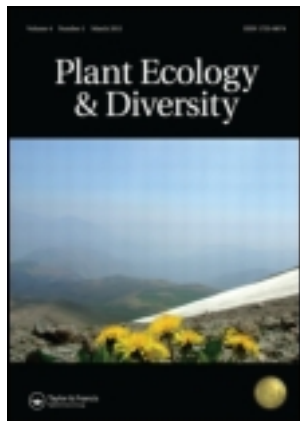


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RESEARCH ARTICLE

Spatial patterns of Smith fir alpine treelines on the south-eastern Tibetan Plateau support that contingent local conditions drive recent treeline patterns

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Background: Recent work has shown little change in the position of the Smith fir treeline on the south-eastern Tibetan Plateau in response to global warming. However, the relationship between tree distribution patterns within the treeline ecotone and low responsiveness is unknown, and additional constraints than climate might be major drivers of these patterns (e.g. microsite availability for regeneration).

Aims: To characterise the spatial patterns of Smith fir alpine treelines and to infer the underlying processes driving their dynamics.

Methods: We investigated spatial patterns of Smith fir trees across two treeline ecotones in the Sygera Mountains, south-eastern Tibetan Plateau. The $O(r)$ -ring statistic was used to analyse the univariate and bivariate spatial point patterns of three size classes (adults, juveniles and seedlings).

Results: Mature trees presented random spatial patterns. Clusters of juveniles and seedlings colonised areas not occupied by mature trees. Seedlings were clustered and established preferentially near juvenile firs, *Rhododendron* mats and over moss-lichen and organic matter substrates, indicating the importance of microsite availability for successful Smith fir recruitment.

Conclusions: Local factors such as microsite availability may play a major role in driving recent Smith fir treeline patterns and determine the lack of significant warming-induced upward shifts of these ecotones.

Keywords: *Abies georgei* var. *smithii*; microsite availability; O -ring statistic; recruitment; south-eastern Tibetan Plateau; spatial pattern; stand structure; treeline

Introduction

Spatial patterns in tree populations are essential for understanding forest structure and dynamics (e.g. Wiegand et al. 2007; Wang et al. 2010). To maximise the ecological information inferred from spatial patterns, precise hypotheses must be evaluated based on the use of adequate analyses (McIntire and Fajardo 2009; Chen et al. 2010). It is also necessary to consider the influence of alternative processes on the formation of spatial patterns at different tree life stages (Eichhorn 2011). For instance, aggregated patterns may arise because of distance-limited seed dispersal (Nathan and Muller-Landau 2000), micro-habitat heterogeneity (Webb and Peart 2000) and facilitation (Callaway 2007). On the contrary, mature trees across size/age classes tend to have random distributions mainly due to density-dependent mortality (Kenkel 1988).

Spatio-temporal patterns of tree populations may be used to infer alpine treeline dynamics (Camarero et al. 2000). The treeline ecotone is defined as a transitional area that separates the upper montane (subalpine) forest from alpine shrublands and grasslands, and including the timberline, treeline and tree species line (Holtmeier 2003; Körner 2003; Nagy and Grabherr 2009). However, the structure and spatial patterns of alpine treelines are largely

unknown in many mountains outside Europe and North America (Malanson 2001; Kullman 2007). In a recent review of treelines, about half of them did not advance upwards during the past century in response to global climate warming (Harsch et al. 2009). A better knowledge of contingent local conditions, such as the spatial pattern of trees, would increase our understanding of why treelines are not responding uniformly to climate warming.

In harsh environments, such as alpine treelines, clumping of recruits can be driven by facilitation and the microsite heterogeneity for tree establishment (e.g. understorey type and cover) (Humphries et al. 2008; Hofgaard et al. 2009; Harper et al. 2011). However, few studies have evaluated how the availability of substrate determines clumped recruitment (but see Batllori et al. 2009, 2010). Contingent local conditions may be essential for understanding the low responsiveness of some treelines to global climate warming (Camarero and Gutiérrez 2004).

The Tibetan Plateau holds the highest alpine treelines in the northern hemisphere (Miehe et al. 2007; Liang et al. 2012). As indicated by long-term tree-ring chronologies developed in the area (Liang et al. 2011b; Zhu et al. 2011), there has been a warming trend in winter and summer temperatures there since the 1820s. It would be expected that

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Tibetan alpine treelines shifted upward in response to rising air temperatures, as other ecological processes have responded to climate warming in the Himalayas (Song et al. 2004; Xu et al. 2009; Wang et al. 2011). The treelines have advanced upslope over the last century in the Hengduan Mountains, Northwest China (Baker and Moseley 2007; Wong et al. 2010), whereas in the Tianshan Mountains the spruce treeline has not shifted upwards during the past 200 years (Wang et al. 2006). On the Tibetan Plateau, the spruce (*Picea likiangensis* (Franch) Pritz var. *balfouriana* (Rehd. et Wils.) Hillier ex Slavina), fir (*Abies spectabilis* (D. Don) Spach) and juniper (*Juniperus przewalskii* Kom.) treelines showed also little change in their position and increasing tree density (Fang et al. 2009; Lv 2011; Gou et al. 2012; Lv and Zhang 2012). Our recent studies have shown that the treeline position of Smith fir (*Abies georgei* var. *smithii* (Viguie & Gaussen) W. C. Cheng & L. K. Fu) showed a little change, while the population density has been increasing significantly in the past 200 years on the south-eastern Tibetan Plateau (Liang et al. 2011b). Such diverse patterns demand better explanations for understanding the varied responses of treeline dynamics to the variability in regional climatic conditions. In this study, we studied the spatial patterns and recent dynamics of Smith fir alpine treelines in the Sygera Mountains, south-eastern Tibetan Plateau (Liang et al. 2009, 2010, 2011b) to assess potential drivers determining the response of treelines to climate warming.

