Multi–Scale Influences of Climate on Upper Treeline Dynamics Along a Latitudinal Gradient in the Rocky Mountains, U.S.A.

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Dedication

I dedicate this dissertation to my wife, Susan. During the course of our marriage, and especially over the past four years, you have continuously offered your unconditional love, patience, and support, while also working tirelessly to ensure that you succeed in your own career and that our family is taken care of. How you do it remains a mystery, yet leaves me in awe. You were always there to celebrate accomplishments and lessen the hardships of defeat. Your willingness to come into the field with me was crucial to my success, particularly after my assistant was injured, and essentially without your help with family–related circumstances on almost a daily basis, I could not have completed this research in such a timely manner. You are a wonderfully loving wife, mother, and teacher and one of my greatest privileges is to be able to share this life with you.

Abstract

The Rocky Mountains have experienced broad-scale increases in temperature during the 20th century. Both paleoecological and contemporary research suggest that upper treeline ecotones are sensitive to temperature fluctuations, yet questions remain as to how the complex interactions between temperature, precipitation, and spatial patterns of tree establishment act to ultimately facilitate or limit treeline advance.The inherent complexities associated with these interactions portend the likelihood of crossing certain bioclimatic thresholds, particularly when considering that they are operating within the context of global climate change. Moreover, the relative importance of these variables is likely to change according to slope aspect and by spatial scale of analysis. My dissertation research uses a multi-scale approach, ranging from contrasting south- and north-facing slopes at a local scale to a regional scale along a latitudinal gradient in the Rocky Mountains to ascertain the influence of temperature and precipitation on upper treeline dynamics. Specifically, this research addresses whether temperature is the predominant influence on tree establishment at upper treeline and eventual treeline advance, and how this varies by spatial scale in the Rocky Mountains (ca. 35°N–44°N).

From a regional perspective, widespread tree establishment is occurring at upper treeline, and has almost exclusively been initiated since ca. 1950. Similar region-wide patterns of tree establishment at upper treeline across various environmental gradients suggest the importance of broad scale climate inputs in driving upper treeline ecotonal dynamics. Perhaps most compellingly, random spatial patterns of tree establishment have the only significant correlations with temperature, suggesting that they are more directly influenced by climatic inputs compared to clustered spatial patterns. Clustered spatial patterns initially form in response to harsh abiotic conditions, but then become more dependent on positive feedback interactions with neighboring vegetation rather than changes in abiotic conditions. Thus, the conclusions of this multi-scale research suggest that upper treeline ecotones in the Rocky Mountains are indeed sensitive to climate and temperature appears to be the most influential climatic component driving these changes. However, the relative influence of climate on treeline dynamics can vary considerably depending on slope aspect, spatial pattern of tree establishment, mountain range, and location relative to 40°N.

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Chapter 1: Upper Treeline – The Rationale and Objectives of this Research

Upper treeline, the highest elevational extent of forest in mountainous regions, is perhaps the most recognizable ecotone, or vegetation boundary, in existence. It provides an inescapable visual contrast of forested versus non-forested environments in countless photographs and artistic depictions of mountain landscapes throughout the world. Upper treeline can be found towards the crest of mountain ranges that attain heights beyond which trees can successfully establish and reproduce. It typically occupies a transition zone of variable length depending on local environmental gradients that begins at the uppermost border of contiguous subalpine forest and extends upslope to isolated stunted and gnarled trees, eventually giving way to treeless alpine tundra. This high-elevation ecotone often affords stunning views of the surrounding landscape and is generally exposed to harsh climate conditions throughout most of the year, with relatively cool, wet, and windy conditions compared to surrounding lowland areas. Yet, in spite of the difficulties commonly associated with accessing and remaining comfortable in this remarkable and unforgiving landscape, upper treeline has captivated the research interests of biogeographers, ecologists, and mountain enthusiasts for decades. As a result, an extensive literature exists on upper treeline. However, as I will detail below in this introductory chapter, some very important questions remain with respect to the influence of climate on these high-elevation ecotones.

In this introductory chapter, I draw from this compilation of scholarly work to place my dissertation research in the proper context. Broadly speaking, the primary purpose of this dissertation research is to determine the influence of climate on upper treeline dynamics at multiple spatial scales along a latitudinal gradient in the Rocky Mountains. In addition, each aspect of this research is situated within the context of global climate change, with one of the primary goals being to provide an empirical field-based study that could potentially improve the ability to forecast the influences of climate change on high-elevation mountain systems. Much of the earliest upper treeline research focused on the importance of growing season temperature in determining its elevational position (e.g., Daubenmire 1954; Tranquillini 1979; Wardle 1971) and with ongoing climate change, this remains at the forefront, yet many researchers have documented the importance of and interactions between other abiotic and biotic factors (e.g., Holtmeier and Broll 2005; Lloyd and Graumlich 1997; Malanson et al. 2007; Smith et al. 2003). Therefore, this research takes a more holistic approach that extends beyond a singular focus on temperature–treeline correspondence. In order to properly conceptualize and understand the rationale and objectives of this research, I have provided a review of relevant literature that provides an important foundational framework for my dissertation.

Placing 20th Century Climate in Context. Increases in global surface temperature over the latter half of the 20th century have highlighted the need for elucidating the biogeographic impacts of climate change on forest ecosystems. Currently, the scientific community is in broad agreement regarding a warming climate (IPCC 2007; Oreskes 2004). Various external forcing agents act upon the global climate system, but anthropogenic-induced greenhouse-gas forcing now comprises the dominant mechanism (Crowley 2000). As a result, climate scientists are increasingly confident that the global mean surface temperatures of the late 20th century exceed those of any time during the past 500 years (IPCC 2007), and potentially extend outside the range of natural variability of the Northern Hemisphere in at least the past two millennia (Jones and Mann 2004; Mann et al. 2008). Moreover, the projected warming of the 21st-century surpasses the best estimates of global temperature change for the last interglacial (Crowley 2000). It seems likely that this unprecedented warming will usher in dramatic changes in vegetation community composition and dynamics, with the possibility of novel community assemblages forming and operating under the influence of a climate system with no previous analog (Williams, Jackson, and Kutzbach 2007). However, considerable uncertainty exists as to the spatial and temporal extent of vegetation change, particularly at regional- to landscape-scales in topographically-complex mountain environments (Bartlein, Whitlock, and Shafer 1997; Beniston 2003; Fagre, Peterson, and Hessl 2003).

While global climate change is expected to result in sustained warmth at previously unprecedented levels across relatively broad continental-scales (Jones and Mann 2004; Jones and Moberg 2003), corresponding trends in precipitation are projected to be less uniform (New et al. 2001). Precipitation inherently exhibits more spatiotemporal variability than temperature, thus further complicating the elucidation of large-scale patterns (New et al. 2001; Walther et al. 2002). However, past and present episodes of drought highlight the importance of understanding precipitation variability, particularly in semi-arid regions, such as western North America (e.g., Gray et al. 2004; Cook et al. 2004) where spatial and temporal variations in annual precipitation have profound effects upon both natural and socioeconomic systems (e.g., Brown and Comrie 2004; Woodhouse 2004). Further, in the western United States, most of the precipitation falls as snow during winter and spring, but there is extensive spatial variation as a result of the rugged topography that dominates the region (Mock 1996). However, Dettinger et al. (1998) identified a north-south seesaw of precipitation that pivots around ca. 40°N in western North America, with opposite moisture conditions existing simultaneously to the north and south of this parallel. In general, the existence of this precipitation dipole creates a potentially unique and valuable region to study the influence of widespread warming (Hamlet et al. 2005; Barnett et al. 2008) coupled with contrasting precipitation regimes. More specifically, this seesaw could prove helpful in revealing detailed biogeographic impacts of anthropogenic climate change on high-elvation forest ecosystems in the Rocky Mountains.

Treeline Ecotones as Biomonitors of Vegetation Change. Ecotones, such as upper treeline, represent a sensitive proxy indicator of the impact of climate change and variability on the distribution of mountain forests (Kullman 1998; Lloyd and Graumlich 1997; LaMarche and Mooney 1967; Risser 1995; Kullman 2001; Camarero and Gutiérrez 2004; Kullman 2002; Lloyd 2005; Kullman and Öberg 2009). An universal explanation for the location of upper treeline has not been formally agreed upon, but its location in most regions appears to be primarily controlled by local thermal regimes (Körner 1998; Körner and Paulsen 2004; Rossi et al. 2007). Generally warmer temperatures that prolong the growing season are therefore expected to have important effects on upper treeline position and ecotonal dynamics (e.g., Lloyd and Fastie 2002; Millar et al. 2004).

Upper treeline vegetation is predicted to respond positionally and structurally to a warming climate, with an upslope advance of tree establishment likely (Grace, Berninger, and Nagy 2002; Kullman 2001). Indeed, paleoecological evidence suggests that upper treeline vegetation has migrated upslope in response to prolonged warm episodes in the past throughout the western United States (e.g., LaMarche and Mooney 1967; Lloyd and Graumlich 1997; Rochefort et al. 1994) and the response of upper treeline to contemporary warming may already be evident. Shifts in the altitudinal extent of upper treeline have been identified in several places including the Canadian Rockies (Danby and Hik 2007; Luckman and Kavanagh 1998, 2000), Alaska (Lloyd and Fastie 2003; Lloyd 2005), and the Swedish Scandes (Kullman 1998, 2001, 2002; Kullman and Öberg 2009) reportedly resulting from 20th century climate changes. However, these studies report asynchronous changes across both space and time. For instance, treeline structure has remained relatively stable on north-facing slopes during the past 400 years, while south-facing slopes have exhibited remarkable change over the same period, accentuated by extensive upslope migration of treeline by seedling establishment (Kullman 1998; Luckman and Kavanagh 2000; Danby and Hik 2007). Differences in treeline response to warmer temperatures based on local topography suggest the potential importance of precipitation and soil moisture regimes in driving ecotonal change. Accordingly, some studies suggest the potential benefits of warmer temperatures on treeline vegetation could be negated without a concurrent increase in precipitation to replenish soil moisture and alleviate water stress (e.g., Daniels and Veblen 2004; Hessl and Baker 1997; Lloyd and Fastie 2002; Weisberg and Baker 1995). Thus, the ramifications of a warming climate on upper treeline dynamics remain uncertain.

Is Climate the Dominant Driver of Upper Treeline Ecotonal Dynamics?

Although the elevational extent of upper treeline is primarily governed by temperature (e.g., Körner and Paulsen 2004) and contains climatically-sensitive tree populations growing at their physiological range limit (e.g., Brubaker 1986), some researchers have argued that it is in disequilibrium with climate and as a result, will move too slowly to be an effective indicator of climate change (e.g., Kupfer and Cairns 1996; Noble 1993; Cairns and Malanson 1997; MacDonald et al. 1998; Payette et al. 1989). Heterogeneous edaphic conditions at upper treeline (e.g., Kupfer and Cairns 1996) and the nearly ubiquitous influence of disturbances in the Rocky Mountains (e.g., Veblen et al. 1994; Walsh et al. 1994; Peet 2000) also raise concerns about upper treeline serving as a sensitive proxy for evaluating changes in climate. This is noteworthy given that rates of disturbance are predicted to increase with continued warming (Overpeck, Rind, and Goldberg 1990) and that previous research has argued that an initial disturbance event will provide the necessary impetus for eventual vegetation change associated with climate change (Davis 1989; Villalba and Veblen 1997).

In subalpine forests of the Rocky Mountains, fire is the dominant disturbance agent (Peet 2000; Veblen et al. 1994) and it is characteristically infrequent and stand-replacing (e.g., Baker and Veblen 1990; Veblen, Hadley, and Reid 1991; Kipfmueller and Baker 2000). Post-fire regeneration could possibly be confused with climate-mediated tree establishment at upper treeline, yet recently burned areas should be relatively easy to identify when selecting appropriate study sites given how long evidence of previous crown fires can persist on the landscape in the form of standing dead snags.

Paleoecological evidence suggests that treeline ecotones in the Rocky Mountains are responsive to climate change (e.g., Fall 1997; Jiménez-Moreno, Fawcett, and Anderson 2008; Stohlgren and Bachand 1997). Moreover, recent research in Canada (Danby and Hik 2007; Luckman and Kavanagh 1998, 2000), Alaska (Lloyd and Fastie

2003), and Sweden (Kullman 1998, 2001, 2002) have identified important vegetation modifications without appreciable time lags, ultimately resulting in the apparent upslope migration of treeline during the 20th century. From a long-term perspective, this rapid rate of vegetation change at upper treeline stands out as a virtually unprecedented anomaly and indicates that contemporary treelines may be at the pinnacle of their existence during the past 7000 years (Kullman 2001; Kullman and Kjällgren 2006). Other research suggests the distribution of tree species changed more rapidly than soil development in many areas at upper treeline (Malanson et al. 2002), and when considered in conjunction with relatively infrequent disturbances, it becomes clear that upper treeline exemplifies an environment that is strongly driven by climate (Baker and Weisberg 1995; Lloyd 2005).

Are Upper Treeline Dynamics Shaped by the Same Climatic Factors? Identical climatic parameters do not uniformly affect seedling establishment, subsequent growth, and eventual treeline advance in all cases (Wang, Zhang, and Ma 2006; Camarero and Gutiérrez 2004; Daniels and Veblen 2004; Earle 1993). However, previous studies have attributed each of these components to global climate change and recognized them as potentially sensitive indicators of upper treeline to climate.

Regeneration success is probably a more suitable indicator of the sensitivity of upper treeline ecotones to environmental change than increasing growth rates of mature trees because accelerated growth does not automatically imply appropriate conditions for seedling establishment (Holtmeier and Broll 2005). Moreover, nearly all of the supporting data from treeline dynamics have been derived from studies on older trees rather than on the mechanisms of seedling establishment (Smith et al. 2003). Seedling establishment within the treeline ecotone is essential for the perpetuation of subalpine forest and has been reported as a measure of forest response to climate variability (Kullman 1993; Noble 1993). Regeneration leads to an increase in tree abundance, which in fact might be a more sensitive monitor of climate change than treeline position (Camarero and Gutiérrez 2004). Several studies in the Rocky Mountains have documented an increase in tree density at upper treeline (e.g., Elliott 2003; Klasner and Fagre 2002; Zier and Baker 2006). However, paleoecological evidence from the Sierra Nevada Mountains in California suggest changes in tree abundance may precede changes in treeline position by up to 400 years (Lloyd and Graumlich 1997). As a result, the relative importance of an increase in tree density with respect to detecting the impacts of global climate change remains unknown, especially in the Rocky Mountains.

The advance of seedling establishment upslope beyond the current limit of treeline is considered the best measure of treeline sensitivity to climatic change (Holtmeier and Broll 2005). Paulsen et al. (2000) claim treeline advance could only occur if a long-term warming trend stimulates tree growth and establishment frequently enough, or if periods of lower temperatures that inhibit these are rare. Yet, observed changes in 20th century climate support the likelihood of this occurring and the initial migration of a plant species is most likely to occur at an ecotone because it represents the biophysical boundary of a species (Stohlgren, Owen, and Lee 2000). However, despite some previously cited reports of upslope treeline advance (cf., Kullman 1998, 2001, 2002; Luckman and Kavanagh 1998, 2000), other studies suggest that seasonal temperature anomalies have prevented the ascent of upper treeline (e.g., Camarero and Gutiérrez

2004; Wang, Zhang, and Ma 2006). Research in the Rocky Mountains found that treeline areas exposed to relatively high levels of sunlight, such as south-facing slopes, may not be suitable for treeline migration due to the combination of an increase in both water stress and diurnal temperature range (Germino, Smith, and Resor 2002; Weisberg and Baker 1995).

In addition to climate, other research has identified the importance of biotic interactions and feedback in regulating upper treeline dynamics (e.g., Alftine and Malanson 2004; Batllori et al. 2009; Bekker 2005; Smith et al. 2003). Biotic interactions have been at the forefront of upper treeline research in the Medicine Bow Mountains of southeastern Wyoming, where contradictory results have emerged with respect to the likelihood of treeline expansion into alpine tundra (e.g., Germino, Smith, and Resor 2002; Maher, Germino, and Hasselquist 2005; Moir, Rochelle, and Schoettle 1999). For example, Moir et al. (1999) argue that it is unlikely that treeline species will be able to spread into the dense tundra grass vegetation, while Germino et al. (2002) and Maher et al. (2005) suggest that the herbaceous ground cover facilitates tree seedling establishment by ameliorating local microclimatic conditions. The latter argument supports other research that demonstrates the ability of scattered tree islands within the alpine tundra to permit seedling establishment on the leeward side by lessening the effects of naturally-harsh climatic conditions (e.g., Batllori et al. 2009; Bekker 2005; Hättenschwiler and Smith 1999; Marr 1977; Szeicz and MacDonald 1995). These studies also demonstrate the possible importance of feedback processes, particularly in relation to wind, when examining the spatial pattern of tree establishment at upper treeline (Alftine and Malanson 2004; Holtmeier and Broll 2005; Resler 2006). Cumulatively, these studies illustrate the lack of a general scientific consensus on whether or not a directional increase in temperature, as predicted by global climate change scenarios, will ultimately result in an elevational expansion of upper treeline.

The Importance of Scale in Upper Treeline Research. It is essential for biogeographic investigations to consider both coarse and fine scales (Resler 2006). This can be achieved by placing upper treeline research in the context of a comparative framework that facilitates the critical evaluation of similarities and differences in the spatial patterns produced by ecotonal dynamics along major latitudinal and biogeographic gradients (Young and León 2007). Comprehensive explanations of geographic variation in vegetation along a latitudinal gradient have been completed in the Rocky Mountains (cf., Allen, Peet, and Baker 1991; Peet 1978), but have excluded comparisons of upper treeline dynamics. Surprisingly, despite inspiring scholarly research for decades, the literature on upper treeline is dominated by local, relatively small-scale studies. More importantly, with only a few exceptions worldwide (e.g., Dalen and Hofgaard 2005; Daniels and Veblen 2004; Kullman and Öberg 2009; Lloyd 2005), little attention has been given to examining the spatial variation of upper treeline in response to climate change on multiple spatial scales, especially in the Rocky Mountains. This is noteworthy because local and regional studies of upper treeline are warranted to more accurately assess the influence of climatic factors that control the spatial and temporal patterns of tree establishment and subsequent survival (Holtmeier and Broll 2005; Smith et al. 2003). Furthermore, key information for understanding the effects of climate change scenarios on mountain forests could be provided by a detailed reconstruction of upper treeline population dynamics (Luckman and Kavanagh 1998; Wang, Zhang, and Ma 2006), which is currently lacking in the Rocky Mountains. When considering the role of scale in upper treeline research, it is important to realize that the influence of climate may not be discernable in the age structure of a single study site, but will likely be most evident in a summary of tree establishment dates across a mountain range or region (Swetnam and Betancourt 1998). Ultimately, a systematic and multi-scale approach to studying the impacts of climate change on upper treeline ecotones is needed in the Rocky Mountains. More specifically, research is needed to compare the influences of contrasting regional climates on the vegetation dynamics of upper treeline and to better understand the influence of fine-scale biotic processes that may interact with broader scale climate inputs.

Research Setting – The Rocky Mountains. The Rocky Mountains are particularly well suited for studying the multi-scale impacts of climate change on upper treeline ecotones along a latitudinal gradient due to their generally north-south orientation. My study area includes sites placed along a north–south transect that spans an approximate ten-degree range in latitude (35°N–45°N) from the Southern Rocky Mountains northward into the Central Rockies (Fig. 1) (Thornbury 1965). My study sites are located in the Sangre de Cristo Mountains of northern New Mexico and southern Colorado (ca. 35°–37°N), Front Range Mountains of Colorado (ca. 38°–40°N), Medicine Bow Mountains of southern Wyoming (ca. 41°N), and Bighorn mountains of northern Wyoming (ca. 44°–45°N). These areas were chosen because they allowed me to examine the influence of climate on upper treeline at the local scale (north- vs. south-facing

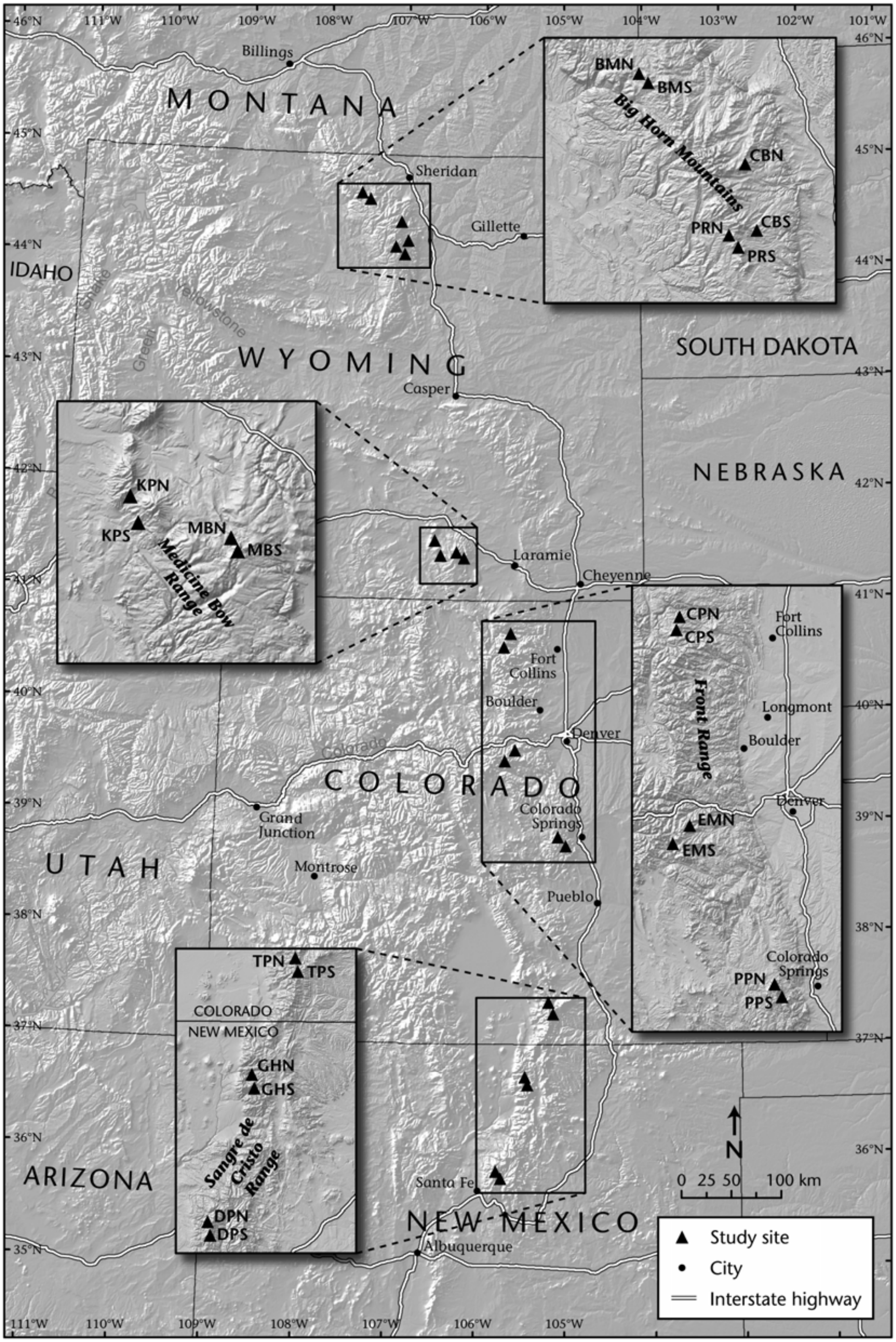

Figure 1. Study area map.

slopes), landscape scale, (mountain range), sub-regional scale (north and south of 40°N), and regional scale (between mountain ranges). In addition, based on climatological studies (e.g., Dettinger et al. 1998; Mitchell 1976) and for comparison purposes, I classify the Southern Rocky Mountains as being south of 40°N and including the Sangre de Cristo and Front Range Mountains. In a similar manner, I classify the Central Rocky Mountains as being north of 40°N and including the Medicine Bow and Bighorn Mountains. This deviates from some classic vegetation gradient studies (Allen, Peet, and Baker 1991; Peet 1978) whereby the Medicine Bow Mountains are included in the Southern Rocky Mountains. However, based on my results below coupled with extensive field observations, this grouping seems appropriate in terms of how upper treeline dynamics within these two areas are primarily influenced by the interactions of abiotic and biotic processes.

Dendroecology as a Research Tool. Dendrochronology, the study of tree rings, offers a valuable tool for studying vegetation change in forest environments (Kipfmueller and Swetnam 2001). Dendroecology is a subfield of dendrochronology that is primarily concerned with applying dendrochronological techniques and principles to address ecologically-based research questions (Fritts and Swetnam 1989). In this case, I used dendroecological methods to reconstruct tree establishment at upper treeline in order to ascertain how contemporary dynamics arose. In the field, this involved using an increment borer to core into a tree, which functions as a manually-turned drill bit, at either 30 cm above the ground or at the base of the tree, depending on the site. The point of this is to sufficiently penetrate the bole of the tree so that the pith can be attained and when this occurs, a cylindrical tree core sample is removed and stored in a paper art straw. In addition, two tree cores are commonly collected, which facilitates crossdating.

Crossdating involves matching the patterns of narrow and wide annual growth rings, which forms the foundation of dendrochronology (Fritts 1976). This was primarily accomplished by using skeleton plots (Stokes and Smiley 1996). Skeleton plotting is done on graph paper and essentially involves drawing the relative narrowness of each annual ring present on a tree core sample. When this is performed on a representative sample of tree cores collected, then the “marker rings” of each tree core should line-up through the use of crossdating. Marker rings are typically narrow annual rings that are produced during years of sub-optimal growing conditions, which generally refers to colder temperatures at upper treeline, although moisture stress can influence this as well. Once a calendar year is assigned to each annual growth ring after crossdating, the age of the tree can be determined and subsequently placed into age-classes representative of the year of tree establishment (e.g., 5-yr or 10-yr age-classes). Age classes are routinely used in dendroecological research because of the uncertainties associated with being able to pinpoint the exact year of tree germination (e.g., coring height above the ground or number of rings missing to the pith). The primary consequence of this is a loss of annual resolution.

Description of Dissertation Research. To accomplish a holistic and comprehensive study of the influences of climate on upper treeline dynamics in the Rocky Mountains, the next three chapters (chapters 2–4) contain specific examinations of climate-treeline interactions. Chapter five provides a summary of the conclusions of this research. Each topical chapter (chapters 2–4) was originally prepared as a separate manuscript for submission to a peer-reviewed journal, so some redundancy exists, particularly in the description of my study area and field methods.

Chapter two examines the specific influences of slope aspect and the spatial pattern of tree establishment on upper treeline dynamics in the Southern Rocky Mountains. The point of this chapter was to use contrasting slope aspects as a proxy for soil moisture conditions, with north-facing slopes presumably experiencing more moist conditions, and to examine the spatial pattern of tree establishment above timberline as a proxy for the degree of climatic influence. The combination of these attributes were used to gauge the overall importance of local site factors such as positive feedback, versus broad-scale climate inputs in driving ecotonal dynamics at upper treeline, and how these interactions may vary over space. A manuscript based on this work has been accepted for publication in *Arctic, Antarctic, and Alpine Research*.

Chapter three assesses the influence of 20th century climate and bioclimatic thresholds on tree establishment in the Southern Rocky Mountains. I wanted to see if the influence of climate was relatively uniform with respect to tree establishment at upper treeline throughout the region. To the best of my knowledge, this chapter represents the first study to explicitly test for the occurrence of thresholds in tree establishment and significantly correlated climate variables. This chapter also examines the temporal synchrony between the crossing of various climate and ecological thresholds. This chapter was written with the intent of submitting it to the journal *Annals of the Association of American Geographers.*

Chapter four represents a synthesis of how spatial pattern, positive feedback, and climate interact to govern upper treeline dynamics along a latitudinal gradient in the Rocky Mountains. A relatively extensive literature exists regarding both treeline structure (i.e. patterns and processes over space) and the influence of climate on upper treeline, yet to the best of my knowledge, this represents the first synthesis of the two to gain a more holistic understanding of how local patterns and processes interact to ultimately influence the level of climate sensitivity at upper treeline Moreover, this chapter examines the degree to which spatial scale plays a role in understanding treeline dynamics. For instance, I assess how small scale processes and patterns manifest themselves at larger spatial scales and in turn, how processes and patterns at large spatial scales are constrained by regional climate. Scales of analysis used include landscape, sub-regional, and regional. This chapter was written with the intent of submitting it to the journal *Global Ecology and Biogeography*.

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Chapter 2. Multi-Scale Influences of Slope Aspect and Spatial Pattern on Ecotonal Dynamics at Upper Treeline in the Southern Rocky Mountains, USA

Given substrate conditions suitable for tree establishment, the location of upper treeline appears to be primarily controlled by local thermal regimes (e.g., Körner and Paulsen 2004; Rossi et al. 2007). Generally warmer temperatures that prolong the growing season are therefore expected to have dramatic effects on upper treeline ecotonal dynamics, including changes in the position and structure of treeline communities (e.g., Grace, Berninger, and Nagy 2002; Kullman 2001; Lloyd and Fastie 2002). However, regional-scale temperature trends can be modified by local-scale interactions between abiotic and biotic factors that help pattern treeline structure (Baker and Weisberg 1995; Luckman and Kavanagh 1998; Smith et al. 2003). Understanding the spatial pattern that results from these dynamic interactions at upper treeline provides a viable approach for evaluating past fluxes and predicting future changes (Young and León 2007).

The local-scale modification of treeline environments is often contingent on the initiation of positive feedback processes, whereby a vegetation community modifies the surrounding environment to promote further establishment (Wilson and Agnew 1992). Positive feedbacks have been shown to affect the dynamics and spatial pattern of upper treeline (e.g., Alftine and Malanson 2004; Bader, Rietkerk, and Bregt 2008; Resler 2006). Two important mechanisms for facilitating new seedling establishment and sustaining positive feedback cycles include krummholz patches (e.g., Bekker 2005; Callaway 1998; Marr 1977) and inanimate objects such as boulders and terrace risers (e.g., Resler 2006; Resler, Butler, and Malanson 2005). The corresponding spatial pattern that these feedback systems create can determine how upper treeline ecotonal dynamics will be influenced by continued broad-scale warming (e.g., Bekker 2005; Camarero, Gutiérrez, and Fortin 2000). Yet, research is lacking on how the interactions between treeline pattern and feedbacks vary with slope aspect and scale.

In mountainous regions, complex topography creates steep environmental gradients that produce ecologically important bioclimatic differences from variations in elevation, aspect, and slope over relatively short distances (e.g., Villalba, Veblen, and Ogden 1994; Fagre, Peterson, and Hessl 2003). As a result, the slope aspect mediation of local-scale site conditions has been shown to influence the age-structure and ecotonal dynamics of upper treeline environments (Bunn, Waggoner, and Graumlich 2005; Danby and Hik 2007; Elliott and Baker 2004; Kullman 1998; Luckman and Kavanagh 2000). Notable differences in the spatial and temporal patterns of tree regeneration based on slope aspect suggest that soil moisture conditions may exert a strong influence on ecotonal dynamics at upper treeline (e.g., Daniels and Veblen 2004; Hessl and Baker 1997). In addition, aspect-mediated changes in the pattern and position of upper treeline are suggestive of a non-linear response to broad-scale warming and could indicate the importance of crossing bioclimatic thresholds (e.g., Kupfer and Cairns 1996; Lloyd 2005; Malanson 2001).

Scale plays an important role in upper treeline research since spatial pattern is driven by processes operating at multiple spatial scales (Holtmeier and Broll 2005; Resler 2006). A multi-scale approach can be achieved by using a comparative framework that pays careful attention to evaluating similarities and differences in the spatial patterns of upper treeline along a latitudinal gradient (cf. Young and León 2007). Comprehensive vegetation studies along a latitudinal gradient have been completed in the Southern Rocky Mountains (SRM) (Allen, Peet, and Baker 1991; Peet 1978), but have excluded regional-scale comparisons of upper treeline dynamics. Furthermore, although numerous studies have been performed at upper treeline in the SRM, the research has focused on relatively small areas in the Colorado Front Range (FR) (e.g., Baker and Weisberg 1995; Daly and Shankman 1985; Humphries, Bourgeron, and Mujica-Crapanzano 2008; Weisberg and Baker 1995a, 1995b; Hessl and Baker 1997). Consequently, at upper treeline in the Rocky Mountains, little attention has been paid to what type of regional-scale patterns emerge when scaling up from a series of detailed local-scale data sets (cf. Allen et al., 1991).

In this chapter I focused on the mediating role of slope aspect and spatial pattern on upper treeline ecotonal dynamics at multiple spatial scales in the SRM to infer process interactions and gauge the importance of feedbacks in determining the potential response of upper treeline to climate change. Dendroecological techniques were used to create a detailed reconstruction of population dynamics that was used in conjunction with proxies for soil moisture (slope aspect) and climate (spatial pattern) to make comparisons between the interacting influences of regional-scale climate and local site conditions. For instance, if climate is the dominant driver of ecotonal dynamics at upper treeline, distinct similarities should exist in tree establishment dates and spatial patterns throughout the region (e.g., Camarero and Gutiérrez 2004; Lloyd and Fastie 2003; Swetnam and Betancourt 1998). Alternatively, if local site conditions created by the complex interplay of climate, geology, and geomorphology are primarily responsible for patterns of tree establishment, then idiosyncratic responses within the region would be expected (e.g., Malanson et al. 2007; Allen and Walsh 1996; Butler et al. 2007). These patterns and responses are also likely to vary with scale.

To test this, I used multiple spatial scales of analysis (local = slope aspect; landscape = mountain range; regional = between mountain ranges) to address the following research questions: 1) does slope aspect influence the spatial and temporal patterns of tree establishment in the Southern Rockies? 2) is the spatial pattern of upper treeline similar throughout the Southern Rockies, thus suggesting climate as the primary control?

Study Area

The study area stretches along ca. 600 km of the generally north-south trending SRM of Colorado and northern New Mexico (Fig. 1). The SRM are situated on the leeward side of the Continental Divide where they rise abruptly along their east slope, with mountain peaks reaching ca. 3800–4200 m a.s.l., ca. 1800–2500 m above the adjacent High Plains of Colorado and New Mexico (Veblen and Lorenz 1991). Towards their crest, treeline elevation varies from ca. 3800 m a.s.l. in the Sangre de Cristos to ca. 3500 m a.s.l. in the Front Range (Peet 1978). My study sites are located along a five-degree range of latitude from 35°N in the Sangre de Cristo Mountains (SDC) (ca. 35°–37°N) to 40°N in the FR (ca. 38°–40°N; Table 1).

The geology of the SRM exhibits considerable spatial variation, but the substrate in high-elevation areas is predominantly composed of Precambrian granitic rock with coarse texture and high silica content, along with gneiss and schist that share similar geochemical properties (Allen, Peet, and Baker 1991; Peet 2000). Pedogenic processes

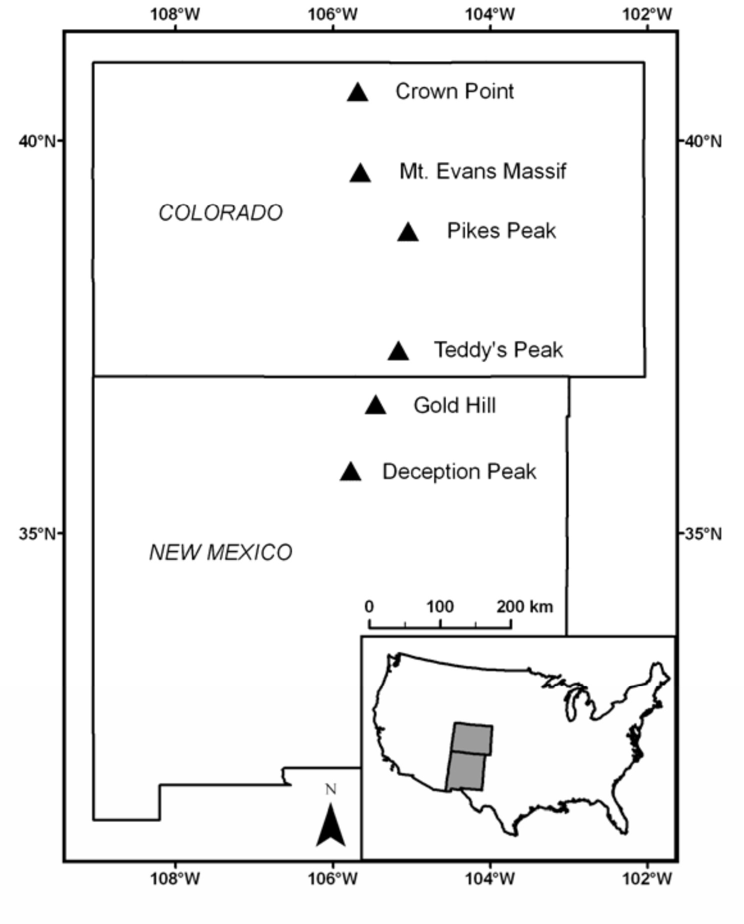


Figure 1. Study area map depicting sites in the Sangre de Cristo (SDC) and Front Range (FR) mountains of the Southern Rocky Mountain (SRM) region.

eventually form relatively acidic, infertile soils from this parent material (Allen, Peet, and Baker 1991).

