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From Himalaya to Hengduan: Alpine Treelines Dynamics Under Climate Change

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Abstract:

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 (Abies spectabilis, Betula utilis, Abies georgei and Larix potaninii) 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 A. spectabilis and B. utilis treelines in Nepal, and lower seedling recruitment with lower shifting rates of treelines of A. georgei and L. potaninii

	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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From Himalaya to Hengduan: Alpine Treelines Dynamics Under Climate Change

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Abstract

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 (*Abies spectabilis*, *Betula utilis*, *Abies georgei* and *Larix potaninii*) 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 *A. spectabilis* and *B. utilis* treelines in Nepal, and lower seedling recruitment with lower shifting rates of treelines of *A. georgei* and *L. potaninii* 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.

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

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1 Introduction

Alpine treelines are the conspicuous transition zone between timberline and treeless alpine vegetation (Körner 2003). Near-natural treelines are typically climate-limited and thus valuable indicators of changing climate (Kullman 2002; Körner and Paulsen 2004; Batllori and Gutiérrez 2008). Alpine treelines have been reported to be shifting upwards in response to global warming (Grace et al. 2002; Holtmeier & Broll 2007; Harsch et al. 2009; Hansson et al. 2020). The formation of the upper distributional limit of the tree life form according to thermal balance (Körner 1998, 2003, 2012; Holtmeir & Broll 2007; Harsch et al. 2009) emphasises that climate warming is expected to promote forest growth at their elevation range edge, to generate densification of ecotone and to advance treelines upward in the elevation (Grace et al. 2002; Dullinger et al. 2004; Smith et al. 2009). However, for comparatively dry and semiarid zones, treeline position is frequently limited by drought stress (Lloyd and Fastie 2002; Wilmking et al. 2004; Qi et al. 2015; Tiwari et al. 2017a). In such regions, current warming may exacerbate moisture stress and even may cause retreat of treelines downslope. For the Himalayan region, evidence suggests treeline shift rates are driven by moisture availability during the dry season (Tiwari et al. 2017a; Sigdel et al. 2018). Great uncertainties still prevail at explaining treeline response to rapidly changing climate because treelines do not always keep pace with climatic change on multi-decadal time scales, as the displacement and adjustment of alpine trees to warmer climate can require decades or even centuries (Kullman 2007).

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

The elevational treeline environment is very heterogeneous, which limits broad generalization on treeline sensitivity to climate because of topographic variation (Daniels and Veblen 2004; Elliott and Kipfmueller 2011; Greenwood et al. 2014) and also because of intense human activities mainly related to declined land use intensity (Schickhoff et al. 2015). Seedling recruitment, stand densification and rate of upward shifting of the treeline can greatly vary between surface gradients (slope) and orientation (aspects) due to substantial difference in soil conditions and intensity of solar radiation (Danby and Hik 2007; Matzinger et al. 2003), and due to other factors such as stand history, dispersal ability of tree species, disturbance and ecological interactions (Schloss et al. 2012).

Various studies have reported upward shifts of the *Abies spectabilis* treeline, both in temperature sensitive (Gaire et al. 2014, Mainali et al. 2014) and moisture sensitive (Tiwari et al. 2017a) ecotones in the Himalaya, although there are some evidences for stable position during the past century (Sigdel et al. 2018). Although there are climatic as well as non-climatic factors involved in determining treeline dynamics, shifting treelines have been reported from Hengduan Mountains (20 m in elevation in the past 100 years) (Liang et al. 2016), in northwestern Yunnan, (Moseley 2006; Baker and Moseley 2007), and in Baima snow mountain in the central part of Hengduan Mountain in China (Wang et al. 2019a).

The Himalaya and Hengduan Mountain regions are rapidly warming regions of the northern hemisphere. Trends in much of the Himalayan region substantially exceed the global average trend of warming (IPCC 2013), with the decreasing number of cold days and nights and increasing number of warmer days and nights making most ecosystems vulnerable to climate change (Shrestha et al. 2012; Sharma and Tsering 2009; Aryal et al. 2012). Moreover, the Hindu Kush Himalayan (HKH) region showed the annual mean warming rates of 0.19 °C/decade during the period 1901–2014, while that of 1951–2014 period was 0.20 °C/decade (Ren et al. 2017), and the substantial increase in length of growing season (Krishnan et al. 2019). Observed trends in Hengduan Mountain show increasing temperature of the warmest and coldest nights by 0.016 ºC/yr and 0.055 ºC/yr respectively, a decrease in the number of frost and ice days, and an increase in the length of the growing season during the past half-century (Ning et al. 2012). However, the widespread increase of air temperature and variation in precipitation trends associated with strong topographic gradients and rain shadow effects are largely responsible for the complex climate system in both Himalayas (Schickhoff 2005) and Hengduan mountains (Ning et al. 2012) raising significant questions about how treelines of the region might respond to climate change.

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

2 Methods

2.1 Study site description

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

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.

We selected four treeline species from these regions, two evergreen; *Abies spectabilis* (D. Don) Spach and *Abies georgei* var. *smithii* (Viguie & Gaussen), 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; Miehe et al. 2015). *Abies georgei* var. *smithii* (Viguie & Gaussen) 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).

The longer axis of each plot was parallel to the altitudinal gradient of subalpine forest to alpine shrub land. For each plot, the location of each individual tree was mapped. The altitudes of lower and upper parts of the plots were recorded by GPS.

2.3 Tree ring series

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

2.4 Stand age structure

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

2.5 Treeline movement

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

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

Data analysis

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

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

To determine which of our potential predictor variables were correlated to RWI, we first performed simple linear regression for each variable and RWI of trees from all sites. This was performed separately for each site. Based on this initial analysis, we dropped predictors which were not significantly correlated ($p > 0.05$) to the ring width indices for the respective comparisons. The remaining predictors were used in a stepwise regression. Variables were included in the model based on Akaike Information Criterion (AIC) adjusted for small sample size such that the summed probability of the models (Buckland et al. 1997, Calcagno and de Mazancourt 2010). To further simplify the multiple regressions and develop the final models, we eliminated variables which were highly correlated and with no biological relevance. Statistical analyses were performed using R 4.0.3 (R Development Core Team 2020).

3. Results

3.1 Tree Ring-width Chronology

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

3.2 Growth climate response

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

Considering regression models with individual variables, some of the topmost influencing variables on tree growth (*A. spectabilis*) across treeline of Trans-Himalayan site (C) were precipitation from May and Winter, and January minimum temperature, April average temperature and growing season temperatures ($p < 0.05$, Figs. 4, 5 and 6). Tree growth of relatively moist L1 site was strongly related to precipitation from January and March, and previous August average temperature, January maximum temperature, March average temperature and growing season average temperature whereas L2 was related to March precipitation, March average temperature, and growing season average temperature. Tree growth of Hengduan site was primarily related to only temperature variables ($p < 0.05$, Figs. 4, 5 and 6). Tree growth in Tb site was strongly related to minimum temperature of January, August and winter months. August average temperature and September average temperature were also related to growth of trees in rage Tb site. RWI of X1 site was corelated to minimum temperature from September (previous), January, September, winter, summer months, and average temperature of May, August, September, growing season months ($p < 0.05$, Figs. 4, 5 and 6). However, the strength of the relationship was slightly different.

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

Multiple regression analysis of climate variables with radial growth yielded a total R^2 = 0.34, 0.51, and 0.52 across relatively dry sites (Tb) and cold alpine site (X1 and X2) of Hengduan Mountains, respectively (Table 2). August average temperature from the previous year was primarily related to RWI of *A. georgi* across the dry treeline (Tb) of Hengduan Mountain. In addition, previous growing season precipitation and current August minimum temperature influence the radial growth of *A. georgei*. Radial growth of *L. potaninii* across the alpine tree line site of Xinagcheng (X1, and X2), was primarily influenced by September minimum temperature from previous year. The other related variables for tree growth of *L. potaninii* were current growing season average temperature in the X1 site while current minimum temperature of September and summer (negative relation) influenced the growth of *L. potaninii* across the X2 site.

