SPATIAL PATTERNS AND TYPOLOGY CHANGES OF AN ADVANCING TREELINE ON PIKES PEAK, CO

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By

Kelsey Kjestine Elwood

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Miroslav Kummel, Ph.D.
Assistant Professor

Howard Drossman, Ph.D.
Professor

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ABSTRACT

Alpine treeline is a valuable indicator of climate change because of its sensitivity to temperature. On Pikes Peak (Southern Rocky Mountains, Colorado), tree density and elevation in the forest-tundra ecotone has increased in the last century, corresponding with a 2°C increase in regional growing-season temperature. The purpose of this study was to provide a detailed analysis of the process of treeline advancement. Spatial clustering within age classes and elevational bands was used to identify harsh environments and track the upper climatic boundary of tree establishment. Overall, clustering (Ripley's K, $p < 0.01$, based on boot-strapping) was more prominent at lower elevations and for older cohorts, indicating the upward migration of the climatic boundary. However, the climatic boundary may be advancing more quickly than treeline as the moving edge changed from a clustered to a randomly dispersed distribution over time: from 1868-1940 the moving edge was clearly clustered, from 1941-1976 it showed mixed results, and from 1977-2010 it displayed a random spatial pattern. Treeline advancement also demonstrated a reach-and-fill pattern, with sudden advancement of treeline, followed by a few decades of infill at lower elevations. The reach-and-fill pattern repeated three times in the last 120 years, with exponential increases in tree density, especially in the last 40 years. The recent explosion of growth and the quickly advancing climatic boundary match temporally with a shift from an abrupt to a diffuse edge typology. To my knowledge, this is the first study that examines in detail the process of changing treeline typology of an advancing treeline.

INTRODUCTION

Globally, climate changes over the last century have led to increased surface temperatures, likely from anthropogenic emissions of greenhouse gases (Fischlin et al., 2007). Average surface temperatures have risen about 0.74°C, but it is expected that temperatures will continue to rise in the future from positive feedback mechanisms and the continued presence of greenhouse gases in the atmosphere (Fischlin et al., 2007). Ecotones, the transitional zone between two distinct habitats, are of special interest to ecologists because they may be particularly sensitive to climatic changes (Walther et al., 2002; Risser, 1993). Alpine and arctic ecotones may be especially affected by global warming because temperature increases have been more pronounced at high altitudes and latitudes (Walther et al., 2005; Fischlin et al., 2007). Growth at treeline, an alpine ecotone representing the transition between closed-canopy forest and the upper limit of tree species growth, is constrained by temperature and therefore may be particularly sensitive to changes in climate. Evaluating changes in treeline elevation, treeline typology, and tree distribution patterns provides valuable insight into the ecological relationship between climate change and subalpine ecosystems. Around the world, there is solid evidence that treelines are advancing to higher elevations, that the treeline migration happens more frequently for treelines with a diffuse edge, and that changes in treeline typology represent particularly significant climate changes (Harsch & Bader, 2011). There is a lack of research, however, exploring whether observed changes in treeline match the rate of climate change or whether climate is changing more quickly than treelines can respond. To explore the relationship between treeline dynamics and climate change, it is first important to understand the mechanisms that control treeline elevation.

Growth at alpine treeline is limited by the upper climatic boundary, which represents the elevation with the harshest environment possible for successful establishment of tree species. Scientists believe that the upper climatic boundary at alpine treeline is primarily controlled by temperature, especially growing-season temperature means (Körner, 1998; Grace et al., 2002). Based on global treeline patterns, it seems that treelines generally establish at elevations corresponding to an average seasonal temperature of about 6°C, possibly representing the maximum isotherm for tree establishment (Körner, 1998; Grace et al., 2002). Körner proposes that temperature may affect tree establishment by limiting cell production and development below a thermal threshold (Körner, 1998; Shi et al., 2008). Körner's growth-limitation hypothesis is supported by experiments that suggest that carbon supply does not limit tree growth at treeline, but rather that low temperatures inhibit carbon use (Shi et al., 2008). The growth-limitation hypothesis also explains why warmer summer temperatures correlate with increased regeneration above treeline and faster radial growth (Bolli et al., 2007; Grace et al., 2002; Feiden, 2010).

With increased temperatures from global climate change, scientists expect that the upper climatic boundary will rise in elevation, allowing tree invasion into previously treeless tundra (Kullman, 2002). Already, many researchers have reported treeline advancement during the last century (e.g., Kullman, 2002; Harsch et al., 2009; Walther et al., 2005; Earnest, 2011; Fieden, 2010). A recent meta-analysis of treeline research found that fifty-two percent of treelines studied were advancing, while only one percent were retreating (Harsh et al., 2009). The global trend in treeline advancement mirrors the global increases in temperature observed in the last century. Elevational changes are important in understanding the relationship between climate and treeline, but treeline typology may also play a critical role affecting treeline dynamics.

Treeline typology may have a significant impact on the response of treeline to temperature change. Treelines are found in many forms, including abrupt, diffuse, krummholz, and island/ribbon forest (adapted from Harsch & Bader, 2011). Harsch & Bader (2011) describe how treeline typologies have feedback mechanisms that reinforce maintenance of the forest edge. Treelines with abrupt edges, for example, redistribute wind and snow patterns in ways that hinder growth beyond the closed canopy forest, preserving the abrupt typology. Because of the feedback mechanisms of treeline typology, major shifts in the structure of the treeline edge may suggest particularly significant climatic changes.

Of particular interest to this study is the transition from an abrupt to a diffuse treeline. Abrupt treelines are identified by a distinct boundary between closed-canopy forest and alpine tundra. The tall growth at the forest edge suggests that abrupt treelines are not growth-limited and therefore growing-season temperature is unlikely to influence growth at abrupt treelines (Harsch & Bader, 2011). Because an abrupt treeline is less influenced by temperatures, the maximum isotherm for tree growth may lay far above the actual treeline. Experiments at an abrupt treeline in New Zealand, for example, suggest that seedlings can survive far beyond the forest edge when artificially shaded (Wardle, 1985). Rather than being temperature-limited, some researchers have proposed that abrupt treelines are limited by tree establishment and survival due to the way that an abrupt treeline alters permafrost distribution and wind patterns (Danby & Hik, 2007). In other words, the abrupt shift between forest and tundra creates a unique microenvironment above the treeline that hinders tree establishment and growth. The characteristics of an abrupt treeline reinforce the continued existence of an abrupt treeline by limiting new establishment above the treeline. Abrupt treelines are more stable during periods of climate change: only major changes in climate could transform an abrupt treeline typology (Harsch et al., 2009; Harsch & Bader, 2011).

Diffuse treelines, on the other hand, seem particularly prone to advancement. According to Harsch et al. (2009), eighty percent of diffuse treelines are advancing compared to only 22 percent for other treeline types. Diffuse treelines have an extended transitional zone between the forest and the species limit, characterized by a gradual decrease in tree height and density with elevation. The gradient of tree growth in diffuse treelines suggests that they are temperature-limited (Harsch & Bader, 2011; Harsch et al., 2009) in accordance with Körner's growth-limitation hypothesis (Körner, 1998). Because of their temperature sensitivity, diffuse treelines are expected to advance with global increases in temperature (Harsch et al., 2009).

Diffuse treelines also have feedbacks that maintain their typology and encourage treeline advancement. Unlike an abrupt treeline, the influence of a diffuse treeline on wind and temperature dynamics seems to contribute to a more favorable microenvironment for tree growth. Tree growth increases the frictional surface for wind flow (Resler et al., 2005). The dispersed growth of a diffuse treeline may facilitate growth in the forest-tundra ecotone by reducing the cooling effect of wind (Holtmeier & Broll, 2005). With slower and warmer winds, temperatures near the surface are able to be thermally coupled with the warm ground rather than with the cool atmosphere. Soil has a higher heat capacity than the surrounding air, allowing the diurnal temperature to remain more constant near the ground surface, which positively benefits tree growth (Grace et al., 2002). The insulated area above the ground surface is considered a boundary layer, within which trees grow more successfully (Körner, 1998). The dispersed trees of a diffuse treeline could increase the scope of the boundary layer, allowing greater establishment and survival at treeline. Advancement in diffuse treelines, therefore, may accelerate further advancement as newly established trees improve the microenvironment and facilitate establishment of more trees (Harsch & Bader, 2011).

The positive feedbacks of treeline typology for both abrupt and diffuse treelines suggest that it is unlikely for treelines to change typology. Only a major shift in climate could transform treeline typology. Because abrupt treelines are not growth limited, the maximum isotherm for tree establishment may lay far above an abrupt treeline. A shift from an abrupt to a diffuse treeline, therefore, may represent an important "tipping-point" in treeline typology, leading to a relatively sudden and accelerated advancement of treeline. Treeline typology is important in understanding the relationship between climate and treeline; however, it does not describe whether the rate of treeline advancement is changing at the same rate as climate. Exploration of changes in spatial distribution patterns provides insight into the relationship between the rate of tree migration and climate change.

Environmental conditions influence the spatial distribution pattern of tree establishment at treeline by altering the relative influence of facilitative and competitive factors among the tree population. Generally, clustering of tree species is more common in harsh environments (Callaway et al., 2002). Trees growing at upper treeline are at the environmental frontier for their species, where clustering is most beneficial. Tree clustering provides shading from the open sky, thermal insulation, moisture retention, wind protection, nutrient availability, soil geology, and other microsite characteristics that can benefit tree establishment (Smith et al., 2003; Germino et al., 2002; Maher & Germino, 2006; Körner 1998).

Tree clustering is beneficial only when facilitation sufficiently compensates for competition among the clustered trees (Callaway et al., 2002). Otherwise, trees that can survive as individuals, away from a cluster, generally grow faster than comparable clustered trees (Roberts, 2010). Clustered tree distribution patterns, therefore, suggest that trees established in a harsh environment. Randomly distributed tree establishment patterns suggest that the environment was milder and that clustering was not necessary or beneficial to tree survival. Changes in the distribution patterns of an advancing treeline can track the movement of the upper climatic boundary through time. The relationship between tree establishment patterns and environmental conditions helps describe the relationship between treeline advancement and climate change.

