

Divergent response of shrub growth to climate warming along a latitude gradient

Jingwen Yang

Qufu Normal University

Qiuliang Zhang

Inner Mongolia Agricultural University

Wenqi Song

Northeast Forestry University

Xu Zhang

North West Agriculture and Forestry University

Xiaochun Wang (✉ wangx@nefu.edu.cn)

Qufu Normal University

Research Article

Keywords: Climate change, Boreal, Shrub, Latitude, Pinus pumila

Posted Date: April 22nd, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-1550413/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Abstract

Understanding the response of shrub growth to climate changes is crucial to accurately predict the dynamic changes of the boreal forest ecosystem. A shrub-ring network base on 12 sites was established to explore the response of *Pinus pumila* growth to climate change along a latitudinal gradient from 44.10° to 52.58° N in northeastern China. The results showed significant differences in the growth trend of *P. pumila* at different latitudes in recent decades. Shrub growth was faster from 1950 to 1980 in the south and central. From 1981 to 2014, *P. pumila* growth increased in the north while slowed in the south and the central regions. The temperature of the previous winter and current spring were the main limiting factors for the growth of *P. pumila* in the north and south. In the central and southern, shrub growth was negatively correlated with precipitation in the previous and current summer. With the increase of latitude, summer temperature inhibits *P. pumila* growth, while summer precipitation positively impacts from 1981 to 2014. At the individual level, it can be better verified that the growth of *P. pumila* is promoted by both water and temperature. The prediction of the model shows that the radial growth trend of the northern shrub is decreasing under warming. Unexpectedly, *P. pumila* growth in the south will benefit from warming under the RCP4.5, RCP6.0, and RCP8.5 scenarios. Therefore, shrubs might not expand northward in the future under the background of climate warming.

Introduction

Climate change, i.e., temperature rise, alpine glacier retreat, snow cover reduction, and large-scale precipitation change, has a significant impact on ecosystem dynamics and social communities (IPCC, 2013). Forests play a crucial role in the carbon, water, and energy cycle of terrestrial ecosystems (Fang et al. 2001; Parker et al. 2015; Sullivan et al. 2021), especially in boreal forests, which account for about 30% of the global forest area (Gauthier et al. 2015). High latitude forest ecosystems are one of the most vulnerable areas to climate change. The change in vegetation composition and distribution in the boreal forest may further stimulate multiple biospheric and atmospheric feedback (Pearson et al. 2013; Mack et al. 2021). There is increasing evidence that recent climate changes have affected the ecological performance of global plant species, from phenology, growth, or reproductive investment to recruitment rates (Jump et al. 2006; Matías et al. 2017; Fang and Zhang, 2020).

Trees in the boreal forest show the temperature gradient signal from south to north to the Arctic treeline, an important area of dendroclimatic and ecological studies (Lange et al. 2020; Rees et al. 2020). Latitude changes will lead to changes in temperature and precipitation, which are the essential factors affecting tree growth (Lens et al. 2004; Mäkinen et al. 2002). Therefore, according to the method of space replacing time, the impact of climate warming can be studied by the change of tree growth on the latitude gradient (Jump et al. 2009; Tito et al. 2020). In boreal forests, the climatic factors that limit tree growth will change along the latitude gradient, usually from the water limit in low latitude to the low-temperature limit in the high latitude (Matias et al. 2017). The maximum summer temperature was significantly negative with the radial growth of larch in low and middle latitudes but non-significant in high latitudes (Jiang et al. 2016). Warming winter and spring temperatures might benefit the *Betula papyrifera* stand located north of 49 °N,

Populus tremuloides at northern latitudes, and *Picea mariana* and *Pinus banksiana* stand located north of 47 °N to promote their radial growth in the next few decades, whereas they might be inhibiting southern stands radial growth (Huang et al. 2010). Also, Pellizzari et al. (2017) found that warm summer conditions were favorable for forming wider rings in the Palor and harmful to the radial growth of the Mediterranean tree.

In the boreal forest, previous studies have shown that the growth of trees in the northern region is limited by frost and moisture, while the water deficit caused by high temperature in the central and southern regions limits the growth of trees (Li et al. 2020). With the continuous global warming, the trees threatened by summer high temperatures will increase by 45.5–63.6% by the end of this century (Li et al. 2020). In the high latitudes of the northern hemisphere, the current high summer precipitation promotes tree growth, and the correlation between summer precipitation and radial growth increases with the decrease in latitude (Henttonen et al. 2014). However, representative data on long-term growth trends in shrubs and their climatic drivers remain poorly understood. Furthermore, only limited knowledge has been available on the growth-climate relationships of shrubs across the latitudinal gradient and their differences in response to global warming.

Shrubs are short woody plants with multiple trunks, which are important in many ecosystems. They play an irreplaceable role in forest water conservation, sand fixation, soil improvement, and maintaining an ecological balance (Myers-Smith et al. 2015a; Xiao et al. 2019). In general, shrubs are more widely distributed than trees because they grow beyond treeline or timberline in high latitudes or altitudes where trees are scarce or completely absent (Takahashi and Aoki, 2015; Shetti, 2018; Yang et al. 2020). However, most dendrochronological studies have focused on the climate responses of tree species, although trees and shrubs may coexist in forests (Morales et al. 2012; Götmark et al. 2016). Shrubs located at the upper distribution edge may experience the highest warming rate and are considered sensitive ecological indicators of the responses of terrestrial ecosystems to changing abiotic and biotic conditions (Körner, 2012; Lu et al. 2021). Therefore, shrubs have great potential in studying the dendrochronology of boreal forest and dryland ecosystems (Buchwal et al. 2020; Shetti, 2018; Takahashi and Aoki, 2015; Winkler et al. 2019; Xiao et al. 2019). Recent studies have suggested that the ring widths of shrubs can be used to indicate long-term moisture and temperature in high altitudes and latitudes (Myers-Smith et al. 2020). Studies on monitoring and reconstructing environment and climate change with shrub chronology have increased significantly in recent years (Myers-Smith et al. 2015a; Pellizzari et al. 2017; Shetti, 2018; Weijers et al. 2012). The dwarf shrub, *Pinus pumila*, is one of the main shrub species in the high-altitude area in northeast China. Its clear annual rings and long-living make it ideal for use in dendroclimatology studies.

Understanding how shrub growth responds to temperature changes on the latitude gradient is crucial to accurately predict the dynamic changes of the boreal forest ecosystem under the background of global change. Little is known about the response of shrub growth along the latitudinal gradient to climate change in China. Therefore, we hypothesize that with the increase in latitude, the temperature may play a more critical role in influencing the radial growth of the shrub, whereas the precipitation affecting the

radial growth may be substantial in the south. In this study, a dendroclimatic investigation was conducted on a dominant boreal shrub species, *Pinus pumila*, along the latitudinal gradient spanning 44°-52° N in northeast China. The objectives of this study are to (1) explore the radial growth characteristics of *P. pumila* along the latitude gradient, (2) investigate changes in the growth-climate relationship of *P. pumila* along the latitudinal gradient, and (3) evaluate the potential changes in the growth of *P. pumila* in the boreal forests of northeast China.

Materials And Methods

Study area

The study area is located in northeast China, with latitudinal gradients from 44.06° N to 52.36° N and 120.17° E to 128.29° E (Table 1, Fig. 1). From 2015 to 2018, we conducted a field investigation at 12 sites. We divided the 12 sampling sites into three regions according to latitude: South (LBS, TS, AES), Central (DBS, ME, HM, YK, XBS), and North (AK, FKS, YA, ZL) (Table 1, Fig. 1). The mean annual precipitation (1950–2014) in the study area ranges from 415.6 mm to 636.2 mm, and more than 68% occurs from June to August (Fig. 1a). The mean annual temperature is between -6.3 °C to 0.5 °C. January and July are the coldest (-38.2 °C, ZL) and hottest (25.3 °C, TS) months, respectively (Table 2). The annual frost-free period is 80-100 days, with early and late frost occurring in September and May.

P. pumila is a multi-trunk, ground-creeping shrub which grows obliquely. In the symbiotic community with other plant species, *P. pumila* forms two types of plant communities: high-altitude subalpine shrub community and low-altitude high canopy tree forest community. The former grows in subalpine areas with fruticulose and herbs. The latter grows under the canopy of boreal trees (e.g., *Larix gmelinii*, *Pinus sylvestris* var. *mongolica*, *Betula ermanii*) (Okuda et al. 2008). The dominant *P. pumila* in the subalpine dwarf forest is mainly distributed in the altitude range of 800-1700 m in northeast China. *Pinus sylvestris* var. *mongolica* and *Larix gmelinii* are the main trees associated with *P. pumila* at low altitude, and they are also the main constructive species of boreal forest in the Daxing'an Mountains, China (Zhang et al. 2019).

