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Reconstruction and spatial analysis of alpine treeline in the Elk Mountains, Colorado, USA

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The alpine treeline is a biogeographic transition zone that is an important indicator of environmental change. Here, I analyze spatial and temporal dynamics of vegetation in the alpine treeline ecotone in the Elk Mountains of western Colorado. I used dendroecological techniques to determine dates of tree establishment, then reconstructed past forest structure and composition and documented the patterns of vegetation change. The elevation of treeline in the Elk Mountains has not advanced upslope for at least 130 years, but tree density and basal area in the alpine ecotone have more than doubled during the 20th century. Spatial patterns of tree establishment are significantly clustered across multiple spatial scales in the alpine zone, while tree distributions in the subalpine forest have shifted from random to clustered patterns. Overall the pattern of treeline dynamics has been different from other sites in the Rocky Mountains where upslope advance has been more prominent. This research highlights the importance of site-specific information to understand variability in the spatial and temporal dynamics of treeline.

Keywords: alpine ecotone; Rocky Mountains; subalpine forest; timberline

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Introduction

The alpine treeline ecotone – the interface between subalpine forest and alpine tundra – is a dynamic vegetation zone responsive to environmental change across many spatial and temporal scales. Studies of the position and structure of treelines throughout the world have shown that the vegetation dynamics of these ecosystems have responded to broad-scale climatic changes over decades to millennia, and treeline dynamics may be an indicator of global-scale environmental change (Danby & Hik, 2007; Jiménez-Moreno, Fawcett, & Anderson, 2008; Smith, Germino, Johnson, & Reinhardt, 2009; Szeicz & Macdonald, 1995; Taylor, 1995). Further, changes in biogeographic patterns at treeline are likely to have ecological consequences such as reduction and fragmentation of habitat for alpine species (Grabherr, Gottfried, & Pauli, 1994), altered hydrologic properties of mountain soils (Harden, Hartsig, Lee, Farley, & Bremer, 2013; McVicar et al., 2007), and changes to carbon and nutrient cycling in montane ecosystems (Greenwood & Jump, 2014; Sjögersten & Wookey, 2005). Predicting the ecological impacts and future forest structure at treeline requires understanding of the spatial and temporal patterns of treeline dynamics.

The response of treeline to environmental change during the last century has varied between geographic locations. The position of alpine treeline (the upper elevation limit

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of trees with an upright growth form) has increased in 52% of mountain ranges worldwide during the 20th century (Harsch, Hulme, McGlone, & Duncan, 2009). However, in locations where treelines have not advanced upslope, structural changes within treeline forests, such as increased tree density (Liang, Wang, Eckstein, & Luo, 2011) and changes in growth form from prostrate to upright trees (Lescop-Sinclair & Payette, 1995), have been observed. Treelines that have advanced upslope during the 20th century differ from non-advancing treelines in the climatic conditions they experience as well as the spatial arrangement of trees in the (Harsch et al., 2009). Therefore, investigations of the spatial structure of treeline ecotones may help explain why some treelines have rapidly migrated upslope while others have remained relatively stable during the past century.

Although the structure and position of alpine treeline is influenced by climate at broad spatial scales (Körner, 1998), vegetation dynamics are modulated by fine-scale biological and topographic conditions (Bekker, 2005; Elliott & Kipfmueller, 2010; Holtmeier & Broll, 2005; Malanson et al., 2007). Biotic and abiotic factors can facilitate tree establishment resulting in clustered tree distributions. Establishment, growth, and reproduction of plants in harsh high-elevation environments are thought to be aided by facilitative effects of neighboring plants whereby neighbors create microclimatic conditions favorable for plant establishment by blocking wind, solar radiation, or frost deposition (Bertness & Callaway, 1994; Callaway, 1998). In these harsh environments, the positive effects from the amelioration of physical stress override the negative effects of competition for resources between individuals (Callaway, 1998; Callaway et al., 2002). Thus, positive feedbacks between established trees and establishing trees result in clustered tree distributions in the treeline ecotone (Bekker, 2005; Maher, Germino, & Hasselquist, 2005; Marr, 1977). Clustered tree distributions can also be produced by periglacial topographic features such as boulders and terrace risers that provide shelter to seedlings (Resler, 2006; Resler, Butler, & Malanson, 2005).

While the spatial pattern of tree distribution in the alpine ecotone is generally expected to be clustered, spatially random tree distributions have been documented at treeline in the Front Range of the Southern Rocky Mountains (Elliott, 2011; Elliott & Kipfmueller, 2011). These spatial patterns were interpreted to mean that sites exerting only moderate physical stress on tree physiology may allow trees to establish without requiring facilitative effects from neighboring individuals or topographic shelters. If favorable climatic conditions eliminate the need for facilitation, then a warming of climate may cause a shift in the pattern of tree establishment from clustered to random. Moreover, a shift in the spatial pattern of tree establishment may result in feedbacks that influence the rate of treeline advance and accelerate or retard future patterns of tree establishment. A shift in the spatial pattern of tree establishment can take several forms (Figure 1), and such a shift could be detected by reconstructing stand structure in both the alpine and subalpine zones.

In this study, I quantify characteristics of the structure and dynamics of the alpine treeline on the west slope of the Southern Rocky Mountains in a region where there is a paucity of information on treeline dynamics. Assessing the variability of treeline responses to environmental change requires information across locations experiencing a wide range of conditions. However, the majority of treeline studies in the Southern Rocky Mountains have been conducted east of the Continental Divide where climatic conditions are much drier than on the west slope (e.g. Allen, Peet, & Baker, 1991; Elliott & Kipfmueller, 2010; Hessl & Baker, 1997). To compare treeline dynamics with

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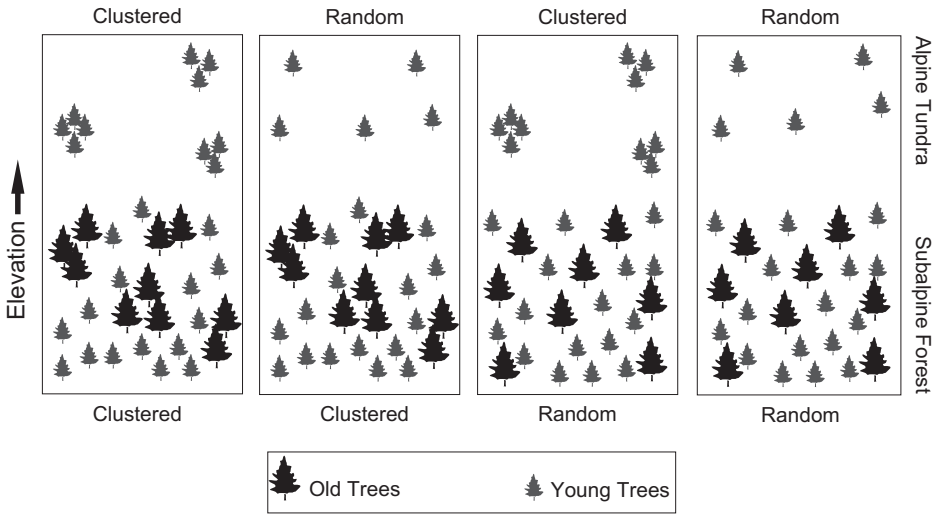

Figure 1. Four scenarios of shifts in the spatial arrangement of trees in the treeline ecotone. Tree establishment in subalpine forests that were formerly located at treeline may have been clustered or random with younger trees filling in gaps as forest density increased. Stability or dynamics of spatial patterns can be assessed by reconstructing past establishment patterns along an elevational transect that spans the subalpine and alpine zones.

other sites in the Southern Rocky Mountains, I use tree establishment dates to assess whether treeline has advanced during the last century and whether tree density has changed within the treeline ecotone.

