Differences and similarities in radial growth of *Betula* species to climate change

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Abstract *Betula platyphylla* and *Betula costata* are important species in mixed broadleaved-Korean pine (*Pinus koraiensis*) forests. However, the specific ways in which their growth is affected by warm temperatures and drought remain unclear. To address this issue, 60 and 62 tree-ring cores of *B. platyphylla* and *B. costata* were collected in Yichun, China. Using dendrochronological methods, the response and adaptation of these species to climate change were examined. A "hysteresis effect" was found in the rings of both species, linked to May–September moisture conditions of the previous year. Radial growth of *B. costata* was positively correlated with the standardized precipitation-evapotranspiration index (SPEI), the precipitation from September to October of the previous year, and the relative humidity in October of the previous year. Growth of *B. costata* is primarily restricted by moisture conditions from September to October. In contrast, *B. platyphylla* growth is mainly limited by minimum temperatures in May–June of both the previous and current years. After droughts, *B. platyphylla* had a faster recovery rate compared to *B. costata*. In the context of rising temperatures since 1980, the correlation between *B. platyphylla* growth and monthly SPEI became positive and strengthened over time, while the growth of *B. costata* showed no conspicuous change. Our findings suggest that the growth of *B. platyphylla* is already affected by warming temperatures, whereas *B. costata* may become limited if warming continues or intensifies. Climate change could disrupt the succession of these species, possibly accelerating the succession of pioneer species. The results of this research are of great significance for understanding how the growth changes of birch species under warming and drying conditions, and contribute to understanding the structural adaptation of mixed broadleaved-Korean pine (*Pinus koraiensis*) forests under climate change.

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Introduction

With the intensification of industrialization and rapid population growth, human activities have an unprecedented impact on Earth's climate, with no parallels in the past two millennia (IPCC 2021). This has translated into extreme changes in climate, such as heightened temperatures and

severe drought, with consequences for tree growth, development, and survival (Nitschke et al. 2017; Peng et al. 2023).

In the Northern Hemisphere, warming is more evident at higher latitudes than at middle and lower latitudes. Consequently, certain regions have experienced pronounced warming and drying (Balting et al. 2021). Over the past 100 years, northeastern China has undergone a marked warming trend coupled with reduced precipitation, resulting in increased aridity (Chorography Compilation Committee of Heilongjiang Province 1997). This warmer and more arid climate has a profound influence on the ecosystems of northeastern China (Gao et al. 2020; Ju et al. 2007).

Betula platyphylla Sukaczev. and *Betula costata* Trantv. belong to the early evolutionary and the late evolutionary species, respectively, of the genus *Betula* (Jiang 1990). *B. platyphylla* is dominant in the natural secondary forests formed following the harvesting of mixed broadleaved-Korean pine (*Pinus koraiensis* Siebold & Zucc.) forests in the Xiaoxing'an Mountains. It is a typical pioneer species of temperate secondary forests, characterized by its adaptability and its resource utilization value. In contrast, *B. costata* is an important associate species within both primary mixed broadleaved-Korean pine forests and secondary forests in the Xiaoxing'an Mountains. Its wood is hard, and the species has significant economic value (Liu 2004). Both *B. platyphylla* and *B. costata* play a vital role in supporting ecosystem structure as well as facilitating forest succession (Hussain et al. 2021). It is therefore important to develop a more comprehensive understanding of the dynamics driving the responses of these species to climate change. Although both belong to the same genus, they are distinct species; understanding their climate change responses is crucial for understanding interspecies variations.

Inconsistencies exist in the factors limiting the growth of *B. platyphylla* across various regions. In the Changbai Mountain area, characterized by relatively abundant precipitation, temperature has a significantly more pronounced influence on radial growth than precipitation (Liu 2018). Temperature also has a significant influence on growth in the Zhangguangcai Mountains. On the relatively cold Kamchatka Peninsula of Russia, growth is mainly affected by summer (May to August) temperatures (Deck et al. 2017). Some surveys have also found that temperature is a major factor in *B. platyphylla* growth at high altitudes (Lyu et al. 2020; Li et al. 2022). However, in the relatively arid mountain steppe-coniferous forests of northern Mongolia, water availability is the critical determinant of growth (Gradel et al. 2017a, 2017b). Similarly, there are no correlations between *B. platyphylla* tree-ring width and temperatures in any month at the highest elevations of Mount Norikura in Japan (Takahashi et al. 2003).

While some research has explored the connection between the growth of *B. platyphylla* and climate (Watanabe et al.

2016; Gradel et al. 2017b; Khan et al. 2019; Li et al. 2022), few studies have addressed climate change responses of *B. costata*. Luo et al. (2012) analyzed the changes in diameter at breast height (DBH), tree height, and volume of *B. costata* in Jilin province but did not consider the influence of climate factors. Yang et al. (2018) studied the correlation between DBH, height and crown width of the species in mixed coniferous broad-leaved forests in the Xiaoxing'an Mountains but did not examine relationships between growth and climate. Studies on wood anatomy of *B. costata* trunks and branches found that xylem anatomical characteristics varied with location and age (Zhao et al. 2019).

