1 Article

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

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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.

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Introduction

The structure 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; Liu and Yin 2013; Greenwood et al. 2014; Liang et al. 2016; 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; Kirdyanov 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 were 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; Landhausser 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).

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 treelie 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 (±

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 (0.5m < 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 (CI = 0.76* 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

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, d). Young trees recruited since the 1990s accounted for the largest proportion of the treeline populations (Fig. 3) and had an approximately reverse J-shaped age structure. Recruitment pulses in the undisturbed larch N1 plot and fir NE3 plot were characterized by wave-like and rapidly rising recruitment patterns, respectively (Fig. 3e, f). Tree recruitment in the three fire-disturbed larch treelines or two undisturbed treelines did not differ significantly ($P > 0.05$, K-S tests) between plots (E1 vs. NE1, E1 vs. NE2 or NE1 vs. NE2; NE3 vs. NE1) (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).

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 occured 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

Discussion

315

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.

320   2011). However, climate warming is only one aspect of environmental change that could alter the

321   structure and position of treelines (Carrer and Urbinati 2006; Batllori and Gutiérrez 2008; Liang

322   and Camarero 2018). Apart from climate, other factors such as fire disturbance could buffer or

323   amplify warming impacts on treeline dynamics locally (Aakala et al. 2014). Given a wide

324   occurrence of fire disturbance in subalpine forests (Yao et al. 2017; Waito et al. 2018), it is a

325   challenge to investigate how fire disturbances mediate the responses of treelines to climate warming.

326   We found that treeline dynamics were jointly driven by fire and climatic warming. At least one

327   fire in the late 1960s drastically affected tree recruitment at the treeline. The lack of tree

328   establishment in fire-disturbed larch treelines during the 1970s could be attributed to the adverse

329   effect of a recent fire, given that the favorable warming conditions since the 1950s on the Tibetan

330   Plateau are generally linked to increased tree growth and recruitment (Liu et al. 2009; Yang et al.

331   2009; Liang et al. 2011, 2016; Liu et al. 2011; Zhu et al. 2011; Chen et al. 2016; Wang et al. 2016a).

332   The initial decrease in recruitment during the first 10 years after the fire could have been due to

333   damage to tree crowns and reduced seed production or to the lack of facilitation from short shrubs

334   which could become sparse after fire disturbance. As a control, a larger episode of recruitment in

335   the 1970s was detected at the undisturbed larch and fir treelines, providing indirect evidence for this

336   hypothesis. Recruitment at fire-disturbed sites, however, increased in the 1980s and increased

337   abruptly in the 1990s, suggesting a major acceleration in recruitment relative to the unburned sites,

338   which remained stable. This finding indicates that disturbances play a pivotal role in mediating the

339   responses of treelines to climatic warming (Aakala et al. 2014), as they do in forests (Turner et al.

340   2016). Young larch trees ranging in age from 20 to 30 years were found near or around the fire-

341   scarred trees across the treeline ecotones. This pattern suggests that a post-fire recruitment release

342   took place from the 1980s onwards, which would have allowed for the growth of post-fire recruited

343   seedlings and them reaching heights ≥ 2 m in recent decades.

344   Climatic warming may have a larger impact on the density than the position of undisturbed fir

345   treelines, whereas nearby fire-disturbed treelines have advanced substantially in the last century. A

346   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. Miehe and Miehe, 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

421

422   **Compliance with ethical standards**

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

424

425   **References**

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580

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, plot size, latitude (Lat), Longitude (Lon), elevation of current treeline (ECT), slope, fire disturbance (FD), tree desnity (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	*Larix potaninii*	28°21.308'	99°01.349'	4359	5	Yes	163
NE1	30 × 280	*Larix potaninii*	28°21.374'	99°01.494''	4417	19	Yes	544
NE2	30 × 270	*Larix potaninii*	28°21.557'	99°01.239'	4387	19	Yes	323
NE3	30 × 200	*Abies georgei*	28°20.955'	99°01.912'	4247	25	No	1295
N1	30 × 200	*Larix potaninii*	28°20.899'	99°01.767'	4305	21	No	188

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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

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Table 3. Comparison between treeline shifts during the three periods (1980-2014 vs. 1961-2014 and 1980-2014 vs. 1911-2014). 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. 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.sl.)			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

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

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Figures Caption

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

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

Figure 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.

