



# Changes of growth-climate relationships of Smith fir forests along an altitudinal gradient

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**Abstract** Temporal changes in the relationship between tree growth and climate have been observed in numerous forests across the world. The patterns and the possible regulators (e.g., forest community structure) of such changes are, however, not well understood. A vegetation survey and analyses of growth-climate relationships for *Abies georgei* var. *Smithii* (Smith fir) forests were carried along an altitudinal gradient from 3600 to 4200 m on Meili Snow Mountain, southeastern Tibetan Plateau. The results showed that the associations between growth and temperature have declined since the 1970s over the whole transect, while response to

standardized precipitation-evapotranspiration indices (SPEI) strengthened in the mid- and lower-transect. Comparison between growth and vegetation data showed that tree growth was more sensitive to drought in stands with higher species richness and greater shrub cover. Drought stress on growth may be increased by heavy competition from shrub and herb layers. These results show the non-stationary nature of tree growth-climate associations and the linkage to forest community structures. Vegetation components should be considered in future modeling and forecasting of forest dynamics in relation to climate changes.

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**Keywords** Climate change · Tree rings · Altitudinal gradient · Community structure · Plant diversity

## Introduction

The relationship between radial growth of trees and climatic factors has long been assumed to be stable over time in climate reconstruction studies (Fritts 1976), rendering it the basis to predict forest carbon fluxes and sinks, or to assess forest health risks in a changing environment (Braswell et al. 1997; Vaganov et al. 1999). However, shifts in tree growth sensitivities from temperatures to moisture in the late twentieth century (Jacoby and D'Arrigo 1995) and the instability of growth-climate response has been widely reported from boreal forest zone to mid- and low-latitude forests (Briffa et al. 1998; Barber et al. 2000; Wilmking and Myers-Smith 2008). Characteristics of the instability and mechanisms behind it differ from one region to the next (Briffa et al. 1998; D'Arrigo et al. 2008; Wilmking and Myers-Smith 2008). Nevertheless, there is a lack of information on how forest community structures affect climate-growth relationships despite the instability of growth-climate response and

its causes have received increasing interest in forest ecology and global climate change.

Declining temperature and increasing moisture sensitivities in tree growth are widely reported for high-latitude forests, possibly due to rising temperatures in combination with increased drought stress (Jacoby and D'Arrigo 1995; Briffa et al. 1998; Driscoll et al. 2005). In addition to changes in climate, nutrient availability and microsite conditions could also change the sensitivity to temperature variations (Wilmking et al. 2004; Wilmking and Juday 2005). A recent study showed that temporal variability in tree growth response to climate is universal and relates to severe disturbances or physiological states of trees (Peltier and Ogle 2020). Similar changes in the relationships between growth and climate were also reported for high-altitude forests such as on the Tibetan Plateau. For example, growth of *Picea crassifolia* Kom. on the northeastern Tibetan Plateau showed a strengthening of correlations of annual radial growth with summer temperatures but with a very high spatial heterogeneity, i.e., positive on some sites and negative on others (Zhang and Wilmking 2010; Wang et al. 2020). In the eastern and southeastern Tibetan Plateau, divergent tree growth response to recent climate warming was observed between *Abies fargesii* Franch and *Larix kongboensis* R.R. Mill (Zhao et al. 2018; Yu et al. 2023). In contrast, studies of tree-ring data in the European Alps showed no unusual late twentieth century divergent growth responses (Büntgen et al. 2008). An examination of the data handling procedure suggested that divergent growth response would have been prevented if the sites and trees were carefully selected and appropriate techniques for tree-ring detrending and growth-climate regression were used (Esper and Frank 2009). To date, the causes and spatial scale of changing tree growth-climate response are still debated.

