

**SWITCH FROM ABRUPT TO DIFFUSE TREELINE TYPOLOGY COINCIDES  
WITH A SWITCH FROM PRECIPITATION TO TEMPERATURE CONTROL  
OF TREE GROWTH**

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## Abstract

Treelines are ecotones between alpine forest and tundra ecosystems and have different typologies including diffuse and abrupt. Treelines can advance in response to climate change if tree growth becomes accelerated and seedling recruitment and survival occurred regularly and quickly enough to allow the treeline to move upward. Abrupt treeline advancement is mostly controlled by seedling recruitment and survival which are typically both controlled by precipitation, especially snow. It can be hypothesized, that tree growth at abrupt treelines responds to the same limiting factors as seedling survivorship; if the precipitation is low enough to kill seedlings, it is likely low enough to reduce growth of adult trees. Treeline advancement at a diffuse treeline is typically limited by tree growth which in turn is typically limited by temperature. Due to climate change, treelines can change typology from abrupt to diffuse and hence change the factors that limit their advancement and limit tree growth. Furthermore, there are several spatial dynamics that can occur between trees at the treeline. Trees growing on the upper edge of the treeline should face a harsher environment than trees within the forest below. In addition, some trees form clusters, which can increase resource competition but also be beneficial for tree growth through facilitation.

The present study analyzes tree growth at an advancing treeline that had recently switched typology from abrupt to diffuse. Based on the reasoning above it is hypothesized that the abrupt to diffuse switch in typology should coincide with a change from precipitation to temperature control of tree growth. Moreover, the study investigates how trees above and below the treeline as well as singletons versus clusters are affected differently by precipitation and temperature. Under abrupt typology, trees above the treeline would be more affected by snow than trees below the treeline. Under diffuse typology, trees above and below the treeline will mainly be affected by temperature.

Lastly, it is predicted that, during the abrupt phase, singletons will be more affected by precipitation than clusters because they lack facilitation benefits.

The study was conducted within a bowl on the western slope of Pikes Peak on the Front Range of the Colorado Rocky Mountains with an *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) monoculture using cores that were collected by Kelsey Elwood in 2011 but were not previously analyzed. Tree ring width was measured to the nearest 0.001mm using a velmex bench with a dissecting microscope. Tree cores were visually and statistically cross dated. Inconsistencies in the cross-dating were used to assess which cores needed to be remeasured. The finalized tree ring widths were detrended with negative exponential function for effects of age and with  $67/n$  spline for long term trends. The detrended ring series were averaged to form the master chronology, which was used to examine correlations climatic variables including monthly temperature and precipitation series. Another master chronology was created and only detrended for effects of age.

Both chronologies showed high variability from 1935 to 1970, with two large peaks of high growth, and low variability of growth after 1970. The chronology detrended only for age showed a gradual increase in tree ring width index from 1970 to 2009, coinciding with an increasing temperature caused by climate change. Tree growth had a statistically significant positive correlation with previous year June and current year March temperatures. Current year May and June temperatures were close to having a statistically significant positive correlation. Precipitation in the form of snow in winter and early spring had a negative effect. During the treeline's abrupt phase, tree growth was mainly limited by spring and winter snow. As the treeline typology changed to diffuse, growth limitation by growing season temperature became more important than growth limitations

fluctuations in growth compared to trees below treeline. However, higher sensitivity to climatic variables for trees above treeline was not found. Clustered trees are more sensitive to temperature changes as is supported by the abundance of fluctuation in the master chronology. Likewise, the groupings of clustered, singletons, above treeline and below treeline did not show differences in their response to temperature and precipitation. Furthermore, springs and falls with high precipitation were correlated with high tree growth and vice versa. An increase in temperature during the months of March, May and June was correlated to an increase in tree growth. Moreover, analysis of 35 years long segments lagged by five years shows that up until the 1960s, precipitation had a major effect on tree growth. More precipitation in April led to a decrease in growth. Since 1980s, temperature was the factor causing the major effect. These changes coincided with the change in treeline typology from abrupt treeline to diffuse treeline.

Cambio de límite arbóreo con tipología abrupta a tipología difusa coincide con un cambio en los factores de control de crecimiento arbóreo de precipitación a temperatura

Resumen en español

Los límites arbóreos son ecotonos entre los ecosistemas de bosques alpinos y tundra, los cuales tienen diferentes tipologías incluyendo difusa y abrupta. Los límites arbóreos pueden avanzar en respuesta al cambio climático si el crecimiento arbóreo se acelera y el reclutamiento de retoños arbóreos, y la sobrevivencia de estos, ocurren lo suficientemente regular y rápidamente para permitir que el límite arbóreo ascienda. La ascensión del límite arbóreo abrupto está mayoritariamente controlada por el reclutamiento y la sobrevivencia de los retoños arbóreos, características que típicamente son controladas por precipitación, especialmente nieve. Se postula la hipótesis que el crecimiento arbóreo en límites arbóreos abruptos responde a los mismos factores limitantes que la sobrevivencia de los retoños arbóreos: si la precipitación es lo suficientemente baja como para no permitir la sobrevivencia de los retoños arbóreos, es probable que también sea lo suficientemente baja para reducir el crecimiento arbóreo adulto. La ascensión del límite arbóreo difuso típicamente es limitada por el crecimiento arbóreo, el cual, a su vez, es típicamente limitado por la temperatura. Dado al cambio climático, los límites arbóreos pueden cambiar de tipología abrupta a tipología difusa y así cambiar los factores que limitan sus ascensos y limitan el crecimiento arbóreo. Además, existen varias dinámicas espaciales que pueden ocurrir entre los árboles situados en el límite del crecimiento arbóreo. Los árboles que crecen en el margen superior del límite arbóreo han de enfrentarse a ambientes más hostiles que los árboles dentro de el bosque que se encuentra debajo. En adición, algunos árboles se agrupan, lo cual puede incrementar su competencia por recursos, pero esto también puede ser benéfico para el crecimiento arbóreo a través de una relación benéfica intraespecífica.

Este estudio analiza el crecimiento arbóreo en un límite arbóreo ascendente que recientemente cambió de tipología abrupta a tipología difusa. Basado en el razonamiento establecido previamente se hipotetiza que el cambio de tipología abrupta a tipología difusa ha de coincidir con un cambio del control del crecimiento arbóreo basado en la precipitación a uno basado en la temperatura. Por otra parte, el estudio investiga cómo árboles por encima y debajo del límite arbóreo, así como los que están o no agrupados, son afectados diferentemente por la precipitación y la temperatura. Bajo una tipología abrupta, los árboles por encima del límite arbóreo serían más afectados por la nieve que los árboles debajo del límite arbóreo. Bajo una tipología difusa, los árboles por encima y por debajo del límite arbóreo serán principalmente afectados por la temperatura. Por último, se predice que, durante la fase abrupta los árboles no agrupados se verán más afectados por la precipitación que los árboles agrupados ya que los árboles no agrupados no tendrán los beneficios de interacciones intraespecíficas.

El estudio fue conducido dentro de un cuenco en la ladera oeste del pico Pikes Peak en la cordillera frontal de las montañas rocosas de Colorado con un monocultivo de *Picea engelmannii* Parry ex Engelm. (Abeto Engelmann) utilizando testigos que fueron coleccionados por Kelsey Elwood en el 2011 pero no fueron previamente analizados. El ancho de los anillos arbóreos fue medido a la milésima de milímetro más cercano utilizando una banca velmex con un microscopio de disección. Los testigos fueron sometidos a la técnica de datación cruzada visual y estadísticamente. Las inconsistencias en la datación cruzada fueron utilizadas para revisar cuáles testigos tendrían que volver a ser medidos. Una vez resueltas las inconsistencias, a los anchos de los anillos arbóreos se les quitaron las tendencias con una función exponencial negativa para remover los efectos de la edad arbórea y con “67/n spline” para las tendencias de largo plazo.

Las series de los anillos arbóreos sin tendencias fueron promediadas para formar una cronología maestra, la cual fue utilizada para examinar correlaciones de variables climáticas incluyendo series mensuales de temperatura y precipitación. Otra cronología maestra fue creada y sólo las tendencias de los efectos de la edad arbórea fueron removidas.

Ambas cronologías mostraron alta variabilidad de 1935 a 1970, con dos picos de alto crecimiento arbóreo y poca variabilidad de crecimiento arbóreo después de 1970. La cronología a la cual solo se le removieron los efectos de la edad mostró un incremento gradual en el índice de ancho de anillo arbóreo desde 1970 al 2009, esto coincide con una temperatura que va en incremento a causa del cambio climático. El crecimiento arbóreo tuvo una correlación estadística y significativamente positiva con las temperaturas de junio del año previo y de marzo del año presente. Las temperaturas del año presente en mayo y junio estuvieron cerca de tener una correlación estadística y significativamente positiva. La precipitación en forma de nieve durante el invierno y el inicio de la primavera tuvo un efecto negativo. Durante la fase abrupta del límite arbóreo, el crecimiento arbóreo estuvo principalmente controlado por la nieve durante la primavera y el invierno. Al ir cambiando la tipología del límite arbóreo hasta llegar a ser difusa, el control del crecimiento arbóreo a través de la temperatura estacional se hizo más importante que los cambios de los controles del crecimiento a comparación de los árboles debajo del límite arbóreo. Sin embargo, no se encontró mayor sensibilidad a variables climáticas en los árboles encima del límite arbóreo. Los árboles agrupados son más sensibles a los cambios de temperatura y esto es apoyado por la abundancia de fluctuaciones en la cronología maestra. Así mismo, los análisis específicos para los árboles en agrupación, sin agrupación, por encima del límite arbóreo y por debajo del límite arbóreo no mostraron diferencias en sus respuestas a la



temperatura y la precipitación. Además, las primaveras y los otoños con alta precipitación fueron relacionados con alto crecimiento arbóreo y viceversa. Un incremento en la temperatura durante los meses de marzo, mayo y junio fueron relacionados a un incremento en el crecimiento arbóreo. Por otra parte, un análisis de segmentos de 35 años traslapado por 5 años muestra que, hasta los años 1960s, la precipitación tuvo un efecto principal en el crecimiento arbóreo. La precipitación en abril está relacionada con un decremento en el crecimiento arbóreo. Desde los 1980s la temperatura fue el factor que causó el mayor efecto. Estos cambios coinciden con el cambio en la tipología del límite arbóreo de abrupto a difuso.

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## Introduction

Treelines represent the upper climatic boundaries for alpine forest ecosystems. Their elevation is temperature dependent. Treelines occur at approximately the same temperature worldwide, but not at the same elevation, likely because the higher elevation has a temperature that is too cold and climate conditions are too harsh to continue to promote alpine tree growth (Körner and Paulsen, 2004) and (Grace, 2002). Over historically long periods of time treelines appear to follow local temperatures. For example, the presence of 6,000-year-old pine stumps preserved 200 meters above the present treeline combined with evidence of warmer temperatures at such site in Scotland 6,000 years ago (Pears, 1968) provides further support to the argument that treeline dynamics track temperature-based climatic boundaries.

