Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau

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Abstract

The alpine treeline is commonly regarded as being sensitive to climatic warming because regeneration and growth of trees at treeline generally are limited by low temperature. The alpine treelines of the Tibetan Plateau (TP) occur at the highest elevations (4900 m a.s.l.) in the Northern Hemisphere. Ongoing climatic warming is expected to shift treelines upward. Studies of treeline dynamics at regional and local scales, however, have yielded conflicting results, indicating either unchanging treeline elevations or upward shifts. To reconcile this conflict, we reconstructed in detail a century of treeline structure and tree recruitment at sites along a climatic gradient of 4 °C and mean annual rainfall of 650 mm on the eastern TP. Species interactions interacted with effects of warming on treeline and could outweigh them. Densification of shrubs just above treeline inhibited tree establishment, and slowed upward movement of treelines on time scale of decades. Interspecific interactions are major processes controlling treeline dynamics that may account for the absence of an upward shift at some TP treelines despite continued climatic warming.

Keywords: alpine treeline ｜treeline dynamics｜ climate change ｜interspecific competition ｜Tibetan Plateau

Significance Statement

Climatic warming is expected to shift alpine treelines upward because regeneration and growth of trees there are limited by low temperature. However, treeline displacement is spatially heterogeneous despite warming climate. Using data on undisturbed spruce and fir treeline plots located on the Tibetan Plateau between 28.4 and 38.5°N, we showed that climatic warming tended

to promote an upward shift of alpine treelines at local and regional scales. However, upslope migration rates were controlled largely by interspecific interactions. Our findings both help to explain why many treelines have not advanced in response to climatic warming and highlight that predictions of treeline shifts based solely on climate may be misleading because interspecific interactions can temper effects of climatic change.

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Introduction

The boundary of vegetation formed by alpine treelines is expected to be sensitive to effects of climatic warming on subalpine and alpine ecosystems (1-3). Despite complex mechanisms controlling treeline ecotones (4), the mean root-zone and air temperature is thought to be the primary constraint on tree growth at the high elevations reached by particular tree species because reduced soil temperatures limit the use of carbohydrates to sustain cell division and create woody plant tissues (3). As the temperature warms, therefore, treelines are expected to increase in elevation (“shift upward”) (e.g., 5-7).

In a global meta-analysis, however, Harsch et al. (8) found that treelines shifted upward during the last century at only 52% of 166 locations examined; the majority of treelines upward shifts was attributed to improved winter conditions. Elsewhere, changes in treeline (“treeline displacement”) were spatially heterogeneous and slow despite accelerating warming (9, 10). In general, treelines are not always keeping pace with climatic warming on multi-decadal time scales, suggesting that upward migration and adjustment of alpine trees to warmer climate conditions may take from several decades to centuries (11), given biotic and climatic factors (e.g. drought, changes in frost damage and insect and pathogen attacks, soil nutrients or water availability limitations). However, little is known about processes that control upward displacement of treelines in response to long-term warming, and whether alpine tree lines will respond quickly or not to climate warming occurring since the mid-1800s and accelerating today.

Treeline displacement results from changes in tree recruitment, growth and mortality (11-13). These demographic processes are controlled by different drivers and involve biotic and climatic responses and limitations (4, 14-17). In addition to physiological responses to temperature warming (3), geomorphic or topographic conditions also limit upward shifts in alpine treelines (18-20). Species competition often is an important force driving stand dynamics and suppression (e.g., 21-27). Theoretically, altered disturbance regimes and interactions between trees and shrubs or grasses also can affect demographic parameters and determine whether treelines shift upward.

Interactions among plants also may shift from competition to facilitation as environmental stress increases (28), but the role of species interactions as regulators of alpine treeline shifts has been little studied. There are some data that suggest that the presence of shrubs may limit recruitment and tree establishment above the treeline (16, 29-31), but regional studies and transplant experiments have not allowed for quantitative assessment of long-term changes in species interactions at treeline.

Treelines provide a valuable place for investigating interactions between plant species since prevailing environmental conditions are harsh and this could lead to shifts from negative (competition) to positive interactions (facilitation; cf. 28, 32, 33). The natural treeline on the Tibetan Plateau (TP) is at the highest elevation 4900 m a.s.l. in the Northern Hemisphere (34). Several climatic proxies show that the past century was the warmest period on the TP over the last millennium (*SI Appendix,* Fig. S1). The TP treelines also are virtually undisturbed by human activities, and both edaphic constraints and slope features allow trees to colonize new areas above the current TP treeline, making the area a good locale for investigating climatic and biotic factors influencing treeline changes (35, 36). Along the eastern TP, tree growth of alpine trees is limited primarily by spring and summer temperatures (see *SI Appendix,* Fig. S1 and references therein). In the past 100 years, the region experienced a warming of 1.2-1.5 °C (*SI Appendix,* Fig. S1). Based on an observed temperature lapse rate of 0.65°C /100 m on the southeastern TP, an upward displacement of more than 200 m in elevation should be expected on the TP if spring and summer temperature were the single factor limiting tree growth and regeneration, and if treelines were in equilibrium with climate.

Recent studies have reported a range of different changes in treelines on the TP. For example, Baker and Moseley (37) estimated an upward shift of the fir treeline by 67 m from comparisons of repeated photographs from 1923 and 2003 taken at the same points in the Baima Snow Mountains (southeastern margin of TP). Plot-based dendroecological reconstructions, however, showed little changes of fir and spruce treelines in the past 200 years on the eastern and southeastern TP (36, 38). Both local and regional studies are needed to determine why upward treeline shifts occur in some sites and not in others. Based on data from 14 treeline plots located on the eastern TP between 28.4 and 38.5°N (Fig. 1), we addressed two questions: (1) has climatic warming been associated with an upward shift of treeline during the past 100 years; and (2) could biotic interactions between trees and other plants modulate treeline responses to warming and account for the inconsistent observations of previous studies?

Results and Discussion

A pronounced warming trend is apparent across the TP (Figs. 1, *SI Appendix* Fig. S1, S2, S3). A total of 14 treeline fir and spruce sites in the eastern part of the region showed increased density of tress (“densification”) during the past 100 years (*SI Appendix*, Fig. S4), in line with previous studies in that region (36, 38). A global meta-analysis of treeline response to climate warming also found an increase in stand density during the last century (8). Based on stand age structure of the studied treeline plots in the TP, we found that tree recruitment increased by more than 50% across all sites in the 1950s and 1960s (Fig. 2). Decadal tree recruitment was significantly correlated ($P <$ 0.01; *SI Appendix,* Table S2) with summer and winter temperatures reconstructed from climatic proxies based on $^{18}O/^{16}O$ ratios in ice cores and tree-ring widths (39, 40; Zhu et al. 2008) (Fig. 2,). Given that the establishment of new trees at treeline usually is limited more by climate than by the distance that seeds can disperse upwards (41), our null hypothesis is that climatic warming of the TP has accelerated and increased tree establishment at the studied sites, and that the treeline moved upwards.

Based on population age structure in the investigated plots across the treeline ecotone, we reconstructed treeline elevation based on the presence of the tallest trees (≥ 2 m) in 50-year intervals. A treeline shift of > 10 m (equal to the maximum tree height in all study plots) in the last 100 years was considered to be biologically meaningful. Except in the Sygera Mountains, treelines shifted upslope by > 10 m during the past century (Table 1, *SI Appendix,* Fig. S4). At one extreme, treeline of a fir-dominated plot in the Ranwu Lake area (RW3) advanced upward in elevation by 69 m, a spruce-dominated plot by 65 m, and three of four *Picea crassifolia*-dominated plots in the northeastern TP by 52 – 80 m.

However, the average rate of upward shift overall was only 2.9 ± 2.9 m per decade (range: 0 - 8.0 m per decade), far less than rates reported in previous meta-analyses (6.1-11.0 m per decade) of alpine plants (42, 43). The average rate over the eastern TP also was much less than the rapid upward shift of 91-119 m reported since the 1960s for the Green Mountains in Vermont, U.S.A. (8). It also is somewhat less than the upward shift of 4-15 m per decade in High Asia (southern Siberia and along the Urals mountain rangel) (Shiyatov 2003; Kharuk et al. 2010; Hagedorn et al.

2014[AME1]). The average treeline shift rate we found for the TP, however, was close to that reported for other alpine treelines in Spanish Pyrenees and northern Siberia (9, Kirdyanov et al. 2012[AME2]), With a warming in summer and annual mean temperature of around 1.2 - 1.5 °C in the past 100 years on the TP (*SI Appendix*, Fig. S1), a slower upward shift implies that drivers other than temperature must be considered to understand treeline dynamics on the TP.

Species interactions could modulate treeline responses to climatic change. Based on the coverage by shrubs (mainly *Rhododendron* species) or herbs and their mean heights above the treeline, we defined a thickness index (TI) of short vegetation as the product of shrub and grass cover multiplied by their mean height (see Methods). A generalized linear model that included species above the treeline, TI, treeline elevation, mean slope of treeline ecotone, changes in winter temperature and precipitation, and mean winter temperature and precipitation near the study sites explained 97.2% of the variance in treeline dynamics (*SI Appendix*, Table S3). However, only two predictor variables – either TI and species composition or TI and vegetation height – were needed to explain 86.6% of the variance in treeline dynamics. Thickness index alone accounted for over 50% of the variance in treeline dynamics in either model (*SI Appendix*, Table S3). Thus, it appears to be reasonable to use TI as a predictor of the rate of upward motion of treelines in response to warming and shrub-herb abundance (Fig. 3).