While previous studies have quantified the spatial arrangement of trees in the treeline ecotone (e.g. Elliott & Kipfmueller, 2010), there is a lack of research on the temporal stability of these patterns. Here, I employ a novel use of a dendroecological reconstruction method to assess temporal variability in the spatial pattern of tree establishment. I explicitly investigate whether spatial patterns have changed over the 20th century by reconstructing stand structure and composition at the beginning of the 20th century and quantifying reconstructed and contemporary tree distributions. Specifically, I address the following research questions: (1) has the elevation of treeline changed during the 20th century? (2) have the density or basal area of treeline forests changed? and (3) has any shift in the spatial pattern of tree establishment occurred over the past century?

Methods

Study area

Structure and dynamics of treeline were investigated on three peaks representative of treeline ecotone forests of the southern portion of the Elk Mountains and northern portion of the West Elk Mountains of western Colorado (Figure 2). The three peaks selected for sampling were Mt. Bellview, Mt. Baldy, and Mt. Axtell, and treeline was sampled on west, southeast, and southwest slopes, respectively (Table 1). To address research questions about treeline dynamics, I restricted analyzes to sites where the presence of alpine vegetation above treeline may indicate that this site has the potential for tree establishment.

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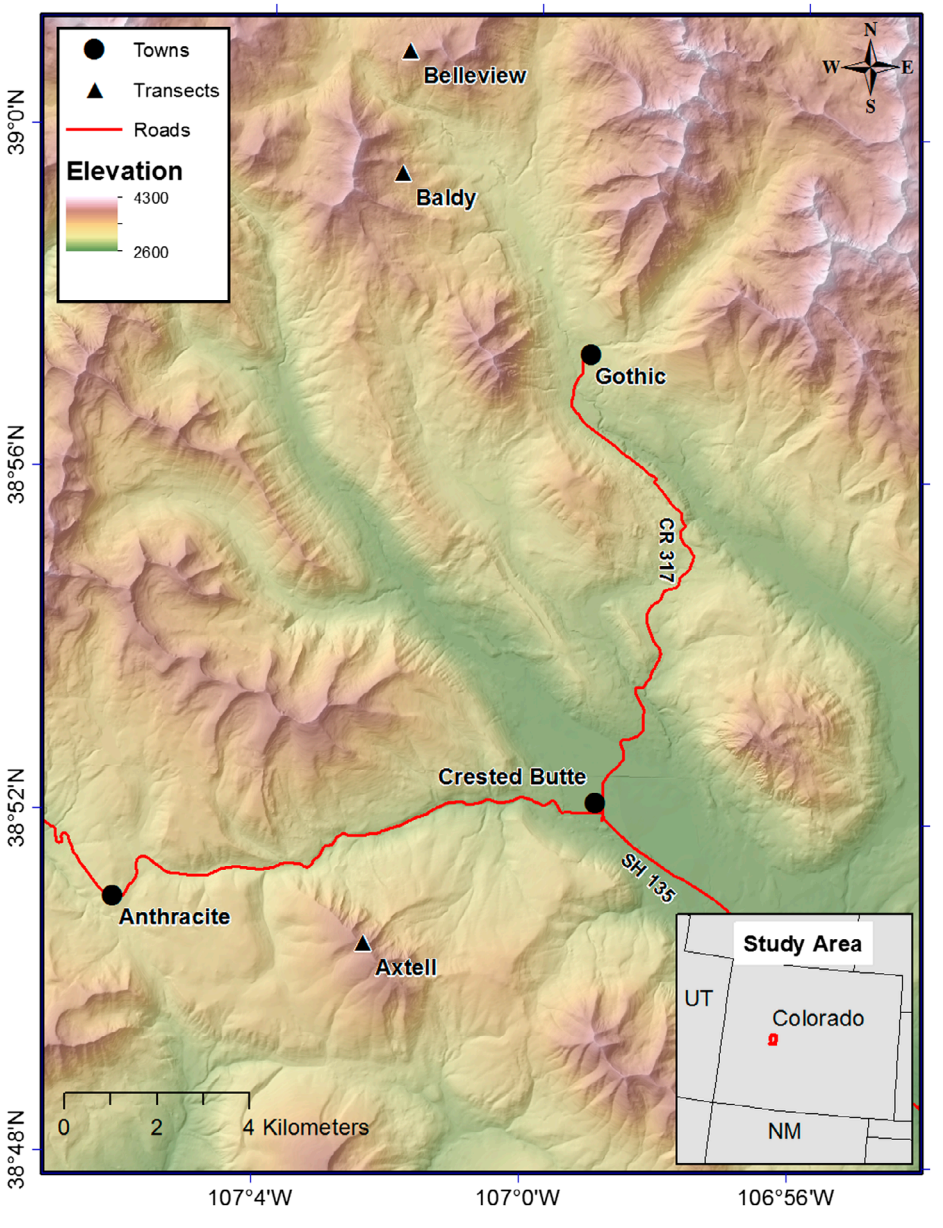

Figure 2. Map of the study area. Elevations are shown in meters.

The Elk and West Elk Mountains are characterized by steep peaks of uplifted sedimentary rocks with numerous igneous intrusions (Prather, 1999). All three study sites reported here are located on weathered laccoliths of granodiorite and quartz monzonite that intruded into sedimentary strata during the mid-Tertiary (Gaskill, DeLong, & Cochran, 1987). The thin, well-drained soils at treeline are classified as very gravelly loam or stony clay loam derived from colluvium and residuum weathered from igneous rock, and they support alpine and subalpine vegetation typical of the Southern Rocky

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Table 1. Characteristics of study sites.

Transect characteristic	Mt. Bellview	Mt. Baldy	Mt. Axtell
Elevation (m)	3545	3478	3666
Slope aspect (°)	270	120	230
Slope angle (°)	16	20	22
Length (m)	680	290	140
Trees	324	121	157
Saplings	47	41	39
Seedlings	67	21	16

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Mountains (Soil Survey Staff, 2015). Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies bifolia*) dominate the subalpine forest and treeline ecotone, and were the only tree species present in this study area. These two species are the most commonly encountered at treeline throughout the Rocky Mountains (Holtmeier, 2009). Some shrubs are present in the understory of the subalpine forest and extend to treeline. The most frequently encountered shrubs in transects were *Ribes spp.* and *Vaccinium spp.*

The study area is characterized by a continental montane climate where most precipitation falls as snow between November and April and some rainfall is associated with convective storms in the summer. Temperature ranges from an average daily minimum of −12.6 °C in January to an average daily maximum of 19.3 °C in July. Average January snowfall is 176 cm (Western Regional Climate Center, n.d.-b). This region receives some of the highest annual winter snowfall totals in Colorado (Western Regional Climate Center, n.d.-a).