Table 1 Characteristics of the 12 study sites with the name of the mountain, the sample code and sample number, longitude and latitude of site, altitude of plots above sea level, and divided region.

| Site | Code | Longitude (E) | Latitude (N) | Altitude (m a.s.l.) | Sample number | Region |
|--------------------|------|---------------|--------------|---------------------|---------------|---------|
| Laobai Mountain | LBS | 128° 03' | 44° 06' | 1685 | 35 | South |
| Tao Mountain | TS | 128° 29' | 46° 38' | 1369 | 31 | South |
| A'er Mountain | AES | 120° 17' | 47° 13' | 1164 | 52 | South |
| Dabai Mountain | DBS | 123° 08' | 51° 18' | 1431 | 28 | Central |
| Mo'erdaoga | ME | 120° 49' | 51° 22' | 1072 | 33 | Central |
| Hanma | HM | 122° 24' | 51° 31' | 1000 | 58 | Central |
| Yikesama | YK | 121° 14' | 51° 32' | 1262 | 36 | Central |
| Xiaobai Mountain | XBS | 123° 32' | 51° 37' | 1400 | 33 | Central |
| Aokelidui Mountain | AK | 122° 03' | 51° 50' | 1104 | 30 | North |
| Fuke Mountain | FKS | 121° 40' | 52° 28' | 1096 | 30 | North |
| Yong'an | YA | 121° 06' | 52° 33' | 1196 | 60 | North |
| Zhalinku'er | ZL | 123° 31' | 52° 35' | 1135 | 58 | North |

Dendrochronological sampling, treatment and analysis

At each site, 10-15 discs of *P. pumila* were sliced with a hand saw near the base of the trunk. These samples were obtained only from isolated, mature and healthy individuals to avoid the fact that competition with other plants may affect stem growth. A total of 140 discs from 12 sites (Fig. 1, Table 1) were sampled on the latitude gradient from south to north. The cross-section of each disc was naturally air-dried and polished with mesh gradually finer sandpaper (120-800 grit) until the ring boundary could be clearly distinguished under the microscope (Fritts, 1976; Cook and Kairiukstis, 1990). Shrub rings were cross-dated and ring width was measured in the laboratory using traditional dendrochronological methods (Fritts, 1976; Cook and Kairiukstis, 1990). Two to four radii in the disc were cross-dated, and the ring width at each radius direction was measured using the Velmex measurement system with a resolution of 0.001 mm. The cross-dating and measurement accuracy were statistically checked using the COFECHA computer program (Holmes, 1983), which determines the degree of synchronization between series according to the correlation with the main series of chronology. Each ring-width series was detrended and standardized by fitting a negative exponential curve or linear line using the ARSTAN program to remove non-climate signals related to age or stand dynamic effects (Cook and Holmes, 1986). The ring-width index was derived by dividing the ring width by the fitting value of each ring. Three kinds of ring-width chronologies (standard, residual and autoregression chronologies) were obtained by averaging all detrended series with a bi-weight robust mean (Cook and Kairiukstis, 1990). The standard chronologies (STD) were used in the subsequent analyses.

Climate data

We used CRU TS 4.04 $0.5^\circ \times 0.5^\circ$ gridded monthly and seasonal temperature and precipitation data to analyze growth-climate relationships for 1950–2014 because no nearby weather stations exist. The data were extracted from the sample area using the KNMI Climate Explorer web page (<http://climexp.knmi.nl>). The CRU database is formed by interpolated values from regional meteorological stations. Climate variables including monthly total precipitation (P), mean (T_{mean}), minimum (T_{min}) and maximum temperature (T_{max}) (Fig. 2) were used for growth-climate response analysis. We define winter as December of last year to February of that year, spring for March-May, spring for June-August, and autumn for September-November.

Climate–Growth Relationship Analysis

To determine the main climate factors limiting the radial growth of each chronology at each site. Pearson correlation was used to determine the relationship between the tree-ring index and monthly and seasonal climate variables. Radial growth is affected by the current and previous year's climate (Fritts, 1976). Therefore, climate variables over 17 months, from May of the previous year to October of the current year, were used for the correlation analysis. Meanwhile, we carried out two periods (1950-1980, 1981-2014) correlation analyses to investigate the temporal stability of the growth-climate response.

The response of each shrub to temperature was categorized into four response types: positive (67% of significant correlations with temperature were positive), negative (33% of significant correlations with temperature were positive), mixed (between 33% and 67% of significant correlations with temperature were positive), or none (no significant correlations with temperature) (Lloyd et al. 2011). Shrubs were similarly categorized concerning their response pattern to precipitation, and the proportion of shrubs exhibiting each response type was tailed for each site. After that, linear mixed-effects models were used to identify the effects of 8 climatic variables (T_{wi} , T_{sp} , T_{su} , T_{au} , P_{wi} , P_{sp} , P_{su} and P_{au}) on the residuals of the previous function, using climatic variables during 1950–2014 as fixed factors and shrub as a random factor. Fitted models followed the equation:

$$RW_i = Xa_i + Zb + e_i$$

where RW_i represents the ring-width in year i ; a is the vectors of fixed effects (seasonal climate variables), b is the vector of random effects (shrub identity), X and Z are the fixed and random effects regressor matrices, respectively; and e_i is the within-group error vector (Camarero et al. 2017). We ranked all the potential models that could be generated with the different explanatory variables according to the Akaike information criterion (AIC). We selected the most parsimonious models, that is the ones with the lowest AIC (Burnham & Anderson, 2002). The final model was selected for each site as the one with the lowest number of variables among those with the lowest AIC (Burnham & Anderson, 2002). In addition, we used the Akaike weights (W_i) of each model to measure the conditional probability of the candidate model, assuming it was the best model. The use of seasonal climatic averages instead of monthly data allowed

the creation of more parsimonious models while maintaining a reliable representation of climatic trends (Matías et al. 2017). The linear mixed model analysis was performed using the LME4 package in R 4.0.3 (R Core Team, 2015). Hierarchical cluster analysis and correlation analysis were performed using the SPSS 22.0 software package (IBM SPSS Inc., Chicago, IL, USA).

Finally, the growth trend of shrub ring width under four emission scenarios of RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5 was simulated by a linear regression forecast under the CMIP5 scenario predicted by HadGEM2-ES for the period 2020–2100.

Results

Comparison of the chronological characteristics and growth trends

The mean age of shrubs at the four sites ranged from 69 to 151 years, and the mean ring width varied from 0.27 to 0.65 mm (Table 2). ME had the highest MS, AK had the highest SD, VF1% and R_{bar} , YK had the highest AC1, and HM had the highest EPS and SNR (Table 2). In short, there was a significant trend among shrub chronological statistics in different sites. All analyses indicated that the 12 chronologies were rich in climatic signals and suitable for analyzing growth-climate relationships.

Table 2 Major characteristics of STD chronologies in 12 sites *Pinus pumila* in northeast China, mean ring width, chronology time span, mean sensitivity (MS), standard deviation (SD), signal-to-noise ratio (SNR), mean intercorrelation between individual series inter-series correlation (R_{bar}), autocorrelation of order 1 (AC1), variance in the first eigenvector (%) (VF1) and expressed population signal (EPS) included in the dendroecological network.

Chronological clustering and correlation analysis

The Pearson correlations analysis result showed a high correlation among the sites in the same region (Fig. 1c). During 1950 to 1980, there was a significant increase in the ring-width index of *P. pumila* in the south and central regions, and a non-significant increase in the northern part. After 1980, the chronology trend was divergent in different regions. There was a slight downward trend in the southern and central chronologies, whereas the northern chronology shows an upward trend (Fig. 2a). There was no significant difference in annual ring width between different regions (Fig. 2b).

Climate response

The radial growth of north shrubs was significantly positively correlated with January and May temperatures (Fig. 3a, b and c). Warm winter conditions enhanced growth in north and south shrubs with stronger temperature-growth correlations (Fig. 3a, b and c). In addition, wet winter conditions were positively associated with north shrub growth. April to June minimum temperatures were related to wider ring widths, particularly in north shrubs. Wet June conditions enhanced shrub growth at three region

| Site | Mean ring width (mm) | Chronology time span | MS | SD | ACI | VF1% | Rbar | EPS | SNR |
|------|----------------------|----------------------|------|------|------|-------|------|------|-------|
| LBS | 0.52 | 1937- 2017 | 0.14 | 0.29 | 0.84 | 27.22 | 0.18 | 0.89 | 8.09 |
| TS | 0.27 | 1907- 2017 | 0.12 | 0.22 | 0.80 | 19.61 | 0.10 | 0.80 | 3.87 |
| AES | 0.44 | 1934-2017 | 0.15 | 0.16 | 0.40 | 23.52 | 0.1 | 0.79 | 3.83 |
| DBS | 0.65 | 1945-2014 | 0.14 | 0.19 | 0.56 | 26.82 | 0.16 | 0.85 | 4.42 |
| ME | 0.53 | 1867-2017 | 0.22 | 0.28 | 0.45 | 28.05 | 0.15 | 0.85 | 4.24 |
| HM | 0.43 | 1891-2018 | 0.17 | 0.21 | 0.46 | 26.98 | 0.22 | 0.94 | 14.81 |
| YK | 0.55 | 1923-2017 | 0.17 | 0.21 | 0.87 | 21.44 | 0.16 | 0.85 | 6.70 |
| XBS | 0.52 | 1946-2014 | 0.14 | 0.16 | 0.38 | 24.50 | 0.21 | 0.92 | 12.15 |
| AK | 0.50 | 1943-2014 | 0.15 | 0.32 | 0.81 | 37.92 | 0.27 | 0.89 | 8.27 |
| FKS | 0.39 | 1881-2014 | 0.17 | 0.23 | 0.62 | 24.76 | 0.19 | 0.87 | 6.66 |
| YA | 0.49 | 1903-2017 | 0.13 | 0.17 | 0.55 | 27.14 | 0.22 | 0.90 | 9.43 |
| ZL | 0.49 | 1949-2017 | 0.19 | 0.23 | 0.54 | 29.49 | 0.24 | 0.92 | 10.75 |

shrubs. It should be noted that the growth of shrubs did not show significant correlations with maximum temperature in summer. In contrast, warm autumn conditions favored the growth of shrubs in the north and south. Previous growing season temperatures positively influence the radial growth of shrubs. The results showed within-region variation in the climate response across latitudes, with at least three different response categories for each region (Figs. 3 and 4).