A higher coverage index implies stronger interspecific competition that may counteract the effects of warming on tree establishment. The TI ranged from 0.9 to 3.0 in five of the six treeline plots near the Ranwu Lake and in the Sygera Mountains, where the alpine vegetation is dominated by dense *Rhododendron* mats 1-3 m in height, and the treelines were stable over the past 100 years. In Plot LZ1-3, fir saplings in dense *Rhododendron* patches cannot survive more than three years because the saplings are smothered by fallen shrub litter. Only one treeline in these two regions (RW3) with a low coverage of herbs (TI= 0.30) shifted significantly upward (69 m). In this case, low shrub cover may have facilitated seedling establishment. Overall, the rate of upward shift in treeline was associated significantly and negatively with TI, suggesting that in addition to climatic amelioration, competition with shrubs and grass controls tree recruitment at treeline on the TP. Under a warming climate, increasing shrub coverage will restrict treeline upward shifts.

In the four regions where the TI ranged from 0.14 to 0.64, we observed upward shifts in treeline from 13 to 80 m over the past century. These low to moderate TI values represented conditions where shrubs did not prevent establishment of fir and spruce seedlings above the treeline, but rather created environmental conditions suitable for recruitment and growth. Species above the treeline (tall shrub, short shrub, grass) was used as separate predictor in evaluating treeline changes. Shrubs seem to be stronger inhibitors of tree seedling growth than grasses because the former begin to grow earlier than the latter (45) and outcompete small tree seedlings. At the site with the lowest TI (0.14) spruce treelines moved upslope by ≈80 m. Our results overall illustrate that tree-shrub competition is unlikely to limit recruitment of tree seedlings when TI < 0.8; under these conditions, upward movement of treeline as a consequence of climatic warming is likely to be observed. Unfortunately, coverage by shrub or grass species above the treeline across all the investigated plots was never sparse enough to capture a lower TI threshold (which we hypothesize that TI is << 0.14), i.e. most alpine communities studied did not act as “tree nurseries”, and tree recruitment was prevented.

In summary, spatially explicit and quantitative assessments of empirical data on TP treeline dynamics in the past century illustrate that climatic warming tended to promote an upward shift of alpine treelines at local and regional scales. Upslope migration rates, however, were controlled largely by interspecific interactions. Given the lack or low intensity of local disturbances to the TP treelines by herbivores, land use, and the lack of local geomorphic constraints (i.e., availability of sites with regolith above the treeline) on tree regeneration at most sites, interactions between trees and short-statured vegetation could well account for the discrepancy between treeline dynamics and climatic warming. Species interactions not only help to explain why many treelines have not advanced in response to climatic warming on a global scale (8), but also highlight that predictions of treeline shifts based on climate envelopes may be misleading because interspecific interactions can temper effects of climatic change.

Material and Methods

The study area encompassed six regions along a latitudinal transect between the southernmost and northernmost regions of the eastern TP (28.4-38.5°N; linear distance = 1150 km). The climates of these two regions are influenced strongly by the southern (Baima Snow Mountains, Ranwu Lake and Sygera Mountains) and East Asian (the source region of Yangtze River) monsoons and westerlies (Qilian Mountains), respectively. Annual precipitation decreases from ≈1000 mm in the south to ≈350 mm in the north. Annual mean air temperature ranges from 8.5 °C at Bomi (2800 m) in the south to 4.7 °C at Wulan (2600 m) in the north. Neither annual nor summer precipitation showed significant trends across all six regions, whereas annual, summer and winter temperatures showed significant warming trends (Fig. 1, *SI Appendix,* Fig. S2, S3). An automated weather station situated at the treeline (4360 m) in the Sygera Mountains, southeastern Tibetan Plateau recorded a mean air temperatures during the growing season of 6.0 ±0.3°C from 2007–2014. This is in agreement with the definition of the growing season since soil temperatures at 10 cm depth are higher than 3.2°C, which is regarded as a global thermal threshold for treelines (3).

The treeline research plots were established on gentle to moderately steep slopes with substrates dominated by regolith and located away from talus slopes and avalanche paths (i.e., study plots were in locations more likely to experience warming-induced changes in treeline in absence of biotic factors). The elevations of the alpine treelines declined from 4478 m on the southeastern TP to 3386 m on the northeastern TP as latitude increased. These treelines are much lower than the permafrost zone, which as a lower altitudinal limit (i.e. the zone above which permafrost occurs) running from 4800 m a.s.l. in the south to 4200 m a.s.1. in the north (Wang and French 1995[AME3]).. These treelines are usually diffuse in shape and are characterized by dominant tree species in each region (Fig. S5), including *Abies georgei*, *A. georgei* var. *smithii*, *Picea likiangensis* var. *balfouriana* and *Picea crassifolia* (Table 1). There typically are no krummholz mat formation or flagged trees in the investigated treeline ecotones.

The position of the upper treeline was defined by the presence of upright trees with a minimum height of 2 m at the maximum altitude and a continuous distribution above the timberline (forest coverage of more than 30%) in the plot (2, 9, 11). The treeline ecotone refers to the transition from the timberline to the treeless alpine vegetation (3). The upper species limit refers to the highest elevation at which species height is generally shorter than 2 m. One to three spatially independent and rectangular plots (30 ×150 m or 30 ×200 m) were established in each region on a topographically uniform area of the treeline ecotone to include the timberline and the species' upper limit (9). The longest side (*y*-axis) of each plot was parallel to the elevational gradient formed by the transition from subalpine forest to alpine shrubland or tundra. The bottom left corner of each plot was designated the origin (x, y) = (0, 0). The altitudes of the lower and upper parts of the plots were determined by GPS at a resolution of ± 5 m. The location of each tree within the plots was mapped by recording the x and y coordinates at the center of the main stem. Coordinates were measured to the nearest 0.1 m and then corrected by accounting for the mean slope of each plot. Diameter at breast height (DBH, 1.3 m), tree height, and horizontal projection of the tree canopy along the x- and y-axes were measured for all trees. Tree height was measured directly for trees shorter than 2 m or with a clinometer for trees taller than 2 m.

The cover and height of the vegetation above the treelines were quantified using the point-intercept method (46, 47). Six transects along the elevational (y-) axis of each plot were established from the upper treeline to 20 m above the treeline. Transects were spaced 6 m apart perpendicular to the slope, i.e., 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 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. To ensure that maximum cover was 100%, multiple contacts at a single sample point were considered to be one contact. The vegetation was dominated by sparse *Rhododendron* shrubs above the fir treeline in the Baima Snow Mountains (Table 1). Near Ranwu Lake and in the Sygera Mountains, however, *Rhododendron* shrubs had an extremely high coverage (> 90%), and the height of the shrubs ranged from 1.0 to 3.1 m. In Yushu and the Qilian Mountains, the area above the treeline was occupied by dwarf-shrub species with a mean height of 0.45 to 0.70 m, respectively.

The thickness index (TI) of short vegetation was calculated as percent cover × vegetation height (m) (Table 1). Cover of plants above treelines can act either as nurseries or biotic bottlenecks for seedling survival, depending on cover and plant height (29, 31). The TI contains the effects of both shrub/herb cover and their height on interspecific interactions. However, the shrub or herb cover above the treeline was > 20% at all sites. A generalized linear model was used to estimate effects of each predictor variable on treeline changes. We estimated the variance explained by each predictor variable using the R software system and the package relaimpo (48). Based on the "successive sweep method," we determined whether TI was a significant predictive variable.

Age structures of tree populations at each site were reconstructed using several methods. First, trees with a DBH > 5 cm were cored to the pith at 1.3 m above ground using a Pressler increment borer. When cores could not reach the pith, we estimated the number of missing innermost rings with a geometric pith locator. Second, ages of saplings and seedlings (height <2.5 m and DBH ≤5 cm) were non-destructively determined in the field by counting terminal bud scars (internodes or branch whorls) along the main stem (9, 36). Counting internodes, however, may underestimate true seedling ages by up to four years (36). Third, to obtain a more accurate estimate of tree age in two height classes – 1.3-2 m and ≥2 m – we determined the age of 20 individuals by counting the internodes (*SI Appendix,* Table S1). As in previous studies (9, 36), we assumed that the times required for seedlings to reach 1.3 or 2 m were statistically the same within each plot. Finally, DBH-age relationships established for each plot were used to estimate ages of trees with rotten stems (*SI Appendix,* Fig. S6).

A simple descriptor of an upward shift of an alpine treeline ecotone is the change in elevation at which the uppermost tree ≥ 2 m was found during successive time periods. The location of the treeline was reconstructed at 50-year intervals using standard dendrochronological methods (36). Based on population age structures in each plot and the uppermost tree ≥ 2 m corresponding to an estimated maximum age, treeline position and recruitment in the following 50-year intervals were reconstructed: 1611-1660, 1661-1710, 1711-1760, 1761-1810, 1811-1860, 1861-1910, 1911-1960 and 1961-2011/2012/2013. Fieldwork was done from mid-May to mid-October in 2011, 2012 and 2013. On this timescale, the expected 5-year error associated with the estimated age for trees 2 m tall is negligible. Maximum tree height was approximately 10 m at the treelines, so we regarded an upward shift of the treeline of more than 10 m in the past 100 years to be significant (36). The presence of old trees at some sites allowed for reconstruction of treeline position back to the early 17th century (*SI Appendix,* Fig. S4). It was evident that there were no remains of dead trees at or above current treeline at all 14 study sites.

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Tables

Table 1. Characteristics of the 14 treeline plots covering six regions from the southeastern to the northern margins of the Tibetan Plateau (site locations in Fig. 1). The main tree species, the mean covers and heights of the dominant alpine shrub or herb species above the treeline, and the corresponding vegetation thickness index (TI), are given. The last column shows the elevational treeline shift estimated for the past 100 years. Tree species include: 1, *Picea crassifolia*; 2, *Picea likiangensis* var. *balfouriana*; 3, *Abies george*i var. *smithii* and 4, *Abies georgei.* Dominant shrub or herb species above the treeline include: S1, *Salix cupularis*; S2, *Caragana jubata*; *S*3*, Stipa* spp.; S4, *Rhododendron aganniphum* var. *schizopeplum*; S5, *Rhododendron nivale*; S5, *Artemisia* spp. and S5, *Rhododendron platyphyllum*.

