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Species-specific drought resilience in juniper and fir forests in the central Himalayas

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ABSTRACT

With increased frequency and intensity of drought occurrence in the changing climate, the drought resilience of forest trees is of widespread interest. Particularly, it is not clear as to how the resilience differs between tree species and whether or not such resilience changes over time. Understanding tree resilience to drought requires observations not only from recent events but also from the historical past, information of which is usually hardly available. Here we defined historical drought based on isotope data and compared drought resilience in *Juniperus tibetica* and *Abies spectabilis* forest in the central Himalayas in five extreme droughts during the past two centuries. We found that juniper trees had a stronger resistance than fir trees in the three extreme droughts in the nineteenth century but this pattern reversed in the two drought events in the twentieth century. The length of response time to droughts and recovery time to pre-drought state were shorter in juniper trees than in fir trees. The proportion of declining trees showed a decreasing trend in fir trees but not in juniper trees. Our results indicate that the species-specific resilience might be related to the anisohydric (junipers) and isohydric (firs) strategies of stomatal regulation in response to droughts plants. The differences in species-specific drought resilience should be taken into account when developing forest management policies against the influence of extreme droughts in future.

1. Introduction

Resilience is the capacity of ecosystems to withstand disturbance and maintain their structures and functions (Holling, 1973; Walker et al., 2004). Tree growth resilience to climate extremes has received increasing attention in studies of forest response to changing climate (Allen et al., 2016; Willis et al., 2018). It has been demonstrated that trees could actively resist the influence of extreme events and recover to pre-disturbance growth state if the resilience threshold is not exceeded (Hodgson et al., 2015; Gazol et al., 2018; Stevens-Rumann et al., 2018; Liu et al., 2019). Previous studies showed that tree resilience to climate extremes varies among species due to differences in growth sensitivity, stomatal and physiological traits (Vitali et al., 2017; Gomes Marques et al., 2018; Serra-Maluquer et al., 2018; Duan et al., 2019; Rahman et al. 2019). Understanding the species-specific resilience is a prerequisite for making management policy to mitigate climatic extremes in forests.

Tibetan juniper (*Juniperus tibetica*) and east Himalayan fir (*Abies spectabilis*) forests are distributed in the central Himalayas with the average elevation more than 3500 m above sea level. Juniper and fir are both long-lived and dominant tree species in high-mountain ecosystems, which contribute to regional carbon stocks and forest productivity (Måren et al., 2015). Tree-ring oxygen isotopes collected from fir trees in the central Himalayas showed that the region has been subjected to drought extremes over the past two hundred years (Xu et al., 2018). The healthy growth of juniper and fir forests in this region suggests that these two species developed strategies of resilience to the recurrent drought extremes. Yet it is not clear as to these strategies in the two species.

In this study, we investigate the characteristics of drought resilience in Tibetan juniper and east Himalayan fir trees in two sites in the central Himalayas. We use tree-ring data to quantify key components of resilience (resistance, length of response time and length of recovery time) and compare them in the two species in the past two centuries. The objectives of our study were to answer two questions: (a) What's the differences in drought resilience between the two species? and (b) Has the resilience of the two species changed in the past two centuries?

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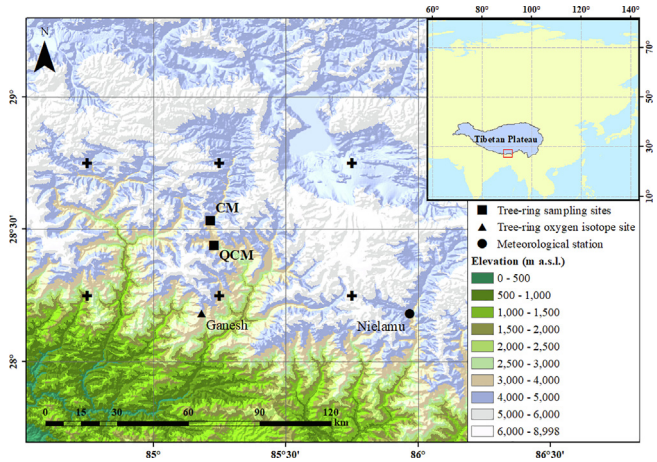

Fig. 1. Location of sampling sites and meteorological station. CM: site wth *Juniperus tibetica*; QCM: site with *Abies spectabilis*; Ganesh: site with tree-ring oxygen isotope record published by Xu (2018); The crosses describe the grid of the CRU scPDSI data (84.5–86°E, 28–29°N) used in this study.

