

# Increased stem density and competition may diminish the positive effects of warming at alpine treeline

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**Abstract.** The most widespread response to global warming among alpine treeline ecotones is not an upward shift, but an increase in tree density. However, the impact of increasing density on interactions among trees at treeline is not well understood. Here, we test if treeline densification induced by climatic warming leads to increasing intraspecific competition. We mapped and measured the size and age of Smith fir trees growing in two treelines located in the southeastern Tibetan Plateau. We used spatial point-pattern and codispersion analyses to describe the spatial association and covariation among seedlings, juveniles, and adults grouped in 30-yr age classes from the 1860s to the present. Effects of competition on tree height and regeneration were inferred from bivariate mark-correlations. Since the 1950s, a rapid densification occurred at both sites in response to climatic warming. Competition between adults and juveniles or seedlings at small scales intensified as density increased. Encroachment negatively affected height growth and further reduced recruitment around mature trees. We infer that tree recruitment at the studied treelines was more cold-limited prior to 1950 and shifted to a less temperature-constrained regime in response to climatic warming. Therefore, the ongoing densification and encroachment of alpine treelines could alter the way climate drives their transitions toward subalpine forests.

**Key words:** climatic warming; codispersion; dendroecology; facilitation; long-term ecological process; paleoecology; plant interactions; point-pattern analysis; timberline.

## INTRODUCTION

Competition is a crucial driver of the structure, spatial patterns, and dynamics of forests (He and Duncan 2000, Comita et al. 2010). Tree-to-tree competition tends to increase with density of conspecifics (Kenkel 1988, Getzin et al. 2006). Therefore, densification and encroachment should intensify competition between trees even near the uppermost limit of their existence, the alpine treeline. Globally, an increase in forest density is being observed more frequently than altitudinal ascents of the uppermost trees at treeline (e.g., Camarero and Gutiérrez 2004, Kullman 2007, Liang et al. 2011), and recent studies have discussed the potential for competition to shape recent treeline dynamics (Grau et al. 2012). However, little is known about the role of competition on long-term population dynamics of trees as climatic warming ameliorates environmental conditions

at treeline (Camarero and Gutiérrez 2004, Holtmeier and Broll 2007, Elliott 2011).

The highest alpine Northern Hemisphere treeline ecotones, such as those located across the Tibetan Plateau, experience extreme environmental conditions (Miehe et al. 2007) and thus provide an excellent system to investigate the impact of climatic warming on competition (Liang et al. 2011). Because low temperature often is the major constraint on tree regeneration, survival, and growth at alpine treelines (Wang et al. 2006, Holtmeier and Broll 2007, Liu and Yin 2013, Renard et al. 2016), recent treeline densification at treelines has been linked to rising temperatures (Liang et al. 2011, Lv and Zhang 2012). However, here we argue that rapid treeline densification would lead not only to increased positive spatial associations (i.e., clustered spatial patterns) among recruits (Batllori et al. 2009), but also to increased competition among adult trees and recruits. Competition in such early stages should be mainly asymmetrical, resulting from, and subsequently amplifying, different growth rates among adjacent individuals (Fajardo and McIntire 2007). Alternatively, if facilitation occurs

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among trees in the harsh conditions at treeline, positive spatial associations between tree height of adults and recruits would be observed. To test these ideas, we first reconstructed the age structure of Smith fir populations within two large plots spanning the upper boundary of treeline ecotones in the Tibetan Plateau and examined the relationship between age structure and recent climatic warming. We then analyzed the spatiotemporal treeline dynamics during the past 150 years by using spatial point-pattern and codispersion analyses. Finally, we inferred the possible impacts of recent densification on competition and treeline dynamics in response to climate.

## METHODS

### *Study area*

The study area is located in the Sygera Mountains in the southeastern Tibetan Plateau (29°10′–30°15′ N, 93°12′–95°35′ E) (Appendix S4: Fig. S1). The closest meteorological station, located in Nyingchi (Linzhi) (29°34′ N, 94°28′ E, 3,000 m above sea level [a.s.l.]), recorded 671 mm mean total annual precipitation (1960–2012 period), >70% of which falls between June and September. A significant warming trend in summer (June to August) and winter (December to February) without a concomitant trend in annual or summer precipitation was detected there beginning in the 1960s (Liang et al. 2011). Another nearby automated meteorological station located at treeline in the Sygera Mountains (29°40′ N, 94°43′ E, 4,390 m a.s.l.) recorded a range in mean annual temperatures from  $-0.2^{\circ}$  to  $0.9^{\circ}\text{C}$  between 2007 and 2013 (Liang et al. 2011). July was the warmest month ( $7.9 \pm 0.5^{\circ}\text{C}$  [mean  $\pm$  SD]) and January was the coldest ( $-8.0 \pm 1.7^{\circ}\text{C}$ ). This treeline station recorded an annual average of 957 mm of precipitation; 62% during the monsoon season (June–September), and snowfall occurred mainly from November to May.

### *Tree species*

Smith fir (*Abies georgei* var. *smithii* (Viguie & Gaussen) W. C. Cheng & L. K. Fu) is the dominant tree species on the north-facing slopes in the Sygera Mountains, where it forms nearly monospecific stands between 3,300 and 4,400 m a.s.l. The maximum elevation for Smith fir treeline varies from 4,250 to 4,400 m a.s.l., depending on local topographical conditions. Diffuse treelines are common on gentle slopes. As wind speeds are generally low, flagged trees or shrubby individuals (“krummholz”) are usually absent in these treelines (Liang et al. 2011). The oldest individual Smith fir near the timberline is around 400 yr old (Liang et al. 2011). July mean minimum air temperature appears to be the primary constraint on the radial growth of adult Smith fir (Liang et al. 2011). Seeds can be dispersed upslope up to 40 m away from parent trees located at treeline (Shen et al. 2014).

### *Field sampling*

We characterized the structure and reconstructed the dynamics of Smith fir at two treeline sites, designated as N1 and N2. Both sites were located on north-facing slopes, and encompassed the treeline ecotone, including the upper treeline (uppermost 2 m tall trees) and the forest limit (elevation at which tree cover  $\geq$  30%). The current altitudinal positions of N1 and N2 were 4,388 and 4,370 m a.s.l., with mean slopes of  $10^{\circ}$  and  $15^{\circ}$ , respectively. These treelines were not locally disturbed by yak (*Bos grunniens* L.) grazing, or logging (Liang et al. 2011), and defoliation due to insect outbreaks or wild herbivores were not observed during field sampling. Above the current treeline, dense 2–3 m tall individual *Rhododendron* shrubs dominated the vegetation, but no stumps or remains of old dead trees were found there.

The age structure of the Smith fir trees (DBH > 5 cm) within two large rectangular plots (150  $\times$  150 m; see Appendix S4: Fig. S2) was characterized following Liang et al. (2011) and Wang et al. (2012). Age was estimated from basal cores taken from the main stem of each tree and collected with an increment borer (see Appendix S1 for additional methodological details). We processed the core samples using standard dendrochronological techniques, including air drying, sanding with successively finer sandpapers, and visually cross-dating the cores under a stereomicroscope (Cook and Kairiukstis 1990). Mean series intercorrelation for plots N1 and N2 were 0.61 and 0.60, respectively, indicating reliable cross-dating. If the pith was not present in the core, a pith geometric locator was used to estimate the innermost distance missing up to the theoretical center of the stem (Wang et al. 2012). Ages of hollow trees were estimated using DBH–age regressions (N1,  $r^2 = 0.88$ ,  $P < 0.001$ ,  $n = 385$ ; N2,  $r^2 = 0.83$ ,  $P < 0.001$ ,  $n = 406$ ; see also Liang et al. 2011). In our collection, missed piths typically occurred only in trees >200 yr old, so any errors in estimated ages using this method would have little effect on recruitment that occurred within the last 150 yr. The germination age of young individuals (DBH < 5 cm and height < 1.3 m, age > 3 yr) was estimated by counting the successive bud scars or internodes observed along their main stem (Camarero and Gutiérrez 2004). Since uncertainties related to age determination were always present, we binned tree ages by decades for analysis (Liang et al. 2011).

To identify temporal changes in the variation in spatial patterns of Smith fir in these two plots, we examined tree size distributions in five consecutive 30-yr intervals beginning with the 1862–1891 period and ending either with 1982–2011 (for N1) or 1982–2013 (N2). For each interval, individual Smith fir trees were grouped into three age classes: seedlings (age  $\leq$  30 yr), juveniles ( $31 \leq$  age  $\leq$  100 yr), and adults (age  $\geq$  101 yr). These age classes produced groups similar to those found when grouping trees by their height or DBH. For instance, a tree aged 30 yr was often approximately 50 cm tall, a

threshold that is often used as a criterion to define the maximum height of seedlings growing in treeline ecotones (Camarero and Gutiérrez 2004). Likewise, trees between 101 and 150 yr in age corresponded to heights > 6 m with DBH > 17.5 cm, which are categories usually employed to consider a tree as a mature, dominant, and reproductive individual (Camarero and Gutiérrez 2004, Wang et al. 2012). Given the lack of long-term forest survey data near treelines (Liang et al. 2011, Wang et al. 2012), grouping trees into age or stage classes provides a repeatable method to investigate the variations of competition through time.

#### *Point-pattern analyses*

To describe how the spatial patterns of the treeline Smith fir population changed through time, we used point-pattern analyses (Wiegand and Moloney 2004, 2014, Wang et al. 2010) implemented in the Programita software (Wiegand and Moloney 2014). We used inhomogeneous versions of the univariate and bivariate  $O(r)$  statistics because they are sensitive to variation in patterns at small spatial scales (Wiegand and Moloney 2004, 2014) and there is environmental heterogeneity within Smith fir treeline ecotones (Wang et al. 2012). The univariate  $O_{11}(r)$  statistic was used to characterize the spatial patterns of the three different age classes, and the bivariate  $O_{12}(r)$  statistic was used to characterize the spatial associations between the three age classes. Values of  $O_{11}(r)$  located above or below the upper and lower envelopes represent significant aggregation or hyperdispersion (regularity), respectively, whereas values of  $O_{12}(r)$  located above or below the upper and lower envelopes represent significant attraction or repulsion, respectively (see Appendix S2 for additional technical details about the analyses).

