

Article

Isolated Trees in Two Tibetan Plateau Treelines Reveal Growth Plasticity to Harsh Conditions of the Little Ice Age

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Abstract: Trees greater than 150 years old growing in the current treelines were most likely isolated tree outposts above previous treelines of the Little Ice Age (LIA). An intuitive question is, how did these isolated trees grow at such a high elevation in the cold environment? Here, we tackle this question using tree-ring width data of the Northern Hemisphere's highest treelines at 4900 m a.s.l. (Basu) and 4680 m a.s.l. (Langkazi) on the Tibetan Plateau. The results showed that an age-related exponential growth trend did not exist in most of the ring-width sequences of the sampled trees. The values of ring widths in the isolated trees had a similar pattern of probability distribution during and after the LIA. The coefficients of variation in ring widths of the isolated trees were significantly greater than those of the non-isolated trees in their common growth period. Synchronicity of annual change in radial growth among trees varied in time. These results indicated that the isolated trees in the LIA developed an adaptive ability to slow down radial growth rate and modulate growth synchronicity among individuals in cold stressful environments. Our study highlights growth plasticity in isolated trees above treelines for coping with harsh conditions in the LIA.



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Keywords: the little ice age; treeline; radial growth; isolated trees; non-isolated trees; climate change; Tibetan Plateau

1. Introduction

On the global scale, the position of altitudinal treelines is determined by growing season temperature which limits the growth and survival of trees [1–3]. Thus, the treeline positions in the Little Ice Age should be lower than that of today. However, in the current treelines on the Tibetan Plateau, we found trees that grew in the Little Ice Age (LIA). Specifically, there were trees as old as 475 years of age in the Basu treeline at an elevation of 4900 m above sea level (a.s.l.) and trees as old as 417 years of age in the Longkazi treeline at an elevation of 4680 m a.s.l. [4]. The phenomenon that current treelines had old trees starting to grow in the LIA also exists in other parts of the world [5–9]. A natural question is: How did the trees establish and survive the cold epoch of the LIA in the position of current treelines?

For the above question, we consider that the old trees in the present treeline position were “isolated tree outposts” growing above the LIA treelines. The isolated trees refer to trees growing apart from each other at an altitude higher than the continuous stands of tree-lines [1,3]. The radial growth of such outpost individuals reflects particular characteristics in adaptation to stresses and disturbances. During the LIA, occasionally beneficial climatic conditions enabled some seeds to spread and colonize above the upper margin of the closed forest [10–12]. Although most seeds and seedlings would die under stressful conditions at the sites above treelines, some seedlings would survive and establish as isolated trees, possibly due to strong growth plasticity to habitat adversity [13–16]. The growth plasticity is an ability in trees to adapt to stresses and disturbances and to recover to a normal state of

growth after environmental perturbations [17–19]. Yet, little is known about such growth plasticity of the isolated trees above treelines.

Having an average elevation greater than 4000 m above sea level, the Tibetan Plateau has received much interest in studies of treeline dynamics. Recent studies have shown that most of the treelines over the eastern Himalaya have reached their thermal treeline positions and will migrate upslope under continued climate warming [20], yet declines in recruitment of shrubs beyond treelines were observed on the Tibetan Plateau [21]. Trees living in a changing climate for hundreds of years adapted to their habitats in a variety of ways. Here we explore the growth plasticity of the isolated trees growing in the Basu treeline and the Langkazi treeline on the Tibetan Plateau. Our previous study of these two treelines investigated the relationships between climate and tree growth using meteorological records in 1978–2014 and demonstrated that the growth of treeline trees was mainly limited by moisture availability in the growing season [4]. Given that the old treeline trees experienced not only the current climate warming but also cold conditions in the LIA, examination of their growth earlier than the period of meteorological observations is of significance for understanding the growth plasticity they might have developed in the course of their growth. To do so, we examine the trend of radial growth in all the sampled trees, compare the annual growth rates of isolated trees in and after the LIA, and investigate the changes in growth synchronicity among isolated trees in the past. Specifically, we attempt to answer three questions: (1) Did the isolated trees reduce their growth rate to cope with the cold conditions in the LIA when the trees were young? (2) Did the isolated trees show different growth patterns in the LIA and after? (3) Did isolated trees keep pace with others in their annual growth to respond to stressful conditions?