3.3 Stand age structure

We found that the seedling density was maximum at L1, L2 and X1 whereas it was minimum at X2 showing considerable spatial heterogenity in tree establishment. We observed a similar recruitment pattern in all transects: the largest number of individuals was recorded for 10–30 years of age (most of them were established during 1990 to 2000). The maximum recruitment occurred at the highest elevation at all sites except X1 and X2, which showed very poor regeneration at upper edge of treeline ecotone, and the treeline retreat in the recent decades (after 1990) (Fig. 7).

3.4 Treeline movement

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

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

4. Discussion

Our goal was to assess how climate factors affect radial growth and spatiotemporal dynamics of different species across timberline and treeline of the Trans-Himalayan region and Hengduan Mountains of China. Along with various studies on climate change impacts on tree growth across these regions (Fan et al. 2009; Liang et al. 2016; Tiwari et al. 2017a), our study expands and adds empirical evidence of tree growth and interactions of climate variables across high altitude. Overall, precipitation and temperature from current and previous year were related to site-specific radial growth. We found that precipitation showed both positive and negative influence and average temperature inversely influence the radial growth of *B. utilis* across moist site (L1, L2) while precipitation and temperatures both showed negative impacts on radial growth of *A. spectabilis* on dry site (C) of Himalayan treeline. In contrast, only temperature of various months and growing season from previous and current year controlled the radial growth of *A. geo*rgei (Tb) and *L. potaninii* (X1, X2). There is higher potential of treeline shifts associated with changing climate across the Trans-Himalayan region, whereas low potential of treeline shift despite climate suitability in the Hengduan Mountain sites in China.

4.1 Climate growth response

Our results showed that the radial growth of trees is strongly controlled by precipitation and temperature at Trans Himalayan sites. The moisture sensitivity of tree growth has been observed in Himalaya and high mountains of the world (Stahle and Hehr 1984, Qi et al. 2015; Lopez et al. 2017, Tiwari et al. 2017a, b; Sigdel et al. 2018). The higher temperature in the early growing season (March-May) induces drought stress, and the rainfall during this period is beneficial for tree growth as evidenced by our findings (fir and birch). And these results are similar with growth climate response in central and eastern Himalaya (Dawadi et al. 2013; Liang et al. 2014; Tiwari et al. 2017a; Gaire et al. 2017), and in treeline-forming *Betula* species (Takahashi et al. 2005; Wang et al. 2013). Sano et al (2015), Gaire et al (2014) and Tiwari et al (2017b) reported importance of spring season moisture coupled with warm-day temperature (Tmax) for radial growth in the region. Gaire et al (2014) also found that growth is typically sensitive to growing season temperature of tree species at fir treelines in eastern Himalaya and central Himalaya, and Schwab et al (2018) showed the stronger correlation between tree radial growth of Himalayan fir and 20^{th} century temperature as indicated by blue intensity (BI) as the climate proxy. Our findings confirm spatial variability in climate and growth response in Himalayan topography, particularly since the eastern Himalaya region is wetter than its drier western counterpart (Shrestha et al. 2012). Spring season warming coupled with higher radiation initiates early melting of snow and increased atmospheric evaporative demands. This amplifies exposure of the ecotone to drought until the onset of summer precipitation (Fritts 1976; Bhattacharya et al. 2006; Cook et al. 2003, Winkler et al. 2018). A frequent existence of narrow and missing growth rings in birch across central Himalayan also highlights that drought stress affects birch radial growth (Liang et al. 2014).

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

4.2 Treeline movement

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

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

The higher frequency of tree establishment at the upper edge of treeline is mainly due to increased temperature accompanied by enough moisture (Cook et al. 2003; Sano et al. 2005; Shrestha et al. 2012). However, the hotter summer (July) may also create desiccation and drought stress in case of depleted soil moisture and affect recruitments (Hughes et al. 2009; Fajardo and McIntire 2012). The higher sensitivity of minimum summer temperature and spring season precipitation with regeneration was also documented in *Picea schrenkiana* from treeline ecotone of Tian Mountains of China (Wang et al. 2006).

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

We reported great variability in position of treeline in the nearby sites (< 5 km) within the same mountain slope, and rate of upward shifting of treeline, and this variability could be the outcome of human impact in the past including logging, grazing and fire that caused the decline in land use intensity as indicated by Schickhoff et al (2015). Different slope exposure and wind velocity (Greenwood et al. 2014), and biotic interactions (Liang et al. 2016) are likely to determine the position of treeline. The maximum shift of treeline was observed at *Betula* site (L2) linked to the increasing average temperature and precipitation in the region. As an early successional species birch also has higher regeneration potential on exposed sites of the upper treeline (Shrestha et al. 2007). Furthermore, the maximum density of tree individuals and higher seedling sapling density within the plot indicated the higher potential for future shift. Our findings agree with treeline shift reports in the Himalaya (Dubey et al. 2003; Gaire et al. 2014) with considerable recruitment in the recent decades especially after 1950s as reported by (Liang et al. 2011b; Shrestha et al. 2015; Schickhoff et al. 2015).

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

Despite favourable climate, considerable gaps in the tree establishment across alpine region (X1, X2) due to low regeneration of larch tress in the recent decades could be associated with poor soil quality and anthropogenic disturbance via logging operations. Our results indicated that Hengduan larch (X1, X2) and silver fir (Tb) have experienced greater influence of disturbances for tree establishment in treeline. The poor regeneration in these sites (X1, X2) might lead to treeline retreat in these sites in the future if adult individuals die or removal through exploitation increases. The potential for such retreat is already evident at X1 and X2, especially after the 1990s. Therefore, we highlight that modifying factors (biological, geomorphology, human interference) in addition to climate may drive tree establishment and stand densification in treelines and it is, therefore, inadvisable to overlook local context when predicting treeline changes across broad regions.

5 Conclusions

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

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Conflict of interest The authors declare that they have no conflict of interest.

Authors' contributions ZZK, FZX, AT conceptualized and designed the research; AT, LSF collected data; AT, AA, AJ performed the analysis and wrote manuscript. The author(s) read and approved the final manuscript.