Tree growth-climate relationships may exhibit significant differences along an altitudinal gradient in the same region (Kharal et al. 2017; Gaire et al. 2023). For example, previous studies have reported that temperature is the limiting factor at the treeline while tree growth is more sensitive to fluctuations in precipitation at lower altitudes (Lv and Zhang 2012; Kharal et al. 2017; Panthi et al. 2020). In addition to climate conditions, forest community structure may vary at different altitudes because decreasing temperatures could restrict some plant species as altitude increases (Rahbek 1995; Ma et al. 2010), resulting in communities at lower altitudes that are more diverse and denser in composition than those at higher altitudes (Kraft et al. 2011). Forest community structure may affect tree growth in two alternative ways by either exaggerating or buffering the climate change effects on growth (Pretzsch and Dieler 2011; Clark et al. 2012, 2016). Despite the important role of vegetation communities on tree growth and its climate response, this has been largely overlooked in previous studies. Therefore, clarifying

the associations between vegetation communities and tree growth-climate response remains an important objective.

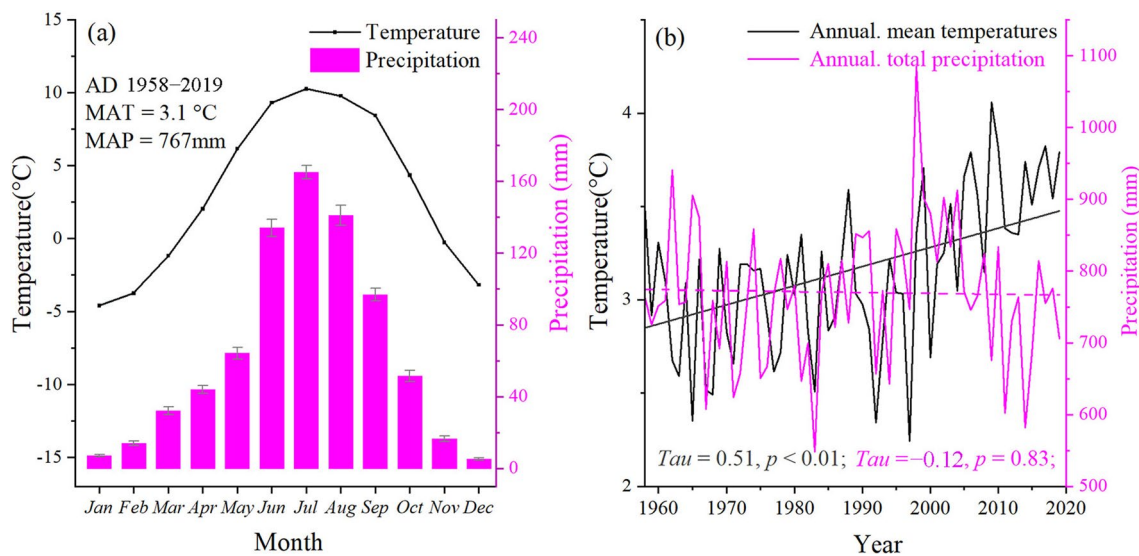
In this study, the temporal characteristics of tree growth-climate response of *Abies georgei* var. *smithii* (Viguiégu-Gaussen) W. C. Cheng & L. K. Fu (Smith fir) along an altitudinal gradient in the Meili Snow Mountain on the southeastern Tibetan Plateau were investigated. Differences in hydrothermal mountain conditions provide a diversity of vegetation communities along an altitudinal gradient. However, the influence of vegetation structure on instability about tree growth-climate associations is not well recognized (Zhang and Wilmking 2010; Yu et al. 2023). The objectives of this study is to identify, along an altitudinal gradient, spatial-temporal patterns of tree growth-climate associations and the link to vegetation structures. It was hypothesized that climate warming-induced changes in tree growth-climate relationships would be exaggerated by denser community structures at lower altitudes. Evidence of such processes would provide insight into the feedback between forest growth and climate changes and contribute to the design of future research on forest dynamics.

## Materials and methods

### Study area and climate

We collected increment cores of Smith fir trees and forest community structure data in 20 m × 20 m vegetation plots from the treeline to the lower limit of the forest distribution located on the southwest of Meili Snow Mountain, southeastern Tibetan Plateau (98.46–98.50°E, 28.528–28.555°N). The regional climate is influenced by the southwest Asian monsoon (Bird et al. 2014; Yu et al. 2016). Because the meteorological station closest to the sampling site started climate observations in 1958, climate data was obtained for 1958–2019 from Climate Unit (CRU) 4.05 dataset (<http://climexp.knmi.nl>). Over the study area, mean annual air temperature is 3.1 °C and annual total precipitation 767 mm, with 78% falling in the monsoon period from May to September (Fig. 1a).

