



Fire facilitates warming-induced upward shifts of alpine treelines by altering interspecific interactions

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Abstract

Key message Moderate-severity fire disturbances can accelerate upslope shifts of alpine treelines by reducing interspecific interactions, providing additional evidence for the species interaction mechanism in controlling treeline dynamics.

Abstract Biotic interactions between trees and other plants may modulate the responses of alpine treelines to climate. Moderate disturbances could, therefore, accelerate upward shifts of alpine treelines as the climate warms by reducing the coverage of competitor plants and resetting interspecific interactions. Larch (*Larix potaninii* var. *macrocarpa*) treelines disturbed by fire on the southeastern Tibetan Plateau are good locales for testing this hypothesis. We characterized treelines in five large rectangular plots spanning undisturbed and fire-disturbed fir (*Abies georgei*) and larch treelines. The fires in the 1960s caused gaps in the reconstructed age structures of the larches during the 1970s but did not lead to downslope shifts in treeline position. Recruitment has instead increased since the 1980s within the disturbed larch treelines, with treelines shifting upward by 11–44 m. In contrast, the undisturbed larch and fir treeline positions remained mostly unchanged. We hypothesize that upslope shifts of alpine treelines are likely a consequence of climatic warming, but fire disturbances can accelerate these dynamics by altering interspecific interactions.

Keywords Climate change · Dendroecology · Fire disturbance · Interspecific competition · Tree recruitment · Treeline shift

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Introduction

The recruitment and position of alpine treelines are considered to be primarily thermally controlled (Körner 2012). In support of this hypothesis, global climatic warming has induced upward treeline encroachment and tree densification at some treeline ecotones (Camarero and Gutiérrez 2004; Chapin et al. 2005; Liang et al. 2011, 2016; Liu and Yin

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2013; Greenwood et al. 2014; Wang et al. 2016a). Many treelines globally, however, are relatively stable despite evidence of regional warming (Harsch et al. 2009). Different responses of regional treelines to warming result from variability of the local processes controlling population dynamics at particular treeline locations (Malanson et al. 2007; Gou et al. 2012; Kirilyanov et al. 2012; Case and Duncan 2014; Lyu et al. 2016; Camarero et al. 2017; Wang et al. 2017; Vitali et al. 2019). For example, regional warming promoted an upward shift of undisturbed spruce and fir treelines on the Tibetan Plateau, but their rates of upslope migration were controlled largely by interspecific interactions (Liang et al. 2016). We would, therefore, expect that upward shifts in treelines could be accelerated or decelerated if competition or facilitation was reduced by local disturbances.

As an important agent of disturbance (Swetnam and Betancourt 1990; Brown et al. 1999; Turner et al. 2016), fire can have a wide variety of impacts depending on the severity of the fire and the dynamics of the treeline communities involved (Stueve et al. 2009; Cansler et al. 2018). For example, highly severe fires can destroy vast areas of contiguous subalpine forests and depress alpine treelines, thereby overriding any positive effect of climatic warming on the dynamics of alpine treelines (Hemp 2005; Brown 2010). The roles played by fires of low to moderate severity in mediating alpine-treeline dynamics, however, are less clear, although some evidence suggests that moderately severe fires facilitate tree recruitment into arctic treeless areas by creating favorable microsites for regeneration where competitive plants have been removed (Certini 1993; Landhauser and Wein 1993; Lloyd and Fastie 2003). Few studies, to date, have determined how fire disturbances modulate the responses of alpine treelines to climate, even though fire-disturbed alpine treelines are found in several mountainous areas (Peñuelas and Boada 2003; Baker and Moseley 2007; Stueve et al. 2009; Aakala et al. 2014).

The Baima Snow Mountains on the southeastern Tibetan Plateau host larch (*Larix potaninii* var. *macrocarpa*) and fir (*Abies georgei*) treelines from 4300 to 4430 m a.s.l. Competition from dense alpine shrublands in these mountains near and above the treeline slows the upward movement of undisturbed treelines induced by warming (Liang et al. 2016). Photographs of landscapes have shown that historical fires have occurred at some treeline ecotones in the mountains (Baker and Moseley 2007). The presence of undisturbed and fire-disturbed treelines in these mountains provides a rare opportunity to investigate the role of fire disturbances in modulating the responses of treelines to climate.

In this study, we assessed and further identified the magnitude and drivers of treeline changes using annually resolved tree-ring records and inferred the mechanisms behind interspecific interactions. Specifically, we (1) reconstructed the spatiotemporal patterns of *L. potanini* var.

macrocarpa and *A. georgei* treelines in the Baima Snow Mountains using dendroecological methods, (2) dated recent fires by cross-dating trees killed by fire and (3) tested the hypothesis that fire disturbance facilitates upward shifts of alpine treelines induced by warming by reducing the coverage of plants near or above the treeline. If this hypothesis was confirmed, climate warming would further contribute to upward treeline advances by enhancing tree growth and recruitment but also by increasing fire incidence and altering plant–plant interactions exerted by alpine vegetation on tree recruits.

