

The Role of Spring Frost Events in Controlling the Expansion of Temperate Tree Species  
Into the Boreal Forest

by

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## ABSTRACT

Increasing global temperatures are driving the migration of temperate tree species into boreal regions. This study utilized elevational climate and composition gradients and tree-rings at Mount Carleton Provincial Park, New Brunswick, to evaluate the relative influence of winter and spring temperatures on the leading-edge of temperate tree species. We found that low spring temperatures impact the relative abundance of red and sugar maple more than winter temperatures toward their elevational limits. Further, we found that annual growth for all species responded more to minimum May temperatures than to winter temperatures. These results suggest that minimum winter temperatures do not explain the upper elevational limits of these species and may not be the main constraint on the northward expansion of these species, as traditionally thought. Instead, minimum spring temperatures post-budburst may be a stronger influence. Our study calls for a reassessment of the traditional assumption that winter temperatures constrain these species.

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# CHAPTER 1: GENERAL INTRODUCTION

## 1.1 Climate change and observed distribution shifts

Climate change, driven by anthropogenic activity, is having a significant impact on the intensity and variability of temperature patterns in eastern Canada (Zhang et al., 2019). These climatic shifts are influencing forest ecosystems, particularly affecting tree species at the edges of their geographic distribution. This is especially evident at high latitudes (Pederson et al., 2004; Fisichelli et al., 2014; Kunstler et al., 2020), where climate warming is amplified (Serreze & Barry, 2011; Walsh, 2014). Early signs of changing distribution patterns are most apparent in these areas, largely because the species affected are near the edge of their climatic tolerances (di Castri & Hadley, 1988).

Current observations reveal that both temperate and boreal tree species are undergoing upward latitudinal and elevational shifts in response to ongoing climate warming, and these shifts are projected to continue (Lenoir et al., 2008; Jump et al., 2009; Boisvert-Marsh et al., 2014; Boulanger et al., 2017). Notably, boreal species at their southern range limits are expected to experience growth reductions and increased mortality as temperatures rise. This decline of boreal species at their southern range limit (D'Orangeville et al., 2016; D'Orangeville et al., 2018; Birch et al., 2016) suggests that new successional pathways are likely to arise in these areas, with boreal species being replaced by temperate species, aligning with a projected northward shift of the temperate-boreal ecotone (Fisichelli et al., 2014; Birch et al., 2016). However, the velocity of range shifts is lagging that of climate change, indicating a complex interplay of factors

influencing species migration and adaptation (Boisvert-Marsh et al., 2014; Sittaro et al., 2017).

## **1.2 Drivers of tree species distribution**

Many factors influence the range limits of temperate tree species, such as soil, seed predation, competition, dispersal, disturbance, and climate (Parmesan & Yohe, 2003; Morin, Augspurger, & Chuine, 2007; Brown & Vellend, 2014; Bonan, 2016). One proposed driver of species' range limits is the post-glacial migration lag hypothesis, suggesting that distributions of certain species have yet to fill their potential range since glacial refugia (Svenning et al., 2008). Other studies have found seed dispersal limitations to be an important factor, where the presence of dispersal barriers has an influence in shaping species' distributions (Lyford et al., 2004; Svenning & Skov, 2004; Angert et al., 2011). Another interesting factor combines dispersal limitation with the idea of unfavourable soil conditions as a function of priority effects. Essentially, some studies suggest that the northward migration of certain temperate species may be hindered by unfavourable soil conditions created by resident boreal species, as boreal needle cover and decayed wood create unfavourable substrates for temperate species establishment (Collin et al., 2018; Carteron et al., 2019; Solarik et al., 2019). Further, in a reciprocal soil transplant study by Brown & Vellend (2014) along an elevational transect, sugar maple (*Acer saccharum* Marsh.) seedlings planted in soils from beyond their natural elevational limit experienced reduced emergence and survival, even when transplanted within the species' natural range, suggesting a significant influence of soil on the distribution of sugar maple. Interestingly they also found that the lowest seedling

emergence and survival occurred in favourable soils transplanted beyond the species' range, suggesting a strong climate control over the elevational limit. However, many of these factors are expected to act regionally or locally, while climate primarily dictates range limits at the continental scale (Lafleur et al., 2010).

Disturbance is another factor that drives tree species distribution patterns (Boisvert-Marsh et al., 2019; Zhang et al., 2015). In western Quebec, climate-driven changes in fire frequency have influenced the distribution of yellow birch (*Betula alleghaniensis* Britt.), particularly at its northern limits (Drobyshev et al., 2014). Similarly, red maple (*Acer rubrum* L.) exhibits varied growth rates across its range, showing increased growth in northern regions where frequent fires increase light availability (Zhang et al., 2015; Leithead et al., 2010). Additionally, fire has been shown to be an important constraint for both white cedar (*Thuja occidentalis* L.) and red pine (*Pinus resinosa* Ait.) at their northern range limits in northwestern Quebec (Flannigan & Bergeron, 1998; Rayfield et al., 2021) The interaction between disturbance and competition on species migration is complicated and varies greatly with location and species. Climate-induced changes in disturbance, however, are altering migration patterns and opening new successional pathways. As disturbances change and boreal forests migrate northward, priority effects are expected to diminish over time, thereby facilitating the establishment of pioneer temperate species in these areas (Boisvert-Marsh & de Blois, 2021).

### **1.3 Importance of temperature on species distribution**

Ultimately, the relative importance and interaction between these drivers of tree species' distribution patterns remains a heavily researched topic in ecological studies, with climate generally recognized as a key factor at the continental scale (Woodward, 1987; Neilson, 1995). Temperature has been shown to play an important role in determining many species' limits. Southern limits, for example, are often constrained by high summer temperatures, limited winter chilling, and drought conditions, while northern limits are typically bound by low temperatures, impacting processes such as germination, seedling establishment, growth, and tree fertility (Sykes et al., 1996; Kimmins, 2004; Case et al., 2005; Pederson et al., 2004; Morin et al., 2007; Fisichelli et al., 2014). Species such as red maple and sugar maple have displayed reduced seed production toward their upper elevational and latitudinal limits (Morin et al., 2007; Graignic et al., 2013), and red maple has been shown to be maintained through vegetative reproduction at its northern distribution limits (Tremblay et al., 2002).

However, while the role of temperature in modulating the northern range limits of temperate tree species is recognized, there is ongoing debate about which specific temperature variable is most crucial. Research shows varying correlations between species' range limits and temperature variables. Some studies link these limits to mean annual temperatures (Thomas, 2004; Thuiller, 2005), others to mean winter temperatures (Iversen, 1944; Walther, Berger & Sykes, 2005), and further research suggests improved predictions when including climatic extremes (Zimmermann et al., 2009). However, many of these variables may not have a direct impact on species distributions and may

act as surrogates to more biologically significant factors, such as spring frost events (Thuiller et al., 2008; Austin & Van Niel, 2011; Kollas et al., 2014).

#### **1.4 Winter and spring temperature effects**

Research by Kollas et al. (2014) and Körner et al. (2016) suggests that occurrences of winter temperatures low enough to physiologically constrain many species are rare. This is because trees have evolved to withstand extreme cold during winter dormancy (Sakai and Larcher, 1987), and these critical thresholds are rarely reached at the limits of many temperate species. Consequently, winter temperatures appear to lack a direct causal link to temperate species' range limits. In contrast, these same studies also highlighted the critical role of spring temperatures in influencing the range limits of temperate species (Kollas et al., 2014; Körner et al., 2016). After the onset of spring phenology, trees are especially vulnerable to low temperatures, increasing the likelihood of damage to new growth (Tao et al., 2021). This risk is heightened at higher latitudes and elevations, where late spring frosts are more prevalent (Kollas et al., 2014; Vitasse et al., 2018a). Additionally, climate change is causing the timing of budburst to advance in many species (Menzel et al., 2003; Vitasse et al., 2018a; Kreyling et al., 2015; Richardson et al., 2018), which may be increasing their susceptibility to spring frost damage. Furthermore, temperate trees in colder climates tend to delay leaf-out timing to reduce their risk of experiencing frost damage, but this often leads to a shorter growing season (Dittmar et al., 2006; Hufkens et al., 2012; Kollas et al., 2014). Consequently, a reduced growing season may inhibit the ability of temperate species to compete with cold-adapted boreal species (Körner et al., 2016). Further, low spring temperatures have

been shown to impact growth, having been associated with significant reductions in the radial growth of many temperate-deciduous species. Studies have shown growth reductions of up to 50% at high-elevation sites in the Swiss Alps (Körner et al., 2016) and declines exceeding 90% in European beech (*Fagus sylvatica* L.) stands following severe frosts (Dittmar et al., 2006).

These observations suggest the importance of spring temperature minima in determining the northern and upper elevational (collectively ‘leading-edge’) range limits of temperate tree species and challenge the traditional emphasis on winter temperatures. Understanding this relationship is especially important in the context of climate change and species migration. Such understanding is vital for both industrial and conservation efforts, as changes in species distribution will impact forestry practices and biodiversity conservation. A proactive approach, considering these evolving dynamics and their drivers, is essential for effective forest management strategies in a changing climate.

## **1.5 Objectives and hypotheses**

The main goal of my research was to identify the key seasonal temperature variables influencing the distribution of temperate tree species at their leading-edge of distribution (cold range limits) in the Acadian Forest region – a unique transitional zone between the temperate forest to the south and the boreal forest to the north. This research particularly focuses on understanding the relative impacts of winter temperatures versus spring temperatures.

In Chapter 2, my investigation focuses on the relationship between current species distribution patterns toward their upper elevational range limits and long-term climate normals across elevational gradients. I posit two alternative hypotheses: (i) the decline in temperate tree species' relative abundance toward their elevational range limit is most strongly associated with increased spring frost severity and frequency; (ii) damaging low winter temperatures are responsible for the decline in temperate tree species' relative abundance toward their elevational range limit.

Chapter 3 investigates the short-term spatiotemporal responses of temperate tree species to annual climate variability, by assessing annual growth responses to temperature variables across elevational gradients. For this, I developed two alternative hypotheses, focusing on the differential growth responses to winter versus spring temperature variables: (i) the radial growth of temperate tree species is more influenced by minimum spring temperatures or spring frost events than minimum winter temperatures (ii) the radial growth of temperate tree species is more influenced by minimum winter temperatures than by spring frost events or minimum spring temperatures.

## **1.6 Thesis structure**

The structure of this thesis is divided into two research chapters, each assessing different mechanisms of climate control on temperate tree species performance. These two research chapters allow us to look at interactions between climate and temperate tree species at the community level, as well as at the tissue level. Chapter 2, titled '*Assessing the relationship between seasonal temperature and Acadian temperate tree species*'

*distribution at their leading-edge*', evaluates the present-day community-level distribution of temperate tree species at their elevational cold range limits as a result of long-term climate. Chapter 3, titled '*The growth of Acadian temperate tree species at their leading-edge is more sensitive to spring than winter temperatures*', examines the relationship between annual growth rings of three temperate tree species and annual temperature variations. Lastly, Chapter 4 discusses the implications and limitations of our results and makes suggestions for future research.

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**CHAPTER 2: ASSESSING THE RELATIONSHIP BETWEEN  
SEASONAL TEMPERATURES AND ACADIAN TEMPERATE  
TREE SPECIES' DISTRIBUTION AT THEIR LEADING-EDGE**

## 2.1 Abstract

Migration of temperate tree species into boreal regions is expected with climate warming, but the actual climate constraints to such migration remain controversial. Traditionally, minimum winter temperatures have been assumed to constrain the leading-edge range limits of temperate species, but such hypotheses are not well supported by quantitative evidence of winter freezing tolerance – at least for many temperate species. Here, we use temperature probes along multiple elevational transects in Mount Carleton Provincial Park, a temperate-boreal transition zone in the Acadian Forest, to test the hypothesis that minimum winter temperature controls the distribution of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) at their leading edge. Our findings suggest that minimum spring temperature and late spring frost are better predictors of the relative abundance of these species at their leading edge. Specifically, April through June spring frosts and minimum spring temperatures appeared to be the strongest predictor of red maple relative abundance, while sugar maple was most strongly associated with May through June frost events. These results indicate the potential importance of using extreme temperature minima during spring phenology when explaining temperate species' leading-edge range limits (cold-range limits) and predicting future range shifts.

## 2.2 Introduction

Anthropogenic climate change is increasing temperatures and altering precipitation patterns throughout Canada (Zhang et al., 2019). These climatic changes are having an impact on tree species' ranges, growth dynamics, and competitive ability, and become especially prevalent among species established at the edge of their geographic distribution (Fisichelli et al., 2014, Kunstler et al., 2020), since the effects of climate warming are particularly pronounced at high latitudes and high elevation (Xu et al., 2013). Climate warming is projected to shift the distribution of boreal and temperate species toward higher latitudes and elevations. This trend has been observed in several studies, though shifts are generally small, and further research is necessary (Beckage et al., 2008; Lenoir et al., 2008; Boisvert-Marsh et al., 2014). A study in the Green Mountains of Vermont reported an upslope migration of the northern hardwood-boreal ecotone of as much as 119 m between 1962 and 2005 in response to a 1.1°C warming (Beckage et al., 2008). In Québec, northward shifts were observed in several temperate tree species between 1970 and 2002, with shifts as great as 20 km for the northern limits of red maple (*Acer rubrum* L.; Boisvert-Marsh et al., 2014). However, the average northward trends were less significant overall, at only  $3.07 \pm 4.37$  km (Boisvert-Marsh et al., 2014). In a follow up study, Boisvert-Marsh, (2019) observed even further northward shifts by several kilometres, most notably for red maple and sugar maple (*Acer saccharum* Marsh.). However, observed shifts in species' distributions toward the north are limited, with some studies even reporting contradictory trends (Foster & D'Amato, 2015). Moreover, research suggests that the average velocity of northward migration for temperate species is less than 50% of the rate of climate change, suggesting that

migration may not occur rapidly enough to prevent biodiversity loss (Corlett & Westcott, 2013; Sittaro et al., 2017).

These limited and occasionally contradictory observations of species' range shifts not only highlight the existing barriers to species migration but also suggest that the mechanisms driving these barriers are not fully understood. At the forest-stand scale, soil characteristics, seed dispersal, and stand disturbances have been identified as important drivers of species distribution (Kellman, 2004; Brown & Vellend, 2014; Zhang et al., 2015; Boisvert-Marsh et al., 2019). While climatic factors also play a role at the smaller scale, such as across hillsides or valleys, temperature is generally recognized as the primary driver of temperate tree species' range limits at the continental scale (Woodward, 1987; Neilson, 1995). This distinction highlights the increasing dominance of climatic factors in shaping distribution patterns over larger geographic areas. Temperature not only influences disturbance regimes and soil processes but also directly influences key life cycle stages, such as seed production, germination, establishment, and growth (Fisichelli et al., 2014). The northern and upper elevational distribution (collectively, 'leading-edge') limits of temperate tree species are commonly referred to as 'cold range limits', as they are typically associated with low temperatures during spring and winter, as well as inadequate temperatures throughout the growing season (Sykes et al., 1996; Kimmins et al., 2004; Case et al., 2005; Pederson et al., 2004; Morin, Augspurger, & Chuine, 2007).

The influence of growing season temperature has been linked to the reproductive success of some species toward their leading-edge. In a classic example, Pigott &

Huntley (1981) found that *Tilia cordata* Mill. is limited in the north mainly by insufficient warmth during the early growing season. Essentially, at these limits, temperatures are not warm enough for flowers to undergo full pollen tube extension and fertilization. Further, in years with warm summers where flowers could fully develop and undergo successful fertilization, insufficient late season temperatures do not allow for full embryo development (Pigott & Huntley, 1981). Similarly, Morin et al. (2007) used a process-based model to accurately reconstruct the distribution of 17 temperate tree species. Through this, they determined that the northern range limits of temperate tree species were mainly due to insufficient growing season temperatures, which impeded their ability to undergo flowering or full fruit maturation.

In addition, climatic models traditionally use mean winter temperature as an important factor in determining the northern limits of temperate tree species (Iversen, 1944; Walther, Berger & Sykes, 2005). This focus stems from the role of winter temperatures in causing freezing injury. Trees acclimate to subfreezing temperatures gradually, increasing their freezing tolerance from the end of the growing season into winter via mechanisms that prevent cell freezing and desiccation (Weiser, 1970). However, abrupt declines in minimum temperatures can disrupt this slow acclimation, resulting in rapid freezing and subsequent tissue damage (White & Weiser, 1964). The degree of freezing resistance can vary significantly across species, with some species exhibiting notable geographic variation in this resistance. For instance, at their northern limits, sugar maple and yellow birch (*Betula alleghaniensis* Britt.) demonstrate freezing tolerances of -42 to -43°C and -44 to -45°C, respectively, whereas red maple withstands

down to  $-54^{\circ}\text{C}$  in northern regions but only  $-25$  to  $-30^{\circ}\text{C}$  in the south (Sakai & Weiser, 1973; George et al., 1974). Furthermore, freezing tolerance can also vary across different tissues of the same species. For example, the xylem of sugar maple withstands temperatures down to  $-40^{\circ}\text{C}$ , while its buds and cortex can endure down to  $-80^{\circ}\text{C}$  (Sakai & Weiser, 1973).

However, the focus on mean winter temperature fails to account for the nuanced impact of climatic extremes (Thuiller et al., 2008), potentially leading to inaccurate predictions of species distribution. Incorporating variables that capture interannual variability and absolute winter minima (Pederson et al., 2004; Zimmerman et al., 2009; Gloning, Estrella, & Menzel, 2013) has proven to refine these predictions by recognizing the significance of transient, extreme events. However, because of the documented freezing resistance of some species, the relevance of winter temperatures remains contentious. While certain species, like sugar maple and yellow birch, often exhibit freezing tolerances near the coldest temperatures encountered at their northern range limits, others such as basswood (*Tilia americana*), can withstand temperatures ( $-80^{\circ}\text{C}$ ) far below those experienced at their northern edges (George et al., 1974). This discrepancy suggests that for some species, low winter temperatures may not pose a physiological barrier, challenging the assumption that winter temperatures predominantly dictate the northern range limits of those species.

Consequently, some studies have questioned the importance of winter temperatures in controlling the northern range limits of temperate species, in comparison to spring cold events. Körner et al. (2016) noted that damaging winter lows at species'

leading edges were uncommon, attributing this resilience to the cold tolerance of these trees during winter dormancy (Sakai and Larcher, 1987). They concluded that winter minimum temperatures likely do not constrain species at their leading edge. Instead, they emphasized the vulnerability of these species to harmful low temperatures in spring post-budburst. Furthermore, they observed similar harmful spring temperatures at both the latitudinal and elevational limits, further highlighting the significant role of spring frost events in controlling the leading-edge distribution of temperate tree species. Moreover, a seed trap study by Tremblay et al. (2002) observed a decline in red maple samara production toward its northern range limits, attributing it to increased spring frost events, leading northern populations to subsist almost exclusively through vegetative reproduction.

