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1 Article

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

5

6 Running head: Fire facilitates upward treeline shifts

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27

28

29 **Abstract**

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

33

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

47

48 **Keywords** Climate change · dendroecology · fire disturbance · interspecific competition · tree
49 recruitment · treeline shift.

50

51

52 **Introduction**

53 The structure and position of alpine treelines are considered to be primarily thermally controlled
54 (Körner 2012). In support of this hypothesis, global climatic warming has induced upward treeline
55 encroachment and tree densification at some treeline ecotones (Camarero and Gutiérrez 2004;
56 Chapin et al. 2005; Liang et al. 2011; Liu and Yin 2013; Greenwood et al. 2014; Liang et al. 2016;
57 Wang et al. 2016a). Many treelines globally, however, are relatively stable despite evidence of
58 regional warming (Harsch et al. 2009). Different responses of regional treelines to warming result
59 from variability of the local processes controlling population dynamics at particular treeline
60 locations (Malanson et al. 2007; Gou et al. 2012; Kirilyanov et al. 2012; Case and Duncan 2014;
61 Lyu et al. 2016, Camarero et al. 2017; Wang et al. 2017; Vitali et al., 2019). For example, regional
62 warming promoted an upward shift of undisturbed spruce and fir treelines on the Tibetan Plateau,
63 but their rates of upslope migration were controlled largely by interspecific interactions (Liang et
64 al. 2016). We would therefore expect that upward shifts in treelines could be accelerated or
65 decelerated if competition or facilitation were reduced by local disturbances.

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

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

88 In this study, we assessed and further identified the magnitude and drivers of treeline changes
89 using annually resolved tree-ring records and inferred the mechanisms behind interspecific
90 interactions. Specifically, we 1) reconstructed the spatiotemporal patterns of *L. potaninii* and *A.*
91 *georgei* treelines in the Baima Snow Mountains using dendroecological methods, 2) dated recent
92 fires by cross-dating trees killed by fire and 3) tested the hypothesis that fire disturbance facilitates
93 upward shifts of alpine treelines induced by warming by reducing the coverage of plants near or
94 above the treeline. If this hypothesis was confirmed, climate warming would further contribute to
95 upward treeline advances by enhancing tree growth and recruitment but also by increasing fire
96 incidence and altering plant-plant interactions exerted by alpine vegetation on tree recruits.

97

98 **Materials and methods**

99 **Study region**

100 The Baima Snow Mountains (27°25'-28°36'N, 98°47'-99°21'E) are in the central Hengduan
101 Mountains, southeastern Tibetan Plateau (Fig. 1). Based on climatic data from the Deqin weather
102 station near the study site (28°23'N, 99°01'E; 4293 m a.s.l.), July (mean monthly air temperature
103 of 7.1 °C) and January (-9.1 °C) are the warmest and coldest months, respectively (Li and Zhang
104 2010). The mean annual precipitation for 1981-2009 was 807 mm, about 70% of which fell during
105 the monsoon season, i.e. from June to August (Li and Zhang 2010). Maximum wind speed varies

106 from 3-5 m s⁻¹ throughout the year. The soil is covered by snow (depth ca. 50-100 cm) mainly
107 during winter. Another meteorological station in nearby Deqin county (28°29'N, 99°55'E; 3485 m
108 a.s.l.), about 30 km from the study area, recorded an increase of 2.4 °C in summer mean
109 temperatures during 1954-2013 ($r = 0.75$, $P < 0.001$), whereas annual or summer precipitation did
110 not show a significant trend during the same period. Temperature reconstructions for the
111 southeastern Tibetan Plateau based on tree rings have also identified significant warming trends in
112 the region during the last 200 years (Zhu et al. 2011).

113

114 **Research plots and sampling design**

115 Conifer treeline plots were selected in the central Baima Snow Mountains. We defined the treeline
116 and forest limits as the highest elevations where trees were at least 2 m tall and where tree cover
117 was at least 30%, respectively (Holtmeier 2009). The treeline ecotone encompasses both
118 boundaries. The dominant tree and shrub species in the central Baima Snow Mountains include
119 larch (*L. potaninii* Batal. var. *macrocarpa* Cheng et Y. W. Law), fir (*Abies georgei* var. *smithii*
120 (Viguie et Gaussen) Cheng et L. K. Fu) and a dwarf scrubland-heath complex consisting of several
121 *Rhododendron* species (e.g. *R. phaeochrysum* Balf. et W. W. Smith, *R. rupicolum* W. W. Smith var.
122 *chryseum* (Balf. Et Ward) Philipson et Philipson, *R. nivale* Hook. var. *boreale* Philipson et
123 Philipson, *R. tapertiforme* Balf. et Ward and *R. yungningense* Balf.). Alpine meadows are the
124 dominant vegetation type above 4500 m.

125 Larch and fir are the main treeline species in the Baima Snow Mountains. Forests of these
126 species grow along an altitudinal gradient from 3500 m to 4300 m and from 3500 to 4200 m a.s.l.,
127 respectively. The positions of the larch and fir treelines vary from 4300 to 4417 m and from 4200
128 to 4450 m, respectively, due to the variable topography and landforms (Table 1). Wind-flagging
129 trees or krummholzs were not observed at the larch and fir treeline.