While few studies have explored species of the same genus, investigations comparing the impacts of climate change on growth across distinct birch species have been rare. It is important to note that different birch species adapt to different habitats. For example, *Betula pendula* Roth. thrives in well-drained soils, whereas *Betula pubescens* Ehrh. is highly tolerant of moist soils and poorly drained heaths (Beck et al. 2016). The core distribution area and maximum climate niche range differ among various birch species. *B. platyphylla* falls within the category of species adapted to low temperatures, low humidity, and has a broad ecological range, while *B. costata* is characterized as a low temperature, low humidity species with a narrower one (Du et al. 2019). Comparative studies of birch microanatomy have also been carried out (Nielsen et al. 2017; Yuan et al. 2021). In western Greenland, variations in vessel lumen area are correlated with spring and summer temperatures, while vessel grouping is primarily influenced by winter temperatures (Nielsen et al. 2017). Although *B. platyphylla*, *B. costata*, and *Betula dahurica* Pallas. are diffuse-porous species, *B. costata* has higher mechanical strength (Gao et al. 1996). *B. platyphylla* responds to climate change by producing more and smaller vessels. Conversely, *B. costata* adapts by enhancing water transport efficiency through large vessels. *B. dahurica* falls between these two extremes, with a moderate number and size of vessels (Bai et al. 2023).

Although the growth response of *B. platyphylla* to climate change has been widely analyzed, little has been carried out to understand other species within the *Betula* genus. The impact of varying climatic conditions on the growth of different birch species warrants further exploration. This paper builds upon prior research and addresses the following questions: (1) Do different birch species respond differently to climatic factors? (2) How do the growth patterns of *B. platyphylla* and *B. costata* reflect extreme drought conditions?

Materials and methods

Study area

The research area is located in Wuying National Forest Park (47.9° N–48.3° N, 129.1° E–129.5° E) in Yichun, northeastern China. It has a typical temperate, continental monsoon climate with warm, humid summers and cold, dry winters and strong seasonal distinctions. The annual mean temperature is − 0.5 °C, with the mean temperatures of the coldest (January) and hottest (July) months − 23.5 and 20.2 °C, respectively. The annual total precipitation is 780 mm, falling from June to August and accounting for about 83% of the annual amount. Early frosts begin in mid-September, and late frosts last until late May; there are only 100–120 days frost-free. Elevation throughout the study area ranges from 285 to 688 m a.sl. The area is part of the Tangwang River system. Soils are dark brown forest soil.

The zonal vegetation is a temperate coniferous and broad-leaved mixed forest dominated by *P. koraiensis* with a variety of temperate broad-leaved species, including *B. platyphylla*, *B. costata*, *Tilia amurensis* Rupr., *Acer tegmentosum* Maxim., and *Quercus mongolica* Fisch. ex Ledeb. Cold-temperate coniferous species include *Picea koraiensis* Nakai. and *Abies nephrolepis* (Trautv. ex Maxim.) Maxim.; common shrub species include *Euonymus alatus* (Thunb.) Sieb., *Corylus mandshurica* Maxim. & Rupr., and *Philadelphus schrenkii* Rupr. *Actinidia kolomikta* (Maxim. & Rupr.) Maxim. is the dominant liana.

Tree-ring sampling and chronology development

Sampling was carried out in July 2015 and 2016. Samples were taken from healthy individuals without obvious signs of pest infestation or fire disturbance. To have the sampling environment as consistent as possible, samples were taken from closed forest areas. The soil type and soil nutrient contents of the sampling points are basically similar. Following traditional dendrochronological methods, a minimum of 25 healthy trees of each species were selected for sampling (Table 2). Two or three cores per tree at breast height (~ 1.3 m) were taken with a 5.15 mm increment borer (Haglöf, Dalarna, Sweden). A total of 60 *B. platyphylla* cores and 62 *B. costata* cores were obtained. The samples were placed in numbered plastic tubes for transport to the laboratory where they were processed. Following the method of Stokes and Smiley (1968), samples were fixed on wooden mounts, air-dried, and polished until the tree-ring boundary was clearly visible under a microscope. The skeleton plot method was used to visually assign each ring to an accurate calendar year. The Velmex tree-ring measurement system (Velmex Inc., Bloomfield, NY, USA) was used to measure tree-ring widths (0.001 mm accuracy). The COFECHA program (Holmes 1983) examined the cross-dating and measurement results. Cores that could not be cross-dated or that correlated poorly with the main sequence were eliminated from the sample set. This process ensured that an accurate calendar year was assigned to each growth ring and eliminated errors in dating and measurement. A smoothing spline 67% of the series length was used to detrend the individual tree-ring series. The process of chronology establishment was completed using the R package dplR (Bunn 2008).

Meteorological data and statistical analyses

Climate data was collected from the Yichun meteorological station (47.73° N, 128.92° E). Monthly mean temperature (T), monthly minimum temperature (T_{min}), monthly maximum temperature (T_{max}), monthly total precipitation (P), relative humidity (RH), and standardized precipitation evapotranspiration index (1-month scale, SPEI-1) were selected for correlation analysis with the tree-ring indices. Relative humidity is the ratio of air humidity to saturated humidity at the same temperature. SPEI has the characteristics of multiple time scales of 1–48 months. SPEI $\leq$ − 2.0 is considered extreme drought; when − 2.0 < SPEI $\leq$ − 1.5, severe drought conditions exist. The SPEI was calculated using the R package SPEI (Vicente-Serrano et al. 2010).

To include the impact of climate on radial growth in the preceding year, we used 17 months of data from May of the preceding year to September of the current year. Correlation analysis was conducted using the standard chronology. Recognizing that climate exerts both persistent and cumulative effects on tree growth, this study simultaneously investigated the relationship between seasonal climatic factors and radial growth for both species. To fully encompass the physiological and ecological significance of climate impacts, the seasons were divided into: winter (December of the previous year to February of the current year), spring (March to May of the current year), summer (June to August of the current year), and autumn (September to November of the current year).