Figure 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 symbos denote an individual that was established during the period indicated at the top of each plot, whereas open symbols respresent trees established during previous periods. Different symbols correspond to different tree establishment periods.
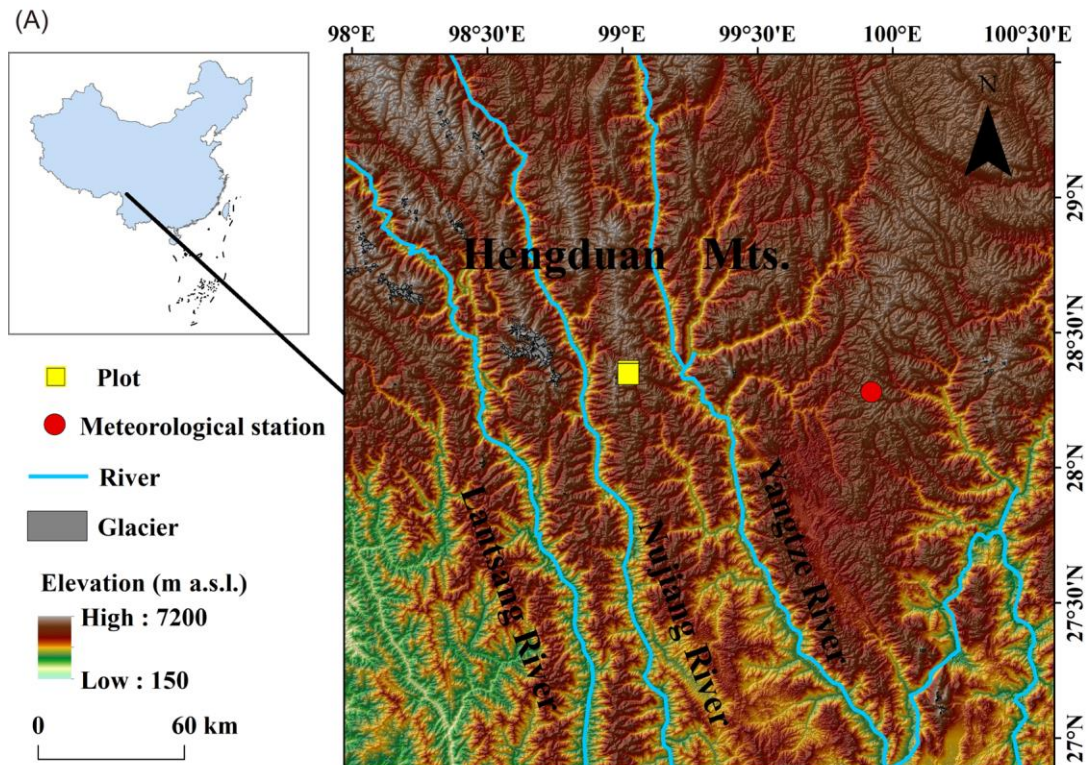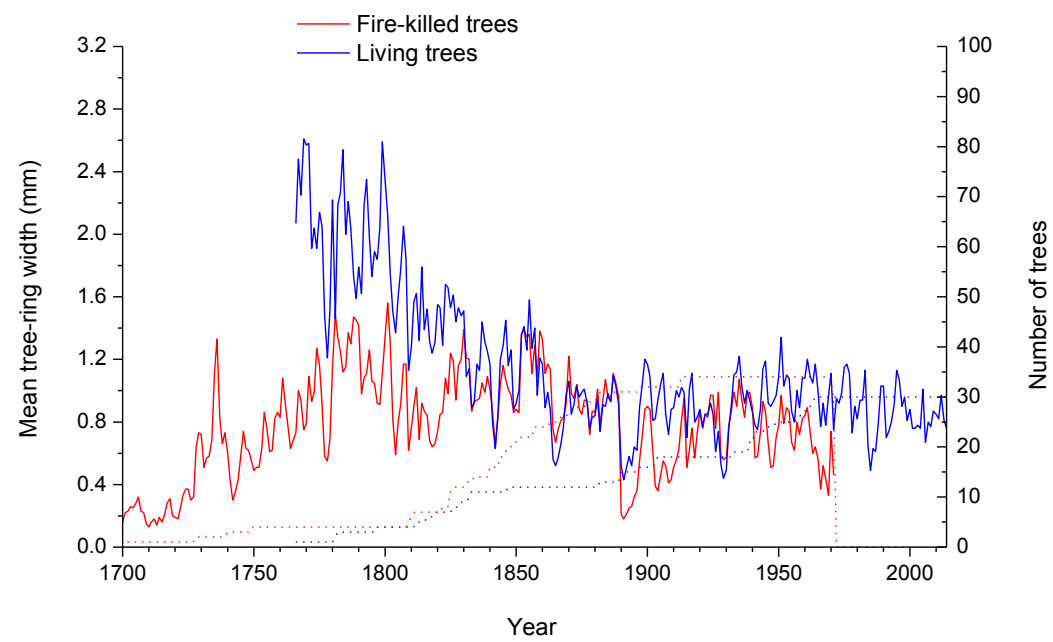
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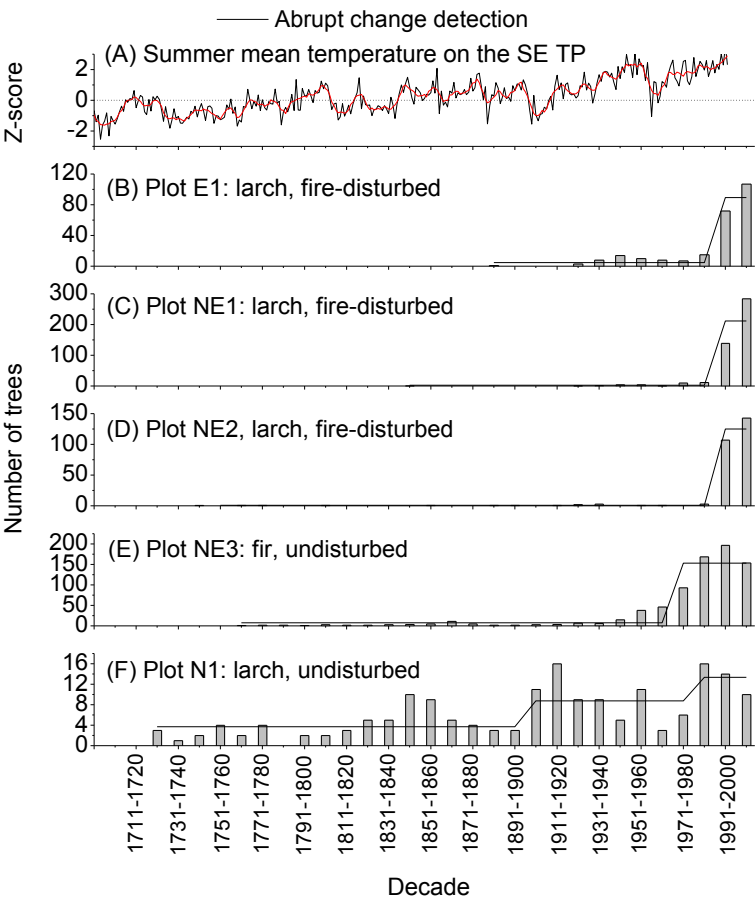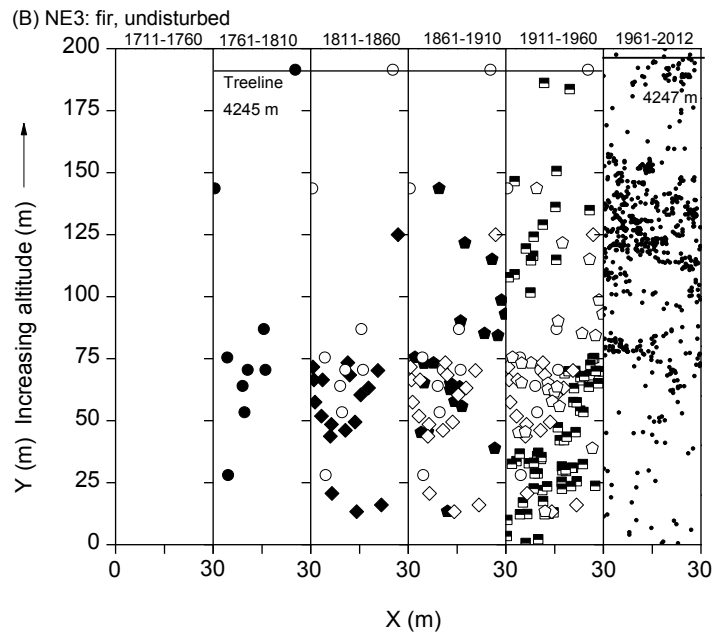621