130 Based on a meta-analysis using a global dataset of 166 treeline sites, there were no clear
131 differences among plant families in their probability of treeline advance (Harsch et al. 2009). On
132 the Tibetan Plateau, we did not find species-related treeline shift rates of four species (*Picea*

133 *crassifolia*, *Picea likiangensis* var. *balfouriana*, *Abies georgei* var. *smithii*, and *Abies georgei*) in
134 the last 100 years (Liang et al. 2016). In the central Himalayas, broadleaf and conifer tree species
135 (*Betula utilis* and *Abies spectabilis*) also did not exhibit specific differences in their shift rates of
136 alpine treelines (Sigdel et al. 2018).

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

147 Some larch treelines in the study area (Fig. 1) have been affected previously by human-caused
148 fire, as indicated by the presence of dead trees and fire-scarred living trees (see more details in
149 Baker and Moseley 2007). Trees killed by fire still had remnants of bark and sapwood on their
150 stems, whereas scarred living trees had fire scars (“cat-faces”) at the stem base (Baker and
151 Moseley 2007). No signs of fires, however, were found across the fir treeline ecotone during field
152 observations from May 2013 to October 2014.

153 Five treeline sites (one fir and four larch sites) on different topographical conditions were
154 selected in the Baima Snow Mountains (Table 1). Rectangular plots with size 30 m × 200 m (2
155 plots), 30 m × 270 m, 30 m × 280 m and 30 m × 500 m were established on topographically
156 uniform areas across treeline ecotones and included the current treelines and forest limits. These
157 treeline plots were surveyed following the methods of previous treeline studies on the Tibetan
158 Plateau (Liang et al. 2011, 2016; Wang et al. 2016b). The longest side (y-axis) of each plot was set
159 parallel to the steepest slope (i.e. following the altitudinal gradient), and the origin (x, y) = (0, 0)

160 was located in its bottom left corner. The altitudes of the lower and upper parts of the plots were
161 determined using a GPS calibrated with a barometric altimeter (Cook and Kairiukstis 1990). The
162 location of each visible tree individual within the plot was mapped (± 0.1 m) using x-y coordinates
163 relative to the plot origin. Other biometric parameters measured and recorded for each tree
164 included: DBH (diameter at breast height, measured at 1.3 m aboveground), tree height, and
165 diameter of the tree canopy horizontally projected along the x and y axes. Tree height was
166 determined with a measuring stick for trees ≤ 2 m (± 0.01 m), or a clinometer for trees > 2 m (\pm
167 0.1 m) (Duncan, 1989).

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

175 The age structure of the trees was obtained by combining several methods. The ages of
176 seedlings (height ≤ 0.5 m) and juveniles ($0.5\text{m} < \text{height} < 2.5$ m) were non-destructively
177 determined in the field by counting the branch whorls along the main stem (Camarero and
178 Gutiérrez 2004). We randomly collected stem disks from 30 seedlings located immediately outside
179 the study plots and also counted the bud scars for these seedlings. The ages of seedlings obtained
180 from counting the internodes (CI) and the rings of stem disks (CR) were significantly correlated
181 ($\text{CI} = 0.76 * \text{CR} + 2.42$; $r = 0.77$, $P < 0.0001$, $n=30$) and reliable for determining tree age (Aakala
182 et al. 2014), although counting the bud scars underestimated the true seedling age by as much as
183 1-4 years (Figure S1).

184 We determined the age of 150 larch individuals and 30 fir individuals at or near the treelines,
185 respectively, by counting the internodes to obtain more accurate estimates of tree ages in the two
186 height classes (1.3-2.5 and ≥ 2.5 m). The larch and fir trees required averages of 18 ± 2 ($n=150$)

187 and 33 ± 5 ($n=30$) years to reach 2 m in height, respectively. As suggested by previous treeline
188 studies (Camarero and Gutiérrez 2004; Liang et al. 2011, 2016), we assumed that a seedling
189 required the same time (18 and 33 years for larch and fir treelines, respectively) to reach 2 m
190 during the past and current climatic conditions. The mean DBH for two undisturbed plots and
191 three fire-disturbed plots was 19.7 ± 12.4 (N1, $n = 145$), 11.2 ± 14.7 (NE3, $n = 286$) and 8.1 ± 6.5
192 (E1, $n = 93$), 5.3 ± 7.1 (NE1, $n = 99$), 6.7 ± 9.7 (NE2, $n = 92$), respectively. The mean height for
193 two undisturbed plots and three fire-disturbed plots was 8.5 ± 5.5 (N1, $n = 167$), 2.5 ± 4.6 (NE3, n
194 $= 777$) and 2.0 ± 2.0 (E1, $n = 246$), 1.1 ± 1.3 (NE1, $n = 458$), 1.6 ± 2.1 (NE2, $n = 270$),
195 respectively.

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

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

210 The mean height and canopy cover of vegetation above the treeline were surveyed as described
211 by our previous treeline study (Liang et al. 2016). Along the elevational (y) axis of each treeline
212 plot, six line-transects were established from the upper treeline to 20 m above the treeline.
213 Transects were spaced 6-m apart perpendicular to the slope: that is, along the axis perpendicular to

214 the maximum slope (x axis) at 0, 6, 12, 18, 24, and 30 m. Percent vegetation cover was calculated
215 based on the number of contacts between plants and a rod located every meter along the
216 elevational axis, and the height of the vegetation in each treeline plot was calculated as the mean
217 height of the vegetation at each sample point. A total of 126 points were recorded above the
218 treeline for each plot. The thickness index (TI), an ecological indicator of interspecific interaction,
219 is defined as the product of alpine shrub cover above the treeline multiplied by mean shrub height
220 (Liang et al. 2016). Such line-transects were set up in each study site.