The objectives of this study were (1) to assess the recruitment habitat (substrate, understorey and overstorey cover) of Smith fir at two treeline ecotones in the Sygera Mountains, south-eastern Tibetan Plateau; and (2) to quantify the spatial patterns of Smith firs of different size classes and their spatial associations using point pattern analyses. We hypothesised that Smith fir treeline populations were spatially aggregated at the seedling stage (clumping of seedlings), and that the spatial associations between seedlings and bigger size classes were mostly positive as expected under harsh environmental conditions, such as those experienced in treeline ecotones (Callaway 2007). Based on the relatively static patterns of Smith fir treeline described recently (Liang et al. 2011b), we expected that most recent recruitment episodes would be clustered. We hypothesised that contingent local conditions, such as facilitation or suitable local conditions, may be major drivers of the recent low responsiveness of Smith fir alpine treelines to climatic change.

Material and methods

Study area and species

The Sygera Mountains (29° 10'–30° 15' N, 93° 12'–95° 35' E) are located in the transition zone between semi-humid and humid climates in the south-eastern Tibetan Plateau. The meteorological station in Nyingchi (Linzi) (29° 34' N, 94° 28' E, 3000 m a.s.l.) recorded a mean total annual precipitation of 677 mm from 1961 to 2006, about 72% of which falls from June to September during

the monsoon season (Liang et al. 2009). Based on data from an automatic meteorological station at the treeline (4390 m a.s.l.) close to plot E (Figure 1), the warmest month was July (mean temperature of 7.9 ± 0.5 °C) with a maximum daily mean air temperature of 10.5 °C, and the coldest month was January (-7.1 ± 2.1 °C) with a mean minimum value of -14.3 °C from 2007 to 2009 (Liu et al. 2011). Annual total precipitation was around 871 mm (Liu and Luo 2011; Liu et al. 2011). If the growing season is defined as the period when the mean daily temperature is above 5 °C in spring and below 5 °C in autumn for at least five consecutive days, the mean temperature of the growing season was 6.8 ± 0.3 °C from 2007 to 2009 (Liang et al. 2011a; Liu et al. 2011). Climate data from the Nyingchi station showed significant increases in spring, summer and winter temperatures since the 1960s (Liang et al. 2009).

Smith fir treelines reach maximum elevations between 4250 and 4400 m in the south-eastern Tibetan Plateau, depending on topography (Xu 1995), whereas shrubs of *Rhododendron* species are dominant above 4400 m. Smith fir dominates most of the east- and north-facing subalpine forests in the study area (Xu 1995), where it grows from 3300–4400 m a.s.l. Growth rates of trees in the studied treelines are low compared with subalpine and montane Smith fir forests and mainly controlled by low summer minimum temperatures, as indicated by tree-ring width and annual shoot increment data (Liang et al. 2010; Wang et al. 2012). For instance, the mean ring width of adults in the studied forests at 4000–4200 m elevation is 1.40 ± 0.53 mm, whereas at 3550–3700 m (henceforth, lower elevation) is 4.16 ± 1.99 mm. Annual height growth in the treeline is about 6.9 cm year⁻¹, while at the lower elevation sites is 11.3 cm year⁻¹ (see Liang et al. 2009, 2010; Wang et al. 2012).

Field sampling

We selected two Smith fir alpine treeline ecotones including the treeline and the forest limit or timberline on east- (plot E) and north-facing (plot N) slopes (Figure 1(a), (b)), as reported by Liang et al. (2011b). The mean slopes of plots E and N were 15° and 10°, respectively. We found no evidence that the two investigated sites were recently disturbed by external factors, such as fire or local anthropogenic activities (logging, grazing) (Liang et al. 2009, 2011b). No browsed trees or remains of charcoal in the soil were found at either study site, and tree density decreased gradually upslope with a few isolated old trees located within the ecotone (Figure 1(b)). The lack of local anthropogenic use may be explained by the poor access to both sites, their remote location and the fact that no grassland areas are available for yak (*Bos grunniens* L.) grazing (Liang et al. 2011b). The soil is podzolic (an organic mat over a grey leached layer) with an average pH value of 4.5.

A rectangular plot (30 m × 150 m) was placed at each site in a topographically uniform area of the treeline ecotone, with the longer side of the plot located along the slope (Liang et al. 2011b). The current treeline and timberline