The treeline itself is an ecotone, an intermediate space of living and non-living components found between two distinct ecosystems. The treeline is therefore the intermediate space between alpine forest and tundra ecosystems. Treeline, since it is an ecotone, it is not a line. It is a transition zone with a complex spatial structure (Körner, 2012; Holtmeier et al. 2003). The bottom boundary of the treeline is called timberline. Here trees are still near each other, and they are tall and developed enough to still represent an alpine forest ecosystem. Above the timberline, there are scattered trees known as outpost trees. Outpost trees are considerably dispersed, and they often cannot fully develop due to low temperatures and harsh climatic conditions. Between the timberline and the outpost trees, there are a variety of tree forms including short trees, tree clusters and krummholz. The upper treeline boundary, after which trees cannot grow and the tundra ecosystem begins, is known as the species limit. The area between the timberline and the species limit is the treeline ecotone. When the ecotone's width is extended, the treeline has a diffuse typology. When the treeline's structure is compressed, it is an

abrupt treeline. When the treeline is composed of tree clusters within a matrix of alpine tundra, it is an island treeline. If the tree forms between the timberline and the species limit are composed chiefly of disfigured trees called Krummholz, the treeline is referred to as a Krummholz treeline. Krummholz treelines form when the trees at the treeline must constantly face freezing, harsh winds with ice crystals. Their unique structure of the individual Krummholz trees allow them to survive freezing temperatures and constant ice damage by being close to the ground (Smith et al., 2002).

Treeline ecotones are especially sensitive to climatic changes like depressing freezing points and solutes' presence and concentration in water and soil. Due to climate change, average Earth surface temperature has increased by 0.74 °C since the beginning of the 20<sup>th</sup> century (IPCC, 2021). Mountainous areas often experience even higher rate of temperature change due to changes in albedo associated with changes in timing of snowmelt, a phenomenon termed mountain climate change amplification (Pepin et al., 2015).

Temperature is a major factor affecting treeline advancement. Specifically, several lines of evidence suggest that summer temperatures are the most influential to high altitudinal and latitudinal treeline advancement. In fact, a considerable proportion of the world's treelines coincide with a mean growing season temperature of 5-6 °C (Harsch et al., 2009). Treelines have been advancing at unprecedented rates, and recruitment levels have reached elevations not previously recorded (Harsch et al., 2009).

As mentioned previously, treelines are ecotones with a complex spatial structure, including four main tree typologies or forms: Diffuse, abrupt, island and krummholz. Significant body of theoretical literature has been developed about the ability of these treelines to respond to climate change, and the mechanisms that govern their dynamics (e.g. harsh and Bader 2011).

However, and importantly, treeline typology as described by Harsch and Bader (2011) is somewhat subjective and is not fully applicable to all situations, as these labels are attempting to use discrete categories to describe something relatively continuous. This continuum also logically means that treelines can change typology over time. In several documented cases, treeline advancement in response to warming temperatures resulted in a change in treeline typology from abrupt to diffuse (Harsch & Bader, 2011). This is concerning because diffuse treelines are more prone to be affected by warming temperatures and advancing quicker than abrupt treelines.

In some cases, the climatic boundary is moving quicker than treelines can respond. Warming temperatures immediately affect the environment that trees are subjected to, and this warming impacts the growth of trees at the treeline in both direct and indirect ways ((Körner, 2012). Nevertheless, treeline advancement requires more than growth of trees at the treeline, it requires seedling recruitment to further populate higher altitudes. Recruitment requires seedling survival and time for seedling growth and maturation (Körner, 2012). Furthermore, seedling recruitment usually does not cover a considerable amount of space quickly because seed rain typically decreases exponentially with distance from the seed-bearing tree (Körner, 2012). Also, in many forest ecosystems, seedling establishment occurs in sporadic infrequent events that are not always predictable (Körner, 2012). In addition, disturbances such as avalanches can also halt, stunt or prohibit seedling recruitment. Consequently, treeline advancement can happen only at finite rates that may be much slower than the movement of the isotherm that constraints equilibria treeline elevations gradually even if global warming is progressive and constant (Körner, 2012). A mechanism that is frequently cited to underlie the sensitivity of treelines to increasing environmental temperature is the growth limitation hypothesis (Körner, 1998).

Temperature places a limit on tree growth because too low temperatures inhibit cell growth and development. Therefore, they create a climatic threshold where tree growth cannot occur below the threshold temperature. Below this limit, wood production is insufficient to sustain tree survival. An earlier competing hypothesis behind the rationale of the effect of warming temperatures on advancing treelines is decreasing CO<sub>2</sub> at higher altitudes. This “source limitation hypothesis” states that the limited availability of CO<sub>2</sub> itself does not allow tree growth because sufficient photosynthesis cannot be performed by the trees without abundant resources including CO<sub>2</sub> (Trembl & Veblen, 2017). Körner’s growth limitation hypothesis (also known as carbon-sink limitation hypothesis) states that it is not CO<sub>2</sub> scarcity that limits tree growth directly. Trees, even at high elevation, can accumulate enough carbon by performing photosynthesis. Even though they have enough resources for growth, low temperatures at the treeline plus low CO<sub>2</sub> availability hinder efficient glucose and carbon utilization. This, in turn, limits tree growth. The growth limitation hypothesis prevails over the source limitation hypothesis and explains why warmer summer temperatures should lead to more regeneration and faster radial growth above treeline (Trembl & Veblen, 2017).

In addition to temperature, there are several other factors that affect tree growth and treeline movement at all treelines. These factors include moisture (Germino et al., 2002; Macias-Fauria & Johnson, 2013), low availability of soil nutrients such as nitrogen (Germino et al., 2002; Macias-Fauria & Johnson, 2013), and high rate of biomass-loss due to wind-driven ice abrasion (Kullman, 2005). Given that multiple factors potentially could impact tree growth and treeline advancement, it is pertinent to ask whether we can predict which one (singly or in combination) will be most important, and whether their importance is situation dependent. Applying Liebig's law of the minimum, it should be the “scarcest” resource that primary affects

tree growth and treeline advancement (*Essential Elements for Plant Growth Law of the Minimum*).

Different types of treelines will be affected in distinct manners and magnitudes by the concept explained by the Körner's growth-limitation hypothesis and hence by temperature. Even though, tree growth and treeline advancement are not the same phenomenon, tree growth is necessary for treeline advancement. While the temperature limitation may operate at any type of treeline, it is hypothesized that diffuse treelines will be more affected by temperature (Harsh and Bader, 2011). In fact, in a diffuse treeline, tree growth and treeline advancement are both limited by temperature. This treeline type, by definition (Harsh and Bader, 2011), has abundant and unrestrained seedling establishment, survival and development into adult trees. High survival rates allow a considerable quantity of mature trees to reach the maximum temperature boundary at diffuse treelines (Trembl & Veblen, 2017). Moreover, dispersed trees of diffused treeline increase the boundary for warmer temperature created by soil's greater ability to generate more warmth than the atmosphere. Thus, diffuse treelines contribute to favorable microclimate for tree growth as they reduce the cooling effect of wind and increase the frictional surface for wind (Körner, 2012). They are not significantly affected by neighbor-neighbor interactions or tree establishment and favorable microclimates can form within the trees. Consequently, diffuse treeline typology, once established, may perpetuate treeline movement through positive feedback (Körner, 2012).

Abrupt treelines have a clear distinction between closed-canopy forest and treeless tundra. In contrast with diffuse treelines, tree growth and treeline movement may or may not be limited by the same factor. While tree growth may possibly still be limited by temperature it could also be impacted by availability of soil moisture or nutrients. Treeline movement is limited



by seedling establishment and survival (Harsch & Bader, 2011). Seedling establishment and survival are affected by “first-level,” “second-level” and “third-level” mechanisms (Harsh and Bader, 2011). Dynamics such as tree growth, dieback, and seedling survival/ mortality are “first-level mechanisms.” Snow, cold climate, harsh winds and other stressors on the trees and seedlings are “second-level mechanisms.” Abrupt treelines are limited by very high seedling mortality far above the treeline. Seedling mortality is significantly reduced below the treeline due to strong facilitation of seedling survivorship inside the forest. Clustering occurs due to facilitation in harsh environments and species environmental tolerance (Callaway et al., 2002). Clustering creates additional neighbor-neighbor dynamics around nutrient sharing, sunlight intake and sheltering; these new dynamics are “third-level mechanisms.” (Harsh and Bader 2011). Clustering helps maintain a warmer soil temperature and prevent winter desiccation (Grace, 1989). While clustering helps plants retain warmth amongst themselves and provide sheltering for seedlings, it also increases competition for space, water, nutrients and sunlight among the trees. Clustering will only be beneficial if it outweighs the costs of competition (Callaway et al., 2002). To advance, a treeline necessitates tree growth. Consequently, seedlings must survive through clustering that does not create “third-level mechanisms” that increase competition to a point of promoting seedling mortality (Russell, 2019).

Treml and Veblen (2017) proposed that precipitation, in particular snow, drives both seedling survivorship and tree growth at the abrupt treelines. Seedling mortality at the treeline ecotone is often determined by neighbor facilitation and snow dynamics; both, too little and too much snow inhibit treeline establishment. Too little snow leads to winter desiccation, (Sullivan, 2016; Resler et al., 2005) and too much snow provides an environment conducive to the spread of pathogenic snow fungi during snow melt. Excessive snow that does not allow the seedlings to

even sprout or show minimal signs of survival is likely also detrimentally affect adult trees. Dendrochronology analysis of adult trees would show that adult trees grow less during seasons of heavy snow fall. Therefore, it would be important to investigate if the growth of adult trees is still depending on temperature and treeline advancement is still depending on seedling recruitment or if, under heavy snow cover, tree growth and treeline advancement are both limited by snow when considering an abrupt typology. Nevertheless, some moderately deep snow can greatly increase seedling survival. Moderate snow depth provides insulation to prevent young root freezing, shelter from harsh abiotic factors such as wind, temperature and ice crystals and serve as a source of nutrients, organic litter and water during snow melt. Furthermore, deeper snow leads to a delayed melting period (Walker et al., 1999). This, in turn, leads to the seedlings growing season occurring later in the summer, meaning that they are growing during warmer, more constant temperatures and recruitment will be more successful (Sullivan, 2016). Warmer soil temperatures will also increase plant and animal activity, decomposition rate and optimize influx and exchange. This will further stimulate growth. Warmer soil temperatures also affect the quantity of permafrost at treelines' upper limit. Increased soil temperatures will cause thawing of the permafrost that is at 0 °C (Walker et al., 1999).

