

Regional Environmental Change

From Himalaya to Hengduan: Alpine Treelines Dynamics Under Climate Change

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| Abstract: | <p>Alpine treelines serve as vital indicators of the impacts of climate change on tree growth and forest distribution. They offer valuable insights into how shifting temperature and precipitation patterns affect ecosystems in treeline ecotones. Analyzing the age structure of tree stands at treelines provides a glimpse into how different generations of trees have responded to changing environmental conditions and aids in predicting future changes. Moreover, studying the spatiotemporal distribution of tree species at treelines helps us gain a comprehensive understanding of how forests adapt to climate variations. Tree rings at treelines can elucidate the climatic factors that limit tree growth and establishment patterns. Mountain environments, characterized by low temperatures at higher elevations, create constraints on tree growth. However, the intricate interplay between temperature and water availability, driven by precipitation gradients, means that predicting treeline shifts based solely on temperature changes is overly simplistic and may not fully reflect the complex reality. To assess the potential for such interactions, we contrasted the dendroecological performance of different tree species (<i>Abies spectabilis</i>, <i>Betula utilis</i>, <i>Abies georgei</i> and <i>Larix potaninii</i>) in the trans-Himalayan zone, Nepal and Hengduan Mountains, China. We reconstructed the stand age structure by using dendrochronology. Statistical determination of climate-growth responses demonstrated that treeline is moisture sensitive in Himalaya, and temperature as well as moisture sensitive in Hengduan region. There was abundant seedling recruitment with consistent range shift of <i>A. spectabilis</i> and <i>B. utilis</i> treelines in Nepal, and lower seedling recruitment with lower shifting rates of treelines of <i>A. georgei</i> and <i>L. potaninii</i></p> | |

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| | in Hengduan Mountains. We identify both moisture and temperature as critical environmental factors in determining tree radial growth and treeline response to climate. However, modifying factors such as microhabitat conditions and biotic interactions are also highly important to improve accuracy of treeline dynamics. |
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1 From Himalaya to Hengduan: Alpine Treelines Dynamics Under Climate Change

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14 Abstract

15 Alpine treelines serve as vital indicators of the impacts of climate change on tree growth and
16 forest distribution. They offer valuable insights into how shifting temperature and precipitation
17 patterns affect ecosystems in treeline ecotones. Analyzing the age structure of tree stands at
18 treelines provides a glimpse into how different generations of trees have responded to changing
19 environmental conditions and aids in predicting future changes. Moreover, studying the
20 spatiotemporal distribution of tree species at treelines helps us gain a comprehensive
21 understanding of how forests adapt to climate variations. Tree rings at treelines can elucidate the
22 climatic factors that limit tree growth and establishment patterns. Mountain environments,
23 characterized by low temperatures at higher elevations, create constraints on tree growth.
24 However, the intricate interplay between temperature and water availability, driven by
25 precipitation gradients, means that predicting treeline shifts based solely on temperature changes
26 is overly simplistic and may not fully reflect the complex reality. To assess the potential for such
27 interactions, we contrasted the dendroecological performance of different tree species (*Abies*
28 *spectabilis*, *Betula utilis*, *Abies georgei* and *Larix potaninii*) in the trans-Himalayan zone, Nepal

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29 and Hengduan Mountains, China. We reconstructed the stand age structure by using
30 dendrochronology. Statistical determination of climate-growth responses demonstrated that
31 treeline is moisture sensitive in Himalaya, and temperature as well as moisture sensitive in
32 Hengduan region. There was abundant seedling recruitment with consistent range shift of *A.*
33 *spectabilis* and *B. utilis* treelines in Nepal, and lower seedling recruitment with lower shifting
34 rates of treelines of *A. georgei* and *L. potaninii* in Hengduan Mountains. We identify both
35 moisture and temperature as critical environmental factors in determining tree radial growth and
36 treeline response to climate. However, modifying factors such as microhabitat conditions and
37 biotic interactions are also highly important to improve accuracy of treeline dynamics.

38 Key words: *Trans-Himalaya; Hengduan Mountain; treeline; timberline; ecotone; range shift;*
39 *limiting factor; regeneration*

40 Total word count: 9594 (including figures and tables)

41 **1 Introduction**

42 Alpine treelines are the conspicuous transition zone between timberline and treeless alpine
43 vegetation (Körner 2003). Near-natural treelines are typically climate-limited and thus valuable
44 indicators of changing climate (Kullman 2002; Körner and Paulsen 2004; Batllori and Gutiérrez
45 2008). Alpine treelines have been reported to be shifting upwards in response to global warming
46 (Grace et al. 2002; Holtmeier & Broll 2007; Harsch et al. 2009; Hansson et al. 2020). The
47 formation of the upper distributional limit of the tree life form according to thermal balance
48 (Körner 1998, 2003, 2012; Holtmeier & Broll 2007; Harsch et al. 2009) emphasises that climate
49 warming is expected to promote forest growth at their elevation range edge, to generate
50 densification of ecotone and to advance treelines upward in the elevation (Grace et al. 2002;
51 Dullinger et al. 2004; Smith et al. 2009). However, for comparatively dry and semiarid zones,
52 treeline position is frequently limited by drought stress (Lloyd and Fastie 2002; Wilmking et al.
53 2004; Qi et al. 2015; Tiwari et al. 2017a). In such regions, current warming may exacerbate

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54 moisture stress and even may cause retreat of treelines downslope. For the Himalayan region,
55 evidence suggests treeline shift rates are driven by moisture availability during the dry season
56 (Tiwari et al. 2017a; Sigdel et al. 2018). Great uncertainties still prevail at explaining treeline
57 response to rapidly changing climate because treelines do not always keep pace with climatic
58 change on multi-decadal time scales, as the displacement and adjustment of alpine trees to
59 warmer climate can require decades or even centuries (Kullman 2007).

60 Tree encroachment into grass and shrub-dominated high-altitude ecosystems is pervasive
61 under warming climate (Formica et al. 2014; Huss et al. 2017; Mainali et al. 2020). In alpine
62 regions, woody plant expansion through densification and infilling of canopy gaps and
63 advancement of treelines has been widely observed under warming climate (Myers-Smith et al.
64 2011; Liang et al. 2011b; Gaire et al. 2014; Camarero et al. 2017). Forest densification within the
65 treeline ecotone can be more responsive to climate change than treeline shifting, due to biotic
66 interactions providing a more benign environment for tree recruitment when sheltered by
67 conspecifics than in open areas above the treeline (Liang et al. 2016; Morley et al. 2020). Hence,
68 treeline shift is a consequence of shifts in vegetation zone associated with abundant tree
69 establishment at the upper edge of the treeline ecotone (Greenwood et al. 2014).

70 The elevational treeline environment is very heterogeneous, which limits broad
71 generalization on treeline sensitivity to climate because of topographic variation (Daniels and
72 Veblen 2004; Elliott and Kipfmüller 2011; Greenwood et al. 2014) and also because of intense
73 human activities mainly related to declined land use intensity (Schickhoff et al. 2015). Seedling
74 recruitment, stand densification and rate of upward shifting of the treeline can greatly vary
75 between surface gradients (slope) and orientation (aspects) due to substantial difference in soil
76 conditions and intensity of solar radiation (Danby and Hik 2007; Matzinger et al. 2003), and due

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4 77 to other factors such as stand history, dispersal ability of tree species, disturbance and ecological
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6 78 interactions (Schloss et al. 2012).
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10 79 Various studies have reported upward shifts of the *Abies spectabilis* treeline, both in
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12 80 temperature sensitive (Gaire et al. 2014, Mainali et al. 2014) and moisture sensitive (Tiwari et al.
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15 81 2017a) ecotones in the Himalaya, although there are some evidences for stable position during
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17 82 the past century (Sigdel et al. 2018). Although there are climatic as well as non-climatic factors
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20 83 involved in determining treeline dynamics, shifting treelines have been reported from Hengduan
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22 84 Mountains (20 m in elevation in the past 100 years) (Liang et al. 2016), in northwestern Yunnan,
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25 85 (Moseley 2006; Baker and Moseley 2007), and in Baima snow mountain in the central part of
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27 86 Hengduan Mountain in China (Wang et al. 2019a).
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30 87 The Himalaya and Hengduan Mountain regions are rapidly warming regions of the
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33 88 northern hemisphere. Trends in much of the Himalayan region substantially exceed the global
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35 89 average trend of warming (IPCC 2013), with the decreasing number of cold days and nights and
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38 90 increasing number of warmer days and nights making most ecosystems vulnerable to climate
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40 91 change (Shrestha et al. 2012; Sharma and Tsering 2009; Aryal et al. 2012). Moreover, the Hindu
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42 92 Kush Himalayan (HKH) region showed the annual mean warming rates of 0.19 °C/decade during
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45 93 the period 1901–2014, while that of 1951–2014 period was 0.20 °C/decade (Ren et al. 2017), and
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47 94 the substantial increase in length of growing season (Krishnan et al. 2019). Observed trends in
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50 95 Hengduan Mountain show increasing temperature of the warmest and coldest nights by 0.016
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52 96 °C/yr and 0.055 °C/yr respectively, a decrease in the number of frost and ice days, and an
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55 97 increase in the length of the growing season during the past half-century (Ning et al. 2012).
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57 98 However, the widespread increase of air temperature and variation in precipitation trends
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60 99 associated with strong topographic gradients and rain shadow effects are largely responsible for
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4 100 the complex climate system in both Himalayas (Schickhoff 2005) and Hengduan mountains
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7 101 (Ning et al. 2012) raising significant questions about how treelines of the region might respond
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9 102 to climate change.

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12 103 In this study we wanted to test if the climatic factors only modulate the treeline dynamics
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15 104 or if there are other driving factors such as land use changes including grazing pressure, fire and
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17 105 human activities. Hence, we sought to determine how treelines in the Trans-Himalaya region and
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20 106 Hengduan Mountains are responding to climate change across adult growth and tree
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22 107 establishment. To do so, we quantified climate-growth relationships at treeline ecotones,
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25 108 analysed spatiotemporal distribution of adults and juveniles in the treeline ecotone, and
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27 109 quantified approximate shifts of the treeline. Specifically, we aimed to (1) identify limiting
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30 110 factors of tree growth at high mountain treelines, and (2) analyze spatiotemporal dynamics of
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32 111 altitudinal treeline.

33 34 35 112 **2 Methods**

36 37 38 39 113 **2.1 Study site description**

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41 114 The study was carried out in the Trans-Himalayan zone of central Nepal and Hengduan
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44 115 Mountains (Southeast Tibet) of China. In central Nepal, the study sites are located at Chimang
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46 116 (28.72° N, 83.69 E, 3500-3638 m asl) and Lete lekh (28.61° N, 83.59° E, 3900-4100 m asl) in
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49 117 the southern part of Mustang District (Fig. 1). Mustang represents a typical rain shadow zone in
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51 118 the central Himalaya, surrounded by high mountains in the southeast and west, and constitutes
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54 119 only about 3.24% land as forests in the southern part (Government of Nepal 2010). The northern
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56 120 part lies in the Trans-Himalayan semi-arid dry zone, and the further north has the Tibetan type of
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59 121 highland forming the driest zone of Nepal (Lomanthang: 200 mm annual rainfall) (Stainton

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1972; Schickhoff 2005). We contrasted a relatively dry region (Chimang) with about 390 mm annual precipitation and a relatively wet region (Lete) with about 1300 mm annual precipitation in our study. In Hengduan Mountain, the study was conducted at Tianbao Mountain in Sangri-La County (Yunnan province; 27.61° N, 99.89° E, 4000 m asl) and at Maan Mountain in Xiangcheng county (Sichuan province; 29.320 N, 100.540 E, 4400 m asl) of China (Fig. 1). Maan Mountain in Xiangcheng County is situated at the western Sichuan and Eastern Tibet coniferous forest region characterised by high mountain, deep valleys, and highlands with a monsoon-influenced humid continental climate on the southeastern edge of Qinghai-Tibet Plateau, where the altitude varies from 1500 to 6000 m (Wang et al. 2012). The meteorological data showed mean annual rainfall of 633 mm with mean summer rainfall (June-September) accounting for about 84% of annual rainfall at Daocheng (northern Hengduan region) (1958-2014 AD as shown by the climate station data: National Meteorological Information Center of China). Meteorological records showed distinct climatic trend in Himalaya and Hengduan Mountains (Fig. 2). Trans Himalayan sites (Lete and Chimang) showed significant warming with a consistent increase of annual temperature during recent decades; these sites showed distinct rainfall pattern; Lete (L1, L2) being relatively moist with a significant increase in annual rainfall, and Chimang (C1, C2) being relatively dry due to stable trend of rainfall.