The role of spring events in defining the leading-edge range limits of temperate tree species is intricately tied to their phenological adaptations. These species have developed strategies to reduce their risk of damage from frost events, using thermal forcing and photoperiod as signals to cue the onset of spring phenology (Lenz et al., 2016a; Vitasse et al., 2014b). However, post-budburst, their susceptibility to low temperatures increases due to a significant reduction in their cold tolerance (Tao et al., 2021). Consequently, temperate species typically exhibit later budburst toward higher elevations and latitudes, due to differences in temperature and photoperiod (Hufkens et al., 2012; Dittmar et al., 2006). Although this strategy reduces frost damage risk, it concurrently shortens the growing season (Kollas et al., 2014), creating a trade-off that

may impede temperate species' ability to compete against cold-adapted boreal species (Körner et al., 2016).

Given the complex role of temperature in influencing the leading-edge range limits of temperate tree species, there is a need for research that examines how different temperature variables influence these patterns. Such studies are essential to understanding how trees will respond to climate change. To understand the influence of temperature on the leading-edge range limits of temperate tree species, we conducted an observational study across five elevational gradient transects in the Mount Carleton Provincial Park in northern New Brunswick, Canada. This area is within the Acadian Forest temperate-boreal ecotone and contains local elevational range limits of temperate deciduous tree species. The main objective was to evaluate the relative effect of minimum spring and winter temperatures, among other temperature related variables, on temperate species abundance near their elevational range limits. As we did not have repeated forest inventory data to conduct a temporal analysis on species composition shifts, we chose to assess the relationship of current-day composition as a response to 70 years of on-site reconstructed climate and determine which temperature variables best explained the spatial variation in each target species' abundance. In our study, "relative abundance" collectively refers to two metrics: relative stem count and relative basal area. Our study focused on three of the most abundant temperate deciduous tree species of the Acadian Forest: red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.). We developed two alternative hypotheses: (i) the decline in temperate tree species' relative abundance toward their elevational range limit

is most strongly associated with the frequency and severity of spring frost; (ii) damaging low winter temperatures are responsible for the decline in temperate tree species' relative abundance toward their elevational range limit.

## **2.3 Methods**

### *2.3.1 Study area*

The study was conducted in Mount Carleton Provincial Park, a protected natural area in the northcentral part of New Brunswick, Canada (Figure 2.1). New Brunswick is part of the Acadian Forest region, a transitional zone between the temperate and boreal forest. The study area is characterized by a warm, humid continental climate, with hot summers and cold winters. Mount Carleton is located in the Highlands Ecoregion of northern New Brunswick and contains the highest elevations in the maritime provinces. Lower elevations generally consist of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) communities on well-drained, fertile soils (Eyre, 1980). Higher elevations are characterized by boreal composition, consisting of spruce-fir communities on well-drained soils which become shallow- to exposed bedrock toward the summits. The montane environment and high latitude of this region within the province make this area ideal for our study, as it provides access to climatic gradients over relatively short distances and can act as a surrogate for latitudinal gradients (Beckage et al., 2008).

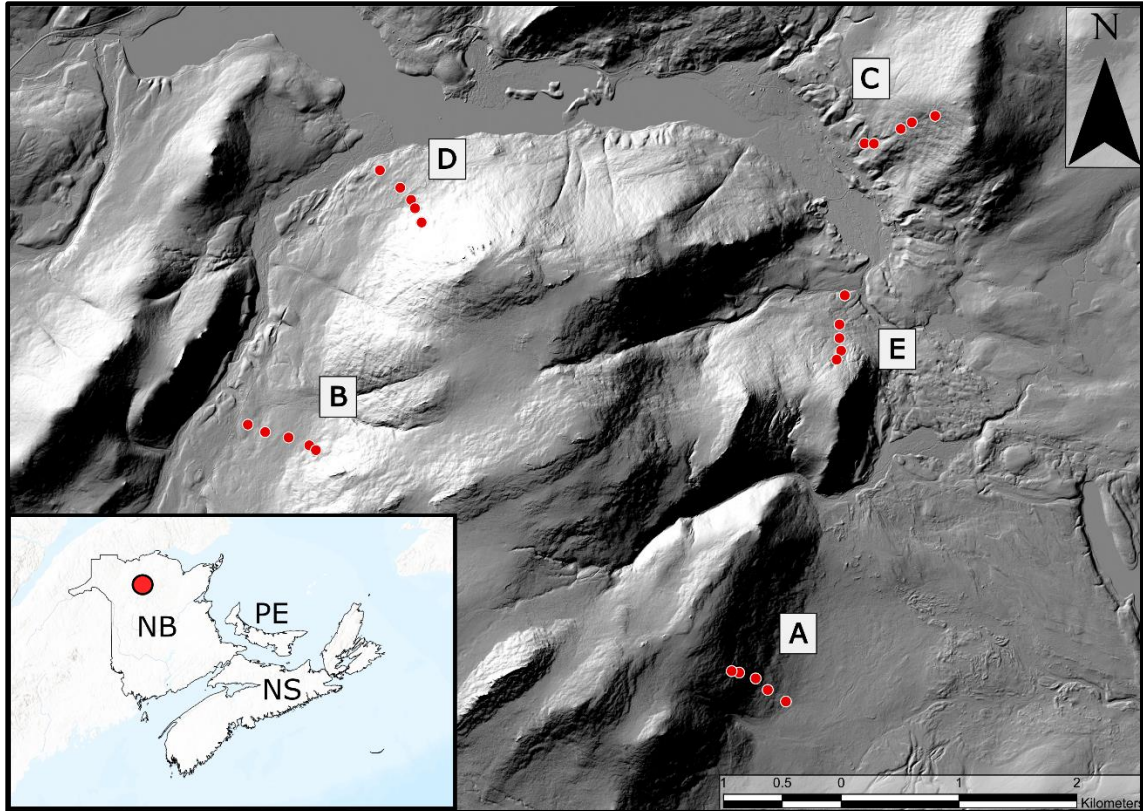


Figure 2.1. Digital elevation model (DEM) of the study area in Mount Carleton, New Brunswick, Canada. Plots of the five elevational transects are represented by the red circles. The inset in the bottom left shows the location of the study area (red dot) in the context of the Maritime provinces. Province abbreviations: NB = New Brunswick, PE = Prince Edward Island, NS = Nova Scotia.

### 2.3.2 Sampling design

Five transects, each consisting of five plots were established in May 2021 to capture the natural transition in species composition from temperate to boreal species along an elevation gradient (Table 2.1). The low-elevation-start of each transect was established in temperate stands dominated by red maple, sugar maple, or yellow birch – the three target temperate deciduous tree species in this study. The rest of the plots of each transect were established parallel to the elevational gradient and tracked the decline in temperate species abundance with increasing elevation, with the last plot established in

boreal-dominated stands, to capture the gradual shift in species composition. Transects were established in undisturbed areas with no visible signs of management activities or major natural disturbances (such as fire or stand-replacing windthrow), and in areas where site characteristics, such as soil properties, coarse fragment content, and slope, appeared relatively consistent. This was essential to ensure minimal effect of site variation on composition changes across space.

Table 2.1. Topographical information for each transect in the study. Includes details about transect slope aspect and elevation of the individual plots within each transect.

Transect	Aspect (°)	Elevation (m)				
		Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
A	102	416	444	478	443	564
B	274	330	346	365	389	419
C	231	292	305	378	413	483
D	304	285	313	334	370	443
E	350	329	356	395	435	416

### 2.3.3 Plot measurements

#### 2.3.3.1 Species composition

Each plot was comprised of a 10 m-radial sampling area representative of the overall site and stand conditions. Within these plots, we categorized all stems with diameter at breast-height (DBH, 1.3 m)  $\geq$  9 cm as trees. For all trees, we recorded the number of individuals per species and the DBH. Tree height was measured using a clinometer (model PM-5/360 PC, Finland).

Within a 5 m radius circular subplot centered within the main plot area, saplings ( $1 \text{ cm} \geq \text{DBH} < 9 \text{ cm}$ ) were identified and recorded using the same protocol as for trees.

For seedling inventory, 1 m radial cardinal plots (one for each cardinal direction) were placed at the boundary of the 5 m subplot. Within these, seedlings were categorized into three distinct height classes: Class 1 ( $1 \geq \text{height} < 15 \text{ cm}$ ), Class 2 ( $15 \geq \text{height} < 30 \text{ cm}$ ), and Class 3 ( $\text{height} \geq 30 \text{ cm}$ , but with a  $\text{DBH} < 1 \text{ cm}$ ).

Ground vegetation cover was assessed within  $1 \text{ m}^2$  quadrats placed at the four cardinal points within each plot, to be used as indicators of site conditions. The ground vegetation cover was evaluated using modified Daubenmire cover classes (Daubenmire, 1956), which categorizes ground cover into eight classes: Class 1:  $<1\%$ ; Class 2:  $1-4\%$ ; Class 3:  $5-14\%$ ; Class 4:  $15-24\%$ ; Class 5:  $25-49\%$ ; Class 6:  $50-74\%$ ; Class 7:  $75-94\%$ ; and Class 8:  $95-100\%$ .

#### *2.3.3.2 Soil characteristics*

To account for the effects of variation in soil characteristics across our elevational gradients, soil pits were excavated at each of the 25 main plots along each transect. Soil horizon depths were measured, and mineral soil samples were collected from a depth of 10 cm below the top of the mineral soil layer. These samples were stored in paper bags and dried at  $65^\circ\text{C}$  for 48 hours before being analyzed for texture, pH, total organic carbon, nitrogen, sulfur, available phosphorus, and exchangeable cations. To monitor temporal variations in soil water potential and volumetric moisture, four probes were installed at a depth of 10 cm below the mineral soil horizon in plots 1, 2, 3, and 4 along

transect C. These plots were chosen as they adequately captured a transition from temperate to boreal composition, and transect C was chosen as it was the earliest to be established in our study. The installed probes collected one year of hourly data from August 2021 to August 2022, utilizing soil data loggers (model ZL6, Zentra, Canada).

#### *2.3.3.3 Leaf phenology and budburst timing*

To investigate the timing of budburst in relation to frost events, nine trail cameras (model BTC-5HD-MAX, Browning, USA), hereafter referred to as 'phenocams', were deployed in plots 1, 2, 3, and 4, along Transect C. These plots were chosen as there were target species saplings in plot 5, which was the highest elevation plot. Transect C was chosen to install the cameras as this was the earliest transect established, allowing us to capture as much of the growing season as possible. Each phenocam was positioned to monitor the budburst and leaf unfolding of a single target species sapling. The phenocams were programmed to capture one photograph daily at 12:00pm, creating a phenological timeseries, allowing us to identify budburst timing.

#### *2.3.3.4 Temperature data*

Hourly temperature data was collected at each plot using temperature loggers (model HOBO MX2201, Onset, USA) from August 2021 to August 2022. Four loggers were affixed to a straight, healthy tree at the center of each plot at heights of 0, 0.5, 1, and 2 m. These heights were chosen to capture fine-scale temperature variations across different tree tissues and species life stages. To avoid inaccurate readings from direct solar exposure, the probes were installed on the north-facing side of the tree with sponges

placed between the tree and the logger to prevent direct contact. Temperature data for plot 5 in transect C is unavailable due to the loss of one probe (likely animal interference), malfunction of another, and snowpack impact on the third.

#### *2.3.4 Data analysis*

##### *2.3.4.1 Historical temperature reconstruction*

A single year of climate data may not accurately represent the conditions under which current forest communities were established. Thus, an on-site historical climate record was necessary in order to represent such conditions. To capture the historical climate gradients across our plots, we reconstructed historical temperature profiles over recent decades using temperature data collected at each plot. This reconstruction was crucial for identifying historical spring frosts and other temperature anomalies. To do this, we utilized the one year of on-site temperature data collected from August 2021 – August 2022 and 70 years of interpolated temperature data to reconstruct daily minimum and maximum temperatures for the period of 1950 to 2020 across all plots at each probe height. Weather data from the high-resolution climate model ANUSPLIN was used for the interpolated temperature dataset. This model was chosen for its 30 m spatial resolution, and high sensitivity to elevational variability and temperature extremes (McKenney et al., 2011). However, the data was only available from 1950 to 2017, so we used an additional temperature dataset covering 1994 – 2020 from the nearest weather station, 30km southeast of our study area, to bridge the temporal gap between the two datasets. First, we fitted linear regression models to the overlapping periods of weather station data and on-site temperature data, with weather station data as the predictor and

on-site temperature probe data as the response. These models demonstrated excellent predictive capacity, with an average  $R^2$  value of 0.94. We used these models to predict daily temperatures for each plot from 1994 to 2020, corresponding to the operational lifespan of the weather station. To extend the temperature reconstruction back to 1950, we repeated this process using the reconstructed 1994–2020 dataset and an interpolated dataset of daily minimum and maximum temperatures. This approach enabled us to produce an uninterrupted historical time series of daily minimum and maximum temperatures from 1950 to 2020, providing a solid foundation for our analysis.

#### *2.3.4.2 Response variable selection*

Due to the gradual reduction in abundance of temperate species toward their upper elevational limits, our analysis utilizes two main response variables: relative stem count and relative basal area. Relative stem count, calculated as the percentage of individuals of a species relative to the total number of individuals in a plot, provides insights into a species' overall ability to establish and survive in a given site compared to other species. Relative basal area, calculated as the percentage of the total plot basal area represented by a species, measures the general performance of a species within a community, even if site conditions do not fully hinder its establishment.

#### *2.3.4.3 Explanatory variable selection*

To assess the long-term climate impact on present-day tree species distribution, our analysis focused on a set of explanatory variables representing 70-year temperature normals, derived from our reconstructed daily temperature dataset (Table 2.2). These

variables were specifically chosen to reflect three critical seasonal periods: winter, spring, and the growing season. For all seasonal variables, minimum temperatures were determined as the absolute lowest daily temperature recorded from 1950 to 2020, to capture extreme climatic events. Likewise, mean temperatures were calculated as the mean daily temperature across the entire time-period.

The winter variables covered the period of January through March, capturing the coldest part of the year. We included mean and minimum winter temperatures based on their application in species distribution models and their documented link with species northern range limits (Iversen, 1944; Walther et al., 2005; Gloning et al., 2013). Additionally, mean summer temperature, covering the period from June 20th to September 23<sup>rd</sup>, was included for its known influence on annual growth patterns (Körner et al., 2016). While we recognize the potential influence of winter thaw events, these were not included in the study, with the focus for the winter variables being on the influence of minimum winter temperatures.

For spring, we examined various timings of temperature to explore the relationships between climate conditions and species phenological stages. For instance, April minimum temperature was included as it coincides with the flowering period of red maple in our study region, and low temperatures after flowering have been shown to adversely affect developing red maple flowers (Tremblay et al., 2002). Likewise, we investigated May minimum temperature, as low temperatures during this period can damage newly expanding leaf tissue. Generally, low temperatures during these periods

are recognized as an important factor in determining the leading-edge range limits of temperate tree species (Kollas et al., 2014; Körner et al., 2016).

Lastly to assess the effects of repeated spring frost events, rather than very rare temperature minimums, we examined the periods of April 1st to June 20th and May 1st to June 20th, noting that no frost events occur after June in our dataset. Frost events were determined as temperatures at or below 0°C. The severity of late spring frosts has been previously documented based on their duration and their timing in relation to the beginning of the growing season (Vitasse & Rebetez, 2018). Following this, we quantified spring frost severity using 'frost GDD,' a metric based on the total growing degree-days (GDD) accumulated from the start of the growing season until the frost event, with GDD accumulation starting at temperatures at and above 4°C (Vitasse & Rebetez, 2018). We then calculated the sum of frost GDD for the entire 70-year period (Table 2.2). This approach, rather than computing annual averages, provides a more accurate assessment of the overall spring frost exposure experienced by mature individuals. Given that most trees in our study are as old as, or older than, our historical temperature record, we deemed this method appropriate.

Table 2.2. List of predictor variables used in analysis, their date range, arithmetic expression, and references of established research justifying the use of such explanatory variables. For calculation, T = temperature, Y = year, and GDD = growing degree days accumulated at the time of a spring frost event ( $T < 0C^\circ$ ).

Predictor	Date range (mm/dd)	Calculation	Reference
Winter min. temp. ( $C^\circ$ )	12/21 - 03/20	$T_{\min} = \min(T(Y_1), T(Y_2), T(Y_3), \dots, T(Y_{70}))$	Gloning et al., 2013
Winter mean temp. ( $C^\circ$ )	12/21 - 03/20	$T_{\text{mean}} = (T(Y_1), T(Y_2), T(Y_3), \dots, T(Y_{70})) / 70$	Iversen, 1944; Walther et al., 2005
May - June frost ( $\sum GDD$ )	05/01 - 06/30	Frost = $\sum[GDD(Y_1) + GDD(Y_2) + GDD(Y_3) + \dots + GDD(Y_{70})]$	Kollas et al., 2014; Vitasse & Rebetez, 2018
May min. temp. ( $C^\circ$ )	05/01 - 05/31	$T_{\min} = \min(T(Y_1), T(Y_2), T(Y_3), \dots, T(Y_{70}))$	Kollas et al., 2014; Körner et al., 2016
April - June frost ( $\sum GDD$ )	04/01 - 06/30	Frost = $\sum[GDD(Y_1) + GDD(Y_2) + GDD(Y_3) + \dots + GDD(Y_{70})]$	Tremblay et al., 2002; Vitasse & Rebetez, 2018
Apr. min. temp. ( $C^\circ$ )	04/01 - 04/30	$T_{\min} = \min(T(Y_1), T(Y_2), T(Y_3), \dots, T(Y_{70}))$	Tremblay et al., 2002
Summer mean temp. ( $C^\circ$ )	06/21 - 09/23	$T_{\text{mean}} = (T(Y_1), T(Y_2), T(Y_3), \dots, T(Y_{70})) / 70$	Körner et al., 2016

### 2.3.5 Statistical analysis

To explain our response variables, we used a non-linear modelling approach, as an explanatory analysis indicated that our data generally displayed a sigmoidal distribution. To identify the non-linear model that best fits our data, we evaluated several models in R, using the 'drc' package, chosen for its robust model-fitting capabilities (Ritz et al., 2015). The modified-Gompertz model was selected due to its limited number of parameters, and because it consistently yielded the best fit to our data according to the Akaike Information Criterion (AIC). Given that relative stem count and relative basal area are proportions constrained to values between 0 and 1, we assigned the upper and lower asymptotic limits as 1 and 0, respectively. This resulted in a simplified 2-parameter model, which is expressed by the following equation:

$$y = 1 - e^{-e^{b_1(x-b_2)}}$$

where  $b_1$  represents the slope,  $b_2$  the inflection point,  $x$  the climate-based explanatory variable, and  $y$  the response of relative stem count or relative basal area.