The purpose of the current study was to analyze the changes in treeline elevation, typology, and establishment distribution patterns of treeline on Pikes Peak in order to more clearly understand the relationship between climate and treeline. Ichose a study site on Pikes Peak, Colorado with known advancement of 18m elevation and 60m surface migration from 1953-2009 (Earnest, 2011; Feiden, 2010). The period of significant advancement of treeline also is associated with a shift from an abrupt to a diffuse treeline based on historical aerial images. With the warmer temperatures and advancing treeline, I hypothesized that the distribution pattern of tree establishment had changed through time. Using spatiotemporal reconstruction, I anticipated clustering to be more prominent for older generations of trees at lower elevations within the forest-tundra ecotone, when the climate was cooler. As the climate warmed over time, I expected younger trees to be randomly distributed at the lower elevations and clustered at higher elevations, elevations beyond the establishment limit of their predecessors. If the rate of tree establishment matched the rate of movement of the upper climatic boundary, I expected that the trees existing at the upper elevational limit for each generation would exhibit clustering, tracking the movement of the upper climatic boundary through time. This study sought to provide unmatched spatial and temporal resolution to describe the specific movement patterns of an advancing treeline. A detailed analysis of the distribution patterns and population wave-front dynamics at treeline is valuable for understanding population movement and distribution in sensitive ecotones with future climate changes.

METHODS

Site description

The study area was a rectangular transect 50 meters wide and 260 meters long (105°5’25” W and 38°51’35” N, center of transect), located within a bowl on the western slope of Pikes Peak on the Front Range of the Colorado Rocky Mountains. The elevation of the transect ranged from 3609 m to 3719 m a.s.l., which spanned the distance from the highest outpost tree to the 2009 treeline (as defined in Earnest, 2011 and Feiden, 2010). The transect ran downslope, perpendicular to contours, with a northwestern aspect. The site was chosen because the treeline is known to be advancing significantly in this area (Feiden, 2010; Earnest, 2011).

I studied only the transitional ecotone between closed-canopy forest and alpine tundra. The treeline boundary was diffuse at this site, with gradually decreasing tree density with increased elevation (Fig. 1). The uppermost limit of the transect represents the tree species maximum (no trees exist above this limit). The only tree species present was *Picea engelmannii* Parry ex Engelm. (Engelmann spruce).

Snow typically covers the site from late September to late May. Other tundra species including grasses and various wildflowers dominate the areas between trees during the growing season. Boulders were found throughout the transect, but significant groupings were found primarily at the top of the transect and a small rock slide near the bottom. Many large trees had multiple upright branches from layering, or the asexual reproduction of a tree from submerged branches that develop their own root systems. Layering is particularly common for krummholz trees, but all of the trees in the transect had a generally upright stature. There was a marked lack of krummholz mats at the site.

Field methods

Every tree, sapling, and seedling greater than 10 centimeters tall (n=630) within the transect was labeled and mapped using a Trimble GeoExplorer GeoXT GPS (Trimble Navigation Limited, Sunnyvale, CA). For simplicity, all *P. engelmannii* trees, saplings, and seedlings in this study are referred to as “trees.” Only trees taller than 10 cm were included because trees smaller than that were difficult to see among the tundra grasses. Each tree was aged, either by coring or counting budscars. Height and percent frost damage were also estimated for each tree. For trees that were large enough to core, age cores were collected at the nearest possible point above the root collar. Age cores were taken at a slight downward angle to maximize ring collection. The distance along the trunk was recorded. When possible, a second core was taken perpendicular to the tree to analyze growth rates. Due to the size of the trees, most growth cores were collected between 20 cm and 100 cm above the ground. All cores were taken above the basal buttress. Cores were generally taken from the downslope, western side of the tree except when collection from that angle was impossible. For trees too small to core, apical budscars were counted to approximate age.

Lab methods

Cores were transported to the lab in labeled plastic straws. In the lab, cores were dried for at least 24 hours at approximately 60°C. Cores were then mounted, relabeled, and belt-sanded (Stokes and Smiley, 1968). Rings were counted using a Velmex linear measuring bench (Velmex, Inc., Bloomfield, NY) with MeasureJ2X dendrochronology software (VoorTech Consulting, Holderness, NH). Ring width was measured to 1/1000 mm. For cores missing the pith, a 1 mm concentric circle transparent film was laid over the core to approximate the distance to the pith (Norton et al., 1987). The distance to the pith and the mean width of the last three complete rings was used to approximate the number of missing rings.

To correct for the number of missing rings due to coring at heights above the root collar and due to budscar error, 39 seedlings (for budscars) and 21 saplings (for coring) were harvested from areas surrounding the transect. Budscar error was corrected by comparing budscar counts to actual rings at the root collar for the harvested seedlings (linear regression, $R^2 = 0.9098$, $n = 39$, $p < 0.0005$). For coring height correction, the saplings were cut at 5 cm intervals starting at the root collar. The number of rings at the root collar was taken as the true age of the plant. The rings at each interval were counted to approximate the missing rings, defined as the difference between the number of rings at the root collar and the number of rings at the particular height. A linear regression of the data provided a reasonable estimate that was used to correct the data ($R^2 = 0.7502$, $n = 184$, $p < 0.001$). For some samples, growth cores provided better age data than age cores. Not all growth samples had recorded core height data. When core height data were unavailable ($n = 17$), I approximated that growth cores of trees 150-250 cm tall were cored at 50 cm, which added 30 years to the core data. For trees greater than 250 cm tall, growth cores were approximated at 100 cm, or an additional 40 years.

GIS and spatial distribution analysis

I examined spatial distribution patterns of tree establishment using Ripley's $K(t)$ (Ripley, 1977), a second-order point pattern analysis that identifies significantly clustered, random, and dispersed distributions at multiple spatial scales (Ripley, 1977; Piegorsch and Bailer, 2005; Haase, 1995). I used the ArcMap10 program of the ArcGIS geographic information system to run Ripley's $K(t)$ analysis (Esri, Inc., Redlands, CA). ArcMap10 calculated $L(t)$, a square-root transformation of $K(t)$, to facilitate visual interpretation of the results (Esri, 2011; Humphries, 2008; Elliott & Kipfmueller, 2010):

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

where t represents the distance between trees. The value of the $L(t)$ function indicates spatial clustering when $L(t) > 0$, random distributions when $L(t) = 0$, and uniform dispersal when $L(t) < 0$. Calculating $L(t)$ with 99 random permutations established a 99 percent confidence envelope for each study plot. Values of $L(t)$ within the confidence envelope were randomly distributed, while values above were clustered and values below were uniformly dispersed. I used the Ripley Edge Correction Method, a toroidal edge correction, to account for the problem of edge effects (Haase, 1995). The study analyzed clustering at 0.5 m distance intervals with a maximum distance of 20 m, which is two-fifths the width of the shortest edge of the study area. It is recommended that analysis does not exceed one-third to one-half of the shortest edge of the study area (Piegorsch and Bailer, 2005).

The GPS locations were precise to about 15 cm. The GPS's elevation readings, however, was less reliable. To correct for elevation, I ran a block statistics function on a contour map of the area in ArcMap10. The contour map was defined in 10 m bands, which were extrapolated to 0.5 m intervals. Each tree was reassigned a new elevation field defined by the nearest contour.

For analysis, the transect was split into four elevational bands and three age cohorts in order to describe changes in spatial patterns across the elevational gradient over time (Fig. 2). I used Jenks natural breaks optimization method (Jenks, 1967) to identify four elevational groups: 3609-3628.5 m a.s.l. (low), 3629-3651.5 m a.s.l. (mid-low), 3652-3680 m a.s.l. (mid-high), and 3681.5-3719 m a.s.l (high). The Jenks optimization method is a statistical tool calculating goodness of variance fit (GVF), which identifies optimal breaks within a data set into categories that minimize variance within a class while maximizing heterogeneity between classes (Jenks, 1967; Kinnaird et al., 2003; Esri FAQ, 2004). Dividing the transect into elevational bands compensated for the decrease in expected tree density as a function of elevation. I also split the trees into three age cohorts to analyze changes in distribution pattern over time. Dividing the age classes revealed the non-stationary population structure of the site. Again, I used Jenks natural breaks to define the three age classes: less than 33 years old (established 1977-2003), 34-69 years old (established 1941-1976), and greater than 70 years old (established 1878-1940). For simplicity, I will hereafter refer to these cohorts as young, middle-aged, and old trees, respectively. Height was divided into groups of 100 cm or less, 100-200 cm, and greater than 200 cm (maximum 1070 cm). Comparing analysis based on height to analysis based on age showed interesting relationships between these two variables.

Spatial analysis of tree density

In addition to Ripley's $K(t)$ clustering analysis, I studied changes in tree density across the elevational gradient through time. Because I was studying an advancing treeline (Fieden, 2010; Earnest, 2011), I expected an increase in tree density over time. I used age to identify the time period of recruitment. I divided the trees into age cohorts of 10 years each for finer resolution of tree establishment over time. I used the finer resolution of tree establishment to construct a time-lapse animation of tree establishment and density patterns through history. I also split the transect into eleven elevational groups of 10 vertical meters ranging from 3609-3719 m a.s.l. to identify the elevational bands where trees recruited at different periods of history. I expected greater recruitment at lower elevations because lower elevations have milder environments than higher elevations. I also expected a gradual increase in maximum elevation of tree recruitment over time, consistent with an advancing treeline. The subdivision of the data set into finer age and elevational classes provided insight into the population wave-front dynamics of an advancing treeline.

RESULTS

Treeline typology

Based on aerial images, the treeline prior to 1957 was abrupt, meaning that there was a clear boundary between the closed-canopy forest and the alpine tundra (Fig. 3a). Although my dendrochronological analysis shows that some trees had established above the abrupt treeline before 1957, these trees were too small to significantly affect treeline typology. As previously described, treeline typologies are generally stable because of reinforcing feedbacks that maintain the typology. A shift in typology, therefore, represents a significant shift in local climate (Harsch & Bader, 2011). It appears that the shift from abrupt to diffuse treeline at the site may have begun after 1957 (Fig. 3b). Around that time, the establishment limit significantly increased, jumping from a maximum at 3651.5 m a.s.l. in 1940 to 3718.5 m a.s.l. by 1977. The maximum elevation of the forest-tundra ecotone increased 67 meters in elevation between 1940-1977. In this same period, the closed-canopy treeline only migrated 6.7 meters in elevation (Earnest, 2011). The species limit migrated about 10 times further than the closed-canopy treeline, producing an elongated forest-tundra ecotone by 1977. Large forest-tundra ecotones are associated with diffuse treelines. Aerial images confirm that treeline typology seems to have shifted to a diffuse treeline after 1957.

Spatial clustering of age cohorts

Because clustering of conifers is correlated with highly stressful environments (Callaway et al., 2002), I analyzed spatial and temporal patterns of clustering in order to identify changes in microclimate across the elevational gradient over time. Overall, tree distribution patterns changed significantly over spatial and temporal scales (Table 1a). Generally, clustering was historically more prevalent at lower elevations and is recently more prevalent at higher elevations.