Fire, livestock grazing, and logging have been the dominant disturbance agents within the region surrounding the study area. No records of major fires exist for this area since the establishment of the Gunnison National Forest in 1905, but evidence of past fire is extensive. Even-aged stands of lodgepole pine (*Pinus contorta*) and pockets of fire-scarred trees and snags occur throughout the region. Langenheim (1962) estimated that the most recent widespread fires in the area occurred between 1890 and 1895 based on establishment dates of lodgepole pines. I observed basal fire scars on dead trees near treeline at the Mount Bellview site, and even-aged stands of lodgepole pine occur at elevations below the Mount Axtell site, but I did not notice any evidence of past fire near treeline on Mount Axtell or Mount Baldy. The intensity of grazing (62,000 cattle and horses) on the National Forest is lower than historical levels, and a trend of decreasing grazing intensity has continued for more than 50 years (Bradford, McConkey, & Reed, 2003). Evidence of grazing was observed near the treeline ecotone, but severe soil erosion from grazing did not appear to be occurring. Timber harvest in support of mining activities began in the 1870s (USDA Forest Service, 1928), but I observed no evidence of logging (e.g. cut stumps) at any of the treeline study sites.

Field methods

Forest structural and compositional data were collected in belt transects that spanned the treeline ecotone. Here I refer to treeline as the elevational limit of individual trees with an upright growth form. Timberline refers to the upper limit of closed-canopy subalpine forest, and the treeline ecotone is the area between treeline and timberline

(Malanson et al., 2007). Potential study sites were identified by examining aerial imagery and selecting representative peaks with alpine tundra vegetation above closed-canopy subalpine forest. Then, sites were visited to verify that treeline was not influenced by avalanche tracks or drastic changes in slope, soil conditions, or substrate. Each transect originated at the highest-elevation tree with an upright growth form and extended down slope perpendicular to slope contours. Trees with a krummholz growth form were not sampled because the microclimate they create may not represent conditions for tree establishment (Körner & Paulsen, 2004). Transects extended 50 m into the subalpine forest zone where interlocking crowns created closed-canopy forest. Each transect was 20 m wide in the area above timberline and 10 m wide below timberline to minimize oversampling in the high density subalpine forest.

Within each transect, all trees (≥5.0 cm diameter at breast height; DBH), saplings (<5.0 cm DBH), and seedlings (0.3–1.4 m tall) were identified to species and their status (live or dead) was noted. The first two years post germination is the most critical life stage for treeline trees, where rates of mortality are high (Germino, Resor, & Smith, 2002). Therefore, seedlings appearing to be recently germinated (<0.3 m tall and < 1 cm basal diameter) were excluded from analysis. The location (x, y coordinates to the nearest 0.1 m) of each tree within the transect was determined by measuring the distance and azimuth of each tree relative to a corner of the transect using a distance tape and compass. The diameter of each dead tree was measured, and the condition of each stem was classified into categories of wood decay using methods prescribed by Maser, Anderson, Cromack, Williams, and Martin (1979). Increment cores were collected from live trees from a height of 30 cm above the ground. Where upright trees exhibited layering of lower branches that created a cluster of small stems, the largest diameter upright stem was cored. Additionally, cross sections of seedlings and saplings were collected at the ground surface. For each seedling and sapling collected, its location along the transect (y coordinate) and whether the seedling or sapling established in open conditions or under existing canopy was noted.

Position of treeline

To determine whether trees establishing upslope have increased the elevation of treeline since the beginning of the 20th century, I quantified age structure of transects. Establishment dates of all trees were estimated using increment cores and cross sections. Cores and cross sections were processed using standard dendrochronology methods (Stokes & Smiley, 1968). Establishment dates were determined by visually crossdating annual rings on all increment cores from sampled trees (Yamaguchi, 1991). Increment cores that missed the pith of the tree were overlaid with a transparent ring template and the number of rings missing from each core was estimated. Annual growth rings were counted from basal cross sections (at the ground surface) and from cross sections 30 cm in height. The difference between ring counts from the two stem heights of each individual was recorded and used as an age-to-coring height correction factor (Villalba & Veblen, 1997). The ages of basal cross sections were also used to determine the establishment dates for seedlings and saplings in each transect. Ages of seedlings and saplings not sampled were estimated using regression of age against basal stem diameter. Separate regressions were used for seedlings establishing in open vs. closed canopy conditions. Distribution of tree ages along transects were summarized with a linear best-fit line from treeline to the bottom of each transect.

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Reconstruction of stand structure

The stability of stand conditions and the spatial arrangement of tree establishment were analyzed by reconstructing stand composition and structure for two periods in the 20th century (1900 and 1960) and comparing past and contemporary (2013) stand structure. Reconstructions were developed by removing trees with an establishment date following the reconstruction date, subtracting diameter increments from trees predating the reconstruction date, and adding dead trees that would have been alive at the reconstruction date back into the stand (Maxwell et al., 2014; Scholl & Taylor, 2010). The year of death for each dead tree was estimated using methods developed by Fulé, Covington, and Moore (1997) and adapted for subalpine forests using growth rates for Engelmann spruce (Meyers & Alexander, 1972). The decay condition of each dead tree was used to predict the death date using a tree decay model (Rogers, Prosser, Garrett, & Ryan, 1984). Dead trees added back into the reconstructed stand had annual diameter increments removed based on average growth increments for each species (i.e. radial growth from reconstruction date to date of death). A potential source of error in this reconstruction is uncertainty in the decay rate of dead wood, which would influence the estimated date of tree death. Therefore, I used a sensitivity analysis to determine the effect of variable decay rates on reconstructed stand composition. For all dead trees added back into reconstructed stands, I calculated the 25th, 50th, and 75th percentile decay rates (Fulé et al., 1997). I then report stand density and basal area as a range of values based on this variable decay rate.

Spatial pattern of tree establishment

The spatial arrangement of trees in contemporary and reconstructed stands were quantified using Ripley's K function (Ripley, 1977) to analyze tree locations as points in two-dimensional space. The K function is a second-order point pattern analysis technique based on calculating the mean number of points occupying circular plots of variable radii surrounding each point in the study area. K functions were calculated for all possible radii using the x, y coordinates of all trees in the transects. Two pieces of information were used to determine if the spatial arrangement of trees was random, clustered, or dispersed. First, a theoretical K function was calculated for each transect assuming complete spatial randomness (CSR) – a point pattern with no first- or second-order effects. Second, an envelope of K functions was produced for each transect using 99 simulations of tree distributions in an area with the same spatial dimensions as the transect. Observed K functions were compared to theoretical functions to assess whether spatial patterns of trees were significantly different from CSR. However, critiques of this method assert that CSR is an unrealistic null hypothesis for point patterns with known first- or second-order effects (Gould, 1970). Both first-order effects (e.g. spatial variation of physical characteristics of the study area) and second-order effects (e.g. competition or facilitation between trees) are reasonably expected to influence the spatial arrangement of tree establishment. Therefore, I rely upon a comparison between simulated and observed K functions to discern spatial distribution of trees. K functions within the envelope of simulated tree distributions were interpreted as being randomly distributed, while K functions outside the simulation envelope were interpreted as clustered or dispersed. Calculations of observed and theoretical K as well as simulations were completed using the spatstat package (Baddeley & Turner, 2005) in *R* (R CoreTeam, 2015).

Results

The three transects varied by slope aspect and length of the treeline ecotone, but were similar in slope angle (Table 1). Elevation of treeline was highest on the southwest-facing slope of Mt. Axtell (3666 m) and lowest on the southeast-facing slope of Mt. Baldy (3478 m). Ages were estimated for 602 total trees. Ages could not be determined for 37 trees (less than 7% of the total trees) due to rot. I counted 127 saplings and 104 seedlings within the transects. The average age of saplings was 49 years (range 36–71), and the average age of seedlings was 20 years (range 9–29). Stem ages were not estimated for krummholz, but trees with krummholz growth form were only observed on Mt. Bellview above the elevation of the highest upright tree (the top of the transect).