The modified-Gompertz model was applied separately for each species and each response variable—relative stem count and relative basal area—against each explanatory variable, resulting in a total of 42 univariate models. Sugar maple was absent from Transect B (Figure 2.2), while red maple was nearly absent from Transect D (Figure 2.2). Due to potential non-climatic influences on their absence or low abundance, these transects were excluded from the analysis for these species. The effectiveness of these variables in explaining variations in our response metrics was determined using several criteria. These included the Akaike Information Criterion (AIC) scores for model comparison, where lower AIC scores indicated a stronger fit, the statistical significance of model parameters (with a p-value threshold of  $< 0.05$  for significance), and the normality of residual distribution, verified using the Shapiro-Wilk test for normality (with a p-value  $> 0.05$  indicating normal distribution). This methodology for model evaluation ensured that only models with statistically significant parameters and normally distributed residuals were considered, thereby enhancing the reliability of our findings.

## 2.4 Results

### 2.4.1 Observed gradients in stand and site characteristics

#### 2.4.1.1 Tree species composition

The relative stem count and relative basal area of temperate species were generally highest in low-elevation plots, gradually declining with elevation (Figures 2.2 and 2.3). Although, transect B displayed an inconsistent pattern, where the only temperate species in the lowest-elevation plot was red maple, which made-up only 25% of plot relative stem count (Figure 2.2). However, temperate species increased in the subsequent plots along transect B, reaching 80% of relative stem count by plot 3, followed by a complete absence of temperate species in plots 4 and 5 (Figures 2.2 and 2.3). Interestingly, the relative stem count of seedlings and saplings did not display a clear pattern with increasing elevation.

#### 2.4.1.2 Soils and ground vegetation

Soil nutrients, horizon depth, texture, organic matter concentration, coarse fragments, moisture, and water potential did not display any clear patterns of change with respect to elevation. However, soil pH did show an elevational pattern (see Supplementary Table S1). Lower elevation plots were generally more alkaline, compared to higher elevation plots which were more acidic. Across the transects, the mean pH of the lowermost plots was  $4.53 \pm 0.40$ , while it was  $4.33 \pm 0.31$  in the uppermost plots. The greatest pH variances were observed on transects B and D, with differences between upper and lower plots of 0.57 and 0.64, respectively. Ground vegetation also exhibited

noticeable patterns corresponding to elevation and pH preferences, transitioning from species favouring neutral to slightly acidic conditions at lower elevations to acidophilic species, such as lowbush blueberry (*Vaccinium angustifolium* Ait.) and Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd) at higher elevations. Additionally, soil horizon depth remained relatively constant, with depth becoming difficult to measure only in the last ~100m of elevation due to rock outcrops.

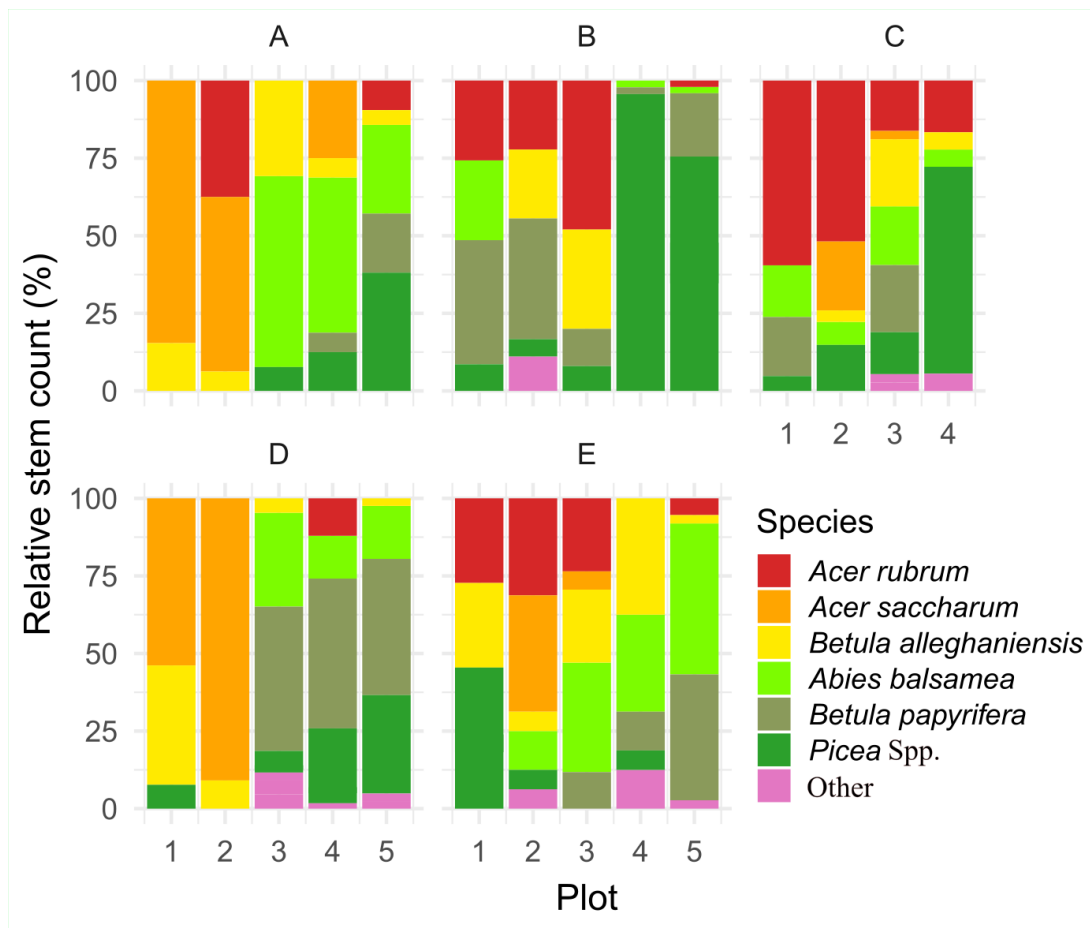


Figure 2.2. Stacked bar chart showing the relative stem count, expressed as a percentage of each species' stem count relative to the total plot stem count. Solid filled bars indicate relative stem count, colored by species, and plots are displayed on the x-axis. "Other" consists of sporadically present species, such as *Acer spicatum* Lam., *Thuja occidentalis* L., and *Prunus pensylvanica* L. f.

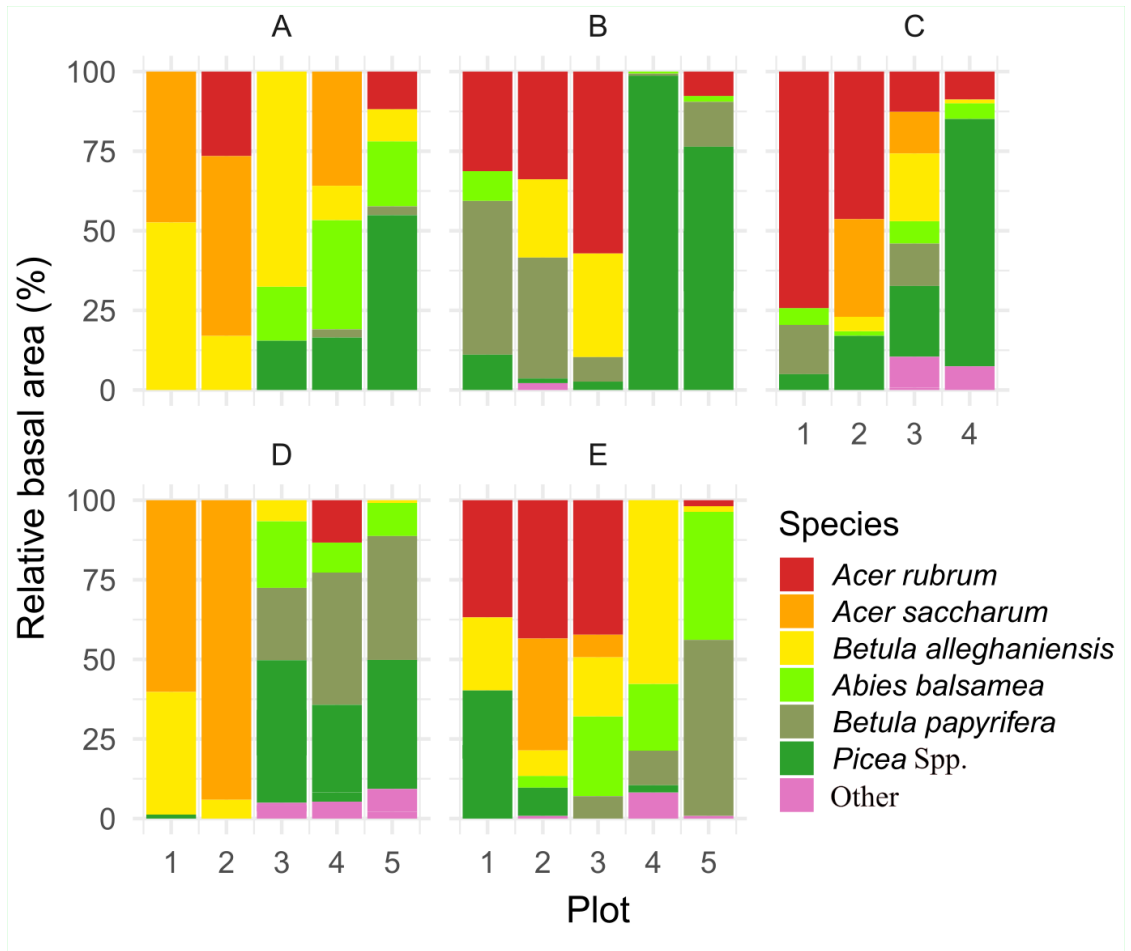


Figure 2.3. Stacked bar chart showing the relative basal area, expressed as a percentage of each species' basal area relative to the total plot basal area. Solid filled bars indicate relative basal area, colored by species, and plots are displayed on the x-axis. "Other" consists of sporadically present species, such as *Acer spicatum* Lam., *Thuja occidentalis* L., and *Prunus pensylvanica* L. f.

#### 2.4.1.3 Budburst timing across species

Phenocam observations from transect C provided insight into the timing of budburst across species and elevations. Across elevations, red maple budburst occurred earliest of all species observed. In the lowest plot (plot 2; 305m), red maple budburst occurred on May 9th. Yellow birch closely followed, with budburst on May 10th in the same plot. At the highest elevation observed (plot 3; 378 m), red maple's budburst

occurred on May 14<sup>th</sup>, 5 days later than its low elevation counterpart. The observed red maple specimen in plot 4 (413 m) was lost before budburst, possibly due to predation or damage from snowpack. At its highest elevation (plot 4; 413 m), yellow birch experienced budburst on May 12<sup>th</sup>, just two days later than its lower elevation counterpart. Sugar maple showed a notably later budburst compared to the other species. At its lowest elevation (plot 1; 292 m), sugar maple budburst occurred on May 14<sup>th</sup>, with a 6-day delay observed at its highest elevation on May 20<sup>th</sup> (plot 3; 378 m).

#### *2.4.1.4 Seasonal and elevational variations in temperature*

Our temperature data analysis suggested that the 0 and 0.5 m probes spent a large portion of the winter buried under snow, indicated by their prolonged stagnation at 0°C (see Supplementary Figure S1). Consequently, we excluded these probes from further analysis, as they do not represent the ambient air temperature experienced by trees with foliage above snowpack. Across the 70-year time series, the mean difference between the 1 and 2 m probe was minimal, at  $0.1 \pm 0.1^\circ\text{C}$ . This difference increased slightly through June, July, and August ( $0.2 \pm 0.1^\circ\text{C}$ ). Given the negligible variation in recorded temperatures between probe heights (see Supplementary Figure S2), we opted to use data from the 1m probes in all subsequent analysis. With this, temperature patterns across transects generally followed similar seasonal trends between the highest and lowest elevation plots, except for transect C, which generally showed opposite trends in temperature variance (Figure 2.4). However, variation between the highest and lowest plot in all transects was small, not surpassing 1°C for both mean and minimum temperatures.

#### *2.4.1.4.1 Trends in mean temperature*

Across the study area, the 70-year mean winter temperature was  $-9.2 \pm 0.3^{\circ}\text{C}$ , with mean April and May temperatures at  $-2.0 \pm 0.3^{\circ}\text{C}$  and  $3.5 \pm 0.3^{\circ}\text{C}$ , respectively. The mean summer temperature rises to  $15.0 \pm 0.3^{\circ}\text{C}$ , followed by a gradual decrease through autumn and back into winter, forming a bell-shaped curve in mean temperature variation (Figure 2.4). When plots were averaged across transects, mean winter temperature in plot 1 was  $-9.1 \pm 0.3^{\circ}\text{C}$  compared to  $-9.5 \pm 0.3^{\circ}\text{C}$  in plot 5. Mean April temperature in plot 1 was  $-1.9 \pm 0.3^{\circ}\text{C}$ , and  $-2.4 \pm 0.4^{\circ}\text{C}$  in plot 5. In May, mean temperatures were  $3.6 \pm 0.2^{\circ}\text{C}$  in plot 1, and  $3.2 \pm 0.4^{\circ}\text{C}$  in plot 5. For summer, the mean temperature in plot 1 was  $15.2 \pm 0.3^{\circ}\text{C}$ , and  $14.8 \pm 0.5^{\circ}\text{C}$  in plot 5.

#### *2.4.1.4.2 Trends in minimum temperature*

Minimum temperatures exhibited more pronounced seasonal and elevational fluctuations compared to mean temperatures (Figure 2.4). Across the study area, the average minimum winter temperature was  $-33.4 \pm 0.5^{\circ}\text{C}$ . For April and May, average minimum temperatures were  $-19.6 \pm 0.4^{\circ}\text{C}$  and  $-8.0 \pm 0.5^{\circ}\text{C}$ , respectively. Focusing on elevational differences, plot 1 had an average minimum winter temperature of  $-33.4 \pm 0.6^{\circ}\text{C}$ , while plot 5 was  $-33.7 \pm 0.3^{\circ}\text{C}$ . Mean April minimum temperature in plot 1 was  $-19.4 \pm 0.4^{\circ}\text{C}$ , and  $-20.0 \pm 0.4^{\circ}\text{C}$  in plot 5. In May, mean minimum temperature was  $-7.7 \pm 0.4^{\circ}\text{C}$  for plot 1, and  $-8.5 \pm 0.5^{\circ}\text{C}$  for plot 5.

### 2.4.1.4.3 Trends in frost GDD

Additionally, our analysis showed an overall upward trend in the cumulative frost GDD sum for May – June over the 70-year period, increasing from the lowest to the highest elevations (Figure 2.5). Notably, the lowest plot in all transects exhibited slightly higher frost GDD values than the second-lowest plot (Figure 2.5). The average frost GDD accumulated over the 70-year span was  $10637 \pm 1108^{\circ}\text{C}\cdot\text{d}$ . Specifically, plot 1 experienced an average frost GDD of  $10414 \pm 1073^{\circ}\text{C}\cdot\text{d}$ , slightly decreasing to  $9909 \pm 1115^{\circ}\text{C}\cdot\text{d}$  in plot 2, before rising to  $11785 \pm 1195^{\circ}\text{C}\cdot\text{d}$  by plot 5.

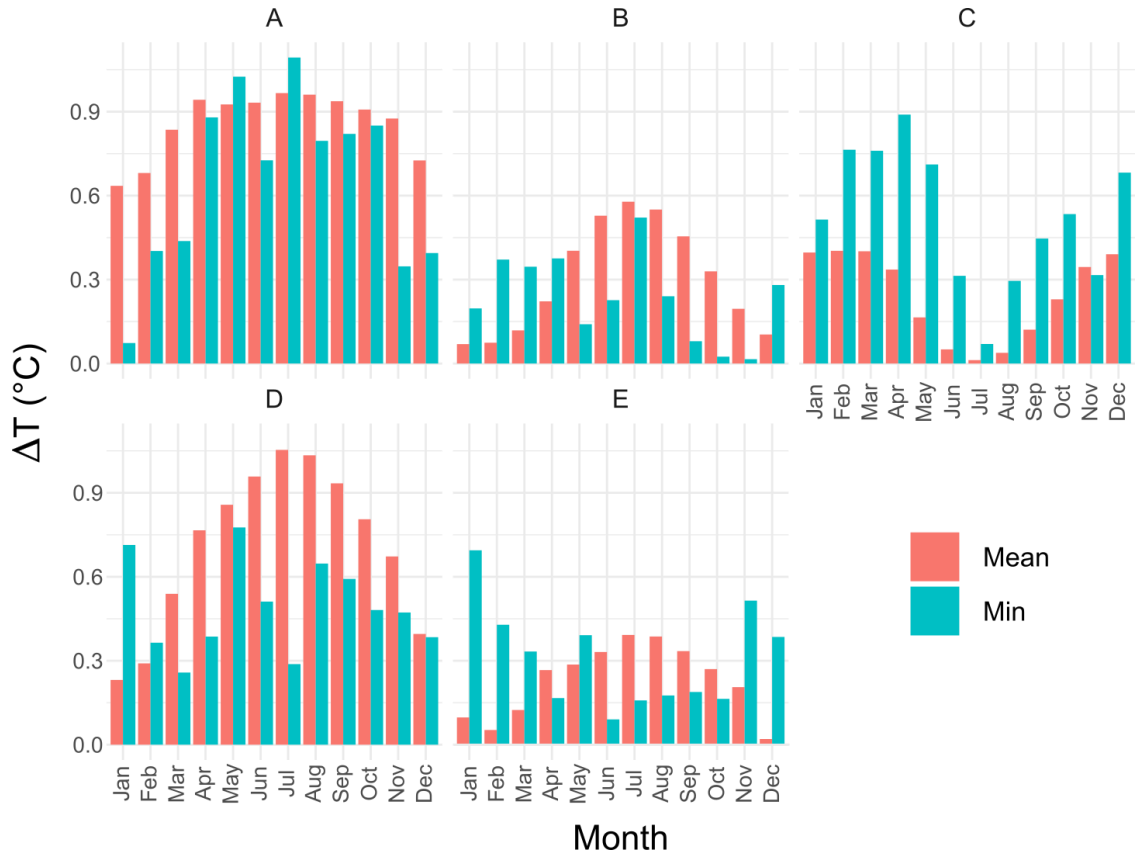


Figure 2.4. Monthly variation in mean and minimum temperatures between the highest and lowest plot in a transect, illustrating the temporal change in the elevational temperature gradient across transects. The depicted values on the y-axis depicted represent the temperature difference between plot 1 (lowest elevation) and plot 5 (highest elevation).