221

222 **Methods**

223 Surviving trees are likely to grow very slowly in the year after crown-damaging fires (Brow and
224 Kaufmann 1999), so we identified the year in which growth rates were suppressed and assumed
225 that was when the historical fire occurred. We used *t*-tests to compare the mean post-fire tree-ring
226 widths of living and fire-killed trees in the final years (e.g. 1969, 1970, 1971) to determine when
227 growth was suppressed. Very narrow rings in some years usually indicated the presence of
228 disturbance (Liang et al., 2015). Samples from fire-scarred living trees were also used to
229 determine the years of the fires. The ages of 30 randomly selected young trees near or around the
230 fire-scarred trees and probably recruited after the fire was estimated by counting their bud scars.
231 Fire occurrence (binary variable) was related to TI to explore their relationships.

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

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

248 Post-fire tree recruitment data in the three fire-disturbed larch plots were compared to
249 determine the effect of fire disturbance on the pattern of tree recruitment at treeline ecotones. Post-
250 fire recruitments for these plots were then compared with those of the undisturbed larch and fir
251 treeline plots. The two-sample Kolmogorov-Smirnov (K-S) test was used to test if the distribution
252 of recruitment series differed significantly within the three fire-disturbed plots. The K-S test was
253 similarly used to identify significant differences in tree recruitment between fire-disturbed and
254 undisturbed plots.

255 We used a sequential algorithm developed by Rodionov (2004) and described by Elliott (2012)
256 to detect abrupt changes in the reconstructed patterns of tree establishment. This is a data-driven
257 approach in which an a priori hypothesis on the timing of regime shifts is not needed, and
258 sequential t tests are performed on time-series data to detect regime shift changes (Rodionov
259 2004). An abrupt change was identified if the cumulative sum of normalized deviations from the
260 mean of a potentially new pattern of establishment differed significantly from the mean of the
261 previous pattern of establishment episodes (Elliott 2012). A significance level of 0.05 and a 7-year
262 cut length were used to test for shifts in the means of the time series of the recruited trees. The
263 analyses of abrupt changes used the STARS program (Rodionov 2004). Such a method has been
264 used to analyze abrupt changes in the recruitment data at treelines in the Rocky Mountains, USA
265 (Elliott 2012).

266

267 **Results**

268 Fire-induced changes in tree growth were compared to determine fire events at the treelines. The
269 maximum and mean lengths of the series of tree-ring widths were 249 and 132 years, respectively.
270 The series of fire-killed trees was cross-dated with series of living trees, with average inter-series
271 correlation of 0.63 ($P < 0.001$). The year of the outer ring in the trees killed by fire varied from
272 1969 to 1971. The mean tree-ring widths of the dead trees in 1969, 1970 and 1971 were
273 significantly narrower than those of the surviving trees ($P < 0.05$ for 1969, 1970 and 1971; $n = 30$
274 trees). A very narrow ring formed in 1969 was consistently observed in the dead trees (Fig. 2).
275 Fire-scars in the surviving larch trees were also dated from 1969 to 1971. Thus, the three years
276 with narrow tree rings represent the impacts of fire on the individual tree.

277 Age structures and recruitment dynamics vary as functions of climate and fire. The estimated
278 year of the fire in the late 1960s (Fig. 2) coincided with the absence of recruits in the NE2 plots
279 and a much reduced tree establishment in the E1 and NE1 plots during the 1970s (Fig. 3b, d).
280 Young trees recruited since the 1990s accounted for the largest proportion of the treeline
281 populations (Fig. 3) and had an approximately reverse J-shaped age structure. Recruitment pulses
282 in the undisturbed larch N1 plot and fir NE3 plot were characterized by wave-like and rapidly
283 rising recruitment patterns, respectively (Fig. 3e, f). Tree recruitment in the three fire-disturbed
284 larch treelines or two undisturbed treelines did not differ significantly ($P > 0.05$, K-S tests)
285 between plots (E1 vs. NE1, E1 vs. NE2 or NE1 vs. NE2; NE3 vs. NE1) (Table 2). In contrast, tree
286 recruitment between the fire-disturbed and undisturbed larch/fir plots differed significantly ($P <$
287 0.05 , K-S tests on E1 vs. N1/ NE3, NE1 vs. N1/ NE3 and NE2 vs. N1/ NE3) (Table 2). Regardless
288 of the local site conditions, recruitment has increased in recent decades for the five study plots
289 (Fig. 3b-f) and was positively correlated with reconstructed summer temperatures on the
290 southeastern Tibetan Plateau (Fig. 3a) (plot E1: $r = 0.59$, $n = 8$; plot N1: $r = 0.57$, $n = 32$; plot
291 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
292 except E1; see also Fig. 3).