Trends in mean annual air temperatures and total precipitation were investigated using the non-parametric Mann–Kendall technique (Yue and Wang 2004). Kendall's tau ( $t$ ) was calculated to evaluate the nonparametric correlation between climate factors and time. The absolute value of  $t$  was used to evaluate the strength of the trend. A positive value implies an increasing trend and a negative one a decreasing trend. Over the period 1958–2019, annual air temperatures showed an increasing trend ( $t=0.51$ ,  $p<0.01$ ) and annual total precipitation an insignificant decreasing trend ( $t=-0.12$ ,  $p=0.83$ ) (Fig. 1b).



**Fig. 1** **a** climatic diagrams and **b** changes 1958–2019. MAT and MAP in (a) are mean annual temperature and mean annual total precipitation, respectively. The solid line is significance ( $p < 0.05$ ) while the dashed line is an insignificant ( $p > 0.05$ ) trend

### Vegetation survey and tree-ring data

Forests growing between 3600 and 4200 m a.s.l. are dominated by Smith fir, which is gradually replaced upwards by *Rhododendron* shrubs and by *Pinus yunnanensis* Franch. at lower elevations. Plots 20 m × 20 m were established every 100 m between 3600 and 4200 m a.s.l. Four 10 m × 10 m shrub quadrats and four 1 m × 1 m herb quadrats were set out in each plot in a diagonal direction. In each quadrat or plot, the plant species were identified, and their abundance, height and cover recorded. For trees, individual DBH (diameter at breast height) and crown width were recorded, and seedlings of each tree species were also recorded. In forest plot, increment cores were taken from Smith fir trees with DBH > 15 cm.

In the laboratory, increment cores were mounted, polished and measured according to standard dendrochronological techniques. The sequences of tree-ring widths were crossdated and the quality of crossdating was validated using the program COFFCHA (Holmes 1983) to ensure each ring was assigned the calendar year of its formation (Schweingruber 1988). To obtain well-replicated chronologies, the tree-ring samples were grouped into three altitudes, treeline (4200 m a.s.l.), middle elevation (3900–4100 m a.s.l.) and lower elevation (3600–3800 m a.s.l.). A standard tree-ring chronology was developed for each elevation group by fitting a negative exponential curve or a straight line of negative slope to the tree-ring sequences to remove any biological growth trends and computing bi-weight robust means of the resulting ring-width indices (Cook 1985).

### Statistical analysis

Climate data covering the study area for 1958–2019 was obtained from Climate Research Unit dataset CRU TS v4.05 (Harris et al. 2020). The climate variables were monthly mean temperature, monthly mean diurnal temperature range, total monthly precipitation, and 6-month scale standardized precipitation- evapotranspiration index (SPEI). The climate-growth relationships were investigated using Pearson correlations with a monthly window from September of the previous year to September of the following year over 1958–2019. In addition, temporal variability of the growth-climate relationships was analyzed using correlations between the tree-ring chronologies and the most correlated climatic variables over a 30-year sliding window. The analyses were carried out using the package *cor* (Best and Roberts 1975) in the R-4.2.2 program (R Core Team 2022).

To characterize the vegetation structure, species information was compiled for each plot, including name, frequency of occurrence, density, coverage, species richness and number of seedlings. The importance value for each plant was obtained by averaging its values of relative frequency, density and coverage.

To evaluate the possible linkages of community structure with tree growth, the mean sensitivity of interannual change of tree-ring widths were calculated for each sample using the following (Lyu et al. 2016a):

$$S = \frac{1}{n-1} \sum_{i=1}^{n-1} \frac{2 |R_{wn} - R_{wn-1}|}{R_{wn} + R_{wn-1}} \quad (1)$$

where,  $S$  is mean tree-ring sensitivity;  $Rw_n$  is the raw ring width for year  $n$ ;  $Rw_{n-1}$  is the ring-width before year  $n$ . The mean sensitivity ranges from 0 to 2; if it is 0, there is no difference among the annual rings, and if it is 2, the tree grows in one year and stops growth in the next. Finally, linear regression analysis was applied to assess the relationship between the percentage of tree growth reduction and forest community structure (Montgomery et al. 2021).