Other factors to consider are “first-level mechanisms” and “second-level mechanisms.” “First-level mechanisms” are spatial characteristics such as growth limitation, seedling mortality and dieback. “Second-level mechanisms” are physiological stress and a damage that the trees face. Neighbor-neighbor interactions directly affect “second-level mechanisms” and “first-level mechanisms” indirectly. Trees close to or in clusters must compete more for water, soil nutrients, sunlight, albedo and space but also receive more shelter from cold wind gusts and ice crystals. “Third- level mechanisms” are the dynamics created by clustering, facilitation and their effect on

“second-level mechanisms.” Clustering reduces sunlight seedlings’ intake and increases competition but also provides shade and sheltering that can prevent freezing (Harsch & Bader, 2011). It can also provide a warmer soil temperature and protection from winter desiccation (Grace, 1989). Trees must balance been in enough snow that they have enough warm soil from which they can obtain nutrients and been in a cluster to ensure surviving as seedlings through sheltering and facilitation despite some competition to further populate and move the treeline upward (Russell, 2019). Since recruitment and establishment of seedlings requires several seasons of moderate snow accumulation, warmer temperatures, proper facilitation through clustering, lack of disturbances and time for maturation, an abrupt treeline advances slowly and does not immediately respond to warmer temperatures. Therefore, abrupt treelines are stable even in the face of climate change (Trembl & Veblen, 2017).

The present study examines the relationship between tree growth and climate variables at a treeline that experienced typology change from abrupt to diffuse as well as how this relates with an increase the treeline’s upward migration rate (Elwood, 2012; Earnest, 2011). The research investigates whether a change from abrupt to diffuse typology coincides with a change with the climatic variables that limit the treeline’s advancement. It is hypothesized that during the abrupt phase tree growth will be sensitive to snow or other precipitation type. If precipitation, especially snow, is detrimental for tree growth, then tree growth will decrease with increasing winter and early spring precipitation. If snow is beneficial for tree growth, then tree growth will increase with increasing winter and early spring precipitation. On the other hand, during the diffuse phase, there will be a change to temperature limitation. Trees will grow faster during warmer temperatures. Furthermore, the study also examines the effect of tree position with respect of being above or below the treeline. It is predicted that, during the abrupt phase,

trees above treeline will be more affected by snow than trees below the treeline. In the later diffuse phase, both trees above and below the treeline will be limited by temperature. Lastly, the relationships between trees existing as singletons and trees existing in a cluster and their response to precipitation, especially snow, and temperature was analyzed. It is further hypothesized that, during the abrupt phase, singletons will be more affected by precipitation and snow because they lack facilitation benefits. When the typology change happens, temperature will now be the main limiting factor. It is predicted that this change in the controlling climatic condition will coincide with the change in treeline advancement speed. While at an abrupt state the treeline advancement will be slow, once the treeline changed to a diffuse state the rate of advancement should increase dramatically.

## Methods

### *Site Description*

Located within a bowl on the western slope of Pikes Peak on the Front Range of the Colorado Rocky Mountains, the study area was a rectangular transect 50 meters wide and 300 meters long ( $105^{\circ}5'25''$  W and  $38^{\circ}51'35''$  N, center of transect) (Figure 1 a) (Blue rectangle on Figure 1 b). The transect pointed downslope. It was perpendicular to contours and had a northwestern aspect. The transect's elevation range was from 3609 m to 3719 m a.s.l. This site was chosen because, at the time the trees were cored, significant treeline advancement was known in this area 18m elevation and 60m surface migration from 1953-2009 (Feiden, 2010; Earnest, 2011) (Figure 1 c). Furthermore, there was a distinct shift from abrupt to diffuse typology. The treeline was clearly abrupt in 1938 and started changing to diffuse after 1980's (Elwood, 2012). Importantly, migration rates changed together with the treeline typologies. The rate was slow until the late 1980's (when the treeline was abrupt). It was fast after 1980 (when the treeline was diffuse) (Feiden, 2010). Furthermore, this also coincided with increasing temperature from 1980s to 1990s (Figure 2) (Miroslav Kummel).

One hundred and fifty meters of forest in the transitional ecotone between closed-canopy forest and alpine tundra were studied. Tree cores were only extracted from this ecotone zone. At the present time the treeline is diffuse. With increasing elevation, tree density gradually decreased. The transect's uppermost limit is the species limit. There are no trees above this limit. A *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) monoculture was the only tree population present (Elkwood, 2012).

Even though there was an Engelmann spruce monoculture, other non-tree tundra species usually grow in between the Engelmann spruce during the growing season. These species include

grasses and several types of wildflowers. From late September to late May, the site is covered in snow. Boulders were found throughout the area. Significant boulder groupings were found mostly at the top of the transect. There was a small rockslide near the bottom. Many large trees had several upright branches from layering or asexual reproduction from trees that had their branches submerged and developed their own root system. Layering is very common in areas where krummholz were present. There was a lack of krummholz trees or mats in the area as all the trees had an upright, straight structure (Elkwood, 2012).

*Natural History of Picea Engelmannii Parry ex Engelm. (Engelmann spruce)*

*Picea Engelmannii* Parry ex Engelm. (Engelmann spruce) is a perennial gymnosperm that grows slowly as a conical tree with a single stem. It is represented by PIEN. Its taxonomic classification is as follows: it belongs to the *Plantae* kingdom (Plants), in the subkingdom *Tracheobionta* (Vascular plants) and in the superdivision *Spermatophyta* (Seed plants). It is in the *Coniferophyta* (Conifers) division, in the *Pinopsida* class and in the *Pinales* order. Lastly, it belongs to the *Pinaceae* (Pine family) family, in the *Picea A. Dietr.* (spruce) genus and in the *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) species. Engelmann spruce natively grows in the western United States and the West part of Canada. It has a long lifespan and actively grows in Spring and Summer. It has deciduous cones with brown seeds and green, densely porous foliage (United States Department of Agriculture).

*Picea Engelmannii* is adapted to fine and medium textured soils but not to coarse textured soils. Its roots are at least 20 inches deep. It does not tolerate anaerobic environments, but it does not require cold stratification. The minimum temperature that it can withstand is -45.56 degrees Celsius. Its tolerance for drought and fire is low, but it tolerates shade well. Its precipitation tolerance range is from 21-160. It does not tolerate salinity. It requires at least 30 days free of

frost and has a medium moisture use. It has a low fertility requirement. It has a pH range from 6.0 to 8.0. Its planting density per acre ranges from 300-700 (United States Department of Agriculture).

*Picea Engelmannii* is routinely available commercially and has medium seed abundance. Its seed period begins in the Summer and ends in the Fall. The seeds do not persist for long in the soil, have low vigor and spread slowly. This pine is pollinated by bare root, container and seed. It blooms in late Spring (United States Department of Agriculture).

*Picea Engelmannii* can be used as a medium fuelwood or as lumber, pulpwood, veneer and naval store/nursery stock products. It is moderately palatable for browse animals, lightly palatable to graze animals and not palatable to humans (United States Department of Agriculture).

#### *Field Methods*

Growth cores were taken were collected between 20cm to 100cm and above the basal buttress. With exception of when this was impossible, all cores were taken at the downslope, western side of the tree (Elkwood, 2012). Cores were extracted by Elkwood in 2011 but were not used for any analysis. Elkwood used cores extracted from the base of the trees to determine tree age and analyzed tree age distribution for her thesis. The present study analyses the growth cores for longitudinal patterns of tree growth.

#### *Dendrochronology Methods*

The study used tree cores extracted in 2011 by Kelsey Elkwood. The cores were mounted on plywood holders and sanded and polished with sandpaper to 800 grids. The sanding and polishing were considered complete when individual xylem cells were clearly visible under a dissecting microscope. Following Trem and Veblen (2017), I selected cores with at least 40 rings

for the study. This resulted in a collection of 131 cores from approximately 600 cores Elwood extracted in 2011. The tree rings in each core were measured to the nearest 0.001mm with a dissecting microscope and a linear Velmex bench. (Velmex, Inc., Bloomfield, NY) coupled with MeasureJ2X dendrochronology software (VoorTech Consulting, Holderness, NH). For cores missing the pith, a 1 mm concentric circle transparent film was laid over the core to approximate the distance to the pith (Norton et al., 1987). The distance to the pith and the mean width of the last three complete rings was used to approximate the number of missing rings. The most abundant distances from the pith were below 5mm. The minimum distance from pith was 1mm. The maximum distance from pith was 16 mm.

Crossdating was done first visually using signal years and then statistically using statistical dendrochronology program COFECHA. COFECHA creates a provisional master tree ring series and then correlates each core to the master chronology. Cores with low correlation are flagged for manual inspection for missing or spurious rings under the dissecting microscope. To further aid the examination COFECHA splits the tree ring series from each core into 25 year segments and shifts the segments around to see if shifted segment produces a better statistical fit. Finding a significantly better correlation when the segment is shifted indicates potential presence of missing or spurious rings. COFECHA uses these to flag the cores to alert the researcher to manually examine the core for missing or spurious rings.

To look for evidence of missing rings the researcher looks for partial rings or for rings that are spaced very closely together, sometimes with only one, two, or three rows of cells comprising the ring. To look for evidence of spurious rings the researcher examines each ring for irregularities of cell size progression. Spurious rings occur when for some reason the tree stops growing for several weeks during the middle of the growing season and re-starts its growth,



giving two rings for one season. These extra rings have a distinct appearance in terms of progression of cell sizes before and after the spurious “false” ring. Cores where the researcher detected these anomalies were re-measured on the Velmex bench and statistical cross dating in COFETCHA was run again with the updated ring series. This iterative process was repeated until COFETCHA stopped identifying new core audits.

The crossdated cores were detrended with (1) a negative exponential model to account for effects of tree age and (2) double detrended with exponential model followed by  $67/n$  spline to account for combined effects of tree age and mid-range climate variability (Trembl and Veblen 2017). The detrending was done in dendrochronology package for R named dplR. After detrending, the data were standardized in dplR by dividing the width of each tree ring in a core by the average. The standardized tree ring series were then averaged to create a master tree ring width chronology. Again, the package dplR was used for this step. The tree ring master chronology was trimmed so that each average tree ring value was supported by at least 20 individual tree cores.

The RStudio package Treeclim was used to correlate the master tree ring width chronology to monthly precipitation and temperature series. Then, a rowing window was utilized to analyze 35-year-long segments overlapping as they lagged by 5 years. Within the rowing window, tree growth was correlated with the temperature and precipitation pattern, the results were recorded in a table, and their significance was adjusted to multiple comparisons, and then the window was moved 5 years forward.

Data from 2009 in ArcGIS organized by Kelsey Elwood was utilized to determine which of the cored and measured trees were above the treeline. The treeline and trees' position were also obtained from ArcGIS. To determine if trees were singletons or in clusters, geoprocessing

and spatial analysis were utilized. One-meter buffers were created around each measured and unmeasured trees to determine if the tree was within one meter of any other trees. Trees that were within at most one meter of any other trees were considered clustered; trees that were not within one meter of any other trees were considered singletons. Using these methods, the trees were categorized into either singletons or clustered and into either been at above or below treeline. The same analysis was done with cores in each group.