#### *Mark correlation function: bivariate patterns with a quantitative mark*

We used the normalized mark correlation functions  $k_{m_1 m_2}(r)$  of tree heights to examine how patterns of growth covaried among age classes. This was justified because tree height was measured for all sampled individuals, and height growth is used to define treeline position (Holtmeier and Broll 2007). Further, competition among trees and its effects on growth are described better by considering heights of neighboring trees than by measuring their DBH (Thorpe et al. 2010). Bivariate point pattern analysis on a quantitative attribute (or “mark”), such as tree height, can be used to explore the impact of individuals of one pattern (e.g., bigger or older individuals) on individuals of a second pattern (e.g., smaller or younger individuals).

Using  $k_{m_1 m_2}(r)$  accounted not only for the spatial coordinates of trees, but also for the product of the heights (the mark in this case) of all pairs of individuals (Stoyan and Penttinen 2000). A value of  $k_{m_1 m_2}(r)$  close to 1 would

indicate that the mark-pair products at a distance  $r$  depended on the spatial location of Smith fir individuals. In contrast, values of  $k_{m_1 m_2}(r) > 1$  or  $k_{m_1 m_2}(r) < 1$  indicated mutual stimulation (excess of mark pair products beyond a value explicable just in terms of locations of individuals) or inhibition, respectively. For instance, low values of the  $k_{m_1 m_2}(r)$  function at short distances would indicate that individuals belonging to pattern 2 (i.e., seedlings, juveniles) were shorter than expected if the points were located that distance apart from points of pattern 1 (i.e., juveniles, adults). The null model was built by fixing the marks of the pattern 1 while randomizing the marks of pattern 2 (Wiegand and Moloney 2014). We analyzed three bivariate patterns (adults vs. juveniles, adults vs. seedlings, juveniles vs. seedlings) of the mark (tree height) in both study plots (see also the bivariate patterns with two quantitative marks in Appendix S2).

#### *Codispersion analysis*

We used codispersion analysis to detect anisotropy in the present day bivariate height relationships among adults, juveniles, and seedlings (Cuevas et al. 2013, Buckley et al. 2016a) using the mean height of each life stage in  $10 \times 10$  m grid cells. This method uses a kernel function, in this case with a 10-m bandwidth, to quantify spatial covariation across a range of directions and spatial lags up to 38 m (one-quarter of the plot width). The observed codispersion values were compared to those generated by a “random labelling” null model that reshuffled the heights of trees 199 times (Buckley et al. 2016b).

#### *Relating regeneration to climate*

The climatic records in the study area, which were available from the 1960s onward, were too short to evaluate linkages between treeline dynamics and directly measured climatic variables. Thus, we used two seasonal temperature reconstructions based on independent dendrochronological proxies to quantify climate–regeneration associations at multi-century scales (Liang et al. 2011). The first series was a summer mean minimum temperature reconstruction based on a tree ring-width chronology of Balfour spruce (*Picea likiangensis* var. *balfouriana* (Rehd. et Wils.) Hillier ex Slavin) growing in the southeastern Tibetan Plateau (Zhu et al. 2011). This reconstruction revealed an intense warming trend since the 1800s. A previous, related study on Smith fir (Liang et al. 2011) indicated that radial and longitudinal growth rates of this species were controlled by summer minimum temperature, and thus we expected that this would be the case in the present study. The second series was a cool-season mean temperature reconstruction (September until April) based on Qilian junipers (*Juniperus przewalskii* Kom.) from Wulan (Zhu et al. 2008), located  $\approx 400$  km northeast from the study area. This second

reconstruction was well correlated with more recent seasonal temperatures measured at our Nyingchi weather station ( $r = 0.64$ ,  $P < 0.001$ ; Liang et al. 2011). It also showed a prominent rise in reconstructed cool-season temperatures during the 20th century. Here, we predicted that cool-season temperatures would limit the survival of tree recruits at treelines, as shown previously (Kullman 2007, Renard et al. 2016).

We correlated the age structure data of Smith fir treeline trees with the reconstructed summer mean minimum and cool-season temperatures from 1760 to 2000. Since recruitment data were reconstructed and treelines may respond slowly to temperature changes (Camarero and Gutiérrez 2004), temperatures were averaged at 10-, 20-, 30-, and 40-yr intervals from 1760 to 2000.

We used the reconstructed age structure of living trees to infer variations in recruitment over time (Camarero and Gutiérrez 2004, Auger and Payette 2010) assuming constant mortality rates (Wang et al. 2006, Liang et al. 2011). This assumption is supported by the following observations. First, the numbers of individuals of all stages (seedlings, juveniles, and adults) have increased over time in our reconstruction, indicating higher recruitment than mortality rates (Appendix S4: Fig. S5). Whereas seedlings are typically the stage most susceptible to mortality (e.g., >90%; Germino et al. 2002), in this study “seedlings” were well-established recruits between 3 and 30 yr old. Given this fact, as well as the increase in older-stage individuals in these plots over recent time periods, mortality rates must clearly have been relatively low and not increasing over the reconstruction time period, even with increased warming. Second, trees used in our population reconstructions were well within the 400-yr lifespan of Smith fir and, aside from possible catastrophic events that may have caused episodic mortality over the past 200 yr (which has not been recorded in local tree-ring chronologies; Liang et al. 2011), the older trees within our study plots should be reflective of the survival rates at the earliest time periods in our study. To further support this, across both sampled plots we found only six dead adult trees (DBH 17–62 cm; height 4–14 m), which accounted for only 3.4% of the total sampled adults, suggesting a relatively low rate of adult tree mortality. Third, treeline position of Smith fir has remained stable over the past 200 yr (Liang et al. 2011), including in relatively cold periods. Thus, there is no evidence along this line of inquiry to indicate significant mortality events. Finally, treeline densification inferred from our age-structure analysis is consistent with results from repeat landscape photography at treelines in Europe, America, and Asia (Camarero and Gutiérrez 2004, Zier and Baker 2006, Devi et al. 2008), as well as at treelines in the Hengduan Mountains of southeastern Tibetan Plateau located near our study region (Baker and Moseley 2007). Thus, it appears reasonable to use the reconstructed age structure at these plots to investigate changes in tree recruitment through time.

#### *Data and code availability*

All data and accompanying R code for the codispersion analyses are available from the Harvard Forest Data Archive, data set HF265 (*available online*).<sup>8</sup>

## RESULTS

### *Spatiotemporal patterns of tree age classes*

Seedlings and juveniles were abundant in both study sites, and formed dense patches at treeline (Fig. 1; Appendix S4: Fig. S3). Intermediate diameter classes ( $35 \leq \text{DBH} \leq 40$  cm) included relatively few individuals (Appendix S4: Fig. S3). The distribution of age classes corresponded to recently expanding Smith fir treeline populations. Trees that had recruited into the population within the past 5–50 yr accounted for 84% (N1) and 89% (N2) of individuals (Appendix S4: Fig. S3). The reconstruction of the spatial patterns also revealed increasing tree density in both plots (Fig. 1). The most recent period (1982–2011/2013) contained the largest number of trees (Fig. 1e; Appendix S3: Table S1). The second largest recruitment peak occurred in 1952–1981 (Fig. 1d).

Adults, juveniles, and seedlings were randomly distributed within the treeline ecotone prior to 1921 (Fig. 1a and b), but seedlings from 1922 to 1951 were spatially clustered in the N1 site (Fig. 1c; Appendix S3: Table S1). Similarly, seedlings from 1952 to 1981 were spatially clustered at scales up to 6–8 m (Fig. 1d).

Adults and seedlings in the 1922–1951 cohort were spatially segregated (i.e., a significant negative spatial association) at distances of 1–5 m in the N1 site (Fig. 1c), whereas no spatial associations between adults and seedlings were found in the N2 site (Fig. 1c). During the 1952–1981 period, adults and seedlings were spatially segregated at 1–6 m scales (Fig. 1d). From the 1980s onward seedlings were negatively associated with adults at 1–5 m scales (Fig. 1e).

No spatial associations were detected between adults and juveniles during the 1922–1951 period in both sites (Fig. 1c), but spatial segregation was found at 2–5 m for these two tree classes during the 1952–1981 and 1982–2011 periods (Fig. 1d, e). No significant spatial associations between adults and juveniles were detected in the N2 site (Fig. 1a–e).

No spatial associations were detected between juveniles and seedlings prior to 1951 in either of the study sites (Fig. 1a–c). However, during the 1952–1981 period, aggregations of juveniles and seedlings were detected at scales of 1–4 m in the N2 site (Fig. 1d). From the 1980s onward, a significant spatial aggregation was detected between juveniles and seedlings at 1–8 m (Fig. 1e).

In sum, spatial segregation was detected between adults and juveniles or seedlings since the 1950s, when Smith fir regeneration also was increasing in density. This