A detailed climate study that exclusively examines both the SDC and FR has not been published. In general, the climate of the SRM is relatively uniform south of ca. 40°–41°N, with infrequent intrusions of Pacific air masses during the winter and an influx of monsoonal moisture producing most summer precipitation (Mitchell 1976). However, due to the paucity of climate stations at high elevations near upper treeline (Barry 1992), I calculated a detailed climate summary for the region using PRISM (Precipitation-elevation Regressions on Independent Slopes Model) climate data from our study sites (Table 1; PRISM Group, Oregon State University, http://www.prismclimate.org, created 10 Oct 2008). PRISM data recognizes the dominant influence of elevation and topography in mountain climates and has been shown to accurately capture precipitation and temperature values in remote mountainous regions where limited data are available (Daly, Neilson, and Phillips 1994; Daly et al. 2001). Mean annual temperature for my study area is 1.3°C, with July and August being the only two months with an average temperature above 0°C at all of the study sites. Within the SRM, mean summer (June-August) growing season temperature is 0.8°C warmer in the SDC (10.9°C vs. 10.1°C, respectively). The SRM receive an average total of 78.5 cm of annual precipitation. Monsoon-induced precipitation during the summer delivers a seasonal maxima in the SDC, while the FR receives most precipitation during the winter (December-February) and spring (March-May) in the form of snow (e.g., Mock 1996).

Vegetation at high-elevation upper treeline sites is primarily composed of *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) and *Abies lasiocarpa* (Hook.) Nutt.

Table 1. Upper treeline study sites and locations in the Southern Rocky Mountains. Abbreviations are given for sites on both south-(S) and north-facing (N) slopes.

Site	Abbreviations (S:N)	Mtn. Range	Lat./Lon. (°N/°W)
Deception Peak	DPS:DPN	Sangre de Cristo	35.8/105.8
Gold Hill	GHS:GHN	Sangre de Cristo	36.6/105.6
Teddy's Peak	TPS:TPN	Sangre de Cristo	37.3/105.2
Pikes Peak	PPS:PPN	Front Range	38.8/105.1
Mt. Evans Massif	EMS:EMN	Front Range	39.6/105.7
Crown Point	CPS:CPN	Front Range	40.6/105.7

(subalpine fir), with some *Pinus aristata* Englem. (Colorado bristlecone pine) on south-facing slopes south of around 39°N and some *Pinus contorta* Dougl. ex Loud. (lodgepole pine) in the northern FR (Peet 2000). *P. engelmannii* often forms monospecific stands in the southernmost areas of the SDC, particularly on north-facing slopes, and *A. lasiocarpa* becomes more prevalent in the northern FR (Peet 1978). Due to relatively steep slopes, krummholz patches are rare, especially in the SDC (Peet 1978).

Evidence of humans occupying areas near timberline dates back thousands of years, although any settlement or land-use patterns were likely ephemeral in such extreme environments (e.g., Veblen and Lorenz 1991; Wolf 1995). Permanent Euro-American settlement within the area often coincided with mining activities, which reached a pinnacle in the mid- to late-1800s (ca. 1850s – 1870) (deBuys 1985; Veblen and Lorenz 1991). Currently, based on extensive field observations, most anthropogenic influence at upper treeline stems from cattle grazing in northern New Mexico and timber harvesting in the northern FR, although neither appears to be widespread.

Methods

Field Sampling. To achieve a multi-scale approach, I placed six nested-belt transects on contrasting north (azimuth 315° to 45°)- and south (azimuth 135° to 225°)-facing slopes in each of the two mountain ranges comprising the SRM region (n = 12 transects). Only sampling on north- and south-facing slopes with generally opposite soil moisture regimes allows me to make inferences regarding the importance of slope aspect and corresponding soil moisture condiions in driving ecotonal dynamics at upper treeline (e.g., Danby and Hik 2007; Daniels and Veblen 2004). Study sites were separated by approximately one degree of latitude (~ 111 km) and transect location was systematically selected to eliminate the influence of potentially confounding variables from both natural and anthropogenic disturbances. In addition, my site selection focused on identifying climatic treelines (cf. Holtmeier and Broll, 2005; Butler et al., 2007), which essentially refers to areas where possible treeline expansion was not limited by local topography or mechanical reasons that make tree growth impossible (e.g. steep and rocky slopes, absence of soil, or avalanche tracks). Every study site was selected *a priori* by analyzing aerial photographs for evidence of recent disturbance events and to ensure that potential treeline expansion was not prohibited by the local geology. Exploratory reconnaissance trips were performed when the suitability of a site was in question.

Individual nested-belt transects began at an outpost tree (term after Paulsen, Weber, and Körner 2000), which was classified as the furthest upright tree (≥ 5 cm diameter at breast height [dbh]) or sapling (< 5 cm dbh, ≥ 1.2 cm diameter at ground level [dgl]) existing within the treeline ecotone, extending downslope perpendicular to the slope contours and through timberline 40 m into relatively closed-canopy forest. Here I define treeline as the uppermost limit of individuals having an upright growth form and timberline as the elevational limit of closed-canopy forest (cf. Daniels and Veblen 2003). Collectively, the zone in-between this demarcation is referred to as the treeline ecotone (cf. Malanson et al. 2007). Krummholz was not sampled because their low stature creates a different microclimate than that experienced by upright trees and thus may not reflect suitable conditions for tree establishment within the treeline ecotone (e.g., Körner and Paulsen, 2004). The width of each nested-belt transect was divided into two parts to ensure an adequate number of saplings to calculate age corrections and analyze regeneration patterns. Above timberline (ATL), I sampled all saplings within a wide 20 m belt and all trees within a narrower 10 m belt on each side of the transect. The north-facing side of Pikes Peak (site = PPN) represents the only exception to this, as I was only able to sample a 10.5 m wide belt ATL due to logistical concerns associated with destructive sampling. Below timberline (BTL), the widths were half as wide at each site (saplings were collected within 10 m and trees were sampled within 5 m) to accommodate for the general increase in tree density. As a result of variations in tree density and the upward position of the outpost tree, overall transect length varied at each site, but each was long enough to include at least 50 trees.

Site conditions were recorded along each transect, including elevation, slope aspect, slope steepness (°), distance from the outpost tree to timberline, and GPS coordinates of the outpost tree. Additionally, I recorded detailed notes for each tree within the transect including dbh (dgl, if applicable), *x* and *y* coordinates to the nearest 0.1 m along the transect (including krummholz), 1 m radius of microtogography (i.e. convex, concave, slope, or lee of shelter), canopy position (canopy, subcanopy, or understory), and coring height. The distance from outpost tree to timberline was measured to quantify the differences in ecotone structure between north- and south-facing slopes (cf. Daniels and Veblen 2003). The location of krummholz patches were noted to provide a detailed account of the spatial patterns of tree establishment within the upper treeline ecotone. Local microtopography was recorded to determine whether tree establishment is predominantly in concave, moisture-gathering areas, on convex surfaces devoid of excess soil moisture, or relegated to sheltered sites, all of which could have implications for possible feedback mechanisms driving vegetation patterns at treeline (e.g., Alftine and Malanson 2004).

Age-Structure Analysis. Age-structure information was collected by extracting two increment cores at 30 cm above the ground from all living trees (≥ 5 cm dbh, ≥ 9 cm dgl) along the transect. Every sapling within the transect was harvested at ground-level and where available, 10–15 were sectioned at 30 cm to determine a correction factor for age-at-coring height. Further, distinctions were made between species and saplings growing ATL in a relatively open environment from those growing in the shade of closed-canopy forest BTL to more accurately determine age-to-coring height corrections for the trees growing in both conditions (cf. Veblen 1992). I inventoried seedlings (< 1.2 cm dgl) as alive or dead throughout the entire transect.

All tree cores and sapling cross sections were dried and mounted following standard dendrochronological procedures (Stokes and Smiley 1996). All tree-ring samples were crossdated using both visual evidence from individual series and by comparing skeleton plots to ensure that accurate dates were assigned to the annual rings of each series (Stokes and Smiley 1996). Pith estimators were used to geometrically determine the number of rings to center when the pith was not obtained during field sampling (Applequist 1958). Any samples that could not be confidently crossdated (e.g., rotten and/or no ring curvature present to estimate distance to pith) were excluded from my analyses (*n* = 19).

Dates of tree establishment were calculated based on tree age at the time of sampling (2007 for SDC and Mt. Evans site, 2008 for rest of FR) and by adding the appropriate age to coring-height correction. Coring-height corrections were calculated for each tree species growing ATL and BTL and were further stratified by slope aspect and mountain range. Mean tree age at 30 cm was determined for each species according to slope aspect and mountain range and added to the age determined from coring. Outliers (± 2 s.d.; $n = 11/159$) were removed before computing final corrections. The average age corrections for 30 cm were compared between trees growing ATL and BTL, slope aspect, and mountain range and were combined if they were not statistically different ($p < 0.05$; t-test). Interestingly, only Pikes Peak exhibited statistically different age adjustments from trees growing above and below treeline. Therefore, aside from the south-facing site on Pikes Peak, age-height corrections were combined into slope aspect for each mountain range, regardless of position along transect (Fig. 2). When a certain species was only sporadically represented throughout the region, age corrections were combined from both mountain ranges to produce a regional age correction (e.g., *P. aristata* and *A. lasiocarpa*).

Once age to coring height corrections were applied, tree establishment dates were grouped into both decadal (pre–1800 to 1890) and five-year (1900–2000) age classes to produce a hybrid age-structure chronology. Separate age-class divisions were created before (10-yr) and after 1900 (5-yr) because of my detailed sampling strategy that produced age to coring height corrections and a low average number of rings to center for the period 1900 to present (Table 2).

The hybrid age-structure data were analyzed to determine whether tree age was statistically different based on slope aspect at local, landscape, and regional scales. Cumulative age distributions were tested for normality using a Kolmogorov–Smirov test and then median age was compared using a Mann–Whitney *U*-Test. I used the

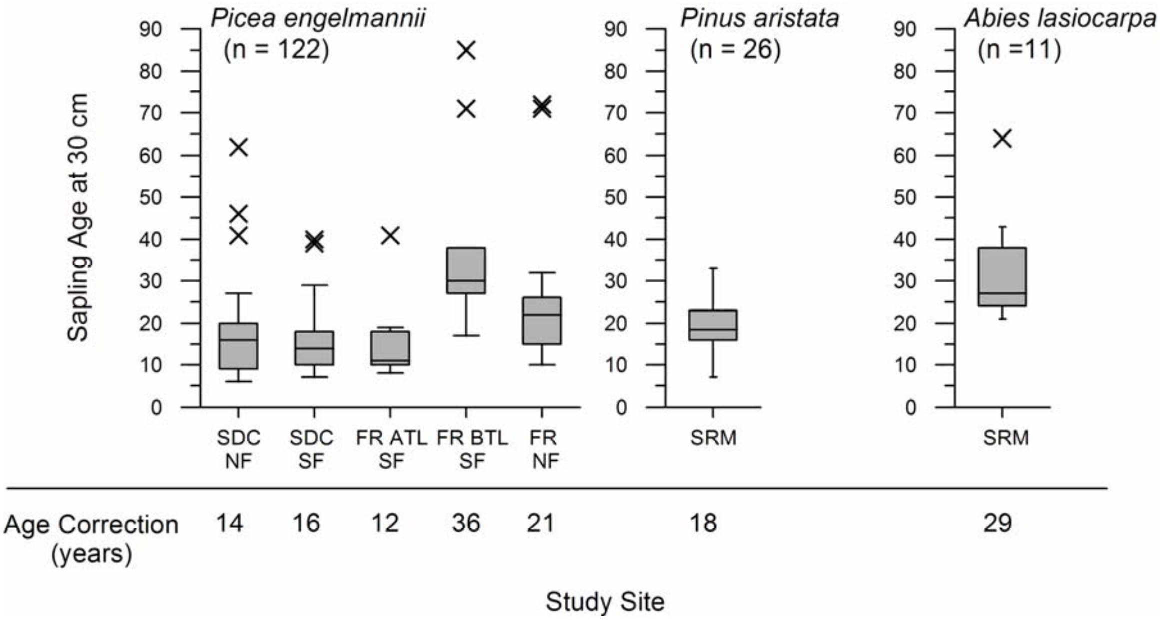


Figure 2. The range of age to coring-height correction data with tree age outliers (± 2 s.d.) denoted by a X. The age of saplings at 30 cm height was determined for each species and further stratified by slope aspect and mountain range. Due to a low *n Abies* and *Pinus* were combined to form a regional age correction. Note that age corrections for south-facing slopes (SF) in the Front Range were stratified based on position above or below timberline because of statistically significant differences between the two ($p < 0.05$; *t*-test). Abbreviations used include: ATL – above timberline; BTL – below timberline; NF – north-facing slopes.

Table 2. Average number of rings to center data for crossdated tree cores in the hybrid age-structure classes (Pre-1900 and 1900-present). Samples do not include cross-section data from harvested saplings that already contain the pith (*n* = 150). Site abbreviations can be found in Table 1.

Site	Pre–1900	(n)	1900–Present	(n)	Total Cores Collected	Pith (%)
DPS	5.6	8	2.8	15	23	30.4
DPN	8	1	3.2	25	26	34.6
GHS	13	3	1.4	36	39	51.3
GHN	4.4	8	2.1	25	33	33.3
TPS	10.5	2	1.3	31	33	54.5
TPN	2.6	9	4.6	11	20	40.0
PPS	7.7	23	2.3	13	36	27.8
PPN	6.6	14	3.2	24	38	28.9
EMS	7.1	18	2.1	14	32	31.3
EMN	5.9	20	3.3	12	32	15.6
CPS	11	1	3.4	26	27	48.1
CPN	4.8	4	6.6	28	32	9.4
Mean/Total	7.3	111	3.0	260	371	33.8

nonparametric Mann–Whitney *U*-Test to discover whether tree ages at upper treeline in the SRM were significantly different according to slope aspect, with the null hypothesis being that the population ages are equal. Any statistically significant differences in tree age ($p < 0.05$) between north- and south-facing slopes could illustrate possible feedback-induced nonlinear responses to climate and help elucidate the stability of high-elevation treeline ecotones throughout the SRM.

Spatial Analysis. I assessed the spatial pattern of tree establishment by computing Ripley's $K(t)$ (Ripley 1977) on the x and y coordinates of each tree (including krummholz) ATL in my transects. Ripley's $K(t)$ function is a second-order point pattern analysis based on the variance between points (tree-to-tree) in two-dimensional space that can identify particular patterns (random, clustered, or uniform) at varying spatial scales (Duncan 1991; Haase 1995; Ripley 1977). However, since $K(t)$ can be difficult to interpret visually, my analysis used the function $L(t)$, a square-root transformation of the function $K(t)$ (Diggle 1983; Ripley 1977; Humphries, Bourgeron, and Mujica-Crapanzano 2008):

$$L(t) = [K(t) / \pi]^{1/2} - t \tag{1}$$

where t represents the distance between trees based on Euclidian measurements.

Computations were performed using Duncan's (1990) spatial analysis program. A toroidal edge correction was used and model simulations were based on a distance step of 1 m and calculated up to 12 m, with the exception of north-facing slopes in the FR, where more compact ecotones limited my analysis to 5 m. These dimensions adhere to the general practice of using a maximum distance equal to half the length of the shortest rectangular plot side. Sites with less than 10 trees above timberline were excluded from the analysis (CPN). In addition, I limited my analyses to these relatively small radii in order to account for the assumptions of stationarity inherent to spatial statistics, (cf. Camarero, Gutiérrez, and Fortin 2000). Monte Carlo simulations (n = 1000) were used to generate confidence intervals for the results of our Ripley's $K(t)$ analyses. The Monte Carlo simulations compare the observed $L(t)$ value of the function to what could be expected from a randomly distributed group of points and the results can then be used to accept or reject the null hypothesis, which is that tree establishment was spatially random (e.g., Haase 1995). Modeled output values that were greater than the upper 99% confidence envelope were clustered, values within the upper and lower 99% confidence envelope were random, and values below the lower envelope were uniform. These values often vary with scale, yet the overall spatial patterns can be used to detect processes operating at upper treeline.

Results

Age Structure. I crossdated 632 trees in the SRM and collected samples from a relatively even proportion of trees from both south- and north-facing slopes (320 and 312, respectively) (Table 3). Transect locations ranged in elevation from 3,733.8 m on a south-facing slope at 35.8°N in the SDC to 3,407.4 m on a north-facing slope at 40.6°N in the FR (Tables 1 and 2). From a regional perspective, this equates to approximately a 65.3 m decline in treeline elevation per degree of latitude north. Steepness of slope (°) showed no statistically significant differences ($p > 0.05$; t-test) between south- and north-facing slopes and ranged from 10°–26° (Table 3). Similarly, ecotone length (distance from

Table 3. Site conditions for each transect. Elevation (m) refers to the location of the outpost tree and treeline – timberline is the distance in (m) from the outpost tree downslope to timberline. Microtopography denotes the most common characteristic measured for each tree (1 m radius) located above timberline.

Site	Elevation (m)	Slope Aspect (°)	Treeline–Timberline (m)	Slope Angle (°)	Dated Trees (n)	Micro – topography (% of trees)
South–Facing						
DPS	3733.8	184	62.4	26	50	Slope (100%)
GHS	3665.2	190	29.0	15	67	Slope (100%)
TPS	3670.1	160	95.0	19	53	Slope (100%)
PPS	3608.5	170	186.0	10	55	Slope (100%)
EMS	3618.9	226	116.0	22	46	Slope (100%)
CPS	3434.2	194	40.0	17	49	Slope (52.4%)
Mean	*3621.8*	*187.3*	*88.1*	*18.2*	*53.3/320*	
North–Facing						
DPN	3716.1	315	28.0	21	56	Slope (100%)
GHN	3658.2	350	68.5	10	52	Slope (100%)
TPN	3634.7	324	45.0	23	47	Slope (100%)
PPN	3600.3	320	10.0	11	51	Slope (100%)
EMN	3542.1	338	10.0	24	57	Slope (99.9%)
CPN	3407.4	320	5.5	14	49	Shelter (50%)
Mean	*3593.1*	*327.8*	*27.8*	*17.2*	*52/312*	
Study Area						
Mean/Total	3607.5	–	58.0	17.7	52.7/632	

outpost tree – timberline) did not vary significantly between slope aspect even though the average distance on south-facing slopes was three times longer than on contrasting north-facing slopes (Table 3). The majority of trees located ATL (*n* = 253) were growing in areas without the ameliorating influence of local microtopography in 11 of 12 sites (Table 3). The only exception was at my northernmost site (CPN), where 50% of trees ATL established in places with shelter from boulders (Table 3). Seedlings, both alive and dead, were more common on north-facing slopes (Fig. 3).

Tree age and spatial configurations of tree establishment varied at each study site, yet some consistent patterns emerged in both the spatial and temporal dynamics (Figs. 4 and 5). On both north- and south-facing slopes, and in the SDC and FR, the treeline ecotone is characterized by abundant regeneration above timberline, with predominantly younger trees occupying the highest positions on the slope and relatively sharp timberline boundaries (Figs. 4 and 5). Collectively, the widespread establishment of younger trees ATL is supported by the age-structure plots, as 93% of the trees have established since 1950 and 64% since 1970 (Figs. 4 and 5). Conversely, subalpine forests BTL are dominated by older trees, with only 42% establishing since 1950 and 20% since 1970 (Figs. 4 and 5). Quantitative comparisons of tree age using Mann-Whitney *U*-Tests provide further evidence of this discrepancy in establishment, as tree ages are significantly younger ($p < 0.05$) ATL compared to below at 11 of 12 sites (Table 4). Interestingly, the only site (GHS) where trees ATL were not significantly younger than ones below was much younger as a whole than its north-facing counterpart when comparing tree ages below timberline and along the entire transect (Table 4). This indicates the universal presence of young trees at this site and helps explain the lack of a

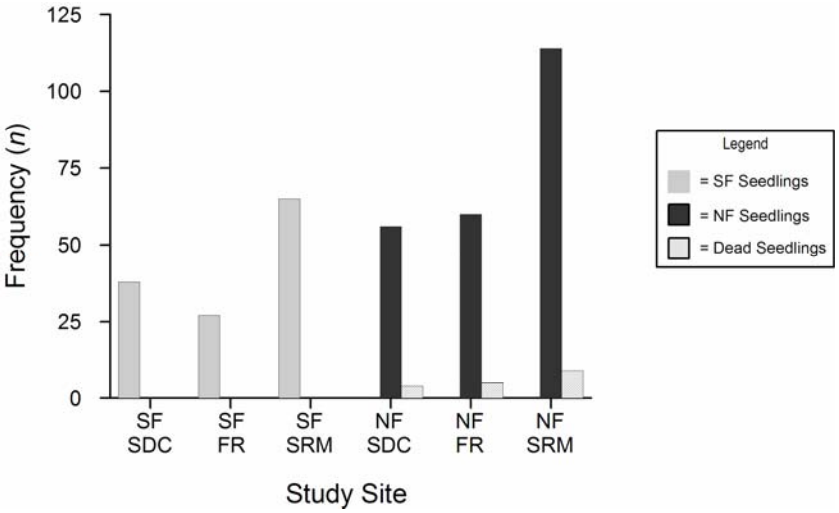


Figure 3. Seedling occurrence stratified by slope aspect and mountain range in the Southern Rocky Mountains.

Figure 4. Spatial and temporal examination of upper treeline study sites in the Sangre de Cristo Mountains (SDC). Transects and age-structure data are shown for adjacent north- and south-facing slopes. The width of the nested-belt transect extended to 40 m above timberline and was reduced to 20 m below. The hybrid age-structure data is divided between decadal (pre-1800–1890) and 5-yr. (1900–2000) age-classes. Note the different y-axis for age-structure of DPN.

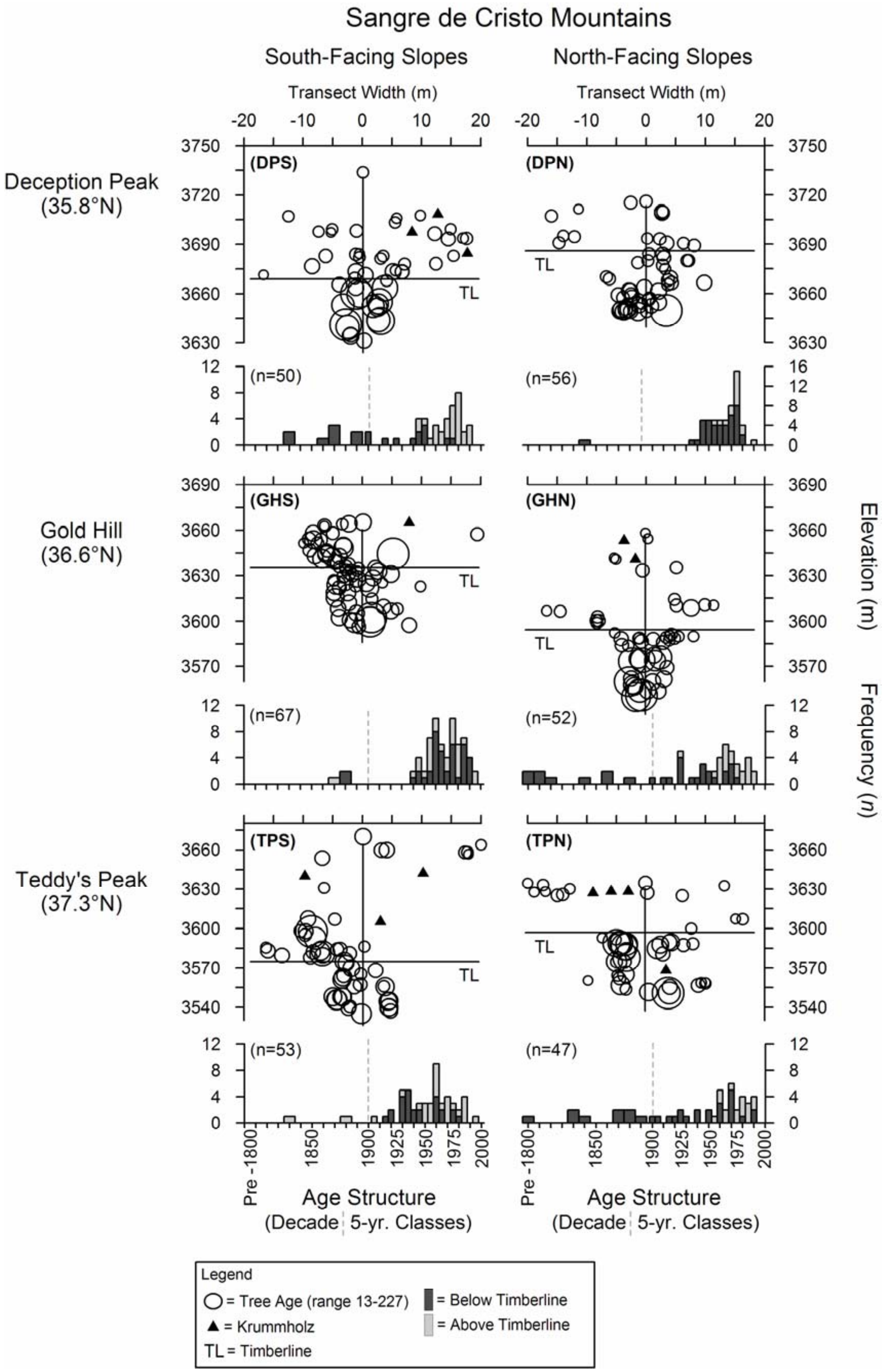
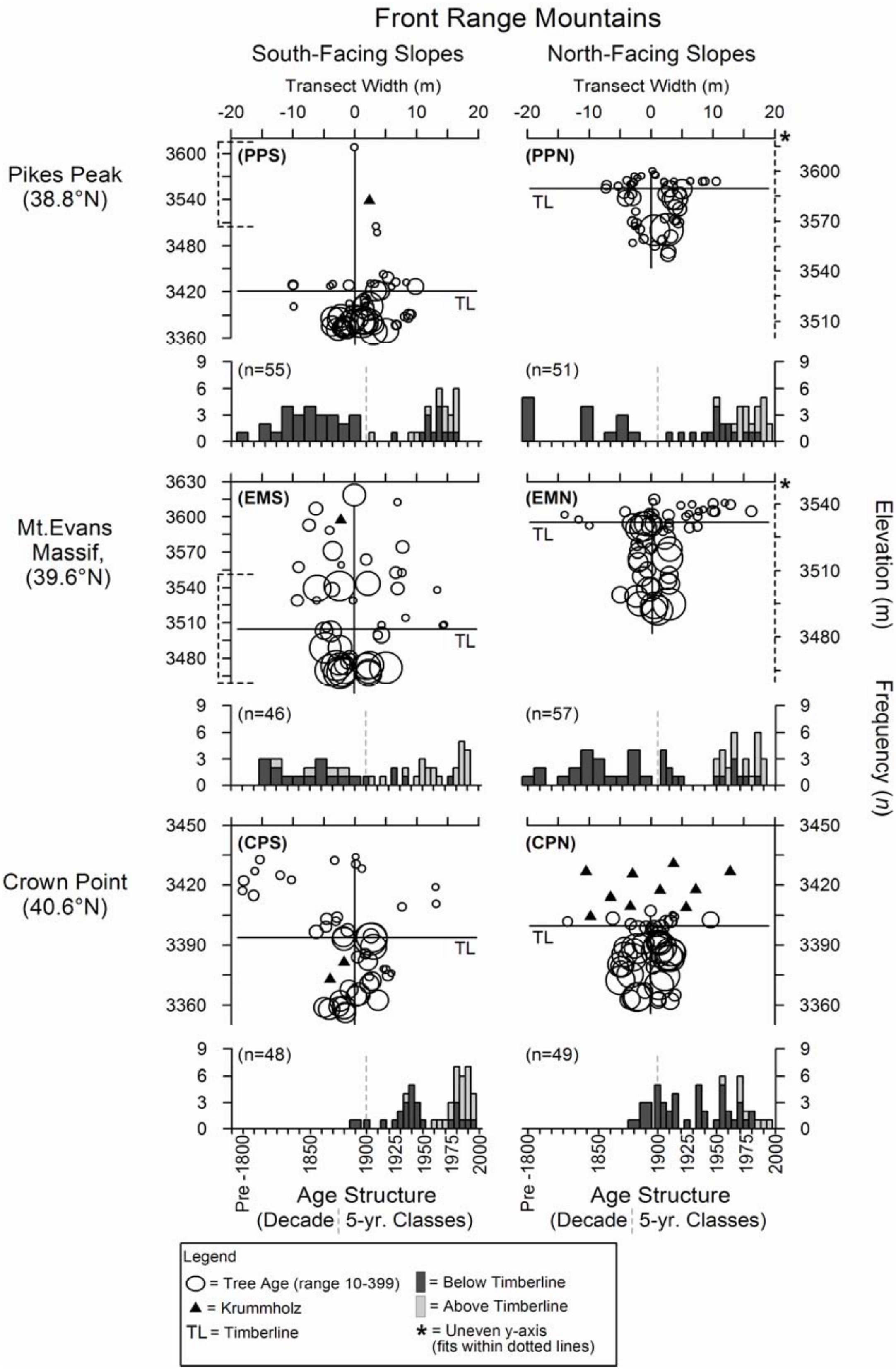

Sangre de Cristo Mountains
South-Facing Slopes
North-Facing Slopes
Transect Width (m)
-20 -10 0 10 20
Deception Peak (35.8°N)
Gold Hill (36.6°N)
Teddy's Peak (37.3°N)
(DPS)
(DPN)
(GHS)
(GHN)
(TPS)
(TPN)
TL
(n=50)
(n=56)
(n=67)
(n=52)
(n=53)
(n=47)
3750
3720
3690
3660
3630
3570
3540
3600
16
12
8
4
0
Elevation (m)
Frequency (n)
Pre -1800
1850
1900
1925
1950
1975
2000
Age Structure
(Decade | 5-yr. Classes)
Legend
○ = Tree Age (range 13-227)
▲ = Krummholz
TL = Timberline
= Below Timberline
= Above Timberline

Figure 5. Spatial and temporal examination of upper treeline study sites in the Front Range Mountains (FR). See caption for Fig. 4. Note that two north-facing transect y-axes (*) are plotted with different elevation values and that their position in relation to the corresponding south-facing transect is marked with a dashed line on the left y-axis. For CPN, the pattern of krummholz mats is not based on exact coordinates and is used to illustrate the belt of krummholz that exist upslope from the outpost tree.



Front Range Mountains
South-Facing Slopes
North-Facing Slopes
Transect Width (m)
-20
-10
0
10
20
Pikes Peak
(38.8°N)
(PPS)
(PPN)
TL
3600
3540
3480
3420
3360
3600
3570
3540
3510
(n=55)
(n=51)
9
6
3
0
Mt.Evans
Massif,
(39.6°N)
(EMS)
(EMN)
3630
3600
3570
3540
3510
3480
(n=46)
(n=57)
Elevation (m)
Frequency (n)
Crown Point
(40.6°N)
(CPS)
(CPN)
3450
3420
3390
3360
(n=48)
(n=49)
Pre -1800
1850
1900
1925
1950
1975
2000
Age Structure
(Decade 5-yr. Classes)
Legend
○ = Tree Age (range 10-399)
▲ = Krummholz
TL = Timberline
■ = Below Timberline
▨ = Above Timberline
* = Uneven y-axis
(fits within dotted lines)

statistically significant difference in tree ages above and below timberline (Table 4; Fig. 4).

The influence of slope aspect on tree age is the most apparent at multiple spatial scales when considering trees growing upslope from timberline. Upslope from timberline, north-facing slopes contain significantly younger trees at all three scales of analysis (Table 4). At the local scale, north-facing slopes contain younger trees at 2 of 12 sites, with one site in each mountain range (Table 4). The relatively low number of local-scale comparisons with significant differences is likely a consequence of young trees being widespread ATL on both south- and north-facing slopes and a relatively small sample depth for the analysis (Figs. 4 and 5). North-facing slopes are significantly younger than south-facing slopes at the landscape scale in the SDC and throughout the SRM (Table 4). Additionally, it is noteworthy to point out that south-facing slopes are not statistically younger than north-facing slopes at any scale in the SRM (Table 4).

Spatial Analysis. Spatial analysis using Ripley's *K(t)* function for trees growing ATL produced different results based on slope aspect and mountain range. South-facing slopes in the SDC have clustered spatial patterns (Table 5). While minor deviations occur within the distance bins, (such as the random pattern detected at GHS from 1–2 m) when analyzing the overall spatial pattern, clustering is the predominant spatial configuration (Table 5). Random spatial patterns exist at most study sites on north-facing slopes in the SDC (excluding GHN) and at every study site in the FR, with the exception of the south-facing site on Pikes Peak (Table 5). For instance, variations in spatial pattern at GHN (random at smallest and largest distances) could have arisen from differences in species

Table 4. Results of Mann-Whitney *U*-Tests comparing tree age distributions. Median tree age was tested using 95% confidence intervals. The bold *p*-values highlight comparisons where the null hypothesis was rejected (ie. statistically different). The bold abbreviation in parentheses indicates the site, mountain range, or slope aspect within the Southern Rocky Mountain region that contains the statistically younger trees between the two values being compared. ATL–BTL values represent intra-site comparisons between tree ages above and below timberline, with other columns representing a comparison of tree age between contrasting south- and north-facing slopes above timberline, below timberline, and throughout the entire transect. Local scale site abbreviations can be found in Table 1 and the other abbreviations include: SF = south-facing slope; NF = north-facing slope.

Site/Comparison	ATL–BTL (*p*)	Above Timberline (*p*)	Below Timberline (*p*)	Entire Transect (*p*)
Local Scale				
DPS	**0.000**			
DPN	**0.002**	0.754	**0.000 (DPN)**	0.498
GHS	0.798			
GHN	**0.000**	0.251	**0.000 (GHS)**	**0.004 (GHS)**
TPS	**0.012**			
TPN	**0.000**	**0.007 (TPN)**	0.207	0.841
PPS	**0.000**			
PPN	**0.000**	**0.012 (PPN)**	0.636	**0.053 (PPN)**
EMS	**0.000**			
EMN	**0.000**	0.177	0.212	0.863
CPS	**0.000**			
CPN	**0.000**	0.260	**0.031 (CPS)**	**0.000 (CPS)**
Landscape Scale				
SDC SF –		**0.029 (NF)**	0.172	0.335
SDC NF		0.240	0.509	0.606
FR SF – FR NF		**0.046 (FR)**	**0.000 (SDC)**	**0.000 (SDC)**
SDC – FR				
Regional Scale				
SRM SF –		**0.016 (NF)**	0.399	0.159
SRM NF				

Table 5. Ripley’s *K(t)* analysis of tree patterns above timberline in the Sangre de Cristo (SDC) and Front Range (FR) Mountains of the Southern Rockies (SRM). The spatial pattern for each distance bin (1–12 m) was determined using a 1–m step and 99% confidence intervals derived from Monte Carlo simulations (*n* = 1000). Spatial pattern is marked as follows: **X** = random; ● = clustered. Area was calculated for the rectangular portion of the transect located above timberline. Site abbreviations can be found in Table 1. Note that relatively small areas above timberline limited the radius of our spatial analysis on north-facing slopes in the FR and the absence of CPN (*n* < 10).

Mtn. Range	Slope Aspect	Site	*n*	Area (m^2)	L(t) (m)												
					1	2	3	4	5	6	7	8	9	10	11	12	Overall Pattern
Sangre de Cristo	South-Facing	DPS	32	2496	●	●	●	●	●	●	●	●	●	●	●	●	Clustered
		GHS	28	1160	**X**	**X**	●	●	●	●	●	●	●	●	●	●	Clustered
		TPS	31	3800	●	●	●	●	●	●	●	●	●	●	●	●	Clustered
	North-Facing	DPN	15	1120	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	Random
		GHN	24	2740	**X**	●	●	●	●	●	●	●	●	**X**	**X**	**X**	Clustered
		TPN	19	1800	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	Random
Front Range	South-Facing	PPS	17	7440	●	●	●	●	●	●	●	●	●	●	●	●	Clustered
		EMS	28	4640	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	**X**	Random
		CPS	22	1600	**X**	**X**	**X**	**X**	**X**	●	**X**	**X**	**X**	**X**	**X**	**X**	Random
	North-Facing	PPN	20	210	**X**	**X**	**X**	**X**	**X**								Random
		EMN	21	400	**X**	**X**	**X**	**X**	**X**								Random

composition or tree size classes present. However, for a general comparison between mountain ranges, the SDC show a stronger aspect-mediated relationship with the spatial pattern of trees ATL, while the patterns in tree establishment ATL in the FR are almost exclusively random in space (Table 5). The aspect mediation of spatial pattern suggests that the importance of feedback processes in driving ecotonal dynamics at upper treeline vary according to slope aspect and within the SRM region

Discussion

Patterns of Tree Establishment. Widespread tree establishment ATL, on both south- and north-facing slopes, is evident throughout the SRM region (Figs. 4 and 5). In addition, the trees sampled on north-facing slopes are significantly younger than trees on south-facing slopes at multiple spatial scales (Table 4). This contrasts sharply with the findings of previous research on upper treeline dynamics where successful tree regeneration ATL was primarily confined to south-facing slopes, with treeline ecotone structure remaining relatively stable on north-facing slopes for the past several hundred years in the Canadian Rockies (Danby and Hik 2007; Luckman and Kavanagh 2000) and Scandes Mountains of Sweden (Kullman 1998). Danby and Hik (2007) specified that tree advance appeared to be limited by the presence of permafrost on north-facing slopes, but the other studies make no mention of the role of frozen soil horizons. The SRM are devoid of permafrost and this region-wide pattern of successful establishment ATL may suggest the importance of climate in determining ecotone structure (e.g., Baker and Weisberg 1995; Lloyd and Fastie 2003).