## Results and Discussion

The present study sought to investigate how climatic variables impacted tree growth above or below the treeline. We examined how climatic variables control growth in relation to treeline typology, climate change and different spatial tree relationships among trees. It was found that a change from abrupt to diffuse typology coincided with a change from precipitation to temperature control of tree growth. Also, clustered trees are more affected by temperature changes than singletons. Nevertheless, there was no indication of higher sensitivity to climatic variables for trees above treeline. Also, there was no significant differences among the responses of clustered or singletons, above treeline and below treeline. Interestingly, seasons with high precipitation were correlated with higher tree growth. Lastly, until the 1960s, precipitation was the major driver of tree growth; however, since the 1980s, temperature was the major driver of tree growth.

The two master tree ring chronologies (Figure 4) utilize all tree cores. They span from 1935 to 2009. One chronology was double detrended for age-related effects (figure 4a) and long-term trends while the other one was only detrended for age-related effects (figure 4b). Tree cores are always detrended for age because all trees go through a juvenile growth spurs and exponential decline of tree growth with age. In addition to decline of growth with age, larger trees distribute wood around a larger circle as the tree grows, making the tree rings narrower with age even when the tree produce constant amount of wood each year. Therefore, trees will show a positive deviation from expected growth during juvenile years and exponentially decreasing growth as they age. This could create a confounding variable specially because trees of all ages are usually found at a study site. Consequently, growth trends must be taken out to allow for appropriate analysis of tree growth. To take out the age-related artefacts the tree ring

series is first detrended with a negative exponential function (Fritts, 2001; Fritts, 2012). It is standard practice to double-detrend the data so that long-term trends do not add too much noise to the data and potentially affect analysis (Treml & Veblen, 2017). However, long-term trends could potentially be key to understanding the lasting effects of warming temperatures on tree growth (Fritts, 2001; Fritts, 2012), and therefore I am including both in my study. Both chronologies show high variability from 1935 to 1970, with two large peaks of high growth, and low variability of growth after 1970 (Figure 4). These two large fluctuations in the general master chronologies show initial tree growth variability. Such variability does not match precisely with neither temperature nor precipitation (Figure 3). However, in terms of peak coincidence, there is a qualitative match with summer and fall temperatures. The chronology detrended only for age shows an increase in tree ring width index through time from 1970 to 2009, coinciding with an increasing temperature caused by climate change (figure 2). A strong correlation between increasing temperatures and increased tree growth was also found in another study done by Mikola (reviewed in Grace et al 2002). Mikola found that, due to climate change, tree growth can accelerate very quickly in response to warming temperatures (Grace et al 2002). Specifically, they found a very high correlation coefficient ( $r = 0.8$ ) between a linear regression of several, consecutive increasing July temperatures and tree ring width index.

Without detrending for long-term trends, tree growth had a statistically significant correlation with previous year June and current year March temperatures, where tree growth increased as temperature increased. Current year May and June temperatures were close to having a statistically significant positive correlation as well (Figure 5 b). It is understandable that previous year June had a statistically significant correlation. A warm June in the previous year would have allowed for a higher rate of photosynthesis. This, in turn, would allow for higher

glucose storage in the trees. Such stored glucose could be correlated with higher growth during the current year since the tree could still utilize sugars from previous storages to grow. As supported by the growth-limitation hypothesis, there is a temperature threshold below which trees cannot utilize available resources to produce glucose and ultimately extract ATP for energy even if resources are plentiful. At a treeline, trees are usually higher than shrubs and at considerably high elevations. Consequently, they are usually subjected to low temperatures that prevent efficient resource utilization. It follows that a warm summer in previous years would not have subjected trees to such temperature threshold and would have allowed trees to produce more glucose than the quantity necessary for mere survival. Production of abundant glucose during a previous year would lead to higher glucose storage that would be used in subsequent years; therefore, accelerating growth in such subsequent years (Korner, 1998; Harsch & Bader, 2011).

The finding that warm temperatures in current year March are positively correlated to tree growth is not expected as the trees are dormant during March because the field site is under snow cover. Higher temperatures during the Spring, especially during March, could be correlated with higher tree growth because warmer weather at this time of the year likely supports faster snow melting and thus increasing the length of the growing season. A study done in *Pinus uncinata* mountain forests found similar results (Sanmiguel-Vallelado et al., 2019). *Pinus uncinata* tree width index was negatively impacted by a longer snow season and higher snowpack that potentially led to slower snow melting. Furthermore, they found that *Pinus uncinata* tree width index increased in forest with shorter snowing season, less snowpack and overall warmer conditions (Sanmiguel-Vallelado et al., 2019). The statistical analysis for the double detrended series showed very similar results, with the small exception where the

temperatures in previous year June were no longer statistically significantly correlated to tree growth. Tree growth can be controlled by several climatic variables, and the importance of these variables can change through time. To investigate if the climatic variables controlling growth changed through time, a lagged correlation analysis was performed. Because the treeline switched from an abrupt to diffuse typology, it was hypothesized that early on during the abrupt state, tree growth should be limited by precipitation and later during the diffused stage, tree growth should be limited by temperature. The results of analysis with and without double detrending are nearly identical. Supporting the hypothesis, these results show that before 1960' tree growth had the strongest correlation with early spring precipitation that comes at the field site as snow. Tree growth decreased in years that had more late spring snow (figure 6). A study in San Juan Mountains in Southwestern Colorado found similar results (Walker et al., 1999) The study found that increased snowfall affects alpine ecosystems more than subarctic ecosystems. Even when snowfall was increased artificially at a field site, tree growth still decreased due to a shorter growing season. In fact, some sites only had 90-100 days long growing seasons (Walker et al., 1999). The decrease of tree growth in years with higher spring snow precipitation is probably due to more snow limiting and shortening the growing season. Snow accumulating in the field prevents tree growth from accelerating and the growth season commencing until some snow melting occurs.

In the abrupt state temperature and precipitation were both important in controlling tree growth, however precipitation was more important than temperature (Treml & Veblen, 2017). Warm falls were also correlated with a decrease in tree growth (Figure 6). This negative correlation is potentially caused by higher temperature desiccating trees at the end of the growing season. Typically, falls have relatively low precipitation on Pikes Peak (Kummel, personal

communication). This may not matter when air is cold, but when air is warm it has higher water vapor deficit and becomes more desiccating as it will remove more water out of the tree through their stomata. This could cause trees to close their stomata more during warm falls. Closing their stomata means that carbon may be limited due to decreased gas exchange. This caused less efficient photosynthesis and cellular respiration. With less efficient glucose production and storage, tree growth will be negatively impacted (Korner, 1998). Interestingly, fall had a non-significant but reasonably strong positive correlation between rainfall and tree growth suggesting that the rainfall would ameliorate any effects of temperature-caused desiccation, adding support to the conjecture that the high temperature at the end of the growing season decreased tree growth via creating a water deficit. While the same rationale is not explicitly mentioned, another study also performed tree ring chronologies and found a negative correlation between fall precipitation and tree growth (Hansen-Bristow et al., 1988). This decrease in tree growth with increased fall interpretation can sometimes be related to a higher potential for freezing and tissue damage since more precipitation could create excess water content.

The last important climatic variable during the abrupt phase was the positive effect of summer rain on tree growth. Summer rain allowed trees to have their stomata open as water was readily available (Germino et al., 2002; Macias-Fauria & Johnson, 2013). Stomata did not have to close as often to conserve water. Having open stomata allows for increased photosynthesis and respiration rates. Summer rain also increases water availability. With higher resource availability, tree growth can happen more efficiently. More rain is also related to less tree desiccation. Therefore, summer rain is positively correlation with tree growth (Figure 6). In a study done with *P. smithiana* and *A. pindrow*, tree ring width increased in response to higher

summer rainfall (Borgaonkar et al., 1994). This corroborates these studies finding that summer rainfall is related to higher tree growth.

During the diffuse phase of the treeline, there was a switch from precipitation controlling tree growth to temperature controlling tree growth. As seen in Figure 6, after 1960 growing season temperature from the previous and current year is considerably more strongly and positively correlated to tree growth than precipitation (look especially at top right corner). This finding is corroborated with the finding in Figure 5, where based on the whole time series analysis, tree growth was positively correlated with previous June temperatures. Since trees are now growing in warmer temperatures, their environment is now also more suitable for resource utilization and glucose production and storage. Therefore, they can produce more glucose during a warm June and utilized it for accelerated growth in subsequent years (Korner, 1998). Faster tree growth under warmer conditions relates to treeline typology change from abrupt to diffuse coinciding with a change from precipitation to temperature control. The treeline at the study site has change from abrupt to diffuse topology, so it follows that tree growth should be more controlled by temperature threshold, than by recruitment, precipitation or other water related thresholds (Harsch & Bader, 2011).

In addition to growth being positively controlled by growing season temperatures, growth was also positively correlated with temperatures in current March. This finding is corroborated with the results presented in figure 5 using the whole time series. Temperature during March was key in controlling tree growth over several decades. As previously discussed, it is likely that increasing March temperatures increased snow melt and led to a longer growing season.

The last driver of tree growth during the diffused phase was a negative effect of precipitation in the form of snow in winter and early spring. As previously discussed, during the



treeline's abrupt phase, tree growth was mainly limited by spring and winter snow. As the treeline typology changed to diffuse, growth limitation by spring and winter snow became less important than growing season temperature. Consequently, the hypothesis of the treeline typology changes from abrupt to diffuse coinciding with a change from precipitation to temperature control is supported.

Treml and Veblen (2017) conducted a similar study to the one described in this thesis where they compared the drivers of tree growth at treeline sites that are currently abrupt diffuse, and Krummholz. Their objective was to test the same hypothesis as this thesis, they hypothesized that tree growth at diffuse treeline sites should be limited by temperature and tree growth at abrupt and Krummholz treeline sites should be limited by precipitation. They used dendrochronology to construct master tree ring chronologies for different treeline typologies including abrupt, diffuse and krummholz. They utilized two tree species while I only utilized one. While I had an *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) monoculture, they had *Picea engelmannii* and *Abies lasiocarpa*. Their results had both interesting similarities and differences compared to the results of my study. They found that the two tree species differed significantly in their responses to climatic variables at each site. Treeline typology was of secondary importance. Specifically, tree growth at diffuse treelines showed ambiguous results that varied considerably by site and tree species. However, they also had results that were like those obtained in this thesis at a few specific sites. They had diffuse treeline sites where tree growth was limited by growing season length and temperature. Those sites where tree growth was controlled by temperature and season length appeared to have experienced increased growth during the last thirty years. It is probable that the differences between this thesis' results and their results is due to them not having tree species and location as controls and instead having it as

additional variables to account for (Trembl & Veblen, 2017). Tree growth at Krummholz treelines was limited by the length of the growing season, which was not expected. Abrupt sites, in contrast, had tree growth limited by growing season precipitation. This finding is congruent with my finding that the tree growth at the treeline at Pikes Peak was sensitive to precipitation during the abrupt phase. It is probable that the differences between this thesis' results and their results are due to this thesis having only a single site and single species, which restricts the generality of my conclusions. On the other hand, having a single site that switched from abrupt to diffuse controls for site-specific variables, while having multiple sites potentially introduces site-specific artefacts that are difficult to control for, and limits the generality of their conclusions, especially given the relatively low sample size of 7 total sites with some but not all having multiple treeline types (Trembl & Veblen, 2017).