The Hengduan Mountain region showed significant warming in recent decades with consistent increase in mean temperature (Fig. 2). Tianbao treeline site (Tb) showed a stronger warming trend than Xiangcheng treeline sites (X1, X2) in the same time period (Figure 2), likely due to the complex topography of the region. Both sites in Hengduan region showed a stable trend in precipitation.

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We selected four treeline species from these regions, two evergreen; *Abies spectabilis* (D. Don) Spach and *Abies georgei* var. *smithii* (Viguie & Gausсен), and two deciduous; *Betula utilis* (D. Don) and *Larix potaninii* Batalin (var. *macrocarpa*). *A. spectabilis* (Himalayan fir) usually grows under moist climatic conditions in sub-alpine Himalaya forests (3000 to 4000 m asl), occasionally extending its upper limit to 4300 m asl. It is usually associated with *B. utilis* and *Rhododendron campanulatum* at its upper limit (Yadav et al. 2004). *Betula utilis* (Himalayan birch) is a moderate-sized (< 20 m tall) broadleaved pioneer tree species and dominates an extensive area of subalpine and alpine forests up to 4500 m elevation, quite close to glaciers on northern slopes of the inner Himalayas (Stainton 1972; Miede et al. 2015). *Abies georgei* var. *smithii* (Viguie & Gausсен) is a common tree species up to 30 m tall and found in subalpine dark coniferous forest on the southeast of Qinghai-Tibet Plateau, growing mostly as alpine-subalpine coniferous forests at 2500-4200 m. Whereas, *Larix potaninii* (Chinese larch) is usually found in mountains and river basins from 2500-4600m asl. growing up to 50 m tall this is one of the earliest species used in dendroclimatic studies in China and is highly sensitive to environment variations, exhibiting tremendous potential for usage in dendroclimatology (Sun et al. 2010).

2.2 Sample collection and processing

Field study and tree core sample collection were carried out during September of 2014 in the Himalayan sites and, during March-June of 2015 in Hengduan sites. Plot-sampling by placing elevation transects (20 m × 90-120 m) across the alpine treeline ecotone were laid to include the uppermost species' limit (irrespective of age) and timberline trees. Altogether we studied 7 transects in monospecific treelines; two at three treeline sites and only one at Shangri-La treeline site. We defined treeline as the uppermost elevation of trees (2 m height) and timberline as the uppermost closed forest with tree cover (trees > 5 m height) of at least 30% (Holtmeier 2003).

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4 168 The longer axis of each plot was parallel to the altitudinal gradient of subalpine forest to alpine
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6 169 shrub land. For each plot, the location of each individual tree was mapped. The altitudes of lower
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9 170 and upper parts of the plots were recorded by GPS.
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11 12 171 **2.3 Tree ring series** 13

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15 172 Tree cores were collected from *A. spectabilis*, *B. utilis*, *A. georgei* and *L. potaninii* using a 5.5
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17 173 mm increment borer. One, two or multiple cores were extracted from the base of each tree (basal
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20 174 tree core: below 30 cm height). Tree cores were air dried and mounted on sample holders with
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22 175 vertical alignment of tracheids. The surface was then sanded using progressively finer sandpaper
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24 176 until the ring boundaries were visible (Fritts 1976). Ring widths were measured at a resolution of
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27 177 0.01 mm with a LINTAB II measuring system (Rinntech, Germany). Tree cores were cross-dated
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30 178 by visual inspection (Stokes and Smiley 1996) and by statistical tests (sign-test and t-test) using
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32 179 the software package TSAP-Win (Rinn 2003). We produced the individual site chronologies for
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34 180 each treeline site, however a composite site chronology was produced by combining Chimang
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37 181 (C1 and C2) treeline sites as the sites were close to each other. Ring-width measurements were
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39 182 detrended with a negative exponential or a linear regression function, with the help of ARSTAN
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42 183 software (Cook 1985). Detrending was performed to maximise the common signal among
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44 184 individual tree-ring series (Cook and Kairiukstis 1990). Variance stabilization (Osborn et al.
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47 185 1997) was applied to adjust for changes in variance associated with declining sample size
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49 186 (number of trees) over time. Descriptive statistics were calculated for the standardized
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52 187 chronologies (Parr and Phillips 1999). The quality of site chronology was indicated by signal-to-
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54 188 noise ratio and expressed population signal (EPS). A level of 0.85 for EPS was considered to
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56 189 indicate satisfactory quality and characteristics of a chronology (Wigley et al. 1984).
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190 **2.4 Stand age structure**

191 We dated the stand age structure of treeline ecotones by ring counts of the basal tree cores of
192 each individual tree. In the case of tree cores with missed pith, the number of missing rings was
193 determined by geometric method (Duncan, 1989) to estimate the age of the tree. The ages of
194 saplings and seedlings (height < 2 m and DBH ≤ 5 cm height) were estimated non-destructively
195 in the field by counting terminal bud scars along the main stem (Camarero and Gutierrez 2004),
196 and the seedling/sapling ratio was calculated for each treeline site. We also recorded all dead
197 trees per transect during the field visit. We surveyed a total of 954 individuals of treeline species
198 (480 trees, 209 saplings and 175 seedlings) in seven treeline ecotones (C1, C2, L1, L2, Tb, X1,
199 and X2) (Fig. 7). The seedlings >20 cm tall were only included in density estimations
200 considering low likelihood of successful establishment of smaller seedlings (< 20 cm tall).

201 **2.5 Treeline movement**

202 The potential advance of the tree species limit for each treeline transect within study area was
203 calculated by subtracting the elevation of oldest position of the tree limit (down slope) from the
204 elevation of the youngest tree (2 m height) position (upslope) and using the following equation
205 (Gamache and Payette 2005).

206 Rate of shift (per year) = Upper most elevation of youngest tree – upper most elevation of oldest
207 tree / Age of oldest tree – Age of youngest tree

208 **Data analysis**

209 Growth–climate response was analyzed by individual regression models and stepwise regression
210 models. Monthly climate comparison of 19-month period from June of the year prior to ring
211 formation, up until December of the year of ring formation, as well as during winter (previous
212 year November-current year February), spring (current year March-May), summer (current year

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213 June-September) and annual climate. These periods include late growing season of previous
214 year, intervening winter/spring and the growing season of the current year of ring formation
215 which allows an evaluation of any effects of preconditioning by climate before the growing
216 season (Fritts 1976; Cook & Kairiukstis 1990; Biondi & Waikul 2004). Analysis of variance
217 (ANOVA) was used to estimate the different in ring-width indices (RWI) between and among
218 the sites with Tukey's Post-hoc test at 95% confidence intervals level ($p = 0.05$). We used
219 multiple regression to determine the coefficient of determination (R^2) and predicted the
220 relationship between RWI and climate variables. We also used Person Correlation to establish
221 the relationship between climate variables and tree establishment year. Climatic data were
222 collected and computed from daily data for the period of 1976–2012 from central Himalaya sites
223 (Thakmarpha and Lumle meteorological stations of Nepal) and Hengduan Mountain sites
224 (Shangri-La and Daocheng meteorological stations of China), and the data were obtained from
225 Department of Hydrology and Meteorology Government of Nepal, and National Meteorological
226 Information Center of China.

227 To determine which of our potential predictor variables were correlated to RWI, we first
228 performed simple linear regression for each variable and RWI of trees from all sites. This was
229 performed separately for each site. Based on this initial analysis, we dropped predictors which
230 were not significantly correlated ($p > 0.05$) to the ring width indices for the respective
231 comparisons. The remaining predictors were used in a stepwise regression. Variables were
232 included in the model based on Akaike Information Criterion (AIC) adjusted for small sample
233 size such that the summed probability of the models (Buckland et al. 1997, Calcagno and de
234 Mazancourt 2010). To further simplify the multiple regressions and develop the final models, we

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235 eliminated variables which were highly correlated and with no biological relevance. Statistical
236 analyses were performed using R 4.0.3 (R Development Core Team 2020).

237 **3. Results**

238 **3.1 Tree Ring-width Chronology**

239 We produced well replicated ring-width chronologies with length from 68 to 374 years from six
240 sites of the central Himalaya and Hengduan Mountains (combining two nearby transects of *A.*
241 *spectabilis* sites in Himalaya) (Fig. 3). These chronologies showed valid statistical criteria used
242 in common dendrochronological studies including mean inter-series correlation (R_{bar}), mean
243 sensitivity, mean ring-width index, standard deviation, first-order autocorrelation and expressed
244 population signal (EPS) values (Table 1). The population representation for sampled trees with
245 $EPS > 0.85$ is usually considered as a reliable indicator. However, we considered tree-
246 chronologies from the year 1976 for subsequent analyses given that available instrumental
247 climate data were limited to this period.

248 **3.2 Growth climate response**

249 After examining growth climate correlations, we emphasized monthly and seasonal
250 variables which revealed a significant relationship with radial growth (Fig. 4, $p < 0.05$). The
251 growth climate analysis demonstrated contrasting climate signal in tree rings from Trans-
252 Himalayan and Hengduan Mountain sites with strong precipitation and temperature signals at
253 Trans-Himalayan sites and mainly temperature signal at Hengduan Mountains (Fig. 4 and Table
254 2).

255 Considering regression models with individual variables, some of the topmost
256 influencing variables on tree growth (*A. spectabilis*) across treeline of Trans-Himalayan site (C)

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257 were precipitation from May and Winter, and January minimum temperature, April average
258 temperature and growing season temperatures ($p < 0.05$, Figs. 4, 5 and 6). Tree growth of
259 relatively moist L1 site was strongly related to precipitation from January and March, and
260 previous August average temperature, January maximum temperature, March average
261 temperature and growing season average temperature whereas L2 was related to March
262 precipitation, March average temperature, and growing season average temperature. Tree growth
263 of Hengduan site was primarily related to only temperature variables ($p < 0.05$, Figs. 4, 5 and 6).
264 Tree growth in Tb site was strongly related to minimum temperature of January, August and
265 winter months. August average temperature and September average temperature were also
266 related to growth of trees in rage Tb site. RWI of X1 site was corelated to minimum temperature
267 from September (previous), January, September, winter, summer months, and average
268 temperature of May, August, September, growing season months ($p < 0.05$, Figs. 4, 5 and 6).
269 However, the strength of the relationship was slightly different.

270 Multiple regression analysis of climate variables with RWI yielded a regression
271 coefficient (R^2) of 0.50, 0.61, and 0.49 across relatively dry sites (C) and moist sites (L1 and L2)
272 of Trans-Himalaya, respectively (Table 2). Annual growth of *A. spectabilis* was primarily
273 influenced by temperature and precipitation. However, the strength of the relationship with
274 temperature (inverse relation with growing season maximum and January minimum temperature)
275 was greater compared to that of precipitation (positive relation with growing season
276 precipitation). Annual growth of *B. utilis* tree across the moist treeline site of Trans-Himalaya
277 (L1 and L2) showed an inverse relationship with January precipitation and growing season
278 average temperature and was positively related to March precipitation. However, at site L2, RWI

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4 279 was related to August precipitation from the previous year (negative) and January maximum
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10 281 Multiple regression analysis of climate variables with radial growth yielded a total $R^2 =$
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12 282 0.34, 0.51, and 0.52 across relatively dry sites (Tb) and cold alpine site (X1 and X2) of
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15 283 Hengduan Mountains, respectively (Table 2). August average temperature from the previous
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17 284 year was primarily related to RWI of *A. georgi* across the dry treeline (Tb) of Hengduan
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20 285 Mountain. In addition, previous growing season precipitation and current August minimum
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22 286 temperature influence the radial growth of *A. georgei*. Radial growth of *L. potaninii* across the
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25 287 alpine tree line site of Xinagcheng (X1, and X2), was primarily influenced by September
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27 288 minimum temperature from previous year. The other related variables for tree growth of *L.*
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30 289 *potaninii* were current growing season average temperature in the X1 site while current
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32 290 minimum temperature of September and summer (negative relation) influenced the growth of *L.*
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34 291 *potaninii* across the X2 site.
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38 292 **3.3 Stand age structure**

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40 293 We found that the seedling density was maximum at L1, L2 and X1 whereas it was minimum at
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43 294 X2 showing considerable spatial heterogeneity in tree establishment. We observed a similar
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45 295 recruitment pattern in all transects: the largest number of individuals was recorded for 10–30
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48 296 years of age (most of them were established during 1990 to 2000). The maximum recruitment
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50 297 occurred at the highest elevation at all sites except X1 and X2, which showed very poor
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53 298 regeneration at upper edge of treeline ecotone, and the treeline retreat in the recent decades (after
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55 299 1990) (Fig. 7).
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300 **3.4 Treeline movement**

301 The treeline position in each plot showed evidence of considerable range shifts ranging from
302 0.11 – 1.74 m year⁻¹, with some sites showing evidence of a changing treeline over centuries.
303 We found site specific elevation of treelines; the treelines were at lower elevation in Himalayan
304 sites. There is evidence that treelines have shifted in all the sites assessed with future potential of
305 shifting besides X1; which did not show tree establishment at upper elevation since 1950. The
306 maximum shift indicated was observed at birch (*B. utilis*) treeline (L2; 1.74 m year⁻¹) followed
307 by larch (*L. potaninii*) treeline (X2; 1.5 m year⁻¹, X1; 1.4 m year⁻¹).