Position of treeline

A slight trend of older trees with increasing distance from treeline was detected in each of the study sites, but this trend in tree age was only significantly different from zero on Mt. Bellview as determined by a *t*-tests on the slope coefficients of regression lines (Figure 3). Trees exceeding 100 years in age were located at or near the top of each

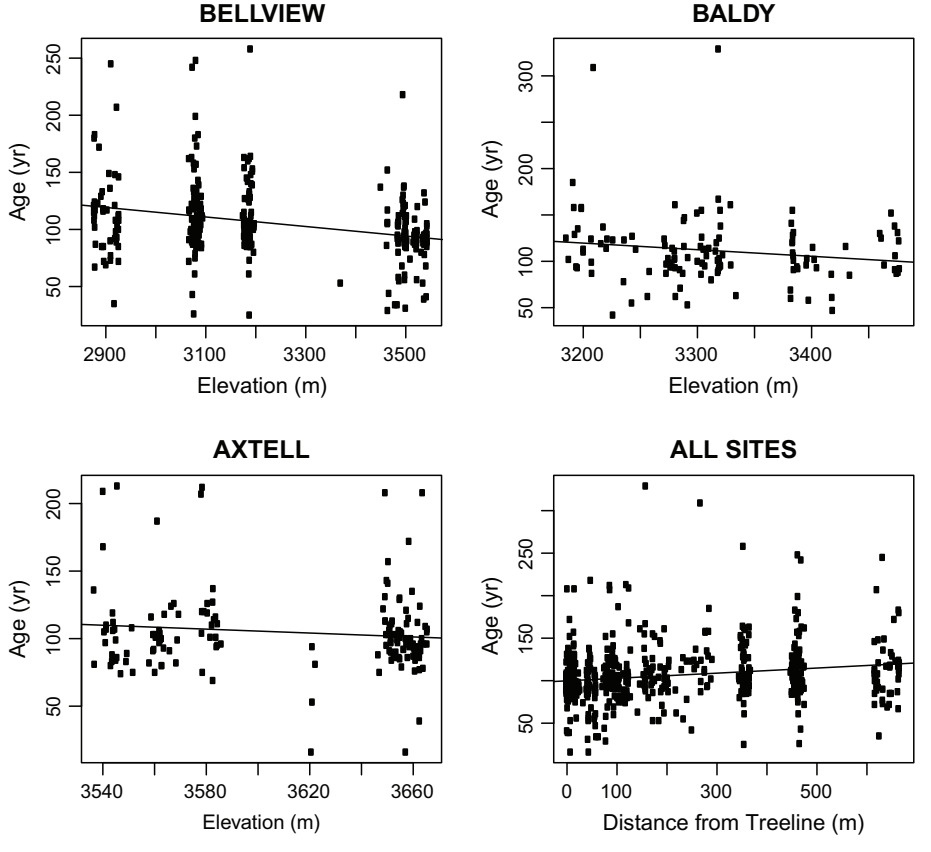

Figure 3. Tree age by elevation. The relationship between elevation and tree age was negative at all sites, but only significantly different from zero at Mt. Bellview ($p < 0.05$; *T*-test).

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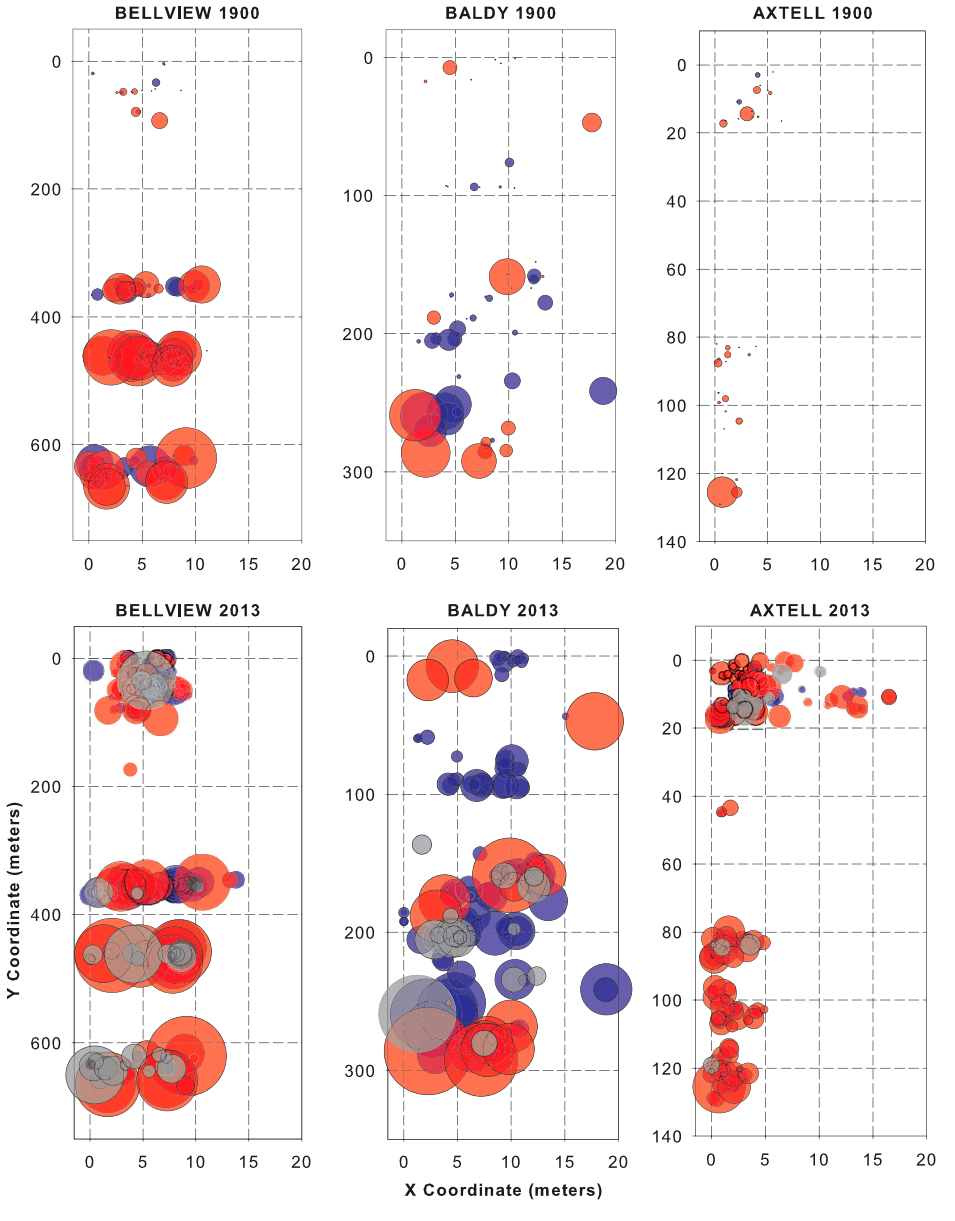

Figure 4. Reconstructed (top three panels) and contemporary (lower three panels) spatial distribution of trees within transects in the treeline ecotone. Red circles indicate individuals of Engelmann spruce, blue circles represent subalpine fir, and gray circles are dead trees. The top of each graph corresponds with the upper limit of upright trees. Note that the *y*-axes have different scales between study sites and *x*-axes have been expanded to show detail. Sizes of point symbols are proportional to tree diameters.

transect (Figure 4). The oldest upright tree at the top of the transect on Mt. Bellview was a 130 year old subalpine fir. The oldest tree at the top of the Mt. Baldy transect was a 138 year old Engelmann spruce, and a 208 year old Engelmann spruce was located within 2 m of treeline on Mt. Axtell.