Soil moisture conditions created by differences in slope aspect have been shown to play an important role in regeneration success at upper treeline (e.g., Daniels and Veblen 2004; Hessl and Baker 1997). As a result, ecotones on mesic north-facing slopes may be more responsive to climate change since better conditions exist for seedling growth (Weisberg and Baker 1995b). Indeed, water stress is common at upper treeline due to greater sun exposure coupled with the existence of relatively thin soils that have low moisture-holding capacities (e.g., Kupfer and Cairns 1996; Sveinbjörnsson 2000). In the SRM, these drought conditions are most likely to exist on south-facing slopes and this slope aspect mediation of moisture regimes could explain the greater number of seedlings on north-facing slopes (Fig. 3).

The nearly ubiquitous presence of trees and saplings ATL has created an environment that despite the variations in ecotone length, indicates a possible upslope advance of treeline, with significantly younger tree populations existing ATL at 92% of my sites (*n* = 11; Table 4). Moreover, tree establishment has been relatively synchronous throughout my study area, with 91% and 64% of all trees ATL establishing since 1950 and 1970, respectively (Figs. 4 and 5). This is noteworthy given that my data set does not include seedling age-structure data, which in the case of north-facing sites, would have contributed to substantial increases in recent establishment dates (post–1970). Similar patterns of treeline advance consisting of progressively younger trees ATL without any evidence of mortality events have been observed throughout Alaska, yet these studies reported considerable variance (> 100 yrs.) in the timing of widespread tree regeneration ATL between mountain ranges (e.g., Lloyd 2005; Lloyd and Fastie 2003). In my case, relatively rapid non-linear shifts in regeneration patterns during the latter half of the 20th century suggest that positive feedback interactions may be important (e.g., Batllori and Gutiérrez 2008; Malanson 2001). Positive feedback becomes influential at upper treeline through increased tree establishment ATL, which creates environmental conditions capable of maintaining the facilitative conditions necessary for eventual treeline advance (e.g., Smith et al. 2003). However, the ability of positive feedback processes to cause sudden changes in recruitment can be contingent on the spatial patterns present (Malanson 1997).

The availability of suitable microsites for tree establishment may be limited in areas without the ameliorating influence of krummholz mats (e.g., Bekker 2005; Szeicz and MacDonald 1995; Weisberg and Baker 1995a). Yet, when considering the spatial patterns present throughout this study, the successful establishment and growth of seedlings into saplings and trees has occurred mainly without the assistance of nearby krummholz mats (Figs. 4 and 5). Although isolated krummholz exist at a majority of my sites, the spatial pattern of saplings and trees ATL is not clustered around them, thus suggesting a possible treeline advance independent of their existence (Figs. 4 and 5).

Treeline advance may rely on the availability of sheltered sites created by variations in local microtopography or from the presence of inanimate objects, such as rocks or boulders (e.g., Resler 2006; Resler, Butler, and Malanson 2005). Previous research in the FR found that the upslope migration of treeline is dependent on the availability of sheltered sites, with few trees growing in open conditions (Daly and Shankman 1985; Ives and Hansen-Bristow 1983). Despite this, the vast majority of tree establishment ATL at 11 of my 12 study sites occurred on a regular sloped surface without shelter (Table 2). Minimal variation in local microtopography appears to be more suitable for tree establishment since snowpack accumulation effectively shortens the growing season and subjects trees to snow mould in concave locations, while convex surfaces fail to maintain a protective snow layer, generally leading to seedling mortality (Ives and Hansen-Bristow 1983).

Differences in the need for sheltered sites in facilitating treeline advance could result from contrasts in wind regimes at a given location. My data suggest that the influence of wind on regeneration ATL becomes more pronounced in the northern portion of my study area around 40°N (e.g., Crown Point; Tables 1 and 2). The propensity of trees to establish in sheltered sites along with the existence of numerous krummholz mats above treeline at CPN imply that the site is typically exposed to windy conditions (Fig. 5). Throughout the western United States, mean wind characteristics often reflect the channeling influences created by local topographic features (Klink 1999), which can be further modified by the spatial patterns of upper treeline (Holtmeier and Broll, 2005). In some cases, the topographic mediation of local wind regimes can affect the need for positive feedback in promoting and sustaining tree establishment ATL (Alftine and Malanson, 2004), while also potentially superseding the relative importance of projected changes in temperature and precipitation regimes associated with global warming (Woodward 1993). Deviations in the ecological significance of wind at upper treeline within my study area demonstrate how the relative importance of processes and patterns can vary as environmental contexts change (cf. Malanson et al., 2007).

Spatial Pattern and Feedback Processes Above Timberline. Vegetation pattern at upper treeline is often strongly influenced by the interactions of climate and slope aspect (e.g., Brown 1994; Danby and Hik 2007). This is illustrated by the spatial pattern of tree establishment on south-facing slopes in the SDC and on Pikes Peak, where clustering suggests that feedbacks may play a critical role in the biological amelioration of harsh growing conditions (Table 5). In the Southern and Central Rocky Mountains, tree establishment was limited on south-facing slopes as a result of relatively high levels of sunlight that led to increases in water stress and diurnal temperature range (Germino and Smith 1999; Germino, Smith, and Resor 2002; Weisberg and Baker 1995a). In my case, tree establishment was not limited on south-facing slopes; rather the pattern of establishment appears to be more dependent on plant interactions, probably as a result of increased climate stress. This is consistent with other research at or near upper treeline in the Italian central Alps (Emanuele et al., 2008), Spanish Central Pyrenees (Camarero et al., 2000), and northern Rocky Mountains (Callaway 1998; Callaway et al. 2002), where spatial clustering or facilitation among plants increased with abiotic extremes.

Relative increases in exposure to solar radiation and subsequent water stress on south-facing slopes in the SDC and on Pikes Peak provides a logical rationale for spatial clustering ATL. The SDC experience the warmest growing season temperatures within our study area (refer to *STUDY AREA*) and the influence of this is most likely amplified on south-facing slopes. Consequently, soil moisture becomes limiting earlier in the growing season compared to contrasting north-facing slopes. Low moisture availability appears to be the primary reason for clustering on Pikes Peak. Given that it is situated slightly east of the main axis of the Southern Rockies (Fig. 1), it experiences a drier climate that more closely resembles the adjacent High Plains (Diaz, Barry, and Kiladis

1982; Peet 1978). In an attempt to compensate for warm and dry conditions, tree establishment appears to be dependent on positive feedback interactions.

Clustered tree patterns that result from positive feedback interactions ATL on south-facing slopes have the ability to ameliorate harsh environmental conditions that would otherwise preclude tree establishment by providing shade to reduce diurnal temperature range, shelter from wind dessication, and/or to help trap snowpack in order to prolong the availability of soil moisture during the growing season (e.g., Bekker 2005; Germino, Smith, and Resor 2002; Smith et al. 2003). Furthermore, Maher and Germino (2006) found competition that arises from clustered spatial patterns to be almost negligible and seedling mortality more likely to result from extreme microclimate conditions without protective cover than from competitive exclusion by neighboring vegetation. Clustered arrangements imply that positive feedback is more important in facilitating upslope establishment and treeline advance. However, my data suggest that both regeneration and potential treeline advancement rates are reduced on south-facing slopes due to the increased reliance on biotic interactions with neighboring vegetation (Table 4). Evidence for this exists at all spatial scales, but becomes most apparent at landscape and regional scales where sites exhibiting clustered spatial patterns ATL are comprised of significantly older trees (Tables 4 and 5). In a similar manner, Bader et al. (2008) concluded that the overriding importance of biotic relationships associated with positive feedback may slow tree establishment ATL in the tropics because it acts to partially uncouple treeline from external climatic influences. Thus, the aspect-mediated spatial clustering within my study area reflects a survival strategy for trees growing in relatively harsh environments (ie. warmer and drier) and perhaps most notably, suggests that the importance of feedback processes can vary by the differences in local climate produced by contrasts in slope aspect.

In contrast to clustered spatial patterns, the random configuration of tree establishment ATL on most of the north-facing slopes in the SDC and throughout the FR (excluding PPS) implies that feedback processes may not be as important in influencing the dynamics of upper treeline (Table 5). Evidence for this exists in my age-structure data, where all of the significantly younger sites are located on north-facing slopes and characterized by a random spatial pattern (including FR at landscape scale; Tables 4 and 5). From an ecological perspective, the existence of random spatial patterns implies that local ameliorating conditions are not needed in order for successful establishment upslope from timberline and eventual treeline advance (not including CPN). When feedbacks are of minimal importance, upper treeline is more likely to remain closely coupled with external climate and as a result, probably respond more directly to changes in the system (Bader, Rietkerk, and Bregt 2008). In addition, the very existence of randomly distributed trees and saplings above timberline is compelling, as it could indicate a recent cessation of harsh climate events, thus negating the need for spatial clustering in order to survive. Therefore, from a regional perspective, my sites on north-facing slopes and in the FR likely provide a more clear representation of the affects of climate variability on ecotonal dynamics at upper treeline because the effects of biotic interaction are reduced.

A more thorough understanding of positive feedbacks is needed in order to identify the potential impacts of climate change on upper treeline ecotones (Alftine and Malanson 2004). This is further complicated by the reported ephemeral nature of feedback–pattern interactions, which have been shown to vary in importance over time and space (Bekker 2005; Malanson 1997). Yet, my research has identified some important relationships between feedback, pattern, and slope aspect that have primarily resulted from contemporary interactions (ie. since 1950) and subsequently, have the ability to strongly mediate the influences of climate change. The slope aspect mediation of spatial patterns and corresponding tree ages suggest that continued warming associated with climate change will most likely produce a non-linear response accompanied by varying degrees of change in ecotonal dynamics at upper treeline (e.g., Danby and Hik 2007; Kupfer and Cairns 1996). More specifically, regeneration on south-facing slopes with clustered patterns of tree establishment will likely continue to decrease if warmer temperatures are not accompanied by an increase in precipitation that improves soil moisture availability. On north-facing slopes with random spatial patterns, it is conceivable that warmer temperatures associated with climate change could eventually begin to limit soil moisture, similar to what I have inferred on south-facing slopes, if a bioclimatic threshold is surpassed without a concurrent increase in precipitation, thus forcing tree establishment into a clustered, biological-ameliorating pattern dependent on feedback interactions. Otherwise, if favorable soil moisture conditions persist, north-facing slopes will likely remain a better barometer for measuring the influence of climate on upper treeline. This research from the SRM has global implications for understanding ecotonal dynamics at upper treeline and ultimately suggests that the mediating role of slope aspect and spatial patterns of tree establishment should be considered when assessing the possible response of upper treeline to climate change.

Conclusions

When considering the general spatiotemporal patterns of tree establishment at a regional scale, the influence of slope aspect is not readily apparent. Successful regeneration is underway on both south- and north-facing slopes and appears to represent more than a series of random establishment events, which can be common ATL (e.g., Lloyd 2005; MacDonald et al. 1998). Region-wide similarities in tree establishment patterns suggest that broad-scale temperature trends can influence upper treeline at a regional scale (e.g., Lloyd and Fastie, 2003). However, the influence of topography becomes more pronounced when examining how small scale processes combine to create detectable patterns at a regional scale (e.g., Alftine and Malanson, 2004). For instance, my data suggest that seedling establishment is strongly influenced by slope aspect (Fig. 3) and this has potential ramifications for future ecotonal dynamics on south-facing slopes, particularly within the context of climate change. A bioclimatic threshold may have been crossed, creating conditions that are typically too warm and dry for successful seedling recruitment. In this case, continued tree establishment on south-facing slopes is most likely contingent on feedback processes associated with a spatial pattern that ameliorates the abiotic conditions of upper treeline ecotones.

The spatial arrangement of tree establishment at upper treeline shows slope aspect-mediated patterns at landscape and regional scales, suggesting a varying importance of feedback processes that, in turn, affect tree ages at multiple spatial scales. In general, significantly younger trees ATL were found on north-facing slopes in the SRM, in the SDC, and within the entire FR compared to the SDC. The lack of statistically different tree ages ATL in the FR can be attributed to the prevalence of random spatial patterns on both south- and north-facing slopes, which seems to indicate areas less reliant on feedback processes, and that could potentially be more sensitive to climate variability. Thus, the influence of climate change on upper treeline ecotonal dynamics in the SRM will likely be mediated by slope aspect, as it has the ability to dramatically alter feedback interactions that can either accelerate or retard rates of tree establishment based on existing spatial patterns.

This study suggests that at a regional scale, climate exerts the primary control on upper treeline dynamics, yet similarities and differences arise from the constraints produced by local-scale processes (cf. Malanson et al., 2007). However, the local-scale differences in spatial pattern were likely initiated in response to slope aspect-mediated climatic inputs, such as the apparent need for spatial clustering on warm and dry south-facing slopes prone to moisture stress. Although different spatial patterns emerged in my study, this suggests that in the SRM, the spatial and temporal alignment of temperature trends and precipitation regimes may play a strong role in governing upper treeline ecotonal dynamics. This interpretation does not conflict with those of other researchers who discussed the subservient role of climate in relation to local geological constraints (e.g., Butler et al. 2007) or the interactions between feedback processes and sheltered sites that may be necessary for treeline advance (e.g., Alftine and Malanson 2004; Bekker 2005; Resler 2006). In fact, these conditions become more prevalent towards 40°N in my study area, which may indicate the presence of a transition zone where pattern and process at upper treeline become primarily controlled by wind and the availability of sheltered sites, compared to my sites, where the interactions of temperature and precipitation are more clearly manifested in the ecotonal dynamics at multiple spatial scales. Climatologists have identified the area around 40°N as a pivot point between different climate regimes (e.g., Mitchell, 1976; Dettinger et al., 1998). When considering upper treeline dynamics, this may represent a type of spatial threshold whereby temperature and precipitation are the primary controlling variables south of this parallel, versus to the north, where site-specific geological and geomorphological characteristics may exert the most influence on ecotonal dynamics. Ultimately, this research highlights the importance of conducting biogeographic research at multiple spatial scales and across environmental gradients in order to ascertain the similarities and differences in key patterns and processes at upper treeline.

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Chapter 3. Evidence of Intra–Regional Variability and Bioclimatic Thresholds at Upper Treeline in Response to 20th Century Climate in the Southern Rocky Mountains, USA

Mountain ecosystems contain forests particularly vulnerable to the influences of a rapidly changing climate (e.g., Beniston 2003; Fagre, Peterson, and Hessl 2003; Marston 2008). Currently, climate scientists are confident that the global mean surface temperatures of the late 20th century exceed those of any time during the past 500 years (IPCC 2007), and potentially extend outside the range of natural variability of the Northern Hemisphere in at least the past two millennia (Jones and Mann 2004; Mann et al. 2008). It seems likely that this unprecedented warming will usher in dramatic changes in vegetation community dynamics, yet considerable uncertainty exists regarding the potential extent of vegetation change at both regional and landscape scales in topographically complex mountain environments (Bartlein, Whitlock, and Shafer 1997).

Upper treeline can serve as a sensitive proxy for revealing the impact of climate variability on the distribution of high-elevation mountain forests (e.g., Camarero and Gutiérrez 2004; Lloyd 2005; Kullman 1998; LaMarche and Mooney 1967). It contains climatically-sensitive tree populations growing at their physiological range limit (e.g., Brubaker 1986; Rochefort et al. 1994; Fritts 1976; Tranquillini 1979) and given substrate conditions suitable for tree establishment, the location of upper treeline appears to be primarily controlled by local thermal regimes (e.g., Körner and Paulsen 2004; Rossi et al. 2007). This is consistent with paleoecological research, which suggests that treeline ecotones in the Rocky Mountains are responsive to climate change (e.g., Fall 1997; Jiménez-Moreno, Fawcett, and Anderson 2008; Stohlgren and Bachand 1997). As a result, generally warmer temperatures that prolong the growing season are expected to have pronounced effects on upper treeline ecotonal dynamics, including changes in the position and structure of treeline communities (e.g., Grace, Berninger, and Nagy 2002; Kullman 2001).

The upslope advancement of tree establishment into alpine tundra represents the best indicator of upper treeline sensitivity to climate (Holtmeier and Broll 2005) and has often been positively correlated with temperature variables (e.g., Camarero and Gutiérrez 2004; Danby and Hik 2007; Lloyd and Fastie 2003; Szeicz and MacDonald 1995; Taylor 1995). Yet, at a regional scale, differences in the relationship between climate and tree establishment commonly arise from the varying importance of finer scale environmental factors (e.g., Baker and Weisberg 1995; Luckman and Kavanagh 1998; Malanson et al. 2007). Examples of potentially confounding local variables that can facilitate, modulate, or possibly override the response of upper treeline to temperature variability include slope aspect and corresponding soil moisture conditions (see Chapter 2; Daniels and Veblen 2004; Hessl and Baker 1997; Lloyd and Fastie 2002; Lloyd and Graumlich 1997; Weisberg and Baker 1995), spatial pattern of tree establishment (see Chapter 2; Camarero, Gutiérrez, and Fortin 2000), properties of soil and geologic substrate (e.g., Allen and Walsh 1996; Butler et al. 2007; Kupfer and Cairns 1996), herbivory (e.g., Cairns et al. 2007), and land-use history (e.g., Batllori and Gutiérrez 2008; Gehrig-Fasel, Guisan, and Zimmermann 2007; Hofgaard 1997). Furthermore, the potential interactions between these variables and temperature can often be contingent on the initiation of positive feedbacks due to biotic factors (e.g., Alftine and Malanson 2004; Bekker 2005). The complexity of treeline-climate interactions thus make it unlikely that future climate change will produce straightforward, linear responses in treeline ecotonal dynamics (e.g., Lloyd 2005; Malanson 2001; Millar et al. 2004).

Nonlinear changes in climate can lead to the crossing of critical bioclimatic thresholds that cause abrupt ecological regime shifts to occur (Anderson et al. 2009; Groffman et al. 2006). These are often initiated by extreme temperature and precipitation events, which are expected to become more frequent with continued climate change (e.g., Easterling et al. 2000). A regime shift occurs at the point in time when a rapid reorganization occurs from one relatively stable state to another (Rodionov and Overland 2005), which can lead to a switch in the primary processes responsible for creating landscape pattern (Contamin and Ellison 2009). Yet, despite the importance of identifying whether threshold-induced regime shifts have occurred at upper treeline since the onset of anomalous warmth during latter half of the 20th century, explicit testing for these abrupt system changes is lacking.

The Southern Rocky Mountains are situated within a relatively homogenous climate region south of ca. 40°N (Dettinger et al. 1998; Mitchell 1976), although for any given climate region, the extent to which climatic inputs control specific biogeographical processes and patterns remain poorly understood (Hessburg, Kuhlmann, and Swetnam 2005). Following these assumptions, I used dendroecological techniques to create a detailed reconstruction of population dynamics at upper treeline in the Southern Rockies to determine the influence of climate variability on tree establishment during the 20th century at landscape (mountain range) and regional (between mountain ranges) scales. Previous studies have examined upper treeline environments in the Southern Rockies, but prior research has primarily focused on relatively small areas in the Colorado Front

Range (e.g., Baker and Weisberg 1995; Daly and Shankman 1985; Hessl and Baker 1997; Humphries, Bourgeron, and Mujica-Crapanzano 2008; Ives and Hansen-Bristow 1983; Wardle 1968; Weisberg and Baker 1995). More importantly, with a few exceptions worldwide (Dalen and Hofgaard 2005; Daniels and Veblen 2004; Lloyd 2005; Kullman and Öberg 2009), little attention has been given to examining the influence of climate change on upper treeline at a regional scale. As a result, I addressed the following research questions concerning 20th century treeline dynamics in the U.S. Southern Rocky Mountains: 1) what is the current state of upper treeline dynamics? 2) how do temperature and precipitation affect tree establishment? 3) are upper treeline dynamics influenced by regime shifts and/or bioclimatic thresholds? 4) what role does scale play in assessing treeline-climate interactions?

Study Area

The study area stretches along ca. 600 km of the generally north-south trending Southern Rocky Mountains of Colorado and northern New Mexico (Fig. 1). The Southern Rockies are situated on the leeward side of the Continental Divide where they rise abruptly along their east slope, with mountain peaks attaining heights of ca. 3800–4200 m. Towards their crest, treeline elevation varies from ca. 3800 m. in the Sangre de Cristos to ca. 3500 m. in the Front Range (Peet 1978). My study sites are located along a five-degree range of latitude from 35°N in the Sangre de Cristo Mountains (ca. 35°–37°N) to 40°N in the Front Range (ca. 38°–40°N; Table 1).

The geology of the Southern Rockies exhibits considerable spatial variation, but the substrate in high-elevation areas is predominantly composed of Precambrian granitic

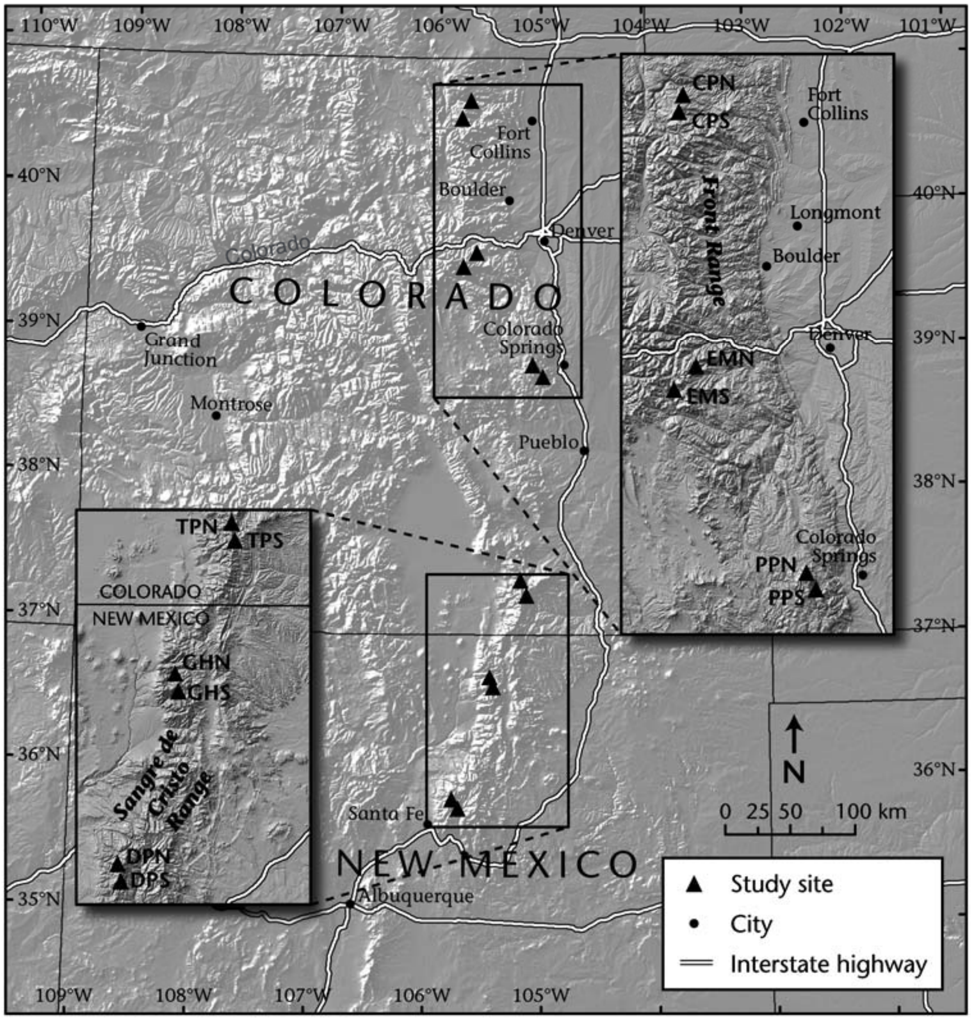

Figure 1. Study area map showing my study sites in the Southern Rocky Mountains. Study site abbreviations are given in Table 1.

Table 1. Upper treeline study sites and locations in the Southern Rocky Mountains. Elevation refers to the mean elevation of both sites on each mountain peak.

Site	Abbreviations[a] (S:N)	Lat./Lon. (°N/°W)	Elevation (m)
Sangre de Cristo Mountains			
Deception Peak	DPS:DPN	35.8/105.8	3725
Gold Hill	GHS:GHN	36.6/105.6	3662
Teddy's Peak	TPS:TPN	37.3/105.2	3653
Front Range Mountains			
Pikes Peak	PPS:PPN	38.8/105.1	3605
Mt. Evans Massif	EMS:EMN	39.6/105.7	3581
Crown Point	CPS:CPN	40.6/105.7	3421

[a] Abbreviations are given for sites on both south- and north-facing slopes.

rock with coarse texture and high silica content, along with gneiss and schist that share similar geochemical properties (Allen, Peet, and Baker 1991; Peet 2000). Local topography plays a pivotal role in pedogenic processes (Cairns, Butler, and Malanson 2002), which in my study area eventually creates relatively acidic, infertile soils (Allen, Peet, and Baker 1991).

The only detailed climate study that examines both the Sangre de Cristo and Front Range was published by Baker (1944), but a modern synthesis for these two mountain ranges is lacking. In general, the climate of the Southern Rockies is relatively uniform south of ca. 40°N, with infrequent intrusions of Pacific air masses during the winter and an influx of monsoonal moisture producing most summer precipitation (Mitchell 1976). The continentality and high elevation of my study area leads to a relatively dry climate with a large seasonal temperature range (Pepin 2000).

Vegetation at high-elevation upper treeline sites is primarily composed of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), with some Colorado bristlecone pine (*Pinus aristata* Engelm.) on south-facing slopes south of around 39°N and some lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in the northern Front Range (Peet 2000). Engelmann spruce often forms monospecific stands in the southernmost areas of the Sangre de Cristos, particularly on north-facing slopes, and fir becomes more prevalent in the northern Front Range (Peet 1978).

Evidence of humans occupying areas near timberline dates back thousands of years, although any settlement or land-use patterns were likely ephemeral in such extreme environments (e.g., Veblen and Lorenz 1991; Wolf 1995). In the surrounding valleys, permanent Spanish settlement began during the 1500s in the Sangre de Cristo Mountains (deBuys 1985) and although exact numbers remain unclear, an estimated 3 million sheep were grazed throughout northern New Mexico during the late 1800s (Denevan 1967). In addition, mining opportunities throughout the Southern Rockies enticed Euro-American settlers, which reached a peak in the mid- to late-1800s (ca. 1850s–1870) (deBuys 1985; Veblen and Lorenz 1991). Mining occurred in the immediate vicinity of Gold Hill (Pearson 1986), but evidence of anthropogenic disturbance at upper treeline is lacking. Currently, based on extensive field observations, most anthropogenic influence at upper treeline stems from cattle grazing in northern New Mexico and timber harvesting in the northern Front Range, although neither appears to be widespread.

Methods

Field Sampling. To gain a regional-scale perspective of the possible influences of climate on upper treeline ecotonal dynamics, I systematically located six mountain peaks to place paired nested-belt transects on contrasting south (azimuth 135° to 225°)- and north (azimuth 315° to 45°)-facing slopes in the Sangre de Cristo and Front Range Mountains (*n* = 12 transects). These mountain peaks were separated by approximately one degree of latitude (~ 111 km) and had upper treeline environments where possible treeline advance was not restricted by local topography or geologic substrate conditions such as rock outcrops with no soil, talus slopes, or avalanche tracks. This type of upper treeline ecotone is generally characterized by a relatively straight line of forest abutted by alpine tundra and is commonly referred to as a climatic treeline (Butler et al. 2007; Holtmeier and Broll 2005). My study sites were selected *a priori* through the analysis of aerial photographs, topographic maps, and through discussions with local USDA Forest Service (USFS) personnel in order to ensure the absence of recent disturbance events (e.g., fire or logging). If a potential site was in question, an exploratory reconnaissance trip was used to confirm the existence of suitable conditions.

Individual nested-belt transects began at an outpost tree (term after Paulsen, Weber, and Körner 2000), which was classified as the furthest upright tree (≥ 5 cm diameter at breast height [dbh]) or sapling (< 5 cm dbh, ≥ 1.2 cm diameter at ground level [dgl]) existing within the treeline ecotone. The transect extended downslope from the outpost tree perpendicular to the slope contours and through timberline 40 m into closed-canopy subalpine forest, which was characterized by relatively dense forests with interlocking canopies. Here I define treeline as the uppermost limit of individuals having an upright growth form and timberline as the elevational limit of closed-canopy forest, with the treeline ecotone existing between these two delineations (Malanson et al. 2007). Krummholz were not sampled because their low stature creates a different microclimate than that experienced by upright trees and, therefore, may not reflect suitable conditions for tree establishment within the treeline ecotone (Körner and Paulsen 2004). The width of each nested-belt transect was divided into two parts to ensure a sufficient number of saplings to calculate age corrections and analyze regeneration patterns. Above timberline (ATL), I sampled all saplings within a wide 20 m belt and all trees within a narrower 10 m belt on each side of the transect. Below timberline (BTL), the widths were half as wide (saplings were collected within 10 m and trees were sampled within 5 m) to accommodate for the considerable increase in tree density. Due to variations in tree density and the elevational position of the outpost tree, overall transect length varied at each site, but each was long enough to include at least 50 trees.

Local site conditions (Table 2) were documented at each transect location, including the elevation and GPS coordinates of the outpost tree, slope aspect, and slope steepness (°). In addition, I recorded detailed notes for each tree that was sampled, such as dbh (dgl, if applicable), coring height, and *x* and *y* coordinates to the nearest 0.1 m along the transect (including krummholz).

Age-Structure Data. Age-structure information was collected by extracting two increment cores at 30 cm above the ground from all living trees (≥ 5 cm dbh, ≥ 9 cm dgl) along the transect. Every sapling within the transect was harvested at ground-level and where available, 10–15 were sectioned at 30 cm to determine a correction factor for age-at-coring height. Further, distinctions were made between species and saplings growing ATL in a relatively open environment from those growing in the shade of closed-canopy forest BTL to more accurately determine age-to-coring height corrections for the trees growing in both conditions (cf., Veblen 1992).

All tree cores and sapling cross sections were prepared following standard dendrochronological procedures (Stokes and Smiley 1996). All tree-ring samples were crossdated using both visual evidence from individual series and by comparing skeleton plots to ensure that accurate dates were assigned to the annual rings of each series (Stokes and Smiley 1996). Pith estimators were used to geometrically determine the number of missed rings when the pith was not obtained during field sampling (Applequist 1958).

Table 2. Site conditions for each transect. Site abbreviations can be found in Table 1 and Elevation (m) refers to the location of the outpost tree. Other abbreviations include: ATL – above timberline; BTL – below timberline. Timberline is defined as the elevational extent of closed-canopy forest.

Site Abbrev.	Elevation (m)	Slope Aspect (°)	Slope Angle (°)	Transect Area ATL (m²)	Trees ATL (n)	Trees BTL (n)	Total Trees (n)
DPS	3734	184	26	2496	32	18	50
DPN	3716.1	315	21	1120	15	41	56
GHS	3665	190	15	1160	28	39	67
GHN	3658.2	350	10	2740	24	28	52
TPS	3670	160	19	3800	30	23	53
TPN	3634.7	324	23	1800	19	28	47
PPS	3609	170	10	7440	17	38	55
PPN	3600.3	320	11	200	20	31	51
EMS	3619	226	22	4640	28	18	46
EMN	3542.1	338	24	210	21	36	57
CPS	3434	194	17	1600	22	27	49
CPN	3407.4	320	14	220	8	41	49

Any samples that could not be confidently crossdated (e.g., rotten and/or no ring curvature present to estimate distance to pith) were excluded from my analyses.

Tree establishment dates were combined into 5-year age classes for the period 1900–2000. Age to coring-height corrections were used by taking the mean age at 30 cm of harvested saplings and adding it to the age determined from crossdating individual tree cores collected from the same height above the ground. More specific details on coring-height corrections can be found in Chapter 2. In addition, while there are known limitations to producing a static age-structure distribution, particularly with regards to understanding past mortality rates (e.g., Johnson, Miyanishi, and Kleb 1994; Veblen 1992), it offers the most viable approach for this study. Furthermore, any evidence of mortality within the general vicinity of my sites was dutifully recorded in order to minimize these limitations.

Climate Data. Due to the paucity of climate stations at higher elevations in the Rocky Mountains (Barry 1992), I obtained PRISM (Precipitation-elevation Regressions on Independent Slopes Model) climate data for each study site (PRISM Group, Oregon State University, http://www.prismclimate.org, created 10 Oct 2008). PRISM data recognizes the dominant influence of elevation and topography in mountain climates and has been shown to accurately capture precipitation and temperature values in remote mountainous regions where limited data are available (Daly, Neilson, and Phillips 1994; Daly et al. 2001).

To the best of my knowledge, PRISM data has not been previously used in other research on upper treeline vegetation dynamics, but is instead more commonly used by climatologists in studies examining climatic trends in the mountainous regions of western North America (e.g., Hamlet et al. 2005; Mote et al. 2005). Overall, PRISM data is perhaps more appropriate for upper treeline research because of the large discrepancies between general climatic conditions at high-elevation sites and surrounding valleys and basins where most climate stations are located. These elevational differences are amplified during convective summer storms, where the amounts of precipitation received can vary by up to an order of magnitude between the foothills and higher elevations (Barry 1992). Moreover, a single weather station in a complex mountain environment cannot be relied upon to be representative of the entire region (Villalba, Veblen, and Ogden 1994).

I obtained PRISM point data for each study site on the six mountain peaks used in this study. In the event that one site was drawing from a different PRISM grid (2.5 minute resolution) than the site with an opposite slope aspect, the transect site located in the PRISM grid with the highest elevation was used to more accurately capture the actual conditions at upper treeline. Data from sites within each mountain range were averaged together to create landscape scale climatological summaries and a regional summary for the Southern Rockies was produced by combining the climate summaries from the Sangre de Cristos and Front Range.

Precipitation, maximum temperature (Tmax), minimum temperature (Tmin), and temperature range data (Trange = Tmax–Tmin) were used to calculate the following annual and seasonal mean values: 1) annual; 2) spring (March–May); 3) summer (June–August); 4) fall (September–November); 5) cool season (November–April). Tmax, Tmin, and Trange data were all used because unlike mean climate conditions (e.g., mean summer temperature), they represent the most likely variables to indicate whether a critical bioclimatic threshold has been crossed. Cool season data were used in lieu of winter data to more accurately capture the entire snowfall period within my study region. To further test for the influence of precipitation on tree establishment, I included arid foresummer (April–June) precipitation. The arid foresummer is a regionally-important period of drought-like conditions throughout the American Southwest that affects the Sangre de Cristo Mountains and typically precedes the onset of monsoon rains in July (Swetnam and Betancourt 1998). All climate variables were averaged into five-year bins (1900–2000) to match the minimum resolution of my age-structure data.

Analyses. Differences in several decadal parameters of upper treeline dynamics during the 20th century were quantitatively assessed with Mann–Whitney *U*-Tests. These were used to see if changes in the dynamics of tree establishment mirror what would be expected under continually warmer conditions during the latter half of the 20th century, such as an upslope advance of treeline coupled with an increase in tree establishment. In addition, these tests were performed to identify any sudden changes indicative of a possible threshold response in treeline dynamics, which could be manifested through exponential increases in specific structural parameters (e.g., tree density). A nonparametric test was used in each case because of the relatively low number of sites for each run ($n = 6$ for landscape scale, $n = 12$ for regional scale) (Lloyd and Fastie 2003). Mann–Whitney *U*-Tests were used to test for differences between the following attributes of upper treeline dynamics at both landscape and regional scales: (1) distance of outpost tree advancement upslope; (2) decade when the outpost tree established at its current elevation; (3) tree density above and below timberline; and (4) changes in tree density from 1900–1950 versus 1950–2000. Tree density data (trees ha^{-1}) were normalized using a natural-log transformation and averaged together (Campbell and Antos 2000) to create a representative value for each slope aspect sampled in both mountain ranges.

To test for the influence of climate on tree establishment during the 20th century, age-structure data (1900–1995) were compared with identical five-year bins of mean climate data using Spearman's rank correlation coefficient (r_s). Correlation analysis was performed on all trees within each transect and also stratified by slope aspect at a landscape and regional scale to assess the potentially contrasting influences of climate caused by variations in local temperature and moisture regimes.