As expected, the oldest trees (established 1878-1940) were clustered at both elevational bands where they were present: the low (3609-3628 m a.s.l.) and mid-low (3628.5-3651.5 m a.s.l.) bands. Only a few individuals (n = 4) existed above the mid-low elevational band, with 92 percent of the cohort existing below 3651.5 m a.s.l.

The middle-aged trees (established 1941-1976) established at much higher elevations than their predecessors. Middle-aged trees established at all elevational bands within the forest-tundra ecotone. At the lowest two elevational bands, trees were no longer clustered like the old cohort but instead were randomly distributed. At the next highest elevational band (mid-high), middle-aged trees were clustered. The mid-high elevational band is directly above the establishment limit of the previous generation of trees. The clustering pattern displayed by the middle-aged trees at the mid-high band mirrors the pattern displayed by the old trees at the mid-low band. Surprisingly, middle-aged trees were distributed randomly at the high elevational band. Possible reasons for the unexpected random distribution at the highest elevation are explained in the discussion.

Young trees (established 1977-2003) exhibited a complex pattern. They were clustered at the low elevational band, randomly distributed at the mid-low elevation, clustered at mid-high, and randomly distributed at the high elevational band. Young trees had a similar distribution pattern as the middle-aged trees with the exception of the low elevational band. At the low elevation, young trees were clustered while middle-aged trees were randomly distributed. The clustering of young trees at the low elevation band is primarily from trees that have established since 1990. Trees established between 1970 and 1990 were primarily randomly distributed. The pattern exhibited by young trees also diverged from my original hypothesis and will be explained further in the discussion.

Height class distributions

There were similar patterns of clustering across elevational bands when classed by height (Table 1b). Trees less than 100 cm tall mirrored the distribution pattern of the youngest cohort as they were clustered at the lowest elevational band, random at mid-low, clustered again at mid-high, and random at the highest elevation. Middle-sized trees (100-200 cm tall) were random at all elevations except at mid-high, same as the middle-aged trees. Tall trees (>200 cm tall), however, did not match the clustering pattern of any age cohort. Tall trees were clustered at mid-low and randomly distributed at the low elevational band. There were no trees taller than 200 cm above the mid-low elevation.

A majority of the trees in the tallest height class were middle-aged (55 percent), which could explain the random distribution at the low elevational band. Tall trees of the oldest age class comprised 44 percent of the tallest tree class, which could explain the clustering of tall trees at the mid-low elevational band. Young trees contribute to the remaining 1 percent.

Although there is not a strong linear correlation between age and height ($R^2 = 0.466$, $p < 0.005$), each height class is dominated by an age cohort such that younger trees dominate the shorter height class and middle-aged trees dominate the middle-sized height class. For trees 100-200 cm tall, 59 percent are middle-aged, 34 percent are young, and 7 percent are old. For trees shorter than 100 cm, the majority are young (84 percent), with 15 percent middle-aged, and 1 percent in the oldest cohort.

Tree density changes

I know that treeline has been advancing at the site since at least the 1930s (Fielden 2010, Earnest 2011). To understand when and where trees established during this period, I subdivided the data into 10 year establishment periods and 10 m elevational bands. Each elevational band comprised an area 50 m wide and approximately 20 m long (1000 m^2). I looked at spatio-temporal changes in tree density to understand the dynamics of the moving edge of treeline at the site.

The density of trees decreased with elevation from a maximum of 127 trees per 1000 m^2 at the lowest end of the transect to 4 trees per 1000 m^2 at the upper end of the transect. The difference in tree density with elevation has become more exaggerated and defined over time with a negative slope of 0.3 trees per meter elevation 100 years ago ($R^2=0.22$, $p = 0.146$), 2.7 trees per meter elevation 50 years ago ($R^2 = 0.80$, $p < 0.001$), to 13.1 trees per meter elevation in 2000 ($R^2 = 0.95$, $p < 0.001$). Most of the increase in the slope has come from accelerated recruitment rates at lower elevations. The number of trees at the highest elevation remained relatively stable, with only 4 trees establishing since 1880. The number of trees at the lowest elevation increased dramatically with over 120 new trees since 1880. The observed increases in density are consistent with an advancing treeline.

The total number of trees markedly increased about 40 years ago with major leaps each subsequent decade. Increased recruitment is particularly evident at the lower elevations (3609-3629 m a.s.l), but is still noticeable throughout the transect (Fig. 4).

Although there is a distinctly negative slope of tree density and altitude in 2000 ($R^2 = 0.95$, $p < 0.001$), the change in tree density is not a steady across all elevations. Rather, my analysis indicated that recruitment was successful in certain elevational pockets more than others, creating peaks of tree density along the elevational gradient.

In the 1880s, the only small clump of trees was at 3639-3649 m a.s.l. For the next 50 years, trees mostly recruited at this same elevational band, with little to no recruitment at lower or higher elevations. The concentrated recruitment at 3639-3649 m a.s.l creates a peak in the tree density at that elevation (Fig. 4). For the following 30 years, trees recruited at or below the same elevational band. The infill of trees behind the density peak creates an inflection point in the graph, which could be interpreted as a moving front of the tree population.

In the last forty years, the front has appeared to move to a higher elevation of approximately 3669-3979 m a.s.l. The inflection point at this elevation is created because there is a significant decrease in tree density at elevations above 3679 m a.s.l. The ontogeny was by simultaneous recruitment at and below 3669-3679 m a.s.l., but with little recruitment above.

Interestingly, dynamics similar to the creation of the first peak at 3639-3649 m a.s.l. appear to be present in more recent years at the top elevational bands. At 3699-3709 m a.s.l. trees began recruiting in the 1930s, but there has been a significant increase in recruitment in the last 40 years. The increased recruitment creates another peak in tree density at a much higher elevation than the majority of the tree population, with little or no trees recruiting at higher or lower nearby elevational bands. Until 30 years ago, there were no trees at the elevational band below the peak. Significant infill of trees behind the peak began 20 years ago. The recruitment pattern of recent years appears to repeat the dynamics described at the much lower elevation about 100 years ago.

The three inflection points described above demonstrate that the treeline is moving in discrete steps. The dynamics show that recruitment is greater at certain elevational pockets, followed by a few decades of infill. I refer to this pattern as a reach-and-fill pattern. It seems that the pattern repeated three times in the last 120 years.

Tree recruitment rates

The pattern of new tree recruitment shows two distinct time periods of recruitment rates, with a major shift about 40 years ago (Fig. 5). Until about 40 years ago, there was slow and relatively even tree establishment along the transect. Each elevational band had 0-3 new trees per decade, with the exception of the lowest elevations (3609-3929 m a.s.l.), which had up to 7 new trees in a decade. The fairly uniform distribution of trees across the elevational gradient creates a very shallow negative slope of tree recruitment with elevation. In the 1960s, the pattern began to shift with a greater difference between recruitment rates at the lower and upper ends of the transect. In the decade of the 1960s, there were 16 new trees per 1000 m^2 at the lowest elevation, 10 new trees for the next highest 1000 m^2 pocket (3619-3629 m a.s.l.), and up to 5 for the remainder of the transect. After that, the pattern changed abruptly. Since the 1970s, there were significant increases in tree density with up to 40 new trees per 10 m elevational band per decade. However, tree recruitment decreased dramatically with increased elevation. For example, the highest elevation had only one tree recruited per decade. The uneven recruitment rate across the elevational gradient creates a steep negative slope of tree recruitment to elevation.

Although the decades since the 1970s had greater recruitment than previous generations of trees, there were significant differences between the patterns of recruitment in the 1970s-1980s and in the 1990s-2000s. The 1970s and 1980s had very similar distributions of new trees across elevational bands. The 1990s-2000s, however, show an anticorrelated pattern of recruitment when compared to the 1970s-1980s, especially the 1980s. The elevation bands with exceptionally high recruitment in the 1980s had especially low recruitment in the 1990s-2000s. Conversely, some elevational bands with low recruitment in the 1980s had very high recruitment in the 1990s-2000s. (Fig. 5)

DISCUSSION

In my analysis, I used patterns of spatial distribution and tree density to gain a better understanding of the relationship between treeline and a changing climate. In the following discussion, I first consider how spatial distribution patterns at the moving front of treeline suggest that the climatic boundary has migrated upslope and may be outpacing tree establishment at the upper limits of the forest-tundra ecotone. Then, I discuss how analyzing the tree density patterns of the forest-tundra ecotone as a function of elevation and age revealed population wave-front dynamics previously not described in the literature. Finally, I describe how the shift in treeline typology may have influenced many of the observed patterns at treeline.

Movement of the upper climatic boundary

In my analysis, tree distribution patterns are used to determine spatiotemporal changes in climatic conditions at treeline. I hypothesized that spatial clustering indicates that trees established in a harsh environment, while random distributions suggest establishment in a milder environment. Generally, my data support the hypothesis that spatial distributions correspond to climatic conditions. However, some surprises within the data were incongruous with the predicted pattern and suggest that other factors also control spatial distribution patterns at treeline. Here, I will first explain the way that the data describe the movement of the upper climatic boundary over time. Then, I will describe the anomalous distribution patterns and explain what other factors may control establishment patterns.

The first hypothesis suggests that tree clustering is a relic of a harsh environment because trees needed the facilitative effects of nearby trees for successful establishment. In harsh environments, the facilitative effects of clustering enhance conifer seedling survival (Callaway et al., 2002; Germino et al., 2002). Tree clustering benefits tree establishment by providing wind protection, snow coverage, and thermal insulation (see Smith et al., 2003; Germino et al., 2002; Maher & Germino, 2006). Alternatively, a random distribution indicates that trees no longer relied on the facilitative effects of neighbors for survival, indicating a milder environment. Random distribution is advantageous to trees because it reduces competition for resources (Callaway et al., 2002). Trees that grow randomly generally grow faster than similarly-sized clustered trees (Roberts, 2010). Based on the hypothesis that clustering indicates a harsh environment and random distributions indicate a milder environment, I expected greater clustering for older generations of trees at lower elevations and for younger generations at higher elevations. The upward shift in clustering pattern would indicate that the upper climatic limit for tree establishment rose in elevation over time. In general, my results support the hypothesis of a moving upper climatic boundary. All trees established prior to 1940 were clustered. After 1940, trees were generally randomly distributed at lower elevations, with clustering at upper elevations.

The clustering of the oldest trees suggests that the environment at treeline was harsh for trees that established before 1940. Trees of the oldest cohort also only established within the lower two elevational bands, below 3651.5 m a.s.l. The clustering pattern below 3651.5 m a.s.l. indicates that the upper climatic limit of tree growth probably was located around 3651.5 m a.s.l. prior to 1940.