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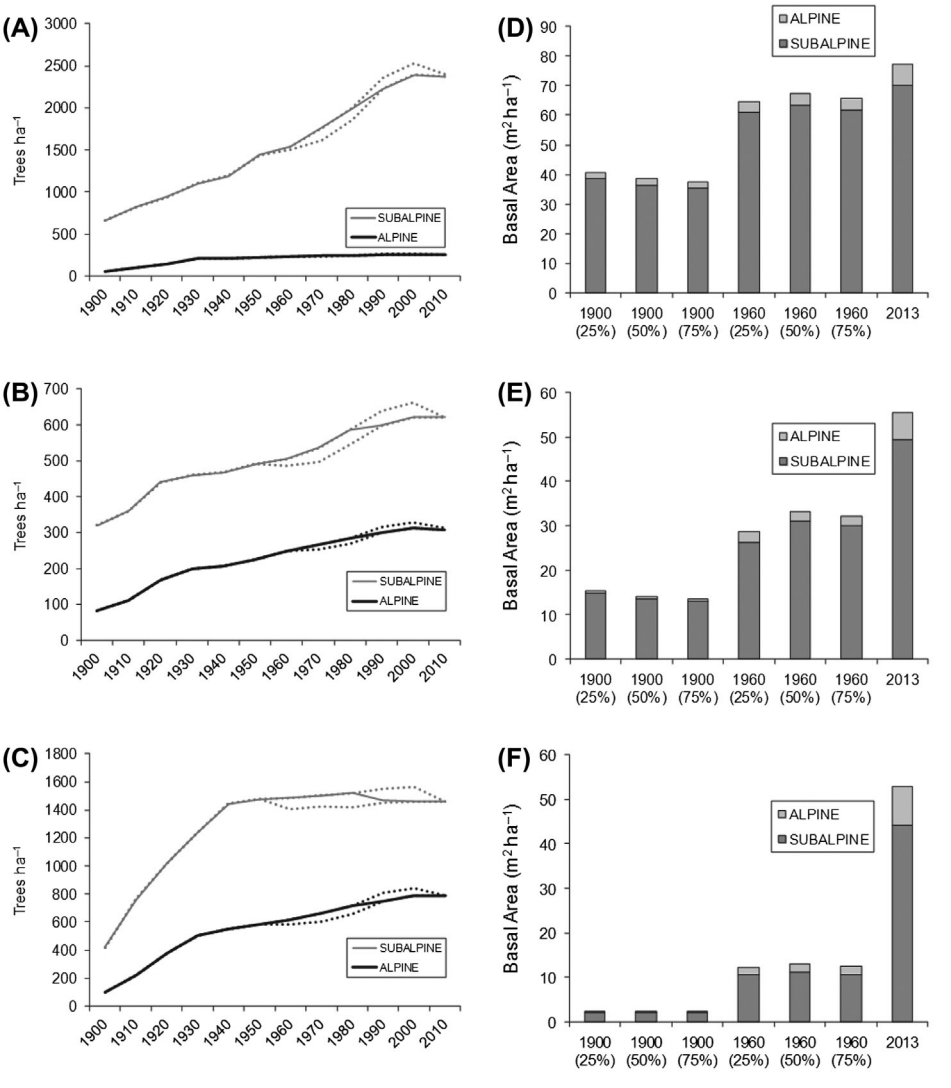

Figure 5. Reconstruction of live tree density (A)–(C) and basal area (D)–(F) in the treeline ecotone. Density in the subalpine zone (black line) and alpine zone (gray line) is shown for Mt. Bellview (A), Mt. Baldy (B), and Mt. Axtell (C). Solid lines indicate tree density using the median (50th percentile) decay rate for dead wood. Dashed lines represent stand reconstructions using faster (75th percentile) and slower (25th percentile) rates of decay. Similarly, basal area in 1900 and 1960 was reconstructed for Mt. Bellview (D), Mt. Baldy (E), and Mt. Axtell (F) using variable rates of dead wood decomposition. Note that *y*-axis scales vary between sites.

Stand structure of the treeline ecotone

The density and basal area of trees in the alpine and subalpine zones have increased during the 20th century (Figure 4). On each peak, tree density in the alpine zone was below 200 trees ha^{-1} in 1900, but median tree density above timberline increased to 255 trees ha^{-1} on Mt. Bellview, 308 trees ha^{-1} on Mt. Baldy, and 786 trees ha^{-1} on Mt. Axtell by 2010 (Figure 5). The largest portion of increase in basal area on Mt.

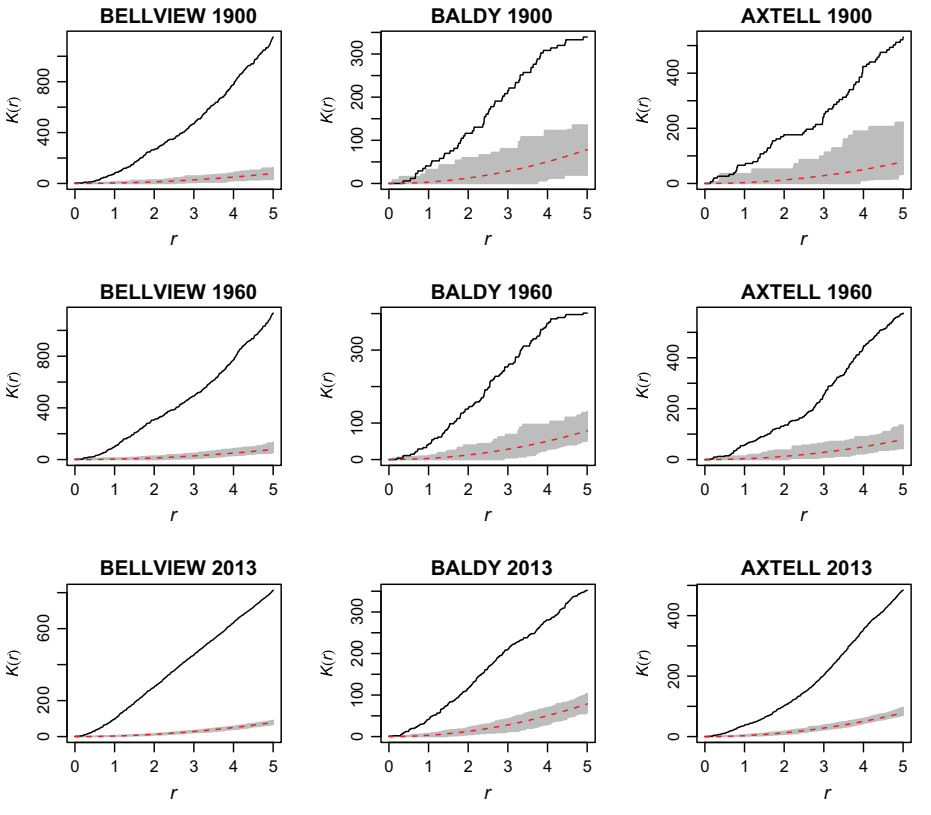

Figure 6. Spatial arrangement of trees in the alpine zone of reconstructed (1900 and 1960) and current (2013) treeline transects. Solid lines are Ripley's K functions across inter-tree distances of increasing radii (r) observed at each site. Dashed lines are predicted K functions assuming complete spatial randomness of tree establishment. Gray envelopes are the range of K functions generated with 99 simulations. A K function above the predicted function indicates a clustered arrangement of trees.