2. Materials and methods

2.1. Study sites and tree-ring data

Two sites in natural high-mountain forests in the central Himalayas were chosen in this study (Fig. 1). One site is Cangmu (CM) where the dominant tree species is Tibetan juniper and the geographical location is 85°12′57″ E, 28°31′59″ N. The other site is Qiucangmu (QCM) where the dominant tree species is east Himalayan fir and the geographical location is 85°13′42″ E, 28°26′20″ N. The growing season of the two species is from May to late September or early October according to the relevant studies (Liang et al., 2010; Li et al., 2019; Xu et al., 2019). Regional annual mean temperature is 3.8 ± 0.5 ℃ (mean ± SD) and annual total precipitation is 638.6 ± 139.8 mm (mean ± SD) based on climate data from years 1967–2018 in the Nielamu national meteorological station (Fig. 1). Maximum temperature and precipitation both occur in July.

Increment cores were collected from relatively old juniper trees in CM site and fir trees in QCM site, which are approximately 10 km apart in distance and located within the same valley with similar soils and climate conditions. The sampling was conducted in elevation between 3400 and 3500 m on the south slope in CM, and between 3500 and 3600 m on the north slope in QCM. We intentionally selected sites that had minimal evidence of past human activities, including trees with an intact large diameter class. Increment cores was extracted at breast height of trees and in the direction parallel to the contour. In order to ensure enough individual trees to be sampled in the remote area, we collected one core per tree from a total number of 20 and 30 trees in the two sites, respectively. The core samples were dried, fixed and sanded to bring the rings clearly visible. Ring widths were measured using a Lintab 6 system (Frank Rinntech, Heidelberg, Germany) with an accuracy of 0.001 mm. Tree rings were crossdated and quality-checked by standard dendrochronological techniques (Schweingruber 1988; Holmes 1983). Growth trend in tree-ring series was removed using a cubic spline of 50% frequency–response cutoff at half length of the series for each individual tree (Cook et al., 1990). Tree-ring chronologies were developed for each site.

2.2. Climate sensitivities and extreme drought events

Monthly mean self-calibrating Palmer Drought Severity Indices (scPDSI) for the six 0.5°×0.5° grids nearest to the two study sites were obtained (Fig. 1) from Climatic Research Unit database (CRU TS 4.03) (https://crudata.uea.ac.uk/cru/data/drought/). Person correlation coefficients between the tree-ring chronologies and scPDSI from October of prior growth year to September of the growth year were calculated for the period 1967 to 2005 to identify the climate-growth relationships.

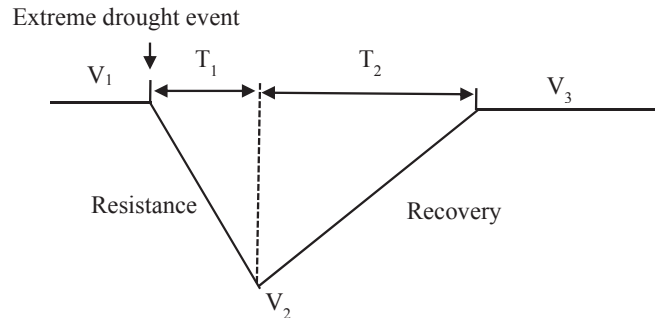

Fig. 2. Definition of tree resilience. $V_{1\text{-}3}$: tree-ring index before, during and after the extreme drought event; $T_{1\text{-}2}$: Time to resist and recover.

Tree-ring cellulose $\delta^{18}O$ sequence from fir trees in Ganesh, approximately 30 km from site QCM and 40 km from site CM, was proved to have significant correlation with scPDSI from June to September (Xu et al., 2018). The data of tree-ring cellulose $\delta^{18}O$, spanning from 1801 to 2000 were downloaded at the National Oceanic and Atmospheric Administration (https://www.ncdc.noaa.gov/paleo/study/22551). Linear trend in $\delta^{18}O$ data was eliminated and the years that the detrended $\delta^{18}O$ values dropped below two standard deviation of the series were defined as extreme droughts.

