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Multi-scale Influences of Slope Aspect and Spatial Pattern on Ecotonal Dynamics at Upper Treeline in the Southern Rocky Mountains, U.S.A.

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Abstract

We focused on the mediating role of slope aspect and spatial pattern on upper treeline ecotonal dynamics at multiple spatial scales in the Southern Rocky Mountains to infer process interactions and gauge the importance of feedbacks in determining the potential response of upper treeline to climate change on contrasting south- and north-facing slopes. Dendroecological techniques were used to reconstruct tree establishment within the upper treeline ecotone and Ripley's *K* was used for spatial pattern analysis. Tree age was determined by using age to coring-height corrections, and the influence of slope aspect was quantitatively assessed at multiple spatial scales using Mann-Whitney *U*-Tests. Widespread tree establishment occurred within the treeline ecotone on both south- and north-facing slopes during the 20th century, but tree ages above timberline are significantly younger on north-facing slopes at all spatial scales (local, landscape, and regional). The spatial pattern of tree establishment above timberline was predominantly random, except for significant clustering on south-facing slopes in the Sangre de Cristo Mountains. The aspect mediation of tree age and spatial pattern suggest that the importance of feedbacks may vary according to slope aspect and that both of these environmental factors should be considered when assessing possible treeline response to climate change.

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Introduction

Given substrate conditions suitable for tree establishment, the location of upper treeline appears to be primarily controlled by local thermal regimes (e.g., Körner and Paulsen, 2004; Rossi et al., 2007). Generally warmer temperatures that prolong the growing season are therefore expected to have dramatic effects on upper treeline ecotonal dynamics, including changes in the position and structure of treeline communities (e.g., Kullman, 2001; Grace et al., 2002; Lloyd and Fastie, 2002). However, regional-scale temperature trends can be modified by local-scale interactions between abiotic and biotic factors that help pattern treeline structure (Baker and Weisberg, 1995; Luckman and Kavanagh, 2000; Smith et al., 2003). Understanding the spatial pattern that results from these dynamic interactions at upper treeline provides a viable approach for evaluating past fluxes and predicting future changes (Young and León, 2007).

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

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

Scale plays an important role in upper treeline research since spatial pattern is driven by processes operating at multiple spatial scales (Holtmeier and Broll, 2005; Resler, 2006). A multi-scale approach can be achieved by using a comparative framework that pays careful attention to evaluating similarities and differences in the spatial patterns of upper treeline along a latitudinal gradient (cf. Young and León 2007). Comprehensive vegetation studies along a latitudinal gradient have been completed in the Southern Rocky Mountains (SRM) (Peet, 1978; Allen et al., 1991), but have excluded regional-scale comparisons of upper treeline dynamics.

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Furthermore, although numerous studies have been performed at upper treeline in the SRM, the research has focused on relatively small areas in the Colorado Front Range (FR) (e.g., Daly and Shankman, 1985; Baker and Weisberg, 1995; Weisberg and Baker, 1995a, 1995b; Hessl and Baker, 1997; Humphries et al., 2008). Consequently, at upper treeline in the Rocky Mountains, little attention has been paid to what type of regional-scale patterns emerge when scaling up from a series of detailed local-scale data sets (cf. Allen et al., 1991).

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

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

Methods

STUDY AREA

The study area stretches along ca. 600 km of the generally north-south-trending SRM of Colorado and northern New Mexico (Fig. 1). The SRM are situated on the leeward side of the Continental Divide where they rise abruptly along their east slope, with mountain peaks reaching ca. 3800–4200 m a.s.l., ca. 1800–2500 m above the adjacent High Plains of Colorado and New Mexico (Veblen and Lorenz, 1991). Towards their crest, treeline elevation varies from ca. 3800 m a.s.l. in the Sangre de Cristos to ca. 3500 m a.s.l. in the Front Range (Peet, 1978). Our study sites are located along a 5° range of latitude from 35°N in the Sangre de Cristo Mountains (SDC) (ca. 35°–37°N) to 40°N in the FR (ca. 38°–40°N).