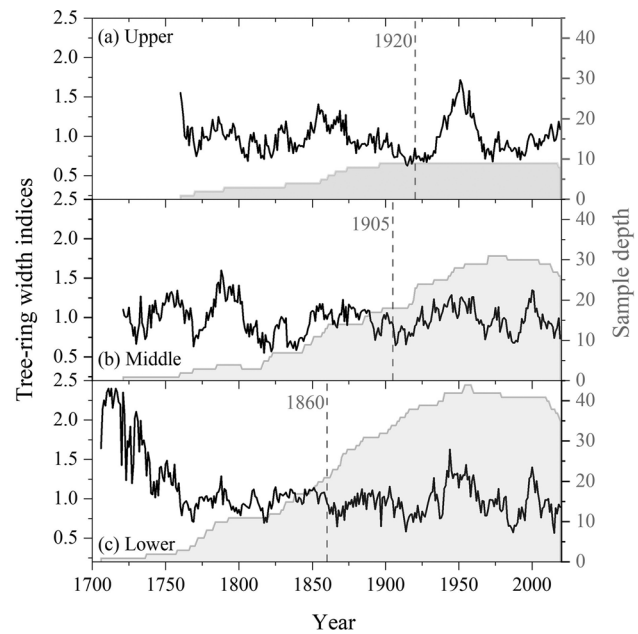
## Results

### Development of tree-ring chronology

Tree-ring sequences, with years ranging from 50 to 314, were cross-dated and subjected to analyses (Table 1). With increasing altitude, the average sensitivity of tree rings decreased from 0.21 to 0.14, and the mean standard deviation from 0.51 to 0.15, indicating a reduced sensitivity and variation in tree rings with increasing altitude. There were no significant differences in the mean auto-correlation and mean inter-series correlations at different altitudes. Values of the expressed population signal (EPS) > 0.85 started from 1860, 1905 and 1920 in the chronologies for upper, middle and lower altitude trees, indicating that chronologies after these years contained strong common signals for the sampling sites (Fig. 2).

### Relationship between tree-ring chronologies and climatic factors

Analyses of growth-climate relationships showed that ring widths were positively correlated with November temperatures of the previous growth year for all altitudes. Positive correlations between ring width and April and July temperatures of the following year were observed at the treeline (Fig. 3a). At middle and lower altitudes, ring widths were positively correlated to SPEI from the previous September to the following September (Fig. 3b). However, there were no significant correlations with monthly SPEI for trees at the treeline. For monthly precipitation



**Fig. 2** Standard tree-ring width chronologies of Smith fir for **a** upper, **b** middle, and **c** lower altitudes on Meili Snow Mountain; dotted lines indicate year from which the values of expressed population signal were greater than 0.85