Materials and methods

Study region

The Baima Snow Mountains (27°25'–28°36'N, 98°47'–99°21'E) are located in the central Hengduan Mountains, southeastern Tibetan Plateau (Fig. 1). Based on climatic records near the study site (28°23'N, 99°01'E; 4293 m a.s.l.), July (mean monthly air temperature of 7.1 °C) and

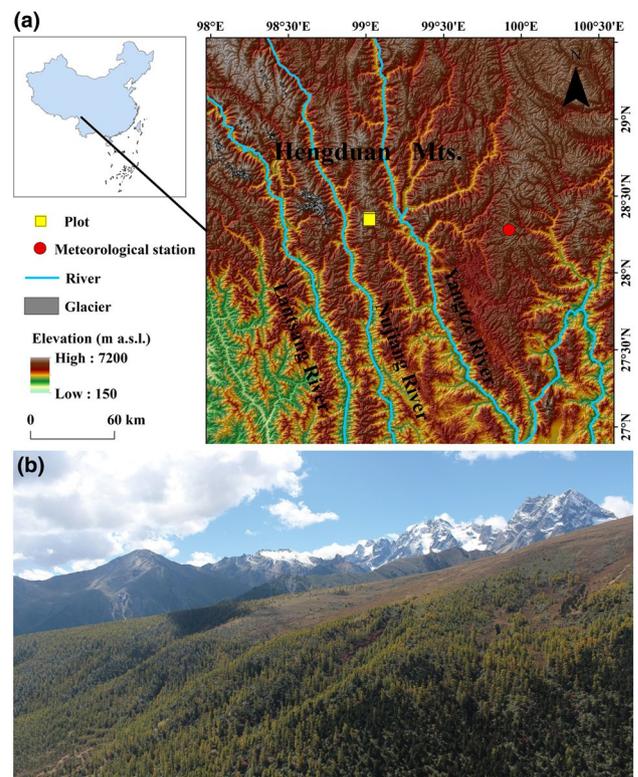


Fig. 1 Location of the Baima Snow Mountains on the southeastern Tibetan Plateau (a), larch (*Larix potaninii* var. *macrocarpa*) and fir (*Abies georgei*) treeline plots in the Baima Snow Mountains (photograph taken by Y. Wang, October 2014) (b). The yellow and green areas in the image correspond to larch and fir treelines, respectively

January ($-9.1\text{ }^{\circ}\text{C}$) are the warmest and coldest months, respectively (Li and Zhang 2010). The mean annual precipitation for 1981–2009 was 807 mm, about 70% of which fell during the monsoon season, i.e., from June to August (Li and Zhang 2010). Maximum wind speed varies from 3 to 5 m s^{-1} throughout the year. The soil is covered by snow (depth ca. 50–100 cm) mainly during winter. The meteorological station in Deqin county ($28^{\circ}29'\text{N}$, $99^{\circ}55'\text{E}$; 3485 m a.s.l.), about 30 km from the study area, recorded an increase of $2.4\text{ }^{\circ}\text{C}$ in summer mean temperatures during 1954–2013 ($r=0.75$, $P<0.001$), whereas annual or summer precipitation did not show a significant trend during the same period. Temperature reconstructions for the southeastern Tibetan Plateau based on tree rings have also identified significant warming trends in the region during the last 200 years (Zhu et al. 2011).

Research plots and sampling design

Conifer treeline plots were selected in the central Baima Snow Mountains. We defined the treelines and forest limits as the highest elevations where trees were at least 2 m tall and where tree cover was at least 30%, respectively (Holtmeier 2009). The treeline ecotone includes both boundaries. The dominant tree and shrub species in the central Baima Snow Mountains include larch (*L. potaninii* Batal. var. *macrocarpa* Cheng et Y. W. Law), fir (*Abies georgei* Orr) and a dwarf scrubland-heath complex consisting of several *Rhododendron* species (e.g., *R. phaeochrysum* Balf. f. et W. W. Smith, *R. rupicola* W. W. Smith var. *chryseum* (Balf. Et Ward) Philipson et Philipson, *R. nivale* Hook. f., *R. tapetiforme* Balf. f. et Ward and *R. yungningense* Balf.). Alpine meadows are the dominant vegetation type above 4500 m.

Larch and fir are the main treeline species in the Baima Snow Mountains. In recent years, larch and fir forests are protected by local government due to their limited distribution. Forests of these species grow along an altitudinal gradient from 3500 m to 4300 m and from 3500 to 4200 m a.s.l., respectively. The positions of the larch and fir treelines vary from 4300 to 4417 m and from 4200 to 4450 m,

respectively, due to the variable topography and landforms (Table 1). Wind-flagging trees or krummholzs were not observed at the larch and fir treeline. Tree individuals $<70\text{ cm}$ were absent above the larch or fir treelines.

Based on a meta-analysis using a global dataset of 166 treeline sites, there were no clear differences among plant families in their probability of treeline advance (Harsch et al. 2009). On the Tibetan Plateau, we did not find species-related treeline shift rates of four species (*Picea crassifolia*, *Picea likiangensis* var. *balfouriana*, *Abies georgei* var. *smithii*, and *Abies georgei*) in the last 100 years (Liang et al. 2016). In the central Himalayas, broadleaf and conifer tree species (*Betula utilis* and *Abies spectabilis*) also did not exhibit specific differences in their shift rates of alpine treelines (Sigdel et al. 2018). Therefore, treeline data are comparative among plant families.

A number of treelines on the Tibetan Plateau have been rarely disturbed by local human activities (Liang et al. 2011, 2016; Gou et al. 2012; Lyu et al. 2016). Based on weekly xylogenesis monitoring, minimum air temperature was the dominant climatic variable associated with xylem growth at such humid and cold treeline (Rossi et al. 2016; Li et al. 2017). Moreover, biotic competition can affect tree growth and regeneration and mediate their responses to climate change (Wang et al. 2016a; Liu et al. 2018). Larch seeds could be dispersed upslope by as much as 84–140 m in elevation from parent trees based on the occurrence of few larch seedlings above the current treeline (Table S1). As shown by a study on the southeastern Tibetan Plateau, fir seedlings were found 40 m higher above its treeline, implying that seed dispersal was not a constraint for treeline shift (Shen et al. 2014).