The geology of the SRM exhibits considerable spatial variation, but the substrate in high-elevation areas is predominantly composed of Precambrian granitic rock with coarse texture and high silica content, along with gneiss and schist that share similar geochemical properties (Allen et al., 1991; Peet, 2000). Pedogenic processes eventually form relatively acidic, infertile soils from this parent material (Allen et al., 1991).

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

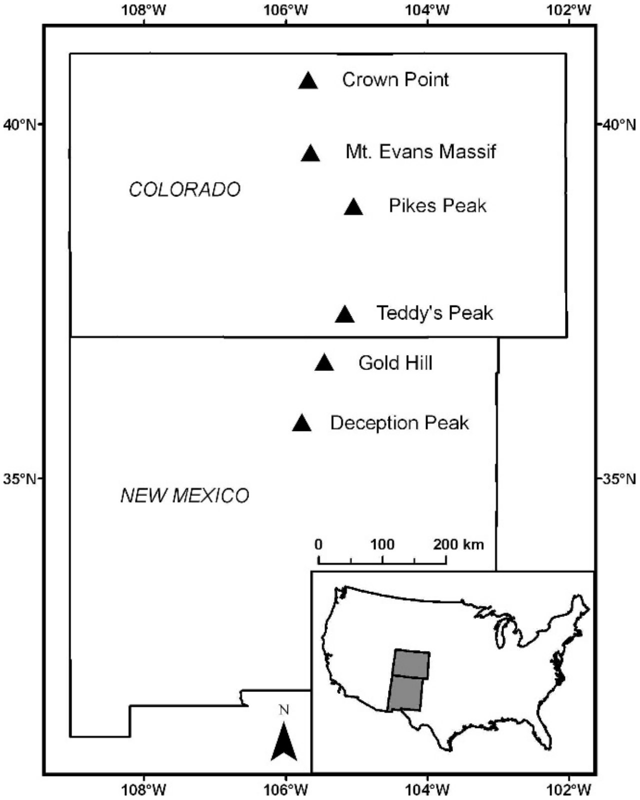

FIGURE 1. Study area map depicting sites in the Sangre de Cristo (SDC) and Front Range (FR) mountains of the Southern Rocky Mountain (SRM) region.

Vegetation at high-elevation upper treeline sites is primarily composed of *Picea engelmannii* Parry ex Engelm. (Engelmann spruce) and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), with some *Pinus aristata* Engelm. (Colorado bristlecone pine) on south-facing slopes south of around 39°N and some *Pinus contorta* Dougl. ex Loud. (lodgepole pine) in the northern FR (Peet, 2000). *P. engelmannii* often forms monospecific stands in the southernmost areas of the SDC, particularly on north-facing slopes, and *A. lasiocarpa* becomes more prevalent in the northern FR (Peet, 1978). Due to relatively steep slopes, krummholz patches are rare, especially in the SDC (Peet, 1978).

TABLE 1

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

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

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

FIELD SAMPLING

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

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

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

AGE-STRUCTURE ANALYSIS

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

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

Dates of tree establishment were calculated based on tree age at the time of sampling (2007 for SDC and Mt. Evans site, 2008 for rest of FR) and by adding the appropriate age to coring-height

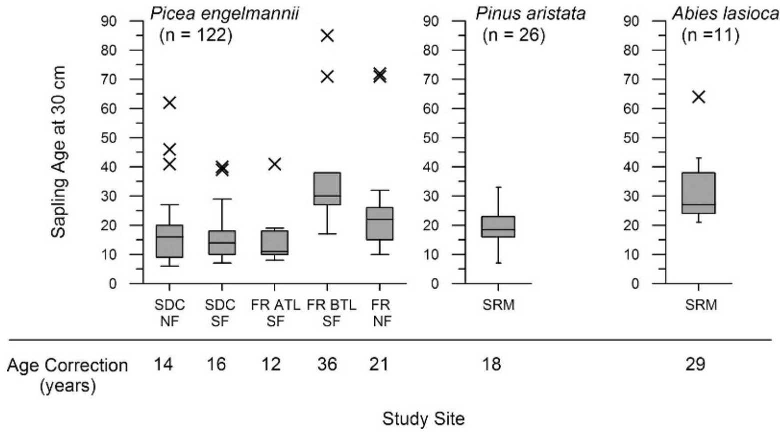

FIGURE 2. The range of age to coring-height correction data with tree age outliers (±2 s.d.) denoted by a X. The age of saplings at 30 cm height was determined for each species and further stratified by slope aspect and mountain range. Due to a low *n Abies* and *Pinus* were combined to form a regional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