Statistical similarities and correlations provide a suitable place to begin when investigating relationships in natural systems, but multiple lines of complimentary evidence improve the ability to independently assess linkages (Levin 1992). As a result, I used climate- and ecologically-based regime shift analysis to identify the possible synchrony between nonlinear threshold changes that can lead to regime shifts in both climate and tree establishment at upper treeline during the 20th century.

Several quantitative methods exist for identifying thresholds and regime shifts (see Anderson et al. 2009). I used a sequential algorithm method developed by Rodionov (2004) that is an exploratory or data-driven analysis where an *a priori* hypothesis on the timing of regime shifts is not needed (available for download at www.BeringClimate.noaa.gov). This separates it from classical intervention analysis, which cannot be used when the pivot point in a time series occurs at an *a priori* unknown time (Anderson et al. 2009). For my analysis, I used a 0.05 significance level to test for shifts in the mean value of the time series and a cut-off length of 10 years. The cut-off length and significance level affect the magnitude of regime shifts that can be detected, with a direct relationship occurring between cut-off length and the time scale of regimes detected (Rodionov and Overland 2005). A 10-year cut-off was used since numerous studies have shown evidence for considerable decadal variability in climate throughout the western United States (McCabe, Palekci, and Betancourt 2004). More complete details for this method of analysis can be found in Rodionov (2004) and an applied example of its use can be found in and Rodionov and Overland (2005).

Results

Treeline Dynamics. Trees that established from 1900–2000 constitute 82% of the trees sampled in the Southern Rockies (*n* = 517/632). These data suggest that the dynamics of upper treeline environments in the Southern Rocky Mountain region have changed considerably during the 20th century. Widespread tree establishment has occurred ATL on both south- and north-facing slopes in the Sangre de Cristo and Front Range Mountains (Figs. 2 and 3). In addition, a majority of these trees ATL are relatively young, with 93% (*n* = 229/246) having established since 1950, compared to only 42% of trees BTL (Figs. 2 and 3). Although past mortality rates remain unknown, there were virtually no trees ATL until the 1950s (Figs. 2 and 3). Additionally, evidence of previous tree mortality was lacking at every site. This suggests that my age-structure data is representative of tree demography during the 20th century, which is accentuated by an abrupt increase in tree establishment initiated around 1950.

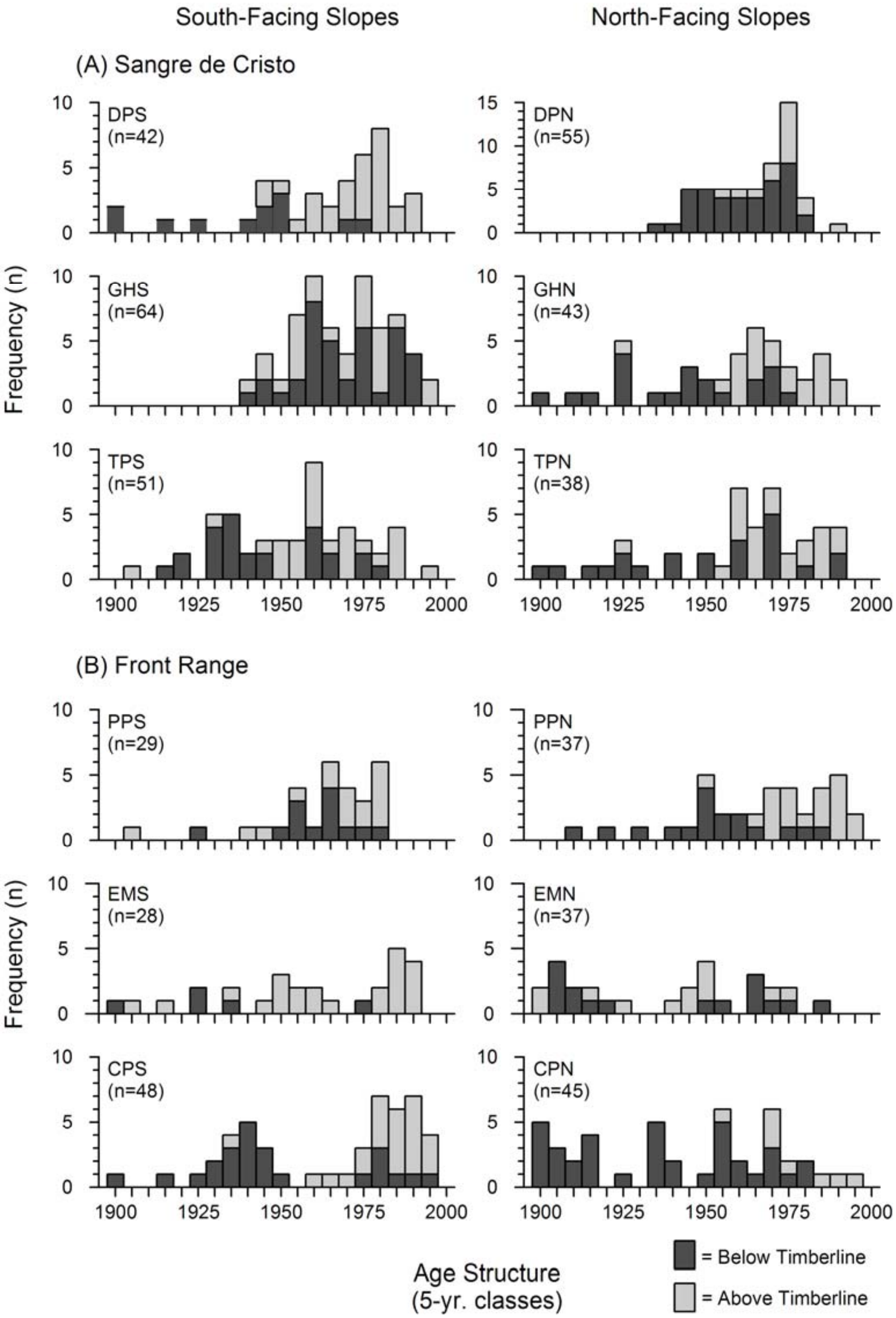

Figure 2. Age-structure data (1900–2000) in 5–year age-classes for each study site in the (A) Sangre de Cristo and (B) Front Range Mountains. Trees are stratified by position relative to timberline (above or below), which is classified as the elevational extent of closed-canopy forest. Details on site abbreviations are listed in Table 1. Note the different y-axis for site DPN in (A).

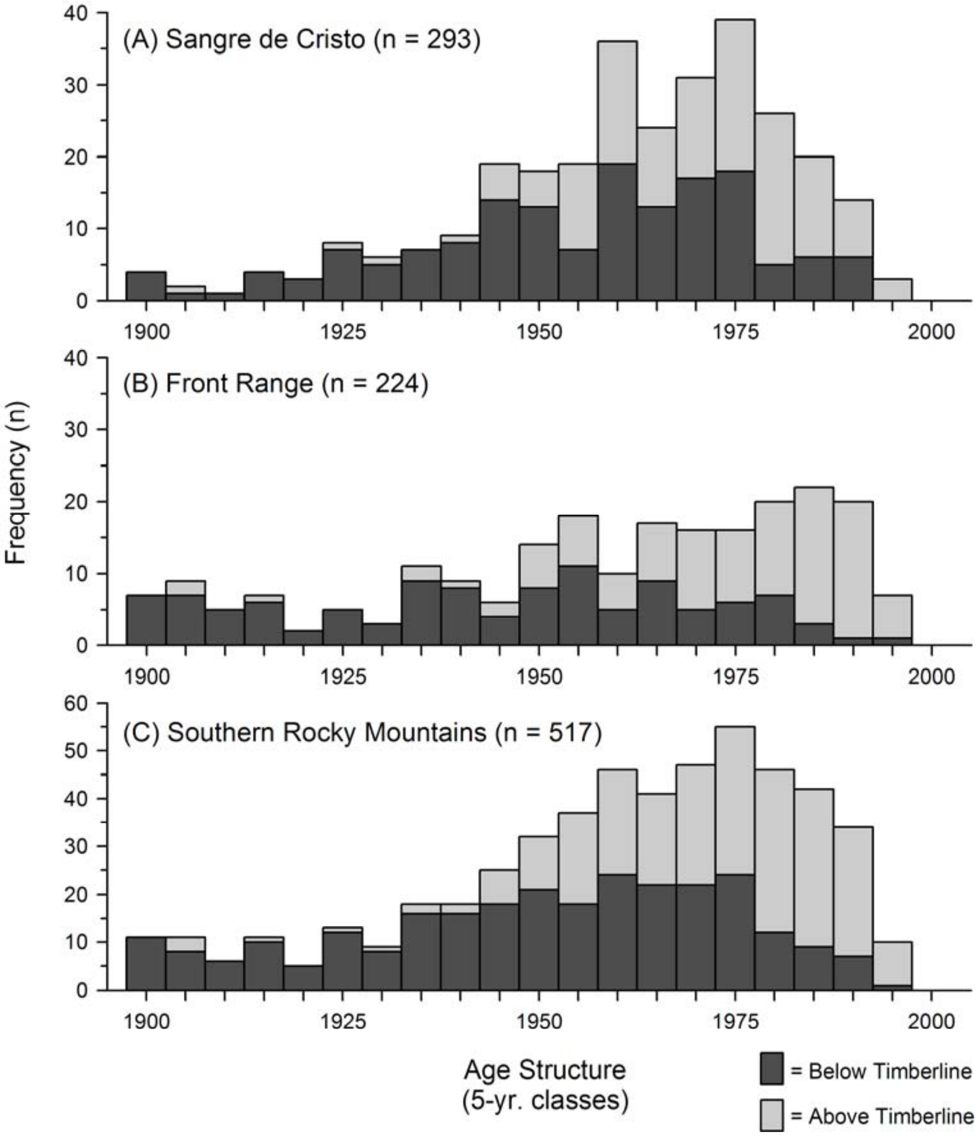

Figure 3. Landscape and regional scale age-structure data (1900–2000) in 5–year age-classes. Trees are stratified by position relative to timberline (above or below). Consult Figure 2 for details on timberline. Note the different y-axis used for the regional scale age-structure data in (C).

There has been an upslope advance of upper treeline at 11 of 12 sites during the 20th century (Fig. 4). Within the region, the mean distance of outpost tree advancement upslope was 57.3 m and at a landscape scale, treeline advancement was more pronounced in the Sangre de Cristo Mountains (mean = 69.8 m vs. 44.8 m in Front Range) (Fig. 4). Differences in outpost tree migration between mountain ranges was not significant (p = 0.07), although this is a result of the anomalously long treeline ecotone at the PPS site (Fig. 4). Changes in the timing of current outpost tree establishment were not statistically different (p = 0.69) between the Sangre de Cristo and Front Range, and 92% (n = 11) of the outpost trees established after 1950 (Fig. 4).

Tree density has increased during the 20th century, with the most marked changes occurring ATL and on north-facing slopes (Fig. 5). Collectively, no significant differences exist between mountain ranges (p = 0.43; data not shown), and similar to the timing and extent of outpost tree migration, the largest increases in density throughout the Southern Rocky Mountains have occurred since 1950 (Fig. 5). Quantitative comparisons of tree density indicate that increases were significantly greater ATL during the latter half of the 20th century (1950–present) in both the Sangre de Cristos and Front Range, as well at a regional scale throughout the Southern Rocky Mountains (Table 3; Fig. 5). Slope aspect also influenced density values during the second half of the 20th century, with significantly larger increases in density occurring on north-facing slopes throughout the region (Table 3; Fig. 5).

Climate. Each climate variable that I calculated was tested for a correlation with tree establishment using Spearman’s rank correlation coefficient, but only

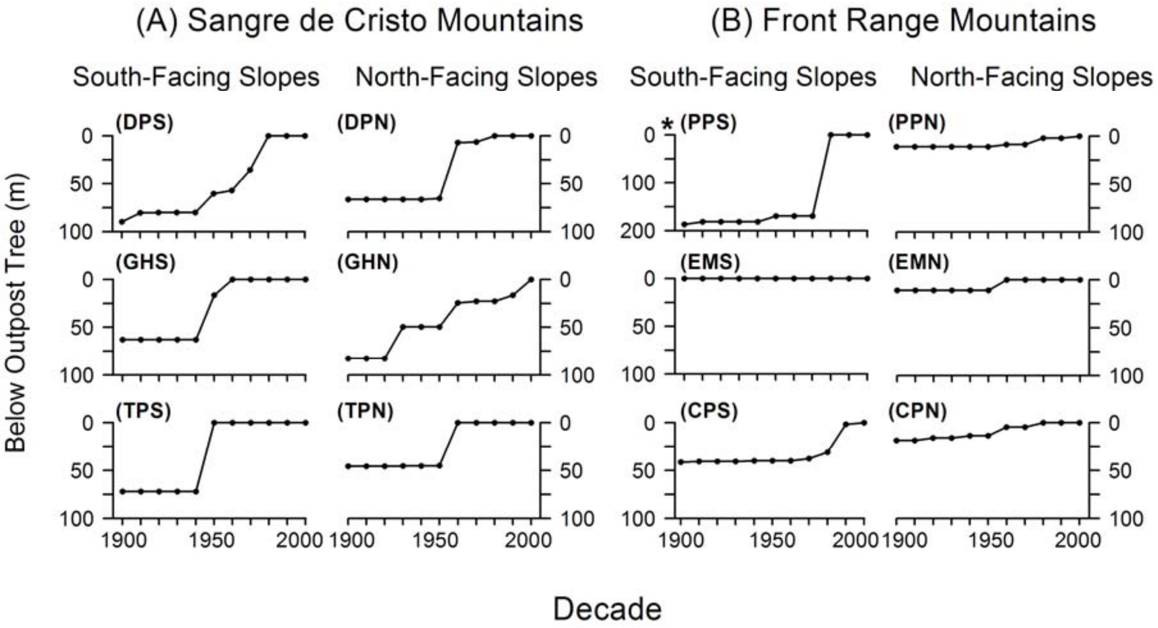

Figure 4. The distance of upslope advancement of the outpost tree during the 20th century at each study site. The uppermost elevation of existing trees within my transects was reconstructed by decade (1900–2000) in relation to its current position to determine the degree of change over time. For example, DPS in part (A) indicates that the current elevation of the outpost tree was reached in 1980 and that the elevational extent of treeline has increased by almost 100 m during the 20th century. Note the different y-axis for site PPS in (B).

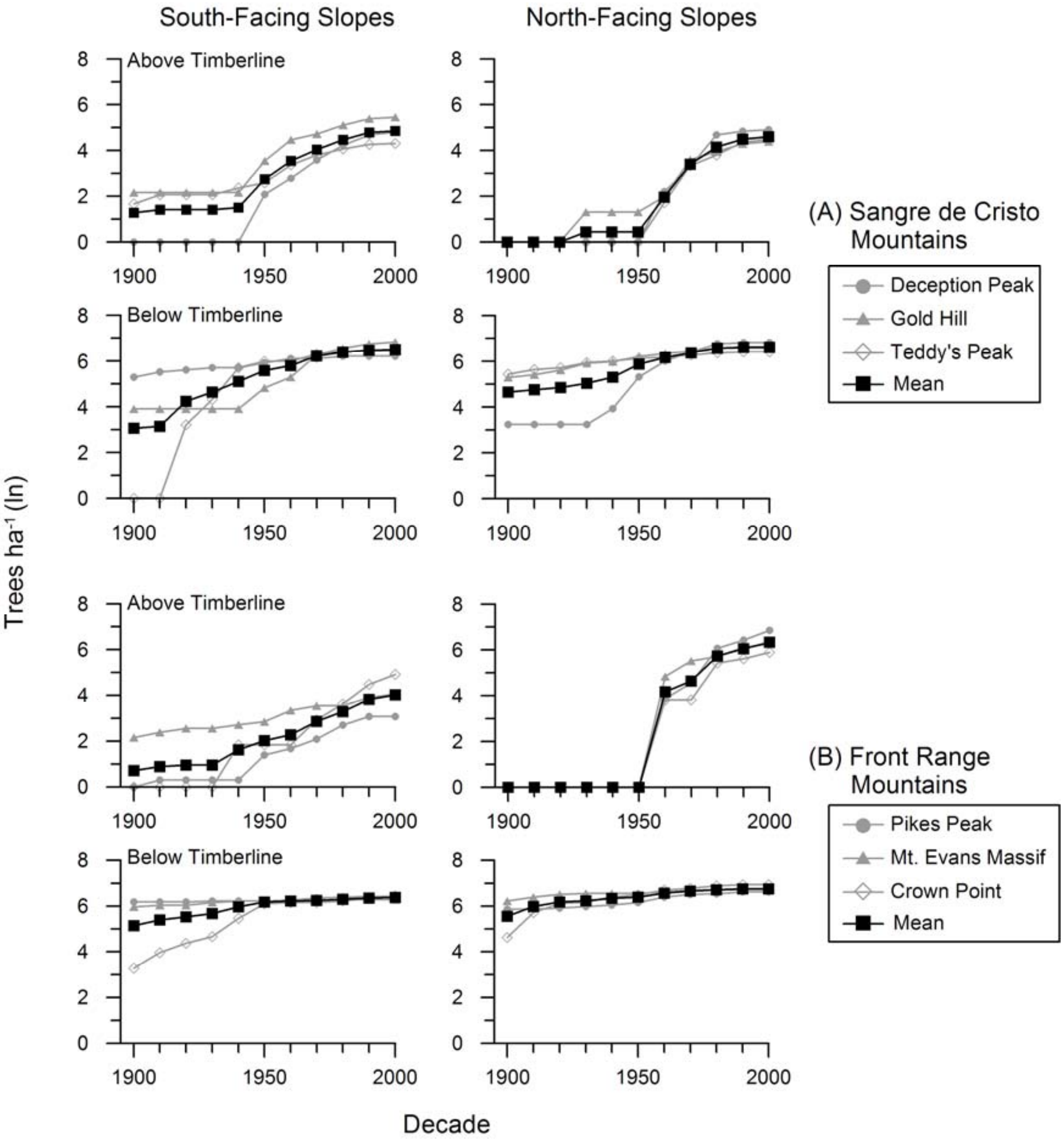

Figure 5. Reconstructed tree density data (trees ha^{-1}) that were normalized by a natural-log transformation and averaged together for a representative value for study sites on contrasting slope aspects and for each mountain range.

Table 3. Quantitative comparisons of changes in density from 1900–1950 vs. 1950–present. Mann-Whitney *U*-Tests were used ($n = 6$) and *p*-values in bold represent comparisons where statistically significant ($p < 0.05$) increases in tree density occurred during the second half of the 20th century (1950–present) compared to the first half (1900–1950).

Comparison	Density Changes (1900–1950 vs.1950–pres.) (*p*)
Landscape Scale	
SDC ATL	**0.0129**
SDC BTL	0.1282
FR ATL	**0.0194**
FR BTL	0.6889
Regional Scale	
SR SF ATL	0.1735
SR NF ATL	**0.0051**
SR SF BTL	0.3785
SR NF BTL	0.2298
*SR ATL	**0.0004**
*SR BTL	0.1124

*Denotes regional comparison where $n = 12$

statistically significant correlations ($p < 0.05$) will be discussed in this paper. These variables include: (1) annual precipitation; (2) arid foresummer precipitation; (3) annual Tmax; (4) spring Tmax; (5) summer Tmax; (6) cool season Tmax; (7) summer Tmin; (8) fall Tmin; (9) annual Trange; (10) spring Trange; (11) summer Trange; (12) fall Trange. Additionally, it is important to note that the degree of significance between tree establishment and climate varies within the Southern Rocky Mountain region.

At a regional scale, a *significant* (hereafter signifying a statistical comparison with a p-value < 0.05) positive correlation exits between tree establishment at upper treeline and annual Tmax, summer Tmax, annual Trange, and summer Trange (Fig. 6). Precipitation appears to be of minimal importance when considering tree establishment at a regional scale and there is no discernable influence of slope aspect (Fig. 6). However, when examined at the landscape scale the regionally significant correlations simply represent the climate-tree establishment relationships that exist in the Front Range dampened by the lack of similar correlations in the Sangre de Cristos (Fig. 6), thus calling into question the usefulness of solely looking at regional scale correlation values over regions that encompass diverse landscapes . In essence, when correlation values are near zero in the Sangre de Cristo, then regional scale coefficients are higher because there is less of a counteracting negative influence on the generally high correlation values from the Front Range.

Tree establishment at upper treeline during the 20th century appears to be the most closely related to climate at a landscape scale in the Front Range Mountains where a strong positive correlation exists with temperature and temperature range values (Fig. 6). Among these positive relationships, trees on north-facing slopes have consistently higher

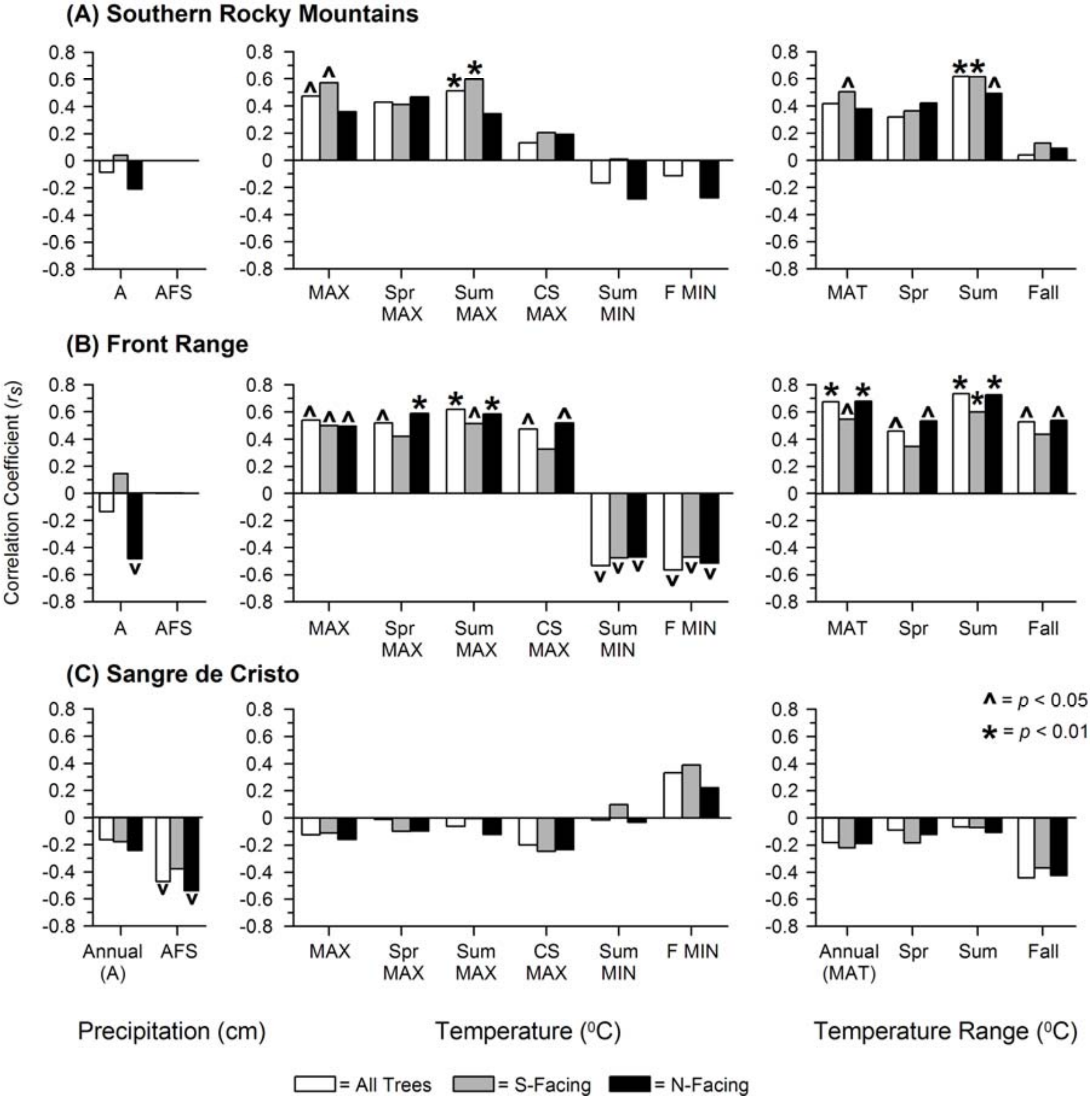

Figure 6. Spearman rank correlation coefficients (r_s) comparing tree establishment with precipitation, temperature, and temperature range data from 1900–1995 at landscape and regional scales. Abbreviations include: AFS – arid foresummer (April–June); MAX – annual maximum temperature; Spr – spring; Sum – summer; CS – cool season; F – fall.

correlation coefficients and are the only ones with a significant inverse relationship with precipitation. Relatively high inverse correlations exist with successful tree recruitment and summer and fall Tmin (Fig. 6). Overall, the combination of significant positive correlations with every seasonal Tmax value except fall, along with negative correlations with minimum temperature variables indicates that generally warmer conditions are the most conducive to tree establishment at upper treeline in the Front Range (Fig. 6).

Tree establishment at upper treeline in the Sangre de Cristo Mountains does not correlate strongly with climate. The only significant relationship between establishment and climate is an inverse correlation with arid foresummer precipitation, which does not apply to south-facing slopes (Fig. 6). This intra-regional differentiation in climate correlations within the Southern Rocky Mountains highlights the importance of focusing on landscape scale assessments of climate-upper treeline relationships. A region-wide comparison appears to contain more noise and perhaps more importantly, minimizes the role of landscape and local scale site conditions in modifying broad scale climate inputs.

Regime shift analysis of tree establishment and the most significantly correlated climate variables provided insight into a possible mechanism for such rapid increases in recruitment since 1950 in the Front Range Mountains. The step change in tree establishment during the early 1950s (1950–1954) indicates that a bioclimatic threshold may have been surpassed in response to climate regime shifts that produced warmer temperatures and a corresponding increase in temperature range (Fig. 7). The most significant regime shift was with annual Tmax in 1950 when a 1.7°C increase in mean conditions occurred that likely initiated coincident regime shifts in both tree establishment and seasonal temperature parameters (Table 4). Tmax is significantly inter-

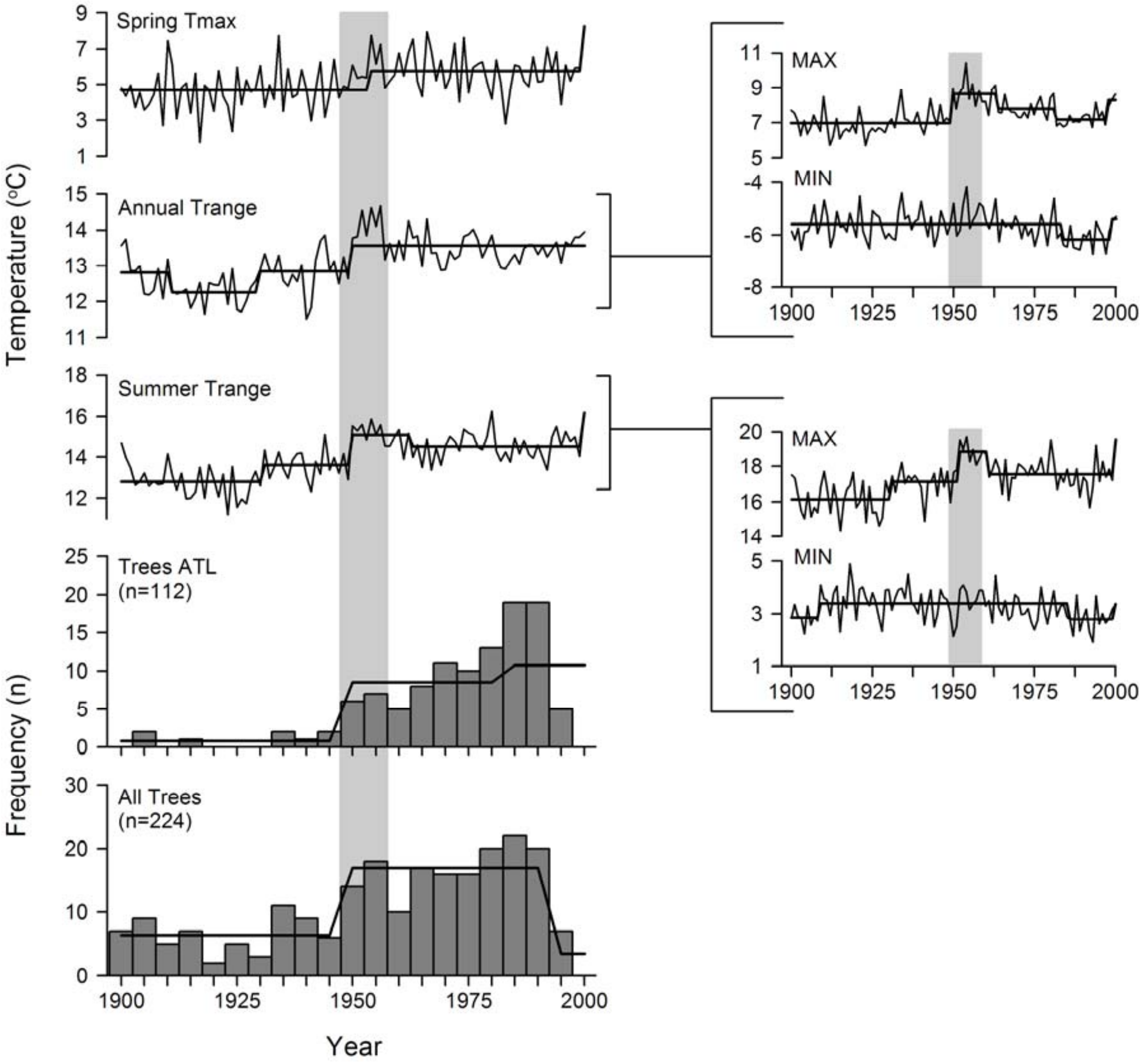

Figure 7. Regime shift analysis of tree establishment and the most strongly correlated temperature variables for the Front Range Mountains. Individual time series that combine to form the temperature range data (Tmax and Tmin) are given to provide further insight into the temperature range variability.

Table 4. Attributes of climate regime shifts. Regime shift refers to the nearest date to the ecological regime shift in tree establishment.

Climate Variable	Regime Shift (yr)	Deviation from Mean (°C)	Length (yrs)	Next Shift (yr)	Next Deviation (°C)
Front Range					
Spring Tmax	1954	+1.1	46	2000	+1.4
Annual Trange	1950	+0.8	55	2005	–1.2
Annual Tmax	1950	+1.7	14	1964	–0.9
Annual Tmin	1984	–0.6	15	1999	+0.8
Summer Trange	1950	+1.5	13	1963	–0.6
Summer Tmax	1952	+1.7	9	1961	–1.3
Summer Tmin	1986	–0.6	14	2000	+0.6
Sangre de Cristo					
Fall Trange	1969	–1.0	35	2004	–1.3
Fall Tmax	1969	–0.9	29	1998	+1.4
Fall Tmin	1997	+2.4	8	2005	–1.5

correlated with each temperature variable plotted in Figure 7 ($r = 0.571–0.767$; $p < 0.00$; Pearson's correlation), except summer Tmin ($r = 0.189$; $p = 0.06$; Pearson's correlation), yet the physical climate mechanism responsible for creating this abrupt increase in annual Tmax remains less clear.

Prior to the abrupt increase in maximum temperature that lead to a regime shift in 1950, there were virtually no trees (8% of current total; $n = 8/112$) growing above the current timberline boundary (Fig. 7). Moreover, during the 1950s, maximum temperatures sustained previously unprecedented warmth relative to the first half of the 20th century, which seems to have initiated a wholesale shift towards more favorable growing conditions at upper treeline. The most compelling aspect of the regime shift analysis is the temporal synchrony between the abiotic mechanism (climate) and biotic response (tree establishment ATL).

In the Sangre de Cristo Mountains, asynchronous conditions exist between the initial regime shift in tree establishment ATL (1955–1959) and corresponding step changes in the most strongly related climate variables (Fig. 8). Overall, the most influential climate parameter governing recruitment at upper treeline appears to be a dry arid foresummer, but evidence for a threshold-induced biotic response to changes in climate is absent (Fig. 8).

Discussion

Upper Treeline Dynamics. The spatiotemporal dynamics of upper treeline environments in the Southern Rocky Mountains have changed dramatically since the middle of the 20th century. Upper treeline has advanced upslope, to varying degrees,

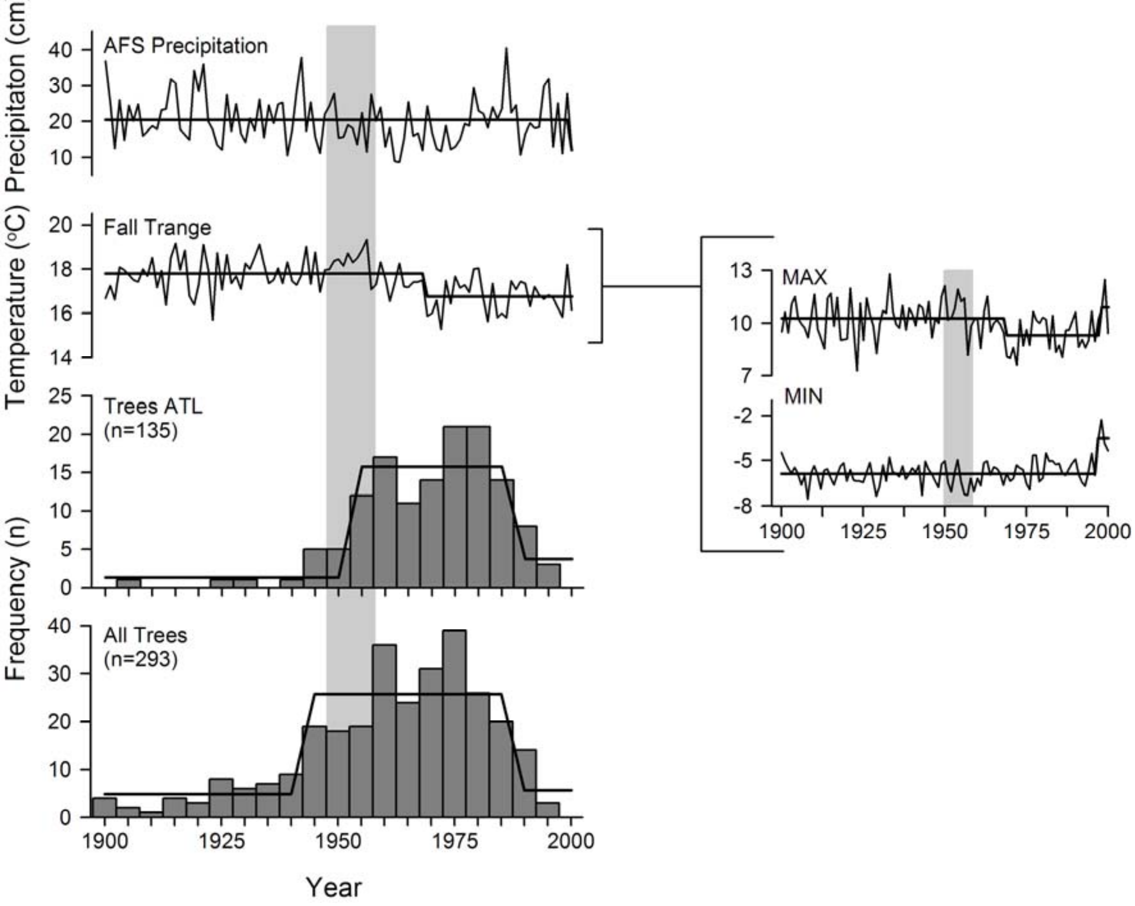

Figure 8. Regime shift analysis of tree establishment and the most strongly correlated temperature variables for the Sangre de Cristo Mountains. Individual time series that combine to form the temperature range data (Tmax and Tmin) are given to provide further insight into the temperature range variability.

throughout the region since 1950. Although random establishment events can be relatively common ATL (MacDonald et al. 1998), concomitant increases in tree density suggest that overall environmental conditions have become more conducive to tree establishment and treeline advance since ca. 1950. Numerous studies have documented an overall increase in tree density at upper treeline during the 20th century (e.g., Batllori and Gutiérrez 2008; Camarero and Gutiérrez 2004; Danby and Hik 2007; Elliott 2003; Klasner and Fagre 2002; Lloyd and Fastie 2003; MacDonald et al. 1998; Szeicz and MacDonald 1995) and in fact, it has been proposed that density increases may be a more sensitive monitor of climate change than treeline position (Camarero and Gutiérrez 2004). The abrupt rise in tree density values ATL suggest a shift to more favorable growing conditions that could facilitate the continuation of treeline advance. However, paleoecological research from the Sierra Nevada and mountains throughout Alaska found that changes in tree abundance ATL preceeded changes in treeline position by an average of 207–400 years (Lloyd 2005; Lloyd and Graumlich 1997). Given the substantially rapid increases in tree density ATL that are approaching the values found BTL, it appears that a bioclimatic threshold may have been surpassed, thereby permitting a potential acceleration of treeline advance.