In terms of tree position with respect to the treeline, it was hypothesized that trees above treeline should be more sensitive to climatic changes compared to trees below treeline. This is potentially due to trees above treeline being exposed to harsher temperatures than trees below treeline (Harsch & Bader, 2011) Several other authors have found these relationships in their studies (reviewed by Grace et al., 2002). The present study found that trees above treeline had higher fluctuations in growth compared to trees below treeline (Figure 7), this is potentially because of increased facilitation with increased tree density. However, the present study did not find higher sensitivity to climatic variables for trees above treeline. The correlation coefficient between tree growth and climatic variables for trees above and below treeline were nearly identical (Figure 8).

Regarding facilitation through clustering, it was hypothesized that, during the abrupt phase, singletons would be more affected by precipitation than clusters because they lack

facilitation benefits (Callaway et al., 2002). Without facilitation benefits, they are exposed to harsher temperatures and at higher risk of winter desiccation. For example, used thermal drone imagery at the field site for the present study and found that trees growing as singletons above treeline had experienced larger temperature fluctuations than trees growing in clusters and in the forest (McGarrigal et al., 2020) (ESA POSTER). The present study surprisingly found that clustered trees may be more sensitive to temperature changes. The master chronology for clustered trees shows more fluctuations than the master chronology for singletons (Figure 7 d; Figure 7 c). The finding could be explained by the fact that clustering allows for a warmer climate around the clustered trees. This could allow trees to grow more because colder temperatures could prevent growth through inhibiting carbon utilization (Korner, 1998). Interestingly and somewhat unexpectedly the correlations between tree growth and climatic variables are nearly identical for trees grown singly and in clusters.

## Conclusion

The climate is undoubtedly warming and most treelines in alpine areas are either maintaining or advancing (Harsch and Bader, 2011). Furthermore, as the planet warms, it is likely that treelines are lagging the advancement of the climatic boundary that would constrain them. This is important to note because it means that even if modern and future attempts to minimize, ameliorate and reverse the effects of climate change and warming temperatures are successful, treelines are likely to continue to advance even after the climatic boundary would either stop advancing or slow down its upward advancement (Körner, 2012). The present study shows that growth control has turned to temperature limitation instead of precipitation limitation as the treeline changed typology and accelerated the rate of advancement. This could mean that climate change and warming temperatures will continue to affect tree growth into the future. Precipitation also affects tree growth specially during fall and summer. Climate change is also affecting precipitation patterns. If significant change does not happen, it is likely that the colder, treeless tundra ecosystem that should exist above treelines' upper climatic boundary will eventually no longer exist on many mountains both regionally and world-wide as the subalpine ecosystem is gradually invading tundra ecosystem. The organisms that depend on tundra-like conditions for survival will no longer have a proper habitat. Consequently, this could lead to the local extinction of tundra plant species. This would endanger their existence and provide a greater space suitable for alpine ecosystems.

## Figures

Figure 1

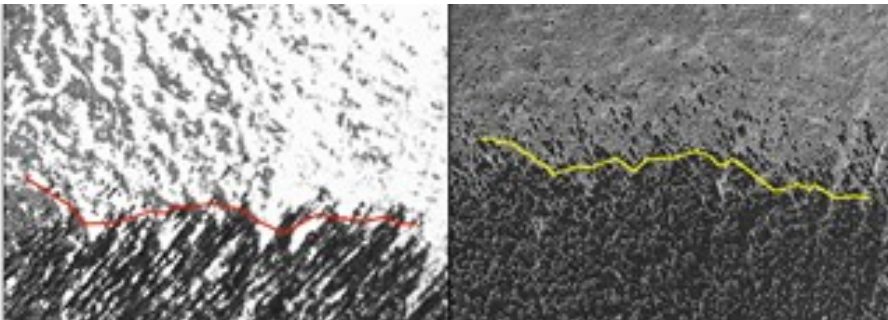
a)



b)



c)

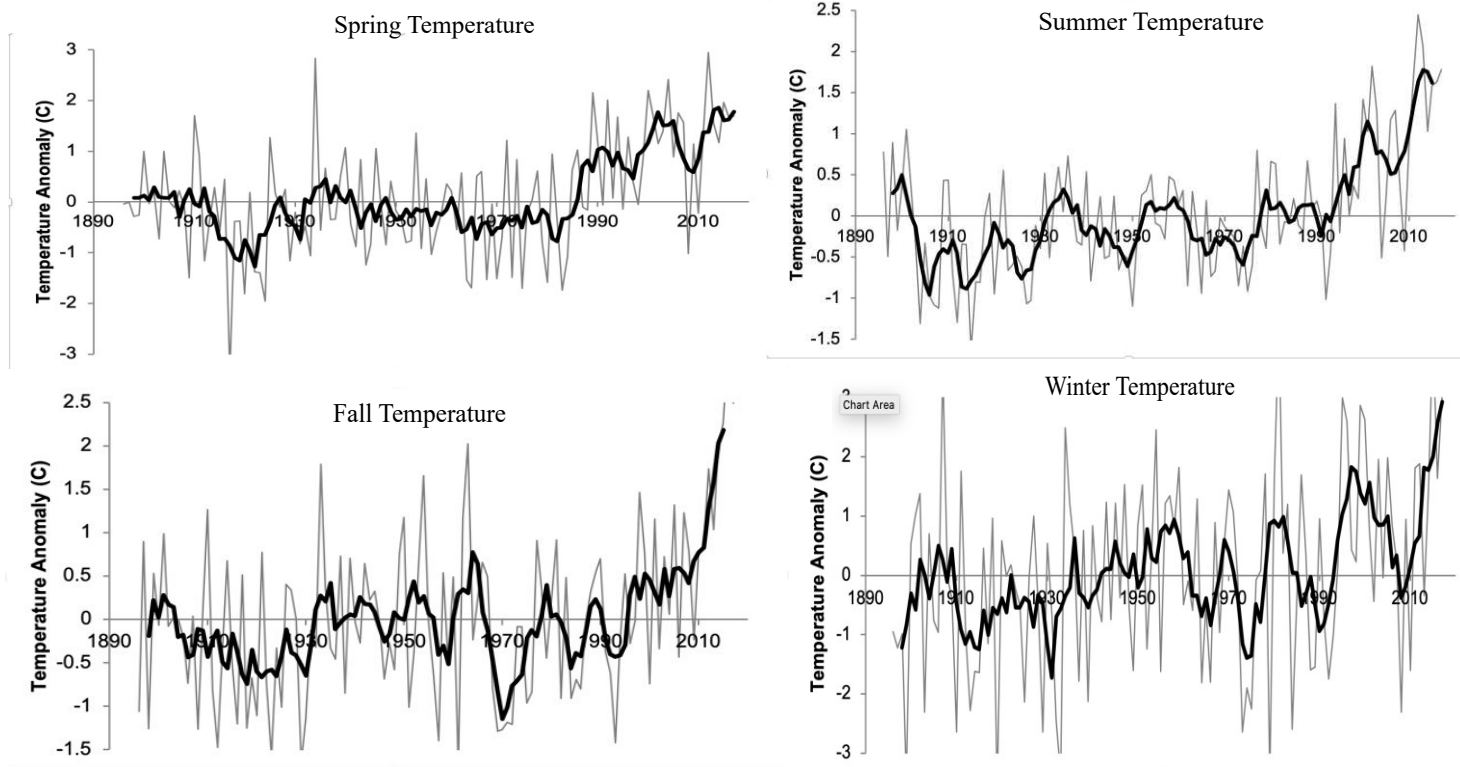


a) An aerial view of the study site is presented.

b) The transect from which the tree cores were obtained is depicted by the blue rectangle.

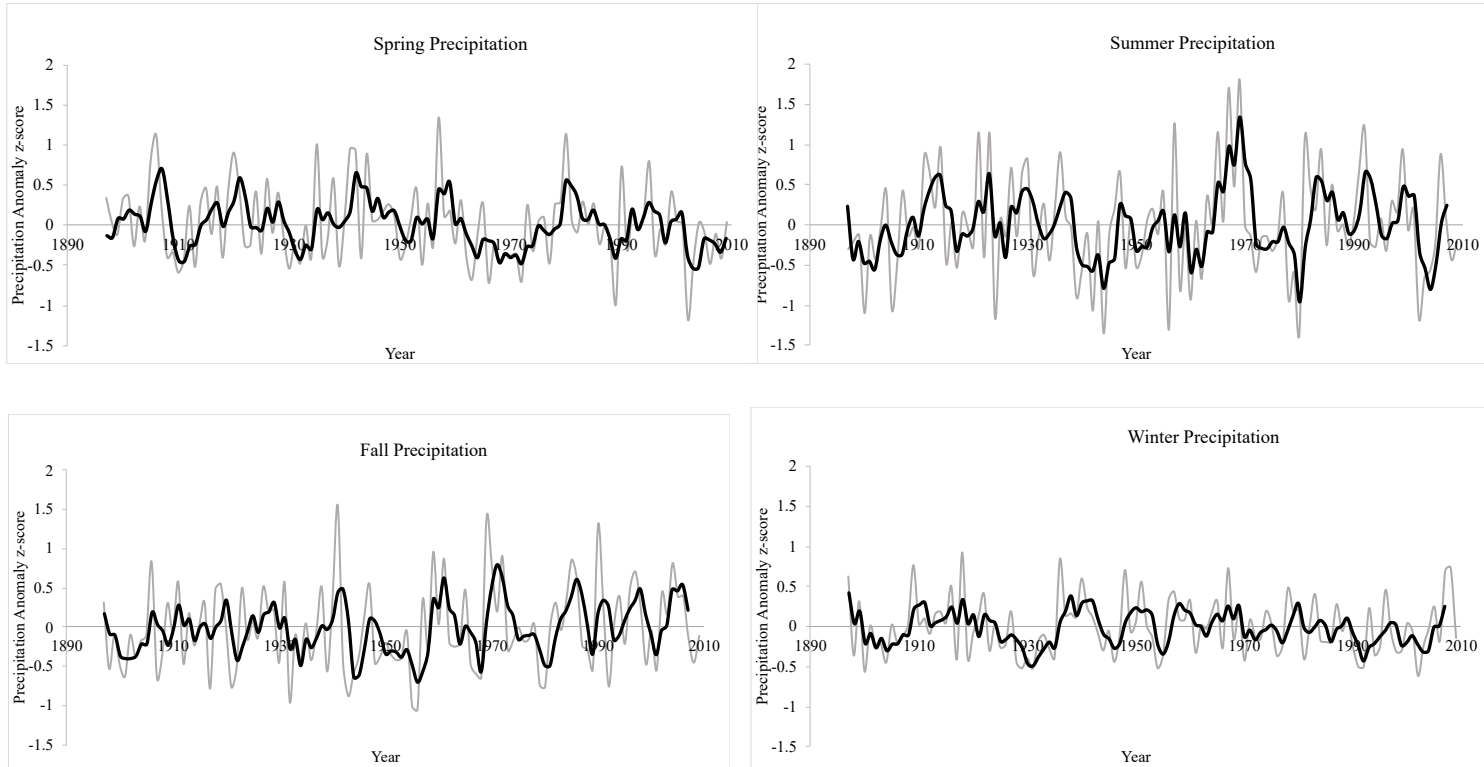
c) (Left) treeline in 1900 (Right) treeline in 2009.