More north shrub individuals responded negatively to temperature than south and central, but there was a substantial minority in which growth was positively correlated with temperature (Fig. 5). Temperature is important in promoting the growth of northern shrubs. However, the minority of shrubs responded positively to temperature, growing more in colder years (Fig. 5a). We found some differences in the correlation between regional chronologies and individuals and climate factors, but this could explain that regional chronologies could be oversimplified, thus producing biased growth estimates. The individuals differ regarding multiple variables, such as size, age, microsite conditions, competition, and genome. While population-based approach emphasizes the mean climatic signal, but at the cost of losing the information given at the level of individuals. Therefore, averaging shrub-ring parameters of many individuals into regional chronologies could be an oversimplification that might bias estimates of future shrub performance.

The relationship between growth and climate in different periods

During 1950-1980, shrub growth was negatively correlated with summer temperature and positively with winter temperature with increasing latitude, and positive summer and winter precipitation-growth

relationships occurred. However, shrub growth was positively correlated with summer temperature and negatively correlated with winter temperature with increasing latitude, which may be due to the excessively high rate of winter temperature increase in high latitudes during 1981-2014. The correlation between shrub growth and summer precipitation decreased with increasing latitude, while that between shrub growth and winter snowfall increased in the recent 30 years. In the first period, shrub growth may be limited by the synergistic effects of summer drought stress and low winter temperatures. However, in the second period, shrub growth in high latitudes might be more susceptible to winter snowfall (Fig. 4 and Fig. 6).

Forecasted growth

The response of shrub growth to warming was divergence on latitude gradient. In response to the changes in climate forecasted by the HadGEM2-ES RCP 2.6 scenario, our models predict growth stable in central regions shrub until 2100 (Table 3, Fig. 6). In comparison, ring width has a slight growth increase in the south and a decrease in the north region. Ring width is expected to continue rising under the RCP 4.5 and RCP 6.0 scenarios in south shrubs. Under the RCP 8.5 scenario, the south shrubs showed rapid growth increasing to 2100 (Fig. 6). In contrast, north and central regions have a decreasing trend in growth under RCP 4.5, RCP 6.0 and RCP 8.5 scenarios.

Table 3 Best linear mixed models explaining the effect of climate on ring width after accounting for seasonal climate factor effects for the different regions across the latitudinal gradients

| Latitude | Growth model | K | AIC | Δ AIC | W_i |
|-------------------------------------------------------------------------|-------------------------------------------------------------------------|-------------------------------------------------------|--------|--------------|-------|
| South | $T_{wi} + T_{sp} + P_{su}$ | 5 | -140.5 | 0 | 0.99 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{su}$ | 7 | -128.8 | 11.7 | 0 |
| | $T_{wi} + T_{sp} + T_{su} + P_{sp} + P_{su}$ | 7 | -127.0 | 13.5 | 0 |
| | $T_{wi} + T_{au} + T_{sp} + T_{su} + P_{sp} + P_{su}$ | 8 | -117.8 | 22.7 | 0 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{sp} + P_{su} + P_{wi}$ | 9 | -108.2 | 32.3 | 0 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{sp} + P_{su} + P_{au} + P_{wi}$ | 10 | -94.5 | 46.0 | 0 |
| | Central | $T_{wi} + T_{su} + T_{au} + P_{sp}$ | 6 | -125.4 | 0 |
| $T_{wi} + T_{sp} + T_{au} + P_{sp} + P_{su}$ | 7 | -111.2 | 14.2 | 0 | |
| $T_{wi} + T_{su} + T_{au} + P_{sp} + P_{su}$ | 7 | -109.8 | 15.6 | 0 | |
| $T_{wi} + T_{au} + T_{su} + P_{wi} + P_{su} + P_{au}$ | 8 | -95.1 | 30.2 | 0 | |
| $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{au} + P_{su}$ | 9 | -89.3 | 36.1 | 0 | |
| $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp} + P_{su} + P_{au}$ | 10 | -79.2 | 46.2 | 0 | |
| North | $T_{wi} + T_{sp} + T_{au} + P_{wi} + P_{sp}$ | 7 | -58.1 | 0 | 0.87 |
| | $T_{wi} + T_{sp} + T_{su} + P_{wi} + P_{sp}$ | 7 | -54.1 | 4.0 | 0.12 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp}$ | 8 | -50.1 | 8.0 | 0.01 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp} + P_{au}$ | 9 | -36.9 | 21.1 | 0 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp} + P_{su}$ | 9 | -36.8 | 21.3 | 0 |
| | $T_{wi} + T_{sp} + T_{su} + T_{au} + P_{wi} + P_{sp} + P_{su} + P_{au}$ | 10 | -23.6 | 34.4 | 0 |

Notes: Selected models are highlighted in bold. The best models were selected on the basis of the Akaike information criteria (AIC). K represents the number of variables included in the model plus constant and error terms, Δ AIC is the difference in AIC respect the best model, and W_i is the relative probability to be the best model for the observed data. T_{wi} , T_{sp} , T_{su} and T_{au} are temperatures of previous winter, spring, summer and autumn of current year, respectively. Similar names for precipitation values (P_{wi} , P_{sp} , P_{su} , P_{au}).

Discussion

Growth associations with climate

Our results show that shrub growth in the southern region is limited by temperature during the growing season (Lloyd et al. 2011; Li et al. 2020). That might be because the average altitude of the sampling sites in the southern region is higher (1310 m), and the precipitation is more than that in the central and northern regions. Therefore, moisture is not the main factor limiting the growth of shrubs in the southern part of the study area. The previous winter temperature promoted the growth of *P. pumila* in the southern and northern parts, whereas it had little effect on the central shrubs. High winter temperatures have been demonstrated to accelerate snow melting, provide sufficient water supply in the following summer and effectively enhance radial growth rates (Lyu et al. 2017; Duan et al. 2017). In addition, warmer winter helps protect the needle and fine root from frost damage (Myers-Smith et al. 2011; Duan et al. 2017). The timing of soil thaw plays a crucial role in initiating the physiological activity of shrubs (Vaganov et al. 1999; Kirilyanov et al. 2003; Lloyd et al. 2011). Previous studies suggest that warmer conditions could promote shrub growth either directly by altering physiological processes or indirectly by enhancing soil microbial activities that supply nutrients for shrub uptake (Myers-Smith et al. 2011). Observations have been on tree/shrub response to warming, including species invasion into the tundra, stand densification and growth increment increase along the northern and alpine treelines during recent decades (Kharuk et al. 2009).

The positive correlations between shrub growth and minimum temperature highlighted the importance of winter and spring temperature in the north (Fig. 4). Similar results indicated that although northern trees were positively correlated with winter and spring temperatures, the growth of stands at more southerly latitudes was negatively correlated with winter and spring temperatures (Huang et al. 2010). Frost is likely to have limited forest growth in high latitudes before the growing season (Li et al. 2020). In cold environments, spring temperatures and the length of the growing season are important factors limiting the production and differentiation of xylem cells (Morales et al. 2012; Lenz et al. 2013; Yang et al. 2020). Higher temperatures in the early growing season may favor coniferous species because their evergreen foliage allows them to take advantage of the warmth (Jiang et al. 2016). Several recent studies have documented significant positive correlations between ring widths or shoot lengths and early and mid-growing season temperatures for some of the most common shrub species found in tundra ecosystems (Myers-Smith et al. 2011). However, winter and spring temperatures seem less critical in the central shrub than in the northern and southern regions of our study area. The effects of summer maximum temperature on shrub growth and growth were not significant, suggesting that the onset climate conditions of the growing season appeared to be more important for positively responding shrubs in the study area (Fig. 4). In contrast, the study of the *L. gmelinii* growth-climate relationships around this region showed that temperatures from June to July represented the most critical factor affecting tree radial growth (Jiang et al. 2016).