Over time, the upper climatic limit seems to have moved upward. After 1940, trees established at elevations far beyond the limit of their predecessors, suggesting that the environment at higher elevations suddenly became suitable for successful establishment. At the mid-high elevational band, directly above the establishment limit of the previous generation, trees established after 1940 were clustered. The clustering of young and middle-aged trees matches the clustering of older trees at the lower elevations, suggesting that the harsh environment of the old trees was now experienced by younger trees at higher elevations. The upward movement of the harshest environment is congruent with an advancing climatic boundary. The upward migration of trees and the clustering pattern indicate that the harsh environment at the upper climatic boundary migrated to the mid-high elevational band after 1940.

The random distribution of young and middle-aged trees at lower elevations provides further evidence that the climatic boundary had advanced after 1940. Random distributions indicate a milder environment because trees did not need the protection of other trees for survival. At elevations below 3651.5 m a.s.l., the old trees were clustered, but younger trees were generally randomly distributed. This suggests that sometime after 1940, the environment at the lower elevations became more moderate and allowed trees to establish as individuals instead of clusters. The lower elevations were no longer at the edge of the climatic boundary. Instead, they were comfortably below the climatic maximum, facilitating easier growth.

Overall, the clustering pattern provides evidence that the environment at treeline has become milder over time and that the upper climatic boundary has migrated upslope. The changes in the climatic boundary correspond to the regional changes in temperatures observed in the last century. Regional summer temperatures (combined June, July, and August monthly averages) have increased about 2.4°C since 1896 (Fig. 6; linear regression, $R^2 = 0.738$, $p < 0.001$). Since global treelines seem to be temperature sensitive to within a degree of 6°C (Körner, 1998), it seems likely that a change of 2.4°C could alter treeline, a hypothesis that is supported by the known advancement of treeline at this site in the last century (Fieden, 2010; Earnest, 2011). Because of the substantial temperature ranges over time and space at this site and the known sensitivity of treeline to temperature, it is reasonable to suggest that a spatio-temporal analysis of treeline could be used to describe the treeline's response to changes in microclimate.

The moving edge: Is treeline climate-limited or recruitment-limited?

It is clear from the preceding discussion that the upper climatic boundary has advanced in the last century. However, it is possible that tree establishment at treeline is not advancing at the same rate as the climatic limit. Some scientists have suggested that the rate of tree migration may not be able to keep pace with changes in temperature (Grace et al., 2002; Fischlin et al., 2007; Camarero and Gutiérrez, 2004). At the highest elevation, middle-aged and young trees display a surprisingly random spatial distribution pattern. Based on the hypothesis that randomly dispersed trees correlate with milder environments, the distribution of trees at the highest elevation suggest that the upper climatic boundary may have already migrated beyond the limit of tree establishment.

If the climate is outpacing treeline advancement, then the treeline is no longer climate-limited, but recruitment-limited. A treeline could be recruitment-limited if the rate of successful establishment of new seedlings is less than the rate of movement of the upper climatic boundary. If the treeline is recruitment-limited, treeline could continue to advance for many more years even if current climatic conditions remained steady. Considering the predicted increase in temperatures, it is likely that treeline will continue to advance for many more decades in the future.

The interesting pattern displayed by the upper limit of tree growth suggests that the moving edge of the tree population is changing. Prior to 1940, the moving edge was clearly clustered as all trees that established above the interior forest exhibited clustering.

From 1941-1977, the spatial distribution showed mixed results as most trees were clustered, with only a few trees establishing in a random pattern at higher elevations. After 1977, the moving edge was randomly distributed. The changes in the moving front correspond well with the possibility of an accelerating climate boundary. The transition from a clustered edge to a randomly dispersed edge suggests that tree growth historically was bound by the upper climatic boundary, but that climate changes have outpaced tree establishment and that treeline is now recruitment-limited.

The likelihood that the climatic boundary is migrating faster than tree establishment is also supported by the dramatic change in temperature experienced in the region. In the last 100 years, average growing season temperatures have risen over 2.4°C since 1896, which corresponds to almost 370 m of vertical movement (based on a standard atmospheric lapse rate of 6.5°C per kilometer; Petty, 2008). During the same period, treeline has only advanced 18 m of elevation. The lag of treeline advancement behind the migration of isotherms has been observed in other studies in Britain and the Alps (e.g., Gear and Huntley, 1991; Grabherr et al., 1994).

It is possible, however, that the random distribution pattern of middle-aged trees at the highest elevational band is erroneous because of the low sample size: only 17 trees of this age cohort exist at the high band, which may reduce the ability to detect clustering. Analytical error seems an incomplete explanation however, as the young trees are also randomly distributed at the high elevational band and had a much larger population ($n = 30$). Additionally, the pattern displayed by the Ripley's *K* analysis for both age cohorts was very clearly random ($p < 0.01$). The random distribution of young trees and high statistical significance of the analysis suggest that the results are accurate and that statistical limitations do not explain why trees are randomly distributed at the high elevational band.

It is also possible that the clustering of young and middle-aged trees at the highest elevational band is due to other microsite factors influencing tree distribution patterns. Abiotic facilitation by boulders, for example, can benefit tree establishment in ways similar to clustering. Boulders provide protection from the wind, decrease exposure to the open-sky, stabilize soil, and retain moisture (Resler et al., 2005; Resler, 2006). Thermal imaging at the study site also showed that rocks warmed up much more quickly in the early morning than trees at treeline, which could provide radiative heat. Because direct sunlight is most harmful to young seedlings when their tissue is cold (Germino et al., 2002; Smith et al., 2003), proximity to a boulder's radiative heat could be particularly beneficial in the early morning and could improve seedling survival. There were many more boulders at the high elevational band than at any other elevation. It is possible that trees at the high elevational band preferentially recruited close to boulders rather than to other seedlings.

To determine whether boulders are responsible for the random distribution pattern at upper treeline, future studies mapping the location of boulders could identify whether trees preferentially recruited near boulders. If boulders favorably influenced tree establishment, it would indicate that trees needed the facilitative effects of boulders for survival. It could therefore be inferred that the upper climatic boundary was located near the elevation of maximum tree growth and that treeline advancement matched the rate of the climatic limit.

However, if future research found that tree establishment did not cluster near boulders, then it could be assumed that trees did not rely on the facilitative effects of either trees or boulders and that the climate was mild enough for independent establishment. The upper climatic boundary, therefore, may have already moved beyond the limits of tree establishment. The differential rate of tree and climate movement seems likely based on the fast rate of temperature change in the region as well as the clearly random distribution of young seedlings. If young seedlings established in a harsh environment, I would expect that trees would display clustering, but further research is needed to confirm which mechanisms are controlling treeline.

The microsite availability hypothesis

Another anomaly in the spatial distribution pattern was the unexpected clustering of young trees at the lowest elevation. Based on the previously discussed evidence that the upper climatic boundary has migrated, it is unlikely that clustering at the low elevation for young trees is driven by climatic conditions. Young trees, established after 1977, that grew at the lowest elevation are far below the climatic limit for tree establishment. Trees of the youngest cohort survive at higher elevations with random distributions, suggesting that the young trees do not need the facilitative effects of other trees at the low elevations. Climatic conditions do not explain the surprisingly clustered distribution of the youngest trees at the lowest elevation.

Instead, it is possible that microsite availability resulted in clustering of the young trees. Limited microsite availability could allow some microsites to be more favorable for tree establishment than other sites. If there are pockets of suitable microsites surrounded by unsuitable terrain, then trees would establish in clusters even though facilitation would not be necessary. Young trees at the lowest elevation had established in an area with the greatest tree density of any elevational band. It is possible that the tree density was significant enough by 1977 that the only remaining viable spots for new seedling recruitment were in small pockets between larger and older trees. All new recruits may have established in these pockets and therefore exhibit clustering. Clustering at the low elevational band has become more prominent over time, with trees established since 1990 showing even more significant clustering. The microsite availability hypothesis would predict that pockets would become more concentrated over time, which potentially explains the increase in clustering for trees less than 20 years old. Especially considering that the last 20 years have seen the warmest summers, it is unlikely that clustering of young trees at the low elevations is driven by climatic conditions.

Tree density and population wave-front dynamics

Examining the treeline at a finer spatiotemporal scale revealed interesting patterns about the population wave-front dynamics of an advancing treeline. It appears that treeline advanced in discrete steps, displaying a reach-and-fill pattern of recruitment. The reach-and fill pattern of recruitment shows that during certain periods, the treeline greatly expanded its reach to higher maximum elevations. Succeeding generations then recruited below the maximum elevation for a few decades until the reach-and-fill pattern was repeated.

The reach-and-fill pattern of movement suggests that altitude is not the only factor influencing tree establishment at my site. If recruitment was elevation-limited, I would expect a steady decrease in tree density as a function of altitude. Instead, a few elevational bands show pronounced peaks of recruitment (Fig. 4). It is possible the wave-like pattern of tree advancement is a product of interannual temperature fluctuation (Paulsen et al., 2000). In slightly warmer years, trees may have been able to jump ahead to higher elevations, followed by a few years filling in lower elevations. However, the low establishment rate at elevations below the peaks suggests that microsite hospitability may also be responsible for the tree density peaks. Microtopography, geology, or biotic factors could influence the ability of trees to establish in some areas more than others (Resler et al., 2005).

If microsite characteristics explain the concentrated presence of "reaching trees," it can be assumed that trees that later established below the tree density peak had established in a slightly less favorable microsite. One reason that trees would eventually establish in less suitable areas is that the ideal microsite is already saturated with existing trees reducing the opportunity for further establishment. A second possibility is that existing trees alter the surrounding environment and improve the ability of trees to establish at nearby sites (Bekker, 2005; Alftine & Malanson, 2004; Smith et al., 2003).

The saturation hypothesis explains the decrease in recruitment for trees that established at low elevations between 3619 and 3639 m a.s.l. in the last 20 years. Since 1990, 36 new trees recruited at those elevations. In the twenty years prior to 1990, however, 131 new trees established. That means that about 7 new trees were recruiting each year between 1970 and 1990, but only 3.6 trees were recruiting each year from 1990-2010; the rate of recruitment decreased by half. Because I know that treeline was advancing during this period and that the upper climatic boundary was far above this elevation, it is likely that the pre-existing density of trees reduced the establishment rate of more trees in this area. The area may be reaching its maximum tree saturation.