2.3. Quantification of tree resilience

We defined three components of tree resilience (Fig. 2). Tree resistance (Rt) is the reduction in tree growth during disturbance relative to pre-disturbance, that is, $R_t = (V_2 - V_1)/V_1$. Length of response time (T_1) is the number of years that tree-ring width reached the minimum value since the extreme drought, reflecting lag effect of the drought. Length of recovery time (T_2) is the number of years that trees return from the lowest growth to the pre-disturbance state.

Where V_1 is the 10-year average of ring indices before the event year; V_2 is the lowest value in ring indices from the event year to three years after the event. V_3 is the 5-year running average of tree-ring indices that is equal or greater than V_1. T_1 is the time from V_1 to V_2, and T_2 is the time from V_2 to V_3. If a tree's T_2 is longer than four years, this tree is considered as a growth declining tree (Anderegg et al., 2015; Wu et al., 2017). All these indices were calculated at the individual tree level for each extreme event in this study.

3. Results

3.1. Tree growth in extreme droughts

The longest tree-ring series at the site CM and QCM are from 1781 to 2005 and 1783 to 2005, respectively. Tree-ring chronologies at the two sites show positive correlation with scPDSI in all months of the year from 1967 to 2005. Juniper and fir chronologies exhibit significant ($p < 0.05$) positive correlation with annual scPDSI ($r = 0.322$ and 0.447, respectively) and positive correlation with June-September scPDSI ($r = 0.226$ and 0.396, respectively).

The detrended tree-ring $\delta^{18}O$ sequence of fir trees from the Ganesh site showed five years that the values are greater than the mean value plus two standard deviations of the series. These five years, 1813, 1833, 1869, 1941 and 1972, were considered as extreme droughts (Fig. 3). The difference in mean value is significant ($p < 0.05$) in the event 1813, 1833 and 1941 (Supplementary Table 1).

We examined the change of the tree ring indices of each tree under

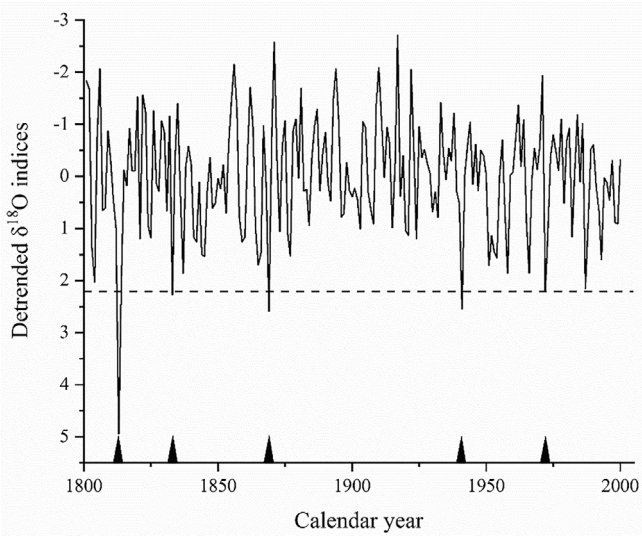

Fig. 3. Detrended tree-ring cellulose $\delta^{18}O$ indices and extreme drought years. The horizontal dash line marks the two standard deviations below the mean values for the detrended $\delta^{18}O$ indices. The triangles highlight the extreme drought years 1813, 1833, 1869, 1941 and 1972.

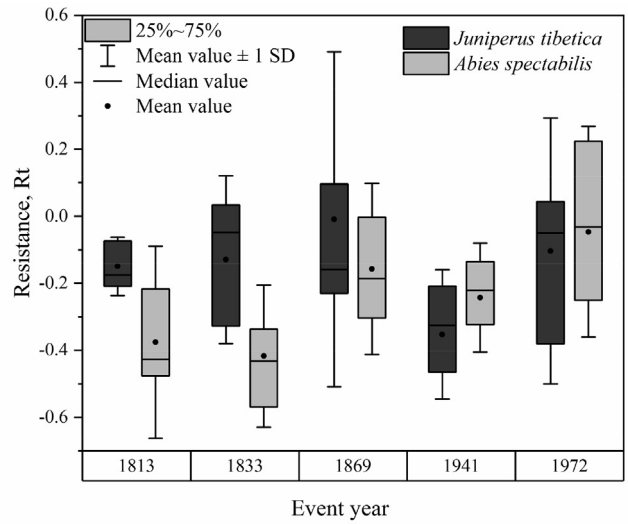

Fig. 4. Resistance of *Juniperus tibetica* and *Abies spectabilis* in five extreme droughts.

each drought event. A total of 178 times of tree response cases were recorded. Growth of most trees reduced rapidly to the lowest in the drought year or within two years after the drought. The growth of a few trees declined, with the tree-ring indices showing a sustained downward trend after the extreme drought. The proportions of trees that reached the lowest growth in the event year and 1 or 2 years after were 25.8%, 25.3% and 25.3%, respectively. The proportion of trees that continued to decline for more than two years was 23.6%. Once tree growth reached the minimum, 88.8% of trees could recover to pre-disturbance growth within just one year. Only 7.9% of the trees did not recover within five years.