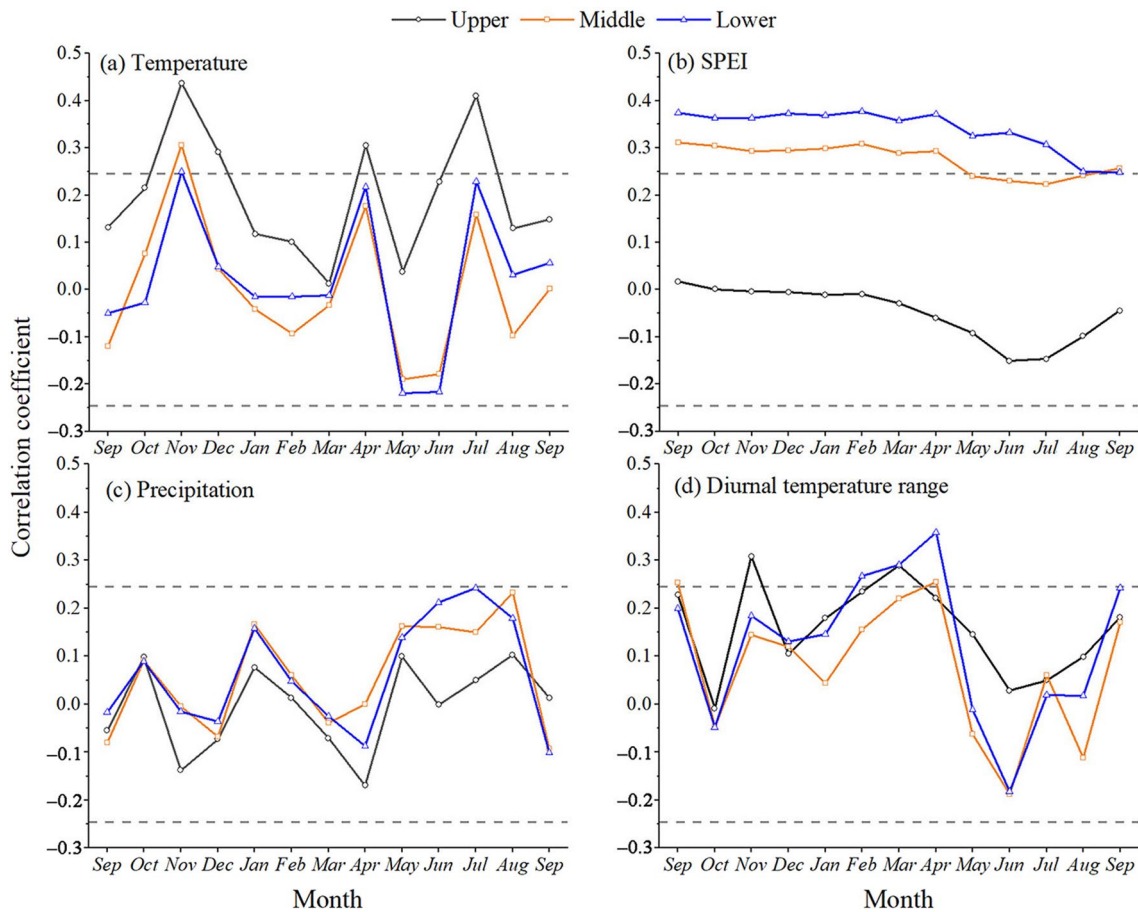
and diurnal temperature differences, tree-ring indices had no significant correlations with total monthly precipitation (Fig. 3c), but a significant correlation with monthly diurnal temperature range in March and April of the following year at middle and lower altitudes (Fig. 3d).

The moving correlation analyses using a 30-year sliding window showed a significant positive correlation between tree rings and November temperatures of the previous year starting in the late-1950s to the mid-1970s for the upper altitude, in the early half of the 1970s for the middle altitude, and in the early 1970s to mid-1980s for the lower altitude (Fig. 4a). Annual growth was significantly positively correlated with annual SPEI from the early 1970s for the lower and middle altitudes, and showed an increasing trend. Tree rings at the treeline were not correlated with SPEI in any window of the analysis (Fig. 4b).

**Table 1** Information and statistics of tree-ring sequences for upper, middle and lower altitudes on the Meili Snow Mountain

Sites	Altitude (m)	No. of trees (ind.)	SD	MS	AR1	Rbar	Year when EPS > 0.85
Upper	4200	9	0.15	0.14	0.88	0.43	1920
Middle	3900, 4000, 4100	31	0.42	0.156	0.87	0.47	1905
Lower	3600, 3700, 3800	44	0.51	0.213	0.85	0.43	1860

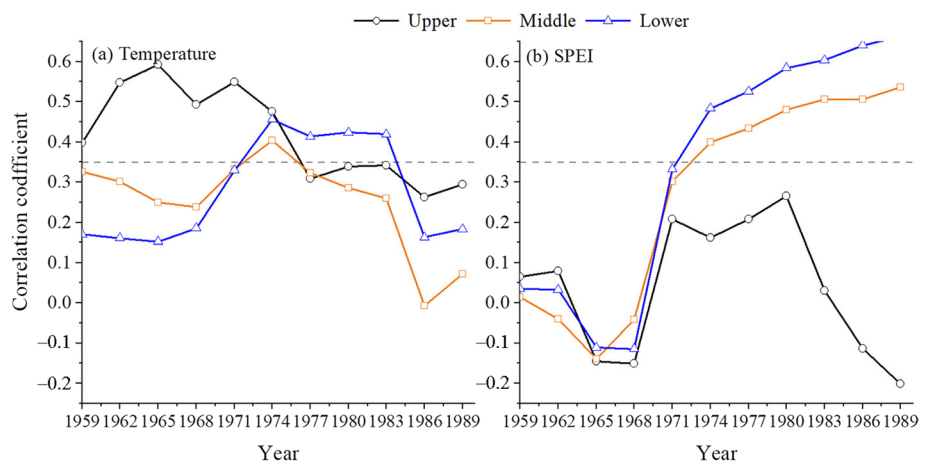
SD, standard deviation; MS, mean sensitivity; AR1, first-order autocorrelation; Rbar, mean inter-series correlation; EPS, expressed population signal