Some larch treelines in the study area (Fig. 1) have been affected previously by fire (likely human-caused), as indicated by the presence of dead trees and fire-scarred living trees (see more details in Baker and Moseley 2007). Trees killed by fire still had remnants of bark and sapwood on their stems, whereas scarred living trees had fire scars (“cat-faces”) at the stem base (Baker and Moseley 2007). No signs of fires, however, were found across the

Table 1 Description of the five study plots used to characterize treeline or timberline dynamics in the Baima Snow Mountains, southeastern Tibetan Plateau

Plot code	Size (m)	Tree species	Lat (N)	Lon (E)	ECT (m)	Slope ($^{\circ}$)	FD	No
E1	30×500	<i>Larix potaninii</i> var. <i>macrocarpa</i>	28°21.308'	99°01.349'	4359	5	Yes	163
NE1	30×280	<i>Larix potaninii</i> var. <i>macrocarpa</i>	28°21.374'	99°01.494''	4417	19	Yes	544
NE2	30×270	<i>Larix potaninii</i> var. <i>macrocarpa</i>	28°21.557'	99°01.239'	4387	19	Yes	323
NE3	30×200	<i>Abies georgei</i>	28°20.955'	99°01.912'	4247	25	No	1295
N1	30×200	<i>Larix potaninii</i> var. <i>macrocarpa</i>	28°20.899'	99°01.767'	4305	21	No	188

Plot codes, plot size (Size), latitude (Lat), Longitude (Lon), elevation of current treeline (ECT), slope, fire disturbance (FD), tree density (No, number of trees per hectare) are shown in the table

fir treeline ecotone during field observations from May 2013 to October 2014.

Five treeline sites (one fir and four larch sites) on different topographical conditions were selected in the Baima Snow Mountains (Table 1). The five sites were 1–5 km apart from each other. Rectangular plots with size 30 m × 200 m (2 plots), 30 m × 270 m, 30 m × 280 m and 30 m × 500 m were established on topographically uniform areas across treeline ecotones and included the current treelines and forest limits. These plots just crossed the forest limits and extended 1–34 m above the current treelines. These treeline plots were surveyed following the methods of previous treeline studies on the Tibetan Plateau (Liang et al. 2011, 2016; Wang et al. 2016b). The longest side (*y*-axis) of each plot was set parallel to the steepest slope (i.e., following the altitudinal gradient), and the origin (*x*, *y*) = (0, 0) was located in its bottom left corner. The elevations of the lower and upper parts of the plots were determined using a GPS calibrated with a barometric altimeter (Cook and Kairiukstis 1990). The location of each visible tree individual within the plot was mapped (± 0.1 m) using *x*–*y* coordinates relative to the plot origin. Other biometric parameters measured and recorded for each tree included: DBH (diameter at breast height, measured at 1.3 m aboveground), tree height, and diameter of the tree canopy horizontally projected along the *x* and *y* axes. Tree height was determined with a measuring stick for trees ≤ 2 m (± 0.01 m), or a clinometer for trees > 2 m (± 0.1 m) (Duncan 1989).

Samples with height > 2.5 m were taken from all recorded trees using an increment borer. Ages of trees > 2.5 m were determined using standard dendrochronological methods after air drying cores, sanding them with successively finer sandpapers, and visually cross-dating them under a stereomicroscope (Liang et al. 2011). If the pith was absent in a core, a pith geometric locator was employed to estimate the distance missing up to the center of the stem (Duncan 1989). The mean series intercorrelation varied from 0.58 to 0.62, indicating a robust cross-dating of annual ring-width series in the five study plots (see also the results in Wang et al. 2012).

The age structure of the trees was obtained by combining several methods. The ages of seedlings (height ≤ 0.5 m) and juveniles (0.5 m $<$ height ≤ 2.5 m) were non-destructively determined in the field by counting the branch whorls along the main stem (Camarero and Gutiérrez 2004). We randomly collected stem disks from 30 seedlings located immediately outside the study plots and also counted the bud scars for these seedlings. The ages of seedlings obtained from counting the internodes (CI) and the rings of stem disks (CR) were significantly correlated ($CI = 0.76 * CR + 2.42$; $r = 0.77$, $P < 0.0001$, $n = 30$) and reliable for determining tree age (Aakala et al. 2014), although counting the bud scars underestimated the true seedling age by as much as

1–4 years (Figure S1). Raw age data were used in the analysis because of such tiny differences.

We determined the age of 150 larch individuals and 30 fir individuals at or near the treelines, respectively, by counting the internodes to obtain accurate estimates of tree ages in the two height classes (1.3–2.5 and ≥ 2.5 m). The larch and fir trees required averages of 18 ± 2 ($n = 150$) and 33 ± 5 ($n = 30$) years to reach 2 m in height, respectively. As suggested by previous treeline studies (Camarero and Gutiérrez 2004; Liang et al. 2011, 2016), we assumed that a seedling required the same time (18 and 33 years for larch and fir treelines, respectively) to reach 2 m during the past and current climatic conditions. Mean DBH and tree height varied among the five treeline plots (Figure S2).