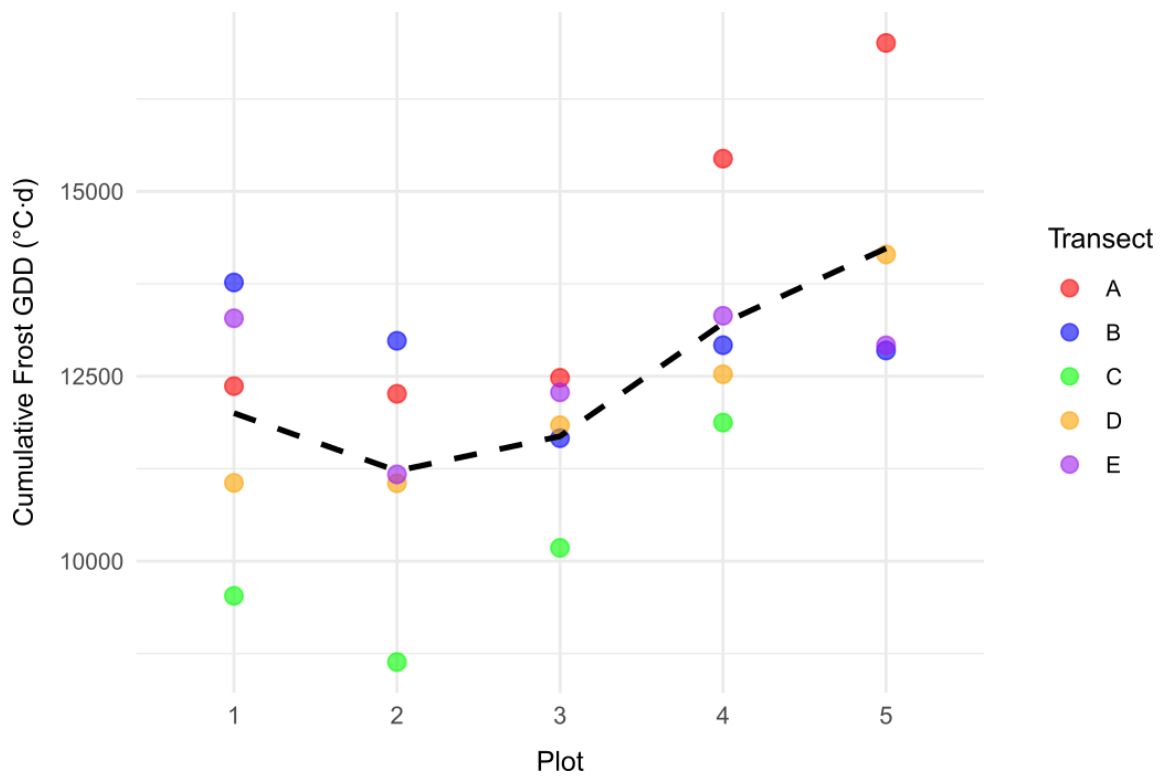


Figure 2.5. Cumulative frost GDD for the period covering May 1st to June 31st, calculated for each plot from 1950 – 2020. Black dashed line represents the average frost GDD sum for plots at similar elevations across all transects.

#### 2.4.2 Seasonal temperature effects on tree stand metrics

Our model analysis revealed that summer temperatures do not significantly influence the relative stem count or basal area of the species under consideration. Additionally, no notable associations were identified between the tested climate variables and either the relative stem count or basal area of yellow birch. However, our findings suggest a predominant influence of spring climate variables over winter variables in determining both the relative stem count and basal area for both maple species.

#### *2.4.2.1 Red maple relationship with seasonal temperature variables*

We observed a pronounced, non-linear response of red maple's relative stem count to early spring temperature minimums. Specifically, the response was most associated with three spring climate variables, namely minimum April temperature (AIC = -25.4, pseudo-R<sup>2</sup> = 0.68; Table 2.3; Figure 2.6a), followed by minimum May temperature (AIC = -21.2, pseudo-R<sup>2</sup> = 0.60; Table 2.3) and April – June frost GDD (AIC = -18.6, pseudo-R<sup>2</sup> = 0.54; Table 2.3). The relationships with minimum temperature were positive, while they were negative for frost GDD (Table 2.3). Following these, the next best association was minimum winter temperature (AIC = -18.3, pseudo-R<sup>2</sup> = 0.52; Table 2.3), followed by mean winter temperature (AIC = -17.2, pseudo-R<sup>2</sup> = 0.50; Table 2.3), both exhibiting a positive relationship with relative stem count. The relative basal area of red maple exhibited a strong positive relationship with minimum May temperature (AIC = -10.3, pseudo-R<sup>2</sup> = 0.49; Table 2.3; Figure 2.6), followed by a negative relationship with May – June frost GDD (AIC = -4.6, pseudo-R<sup>2</sup> = 0.31; Table 2.3).

#### *2.4.2.2 Sugar maple relationship with seasonal temperature variables*

For the relative stem count of sugar maple, May – June frost GDD was the only variable that resulted in a model with fully significant parameters (AIC = 7.0, pseudo-R<sup>2</sup> = 0.38; Table 2.3; Figure 2.6c), which had a negative relationship with relative stem count. Following this, were positive relationships with mean winter temperature, minimum May temperature, and minimum April temperature, all of which lacked parameter significance (Table 2.3). Similarly, May – June frost GDD was the only

variable with fully significant parameters for sugar maple relative basal area, which yielded the strongest negative relationship (AIC = 1.8, pseudo- $R^2 = 0.49$ ; Table 2.3; Figure 2.6d). This was followed by mean winter temperature and winter mean temperature (Table 2.3), which lacked parameter significance.

Table 2.3 Model results for each tested climate variable affecting relative stem count and relative basal area, including parameter estimates with standard errors, AIC values, and pseudo-R<sup>2</sup>. Table only includes models exhibiting normal distribution of residuals, as these are deemed to be a good fit. Significance of parameter estimates is marked by asterisks: \*\*\* indicates p < 0.001, \*\* indicates p < 0.01, and \* indicates p < 0.05.

Species	Response variable	Explanatory variable	b <sub>1</sub> (estimate ± SE)	b <sub>2</sub> (estimate ± SE)	AIC	Pseudo-R <sup>2</sup>
<i>Acer rubrum</i>	Rel. stem count	April T <sub>min</sub> (C°)	1.66 ± 0.29***	-18.6 ± 0.13***	-25.4	0.68
		May T <sub>min</sub> (C°)	1.71 ± 0.36***	-6.99 ± 0.15***	-21.2	0.60
		April 1 - June 30 frost (ΣGDD)	-4.58E-04 ± 1.10E-04***	1.32E+04 ± 6.40E+02***	-18.6	0.54
		Winter T <sub>min</sub> (C°)	1.44 ± 0.35***	-32.2 ± 0.20***	-18.3	0.52
		Winter T <sub>mean</sub> (C°)	2.24 ± 0.55***	-8.46 ± 0.14***	-17.2	0.50
		May 1 - June 30 frost (ΣGDD)	-3.96E-04 ± 1.08E-04**	8.17E+03 ± 8.61E+02***	-15.8	0.46
<i>Acer rubrum</i>	Rel. BA	May T <sub>min</sub> (C°)	1.66 ± 0.44**	-7.08 ± 0.19***	-10.3	0.49
		May 1 - June 30 frost (ΣGDD)	-3.48E-04 ± 1.30E-04*	8.19E+03 ± 1.25E+03***	-4.6	0.31
<i>Acer saccharum</i>	Rel. stem count	May 1 - June 30 frost (ΣGDD)	-1.12E-03 ± 2.04E-04***	1.10E+04 ± 3.05E+02***	7.1	0.38
		Winter T <sub>mean</sub> (C°)	7.22 ± 4.62	-9.00 ± 0.08***	8.5	0.31
		May T <sub>min</sub> (C°)	2.41 ± 2.34	-7.38 ± 0.39***	11.6	0.16
		April T <sub>min</sub> (C°)	1.92 ± 1.75	-18.9 ± 0.54***	12.2	0.13
<i>Acer saccharum</i>	Rel. BA	May 1 - June 30 frost (ΣGDD)	-1.45E-03 ± 3.04E-04***	1.11E+04 ± 2.15E+02***	1.8	0.49
		Winter T <sub>mean</sub> (C°)	10.2 ± 6.31	-9.02 ± 0.04***	4.0	0.40
		May T <sub>min</sub> (C°)	5.70 ± 9.21	-7.55 ± 0.17***	7.4	0.25

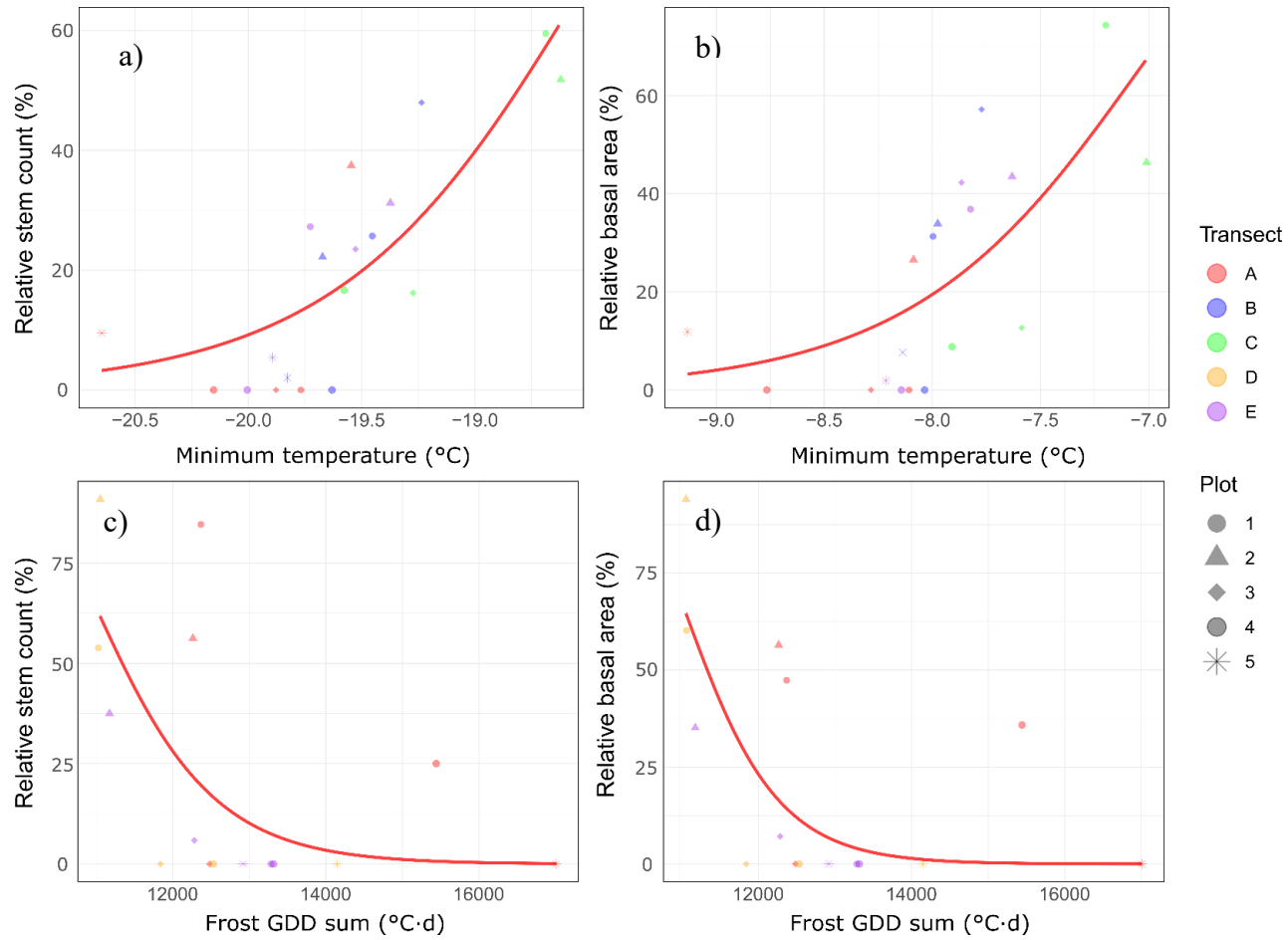


Figure 2.6. Modelled species relative stem count and relative basal area as a function of climate predictors. (a) Red maple relative stem count vs. minimum April temperature; (b) Red maple relative basal area vs. minimum May temperature; (c) Sugar maple relative stem count vs. frost GDD sum; (d) Sugar maple relative basal area vs. frost GDD sum.

## 2.5 Discussion

In this study, we compared the effects of various temperature variables from a 70-year record of reconstructed on-site temperature data on the present-day relative abundance of temperate tree species at their upper elevational range limits in Atlantic Canada. Our aim was to determine whether low spring or winter temperatures more strongly influenced the relative abundance of temperate tree species at their leading-edge range limits, to identify which variable plays a larger role in controlling these range limits. Our findings support our first hypothesis, demonstrating that temperate species relative abundance has a stronger relationship with minimum spring temperatures at their elevational range limits than minimum winter temperatures. While these results are contradictory to the traditional assumption that winter temperatures control the leading-edge range limits of many tree species (Iversen, 1944; Walther, Berger & Sykes, 2005), our results are in line with more recent studies which find that low spring temperatures are a more likely control of these range limits (Kollas et al., 2014; Körner et al., 2016).

### 2.5.1 *Climate observations*

The narrow range of elevational variability in winter temperatures suggests that species experience similar winter conditions across transects. This uniformity is likely influenced by phenomena such as cold air drainage and temperature inversions (Daly, Conklin, & Unsworth, 2010), which are common in winter and may attenuate the elevational temperature gradient with elevation. Additionally, the high albedo of winter snow cover reflects more solar energy, potentially stabilizing temperatures across elevational gradients (Bonan, 2016). Further, the larger gradients in temperature observed

during the growing season can be explained by differences in solar radiation, with lower elevations receiving more solar radiation due to the sun's higher angle, creating a more pronounced temperature gradient compared to winter (Bonan, 2016). The south-facing slope of transect C, subject to increased direct solar insolation (Nie et al., 1992; Uhlmann et al., 2008, and its proximity to the buffering effect of Little Nictau Lake (Bonan, 2016), could explain its divergent temperature pattern, with higher mean temperature variation during the winter relative to the growing season. Notably, minimum temperatures displayed more elevational variation than mean temperatures, with peaks around the months of April and May across plots and transects. However, this is likely due to the effect of averaging temperature statistics. Overall, spring and growing season temperatures exhibited the widest range in elevational variation. This variation may be explained by differences in solar radiation, with lower elevations receiving more due to the sun's higher angle, creating a more pronounced temperature gradient compared to winter (Bonan, 2016). The south-facing slope of transect C, subject to increased direct solar insolation (Nie et al., 1992; Uhlmann et al., 2008) and its proximity to the buffering effect of Little Nictau Lake (Bonan, 2016), could explain its divergent temperature pattern, with higher mean temperature variation during the winter relative to the growing season.

### *2.5.2 General trends in species-climate relationships*

Our analysis revealed significant relationships between local climate and the relative abundance of red maple and sugar maple, but not yellow birch. The relatively low sensitivity of red maple to site factors (Abrams, 1998) could explain why we

detected this relationship. The climate signal was also significant for sugar maple, though less pronounced, potentially reflecting its greater sensitivity to specific site and stand conditions (Godman et al., 1990), despite earlier findings of climate-controlled regeneration (Graignic et al., 2014). The regeneration of sugar maple seedlings has been found to be highly dependent on the presence and abundance of mature conspecifics (Graignic et al., 2014), along with certain soil types (Brown & Velden, 2014). For yellow birch, their low climatic sensitivity found here aligns with findings by Drobyshchev et al. (2014), who found yellow birch distribution along latitudinal gradients to be more influenced by site-specific factors, like suitable substrates and seed availability, rather than climate. However, climate may still play a certain role, as significant yellow birch dieback has been reported in response to winter thaw events and spring frosts (Bourque et al., 2005).

### *2.5.3 Influence of winter temperatures*

The narrow range in winter temperatures across elevation may help explain the weaker relationship with temperate species relative abundance indices, as it suggests that across elevations, species experience similar winter temperatures. Additionally, this temperature range does not appear great enough to explain the drastic shift from temperate to boreal composition along the transects. Further, our findings of a weaker relationship with minimum winter temperatures align with the experimentally determined winter cold tolerance of our target species. At their northern limits, sugar maple and yellow birch can tolerate freezing temperatures down to approximately  $-42^{\circ}\text{C}$  and  $-45^{\circ}\text{C}$ , respectively, while red maple can withstand temperatures as low as  $-54^{\circ}\text{C}$  (Sakai &

Weiser, 1973; George et al., 1974). The coldest temperature in our reconstructed temperature record was  $-34^{\circ}\text{C}$ , which is well within the tolerance range of these species.

#### *2.5.4 Influence of growing season temperatures*

Although growing season temperatures demonstrated considerable variability with elevation, they did not exhibit a significant relationship with the relative abundance of any target species. This suggests that if damaging cold temperatures are the main cause of temperate species decline toward their leading-edge range limits, the lack of a relationship with growing season temperature may be due to the absence of frost events during the growing season. Therefore, changes in growing season temperatures along elevational gradients may have minimal impact on species abundance. Moreover, studies have found that growing season length, rather than growing season temperature, has a stronger relationship with radial growth (Jochner et al., 2018). It has also been suggested that growing season length co-controls temperate species' leading-edge range limits with spring frost events. Specifically, spring frost risk mitigation, achieved through later budburst, shortens the growing season. This reduction in growing season length diminishes tree growth and competitive ability, which may have substantial consequences at the species' range limits, where climatic conditions present considerable constraints (Kollas et al., 2014; Körner et al., 2016).

#### *2.5.5 Influence of spring temperatures*

Overall, we found that spring temperature variables exhibited a stronger influence on the relative abundance of red and sugar maple than winter temperatures. This aligns

with recent studies in Europe from Kollas et al. (2014) and Körner et al. (2016), who identified anomalous minimum spring temperatures after budburst as stronger determinants of the leading-edge range limits of temperate deciduous tree species. The two maple species did vary in their sensitivity to spring temperatures. The decline in red maple relative stem count tracked colder April and May temperatures, consistent with its early flowering and in line with previous findings by Tremblay et al. (2002), who attributed red maple's northern limit to reduced fecundity due to spring frost flower damage. The relative abundance of sugar maple trees also tracked lower May temperatures, but not April temperatures. The weaker role of April aligns with the delayed budburst of sugar maple, which we observed to lag by approximately 4-5 days behind red maple in study site. This highlights sugar maple's vulnerability to late spring frosts, which have been shown to inhibit canopy development (Hufkens et al., 2012) and radial growth (Dittmar et al., 2006; Vitasse et al., 2019). Following budburst, reduced frost tolerance heightens the risk of tissue damage (Sakai & Larcher, 1987). The repair of these damaged tissues in response to frost damage requires substantial NSC allocation, often leading to growth reductions (Rubio-Cuadrado et al., 2021). In extreme cases, growth reductions as great as 90% have been documented (Dittmar et al., 2006).