<sup>8</sup> <http://harvardforest.fas.harvard.edu/data-archive>

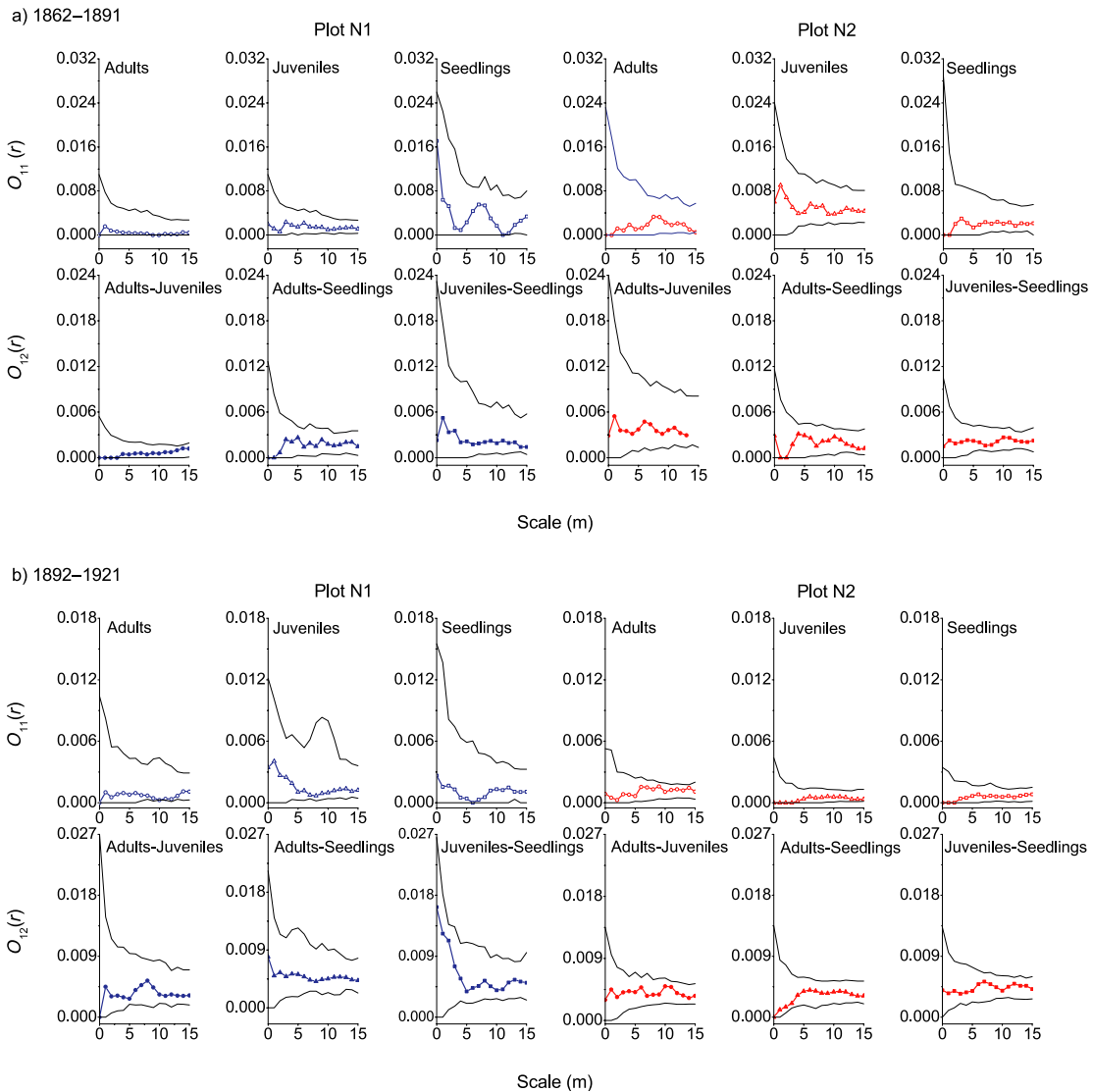


FIG. 1. Univariate and bivariate spatial patterns and analyses obtained for the two Smith fir treeline sites. We considered three age classes of Smith fir individuals (adults, juveniles, and seedlings). Spatial pattern analyses were conducted during the past 150 years over the following 30-yr intervals: (a) 1862–1891, (b) 1892–1921, (c) 1922–1951, (d) 1952–1981, and (e) 1982–2011/2013. Figures in the first row of each panel correspond to the univariate ( $O_{11}(r)$ ) statistic, whereas figures in the second row correspond to bivariate ( $O_{12}(r)$ ) statistic point-pattern analyses, respectively. Colored lines with symbols indicate the  $O_{11}(r)$  or  $O_{12}(r)$  statistics, whereas black lines correspond to the upper and lower 99% bounds of the simulation envelopes. In the univariate case, values of the calculated statistic located above or below the upper and lower envelopes indicate significant aggregation or hyperdispersion (regularity), respectively. In the bivariate case, values of the calculated statistic located above or below the upper and lower envelopes indicate significant attraction or repulsion, respectively (see also Appendix S3: Table S1).

spatial segregation has intensified since the 1980s when regeneration accelerated, whereas spatial aggregation between juveniles and seedlings also has increased recently (Appendix S3: Table S1).

#### *Bivariate mark-correlation functions of tree height and recruitment*

Juvenile trees were shorter than expected when they were located 1–3 m from adults in the N1 site and 1–4 m from adults in the N2 site (Fig. 2). On average, seedlings

also were shorter than expected when located < 1 m from adults in the N1 site and 1–3 m in the N2 site. Seedlings located 1–3 m from juveniles had larger height values than expected in the N2 site.

At 15 m from each target tree, height of adults and juveniles showed both segregation and aggregation with respect to the density of individuals recruited during the last 30 yr (Appendix S4: Fig. S4). Segregation was due to neighboring trees having different heights, whereas aggregation was due to the clustering of recruitment within 4–5 m of adult trees.

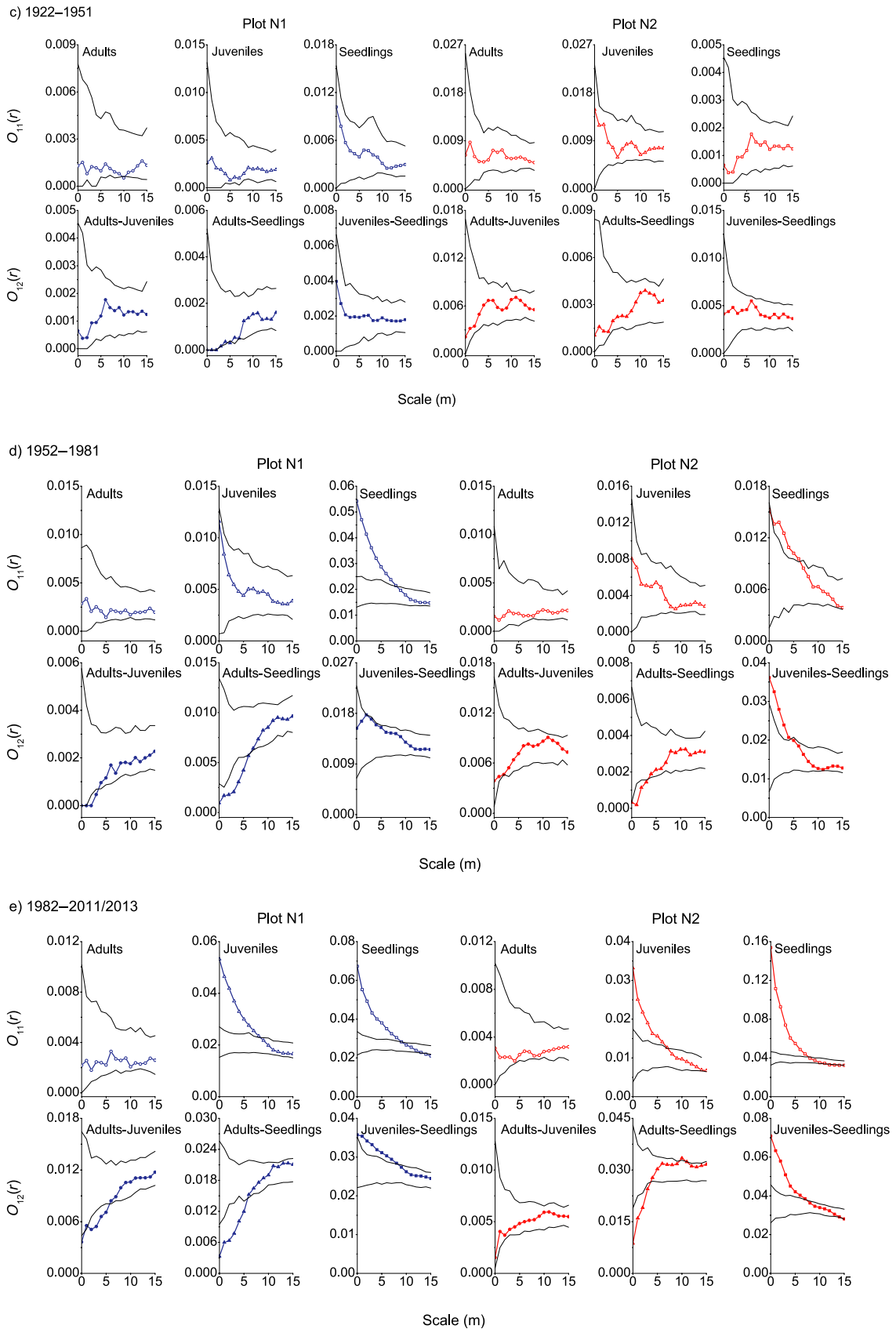


FIG. 1. (Continued).