308 We observed greater variation in the position of the treeline and tree species limit across
309 treeline site (C1) where *A. spectabilis* seedling was recorded at 38 m above the treeline (C1). In
310 some sites, the treeline itself represented the species limit (L2, Tb, X1, X2). The position of the
311 treeline varied greatly among the transects (C1; 3637 m asl, C2; 3513 m asl, L1; 3950 m asl, L2;
312 4100 m asl X1; 4444 m asl, X2; 4490 m asl) within a short distance (< 5 km) and in the same
313 mountain slope. We also observed a poor tree establishment at X1 and X2 sites in the recent
314 decades, with treeline itself representing the upper species limit.

315 **4. Discussion**

316 Our goal was to assess how climate factors affect radial growth and spatiotemporal
317 dynamics of different species across timberline and treeline of the Trans-Himalayan region and
318 Hengduan Mountains of China. Along with various studies on climate change impacts on tree
319 growth across these regions (Fan et al. 2009; Liang et al. 2016; Tiwari et al. 2017a), our study
320 expands and adds empirical evidence of tree growth and interactions of climate variables across
321 high altitude. Overall, precipitation and temperature from current and previous year were related

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322 to site-specific radial growth. We found that precipitation showed both positive and negative
323 influence and average temperature inversely influence the radial growth of *B. utilis* across moist
324 site (L1, L2) while precipitation and temperatures both showed negative impacts on radial
325 growth of *A. spectabilis* on dry site (C) of Himalayan treeline. In contrast, only temperature of
326 various months and growing season from previous and current year controlled the radial growth
327 of *A. georgei* (Tb) and *L. potaninii* (X1, X2). There is higher potential of treeline shifts
328 associated with changing climate across the Trans-Himalayan region, whereas low potential of
329 treeline shift despite climate suitability in the Hengduan Mountain sites in China.

4.1 Climate growth response

331 Our results showed that the radial growth of trees is strongly controlled by precipitation and
332 temperature at Trans Himalayan sites. The moisture sensitivity of tree growth has been observed
333 in Himalaya and high mountains of the world (Stahle and Hehr 1984, Qi et al. 2015; Lopez et al.
334 2017, Tiwari et al. 2017a, b; Sigdel et al. 2018). The higher temperature in the early growing
335 season (March-May) induces drought stress, and the rainfall during this period is beneficial for
336 tree growth as evidenced by our findings (fir and birch). And these results are similar with
337 growth climate response in central and eastern Himalaya (Dawadi et al. 2013; Liang et al. 2014;
338 Tiwari et al. 2017a; Gaire et al. 2017), and in treeline-forming *Betula* species (Takahashi et al.
339 2005; Wang et al. 2013). Sano et al (2015), Gaire et al (2014) and Tiwari et al (2017b) reported
340 importance of spring season moisture coupled with warm-day temperature (Tmax) for radial
341 growth in the region. Gaire et al (2014) also found that growth is typically sensitive to growing
342 season temperature of tree species at fir treelines in eastern Himalaya and central Himalaya, and
343 Schwab et al (2018) showed the stronger correlation between tree radial growth of Himalayan fir
344 and 20th century temperature as indicated by blue intensity (BI) as the climate proxy. Our

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345 findings confirm spatial variability in climate and growth response in Himalayan topography,
346 particularly since the eastern Himalaya region is wetter than its drier western counterpart
347 (Shrestha et al. 2012). Spring season warming coupled with higher radiation initiates early
348 melting of snow and increased atmospheric evaporative demands. This amplifies exposure of the
349 ecotone to drought until the onset of summer precipitation (Fritts 1976; Bhattacharya et al. 2006;
350 Cook et al. 2003, Winkler et al. 2018). A frequent existence of narrow and missing growth rings
351 in birch across central Himalayan also highlights that drought stress affects birch radial growth
352 (Liang et al. 2014).

353 In contrast to Himalayan sites, we found strong temperature sensitivity of tree radial
354 growth in Hengduan Mountain sites (Fig. 4). The RWI of *A. georgei* across timberline was
355 significantly correlated to minimum temperature of August, and to precipitation of previous
356 year's August showing sensitivity to moisture as well (Fig.5). The radial growth of *A. georgei*
357 (Tb) was positively correlated with minimum temperature and mean temperature during winter
358 and summer months, highlighting the potential for a positive impact of increasing temperature
359 for densification and upward shifting of treelines. However, winter temperature sensitivity of
360 ring width of several treeline conifers was also reported from SE Tibet and NW Yunnan
361 (Bräuning and Mantwill 2004; Bräuning and Griebinger 2006; Fan et al. 2009). In such cases, it
362 was expected that warmer conditions during winter improve the storage of higher levels of
363 carbohydrates to regulate root system activity and improve plant productivity (He et al. 2013).
364 Our finding on the significant influence of previous year's September temperature on radial
365 growth of Larch tree across treeline (X1, X2) agrees with past studies (Sun et al. 2010; Ou and
366 Qian 2006; Zhang et al. 2016).

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368 **4.2 Treeline movement**

369 Our results demonstrate species specific stem density in the treeline ecotones, birch with
370 maximum and larch with minimum stand density. Site specific treeline dynamics has been
371 already reported from Himalayan region (Gaire et al. 2017; Sigdel et al. 2018). We found
372 improved tree establishment (as per age of individuals) and treeline shifts only at moist sites for
373 birch (L1, L2), where temperature and precipitation both are increasing significantly. Similarly,
374 elevated temperature in May at alpine environment for larch trees (X1, X2) in the past was
375 primarily related to improved radial growth.

376 Stand densification has been widely reported in various treelines ecotones in Himalaya
377 and Tibet (Gaire et al. 2014; Liang et al. 2011a, 2016; Lv and Zhang 2012). Given the higher
378 density of juveniles that preferentially established in recent decades (Fig 7), all the ecotones now
379 indicate potential for range shift of treelines. While demographic niche differentiation can lead
380 seedling location to be a poor indicator of subsequent successful transition to adulthood, this
381 transition from seedlings into trees is considered as the critical determinant of sustainable
382 regeneration and treeline movement (Vetaas 2000; Camarero and Gutierrez 2007; Lv and Zhang
383 2012). The incidence of saplings at or above the adult distribution limit in Fig. 6 demonstrates
384 the potential for ongoing shifts of the treeline ecotones of our study sites.

385 The higher frequency of tree establishment at the upper edge of treeline is mainly due to
386 increased temperature accompanied by enough moisture (Cook et al. 2003; Sano et al. 2005;
387 Shrestha et al. 2012). However, the hotter summer (July) may also create desiccation and
388 drought stress in case of depleted soil moisture and affect recruitments (Hughes et al. 2009;
389 Fajardo and McIntire 2012). The higher sensitivity of minimum summer temperature and spring

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390 season precipitation with regeneration was also documented in *Picea schrenkiana* from treeline
391 ecotone of Tian Mountains of China (Wang et al. 2006).

392 In agreement with our study, the positive relationship between climate and regeneration
393 of *A. spectabilis* during warm winter and relatively cold summer was reported by Cook et al
394 (2003). We affirm the important role of temperature in growth and regeneration of *A. spectabilis*
395 at the treeline as mentioned by Gaire et al (2014), although the correlation with radial growth in
396 our case is not significant. Contrary to our findings, Liang et al (2014) found higher moisture
397 stress to the radial growth of *B. utilis* in Nepal Himalaya due to the decreasing trend of
398 precipitation in the region. We observed a stronger positive relationship between temperature
399 and densification of stand of *A. spectabilis* compared to that of rainfall. It indicated that the
400 juveniles are favored by warming temperature and the adults to precipitation (Lv and Zhang
401 2012).

402 We reported great variability in position of treeline in the nearby sites (< 5 km) within the same
403 mountain slope, and rate of upward shifting of treeline, and this variability could be the outcome
404 of human impact in the past including logging, grazing and fire that caused the decline in land
405 use intensity as indicated by Schickhoff et al (2015). Different slope exposure and wind velocity
406 (Greenwood et al. 2014), and biotic interactions (Liang et al. 2016) are likely to determine the
407 position of treeline. The maximum shift of treeline was observed at *Betula* site (L2) linked to the
408 increasing average temperature and precipitation in the region. As an early successional species
409 birch also has higher regeneration potential on exposed sites of the upper treeline (Shrestha et al.
410 2007). Furthermore, the maximum density of tree individuals and higher seedling sapling density
411 within the plot indicated the higher potential for future shift. Our findings agree with treeline
412 shift reports in the Himalaya (Dubey et al. 2003; Gaire et al. 2014) with considerable recruitment

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413 in the recent decades especially after 1950s as reported by (Liang et al. 2011b; Shrestha et al.
414 2015; Schickhoff et al. 2015).

415 We report higher regeneration, increased tree establishment and invasion into treeless
416 areas above the forest limit, as directional changes readily attributed to effects of climate change.
417 However, in most cases, pastoral abandonment or other human impacts also drives treeline
418 dynamics (Holtmeier 2009; Schickhoff 2011), excessive grazing pressure and widespread fire
419 were reported as the main agents for altering treelines in Himalaya (Beug and Miede 1999, Wang
420 et al. 2019b). Along with the sampled transects, we did not observe any recent cut stumps and
421 any recent fire incidence in all the sampled ecotone showing diminished anthropogenic pressure
422 in recent years. However, a proportion of tree cores (13% in C1 and 17% in C2) showed fire
423 scars dated back to 20 to 30 years indicating the incidence of past fire. Also, we found evidence
424 of cattle herbivory in all the sampled ecotone, indicating that disturbance factors are one of the
425 key drivers of treeline dynamics as explained by Schickhoff et al (2015). Notably, our study site
426 in Himalaya was included in Annapurna Conservation Area established in 1992, which
427 considerably controlled forest fire and firewood collection. Furthermore, changes in land use
428 have been associated with the gradual shifting of local people from livestock farming to
429 agriculture, low consumption of firewood (provision of hydroelectricity) and migration of people
430 to lower valleys (Jaquet et al. 2016; KC et al. 2017). These changes in land use pressure and fire
431 frequency will undoubtedly have contributed to facilitate forest expansion towards higher
432 elevations in conjunction with the climatically driven changes reported above.

433 Despite favourable climate, considerable gaps in the tree establishment across alpine
434 region (X1, X2) due to low regeneration of larch trees in the recent decades could be associated
435 with poor soil quality and anthropogenic disturbance via logging operations. Our results

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436 indicated that Hengduan larch (X1, X2) and silver fir (Tb) have experienced greater influence of
437 disturbances for tree establishment in treeline. The poor regeneration in these sites (X1, X2)
438 might lead to treeline retreat in these sites in the future if adult individuals die or removal
439 through exploitation increases. The potential for such retreat is already evident at X1 and X2,
440 especially after the 1990s. Therefore, we highlight that modifying factors (biological,
441 geomorphology, human interference) in addition to climate may drive tree establishment and
442 stand densification in treelines and it is, therefore, inadvisable to overlook local context when
443 predicting treeline changes across broad regions.

5 Conclusions

445 We report site specific growth climate responses and treeline inertia based on tree rings and
446 demographic assessment of treeline ecotones at the Trans-Himalayan region of Nepal and
447 Hengduan Mountain regions of China. It was observed that radial growth across the Trans-
448 Himalaya is strongly determined by both precipitation and temperature while in the alpine region
449 of Hengduan Mountains temperature alone has a strong influence. While the Trans-Himalaya
450 region is experiencing rapid shifts in treeline with higher recruitment of tree species across
451 treeline ecotone, Hengduan treelines are experiencing slow recruitment and upward movement of
452 treeline. The contrasting local patterns of climate change are one of the critical drivers of these
453 differences in treeline shifts at high altitudes in face of warming temperatures and higher
454 variation in precipitation trends. We emphasize that impact of changing growth in trees may
455 influence treeline inertia; however, the geomorphological factors, human disturbance and biotic
456 interaction are also the strong drivers for the changes in treeline ecotones. Our results point to the
457 importance of better assessment and integration of local anthropogenic context, impacts of

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458 belowground environmental factors and biotic interactions on juveniles and adults to increase
459 accuracy of prediction on treeline dynamics under changing climate.