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

298 Based on population age structure in the investigated treeline plots, we reconstructed treeline
299 elevation based on the presence of the tallest trees (≥ 2 m) at a 50-y interval. The treelines in the
300 undisturbed larch (N1) and fir (NE3) plots advanced 0 and 2 m in elevation during the last 50
301 years but advanced 4 and 2 m in elevation during the last 100 years, respectively (Table 3; Fig. 4
302 a, b). The larch treeline plots (E1, NE1, NE2) contained some fire-induced dead trees, but the fire
303 did not cause a downslope shift of the treelines (Table 3; Fig. 4c-e). Furthermore, densification
304 mainly occurred above the post-fire treeline. The fire-disturbed larch treeline in the E1, NE1 and
305 NE2 plots advanced 11 m, 44 m and 22 m in elevation in the last 50 years, respectively, and the
306 larch treeline in plot NE2 shifted upward by 22 m in the last 100 years (Table 3; Fig. 4). The fire-
307 disturbed treelines have advanced by 11-44 m since the 1980s (Table 3; Fig. 4). Fire disturbance
308 explained 91.7-100% of the larch-treeline dynamics for the last 50 years (Table 3). In particular,
309 the treeline in the NE2 plot during the last 100 years advanced only after the fire disturbance.

310 Coverage of alpine shrubs above the treeline was related to fire occurrence. Dense
311 *Rhododendron* shrubs dominated the undisturbed treelines (NE3 and N1), with TIs of 1.64 and
312 1.87, respectively (Table 3). In contrast, shrubs dominated the fire-disturbed treelines, with TIs
313 ranging from 0.23 to 0.67 (Table 3).

314

315 Discussion

316 The warming in the last century is unprecedented over the last 1,000 yrs on the Tibetan Plateau (Liu
317 et al. 2005; Bräuning 2006; Thompson et al. 2006; Zhu et al. 2008). Global warming is expected to
318 have considerable effects on species' range limit such as alpine treelines, where tree growth is
319 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 a challenge 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; Liu et al. 2011; 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. 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

347 of increasing temperature. A previous study indicated that fire was used as a traditional tool to halt
348 the advance of woody species in the Baima Snow Mountains (Baker and Moseley, 2007). Thus, it
349 is likely that the 1969 fire was anthropogenic in origin rather than the more frequent “natural”
350 fires that occur at high latitudes (Yao et al. 2017; Waito et al. 2018). Grazing disturbance also
351 cannot be excluded. Comparative research on the treeline ecotone in other areas of the Tibetan
352 Plateau under human impact has found effects of animal grazing, especially in sites where nearby
353 human settlements exist (e.g. Miede and Miede, 2000). Grazing pressure may explain the lack of
354 recruitment before the 1960s at disturbed treelines. However, considering that livestock grazing
355 has always occurred near the disturbed treelines and that grazing intensity tends to increase with
356 the rise of local population (Baker and Moseley, 2007), grazing pressure did not likely reverse the
357 increasing trend in tree recruitment and limit treeline expansion.

358 Historical fire disturbances may have promoted upward shifts of treelines by reducing the
359 competitive pressure from alpine plants. A past fire had an initial negative effect on the
360 recruitment dynamics in the 1970s at the larch treelines but did not depress their elevations. More
361 importantly, trees have encroached and densified in the areas beyond the post-fire treeline
362 elevation, indicating a large upward treeline shift after the fire. The magnitude of advancement of
363 fire-disturbed larch treelines since 1980 explained most of the treeline advance during the last 50
364 and 100 years, suggesting that fire has played an important role in driving the upward movement
365 of treelines. In contrast, undisturbed larch or fir treelines have remained stable, providing further
366 evidence that fire could trigger or even promote upward treeline shifts. Fire may presumably
367 create favorable microsites for successful recruitment by removing competing vegetation and
368 clearing dense shrubs.

369 The TIs calculated for the alpine plant communities near or above the alpine treeline indicated
370 that the intensity of interspecific interactions differed between the undisturbed and fire-disturbed
371 treelines. Tree–shrub competition at undisturbed treelines is likely to limit recruitment of tree
372 seedlings for TIs > 0.8 (Liang et al. 2016). TIs < 0.8 at fire-disturbed treelines represented
373 conditions where low-density shrubs did not prevent tree recruitment above the treeline but

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

385 Other studies in boreal forests also showed that moderate-severity fire disturbances can
386 potentially accelerate the northward movement of treelines by positively influencing biotic factors
387 such as seed availability and seedling establishment, supporting our main results. In fact, the
388 ecological benefits of fire disturbances have been recognized (Stephens and Ruth 2005; Carswell
389 2018). However, high-severity fire disturbance would result in the contractions of forest
390 distribution and treeline retreat, thereby posing a major threat to some forest types (Bond and
391 Keeley 2005; Rolstad et al. 2017). In addition, the impacts of high-severity fires on forests might
392 be linked to tree species-specific traits (e.g., regeneration or adaptive strategy). For instance, North
393 American boreal black spruce forest generally takes advantage of fire because it produces semi-
394 serotinous cones that release seeds massively during a fire event and contribute to treeline
395 regeneration and expansion (Auger and Payette 2010). These studies highlighted that a deeper
396 understanding of fire-disturbed treeline dynamics under climate change should consider non-
397 climatic factors.

398 In summary, upward shifts of conifer treelines at our study sites likely were a consequence of
399 climatic warming, but disturbance by fire may have accelerated the rates by reducing competition
400 between tree seedlings and alpine shrubs. The elevation of undisturbed fir and larch treelines has

401 remained relatively stable despite climatic warming, presumably due to stronger interspecific
402 competition. Fires of low to moderate severity and other disturbances (e.g. grazing), which relax
403 negative species interactions, could therefore act as triggers to accelerate treeline dynamics and
404 couple these dynamics more strongly to climatic warming. As shown by this study, fire
405 disturbance provides a simplified model to detect how species interactions drive treeline shifts. It
406 provides additional evidence for the species interaction mechanism in controlling treeline
407 formation and its response to climatic change. Further work is expected to quantitatively evaluate
408 the effects of different fire severities on species interactions as well as on treeline shift rates.