The differences in individual-level responses to precipitation were consistent that moisture would positively affect more northern regions (Fig. 3d and Fig. 4b). Negative responses to temperature became more in the north, inconsistent with a pattern that previous studies found positive responses to warming were more frequent at the individual level in the north (Lloyd et al. 2011). More than half of the individuals in the north responded negatively to temperature (Fig. 4a), which may result from the

synchronous constraint effect of hydrothermal coupling on the growth of *P. pumila* (Yang et al. 2020). There were some differences in the response of *P. pumila* to climate factors at the population level and individual level (Figs. 3 and 4). Chronology could highlight the climatic information compared to individual shrubs but might bias the subsequent inferences, especially for some dwarf shrubs growing in harsh habitats. Each plant experiences different microenvironmental conditions. The variation from individual to individual within the population is the reality of nature, whereas the mean value is just a statistical abstraction (Carrer, 2011).

The different responses of the two periods (1950-1980 and 1981-2014)

From 1950 to 1980, the radial growth of *P. pumila* may have been limited by summer moisture deficit and low winter temperatures. However, *P. pumila* growth in the north region might be more susceptible to winter snowfall from 1981 to 2014 (Fig. 4 and Fig. 6). A previous study found that junipers have grown more since the 1950s, and this growth enhancement accelerated in the 1980s in the Polar and Mediterranean biomes (Pellizzari et al. 2017). Anthropogenic forcing on the weakening in the temperature seasonality in the Northern Hemisphere and that future human influence may further contribute to a weakening of the annual temperature cycle with subsequent effects on biological and ecological systems, particularly in the high latitudes (50°-70 °N) (Duan et al. 2017; Qian and Zhang, 2015; Rosenzweig et al. 2008). Northern China has shown more substantial warming than southern China over the past 60 years (Xu et al. 2021). The amount of seasonal warming during 1958-2017 was highest in winter and lowest in summer (Xu et al. 2021). The winter warming degree exceeds summer warming started in the late nineteenth century with magnitudes of annual temperature cycles decreasing by 0.45°C/100a (Duan et al. 2017). Winter temperature harms the radial growth of *P. pumila* with increasing latitude during 1981-2014. If the annual temperature cycle continues to change in this pattern, winter temperatures and summer precipitation might become limiting factors for shrub growth in the future.

Growth and distribution of shrubs in the context of global warming

Unexpectedly, the growth of *P. pumila* in the north showed a significant downtrend under rapid warming, while it has an uptrend in the south based on the model. The relationship between climate factors and shrub growth is not a perfectly linear relationship on account shrub growth is affected by a combination of climate factors (Zheng et al. 2021). In addition, there is a compensatory effect of climate on the radial growth of trees (Jiang et al. 2015; Cao et al. 2016). The model results are based on the fact that climate factors are linearly related to shrub growth (Bonan, 2018). When temperatures exceed a threshold, shrub growth will probably not follow the trend predicted by the model. Global warming has led to early spring and later autumn, in which phenology is advanced and prolonging the length of the growing season (Huang et al. 2011; Rossi et al. 2016). The effects of climate warming on ecosystems are more significant at northern latitudes and high altitudes, and the effects vary across species (Huang et al. 2010). Many study results showed that shrubs have increased growth trends and expansion to higher latitudes and altitudes (Myers-Smith et al. 2015b; Myers-Smith et al. 2020). In contrast, a recent study found that the percentage of trees (larch and pine) threatened by high temperatures in summer will

increase by 45.5% to 63.6% (Li et al. 2020). Another important finding was that close to 100% of trees will be negatively affected by high temperatures during the growing season in the south (Li et al. 2020). Analyzing raw measured ring widths, rather than standardized data, can give important insights into shrub growth trends, patch dynamics, and change over time drivers (Myers-Smith et al. 2015). The ring width response to the climate forecast changes indicated that under HadGEM2-ES different scenarios, the shrub has an increasing trend in the south until 2100 (Fig. 6). However, shrub growth has a slight decline or a steady growth trend in the north and central (Fig. 6).

The model results showed a significant decrease in the growth of the northern and central parts of *P. pumila* under rapid warming (Fig. 6). Shrub productivity and recruitment increased significantly compared to trees in alpine and boreal environments (Frost and Epstein, 2014; Myers-Smith et al. 2015; Shetti, 2018). In contrast, water stress caused by climate change has triggered many large-scale tree diebacks and mortality events in some boreal forest regions (Zhu et al. 2018; Anderegg et al. 2019). Gazol and Camarero (2012) suggested that shrubs may be less influenced by temperature than trees because they are more likely to be affected by microclimate, topography, and soil temperature.

Comparing the response of shrubs and trees to climate change at different latitudinal indicated that shrubs showed enhanced growth at the extreme latitudinal Polar, Alpine and Mediterranean sites, whereas trees increased their growth rates in Alpine and Polar regions mostly declined in Mediterranean sites (Pellizzari et al. 2017). Shrubs are more likely to benefit from ongoing warming than trees when there is enough precipitation (Myers-Smith et al. 2015). Therefore, shrubs might become the dominant plant lifeform in areas where trees are sensitive to warming and drought with rising temperatures. For example, Siberian pine (prostrate growth form) should enjoy a competitive advantage due to its higher temperature response in a warming climate (Kharuk et al. 2009). Notably, similar changes are predicted in the European Alps: an increasing proportion of *Pinus cembra* versus *L. decidua* at higher altitudes (Kharuk et al. 2009). With the projected increase in drought, Siberian pine and fir would retreat from their southern low-elevation ranges in Siberia and be substituted by drought-tolerant species (Kharuk et al. 2021). Even if shrubs gradually replace trees in some regions, it will take a long time because the changes in tree distribution have not kept pace with climate change. The shrub distribution and coverage change might have a feedback effect on the global change (Myers-Smith et al. 2011). Another study suggested that high temperatures and moisture deficits in summer still had a negative impact on the growth of *P. pumila* (Yang et al. 2020). Climate conditions in the future will restrict shrub growth and regeneration, with accompanying response gradients forcing the forests to move northwards or upwards possibly.

Conclusions

To assess the dynamic changes of shrub growth in boreal forests under the context of global warming, we investigated the radial growth response of dominant shrub species *Pinus pumila* to climate along the latitudinal gradient from 44 to 52°N in northeastern China. Our results suggest that continued climate warming is likely to have pronounced effects on the boreal shrubs. The temperature of the previous

winter and the current spring promoted the growth of shrubs in the south and north. The maximum temperature in summer had little effect on shrub growth across the latitude gradient. At the individual level, the growth of northern shrubs was promoted by precipitation, while temperature inhibited growth. The LMEs predict that under the RCP2.6 scenario, the north shrub shows a slight decline. While under the scenarios of RCP4.5 and RCP6.0 and RCP8.5, shrub growth in the south showed an upward trend. Thus, there were differences in the response of shrub growth to warming across the latitudinal gradient. As a dominant shrub species in boreal forests, *Pinus pumila* might not expand northward and substitute the original tree species in some areas under the background of warming. Future research could focus on the individual level, and understanding individual differences in response is crucial to predicting the dynamic change and assessing the role of boreal forests in global carbon equilibrium. Shrubs serve as water conservation, fix sand, improve soil, provide food and shelter for small animals, and lead to positive or negative feedback on climate changes. Therefore, it is essential to adopt sustainable forest management strategies for the boreal forest shrubs of the Northern Hemisphere.

Declarations

Acknowledgments

We gratefully acknowledge the forestry bureau workers who helped us work in the field. We also are grateful to the anonymous reviewers for their contributions to improving this paper.

Data availability

The datasets generated and analyzed during this study are available from the corresponding author on reasonable request.

Author's contributions

JY and XW designed the study and edited the manuscript. JY, XZ and WS prepared field experiments, prepared tables and collected literature. XW got grants from the foundation, supervised data collection. QZ edited the manuscript. JY, QZ, WS, XZ and XW contributed to the whole manuscript preparation and design and wrote the main manuscript text. All authors reviewed the manuscript.

Funding

This research was supported by grants from the National Natural Science Foundation of China (41877426), the Fundamental Research Funds for the Central Universities (2572017DG02), and the Fund of Eco-meteorological Innovation Open Laboratory in Northeast China, China Meteorological Bureau (stqx2018zd02).

Conflicts of interest

The authors declare that they have no conflict of interest.