3.2. Difference of tree resistance and recovery in juniper and fir trees

Resistance of junipers and firs differed in the five extreme drought events. The mean resistance values among trees in the five events were −0.15, −0.13, −0.01, −0.35 and −0.1 for juniper trees and were −0.38, −0.42, −0.16, −0.24 and −0.05 for fir trees. In the first three cases, the resistance of junipers was stronger than that of firs. But in the last two cases, firs showed stronger resistance (Fig. 4).

The mean lag time to the five drought events were 0.8, 1.9, 0.6, 1.6 and 1.6 years for junipers and 2.4, 1.6, 1.2, 1.6, 1.7 years for firs, respectively. The proportion of trees that $T_1 = 0$ was generally higher in junipers than firs. The proportion of trees that T_1 greater than 2 was the highest in firs in 1813 and decreased in the following drought events, whereas junipers did not show such a trend (Fig. 5).

The juniper's recovery time is mostly one year, except for the last one, which was 1.3 years. The mean recovery time for firs to the five drought events were 3, 1.5, 1.2, 1.3 and 1.1 years, respectively. In the most recent event, a few juniper trees showed decline in growth. As to firs, there was 50% of the trees showed growth decline after the drought year 1813. The proportion of declining trees reduced in the rest of the drought events (Fig. 6).

4. Discussion

4.1. Quantification of tree resilience

Resilience, which shows a combination process of resistance and recovery, has been quantified in a variety of ways with respect to particular studies (Palumbi et al., 2008; DeSoto et al., 2020). In dendroecological studies, Lloret et al. (2011) proposed formulas to calculate tree resistance, recovery, resilience and relative resilience using tree-ring indices. Many studies have applied these indices in describing tree resilience to climate extremes in the past (Merlin et al., 2015; Vitali et al., 2017; Gazol et al., 2018; Gomes Marques et al., 2018; Fang and Zhang, 2019; Rahman et al., 2019). Here we modified the calculation of tree resistance using the growth minimum to represent the effect of climate extremes rather than the tree-ring index in the year of climate extremes. We also included the length of response time and length of recovery time as additional components to describe tree resilience. We did not calculate these parameters using site tree-ring chronology, rather we used tree-ring indices from individual trees so as to produce a detailed view of the growth response to climate extremes at tree level. In effect, resilience of forest ecosystems is determined by that of internal individuals (Scheffer et al., 2018), that is, the health status of individual trees plays a vital role in maintaining forest resilience.

4.2. Differences in drought resilience in juniper and fir trees

Although the radial growth of both juniper and fir trees are limited by annual moisture availability in the central Himalayas, their response to extreme droughts is different. We found that, when extreme drought occurs, junipers reduced their growth to the minimum in fewer years than firs, and also recovered to pre-drought state more quickly than firs. This difference in growth response to extreme droughts may be related to species-specific physiology. Firs are considered isohydric plants that maintain a relatively constant midday water potential by reducing or closing their stomatal conductance during extreme droughts; whereas junipers are anisohydric species that have higher rates of gas exchange and allow midday water potential to decline with decreasing soil water potential (Lo Gullo and Salleo 1988; Mcdowell et al., 2008; Gaylord et al., 2013; Wei et al., 2019). This difference in stomatal regulation of water status may be an important cause for juniper trees to have quick growth reduction in response to extreme droughts and a quick recovery after the droughts.

Our research was based on two sampling sites with close distances and similar climatic conditions where junipers and firs do not have significant difference in tree ages. The design of sampling and resilience analyses made the long-term species-specific resistance and recovery process more easily detectable. The extent to which our observation applies still needs more data from a larger region to demonstrate.