The other explanation for the infill of trees in possibly less favorable microsites is that the presence of trees at the higher elevational peaks provided facilitative effects that improved nearby environments. Tree growth increases the frictional surface for wind flow, which can reduce wind speed, alter snow distribution patterns, and decrease thermal loss from convection (Resler et al., 2005; Oke, 1987; Hiemstra et al., 2002; Grace, 1988). Trees that established in more hospitable microsites may have provided protection to compensate for sites that may be less hospitable (Germino et al., 2002; Smith et al., 2003; Resler et al., 2005). The facilitation hypothesis also explains the leap-frogging, repetitive pattern of the reach-and-fill model. The increased tree density at lower elevations provides protection for the establishment of higher elevational pockets.

The reach-and-fill pattern of recruitment is consistent with paleoecological records of plant migration. Researchers have found that spruce migrations in the Holocene, for example, followed a “long-jump-and-outliner model of spread” (Bradshaw and Zackrisson, 1990; Pitelka, 1997). The historical establishment of island populations accelerated the rate of population migration, with trees quickly establishing in the intermittent space between the general population and the outlier population (Pitelka, 1997). Although the temporal and spatial scale of the historical records is many orders of magnitude larger than the scale observed in this study, the similar population wave-front dynamic pattern may suggest that the “reach-and-fill” pattern of recruitment is a common characteristic of tree migration.

Population demographics and indications of treeline typology change

The age demographics of treeline suggest that trees younger than 40 years old dominate treeline. According to Fieden (2010), who researched the same treeline as this study, there are two possible explanations for the unbalanced presence of young trees in the forest-tundra ecotone: either it is a relic of differential tree mortality or it is evidence of a migrating treeline. Fieden (2010) first argues that it is possible that the large number of young trees could be a result of the greater opportunity for mortality of older and taller trees. Mortality of older trees could significantly influence analysis of static stand structures (Johnson, 1996) because the compounded rate of mortality of trees over time suggests that not all trees survive to become old. Additionally, tall trees do not have the thermal advantage of being close to the ground, which would increase mortality for taller – and possibly older – trees. In general, trees taller than 2 m are considered likely to be thermally coupled with the atmosphere instead of the ground. At my site, almost all trees are below this height. It is unlikely that tree height significantly increased mortality of older trees. Furthermore, there were few signs of tree mortality, with fewer than 5 dead trees found within the transect (n=630 trees). The site is also cold and dry, which reduces rates of decomposition. Tree stumps from a timber sale almost 100 years ago retain their integrity despite being several hundred vertical meters below the transect in the moister, warmer interior forest. It is therefore unlikely that indications of previously living trees were missed.

Feiden's (2010) second explanation seems more probable. Fieden argues that the skewed age distribution is evidence of an advancing treeline. The known advancement of treeline suggests that there would be a net increase in trees in the forest-tundra ecotone in the last century, a hypothesis that is supported by aerial photograph analysis (Fieden, 2010). Growth rates have also increased significantly during the period of high recruitment, which reduces the likelihood of mortality (Fieden, 2010). Based on Fieden's evidence and my data, it seems that the influence of mortality is insignificant in this study.

The age distributions also correspond with the possible shift from an abrupt to a diffuse treeline. Aerial photographs suggest that treeline typology shifted from abrupt to diffuse sometime after 1957. The explosion of tree growth in the last 40 years may be a result of the transition between the two typologies. Abrupt treelines are often found at lower elevations than other treelines (Harsch & Bader, 2011), which means that the upper climatic boundary may be artificially suppressed at the abrupt edge. It is possible that, as treeline switched to diffuse, there was a relatively sudden uphill leap of the climatic boundary, as the reinforcing feedbacks that maintained an abrupt treeline broke apart. Whereas the abrupt treeline had been controlled by dieback and seedling mortality, the diffuse treeline was controlled by growth and therefore allowed seedlings to establish beyond the forest boundary (Harsch & Bader, 2011). The typological changes at the forest edge may have allowed for the rapid densification of the treeline ecotone.

The potential time period of the typology shift also corresponds with the significant jump in the maximum elevation of tree growth described in the spatial distribution patterns of treeline. Prior to 1940, all trees established below 3651.5 m a.s.l. Sometime between 1940 and 1977, however the maximum elevation jumped to 3718.5 m a.s.l., which is a gain of 67 m elevation. During this same period, the closed-canopy forest migrated about 6.7 m elevation (Fieden, 2010). The span of the forest-tundra ecotone, therefore, expanded about 10 times more quickly than treeline advanced. An expansive forest-tundra ecotone is indicative of a diffuse treeline. It is likely, therefore, that the shift in typology occurred sometime before 1977.

The rapid expansion of the forest-tundra ecotone compared to the forest boundary reinforces the importance of seedling establishment and survival in treeline advancement (Germino et al., 2002; Maher & Germino, 2006; Smith et al., 2003). Studies suggest that densification within the treeline ecotone may be a more immediate response to climate changes than migration of the forest edge (Camarero & Gutiérrez, 2004). Young seedlings respond immediately to climate changes because tree establishment depends heavily on environmental conditions (Kullman, 2002). Waiting for trees to reach the height of a closed-canopy forest, however, may take several years, creating a significant lag between climate change and treeline advancement (Grace et al., 2002). The rapid densification of the treeline ecotone observed on Pikes Peak, therefore suggests that recent climate changes have improved the ability for trees to establish in recent decades. If the temperature continues to warm, the seedlings of today will grow tall enough to form closed-canopy forest at higher elevations.

CONCLUSIONS

Overall, clustering was more prominent at lower elevations and for older cohorts, suggesting that the environment was historically harsher than it is today. The spatial distribution of trees at the moving edge changed from clustered to randomly dispersed: from 1868-1940 the moving edge was clearly clustered, from 1941-1976 it showed mixed results, and from 1977-2010 it displayed a random spatial pattern. The pattern at the moving edge indicates the upward migration of the climatic boundary, while also potentially indicating that the boundary is advancing more quickly than treeline. If this is the case, current treeline advancement may be recruitment-limited instead of climate-limited.

Treeline advancement also demonstrated a reach-and-fill pattern, with sudden advancement of treeline, followed by a few decades of infill at lower elevations. “Reaching trees” recruited more heavily at certain elevational bands, creating peaks of tree density. In following decades, tree recruitment concentrated below these peaks with little or no recruitment above. This pattern repeated three times in the last 120 years. In general, tree recruitment increased significantly in the last 30-40 years.

Evidence that the climatic boundary is outpacing tree establishment in the forest-tundra ecotone suggests that treeline advancement is likely to continue in the future. Forest expansion into the alpine tundra has significant ecological and climatological impacts. The encroachment of trees threatens the health and stability of alpine species and the tundra ecosystem (Walther et al., 2005). Globally, advancing treelines in both alpine and arctic environments may increase the net forest coverage of the world’s surface. Though the climatic effects of forest invasion are unclear – forests provide a carbon sink for climate cooling, but also reduce surface albedo for climate warming– it is an important consideration in understanding the dynamics of climate change (Grace et al., 2002).

The shift in treeline typology from an abrupt to a diffuse treeline and the subsequent explosion of tree growth above the forest boundary may indicate that treeline advancement is likely for many other treelines around the world. Currently, only about 22 percent of abrupt treelines are advancing (Harsch and Bader, 2011). However, my study provides evidence that significant changes in climate can initiate shifts in typology and that many other abrupt treelines may become diffuse with rising temperatures. Since over 80 percent of diffuse treelines are advancing (Harsch and Bader, 2011), it is likely that a change from an abrupt to a diffuse typology would initiate an explosion of tree growth above treeline, such as observed on Pikes Peak, and would further amplify the ecological and climatic effects of forest invasion.

The purpose of the current study was to analyze the population dynamics of an advancing treeline as it shifted from an abrupt to a diffuse typology. This study provided unique insight into distribution patterns and population wave-front dynamics at treeline. Although other studies have evaluated treeline advancement (e.g., Kullman, 2002; Harsch et al., 2009; Walther et al., 2005; Earnest, 2011; Fieden, 2010), few have the spatial or temporal resolution of this study to describe the specific movement patterns. For the first time in treeline research, the precise changes in the moving front of tree species are described. The patterns described by this study allow for better understanding of future changes in treeline dynamics with imminent climate change.

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REFERENCES

Alftine, K. J. & Malanson, G. P. (2004). Directional positive feedback and pattern at an alpine treeline. *Journal of Vegetation Science*, 15, 3–12.

Bekker, M. F. (2005). Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research*, 37(1), 97-107.

Bolli, J. C., Rigling, A., Bugmann, H. (2007). The influence of changes in climate and land-use on regeneration dynamics of Norway Spruce at the treeline in the Swiss Alps. *Silva Fennica*, 41(1), 55-70. Retrieved from http://www.metla.fi/silvafennica/full/sf411055.pdf

Bradshaw, R. H. W., & Zackrisson, O. (1990) A two-thousand-year history of a northern Swedish boreal forest stand. *Journal of Vegetation Science*, 1, 519-528.

Callaway, R., Brooker, R. W., Choler, P., Kikvidze, Z., Lortie, C. J., Michalet, R., Paolini, L., Pugnaire, F. I., Newingham, B., Aschehoug, E., T., Armas, C., Kikodze, D., & Cook, B. J. (2002). Positive interactions among alpine plants increase with stress. *Letters to Nature*, 417, 844-848.

Camarero, J.J. & Gutiérrez, E. (2004). Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change*, 63, 181–200.

Danby, R.K. & Hik, D.S. (2007). Variability, contingency and rapid change in recent subarctic tree line dynamics. *Journal of Ecology*, 95, 352–363.

Earnest, C. (2011). *Treeline dynamics on Pikes Peak, CO: Is the treeline moving and what is controlling the rate of movement?* Thesis, The Colorado College, Colorado Springs, CO.

Elliott, G. P. & Kipfmueller, K. F. (2010). Multi-scale influences of slope aspect and spatial pattern on ecotonal dynamics at upper treeline in the southern Rocky Mountains, U.S.A. *Arctic, Antarctic, and Alpine Research*, 42(1), 45-56.

Esri (2011). Multi-distance spatial cluster analysis (Ripley's K function) (spatial statistics). In *ArcGIS10 Help*.

Esri. (2012). FAQ: What is the Jenks optimization method?. In *Esri Support*. Retrieved from http://support.esri.com/en/knowledgebase/techarticles.

Feiden, M. (2010). *Treeline dynamics on the west slope of Pikes Peak*. Thesis, The Colorado College, Colorado Springs, CO.

Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J., & Velichko, A.A. (2007) Ecosystems, their properties, goods, and services. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden & C.E. Hanson, Eds., Cambridge University Press, Cambridge, 211-272.