Study site	Tree species	Vegetation above treeline	Treeline elevation (m)	Vegetation cover (%)	Height of vegetation (m)	Vegetation TI	Treeline shift (m) over past 100 years (m)
QL1	1	S1	3385.8	90	0.70	0.63	51.5
QL2	1	S2	3496	20	0.70	0.14	79.9
WL1	1	S1	3876.9	70	0.80	0.56	13.2
WL2	1	S1	3846.5	80	0.80	0.64	53.6
DZ1	2	S3	4194.8	90	0.45	0.41	64.6
LZ1	3	S4	4390	90	3.0	2.70	0.0
LZ2	3	S4	4387.3	90	3.1	2.79	0.8
LZ3	3	S4	4376.7	90	3.30	2.97	0.0

RW1	3	S5	4471.3	85	1.0	0.85	3.6
RW2	3	S5	4447.8	83	1.1	0.91	5.4
RW3	2	S6	4478.3	85	0.40	0.34	68.5
BM1	4	S7	4396.8	76	0.60	0.46	28.1
BM2	4	S7	4397.9	82	0.55	0.45	18.7
BM3	4	S7	4427.9	89	0.70	0.62	19.5

Figure legends

Figure 1. Location of treeline plots along a latitudinal transect across the eastern Tibetan Plateau (top). Variations in the mean temperature and total precipitation in summer (June-August) since the year with available instrumental records at five meteorological stations located close to the study treeline plots (bottom). A, Zhangye in the middle Qilian Mountains; B, Yushu in the source region of the Yangtze River; C, Nyingchi in the valley of the Sygera Mountains; D, Bomi close to the Ranwu Lake; E, Deqin close to the Baima Snow Mountains. Variations in summer (June – August) mean temperature (low left) and total precipitation (low right) from instrumental records at five meteorological stations located close to the study treeline plots. The instrumental records at Wulan only began in 2001 and are thus not shown. The mean summer temperature at the five stations showed significant and sustained warming trends (statistics are presented), but summer precipitation did not present significant trends.

Figure 2. Trends in (A), winter-temperature reconstruction based on timberline tree rings on the northeastern Tibetan Plateau (Zhu et al. 2008); (B), ice-core $\delta^{18}O$ ($^{18}O/^{16}O$ ratios) series integrated from the Dunde, Guliya, Puruogangri and Dasuopu glaciers on the Tibetan Plateau (39) indicating summer temperature; (C) summer-temperature reconstruction based on timberline tree rings on the southeastern Tibetan Plateau (40); and decadal tree regeneration at treelines in the six studied regions (D-I) across the Tibetan Plateau and related proxies. The two summer climatic proxies are correlated for decadal intervals back to 1601 (r=0.77; $p<0.001$). See Table 1 and Figure 1 for research regions and forest plots. Red lines in A and C shows decadal moving averages.

Figure 3. The vegetation thickness index (TI) relates changes in treeline elevation across the Tibetan Plateau in the past 100 years to the product of cover and height of shrubs and herbs.

Figures

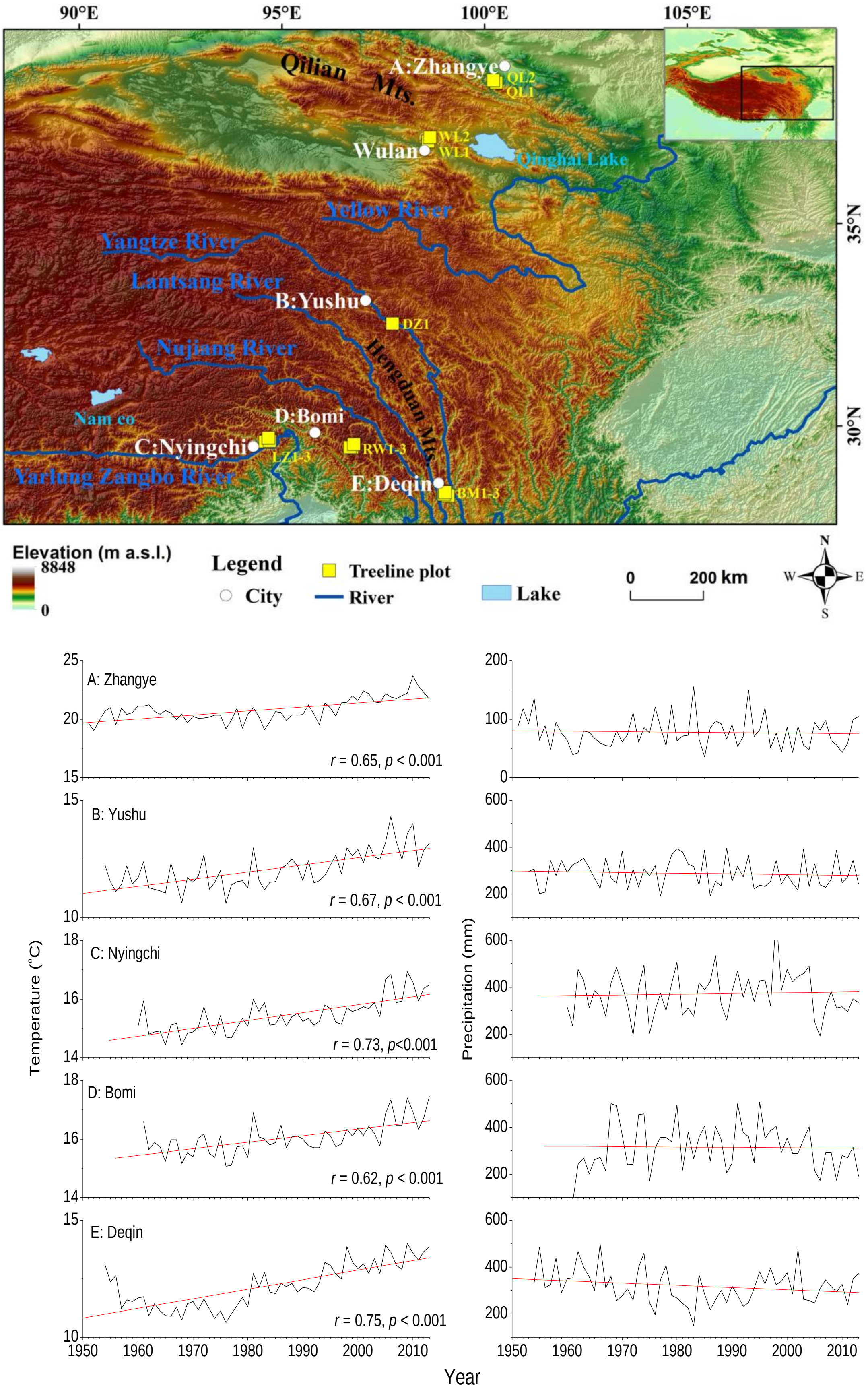

Figure 1

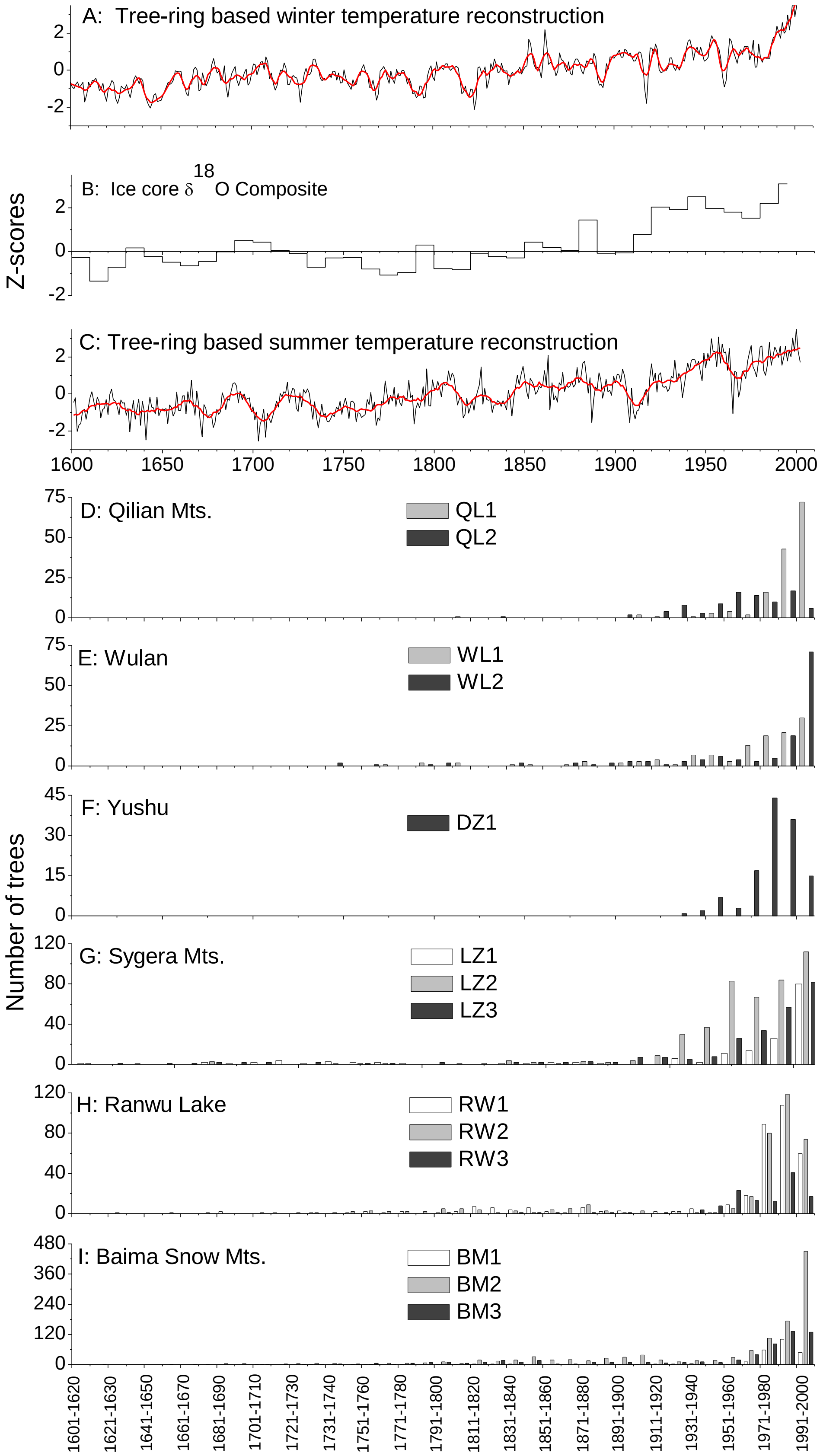
A: Tree-ring based winter temperature reconstruction
B: Ice core δ18O Composite
C: Tree-ring based summer temperature reconstruction
Z-scores
2
0
-2
1600
1650
1700
1750
1800
1850
1900
1950
2000
D: Qilian Mts.
QL1
QL2
E: Wulan
WL1
WL2
F: Yushu
DZ1
G: Sygera Mts.
LZ1
LZ2
LZ3
H: Ranwu Lake
RW1
RW2
RW3
I: Baima Snow Mts.
BM1
BM2
BM3
Number of trees
75
50
25
0
45
30
15
120
80
40
480
360
240
1601-1620
1621-1630
1641-1650
1661-1670
1681-1690
1701-1710
1721-1730
1731-1740
1751-1760
1771-1780
1791-1800
1811-1820
1831-1840
1851-1860
1871-1880
1891-1900
1911-1920
1931-1940
1951-1960
1971-1980
1991-2000