Axtell occurred after 1960, while both Mt. Bellview and Mt. Baldy experienced a larger increase in basal area between 1900 and 1960. The largest increase in basal area in the alpine zone occurred on Mt. Axtell with a basal area of 0.16 m^2 ha^{-1} in 1900 increasing to 9.0 m^2 ha^{-1} in 2013.

Spatial pattern of tree establishment

In the alpine zone, trees were significantly clustered at between-tree distances greater than 0.5 m (Figure 6). The degree of clustering (the difference between the observed K function and the envelope of K functions from simulated tree distributions) increased over larger inter-tree distances. The same spatial pattern was evident in reconstructed stands (1900 and 1960) as well as contemporary stands (2013). Trees in the subalpine zone differed in their spatial arrangement among sites (Figure 7). On Mt. Bellview, trees were randomly distributed in 1900 and 1960; but in the contemporary stand, trees are clustered at distances over 0.5 m. Trees were randomly distributed at all time periods on Mt. Baldy, and clustered at all time periods on Mt. Axtell.

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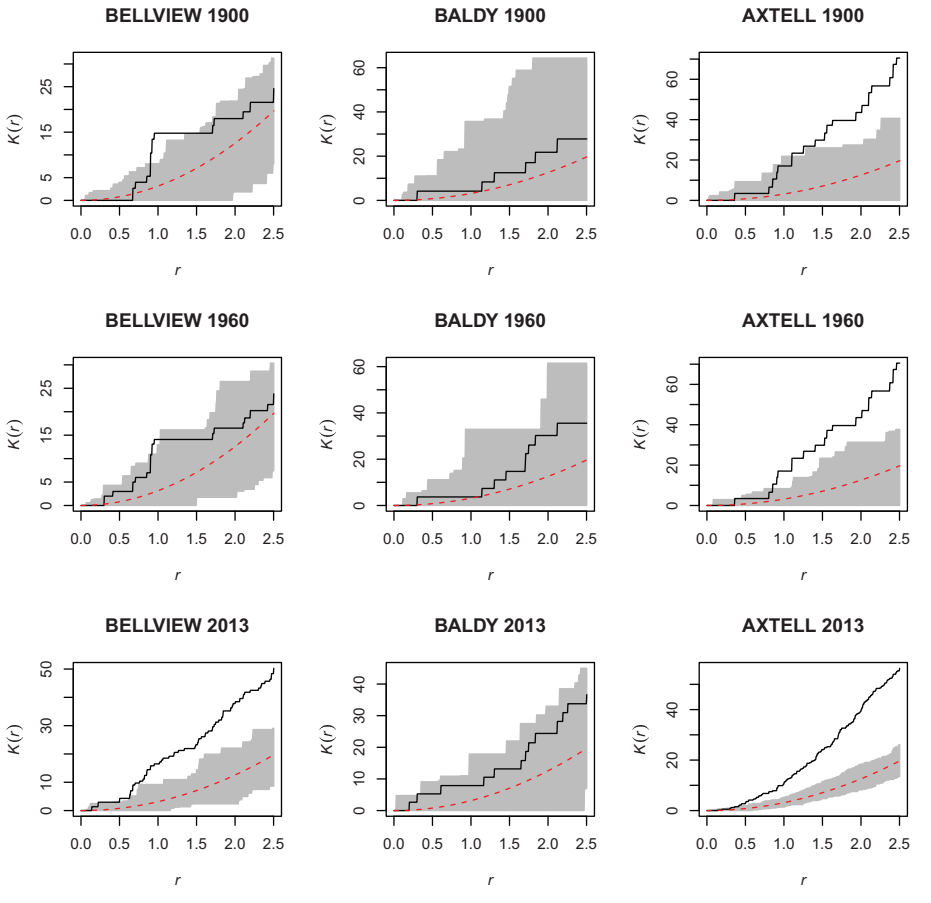

Figure 7. As in Figure 6, but for the subalpine zone.

Discussion

The total area of alpine tundra in the Elk Mountains is limited in spatial extent and landscape position. The study sites presented here were representative of treelines in the region where the presence of soil and alpine vegetation indicates at least the potential for tree establishment. In my reconnaissance of the study area, I found a distinct lack of treeline on north-facing slopes except on peaks where treeline was limited by rock outcrops and a complete lack of soil. On most north-facing slopes, at least a few upright trees extended to ridge tops. Southerly aspects present particularly harsh conditions for the establishment of trees, which can result in variability of treeline in relation to slope aspect. Mortality in pre-establishment seedlings is higher on south-facing slopes and the south side of tree islands in the Rocky Mountains due to the effects of increased sun exposure, drought stress, and extreme diurnal temperature fluctuations (Germino et al., 2002). Additionally, Elliott (2011) encountered clustered tree distributions more commonly on south than north facing slopes at Rocky Mountain treeline sites east of the continental divide. Clustered distributions may indicate increased importance of positive feedbacks for tree establishment on exceptionally harsh sites.

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The elevation of treeline in the Elk Mountains has not advanced upslope during the 20th century. I did detect a slight negative relationship between tree age and elevation at all three sites, but the trend was statistically significant in only one site, Mt. Bellview. Although the trend of younger trees at higher elevations does indicate infilling of the treeline ecotone, trees predating the 20th century were located at the upper limit of treeline. In each transect, the age of highest elevation upright tree exceeded 130 years. The lack of tree establishment at elevations above the current treeline represents a pattern different from other sites in the Rocky Mountains where trees have established at new maximum elevations during the 20th century (e.g. Bekker, 2005; Elliott, 2011).

Although the maximum elevation of trees in the Elk Mountains seems unchanged during the 20th century, the alpine treeline ecotone has experienced a substantial increase in tree density and basal area over this same period. Other sites in the Rocky Mountains experienced a similar degree of densification, but the timing of tree establishment in the Elk Mountains differed from these previous studies. For example, several investigations in the Rocky Mountains found that the majority of trees established during the mid to late 20th century (Bekker, 2005; Elliott, 2011; Hessl & Baker, 1997), but here I found that all three of my study sites experienced greater increases in tree density during the first half of the 20th century and gradual density increases in the later decades. Additionally a smaller proportion (71%) of trees established in the 20th century in the Elk Mountains compared to several sites east of the continental divide (84%; Elliott, 2011).

The increase in tree density is also associated with a dramatic increase in biomass as indicated by stand basal area. The timing of basal area increase differed from that of density; basal area increased more dramatically between 1960 and 2013 than between 1900 and 1960. Quantifying the increase in basal area has been a less common practice than documenting increases in density or shifts in treeline elevation, but biomass is perhaps a more important metric in the context of understanding the carbon cycle implications of ecosystem change at treeline (Grafius & Malanson, 2015). The main source of change in the alpine ecotone of the Elk Mountains is the addition of biomass in the form of larger trees and higher tree density. Therefore, the largest vegetation change is likely to come from infilling of the treeline ecotone rather than expansion of forests to higher elevations.