The region-wide pattern of successful tree establishment ATL coupled with the temporal synchrony of increased regeneration since 1950 (93% of trees above timberline) imply the importance of climate in regulating upper treeline dynamics (Camarero and Gutiérrez 2004; Lloyd and Fastie 2003; Swetnam and Betancourt 1998). This is evidenced by the widespread establishment of relatively young trees ATL on both south- and north-facing slopes in the Front Range and Sangre de Cristos. This contrasts sharply with the results of previous research on upper treeline dynamics where successful tree regeneration ATL was primarily confined to south-facing slopes, with the position and structure of treeline ecotones remaining relatively stable on north-facing slopes for the past several hundred years in the Canadian Rockies (Danby and Hik 2007; Luckman and Kavanagh 2000) and Scandes Mountains of Sweden (Kullman 1998). Moreover, trees on north-facing slopes are significantly younger than their counterparts on south-facing slopes at a regional scale and in the Sangre de Cristo Mountains (see Chapter 2). Marked variability in the dynamics of upper treeline environments from region to region indicates that different controlling factors may be more clearly manifested in certain locations. In this case, the apparent minimal influence of slope aspect on tree establishment and tree age ATL in the Front Range could indicate more uniform climate sensitivity at upper treeline compared to the Sangre de Cristos.

Influence of 20th Century Climate on Upper Treeline Dynamics. Traditional ecological theory regarding upper treeline characterizes this ecotone as a temperature-limited system (Jobbágy and Jackson 2000; Körner and Paulsen 2004). This is consistent with previous research that has associated both increases in tree density and subsequent treeline advance with general warming trends since the termination of the Little Ice Age ca. 1850 (e.g., Danby and Hik 2007; Hessl and Baker 1997; LaMarche and Mooney 1967; Lloyd and Fastie 2003; Payette and Filion 1985; Vittoz et al. 2008). In addition, research on the linkages between tree establishment and climate at upper treeline has reported significant positive correlations with summer Tmax (Elliott and Baker 2004) and overall summer warmth (e.g., Kullman 2007, 2002; Szeicz and MacDonald 1995; Taylor

1995). The results of this research coincide with these findings at a regional scale in the Southern Rocky Mountains where tree establishment during the 20th century is significantly correlated with generally warm conditions (e.g., annual Tmax, summer Tmax, and summer Trange). However, some notable differences arise when considering how temperature–tree recruitment relationships vary at smaller spatial scales, including between mountain ranges and with variations in slope aspect.

Diurnal temperature range has remained relatively constant given the comparable increases in both minimum and maximum temperature since 1979, although a large range of variability exists across regions (IPCC 2007). In my case, temperature range has increased across the study area and is positively correlated with tree establishment. Research at upper treeline in the Spanish Pyrenees suggests that an increase in temperature variability will reduce both favorable growing season conditions and overall tree recruitment (Camarero and Gutiérrez 2004), yet temperature range data has never been explicitly examined with respect to tree establishment. This research indicates that it is not just the range of temperature that is important, but how its individual components (Tmin and Tmax) are changing. In the Front Range, an increase in maximum temperatures created a larger temperature range that appears to have facilitated a substantial increase in tree establishment that led to a shift in the position of treeline. Taken together, examining temperature range data provides a valuable means to discern how maximum and minimum temperatures are co-varying or mirroring each other to produce climate trends that could potentially result in the surpassing of critical bioclimatic thresholds.

The frequency and duration of extreme climate events can provide the necessary mechanism for crossing ecological thresholds that lead to widespread vegetation change (Parmesan, Root, and Willig 2000). In the context of upper treeline research, Paulsen et al. (2000) suggest that treeline advance could only happen if a long-term warming trend stimulated growth frequently enough without the interruption of extreme cold events that inhibit tree establishment. This has occurred in the Swedish Scandes, where prolonged winter warming during the last decades of the 20th century facilitated both an increase in tree establishment ATL and subsequent treeline advance (e.g., Kullman 2007, 2002; Kullman and Öberg 2009). A similar pattern is evident in my data from the Front Range and is most obvious on north-facing slopes, where tree establishment is significantly correlated with cool season Tmax. Generally warmer winters have been shown to reduce tree desiccation and mortality (e.g., Hadley and Smith 1986; Kullman 2002). Moreover, random, feedback-independent spatial patterns of tree establishment ATL in the Front Range could indicate a lack of harsh climate episodes (see Chapter 2). If the spatial pattern of tree establishment ATL is indeed an accurate proxy for climatic inputs, then this provides compelling empirical evidence that the onset of overall warmer conditions since the 1950s has lead to a reduction in harsh climate events and related tree mortality at upper treeline throughout the Front Range.

Consistently higher correlations between tree establishment and climate on north-facing slopes, particularly in the Front Range, suggest that the slope aspect mediation of tree establishment patterns can determine to what extent climate governs upper treeline dynamics (see Chapter 2). In addition, my work in Chapter 2 determined that trees ATL in the Front Range are almost exclusively growing in a random spatial pattern (excluding

PPS), whereas the spatial patterns of tree establishment varies by slope aspect in the Sangre de Cristos, with clustered arrangements on south-facing slopes and primarily random configurations on north-facing ones (excluding GHN). This is important because trees positioned in a random spatial pattern exhibit significant correlations with 20th century climate in the Front Range and on north-facing slopes in the Sangre de Cristos. This supports the conclusion that north-facing slopes represent a better barometer for measuring the influence of climate on tree establishment at upper treeline, primarily because trees growing in a random spatial pattern are more sensitive to climate and less dependent on local biotic feedback interactions (see Chapter 2; Bader, Rietkerk, and Bregt 2008). The cumulative slope aspect-mediated influences of spatial pattern and climate on tree establishment at a landscape and regional scale in the Southern Rockies portends the likely importance of soil moisture in upper treeline dynamics.

Significant influences of soil moisture on upper treeline dynamics are confined to north-facing slopes in the Front Range and Sangre de Cristos, where an inverse relationship exists between precipitation (annual and arid foresummer) and tree establishment. In the Sangre de Cristos, rapid shifts in a low-elevation ecotone boundary occurred during prolonged drought conditions that led to widespread tree mortality in the bordering montane forest (e.g., Allen and Breshears 1998). In my study, a dry late spring and early summer favors tree establishment and since July and August represent the only months where the average minimum temperature is above 0°C at all my study sites (see Chapter 2), the negative correlations with precipitation imply that periods of reduced snowpack favor tree establishment on north-facing slopes. Given the generally cooler conditions created by less direct sun exposure on north-facing slopes (Arno and

Hammerly 1984), it is conceivable that tree recruitment is more dependent on the dynamics of spring snow conditions. For example, reduced spring snowpack has been shown to favor tree establishment at upper treeline (e.g., Kullman 2002; Taylor 1995) and along with warmer spring temperatures, has facilitated the upslope advance of treeline in the Canadian Rockies (Luckman and Kavanagh 1998). Similarly, on north-facing slopes in the Front Range, warmer spring temperatures and reduced spring snowpack have led to considerable increases in both tree establishment and density ATL. The slope aspect mediation of moisture influences at upper treeline indicates that the effects of temperature-precipitation interactions can exhibit intra-regional variability between sites (cf., Daniels and Veblen 2004) and suggests that certain key bioclimatic thresholds may have been crossed.

Evidence for Thresholds at Upper Treeline. The temporal synchrony of regime shifts in both tree establishment and significant climate variables beginning in 1950 suggests the crossing of a critical bioclimatic threshold that caused dramatic changes in treeline vegetation to occur without appreciable time lags. An abrupt increase in annual Tmax represents the most influential temperature variable that helped drive the ecological regime shift and coinciding shifts in seasonal temperature variables. Although the physical climate mechanism responsible for causing a sudden rise in maximum temperature ca. 1950 is less clear, a couple of feasible scenarios exist. In the Front Range, synoptic climatological patterns since the early 1950s suggest that the increases in temperature resulted from processes external to the Rocky Mountain region (Pepin 2000). However, internal feedbacks within the climate system could have helped perpetuate this warmth, whereby uncharacteristically warm spring temperatures accelerate snowmelt, which in turn increases the likelihood of anomalously warm summers and less snow the following year (Cayan 1996; Serreze et al. 1999). In the Front Range, the climate regime shift in annual Tmax was accompanied by a dramatic increase in spring and summer maximum temperature, along with below average snowfall and summer rain (Fig. 9). Collectively, this suggests that internal feedbacks within the climate system could have contributed to the effects stemming from larger scale climate processes that are beyond the scope of this research.

At a landscape scale in the Front Range Mountains, annual Tmax is the most influential climate mechanism driving this ecological regime shift and coinciding shifts in seasonal temperature variables. Various modeling and field-based studies have concluded that upper treeline dynamics are likely to be influenced by the crossing of certain climate thresholds that produce complex, nonlinear changes, particularly as the effects of global climate change scenarios become realized (Camarero and Gutiérrez 2007; Danby and Hik 2007; Kullman 2007; Kupfer and Cairns 1996; Lloyd 2005; Malanson 2001; Millar et al. 2004). My research corroborates the findings of these studies with the identification of synchronous climate and ecological regime shifts at upper treeline. Essentially, the strong correlations that exist between tree establishment and various temperature indices in the Front Range appear to be contingent on the timing of threshold-induced regime shifts that occurred from 1950–1954. Paradoxically, my results suggest that the regime shifts associated with surpassing bioclimatic thresholds helped keep treeline vegetation more closely aligned with variations in climate. That is, if the abiotic mechanism (climate – annual Tmax) did not trigger a synchronous biotic response (primarily tree establishment

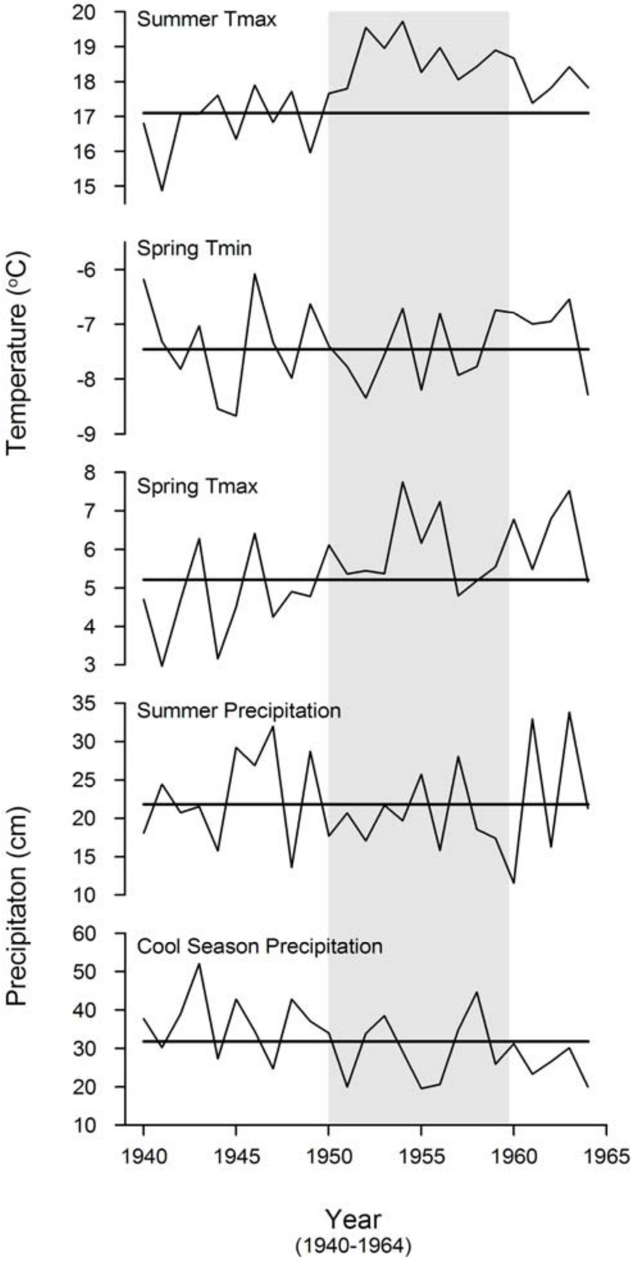

Figure 9. Precipitation (cool season and summer) and temperature (spring Tmin, spring Tmax, and summer Tmax) data for the Front Range from 1940–1964 plotted against the 20th century mean (1900–1999). Data are plotted to highlight the prevalence of warm and dry conditions during the 1950s when important ecological and climate regime shifts occurred (see Figs. 7 and 8).

above timberline), then a growing imbalance would have formed between the two and as a consequence, significant linear correlations would have broken down.

Role of Scale in Treeline–Climate Interactions. Scale is fundamental to most geographic inquiry (McMaster and Sheppard 2004) and is essential when considering the processes operating across multiple scales that have important biogeographic implications for upper treeline ecotonal dynamics (Resler 2006). At a regional scale, climate is often the dominant driver of upper treeline dynamics (e.g., Malanson et al. 2007) and tree demography (Swetnam and Betancourt 1998; Villalba and Veblen 1997). My results indicate that regional scale processes acting across broad environmental gradients are leading to variable degrees of treeline advance throughout the Southern Rockies. Similar widespread changes throughout a topographically complex region suggest that climate is the most likely mechanism (e.g., Camarero and Gutiérrez 2004; Lloyd and Fastie 2003). However, the influence of climate is the most pronounced at a landscape scale and in the Front Range Mountains. Landscape scale variation, in turn, highlights the heterogeneity inherent to complex mountain environments where finer scale processes can modify responses to climate change (e.g., Dalen and Hofgaard 2005; Holtmeier and Broll 2005; Kullman and Öberg 2009; Malanson et al. 2007). Hence, a multi-scale approach provides the most comprehensive way to disentangle the hierarchy of key processes responsible for governing upper treeline dynamics, particularly when assessing the role of climate.

Conducting research at a relatively small spatial scale increases the likelihood of creating biased generalizations that do not hold true when extrapolating to larger spatial scales (Kullman and Öberg 2009). This represents the most likely explanation for a portion of my results that contrast with Hessl and Baker (1997), who concluded that tree establishment at upper treeline in the northern Front Range was favored by several consecutive years of high snowfall, as long as warm temperatures coincided with this period. However, issues relating to study site selection and spatial scale likely account for a majority of this variation. For example, this discrepancy could simply represent a more site-specific response that resulted from sampling areas with relatively xeric conditions, which would more closely resemble south-facing slopes where a positive, albeit insignificant, relationship exists with precipitation. Additionally, my data set includes trees collected from sites that span the entire Front Range, from Pikes Peak in the south (ca. 38°N) to just north of Rocky Mountain National Park (ca. 40°N) where Hessl and Baker (1997) sampled. Consequently, the relationship they documented may not hold at a larger regional scale, particularly given the location of Pikes Peak, which is situated slightly east of the main Southern Rocky Mountain axis and thus, experiences a drier climate more characteristic of the adjacent High Plains (Diaz, Barry, and Kiladis 1982; Peet 1978). Cumulatively, this illustrates the benefits of performing multi-scale research at upper treeline, where in order to gain a comprehensive understanding of the complexities created by topoclimatically diverse mountain regions, multiple spatial scales of inquiry are typically required.

From a temporal scale perspective, climate-treeline interactions in the Front Range deviate from some basic assumptions regarding the anticipated time it takes for variations in climate to initiate changes in vegetation. For instance, over the course of geologic time (10^3–10^6 years) and vast spatial areas (i.e. continents), climate is the principal mechanism responsible for vegetation change in general (e.g., Prentice 1992) and treeline fluctuations in particular (e.g., Jiménez-Moreno, Fawcett, and Anderson 2008). At shorter time scales, spanning decades to centuries, age-structure data typically reveal both climate variations and post-disturbance regeneration (Villalba and Veblen 1997). Thus, it is unlikely that a steady state between climate and vegetation will be attained at a regional scale (e.g., Swetnam and Betancourt 1998). However, the rapid response of tree establishment at upper treeline to similarly abrupt variations in 20th century maximum temperature contrasts with these assumptions, as these landscape scale changes occurred without appreciable time lags. This differs substantially from the predictions of previous research on upper treeline that suggested a considerable lag time may exist between changes in climate and treeline dynamics (Delcourt and Delcourt 1992; Lloyd and Graumlich 1997; MacDonald et al. 1998; Noble 1993; Payette et al. 1989). Alternatively, the apparent tight coupling between climate and tree establishment in the Front Range corresponds to what Kullman (1998, 2001, 2002) and Luckman and Kavanagh (1998; 2000) found with the upslope advance of treeline in the Swedish Scandes and Canadian Rocky Mountains, respectively. From a long-term perspective, researchers in Sweden claim that this rapid rate of vegetation change at upper treeline stands out as a virtually unprecedented anomaly and indicates that contemporary treelines may be at the pinnacle of their existence during the past 7000 years (Kullman 2001; Kullman and Kjällgren 2006). The complete lack of dead trees ATL at my study sites throughout the Southern Rocky Mountains supports this work and perhaps even more importantly, my research suggests that 20th century climate surpassed critical bioclimatic thresholds, ultimately creating a more closely aligned vegetation-climate system at upper treeline in the Front Range.

Conclusions

This research has global implications for climate change investigations that examine the influence of future warming scenarios on the position and dynamics of upper treeline ecotones. Identifying and understanding the causes of regional variability in climate-dependent ecological processes, such as the elevational advance of treeline, constitute vital unanswered questions that may strongly influence the development of future climate change scenarios for complex mountain environments (Lloyd 2005; Kullman 2007).

A region-wide shift towards conditions more conducive to tree establishment occurred around 1950, and appears to have lasted to present. This wholesale switch initiated considerable changes in upper treeline dynamics that facilitated the upslope advance of upper treeline, to varying degrees, at all but one site. Additionally, it coincided with abrupt increases in tree density, particularly ATL and on north-facing slopes. While the regional extent of these changes is noteworthy, significant intra-regional variation exists in the causal mechanisms most likely responsible for the observed changes at upper treeline in the Front Range and Sangre de Cristo mountains.

In the Front Range, climate plays a pivotal role in upper treeline dynamics, and although landscape scale variations in climate sensitivity result from changes in slope aspect and spatial pattern of tree establishment (see Chapter 2), recruitment at upper treeline was closely aligned with the climate system during the 20th century. This represents the first attempt to specifically quantify the influence of temperature range variability on tree establishment at upper treeline, which yielded the highest positive correlations throughout the year. However, the regime shift to warmer maximum temperatures in 1950 was the primary mechanism responsible for driving the dramatic changes in upper treeline dynamics. It conceivably caused a synchronous regime shift in tree establishment on the scale of 5-year age-structure classes and overall, without the concurrent regime shifts in temperature and tree establishment, the significant linear correlations would probably have been diminished. This provides compelling evidence suggesting that the crossing of bioclimatic thresholds (i.e., regime shifts) does not necessarily result in a lagged vegetation response accompanied by nonlinear interactions with climate. In this case, the significant linear correlations were contingent on the threshold responses that led to both ecological and climate regime shifts. Thus, explicitly testing for threshold-induced regime shifts at upper treeline greatly improves the ability to assess mechanistic linkages between climate and tree establishment in these complex high-elevation mountain systems.

The influence of climate on upper treeline in the Sangre de Cristo Mountains is not easily discernable. Virtually no significant correlations exist between tree establishment and climate and the timing of regime shifts in tree establishment is asynchronous with corresponding step changes in climate. More research is needed to clarify this marked intra-regional variation, but some possible reasons for the discrepancies include the spatial pattern of tree establishment, whereby trees on south-facing slopes are exclusively clustered in space, potentially rendering them less dependent on climate inputs and instead, more reliant on interactions with neighboring biota (see Chapter 2). Other potentially confounding variables include the long history of human alteration and land-use practices that places this research into the context of a European-based model, where several studies have reported similar human interference in ascertaining the role of climate in upper treeline dynamics (e.g., Camarero and Gutiérrez 2007; Gehrig-Fasel, Guisan, and Zimmermann 2007; Hofgaard 1997; Motta, Morales, and Nola 2006). The widespread tree establishment ATL could also represent aforestation stemming from the severe 1950s drought where high rates of tree mortality were reported at lower elevations in nearby areas (e.g., Swetnam and Betancourt 1998). However, even if prior disturbance caused the lack of meaningful vegetation-climate relationships at upper treeline during the 20th century, climate is still important, as the spatiotemporal alignment of temperature and precipitation regimes would still have to be suitable for the prolific regeneration underway since ca. 1950.

Overall, this research has helped develop a more holistic understanding of upper treeline dynamics at multiple spatial scales in the Southern Rocky Mountains. It is clear that considerable intra-regional variability exists within the Southern Rockies and that the influence of climate can lead to the crossing of critical bioclimatic thresholds at upper treeline. In addition, broad scale climate inputs can be modified by both slope aspect and the spatial pattern of tree establishment (see Chapter 2). Given the current status of upper treeline dynamics in the Southern Rockies, the future response to climate is not straightforward. Sustained warmth associated with anthropogenic-induced global climate change will likely continue to warm systems beyond ecological thresholds, leading to more frequent and abrupt regime shifts (Anderson et al. 2009). Ultimately, the complexity and scale-dependent interactions of these variables suggests that idiosyncratic responses to climate will likely occur within a region, with more congruent patterns emerging at a landscape scale, particularly on slopes with similar aspects and spatial patterns of tree establishment.

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Chapter 4. Multi–Scale Dynamics of Upper Treeline Along a Latitudinal Gradient in the Rocky Mountains, USA: Implications of Pattern, Feedback, and Climate

In the presence of substrate conditions suitable for tree establishment, upper treeline appears to be primarily controlled by local thermal regimes (e.g., Körner and Paulsen 2004; Rossi et al. 2007). Generally warmer temperatures that produce longer growing seasons are therefore expected to cause considerable changes in the position and structure of upper treeline environments (Grace, Berninger, and Nagy 2002; Kullman 2001). This is consistent with paleoecological research that indicates upper treeline reached its highest elevational extent during the prolonged warmth of the early Holocene 10,000–7,000 yrs. B.P. (e.g., Fall 1997; Jiménez-Moreno, Fawcett, and Anderson 2008; LaMarche 1973). However, some contemporary studies suggest that the facilitative affects of warmer temperatures on upper treeline vegetation could be negated without a concomitant increase in precipitation to replenish soil moisture and alleviate water stress (Daniels and Veblen 2004; Hessl and Baker 1997; Lloyd and Fastie 2002; Lloyd and Graumlich 1997; Weisberg and Baker 1995). Thus, the ramifications of a warming climate on upper treeline dynamics remain uncertain.

Although global climate change is expected to result in sustained warmth at previously unprecedented levels across broad spatial scales (Jones and Moberg 2003; Mann et al. 2008), corresponding trends in precipitation are projected to be less uniform (New et al. 2001). In spite of this, Dettinger et al. (1998) identified a north-south seesaw of precipitation that pivots around ca. 40°N in western North America, with opposite moisture conditions existing simultaneously to the north and south of this parallel. In general, the existence of this precipitation dipole creates a potentially unique and valuable region to study the influence of widespread warming (Barnett et al. 2008) coupled with contrasting precipitation regimes north and south of 40°N. More specifically, this seesaw could help reveal detailed biogeographical impacts of 20th century climate change on upper treeline dynamics in the Rocky Mountains.

Successful tree establishment at upper treeline is often contingent on the initiation of positive feedback (Wilson and Agnew 1992), especially in the extreme environments found at upper treeline in the Rocky Mountains (Smith et al. 2003). Positive feedback ameliorates local climate conditions and is initiated once a tree becomes established, often in the sheltered lee of boulders (Batllori et al. 2009; Resler, Butler, and Malanson 2005). Further, positive feedback can affect the dynamics and spatial pattern of upper treeline (e.g., see Chapter 2; Alftine and Malanson 2004; Bader, Rietkerk, and Bregt 2008; Resler 2006) and possibly determine the degree of climatic influence (see Chapter 2; Bekker 2005). The complexity of these interactions and how they relate to tree establishment at upper treeline portends the likelihood of a nonlinear response to changes in climate (Danby and Hik 2007; Kupfer and Cairns 1996; Lloyd 2005; Malanson 2001). More importantly, nonlinear changes in climate can lead to the crossing of critical bioclimatic thresholds that cause abrupt ecological regime shifts to occur (Anderson et al. 2009; Groffman et al. 2006), potentially leading to a switch in the primary processes responsible for creating landscape pattern (Contamin and Ellison 2009). Yet, research that explicitly examines the collective behavior of these complex relationships and how they combine to influence tree establishment at upper treeline is lacking.

In this study, I used a multi-scale approach along a latitudinal gradient that bisects the reported precipitation dipole (ca. 40°N) in the Rocky Mountains (35°N–44°N) to gain a more holistic understanding of how interactions between spatial pattern, positive feedback, and climate ultimately influence tree establishment at upper treeline. With a few notable exceptions worldwide (Dalen and Hofgaard 2005; Daniels and Veblen 2004; Kullman and Öberg 2009; Lloyd 2005; Villalba and Veblen 1997), little attention has been given to examining the spatial variation of upper treeline in response to climate change on multiple spatial scales, especially in the Rocky Mountains. Scale plays an important role in upper treeline research since spatial pattern is driven by processes operating at multiple spatial scales (Holtmeier and Broll 2005; Resler 2006). Further, using a comparative framework along a latitudinal gradient can aid in the differentiation of key patterns and processes driving upper treeline dynamics (Young and León 2007).

The goal of this research is to determine how local ecological processes and patterns at upper treeline influence and are affected by large-scale climate (sensu Brown 1995). For instance, climate typically exerts a top-down control on ecological patterns and processes (Hessburg, Kuhlmann, and Swetnam 2005), while it has also been shown that local scale interactions can help structure and sustain larger scale vegetation patterns (Alftine and Malanson 2004). However, the point at which key processes and patterns manifest themselves in the dynamics of upper treeline environments is likely to change between different scales of analysis (cf., Levin 1992). For this study, spatial scales of analysis include landscape (mountain range), sub-regional (north and south of 40°N), and regional (entire latitudinal gradient) and were used to address the following research questions: 1) Have warmer temperatures resulted in an increase in tree establishment at upper treeline during the twentieth century? 2) How do the relative influences of spatial pattern, positive feedback, and climate contribute to successful tree establishment at upper treeline? 3) Does the importance of these interactions vary by spatial scale of analysis along a latitudinal gradient in the Rocky Mountains?

Study Area

My study area stretches along a ca. 1000 km north-south latitudinal gradient (ca. 44°–35°N) east of the Continental Divide in the Rocky Mountains (Fig. 1). Moving from north to south, my study sites are located in the Bighorn (BH; ca. 44°N), Medicine Bow (MB; ca. 41°N), Front Range (FR; ca. 38°–40°N), and Sangre de Cristo (SDC; ca. 35°–37°N) mountain ranges. Towards their crest, the elevation of upper treeline varies from ca. 3000 m in the BH to ca. 3800 m in the SDC (Tables 1 and 2) (Despain 1973; Peet 1978).

The geologic substrate of upper treeline environments is primarily composed of Precambrian granitic rock, along with gneiss and schist that share similar geochemical properties (Allen, Peet, and Baker 1991; Knight 1994). In the BH, the central granitic core is overlain by sedimentary layers that extend to ca. 2500–2900 m (Despain 1973). Pedogenic processes typically form shallow, infertile, and coarse-textured soils from this parent material (Allen, Peet, and Baker 1991; Knight 1994).

Detailed climate characteristics of my study area were described by Baker (1944), but a contemporary synthesis is lacking. In general, the climate of the Rocky Mountains is relatively uniform south of ca. 40°N, with infrequent intrusions of Pacific air masses during the winter and an influx of monsoonal moisture producing most summer

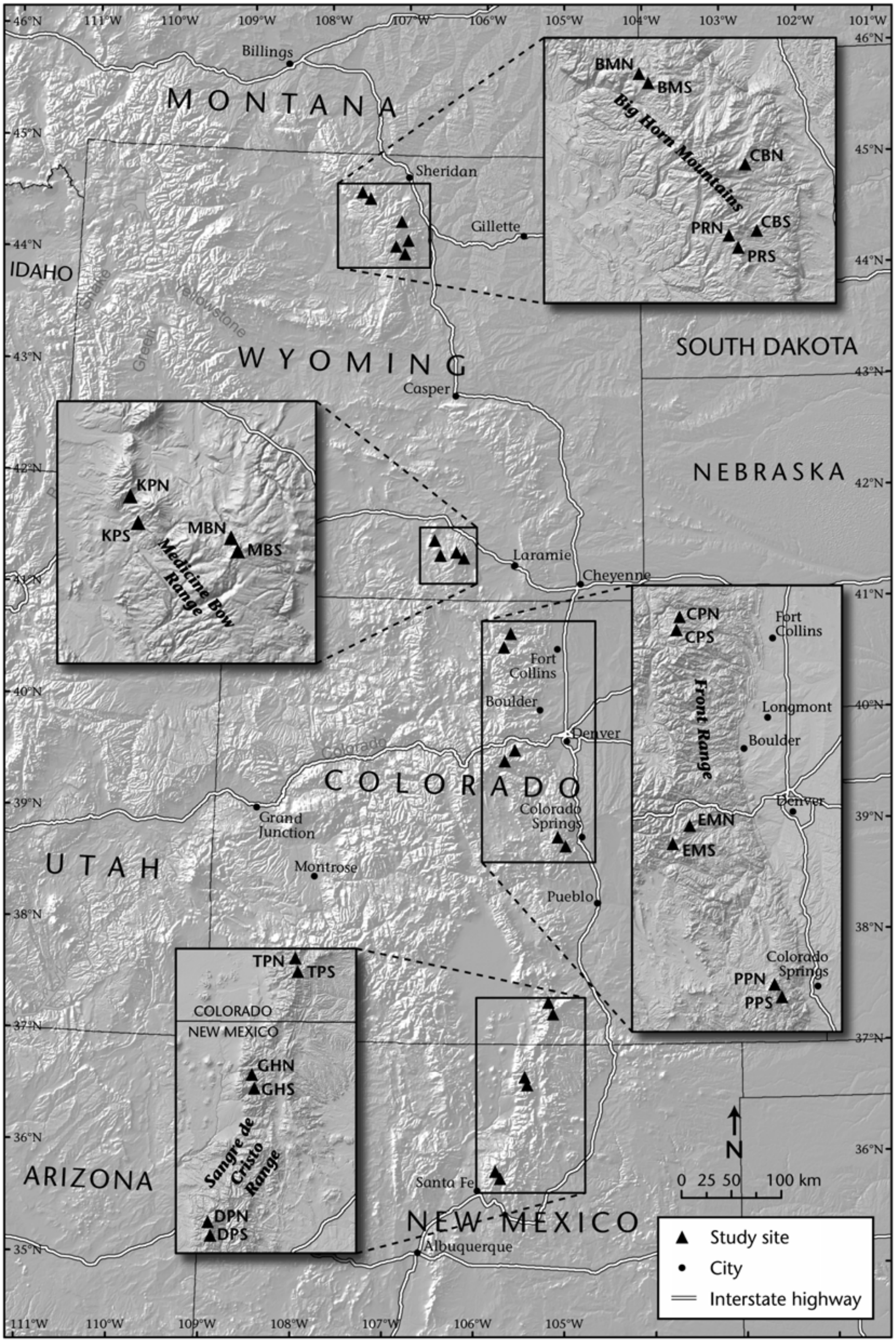


Figure 1. Study area map of my study sites in the Rocky Mountains.

Table 1. Study site names and commonly used abbreviations for the mountain ranges and upper treeline study sites in the Rocky Mountain region. Latitude (°N) and elevation (m) values represent the mean of both south- and north-facing sites.

Mtn. Range/Study Site	Site Code (S:N)*	Latitude (°N)	Elevation (m)
Bighorn Mountains (BH)			
Bruce Mountain	BMS:BMN	44.6	3003
Central Bighorn	CBS:CBN	44.3	2990
Powder River Pass	PRS:PRN	44.1	3005
Medicine Bow Mountains (MB)			
Kannaday Peak	KPS:KPN	41.4	3213
Medicine Bow Massif	MBS:MBN	41.3	3327
Front Range Mountains (FR)			
Crown Point	CPS:CPN	40.6	3421
Mt. Evans Massif	EMS:EMN	39.6	3581
Pikes Peak	PPS:PPN	38.8	3605
Sangre de Cristo Mountains (SDC)			
Teddy’s Peak	TPS:TPN	37.3	3653
Gold Hill	GHS:GHN	36.6	3662
Deception Peak	DPS:DPN	35.7	3725

*Abbreviations are given for site codes on both south- and north-facing slopes

Table 2. Study site characteristics. Note that (*) denotes a total value rather than the mean.

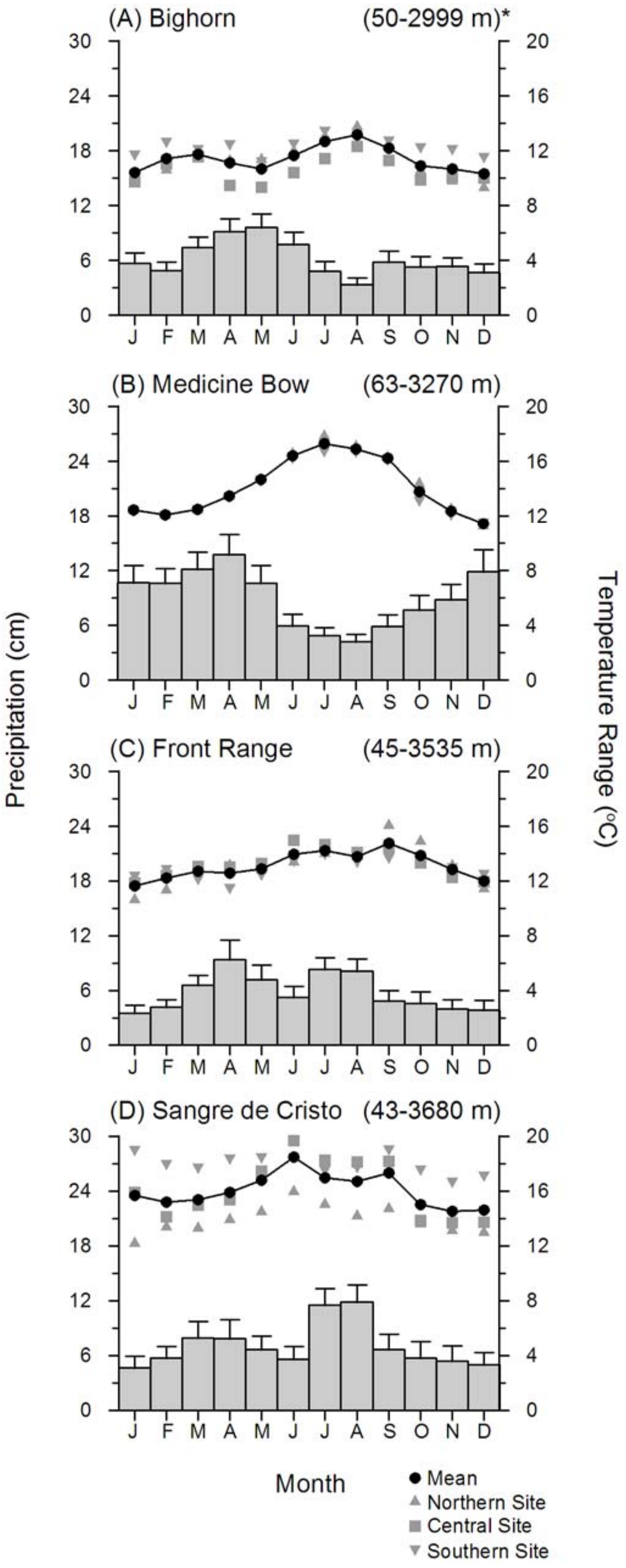
Mtn. Range	Site Code	Lat (°N)	Long (°W)	Elev (m)	Aspect (°)	Slope (°)	Trees (n)	Trees 1900–2000 (n)	Seedlings (n)
Central Rockies									
BH	BMN	44.6	107.5	2999	10	17	59	56	5
BH	BMS	44.6	107.5	3007	210	19	46	36	8
BH	CBN	44.4	107.0	3090	350	3	23	18	4
BH	CBS	44.2	107.0	2889	152	16	40	36	0
BH	PRN	44.1	107.1	2982	320	16	39	25	5
BH	PRS	44.1	107.1	3027	204	15	49	45	8
MB	KPN	41.4	106.5	3264	18	21	83	70	36
MB	KPS	41.4	106.5	3161	130	20	76	72	49
MB	MBN	41.3	106.3	3349	330	18	61	51	23
MB	MBS	41.3	106.2	3304	132	11	81	74	37
*Mean/*Total*		–	–	*3107*	–	*16*	**557*	**483*	**175*
Southern Rockies									
FR	CPN	40.6	105.6	3407	320	14	49	45	0
FR	CPS	40.6	105.6	3434	194	17	49	48	15
FR	EMN	39.6	105.6	3542	338	24	57	37	20
FR	EMS	39.5	105.7	3619	226	22	46	28	7
FR	PPN	38.8	105.0	3600	320	11	51	37	45
FR	PPS	38.8	105.0	3609	170	10	55	29	5
SDC	TPN	37.3	105.1	3635	324	23	47	38	20
SDC	TPS	37.3	105.1	3670	160	19	53	51	7
SDC	GHN	36.6	105.4	3658	350	10	52	43	23
SDC	GHS	36.6	105.4	3665	190	15	67	64	26
SDC	DPN	35.7	105.7	3716	315	21	56	55	17
SDC	DPS	35.7	105.7	3734	184	26	50	42	6
*Mean/*Total*		–	–	*3607*	–	*18*	**632*	**517*	**191*

precipitation (Mitchell 1976). The continentality and high elevation of my study area leads to large variations in monthly and annual temperature range (Figs. 2 and 3). The proportion of annual precipitation that falls as snow increases along a south-north axis and a seasonal precipitation maximum occurs during the spring, except in the SDC, where monsoonal moisture creates a summer maximum (Fig. 2).