The impact of drought events on the growth of *B. platyphylla* and *B. costata* was examined using the standardized precipitation evapotranspiration index on 3-month (SPEI-3) and 12-month (SPEI-12) scales (Fig. 1). SPEI-3 captures seasonal (short-term) variations in drought, whereas SPEI-12 reflects annual (long-term) changes. To reveal the specific conditions of drought, SPEI-3 values for February, May, August, and November were selected to represent seasonal drought patterns. The annual drought condition was characterized by the SPEI-12 value in December (Schwalm et al. 2017).

The R package dplR was used to conduct superposed epoch analysis (SEA) on the selected drought years (Table 1) (Bunn 2008). The goal was to clarify distinctions in the
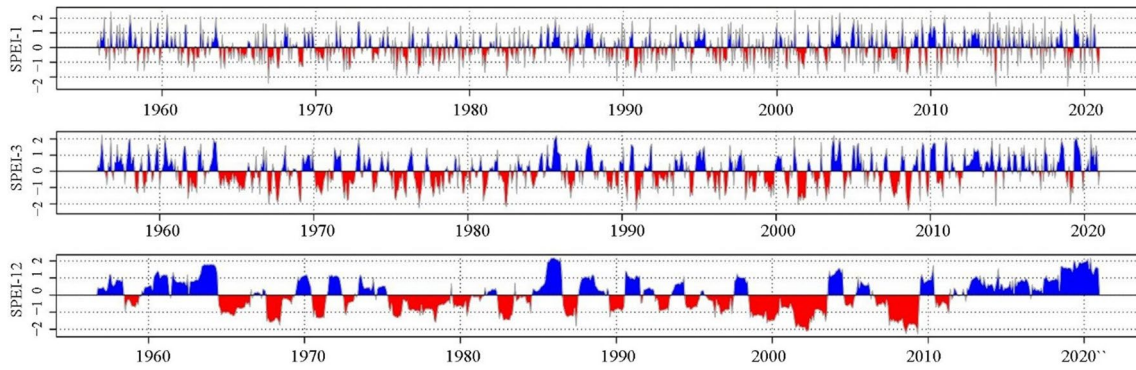
Fig. 1 Variations in the standardized precipitation evapotranspiration index (SPEI) in Yichun, China; 1-month scale (upper panel), 3-month scale (middle panel), and 12-month scale (lower panel)

Table 1 Drought events in different seasons and years in Yichun, China

|	Event year	
	Severe drought	Extreme drought
SPEI-3		
Winter	1967, 1969	–
Spring	1975, 1990, 1996, 2009	–
Summer	1967, 2001	2008
Autumn	1961, 2001, 2008, 2010	1976
SPEI-12		
Annual	1967, 2001, 2007, 2008	–

mechanisms of growth restraint and release between *B. platyphylla* and *B. costata* following seasonal and annual drought events. The SEA approach reduces the interference of background factors and directs attention toward the specific influences of interest. This technique is commonly used

to analyze the impact of extreme weather events on the radial growth of trees. In this context, the year of the drought event is used as the critical time point, while alterations in tree-ring width are used as indicators of response changes.

Over the past 62 years (1956–2017), there has been a significant increase (0.36 °C/10 years) in temperatures at Wuying Forest Farm in Yichun, China. At the same time, the region's climate has exhibited a drying trend (Fig. 2). To explore the impacts of these climate trends on radial growth, a 20-year moving correlation analysis was used. The goal was to establish links between tree growth patterns and climate warming as indicated by the SPEI.

For both species, the correlation and response coefficients were calculated at 20-year intervals starting from 1963 and 1964, respectively. The analysis subsequently progressed backward one year at a time. Pearson correlation analysis between tree-ring chronologies and climate variables was performed using the R package Treeclim (Zang and Biondi 2015). In addition, an evaluation of the correlation between

Fig. 2 Variations in the annual mean temperature and total precipitation from 1956 to 2017; the small panel at the right shows the mean temperature and mean precipitation during 1958–1967, 1968–1977, 1978–1987, 1988–1997, 1998–2007, and 2008–2017
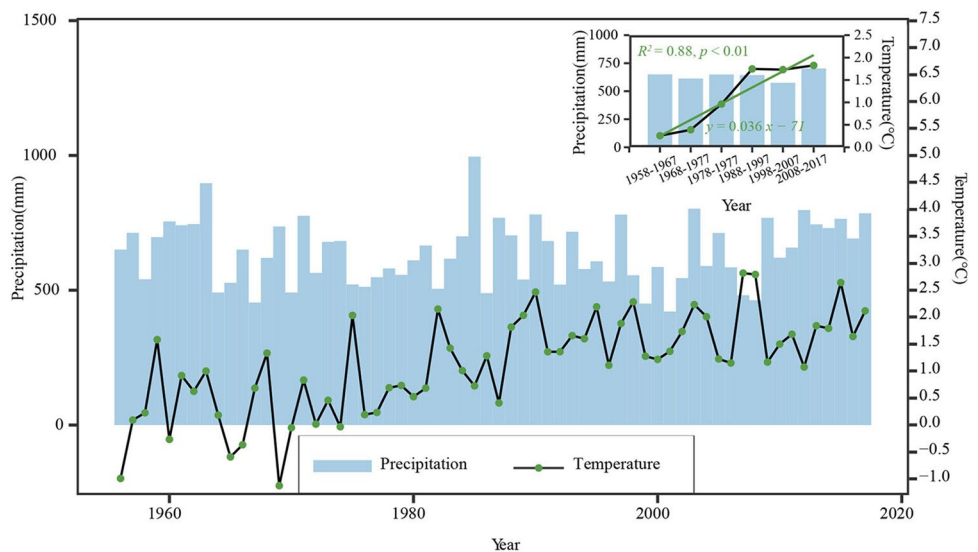
seasonal climate variables and the radial growth of *B. platyphylla* and *B. costata* was carried out using the Seascorr function within the Treeclim R package (Zang and Biondi 2015). Visuals were generated using the R package ggplot2 (Villanueva and Chen 2019) and Microsoft Excel 2019.