Firs are more likely to have resistance collapse in extreme drought

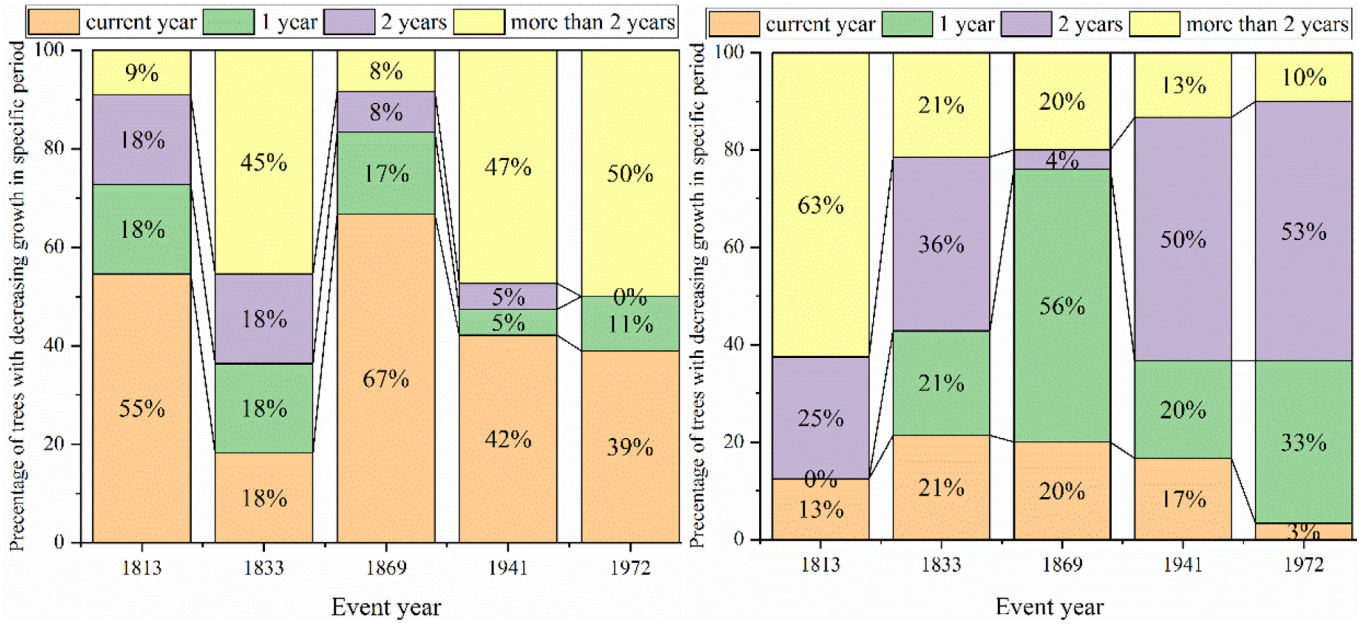

Fig. 5. Lag time to droughts in *Juniperus tibetica* (left) and *Abies spectabilis* (right) in the five extreme drought events of the past two centuries.

years. In the year 1813 that the intensity of drought was the most severe, firs had 63% of trees showing growth minimum two years later the event and 50% of trees spending more than four years to recover to pre-drought state. We hypothesize that, being an isohydric species, some fir trees might die because of hydraulic failure in the severe intensity of drought, thus reducing resource pressure on the surviving trees and lagged the process of growth reduction. Sánchez-Salguero et al. (2015) showed that *Abies* exhibited rapid stomatal closure in severe drought and carbon uptake significantly reduced under water limitation. This isohydric strategy of *Abies* under drought suppression has been proved by other studies (Zang et al., 2014; Yin and Bauerle, 2017). In response to droughts, the surviving trees might close their stomata and maintain growth by consuming carbohydrate reserves, thus the carbon starvation led to a prolonged process of recovery. In response to severe droughts, the water transfer in fir trees may be irreversibly disrupted due to water cohesion breakdown and massive vessel embolisms, which lead to tree mortality (Bréda et al., 2006). Fang et al. (2018) reported drought induced tree mortality in the late 18th century in the northern Tibetan Plateau. Unfortunately, information of forest mortality in history was not available in the region.