References

1. Anderegg WR, Anderegg LD, Huang CY (2019) Testing early warning metrics for drought-induced tree physiological stress and mortality. *Glob Change Biol* 25(7): 2459–2469.
2. Bonan GB (2008) Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320(5882): 1444–1449.
3. Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Shiyatov SG, Vaganov EA (1998) Reduced sensitivity of recent tree-growth to temperature at high northern latitudes. *Nature* 391(6668): 678–682.
4. Buchwal A, Sullivan PF, Macias-Fauria M, Post E, Myers-Smith IH, Stroeve JC, Blok D, Tape KD, Forbes BC, Ropars P, Lévesque E, Elberling B, Angers-Blondin S, Boyle JS, Boudreau S, Boulanger-Lapointe N, Gamm C, Hallinger M, Rachlewicz G, Young A, Zetterberg P, Welker JM (2020) Divergence of Arctic shrub growth associated with sea ice decline. *PNAS* 117(52):33334–33344.
5. Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, Heidelberg.
6. Camarero JJ, Linares JC, García-Cervigón AI, Batllori E, Martínez I, Gutiérrez E (2017) Back to the future: the responses of alpine treelines to climate warming are constrained by the current ecotone structure. *Ecosystems* 20(4):683–700.
7. Cao CF, Zhou FF, Dong ZP, Li YJ, Zhang Y, Li DW, Gan ZF, Fang KY (2016) Study on nonlinear climate growth patterns of *Pinus taiwanensis* in Daiyun Mountain, Fujian Province. *J Subtrop Res Environ* 11(1):44–51.
8. Carrer M (2011) Individualistic and time-varying tree-ring growth to climate sensitivity. *PLoS One* 6(7):e22813.
9. Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. *Science* 263(5144):185–190.
10. Duan J, Esper J, Büntgen U, Li J, Xoplaki E, Zhang H, Wang L, Fang Y, Luterbacher J (2017) Weakening of annual temperature cycle over the Tibetan Plateau since the 1870s. *Nat Commun* 8(1):1–7.
11. Fang OY, Zhang QB (2020) Tree resilience to drought increases in the Tibetan Plateau. *Glob Change Biol* 25(1):245–253.
12. Fang J, Chen A, Peng C, Zhao S, Ci L (2001) Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* 292(5525):2320–2322.
13. Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Glob Change Biol* 20(4):1264–1277.
14. Gauthier S, Bernier P, Kuuluvainen T, Shvidenko AZ, Schepaschenko DG (2015) Boreal forest health and global change. *Science* 349(6250):819–822.
15. Gazol A, Camarero JJ (2012) Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. *Plant Ecol* 213(10):1687–1698.

16. Girardin MP, Bernier PY, Gauthier S (2011) Increasing potential NEP of eastern boreal North American forests constrained by decreasing wildfire activity. *Ecosphere* 2(3):1–23.
17. Henttonen HM, Mäkinen H, Heiskanen J, Peltoniemi M, Laurén A, Hordo M (2014) Response of radial increment variation of Scots pine to temperature, precipitation and soil water content along a latitudinal gradient across Finland and Estonia. *Agr Forest Meteorol* 198:294–308.
18. Huang JG, Bergeron Y, Zhai L, Denneler B (2011) Variation in intra-annual radial growth (xylem formation) of *Picea mariana* (Pinaceae) along a latitudinal gradient in western Quebec, Canada. *Am J Bot* 98(5):792–800.
19. Huang JG, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. *Glob Change Biol* 16(2):711–731.
20. IPCC (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.
21. Jiang Y, Zhang J, Han S, Chen Z, Setälä H, Yu J, Zheng X, Guo Y, Gu Y (2016) Radial growth response of *Larix gmelinii* to climate along a latitudinal gradient in the greater Khingan mountains, northeastern China. *Forests* 7(12):295–306.
22. Jiang Y, Zhou G, Wang Y, Wang H, Shi Y (2015) Advances in the adaptability of zonal *Stipa* plants to CO₂ and climate change in Inner Mongolia. *Acta Ecol Sinica* 35(14):4559–4569.
23. Jump AS, Mátyás C, Peñuelas J (2009) The altitude–for–latitude disparity in the range retractions of woody species. *Trends Ecol Evol* 24(12):694–701.
24. Jump AS, Hunt JM, Peñuelas J (2006) Rapid climate change–related growth decline at the southern range edge of *Fagus sylvatica*. *Glob Change Biol* 12(11):2163–2174.
25. Kharuk VI, Im ST, Petrov IA, Dvinskaya ML, Shushpanov AS, Golyukov AS (2021) Climate-driven conifer mortality in Siberia. *Glob Ecol Biogeogr* 30(2):543–556.
26. Kharuk VI, Ranson KJ, Im ST, Dvinskaya ML (2009) Response of *Pinus sibirica* and *Larix sibirica* to climate change in southern Siberian alpine forest–tundra ecotone. *Scand J For Res* 24(2):130–139.
27. Körner C (2012) Treelines will be understood once the functional difference between a tree and a shrub is. *Ambio* 41(3):197–206.
28. Lange J, Carrer M, Pisaric MFJ, Porter TJ, Seo J, Trouillier M, Wilmking M (2020) Moisture-driven shift in the climate sensitivity of white spruce xylem anatomical traits is coupled to large-scale oscillation patterns across northern treeline in northwest North America. *Glob Change Biol* 26(3):1842–1856.
29. Lens F, Luteyn JL, Smets E, Jansen S (2004) Ecological trends in the wood anatomy of *Vaccinioideae* (Ericaceae s.l.). *Flora–Morphol, Distribu, Func Ecol Plants* 199(4):309–319.
30. Li W, Jiang Y, Dong M, Du E, Zhou Z, Zhao S, Xu H (2020) Diverse responses of radial growth to climate across the southern part of the Asian boreal forests in northeast China. *For Ecol Manage* 458:117759.

31. Liang E, Shao X, Eckstein D, Liu X (2010) Spatial variability of tree growth along a latitudinal transect in the Qilian Mountains, northeastern Tibetan Plateau. *Can J For Res* 40(2):200–211.
32. Lloyd AH, Bunn AG, Berner L (2011) A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Glob Change Biol* 17(5):1935–1945.
33. Lu X, Liang E, Camarero JJ, Ellison AM (2021) An unusually high shrubline on the Tibetan Plateau. *Ecology* e03310.
34. Lyu L, Suvanto S, Nöjd P, Henttonen HM, Mäkinen H, Zhang Q (2017) Tree growth and its climate signal along latitudinal and altitudinal gradients: comparison of tree rings between Finland and the Tibetan Plateau. *Biogeosciences* 14(12):3083–3095.
35. Mack MC, Walker XJ, Johnstone JF, Alexander HD, Melvin AM, Jean M, Miller SN (2021) Carbon loss from boreal forest wildfires offset by increased dominance of deciduous trees. *Science* 372(6539):280–283.
36. Mäkinen H, Nöjd P, Kahle HP, Neumann U, Tveite B, Mielikäinen K, Spiecker H, (2002) Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. *For Ecol Manag* 171(3):243–259.
37. Matías L, Linares JC, Sánchez-Miranda Á, Jump AS (2017) Contrasting growth forecasts across the geographical range of Scots pine due to altitudinal and latitudinal differences in climatic sensitivity. *Glob Change Biol* 23(10):4106–4116.
38. Morales AIGC, Mendoza JMO, Gozalbo ME, Martínez JJC (2012) Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. *Dendrochronologia* 30(4):279–286.
39. Myers–Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environ Res Lett* 6(4):21–35.
40. Myers–Smith IH, Hallinger M, Blok D, Sass-Klaassen U, Rayback SA, Weijers S, Trant AJ, Tape KD, Naito AT, Wipf S, Rixen C, Dawes MA, Wheeler JA, Buchwal A, Baittinger C, Macias-Fauria M, Forbes BC, Lévesque E, Boulanger-Lapointe N, Beil I, Ravolainen V, Wilmking M (2015a) Methods for measuring arctic and alpine shrub growth: a review. *Earth Sci Rev* 140:1–13.
41. Myers–Smith IH, Kerby JT, Phoenix GK, Bjerke JW, Epstein HE, Assmann JJ, John C, Andreu-Hayles L, Angers-Blondin S, Beck PSA, Berner LT, Bhatt US, Bjorkman AD, Blok D, Bryn A, Christiansen CT, Cornelissen JHC, Cunliffe AM, Elmendorf SC, Forbes BC, Goetz SJ, Hollister RD, de Jong R, Loranty MM, Macias-Fauria M, Maseyk K, Normand S, Olofsson J, Parker TC, Parmentier FJW, Post E, Schaepman-Strub G, Stordal F, Sullivan PF, Thomas HJD, Tømmervik H, Treharne R, Tweedie CE, Walker DA, Wilmking M, Wipf S (2020) Complexity revealed in the greening of the Arctic. *Nat Clim Chang* 10(2):106–117.