Results

Tree growth and chronology statistics

The longest effective time spans captured for *B. platyphylla* and *B. costata* were 55 and 53 years, respectively (Table 2). *B. platyphylla* was more sensitive to climate variations, as shown by its higher mean sensitivity and mean correlation compared to *B. costata*. The robustness of the chronologies is underscored by the high signal-to-noise ratios and expressed population signals observed for both species. These indicators suggest that variations in their ring widths accurately reflect changes in the surrounding environmental conditions. Overall, the dendrochronological analyses of both provide valuable information about the relationship between growth patterns and climatic influences.

Relationships between radial growth and climatic factors

Figure 3 illustrates both shared patterns and distinctive characteristics in the relationship between the radial growth of both species and various climate factors. The radial growth of *B. costata* was positively correlated with precipitation and SPEI from September to October of the preceding year, as well as with relative humidity in October of the previous year (Fig. 3b, f). However, its growth was negatively correlated with mean temperature and minimum temperature in September of the current year (Fig. 3a, c). Overall, the growth of *B. costata* was primarily constrained by moisture conditions from September to October. Similarly, the radial growth of *B. platyphylla* was positively correlated with precipitation and SPEI in both May and September of the previous year, as well as with SPEI in February of the current year (Fig. 3f). For both species, the moisture conditions (monthly precipitation, relative humidity, and SPEI) from May to November

of the preceding year had a more significant influence on growth compared to moisture conditions of the current year (Fig. 3).

From July of the preceding year to August of the current year, the radial growth of *B. platyphylla* was more consistent in response to temperature variables (mean temperature, minimum temperature, and maximum temperature) as compared to moisture variables (Fig. 3). The contributions of mean temperature and minimum temperature from May to September of the current year to radial growth were greater than that of climatic factors during the preceding year. Both monthly mean temperature and SPEI during the growing season were positively correlated with *B. platyphylla* growth, with SPEI showing a stronger influence. Moreover, radial growth of *B. platyphylla* was positively correlated with the minimum temperature in June of the preceding year and May to June of the current year. In summary, *B. platyphylla* growth is mainly limited by minimum temperatures during the May to June period of both the previous and current years (Fig. 3).

The effect of seasonal temperature on radial growth was less than the effect of monthly temperature (Table 3). Summer mean temperature and precipitation were positively correlated with *B. platyphylla* growth, while the minimum temperature was significantly positively correlated with *B. platyphylla* growth.

Effects of extreme drought on radial growth

The radial growth responses of *B. platyphylla* and *B. costata* to extreme drought were generally consistent, but *B. platyphylla* exhibited a greater sensitivity (Fig. 4). This aligns with the conclusion that the growth of *B. platyphylla* is more sensitive to seasonal climate shifts than *B. costata*. The occurrence of extreme drought resulted in a reduction in radial growth of both species (Fig. 4a). Following a drought episode, radial growth of both exhibited a gradual recovery. By the fifth-year post-drought, the radial growth of both species had returned to pre-drought levels (Fig. 4a, d, e). Compared to other seasonal droughts, extreme summer droughts had a greater impact on the growth of the two species (Fig. 4d).

Table 2 Statistical characteristics of the chronologies of *B. platyphylla* and *B. costata*

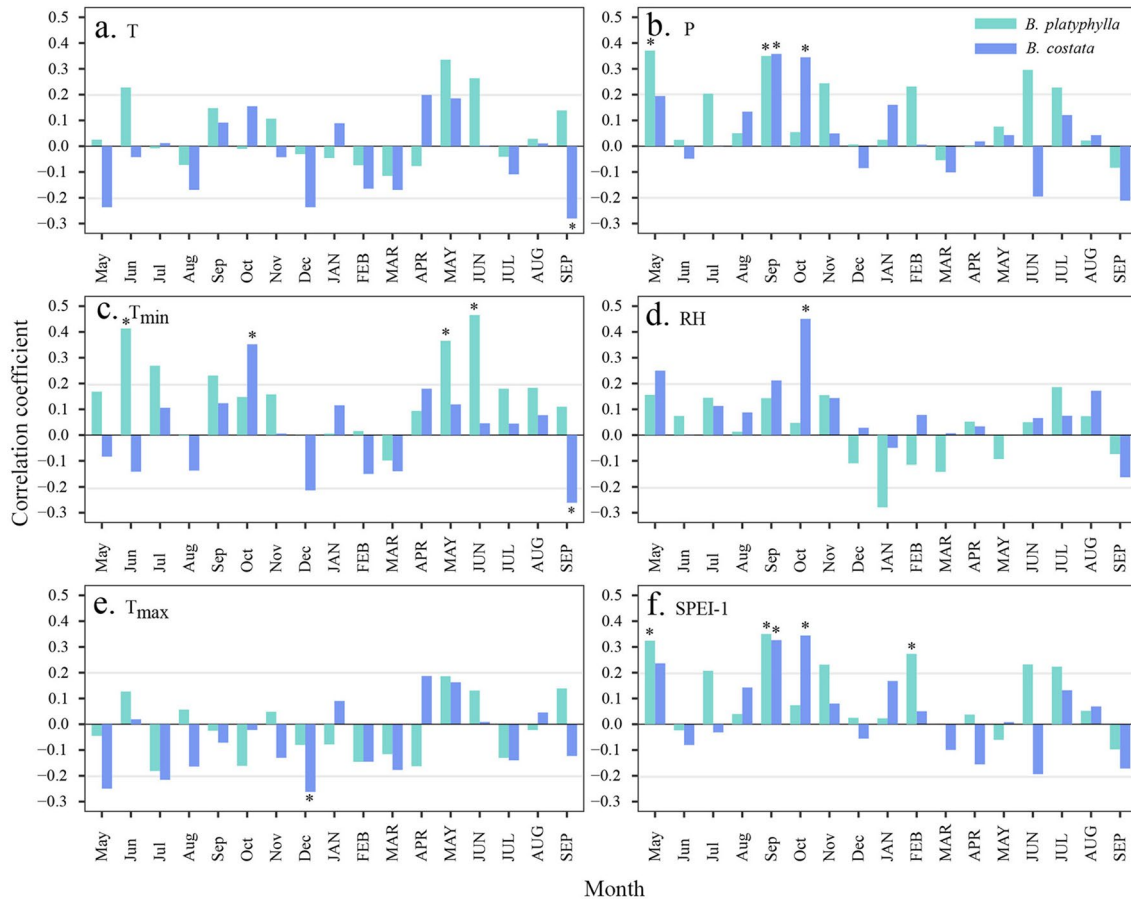| Species	Altitude (m)	# of Cores	Time span	Mean sensitivity	Standard deviation	Mean correlation	First-order autocorrelation	Signal-to-noise ratio	Expressed population signal
B. platyphylla	294	60	1963–2017	0.359	0.286	0.501	0.339	14.451	0.935
B. costata	352	62	1964–2016	0.286	0.149	0.506	0.205	15.16	0.938