Figure 2

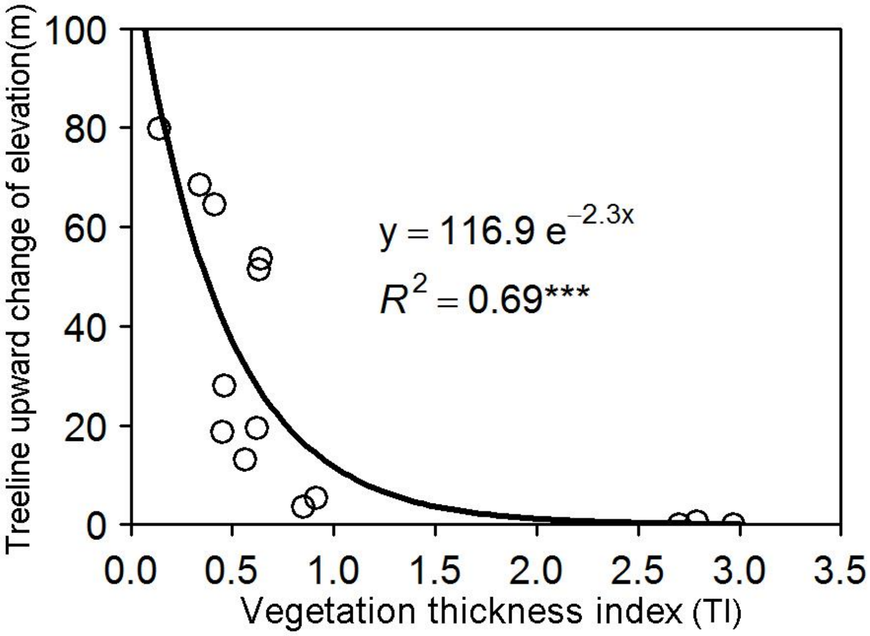
Treeline upward change of elevation(m)
100
80
60
40
20
0
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Vegetation thickness index (TI)
$y = 116.9\, e^{-2.3x}$
$R^2 = 0.69^{***}$

Figure 3

Supporting Information Appendix

Table S1. Ages of trees reaching heights of 1.3 and 2 m in the treeline plots across the eastern Tibetan Plateau. Values are means ± one SE of the mean.

Region	Treeline plot	Tree age at 1.3 m (years)	Tree age at 2.0 m (years)
Qilian Mountains	QL1	19 ± 2	26 ± 2
	QL2	17 ± 2	26 ± 3
Wulan	WL1	23 ± 4	31 ± 4
	WL2	20 ± 3	30 ± 4
Yushu, source region of Yangtze River	DZ1	19 ± 3	25 ± 2
Sygera Mountains	LZ1	31 ± 7	34 ± 5
	LZ2	31 ± 7	34 ± 5
	LZ3	32 ± 4	36 ± 3
Ranwu Lake	RW1	22 ± 4	27 ± 3
	RW2	23 ± 5	28 ± 4
	RW3	21 ± 3	28 ± 4
Baima Snow Mountains	BM1	28 ± 3	33 ± 5
	BM2	29 ± 4	36 ± 6
	BM3	30 ± 4	39 ± 6

Table S2. Pearson correlation coefficients (first row for each plot) and significance levels (second row for each plot) calculated by relating tree recruitment data at 14 treeline plots and reconstructed mean summer and winter temperatures in decadal intervals. Temperatures were reconstructed from either tree-ring or ice-core δ^{18}O data (see Fig. 2).

Treeline plot	Summer-temperature proxy		Winter-temperature proxy
	Tree-ring width data	Oxygen isotopes	Tree-ring width data
QL1	0.599	0.566	0.771
	0.007	0.012	< 0.001
QL2	0.749	0.726	0.482
	0.001	0.001	0.042
WL1	0.797	0.717	0.774
	< 0.001	< 0.001	< 0.001
WL2	0.674	0.588	0.764
	< 0.001	0.003	< 0.001
DZ1	0.633	0.440	0.184
	0.127	0.323	0.662
LZ1	0.634	0.553	0.708
	< 0.001	0.002	< 0.001
LZ2	0.737	0.660	0.764
	< 0.001	< 0.001	< 0.001
LZ3	0.683	0.646	0.746
	< 0.001	< 0.001	< 0.001
RW1	0.584	0.557	0.567
	< 0.001	0.001	< 0.001
RW2	0.563	0.541	0.575
	< 0.001	< 0.001	< 0.001
RW3	0.682	0.635	0.588
	0.001	0.003	< 0.001
BM1	0.553	0.549	0.542
	0.002	0.002	< 0.001
BM2	0.677	0.636	0.713
	< 0.001	< 0.001	< 0.001
BM3	0.647	0.610	0.673
	< 0.001	< 0.001	< 0.001

Table S3. Percentage of variance explained by the models predicting treeline migration rate. All the models included species above the treeline, height or vegetation cover (VC) of species above the treeline, the thickness index (TI) of short vegetation, treeline elevation, mean slope of treeline ecotone (Slope), mean/sum annual, summer and winter temperature (AT, ST, WT)/precipitation (AP, SP, WP), changes in annual, summer and winter temperature (CAT, CST and CWT), changes in annual, summer and winter precipitation (CAP, CSP and CWP) of the study areas. A generalized linear model (GLM) was used to predict treeline dynamics. The relative contribution of the top three or two variables is indicated by the different asterisks (*, ** and *** mean $p<0.05$, $p<0.01$ and $p<0.001$, respectively).

Dependent variable	Independent variables										Model R^2 (percentage)
Treeline Changes	Species **	TI ***	Height *	VC *	Elevation	Slope	AT	AP	CAT	CAP	97.1
	Species **	TI ***	Height ***	VC *	Elevation	Slope	ST	SP	CST	CSP	96.8
	Species **	TI **	Height *	VC *	Elevation	Slope	WT	WP	CWT	CWP	97.2
	Species ***	TI ***	Height *	VC							82.8
	Species *	TI ***	Height **								86.6
		TI **	Height *								85.9
	Species **	TI	Height ***	Species*TI							82.8
	Species	TI ***	Height **	TI*height							82.8
	Species *	TI ***	Height	Species*TI							82.8
	Species **	TI ***		Species*TI							82.7
	Species *	TI **									86.6