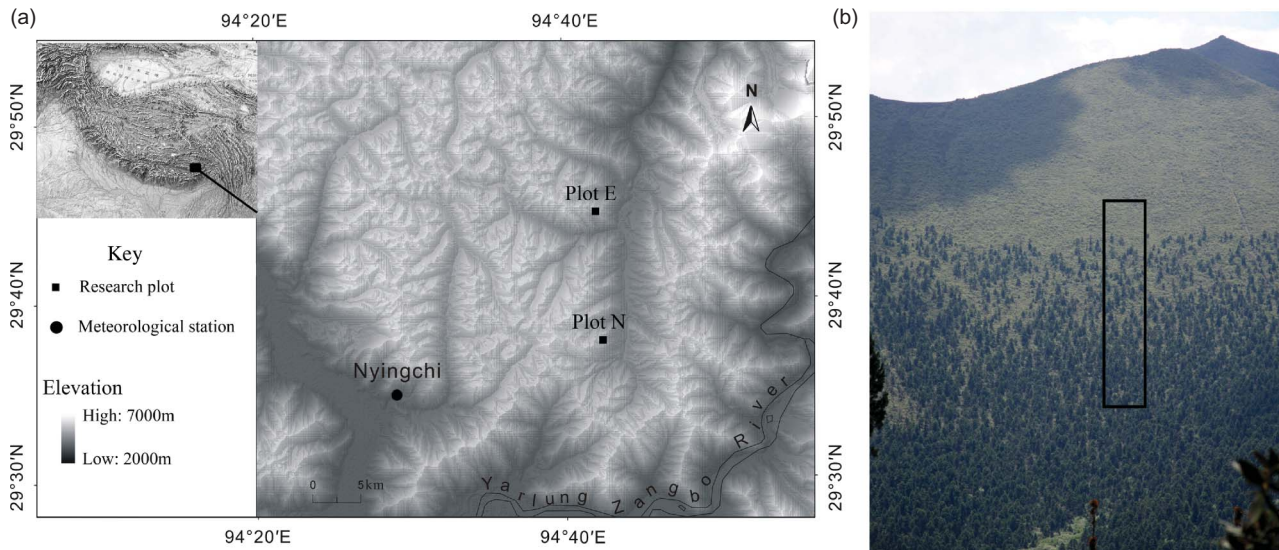


Figure 1. Location of the two study plots and the closest meteorological station (Nyingchi) in the Sygera Mountains, south-eastern Tibetan Plateau, the inset shows the location of the study area on the Tibetan Plateau (a); landscape view of the approximate location of plot N crossing a *Smith fir* treeline located at around 4420 m (rectangle, photograph taken by E. Liang) (b).

were included in each plot (Camarero and Gutierrez 2004). Point $(x, y) = (0, 0)$ was situated at the lower left corner facing upslope.

Several variables were measured for each *Smith fir* individual within both plots: coordinates of the main stem for each living *Smith fir* (x and y coordinates), diameter at breast height (DBH), measured at 1.3 m, tree height, the mean diameter of the vertical crown projections (two projections were measured along the x and y directions and they were averaged). Tree height was determined by using a measuring stick if the tree was lower than 2 m, and with a clinometer if the tree was taller than 2 m. The error of height measurement was ± 50 cm (Liang et al. 2011b). No gradient of tree height (e.g. decreasing height as elevation increases) was observed within the two investigated treeline ecotones. Trees in the upper parts were around 8 m and 12 m tall in plots E and N, respectively.

Since spatial pattern is dependent on tree size and age (Nanami et al. 2011), *Smith fir* individuals were classified into three groups according to their size: adults, DBH > 17.5 cm; juveniles, DBH ≤ 17.5 cm and $0.5 < \text{height} < 2.5$ m; seedlings, height ≤ 0.5 m. The DBH of 17.5 cm corresponds to a tree height more than 6 m and tree age of around 100 years, with trees having DBH > 17.5 cm showing canopy emergence (diameter around 3.5 m). No krummholz individuals were found in either plot. Dead individuals located within both plots were few.

To estimate tree age, one to two radial cores were taken at the stem base using a Pressler increment borer in those trees with DBH > 5 cm. We processed the wood samples following standard dendrochronological practices after air drying, sanding with successively finer sandpapers, and visual cross-dating of cores under a stereomicroscope (Cook and Kairiukstis 1990). No missing rings were detected (Liang et al. 2009). If the pith was absent from a core, a pith geometric locator was used to estimate the

distance missing up to the centre of the stem (Applequist 1958). The mean series intercorrelation was 0.61 and 0.59 at plots N and E, respectively, indicating a reliable cross-dating. Then, we established relationships between DBH and age for mature trees to obtain ages of decayed trees with rotten piths. A total of 58 and 75 individuals were aged by means of core extraction at the tree base in plots N and E, respectively. Despite the uncertainties associated with age determination by core extraction we used age data with yearly resolution throughout the study, given the successful cross-dating of samples. We estimated the age of seedlings and small juveniles in a non-destructive way by counting the number of internodes or branch whorls along their main stems. We did not include seedlings younger than 3 years because of their high mortality rates. We observed that the youngest seedlings showed very low survival rates (Y. Wang, pers. observ.) and that few of them became established, which precluded us from including them in our analyses.

The substrate-understorey and overstorey types were investigated using the point intercept method (Barbour et al. 1987). Six transects along the altitudinal y axis were placed to record substrate-understorey and overstorey types. Transects were located every 6 m, perpendicular to the slope, i.e. along the x axis ($x = 0, 6, 12, 18, 24$ and 30 m) going from the lower ($y = 0$, forest) to the upper edge of the plot ($y = 150$, above treeline) (Camarero and Gutierrez 2002). The main overstorey (*fir*, *gap*, *Rhododendron*) and understorey-substrate (bare soil, organic matter, rock, herbaceous and moss-lichen cover) types were calculated based on the number of contacts with a rod located every 1 m along the y axis. A total of 906 points were recorded in each plot. We assessed the differences in the distribution of the observed and the expected numbers of seedlings as a function of overstorey and substrate types in both study plots by using the G test

(Sokal and Rohlf 1995). The expected numbers of seedlings were the total number of observed recruits proportionally distributed according to the observed contacts of substrate-understorey and overstorey types. It should be mentioned that the G test provides an overall test of deviations from randomness, but does not explicitly indicate which drivers determine the observed patterns.