Fig. 3 Correlation coefficients between the tree-ring indices of *B. platyphylla* (1963–2017) and *B. costata* (1964–2016) and major monthly climate factors; T: monthly mean temperature; T_{min}: monthly minimum temperature; T_{max}: monthly maximum temperature; P: monthly total precipitation; RH: monthly relative humidity; SPEI-1: monthly standardized precipitation evapotranspiration index. The gray line is an auxiliary line that can clearly indicate where the correlation coefficients of 0.2 and −0.2 are. *, $P < 0.05$

Table 3 Correlation coefficients between tree-ring index of *B. platyphylla* (1963–2017) and *B. costata* (1964–2016) and seasonal climate factors

Climate factors	*B. platyphylla*				*B. costata*			
	Win	Spr	Sum	Aut	Win	Spr	Sum	Aut
T	− 0.06	0.01	0.16	0.09	− 0.14	0.03	0.01	0.08
T_{min}	0.02	0.09	0.34*	0.15	− 0.11	0.01	0.11	0.06
T_{max}	− 0.14	− 0.09	0.05	0.01	− 0.17	0.05	0.01	0.10
P	0.15	0.02	0.16	− 0.04	0.01	0.05	0.01	− 0.13
RH	− 0.21	− 0.04	0.09	0.01	0.02	0.03	0.11	0.07
SPEI-1	0.14	− 0.05	0.16	0.11	0.08	− 0.13	0.00	− 0.04

Win Previous winter, *Spr* Spring, *Sum* Summer, *Aut* Autumn

*P < 0.05

Temporal stability of the relationship between radial growth and climate

The relationship between *B. platyphylla* radial growth and monthly SPEI changed in 1980 (Fig. 5). Before 1980, there was a negative correlation between growth and SPEI. After 1980, *B. platyphylla* growth became significantly positively correlated with SPEI from September of the previous year to July of the current year. This correlation increased over time (Fig. 5).

In contrast to *B. platyphylla*, the relationship between the growth *B. costata* and the SPEI from May of the previous year to May of the current year did not change significantly in 1980 (Fig. 6). The significant negative correlation
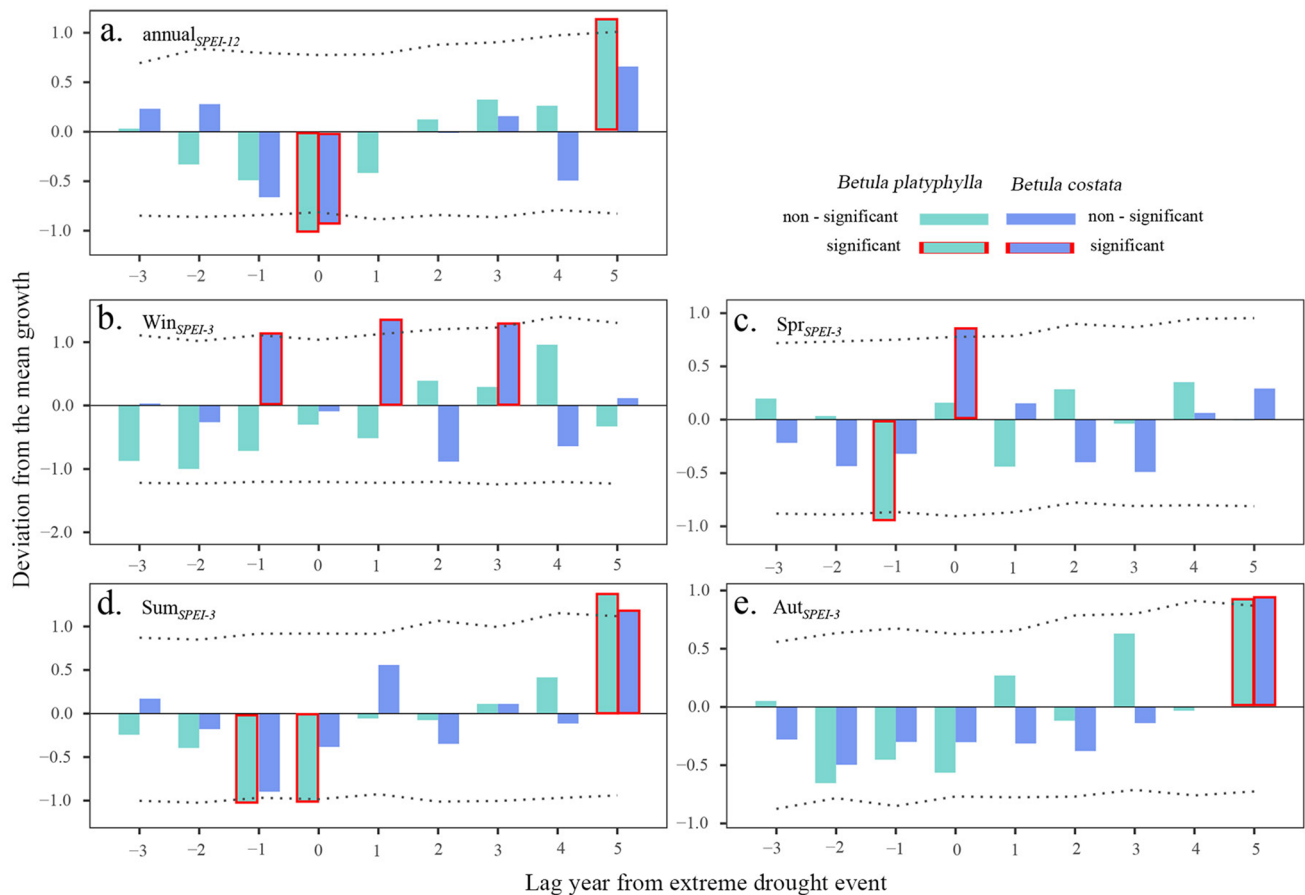
Fig. 4 Superposed epoch analysis of the radial growth of *B. platyphylla* and *B. costata* during drought event years; a: year of extreme drought based on the SPEI-12 filter; b: extreme drought events occurring during the preceding winter based on the SPEI-3 filter; c: extreme drought events occurring in spring based on the SPEI-3 filter; d: extreme drought events occurring in summer based on the SPEI-3 filter; e: extreme drought events occurring in autumn based on the SPEI-3 filter. Dotted lines represent 95% confidence intervals