42. Myers–Smith IH, Elmendorf SC, Beck PS, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger-Lapointe N, Rixen C, Lévesque E, Schmidt NM, Baittinger C, Trant AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, Jørgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen V, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M (2015b) Climate sensitivity of shrub growth across the tundra biome. *Nat Clim Change* 5(9):887–892.
43. Okuda M, Sumida A, Ishii H, Vetrova VP, Hara T (2008) Establishment and growth pattern of *Pinus pumila* under a forest canopy in central Kamchatka. *Ecol Res* 23(5):831–840.
44. Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautiainen A, Sitch S, Hayes D (2011) A Large and Persistent Carbon Sink in the World's Forests. *Science* 333(6045):988–993.
45. Parker TC, Subke JA, Wookey PA (2015) Rapid carbon turnover beneath shrub and tree vegetation is associated with low soil carbon stocks at a subarctic treeline. *Glob Change Biol* 21(5):2070–2081.
46. Pearson RG, Phillips SJ, Loranty MM, Beck PSA, Damoulas T, Knight SJ, Goetz SJ (2013) Shifts in Arctic vegetation and associated feedbacks under climate change. *Nat Clim Chang* 3(7):673–677.
47. Pellizzari E, Camarero JJ, Gazol A, Granda E, Shetti R, Wilmking M, Moiseev P, Pividori M, Carrer M (2017) Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. *Glob Change Biol* 23(8):3169–3180.
48. Qian C, Zhang X (2015) Human influences on changes in the temperature seasonality in mid–to high–latitude land areas. *J Clim* 28(15):5908–5921.
49. R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.R-project.org/>.
50. Rees WG, Hofgaard A, Boudreau S, Cairns D, Harper K, Mamet S, Mathisen I, Swirad Z, Tutubalina O (2020) Is subarctic forest advance able to keep pace with climate change?. *Glob Change Biol* 26(7):3965–3977.
51. Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, Tryjanowski P, Liu C, Rawlins S, Imeson A (2008) Attributing physical and biological impacts to anthropogenic climate change. *Nature* 453(7193):353–357.
52. Rossi S, Anfodillo T, Čufar K, Cuny H, Deslauriers A, Fonti P, Frank D, Gričar J, Gruber A, Huang J, Jyske T, Kašpar J, King G, Krause C, Liang E, Mäkinen H, Morin H, Nöjd P, Oberhuber W, Prislan P, Rathgeber CBK, Saracino A, Swidrak I, Tremli V (2016) Pattern of xylem phenology in conifers of cold ecosystems at the Northern Hemisphere. *Glob Change Biol* 22(11):3804–3813.
53. Shetti R (2018) Potential of Shrubs in the Evolving Field of Arctic and Alpine Dendroecology: Methods in Shrub Dendro–ecology, Understanding the Processes Influencing Shrub Growth in the Arctic and Alpine Ecosystems. PhD Thesis. University of Greifswald, Greifswald, Germany.
54. Sullivan PF, Brownlee AH, Ellison SBZ, Cahoon SMP (2021) Comparative drought sensitivity of co-occurring white spruce and paper birch in interior Alaska. *J Ecol* 109(6):2448–2460.

55. Takahashi K, Aoki K (2015) Effects of climatic conditions on annual shoot length and tree-ring width of alpine dwarf pine *Pinus pumila* in central Japan. *J Plant Res* 128(4):553–562.
56. Tito R, Vasconcelos HL, Feeley KJ (2020) Mountain ecosystems as natural laboratories for climate change experiments. *Front For Glob Change* 3:38–45.
57. Weijers S, Greve AI, Bronken EP, Broekman R, Loonen MJJE, Rozema J (2012) No divergence in *Cassiope tetragona*: persistence of growth response along a latitudinal temperature gradient and under multi-year experimental warming. *Ann Bot* 110(3):653–665.
58. Winkler DE, Belnap J, Hoover D, Reed SC, Duniway MC (2019) Shrub persistence and increased grass mortality in response to drought in dryland systems. *Glob Change Biol* 25(9): 3121–3135.
59. Xiao SC, Ding AJ, Tian QY, Han C, Peng XM (2019) Site- and species-specific climatic responses of two co-occurring shrubs in the temperate Alxa Desert Plateau, northwest China. *Sci Total Environ* 667:77–85.
60. Xu C, Hou M, Yan X, Zhang X (2021) Temporal variability of seasonal warming rates in China. *Int J Climatol* 41: e1597-e1607.
61. Yang J, Cooper DJ, Li Z, Song W, Zhang Y, Zhao B, Han S, Wang X (2020) Differences in tree and shrub growth responses to climate change in a boreal forest in China. *Dendrochronologia* 63:125744.
62. Zhang X, Manzanedo RD, D'Orangeville L, Rademacher TT, Li J, Bai X, Hou M, Chen Z, Zou F, Song F, Pederson N (2019) Snowmelt and early to mid-growing season water availability augment tree growth during rapid warming in southern Asian boreal forests. *Glob Change Biol* 25(10):3462–3471.
63. Zhu L, Cooper DJ, Yang J, Zhang X, Wang X (2018) Rapid warming induces the contrasting growth of Yezo spruce (*Picea jezoensis* var. *microsperma*) at two elevation gradient sites of northeast China. *Dendrochronologia* 50:52–63.

Figures

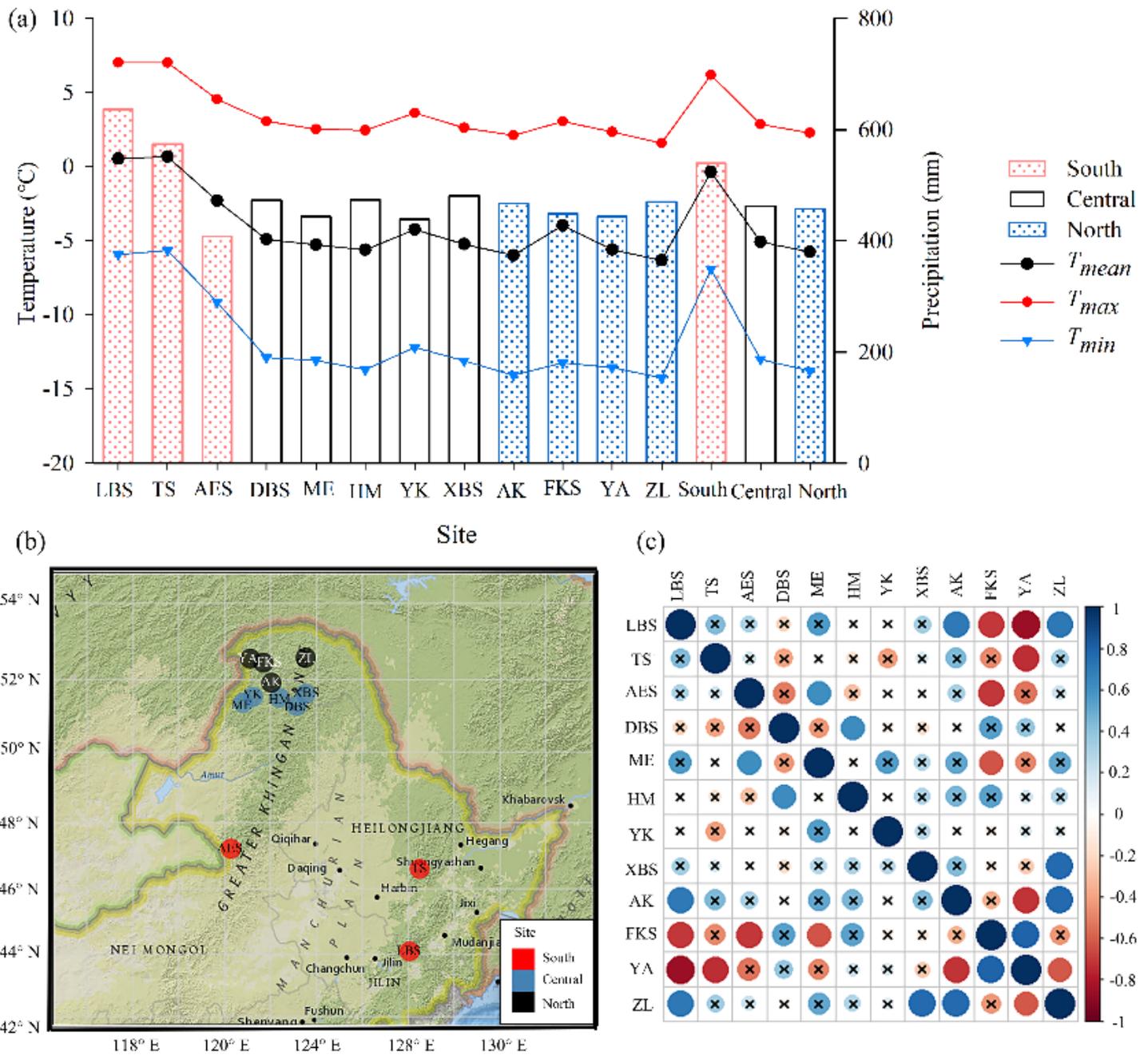


Figure 1

Climate data of sampling sites, including mean temperature (black dotted line), maximum temperature (red dotted line), minimum temperature (blue triangular line) and precipitation (columns), red columns represent the southern region (LBS, TS, AES), white columns represent central region (DBS, ME, HM, YK, XBS), blue columns represent northern region (AK, FKS, YA, ZL) (a); the distribution map of sampling sites (b), red circles represent the southern site, blue circles represent the central site, and black circles represent the northern site; correlation matrix of standard chronologies (c) "x" represents $p > 0.05$.