2. Materials and Methods

2.1. Study Sites and Tree-Ring Data

Our study sites are located in the Basu treeline (96.75° E, 29.74° N, 4900 m a.s.l.) and the Langkazi treeline (90.58° E, 28.9° N, and 4680 m a.s.l.) of the Tibetan Plateau (Figure 1). The slope of the Basu treeline is west facing, and the slope of the Lankazi treeline is south facing. Both treelines have a slope of about 30 degrees and are characterized by a single tree species of *Juniperus Tibetica*. The distance between the isolated trees was about 3 to greater than 10 m. The altitude of the treeline trees was between 4850 to 4900 m in the Basu treeline and 4630 to 4680 m in the Langkazi treeline. The understory of the treelines is stony and covered by sparse herbaceous plants. The climate of the two sites is dominated by Southwest Asian monsoon [22,23]. According to climate records from meteorological stations nearest to the study sites, mean annual air temperatures in Basu and Langkazi are 4.7 °C and 6.8 °C, respectively, and annual total precipitations are 448 mm and 432 mm, respectively (see Figure 2 of our previous study in literature [4]).

At the treelines, trees with a relatively large diameter in stem were chosen for sampling. Increment cores were extracted from tree stems at a height roughly 30 cm above the ground. No scars or wounds were observed on the stems of the sampling trees. After measuring and cross-dating the increment cores, data of tree-ring widths from 27 trees in the Basu treeline and 21 trees in the Langkazi treeline were obtained [4].

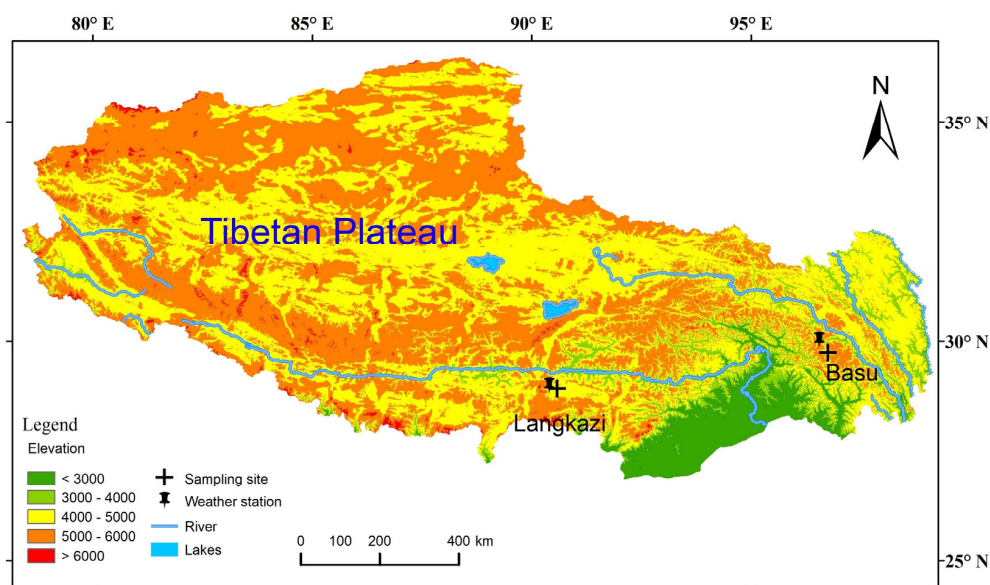


Figure 1. Location of the study sites on the Tibetan Plateau.