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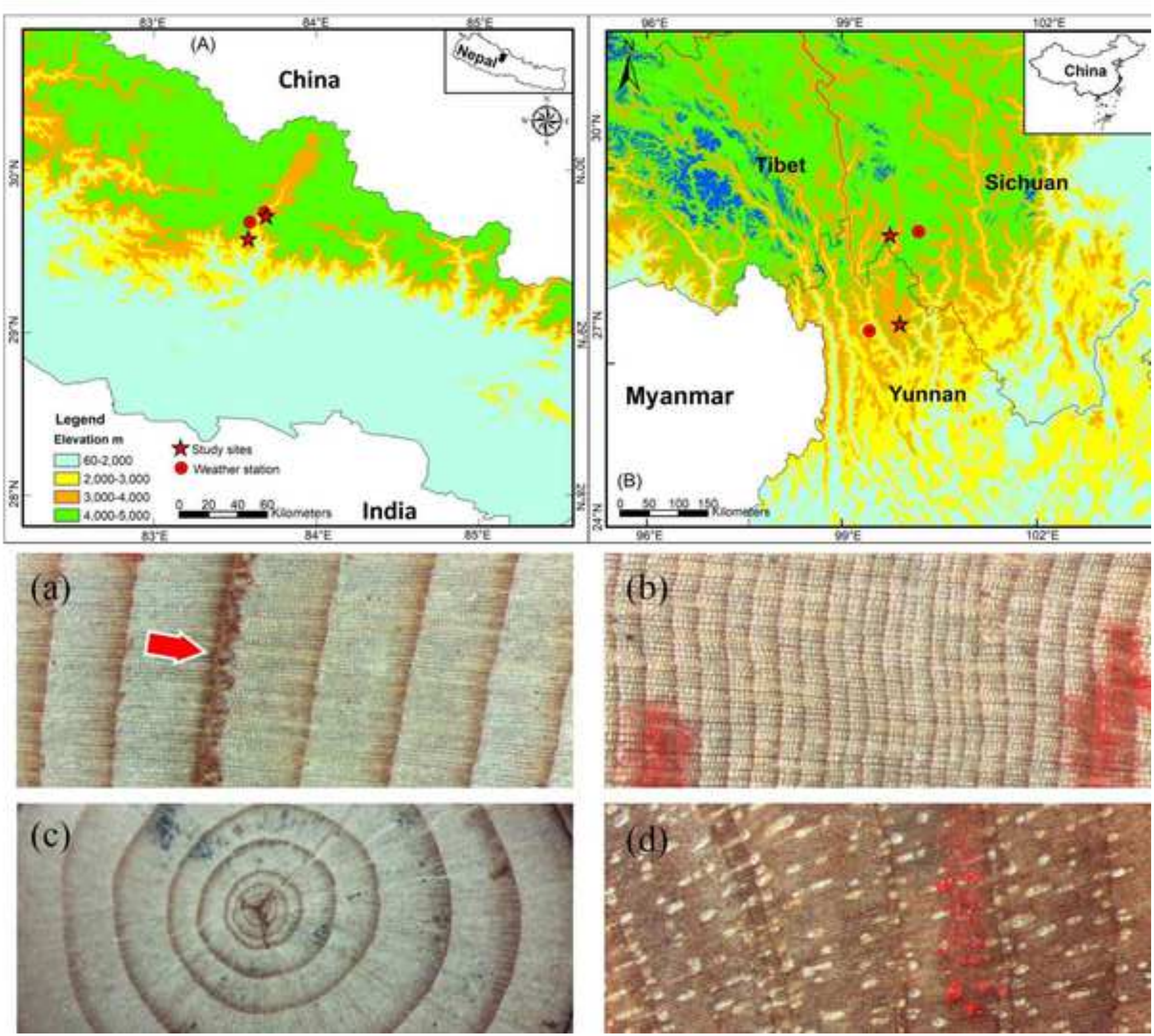
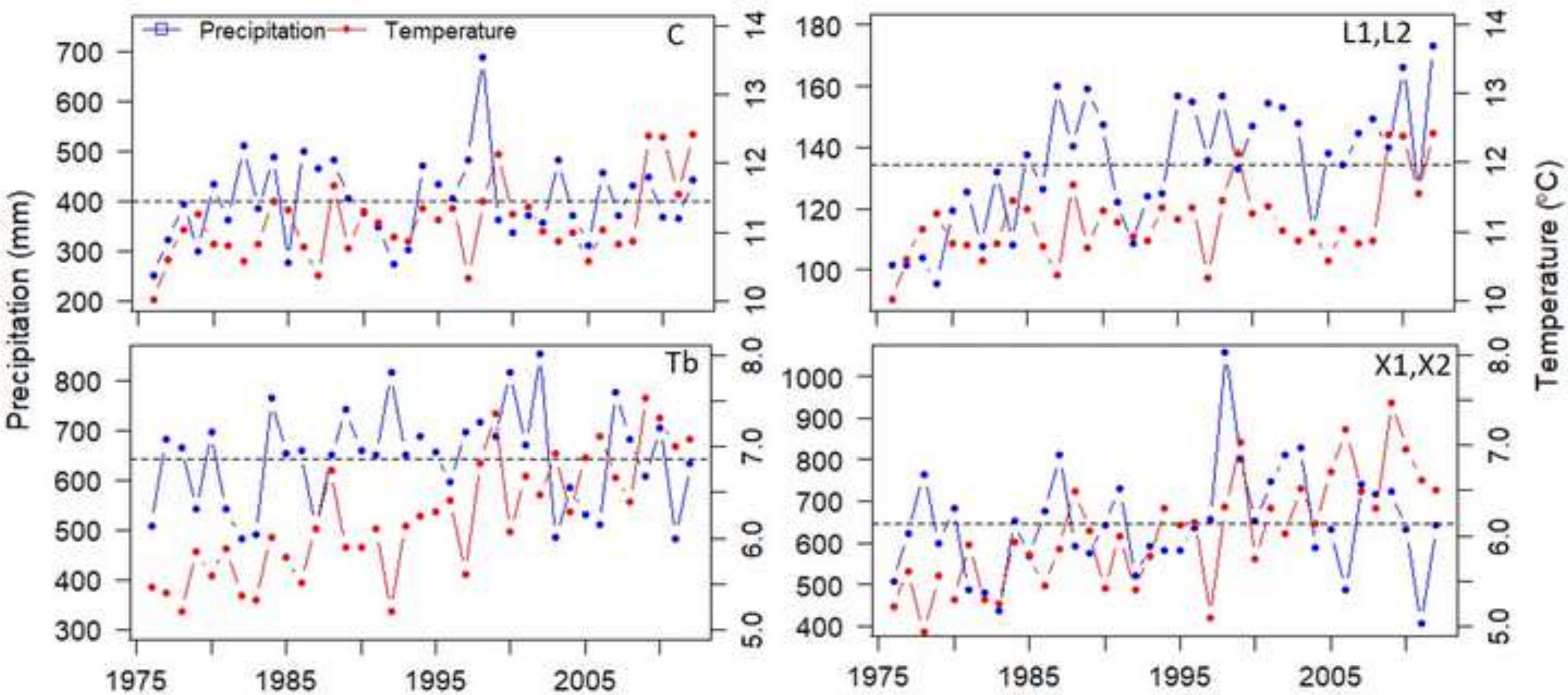
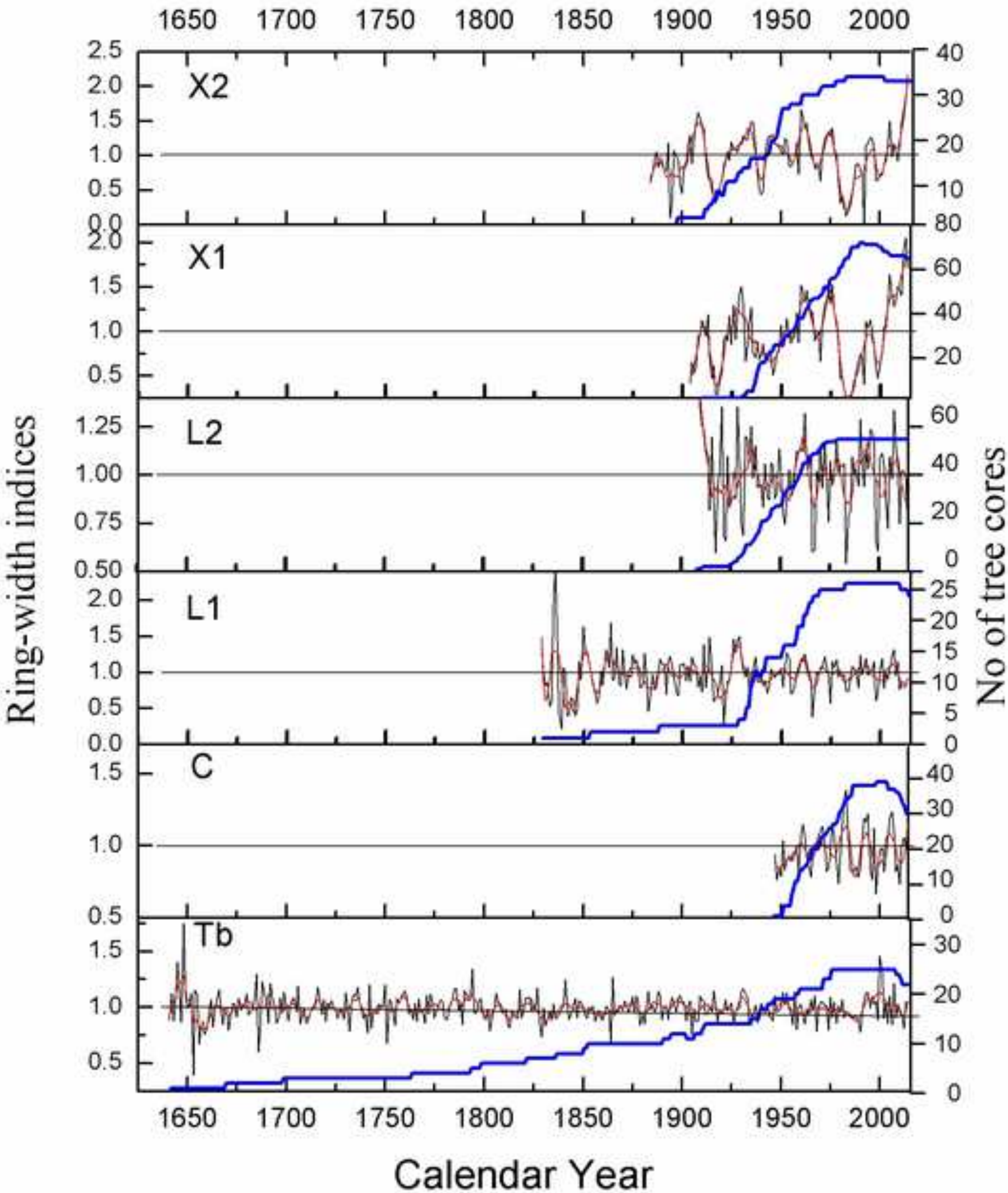
Comments	**Response**
Although it is a bit general, please try to improve the first part of the abstract (L15-22). Now it seems more than a few sentences a bit disconnected.	We have revised the first part of abstract (Lines 15–26)
L59. Please add some additional references to reinforce this point.	Thank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