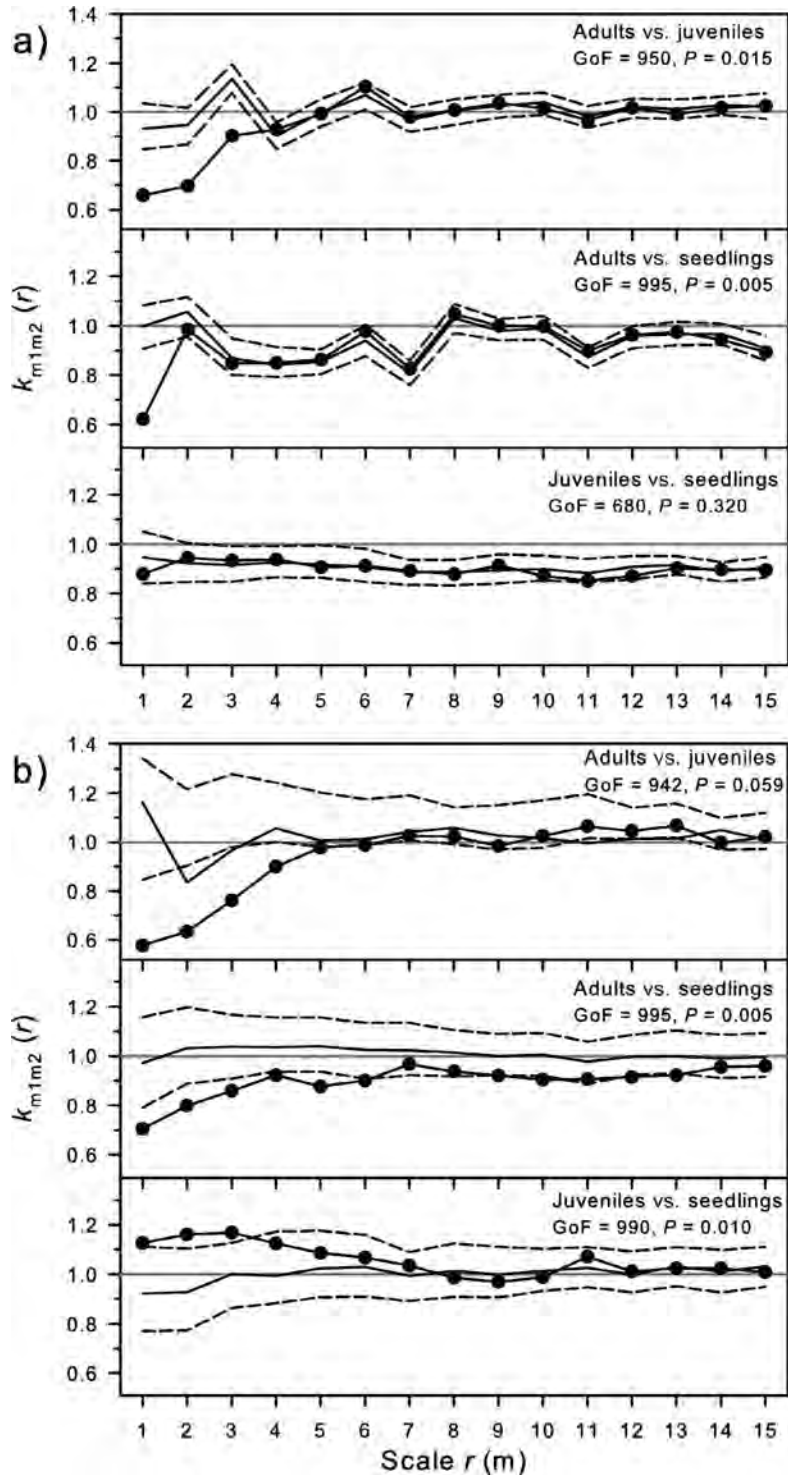


FIG. 2. Mark correlation functions ( $k_{m1m2}(r)$ ) based on the spatial patterns of tree height in (a) N1 and (b) N2 treeline sites. The functions were calculated by relating the spatial locations of adults vs. juveniles, adults vs. juveniles, or juveniles vs. seedlings. The continuous lines with symbols correspond to the calculated functions, whereas continuous and dashed lines show the null model and the 99% bounds of the simulation envelopes, respectively. The goodness-of-fit (GoF) tests and their significance levels ( $P$ ) are also shown. Note that values of  $k_{m1m2}(r)$  close to 1 indicate that the mark-pair products at a distance  $r$  depend only on the spatial location of Smith fir individuals.

Examination of  $k$  of ( $r$ ) suggested that nearby trees were shorter than expected. The bivariate mark correlation function  $k_{m_1m_2}(r)$  revealed spatial associations between height and recruitment patterns (Appendix S2; Appendix S4: Fig. S4). The function  $I_{m_1m_2}(r)$  indicated a negative correlation between height and recruitment density at smaller scales. Specifically, tall trees tended to have fewer neighbors within 4–5 m than did shorter trees. Tree height and the density of individuals recruited during the last 30 yr were negatively associated in both sites (N1,  $r = -0.248$ ,  $P = 0.018$ , radius = 15 m; N2,  $r = -0.173$ ,  $P = 0.001$ , radius = 5 m), although neither of these correlation coefficients were significant after correcting for the presence of spatial autocorrelation ( $P$  corrected = 0.199; N2:  $P$  corrected = 0.653).

Codispersion analyses

Heights of adults and juveniles in the N1 site, and also of adults and seedlings, were negatively correlated at most spatial lags and directions, except for a positive correlation observed in large lags along the northwest direction toward the treeline boundary (interpreted in Fig. 3 as a change in color in observed codispersion values moving from the bottom of the codispersion graph toward the upper left corner of the graph), possibly reflecting the situation that consistently shorter tree heights near the treeline might be more similar to the heights of juveniles and seedlings lower down in the forest, causing a change in codispersion from negative to positive at these larger lags (Fig. 3). These patterns were significantly different from expected-under a null

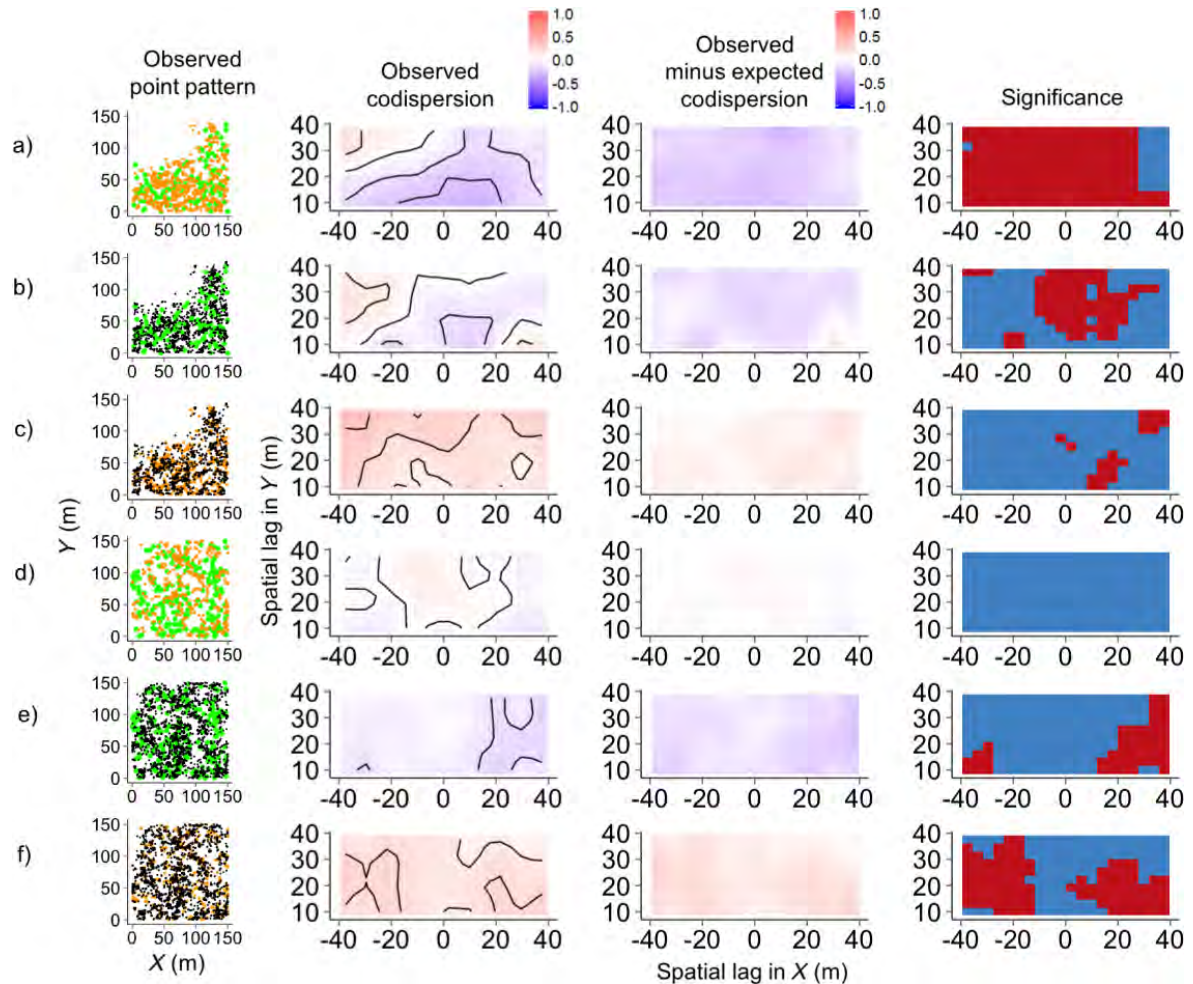


FIG. 3. Recent bivariate point-pattern maps (far left panel) for adult trees (large, green points), juveniles (intermediate, orange points) and seedlings (small, black points) in the (a–c) N1 and (d–f) N2 treeline sites and their resultant codispersion analyses of height. Codispersion graphs show the observed codispersion values for associations between the heights of (a and d) adults and juveniles, (b and e) adults and seedlings, and (c and f) juveniles and seedlings for a range of spatial lags within each site (left; contour lines = 0.1), the observed values minus the values expected under a “random labeling” null model (center), and the significance (red), or not (blue), at the  $P < 0.05$  level. The random labeling model was used to calculate 199 expected codispersion values for randomly assigned heights at the observed tree positions.



model where tree spatial positions were fixed but observed heights were randomly assigned—for most spatial lags and directions for adults and juveniles. However, these patterns were significant only for adults and seedlings at small spatial lags (<20 m) moving toward the treeline. In contrast, the heights of adults and juveniles in the N2 site were not significantly correlated, and adults and seedlings were only weakly negatively related (Fig. 3). In both sites, juveniles and seedling heights were positively correlated at all spatial lags and directions, although this was not significant for most spatial lags and directions in the N1 site, and for lags greater than 15 m in most directions in the N2 site (Fig. 3).

#### *Recruitment dynamics and climate*

Age structures suggested an increase in tree density in recent decades (Fig. 4). In both sites, tree recruitment was positively and significantly related to summer and winter temperatures at 10 to 40-yr long scales (Fig. 4; Appendix S3: Table S2). However, the highest correlations were found between tree recruitment data and averaged summer minimum temperatures at 30-yr intervals in the N1 site and at 20-yr intervals in the N2 site (Appendix S3: Table S2). Tree recruitment in plot N1 during the 1960s and 1970s increased by 84% and 121% in comparison with the previous decade. Similarly, tree recruitment in plot N2 in the 1960s and

1970s increased by 95% and 376% as compared to the previous decade. In comparison with the 1922–1951 period, recruitment in the 1952–1981 period increased by more than 5 and 2.5 times in the N1 and N2 sites, respectively. Since the 1980s, tree recruitment has continued to increase, but at lower rates than in previous decades.