The anomalous pattern of treeline dynamics in the Elk Mountains compared to other locations in the Rocky Mountains may be due to structural characteristics of stands. While approximately half of studied treelines worldwide have experienced recent increases in elevation or latitude (Harsch et al., 2009), several previous studies have found situations where treeline has been stationary, but density has increased (Danby & Hik, 2007; Liang et al., 2011; Szeicz & Macdonald, 1995). Treeline dynamics of increasing density without upslope advance of treeline is not unusual worldwide, but many treelines in the Rocky Mountains have shown both increased density and upslope advance (Holtmeier & Broll, 2007). Harsch et al. (2009) suggested that diffuse treelines with upright trees are the most likely to experience advance, while treelines with abrupt transitions from forest to tundra and treelines with extensive areas of krummholz trees are more likely to be stationary. The treeline site on Mt. Bellview is consistent with this observation because a zone of krummholz trees extends more than 50 m above the highest elevation upright tree. However, the treelines have also been stationary on Mt. Baldy and Mt. Axtell for more than a century despite the fact that the gradual transition between forest and tundra at each of these sites is characterized by a decrease in tree density with proximity to treeline.

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The discrepancy between the characteristics of advancing treelines proposed by Harsch et al. (2009) and the stand structure on Mt. Baldy and Mt. Axtell may point to an alternative environmental factor such as climate or topography limiting treeline advance. The Elk Mountains receive more precipitation and generally have deeper snowpack than sites with advancing treelines on the east slope of the Rockies (e.g. Elliott & Kipfmueller, 2010). Increased depth of snow pack that leads to a shortened snow-free period may limit the establishment of seedlings in the Elk Mountains. Alternatively, a lack of suitable shelters may preclude upslope seedling establishment (Resler et al., 2005). More work is needed to identify specific mechanisms limiting treeline advance in this region.

A high quality reconstruction of the treeline ecotone at the beginning of the 20th century was possible, and this reconstruction confirms that treeline elevation has remained stationary while tree density and basal area have increased. Similar reconstructions using dendrochronology have been used in fire-prone forests of western North America to quantify the effects of fire exclusion on stand structure (Fulé et al., 1997; Maxwell et al., 2014; Scholl & Taylor, 2010). Dendroecological reconstructions are possible in forests where decay of dead wood is slow, and where past disturbances such as fire or logging have not destroyed evidence of historical stand conditions (Fulé et al., 1997). High-quality stand reconstructions are possible in the Elk Mountains because of the slow rate of wood decay at alpine treeline (Peet, 1981) as well as the fact that no large-scale logging or stand-replacing fire has occurred in this location for more than a century. Furthermore, reconstructions of past stand structure and composition were robust to changes in rates of decay. In reconstructions of both density and basal area, stands with differing dead wood decay rates were more similar to each other than to the same stand reconstructed at a different date. This high-precision stand-level reconstruction allowed for a detailed spatial analysis of stand conditions.

The spatial pattern of tree establishment above timberline is characterized by clustered trees, and this pattern has been stable for at least a century. Tree establishment was significantly clustered at all three sites in both contemporary and reconstructed stands. The clustered pattern of establishment may arise from the positive interactions between neighboring trees under harsh environmental conditions. Callaway et al. (2002) found that the importance of facilitation among alpine plants increases with abiotic stress. My results indicate that facilitation is likely an important factor in tree establishment in the alpine zone and facilitation has been important since at least 1900. Tree establishment has been shown to be random in the alpine zone of the Front Range of the Rocky Mountains (Elliott, 2011), but whether random tree establishment represents a shift in spatial pattern associated with a change in biotic interactions remains unclear. Further work is needed in locations with random tree establishment above treeline to investigate whether the relative importance of facilitation or abiotic factors have changed over time.

Reconstructions of tree distributions in the subalpine zone suggests that the spatial pattern of tree establishment was dynamic, and that shifts in spatial patterns differed by site. In the subalpine forest on Mt. Bellview, tree distributions were random in reconstructed stands, but clustered in the contemporary stand. Similarly, subalpine forests on Mt. Axtell experienced a trend of clustered tree distributions across more spatial scales over time. These shifts in pattern suggest that facilitation may have been less important for tree establishment a century ago, but younger trees are currently establishing under older, established trees. In these subalpine forests, Engelmann spruce is often observed establishing in non-forested sites and shade tolerant subalpine fir can establish under

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spruce canopy (Callaway, 1998; Holtmeier & Broll, 2007; Peet, 1981). This pattern of forest succession from spruce to fir establishment may account for the spatial dynamics observed here.

This study illustrates differences in treeline dynamics between the west slope of the Rocky Mountains and previously studied sites near the continental divide, and applies a novel approach to understanding the temporal variability in spatial patterns at treeline. The spatial and temporal variability in response to environmental change highlights the importance of site-specific investigations of treeline dynamics for the discernment of biogeographic patterns and ecological processes.

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References

Allen, R., Peet, R., & Baker, W. (1991). Gradient analysis of latitudinal variation in Southern Rocky Mountain forests. *Journal of Biogeography, 18*, 123–139.

Baddeley, A., & Turner, R. (2005). Spatstat: An R package for analyzing spatial point patterns. *Journal of Statistical Software, 12*(6), 1–42.

Bekker, M. F. (2005). Positive feedback between tree establishment and patterns of aubalpine forest advancement, Glacier National Park, Montana, U.S.A. *Arctic, Antarctic, and Alpine Research, 37*, 97–107. doi:10.1657/1523-0430(2005) 037[0097:PFBTEA]2.0.CO;2

Bertness, M., & Callaway, R. (1994). Positive interactions in communities. *Trends in Ecology & Evolution, 9*, 191–193.

Bradford, D., McConkey, J., & Reed, F. (2003). A range management review. *Rangelands, 25*, 3–12.

Callaway, R. (1998). Competition and facilitation on elevation gradients in subalpine forests of the Northern Rocky Mountains, USA. *Oikos, 82*, 561–573.

Callaway, R., Brooker, R., Choler, P., Kikvidze, Z., Lortie, C., Michalet, R., … Cook, B. (2002). Positive interactions among alpine plants increase with stress. *Nature, 417*, 844–848. doi:10.1038/nature00805.1

Danby, R. K., & Hik, D. S. (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology, 95*, 352–363. doi:10.1111/j.1365-2745.2006.01200.x

Elliott, G. P. (2011). Influences of 20th-century warming at the upper tree line contingent on local-scale interactions: Evidence from a latitudinal gradient in the Rocky Mountains, USA. *Global Ecology and Biogeography, 20*, 46–57. doi:10.1111/j.1466-8238.2010.00588.x

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*, 45–56. doi:10.1657/1938-4246-42.1.45

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Elliott, G. P., & Kipfmueller, K. F. (2011). Multiscale influences of climate on upper treeline dynamics in the Southern Rocky Mountains, USA: Evidence of intraregional variability and bioclimatic thresholds in response to twentieth-century warming. *Annals of the Association of American Geographers, 101*, 37–41.

Fulé, P. Z., Covington, W. W., & Moore, M. M. (1997). Determining reference conditions for ecosystem management of southwestern ponderosa pine forests. *Ecological Applications, 7*, 895–908.

Gaskill, D. L., DeLong, J. E., & Cochran, D. M. (1987). *Geologic map of the Mt. Axtell quadrangle, Gunnison County, Colorado*(Geologic Map No. 1604. 1:24,000). Reston, VA: U.S. Geological Survey.