**Fig. 3** Pearson correlation coefficients between standard tree-ring chronologies and **a** mean monthly air temperature and **b** standardized precipitation evapotranspiration indices SPEI, **c** total monthly precipi-

tion and **d** monthly mean diurnal temperature range from the previous September to September of the following year for 1958–2019

**Fig. 4** Moving correlations between **a** standard tree-ring chronologies and November temperatures of the previous year and **b** annual SPEI with a sliding 30-year window for 1958–2019



**Characteristics of forest community structure along the altitudinal gradient**

Along the altitudinal gradient, there were 130 plant species.

For the upper, middle and lower altitudes, the number of tree species were 3, 5 and 6, the number of shrub species 3, 6 and 10, and the number of herb species 13, 13 and 0, respectively. *Rhododendron* spp. are common in the shrub

layer at all altitudes, and their importance increases with altitude. Species composition became simpler with altitude (Table. S1). The species richness (SR) and shrub cover (SC) lessened with altitude (Fig. S1). In addition, the number of Smith fir seedlings decreased significantly with increased shrub cover and species richness ( $r = -0.82$ ,  $p < 0.01$ ;  $r = -0.83$ ,  $p < 0.01$ ) (Fig. 5).

### Relationship between annual rings and forest community structure

The mean interannual tree-ring sensitivity in different communities decreased with increasing altitude from 1970 to 2019, consistent with the changes in shrub cover and species richness (Fig. S1). Correlation analysis showed that this growth sensitivity was positively correlated with shrub cover and species richness ( $r = 0.82$ ,  $p < 0.01$ ;  $r = 0.83$ ,  $p = 0.005$ ) (Fig. 6).