Vegetation at upper treeline is primarily composed of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (Peet 2000). Other tree species that contribute to local floristic diversity based on environmental conditions include Colorado bristlecone pine (*Pinus aristata* Engelm.) in the south (below 39°N), lodgepole pine (*Pinus contorta* Dougl. ex Loud.) north of the FR, and isolated whitebark pine (*Pinus albicaulis* Engelm.) in the BH (Despain 1973; Peet 2000). Krummholz is more common north of ca. 40°N in the MB and BH.

Evidence of humans occupying areas near timberline dates back thousands of years, although any settlement or land-use patterns were likely ephemeral in such extreme environments (Thybony, Rosenberg, and Rosenberg 1985; Veblen and Lorenz 1991; Wolf 1995). Permanent Spanish settlements arose in the 1500s in the lowlands surrounding the SDC (deBuys 1985) and prospecting opportunities lured Euro-American settlers during the nineteenth century mining boom (ca. 1850–1870s) (Pearson 1986; Veblen and Lorenz 1991). In addition to mining, notable anthropogenic disturbances that coincided with this period (mid- to late-1800s) included logging (Thybony, Rosenberg, and Rosenberg 1985; Veblen and Lorenz 1991) and sheep grazing (Rueth, Baron, and Joyce 2002). Currently, based on extensive field observations, most human-induced

Figure 2. Climate diagrams displaying monthly precipitation (bar graph) and temperature range (line graph). Precipitation bars are plotted with 1 standard deviation showing. Temperature range data are displayed for each mountain peak within the mountain range to show variability around the mean. (*) is used to show the percentage of cool season precipitation (Nov.–Apr.) and the mean elevation of my study sites in each mountain range.


(A) Bighorn
(50-2999 m)*
(B) Medicine Bow
(63-3270 m)
(C) Front Range
(45-3535 m)
(D) Sangre de Cristo
(43-3680 m)
Precipitation (cm)
Temperature Range (°C)
0
6
12
18
24
30
0
4
8
12
16
20
J F M A M J J A S O N D
Month
● Mean
▲ Northern Site
■ Central Site
▼ Southern Site

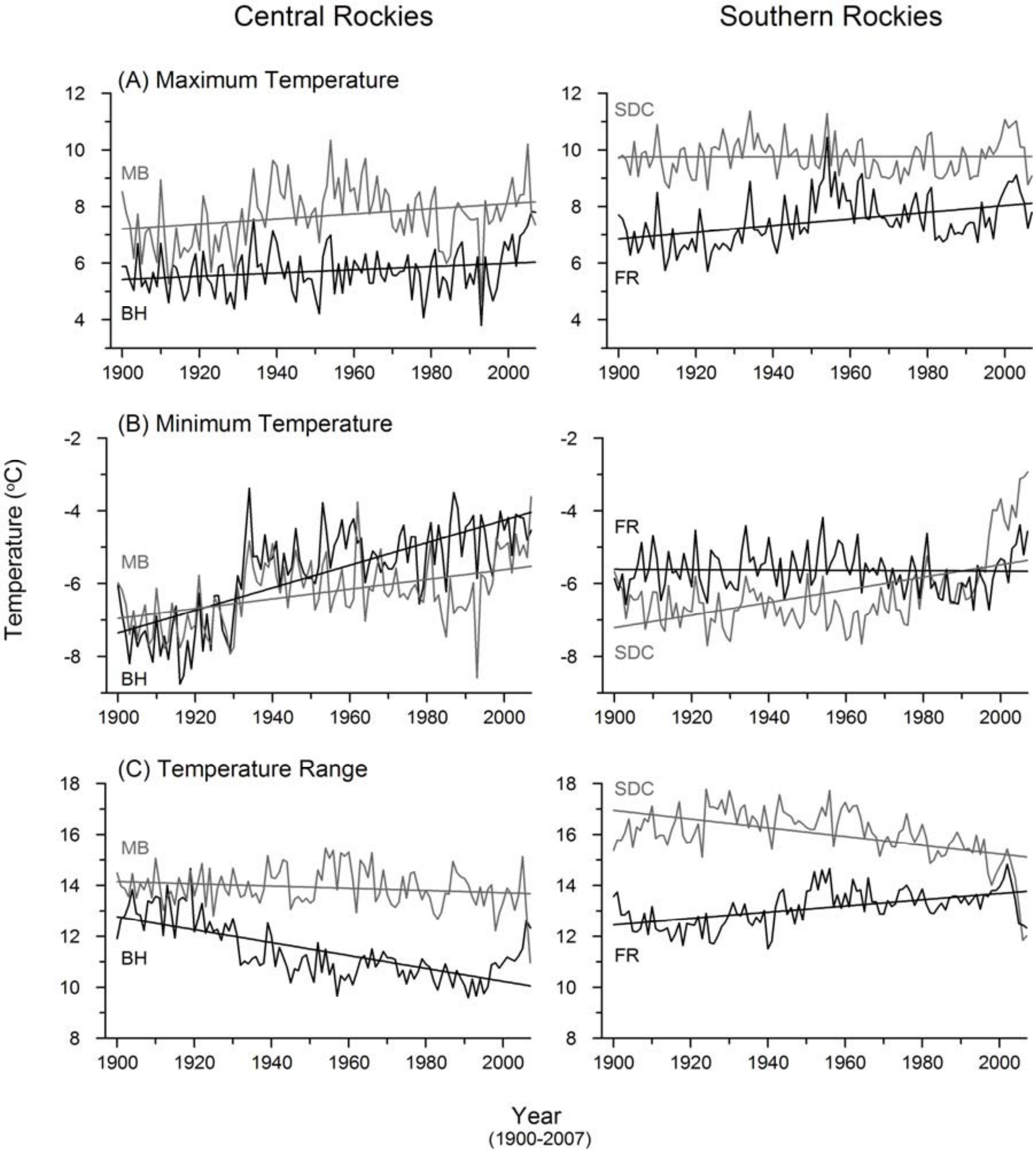


Figure 3. Maximum temperature, minimum temperature, and temperature range data with linear trend lines for each mountain range in my study area.

disturbance stems from cattle grazing in the SDC and BH along with timber harvesting in the FR and MB, although neither appears to be widespread at upper treeline.

Methods

Field Sampling. To understand treeline dynamics along a latitudinal gradient (ca. 44°N–35°N) in the Rocky Mountains, I systematically placed paired nested-belt transects on contrasting south (azimuth 135° to 225°)- and north (azimuth 315° to 45°)-facing slopes on eleven mountain peaks throughout the Central (BH and MB) and Southern (FR and SDC) Rocky Mountains (n = 22 transects). One exception to this occurred in the central BH, where a lack of appropriate sites on the same mountain peak, coupled with logistical constraints associated with sampling in Wilderness, forced me to place transects on two separate mountains located in the same general vicinity (sites CBN and CBS; Fig. 1). Transect location was intentionally selected to eliminate the influence of potentially confounding variables from both natural and anthropogenic disturbances. In addition, my site selection focused on identifying climatic treelines (cf. Butler et al. 2007; Holtmeier and Broll 2005), which essentially refers to areas where possible treeline expansion was not limited by local topography or mechanical reasons that make tree growth impossible (e.g. steep and rocky slopes, absence of soil, or avalanche tracks). My study sites were selected *a priori* through the analysis of aerial photographs, topographic maps, and through discussions with local USDA Forest Service (USFS) personnel in order to ensure the absence of recent disturbance events (e.g., fire or logging). If a potential site was in question, an exploratory reconnaissance trip was used to confirm the existence of suitable conditions.

Individual nested-belt transects began at an outpost tree (term after Paulsen, Weber, and Körner 2000), which was classified as the furthest upright tree (≥ 5 cm diameter at breast height [dbh]) or sapling (< 5 cm dbh, ≥ 1.2 cm diameter at ground level [dgl]) existing within the treeline ecotone. The transect extended downslope from the outpost tree perpendicular to the slope contours and through timberline 40 m into closed-canopy subalpine forest, which was characterized by relatively dense trees with interlocking or adjoining canopies. Here I define treeline as the uppermost limit of individuals having an upright growth form and timberline as the elevational limit of closed-canopy forest, with the treeline ecotone existing between these two delineations (Malanson et al. 2007). Krummholz were not sampled because their low stature creates a different microclimate than that experienced by upright trees and, therefore, may not reflect suitable conditions for tree establishment within the treeline ecotone (Körner and Paulsen 2004). The width of each nested-belt transect was divided into two parts to ensure a sufficient number of saplings to calculate age corrections and analyze regeneration patterns. Above timberline (ATL), I sampled all saplings within a wide 20 m belt and all trees within a narrower 10 m belt on each side of the transect. Below timberline (BTL), the widths were half as wide (saplings were collected within 10 m and trees were sampled within 5 m) to accommodate for the considerable increase in tree density. Due to variations in tree density and the elevational position of the outpost tree, overall transect length varied at each site, but each was long enough to include at least 50 trees.

Local site conditions were documented at each transect location, including the elevation and GPS coordinates of the outpost tree, slope aspect, and slope steepness (°).

In addition, I recorded detailed notes for each tree that was sampled, such as dbh (dgl, if applicable), coring height, species, *x* and *y* coordinates to the nearest 0.1 m along the transect (including krummholz), and 1 m radius of microtopography. The location of krummholz patches were noted to provide a detailed account of the spatial patterns of tree establishment within the upper treeline ecotone. Local microtopography was recorded to determine whether tree establishment is contingent on shelter availability ATL (e.g., Daly and Shankman 1985; Resler, Butler, and Malanson 2005) and to help gauge the importance of positive feedback in driving upper treeline dynamics (e.g., Alftine and Malanson 2004; Smith et al. 2003).

Age-Structure Data. Age-structure information was collected by extracting two increment cores at 30 cm above the ground from all living trees (≥ 5 cm dbh, ≥ 9 cm dgl) along the transect. Every sapling within the transect was harvested at ground-level and where available, 10–15 were sectioned at 30 cm to determine a correction factor for age-at-coring height. Further, distinctions were made between species and saplings growing ATL in a relatively open environment from those growing in the shade of closed-canopy forest BTL to more accurately determine age-to-coring height corrections for the trees growing in both conditions (cf., Veblen 1992). I inventoried seedlings (< 1.2 cm dgl) by species and as alive or dead throughout the entire transect.

All tree cores and sapling cross sections were prepared following standard dendrochronological procedures (Stokes and Smiley 1996). All tree-ring samples were crossdated using both visual evidence from individual series and by comparing skeleton plots to ensure that accurate dates were assigned to the annual rings of each series (Stokes and Smiley 1996). Pith estimators were used to geometrically determine the number of missed rings when the pith was not obtained during field sampling (Applequist 1958). Any samples that could not be confidently crossdated (e.g., rotten and/or no ring curvature present to estimate distance to pith) were excluded from my analyses.

Dates of tree establishment were calculated based on tree age at the time of sampling (2007 for SDC and Mt. Evans site, 2008 for rest of sites) and by adding the appropriate age to coring-height correction. Age to coring-height corrections were done for both the SR (see Chapter 2) and CR. They were calculated by taking the mean age at 30 cm of harvested saplings and adding it to the age determined from crossdating individual tree cores collected from the same height above the ground. Coring-height corrections were computed for each species and further stratified by position relative to timberline (ATL vs. BTL) and mountain range. Outliers (± 2 s.d.; $n = 14/248$) were removed before applying final corrections. Final age-correction values at 30 cm were compared between trees growing ATL and BTL and combined if they were not statistically different ($p < 0.05$; *t*-test).

Once age to coring height corrections were applied, tree establishment dates were grouped into both decadal (pre–1800 to 1890) and five-year (1900–2000) age classes to produce a hybrid age-structure chronology. Separate age-class divisions were created before (10-yr) and after 1900 (5-yr) because of my detailed sampling strategy that produced age to coring height corrections and a low average number of rings to center for the period 1900 to present (Table 3). In addition, while there are known limitations to producing a static age-structure distribution, particularly with regards to understanding past mortality rates (e.g., Johnson, Miyanishi, and Kleb 1994; Veblen 1992), it offers the

Table 3. Number of rings to center data for crossdated tree cores in the hybrid age-structure classes (Pre-1900 and 1900-present). Coring height corrections do not include cross-section data from harvested saplings that already contain the pith. Site abbreviations can be found in Table 1.

Study Site	Pre–1900	(n)	1900–Present	(n)	Total Cores Collected (n)	Cross Sections (n)
BMN	3.3	3	2.6	37	40	20
BMS	4.7	9	3.0	29	38	8
CBN	10.6	5	1.5	3	8	15
CBS	1.8	4	4.5	29	33	7
PRN	6.8	14	3.6	14	28	12
PRS	8.8	5	2.8	26	31	18
KPN	7.8	13	0.9	22	35	48
KPS	6.0	4	1.7	18	22	54
MBS	5.1	7	3.4	10	17	64
MBN	4.1	10	4.3	18	28	33
CPN	4.8	4	6.6	28	32	17
CPS	11	1	3.4	26	27	22
EMN	5.9	20	3.3	12	32	25
EMS	7.1	18	2.1	14	32	14
PPN	6.6	14	3.2	24	38	13
PPS	7.7	23	2.3	13	36	19
TPN	2.6	9	4.6	11	20	27
TPS	10.5	2	1.3	31	33	20
GHN	4.4	8	2.1	25	33	18
GHS	13	3	1.4	36	39	28
DPN	8	1	3.2	25	26	30
DPS	5.6	8	2.8	15	23	27
*Mean/*Total*	*6.6*	**185*	*2.9*	**466*	**651*	*24.5/*539*

most viable approach for this study. Furthermore, any evidence of mortality within the general vicinity of my sites was dutifully recorded in order to minimize these limitations.

Climate Data. Due to the paucity of climate stations at higher elevations in the Rocky Mountains (Barry 2008), I obtained PRISM (Precipitation-elevation Regressions on Independent Slopes Model) climate data for each study site (PRISM Group, Oregon State University, http://www.prismclimate.org, created 1 Jun 2009). PRISM data recognizes the dominant influence of elevation and topography in mountain climates and has been shown to accurately model precipitation and temperature values in topoclimatically complex mountain regions (Daly, Neilson, and Phillips 1994; Daly et al. 2001).

To the best of my knowledge, PRISM data has not been previously used in other research on upper treeline vegetation dynamics, but is instead more commonly used by climatologists in studies examining climatic trends in the mountainous regions of western North America (e.g., Hamlet et al. 2005; Mote et al. 2005). Overall, PRISM data is perhaps more appropriate for upper treeline research because of the large discrepancies between general climatic conditions at high-elevation sites and surrounding lowlands where most climate stations are located. Moreover, a single weather station cannot adequately capture the diverse climate conditions inherent to topographically complex mountain environments (Barry 2008).

I obtained PRISM point data for each study site on the eleven mountain peaks used in this study. In the event that one site was drawing from a different PRISM grid (2.5 minute resolution) than the site with an opposite slope aspect, the transect site located in the PRISM grid with the highest elevation was used to more accurately convey local conditions at upper treeline. Data from sites within each mountain range were averaged together to create landscape scale climatological summaries, which were combined to produce a sub-regional climate summary for the Central Rocky Mountains (CR; MB and BH) and Southern Rocky Mountains (SR; FR and SDC). Based on the regional climatology of my study area (cf. Dettinger et al. 1998; Mitchell 1976) and for comparison purposes, I assigned mountain ranges north of 40°N to the CR and these data were averaged together with the SR to create a regional climate summary for the Rocky Mountains.

Precipitation, maximum temperature (Tmax), minimum temperature (Tmin), and temperature range data (Trange = Tmax–Tmin) were used to calculate the following annual and seasonal mean values: 1) annual; 2) spring (March–May); 3) summer (June–August); 4) fall (September–November); 5) cool season (November–April). Tmax, Tmin, and Trange data were all used because they represent the most likely variables to indicate whether a critical bioclimatic threshold has been crossed, opposed to overall mean conditions. Cool season data were used in lieu of winter data to more accurately capture the entire snowfall period within my study region. All climate variables were averaged into five-year bins (1900–2000) to match the minimum resolution of my age-structure data.

Age-Sturcture Analysis. The hybrid age-structure data were analyzed to determine whether tree age was statistically different between mountain ranges and contrasting slope aspects at landscape, sub-regional, and regional scales. Cumulative age distributions were tested for normality using a Kolmogorov–Smirov test and then median age was compared using a Mann–Whitney *U*-Test. This nonparametric test was used to determine whether tree ages at upper treeline were significantly different throughout the Rocky Mountains, with the null hypothesis being that the population ages are equal. Any statistically significant differences in tree age ($p < 0.05$) between mountain ranges and/or slope aspects contained therein could indicate the result of different processes driving ecotonal dynamics at upper treeline.

The distance of outpost tree advancement upslope (m) and increases in tree density ATL (trees ha^{-1}) were reconstructed for the 20th century and grouped into two cateogories: 1) pre–1950; 2) post–1950. As an example to help clarify, the reconstructed elevation of the outpost tree in 1900 was subtracted from the elevation attained in 1950 in order to obtain an overall change value for the first half of the 20th century. Post–1950 values were computed by subtracting the value in1950 from the one in 2000. Tree density data were normalized using a natural-log transformation to compensate for large differences in ecotone area. Taken together, these data were compiled to determine whether treeline advance occurred during the 20th century and if so, to assess whether outpost tree establishment represented a single random event or was part of a switch to more favorable environmental conditions.

Spatial Analysis. Assessing the spatial pattern of tree establishment can help elucidate the relative importance of positive feedback and climate in governing upper treeline dynamics. I measured the spatial pattern of tree establishment by computing Ripley's $K(t)$ (Ripley 1977) on the x and y coordinates of each tree (including krummholz) ATL in my transects. Ripley's *K*(*t*) function is a second-order point pattern analysis based on the variance between points (tree-to-tree) in two-dimensional space that can identify particular patterns (random, clustered, or uniform) at varying spatial scales (Duncan 1991; Haase 1995; Ripley 1977). However, since *K*(*t*) can be difficult to interpret visually, my analysis used the function *L*(*t*), a square-root transformation of the function *K*(*t*) (Diggle 1983; Ripley 1977; Humphries, Bourgeron, and Mujica-Crapanzano 2008):

$$L(t) = [K(t) / \pi]^{1/2} - t \tag{1}$$

where *t* represents the distance between trees based on Euclidian measurements.

Computations were performed using Duncan's (1990) spatial analysis program. A toroidal edge correction was used and model simulations were based on a distance step of 1 m and calculated up to 12 m, with the exception of north-facing slopes in the FR, where more compact ecotones limited my analysis to 5 m. These dimensions adhere to the general practice of using a maximum distance equal to half the length of the shortest rectangular plot side. Sites with less than 10 trees above timberline were excluded from my analysis (CPN). Further details on my Ripley's *K* analysis can be found in Chapter 2.

Climate Analysis. To test for the influence of climate on tree establishment during the 20th century, age-structure data (1900–1995) were compared with identical five-year bins of mean climate data using Spearman's rank correlation coefficient (r_s). Correlation analysis was performed on all trees within each transect at a landscape, sub-regional, and regional scale to assess the potentially contrasting influences of climate along a latitudinal gradient.

Statistical similarities and correlations provide a suitable place to begin when investigating relationships in natural systems, but multiple lines of complimentary evidence improve the ability to independently assess linkages (Levin 1992). As a result, I used climate- and ecologically-based regime shift analysis to identify the possible synchrony between nonlinear threshold changes that can lead to regime shifts in both climate and tree establishment at upper treeline during the 20th century.

Several quantitative methods exist for identifying thresholds and regime shifts (see Anderson et al. 2009). I used a sequential algorithm method developed by Rodionov (2004) that is an exploratory or data-driven analysis where an *a priori* hypothesis on the timing of regime shifts is not needed (available for download at www.BeringClimate.noaa.gov). This separates it from classical intervention analysis, which cannot be used when the pivot point in a time series occurs at an *a priori* unknown time (Anderson et al. 2009). For my analysis, I used a 0.05 significance level to test for shifts in the mean value of the time series and a cut-off length of 10 years. The cut-off length and significance level affect the magnitude of regime shifts that can be detected, with a direct relationship occurring between cut-off length and the time scale of regimes detected (Rodionov and Overland 2005). A 10-year cut-off was used since numerous studies have shown evidence for decadal variability in climate throughout the western United States (McCabe, Palekci, and Betancourt 2004). More complete details for this method of analysis can be found in Rodionov (2004) and an applied example of its use can be found in and Rodionov and Overland (2005).

Results

Age Structure. I crossdated 1189 trees at upper treeline in the Rocky Mountains, with an average of 297 trees per mountain range (Table 2). The uppermost elevation of my transects had a range of 735 m, with treeline reaching 3734 m at the southernmost extent of the SDC at ca. 35°N, down to 2889 m in the BH at ca. 44°N (Table 2).

Tree establishment increased dramatically along the entire latitudinal gradient during the 20th century (Fig. 4). A majority of trees at each site are relatively young, as 84% and 66% of them have established since 1900 and 1950, respectively (Fig. 4). Moreover, increases in tree establishment are the most pronounced ATL (BTL), where 94% (42%) and 70% (23%) of trees have established since 1950 and 1970, respectively (Fig. 4). Within upper treeline environments in the Rocky Mountains, trees ATL on north-facing slopes are significantly younger ($p < 0.05$) and contain more seedlings (alive and dead) than their counterparts on south-facing slopes (Table 4; Fig. 5). Although past mortality rates remain unknown, my age-structure data indicate that there were virtually no trees ATL at a regional scale until the late 1940s (Fig. 4). Additionally, there is no evidence of previous tree mortality at or above timberline throughout my study area. This suggests that my age-structure data are representative of tree demography during the 20th century, which is accentuated by an abrupt increase in tree establishment initiated around ca. 1950.

From a spatial and temporal perspective, there is abundant tree regeneration occurring ATL throughout my study area (Figs. 6–9) that has led to marked variability in upslope advancement during the 20th century (Fig. 10). However, substantial increases in

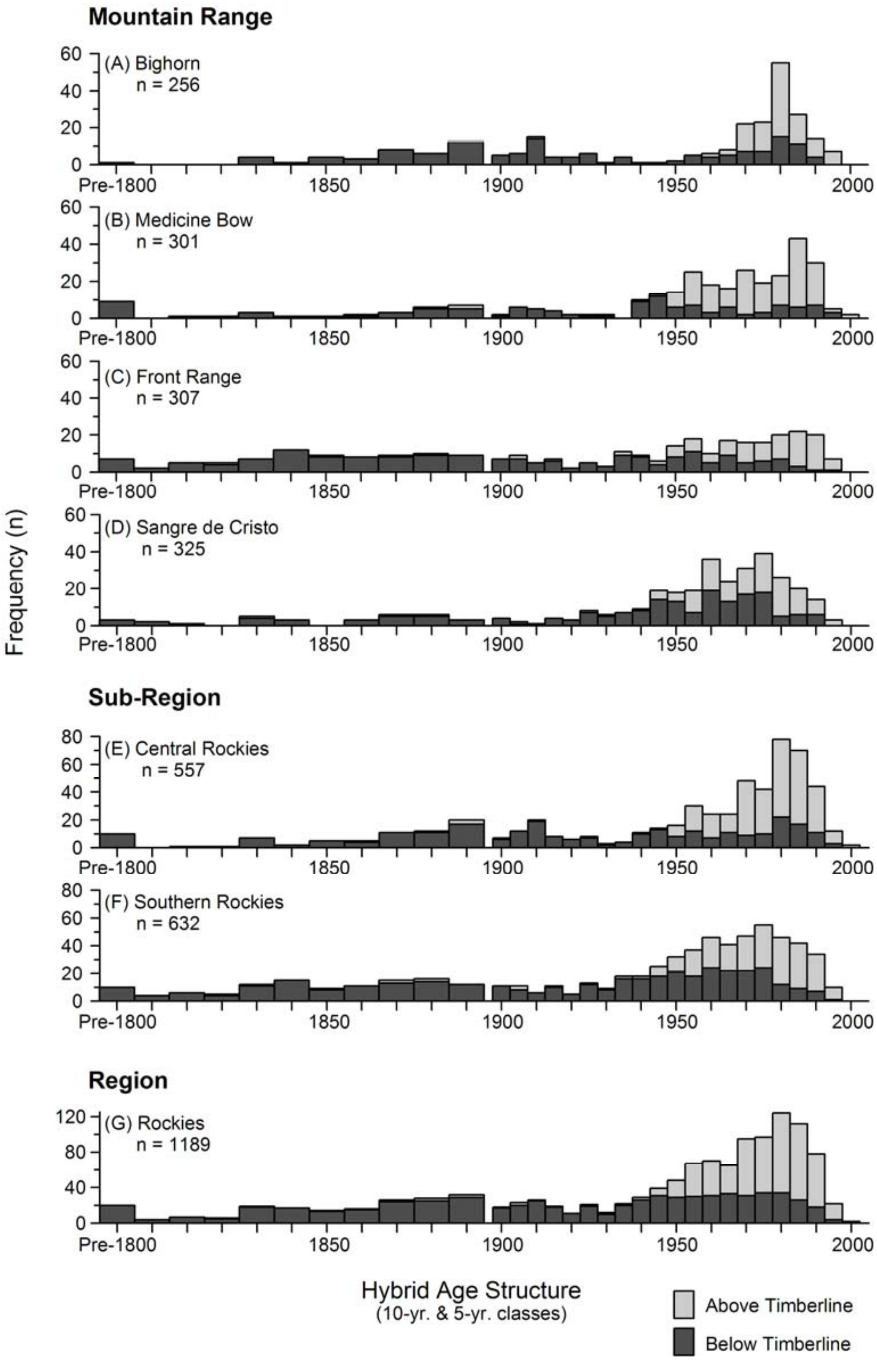


Figure 4. Hybrid age-structure data for trees above and below timberline at multiple spatial scales (landscape, sub-regional, and regional) along a latitudinal gradient (35°–44°N) in the Rocky Mountains. Trees that established before 1900 are in 10-year age-classes and 5-year age-classes are used for post–1900 establishment dates.

Table 4. Results of Mann-Whitney *U*-Tests comparing tree age distributions. Median tree age was tested using 95% confidence intervals. The bold *p*-values highlight comparisons where the null hypothesis was rejected (ie. statistically different). The bold abbreviation in parentheses indicates the mountain range or region with the statistically younger trees in the comparison. Columns represent the cumulative tree ages above timberline (closed canopy forest) and within the entire transect (above and below timberline). Refer to Table 1 for mountain range and regional comparison abbreviations. Other abbreviations include: SF–south-facing slope; NF–north-facing slope.

Comparison	Trees Above Timberline	Trees in Entire Transect
Landscape Scale		
BH–MB	**W=14006.5; *p*=0.002 (BH)**	W=72057.0; *p*=0.738
BH–FR	**W=11576.5; *p*=0.048 (BH)**	**W=63251.5; *p*=0.000 (BH)**
BH–SDC	**W=10901.5; *p*=0.000 (BH)**	**W=70357.0; *p*=0.045 (BH)**
MB–FR	W=27101.0; *p*=0.438	**W=80281.0; *p*=0.000 (MB)**
MB–SDC	W=27465.5; *p*=0.126	W=900465.5; *p*=0.065
FR–SDC	**W=13273.0; *p*=0.046 (FR)**	**W=106766.0; *p*=0.000 (SDC)**
SF BH–NF BH	W=3171.5; *p*=0.0125	W=18173.5; *p*=0.163
SF MB–NF MB	W=10218.5; *p*=0.574	**W=21425.0; *p*=0.003 (SFMB)**
SF FR–NF FR	W=3943.0; *p*=0.240	W=22699.0; *p*=0.606
SF SDC–NF SDC	**W=6406.0; *p*=0.030 (SDCNF)**	W=26812.5; *p*=0.335
Sub-Regional Scale		
CR–SR	**W=74518.5; *p*=0.011 (CR)**	**W=302645.0; *p*=0.000 (CR)**
SF CR–NF CR	W=25334.0; *p*=0.180	W=7997.5; *p*=0.432
SF SR–NF SR	**W=20337.5; *p*=0.016 (NFSR)**	W=97896.0; *p*=0.159
Regional Scale		
RM SF–RM NF	**W=90625.5; *p*=0.015 (RMNF)**	W=353143.0; *p*=0.070

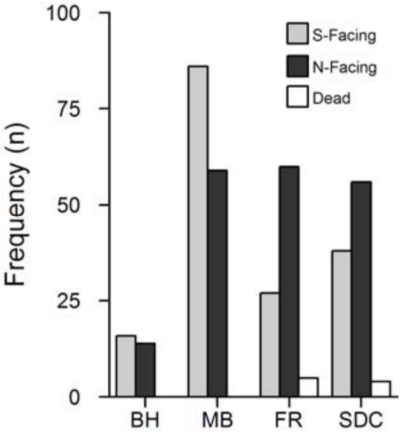


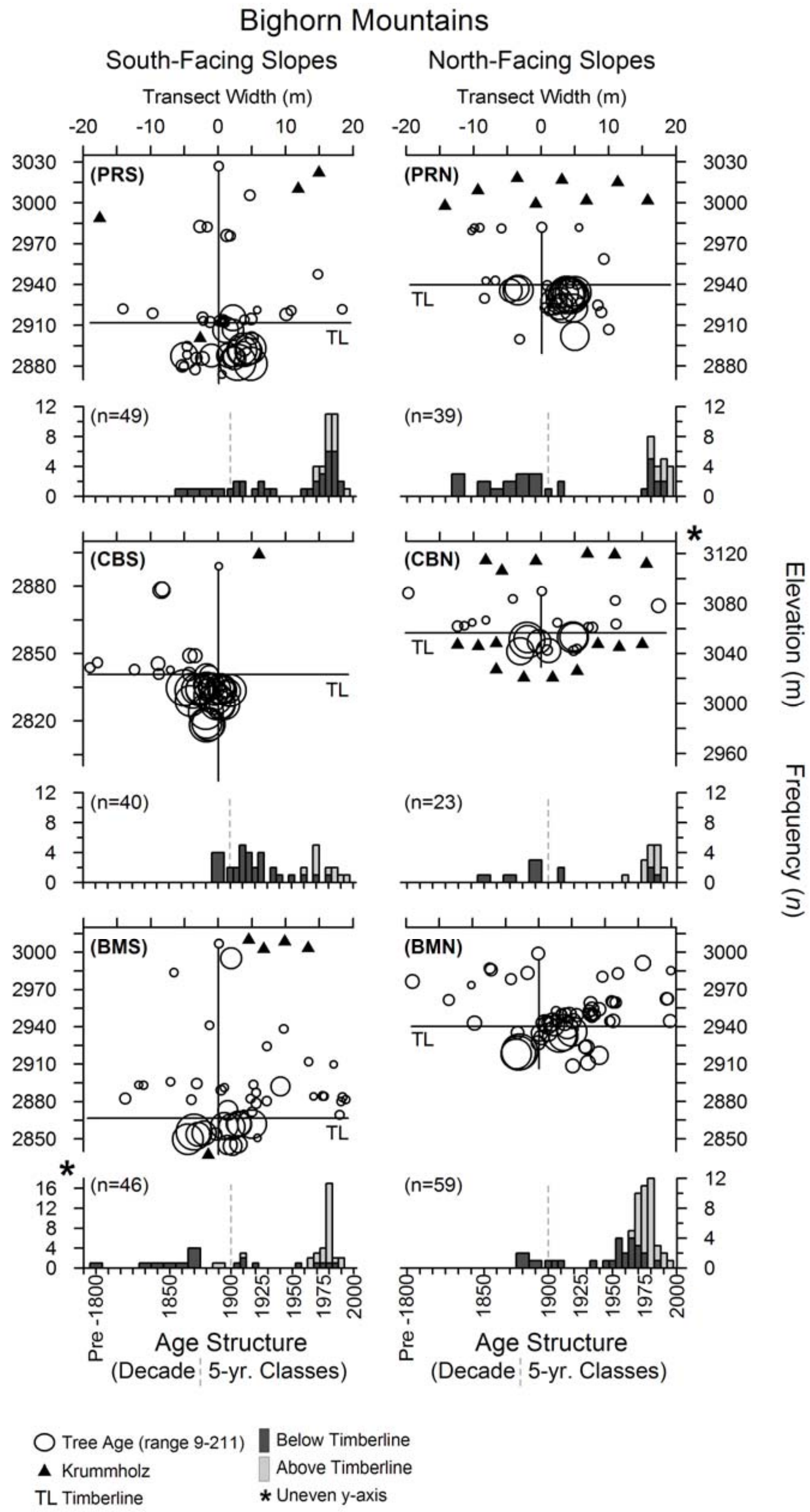
Figure 5. Seedling frequency stratified by slope aspect and mountain range.

tree density have occurred since 1950 along the entire latitudinal gradient (Figs. 4 and 10). At a sub-regional scale, trees ATL are significantly younger in the CR compared to the SR (Table 4). Within these sub-regions, slope aspect does not exert a strong influence on tree age in the CR, while trees on north-facing slopes are significantly younger in the SR (Table 4).

Local environmental conditions change along the latitudinal gradient, as upper treeline environments become more patchy and contain more krummholz above the outpost tree in the CR (Figs. 6–9). In addition, the importance of microtopographical shelter varies by sub-region, with 49% (8%) of trees growing in the lee of boulders in the CR (SR) (Table 5). Shelter is the most important for outpost tree establishment in the BH (Fig. 10), which also contain the youngest trees in my study area (Table 4).

Spatial Analysis. Spatial analysis using Ripley's *K(t)* function for trees growing ATL produced variable results based on sub-region, mountain range, and slope aspect. In the CR, there is no discernible mediation of spatial pattern by slope aspect. For example, tree establishment in the BH is primarily random on both north- and south-facing slopes (n = 2/3 sites) and entirely clustered in the MB (Table 5). In the SR, however, slope aspect is more influential in determining the corresponding spatial patterns of tree establishment ATL, particularly in the SDC. For instance, south-facing slopes in the SDC harbor clustered patterns of trees, while north-facing slopes have primarily random spatial configurations of trees (excluding GHN) (Table 5). Alternatively, random spatial patterns exist at every site in the FR with the exception of the southernmost site, PPS (Table 5). Collectively, the existence of spatially clustered patterns implies the

Figure 6. Spatial and temporal examination of upper treeline study sites in the Bighorn Mountains (BH). Transects and age-structure data are shown for adjacent north- and south-facing slopes. The width of the nested-belt transect extended to 40 m above timberline and was reduced to 20 m below. The hybrid age-structure data is divided between decadal (pre-1800–1890) and 5-yr. (1900–2000) age-classes. Note the different y-axis for elevation of CBN and age-structure of BMS. The patterns of krummholz mats is not based on exact coordinates and are used to illustrate the belt of krummholz that exist upslope from the outpost tree.