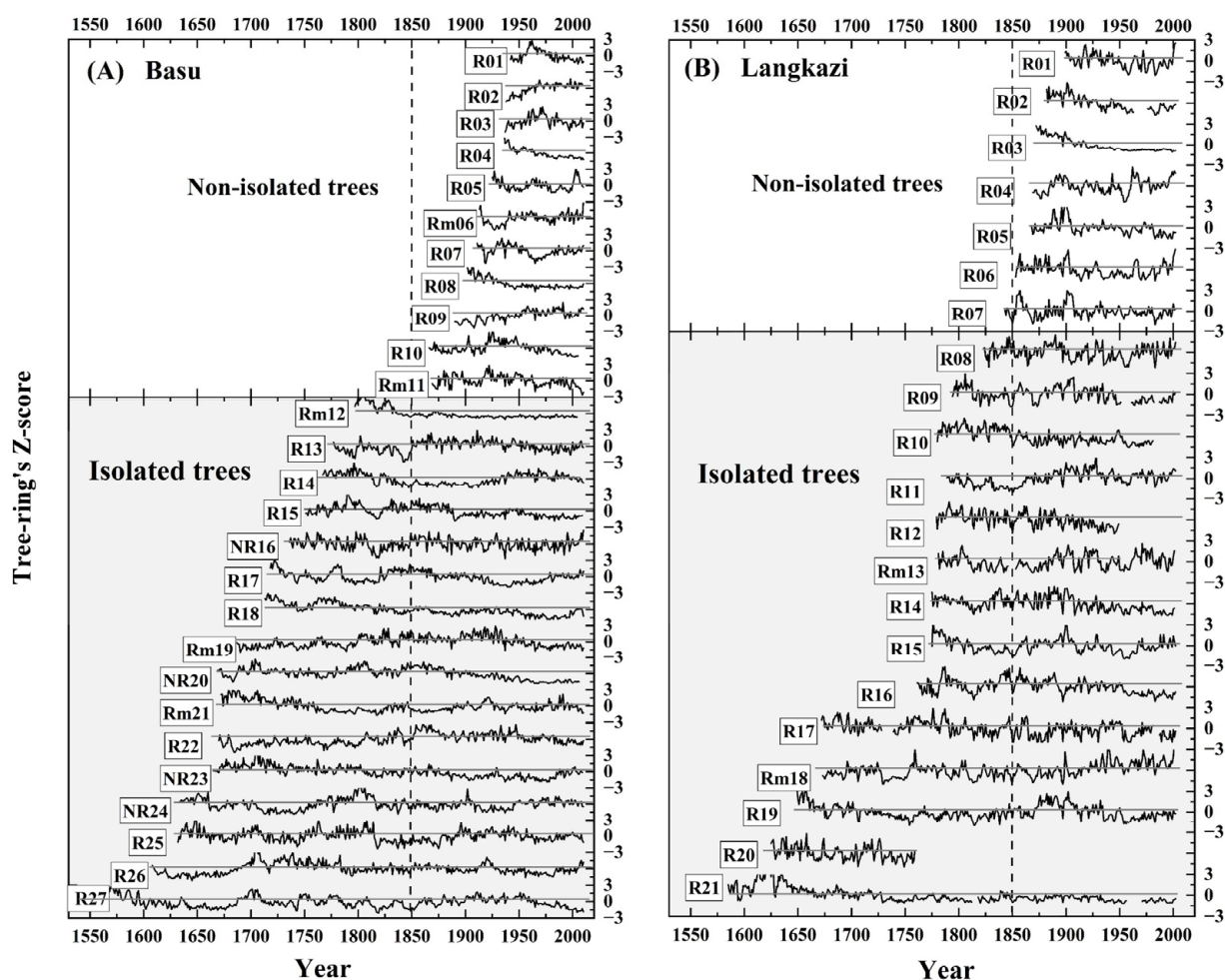


Figure 2. Z-scores of the ring-width sequences of each sampled *Juniperus tibetica* tree in the Basu treeline (A) and the Langkazi treeline (B) in Tibet. “R” refers to samples reaching the stem pith. “Rm” refers to samples that are close to the stem pith. “NR” refers to samples not reaching the stem pith. A horizontal line passing the mean of the series was drawn for each tree-ring sequence.

2.2. Comparison of Radial Growth Rates during the Little Ice Age and after

To compare the temporal pattern of radial growth among individual trees, we transformed the ring-width sequences into Z-score sequences. The Z-scores were obtained by subtracting the mean of ring widths of a sequence from each ring width and dividing the difference by the standard deviation of the sequence [24]. The growth trends, if any, would be retained in the Z-score sequences.

We compared the radial growth of the isolated trees during the Little Ice Age and after by examining the distribution of kernel probability density of the ring-width data from the isolated trees before and after the year 1850, which marked the beginning of the industrial revolution and anthropogenic rise in atmospheric CO₂ concentration [25]. The kernel density estimation is a non-parametric way to identify unknown density distribution about a set of data. The basic idea of this estimation is to construct a histogram with an adequate bandwidth [24]. In our study, the optimal bandwidth was defined using a pointwise estimator [26].