Fire-scarred living or dead trees were found in the three of the larch plots (E1, NE1 and NE2) but not in the NE3 and N1 plots. The alpha-numeric codes correspond to treeline plots located on different slope aspects. For instance, E1 represents one plot on east-facing slope. We estimated the years of fires in the E1, NE1 and NE2 plots by collecting 34 cores 1.3 m above the ground from 17 trees killed by fire. We also collected 30 cores from mature living trees near the undisturbed larch forest limits. The sampled dead trees had retained the main stem bark and sapwood, so the year of a recent fire was identified by cross-dating the tree-ring samples from the living trees at the undisturbed larch treelines with those from the dead trees at the fire-disturbed larch treelines.

Treeline position was defined where erect trees had a minimum height of 2 m at the uppermost elevation within each plot (Camarero and Gutiérrez 2004; Liang et al. 2011). The treeline position at 50-year intervals was reconstructed by calculating the years required for trees to reach 2 m in height (Liang et al. 2011). The 4-year error associated with age estimation for trees 2 m tall was negligible for the time scales of 50 years used in the reconstructions of the treeline dynamics reported here.

The mean height and canopy cover of dominant vegetation above the treeline were surveyed as described by our previous treeline study (Liang et al. 2016). Along the elevational (*y*) axis of each treeline plot, six line-transects were established from the upper treeline to 20 m above the treeline. Transects were spaced 6-m apart perpendicular to the slope: that is, along the axis perpendicular to the maximum slope (*x* axis) at 0, 6, 12, 18, 24, and 30 m. Percent vegetation cover was calculated based on the number of contacts between plants and a rod located every meter along the elevational axis, and the height of the vegetation in each treeline plot was calculated as the mean height of the vegetation at each sample point. A total of 126 points were recorded above the treeline for each plot. Such line-transects were set up in each study site. Based on field observations, shrubs were dominant plants below and above the treeline. Since

shrub height and cover varied little with elevation below the treeline, thus plant–plant interactions might play non-dominant roles in accounting for the infilling (increased tree density) below the treeline. The thickness index (TI), an ecological indicator of interspecific interaction, is defined as the product of alpine shrub cover above the treeline multiplied by mean shrub height (Liang et al. 2016). Specifically, TIs < 0.8 and > 0.8 represent facilitation from short shrubs and competition from tall shrubs, respectively (Liang et al. 2016).

Methods

Surviving trees are likely to grow very slowly in the year after crown-damaging fires (Brown et al. 1999), so we identified the year in which growth rates were suppressed and assumed that was when the historical fire occurred. We used *t* tests to compare the mean post-fire tree-ring widths of living and fire-killed trees in the final years (e.g., 1969, 1970, 1971) to determine when growth was suppressed. Very narrow rings in some years usually indicated the presence of disturbance (Liang et al. 2015). Samples from fire-scarred living trees were also used to determine the years of the fires. The ages of 30 randomly selected young trees near or around the fire-scarred trees within three burned plots and probably recruited after the fire was estimated by counting their bud scars.

Climatic records for the study area are available only from the 1950s onwards, so temperature reconstructions based on independent dendrochronological proxies were used to evaluate the long-term impact of climate on changes in recruitment. We used the series for summer mean minimum temperatures derived from a chronology of tree-ring widths for Balfour spruce (*Picea likiangensis* (Franch.) Pritz. var. *balfouriana* (Rehd. et Wils.) Hill. ex Slavin) developed on the southeastern Tibetan Plateau (Zhu et al. 2011). The data for reconstructed temperatures indicated a substantial warming trend in the last 200 years ($P < 0.01$, slope of linear fit: 0.012) (Zhu et al. 2011).

Age structure of living trees represents the trade-off between the net results of recruitment and mortality through time (Camarero and Gutiérrez 2004; Liang et al. 2011; Wang et al. 2016a). Since recruitment rate of trees is mainly limited by low temperature at undisturbed treelines (Liang et al. 2016; Wang et al. 2016a), it is reasonable to assume that expanding population structure appears under climate warming, and vice versa. In this study, the recruitment history reconstructed by age structure was consistent with the repeated landscape photography at *Larix* treelines in the Baima Snow Mountains located within our study region (Baker and Moseley 2007). Therefore, we used

the reconstructed age structure at treeline plots to discuss changes in tree recruitment through time.

Post-fire and pre-fire tree recruitment data in the three fire-disturbed larch plots were compared to determine the effect of fire disturbance on the pattern of tree recruitment at treeline ecotones. Post-fire recruitments for these plots were then compared with those of the undisturbed larch and fir treeline plots. The two-sample Kolmogorov–Smirnov (K–S) test was used to test if the distribution of recruitment series differed significantly between all pairs of plots.

We used a sequential algorithm developed by Rodionov (2004) and described by Elliott (2012) to detect abrupt changes in the reconstructed patterns of tree establishment. This is a data-driven approach in which an a priori hypothesis on the timing of regime shifts is not needed and sequential *t* tests are performed on time-series data to detect regime shift changes (Rodionov 2004). An abrupt change was identified if the cumulative sum of normalized deviations from the mean of a potentially new pattern of establishment differed significantly from the mean of the previous pattern of establishment episodes (Elliott 2012). A significance level of 0.05 and a 7-year cut length were used to test for shifts in the means of the time series of the recruited trees. The analyses of abrupt changes used the STARS program (Rodionov 2004). Such a method has been used to analyze abrupt changes in the recruitment data at treelines in the Rocky Mountains, USA (Elliott 2012).