Gear, A. J. & Huntley, B. (1991). Rapid changes in the range limits of Scots Pine 4000 years ago. *Science*, 251, 544-547.

Germino, M. J., Smith, W. K., & Resor, A. C. (2002). Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology*, 162, 157-168.

Grabherr, G., Gotfried, M., & Pauli, H. (1994). Climate effects on mountain plants. *Nature*, 369, 448.

Grace, J. (1988). Plant Responses to Wind. *Agriculture, Ecosystems and Environment*, 22/23, 71-88.

Grace, J., Berninger, F., Nagy, L. (2002). Review: Imacts of climate change on the tree line. *Annals of Botany*, 90, 537-544.

Haase, P. (1995). Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. *Journal of Vegetation Science*, 6, 575-582.

Harsch, M. A. & Bader, M. Y. (2011). Treeline form – a potential key to understanding treeline dynamics. *Global Ecology and Biogeography*, 20, 582-596.

Harsh, M. A., Hulme, P. E., McGlone, M. S., Duncan, R. P. (2009). Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters*, 12, 1040-1049.

Hiemstra, C. A., Liston, G. E., Reiners, W. A. (2002). Snow redistribution by wind and interactions with vegetation at upper treeline in the Medicine Bow Mountains, Wyoming, U.S.A. *Arctic, Antarctic, and Alpine Research*, 34(3), 262-273.

Holtmeier, F-K & Broll, G. (2005). Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14, 395–410.

Humphries, H. C., Bourgeron, P. S., & Mujica-Crapanzano, L. R. (2008). Tree spatial patterns and environmental relationships in the forest-alpine tundra ecotone at Niwot Ridge, Colorado, USA. *Ecological Research*, 23, 589-605.

Jenks, G. F. (1967). The Data Model Concept in Statistical Mapping. *International Yearbook of Cartography*,7, 186–190.

Johnson, E. A., Miyanishi, K., & Kleb, H. (1996). The hazards of interpretation of static age structures as shown by stand reconstructions in a *Pinus contorta-Picea engelmannii* forest. *Journal of Ecology*, 82, 923-931.

Kinnaird, M. F., Sanderson, E. W., O'Brien, T. G., Wibisono, H. T., & Woolmer, G. (2003) Deforestation Trends in a Tropical Landscape and Implications for Endangered Large Mammals. *Conservation Biology*. 17(1), 245-257.

Korner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia*, 115, 445-459.

Maher, E. L. & Germino, M. J. (2006). Microsite differentiation among conifer species during seedling establishment at alpine treeline. *Ecoscience*, 13(3), 334-341.

Malanson, G. P. (1997). Effects of feedbacks and seed rain on ecotone patterns. *Landscape Ecology*, 12(1), 27-38.

Norton, D.A., Palmer, J.G. & Ogden, J. (1987). Dendroecological studies in New Zealand, Part 1. An evaluation of tree age estimates based on increment cores. *New Zealand Journal of Botany* 25: 373-383.

Oke, T. R. (1978). *Boundary Layer Climates*. New York, NY: John Wiley.

Paulsen, J., Weber, U. M., & Körner, Ch. (2000). Tree growth near treeline: Abrupt or gradual reduction with altitude? *Arctic, Antarctic, and Alpine Research*, 32(1), 14-20.

Petty, G. W. (2008). *A first course in atmospheric thermodynamics*. Madison, WI: Sundog Publishing.

Piegorsch, W. W., & Bailer, A. J. (2005). Spatially correlated data. In *Analyzing Environmental Data* (pp. 275-323). Chichester, West Sussex, England: John Wiley & Sons.

Pitelka, L. F. & the Plant Migration Workshop Group (1997). Plant migration and climate change: A more realistic portrait of plant migration is essential to predicting biological responses to global warming in a world drastically altered by human activity. *American Scientist*, 85, 464-473.

Resler, L. M. (2006). Geomorphic controls on spatial pattern and process at alpine treeline. *Professional Geographer*, 58, 124–138.

Resler, L. M., Butler, D. R., & Malanson, G. P. (2005) Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography*, 26, 112–125.

Ripley, B. D. (1977). Modeling spatial patterns. *Journal of the Royal Statistical Society Series B – Methodological*, 39, 172-212.

Risser, P. G. (1993). Ecotones at local to regional scales from around the world. *Ecological Applications*, 3, 367-368.

Roberts, V. M. S. (2010). *Potential feedback mechanisms operating among Engelmann Spruce at alpine treeline on Pikes Peak, CO*. Thesis*,* The Colorado College, Colorado Springs, CO.

Shi, P., Körner, C., & Hoch, G. (2008). A test of the growth-limitation theory for alpine tree line formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional Ecology*, 22, 213-220.

Smith, W. K., Germino, M. J., Hancock, T. E., & Johnson, D. M. (2003). Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23, 1101-1112.

Stokes, M.A. & Smiley, T.L. (1968). *An Introduction to Tree-ring Dating*. Chicago: University of Chicago Press.

Walther, G.-R., Beißner, S., & Pott, R. (2005). Climate Change and High Mountain Vegetation Shifts. (G. Broll & B. Keplin, Eds.) *Change*, 77-97.

Wardle, P. (1985). New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craigieburn Range, Canterbury. *New Zealand Journal of Botany*, 23, 219–234.

APPENDIX

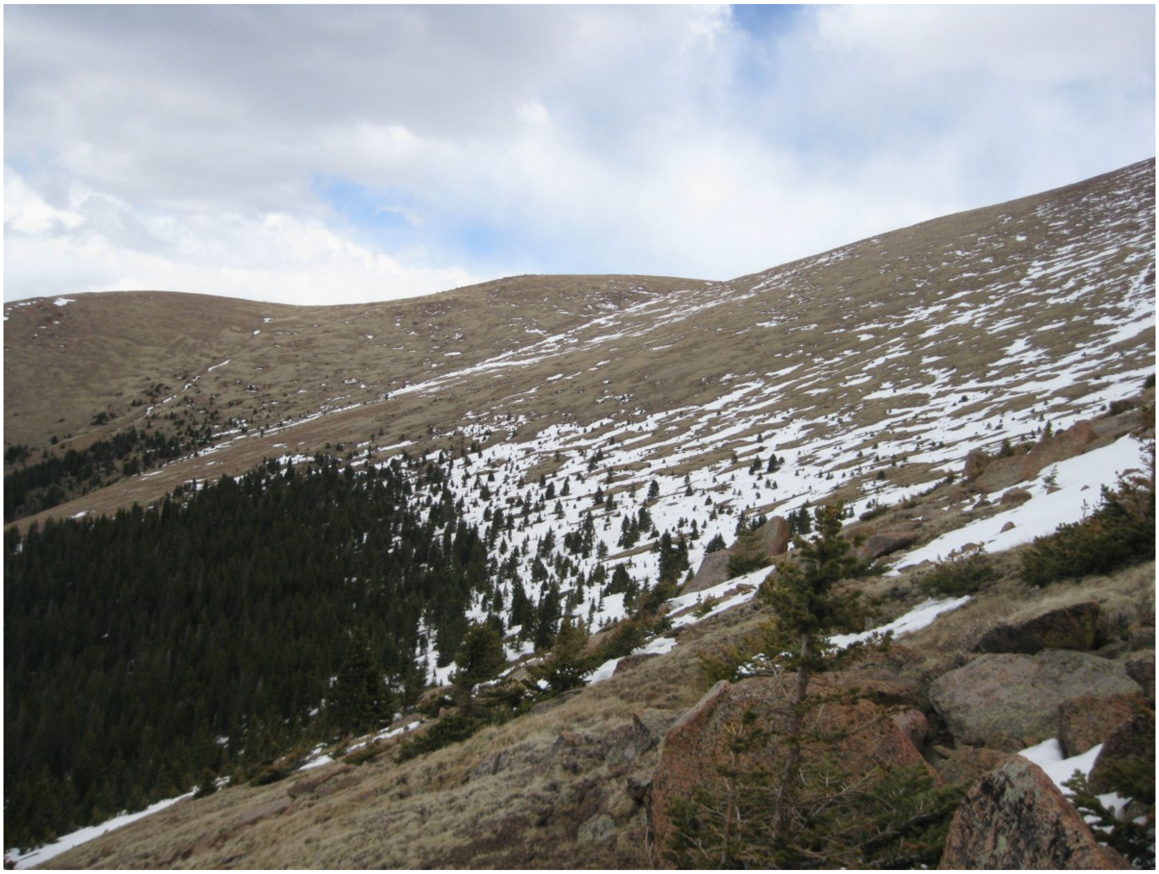


Figure 1. Side view of study site on Pikes Peak. Note the distinct forest boundary (a possible relic of a historically abrupt treeline) with diffuse growth above. The forest-tundra ecotone expands from the forest edge to the highest outpost seedling near the top of the ridge.