Point pattern analyses

Point pattern analyses include numerous statistical methods (Stoyan and Stoyan 1994), but the second-order Ripley $K(r)$ function has been among the most commonly used in plant and forest ecology (Ripley 1981). However, the Ripley $K(r)$ function presents a 'cumulative effect' which may distort the spatial analyses of point patterns showing intense interactions at small scales, such as the case of seedlings in forests (Wiegand and Moloney 2004). The latter authors proposed to use the $O(r)$ -ring statistic instead of the $K(r)$ function. The $O(r)$ statistic replaces the circles used for calculation of the $K(r)$ function by concentric rings, and it is based on the number of neighbouring points in a ring of radius r , therefore isolating specific distance classes. In addition, it is a scale-dependent probability density function with the interpretation of a neighbourhood density, being more intuitive than an accumulative measure as the $K(r)$ function (Wiegand and Moloney 2004). Since pattern heterogeneity is common in treeline ecotones (Camarero et al. 2000) we used the inhomogeneous version of the $O(r)$ statistic as proposed by Baddeley et al. (2000).

In this study, the univariate $O_{11}(r)$ statistic was used to investigate the spatial pattern of three different size classes of Smith fir treelines (adults, juveniles and seedlings), and the bivariate $O_{12}(r)$ statistic was used to characterise the spatial associations of pairs of those in the three different size classes. In the univariate case, we used a heterogeneous Poisson process as a null model corresponding to complete spatial randomness (CSR) to determine if the observed pattern of each size class was random, clumped or regular. The intensity function was based on a Kernel smoothing algorithm applied to tree density data, which involves the decision on an appropriate radius R of the moving window. To avoid edge effect, the bandwidth R (the scale of smoothing) should be greater than r (the maximum scale of analysis, being $r \leq 15$ m in our study case) (Wiegand and Moloney 2004). In our case, 20 or 30 m can be selected as appropriate R values (T. Wiegand, pers. comm.). Since similar outputs were obtained for $R = 20$ m or 30 m we focused on the results derived from $R = 20$ m. We compared the observed data with the upper or lower 99% bounds of the simulation envelopes based on 999 Monte Carlo simulations. If the calculated $O_{11}(r)$ was above or below the upper or lower confidence envelopes the pattern was significantly aggregated or regular at the analysed spatial scale.

In the bivariate case, we assumed that adults might affect smaller trees (juveniles, seedlings), but not vice versa. Thus we used an antecedent condition as the null model, which randomises the locations of the juveniles and

keeps the locations of the mature trees fixed (Wiegand and Moloney 2004). If the $O_{12}(r)$ statistic was above or below the upper or lower confidence envelopes, the pattern corresponded to significant positive or negative associations, respectively. Values of $O_{11}(r)$ and $O_{12}(r)$ falling within the confidence envelopes indicate no significant departure from CSR or independent spatial associations, respectively. The $O_{11}(r)$ and $O_{12}(r)$ were calculated at spatial scales (r) of 1 m up to half the shortest side of the plot (15 m), with a circle of radius equal to 20 m. The Programita software was used to perform the point pattern analyses (Wiegand and Moloney 2004).

Results

Size structure

In plots E and N, the small-diameter individuals (DBH = 0–10 cm) dominated the treeline and mid-size classes (DBH = 20–50 cm) contained few trees (Figure 2(a)). Most sampled trees were younger than 100 years (Figure 2(b)). Diameter distributions were approximately reverse J-shaped at both sites. Significant relationships were found between tree age and DBH in both sites (plot E, $R^2 = 0.78$, $n = 75$; plot N, $R^2 = 0.78$, $n = 58$; $P < 0.001$ in both cases), indicating that tree diameter was an appropriate variable for classifying Smith fir life stages in the treeline. Significant positive non-linear relationships were also found between DBH vs. crown diameter and tree height in both plots (Figure 3), indicating that changes in diameter corresponded well to changes of the vertical structure of Smith fir treelines.

Distribution of seedlings as a function of microsite type

Based on the point intercept method, the cover of Smith fir accounted for 14.2% and 13.9% of total cover in E and N plots, respectively. Most Smith fir seedlings established preferentially near *Rhododendron* shrubs and over moss-lichen and organic matter substrates in both plots (Table 1). More seedlings than expected were found beneath *Rhododendron* and fewer than expected in herbaceous vegetation.

Spatial patterns of tree size classes within the treeline

Most recent recruitment did not occur in the uppermost areas of the plots, and young and old trees were uniformly distributed along the altitudinal gradient in both studied plots (Figures 4 and 5). In both plots, the regressions of age distribution against the altitude had a non-significant correlation coefficient ($P > 0.05$). Therefore, tree age and its relative altitude within the plot were not significantly related.

The patterns of adults did not significantly differ from spatial randomness in the two plots, and those of juveniles showed significant aggregation from 1 m up to 7 m (Figures 5, 6a–b, 6d–e). Seedlings showed significant aggregation up to 6 m in plot E and up to 7 m in plot N (Figures 5, 6c, 6g).