between growth and SPEI existed before 1972 and then gradually weakened. After 1986, the relationship became significantly positive (Fig. 6).

As temperatures in northeastern China rise, drought increasingly becomes a limiting factor for the radial growth of both species (Figs. 5 and 6). *B. platyphylla* is more sensitive to drought than *B. costata*. Growth is more strongly impacted by extreme droughts before the growing season than *B. costata*. However, drought during the growing season had a greater impact on *B. costata* growth (Figs. 5 and 6).

Discussion

Comparison of climate factors limiting radial growth

Moisture is a primary limiting factor for the radial growth of both *B. platyphylla* and *B. costata*. *B. platyphylla*, in particular, is affected by moisture conditions before the growing season (May to November), indicating moisture conditions have a hysteresis effect on ring width growth, leading to the influence being significant in the following year (Yu et al. 2016; Jiao et al. 2022; Li et al. 2022). This agrees with a study on *B. platyphylla* from the Hanshan region of Inner Mongolia, China (Jia 2019), which found that moisture conditions of the previous year affected the growth of the birch in the current year. The Xiaoxing'an Mountains have a typical temperate, continental monsoon climate with four distinct seasons, well-defined variations in temperature and sunlight throughout the year. Due to these changes, which particularly affect growth at high latitudes, periods of active growth alternate with periods of cold-resistant dormancy on an annual cycle (Weiser 1970). This cycle is the basis of tree survival and is regulated by the interaction of genetic and environmental factors (Sutinen et al. 2009). Moisture conditions during the preceding year affect the amount of nutrients synthesized for growth in the following year, determines their greening state at the start of the new growing season, and regulates xylem development (Marqués et al. 2022).