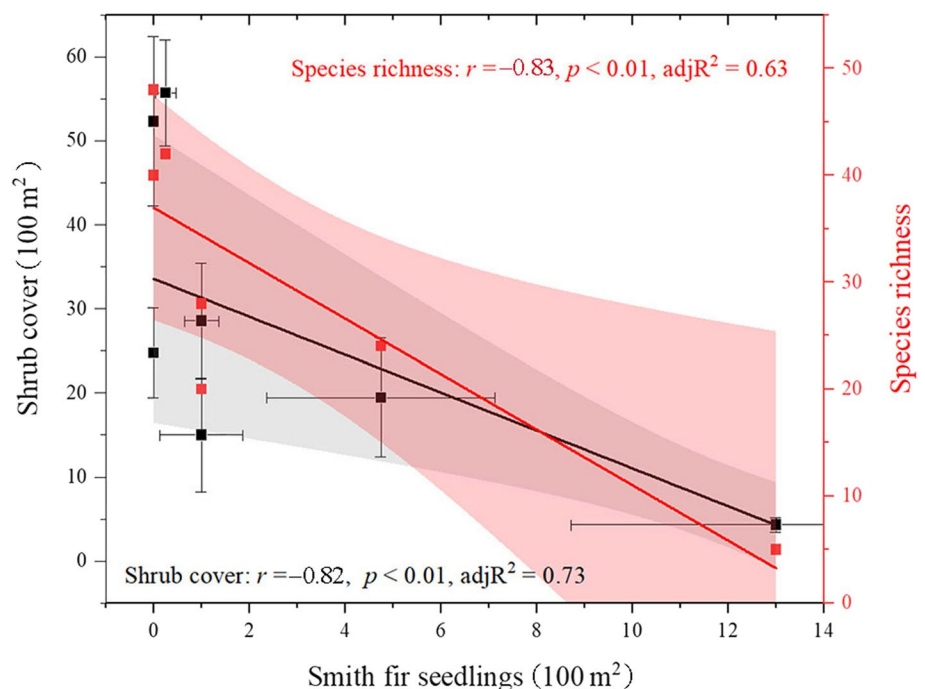
### Discussion

In this study, there were significant differences in climate-growth relationships at different altitudes. Growth at the treeline was regulated by temperature (Fig. 3a), which is in agreement with the ‘temperature limitation hypothesis’ (Körner 1998; Körner and Paulsen 2004). Specifically, the positive effects from previous November temperatures on growth may be related to higher temperatures would prolong the growing season and enhance photosynthesis (Esper et al. 2007). In contrast, drought stress was a

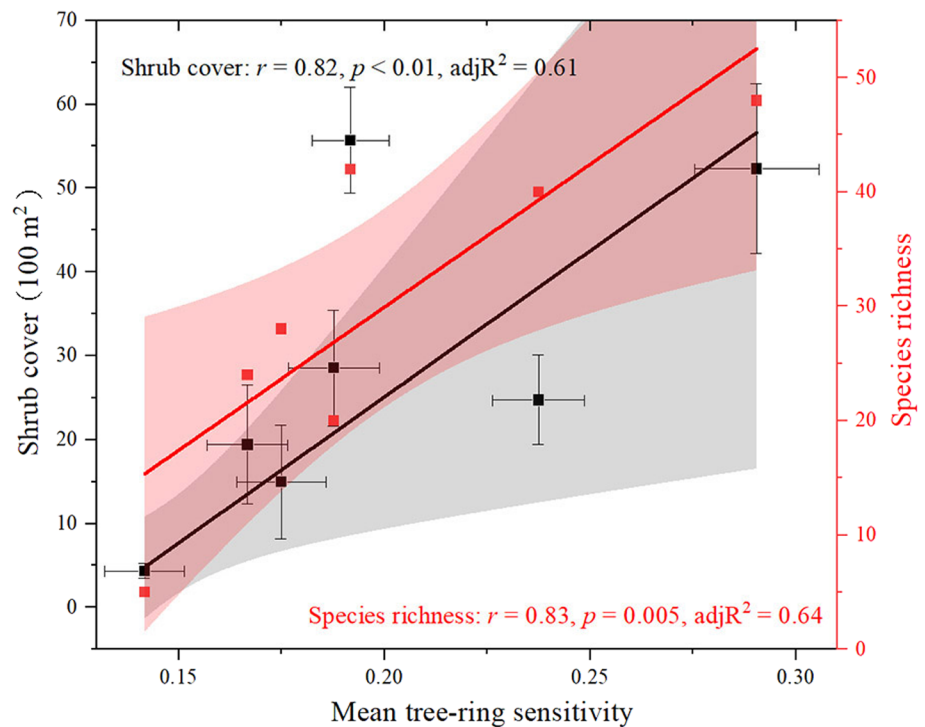
key factor limiting tree growth at middle and lower altitudes (Fig. 3b). The pattern that temperature limitation at the treeline with moisture limitation at middle and low altitudes has been reported elsewhere (Di Filippo et al. 2007; Lv and Zhang 2012; Loehle et al. 2016). Because the May–September rain in the Meili Snow Mountain area accounts for 78% of the annual amount (Fig. 1a), the positive correlation between ring widths and SPEI were strongest before the growing season (Fig. 3b). Pre-growing season climate effects on growth have also been reported in previous studies on the Tibetan Plateau (Liang et al. 2008; Zhang and Wilmking 2010; Gao et al. 2022).

The best correlated drought stress on tree growth (as indicated by the correlation) was not stable over time. Our results show that variations in ring widths were mainly controlled by temperatures at the treeline, but have gradually weakened since the 1970 (Fig. 4a). The diminished temperature effects on tree growth may be related to temperature increase (Kuang and Jiao 2016; Thakuri et al. 2019). Rising temperatures alleviated the low-temperature limitation on tree growth and thus accelerated photosynthesis (Salerno et al. 2015; Thakuri et al. 2019) and ultimately growth (Körner et al. 2016; Sigdel et al. 2018; Anderson et al. 2020). At the same time, associations between SPEI and tree growth were strengthened in middle and lower altitude forests (Fig. 4b), indicating that the drought limitation on tree growth have been strengthened by accelerated warming over past decades (Koerner 2015; Ren et al. 2018; Gao et al. 2020). Similarly, intensified drought on growth was also observed in other parts of the Tibetan plateau (Liang et al. 2016a; Zhang et al. 2017; Yang et al. 2022).