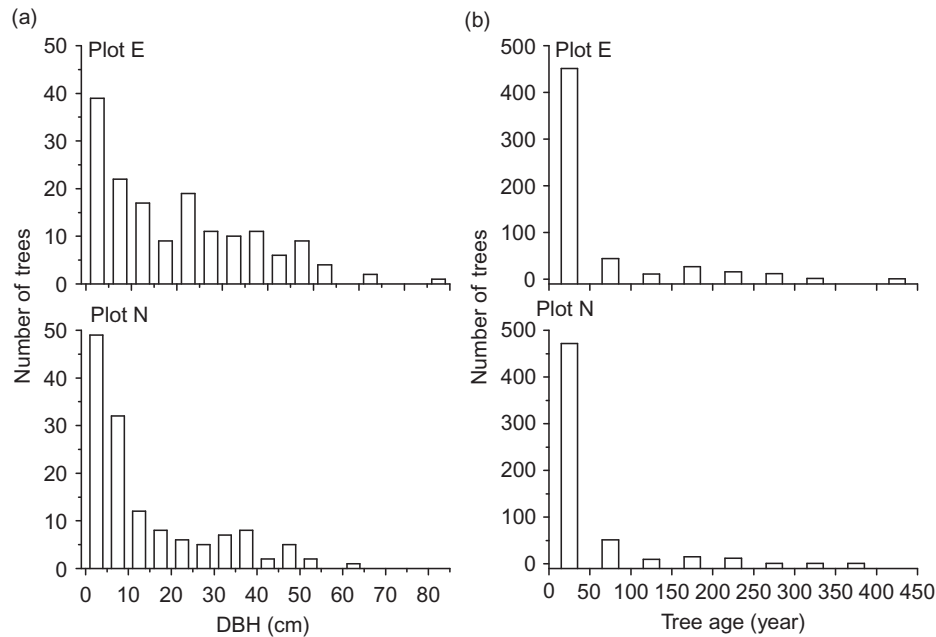


Figure 2. Distribution of diameter at breast height (DBH, 5 cm classes) (a) and ages (in 50-year classes) in plots E and N (b). The age structures were taken and modified from data presented in Liang et al. (2011b).

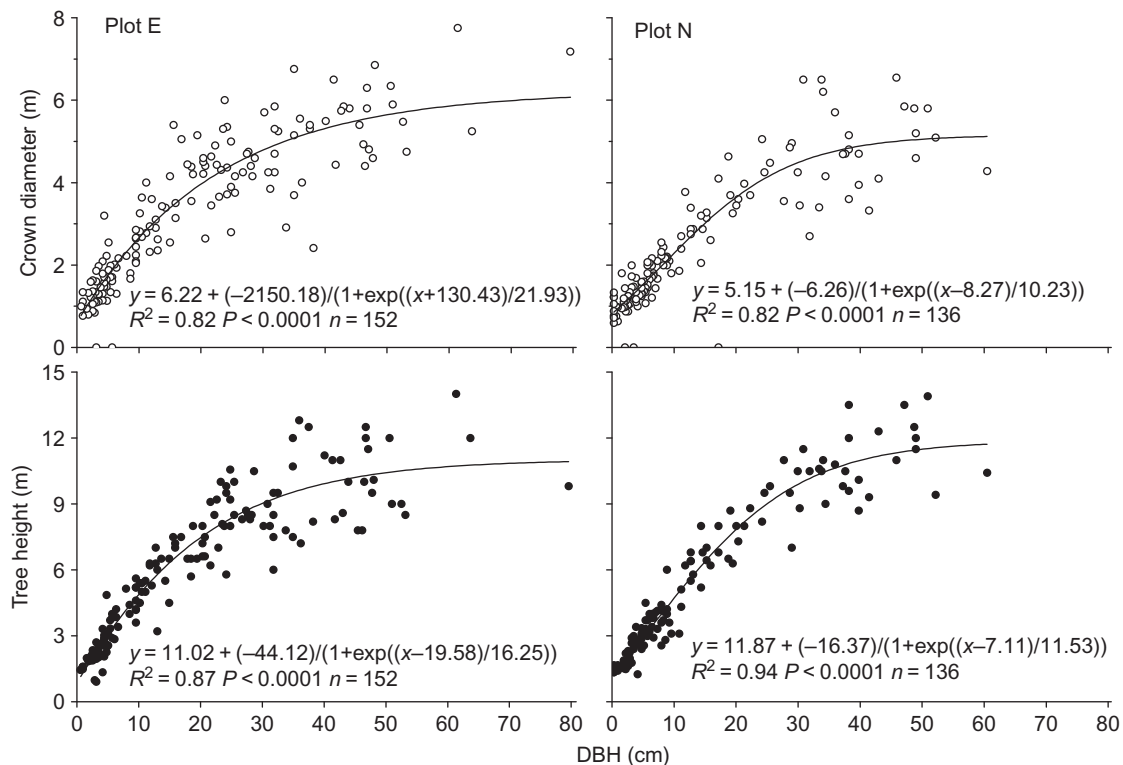


Figure 3. Non-linear relationships found between tree diameter at breast height (DBH) vs. crown diameter and tree height in plots E and N.

The pairs adults–juveniles and adults–seedlings in both plots showed significant negative associations at short distances up to 5 m (Figures 7a–b, 7d–e). Juveniles and seedlings presented significant positive associations up to 6 m and 7 m in plots E and N, respectively (Figures 7c, 7f).

Discussion

The recent increasing tree density observed at Smith fir treelines is characterised by the formation of seedling and juvenile clusters which colonise areas not occupied by adult trees. Density-dependent competition could be a factor in constraining Smith fir recruitment, as Caccia and Ballare

Table 1. Observed and expected frequencies of Smith fir seedlings as a function of different overstorey (fir, gap, near *Rhododendron* shrubs) and understorey-substrate (bare soil, organic matter, rocks, herbaceous vegetation and moss-lichen) types in plots E and N. The last column shows the G statistic and its corresponding significance level (P).