460
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476 **Ethics approval and consent to participate** Not applicable

477 **Consent for publication** Not applicable.

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4 478 **Competing interests** All authors declare that they have no competing interests.
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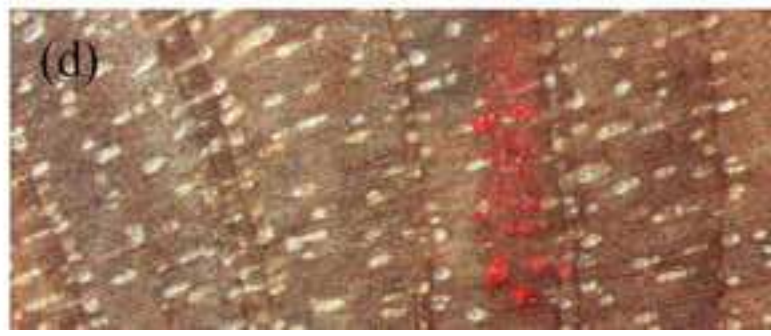
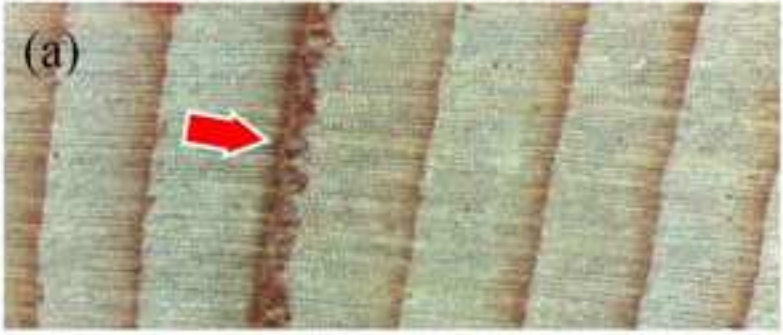
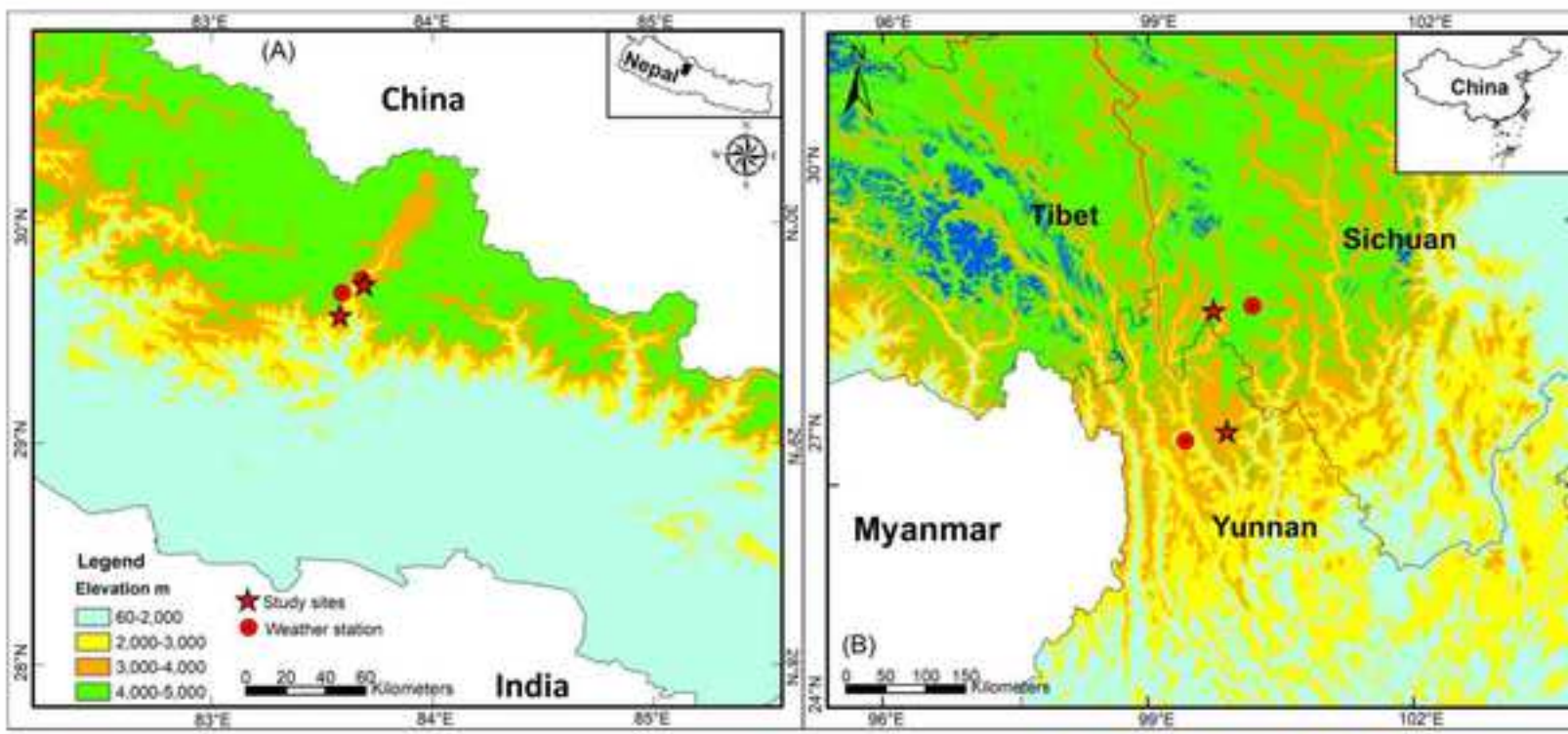
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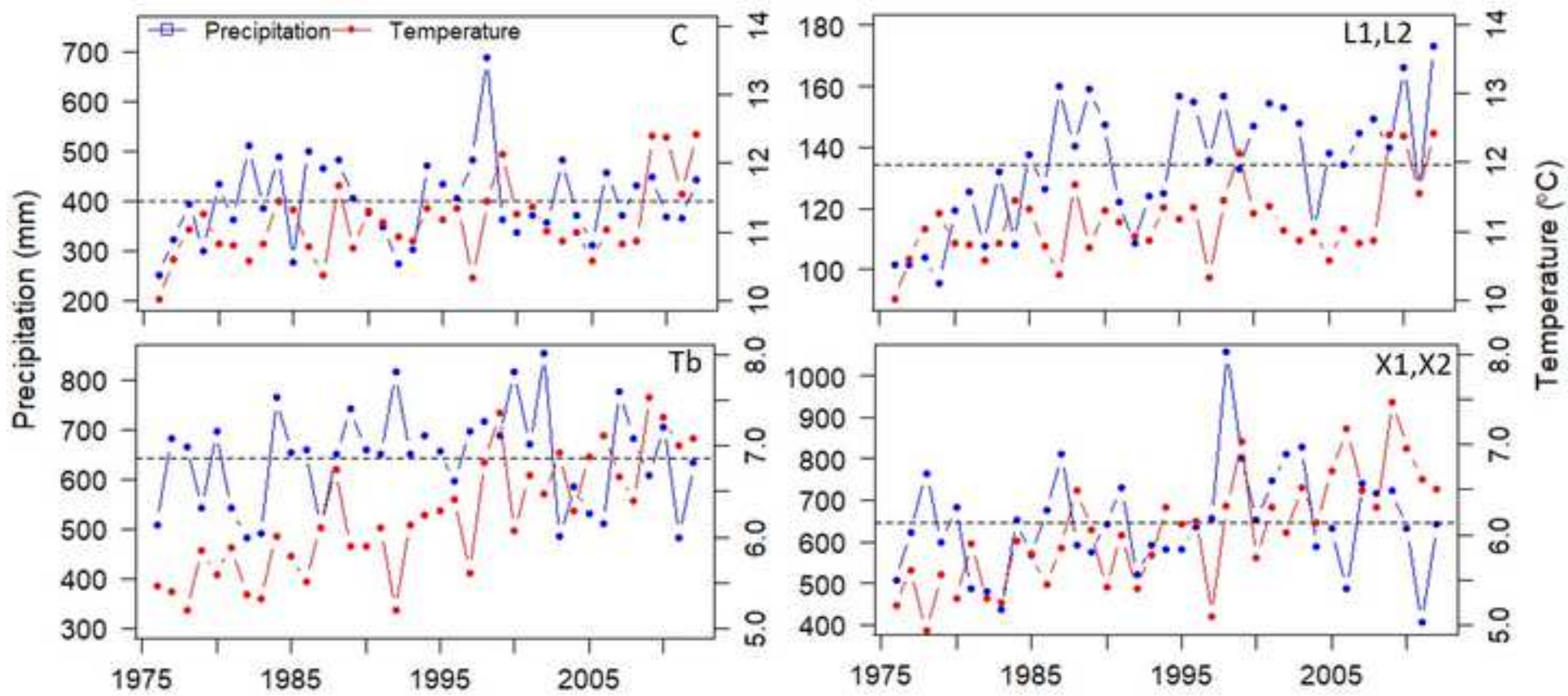
761 Winkler DE, Butz RJ, Germino MJ, Reinhardt K, Kueppers LM (2018) Snowmelt Timing
762 Regulates Community Composition, Phenology, and Physiological Performance of
763 Alpine Plants. *Front Plant Sci.* 9:1140. doi:10.3389/fpls.2018.01140
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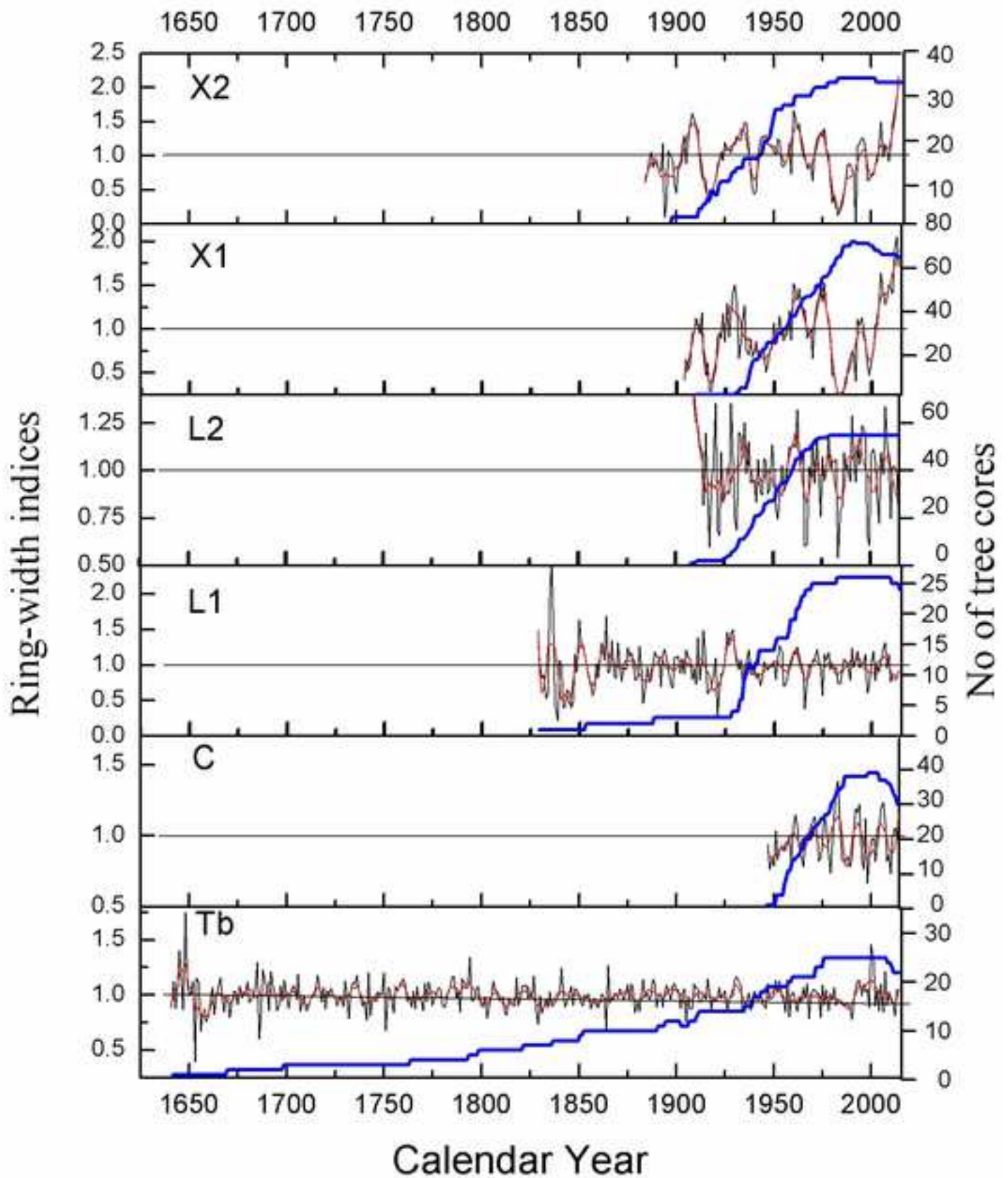
765 Winkler DE (2019) Contemporary Human Impacts on Alpine Ecosystems: The Direct and
766 Indirect Effects of Human-Induced Climate Change and Land Use. Editor(s): Michael I.
767 Goldstein, Dominick A. Della Sala, *Encyclopedia of the World's Biomes*, Elsevier, 2020,
768 Pages 574-570. <https://doi.org/10.1016/B978-0-12-409548-9.11879-2>