Figure 2



Seasonal temperature trends are shown from 1890 to 2010.

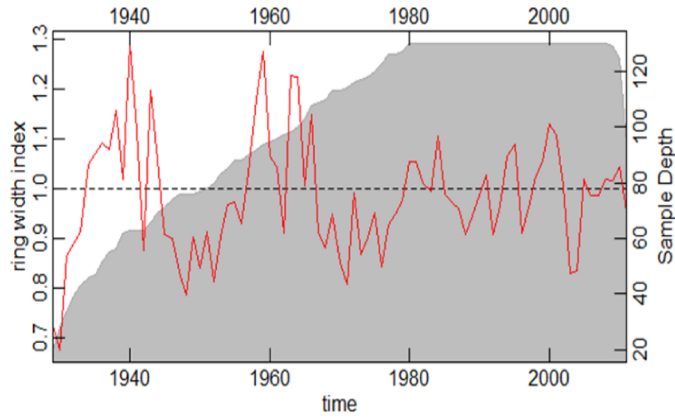
Figure 3



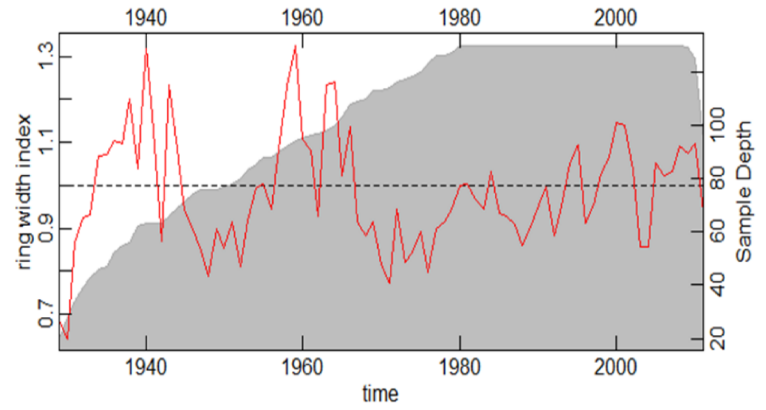
Seasonal precipitation trends are shown from 1890 to 2010

Figure 4

a)



b)

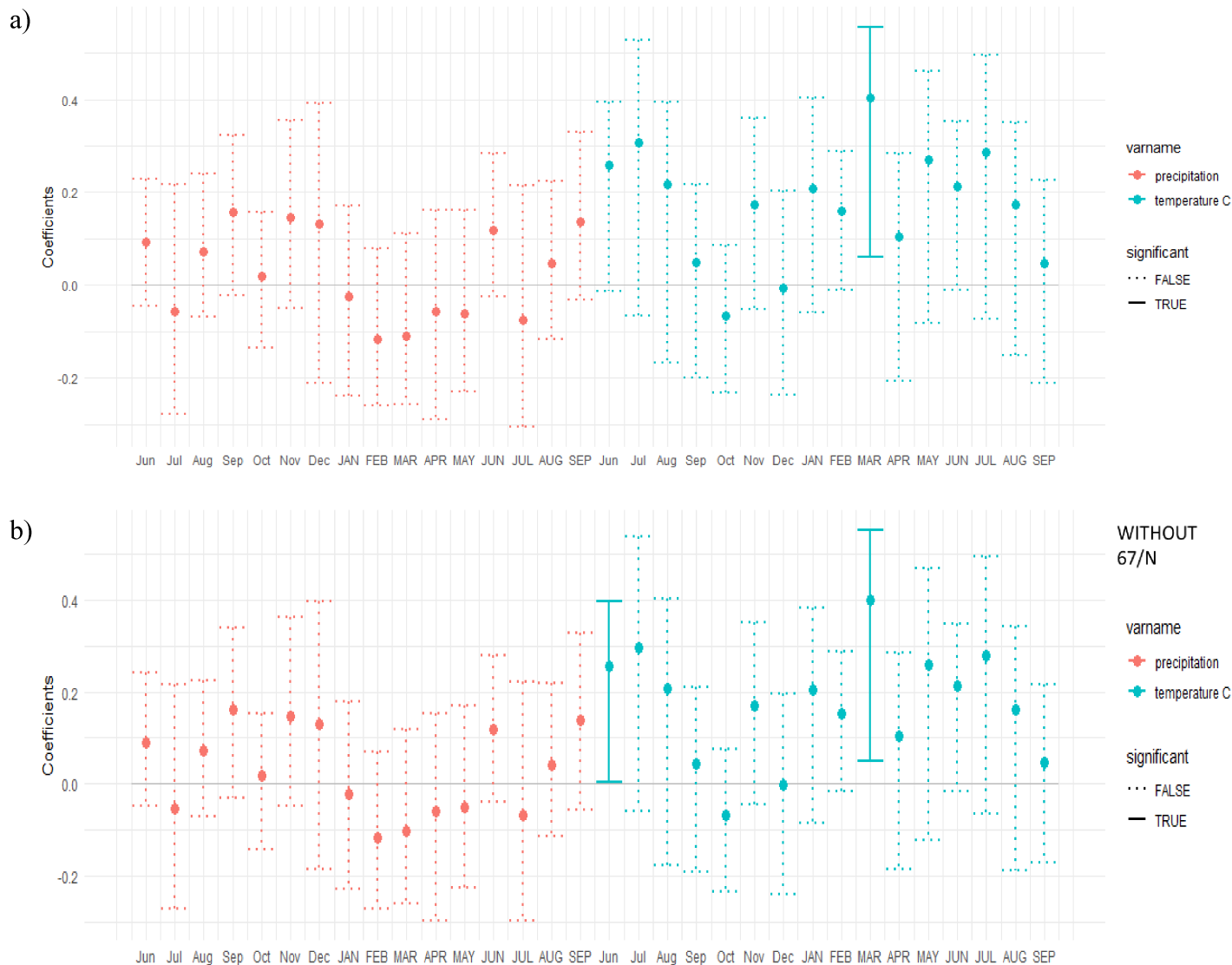
WITHOUT  
67/N

a) Double-detrended (detrended for age and long-term trends) master chronology showing ring width index from 1935 to 2011.

b) Single-detrended (detrended for age) master chronology showing ring width index from 1935 to 2011.



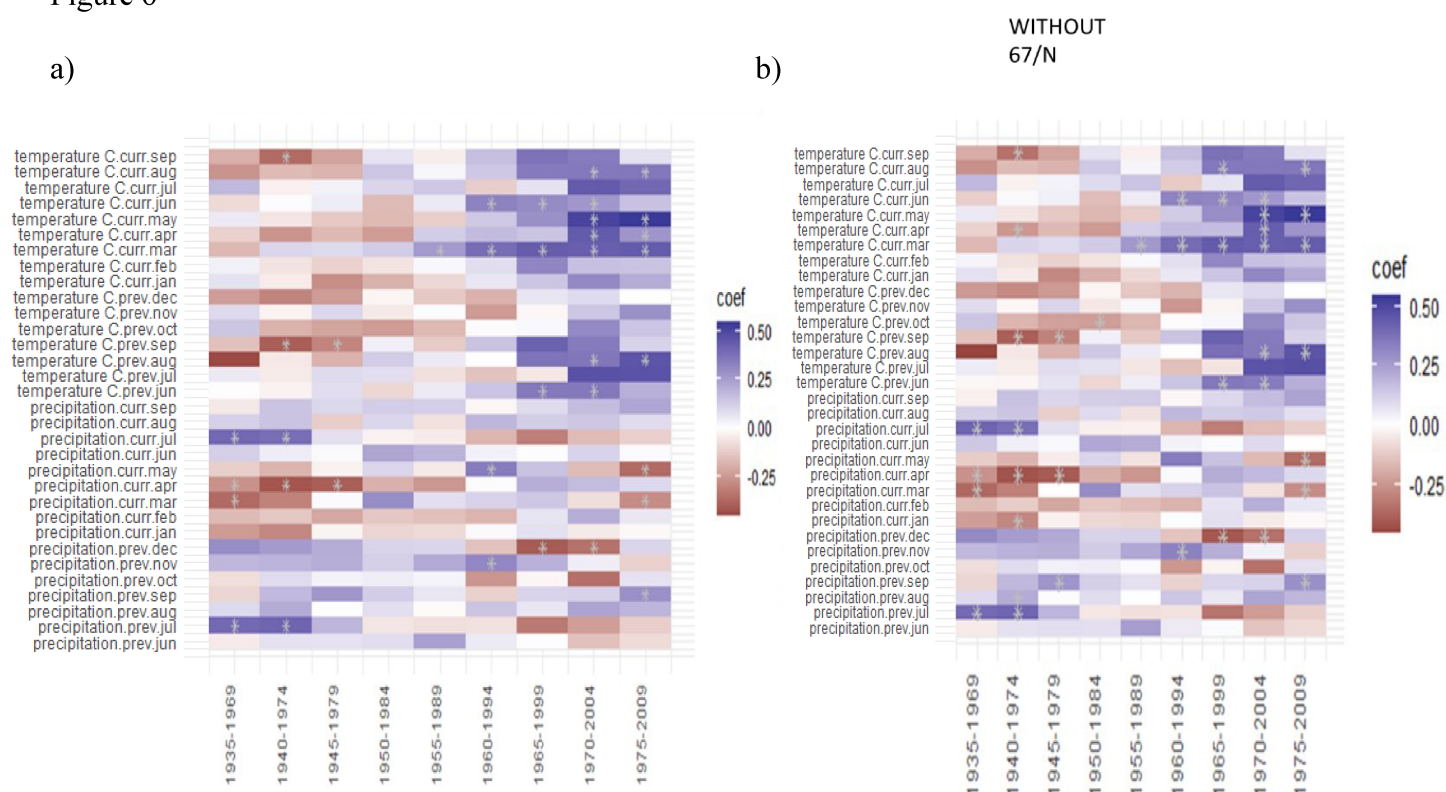
Figure 5



a) Double-detrended (for age and long-term trends) correlations for monthly precipitation (red) and temperature in  $^{\circ}\text{C}$  (blue). Solid lines represent true significant correlations. Dotted lines correlations represent false significant correlations.

b) Single-detrended (for age trends) correlations for monthly precipitation (red) and temperature in  $^{\circ}\text{C}$  (blue). Solid lines represent true significant correlations. Dotted lines correlations represent false significant correlations.