Bighorn Mountains
South-Facing Slopes
North-Facing Slopes
Transect Width (m)
-20
-10
0
10
20
(PRS)
(PRN)
(CBS)
(CBN)
(BMS)
(BMN)
TL
3030
3000
2970
2940
2910
2880
2850
2820
3120
3080
3040
2960
(n=49)
(n=39)
(n=40)
(n=23)
(n=46)
(n=59)
12
8
4
0
16
*
Elevation (m)
Frequency (n)
Pre-1800
1850
1900
1925
1950
1975
2000
Age Structure
(Decade | 5-yr. Classes)
Tree Age (range 9-211)
Krummholz
TL Timberline
Below Timberline
Above Timberline
* Uneven y-axis

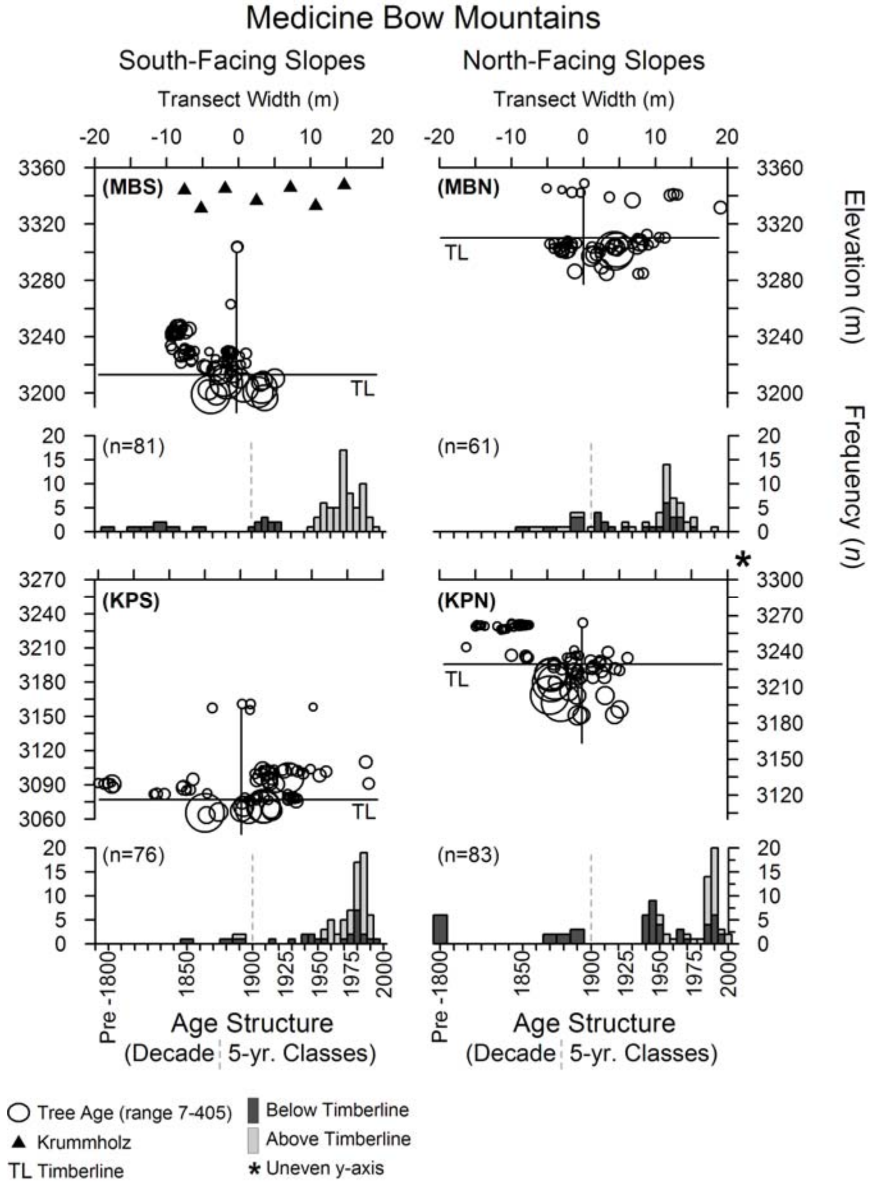
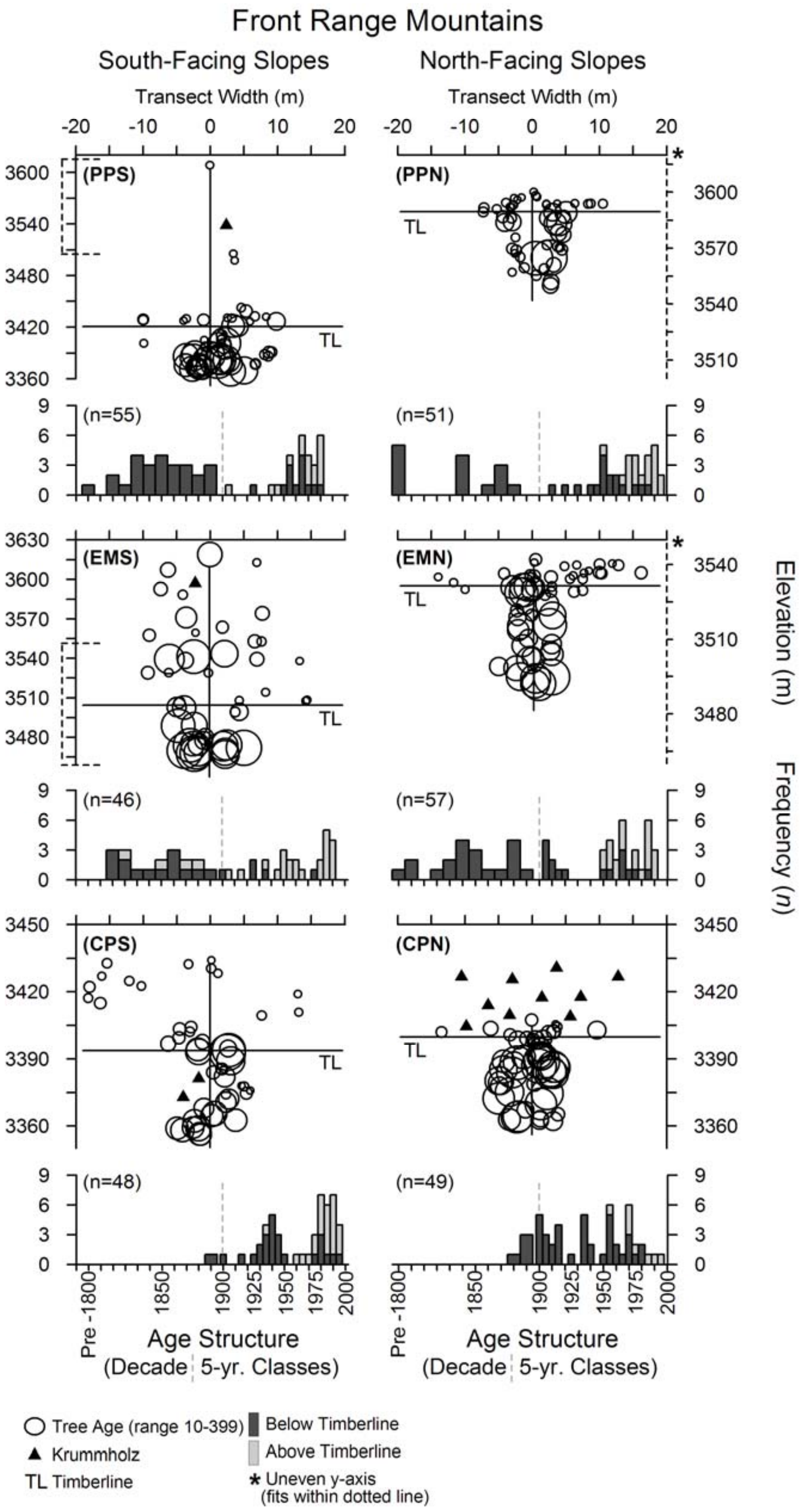


Figure 7. Spatial and temporal examination of upper treeline study sites in the Medicine Bow Mountains (MB). See caption for Fig. 6. Note the different y-axis for KPN.

Figure 8. Spatial and temporal examination of upper treeline study sites in the Front Range Mountains (FR). See caption for Fig. 6. Note that two north-facing transect y-axes (*) are plotted with different elevation values and that their position in relation to the corresponding south-facing transect is marked with a dashed line on the left y-axis. For CPN, the pattern of krummholz mats is not based on exact coordinates and is used to illustrate the belt of krummholz that exist upslope from the outpost tree.


Front Range Mountains
South-Facing Slopes
North-Facing Slopes
Transect Width (m)
-20 -10 0 10 20
(PPS)
(PPN)
(EMS)
(EMN)
(CPS)
(CPN)
TL
3360 3420 3480 3540 3600
3510 3540 3570 3600
3480 3510 3540 3570 3600 3630
3480 3510 3540
3360 3390 3420 3450
(n=55)
(n=51)
(n=46)
(n=57)
(n=48)
(n=49)
0 3 6 9
Elevation (m)
Frequency (n)
Pre-1800 1850 1900 1925 1950 1975 2000
Age Structure
(Decade | 5-yr. Classes)
Tree Age (range 10-399)
Krummholz
TL Timberline
Below Timberline
Above Timberline
* Uneven y-axis (fits within dotted line)

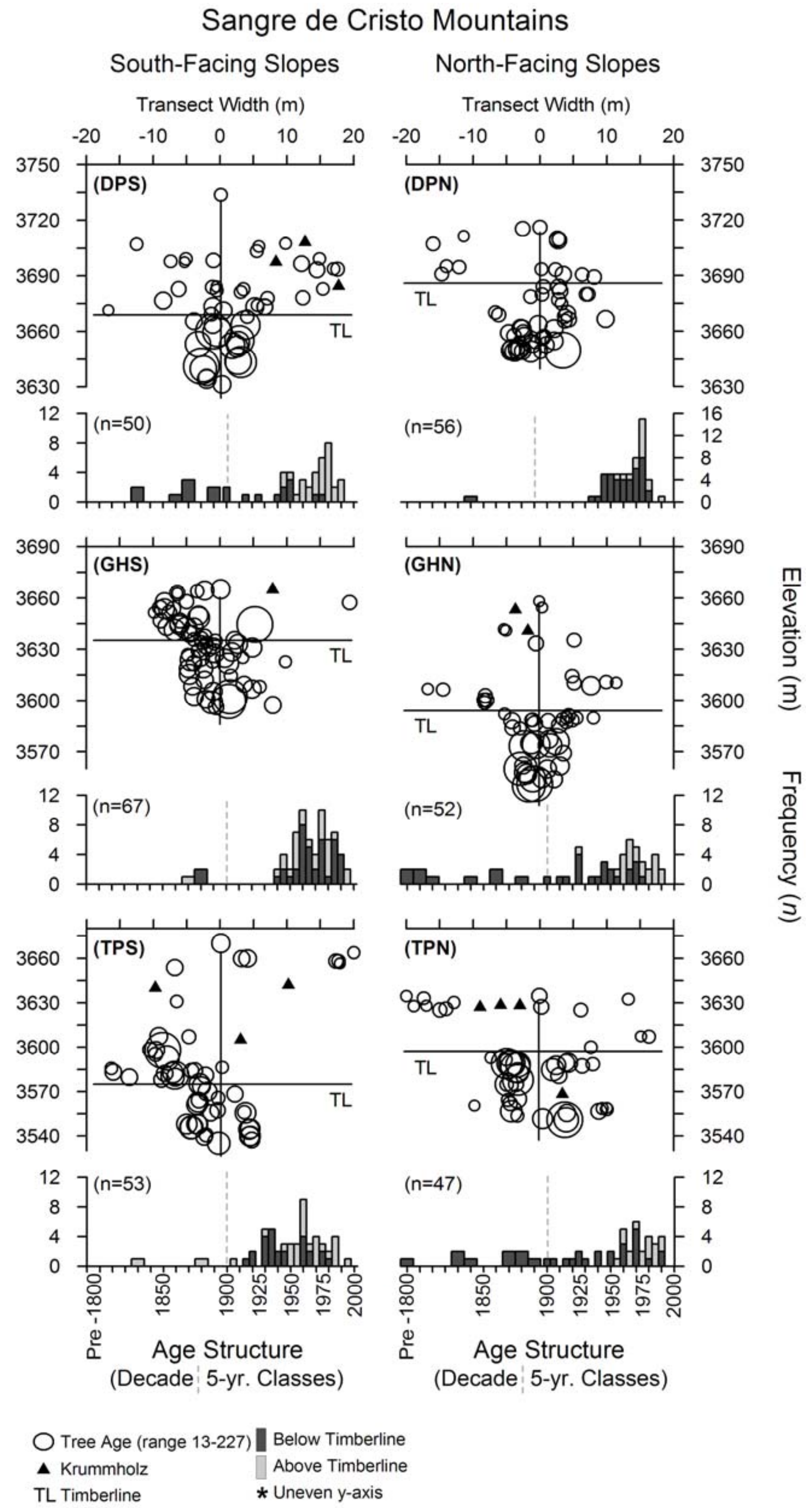


Figure 9. Spatial and temporal examination of upper treeline study sites in the Sangre de Cristo Mountains (SDC). See caption for Fig. 6. Note the different y-axis for age-structure of DPN.

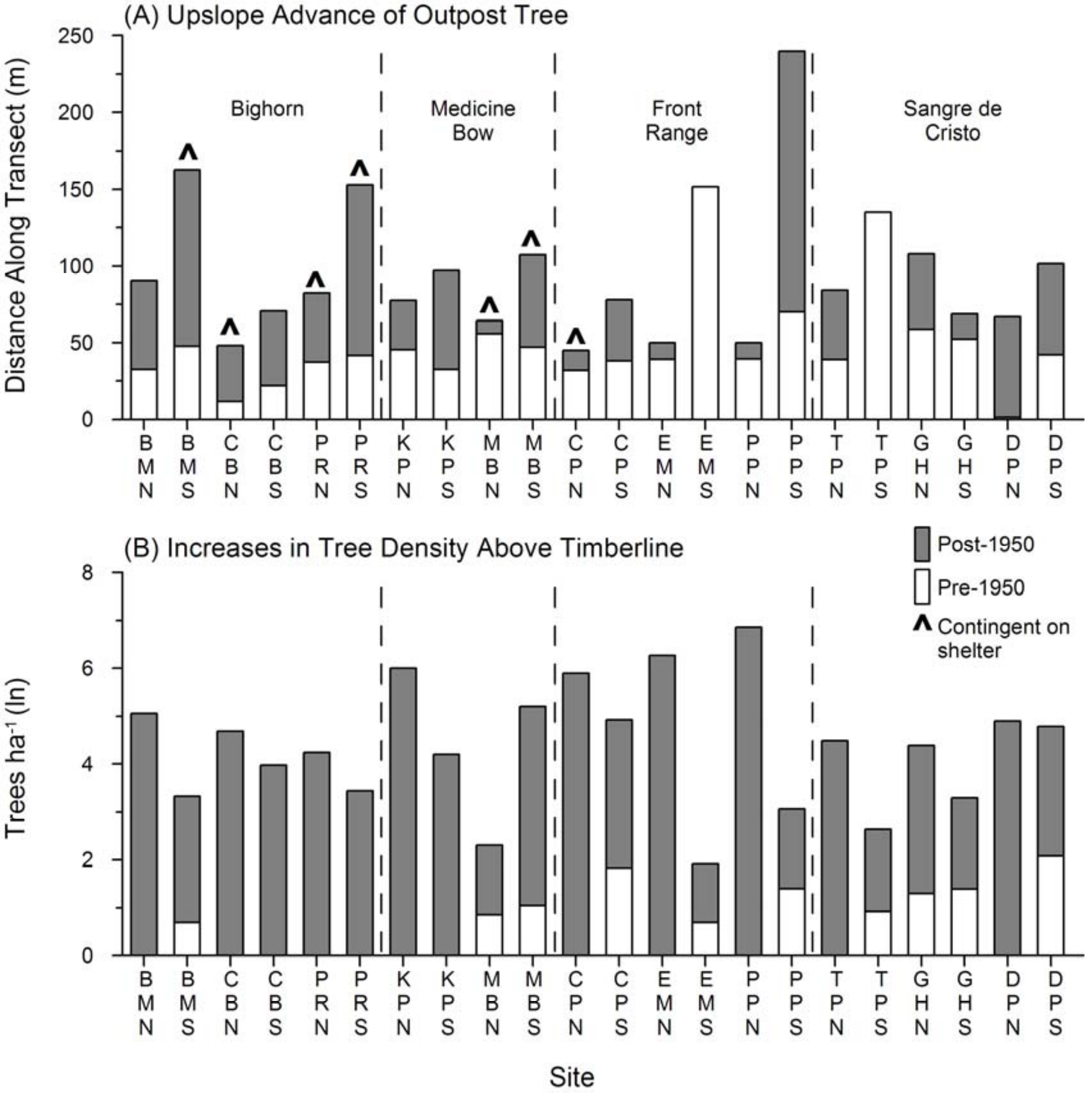


Figure 10. (A) Distance of outpost tree advancement upslope from 1900–1950 and 1950–present at each study site. (B) Increases in tree density above timberline from 1900–1950 compared to 1950–present at each study site.

importance of positive feedback in facilitating and perpetuating tree establishment ATL, which is the case throughout the MB and on south-facing slopes in the SDC. On the other hand, random spatial configurations imply that positive feedback plays a minimal role in creating conditions favorable for tree establishment in the FR and BH.

Climate. Each climate variable that I calculated was tested for a correlation with tree establishment using Spearman's rank correlation coefficient, but only correlations that were highly significant ($p < 0.01$) at a regional scale will be discussed in this chapter. In general, these values include minimum temperature and temperature range data. Specifically, the climate variables include: (1) spring Tmin; (2) cool season Tmin; (3) summer Trange; (4) cool season Trange. In addition, it is important to note that the degree of significance between tree establishment and climate varies at sub-regional and landscape scales along the latitudinal gradient in the Rocky Mountains.

At a regional scale along the latitudinal gradient, a *significant* (hereafter signifying a statistical comparison with a p-value < 0.01) positive correlation exists between tree establishment at upper treeline during the 20th century and minimum spring and minimum cool season temperature (Fig. 11). Conversely, tree establishment has a significant negative correlation with summer Trange and cool season Trange (Fig. 11). Each of these Tmin and Trange variables has the potential to reveal important biogeographical insight into upper treeline dynamics, particularly with regards to seasonal variability. However, the Tmin variables are significantly inter-correlated (r = 0.47–0.64; $p < 0.01$; Pearson's correlation), along with the Trange data ($r = 0.44$; $p < 0.01$; Pearson's correlation). Essentially, this means that any climatic change argument

Table 5. Ripley's *K(t)* analysis of tree patterns above timberline in the Rocky Mountains. Results are stratified by mountain range and slope aspect. The spatial pattern of tree establishment was determined from L(*t*) values using 1 m increments (1–12 m; excluding FR North–5 m) and 99% confidence intervals derived from Monte Carlo simulations (*n* = 1000). The overall spatial pattern of trees above timberline (ATL) is listed along with the percentage of 1 m increments that match the particular pattern. Site and mountain range abbreviations can be found in Table 1 and area was calculated for the rectangular portion of the transect located ATL. Microtopographical shelter refers to trees establishing next to boulders and species indicates the most frequently inventoried ATL. The abbreviation given for species is the first two letters of the genus and species, respectively. For example, the Latin name for Engelmann spruce is *Picea engelmannii* – Pi_en = PIEN.

Mtn. Range	Slope Aspect	Site	Trees ATL (n)	Area ATL (m^2)	Spatial Pattern (% L(*t*) Values)	Trees in Shelter ATL (%)	Species ATL
BH	*North*	BMN	34	2160	Clustered (100)	10	PIEN
		CBN	13	1200	Random (100)	100	ABLA
		PRN	12	1736	Random (67)	69	ABLA
	South	BMS	28	5280	Clustered (83)	87	ABLA
		CBS	10	1880	Random (75)	30	PICO
		PRS	16	4456	Random (100)	100	ABLA
MB	*North*	KPN	35	1200	Clustered (100)	2	PIEN
		MBN	30	1760	Clustered (100)	10	PIEN
	South	KPS	52	3520	Clustered (100)	0	ABLA
		MBS	64	3520	Clustered (100)	1	PIEN
FR	*North*	CPN	8	220	na (n<10)	50	ABLA
		EMN	21	400	Random (100)	0	PIEN
		PPN	20	210	Random (100)	0	PIEN
	South	CPS	22	1600	Random (92)	48	PIEN
		EMS	28	4640	Random (100)	0	PIEN
		PPS	17	7440	Clustered (100)	0	PIEN
SDC	*North*	TPN	19	1800	Random (100)	0	PIEN
		GHN	24	2740	Clustered (67)	0	PIEN
		DPN	15	1120	Random (100)	0	PIEN
	South	TPS	31	3800	Clustered (100)	0	PIAR
		GHS	28	1160	Clustered (83)	0	PIAR
		DPS	32	2496	Clustered (100)	0	PIEN

focused solely on a single Tmin or Trange variable is limited due to their highly significant inter-correlations. However, seasonal changes in temperature can lead to important changes in ecological processes and patterns at upper treeline.

At a sub-regional scale, the most notable correlation between tree establishment and climate is with summer Trange. Trees in the SR have a significant positive correlation, while a significant inverse correlation exists in the CR (Fig. 11). Overall, trees in the CR have more significant correlations with climate, although this breaks down at a landscape scale with no significant climate correlations in the MB or BH (Fig. 11). The FR is the only mountain range with a significant relationship between tree establishment and climate that appears to be favored by an increase in both summer and cool season Trange (Fig. 11). Correlations in the FR, along with the opposite significance of summer Trange above and below 40°N in the CR and SR, respectively (Fig. 11), represent the most notable distinctions with respect to my correlation analysis. Cumulatively, this suggests that contrasting climate mechanisms may be responsible for driving ecotonal dynamics at upper treeline in the CR and SR.

Regime shift analysis of tree establishment at a regional scale in the Rocky Mountains and significantly correlated climate variables provided insight into possible mechanisms for dramatic region-wide increases in tree establishment since 1950. At a regional scale, a regime shift in tree establishment during the 1950s (1950–1954 for all trees; 1955–1959 for trees ATL) indicates that a threshold was surpassed, most likely in response to an increase in minimum temperatures that triggered climate regime shifts between 1929–1934 (Fig. 12). This suggests that tree establishment had a lagged

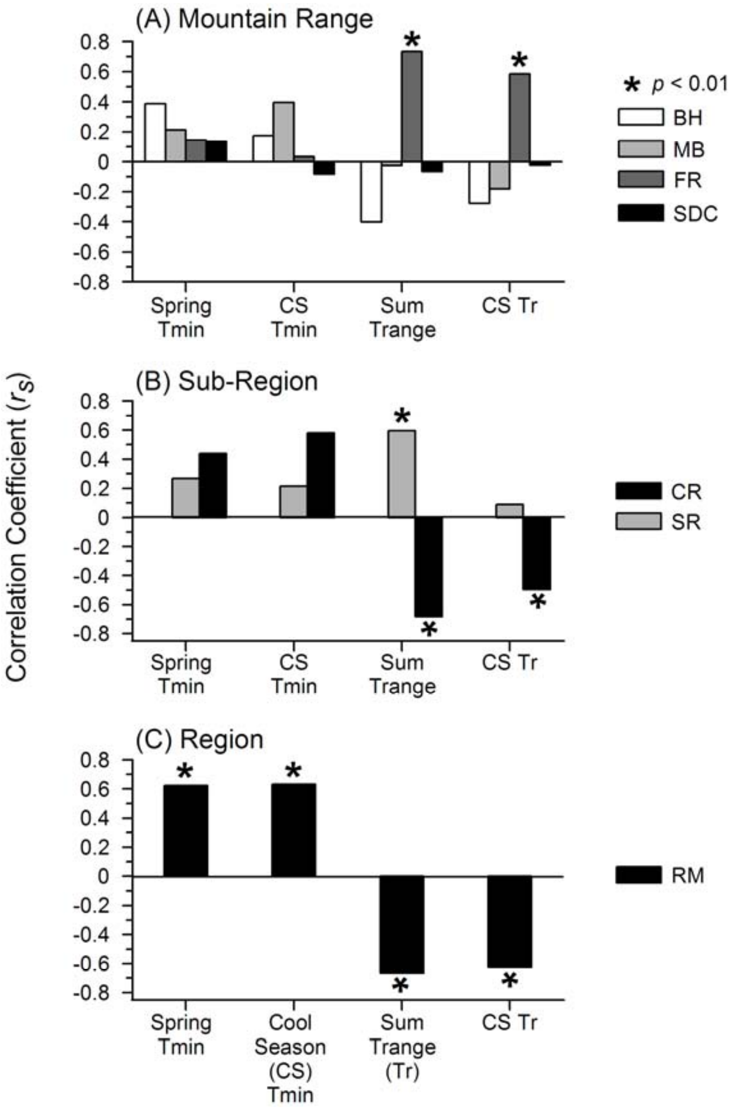


Figure 11. Significant ($p < 0.01$) Spearman rank correlation coefficients (r_s) comparing tree establishment with minimum temperature (Tmin) and temperature range (Tr) data at (A) landscape, (B) sub-regional, and (C) regional scales. Other abbreviations include: Sum – summer.

response of about 20 years to step changes in climate at a regional scale (Fig. 11). The most likely mechanism that facilitated a regime shift in tree establishment was a change towards warmer minimum and maximum temperatures during both the summer and cool season, respectively (Figs. 11 and 12). Increased tree establishment also corresponds with a decrease in cool season precipitation (Fig. 13).

A compelling difference exists in vegetation response to climate at a sub-regional scale in the CR and SR. For example, a lag time exists in the CR of approximately 20 years between a change in the abiotic forcing mechanism (climate) and subsequent biotic response (tree establishment), whereas in the SR, the ecological (trees ATL) and climate regime shifts appear to occur in relative synchrony during the early 1950s (Fig. 14). Synchronous conditions also exist in the FR and for comparison purposes, the BH regime shifts were plotted to assess the role of random spatial patterns in determining how ecological and climate step changes co-vary (Fig. 15). Overall, this suggests that tree establishment at upper treeline in the FR is more strongly driven by climate variability and that both climate and ecological thresholds play an important role in the dynamics of tree establishment at upper treeline.

Discussion

Upper Treeline Dynamics. The elevational extent of upper treeline increased during the 20th century and was accompanied by dramatic increases in tree density since 1950. Isolated establishment events ATL can be relatively common in some treeline environments (MacDonald et al. 1998), yet concurrent increases in tree density ATL suggest that a wholesale change occurred towards conditions more conducive to tree

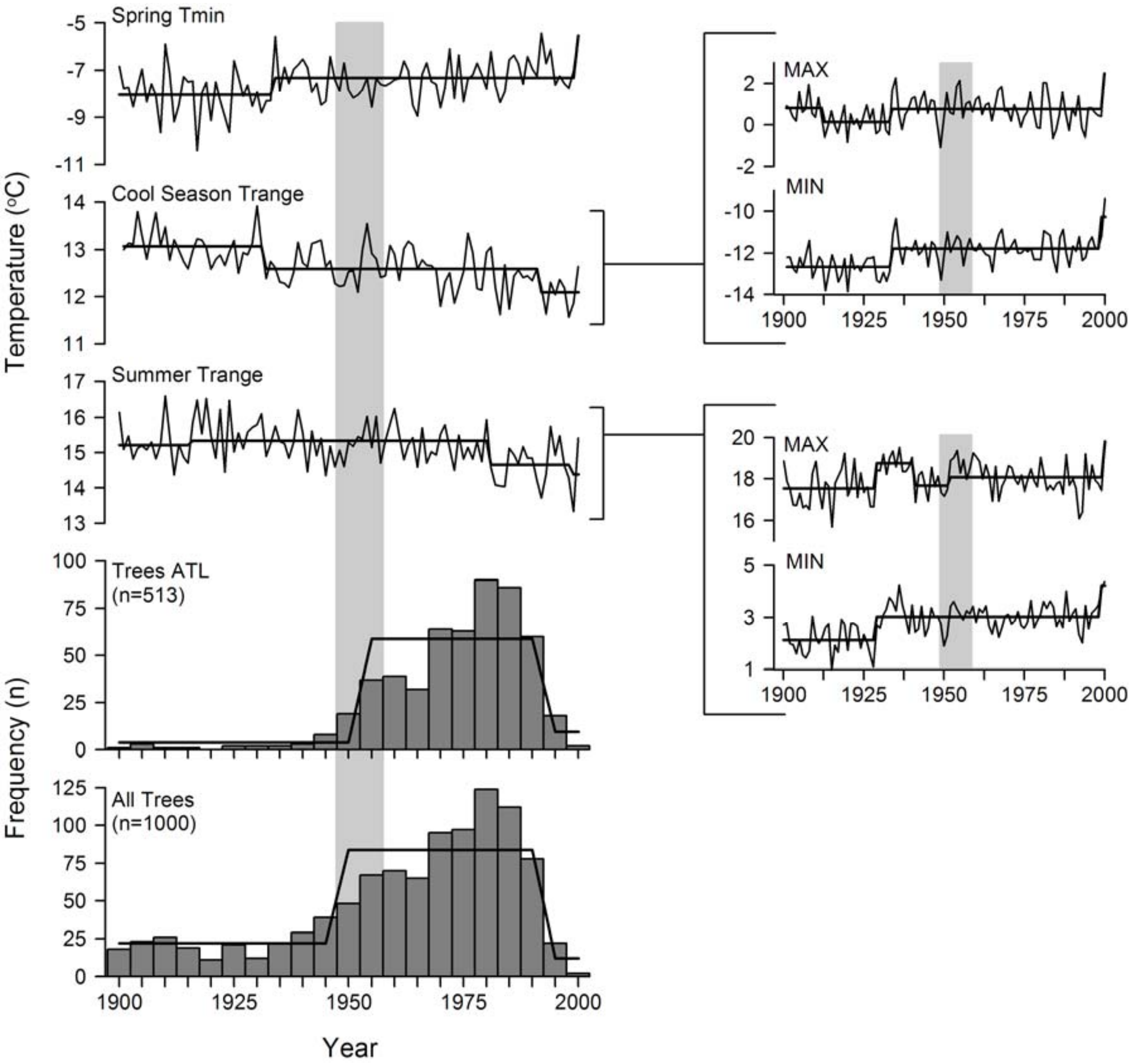


Figure 12. Regime shift analysis of tree establishment above timberline and the most strongly correlated temperature variables for the Rocky Mountain region. Individual time series that combine to form the temperature range data (Tmax and Tmin) are given to provide further insight into the temperature range variability.

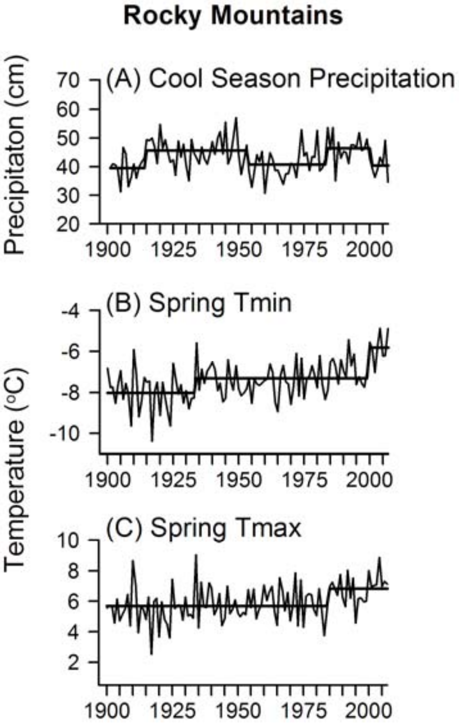


Figure 13. Climate time series and corresponding regime shifts of (A) cool season precipitation, (B) spring minimum temperature (Tmin), and (C) spring maximum temperature (Tmax) for the Rocky Mountain region.

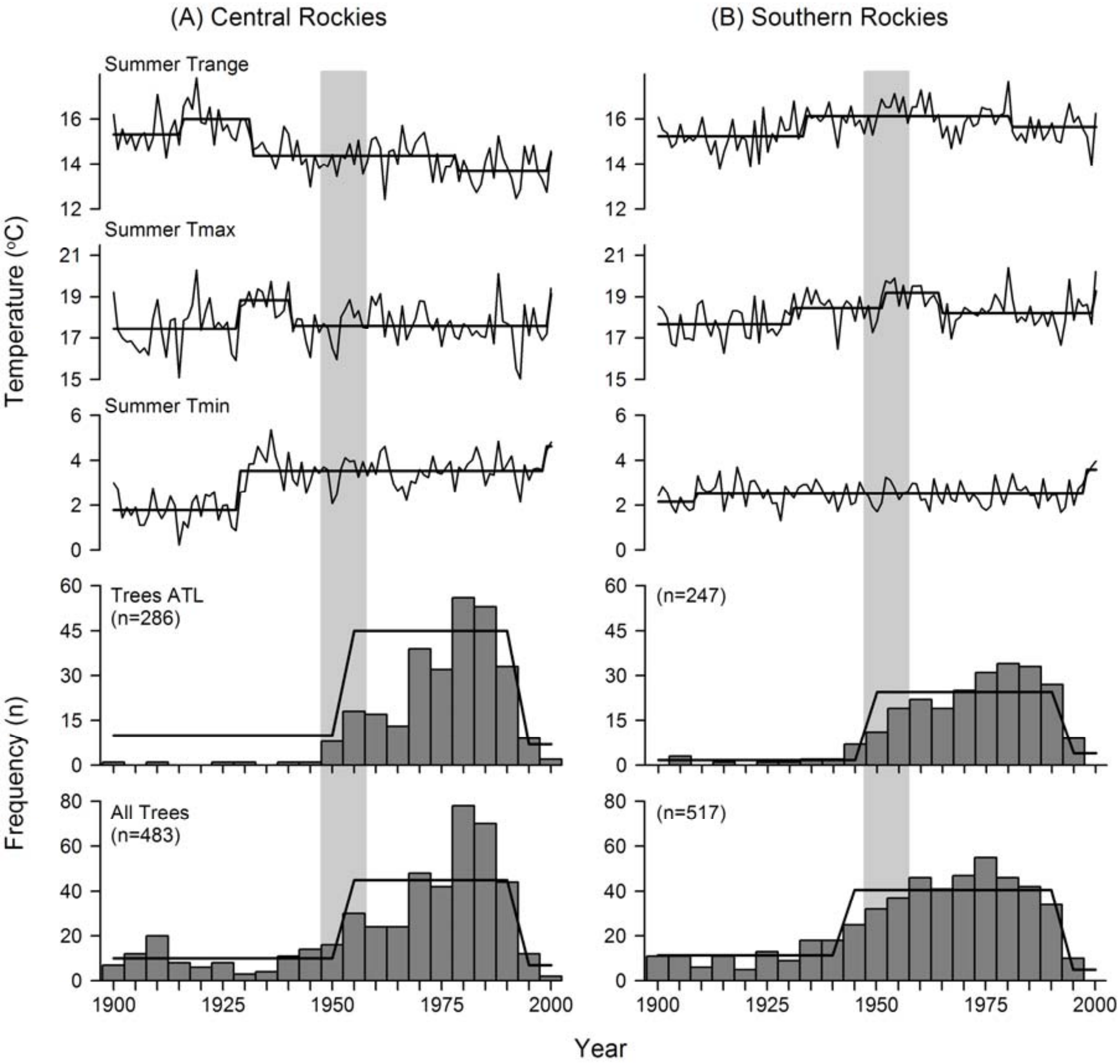


Figure 14. Climate and ecological regime shift analysis at a sub-regional scale for the (A) Central Rockies and (B) Southern Rockies. Climate time series consist summer temperature range (Trange), summer maximum temperature (Tmax), and summer minimum temperature (Tmin).

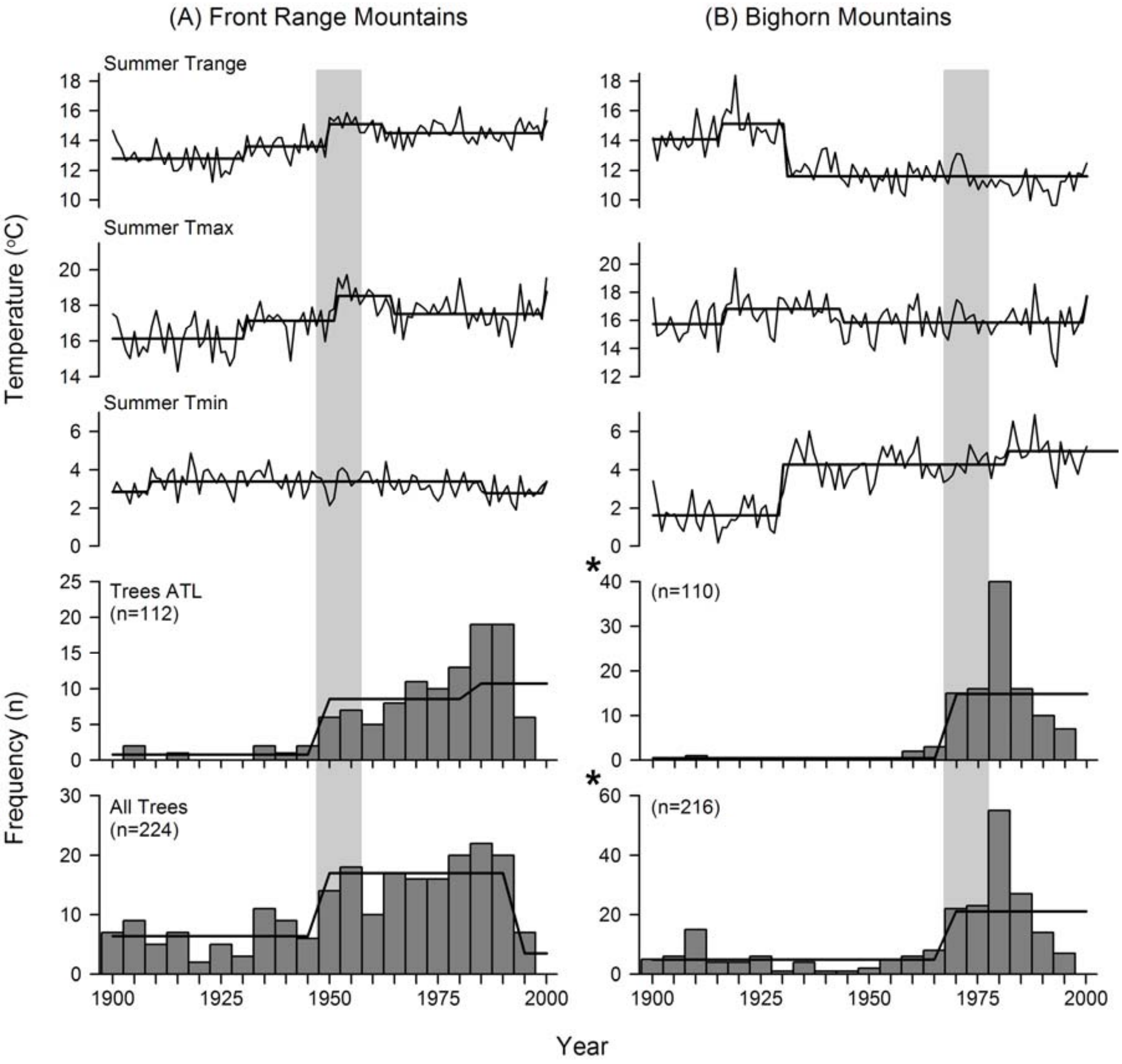


Figure 15. Climate and ecological regime shift analysis at a landscape scale for the (A) Front Range and (B) Bighorn Mountains. Climate time series consist summer temperature range (Trange), summer maximum temperature (Tmax), and summer minimum temperature (Tmin). Note the different (*) y-axes for trees in the Bighorns.

establishment. An increase in tree density at upper treeline during the 20th century is a commonly reported occurrence (Batllori and Gutiérrez 2008; Danby and Hik 2007; Klasner and Fagre 2002; Lloyd and Fastie 2003; Szeicz and MacDonald 1995) and may be a more suitable indicator of treeline climate sensitivity than upslope advancement (Camarero and Gutiérrez 2004). Despite the nearly ubiquitous rise of upper treeline during the 20th century in the Rocky Mountains, intra-regional variability exists in the degree of facilitation required for tree establishment ATL.