#### DISCUSSION

Our results indicate that regional warming has promoted treeline encroachment and densification since the 1950s, coincident with a warming rate that is unprecedented in the last 1,000 yr (Liu et al. 2005). Under the reasonable assumption of no significant changes in adult tree mortality rate, rising tree density in our plots is most likely attributable to an increased rate of tree recruitment that has been associated with climatic warming. Our findings are in line with results from similar studies in Europe and North America (Camarero and Gutiérrez 2004, Elliott 2011) and previous findings in the southeastern Tibetan Plateau (Liang et al. 2011). Our finding that increased tree density was related to warming also is consistent with other studies that have found that tree regeneration and growth in alpine treelines are primarily constrained by low temperatures (Harsch et al. 2009, Körner 2012). Nevertheless, the temporal scale is important because long-term tree recruitment responded positively to 20- and 30-yr

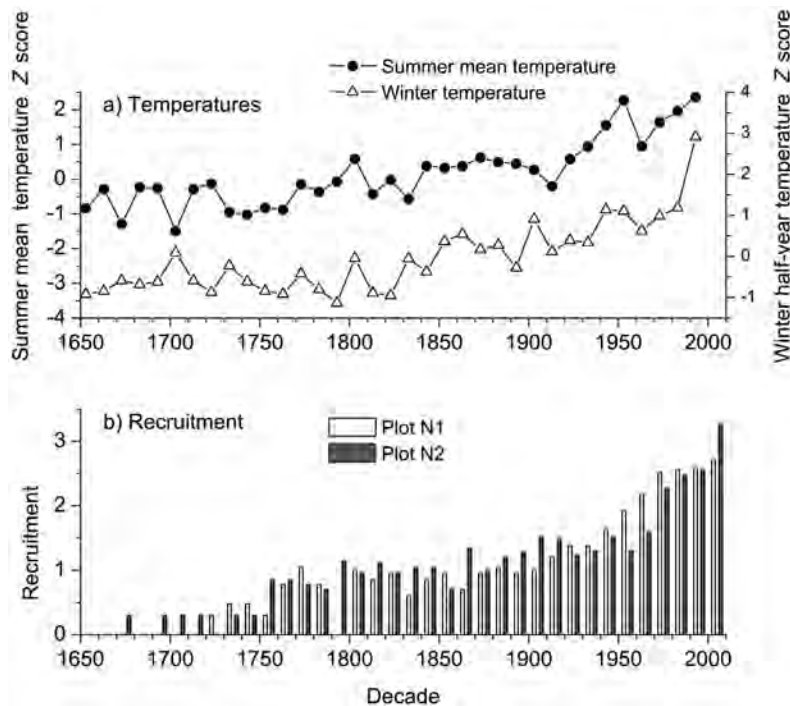


FIG. 4. Variations in (a) reconstructed summer mean minimum and winter half-year mean temperatures and (b) temporal dynamics of (log[no. individuals + 1]-transformed) Smith fir recruitment at decadal resolution in the two treeline plots (white and gray bars correspond to N1 and N2 plots, respectively).

averaged summer minimum temperatures, implying a relatively slow response of recruitment to climatic warming in our study system. These findings point to the possibility that a lagged recruitment response to climate might be a common feature of other cold-limited treelines (Camarero and Gutiérrez 2004, Kullman 2007), although coarse resolution of recruitment data limited our ability to test for a lagged response. Other factors explaining this lag could be the wave-like recruitment observed at alpine treelines that is often related to episodic masting (Körner 2012).

Competition among canopy trees is a key feature of dense forests (Oliver and Larson 1996), but the role of competition as a result of densification in structuring alpine treeline forests has not been studied extensively. Our results suggest that competition has been increasing at our study sites. First, both increasing tree density and significant spatial segregation between seedlings or juveniles and adults at small scales (1–5 m) have occurred since the 1950s (periods 1952–1981 and 1982–2011/2013). Liang et al. (2011) and Wang et al. (2012) found no evidence for major disturbances in our study region. The coupling of densification and spatial segregation further suggests that increased competition between recruits and mature trees is occurring among trees growing along the studied Tibetan treelines.

Second, the intensity of spatial segregation between juveniles or seedlings and adults at small scales increased during 1982–2013 relative to 1952–1981, suggesting that warming-induced densification has increased small-scale competition. Further, the spatial patterns of Smith fir changed from clumped seedlings during the earliest periods (prior to 1950) toward randomly or regularly located juveniles or adults in the most recent periods (1952–1981, 1981–2013), implying that competition has become increasingly important in shaping the spatial distribution of these trees. An alternative explanation for this pattern could be that the post-1950s warming resulted in a relaxation of cold stress strengthening the coupling of treelines with climate and thus making tree recruitment less reliant on neighborhood facilitation. Tree clumping prior to the 1950s could indicate an association between cold stress and facilitation of recruitment through seedling protection from sunlight, frost, or wind stress (Maher and Germino 2006). Nevertheless, if density continues to increase, competition likely will have a negative impact on growth and survival, shifting processes in these forests toward those more like closed-canopy ecosystems (Getzin et al. 2006).

The spatial segregation of seedlings away from adult trees and the observed clustering of seedlings also are suggestive of a positive feedback-induced facilitation, an interaction that is known to play an important role in driving recruitment at treelines (e.g., Maher and Germino 2006). Whereas competition could play a dominant role in shaping future treeline dynamics under warmer climatic conditions (Tingstad et al. 2015), facilitation may still be a relevant process explaining

aggregated recruitment patterns. For instance, the spatial aggregation that we detected between juveniles and seedlings suggests that juveniles may create favorable sites for seedling establishment (Callaway 2007). In addition, the aggregated spatial patterns of seedlings may promote a more favorable microenvironment by enhancing snow retention, which increases recruit survival (Batllori et al. 2009). Such enhanced facilitative mechanisms suggest that frequent bottlenecks in seedling establishment at treelines can be alleviated partially (Holtmeier and Broll 2007).

Increasing recruitment and competition within the Smith fir treeline population over the past 60 yr follows expectations of the stress-gradient hypothesis, i.e., an increase in competition as abiotic stress diminishes (Choler et al. 2001, Callaway 2007, Chu et al. 2008, He et al. 2013). Temperatures in the decades since the 1950s have been among the warmest during the past 1000 yr in the Tibetan Plateau (Liu et al. 2005, Zhu et al. 2008), and it is reasonable to assume that low-temperature stress has been alleviated at Tibetan treeline, especially in comparison to the Little Ice Age. Ultimately, however, increasing competition will induce self-thinning of treeline populations, further suppressing the growth of recruits and inhibiting new recruitment.

The development of denser treeline forests in the Tibetan Plateau to the point where competitive processes predominate has important implications for future interactions between climatic change and forest dynamics. Given that future temperatures in the Tibetan Plateau are projected to increase 2.6–5.2°C by 2,100 (Chen et al. 2013), we conclude that competition will play a more important role in driving treeline dynamics than it has in the past. At some point, increasing competition between adults and juveniles or seedlings could counteract any positive effects of future warming on tree growth in these treeline forests. Additional sites and species should be scrutinized in a global comparison of alpine treelines to properly quantify the pattern and pace of their transitions toward more-dense subalpine forests. Nonetheless, our results suggest that increasing densification as a result of warming at alpine treeline ecotones in future years may promote a potential switch from facilitation to competition, particularly as more juveniles and seedlings transition to adults. To better understand how treelines may respond to future warming, further investigation into climate-driven switches between facilitation and competition over time and space (e.g., Renard et al. 2016) is warranted.

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## LITERATURE CITED

- Auger, S., and S. Payette. 2010. Four millennia of woodland structure and dynamics at the Arctic treeline of eastern Canada. *Ecology* 91:1367–1379.
- Baker, B. B., and R. K. Moseley. 2007. Advancing treeline and retreating glaciers: implications for conservation in Yunnan, PR China. *Arctic, Antarctic and Alpine Research* 39:200–209.
- Battlori, E., J. J. Camarero, J. M. Ninot and E. Gutiérrez. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones: implications and potential responses to climate warming. *Global Ecology and Biogeography* 18:460–472.
- Buckley, H. L., B. S. Case, and A. M. Ellison. 2016a. Using codispersion analysis to characterize spatial patterns in species co-occurrences. *Ecology* 96:32–39.
- Buckley, H. L., B. S. Case, J. K. Zimmerman, J. Thompson, J. A. Myers and A. M. Ellison. 2016b. Using codispersion analysis to quantify and understand spatial patterns in species-environment relationships. *New Phytologist* doi: 10.1111/nph.13934.
- Callaway, R. M. 2007. Positive interactions and interdependence in plant communities. Springer, Dordrecht, The Netherlands.
- Camarero, J. J., and E. Gutiérrez. 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change* 63:181–200.
- Chen, H., et al. 2013. The impact of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. *Global Change Biology* 19:2940–2955.
- Choler, P., R. Michalet, and R. M. Callaway. 2001. Facilitation and competition on gradients in alpine plant communities. *Ecology* 82:3295–3308.
- Chu, C., F. T. Maestre, S. Xiao, J. Weiner, Y. Wang, Z. Duan, and G. Wang. 2008. Balance between facilitation and resource competition determines biomass-density relationships in plant populations. *Ecology Letters* 11:1189–1197.
- Comita, L. S., H. C. Muller-Landau, S. Aguilar, and S. P. Hubbell. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329:330–332.
- Cook, E. R., and L. A. Kairiukstis. 1990. Methods of dendrochronology: applications in the environmental sciences. Kluwer, Dordrecht, The Netherlands.
- Cuevas, F., E. Porcu, and R. Vallejos. 2013. Study of spatial relationships between two sets of variables: a nonparametric approach. *Journal of Nonparametric Statistics* 25:695–714.
- Devi, N., F. Hagedorn, P. Moiseev, H. Bugmann, S. Shiyatov, V. Mazepa, and A. Rigling. 2008. Expanding forests and changing growth forms of Siberian larch at the Polar Ural treeline during the 20th century. *Global Change Biology* 14:1581–1591.
- 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.
- Fajardo, A., and E. J. McIntire. 2007. Distinguishing microsite and competition processes in tree growth dynamics: an a priori spatial modeling approach. *American Naturalist* 169:647–661.
- Germino, M. J., W. K. Smith, and A. C. Resor. 2002. Conifer seedling distribution and survival in alpine-treeline ecotone. *Plant Ecology* 162:157–168.
- Getzin, S., C. Dean, F. He, J. A. Trofymow, K. Wiegand and T. Wiegand. 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* 29:671–682.
- Grau, O., J. M. Ninot, J. M. Blanco-Moreno, R. S. P. van Logtestijn, J. H. C. Cornelissen, and T. V. Callaghan. 2012. Shrub-tree interactions and environmental changes drive treeline dynamics in the Subarctic. *Oikos* 121:1680–1690.
- Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* 12:1040–1049.
- He, F., and R. P. Duncan. 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. *Journal of Ecology* 88:676–688.
- He, Q., M. D. Bertness, and A. H. Altieri. 2013. Global shifts towards positive species interactions with increasing environmental stress. *Ecology Letters* 16:695–706.
- Holtmeier, F. K., and G. Broll. 2007. Treeline advance—driving processes and adverse factors. *Landscape Online* 1:1–33.
- Kenkel, N. C. 1988. Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. *Ecology* 69:1017–1024.
- Körner, C. 2012. Alpine treelines: functional ecology of the global high elevation tree limits. Springer, Basel, Switzerland.
- Kullman, L. 2007. Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implication for tree line theory and climate change ecology. *Journal of Ecology* 95:41–52.
- Liang, E., Y. Wang, D. Eckstein, and T. Luo. 2011. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytologist* 190:760–769.
- Liu, H., and Y. Yin. 2013. Response of forest distribution to past climate change: an insight into future predictions. *Chinese Science Bulletin* 58:4426–4436.
- Liu, X., D. Qin, X. Shao, T. Chen, and J. Ren. 2005. Temperature variations recovered from tree-rings in the middle Qilian Mountain over the last millennium. *Science China Series D: Earth Sciences* 48:521–529.
- Lv, L., and Q. Zhang. 2012. Asynchronous recruitment history of *Abies spectabilis* along an altitudinal gradient in the Mt. Everest region. *Journal of Plant Ecology* 5:147–156.
- Maher, E. L., and M. J. Germino. 2006. Microsite differentiation among conifer species during seedlings establishment at alpine treeline. *Ecoscience* 13:334–341.
- Miehe, G., S. Miehe, J. Vogel, S. Co, and L. Duo. 2007. Highest treeline in the northern hemisphere found in southern Tibet. *Mountain Research and Development* 27:169–173.
- Oliver, C. D., and C. B. Larson. 1996. Forest stand dynamics. John Wiley and Sons, New York, New York, USA.
- Renard, S. M., E. J. McIntire, and A. Fajardo. 2016. Winter conditions—not summer temperature—influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. *Journal of Vegetation Science* 27:29–39.
- Shen, W., L. Zhang, X. Liu, and T. Luo. 2014. Seed-based treeline seedlings are vulnerable to freezing events in the early growing season under a warmer climate: evidence from a reciprocal transplant experiment in the Sergyemala Mountains, southeast Tibet. *Agricultural and Forest Meteorology* 187:83–92.
- Stoyan, D., and A. Penttinen. 2000. Recent applications of point process methods in forestry statistics. *Statistical Science* 15:61–78.
- Thorpe, H. C., R. Astrup, A. Trowbridge, and K. D. Coates. 2010. Competition and tree crowns: a neighborhood analysis