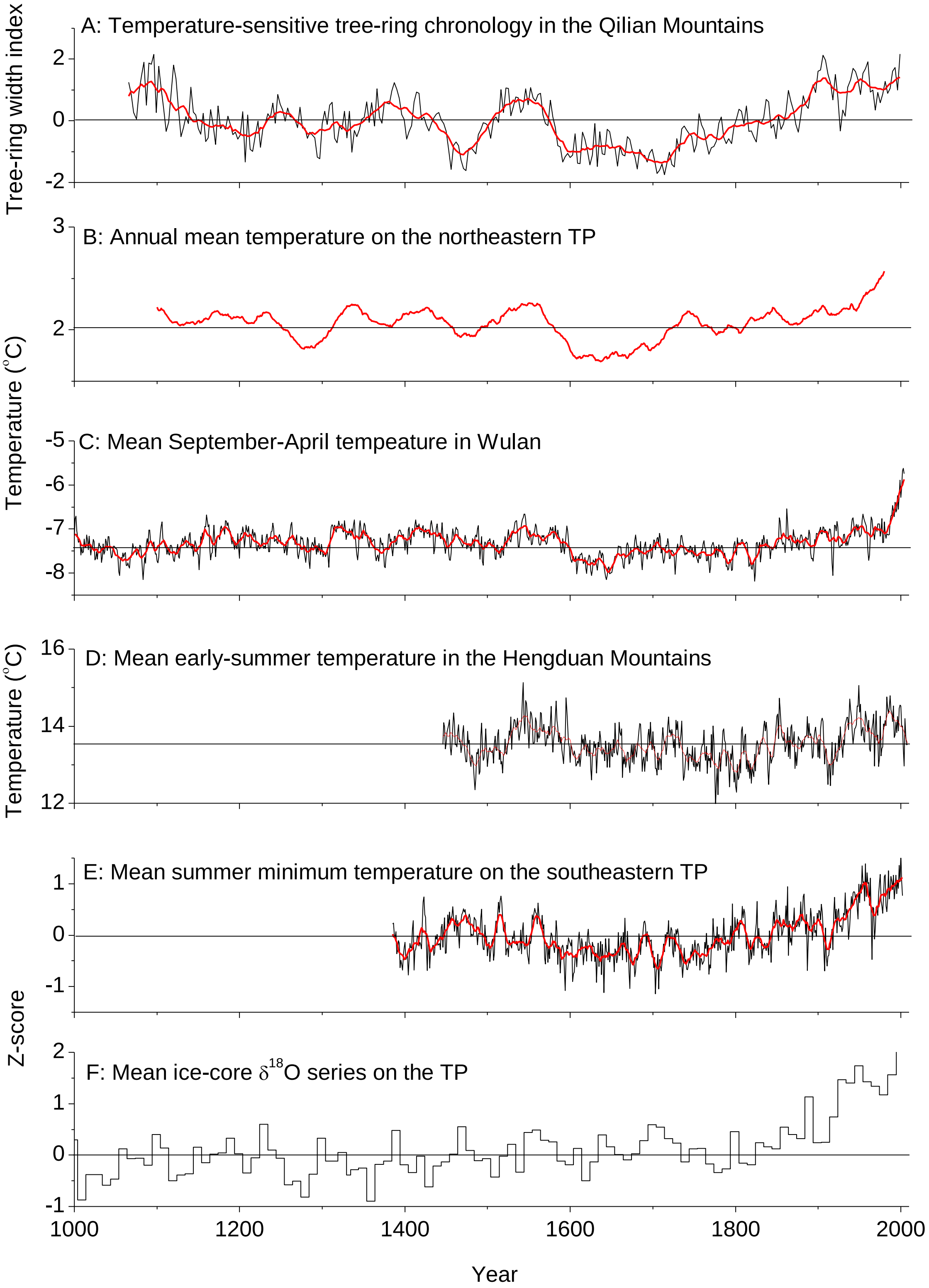

Fig. S1. Variations in temperature on the Tibetan Plateau as indicated by tree-ring and ice-core δ^{18}O series. A. Standardized December-April temperature-sensitive tree-ring-width index in the Qilian Mountains of the northeastern Tibetan Plateau (1); B. Annual-temperature reconstruction based on tree rings (40-year moving average) on the northeastern Tibetan Plateau (2); C. Reconstructed mean temperatures from the previous September to the current April for the Wulan area based on tree-ring chronologies (3); D. Mean early-summer (June-July) temperature reconstruction based on tree rings in the Hengduan Mountains of the southeastern Tibetan Plateau (4); E. Mean summer minimum temperature based on tree rings on the southeastern Tibetan Plateau (5); F. decadal ice-core $\delta^{18}O$ series (an indicator of summer temperature) from the Dunde, Guliya, Puruogangri and Dasuopu glaciers on the Tibetan Plateau (6). Except for B, the thick gray curves represent the 10-year low-pass-filtered values, and the horizontal lines represent the long-term means. The Z-score is calculated by dividing the score deviation (data of each year - mean of the series) by the standard deviation of the series.

In addition to the research presented above, tree growth at the treelines/timberlines in our study area responded significantly and positively to summer temperature in the Baima Snow Mountains (7) and the Sygera Mountains (8) of the southeastern TP, Yushu in the source region of the Yangtze River (9) and Wulan of the northeastern TP (10).

References

1. Liu X, Qin D, Shao X, Chen T, Ren J (2005) Temperature variations recovered from tree-rings in the middle Qilian Mountain over the last millennium. *Sci China Ser D – Earth Sci* 48:521–529.
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6. Thompson LG, et al. (2006) Abrupt tropical climate change: past and present. *Proc Natl Acad Sci USA* 103:10536–10543.
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9. Liang E, Shao X, Qin N (2008) Tree-ring based summer temperature reconstruction for the source region of the Yangtze River on the Tibetan Plateau. *Glob Planet Change* 61:313-320
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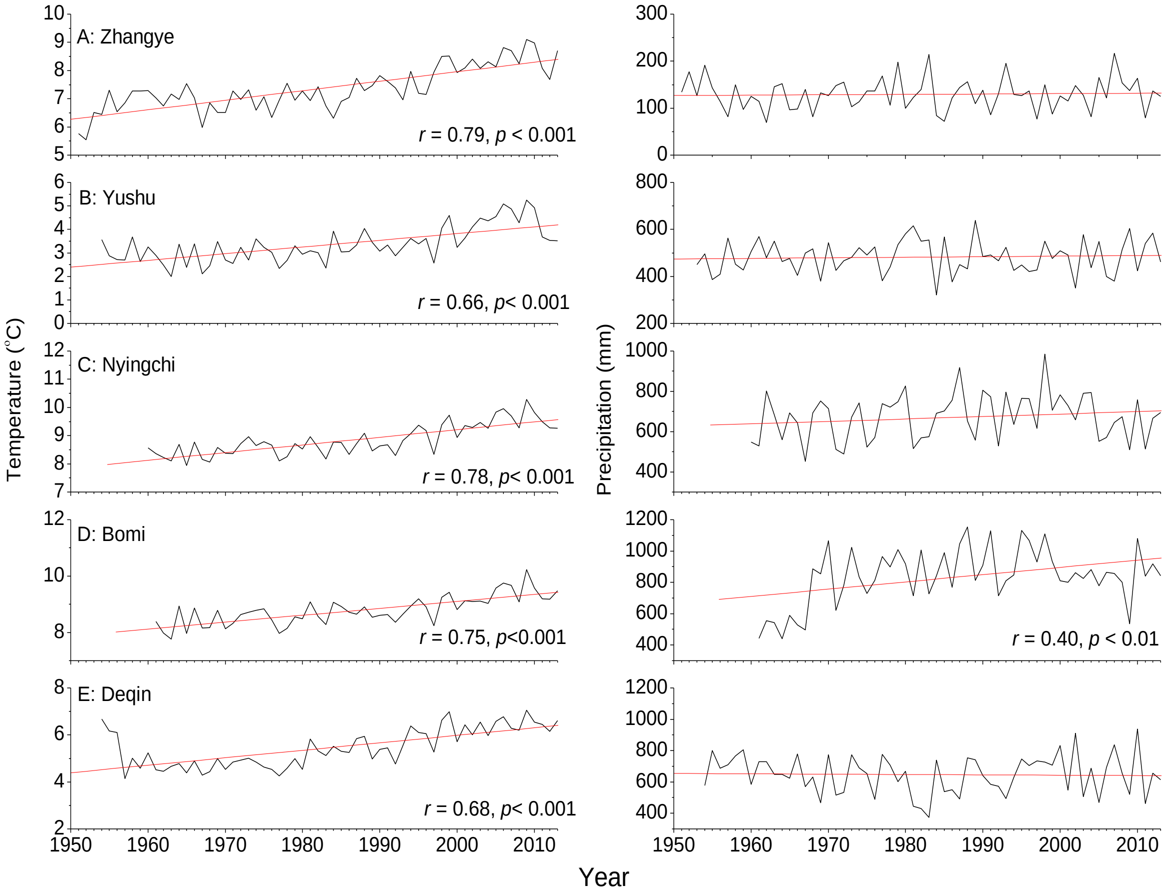


Fig. S2. The annual mean temperatures showed a significant and sustained warming tendency at five meteorological stations located close to the study treeline plots, whereas precipitation values did not such trend (see Figure. 1) except for a slight increasing trend in Bomi. The instrumental records at Wulan only began in 2001 and are thus not shown[C4].