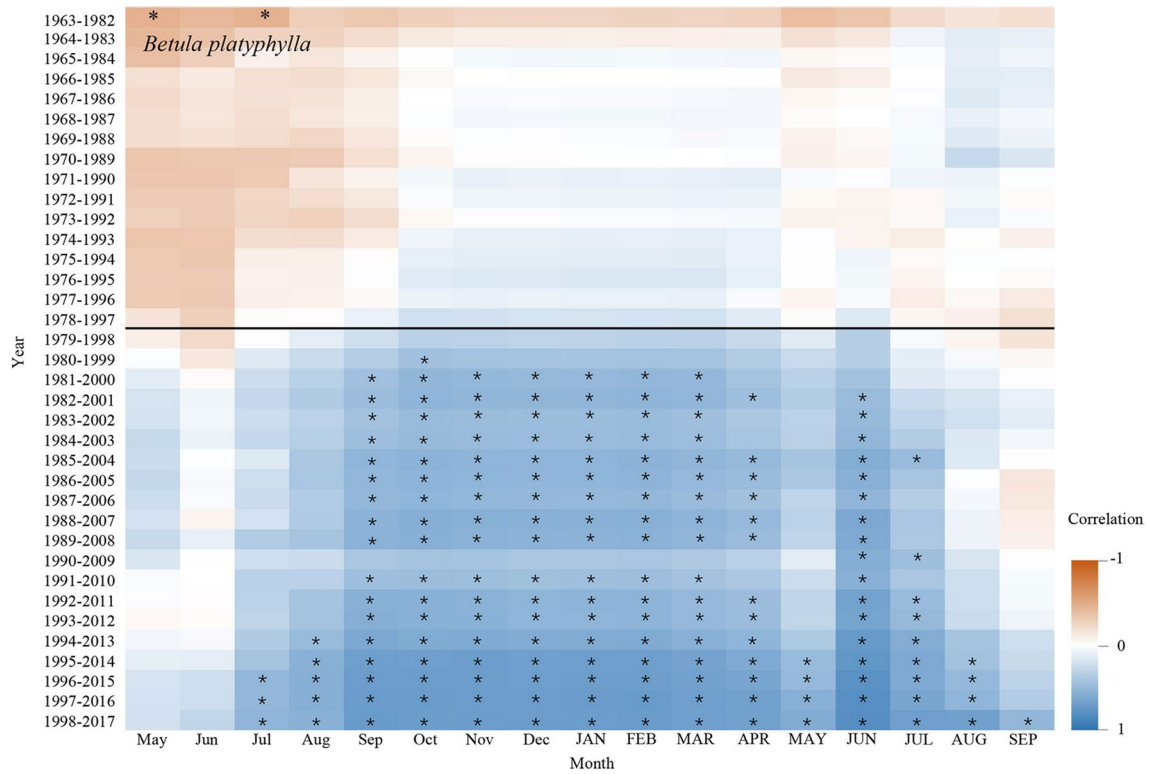
Fig. 5 Moving correlation analysis between the tree-ring index of *B. platyphylla* and monthly SPEI. Warm colors represent negative correlation; Cool colors represent positive correlation; The asterisk "*" represents a significance level of 0.05 for that month and period
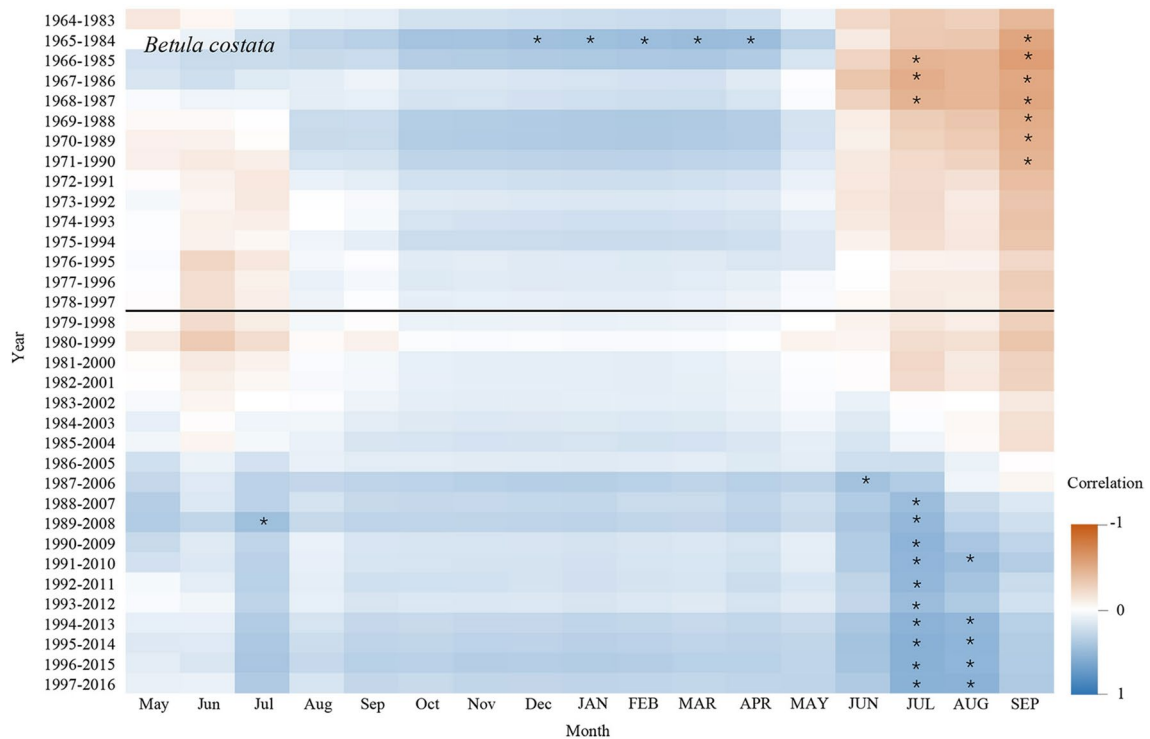

Fig. 6 Moving correlation analysis between the tree-ring index of *B. costata* and monthly SPEI. Warm colors represent negative correlation; Cool colors represent positive correlation; The asterisk "*" represents a significance level of 0.05 for that month and period

Low May and June temperatures also have a significant influence on the growth of *B. platyphylla*. During these months of early growth, trees need more water (Liang et al. 2001). In the Yichun region, winter is cold and long, and the soil remains frozen for a long time (Liu et al. 2019). The increase in minimum temperatures in May causes snow to melt and soil temperatures to rise, increasing soil moisture and promoting root activity and aboveground growth (Toromani et al. 2011). Thus, radial growth benefits from the May increase in minimum temperatures. Temperature affects photosynthesis which in turn impacts transpiration. The increase in minimum temperatures in June enhances photosynthesis and transpiration (Gao et al. 2022). A key characteristic of the climate in Wuying is that temperature and precipitation increase over the same period, concentrated from June to August (Qi and He 2021). Abundant rainfall replenishes the water lost by transpiration due to photosynthesis, allowing radial growth to increase. This result is in line with the results of studies of other broad-leaved tree species in the Zhangguangcai Mountains by Su and Wang (2017).