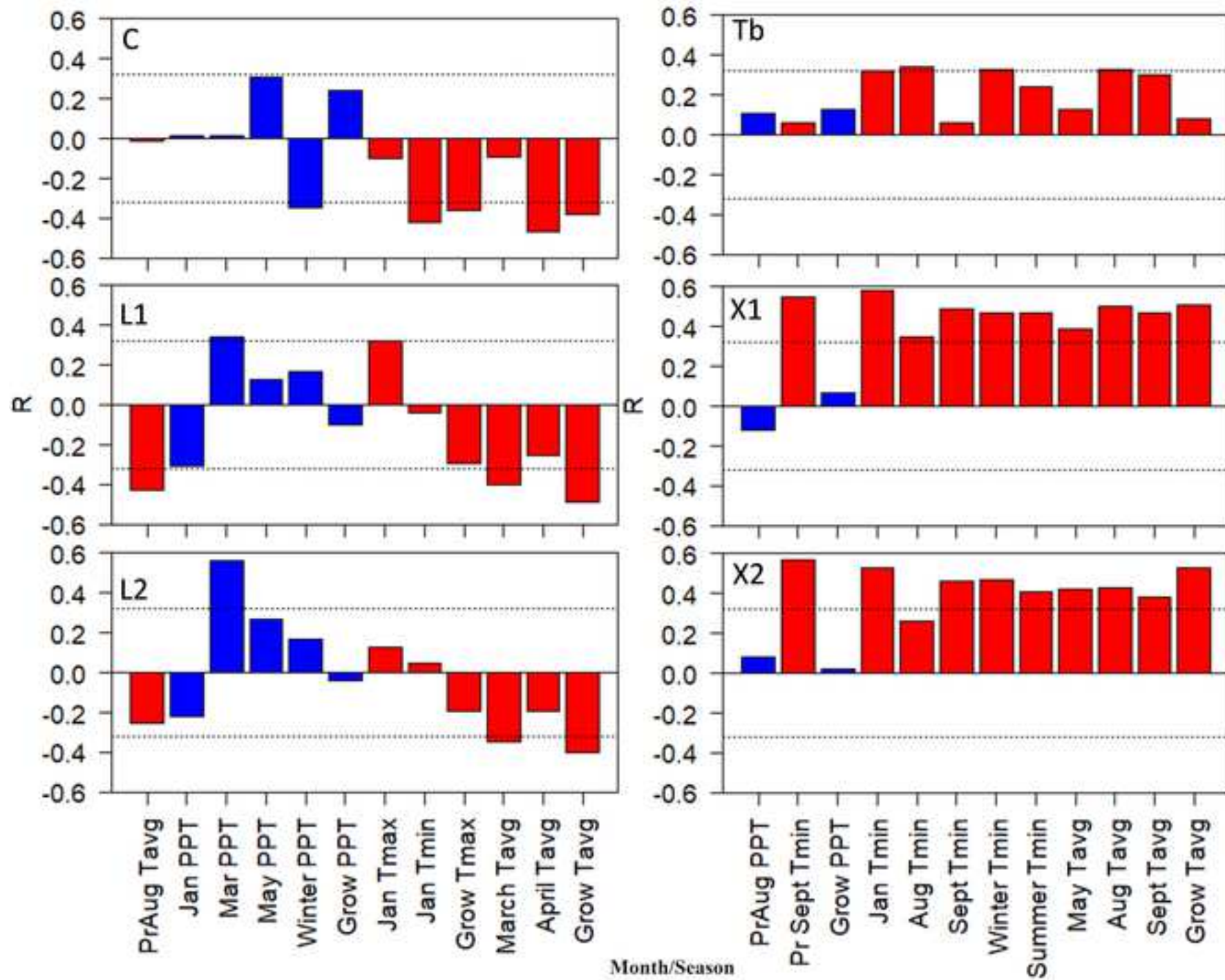
769 Yadav RR, Singh J, Dubey B, Chaturvedi R (2004) Varying strength of relationship between
770 temperature and growth of high-level fir at marginal ecosystems in western Himalaya,
771 India. *Curr. Sci.* 86 (8):1152–1156.