622 **Figure 1**

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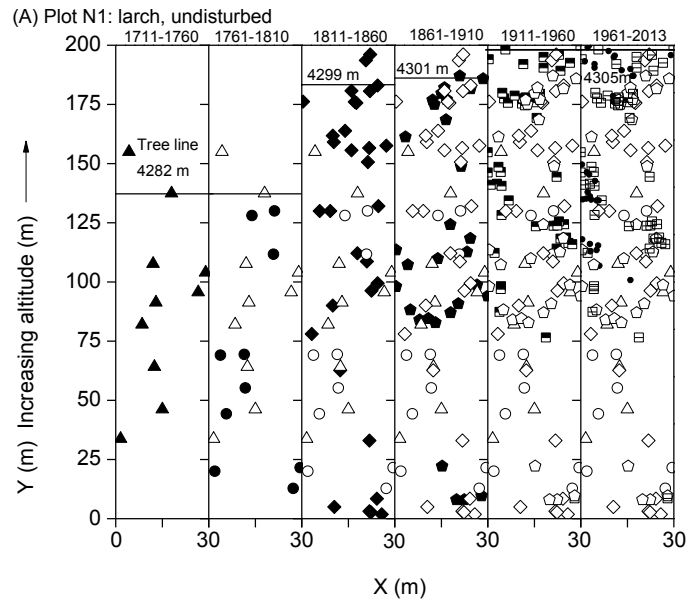
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Figure 2

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631 **Figure 3**

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(A) Plot N1: larch, undisturbed

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(B) NE3: fir, undisturbed

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635   **(Continued)**

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(C) E1: larch, fire-disturbed

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(D) NE1: larch, fire-disturbed
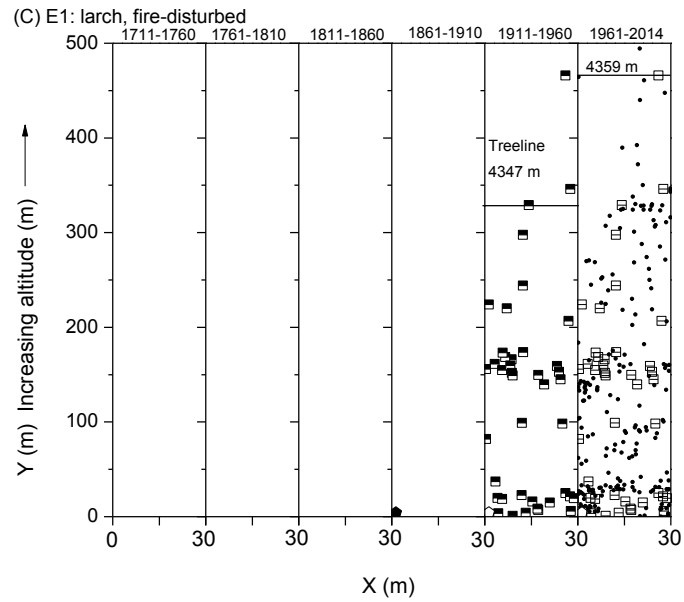
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639   **(Continued)**