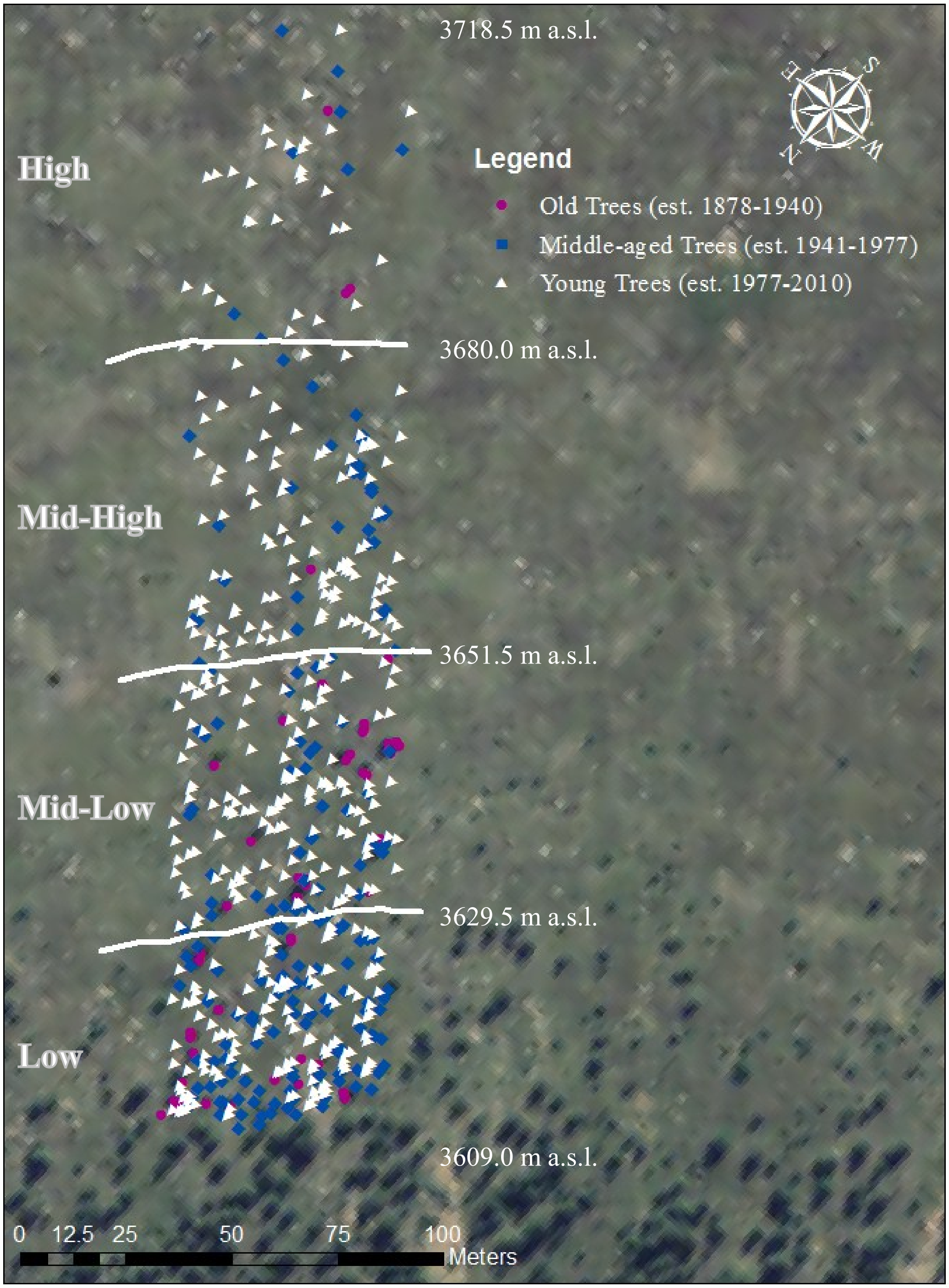


Figure 2. Aerial view of study site depicting elevational bands (high, mid-high, mid-low, and low) and age cohorts (old, middle-aged, and young).

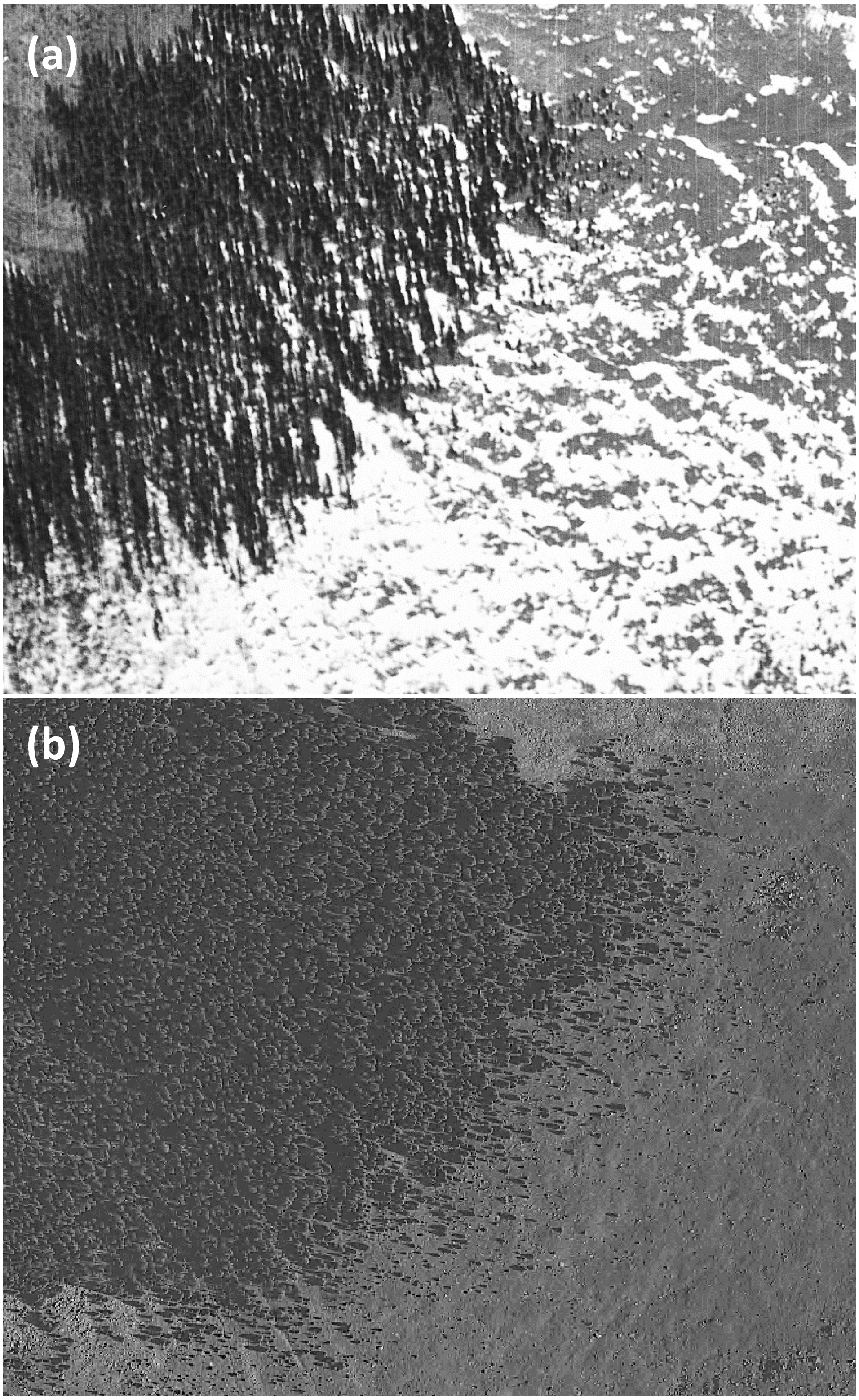
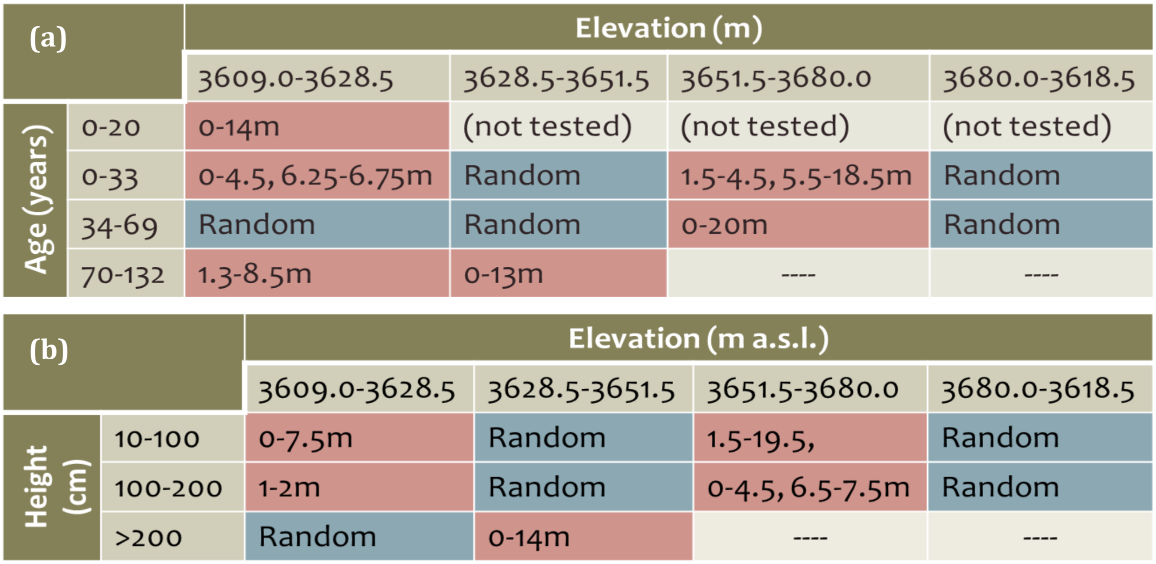


Figure 3. Historical aerial images of the study area on Pikes Peak. **(a)** Image from 1938 displaying an abrupt edge typology with tall growth at the forest boundary and few trees established beyond the forest edge. The treeline did not move between 1938-1957, suggesting that treeline was still abrupt in 1957 **(b)** Image from 2009 showing a diffuse treeline with a gradual decrease in tree density away from the forest edge. (Images adapted from Feiden, 2010).



(a)		Elevation (m)			
		3609.0-3628.5	3628.5-3651.5	3651.5-3680.0	3680.0-3618.5
Age (years)	0-20	0-14m	(not tested)	(not tested)	(not tested)
	0-33	0-4.5, 6.25-6.75m	Random	1.5-4.5, 5.5-18.5m	Random
	34-69	Random	Random	0-20m	Random
	70-132	1.3-8.5m	0-13m	----	----

(b)		Elevation (m a.s.l.)			
		3609.0-3628.5	3628.5-3651.5	3651.5-3680.0	3680.0-3618.5
Height (cm)	10-100	0-7.5m	Random	1.5-19.5,	Random
	100-200	1-2m	Random	0-4.5, 6.5-7.5m	Random
	>200	Random	0-14m	----	----

Table 1. Results of Ripley's K clustering analysis. Red boxes indicate a clustered pattern with the spatial scales of clustering listed. Blue boxes represent random distributions and tan boxes indicate that Ripley's K was not performed. Spatial analysis was not conducted for trees older than 70 and taller than 200 cm at the upper elevational bands because there were not sufficient populations for analysis. **(a)** Clustering analysis based on age cohort. Note that the first age class (age 0-20) is a smaller subdivision of the young trees (age 0-33). Spatial analysis was conducted for trees less than 20 years old at the lowest elevational band to show that trees less than 20 were clustered at a greater span of spatial scales than trees up to 33 years old. **(b)** Clustering analysis based on height class. The only differences between the age and height analyses were at the lowest elevational band.