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

Once age to coring-height corrections were applied, tree establishment dates were grouped into both decadal (pre-1800 to 1890) and five-year (1900–2000) age classes to produce a hybrid age-structure chronology. Separate age-class divisions were created before (10-yr) and after 1900 (5-yr) because of our detailed sampling strategy that produced age to coring height corrections and a low average number of rings to center for the period 1900 to present (Table 3).

The hybrid age-structure data were analyzed to determine whether tree age was statistically different based on slope aspect at local, landscape, and regional scales. Cumulative age distributions were tested for normality using a Kolmogorov-Smirov test and then median age was compared using a Mann-Whitney *U*-Test. We used the nonparametric Mann-Whitney *U*-Test to discover whether tree ages at upper treeline in the SRM were significantly different according to slope aspect, with the null hypothesis being that the population ages are equal. Any statistically significant differences in tree age ($p < 0.05$) between north- and south-facing slopes could illustrate possible feedback-induced nonlinear responses to climate and help elucidate the stability of high-elevation treeline ecotones throughout the SRM.

SPATIAL ANALYSIS

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

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

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

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

Results

AGE STRUCTURE

We crossdated 632 trees in the SRM and collected samples from a relatively even proportion of trees from both south- and

TABLE 2

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

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

north-facing slopes (320 and 312, respectively) (Table 2). Transect locations ranged in elevation from 3733.8 m on a south-facing slope at 35.8°N in the SDC to 3407.4 m on a north-facing slope at 40.6°N in the FR (Tables 1 and 2). From a regional perspective, this equates to approximately a 65.3 m decline in treeline elevation per degree of latitude north. Steepness of slope (°) showed no statistically significant differences ($p > 0.05$; *t*-test) between south- and north-facing slopes and ranged from 10°–26° (Table 2). Similarly, ecotone length (distance from outpost tree–timberline) did not vary significantly between slope aspect even though the average distance on south-facing slopes was three times longer than on contrasting north-facing slopes (Table 2). The majority of trees located ATL (n = 253) were growing in areas without the ameliorating influence of local microtopography in 11 of 12 sites (Table 2). The only exception was at our northernmost site (CPN), where 51% of trees ATL established in places with shelter from boulders (Table 2). Seedlings, both alive and dead, were more common on north-facing slopes (Fig. 3).

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

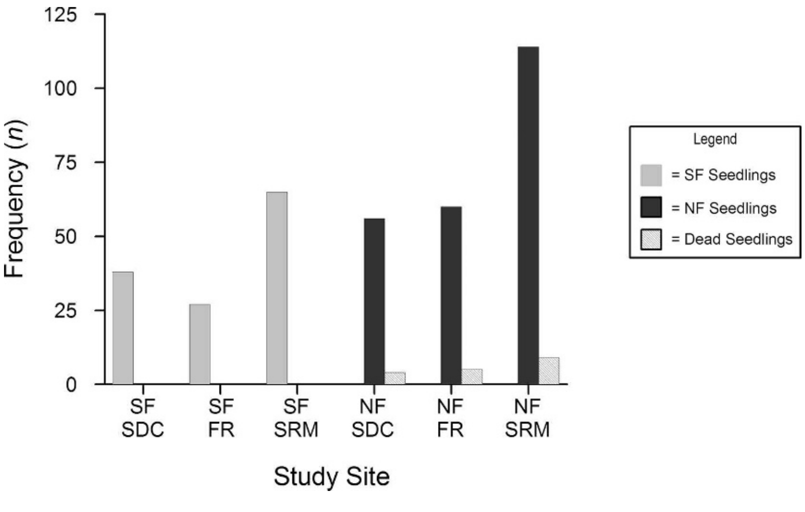

FIGURE 3. Seedling occurrence stratified by slope aspect and mountain range in the Southern Rocky Mountains.

TABLE 3.