- of three boreal tree species. *Forest Ecology and Management* 259:1586–1596.
- Tingstad, L., S. L. Olsen, K. Klanderud, V. Vandvik, and M. Ohlson. 2015. Temperature, precipitation and biotic interactions as determinants of tree seedlings recruitment across the tree line ecotone. *Oecologia* 179:599–608.
- Wang, T., Q. Zhang, and K. Ma. 2006. Treeline dynamics in relation to climatic variability in the central Tianshan Mountains, northwestern China. *Global Ecology and Biogeography* 15:406–415.
- Wang, X., T. Wiegand, Z. Hao, B. Li, J. Ye, and F. Lin. 2010. Species associations in an old-growth temperate forest in north-eastern China. *Journal of Ecology* 98:674–686.
- Wang, Y., J. J. Camarero, T. Luo, and E. Liang. 2012. Spatial patterns of Smith fir alpine treelines on the south-eastern Tibetan Plateau support that contingent local conditions drive recent treeline patterns. *Plant Ecology and Diversity* 5:311–321.
- Wiegand, T., and K. A. Moloney. 2004. Rings, circles and null-models for point pattern analysis in ecology. *Oikos* 104:209–229.
- Wiegand, T. and K. A. Moloney. 2014. *Handbook of spatial point-pattern analysis in ecology*. Chapman & Hall/CRC, Boca Raton, Florida, USA.
- Zhu, H., Y. Zheng, X. Shao, X. Liu, Y. Xu, and E. Liang. 2008. Millennial temperature reconstruction based on tree-ring widths of Qilian juniper from Wulan, Qinghai Province, China. *Chinese Science Bulletin* 53:3914–3920.
- Zhu, H., X. Shao, Z. Yin, P. Xu, Y. Xu, and H. Tian. 2011. August temperature variability in the southeastern Tibetan Plateau since AD 1385 inferred from tree rings. *Palaeogeography, Palaeoclimatology, Palaeoecology* 305:84–92.
- Zier, J. L., and W. L. Baker. 2006. A century of vegetation changes in the San Juan Mountains, Colorado: an analysis using repeat photography. *Forest Ecology and Management* 228:251–262.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1111/1365-3113.1264>.1/supinfo

## **Increased stem density and competition may diminish the potential positive effects of warming at alpine treeline**

Yafeng Wang, Neil Pederson, Aaron M. Ellison, Hannah L. Buckley, Bradley S. Case, Eryuan Liang, J. Julio Camarero

### **Appendix S1**

#### **Field sampling**

Smith fir was the only tree species in each plot that reached canopy status. Soils in the plots were slightly acidic (pH = 5–6), and understory vegetation was a mix of mosses and lichens ( $\approx 60\%$  cover). A few herbaceous plants (e.g., *Rubus thibetanus* Franch., *Bergenia purpurascens* (Hook. f. & Thomson) Engl.) were found at the treeline ecotone, but they accounted for  $< 3\%$  of the ground cover. Fir seedlings establish atop these and in organic matter (Wang et al. 2012).

At each of the two sites, we established a square  $150 \times 150$ -m plot in a topographically uniform area parallel to the local slope. Note that the plot at site N1 was an extension of the  $30 \times 150$ -m N1 plot previously studied by Liang et al. (2011). The upper portion of each plot encompassed the current treeline. The relative origin for each plot ( $x, y = 0, 0$ ) was located at the lower left corner of the plot facing upslope (see Camarero and Gutiérrez 2004). The upper left part of the N1 site was occupied by dense *Rhododendron* dense thickets, and that is the reason why this portion of the plot was excluded from our analyses.

Every tree within each plot was mapped and measured in early November 2011 (N1) and June 2014 (N2) following the previous field sampling protocol used by Liang et al. (2011). Diameter at breast height (DBH) measured at 1.3 m aboveground and the horizontal diameters of the canopy parallel to the  $x$  and  $y$  axes of the plot were measured. If the height of an individual tree

was < 2 m, we measured its height with a tape. Otherwise tree height was determined using a clinometer ( $\pm 0.25$  m). A total of 2053 (for N1) and 3057(N2) trees were sampled and mapped, but only six dead individuals were found.

#### LITERATURE CITED

- Camarero, J. J., and E. Gutiérrez. 2004. Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the Spanish Pyrenees. *Climatic Change* 63:181-200.
- Liang, E., Y. Wang, D. Eckstein, and T. Luo. 2011. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. *New Phytologist* 190:760-769.
- Wang, Y., J. J. Camarero, T. Luo, and E. Liang. 2012. Spatial patterns of Smith fir alpine treelines on the south-eastern Tibetan Plateau support that contingent local conditions drive recent treeline patterns. *Plant Ecology and Diversity* 5:311-321.

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### **Appendix S2**

#### **Point-pattern analyses**

##### *Univariate point-pattern analyses*

The univariate  $O_{11}(r)$  statistic as implemented in the Programita software package (Wiegand and Moloney 2014) was used to characterize the spatial patterns of the three different age classes (adults, juveniles, and seedlings). We used a heterogeneous Poisson process as a null model for complete spatial randomness (CSR), and calculated simulation envelopes to determine if the observed pattern of each age class was random, clumped, or regularly spaced. A 99% simulation envelope of  $O_{11}(r)$  was constructed from 999 Monte Carlo simulations. If the observed  $O_{11}(r)$  was above or below the simulation envelopes, the pattern was considered to be significantly aggregated or hyperdispersed (regular), respectively, at a particular spatial scale. Since spatial relationships for Smith fir treeline populations previously had been detected at scales of 1–7 m (Wang et al. 2012), we estimated  $O_{11}(r)$  at a spatial resolution of 1 m and tested for departure from CSR for scales from 1 to 15 m. Finally, because simulation envelope tests were calculated at multiple spatial scales, the Type I error rate can be inflated (Wiegand and Moloney 2014). Therefore, we also applied a Goodness-of-Fit (GoF) test to collapse that scale-dependent information into a single test statistic for formal hypothesis testing.

### *Bivariate point pattern analyses*

We used the bivariate  $O_{12}(r)$  statistic as implemented in the Programita software package (Wiegand and Moloney 2014) to characterize the spatial associations between the three age classes. We assumed that adults or juveniles impact juveniles or seedlings, respectively, but not vice versa. Hence, we used an antecedent condition as the null model, and only randomized the locations of either juveniles or seedlings while keeping the locations of adults or juveniles, respectively, fixed (Wiegand and Moloney 2014). As in the univariate case, if the  $O_{12}(r)$  statistic was above or below the boundaries of a 99% simulation envelopes, the pattern was considered to show significant positive (attraction) or negative (repulsion) associations, respectively, at a given spatial scale. Again, we used a 1-m resolution and tested for CSR at scales from 1–15 m, and applied a GoF test to minimize Type I error rates.

### ***Mark correlation function: bivariate patterns with two quantitative marks***

To detect if competition affected recent regeneration, we compared the locations and heights of adults and juveniles with the densities of individuals recruited during the last 30 years at a radius of 5, 10 and 15 m from each focal tree. We calculated the density of seedlings found around either adults or juveniles by using the spatstat package (Baddeley and Turner 2013) within the R statistical software, version 3.0.1 (R Development Core Team 2015). Similar to our prior analysis, we performed a bivariate mark correlation analysis by calculating the spatial relationship between height and recruitment density in the tree neighborhood using the Programita software. In this case, we used two additional bivariate mark-correlation functions to identify the spatial pattern of tree height (first  $r$ -mark correlation function  $k_{m1}(r)$ ) while highlighting the



relationships between height and recruitment patterns (Moran's  $I$ -type summary statistic  $I_{m1m2}(r)$ ); see Wiegand and Moloney 2014).