In addition, we compared the growth variations in the isolated trees and non-isolated trees in their common growth periods, which were 1942–2010 for the Basu site and 1900–2002 for the Langkazi site. We calculated the coefficient of variation for each ring-width sequence in the common growth period and compared the distribution of these coefficients of variation in the isolated trees and non-isolated trees using a box-and-whisker plot [27]. The coefficient of variation is a measure of the degree of data dispersion excluding the influence of the mean of data. The difference in the coefficients of variation between the isolated trees and non-isolated trees could be shown by the degree of overlap in the two notch boxes.

2.3. Comparison of Growth Synchronicity among Trees over Time

We investigated the growth synchronicity among isolated trees by examining the Gleichläufigkeitskoeffizient (GLK) index, which is a non-parametric measure of the coherence of year-to-year change in radial growth between two trees [28,29]. The GLK indices in an 11-year sliding window from each pair of the isolated trees were computed and averaged to form a GLK time series for each treeline site using the R package “dplR” [29]. The length of the sliding window determines the feature of signals that are observed. We consider that the 11-year window is an adequate length to examine year-to-year growth synchronicity in relation to habitat changes. A longer length of window would decrease the resolution of observations. In addition, we averaged the ring-width sequences of the isolated trees to obtain a chronology for each treeline to examine whether or not there exists a relationship between the tree-ring chronology and the GLK series.

3. Results

3.1. Age of the Tree-Ring Samples

Examination of the 27 tree-ring samples that were collected in the Basu treeline showed that 23 samples closely reached the stem pith and thus their ages could be estimated with certain confidence. The remaining four samples that did not reach the stem pith were considered as isolated trees because their innermost rings extended earlier than the year 1850. Among the 23 sampled trees that closely reached the stem pith, 12 trees grew earlier than the year 1850 and 11 trees grew after the year 1850. The former 12 trees were considered as isolated trees growing in the LIA, and the latter 11 trees were considered as non-isolated trees. The oldest tree was 474 years of age (Sample No. R27, tree rings between 1537–2010) (Figure 2A).

In the Langkazi treeline, all of the 21 tree-ring samples closely reached the stem pith. Fourteen out of the twenty-one sampled trees grew earlier than the year 1850 and were considered as isolated trees. The remaining seven sampled trees grew after the year 1850 and were considered as non-isolated trees. The oldest tree in the samples was 418 years of age (Sample No. 21, tree rings between 1585–2002) (Figure 2B).

3.2. Radial Growth Rates during the Little Ice Age and after

In the Basu treeline, the ring-width sequences showed a decreasing trend in their juvenile period of tree growth in five isolated trees (Rm12, R16, R17, R21, and R27) and in three non-isolated trees (R04, R05, and R08) (Figure 2A). In the Langkazi treeline, a decreasing growth trend in the juvenile stage was exhibited in five isolated trees (R9, R10, R15, R19, and R21) and two non-isolated trees (R02 and R03) (Figure 2B). Most of the trees did not show an age-related decreasing growth trend.

The statistical distribution of the measured ring widths of the isolated trees showed a similar pattern before and after the year 1850 (Figure 3). The ring widths of isolated trees in the Basu treeline were overall narrower and had a lower proportion of wide rings than those in the Langkazi treeline.