#### *2.5.6 Study limitations*

Our research specifically aimed to pinpoint the most significant seasonal temperature variables influencing the distribution of temperate tree species across elevational gradients, with a strong focus on determining the relative influences of spring versus winter variables. Despite our findings that spring temperature minimums play a

critical role in the elevational distribution patterns of red and sugar maple, we acknowledge the multitude of factors involved in species distribution patterns that were not studied here. For instance, the observed decline in soil pH with elevation may also contribute to the observed compositional gradients. However, no strong correlation between seedling relative abundance and soil pH was evident at our study sites. Nonetheless, our focus on climate in this study does not exclude that climate, stand, and soil characteristics likely interact in controlling the distribution of these species at their leading edge.

In this first study in Atlantic Canada, we compare the effect of various climate variables and find that minimum spring temperatures are the best predictor for the relative abundance of temperate tree species at their leading-edge range limit. Our findings suggest that we reevaluate the prominence of winter temperature variables in species distribution models. Given our use of interpolated climate data and only a single forest inventory collection, studies extending beyond our single year of climate and inventory data collection would enhance data reliability and provide a more comprehensive understanding of interannual impacts and responses to long-term climate trends. Additionally, our study assessed the distribution of these species at their upper elevational limits. While elevational gradients are thought to emulate latitudinal gradients in terms of climate, we cannot conclude that the exact relationships uncovered in this study are consistent with those at the northern range limits of these species. Further, our study takes place at the cold range limits of our target species, where they are exposed to unique conditions. Thus, we suggest that our conclusions cannot be extrapolated to the

entirety of these species' ranges. Lastly, given the importance of annual growth as a mechanism driving species distribution shifts toward their leading edges, we advocate for further research that assesses the short-term, annual impact of temperature variables, such as spring frost, on tree growth. Investigating these aspects could significantly enrich process-based modelling efforts by providing a detailed, high-resolution understanding of how species respond to climate variability.

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**CHAPTER 3: THE GROWTH OF ACADIAN TEMPERATE  
TREE SPECIES AT THEIR LEADING-EDGE IS MORE  
SENSITIVE TO SPRING THAN WINTER TEMPERATURES**

### 3.1 Abstract

Under a warming climate, the projected migration of temperate tree species into boreal regions raises complex ecological questions, as the relative importance of specific climatic drivers remains poorly understood. Winter temperatures are commonly assumed to be the main constraint to the leading-edge range limits of temperate species. However, evidence of winter cold tolerance in many temperate species challenges this hypothesis, suggesting other limiting factors may be at play. Here, we used a dendrochronological approach combined with on-site daily temperature monitoring across five elevational temperate-boreal gradients in northern New Brunswick to investigate climatic drivers of growth for red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britt.) at their upper elevational range limit. We found that minimum spring temperatures are a better predictor of growth than winter or growing season temperatures for all studied species, highlighting the dominant role of spring conditions at colder sites for these species. For red and sugar maple, we found that warmer spring temperatures are generally associated with increased growth, while yellow birch displayed site-specific, contrasted trends in growth coupling with spring conditions. These results challenge the limiting role of winter temperatures on the leading-edge range limits of temperate trees and could help enhance our ability to forecast range shifts of temperate tree species under climate change.

### 3.2 Introduction

Climate change is expected to influence the distribution, growth, and competitive interactions among tree species, particularly affecting communities established at the edge of their distributional ranges (Fisichelli et al., 2014; Kunstler et al., 2020). The temperate-boreal ecotone, representing the transition from southern temperate to northern boreal forests, is predicted to shift northwards due to climate change (Jump et al., 2009; Boulanger et al., 2017; Taylor et al., 2017)—a phenomenon that has already been documented (Boisvert-Marsh et al., 2014; Lenoir et al., 2008). However, our capacity to anticipate future shifts in forest composition remains limited, despite its importance for forest management.

Climate is considered as the predominant force shaping species' range limits at the continental scale, with temperature having a particularly important role (Woodward, 1987; Lafleur et al., 2010). The influence of low temperatures in setting the extreme upper range boundaries for angiosperm survival at the alpine or arctic limits is well understood (Körner, 2003a, 2012). However, the role of temperature becomes less clear for populations not at these extreme limits, such as those reaching their northern limits at the temperate-boreal ecotone (Körner et al., 2016). Traditionally, it has been presumed that mean and minimum winter temperatures are critical factors influencing the leading-edge distribution of temperate tree species (Iversen, 1944; Walther, Berger & Sykes, 2005), largely because of the damaging effect of low winter temperatures on plant tissues (White & Weiser, 1964; Weiser, 1970). However, many species, including red maple (*Acer rubrum* L.), demonstrate winter cold tolerance thresholds at their northern limits far

lower than the coldest temperatures they are likely to encounter (George et al., 1974; Kollas et al., 2014), suggesting that factors other than winter cold exposure may have a stronger influence.

Spring frost events may be another factor constraining the leading edge of temperate tree species. After budburst, the cold tolerance of temperate tree species is greatly reduced (Vitasse et al., 2014b; Tao et al., 2021), and subsequent spring frost events have been reported to cause considerable damage to newly formed leaves and flowers, leading to severe growth declines (Dittmar et al., 2006; Hufkens et al., 2012). Tree growth is crucial for the overall health of trees, with reduced growth rates being strongly associated with an increased probability of mortality (Wyckoff & Clark, 2000, 2002; Berdanier & Clark, 2016). Contrary to winter temperatures, low spring temperatures have been related to 50% reductions in radial growth of temperate-deciduous species at high-elevation sites in the Swiss Alps (Körner et al., 2016). Dittmar et al. (2006) reported declines of 90% or more in the growth of *Fagus sylvatica* L. stands following severe spring frosts, especially at higher elevations where frost damages are more frequent. Vanoni et al. (2016) observed abrupt decreases in growth among 848 standing dead trees across 14 forest reserves in Switzerland, attributing these declines to drought and frost. Similarly, Vitasse et al. (2019) observed growth reductions in two European deciduous species in Switzerland following severe spring frost events. This phenomenon is likely due to the energy expended on repairing or replacing damaged tissue, which subsequently reduces carbon allocation to growth (Rubio-Cuadrado et al., 2021). Over the long-term, the cumulative effects of these damaging events, such as

multi-year growth reductions, can diminish species' competitive fitness and lead to mortality (Berdanier & Clark, 2016). Therefore, climate-induced low growth is likely a significant factor determining the leading-edge range limits of temperate tree species (Kollas et al., 2014; Körner et al., 2016), with low survival probabilities hindering their expansion.

Understanding species-specific vulnerabilities to climate anomalies is essential not only for developing process-based models that incorporate competition, growth, and other ecological processes but also for explaining overall tree species' range shifts and their responses to climate change. This knowledge is crucial for projecting species' distributions under future climate scenarios and informing effective forest management strategies. While such research is extensively conducted in Europe on major species like European beech (*Fagus sylvatica* L.; Dittmar et al., 2006) and Norway spruce (*Picea abies* (L.) Karst.; Vitasse et al., 2018a, b), many temperate deciduous tree species of the Acadian Forest, are underexplored in this context. In the Acadian Forest region, red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.) are three of the most abundant temperate deciduous tree species, each demonstrating elevational range limits within high elevation areas of New Brunswick. The early spring flowering of red maple makes it particularly susceptible to spring frost, leading to reduced fecundity and lack of sexual reproduction at its northern limits due to flower damage (Tremblay et al., 2002). Further, recent dendroclimatic research has linked sugar maple growth declines to winter thaw-freeze events (Moreau, Achim, & Pothier, 2020), while similar events have been tied to yellow birch die back in

New Brunswick (Bourque et al., 2005). However, to our knowledge, there have been no studies in the Acadian Forest that have assessed these three species concurrently to understand their growth responses to a variety of climatic variables and how the spatial variability in these responses.

In this study, our objective was to assess the relative effects of spring and winter temperature anomalies on interannual growth variations in red maple, sugar maple, and yellow birch trees along elevational climatic gradients, to determine which factor is more influential. We developed two alternative hypotheses: (i) the radial growth of temperate tree species is more influenced by minimum spring temperatures or spring frost events than minimum winter temperatures; (ii) the radial growth of temperate tree species is more influenced by minimum winter temperatures than by spring frost events or minimum spring temperatures. This approach allows us to explore the relative effects of low temperature extremes on tree growth, which may help improve our understanding of its influence on these species' leading-edge range (or cold range) limits. In turn, we hope this knowledge can improve the accuracy of process-based models in forecasting the impacts of climate change on future species distributions.

### **3.3 Methods**

#### *3.3.1 Sampling design*

We established 25 plots, evenly distributed across 5 elevational transects within Mount Carleton Provincial Park (New Brunswick, Canada), a temperate-boreal transition zone in the Acadian Forest region. These transects were placed along elevational

gradients to capture the full range from low-elevation temperate forests to the upper elevational limits of these temperate species, where plots are predominantly boreal in composition. The plots within each transect were strategically placed to illustrate this gradual shift from a dominance of temperate hardwood species, including red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.) in the lower plots, to a predominantly boreal species composition in the higher plots, consisting of spruce (*Picea* spp.) and balsam fir (*Abies balsamea* (L.) Mill.). Within these sites, a comprehensive forest inventory was conducted, and temperature loggers were installed to collect hourly temperature data from August 2021 to August 2022. For more details on the sampling design, see Chapter 2, section 2.3.

### 3.3.2 Site Selection

Site selection followed three primary criteria. Firstly, transects were established along elevational gradients to capture the transition from temperate to boreal forest composition. Transects locations were placed along elevational gradients that display a shift from temperate hardwood species, such as red maple, sugar maple, and yellow birch at lower elevations, to boreal species, including spruce and fir at higher elevations. At lower elevations, plots featured a high abundance of red maple, sugar maple, and yellow birch, with the abundance of these species declining with increasing plot elevation. Lastly, we selected sites with minimal evidence of major, stand-replacing disturbances, changes in soil composition, and topographical variation.

Since temperature and the abundance of temperate tree species typically decrease with elevation, placing sites along elevational gradients is a convenient method for capturing a gradient of temperature and species composition. However, it is important to note that the compositional and climatic relationship with elevation is not perfectly consistent. Thus, the spatial component implied by having separate transects is not explicitly used in our study; rather, it is the climate and associated biological responses of trees in different plots that is of primary importance.

### *3.3.3 Tree-ring sampling and chronologies*

Within the 25 study plots, we collected diameter at breast height (DBH) on all target tree species ( $\text{DBH} \geq 9$  cm) during the summer of 2021. We also took two growth increment cores per tree at a height of 1.3 m during summer 2021, resulting in a total of 51 red maple, 31 sugar maple, and 22 yellow birch trees. Samples were stored in plastic straws during fieldwork and then glued onto slotted wood mounts with the long side of the wood fibers in a vertical orientation. Samples were surfaced using a WSL-Core-Microtome (WSL, Birmensdorf, Switzerland) and sanded with 400 grit sandpaper to achieve clear growth-ring visibility. Tree cores were scanned using a Laxco™ SeBaCam Digital Microscope Camera (LAXCO, U.S.) under 5.1 megapixels (mp). Individual images were merged automatically to cover entire cross sections using SeBaView software ver. x64 (LAXCO, U.S.). Annual ring boundaries were measured at a 0.01-mm accuracy from digital images using CooRecorder 9.5 (CYBIS Elektronik & Data AB, Saltsjöbaden, Sweden). Cross-dating was performed using CDendro 9.5 (CYBIS Elektronik & Data AB, Saltsjöbaden, Sweden), and validated with the R Studio package

“dplR” (R Core Team, 2023; Bunn, 2008; Bunn, 2010; Bunn et al., 2023) and COFECHA (Holmes, 1983). Cross-dating was based on the comparison of individual growth curves to the mean growth curve per species and plot. Threshold individual correlations under 0.3 were used to identify poorly dated individual series, which were then carefully inspected to eliminate false annual growth estimates caused by partially missing ring boundaries. Cross-dated ring width series were then averaged annually per tree. Plots with less than two trees of a given target species were excluded from further analysis to avoid cross-dating errors.

Given the study’s design, which naturally leads to a reduction in sample size (less temperate species) across the compositional gradients, employing the express population signal (EPS; Wigley et al., 1984) to evaluate ring-width chronologies was considered unsuitable due to its reduced reliability at lower sample sizes (Buras, 2017). Therefore, the quality of plot-level cross-dating was assessed using the mean series intercorrelation.

#### *3.3.4 Response variables*

For our response variable, we used the ring-width index (RWI) because it is more representative of relative growth changes over time than raw ring width measurements, as it accounts for age-related growth trends and other non-climatic influences (Cook & Kairiukstis, 1990). To calculate RWI, we detrended the tree-ring series to remove low-frequency radial growth trends related to age and other biological effects using a 30-year smoothing spline with a 50% frequency response (Cook & Peters, 1981). The detrending was conducted using the “dplR” package in R (R Core Team, 2023; Bunn, 2008; Bunn, 2010). After detrending, the RWI was computed using the following equation:

$$RWI_t = \frac{RW_t}{\overline{RW_t}}$$

where  $RW_t$  is the observed ring-width in year  $t$  and  $\overline{RW_t}$  is the fitted value from the smoothing spline for year  $t$ .

### 3.3.5 Climate variables

Reconstructed climate data for each site (described in Chapter 2) were aggregated into annual statistics for the period 1950-2020. To test our hypotheses regarding the roles of spring and winter temperatures on tree growth, we derived several candidate variables to characterize the winter and spring seasons, as well as the growing season (Chagnon et al., 2023). Growing season variables included growing-season degree days ('GS<sub>dd</sub>') above 4° and mean growing-season temperature ('GST<sub>mean</sub>'; Körner et al., 2016). Growing degree days have long been associated with tree growth (Kauppi & Posche, 1985; Kauppi, Posche, and Pirinen, 2014), and changes in growing season length have similarly been linked to growth (Kollas et al., 2014; Gao et al., 2022). The start date of the growing season was determined as the fifth consecutive day with a maximum temperature of 4°C or higher, and the end date as the fifth consecutive day with a minimum temperature falling below 0°C after August 1<sup>st</sup> (Chagnon et al., 2023; Huang et al., 2010; Moreau et al., 2020b).

The severity of late spring frosts has been previously reported in terms of duration as well as timing relative to the start of the growing season (Vitasse & Rebetez, 2018). Spring frost duration was estimated as the number of days with minimum temperatures

dropping below 0°C ('LSF<sub>length0</sub>'), -2°C ('LSF<sub>length2</sub>'), and -4°C ('LSF<sub>length4</sub>') following the start of the growing season (Chuine, 2010; Vitasse et al., 2019; Zohner et al., 2020b). Spring frost timing was calculated as the cumulative warming in GDD prior to the last frost event ('LSF<sub>warming</sub>'). In addition, we also calculated mean May minimum temperature ('May<sub>min</sub>') and mean April minimum temperature ('Apr<sub>min</sub>'); Kollas et al., 2014; Körner et al., 2016). Winter variables included winter thaw days, calculated as the number of days in winter with temperatures  $\geq 4^{\circ}\text{C}$  ('WT<sub>length</sub>'), as well as the thaw intensity, calculated as the sum of degree days above 4°C in winter ('WT<sub>warming</sub>'). These variables were chosen due to the documented impacts of winter thaw on temperate tree species' growth (Moreau, Achim, & Pothier, 2020), and overall survival (Bourque et al., 2005). Lastly, we included mean winter minimum temperature ('Winter<sub>min</sub>'), which has been linked to growth reductions (Pederson et al., 2003), and is traditionally associated with tree species' leading-edge range limits (Iversen, 1944; Walther, Berger & Sykes, 2005).

To ensure that we are assessing growth responses to climate variability rather than low-frequency trends such as those related to climate change, climate variables were detrended using the same method applied to the tree-ring series (Chagnon et al., 2023; Klesse, 2021; Ols et al., 2023). Subtractive detrending was applied to variables capable of negative values, such as temperature, while division was used for variables having only positive values. This applies to 'transient' or 'event' variables, such as the number of spring frost days. This detrending was limited to variables that exhibited low-frequency

trends identified through visual inspection. Stochastic fluctuations with no discernible patterns over time were not detrended (Chagnon et al., 2023).

### *3.3.6 Variable selection and growth modelling*

We conducted an exploratory variable selection process to identify the most significant variables for each season, focusing on both traditional climate variables and transient events to construct a final growth model. Traditional climate variables, such as average minimum temperatures, have been widely used in classic dendrochronological studies to characterize growth-climate relationships (Carrer & Urbinati, 2004; Mérian & Lebourgeois, 2011). Additionally, we chose to investigate the impacts of extreme, transient phenomena, such as spring frost events or winter thaws. In more recent studies, the use of these transient or extreme event variables have displayed strong relationships with growth (Dittmar et al., 2006; Moreau et al., 2020a). For spring and winter, we selected one traditional climate variable, and one transient event variable. Growing season was included to provide a baseline for seasonal growth, and as such, we chose a single traditional climate variable for growing season. To test the strength of individual climate variables, we constructed univariate linear mixed effects models for each candidate variable, using tree-level ring-width index (RWI) as the response variable, and ‘tree’ as a random effect, while a function was incorporated to account for the first-order autocorrelation structure in the tree-ring series (Monserud, 1986; Chagnon et al., 2023). To ensure final model robustness and allow for comparison between plots and species, the univariate analysis was conducted on the entire ring-width dataset, without stratification by plot or species. For spring and winter seasons, one transient event and

one traditional climate variable were retained for inclusion in a final model. These variables were chosen based on the second-order Akaike Information Criterion (AICc), which is more appropriate for use with smaller sample sizes (Sugiura, 1978; Mazerolle, 2006), as well as the effect-size estimate. The best variables to be retained were those with the lowest AICc score and the highest effect-size estimate. To assess the potential effects of the previous season's climate, we included variables from the previous spring and growing season, referred to as 'lagged' variables.