**Fig. 5** Changes in Smith fir seedlings, shrub cover and species richness for each 20 m × 20 m plot. The solid line and shadow show the mean and 95% confidence interval of the linear regression.  $\text{adjR}^2$  is R squared adjusted by degree of freedom



**Fig. 6** Relationship between mean tree-ring sensitivity and forest community structure indices shrub cover and species richness 1970–2019; solid line and shadow show the mean and 95% confidence interval of the linear regression.  $\text{adjR}^2$  means R squared adjusted by degrees of freedom



In addition to climatic forcing, other factors such as community structure also affect tree growth and modify growth sensitivity to environmental changes (Pretzsch et al. 2013; Primicia et al. 2015). In this study, tree growth was more sensitive to climate changes in denser forest communities with higher species richness (Fig. 4 and Fig. S1), indicating that community structure may have exaggerated the sensitivity of tree growth to climate changes. Higher stand density may enhance growth sensitivity to moisture variations at lower altitude forests (Grosiord et al. 2014; Primicia et al. 2015), because the competition for water would further exaggerate drought stress, leading to increased growth variability (Brown et al. 2005; Barbier et al. 2008; Raz-Yaseef et al. 2010). The effects of competition from shrubs on tree growth has also been reported for the Tibetan Plateau (Liang et al. 2016b; Lyu et al. 2016b; Wang et al. 2016). Similarly, the importance of stand characteristics was found to be three times greater than that of climate variables to forest growth in some forests of northeastern China (Dong et al. 2024).

Our results disclose that fewer Smith fir seedlings occur in lower altitude than upper altitude forests (Fig. 5). Intense competition from shrubs would make establishment of seedlings difficult (Keeling and Phillips 2007; Luo and Chen 2015; Poorter et al. 2017). Besides, fewer Smith fir seedlings also may be related to restricted sunlight (Szefer et al. 2020; Royo and Carson 2022), so that seeds cannot germinate when shrub cover is high (Robson et al. 2009; Annighöfer 2018).

Therefore, future climate change may alter forest structure through competitive disturbance and inhibition of stand regeneration.

It should be acknowledged that an altitude gradient is largely corresponding to a temperature gradient, which could directly remove some species and thus change species composition along (Rahbek 1995; Rahman et al. 2020). Therefore, the effect of altitude and community on growth-climate response cannot be separated, leading to a lack of evidence to support how tree growth patterns are modified by community structure. Although both forest community and tree growth will respond to climate changes, community structure cannot adjust immediately to climate warming like tree growth because the formation of a new community structure requires a relatively long period of time (Littell et al. 2008; Zhu et al. 2012). Therefore, tree growth-climate relationships are controlled by inter-annual climate variations directly and modified by forest community structure through competition or simultaneously facilitated indirectly. Given the limited understanding on the effects of community structure on forest dynamics, more research is needed to explore the effects of community structure on tree growth-climate relationships in forests with diverse geographic, climatic, taxonomic and ontogenetic backgrounds to obtain a reliable understanding of forest dynamics.

## Conclusions

In this study, changes in the relationship between tree growth and climate and its link to forest community structure along an altitudinal gradient were investigated. Accelerated climate warming had alleviated the low-temperature limitation on tree growth at the treeline and enhanced drought stress on the middle and lower altitudes after 1970. The higher shrub cover and species richness may have further exaggerated growth sensitivity to drought. Our findings shed new light on the linkage of tree-growth response to climate and vegetation structure and reveal the instability of growth-climate relationships.

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**Author contributions** Conceptualization and methodology, QBZ, LL, JCZ; formal analysis, JCZ; writing—original draft preparation, JCZ; writing—review and editing, QBZ, LL; funding acquisition, QBZ, LL. All authors have read and agreed to the published version of the manuscript.

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