Figure 6

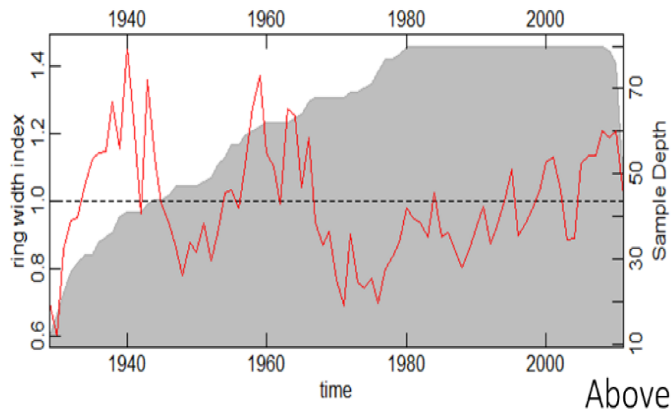


a) Sliding window from 1935 to 2009 lagged by 5 years and double-detrended (for age and long-term trends). Red squares mean negative correlations. Blue squares mean positive correlations. Lighter colors mean weaker correlations. Darker colors mean stronger correlations. White squares mean inexistent correlations.

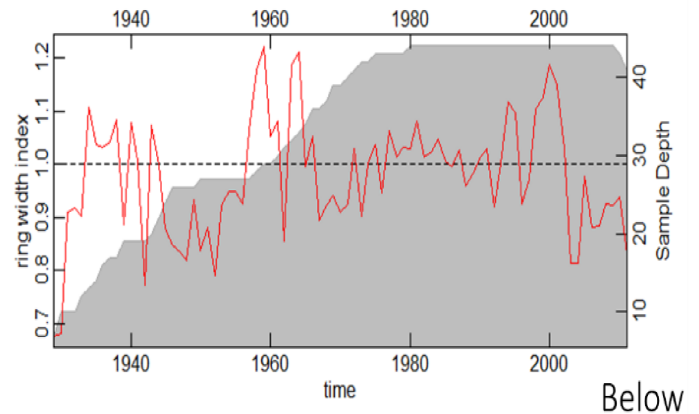
b) Sliding window from 1935 to 2009 lagged by 5 years and single-detrended (for age trends). Red squares mean negative correlations. Blue squares mean positive correlations. Lighter colors mean weaker correlations. Darker colors mean stronger correlations. White squares mean inexistent correlations.

Figure 7

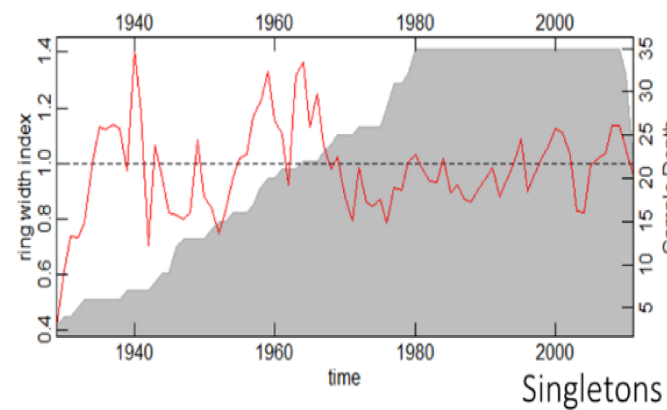
a)



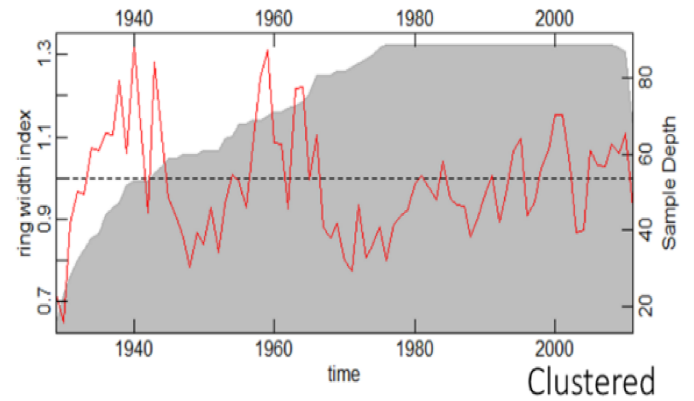
b)



c)



d)



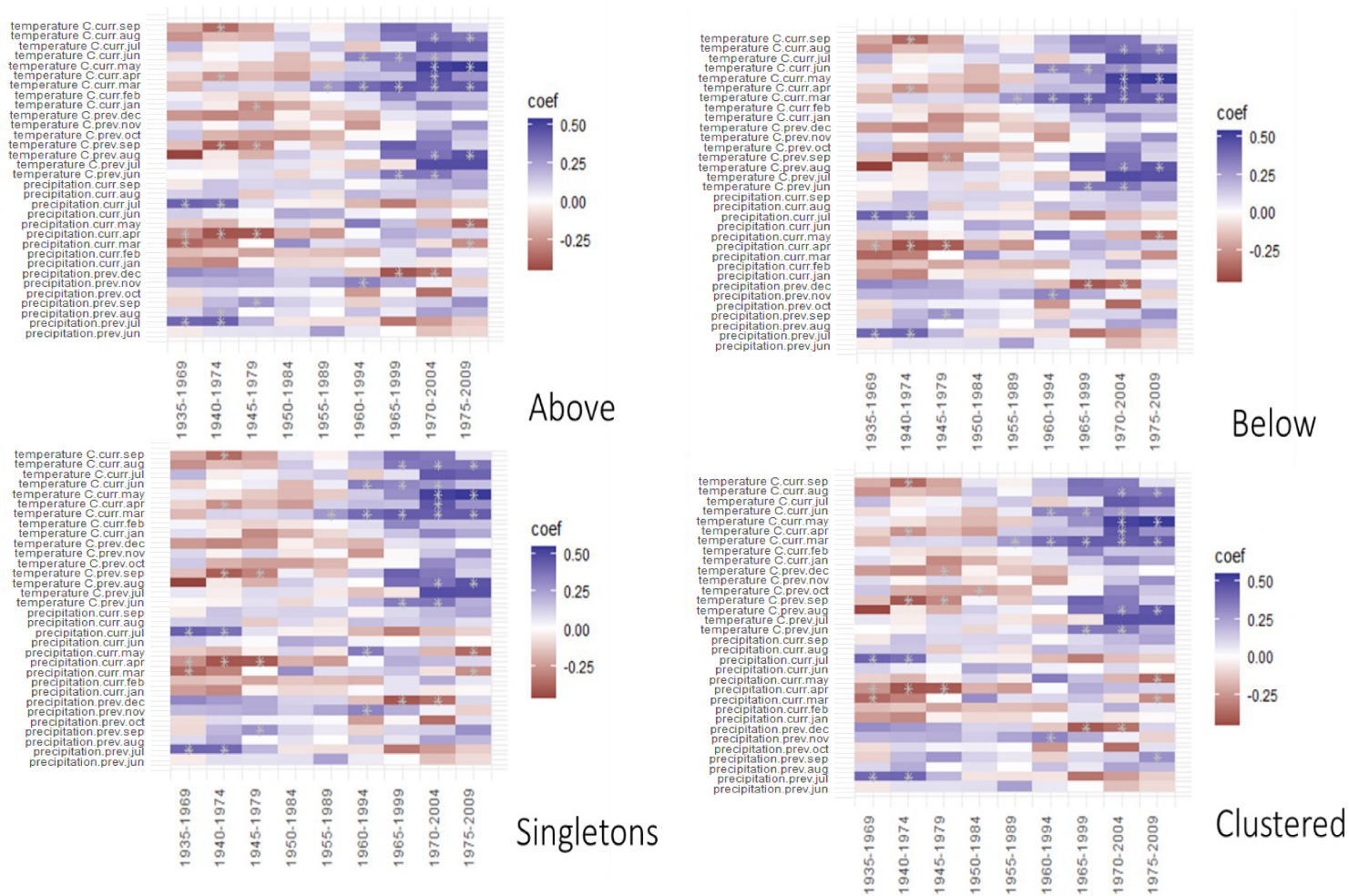
a) Single-detrended (for age trends) master chronology for trees above treeline spanning from 1935 to 2009.

b) Single-detrended (for age trends) master chronology for trees below treeline spanning from 1935 to 2009.

c) Single-detrended (for age trends) master chronology for singletons spanning from 1935 to 2009.