To test our hypotheses, we fitted the final mixed-effects model individually to each plot for each target species, using the "nlme" package (Pinheiro et al., 2022; Pinheiro & Bates, 2000) in R (R Core Team, 2023), with the tree-level RWI as the response variable. Each model also incorporated tree as a random effect and included a function to address the first-order autocorrelation in the tree-ring series. We compared the magnitude and direction of estimated coefficients for each climate predictor to determine their importance. We then tried to relate the variability in coefficients across plots to the variability in long-term climate normals across these plots. To do so, we correlated the coefficients to various 70-year climate normals for each plot, including the average May and winter  $T_{\min}$ , summer  $T_{\max}$ , growing season degree days, start and end dates of the growing season, growing season temperature, mean annual temperature, number of late spring frosts with temperatures below  $0^{\circ}\text{C}$ , and the number of winter thaw days with temperatures above  $4^{\circ}\text{C}$ .

Our analysis did not explicitly incorporate any variables related to 'transect' or elevation, as transects were merely used to capture gradients in species composition,

growth responses, and temperature. In addition, transects were used to increase sample size and coverage, which was especially important to offset the implicit declining sample size toward the range limits of our target species.

## **3.4 Results**

### *3.4.1 Elevational climate gradients*

Our study sites exhibited consistent seasonal and elevational temperature patterns. However, Transect C was an exception, displaying less elevational variability in temperatures during summer, compared to the other transects. Consequently, we excluded it from this climate summary. We found marginal variations in winter minimum temperature along the elevation gradient, ranging from  $-14.5 \pm 7.0^\circ\text{C}$  in plot 1 to  $-14.8 \pm 6.9^\circ\text{C}$  in plot 5. In spring (April and May), elevational variations in minimum temperatures increased, from  $-2.0 \pm 3.9^\circ\text{C}$  and  $3.45 \pm 3.6^\circ\text{C}$ , April, and May, respectively, in plot 1, to  $-2.5 \pm 3.9^\circ\text{C}$  and  $3.1 \pm 3.6^\circ\text{C}$ , respectively, in plot 5. Summer maximum temperatures exhibited a more noticeable elevational difference, with plot 1 recording a slightly warmer average of  $18.9 \pm 5.4^\circ\text{C}$  compared to  $18.4 \pm 5.4^\circ\text{C}$  in plot 5 (for more details on elevational climate gradients, refer to Chapter 2, section 2.4.1.4).

### *3.4.2 Tree characteristics across elevational gradients*

The 51 red maple trees sampled over 11 plots displayed an average age of 60 years, ranging between 29 and 88 years. Between 1950 to 2020, their mean annual ring-width was 1.23 mm, with a high mean series intercorrelation after cross-dating of 0.53 (Table 3.1). Thirty-one sugar maple trees were sampled within 6 plots, with an average

age of 65 years, ranging from 39 to 125 years. Their mean annual ring-width was 1.28 mm (Table 3.1), with a high mean series intercorrelation was 0.51 (Table 3.1). Lastly, we sampled 22 yellow birch trees across 5 plots, with an average age of 61 years, ranging from 37 to 98 years. Yellow birch showed a mean annual ring-width of 1.33 mm, with a slightly lower mean series intercorrelation of 0.43 (Table 3.1).

Table 3.1. Characteristics of plots and trees of the target species, including the number of trees per plot, plot elevation, age, DBH, ring-width (1950-2020 mean), and mean series intercorrelation.

<i>Species</i>	<i>Trees</i>	<i>Plots</i>	<b>Elevation (m)</b>			<b>Age (yrs)</b>			<b>DBH (cm)</b>			<b>Ring-width (mm)</b>			<b>Mean intercorr. (0,1)</b>		
			<i>min</i>	<i>max</i>	<i>mean</i>	<i>min</i>	<i>max</i>	<i>mean</i>	<i>min</i>	<i>max</i>	<i>mean</i>	<i>min</i>	<i>max</i>	<i>mean</i>	<i>min</i>	<i>max</i>	
Red maple	51	11	290	564	60	29	88	22.2	10	52.2	1.23	0.10	4.32	0.53	0.42	0.63	
Sugar maple	31	6	285	444	65	39	125	26	10	68.1	1.28	0.05	4.82	0.51	0.39	0.60	
Yellow birch	22	5	285	478	61	37	98	28.2	50	70.3	1.33	0.04	6.02	0.43	0.39	0.48	

### 3.4.3 Variable selection

Following the univariate model selection process, five climatic variables were selected for inclusion in our final model, based on their AICc values and effect sizes (Table 3.2). For growing season, mean temperature was the most influential variable, with the lowest AICc score (607.10) and the largest effect size ( $\beta = -10.5 \pm 3.4$ ;  $p < 0.01$ ; Table 3.2). For spring, minimum May temperature was the strongest climatic predictor ( $\beta = 12.6 \pm 3.3$ ;  $p < 0.001$ ), along with late spring frost days below  $0^{\circ}\text{C}$  ( $\beta = 14.7 \pm 3.3$ ;  $p < 0.001$ ). For winter, minimum winter temperature was selected ( $\beta = -1.6 \pm 3.3$ ;  $p > 0.05$ ; Table 3.2), along with winter thaw length (the number of winter days above  $4^{\circ}\text{C}$ ;  $\beta = -8.1 \pm 3.3$ ;  $p < 0.05$ ; Table 3.2). This variable selection process led to the development of the following final model, in which we also included a one-year lagged climate variable for the spring and winter variables, to assess the impacts of the previous season:

$$RWI \sim meanGST + meanGST_{lag} + avg\_may\_min + avg\_may\_min_{lag} \\ + LSFlength0 + LSFlength0_{lag} + avg\_winter\_min + WTlength$$

Table 3.2. Model performance statistics for the candidate variable selection process, including coefficient estimates with standard errors, and AICc scores. Selected variables are presented in bold. Significance of parameter estimates is marked by asterisks: \*\*\* indicates  $p < 0.001$ , \*\* indicates  $p < 0.01$ , and \* indicates  $p < 0.05$ . All standard errors are multiplied by  $10^3$ .

Category	Type	Variable	Estimate±SE	AICc
<i>Growing season</i>	Traditional	<b>Mean growing season temp. (°C)</b>	<b>-10.5±3.4**</b>	<b>607.1</b>
	Transient	Growing season degree days ( $\sum$ GDD)	-3.3±3.4	615.89
	Transient	Summer max. temp. (°C)	-6.4±3.4	613.2
<i>Spring</i>	Traditional	<b>May min. temp. (°C)</b>	<b>-12.6±3.3***</b>	<b>601.96</b>
	Traditional	April min. temp. (°C)	-3.2±3.2	615.93
	Transient	<b>Frost length 0 (<math>\sum</math>days <math>\leq</math> 0°C)</b>	<b>14.7±3.3***</b>	<b>597.4</b>
	Transient	Frost length -2 ( $\sum$ days $\leq$ -2°C)	4.2±3.3	615.28
	Transient	Frost length -4 ( $\sum$ days $\leq$ -4°C)	10.0±3.1**	606.83
<i>Winter</i>	Traditional	<b>Winter min. temp. (°C)</b>	<b>-1.6±3.3</b>	<b>616.61</b>
	Transient	<b>Thaw length (<math>\sum</math>days <math>\geq</math> 4°C)</b>	<b>-8.1±3.3*</b>	<b>610.89</b>
	Transient	Thaw GDD ( $\sum$ GDD)	-0.11±3.1	616.99

#### 3.4.4 General growth-climate response

Fitting our final model to each species per plot, we found that May minimum temperature is the strongest predictor of growth for all three studied species. However, the direction of the response was inconsistent. For red maple, growth response to mean May minimum temperature was positive in 6 out of 11 plots, with a peak effect size of 3.27 (Figure 3.1). Similarly, sugar maple exhibited a positive growth response in half of its plots (3 out of 6), with a similar maximum effect size of 3.28 (Figure 3.1). Lastly, yellow birch displayed a positive growth response to May minimum temperatures in two out of five plots (Figure 3.1). The number of late-spring frost events was the second most impactful climate variable on growth, with the most significant effects of -0.205 for red maple, 0.164 for sugar maple, and -0.250 for yellow birch (Figure 3.1). Mean growing

season temperature, winter thaw days, and mean minimum winter temperature exerted relatively minor effects on growth (Figure 3.1). The largest response to mean growing season temperature was 0.18 for red maple, 0.17 for sugar maple, and -0.13 for yellow birch (Figure 3.1). For winter thaw days, the most substantial effect for red maple was -0.06, with sugar maple having equal positive and negative effects of 0.03 to -0.03 (Figure 3.1). Yellow birch's largest growth response to winter thaw days was -0.05 (Figure 3.1). Lastly, the largest response to mean minimum winter temperature was -0.04 for red maple, 0.04 for sugar maple, and -0.04 to 0.04 for yellow birch (Figure 3.1).

#### *3.4.5 Spatial-variability in growth-climate responses*

Spatial variability was determined as the range in effect sizes for plot-level growth responses to a temperature variable. While May minimum temperature was the best predictor of growth, it also demonstrated the highest variability in growth responses across plots, for all species examined. The range of effects on red maple and sugar maple varied from -1.06 to 3.27 and -1.21 to 3.28, respectively across plots, while yellow birch had a narrower range of effects, from -2.45 to 0.35 (Figure 3.1). Following May minimum temperatures, late-spring frost events displayed the most spatial variability in growth response for red maple and yellow birch ( $\beta = -0.20$  to 0.18 and  $\beta = -0.25$  to 0.13, respectively), while sugar maple growth response ranged from -0.01 to 0.17 (Figure 3.1). In contrast, winter variables demonstrated the least spatial variability in its effect on growth. For red and sugar maple, the winter variable showing the most spatial variability was winter thaw days, which ranged from -0.06 to 0.05 and -0.03 to 0.03, respectively (Figure 3.1). For yellow birch, the winter variable with the most spatial variability in

effect sizes was mean winter minimum temperature. Its effect sizes ranged from -0.04 to 0.04, only slightly surpassing that of winter thaw days ( $\beta = -0.05$  to 0.02; Figure 3.1). The range of responses to mean growing season temperature for red maple, sugar maple, and yellow birch were -0.15 to 0.18, -0.04 to 0.17, and -0.13 to 0.11, respectively (Figure 3.1). Lastly, the lagged variables appeared to align in their effect size magnitude, but differed in directional responses, making it challenging to properly interpret the effects of previous season's climate (Figure 3.1).

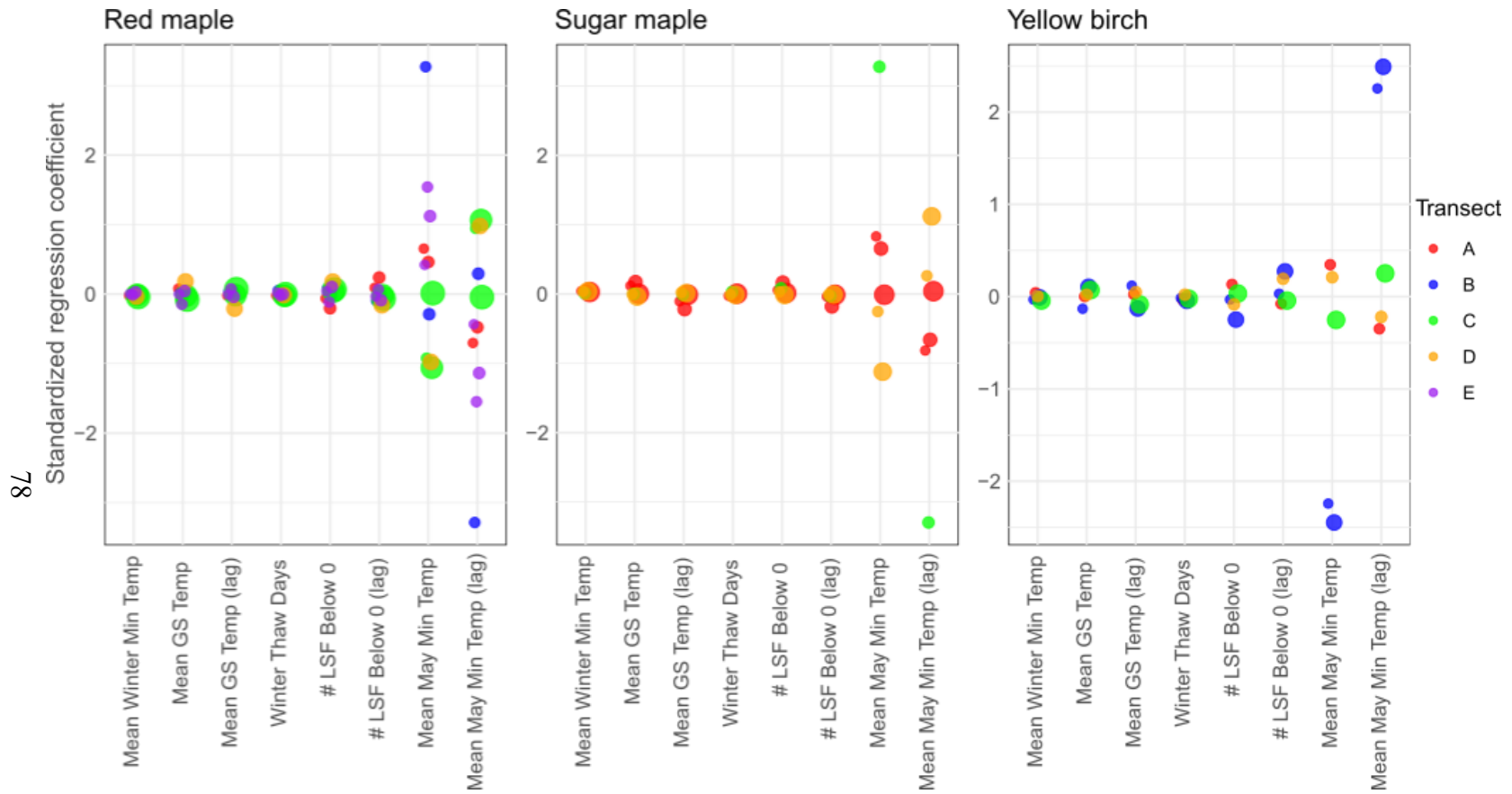


Figure 3.1. Standardized regression coefficients of the plot-specific linear regression model predicting tree growth in response to climate variables for each target species. Points represents individual plots, and point size indicates number of observations (trees) for a given species in a plot.

#### *3.4.6 Long-term climate characterization of plots and growth response variability*

When correlating model variable coefficients to plot climate normals, we found that the effect of May minimum temperature on growth varied with long-term plot climate for all three species (Table 3.3). For yellow birch, the growth response to mean May minimum temperature was most related to the 70-year mean of growing season start date ( $r = -0.52$ ), growing season length ( $r = 0.43$ ) and number of winter thaw days (0.50; Table 3.3). For all factors, more positive May minimum temperature coefficients were associated with warmer plots. However, the non-normal distribution of yellow birch's growth responses made it difficult to interpret a pattern in their spatial variability, and so they are not discussed. For sugar maple, the growth response to mean May minimum temperature was strongly related to 70-year mean of minimum winter temperature ( $r = 0.88$ ), followed by minimum May temperatures ( $r = 0.32$ ) and the timing of the end of the growing season ( $r = 0.30$ ; Table 3.3). Similarly to yellow birch, these correlations all indicated that more positive May minimum temperature coefficients were associated with warmer plots (Table 3.3). For red maple, the growth response to mean May minimum temperature varied strongly with the 70-year mean of minimum winter temperature ( $r = -0.62$ ), maximum summer temperature ( $r = 0.38$ ) and mean growing season temperature ( $r = 0.34$ ; Table 3.3). However, the directions of the effects were inconsistent, with most positive growth responses to May temperatures found at plots with lower winter temperatures as well higher summer temperatures.

Table 3.3. Pearson’s correlation values between the regression coefficients for the mean May minimum temperature spatial growth-response analysis and the 70-year normals for plot climate characterization. All characterization variables here represent 70-year averages.

<b>Plot Characterization Variable</b>	<b>Pearson’s correlation (r)</b>		
	<b>Red maple</b>	<b>Sugar maple</b>	<b>Yellow birch</b>
Minimum winter temperature	-0.62	0.88	0.12
Mean annual temperature	-0.11	0.22	0.29
Minimum May temperature	-0.28	0.32	0.26
Maximum summer temperature	0.38	-0.12	0.23
Growing season degree days	0.06	0.10	0.30
Start of growing season	0.16	-0.23	-0.52
End of the growing season	-0.20	0.30	0.35
Growing season length	-0.19	0.27	0.43
Mean growing season temperature	0.34	-0.15	0.09
Number of spring frost days	0.05	-0.15	0.42
Number of winter thaw days	-0.09	0.25	0.50

### 3.5 Discussion

In this study, we compared the annual growth-climate coupling of three temperate deciduous tree species along elevational gradients at their upper elevational limits. Our aim was to compare the impacts of spring and winter temperatures on the growth of these species toward their leading-edge range limits, to help understand the constraining role of climate on the northward and upward migration of these species under climate change. Our findings suggest that spring temperatures have a greater influence on the growth of red maple, sugar maple, and yellow birch, than low winter temperature toward their upper elevational limits.

### *3.5.1 Winter temperature tolerance in temperate tree species*

While our results emphasize the dominant role of spring temperatures, they notably diverge from past findings which have often highlighted winter temperatures as critical for tree growth and establishment at temperate tree species' cold range limits (Iversen, 1944; Walther, Berger & Sykes, 2005). However, our findings that winter temperatures do not strongly correlate with growth are consistent with the established winter cold tolerance of the tree species studied. For instance, at their northern limits, sugar maple and yellow birch exhibit freezing tolerances down to approximately -42°C and -45°C respectively, while red maple can withstand temperatures as low as -54°C (Sakai & Weiser, 1973; George et al., 1974). These thresholds are well below the coldest temperatures recorded in our study, suggesting that winter temperatures are not a limiting factor for these species at our study sites.

### *3.5.2 Role of spring temperatures in tree growth toward range limits*

In addition to the predominant role of minimum May temperatures, we found that spring-frost events had the second most influential effect on growth. These results support our first hypothesis that spring temperatures are more important than winter temperatures in influencing the annual growth of temperate tree species, especially at their leading-edge range limits. These results align with previous findings that low spring temperatures are responsible for substantial growth reductions of temperate tree species (Dittmar et al., 2006; Hufkens et al., 2012). The strong effect of minimum spring temperature on growth could be linked to its control over cambium dormancy and changes in the start of growth, which can increase growing season length and impact

competitive ability (Kollas et al., 2014; Lenz et al., 2016). This could explain the positive growth response of red maple to warmer May temperatures in colder plots, where growth could be more limited by cold spring temperatures toward its upper elevational limits. Such explanation contrasts with recent studies of temperate stands that conclude that the timing of spring growth onset is not related to the total annual growth in temperate forests (Dow et al. 2022). However, we cannot exclude that the cold climate of our study sites (at the limit of the species range) exerts such a constraint on annual growth that is partly alleviated by earlier spring onsets.