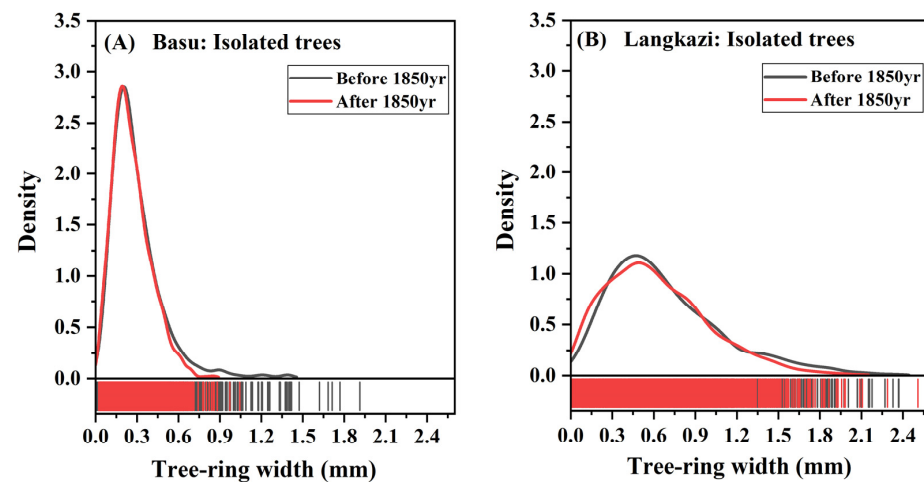


Figure 3. Distribution curve of kernel probability density of the ring-width data from the isolated trees before and after the year 1850 for the Basu treeline (A) and the Langkazi treeline (B) in Tibet.

Coefficients of variation of the ring-width sequences were different for the isolated trees and non-isolated trees during their common growth period, that is, 1942–2010 for the Basu treeline and 1900–2002 for the Langkazi treeline (Figure 4). The coefficients of variation in ring-width data of the isolated trees were greater than those of the non-isolated trees in both treelines.

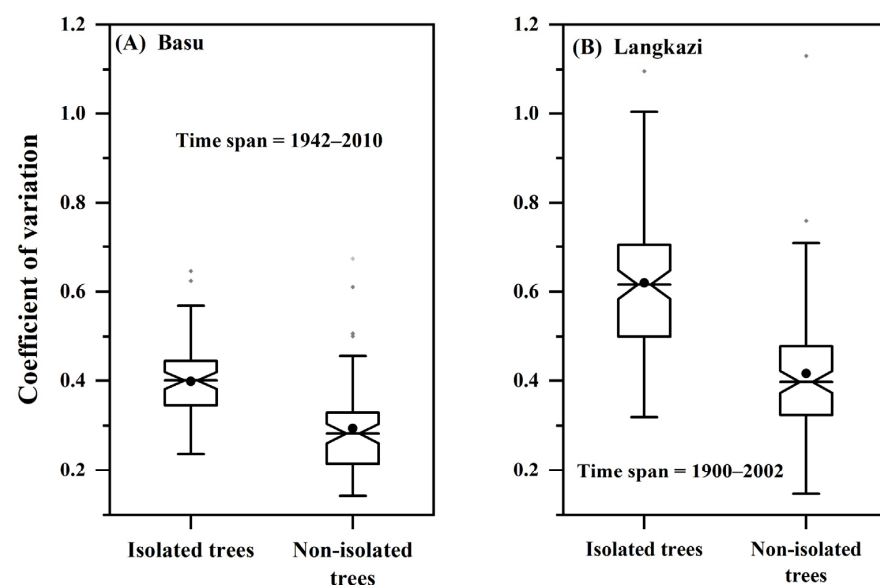


Figure 4. Coefficients of variation of ring-width data for the isolated trees and non-isolated trees in

their common growth period of 1942–2010 for the Basu treeline (A) and 1900–2002 for the Langkazi treeline (B) in Tibet. The position of the notch represents the median value; the upper and lower edges of the box represent the 1st and 3rd quartiles; dots outside of the line represent outliers (beyond 1.5 interquartile range of the box). If two notch boxes do not overlap, this indicates a significant difference between the two medians.

3.3. Growth Synchronicity among Trees over Time

The 11-year sliding window of GLK values for ring widths of the isolated trees showed fluctuation over time in both treelines (Figure 5). The mean GLK values in the Basu treeline was 0.59, whereas that of the Langkazi treeline was 0.66. At the Basu treeline, high synchronicity of tree growth occurred in the 1740s, 1780s, mid-1810s to mid-1820s, 1860s, and 1950s–1960s, and low synchronicity occurred in late 1720s, 1770s, around 1800, early 1840s, early 1870s, late 1930s, early 1970s, and late 1990s. At the Langkazi treeline, high synchronicity of tree growth occurred in early 1810s, early 1840s, 1870s, 1910s–1920s, and 1970s, and low synchronicity occurred in the 1780s to early 1800s, 1830s, around 1900, late 1940s, and early 1960s. The rise and fall of the GLK values did not show a consistent relationship with changes in the mean of ring-width sequences. The patterns of the GLK curves and tree-ring chronologies did not match between the two treelines.