409

410 **Author contribution statement** E.L. designed the research; Y.W., X.L. and E.L. performed the
411 research; All authors analyzed data and wrote the paper.

412

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421

422 **Compliance with ethical standards**

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

424

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580

581 **Table 1.** Description of the five study plots used to characterize treeline or timberline dynamics in
582 the Baima Snow Mountains, southeastern Tibetan Plateau. Plot code, plot size, latitude (Lat),
583 Longitude (Lon), elevation of current treeline (ECT), slope, fire disturbance (FD), tree density
584 (No, number of trees per hectare) are shown in the table.

Plot code	Plot size (m)	Tree species	Lat (N)	Lon (E)	ECT (m)	Slope (°)	FD	No
E1	30 × 500	<i>Larix potaninii</i>	28°21.308'	99°01.349'	4359	5	Yes	163
NE1	30 × 280	<i>Larix potaninii</i>	28°21.374'	99°01.494''	4417	19	Yes	544
NE2	30 × 270	<i>Larix potaninii</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>	28°20.899'	99°01.767'	4305	21	No	188

585

586

587 **Table 2.** Significance levels of two-sample Kolmogorov-Smirnov (K-S) tests showing the
 588 difference 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. NE	0.586	Undisturbed vs. undisturbed

589

590

591 **Table 3.** Comparison between treeline shifts during the three periods (1980-2014 vs. 1961-2014 and 1980-2014 vs. 1911-2014). The percentages were
 592 calculated by dividing the treeline shifts inferred for 1980-2014 and 1961-2014 or 1911-2014, respectively. The vegetation thickness index (TI, plant height
 593 \times cover) was used to indicate the species interactions beyond the treeline. TIs < 0.8 and > 0.8 represent facilitation and competition, respectively

Treeline plot	Tree species and fire disturbance	Mean shrub height above treeline (m)	Mean shrub cover above treeline (%)	TI	Magnitude of treeline shift (m a.s.l.)			Percentage (%)
					1911–2014	1961–2014	1980–2014	
E1	Larch, disturbed (1)	0.45 ± 0.07	90 ± 3.8	0.41	unknown	12	11	91.7, unknown
NE1	Larch, disturbed (1)	0.30 ± 0.06	75 ± 7.2	0.23	unknown	44	44	100, unknown
NE2	Larch, disturbed (1)	0.75 ± 0.07	89 ± 5.1	0.67	22	22	22	100, 100
NE3	fir, undisturbed (0)	2.2 ± 0.29	85 ± 3.8	1.87	2	2	NA	NA, NA
N1	Larch, undisturbed (0)	2.0 ± 0.26	82 ± 6.5	1.64	4	NA	NA	NA, NA

594 (see more details in Liang et al., 2016). Periods without trees are shown as “unknown”. Fire occurrence was indicated by binary variable (1, 0).

595

596

597

598 **Figures Caption**

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

603

604 **Figure 2.** Growth patterns for living and fire-killed larch trees forming the treeline. The grey and
605 black dashed lines denote the number of living and fire-killed trees, respectively.