Warmer spring temperatures also lead to earlier budburst (Menzel et al., 2006), possibly exposing new leaves and flowers to damaging frost events. This exposure can impair photosynthesis, causing trees to grow a second leaf flush and reduce carbon allocation to growth, offering a potential explanation for the negative response to warm May temperatures (Dittmar et al., 2006; Hufkens et al., 2012; Rubio-Cuadrado et al., 2021). For red maple, it is possible that the benefits incurred by an earlier start to the growing season could outweigh the negative effects of increased frost exposure due to early budburst. This interplay between growing-season length and spring frost is discussed by Kollas et al. (2014), who suggests that both factors co-control the cold range limits of temperate tree species. However, little research has been conducted on the specific growth responses of red maple to spring frost and growing season length. In the case of sugar maple, the lack of positive growth response to warmer May temperatures in colder plots may indicate that the increased risk of spring frost damage incurred due to early budburst may outweigh any positive benefit from a longer growing season. This

aligns with research by Hufkens et al. (2012), who found that sugar maple is especially prone to early budburst and subsequent negative impacts from spring frost events.

### *3.5.3 General insights into variable climatic influences on tree growth*

Our research reveals that spring minimum temperatures have a more pronounced effect on the growth of temperate tree species than winter temperatures. Notably, we found considerable spatial heterogeneity in how these species react to spring temperatures. This variability in growth response displays considerable patterns along climatic gradients. Further, the contrasting growth responses to minimum spring temperatures between studied species indicate distinct, species-specific climate interactions. These differences reflect unique phenological strategies, which further emphasize the complex interplay between climatic variables and tree growth dynamics. We can only speculate on the biological mechanisms underpinning these climatic relationships and their covariation with local climate. Such dependency on local climate conditions, including variations in fall, winter, and spring temperatures, may influence phenological events such as budburst and leaf-fall, which are also largely controlled by daylength (Ren et al., 2020). The timing of these phenological phases is crucial as they directly affect the length of the growing season and, consequently, the overall growth and competitive dynamics of these tree species, as well as their risk of frost exposure.

### *3.5.4 Future research*

Given this complexity, further research is essential to disentangle the multifaceted influences of climate on bud phenology as well as cambium activity. Additionally, we

found that the non-normal distribution of yellow birch's growth responses to climate variables complicated the interpretation of their spatial variability. To address this, further investigation is required to explore yellow birch's distinctive interactions with site conditions and climate variations, possibly with a large focus on winter warming—a factor previously identified as crucial for the health of this species in New Brunswick (Bourque et al., 2005). Additionally, since our study assessed these climatic relationships only at the upper elevational limits of these species, further research at their northern range limits is necessary to fully understand these leading-edge dynamics. Lastly, we recommend multi-year monitoring of phenology, alongside comprehensive climate, and plot measurements, to deepen our understanding of the interactions between climate variables and tree growth. Such studies would help clarify the mechanisms through which climate impacts phenology and growth patterns, thereby enhancing species growth and distribution models. This, in turn, we hope will aid in informing forest conservation and management strategies in the context of changing climate conditions.

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## CHAPTER 4: GENERAL DISCUSSION

### 4.1 Summary of results

The aim of this project was to assess the relative importance of spring and winter temperatures in constraining the migration of temperate tree species into the boreal forest. This was achieved by examining the relationship between species compositional gradients and local long-term climate, as well as analyzing the annual growth response of individual trees to yearly climate variations across different climatic gradients. The first study evaluated the present-day species' relative abundance across elevational gradients and its relationship with 70 years of climate data. This study found non-linear relationships between temperature variables and both the relative stem count and relative basal area of red maple and sugar maple. Among all temperature variables examined, red and sugar maple exhibited the strongest relationships with spring temperature variables. Specifically, red maple relative stem count and relative basal area responded more strongly to minimum spring temperature than winter temperature, while the relative stem count and relative basal area of sugar maple responded most strongly to the frequency and severity of spring frost events.

Our second experiment investigated the annual growth response of tree-rings to climatic variability, revealing that minimum temperatures in May had a more substantial impact on the growth of our target species than any winter variables assessed. This finding is supported by earlier research which highlighted the impacts of spring temperatures on growth (Dittmar et al., 2006; Vanoni et al., 2016; Vitasse et al., 2019) and aligns with studies by Kollas et al. (2014) and Körner et al. (2016), which further

suggested that winter temperatures are unlikely to be the limiting factors for the cold range limits of temperate tree species. Moreover, the growth responses to minimum May temperatures displayed considerable spatial heterogeneity, with notable differences in responses between species. This variability is likely due to unique phenological growth strategies (Hufkens et al., 2012), which are highly adapted to the local climate (Ren et al., 2020).

Overall, our findings demonstrate that growth and relative abundance do not correlate strongly with winter temperatures, aligning with studies quantifying the winter cold tolerance of our target species (Sakai & Weiser, 1973; George et al., 1974). Overall, the substantial influence of spring temperatures on the growth and relative abundance of our target species corroborates past findings emphasizing the significant impact of spring frost events on the growth and establishment of temperate tree species (Dittmar et al., 2006; Hufkens et al., 2012), particularly at their cold range limits (Kollas et al., 2014; Körner et al., 2016). These results challenge the traditional view that low winter temperatures are the primary determinant of the northern range limits of temperate tree species (Iversen, 1944; Walther, Berger & Sykes, 2005).

## **4.2 Limitations and future research**

Given the varied species responses to spring temperatures, we recommend conducting phenology-focused research to further understand species-specific adaptations, as we could only speculate on the phenology-driven species-specific responses observed in our results. Further, our study only covers a single year of data collection, with only a single plot inventory. We suggest that multi-year monitoring of

phenology, climate, and plot measurements would provide better insight on the interactions between climate variability and growth. A long-term study would also allow shifts in species distribution to be observed in relation to climate change, similar to research by Boisvert-Marsh et al., (2014, 2019).

To address the complex climatic responses of yellow birch that we observed in both chapters 2 and 3, further investigation is required to explore yellow birch's distinctive interactions with site conditions and climate variability. We suggest a strong focus on winter thaw events may provide valuable insight here (Bourque et al., 2005).

Lastly, it is important to note that the relatively small sample size of our study poses limitations on the generalizability of our results across different climatic gradients. Since our study was conducted across elevational gradients, exploring latitudinal gradients could reveal additional factors, such as genetic variation, that impact species responses. To address these concerns, future research should consider increasing the sample size, adding more transects, and incorporating studies across both elevational and latitudinal gradients to better discern the impacts of climate variability.

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# APPENDIX

## Supplementary data

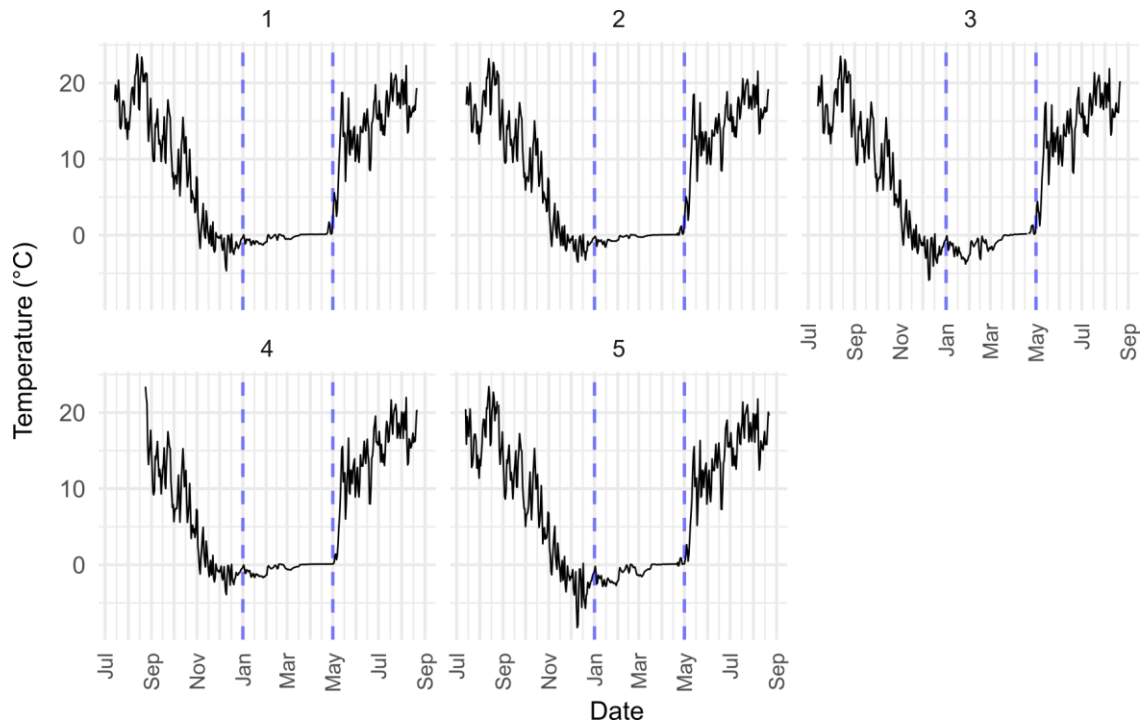


Figure S1. Average daily temperature of the 0m temperature probe, averaged by plot using raw temperature data. X-axis starts in 2021 and ends in 2022. Black line represents the daily mean temperature, computed from hourly temperature data. Blue, vertical dashed lines capture the approximate period in which the 0m probe is affected by snow cover. Each facet represents a single plot.

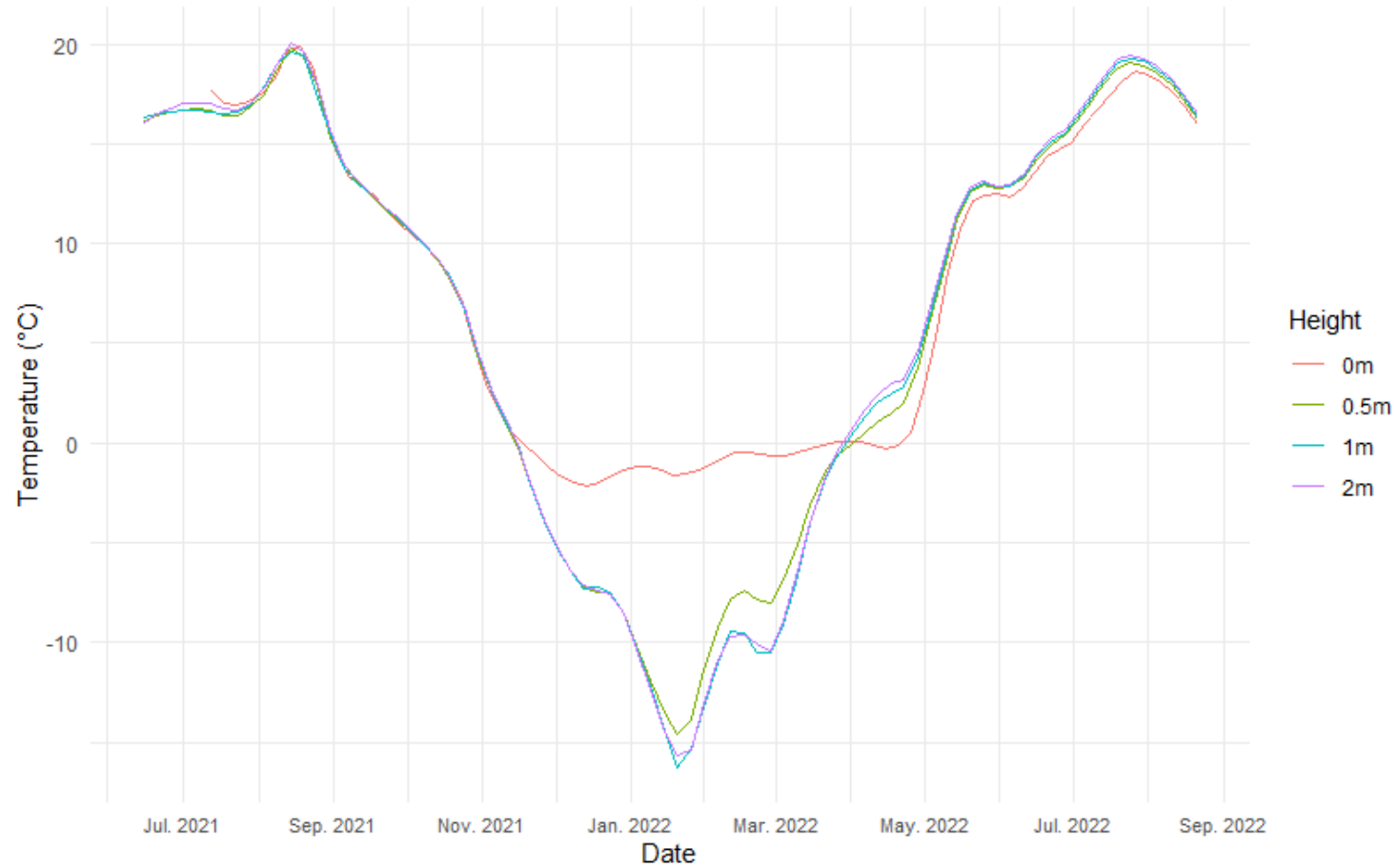


Figure S2. Average daily temperature using 1 year of raw temperature probe data between summer 2021 and 2022, averaged by temperature probe height. To aid in visualization, light loess smoothing was applied to the data at a span of 0.15. Daily averages are computed from hourly data.

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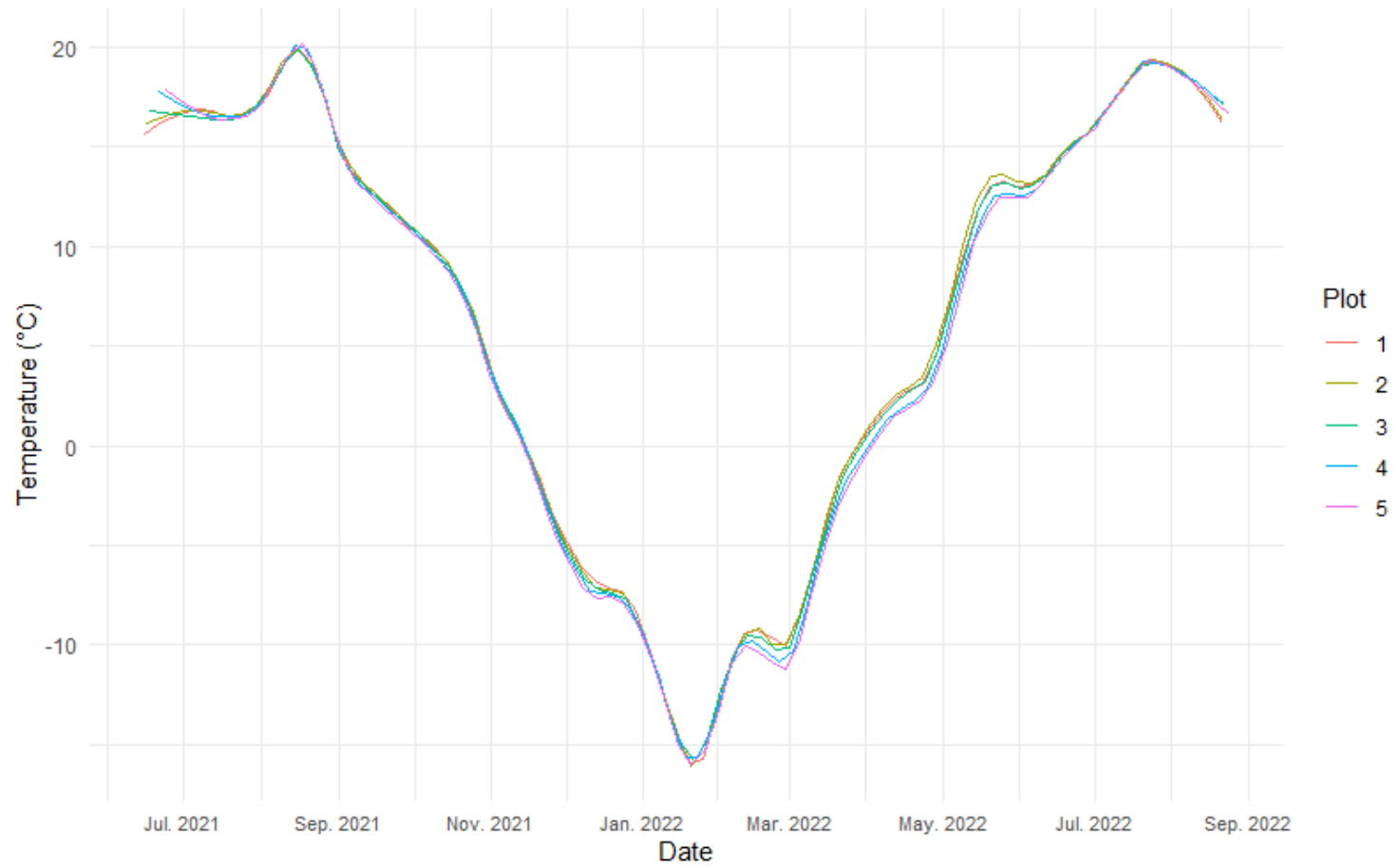


Figure S3. Average daily temperature for each plot using 1 year of raw temperature probe data between summer 2021 and 2022, averaged across plots. To aid in visualization, light loess smoothing was applied to the data at a span of 0.15. Daily averages are computed from hourly data.