Plot	Level	understorey or overstorey type	Observed number of seedlings	Expected number of seedlings	$G(P)$
E	understorey-substrate ($n = 190$)	bare soil	3	4	61.0 (< 0.001)
		organic matter	34	23	
		rocks	8	11	
		herbaceous vegetation	5	57	
		moss-lichen	140	95	
	overstorey ($n = 189$)	fir	13	27	
gap	51	79			
		<i>Rhododendron</i>	125	83	
N	understorey-substrate ($n = 325$)	bare soil	3	13	72.2 (< 0.001)
		organic matter	91	49	
		rocks	15	19	
		herbaceous vegetation	8	65	
		moss-lichen	208	179	
	overstorey ($n = 324$)	fir	16	42	
gap	97	120			
		<i>Rhododendron</i>	211	162	

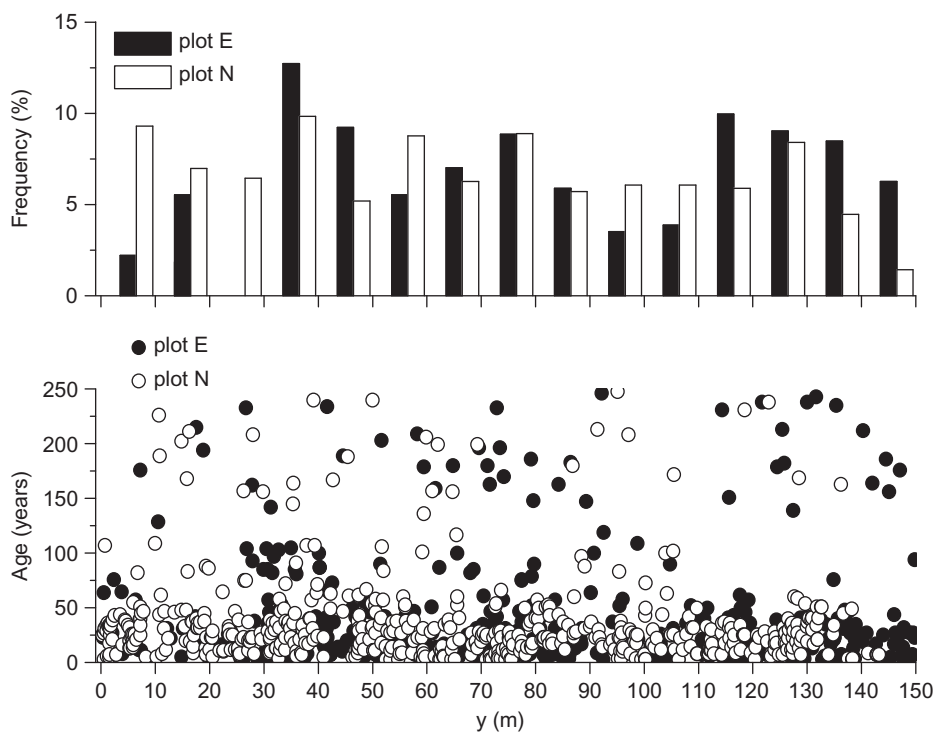


Figure 4. Relative frequency of all individuals along the altitudinal y axis in both studied plots (upper graph) and age-altitude relationships (lower graph). Increasing altitude corresponds to higher values along the y axis, i.e. including the Smith fir alpine treelines at 4360 m a.s.l. in Plot E and 4420 m a.s.l. in Plot N. $y = 0$, represents the bottom short side of a rectangular plot (30 m \times 150 m) that was placed at each site in a topographically uniform area of the treeline ecotone, with the longer side of the plot located along the slope; the current treeline and timberline were included in each plot.

(1998) showed for *Pseudotsuga menziesii* (Mirb.) Franco, whose established saplings reduced growth and survival of neighbouring conspecific seedlings. However, such a hypothesis cannot be tested with the available data since we did not include the youngest seedlings (1- to 2-year-old recruits) in the present study.

As expected, the spatial patterns of trees, even in harsh environments, such as alpine treelines, depended on

their growth stage, since seedlings and juveniles appeared clumped, whereas adult trees were randomly distributed. The latter result may be also biased due to the low number of adults located within the plots. Our findings do support the hypothesis that Smith fir treeline seedlings tend to cluster. Spatial patterns of Smith fir shift from the clumping of recruits towards the random distribution of mature and older trees, confirming that in later life stages

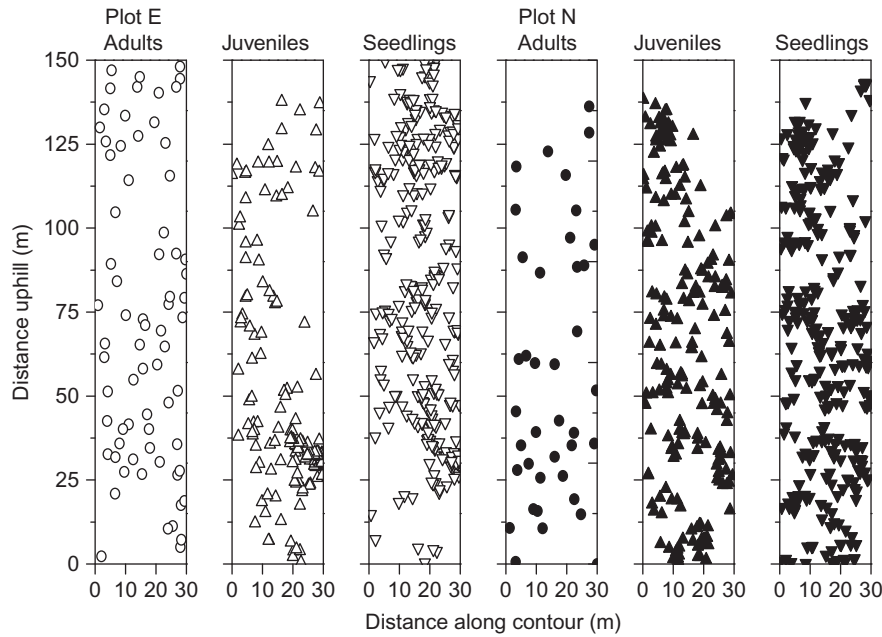


Figure 5. Spatial positions of sampled Smith fir trees within plots E and N. Individuals were grouped into three size classes (adults, juveniles and seedlings). Increasing altitude corresponds to higher values along the y axis. The number of individual is 556 in Plot E (adults = 70, juveniles = 160, seedlings = 326) and 562 in Plot N (adults = 39, juveniles = 218, seedlings = 305).