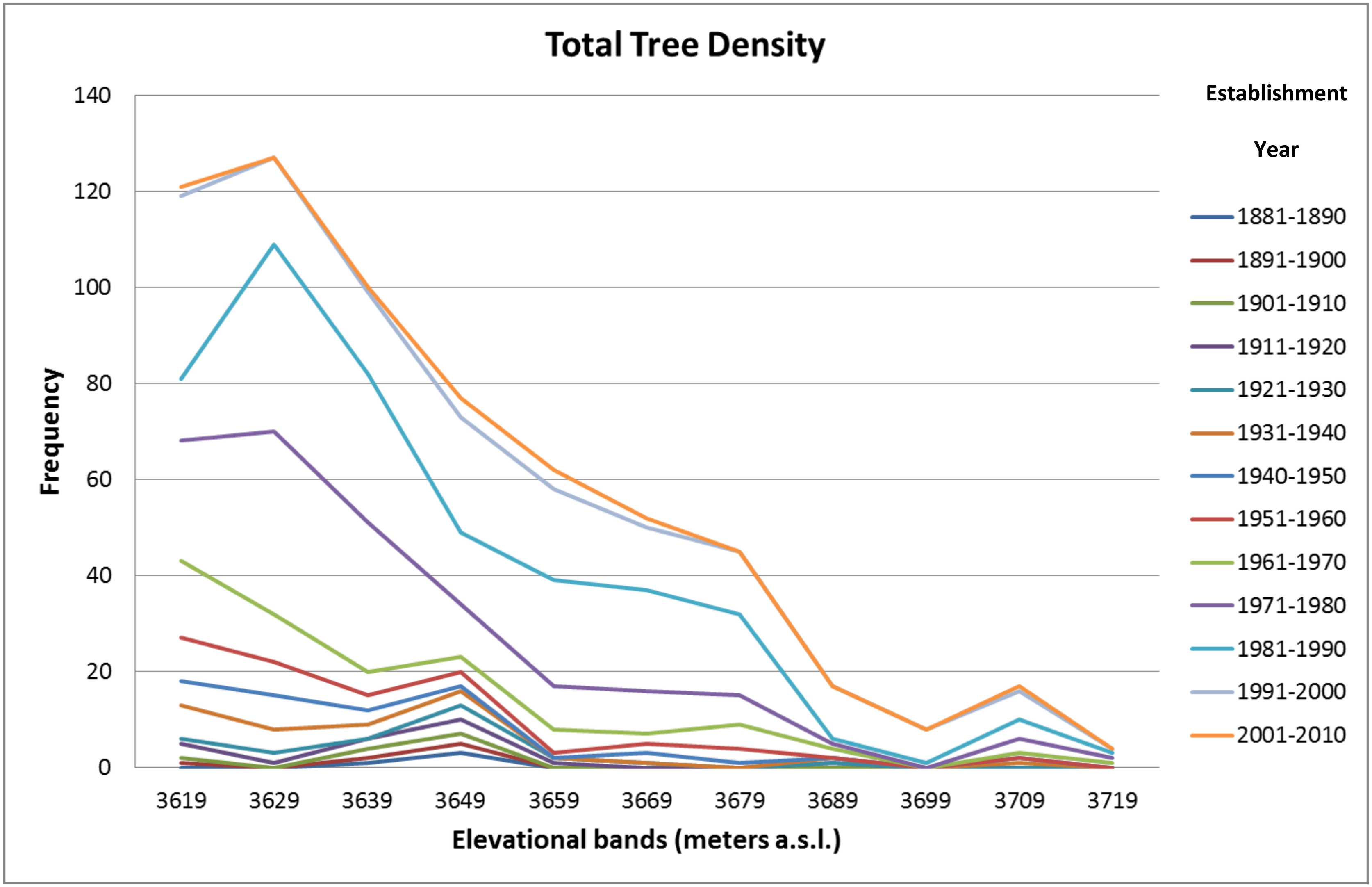


Figure 4. Total tree density by decade and elevational band. There are three noticeable peaks in tree density at 3649 m a.s.l., 3709 m a.s.l., and 3679 m a.s.l.

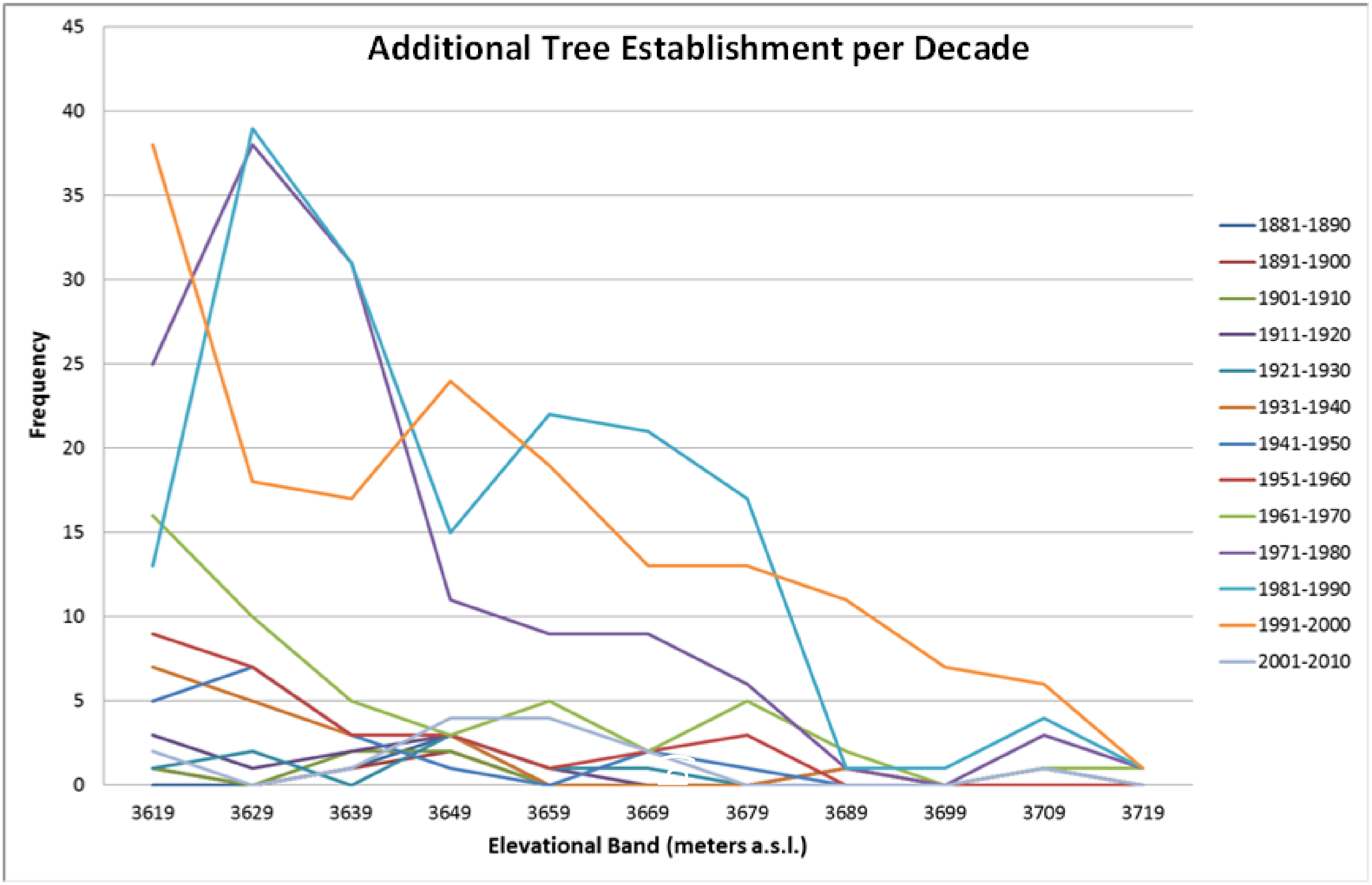


Figure 5. Additional tree establishment per decade. New tree establishment has increased significantly since the 1960s.

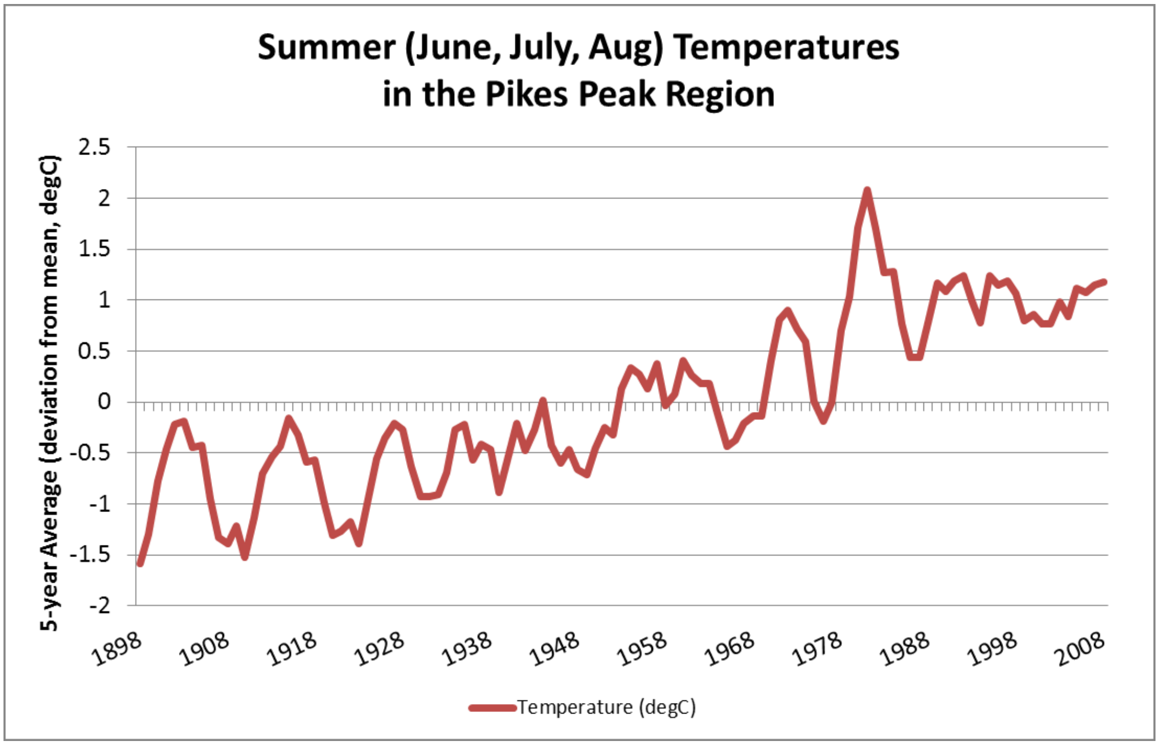


Figure 6. Average growing season temperature at Lake George, Colorado (38°54'N, 105°28'W). Lake George is about 26 km northwest and 1000 m lower than my study site. Average temperatures for June, July, and August have increased over 2.6°C since 1898 (Feiden, 2010).