Figure

Click here to access/download;Figure;Figure 1.jpg



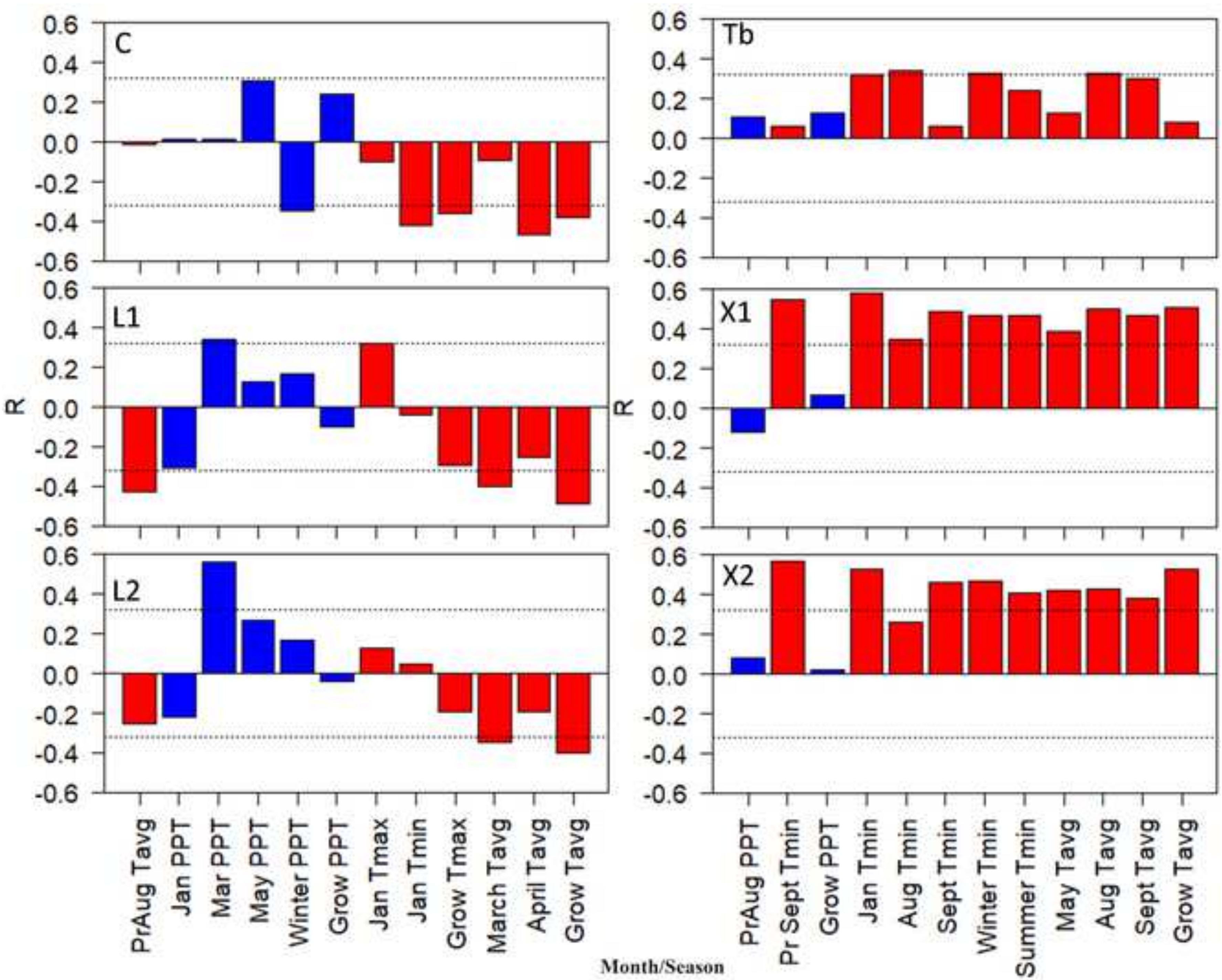

Precipitation
Temperature
C
L1,L2
Tb
X1,X2
Precipitation (mm)
Temperature (°C)
1975
1985
1995
2005

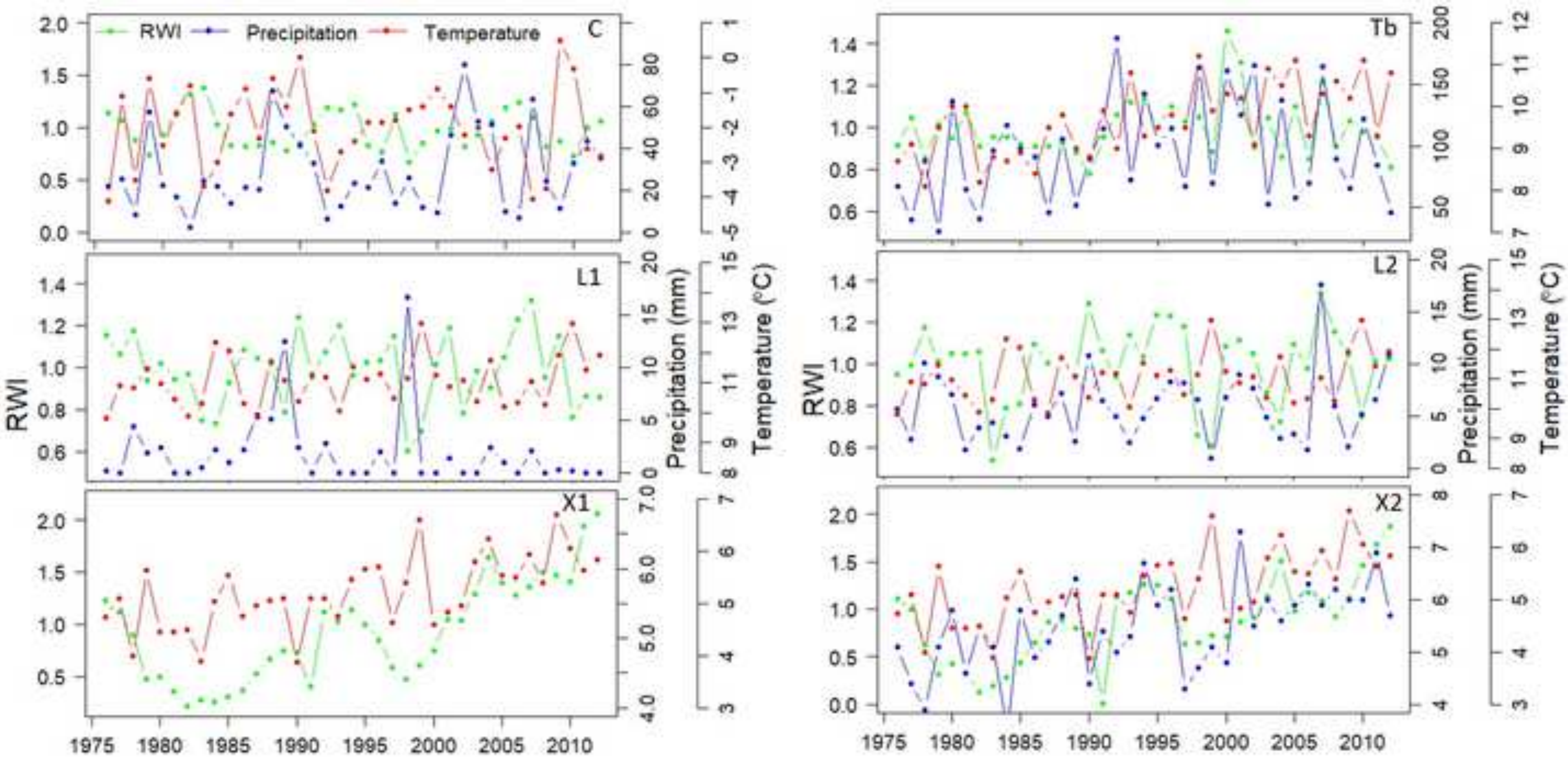


X2
X1
L2
L1
C
Tb
1650
1700
1750
1800
1850
1900
1950
2000
Ring-width indices
No of tree cores
Calendar Year