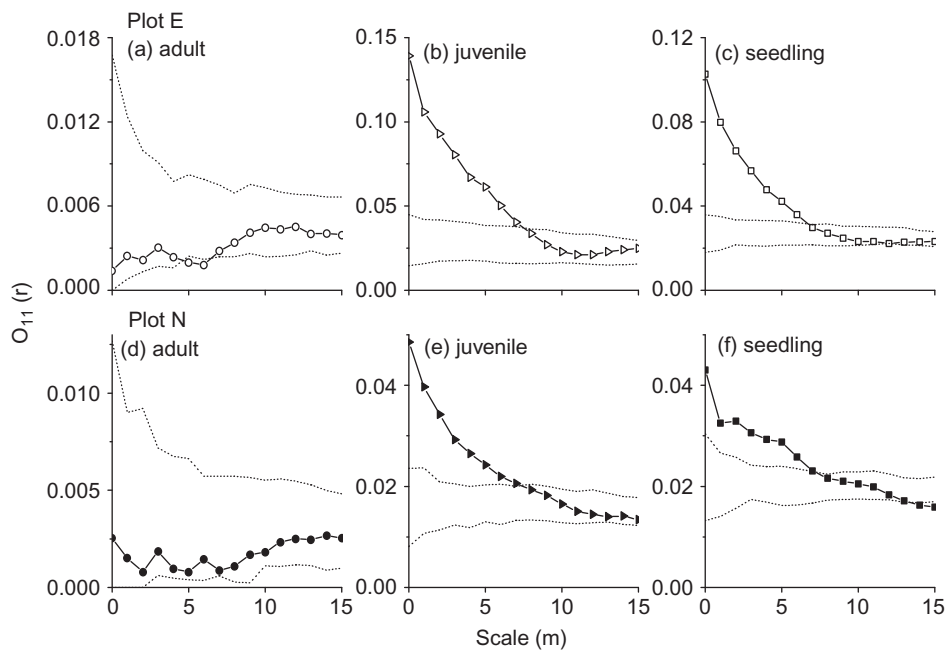


Figure 6. Univariate point pattern analyses for three size classes (adults, juveniles and seedlings) in plots E and N. Lines with symbols indicate the $O_{11}(r)$ -ring statistics, whereas thin lines correspond to the upper and lower 99% bounds of the simulation envelopes. Points above and below the upper and lower envelopes indicate significant aggregation and regularity, respectively. Graphs *a, b, c* represent adults, juveniles and seedlings in plot E, respectively. Graphs *d, e, f* represent adults, juveniles and seedlings in plot N, respectively.

competition may become a factor that contributes to shaping alpine treelines. This has been also observed in dense *Abies densa* Griff. - *Rhododendron hodgsonii* Hooker forests in Bhutan (Gratzer and Rai 2004). As shown in tropical rain forests, the spatio-temporal trend as trees grow is to occupy the available space and neighbours compete is a general pattern (He et al. 1997). The overall clustering of juveniles and seedlings in our study

agrees with the expected importance of facilitative mechanisms from neighbouring conspecific trees in stressful environments, such as alpine treelines (Bekker 2005; Callaway 2007; Zhang et al. 2009). Constraining climatic and abiotic factors of tree establishment and growth at the treeline encompass low air and soil temperatures, a short growing season, and soil instability due to freeze-thaw processes (Körner 2003). Such limiting factors

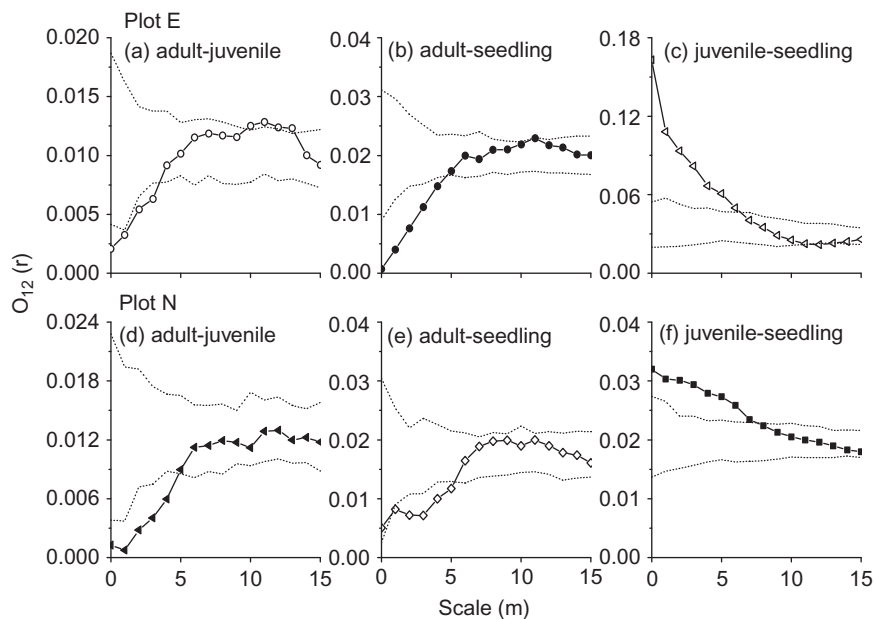


Figure 7. Bivariate point pattern analyses between the three different size classes (adults, juveniles and seedlings) at plots E (upper graphs) and N (lower graphs). Lines with symbols indicate the $O_{12}(r)$ -ring statistics, whereas thin lines correspond to the upper and lower 99% bounds of the simulation envelopes. Points above and below the upper and lower envelopes indicate significant positive and negative associations, respectively. Graphs *a*, *b*, *c* represent adult–juvenile, adult–seedling and juvenile–seedling pairs in plot E, respectively. Graphs *d*, *e*, *f* represent adult–juvenile, adult–seedling and juvenile–seedling pairs in plot N, respectively.