Results

Fire-induced changes in tree growth were compared to determine fire events at the treelines. The maximum and mean lengths of the series of tree-ring widths were 249 and 132 years, respectively. The series of fire-killed trees was cross-dated with series of living trees, with average inter-series correlation of 0.63 ($P < 0.001$). The year of the outer ring in the trees killed by fire varied from 1969 to 1971. The mean tree-ring widths of the dead trees in 1969, 1970 and 1971 were significantly narrower than those of the surviving trees ($P < 0.05$ for 1969, 1970 and 1971; $n = 30$ trees). A very narrow ring formed in 1969 was consistently observed in the dead trees (Fig. 2). Fire scars in the surviving larch trees were also dated from 1969 to 1971. Thus, the three years with narrow tree rings represent the impacts of fire on the individual tree.

Age structures and recruitment dynamics vary as functions of climate and fire. The estimated year of the fire in the late 1960s (Fig. 2) coincided with the absence of recruits in the NE2 plots and a much reduced tree establishment in the E1 and NE1 plots during the 1970s (Fig. 3b, c, d). Young trees recruited since the 1990s accounted for the largest proportion of the treeline populations (Fig. 3) and had an

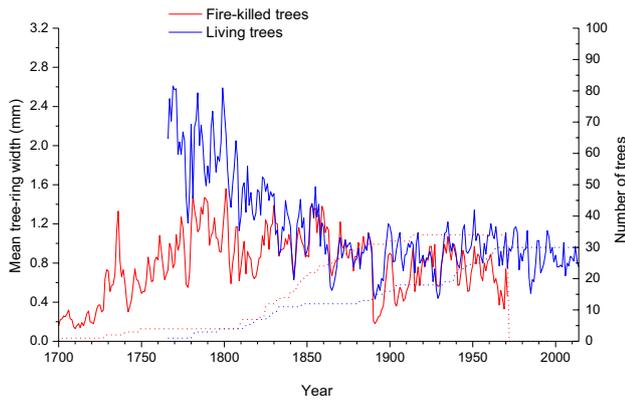


Fig. 2 Growth patterns for living (blue lines) and fire-killed (red lines) larch trees forming the treeline. The dotted lines show the numbers of living and fire-killed trees, respectively

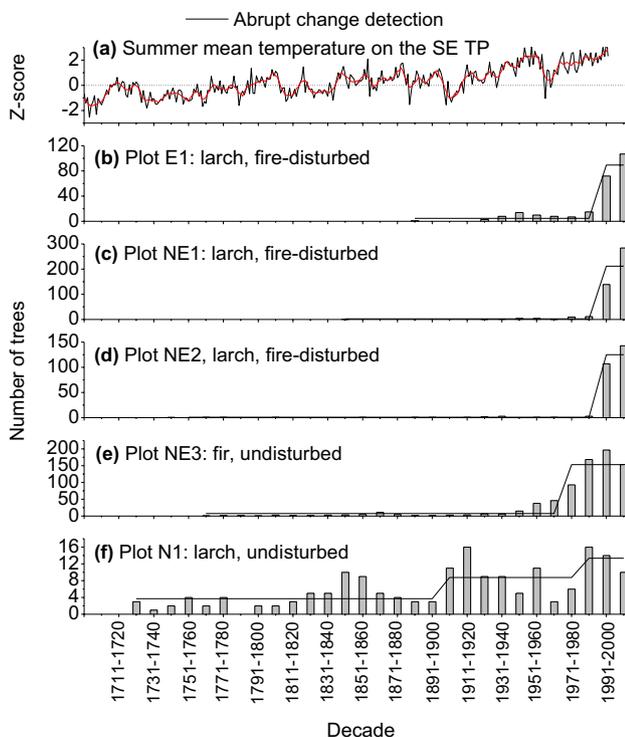


Fig. 3 Long-term changes in summer temperature and abrupt changes in tree recruitment at the treeline. Temperature series was reconstructed from tree rings on the southeastern Tibetan Plateau (SE TP) (Zhu et al. 2011) (a). Analyses of data for abrupt changes (black horizontal lines) in tree recruitment reconstructed for the treelines (b–f). Shifts were detected in the 1990s (b–d), 1970s (e), 1900s and 1980s (f), corresponding to abrupt increases in tree recruitment. All study plots correspond to larch treelines, except the NE3 plot which was located at a fir treeline

approximately reverse J-shaped age structure. Recruitment pulses in the undisturbed larch N1 plot and fir NE3 plot were characterized by wave-like patterns and rapidly rising

trends, respectively (Fig. 3e, f). Tree recruitment in the three fire-disturbed larch plot pairs (E1 vs. NE1, E1 vs. NE2 or NE1 vs. NE2) or two undisturbed plot pairs (NE3 vs. N1) did not differ significantly ($P > 0.05$, K–S tests) (Table 2). In contrast, tree recruitment between the fire-disturbed and undisturbed larch/fir plots differed significantly ($P < 0.05$, K–S tests on E1 vs. N1/NE3, NE1 vs. N1/NE3 and NE2 vs. N1/NE3) (Table 2). Regardless of the local site conditions, recruitment has increased in recent decades for the five study plots (Fig. 3b–f) and was positively correlated with reconstructed summer temperatures on the southeastern Tibetan Plateau (Fig. 3a) (plot E1: $r = 0.59$, $n = 8$; plot N1: $r = 0.57$, $n = 32$; plot NE1: $r = 0.56$, $n = 16$; plot NE2: $r = 0.44$, $n = 26$; plot NE3: $r = 0.71$, $n = 24$; $P < 0.05$ for all plots except E1; see also Fig. 3).