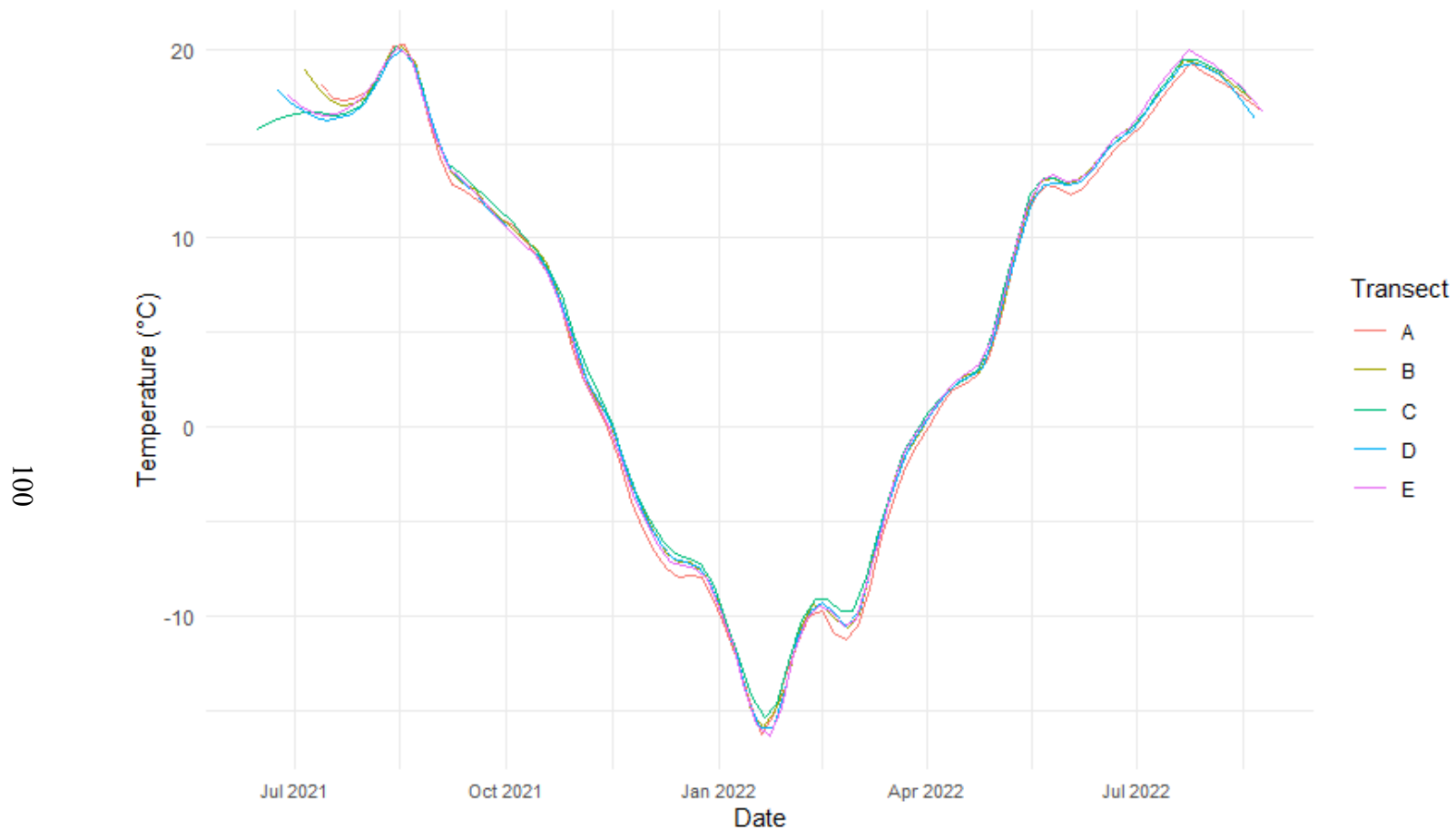


Figure S4. Average daily temperature for each plot using raw temperature probe data between summer 2021 and 2022, averaged by transect. To aid in visualization, light loess smoothing was applied to the data at a span of 0.15. Daily averages are computed from hourly data.

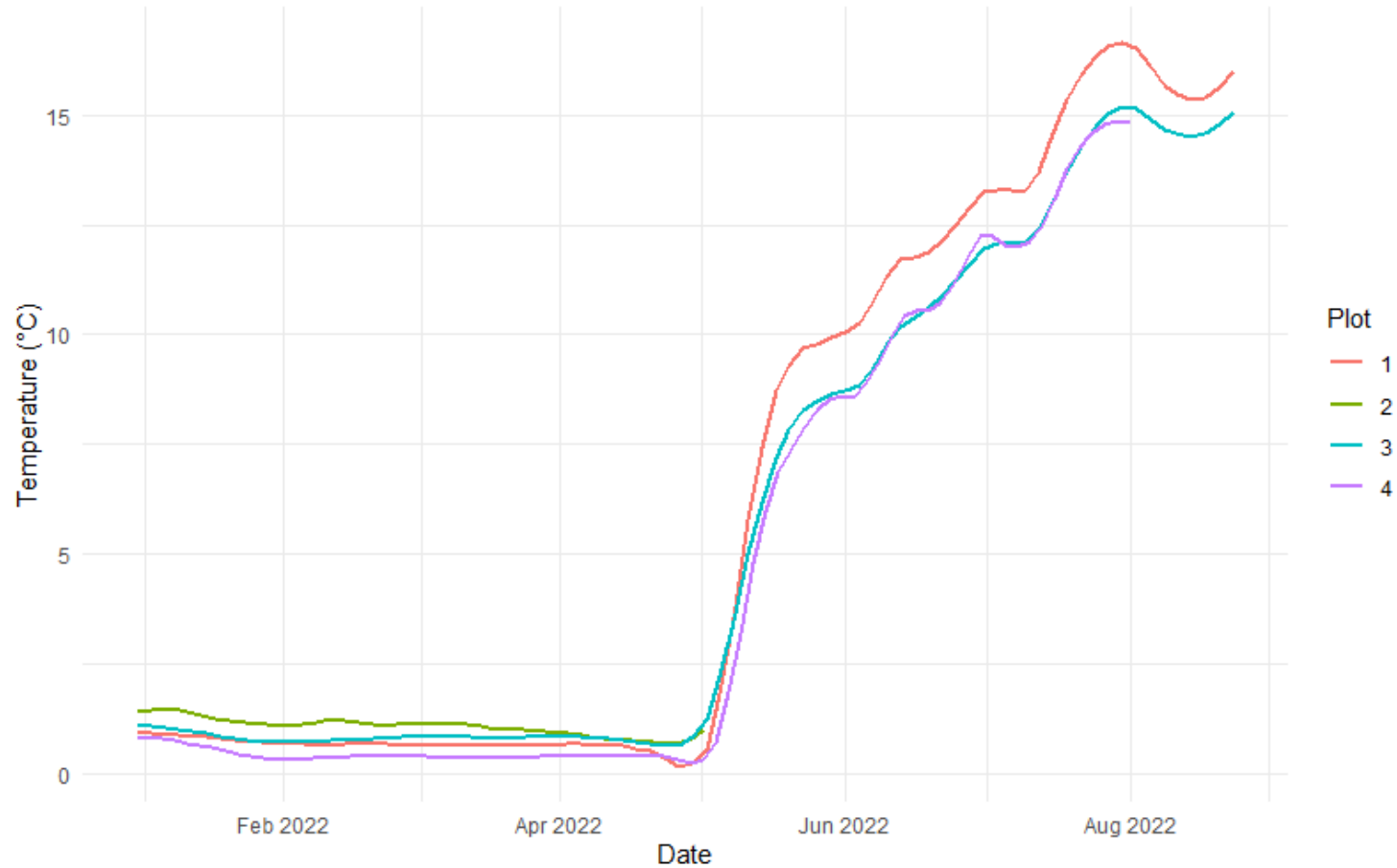


Figure S5. Average daily soil temperature from plot C. Shows data from January 1<sup>st</sup>, 2022, to late August 2023 when the data loggers were removed. Soil temperature probes were installed at 10cm below the start of the mineral soil. Daily average is computed from hourly data. Light loess smoothing is applied at a span of 0.15.

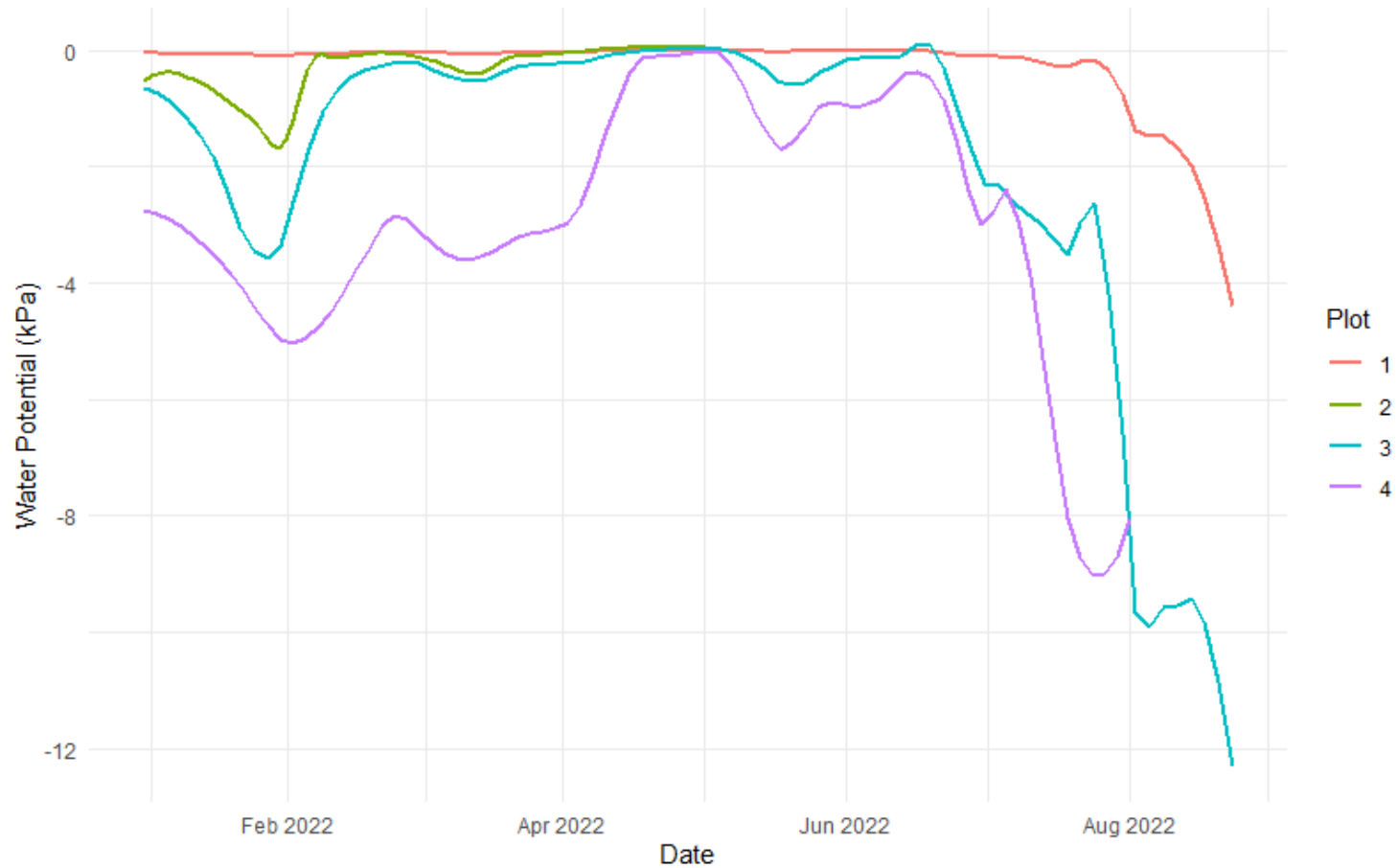


Figure S6. Average daily soil water potential from plot C. Shows data from January 1<sup>st</sup>, 2022, to late August 2023 when the data loggers were removed. Probes were installed at 10cm below the start of the mineral soil. Daily average is computed from hourly data. Light loess smoothing is applied at a span of 0.15.

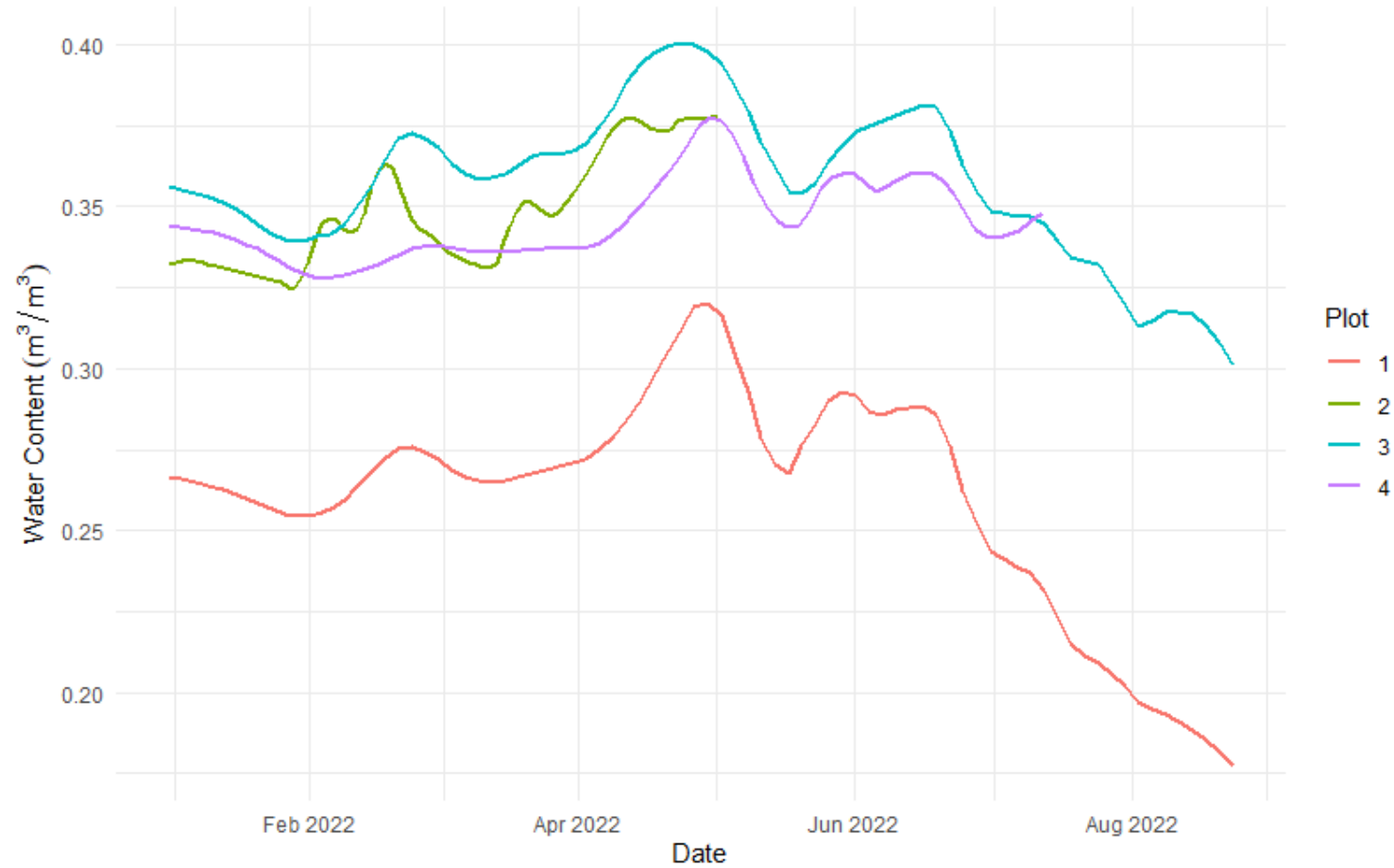


Figure S7. Average daily soil volumetric water content from plot C. Shows data from January 1<sup>st</sup>, 2022, to late August 2023 when the data loggers were removed. Probes were installed at 10cm below the start of the mineral soil. Daily average is computed from hourly data. Light loss smoothing is applied at a span of 0.15.

Table S1. Soil analysis data from study plots. O.M. is organic matter, Tot. N is total nitrogen, and C/N is carbon to nitrogen ratio. In transect D, plots 1 and 3 were missing soil samples. Clay, silt, and sand are missing from transect A, plot 1 due to insufficient soil in sample.

Transect	Plot	O.M. %	Tot.N %	C/N	C %	S %	pH	Exchangeable					Clay %	Silt %	Sand %	Rocks %
								Na	K meq/100 g	Ca	Mg	P ppm				
A	1	12.83	0.556	13.4	7.46	0.049	3.98	0.03	0.14	0.31	0.30	16	-	-	-	47.1
	2	13.02	0.482	15.7	7.57	0.057	4.22	0.02	0.11	0.21	0.15	11	11	39	50	41.1
	3	9.90	0.504	11.4	5.75	0.032	4.23	0.05	0.32	1.22	0.26	28	9	46	45	34.2
	4	18.49	0.714	15.1	10.75	0.059	4.65	0.02	0.13	0.07	0.08	4	7	22	71	43.1
	5	3.41	0.160	12.4	1.98	0.012	4.01	0.07	0.06	0.00	0.02	4	11	47	42	6.7
B	1	10.77	0.421	14.9	6.26	0.026	4.62	0.09	0.24	2.03	0.40	5	21	54	25	20.7
	2	6.75	0.284	13.8	3.92	0.019	4.6	0.02	0.09	0.07	0.07	3	9	49	41	22.8
	3	15.09	0.534	16.4	8.77	0.045	4.48	0.01	0.08	0.00	0.07	3	8	31	61	43.4
	4	14.17	0.405	20.3	8.24	0.05	4.69	0.02	0.11	0.00	0.07	2	6	37	57	24.5
	5	9.68	0.286	19.6	5.63	0.034	4.05	0.03	0.09	0.03	0.08	3	6	36	57	24.4
C	1	4.65	0.237	11.4	2.7	0.002	4.95	0.01	0.05	1.67	0.30	5	7	33	60	34.7
	2	4.61	0.280	9.6	2.68	0.018	4.79	0.22	0.11	1.19	0.28	4	27	38	34	23.7
	3	7.28	0.292	14.50	4.230	0.053	4.61	0.05	0.07	0.30	0.18	7	10	34	56	33.3
	4	7.89	0.287	16.00	4.590	0.052	4.58	0.01	0.05	0.03	0.03	3	7	22	71	31.9
	5	5.63	0.199	16.50	3.270	0.011	4.31	0.04	0.06	0.07	0.03	5	9	25	66	42.6
D	2	4.53	0.322	8.2	2.63	0.029	4.96	0.06	0.11	6.74	0.64	3	11	47	41	59.0
	4	6.77	0.275	14.3	3.93	0.011	4.66	0.01	0.04	0.07	0.03	2	7	18	75	41.9
	5	4.98	0.221	13.1	2.9	0.019	4.68	0.03	0.06	0.00	0.02	1	6	17	77	86.0
E	1	5.17	0.268	11.2	3.01	0.059	4.58	0.08	0.05	1.79	0.33	5	9	44	47	38.5
	2	7.91	0.355	13	4.6	0.014	4.59	0.03	0.05	0.16	0.05	8	9	37	55	33.9
	3	7.19	0.298	14	4.18	0.056	4.34	0.02	0.09	1.15	0.28	38	16	35	49	89.5
	4	10.03	0.399	14.6	5.83	0.02	4.33	0.02	0.12	1.40	0.56	9	20	33	47	61.0
	5	8.69	0.371	13.6	5.06	0.029	4.6	0.03	0.12	0.32	0.12	6	14	33	53	54.1

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