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

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

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

SPATIAL ANALYSIS

Spatial analysis using Ripley's $K(t)$ function for trees growing ATL produced different results based on slope aspect and mountain range. South-facing slopes in the SDC have clustered spatial patterns (Table 5). While minor deviations occur within the distance bins (such as the random pattern detected at GHS from 1 to 2 m) when analyzing the overall spatial pattern, clustering is the predominant spatial configuration (Table 5). Random spatial patterns exist at most study sites on north-facing slopes in the SDC (excluding Gold Hill north-facing site [GHN]) and at every study site in the FR, with the exception of the south-facing site on Pikes Peak (Table 5). For instance, variations in spatial pattern at GHN (random at smallest and largest distances) could have arisen from differences in species composition or tree size classes present. However, for a general comparison between mountain ranges, the SDC show a stronger aspect-mediated relationship with the spatial pattern of trees ATL, while the patterns in tree establishment ATL in the FR are almost exclusively random in space (Table 5). The aspect mediation of spatial pattern suggests that the importance of feedback processes in driving ecotonal dynamics at upper treeline vary according to slope aspect and within the SRM region.

Discussion

PATTERNS OF TREE ESTABLISHMENT

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

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

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

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

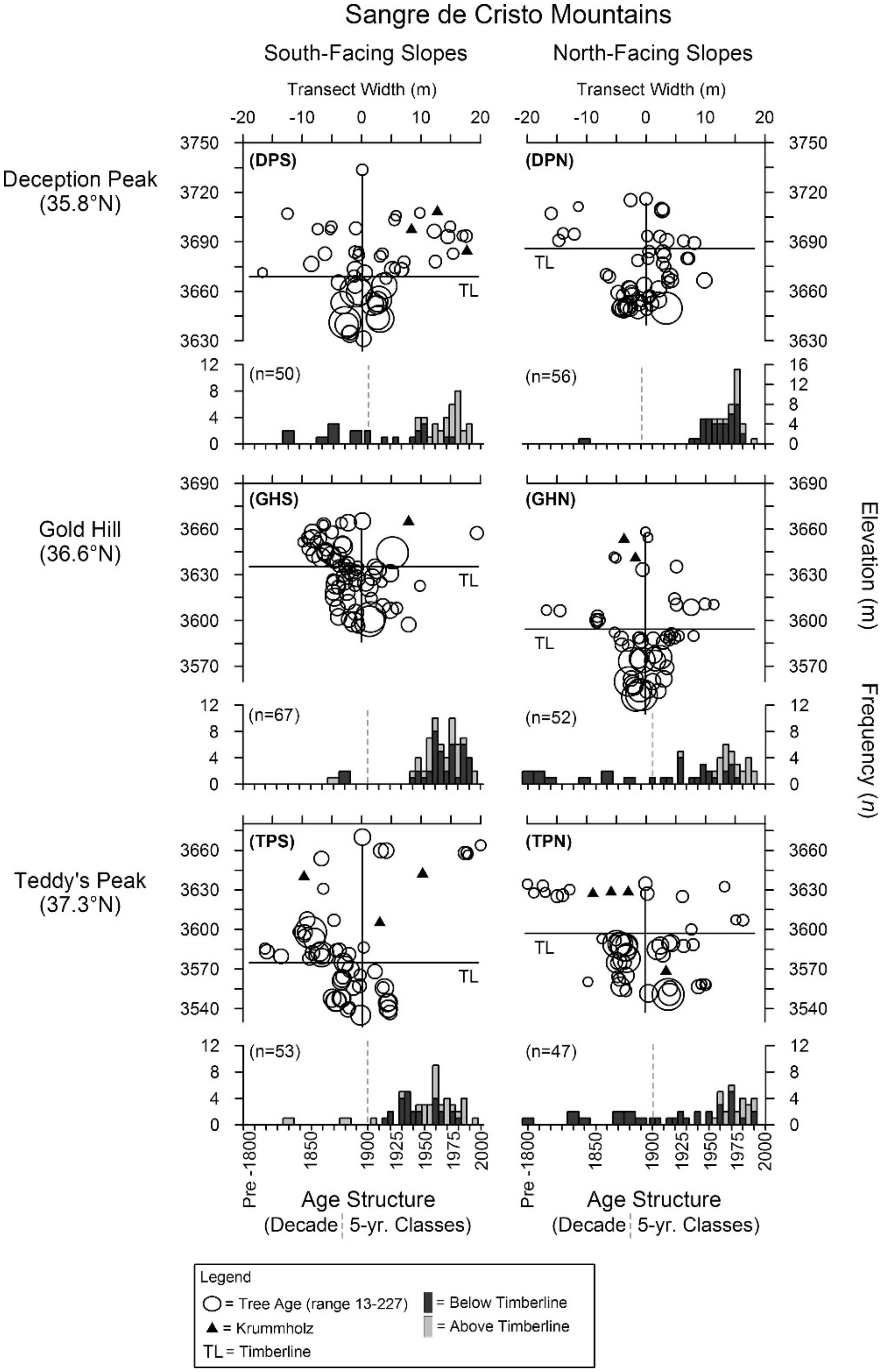

FIGURE 4. Spatial and temporal examination of upper treeline study sites in the Sangre de Cristo Mountains (SDC). Transects and age-structure data are shown for adjacent north- and south-facing slopes. The width of the nested-belt transect extended to 40 m above timberline and was reduced to 20 m below.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

clustered around them, thus suggesting a possible treeline advance independent of their existence (Figs. 4 and 5).

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

Differences in the need for sheltered sites in facilitating treeline advance could result from contrasts in wind regimes at a given location. Our data suggest that the influence of wind on regeneration ATL becomes more pronounced in the northern portion of our study area around 40°N (e.g., Crown Point; Tables 1 and 2). The