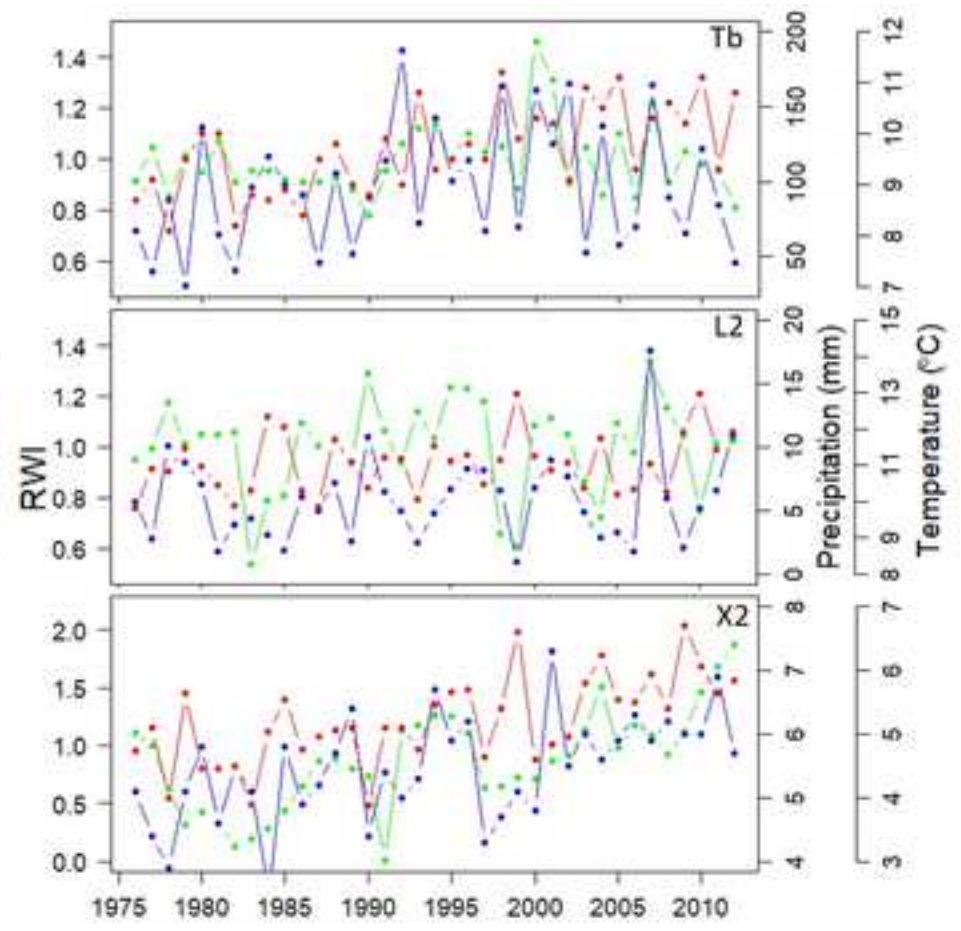
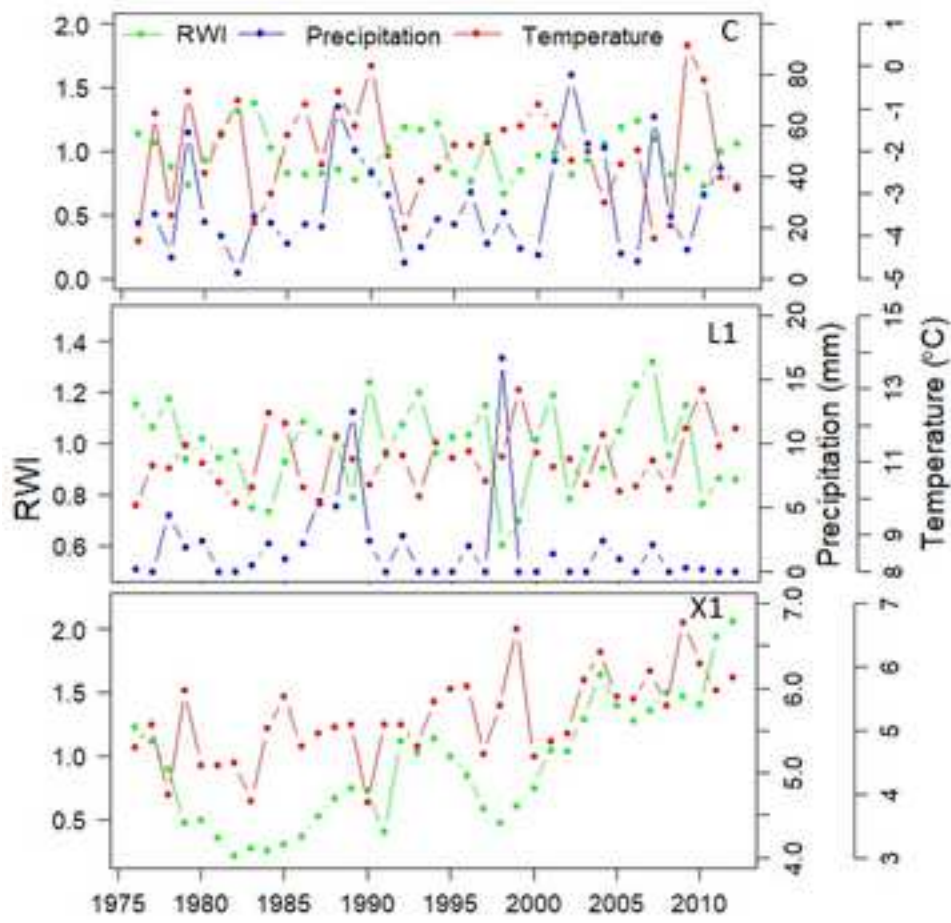
| | | |
|----|--|--|
| 1 | | |
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| 4 | Comments | Response |
| 5 | | |
| 6 | Although it is a bit general, please try to improve the first part of the abstract | We have revised the first part of abstract |
| 7 | (L15-22). Now it seems more than a few sentences a bit disconnected. | (Lines 15–26) |
| 8 | | |
| 9 | L59. Please add some additional references to reinforce this point. | Thank you, we have added these references in |
| 10 | | the revised version: Camarero et al. 2017, |
| 11 | | Liang 2011b, Gaire 2014. (Line 64) |
| 12 | | |
| 13 | | |
| 14 | L67. physiographic and topographic. Not sure about their differences. Please | We removed physiography as a redundancy. |
| 15 | specify or rephrase. | (Line 71) |
| 16 | | |
| 17 | L100. Other factors. Such as? Please specify a bit to reinforce your initial | We have elaborated driving factors in the |
| 18 | hypotheses. | revision: factors such as land use changes |
| 19 | | including grazing pressure, fire and human |
| 20 | | activities. (Line 104–105) |
| 21 | | |
| 22 | | |
| 23 | L112-115. Please try to do not repeat here the term “Mustang” so many | We have removed repetition of Mustang and |
| 24 | times. | revised the paragraph. (Line 117–121) |
| 25 | | |
| 26 | Figure 1. Please, improve the figure. The style should be more homogeneous | We improved Figure 1 |
| 27 | (e.g. same colours range for the altitudes of both sites, indeed panel B does | |
| 28 | not include a proper legend here), the spatial scale is very different, the B | |
| 29 | panel includes national borders, ... | |
| 30 | | |
| 31 | L157. Field investigation. This term sounds a bit weird to me, could you | We replaced it with field study, Line 161 |
| 32 | please replace by other fitting better? | |
| 33 | | |
| 34 | L163. forest with tree density ... at least 30%. Tree density should be in | This appear a bit tricky, actually it is not the |
| 35 | number of trees per area. The descriptor 30% is more related to canopy | density that determines timberline hence we |
| 36 | cover, tree cover density, Please rephrase. | mentioned timberline as the uppermost |
| 37 | | closed forest with tree cover (trees > 5 m |
| 38 | | height) of at least 30% (Holtmeier 2003) |
| 39 | | (Line 167) |
| 40 | | |
| 41 | | |
| 42 | L240. Please avoid references in the Results section. This section should be | Reference removed in the revised version, |
| 43 | focused in describing your findings not comparing them with literature. | (Line 244) |
| 44 | | |
| 45 | L240. Please avoid starting a new sentence with an abbreviation, a number, | We have revised this sentence, Line 244 |
| 46 | etc. | |
| 47 | | |
| 48 | | |
| 49 | L249. Fig.4 and Table 2. Please correct. | We corrected it, Line 253–254 |
| 50 | | |
| 51 | L420-427. I agree with the relevance of socio-economic factors in this type | We have added these important references, |
| 52 | of studies. It would be great if you can add some additional references here | Jaquet et al. 2016, KC et al. 2017. Line 430 |
| 53 | to reinforce this specific point. | |
| 54 | | |
| 55 | Style: please follow format requirements in the whole manuscript. Also, | We have followed format requirements and |
| 56 | please check the reference format and adapt them to the journal instruction | improved reference. |
| 57 | for authors. | |
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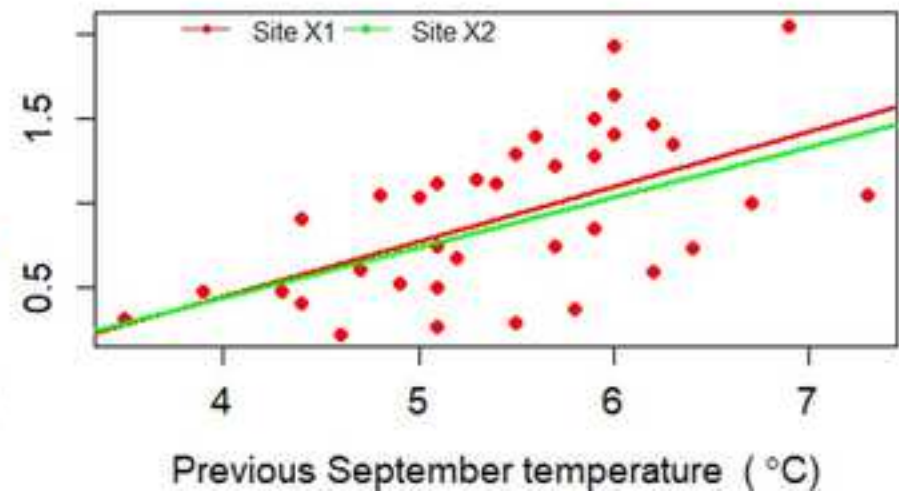
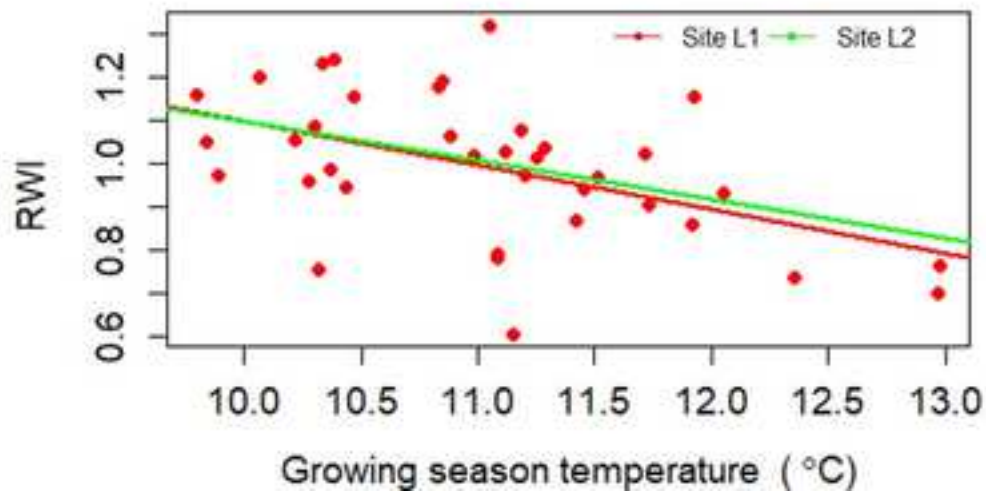
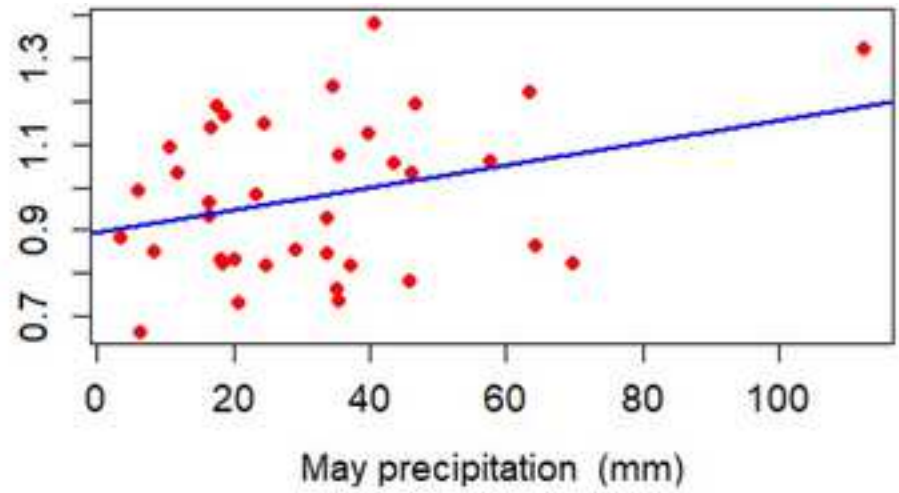
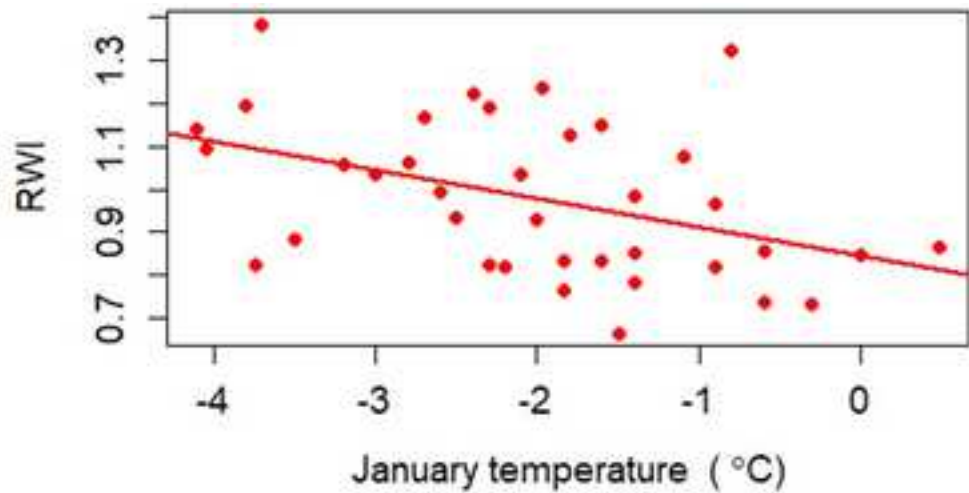