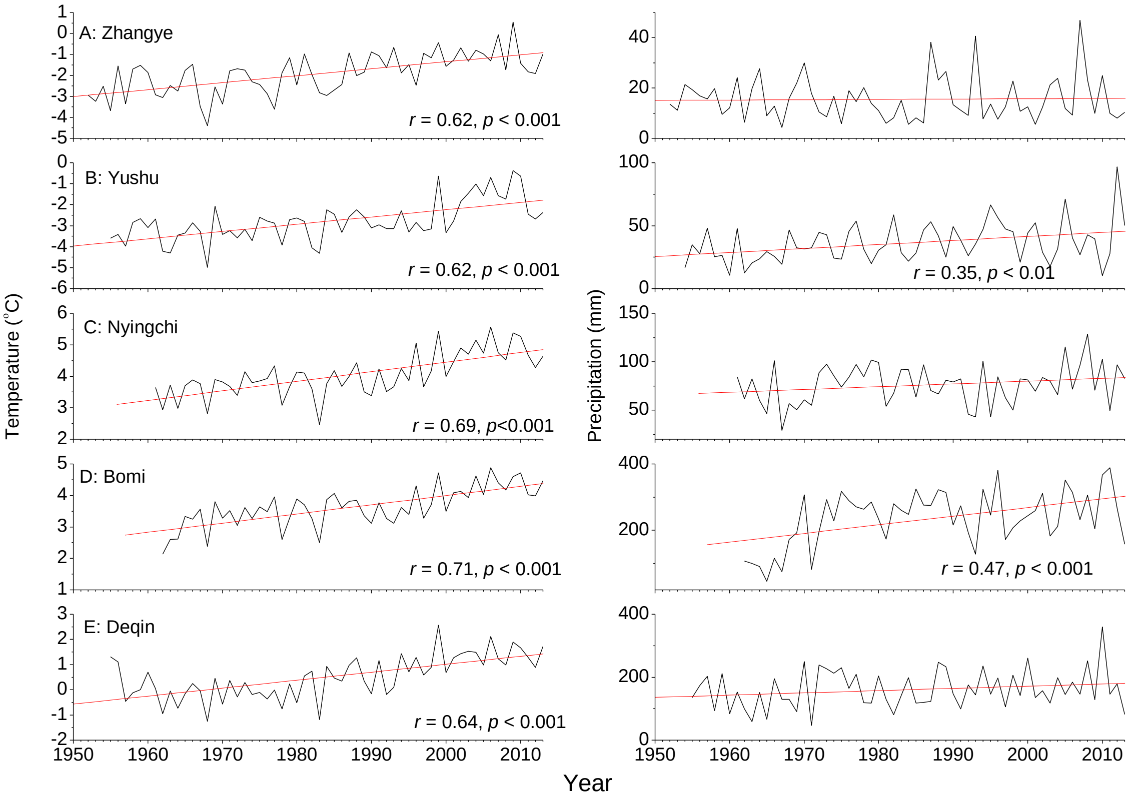
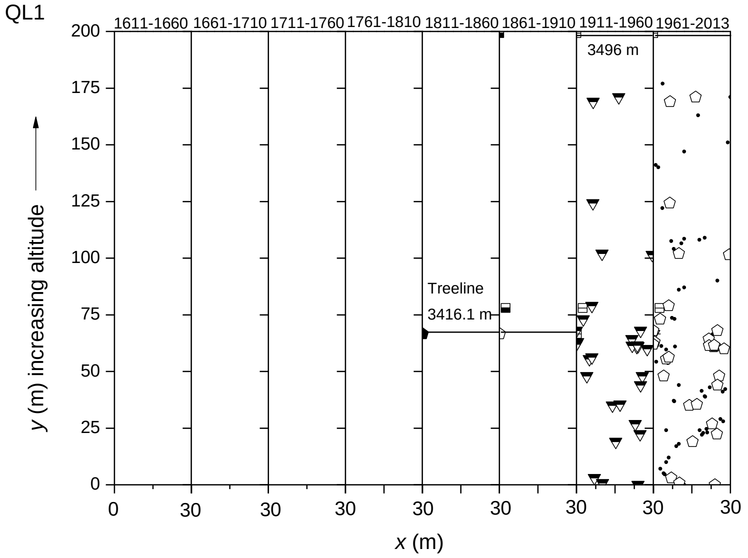
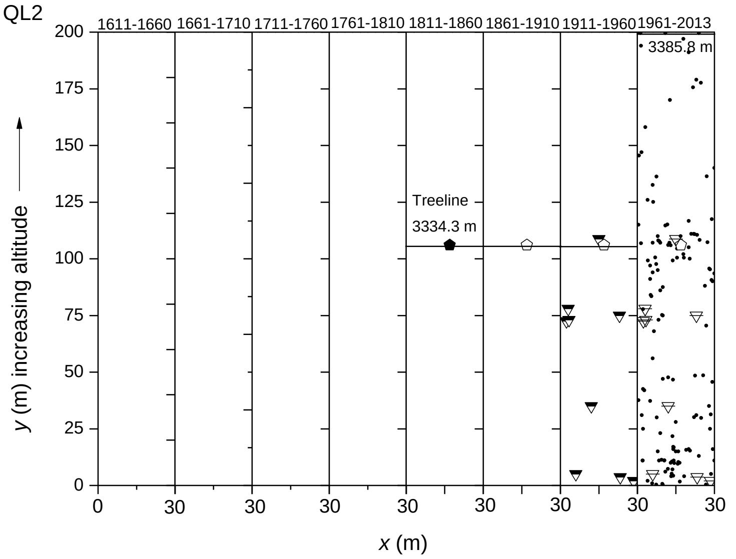
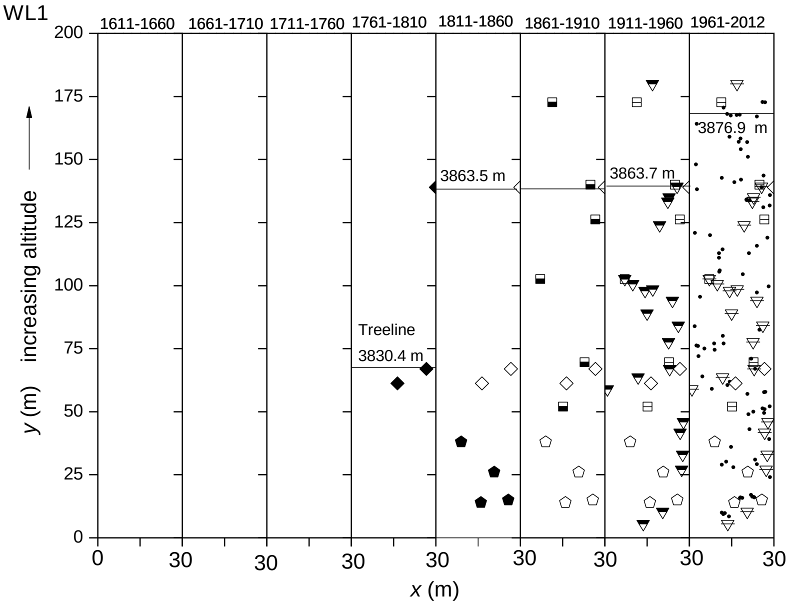
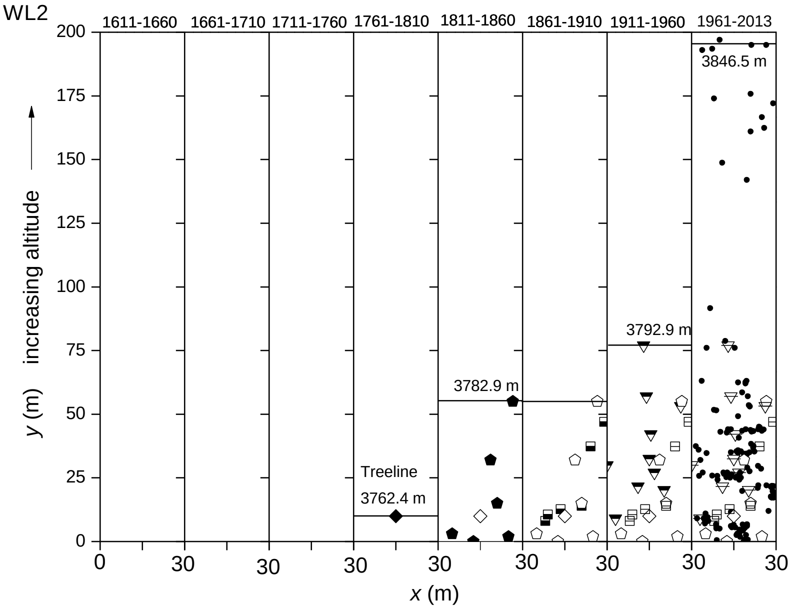


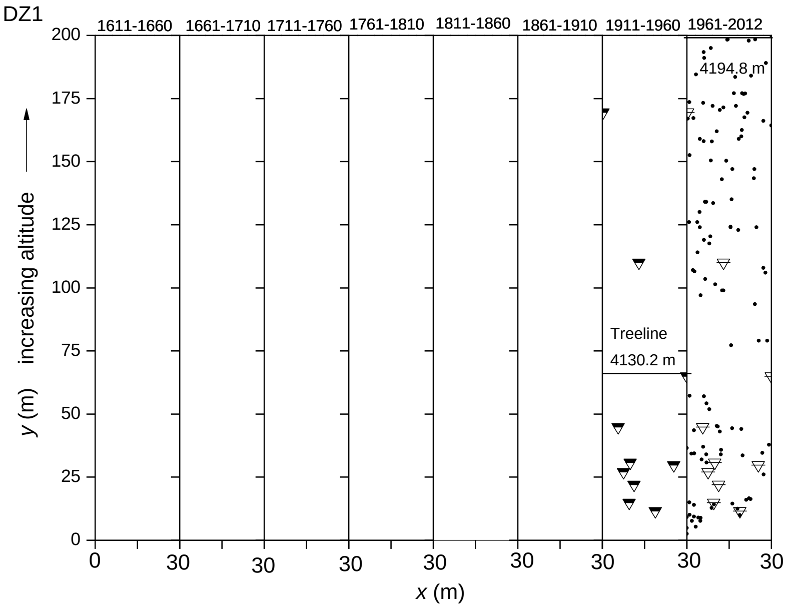
Fig. S3. The mean temperatures during the half year when study sites were covered by snow (November-April) showed a significant and sustained warming tendency at five meteorological stations located close to the study treeline plots (see Figure. 1). Except for a significant and increasing trend in precipitation during winter-half year at Yushu and Bomi, the other stations did not show significant trends. The instrumental records at Wulan began in 2001 and they are too short to analyze trends.