Abrupt changes in recruitment were detected within treeline plots. Tree establishment increased abruptly in the 1990s within the three fire-disturbed plots (E1, NE1 and NE2; see Fig. 3b–d). Recruitment also increased abruptly in the 1970s in the undisturbed fir NE3 plot (Fig. 3e) and in the 1980s in the undisturbed larch N1 plot (Fig. 3f). An abrupt change in recruitment in the 1900s was also detected in the N1 plot (Fig. 3f).

Based on population age structure in the investigated treeline plots, we reconstructed treeline elevation based on the presence of the tallest trees (≥ 2 m) at a 50-year interval. The treelines in the undisturbed larch (N1) and fir (NE3) plots advanced 0 and 2 m in elevation during the last 50 years but advanced 4 and 2 m in elevation during the last 100 years, respectively (Table 3; Fig. 4a, b). The larch treeline plots (E1, NE1, NE2) contained some fire-induced dead trees, but the fire did not cause a downslope shift of the treelines (Table 3; Fig. 4c–e). Densification mainly occurred above the post-fire treeline. The fire-disturbed larch treeline in the E1, NE1 and NE2 plots advanced 11 m, 44 m and 22 m

Table 2 Significance levels of two-sample Kolmogorov–Smirnov (K–S) tests showing the differences between recruitment series within the five study plots

Recruitment data of plot pairs	Significance level of the K–S test (p)	Disturbance regimes
E1 vs. NE1	0.576	Fire-disturbed vs. fire-disturbed
E1 vs. NE2	0.099	Fire-disturbed vs. fire-disturbed
NE1 vs. NE2	0.517	Fire-disturbed vs. fire-disturbed
E1 vs. N1	0.0041	Fire-disturbed vs. undisturbed
E1 vs. NE3	0.0011	Fire-disturbed vs. undisturbed
NE1 vs. N1	0.0032	Fire-disturbed vs. undisturbed
NE1 vs. NE3	0.0003	Fire-disturbed vs. undisturbed
NE2 vs. N1	0.0019	Fire-disturbed vs. undisturbed
NE2 vs. NE3	0.0041	Fire-disturbed vs. undisturbed
NE3 vs. N1	0.586	Undisturbed vs. undisturbed

Table 3 Comparisons between treeline shifts during the three periods (1980–2014 vs. 1961–2014 and 1980–2014 vs. 1911–2014)

Treeline plot	Tree species and fire disturbance	Shrub height (m)	Shrub cover (%)	TI	Magnitude of treeline shift (m a.s.l.)			Percentage (%)
					1911–2014	1961–2014	1980–2014	
E1	Larch, disturbed	0.45 ± 0.07	90 ± 3.8	0.41	Unknown	12	11	91.7, unknown
NE1	Larch, disturbed	0.30 ± 0.06	75 ± 7.2	0.23	Unknown	44	44	100, unknown
NE2	Larch, disturbed	0.75 ± 0.07	89 ± 5.1	0.67	22	22	22	100, 100
NE3	fir, undisturbed	2.2 ± 0.29	85 ± 3.8	1.87	2	2	0	NA, NA
N1	Larch, undisturbed	2.0 ± 0.26	82 ± 6.5	1.64	4	0	0	NA, NA

(see more details in Liang et al. 2016). Periods without trees are shown as “unknown”

The percentages were calculated by dividing the treeline shifts inferred for 1980–2014 and 1961–2014 or 1911–2014, respectively. The vegetation thickness index (TI, plant height × cover) was used to indicate the species interactions beyond the treeline. Shrub height and cover above the treeline (Shrub height, Shrub cover; mean ± SD) were used in the table

in elevation in the last 50 years, respectively, and the larch treeline in plot NE2 shifted upward by 22 m in elevation in the last 100 years (Table 3; Fig. 4). The fire-disturbed treelines have advanced by 11–44 m in elevation since the 1980s (Table 3; Fig. 4). The magnitude of advancement of fire-disturbed larch treelines since 1980 constituted 91.7–100% of the treeline advance during the last 50 and 100 years (Table 3). In particular, the treeline in the NE2 plot during the last 100 years advanced only after the fire disturbance.

Coverage of alpine shrubs above the treeline was related to fire occurrence. Tall *Rhododendron* shrubs dominated the undisturbed treelines (N1 and NE3), with TIs of 1.64 and 1.87, respectively (Table 3). In contrast, short *Rhododendron* shrubs dominated the fire-disturbed treelines, with TIs ranging from 0.23 to 0.67 (Table 3).

Discussion

The warming in the last century is unprecedented over the last 1000 years on the Tibetan Plateau (Liu et al. 2005; Bräuning 2006; Thompson et al. 2006; Zhu et al. 2008). Global warming is expected to have considerable effects on species' range limit such as alpine treelines, where tree growth is primarily limited by low temperatures (Fang et al. 2009; Liu et al. 2009; Yang et al. 2009; Zhu et al. 2011). However, climate warming is only one aspect of environmental change that could alter the structure and position of treelines (Carrer and Urbinati 2006; Batllori and Gutiérrez 2008; Liang and Camarero 2018). Apart from climate, other factors such as fire disturbance could buffer or amplify warming impacts on treeline dynamics locally (Aakala et al. 2014). Given a wide occurrence of fire disturbance in subalpine forests (Yao et al. 2017; Waito et al. 2018), it is important to investigate how fire disturbances mediate the responses of treelines to climate warming.