may be ameliorated through facilitating effects among neighbouring conspecific trees (Bekker 2005). Positive feedbacks may explain clustered patterns of recruits within alpine treeline ecotones because the establishment of a seedling in a favourable location, such as near *Rhododendron* mats in our case, or protected by microtopographical features at other alpine treelines (Resler 2006), may favour the establishment of further recruits. This idea is supported by the positive spatial associations observed between juveniles and seedlings in both plots. However, further field experiments are required to evaluate and to understand the actual role played by facilitation in treeline dynamics (see for instance Batllori et al. 2009).

Local microsite heterogeneity at both sites possibly contributed to the formation of the clumped groups of seedlings, as Getzin et al. (2008) and Chen et al. (2010) have claimed for other forests. However, the intensity of the clumping distribution of seedlings was stronger in plot E than in plot N, which is possibly related to a lower abundance of organic matter substrate types in the former (15%) than in the latter (30%). Smith fir seedlings were abundant over moss–lichen substrates, which suggest that bryophyte mats provide an excellent microsite for the establishment of seedlings as has been observed in similar Asian fir species (Sugita and Nagaike 2005). Most seedlings established near *Rhododendron* shrubs and near conspecific juveniles, which indicates that recruitment is mainly constrained to these particular sites. Gratzer et al. (2004) showed that an overstorey of *Abies densa* and an understorey of *R. hodgsonii* allowed enough radiation to reach seedlings and saplings of *Abies densa* for

their survival and persistence as seedling and sapling banks. This agrees with other studies in Himalayan *A. densa* - *R. hodgsonii* forests where the interspecific segregation between the two species increased with age, but was absent or weak among low plants with heights below 1 m (Gratzer and Rai 2004). In addition, moderate plant cover at the treelines may buffer seedlings from experiencing extremely low temperatures and sky exposure (Smith et al. 2003). However, *Rhododendron* shrubs dominate above the treeline, and their density and cover increase upslope, plausibly creating microsites that are too shady, unfavourable for the successful establishment of Smith fir seedlings. In fact, young Smith fir seedlings (1- to 2-year-old) beyond the current treeline were scarce. Further studies may also assess whether overstorey and understorey variables (cover, composition) are spatially coupled or not within the treeline ecotone.

The observed negative associations between Smith fir seedlings or juveniles and adults suggest that tree cover may prevent the growth of recruits by effectively reducing the radiation received by recruits (Canham et al. 1990), as has been observed in other alpine treelines (Hughes et al. 2009). In addition, seedlings also avoided gaps or microsites with bare soil, which may be linked to the formation there of deep snowpacks in winter, possible in concave microsites, preventing recruitment in spring. The lack of gradients characterised by decreasing tree height going upwards across the treeline ecotone in both investigated sites, i.e. the presence of abrupt changes in tree height near the treeline, could be a fingerprint of little change in the treeline position in the past decades (Liang et al. 2011b).

Recent recruitment patterns in the treeline may determine future changes in treeline dynamics and altitudinal position. However, recruitment is a complex process which depends on the interplay of multiple biotic and abiotic factors (Clark et al. 1998). In climatically harsh environments, such as alpine treelines, Smith fir treeline upward advances require abundant viable seeds but also available safe sites for seedling establishment (Batllori et al. 2009). Based on our observations, Smith fir recruits mainly establish near *Rhododendron* shrubs, but this shrubby species becomes dominant above the treeline where it may form microsites too shady for the establishment of Smith fir, thus preventing the uphill advance of the Smith fir treeline. Since the abundance of safe microsites was mainly created by suitable canopy cover, local microsite availability plays a more important role in driving recent treeline dynamics than regional climatic trends. In addition, a lack of disturbances which could enhance the opening of shady microsites above the treeline may also hamper the upward shift of similar alpine treelines (Liang et al. 2011b). Limited seed dispersal due to low-speed winds (mean velocity ca. 0.9 m s^{-1}) in the Sygera Mountains may be another important factor influencing the clustered patterns of seedlings and juveniles in both plots (Liang et al. 2011b; Liu et al. 2011). Altogether, similar, undisturbed alpine treelines may be much less responsive to climate warming in terms of upward shifts than previously expected.

Conclusions

The recent infilling of the Smith fir treeline ecotone was characterised by the intense clumping of abundant seedlings and random spatial patterns of adult trees, supporting our hypothesis. Smith fir seedlings established mainly on moss-lichen and organic matter substrates and near *Rhododendron* dwarf shrub is likely to constrain successful Smith fir recruitment above the treeline. As expected, the discordance between the minor changes in Smith fir treeline position and the pronounced regional climate warming might be explained by contingent local microsite availability, which seems to be essential for the successful recruitment of tree seedlings at alpine treelines. If local factors balance climate impacts for determining recent treeline dynamics, upward shifts of alpine treeline ecotones in response to global warming may be less widespread than previously expected.

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