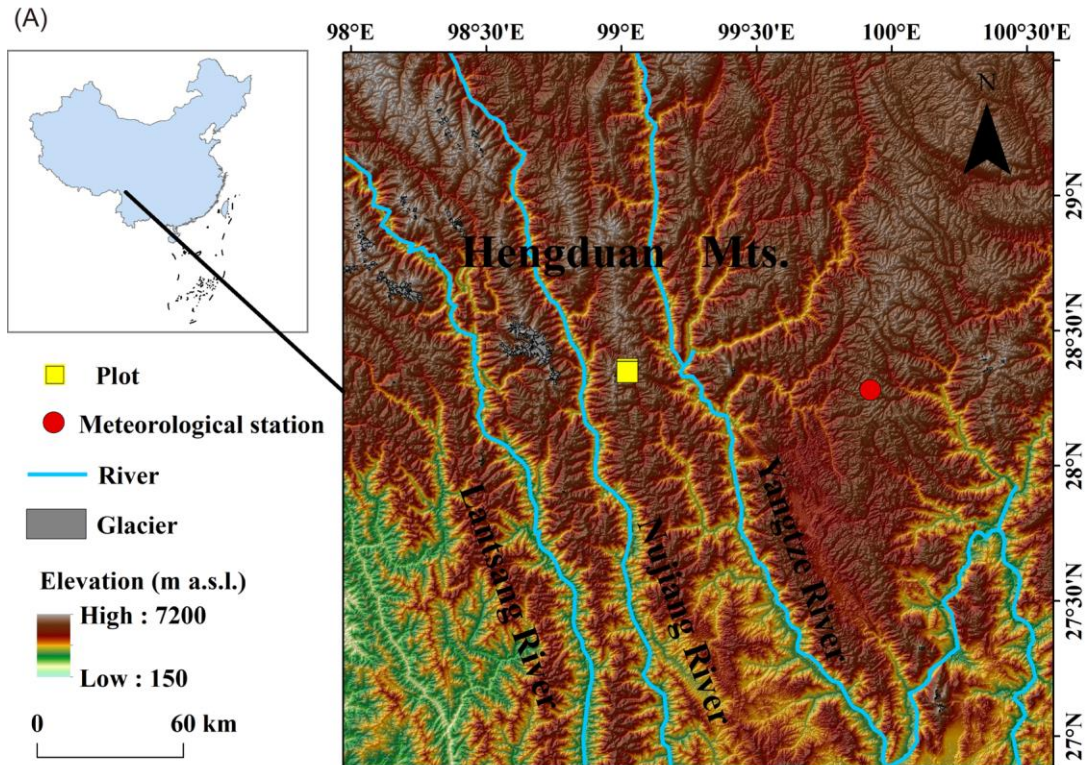
606

607 **Figure 3.** Long-term changes in summer temperature and abrupt changes in tree recruitment at the
608 treeline. Temperature series was reconstructed from tree rings on the southeastern Tibetan Plateau
609 (SE TP) (Zhu et al., 2011) (a). Analyses of data for abrupt changes (black horizontal lines) in tree
610 recruitment reconstructed for the treelines (b-f). Shifts were detected in the 1990s (b-d), 1970s (e),
611 1900s and 1980s (f), corresponding to abrupt increases in tree recruitment. All study plots
612 correspond to larch treelines, except the NE3 plot which was located at a fir treeline.

613

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

619



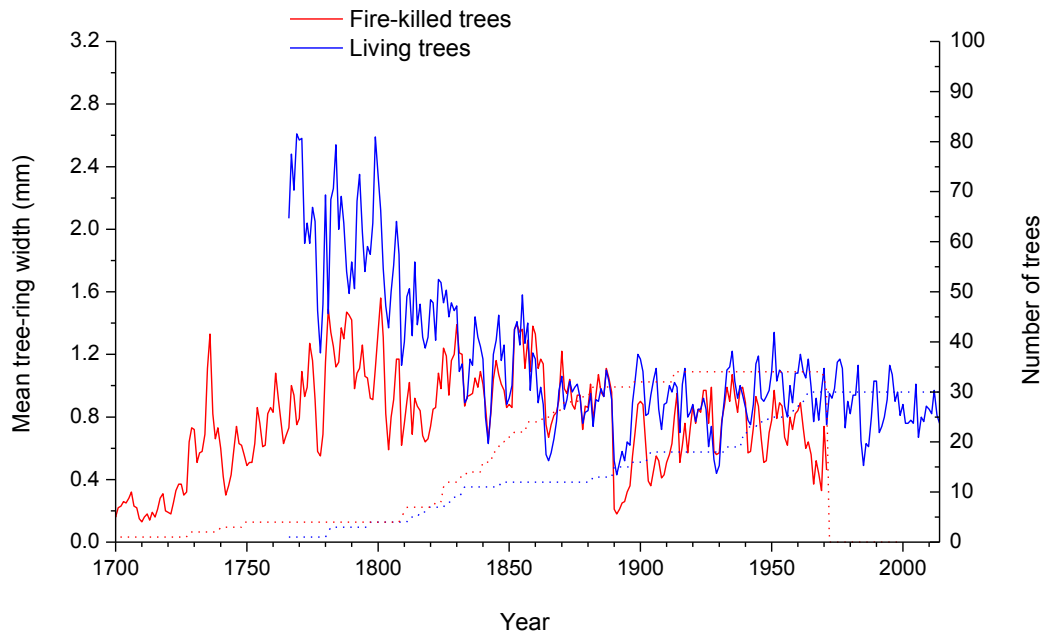
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621

622 **Figure 1**

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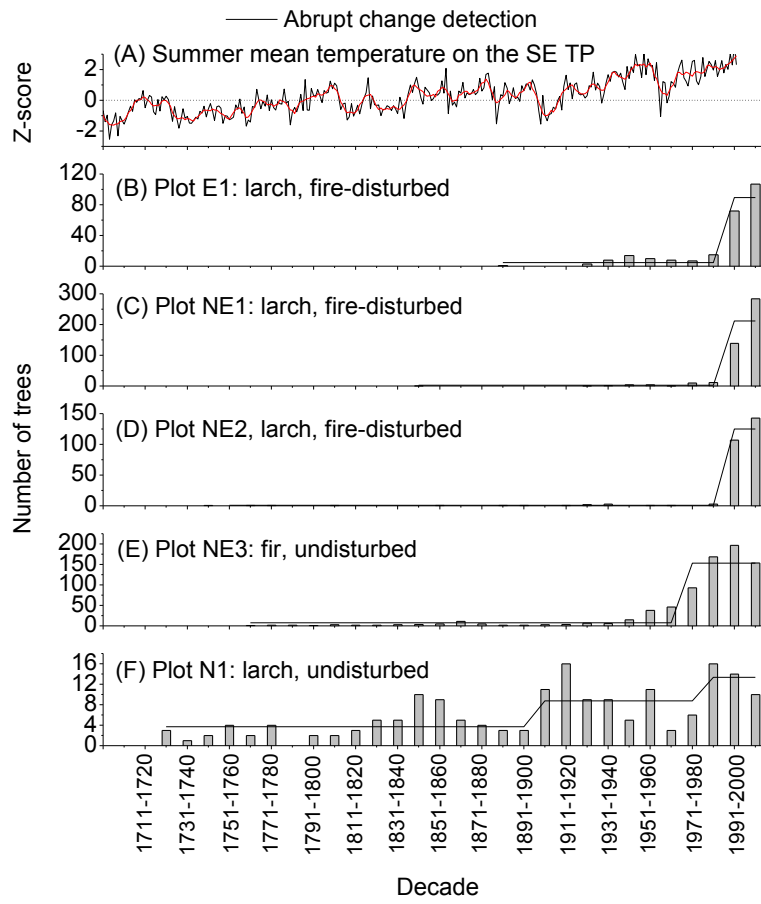
625