4.3. Changes in drought resilience of juniper and fir trees through time

The response of tree growth to climate extremes varies from one event to the other depending on the intensity of climate extremes, climate conditions following the extremes, tree species and other disturbances (McNulty et al., 2014; Bennett et al., 2015; Gazol and Camarero, 2016; Gao et al., 2018; Huang et al., 2018; Serra-Maluquer et al., 2018). A few studies quantified resilience to extreme droughts not only from recent observations but also from the historical past due to the difficulties in obtaining information (Cole et al., 2014; Willis et al., 2018). A two century-long record of stable oxygen isotopes from annual growth rings of fir trees in our study region was recently published and available for us to make comparative studies (Xu et al.,

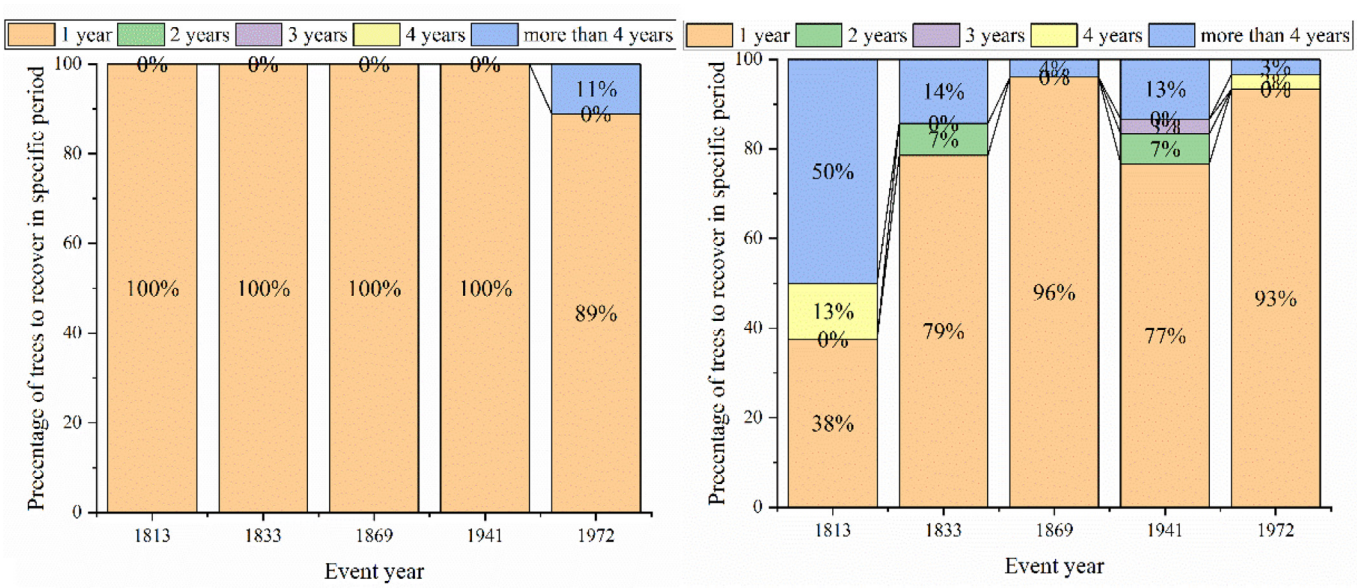

Fig. 6. Recovery of *Juniperus tibetica* (left) and *Abies spectabilis* (right) in the five extreme drought events of the past two centuries.

2018). In the central Himalayas, stable oxygen isotopes of tree rings were widely considered as a robust signal of precipitation related to the Asian summer monsoon despite differences in species and elevations (Zeng et al., 2016; Wernicke et al., 2017; An et al., 2019; Grießinger et al., 2019; Xu et al., 2019). This allowed us to identify extreme drought events in the past two centuries and examine the changes in growth response of juniper and fir trees to these extreme droughts.

Our study showed the changes in the drought resilience of juniper and fir trees in last two centuries. The drought resistance of fir trees was relative lower than that of juniper trees in the three drought events in the nineteenth century, but the resistance became stronger than juniper trees in the two events in the twentieth century (Fig. 4). The proportion of declining trees showed a decreasing trend in fir trees but not in juniper trees (Fig. 6). We supposed warming climate over recent decades might be a factor favorable to the drought resilience of fir trees but not juniper trees. The mechanism for the change in tree resilience is not clear so far, but the changing characteristics brings a new perspective to the assessment of forest growth under climate change. The species-specific drought resilience and their changes over time should be taken into account when developing plans for forest management to cope with the changing climate.

CRediT authorship contribution statement

Ouya Fang: Methodology, Software, Formal analysis, Visualization. **Hongyan Qiu:** Investigation, Resources, Data curation. **Qi-Bin Zhang:** Conceptualization, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2020.106615.

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