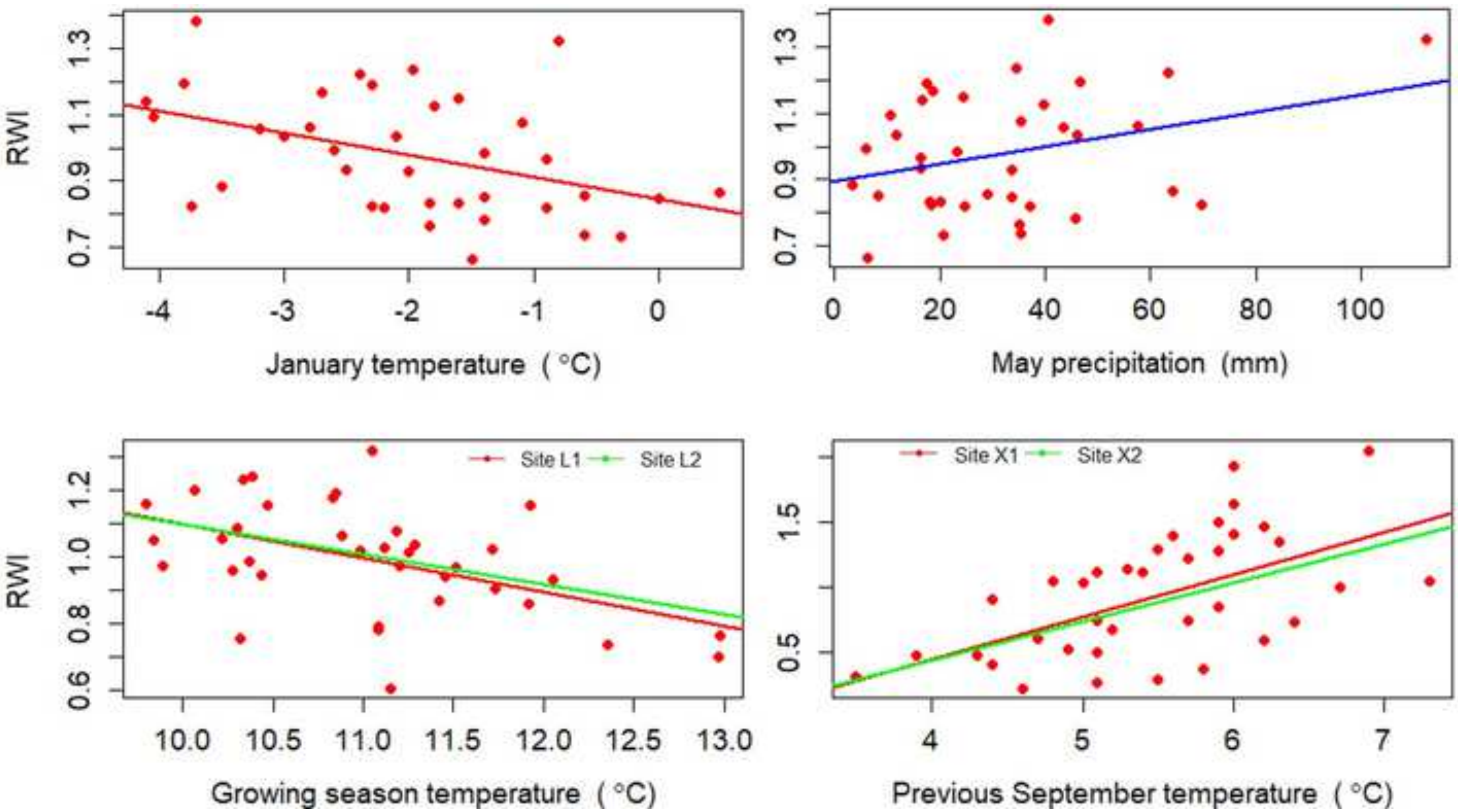
Figure

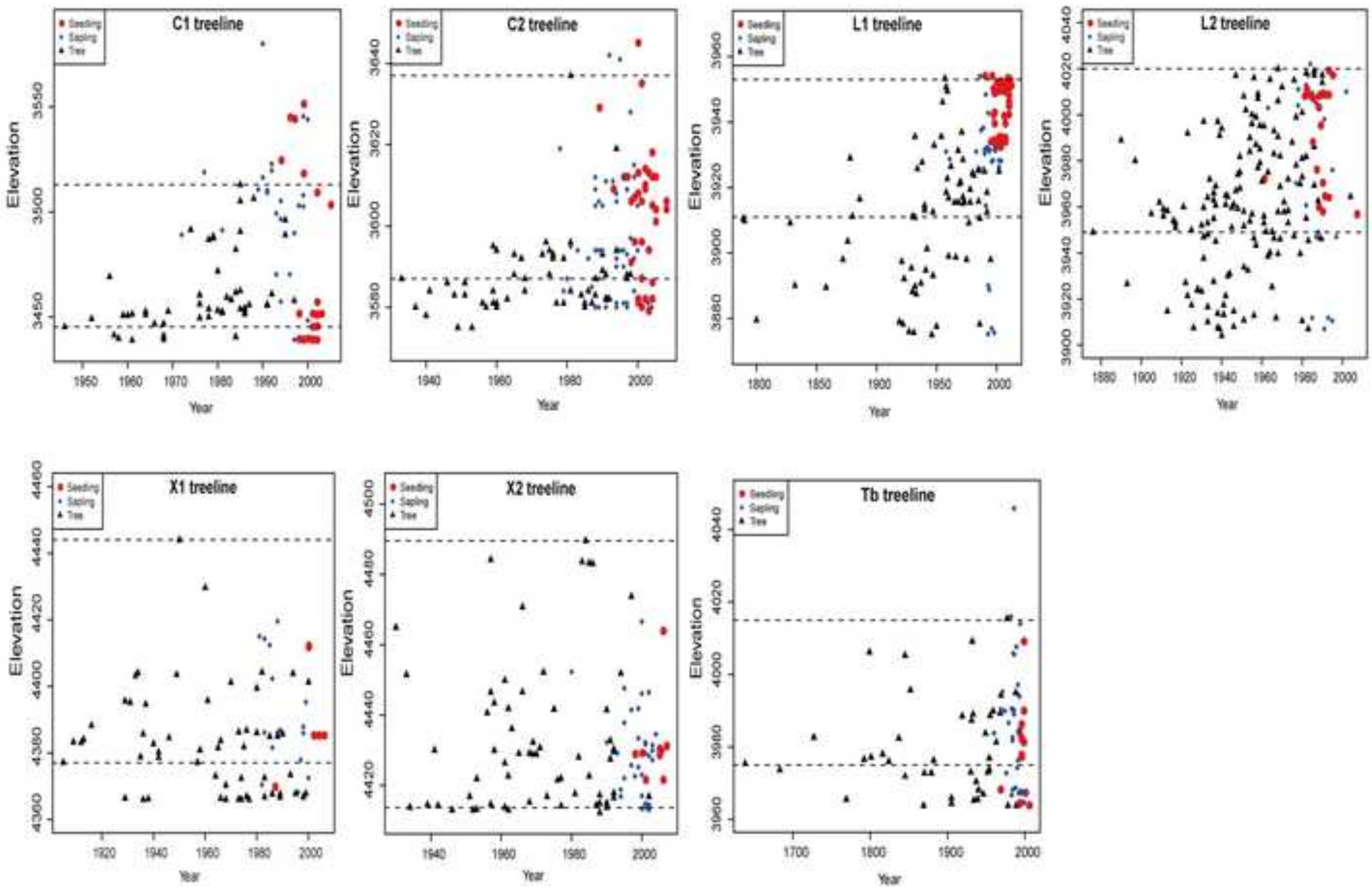
Click here to access/download;Figure;Figure 4.jpeg