The availability of sheltered sites in the lee of boulders ATL become increasingly important in facilitating the upslope advancement of the outpost tree north of 40°N. Upper treeline advance contingent on the existence of sheltered sites could result from generally windy conditions at a given location (Daly and Shankman 1985) and these findings are in agreement with studies from the Northern Rockies (Resler 2006; Resler, Butler, and Malanson 2005) and Spanish Pyrenees (Batllori et al. 2009). However, my results are unique with respect to the possible discovery of a spatial threshold at 40°N, whereby the predominant processes governing upper treeline dynamics switch to the north and south of this parallel. Intra-regional variation in the ecological significance of processes driving treeline dynamics highlights the site-dependent nature of treeline response to climate (Dalen and Hofgaard 2005; Kullman and Öberg 2009; Malanson et al. 2007). Based on the varying degree of facilitation required for treeline advance within my study region, it appears that the influence of wind is more important north of 40°N, but this difference cannot overshadow or provide a suitable explanation for the generally synchronous changes in tree density and establishment at a regional scale along the entire latitudinal gradient.

The prominent pattern of successful tree establishment ATL along the entire latitudinal gradient coupled with the temporal synchrony of increased regeneration since 1950 (94% ATL) suggest the importance of climate in governing upper treeline dynamics (Batllori and Gutiérrez 2008; Lloyd and Fastie 2003; Millar et al. 2004; Swetnam and Betancourt 1998). In essence, there were virtually no trees in current areas ATL prior to 1950 and the subsequent initiation of widespread establishment is evidenced by the abundance of relatively young trees ATL in all mountain ranges, regardless of slope aspect. This contrasts sharply with the results of previous research on upper treeline dynamics where successful tree regeneration ATL was primarily confined to south-facing slopes, with the position and structure of treeline ecotones remaining relatively stable on north-facing slopes for the past several hundred years in the Canadian Rockies (Danby and Hik 2007; Luckman and Kavanagh 2000) and Scandes Mountains of Sweden (Kullman 1998). Further, north-facing slopes contain significantly younger trees ATL at a regional scale, in the SR (see Chapter 2), and in the SDC, which implies that the initiation of tree establishment began later than on opposing south-facing slopes.

A delayed response in tree regeneration on north-facing slopes, in addition to the slope aspect mediation of tree age, suggests that a bioclimatic threshold may have been surpassed, possibly related to soil moisture conditions. In addition, a rapid onset of tree regeneration ca. 1950 could be partly attributed to positive feedback resulting from the initial establishment of a few individuals ATL that subsequently ameliorated local environmental conditions, thereby facilitating continued regeneration (Alftine and Malanson 2004; Lloyd 2005; Smith et al. 2003; Wilson and Agnew 1992). However, the ability of positive feedback processes to cause sudden changes in recruitment can be contingent on the spatial patterns present (Malanson 1997), which in turn can affect vegetation–climate interactions at upper treeline (see Chapters 2 and 3; Bader, Rietkerk, and Bregt 2008; Bekker 2005).

Relative Influences of Pattern, Feedback, and Climate on Tree Establishment at Multiple Spatial Scales. The relative effects of spatial pattern and positive feedback on the degree of climatic influence at upper treeline is most apparent at a landscape scale and diminishes in importance at sub-regional and regional scales. Identifying variation in the importance of certain patterns and processes operating at different spatial scales forms the basis for understanding the driving mechanisms and for predicting future change in treeline environments (sensu Levin 1992). However, the underlying mechanisms often operate at a different spatial scale than which it is manifested, presumably from either the aggregation of small spatial scale interactions or as emergent patterns constrained by processes functioning at larger spatial scales (Levin 1992). The remainder of the discussion will attend to how tree establishment at upper treeline is affected by the relative influence of spatial pattern, feedback, and climate and how this varies by spatial scale of analysis along a latitudinal gradient in the Rocky Mountains.

In my study region, the interaction between abiotic and biotic processes at a local site scale combine to form important spatial patterns that emerge at a landscape scale, which influence climate correlations with tree establishment and temporal rates of vegetation change. For example, when trees are situated in a random spatial pattern they are less reliant on positive feedback with neighboring vegetation and thus, more closely aligned with climate (see Chapter 2; Bader, Rietkerk, and Bregt 2008). Evidence for this exists with trees at upper treeline in the FR, which have the only significant climate correlations at a landscape scale that occurs between tree establishment and summer and cool season Trange. Yet, even more compelling is the synchronous regime shifts that occurred with tree establishment and summer Trange and Tmax during the early 1950s (1950–1954). The apparent tight coupling between climate and tree establishment in the Front Range corresponds to what Kullman (1998, 2001, 2002) and Luckman and Kavanagh (1998; 2000) found with the upslope advance of treeline in the Swedish Scandes and Canadian Rocky Mountains, respectively. Taken together, the combination of trees growing in a random spatial pattern in the FR along with significant climate correlations and synchrony between abiotic (temperature) and biotic (tree establishment) regime shifts provides a strong case for the role of spatial pattern in determining treeline sensitivity to climate. However, given the lack of climate correlations in the BH, where trees are predominantly situated in a random spatial pattern, some important caveats exist with respect to the interactions between climate and spatial patterns of tree establishment at upper treeline.

Despite the primarily random pattern of tree establishment ATL in the BH (4/6 sites), there are no significant correlations with climate or synchronous switches between ecological and climate regime shifts. The explanation for this can be attributed to the need for sheltered microsites in order for successful tree establishment to occur ATL (Fig. 16). This suggests that wind is a primary driver of upper treeline dynamics in the BH, as the abundance of krummholz throughout upper treeline environments would suggest (e.g., Holtmeier and Broll 2005). The ramifications of this for understanding pattern-feedback-climate interactions in the BH are as follows. First, trees are in a random spatial pattern almost exclusively as a result of boulders being randomly distributed across the landscape. Second, the site (BMN) with minimal trees growing in the lee of boulders (10%) exhibits a clustered spatial pattern, which suggests that when shelter is not available, that positive feedback-driven clustered patterns are required to ameliorate the generally harsh (windy) climate conditions. Finally, when considering the need for sheltered sites, the influence of temperature on tree establishment appears to be subservient to the role of local microtopography (e.g., Butler et al. 2007; Resler, Butler, and Malanson 2005).

Boulders create ideal microsite conditions for establishment ATL because they create shelter from the wind, reduce direct sun exposure, and do not compete with trees for limited resources (Resler, Butler, and Malanson 2005). In addition, depending on the size of the boulder, it can reduce wind speed and enhance snow deposition in the immediate vicinity (Hiemstra, Liston, and Reiners 2002). Pockets of snow deposition can increase the chances of seedling survival (Hättenschwiler and Smith 1999), which can thereby initiate the facilitative properties associated with positive feedback and eventual treeline advance (Johnson, Germino, and Smith 2004; Resler 2006; Smith et al. 2003). Although, given the relative dearth of seedlings in the BH coupled with my extensive field observations, the influence of positive feedback appears to be confined to microsites in close proximity to shelter. Overall, given the overwhelming majority of tree establishment in the lee of a boulder, upper treeline dynamics in the BH appear to be operating under the predominant influence of microsite wind-shelter interactions, rather than from landscape scale increases in temperature during the 20th century.

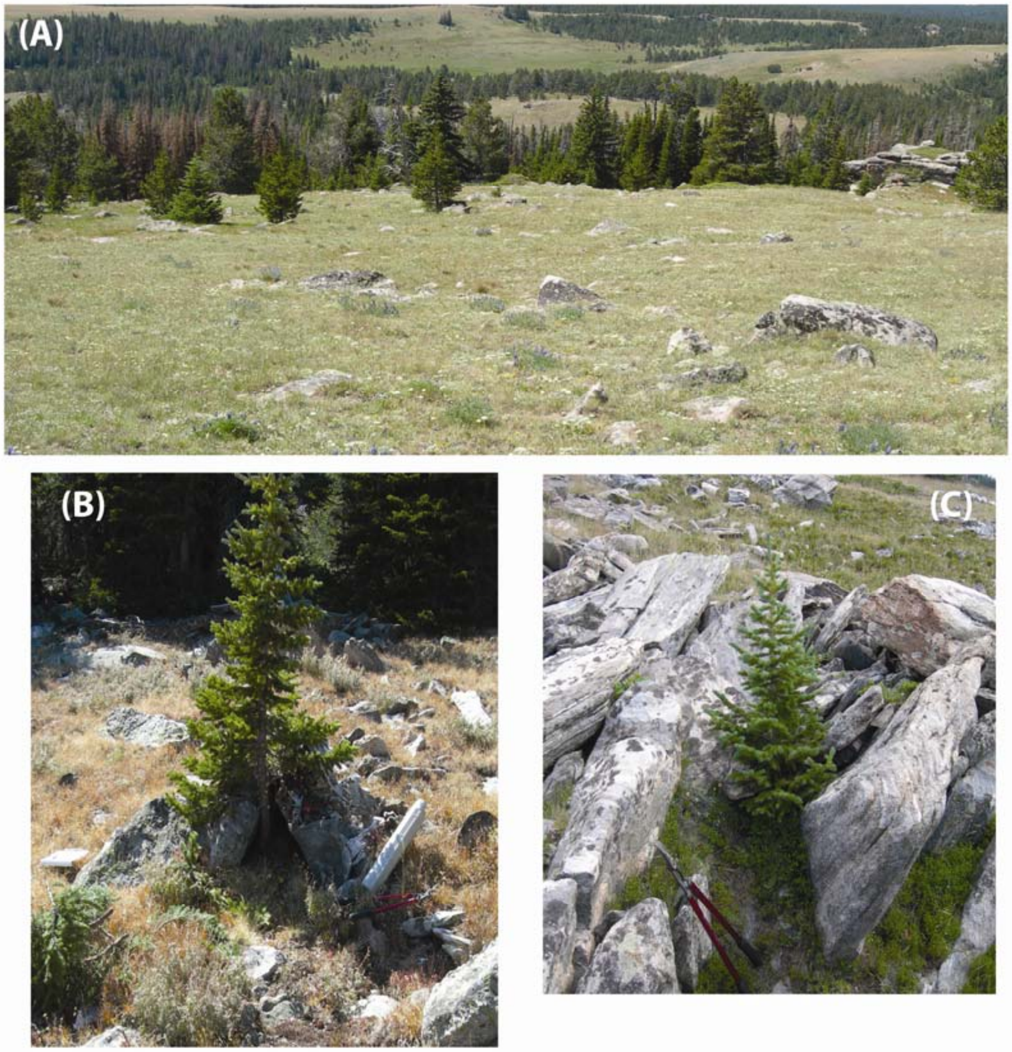


Figure 16. Examples of tree establishment above timberline (ATL) in the sheltered lee of boulders in the Bighorn Mountains (BH). Photos are from the following study sites: (A) BMS; (B) CBN; (C) PRS. Refer to Table 1 for site abbreviations. Note in photo (A) how tree establishment downslope within the treeline ectone is only found in areas with sufficient shelter from nearby boulders.

Widespread tree establishment ATL in the BH did not begin until 1970 and they contain the youngest trees in my study region. I cannot rule out the possibility that this onset of establishment represents a disturbance-induced pulse of regeneration (i.e. following a fire), but the likelihood of a landscape-wide fire at each one of my sites during this period is very low. In addition, no charcoal or visible fire-scar evidence exists at my sites. Instead, the majority of tree establishment ATL since 1970 suggests that climate conditions may have become more favorable during the late 20th century to permit successful regeneration in areas with sufficient shelter. Previous research documented a pronounced influence of climate at upper treeline as a result of infrequent disturbance events (e.g., Baker and Weisberg 1995; Lloyd 2005) and thus, a dual contingency may exist with respect to upper treeline advance, whereby tree establishment is dependent on both shelter availability and warmer temperatures. Under this scenario, upper treeline vegetation was unable to capitalize on the existing sheltered sites until temperatures warmed past a bioclimatic threshold, thereby permitting establishment to occur upslope, so long as sheltered microsites were available.

This double contingency-linked requirement for tree establishment ATL in the BH could help explain the lag time between abrupt climate regime shifts in the first half of the 20th century (1917–1944) to the eventual regime shift in tree establishment during the early 1970s. Despite the apparent synchrony between ecological and climate regime shifts in the FR, a majority of previous studies at upper treeline suggest that a considerable lag time may exist between changes in climate and treeline dynamics (Delcourt and Delcourt 1992; Lloyd and Graumlich 1997; MacDonald et al. 1998; Noble 1993; Payette et al. 1989). In the case of the BH, even though random patterns exist, the contingencies required for successful tree establishment ATL complicate the influences of climate, so that tree responses resemble what I found in areas with clustered spatial patterns (see Chapters 2 and 3). Collectively, although temperature likely plays a role in facilitating the observed patterns of tree establishment in the BH, my results suggest that it is likely of secondary importance compared to shelter from the wind.

Tree regeneration ATL in the MB and SDC is predominantly clustered and has no significant correlations with climate. This can be explained by the overriding importance of local biotic relationships associated with positive feedback that act to reduce the climatic sensitivity of tree establishment at treeline (see Chapter 2; Bader, Rietkerk, and Bregt 2008). Comparisons of tree age ATL at a landscape scale support this, as significantly older trees are found in the MB and SDC, likely as a result of an increased lag time between climate inputs and corresponding tree establishment.

Upper treeline environments in the MB and SDC experience relatively harsh conditions for my study region, with relatively large annual temperature ranges compared to the FR and BH. Consequently, the increased climate stress renders trees more dependent on plant interactions. This is consistent with other research at or near upper treeline in the Italian Alps (Emanuele et al. 2008), Spanish Pyrenees (Camarero, Gutiérrez, and Fortin 2000), and Northern Rocky Mountains (Callaway 1998; Callaway et al. 2002), where spatial clustering or facilitation among plants increased with abiotic extremes. Clustered tree patterns that result from positive feedback interactions ATL have the ability to ameliorate harsh environmental conditions that would otherwise preclude tree establishment by providing shade to reduce diurnal temperature range, shelter from wind dessication, and/or to help trap snowpack in order to prolong the availability of soil moisture during the growing season (e.g., Bekker 2005; Germino, Smith, and Resor 2002; Smith et al. 2003). Furthermore, Maher and Germino (2006) found competition that arises from clustered spatial patterns to be almost negligible and seedling mortality more likely to result from extreme microclimate conditions without protective cover than from competitive exclusion by neighboring vegetation. Cumulatively, the landscape scale variability in the spatial pattern of tree establishment ATL suggests that the primary mechanisms governing upper treeline dynamics differ between mountain ranges and as a result, so does the importance of positive feedback in facilitating the upslope advance of treeline.

Although clustered spatial patterns dependent on positive feedback exist in both the MB and SDC, these biotic configurations appear to be driven by separate abiotic processes. For instance, in the MB, strong winds are common, particularly during the winter, and result from prevailing westerly winds that get funneled through a low point in the Continental Divide approximately 70 km to the west (Knight 1994). Thus, wind plays a major role in the distribution and pattern of vegetation at upper treeline, with patches of trees generally corresponding to areas of cool season snow accumulation that prolong soil moisture availability during the relatively dry summer growing season (e.g., Hiemstra, Liston, and Reiners 2002; Malanson et al. 2007; Wooldridge et al. 1996). At upper treeline, summer drought conditions caused by reduced snowpack have been attributed to an increase in seedling mortality (Hättenschwiler and Smith 1999) and this predisposes conifer needles to death or injury from cuticle abrasion during the winter (Hadley and Smith 1986). However, anomalously high snowpack that persists throughout much of the summer can limit seedling establishment by shortening the growing season (Moir, Rochelle, and Schoettle 1999). Amelioration of harsh abiotic conditions through positive feedback-induced spatially clustered patterns of tree establishment ATL therefore provides an efficient means for trees to withstand windy and dry growing seasons that depend on cool season snowpack to supply soil moisture. Perhaps more importantly, this indicates that despite a similar need for reduced wind exposure in the BH, trees in the MB rely on positive feedback to create biologically-ameliorating patterns of establishment (i.e. clustered) rather than microtopographical shelter in the form of boulders.

In the SDC, clustered patterns of tree establishment ATL appear to result from temperature-induced moisture stress. This helps explain the slope aspect mediation of spatial pattern (see Chapter 2), whereby clustering is primarily confined to warm and dry south-facing slopes. Moisture stress is likely exacerbated on south-facing slopes in the SDC since they experience the warmest maximum temperatures in my study region. Furthermore, tree establishment at upper treeline in the CR and SR was limited on south-facing slopes as a result of relatively high levels of sunlight that led to increases in water stress and diurnal temperature range (Germino and Smith 1999; Germino, Smith, and Resor 2002; Weisberg and Baker 1995). In my case, tree establishment was not limited on south-facing on slopes; rather the spatial pattern is more dependent on positive feedback, likely as a result of heightened moisture stress.

At a sub-regional scale, there is no discernible influence of spatial pattern on correlations with climate and a decrease in summer and cool season Trange has apparently led to an increase in tree establishment. Interestingly, trees in the CR and SR have an opposite correlation with summer Trange due to the relative variation in minimum and maximum temperatures north and south of 40°N, respectively. In the CR, summer Tmin has increased dramatically during the 20th century and consequently, reduced the overall temperature range during the summer. This corroborates the findings of the latest IPCC Report (2007) that discusses the strong spatial variability of minimum temperature trends, particularly since summer minimum temperature has exhibited no trend throughout most of the 20th century in the SR. Given the significant correlation with tree establishment, considerable increases in minimum temperature throughout the CR appear to have favored successful regeneration at upper treeline. Alternatively, summer Tmax has increased in the SR south of 40°N and led to a larger summer Trange with enhanced tree establishment. In addition to the identification of alternate precipitation regimes (Dettinger et al. 1998) and air mass trajectories (Mitchell 1976) to the north and south of 40°N, this research has provided evidence for contrasting changes in 20th century minimum and maximum temperature trends above and below this parallel. Perhaps more noteworthy, conditions have apparently become more favorable for tree establishment during this time, despite both a decrease and increase in summer Trange in the CR and SR, respectively. Thus, from a sub-regional scale perspective, the influence of the precipitation dipole at 40°N appears to be of minimal importance compared to broad scale temperature trends in governing tree establishment at upper treeline in the SR and CR.

Although the spatial patterns of tree establishment do not appear to influence significant correlations with climate at a sub-regional scale, my regime shift analysis suggests that pattern can play a secondary role in the overall sensitivity of upper treeline environments to climate. For example, even at a sub-regional scale, synchronous regime shifts occurred between climate (summer Tmax) and tree establishment in the SR. Conversely, substantial time lags exist between the initial step change in climate and corresponding regime shifts in tree establishment in the CR. Yet, in both cases, the predominant spatial patterns of tree establishment at a landscape scale and related importance of positive feedback can provide insight into these relationships. For instance, in the CR, tree establishment ATL is contingent on local site conditions that ameliorate generally harsh, windy conditions through random shelter availability in the BH and positive feedback in the MB. The overriding importance of shelter and biotic feedback interactions therefore act to override the immediate influence of warmer temperatures and as a consequence, create considerable time lags in tree response to climate. On the other hand, the widespread existence of random spatial patterns in the SR renders the trees less dependent on local interactions involving positive feedback and thus, more responsive to corresponding changes in temperature. As a result, my analyses suggest that while the influence of temperature on tree establishment is significant at a sub-regional scale, the temporal response of upper treeline vegetation to changes in climate can be modified depending on the relative influence of positive feedback in creating spatial patterns at a landscape scale. Ultimately, this research supports the likelihood of a spatial threshold at 40°N, whereby pattern and process at upper treeline are primarily controlled by wind and site-specific shelter availability to the north (CR), versus to the south (SR), where the interaction between temperature and precipitation exerts the most control.

Tree establishment at upper treeline during the 20th century along the entire latitudinal gradient in the Rocky Mountains reflects the influence of macroscale climate inputs that supplant the influences of positive feedback, spatial pattern, and alternate precipitation regimes at a sub-regional scale. At large spatial scales, upper treeline is characterized as a temperature-limited system (Jobbágy and Jackson 2000; Körner 1998b; Körner and Paulsen 2004) in which climate exerts the primary control on the dynamics of tree establishment (e.g., Camarero and Gutiérrez 2004; Holtmeier and Broll 2005; Lloyd and Fastie 2003; Malanson et al. 2007). Moreover, the influence of climate on tree demography is most apparent at a regional scale (Swetnam and Betancourt 1998; Villalba and Veblen 1997). In my case, a regime shift in tree establishment occurred during the early 1950s that is especially pronounced for trees ATL and is coincident with an overall increase in minimum temperature throughout the year. Previous studies have attributed increases in regeneration and related treeline advance to generally warmer conditions since the termination of the Little Ice Age ca. 1850 (e.g., Danby and Hik 2007; Hessl and Baker 1997; LaMarche and Mooney 1967; Lloyd and Fastie 2003; Payette and Filion 1985; Vittoz et al. 2008). However, the pervasive influence of minimum temperature and corresponding seasonal interactions provide some notable distinctions.

Collectively, the regional climate conditions responsible for dramatic increases in tree establishment at upper treeline during the latter half of the 20th century resulted from warmer minimum temperatures that caused a reduction in temperature range in the spring, summer, and cool season. This differs from the findings of the recent IPCC Assessment (2007) that documented a comparable increase in both minimum and maximum temperatures, leading to a relatively constant trend in temperature range. However, an increase in minimum temperature has been linked to an enhanced response in treeline vegetation to climate in the Sierra Nevada (Millar et al. 2004) and in northwestern China when accompanied by high spring precipitation (Wang, Zhang, and

Ma 2006). In addition, recent research has demonstrated the importance of warmer winters in facilitating both tree establishment and subsequent treeline advance (Kullman 2007, 2002; Kullman and Öberg 2009). Ulitmately, warmer minimum temperatures are an important catalyst for changes in upper treeline dynamics because they can directly influence plant physiology by determinging the length of both the growing season and frost-free period.

In my study, there is synchrony at a regional scale between the step change in establishment (1950–1954) and corresponding reduction in cool season precipitation (1954) and a similar pattern exists at a sub-regional scale in the CR (Fig. 17). The acquisition of century-long snowfall data are limited in the Rocky Mountains, yet temperature data show that warming throughout the Rocky Mountain region has been the most pronounced in the spring (e.g., Groisman et al. 2004; Schwartz, Ahas, and Aasa 2006; Westerling et al. 2006) and the most variable during the cool season (November–April) (Wallace, Zhang, and Bajuk 1996). In my case, despite the absence of statistically significant correlations with precipitation, the interactions between warmer temperatures in general and snow in particular likely play an ecologically significant role in regulating upper treeline dynamics. The interactions between cool season temperature and snowpack conditions have been shown to exert a strong control on tree establishment and growth at upper treeline by influencing soil moisture conditions, the availability of regeneration safe-sites, and the length of the growing season (e.g., Hättenschwiler and Smith 1999; Hessl and Baker 1997; Holtmeier and Broll 2005; Kullman and Öberg 2009). Further, although earlier snow-free conditions coupled with warmer temperatures have produced conflicting results with respect to treeline advance (e.g., Camarero and

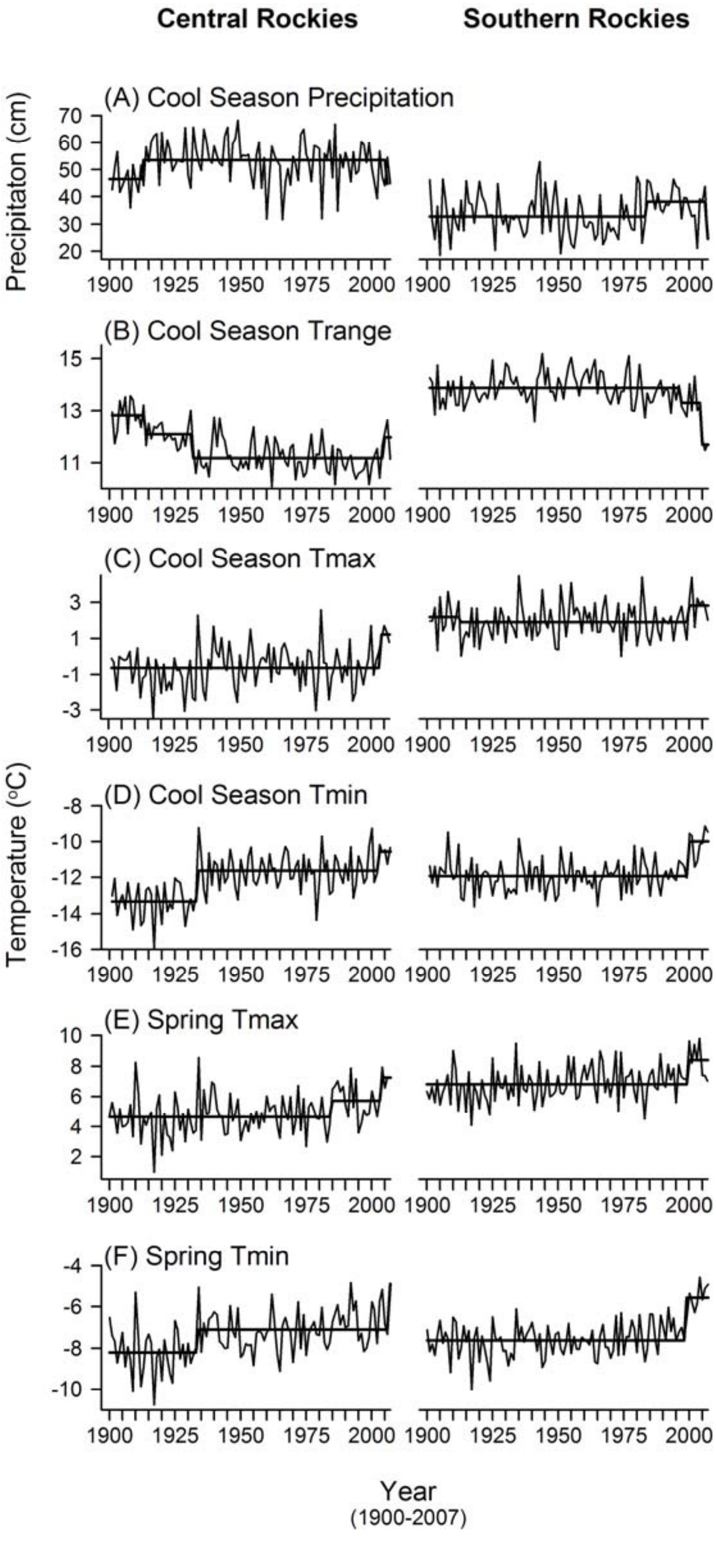


Figure 17. Climate time series and corresponding regime shifts at a sub-regional scale in the Central and Southern Rockies for important climate variables related to snowpack conditions.

Gutiérrez 2004; Kullman 2002; Luckman and Kavanagh 1998; Taylor 1995), my research suggests that these conditions could have facilitated the abrupt increases in tree establishment and related upslope advance of treeline, along with the differences in tree age and spatial patterns present throughout my study region, particularly in the SR.

Overall, if climate does indeed exert a top-down control on ecological processes at a regional scale (e.g., Hessburg, Kuhlmann, and Swetnam 2005), then the following scenario seems plausible for the aforementioned region-wide changes in patterns and processes observed at upper treeline during the 20th century in the Rocky Mountains. To begin, the initial regime shift increases in temperature during the early- to mid-1900s set the stage for tree establishment to take advantage of a regional reduction in snowpack after 1954. Once the temporal alignment of warmer conditions and less snowpack occurred, trees were able to colonize ATL on warm south-facing slopes first. For comparison, this potential double contingency resembles what I found in the BH with respect to temperature and shelter availability. However, after several consecutive years of reduced snowpack, tree establishment began to become moisture-limited on south-facing slopes, which could be why they contain older trees. Coincidentally, while trees on south-facing slopes were becoming drought-stressed, a threshold was passed on north-facing slopes, initiating widespread establishment that occurred later on and thus, younger trees. Furthermore, the onset of these drought-like conditions may have provided the catalyst for feedback-driven clustered spatial patterns on south-facing slopes, such as in the SDC. This scenario would apply less to the CR, yet my research suggests that the SR are more closely aligned with climate, although clustering in the MB and the existence of boulders in the BH would act in a similar manner to help trap snowpack and prolong available soil moisture. Clustered spatial patterns of tree establishment on the south-facing slopes of my four southernmost mountain peaks in the SR also support the possibility that this chain of events occurred, as they are subject to the warmest conditions in my study region and consequently, probably the most drought-stressed. In addition, the lack of spatial clustering on south-facing slopes to the north of Pikes Peak may indicate that conditions were never severe enough (warm and dry) to depend on positive feedback and subsequent clustering (see Chapters 2 and 3). This also implies that continued warming could surpass a critical threshold that would force tree establishment ATL to depend more on positive feedback and therefore become clustered (see Chapter 2). Ultimately, despite the lack of statistically significant correlations with annual or seasonal precipitation at a regional scale, tree establishment at upper treeline is undoubtedly influenced by the spatiotemporal interactions of temperature and precipitation. However, these interactions may become more pronounced at smaller spatial scales where they can be inferred by assessing the spatial patterns of tree establishment in conjunction with climate data.

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Chapter 5. Conclusions and Synthesis of this Research

The conclusions of this multi-scale research suggest that upper treeline ecotones in the Rocky Mountains are indeed sensitive to climate, yet its relative influence on treeline dynamics can vary dramatically depending on slope aspect, spatial pattern of tree establishment, mountain range, and location relative to 40°N. Moreover, the most influential aspect of climate throughout my study region appears to be temperature, although wind–snow interactions can sometimes override the direct effect of temperature at smaller spatial scales, such as in the Medicine Bow Mountains. When considering scale, there is no absolute best spatial scale of analysis because it depends entirely on the research questions at hand (Brown 1995; Levin 1992). In my case, using a multi-scale approach ranging from the local scale (slope aspect) to regional scale along a latitudinal gradient proved to be helpful in ascertaining the role of key processes and patterns responsible for vegetation interactions with climate at upper treeline. In the following paragraphs, I will highlight the main findings of this research and how they relate to future upper treeline response to continued warming.

Local Scale (Slope Aspect). The most important result of my local scale analysis was the slope aspect mediation of spatial patterns of tree establishment. This was the most pronounced in the Sangre de Cristo Mountains, where most of the mesic north-facing slopes contained a random pattern of tree establishment, while clustered spatial patterns existed on more xeric south-facing slopes. North-facing slopes also harbor significantly younger trees as a result of more favorable growing conditions, evidenced by random spatial patterns.

These results indicate that north-facing slopes represent a better barometer for measuring the influence of climate on upper treeline ecotones in the Rocky Mountains. Moreover, this situation will likely remain under continued warming unless moisture becomes limiting on mesic north-facing slopes, at which point the dynamics will more closely resemble that of their south-facing counterparts.

Landscape Scale (Mountain Range). The most compelling result from this research was the discovery that spatial patterns of tree establishment above timberline at a local scale can influence landscape scale climate correlations along a latitudinal gradient and the temporal response of upper treeline to changing climate conditions. Essentially, treeline ecotones containing trees growing in a random spatial pattern are more sensitve to climate because of the reduced dependence on positive feedback, whereas the opposite holds true for clustered spatial patterns, which are more reliant on local feedback interactions with neighboring vegetation. Given that moisture limitation appears to be one driving mechanism behind the formation of spatially clustered trees, it can be assumed that areas of upper treeline with randomly distributed trees maintain adequate soil moisture conditions during the growing season. In my study, these conditions were primarily confined to the Front Range and north-facing slopes in the Sangre de Cristo Mountains, which suggests that these areas are more sensitive to immediate changes in temperature.

An important caveat to increased climate sensitivity with random spatial patterns exists in the Bighorn Mountains, where despite the random arrangement of trees above timberline, no significant correlations exist between climate and tree establishment. This is a direct result of contingencies related to shelter availability above timberline, and thus, the spatial pattern is determined by the location of boulders rather than by initial tree establishment. However, trees that establish in the lee of a boulder could provide local ameliorating conditions necessary for the onset of positive feedback, although this does not appear to be the case yet, given the relative lack of seedlings in close proximity to sheltered sites.

A relatively large compilation of literature exists on strictly treeline–climate interactions and to a lesser extent, on how treeline structure (i.e. pattern) can vary based on local site conditions. Yet, to the best of my knowledge, this represents the first study to explicitly combine the two to gain a more holistic understanding of upper treeline–climate dynamics. Moreover, these results have global implications for how upper treeline environments will respond to continued warming, which is likely to be most pronounced in ecotones with random spatial patterns of tree establishment, as long as temperatures do not warm past thresholds that create moisture limitations. In that case, a threshold will most likely be surpassed whereby spatial clustering is required for continued successful regeneration in order to help trap snowpack, which would prolong moisture availability into the summer growing season.

Sub-Regional Scale (North and South of 40°N). The most notable result from my sub-regional scale analysis was the discovery of an apparent spatial threshold at 40°N, whereby tree establishment at upper treeline is more directly influenced by changes in climate (temperature and precipitation) to the south of this parallel. Upper treeline dynamics appear to be more strongly influenced by wind and corresponding patterns of snow accumulation to the north of 40°N, although it is clear that warmer temperatures during the latter half of the 20th century have created more favorable conditions for establishment. In this case, warmer temperatures play a secondary role and in order for them to be the most effective in governing upper treeline dynamics, other contingencies must exist, such as sheltered sites or sufficient snowpack accumulation.

In addition to the spatial threshold, tree establishment at upper treeline was favored by opposite temperature range variables (minimum and maximum temperature) to the north and south of 40°N. For instance, in the Central Rocky Mountains, warmer minimum temperatures have decreased both summer and cool season temperature range and as a result, apparently created conditions more favorable for tree establishment. Conversely, warmer maximum temperatures have increased the summer temperature range in the Southern Rockies, which has led to a corresponding increase in successful tree establishment at upper treeline. Taken together, my sub-regional scale results indicate that the influence of the precipitation dipole situated at ca. 40°N is minimal, and that temperature and wind regimes exert the most direct control on upper treeline dynamics.

This research therefore suggests that upper treeline response to continued warming will likely vary to the north and south of 40°N. An increase in minimum temperature needs to be accompanied by a decrease in regional wind speeds in order for upper treeline ecotones in the Central Rocky Mountains to respond the most directly to climate change. Alternatively, in the Southern Rocky Mountains, continued increases in maximum temperature will likely continue to favor tree establishment, as long as the system is not warmed beyond critical thresholds that create widespread moisture limitations and thus, clustered spatial patterns.

Regional Scale (ca. 35°N–ca. 44°N). At a regional scale, the most noteworthy result of this research was the significant influence of warmer minimum temperatures. Considerable increases occurred during the cool season, spring, and summer, which reduced the temperature range and additionally, appears to have acted in conjunction with a period of reduced snowpack during the late 20th century to create favorable conditions for tree establishment region-wide, particularly above timberline. Evidence for a wholesale switch to more favorable conditions can be seen in my regional age-structure and tree density data from above timberline, which both illustrate the dramatic increases that coincided with this period.

This suggests that the global climate change signature up to this point in my study area reflects an overall increase in warmth, accentuated by a decrease in severe minimum temperatures that have reduced seasonal temperature ranges. These conditions, coupled with a reduction in cool season precipitation, appear to have favored both an increase in tree establishment at upper treeline and subsequent treeline advance. Thus, although temperature exerts the most direct control on upper treeline dynamics at a regional scale, the interaction between temperature and snowpack remains critical for understanding the future response of upper treeline ecotones to continued warming. More importantly, in order to gain a comprehensive understanding of how key processes and patterns responsible for governing upper treeline dynamics interact with climate, a multi-scale approach across environmental gradients is needed.

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