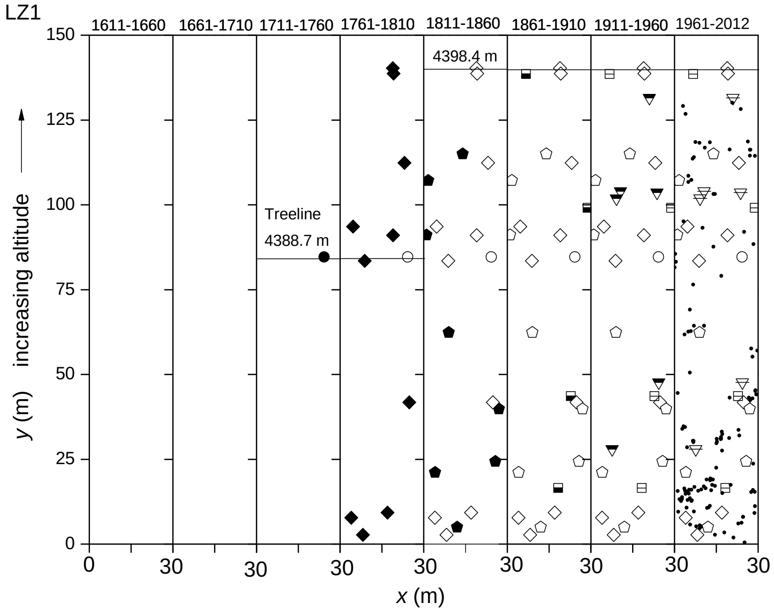

QL1
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2013
3496 m
Treeline
3416.1 m
y (m) increasing altitude
200
175
150
125
100
75
50
25
0
0
30
30
30
30
30
30
30
30
x (m)

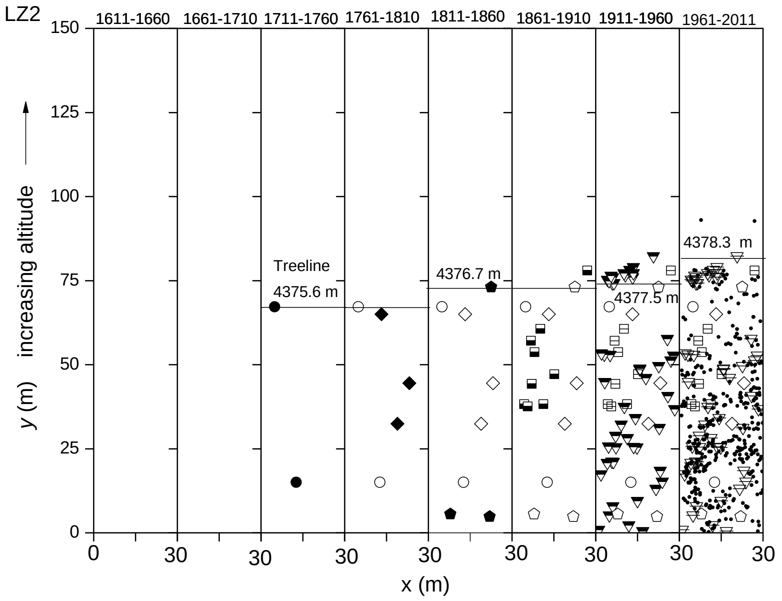

QL2
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2013
3385.8 m
Treeline
3334.3 m
y (m) increasing altitude
200
175
150
125
100
75
50
25
0
0
30
30
30
30
30
30
30
30
x (m)

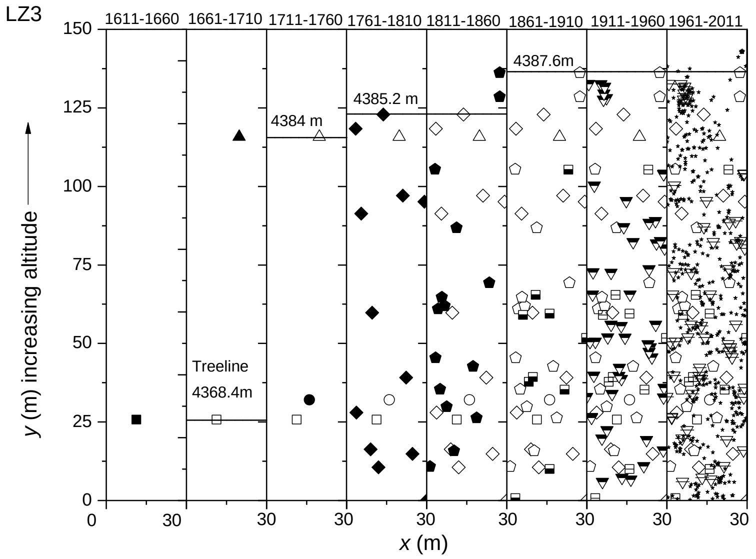

WL1
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
y (m) increasing altitude
0
25
50
75
100
125
150
175
200
Treeline
3830.4 m
3863.5 m
3863.7 m
3876.9 m
0
30
x (m)

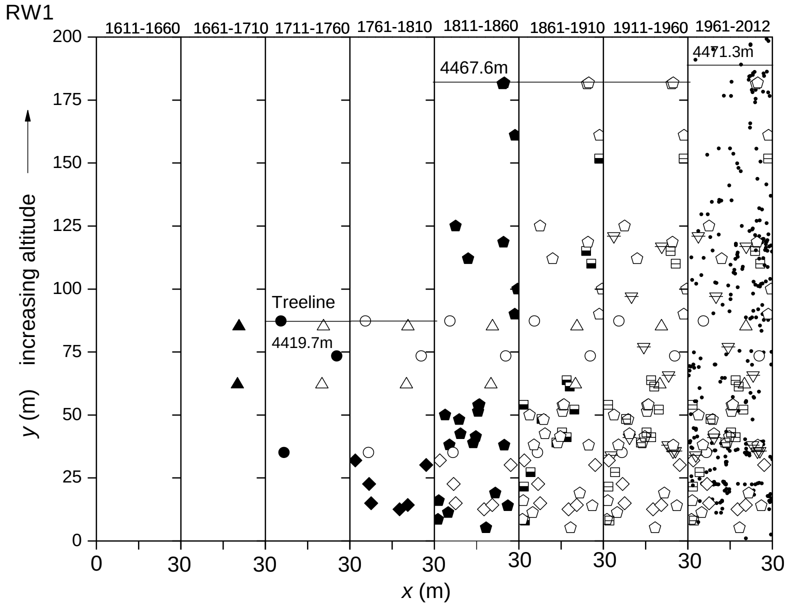

WL2
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2013
y (m) increasing altitude
0
25
50
75
100
125
150
175
200
Treeline
3762.4 m
3782.9 m
3792.9 m
3846.5 m
0
30
x (m)

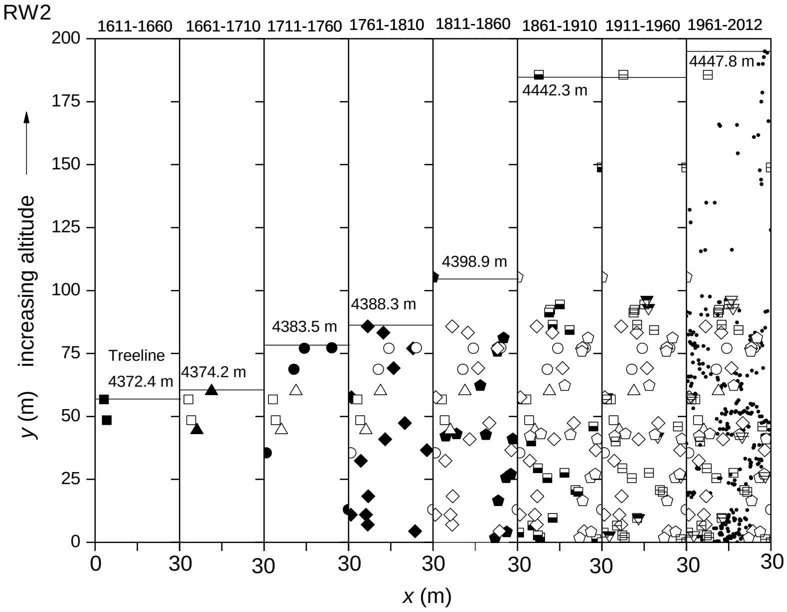

DZ1
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
4194.8 m
Treeline
4130.2 m
y (m) increasing altitude
200
175
150
125
100
75
50
25
0
0
30
30
30
30
30
30
30
30
x (m)


LZ1
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
4398.4 m
Treeline
4388.7 m
y (m) increasing altitude
150
125
100
75
50
25
0
0
30
30
30
30
30
30
30
30
x (m)

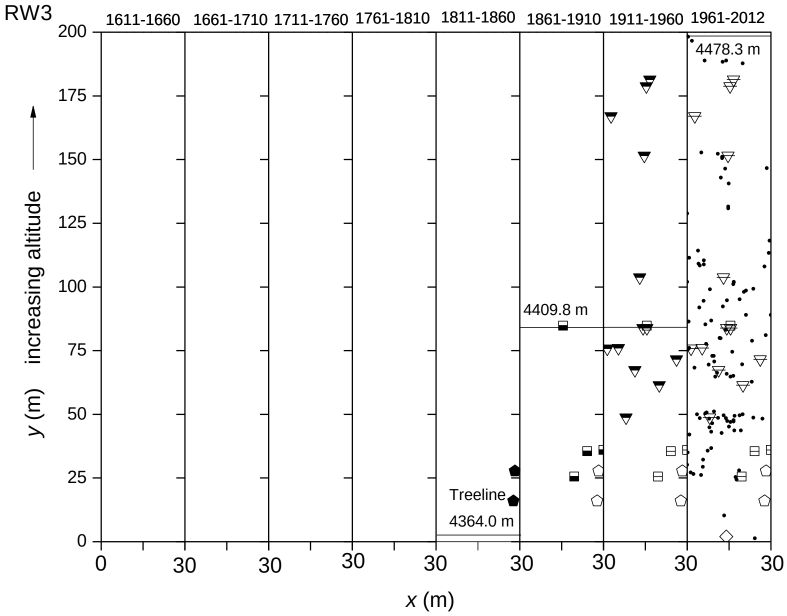

LZ2
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2011
y (m) increasing altitude
150
125
100
75
50
25
0
Treeline
4375.6 m
4376.7 m
4377.5 m
4378.3 m
0
30
30
30
30
30
30
30
30
x (m)


LZ3
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2011
y (m) increasing altitude
150
125
100
75
50
25
0
Treeline
4368.4m
4384 m
4385.2 m
4387.6m
0
30
30
30
30
30
30
30
30
x (m)