626 **Figure 2**

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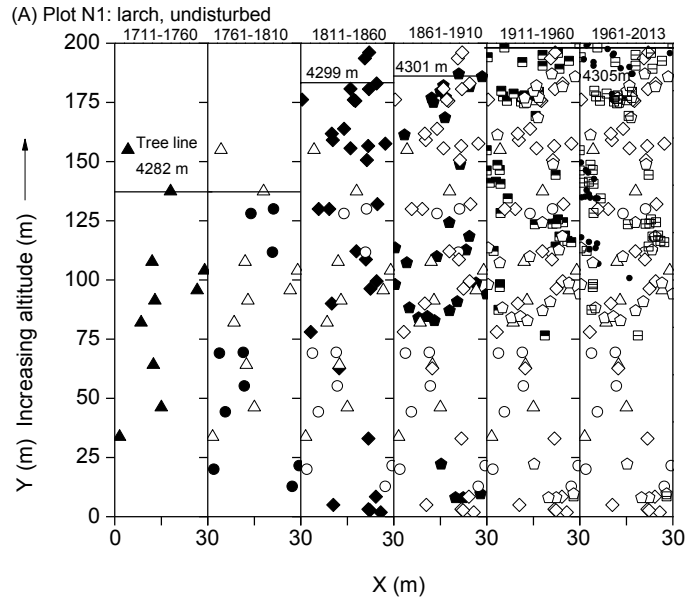
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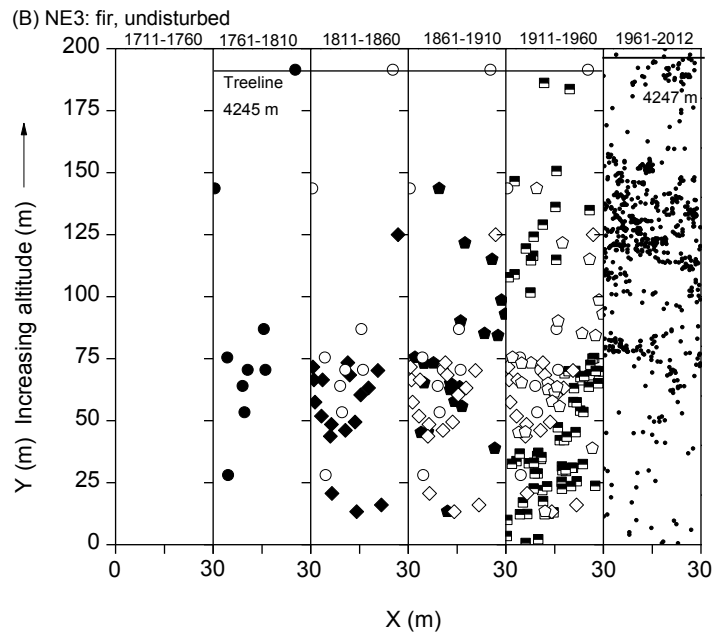
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631 **Figure 3**

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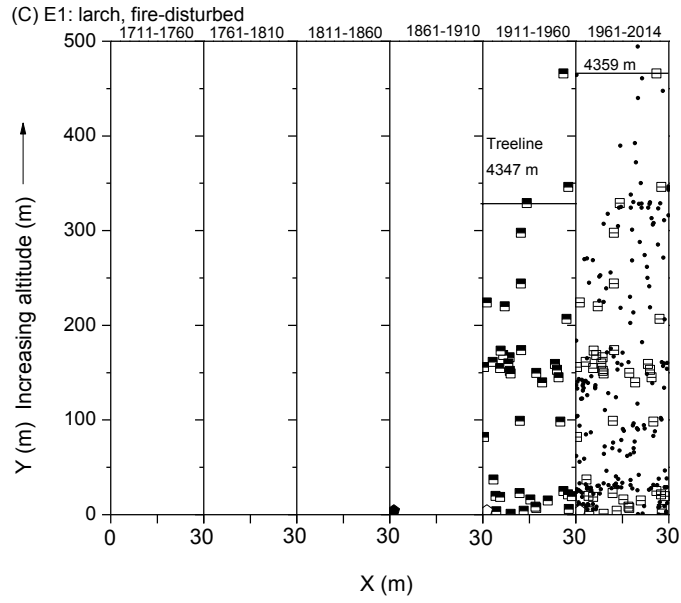
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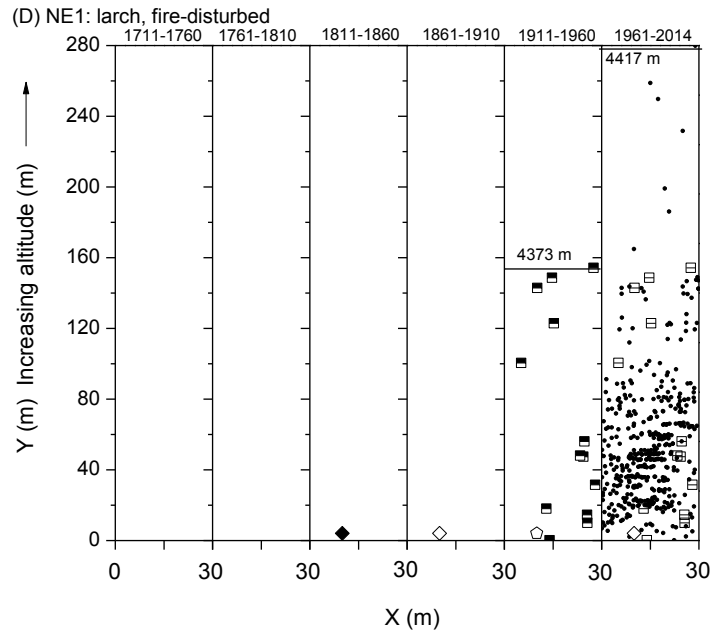
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635 (Continued)