## References

Baddeley, A.J., and Turner, R. 2013. Package 'Spatstat': Spatial Point Pattern analysis.  
<http://mirrors.ustc.edu.cn/CRAN/>.

R Development Core Team. 2015. R: a language and environment for statistical computing. R  
Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.

Wang, Y., J. J. Camarero, T. Luo, and E. Liang. 2012. Spatial patterns of Smith fir alpine  
treelines on the south-eastern Tibetan Plateau support that contingent local conditions drive  
recent reeline patterns. *Plant Ecology and Diversity* 5:311-321.

Weigand, T., and K. A. Moloney. 2014. Handbook of spatial point pattern analysis in ecology.  
Chapman & Hall/CRC, Boca Raton, Florida, USA.

## Increased stem density and competition may diminish the potential positive effects of warming at alpine treeline

Yafeng Wang, Neil Pederson, Aaron M. Ellison, Hannah L. Buckley, Bradley S. Case, Eryuan Liang, J. Julio Camarero

### Appendix S3

**Table S1.** Statistical parameters summarizing the univariate and bivariate point pattern analyses of Smith fir individuals (adults, juveniles and seedlings) growing in two treeline sites. The analyses were calculated for five 30-year periods (see also Fig. 1). Displayed statistics are: nn, mean distance to the nearest neighbor;  $\lambda$ , intensity or density of the pattern within an area delimited by a convex hull; and GoF, Goodness-of-Fit test calculated for each point-pattern analysis (considering the analyzed distance interval from 1 to 15 m) with its corresponding significance level ( $P$ ). Significant ( $P < 0.05$ ) GoF values are in bold. The first two statistics were calculated only for the univariate case.

Site	Spatial pattern analysis of tree individuals	Periods															
		1862-1891			1892-1921			1922-1951			1952-1981			1982-2011/2013			
		nn (m)	$\lambda$ (ind ha <sup>-1</sup> )	GoF ( $P$ )	nn (m)	$\lambda$ (ind ha <sup>-1</sup> )	GoF ( $P$ )	nn (m)	$\lambda$ (ind ha <sup>-1</sup> )	GoF ( $P$ )	nn (m)	$\lambda$ (ind ha <sup>-1</sup> )	GoF ( $P$ )	nn (m)	$\lambda$ (ind ha <sup>-1</sup> )	GoF ( $P$ )	
N1	Adults	11.1	28	690 (0.31)	8.3	43	660 (0.34)	7.4	50	475 (0.52)	5.9	60	190 (0.81)	5.2	85	400 (0.60)	
	Juveniles	7.8	36	90 (0.91)	7.8	40	670 (0.33)	6.5	49	450 (0.55)	4.1	117	<b>985</b> (0.02)	1.7	450	<b>995</b> (0.005)	
	Seedlings	9.0	31	915 (0.09)	9.2	41	635 (0.37)	5.2	80	<b>980</b> (0.02)	1.7	389	<b>990</b> (0.01)	1.3	687	<b>995</b> (0.005)	
N2	Univariate analyses	Adults	12.9	17	708 (0.29)	8.6	33	715 (0.28)	7.1	47	541 (0.86)	6.3	64	390 (0.61)	5.2	97	506 (0.49)
	Juveniles	8.3	32	284 (0.72)	7.9	37	66 (0.93)	6.1	60	914 (0.08)	4.6	75	<b>999</b> (0.002)	2.3	210	<b>1000</b> (0.001)	

N1	Seedlings	11.2	20	564 (0.44)	7.5	37	<b>982</b>	6.3	31	<b>999</b>	3.2	130	<b>1000</b>	1.0	1048	<b>1000</b>
							(0.019)			(0.002)			(0.001)			(0.001)
	Adults - juveniles	---		35 (0.96)	---		435 (0.56)	---		680 (0.32)	---		<b>990</b>	---		<b>990</b> (0.01)
	Adults - seedlings	---		760 (0.24)	---		580 (0.42)	---		<b>980</b> (0.02)	---		<b>995</b>	---		<b>995</b> (0.005)
	Juveniles -	---		590 (0.41)	---		545 (0.45)	---		510 (0.49)	---		<b>985</b>	---		<b>998</b> (0.001)
Bivariate analyses	seedlings															
N2	Adults - juveniles	---		621 (0.38)	---		102 (0.89)	---		924	---		<b>984</b>	---		<b>983</b>
	Adults - seedlings	---		115 (0.88)	---		919 (0.08)	---		906 (0.09)	---		<b>1000</b>	---		<b>1000</b>
	Juveniles -seedlings	---		281(0.97)	---		113 (0.88)	---		148 (0.85)	---		<b>1000</b>	---		<b>1000</b>
													(0.001)			(0.001)

---

**Table S2.** Pearson correlation coefficients obtained by relating recruitment data ( $y$ , dependent variable or predictor) with reconstructed summer mean minimum and winter half-year mean temperatures ( $x$ , independent variables or predictors) for the Tibetan Plateau (period 1760-2000, see Fig. 3). Temperatures were averaged over four different time periods (10, 20, 30 and 40 years). The different  $P$  values are indicated by different symbols (one, two, and three asterisks correspond to  $P < 0.05$ ,  $P < 0.01$  and  $P < 0.001$ , respectively). –

Site	Period of temperature average in years (No. considered periods)	Summer temperature		Winter temperature	
		$r$	Regression function obtained between recruitment data and temperature	$r$	Regression function obtained between recruitment data and temperature
N1	10 (24)	0.740***	$y = 0.0055x + 0.195$	0.716***	$y = 0.0017x - 7.363$
	20 (12)	0.729*	$y = 0.0056x + 0.194$	0.784*	$y = 0.0018x - 7.366$
	30 (8)	0.668	$y = 0.0057x + 0.184$	0.619	$y = 0.0018x - 7.364$
	40 (6)	0.861*	$y = 0.0054x + 0.205$	0.785	$y = 0.0017x - 7.359$
N2	10 (24)	0.674***	$y = 0.0063x + 0.231$	0.719***	$y = 0.0022x - 7.362$
	20 (12)	0.773*	$y = 0.0065x + 0.225$	0.701	$y = 0.0022x - 7.363$
	30 (8)	0.629	$y = 0.0067x + 0.214$	0.611	$y = 0.0021x - 7.358$
	40 (6)	0.743*	$y = 0.0073x + 0.185$	0.771	$y = 0.0023x - 7.369$

**Increased stem density and competition may diminish the potential positive effects of warming at alpine treeline**

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**Appendix S4**

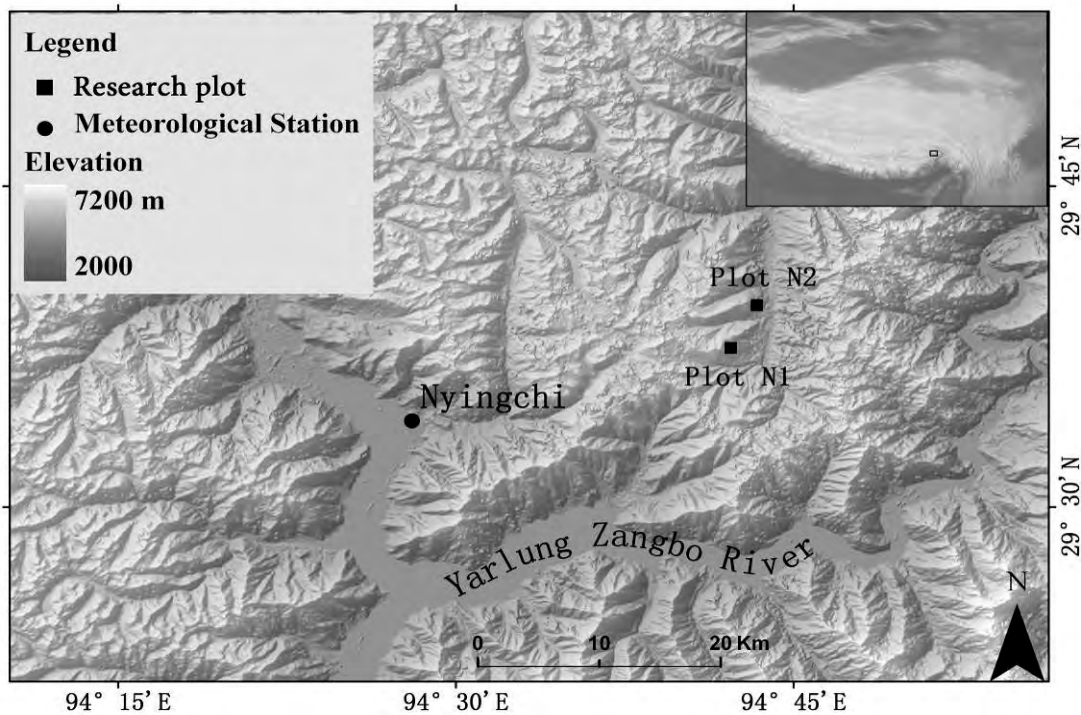


Figure S1. Map showing the locations of the studied Smith fir treeline sites situated in the Sygera Mountains, southeast Tibetan Plateau, eastern Asia (see upper inset) and the Nyingchi meteorological station located at 3,000 m a.s.l. The upper limits of N1 and N2 sites are 4390 and 4370 m a.s.l., respectively.