We found that treeline dynamics were jointly driven by fire and climatic warming. At least one fire in the late 1960s

drastically affected tree recruitment at the treeline. The lack of tree establishment in fire-disturbed larch treelines during the 1970s could be attributed to the adverse effect of a recent fire, given that the favorable warming conditions since the 1950s on the Tibetan Plateau are generally linked to increased tree growth and recruitment (Liu et al. 2009; Yang et al. 2009; Liang et al. 2011, 2016; Zhu et al. 2011; Chen et al. 2016; Wang et al. 2016a). The initial decrease in recruitment during the first 10 years after the fire could have been due to damage to tree crowns and reduced seed production or to the lack of facilitation from short shrubs which could become sparse after fire disturbance. As a control, a larger episode of recruitment in the 1970s was detected at the undisturbed larch and fir treelines, providing indirect evidence for this hypothesis. Recruitment at fire-disturbed sites, however, increased in the 1980s and increased abruptly in the 1990s, suggesting a major acceleration in recruitment relative to the unburned sites, which remained stable. This finding indicates that disturbances play a pivotal role in mediating the responses of treelines to climatic warming (Aakala et al. 2014), as they do in forests (Turner et al. 2016). Young larch trees ranging in age from 20 to 30 years were found near or around the fire-scarred trees across the treeline ecotones, providing evidence that post-fire tree establishment appeared between 1980s and 1990s. This pattern suggests that a post-fire recruitment release took place from the 1980s onwards, which would have allowed for the growth of post-fire recruited seedlings and them reaching heights ≥ 2 m in recent decades.

Climatic warming may have a larger impact on the density than the position of undisturbed fir treelines, whereas nearby fire-disturbed treelines have advanced substantially in the last century. A lack of disturbance may thus be responsible for the apparent fir-treeline stability, despite the trends of increasing temperature. Infilling refers to increase of tree individuals with any size (e.g., height > 1 cm) across the treeline ecotone, while treeline advance means that trees > 2 m appear beyond the current treeline. Based on

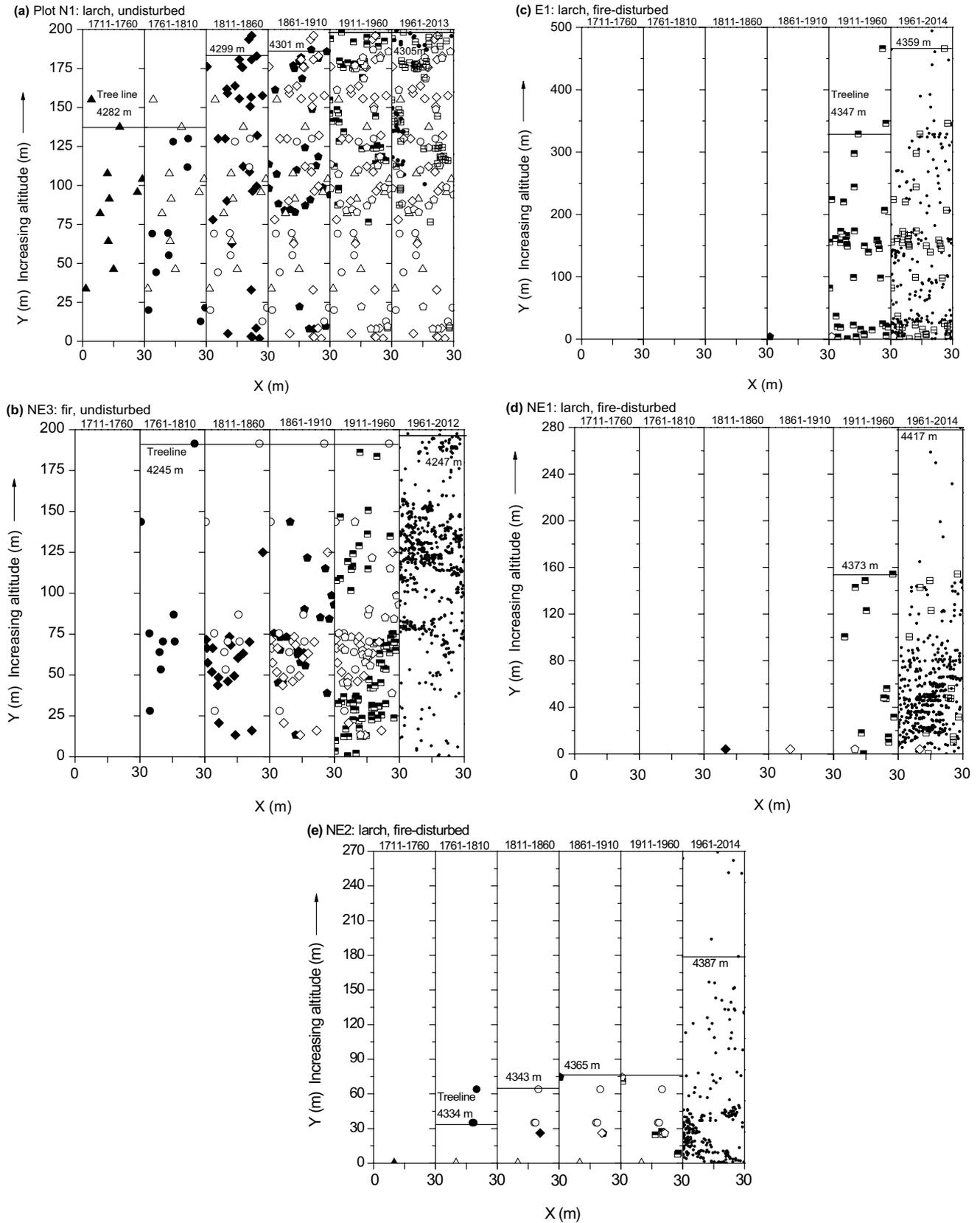


Fig. 4 Spatio-temporal variability in tree density and treeline position (uppermost elevation of living trees ≥ 2 m) at five treeline plots located in the Baima Snow Mountains, southeastern Tibetan Plateau. Closed symbols denote an individual that was established during the period indicated at the top of each plot, whereas open symbols represent trees established during previous periods. Different symbols correspond to different tree establishment periods