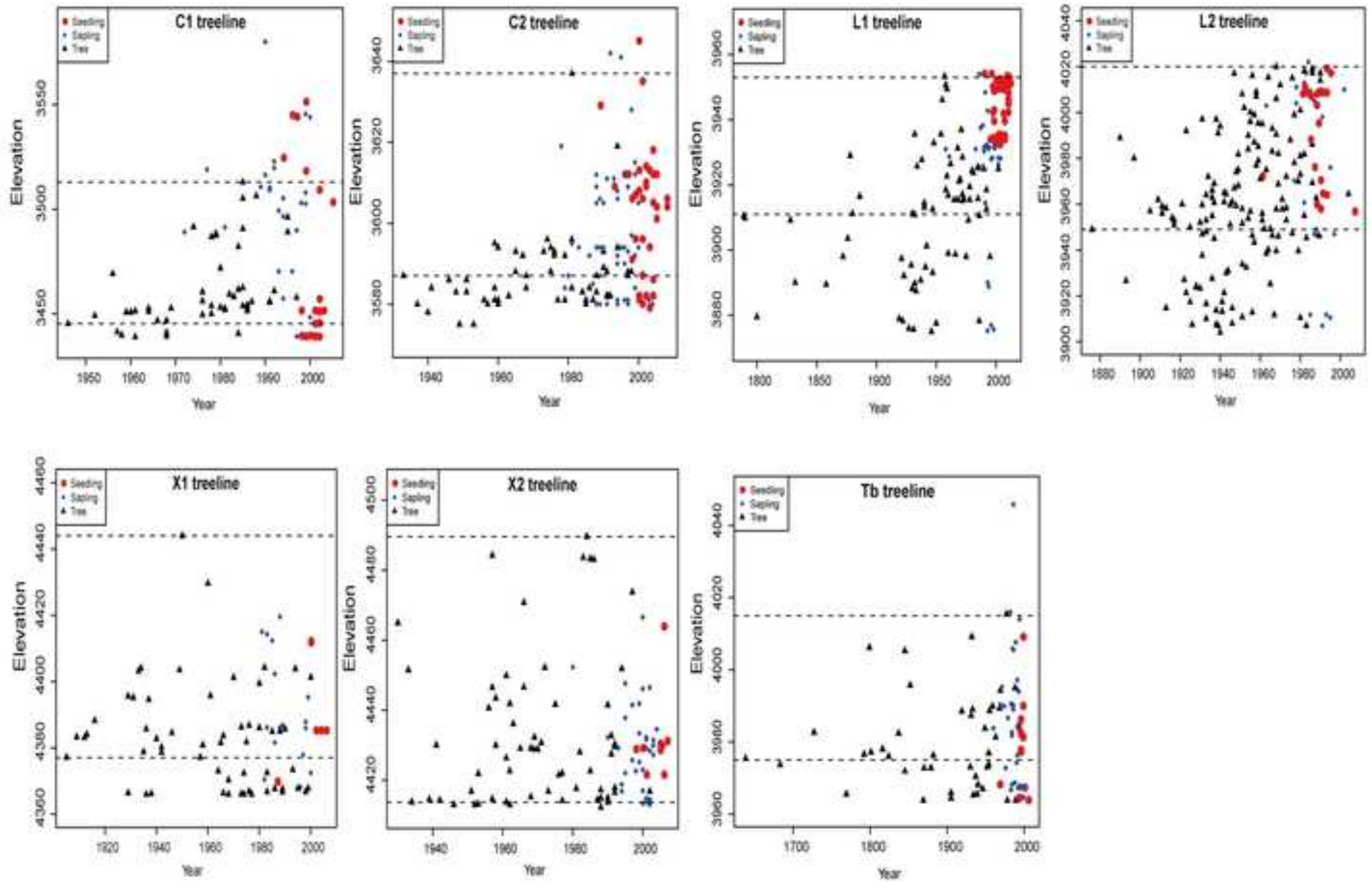












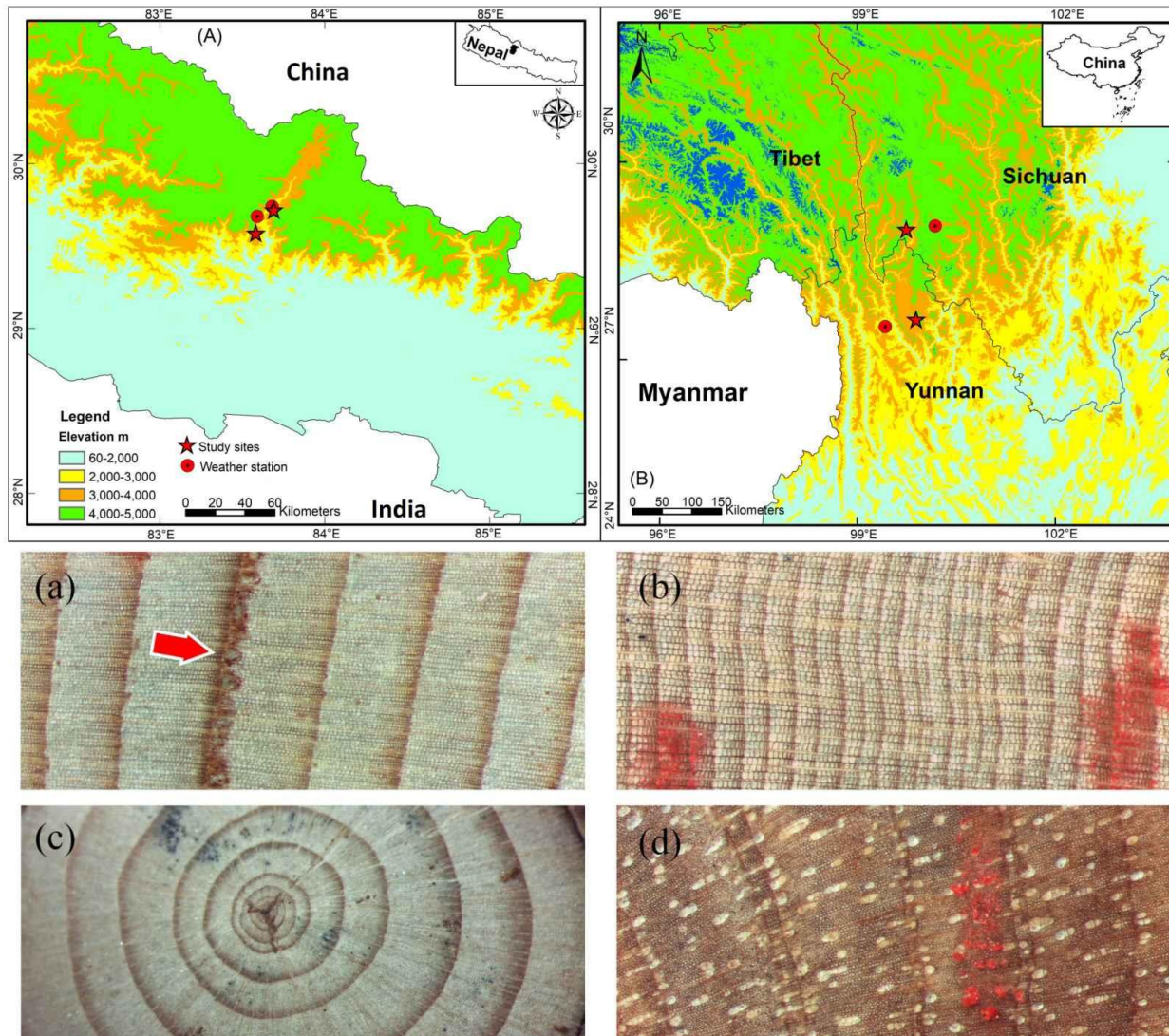


Figure 1. Location of study area across trans-Himalaya region of Nepal (A) and Hengduan mountains of China (B) (upper panels). Section of tree cores including (a) *Abies spectabilis* (red arrow showing frost ring), (b) *Larix potaninii*, (c) *Abies georgei*, and (d) *Betula utilis*

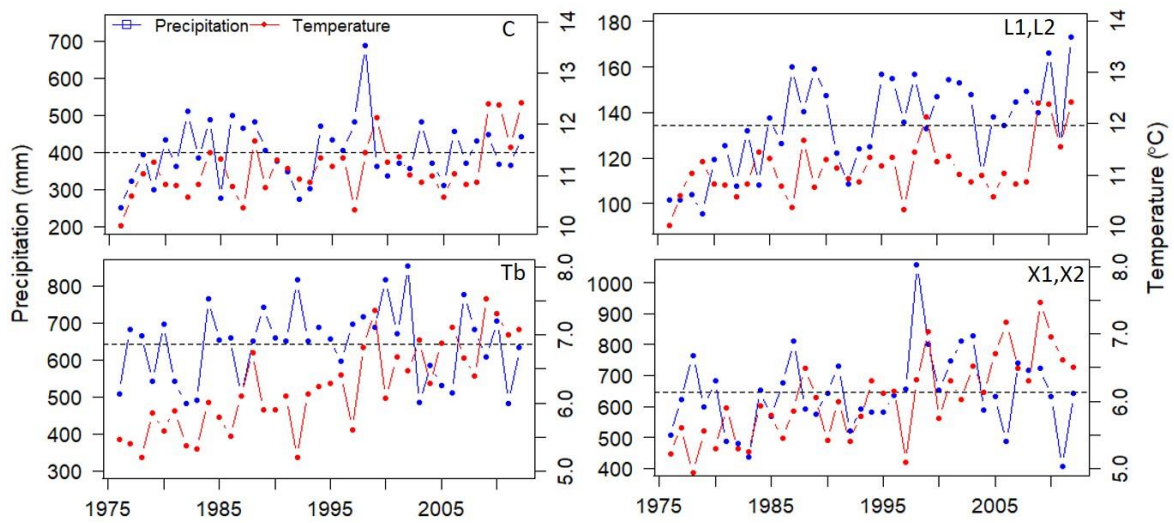


Figure 2. A 37 years' average monthly temperature and precipitation of the study area with an average precipitation (dotted line). Time series of average annual precipitation and temperature of all study sites with an average precipitation (dotted line) for 37 years. Temperature and precipitation were computed from daily data obtained from Department of Hydrology and Meteorology Government of Nepal, and National Meteorological Information Center of China.

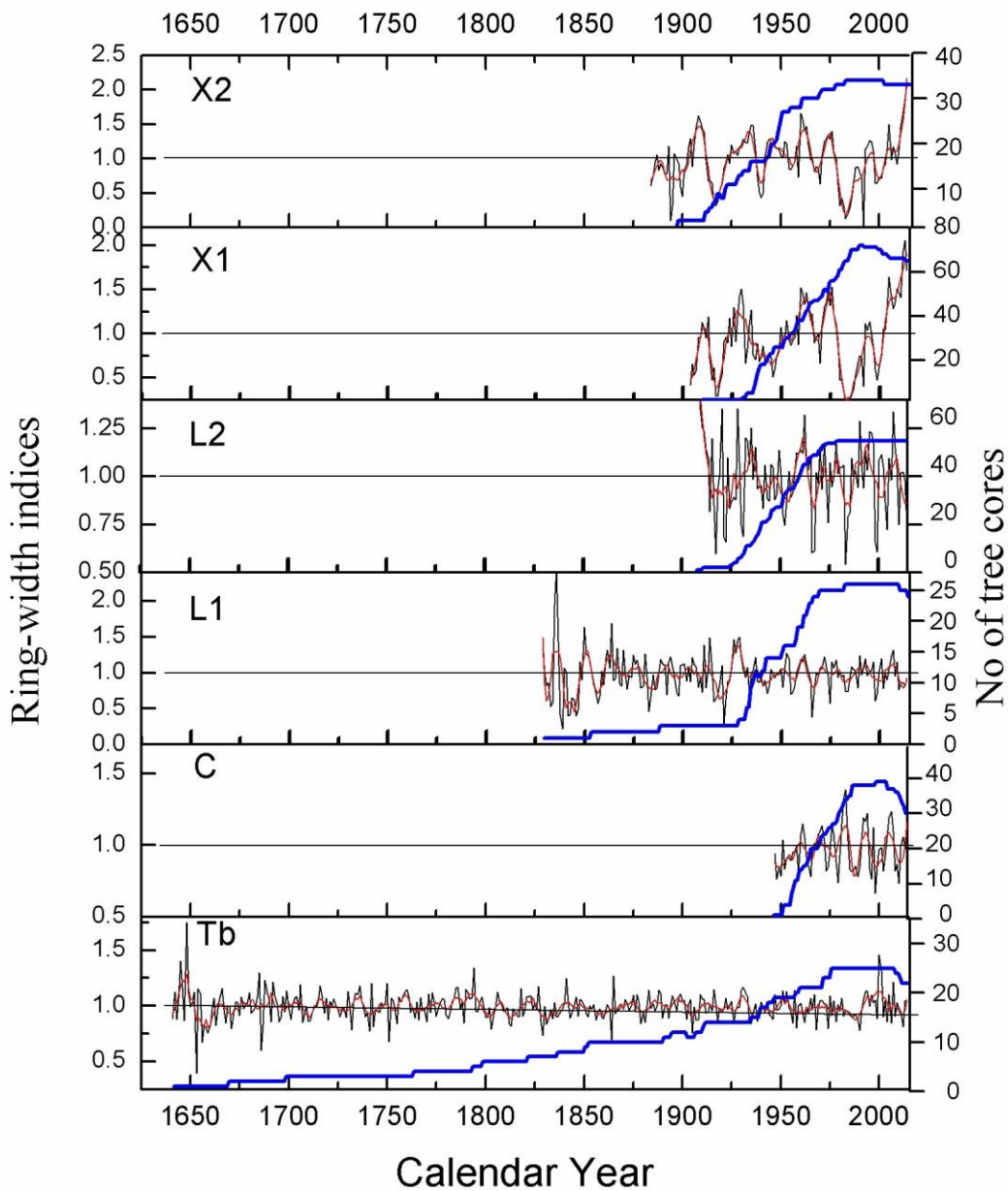


Figure 3. Standardized tree-ring width index (RWI) chronology with sample size with scale on the right axis for the study sites after 1987. The red smoothing line is a five year's cubic spline fit; blue lines indicate number of tree cores.

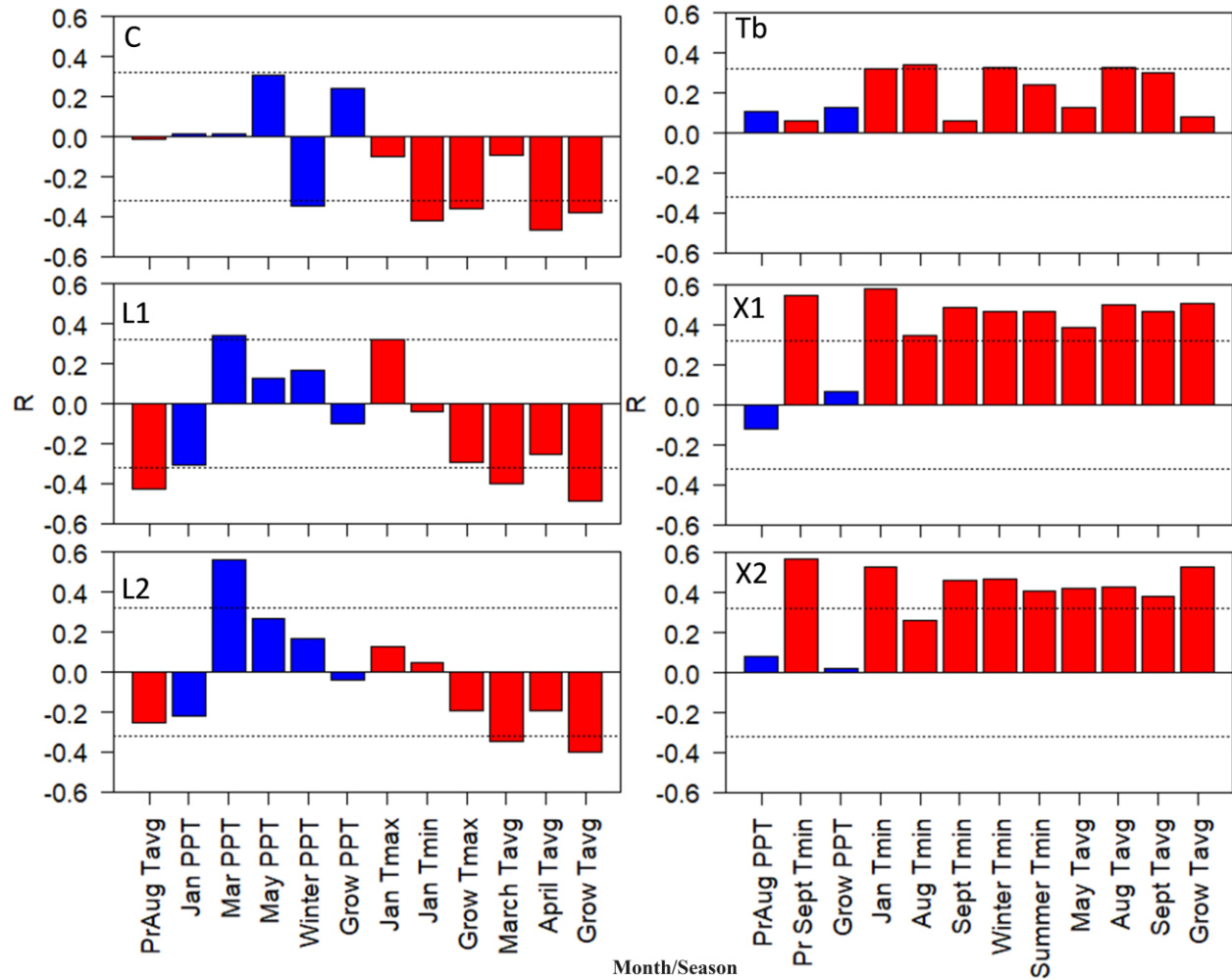


Figure 4. Correlations of tree ring width (RWI) chronologies of different sites across Trans Himalayan and Hengduan regions. Horizontal dotted lines at $r = 0.32$ and $r = -0.32$ form a 95% CI; significant correlations ($p < 0.05$). Blue, and red colors indicate precipitation, and temperature, respectively. (Abbreviations: pr = previous, PPT = precipitation, Tmin = minimum temperature, Tmax = maximum temperature, Grow = growing season). All variables with one or more significant correlations are presented.