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

Gould, P. R. (1970). Is *statistix inferens* the geographical name for a wild goose? *Economic Geography, 46*, 439–448.

Grabherr, G., Gottfried, M., & Pauli, H. (1994). Climate effects on mountain plants. *Nature, 369*, 427–505.

Grafius, D. R., & Malanson, G. P. (2015). Biomass distributions in dwarf tree, krummholz, and tundra vegetation in the alpine treeline ecotone. *Physical Geography, 36*, 337–352. doi:10.1080/02723646.2015.1050954

Greenwood, S., & Jump, A. S. (2014). Consequences of treeline shifts for the diversity and function of high altitude ecosystems. *Arctic, Antarctic, and Alpine Research, 46*, 829–840. doi:10.1657/1938-4246-46.4.829

Harden, C. P., Hartsig, J., Lee, J., Farley, K., & Bremer, L. (2013). Effects of land-use change on water in Andean páramo grassland soils. *Annals of the Association of American Geographers, 103*, 375–384.

Harsch, 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. doi:10.1111/j.1461-0248.2009.01355.x

Hessl, A. E., & Baker, W. (1997). Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. *Arctic and Alpine Research, 29*, 173–183.

Holtmeier, F. K. (2009). *Mountain timberlines: Ecology, patchiness, and dynamics*. Dordrecht: Springer.

Holtmeier, F., & 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. doi:10.1111/j.1466-822x.2005.00168.x

Holtmeier, F., & Broll, G. (2007). Treeline advance – Driving processes and adverse factors. *Landscape Online, 1,* 1–32. doi:10.3097/LO.200701

Jiménez-Moreno, G., Fawcett, P. J., & Anderson, S. R. (2008). Millennial- and centennial-scale vegetation and climate changes during the late pleistocene and holocene from northern New Mexico (USA). *Quaternary Science Reviews, 27*, 1442–1452. doi:10.1016/j.quascirev.2008.04.004

Körner, C. (1998). A re-assessment of high elevation treeline positions and their explanation. *Oecologia, 115*, 445–459. doi:10.1007/s004420050540

Körner, C., & Paulsen, J. (2004). A world-wide study of high altitude treeline temperatures. *Journal of Biogeography, 31*, 713–732. doi:10.1111/j.1365-2699.2003.01043.x

Langenheim, J. H. (1962). Vegetation and environmental patterns in the Crested Butte area, Gunnison County, Colorado. *Ecological Monographs, 32*, 249–285. doi:10.2307/1942400

Lescop-Sinclair, K., & Payette, S. (1995). Recent advance of the Arctic treeline along the eastern coast of Hudson Bay. *The Journal of Ecology, 83*, 929–936.

Liang, E., Wang, Y., Eckstein, D., & Luo, T. (2011). Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytologist, 190*, 760–769. doi:10.1111/j.1469-8137.2010.03623.x

Maher, E., Germino, M., & Hasselquist, N. (2005). Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine-treeline ecotone. *Canadian Journal of Forest Research, 35*, 567–574.

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Malanson, G. P., Butler, D. R., Fagre, D. B., Walsh, S. J., Tomback, D. F., Daniels, L. D., … Millar, C. I. (2007). Alpine treeline of western North America: Linking organism-to-landscape dynamics. *Physical Geography, 28*, 378–396. doi:10.2747/0272-3646.28.5.378

Marr, J. (1977). The development and movement of tree islands near the upper limit of tree growth in the Southern Rocky Mountains. *Ecology, 58*, 1159–1164.

Maser, C., Anderson, R. G., Cromack, K. J., Williams, J. T., & Martin, R. E. (1979). Dead and down woody material. In J. W. Thomas (Ed.), *Wildlife habitats in managed forests – The Blue Mountains of Oregon and Washington* (Vol. 553, pp. 78–95). Washington, DC: USDA Forest Service.

Maxwell, R., Taylor, A., Skinner, C., Safford, H., Isaacs, R., Airey, C., & Young, A. (2014, March). Landscape-scale modeling of reference period forest conditions and fire behavior on heavily logged lands. *Ecosphere, 5*, 1–28. doi:10.1890/ES13-00294.1

McVicar, T. R., Li, L., Van Niel, T. G., Zhang, L., Li, R., Yang, Q., … Gao, P. (2007). Developing a decision support tool for China's re-vegetation program: Simulating regional impacts of afforestation on average annual streamflow in the Loess Plateau. *Forest Ecology and Management, 251*, 65–81. doi:10.1016/j.foreco.2007.06.025

Meyers, C. A., & Alexander, R. R. (1972). *Bark thickness and past diameters of Engelmann Spruce in Colorado and Wyoming*. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Peet, R. K. (1981). Forest vegetation of the Colorado Front Range. *Vegetatio, 45*, 3–75.

Prather, T. (1999). *Geology of the Gunnison Country* (2nd ed.). Gunnison, CO: B&B Printers.

R CoreTeam. (2015). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Resler, L. M. (2006). Geomorphic controls on spatial pattern and process at alpine treeline. *The 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). Modelling spatial patterns. *Journal of the Royal Statistical Society, Series B, 39*, 172–212.

Rogers, J. J., Prosser, J. M., Garrett, L. D., & Ryan, M. G. (1984). *ECOSIM: A system for projecting multiresource outputs under alternative forest management regimes. USDA Forest Service Administrative Report*. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

Scholl, A. E., & Taylor, A. H. (2010). Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications, 20*, 362–380.

Sjögersten, S., & Wookey, P. A. (2005). The role of soil organic matter quality and physical environment for nitrogen mineralization at the forest-tundra ecotone in Fennoscandia. *Arctic, Antarctic, and Alpine Research, 37*, 118–126.

Smith, W. K., Germino, M., Johnson, D., & Reinhardt, K. (2009). The altitude of alpine treeline: A bellwether of climate change effects. *Botanical Review, 75*, 163–190.

Soil Survey Staff. (2015). *Web soil survey*. Natural Resources Conservation Service, United States Department of Agriculture. Retrieved June 1, 2015, from http://websoilsurvey.nrcs.usda.gov/

Stokes, M. A., & Smiley, T. L. (1968). *An introduction to tree-ring dating*. Tucson: University of Arizona Press.

Szeicz, J., & Macdonald, G. (1995). Recent white spruce dynamics at the subarctic alpine treeline of north-western Canada. *The Journal of Ecology, 83*, 873–885.

Taylor, A. H. (1995). Forest expansion and climate change in the mountain hemlock (Tsuga mertensiana) zone, Lassen Volcanic National Park, California, U.S.A. *Arctic and Alpine Research, 27*, 207–216.

USDA Forest Service. (1928). *National Forests of Colorado* (U.S. Department of Agriculture Miscellaneous Publication No. 18). Washington, DC: United States Department of Agriculture.

Villalba, R., & Veblen, T. T. (1997). Improving estimates of total tree ages based on increment core samples. *Ecoscience, 4*, 535–542.

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Western Regional Climate Center. (n.d.-a). *Average annual precipitation, Colorado*. Retrieved June 12, 2015, from http://www.wrcc.dri.edu/pcpn/co.gif

Western Regional Climate Center. (n.d.-b). *Station monthly time series: Snodgrass (RMBL) Colorado*. Retrieved June 12, 2015, from http://www.wrcc.dri.edu/cgi-bin/rawMAIN3.pl?corsno

Yamaguchi, D. K. (1991). A simple method for cross-dating increment cores from living trees. *Canadian Journal of Forest Research, 21*, 414–416.

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