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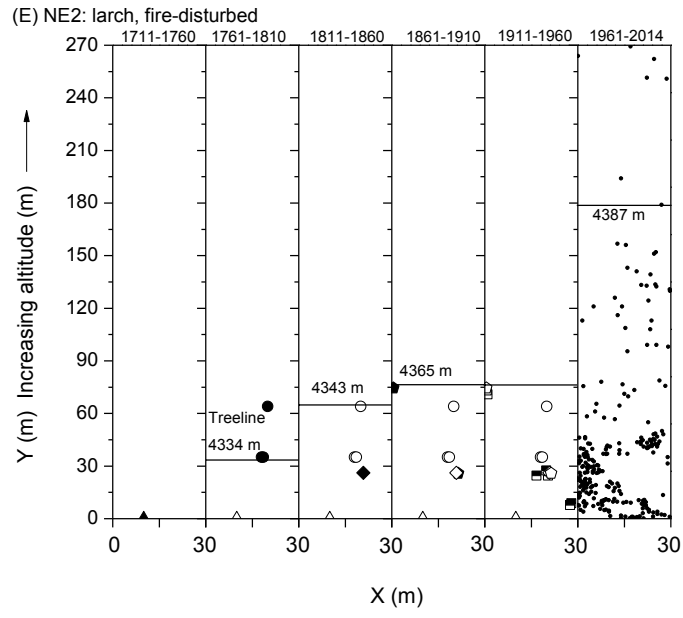
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639 (Continued)

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641

642 **Figure 4**

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644

645 **Supplementary information**

646 **Table S1.** Information about eight larch (*Larix potaninii*) seedlings located above current larch
647 treelines in the Baima Snow Mountains, southeastern Tibetan Plateau.

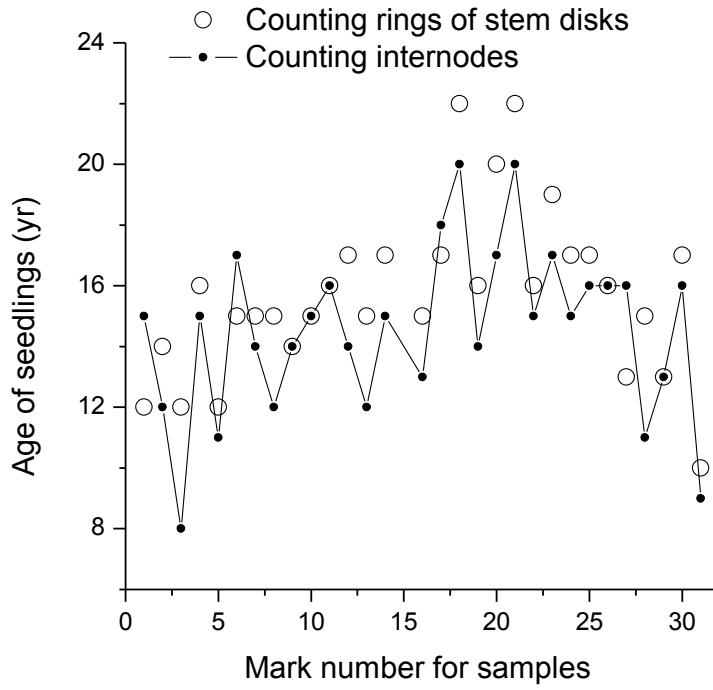
Seedling	Latitude (N), Longitude (E)	Altitude (m a.s.l)	Height (m)	Age (years)	Nearby plot
1	28°21.737', 99°01.215'	4416	0.60	25	E1
2	28°21.181', 99°01.182'	4416	0.35	18	E1
3	28°21.232', 99°01.178'	4435	0.40	19	E1
4	28°21.286', 99°0.955'	4499	0.40	26	E1
5	28°21.364', 99°01.158'	4448	0.67	23	NE1
6	28°21.642', 99°01.368'	4482	0.65	24	NE1
7	28°21.301', 99°0.945'	4501	0.65	21	NE1
8	28°21.313', 99°0.956'	4505	0.24	32	NE2

648

649

650

651 **Figure S1** Ages of seedlings obtained from counting the internodes and the rings of stem disks at
652 the treeline in the Baima Snow Mountains.



653

654