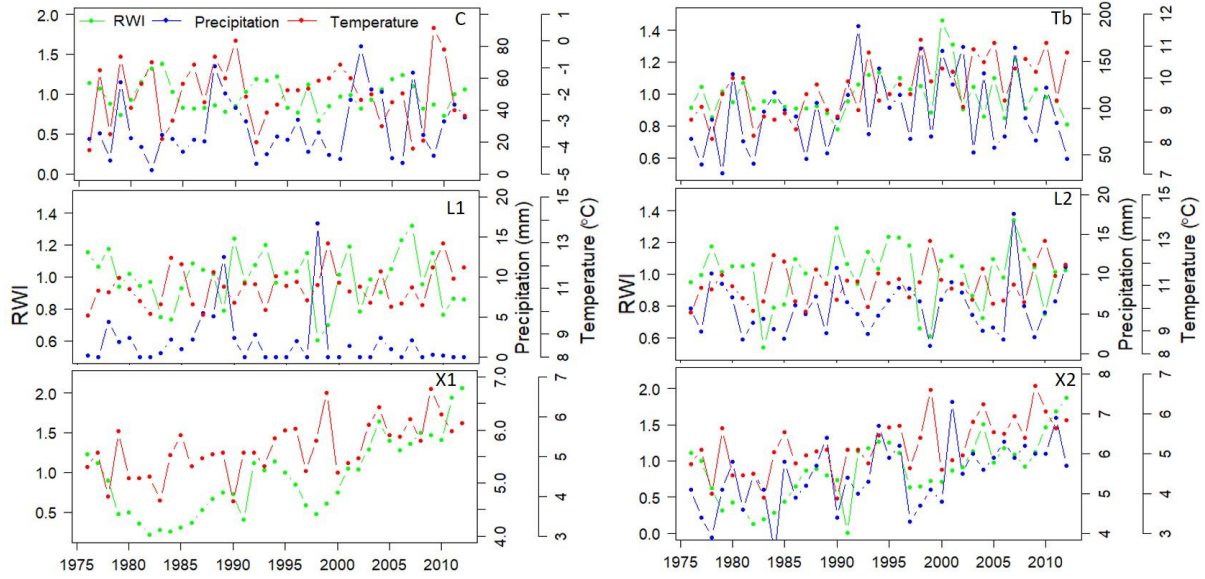


Figure 5. Time series of standardized annual RWI and current year growing season (March-May) maximum temperature and total precipitation across study area. See table 1 for the site description.

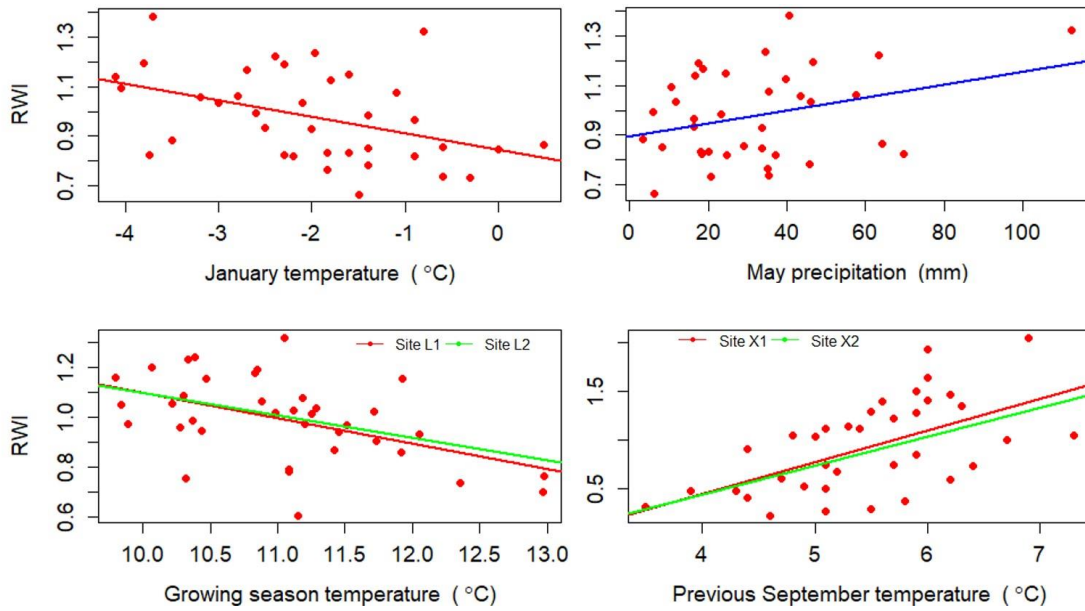


Figure 6. Relationship between standardized RWI and (a) January minimum temperature and (b) May precipitation for *A. spectabilis*, (c) growing season average temperature for *B. utilis*, and (d) previous year September minimum temperature for *L. potaninii*.

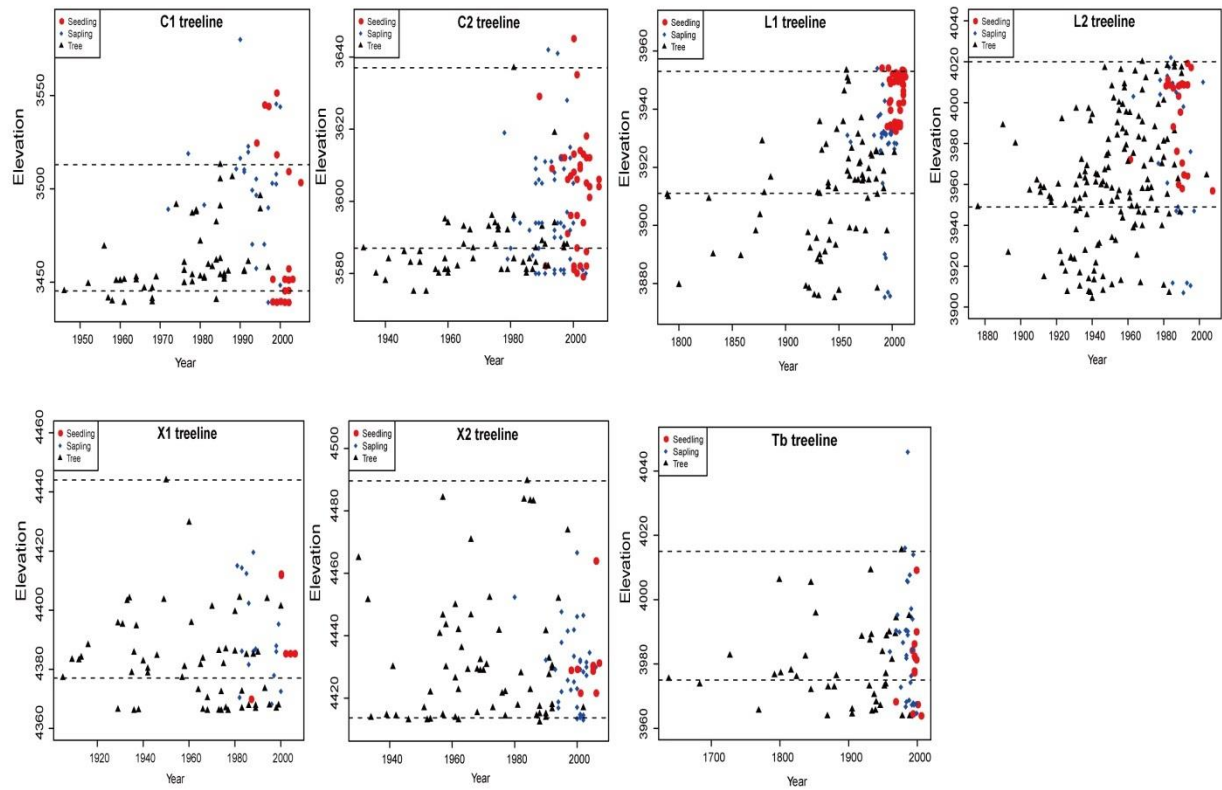


Figure 7. Spatiotemporal dynamics of treeline in the treeline plots, horizontal axis showing year of tree establishment, and vertical axis showing elevation of tree specimen in each treeline ecotone. The upper dashed line in each plot represents elevation of modern treeline, the lower dashed line in each plot represents the position of oldest tree in the plot. See table 1 for site descriptions.

Table 1 Summary statistics including average tree-ring series length, inter series correlation of chronology with master chronology (r_{bt}), mean sensitivity, autocorrelation (AC), and expression population signals (EPS) value for study site. See Tables 1 and 2 for study area descriptions.

| Site | Chronology (years) | Trees (cores) | r_{bt} | Mean sensitivity | EPS | All series Rbar | 1 st order AC |
|------------------------------|--------------------|---------------|----------|------------------|-------|-----------------|--------------------------|
| <i>A. spectabilis</i> C | 68 | 36 (40) | 0.47 | 0.326 | 0.931 | 0.187 | 0.612 |
| <i>B. utilis</i> L1 | 186 | 21(23) | 0.49 | 0.382 | 0.907 | 0.226 | 0.062 |
| L2 | 107 | 52 (56) | 0.51 | 0.324 | 0.954 | 0.415 | 0.026 |
| <i>A. georgei</i> ATE(Tb) | 374 | 19 (26) | 0.45 | 0.106 | 0.756 | 0.284 | -0.001 |
| <i>L. potaninii</i> X1 | 111 | 54 (76) | 0.52 | 0.235 | 0.875 | 0.514 | 0.539 |
| X2 | 131 | 20 (35) | 0.54 | 0.230 | 0.969 | 0.463 | 0.789 |

Table 2 The results of multiple regression for annual wood RWI across the study. The coefficient of determination (R^2) for each variable was estimated using stepwise regression model. The negative sign indicates a negative relationship. Abbreviation: pr - previous year, ppt – precipitation, t - temperature, max: maximum, min: minimum, Grow – growing season. See Table 1 for site code.

| Trans-Himalaya | | | | | | | | | | | | |
|-----------------------|----------------|------------|------------|------------|---------------|-------------|-------------|--------------|-------------|--------------|-------|--|
| Sites | pr Aug tavg | Jan ppt | Mar ppt | May ppt | Winter ppt | Grow ppt | Jan tmax | Grow tmax | Jan tmin | Grow tavg | Total | |
| C | | | | 0.10 | -0.10 | | | -0.05 | -0.25 | | 0.50 | |
| L1 | -0.10 | -0.11 | 0.07 | | | | 0.09 | | | -0.24 | 0.61 | |
| L2 | | -0.07 | 0.26 | | | | | | | -0.16 | 0.49 | |

| Hengduan Mountain | | | | | | | | | | |
|--------------------------|---------------|----------------|-------------|-------------|--------------|-------------|--------------|----------------|-------|--|
| Sites | pr Aug ppt | pr Sep tmin | Grow ppt | Aug tmin | Sept tmin | Aug tavg | Grow tavg | Summer tmin | Total | |
| Tb | 0.10 | | 0.10 | 0.14 | | | | | 0.34 | |
| X1 | | 0.31 | | | | | 0.21 | | 0.51 | |
| X2 | | 0.33 | | | 0.13 | | | -0.06 | 0.52 | |