RWI
Precipitation
Temperature
C
Tb
L1
L2
X1
X2
RWI
RWI
Precipitation (mm)
Temperature (°C)
Precipitation (mm)
Temperature (°C)
1975
1980
1985
1990
1995
2000
2005
2010


RWI
1.3
1.1
0.9
0.7
-4
-3
-2
-1
0
January temperature (°C)
1.3
1.1
0.9
0.7
0
20
40
60
80
100
May precipitation (mm)
RWI
Site L1
Site L2
1.2
1.0
0.8
0.6
10.0
10.5
11.0
11.5
12.0
12.5
13.0
Growing season temperature (°C)
Site X1
Site X2
1.5
0.5
4
5
6
7
Previous September temperature (°C)


C1 treeline
C2 treeline
L1 treeline
L2 treeline
X1 treeline
X2 treeline
Tb treeline
Seedling
Sapling
Tree
Elevation
Year

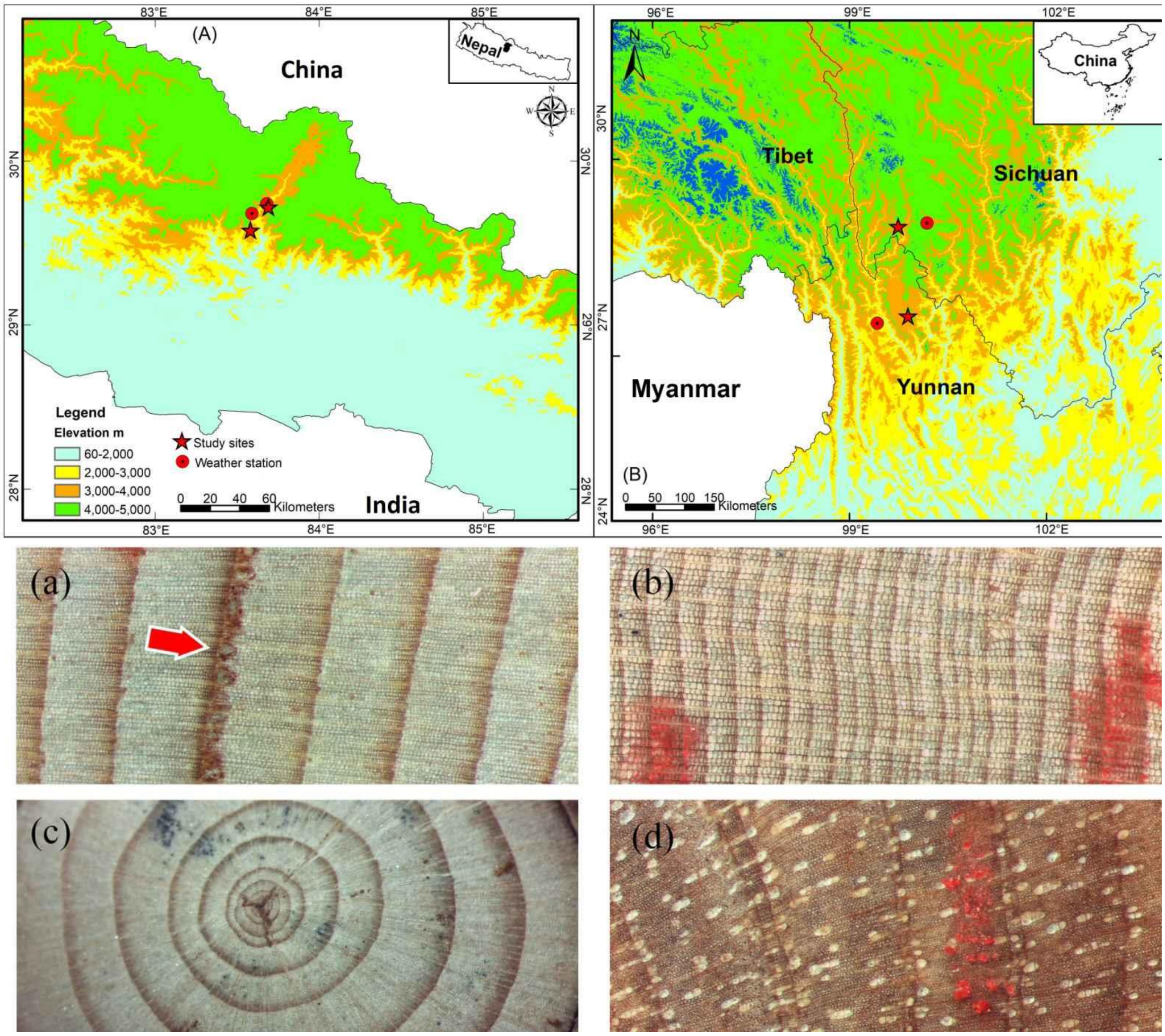


Figure 1. Location of study area across trans-Himalaya region of Nepal (A) and Hengduan mountains of China (B) (upper panels). Section of tree cores including (a) *Abies spectabilis* (red arrow showing frost ring), (b) *Larix potaninii*, (c) *Abies georgei*, and (d) *Betula utilis*

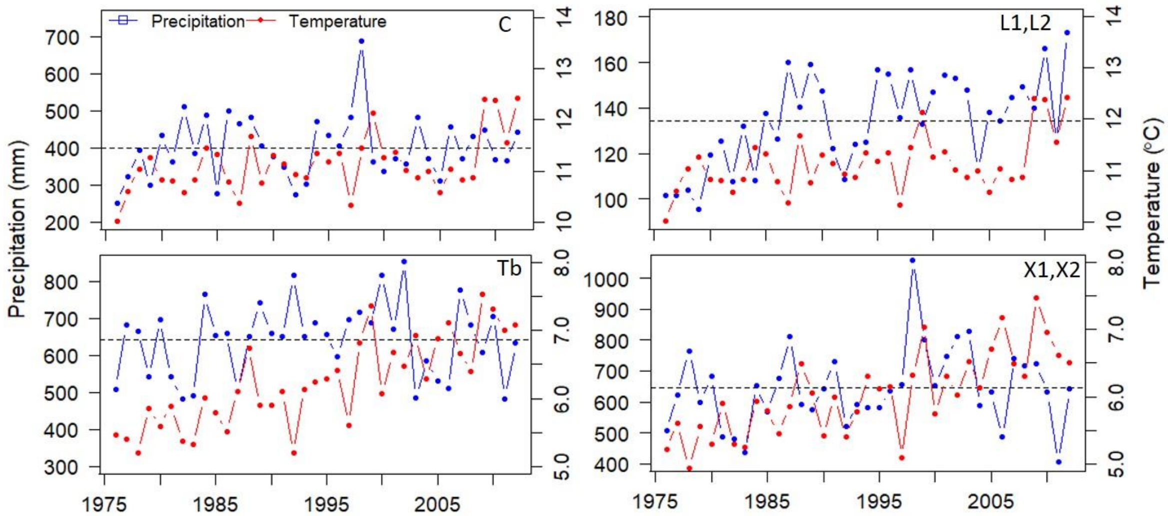


Figure 2. A 37 years' average monthly temperature and precipitation of the study area with an average precipitation (dotted line). Time series of average annual precipitation and temperature of all study sites with an average precipitation (dotted line) for 37 years. Temperature and precipitation were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