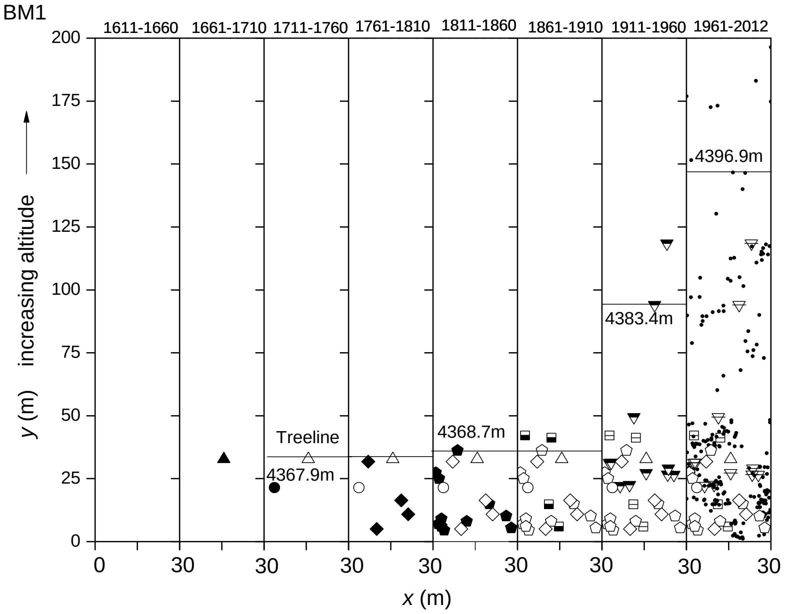

RW1
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
y (m) increasing altitude
200
175
150
125
100
75
50
25
0
Treeline
4419.7m
4467.6m
4471.3m
0
30
30
30
30
30
30
30
30
x (m)


RW2
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
Treeline
4372.4 m
4374.2 m
4383.5 m
4388.3 m
4398.9 m
4442.3 m
4447.8 m
y (m) increasing altitude
x (m)
0
25
50
75
100
125
150
175
200
30

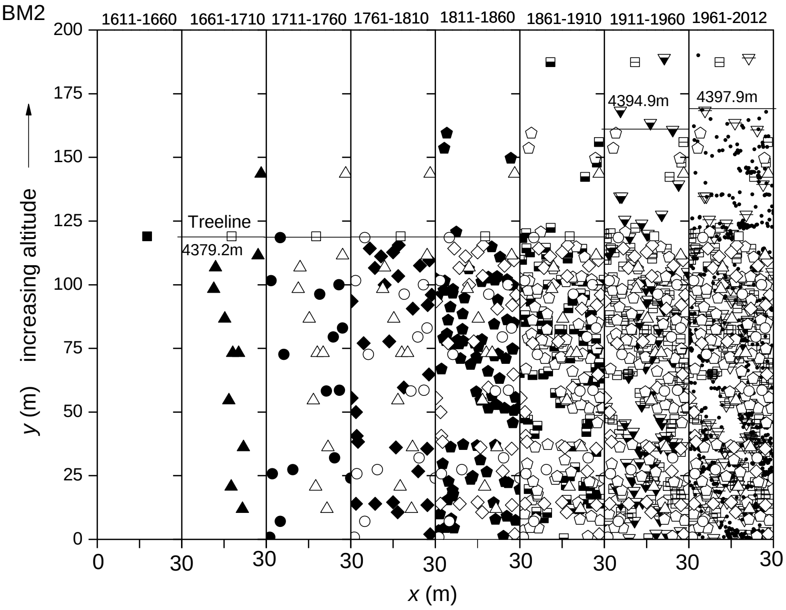
604


RW3
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
Treeline
4364.0 m
4409.8 m
4478.3 m
y (m) increasing altitude
x (m)
0
25
50
75
100
125
150
175
200
30

605


BM1
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
200
175
150
125
100
75
50
25
0
y (m) increasing altitude
Treeline
4367.9m
4368.7m
4383.4m
4396.9m
0
30
x (m)

606


BM2
1611-1660
1661-1710
1711-1760
1761-1810
1811-1860
1861-1910
1911-1960
1961-2012
200
175
150
125
100
75
50
25
0
y (m) increasing altitude
Treeline
4379.2m
4394.9m
4397.9m
0
30
x (m)

607

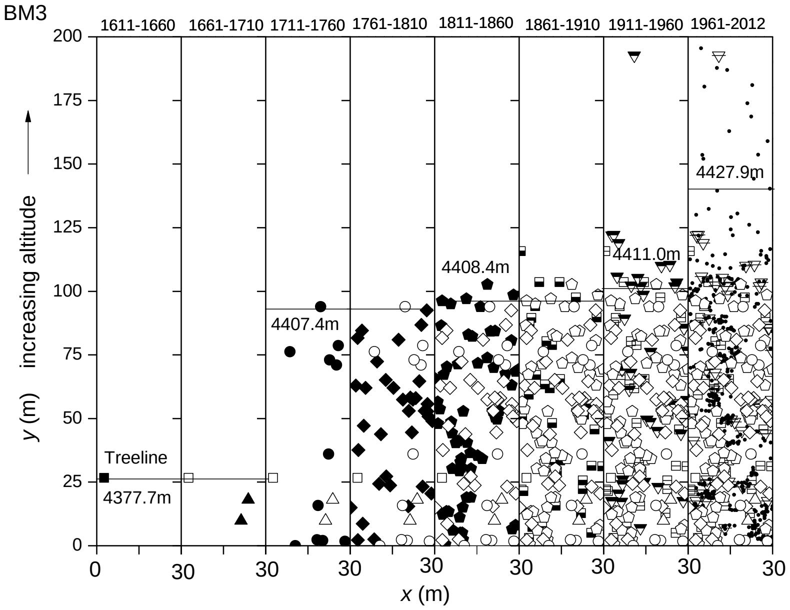


Fig. S4. Spatiotemporal variability in tree density and treeline position (maximum elevation reached by trees with stems at least 2 m high indicated in each plot) reconstructed at the alpine treeline plots along a north-south latitudinal transect across the eastern Tibetan Plateau. Each closed symbol represents an individual that was established during the period indicated at the top of the rectangular plot, and open symbols represent trees established during periods previous to that indicated at the top. Different symbols correspond to different establishment periods (e.g. triangles indicate trees established 1661–1710). Plot LZ3 corresponds to the treeline dataset presented in Liang et al. (2011).

Fig. S5. A typical Smith fir (*Abies george*i var. *smithii*) treeline ecotone (plot LZ1) where dense rhododendron shrub (*Rhododendron aganniphum* var. *schizopeplum*) dominates above the treeline ecotone (photo by Eryuan Liang).

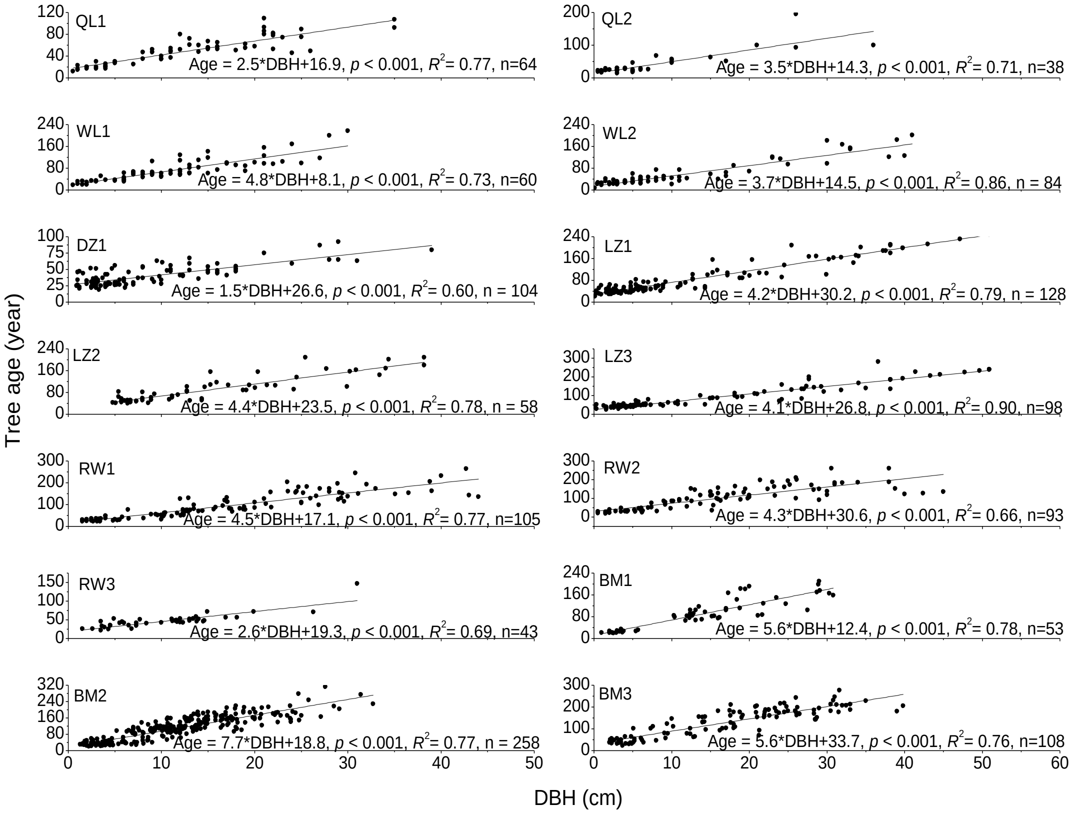


Fig. S6. Relationships between tree age and diameter at breast height (DBH, measured at 1.3 m aboveground) in the treeline plots along a latitudinal transect across the eastern Tibetan Plateau.