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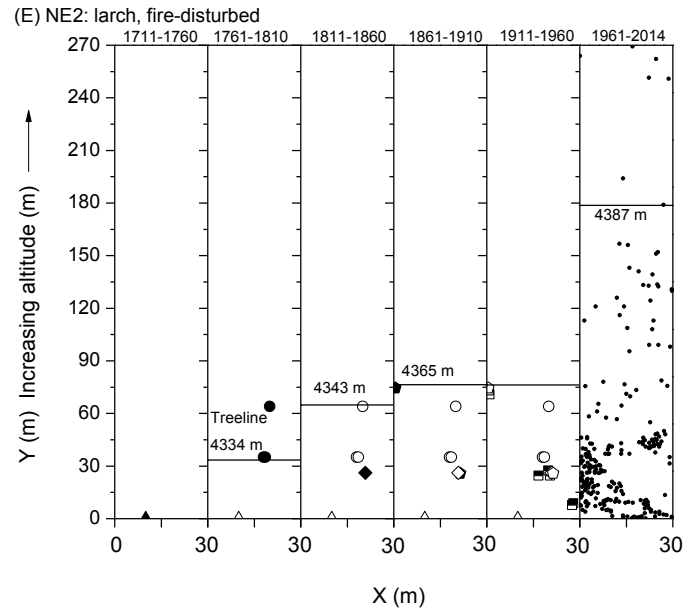(E) NE2: larch, fire-disturbed
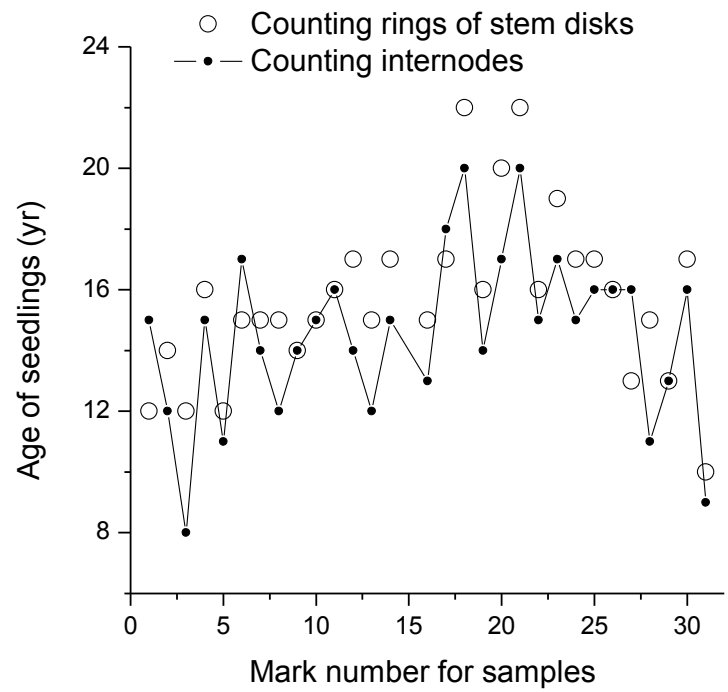
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642 **Figure 4**

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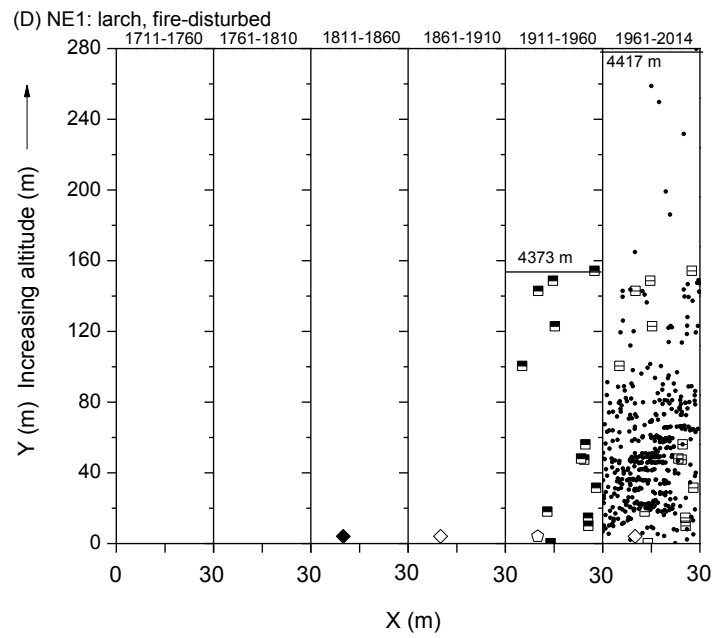
Supplementary information

Table S1. Information about eight larch (*Larix potaninii*) seedlings located above current larch

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

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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.

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