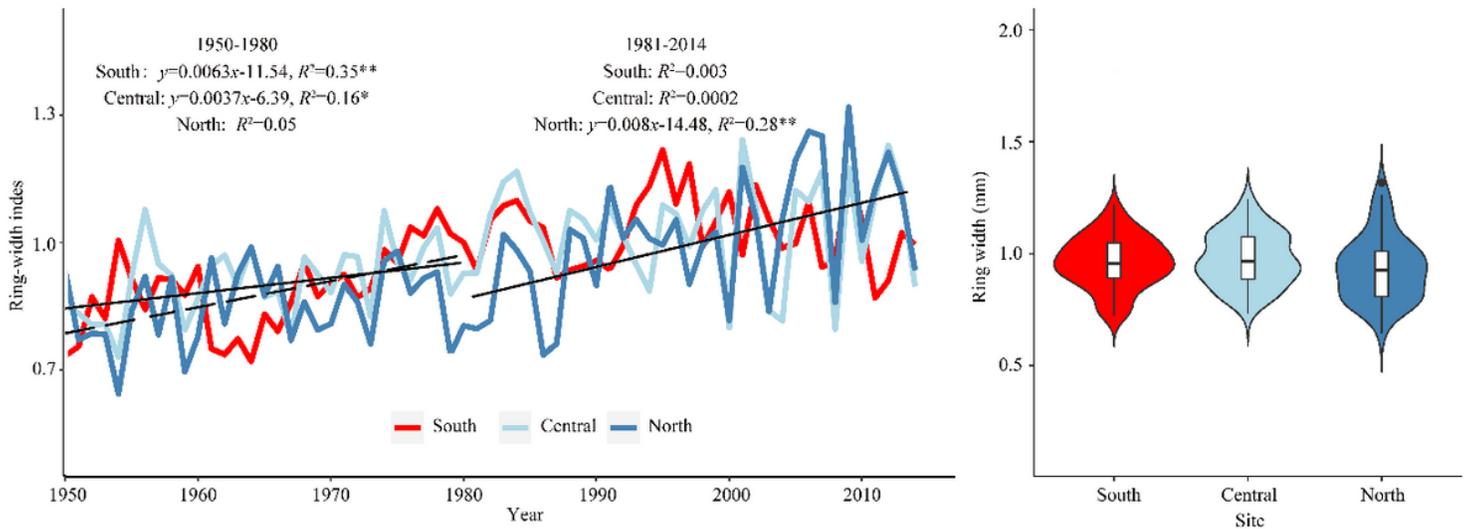


Figure 2

Standard chronologies of different regions (a). Violin plots show the full distribution of data, with white dots referring to the median, and colored dots describing mean shrub-ring width in different regions. The extent of the black lines in the violins represents the interquartile ranges, and the light bars show the 95% confidence intervals, “**” represents $p<0.01$. “*” represents $p<0.05$.

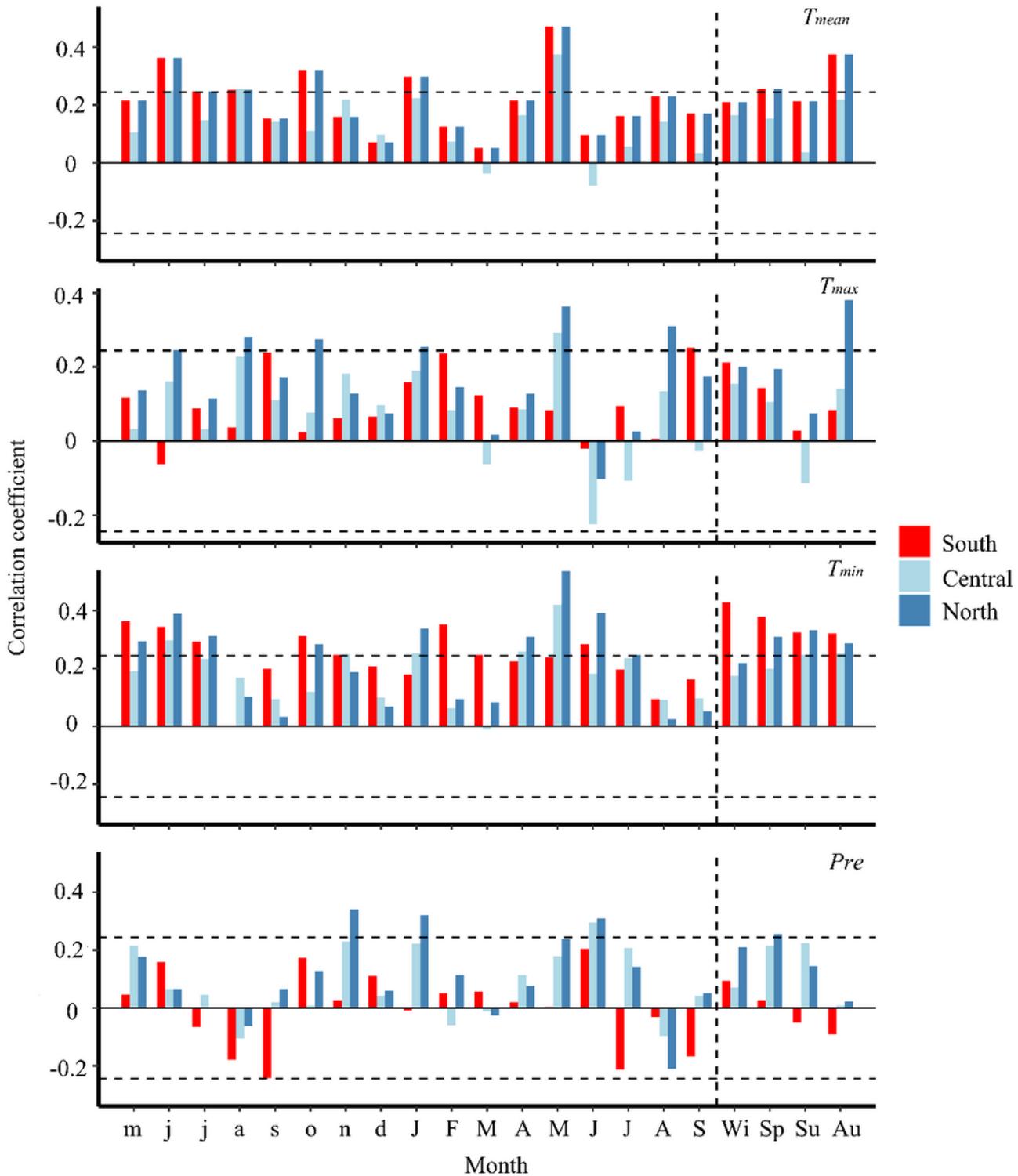


Figure 3

Correlations between regional chronologies and monthly climate factors for 1950-2014. Climate parameters include mean temperature (a), maximum temperature (b), minimum temperature (c) and total precipitation (d). Horizontal dash lines represent significance at $p < 0.05$. Lowercase and uppercase letters on the represent the prior- and current-year months. Wi, Sp, Su and Au represents the prior winter, current spring, summer and autumn, respectively.

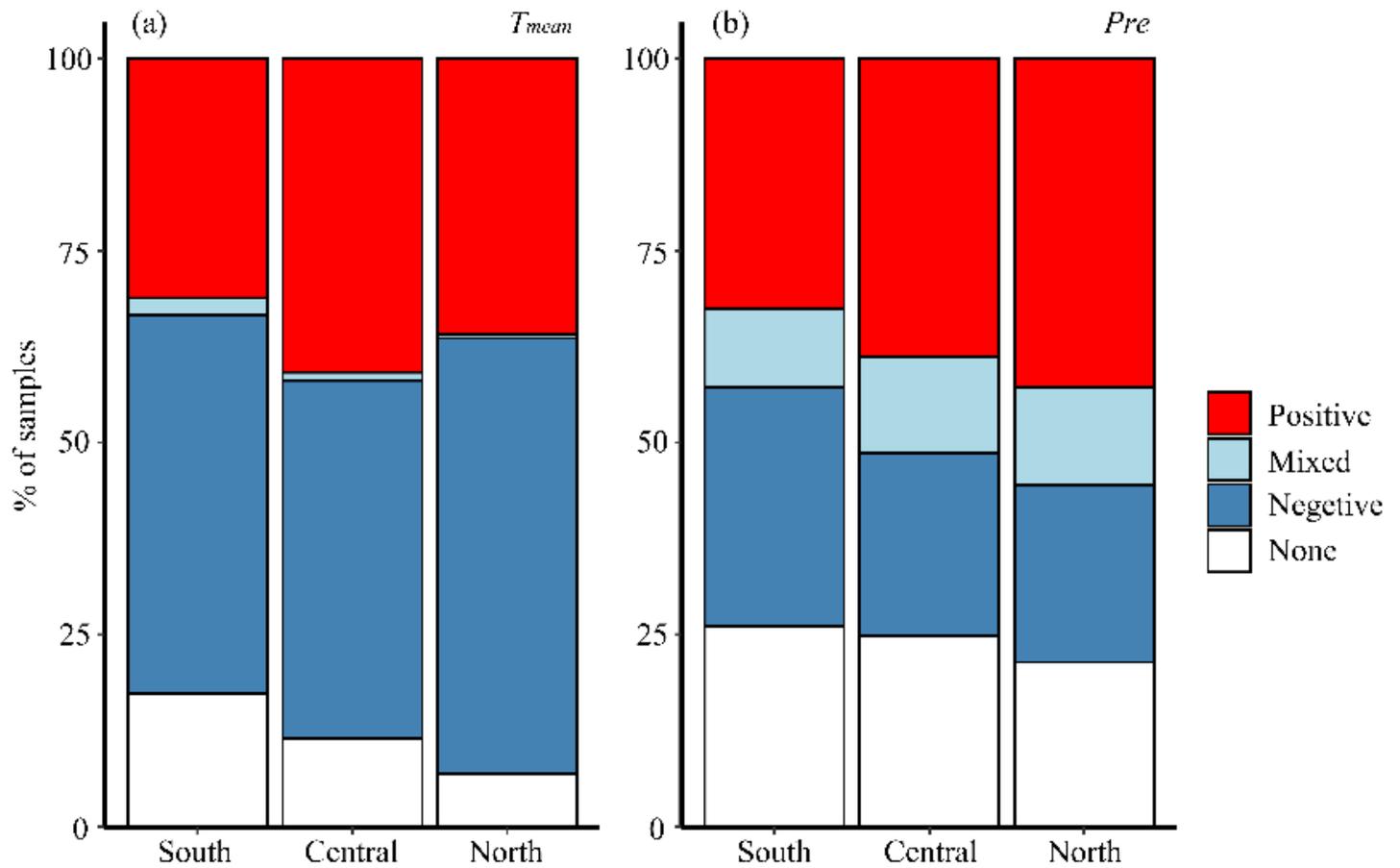


Figure 4

Patterns of response to mean temperature (a) and precipitation (b). Response categories are defined in the Methods. Bars indicate the percent of shrubs at each region in each response category. Sites are arranged from southernmost (LBS) to northernmost (ZL).