B. platyphylla and *B. costata* show differences in their sensitivity to temperatures in September, an important factor affecting *B. costata* growth in particular. Previous studies have found that rising air temperatures can either promote (Vitasse et al. 2019a, 2019b) or inhibit (Greenwood et al. 2017; Brodribb et al. 2020) radial growth depending on the season and the environmental conditions. September is the end of the growing season for *B. costata* (Han et al. 2019). At this time, precipitation decreases, and evaporation is made worse by rising temperatures. When an internal water deficit is reached, the stomata of *B. costata* close, causing a decrease in photosynthesis. This results in a short period of "physiological drought" that restricts growth (Lavrič et al. 2017). The growth of *B. costata* is more strongly affected by September temperatures because it is a mid-succession species, whereas *B. platyphylla* is an early-succession species and therefore more accustomed to temperature changes. Genetic-controlled variations in the traits of the two birch species affect their physiological characteristics, resulting in a significantly different radial growth-climate relationships related to the evolutionary adaptation of species to their environments (White et al. 2007). In general, early succession stage habitats are characterized by openness and abundant light. Due to the buffering effect of vegetation, middle or late succession stage habitats are generally closed and stable, with less drastic changes in environmental conditions (Bazzaz 1996). Early succession species are therefore better adapted to fluctuations in light, temperature, and precipitation. In contrast, species in late succession stages are more susceptible to environmental factors such as drought (Li and Ma 2002). It is therefore unsurprising that *B. costata* growth is more sensitive to moisture conditions from

September–October, whereas *B. platyphylla* growth is limited by May to June minimum temperatures.

Effects of extreme drought on radial growth

The effects of extreme drought on the radial growth of both species varied from season to season. Extreme drought in summer decreased *B. costata* growth and significantly reduced the ring width of *B. platyphylla*. Summer is the primary season for growth and development; insufficient water can be a major factor in delaying or even halting wood formation (Pérez-de-Lis et al. 2016). Therefore, the influence of extreme drought in summer on tree growth are of particular importance.

In this study, ring width did not decrease significantly in the four years following summer, autumn, and annual extreme drought events. However, the recovery process was slow and fluctuated slightly until growth release occurred in the 5th year following a drought. A decline in the radial growth of trees experiencing drought conditions leads to the accumulation of non-structural carbohydrates (Gricar et al. 2018), and both gymnosperms and angiosperms have a certain resilience after drought (DeSoto et al. 2020). Our results agree with Ovenden et al. (2021) findings that the growth recovery of *Pinus sylvestris* L. was significant 4–5 years after a drought. Li et al. (2021) reported that *Pinus massoniana* Lamb. remained in a recovery phase for two years following an extreme drought, then experienced rapid growth in the third year due to relatively warm and humid conditions in the study area (yearly mean temperature was 20.5 °C and annual rainfall 1600 mm). In this study area, *B. platyphylla* and *B. costata* are pioneer species of community succession and the principal species for afforestation of barren hills and bare land (Hussain et al. 2021) due to their drought tolerance and environmental adaptability. This study area has a temperate, continental monsoon climate, with much lower annual precipitation and mean temperatures than the subtropical marine monsoon climate described by Li et al. (2021). We therefore concluded that *B. platyphylla* and *B. costata* in the Xiaoxing'an Mountains remain in the growth recovery phase for about four years following an extreme drought, then recover rapidly in the 5th year.

Our analysis shows that *B. platyphylla* growth recovered more swiftly from the effects of an extreme drought than *B. costata*. Previous studies have found that many early succession species have higher photosynthetic rates when leaf water potential is reduced (Li and Ma 2002). As a result, early succession species typically recover faster once water stress is relieved (Geis et al. 1971).

Before 1980, the SPEI from September to April showed an insignificant negative correlation with *B. platyphylla* growth. After 1980, the correlation became significant and positive, and increased over time. *B. costata* is significantly

less drought-limited than *B. platyphylla*. Although its growth is sensitive to SPEI from July to September, the correlation did not change significantly in or around 1980. Paleoclimate reconstruction studies point to unprecedented warming in the twentieth century. A body of growing data indicates that temperature has increased significantly in northeastern China since 1980 (Zhu et al. 2007). Rising temperatures in Wuying area of Yichun, China from 1956 to 2017 led to enhanced soil water evaporation and faster vegetation transpiration. Precipitation, meanwhile, did not change significantly and therefore could not supplement the evaporated soil water. As a result, soil water content decreased, becoming an important limiting condition for the radial growth of *B. platyphylla* and *B. costata*. In general, early succession species often reduce leaf temperature through higher transpiration (Li and Ma 2002). However, intense transpiration also accelerates water loss and exacerbates drought stress in early succession species (Lavrič et al. 2017). This is consistent with our finding that *B. platyphylla* growth is more significantly restricted by drought than *B. costata*.

Conclusions

We compared the growth responses of different birch species to climate change in Xiaoxing'an Mountains, China. Radial growth of *B. platyphylla* and *B. costata* was affected by moisture conditions of the previous year and temperatures of the current year. Minimum temperatures from May to June and moisture from September to October are major factors limiting the growth of *B. platyphylla* and *B. costata*, respectively. With rapid warming after 1980, the correlations between the growth of these two species and climate factors have changed, with water availability becoming an increasingly important limiting factor. At present, the growth of *B. platyphylla* is more restricted by water conditions than *B. costata*. *B. platyphylla* growth is already affected by the warming and drying trend of the last decade; *B. costata* will also be limited in the future if warming continues. This suggests that climate change may be interfering with the succession processes of *B. platyphylla* and *B. costata*, accelerating the succession of pioneer species. Forest managers need to respond to these changes by adjusting the composition and proportion of tree species over time and by promoting forest succession process. Further physiological and ecological experiments are needed to explore the mechanisms by which different birch species respond to changes in climate change. These studies are crucial for developing effective management measures and promoting healthy forest development.

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