our results, the larch and fir trees required averages of 18 and 33 years to reach 2 m in height, respectively. Thus, treeline advance needs more time than infilling when disregarding changes of abiotic factors along the elevational gradient. Fire could promote recruitment and infilling by removing understory vegetation which competes with tree seedlings, whereas tree growth and treeline advance could be negatively affected by fire. A previous study indicated that fire was used as a traditional tool to halt the advance of woody species in the Baima Snow Mountains (Baker and Moseley 2007). Thus, it is likely that the 1969 fire was anthropogenic in origin rather than the more frequent “natural” fires that occur at high latitudes (Yao et al. 2017; Waito et al. 2018). Grazing disturbance also cannot be excluded. Comparative research on the treeline ecotone in other areas of the Tibetan Plateau under human impact has found strong effects of animal grazing, especially in sites where nearby human settlements exist (e.g., Miede and Miede 2000). Grazing pressure may explain the lack of recruitment before the 1960s at disturbed treelines. However, considering that livestock grazing has always occurred near the disturbed treelines and that grazing intensity tends to increase with the rise of local population (Baker and Moseley 2007), grazing pressure did not likely reverse the increasing trend in tree recruitment and limit treeline expansion.

Historical fire disturbances may have promoted upward shifts of treelines by reducing the competitive pressure from alpine plants. A past fire had an initial negative effect on the recruitment dynamics in the 1970s at the larch treelines but did not depress their elevations. More importantly, trees have encroached and densified in the areas beyond the post-fire treeline elevation, indicating a large upward treeline shift after the fire. The magnitude of advancement of fire-disturbed larch treelines since 1980 constituted most of the treeline advance during the last 50 and 100 years, suggesting that fire has played an important role in allowing the upward movement of treelines. In contrast, undisturbed larch or fir treelines have remained stable, providing further evidence that a fire was necessary to trigger or even promote upward treeline shifts.

The TIs calculated for the alpine plant communities near or above the alpine treeline indicated that the intensity of interspecific interactions differed between the undisturbed and fire-disturbed treelines. Tree–shrub competition at undisturbed treelines is likely to limit recruitment of tree seedlings for $TIs > 0.8$ (Liang et al. 2016). $TIs < 0.8$ at

fire-disturbed treelines represented conditions where low-density shrubs did not prevent tree recruitment above the treeline but created environmental conditions suitable for tree establishment (Liang et al. 2016). A previous study found that alpine shrubs [*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle and *Purshia tridentata* (Pursh) DC] in the Intermountain West of USA need > 50 years to recover after moderately severe fires (Ziegenhagen and Miller 2009). On the southeastern Tibetan Plateau, *Rhododendron* shrubs can reach an age of up to 400 years (Lu et al. 2015; Bi et al. 2017). In harsh environments at alpine treelines, recovery after fire is slow. Thus, fire may lead to substantial changes in shrub cover, not shrub species composition. Current TIs, therefore, are likely to be much higher than those observed immediately after fire events. Over the past 30 years, post-fire tree–shrub interactions might have changed from low-intensity to high-intensity facilitation at and beyond the treeline. The difference in shrub height between burned and unburned treelines indicated that recent fires may alter species interactions and hence modulate treeline responses to warming.

Other studies in boreal forests also showed that moderate-severity fire disturbances can potentially accelerate the northward movement of treelines by positively influencing biotic factors such as seed availability and seedling establishment (Certini 1993; Landhausser and Wein 1993), supporting our main results. In fact, the ecological benefits of fire disturbances have been recognized (Stephens and Ruth 2005; Carswell 2018). However, high-severity fire disturbance would result in the contractions of forest distribution and treeline retreat, thereby posing a major threat to some forest types (Bond and Keeley 2005; Rolstad et al. 2017). In addition, the impacts of high-severity fires on forests might be linked to tree species-specific traits (e.g., regeneration or adaptive strategy). For instance, North American boreal black spruce forest generally takes advantage of fire because it produces semi-serotinous cones that release seeds massively during a fire event and contribute to treeline regeneration and expansion (Auger and Payette 2010). These studies highlighted that a deeper understanding of fire-disturbed treeline dynamics under climate change should consider non-climatic factors.

In summary, upward shifts of conifer treelines at our study sites likely were a consequence of climatic warming, but disturbance by fire may have accelerated the rates by altering interactions between tree seedlings and alpine shrubs. The elevation of undisturbed fir and larch treelines has remained relatively stable despite climatic warming, presumably due to stronger interspecific competition. Fires of low to moderate severity and other disturbances (e.g., grazing), which modify species interactions, could therefore act as triggers to accelerate treeline dynamics and couple these dynamics more strongly to climatic warming. As shown by

this study, fire disturbance provides a simplified model to detect how species interactions drive treeline shifts. It provides additional evidence for the species interaction mechanism in controlling treeline formation and its response to climatic change. Further work is expected to quantitatively evaluate the effects of different fire severities on species interactions as well as on treeline shift rates.

Author contribution statements EL designed the research; YW, XL and EL performed the research; all authors analyzed the data and wrote the paper.

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Compliance with ethical standards

Conflict of interest We declare that there are no conflicts of interest.

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