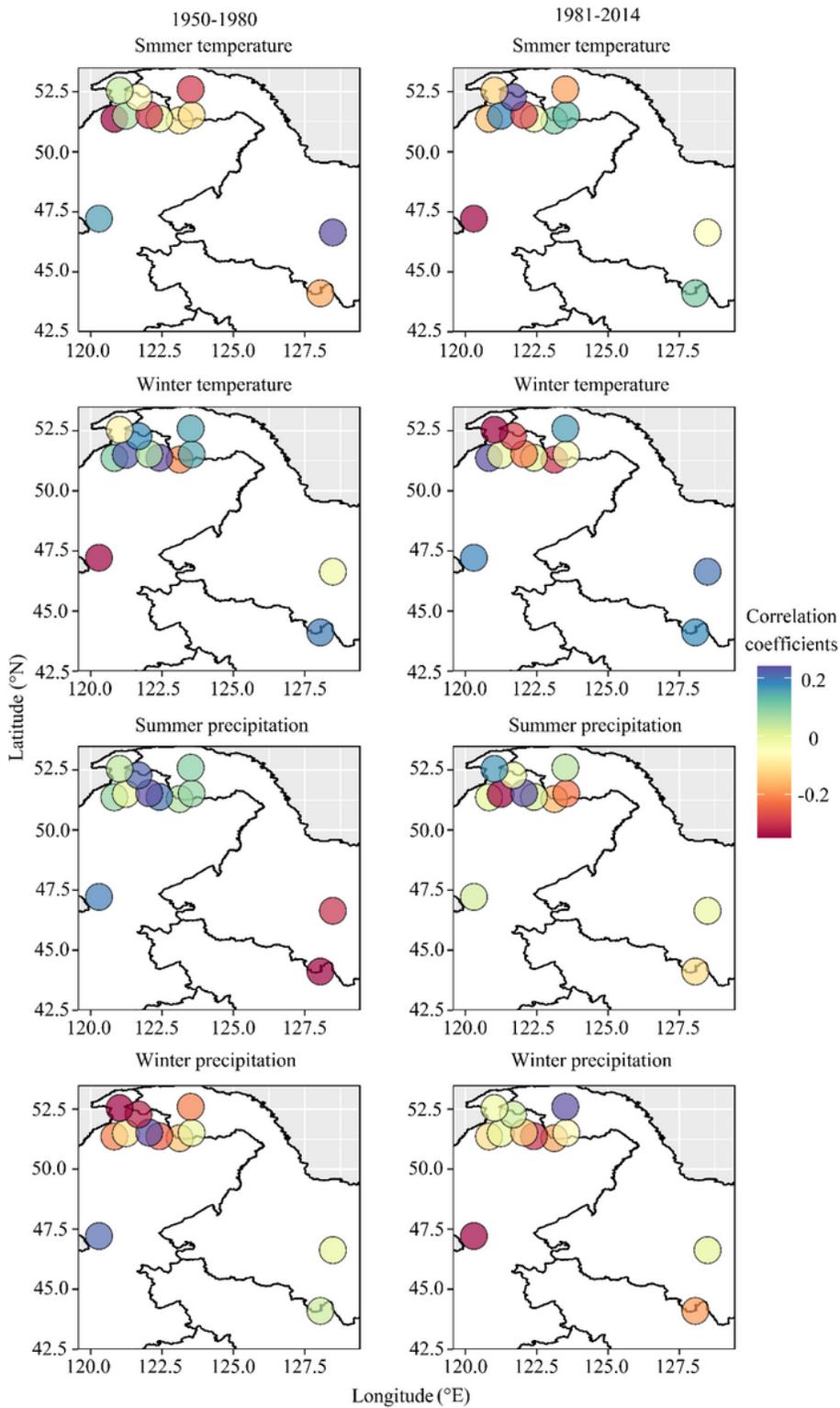


Figure 5

Shrub-ring width index correlation with summer temperature, winter temperature, summer precipitation and winter precipitation during 1950-1980 and 1981-2014.

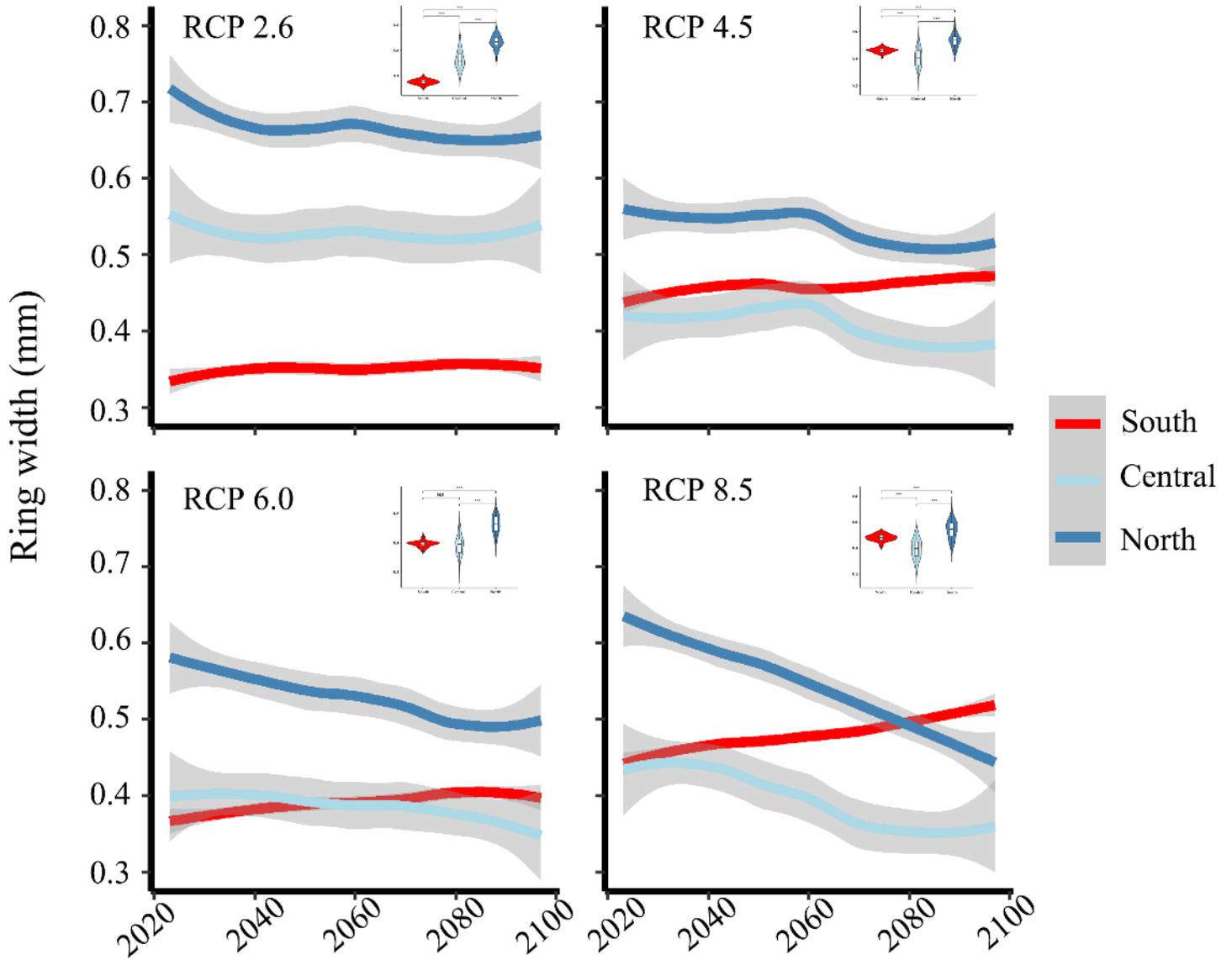


Figure 6

RW growth (RW, ring-width; values are means±SE) under RCP 2.6 (a) RCP 4.5 (b), RCP 6.0 (c), RCP 8.5 (d) scenarios in each region (red, light blue and steelblue lines refer to the South, Central and North, respectively); the violin represents shrub ring width.