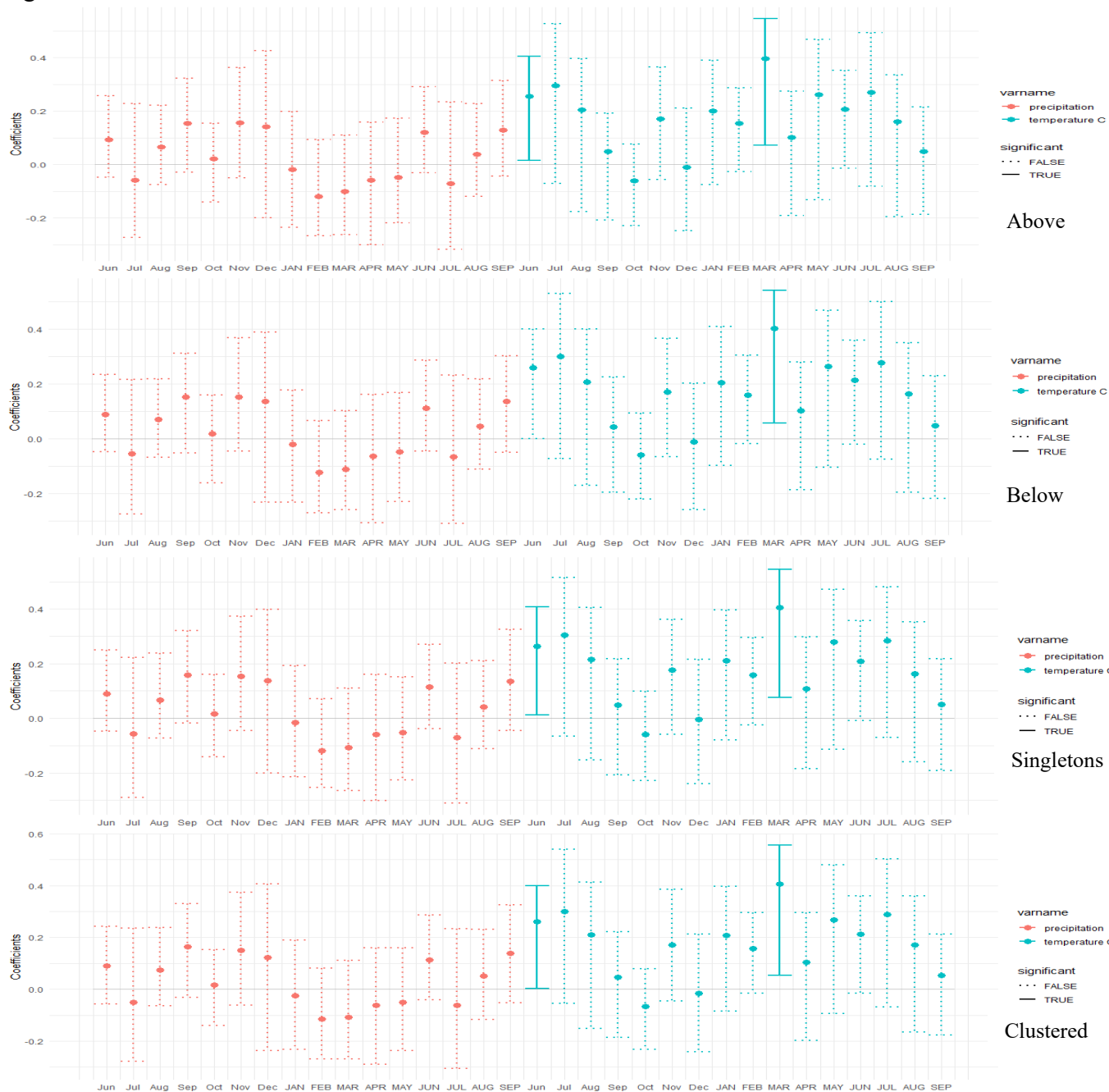
d) Single-detrended (for age trends) master chronology for clustered trees spanning from 1935 to 2009.

Figure 8



Sliding window from 1935 to 2009 lagged by 5 years and single-detrended (for age trends). Red squares mean negative correlations. Blue squares mean positive correlations. Lighter colors mean weaker correlations. Darker colors mean stronger correlations. White squares mean inexistent correlations.

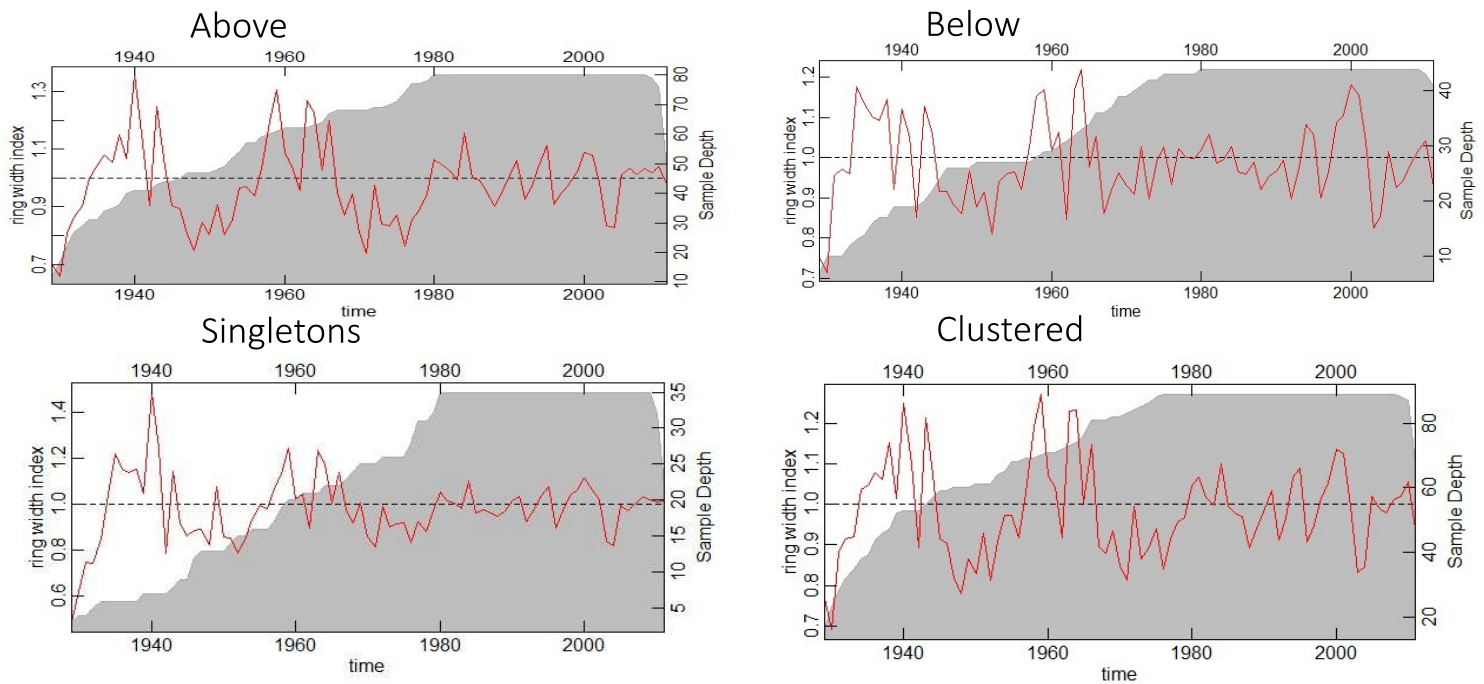
Figure 9



Single-detrended (for age trends) correlations for monthly precipitation (red) and temperature in  $^{\circ}\text{C}$  (blue). Solid lines represent true significant correlations. Dotted lines correlations represent false significant correlations.

## Appendix

Figure 1



- Double-detrended (for age trends) master chronology for trees above treeline spanning from 1935 to 2009.
- Double-detrended (for age trends) master chronology for trees below treeline spanning from 1935 to 2009.
- Double-detrended (for age trends) master chronology for singletons spanning from 1935 to 2009.
- Double-detrended (for age trends) master chronology for clustered trees spanning from 1935 to 2009.

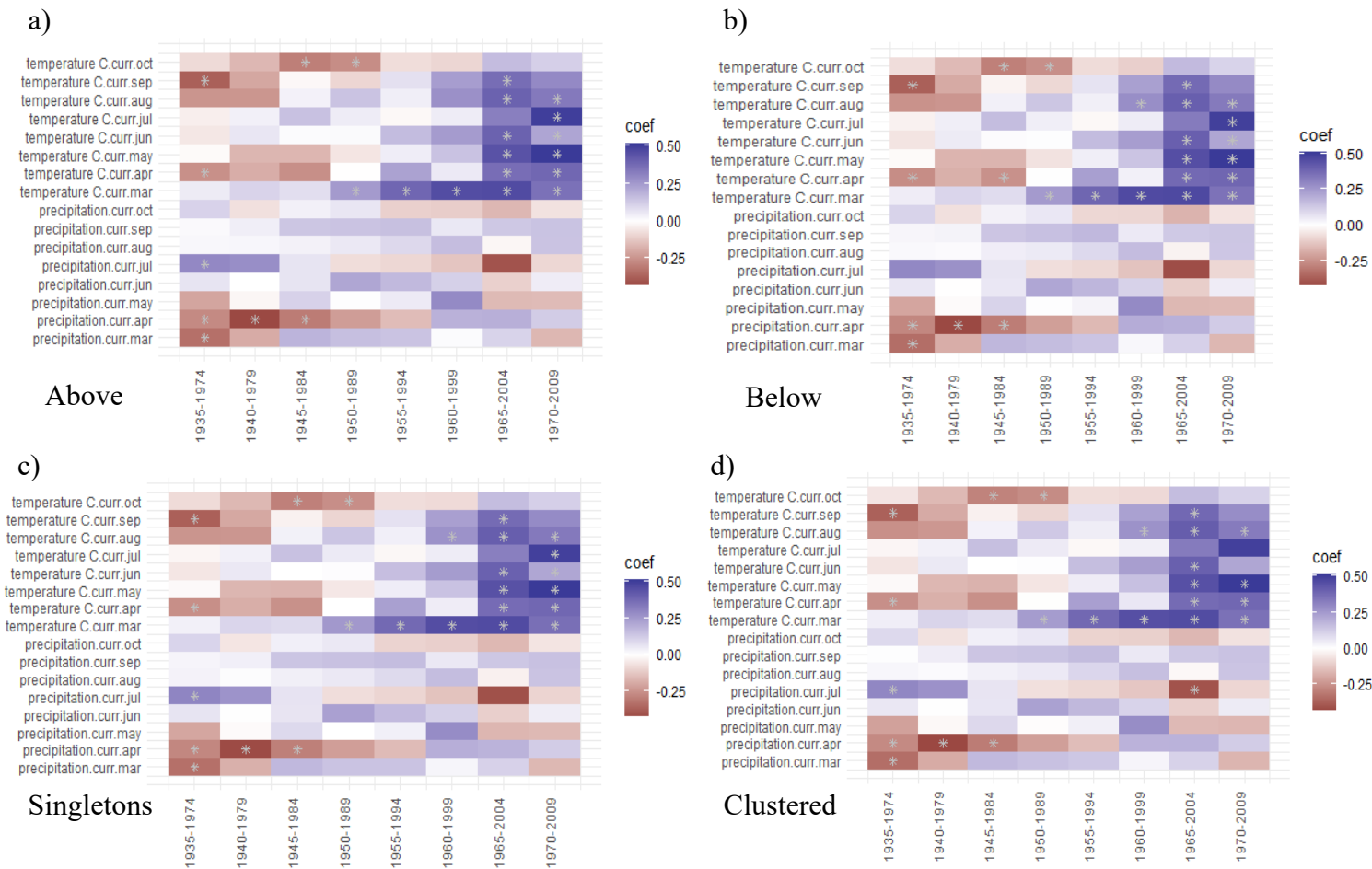
Figure 2



Double-detrended (for age trends) correlations for monthly precipitation (red) and temperature in  $^{\circ}\text{C}$  (blue). Solid lines represent true significant correlations. Dotted lines correlations represent false significant correlations.



Figure 3



Sliding window from 1935 to 2009 lagged by 5 years and single-detrended (for age trends). Red squares mean negative correlations. Blue squares mean positive correlations. Lighter colors mean weaker correlations. Darker colors mean stronger correlations. White squares mean inexistent correlations.



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On my honor, I have neither given nor received any unauthorized aid on this thesis.

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