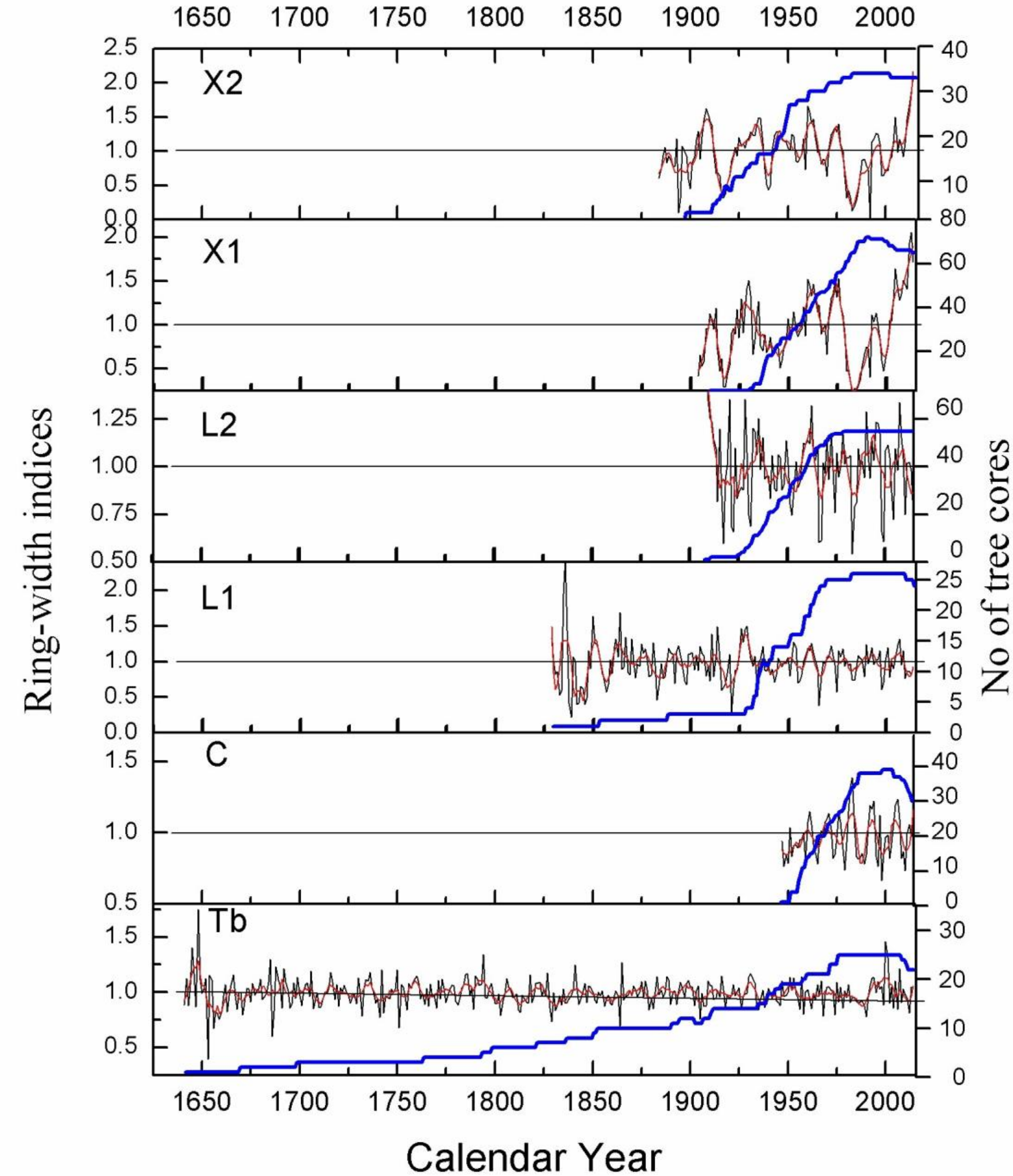


Figure 3. Standardized tree-ring width index (RWI) chronology with sample size with scale on the right axis for the study sites after 1987. The red smoothing line is a five year's cubic spline fit; blue lines indicate number of tree cores.

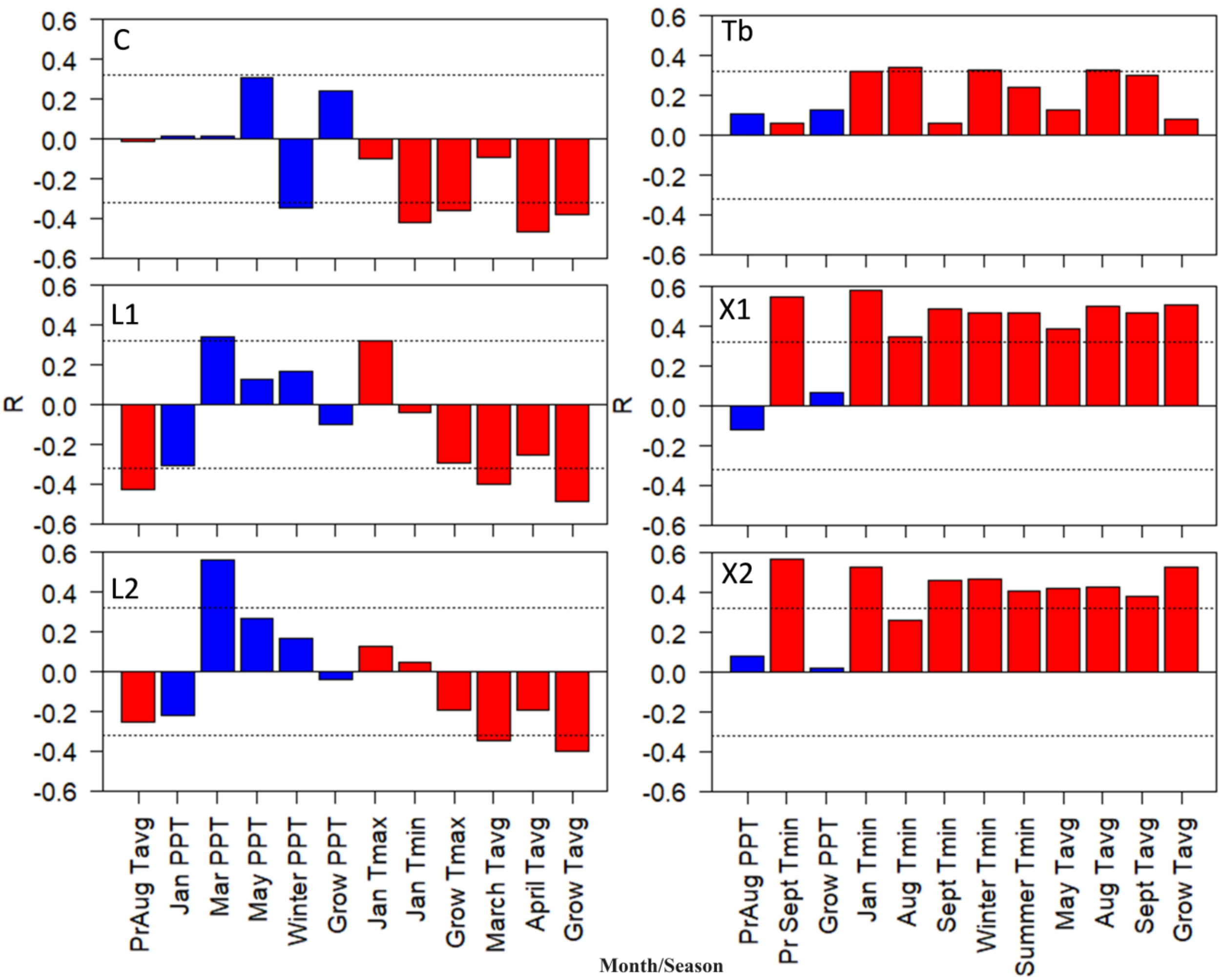


Figure 4. Correlations of tree ring width (RWI) chronologies of different sites across Trans Himalayan and Hengduan regions. Horizontal dotted lines at r = 0.32 and r = -0.32 form a 95% CI; significant correlations ($p < 0.05$). Blue, and red colors indicate precipitation, and temperature, respectively.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