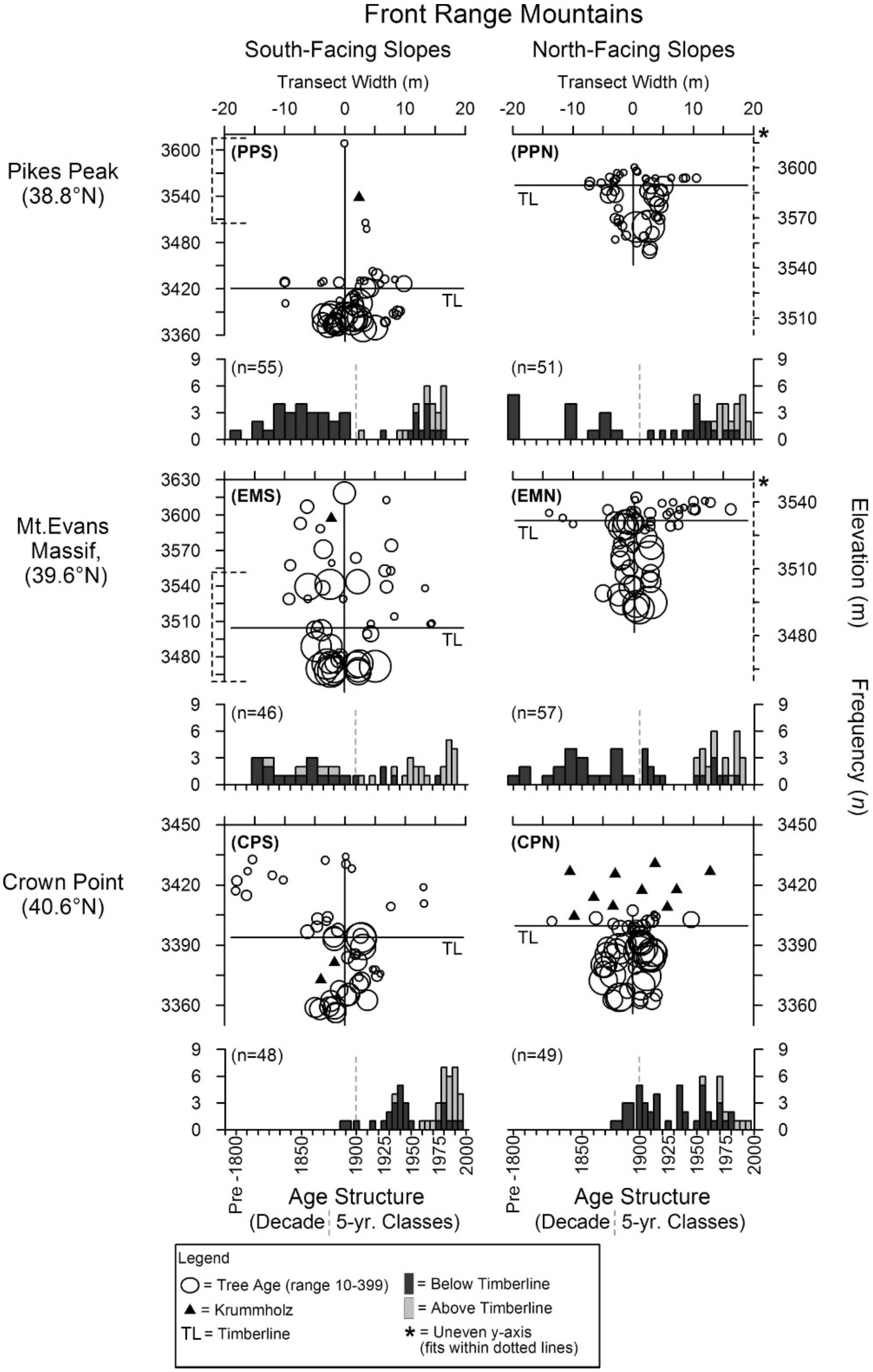

FIGURE 5. Spatial and temporal examination of upper treeline study sites in the Front Range Mountains (FR). See caption for Figure 4. Note that two north-facing transect *y*-axes (*) are plotted with different elevation values and that their position in relation to the corresponding south-facing transect is marked with a dashed line on the left *y*-axis. For CPN, the pattern of krummholz mats is not based on exact coordinates and is used to illustrate the belt of krummholz that exists upslope from the outpost tree. PP—Pike's Peak; EM—Mt. Evans Massif; CP—Crown Point.

propensity of trees to establish in sheltered sites along with the existence of numerous krummholz mats above treeline at CPN imply that the site is typically exposed to windy conditions (Fig. 5). Throughout the western United States, mean wind characteristics often reflect the channeling influences created by local topographic features (Klink, 1999), which can be further modified by the spatial patterns of upper treeline (Holtmeier and Broll, 2005). In some cases, the topographic mediation of local wind regimes can affect the need for positive feedback in promoting and sustaining tree establishment ATL (Alftine and Malanson, 2004) while also potentially superseding the relative importance of projected changes in temperature and precipitation regimes associated with global warming (Woodward, 1993). Deviations in the ecological significance of wind at upper treeline within our study area demonstrate how the relative importance of processes and patterns can vary as environmental contexts change (cf. Malanson et al., 2007).

SPATIAL PATTERN AND FEEDBACK PROCESSES ABOVE TIMBERLINE

Vegetation pattern at upper treeline is often strongly influenced by the interactions of climate and slope aspect (e.g., Brown, 1994; Danby and Hik, 2007). This is illustrated by the

TABLE 4

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

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

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

Relative increases in exposure to solar radiation and subsequent water stress on south-facing slopes in the SDC and on Pikes Peak provide a logical rationale for spatial clustering ATL. The SDC experience the warmest growing season temperatures within our study area (refer to *STUDY AREA*) and the influence of this is most likely amplified on south-facing slopes. Consequently, soil moisture becomes limiting earlier in the growing season compared to contrasting north-facing slopes. Low moisture availability appears to be the primary reason for clustering on Pikes Peak. Given that it is situated slightly east of the main axis of the Southern Rockies (Fig. 1), it experiences a drier climate that more closely resembles the adjacent High Plains (Peet, 1978; Diaz et al., 1982). In an attempt to compensate for warm and dry conditions, tree establishment appears to be dependent on positive feedback interactions.

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

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

A more thorough understanding of positive feedbacks is needed in order to identify the potential impacts of climate change on upper treeline ecotones (Alftine and Malanson, 2004). This is further complicated by the reported ephemeral nature of feedback-pattern interactions, which have been shown to vary in importance

TABLE 5

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

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

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

Conclusions

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

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

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

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