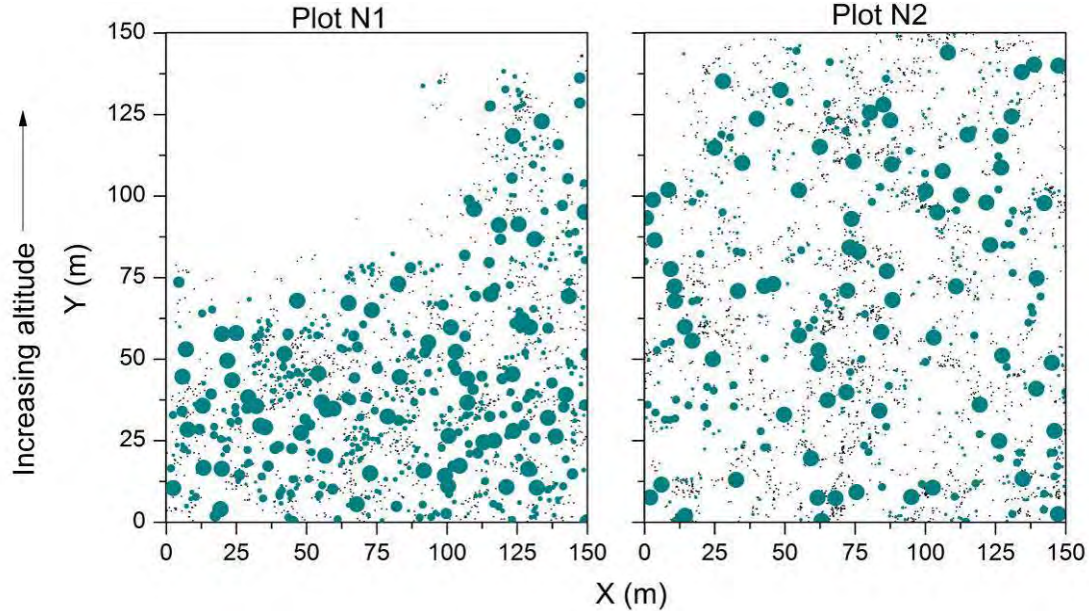


Figure S2. Spatial positions of mapped Smith fir individuals located within the study treeline plots located at N1 ( $n = 2053$ ) and N2 ( $n = 3057$ ) sites. The color circles denote individual trees; the point size is proportional to each tree's diameter at breast height ( $DBH^{0.5}$ ). The small points show individuals that recruited into the plots during the last 30 years. Increasing altitude corresponds to higher values along the y axis. Note that dense patches of tall *Rhododendron* individuals dominate above the treeline in the upper left area of N1 site.

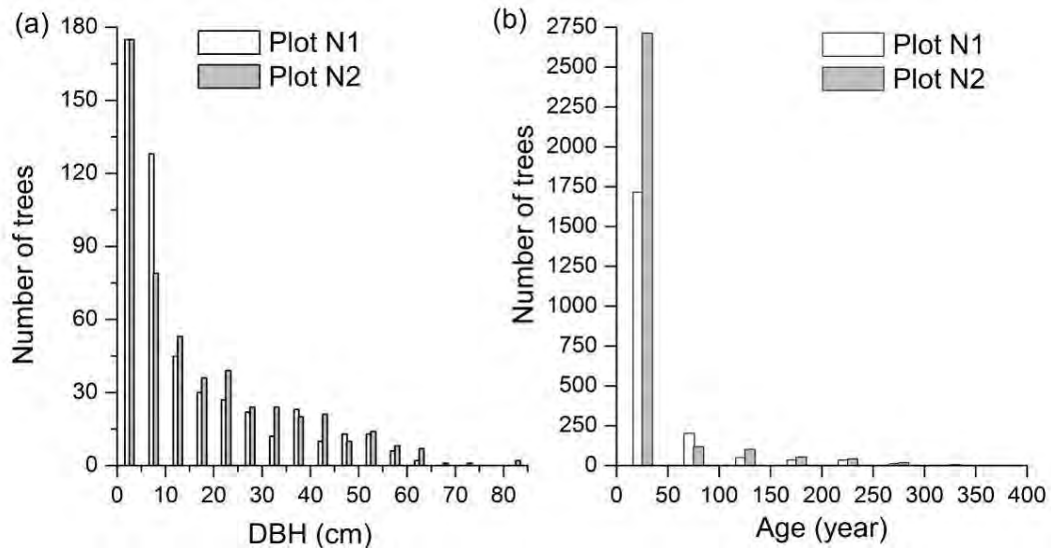


Figure S3. Distribution of sampled trees according to their diameter at breast height (DBH, a) and age (b) in the study treelines (white bars and gray bars correspond to N1 and N2 sites).

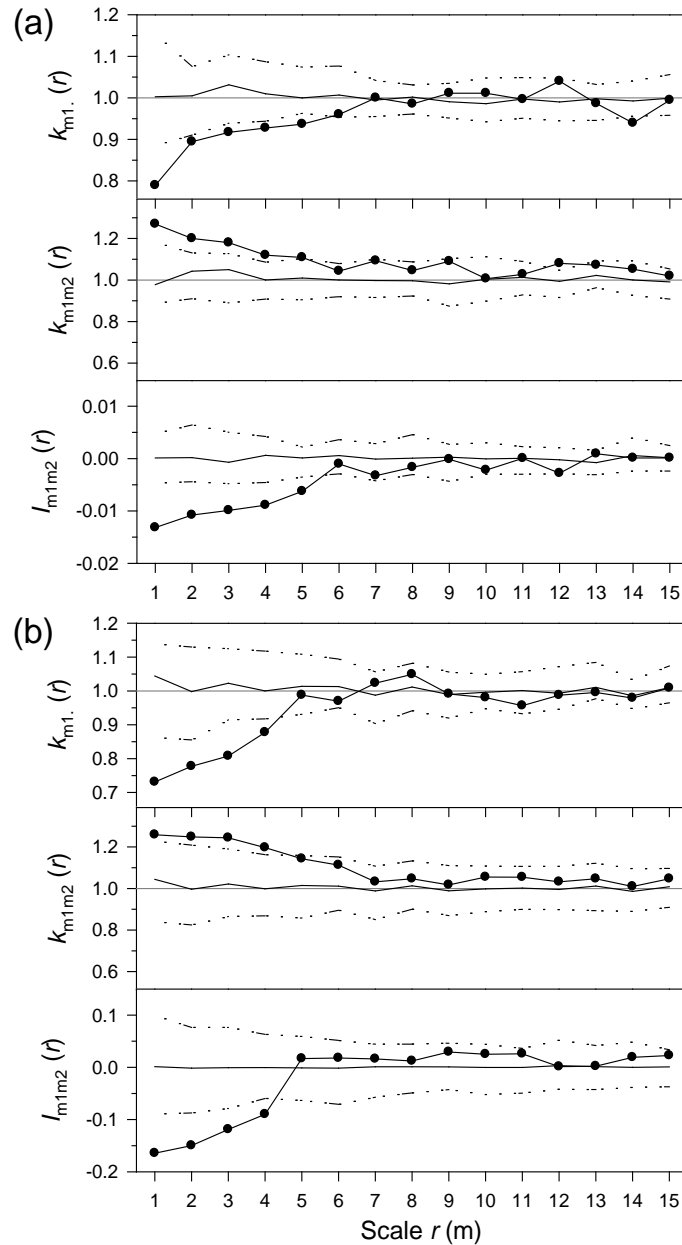


Figure S4. Bivariate mark correlation functions ( $k_{m1}(r)$ ,  $k_{m1m2}(r)$ ,  $I_{m1m2}(r)$ ; upper figures) plotted as a function of scale ( $r$ ) and based on the spatial patterns of tree height and the density of recruits in N1 (a) and N2 (b) treeline sites. Recruitment density corresponds to seedlings germinated during the last 30 years and found at a radius of 15 m from each target tree.  $k_{m1}(r)$  was used to test if the height of recruits was shorter than expected, whereas the interactions of different age classes (adults, juveniles and seedlings) were tested by comparing their heights and



locations with the  $k_{m1m2}(r)$  function. The  $I_{m1m2}(r)$  function was used to investigate the impact of the height of adults on the density of recruits.

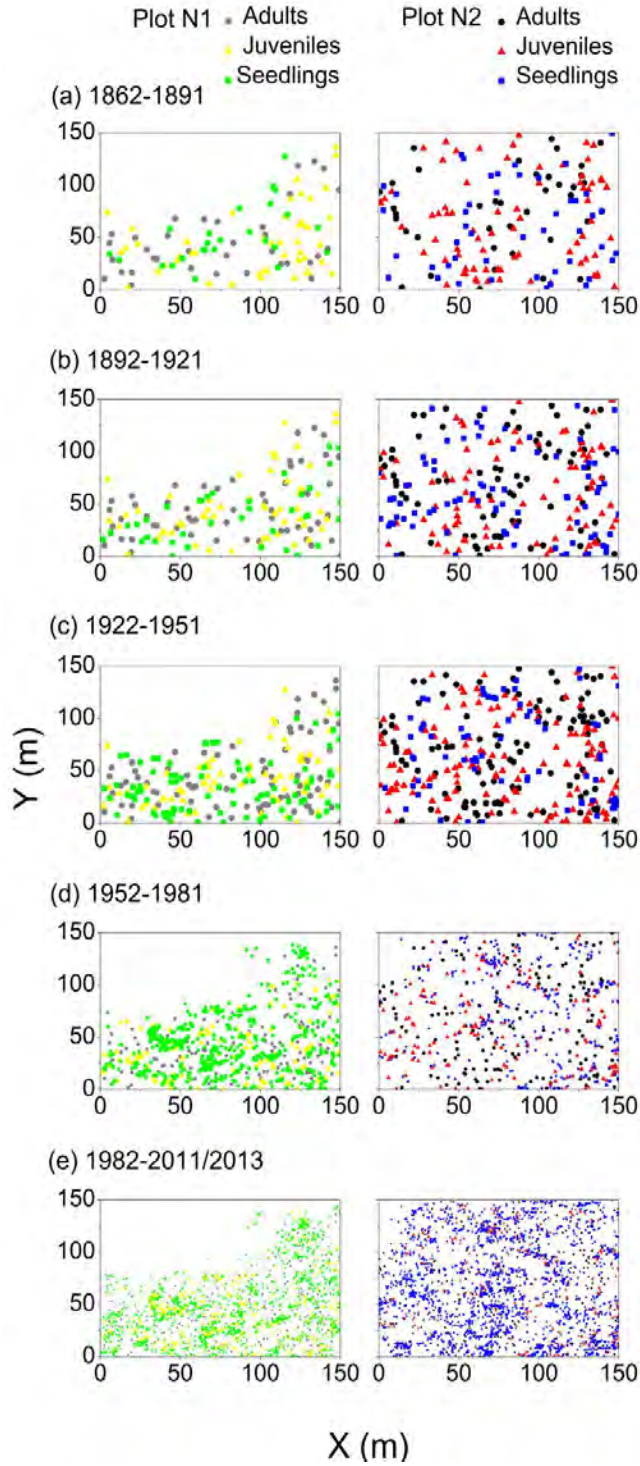


Figure S5. Spatial locations for three age classes (adults, juveniles and seedlings) within two treeline plots in the past 150 years (at each 30-year time interval).