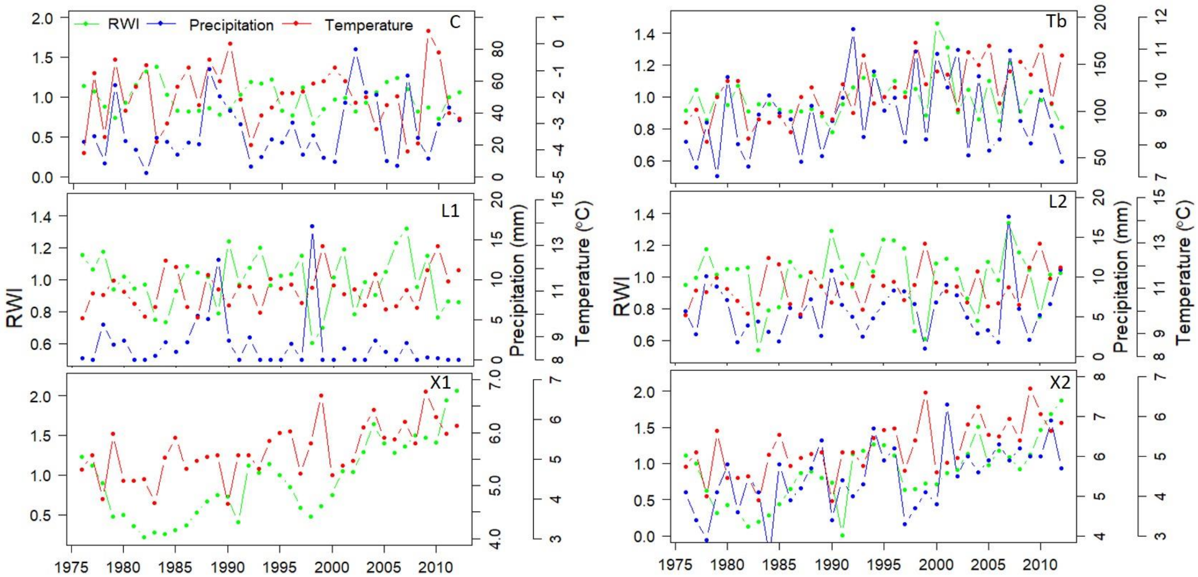


Figure 5. Time series of standardized annual RWI and current year growing season (March-May) maximum temperature and total precipitation across study area. See table 1 for the site description.

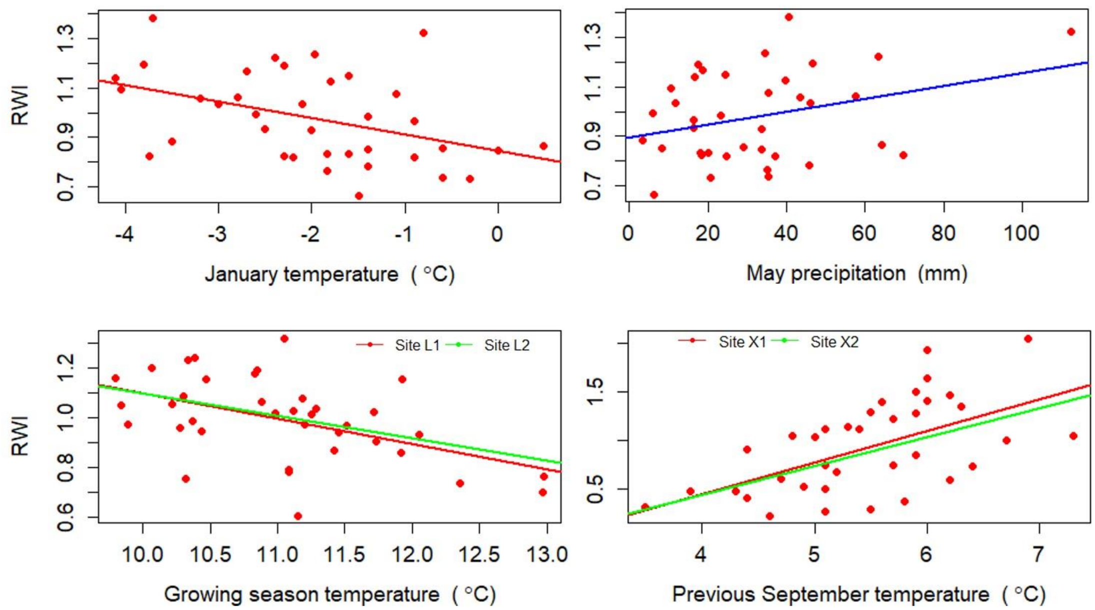


Figure 6. Relationship between standardized RWI and (a) January minimum temperature and (b) May precipitation for *A. spectabilis*,(c) growing season average temperature for *B. utilis*, and (d) previous year September minimum temperature for *L. potaninii*.

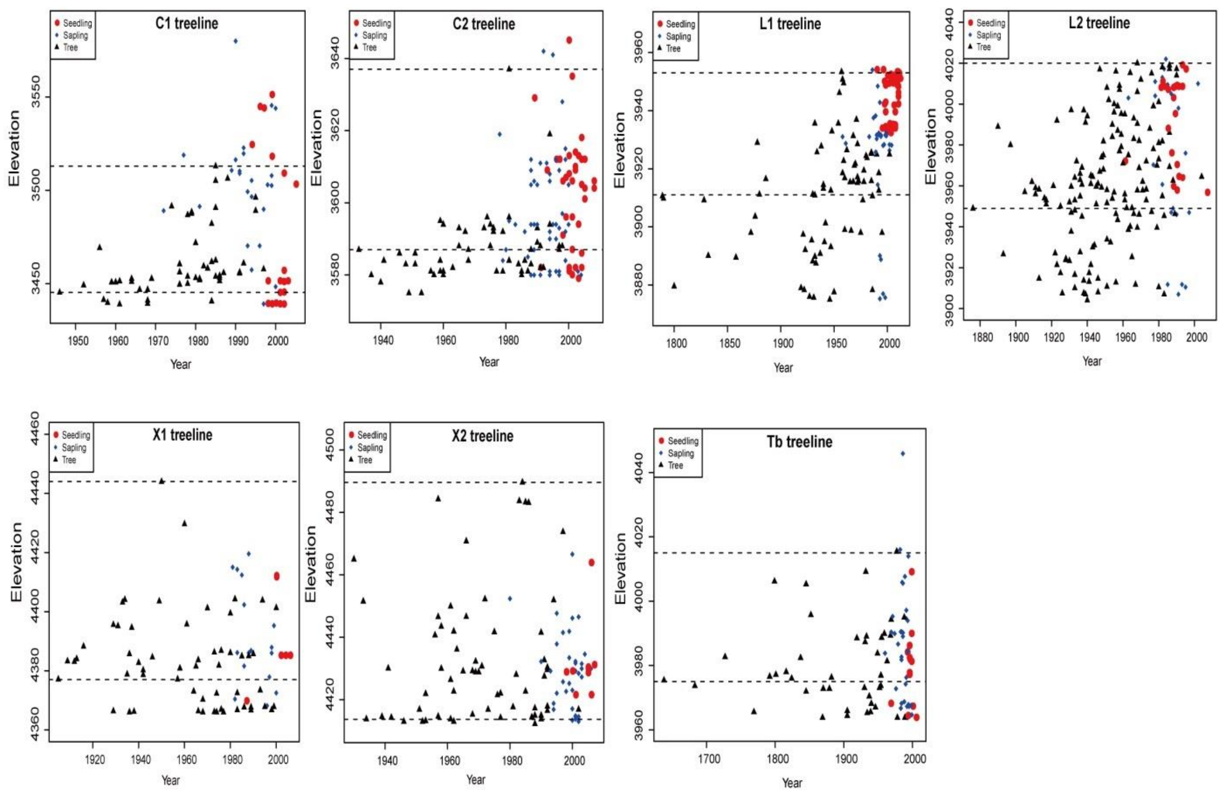


Figure 7. Spatiotemporal dyanmics of treeline in the treeline plots, horizontal axis showing year of tree establishment, and vertical axis showing elevation of tree specimen in each treeline ecotone. The upper dashed line in each plot represents elevation of modern treeline, the lower dashed line in 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)**	$\mathbf{r_{bt}}$	**Mean sensitivity**	**EPS**	**All series Rbar**	**1st order AC**
A. spectabilis C	68	36 (40)	0.47	0.326	0.931	0.187	0.612
B. utilis 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
A. georgei ATE(Tb)	374	19 (26)	0.45	0.106	0.756	0.284	-0.001
L. potaninii 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