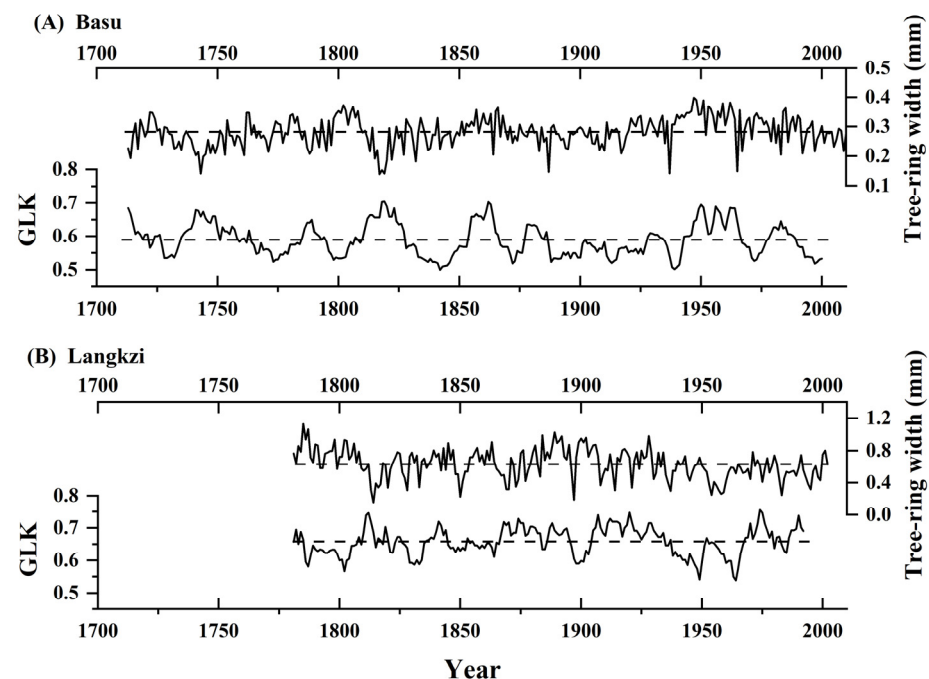


Figure 5. Chronologies of the averaged ring-width sequences of the isolated trees in comparison with the 11-year sliding window of GLK values (placed in the first year of the window) of ring-width sequences of the isolated trees for the Basu treeline (A) and the Langkazi treeline (B) in Tibet. Horizontal broken lines represent the mean for each series.

4. Discussion

4.1. Absence of Age-Related Growth Trends in Treeline Trees

Tree-ring widths are usually wide when trees are young because of the small stem circumference at this stage; when trees grow older, the stem circumference increases and the tree-ring widths decrease, leading to an age-related growth trend in time series of tree-ring widths [30,31]. In this study, however, the age-related growth trends disappeared in most of the trees at both treelines (Figure 2). Independent climatic reconstructions on

the Tibetan Plateau showed that the mean annual air temperature was about 2 °C lower before the mid-19th century than after [22,32]. Although it was reported that tree growth at the two treelines was limited by moisture availability [4], the disappearance of age-related growth trends in trees of different ages suggested that harsh conditions at the treelines might play a role in suppressing the radial growth of trees at their juvenile stage no matter when they established. The growth reduction in young age could also be considered as trees' strategy to trade-off between radial growth and resistance to stressful cold conditions for survival [17,33–36]. In addition, stressful cold environments that cause slow tree growth might also inhibit activities of plant enemies that otherwise would kill more trees [37,38]. It was reported that the poor growth habitats in cliffs harbored old individual trees whose age-related growth trends in the early stage disappeared, indicating resource allocation to survival rather than growth [39–41]. Here we demonstrate that the isolated trees survived the cold conditions by taking advantages of growth plasticity.

The slower rate of tree growth in the Basu treeline than the Langkazi treeline (Figure 3) might be explained by the difference in temperature between the two sites. Meteorological records showed that mean annual air temperature in the Basu area was 2.1 °C colder than that of Langkazi, and total annual precipitation was similar in the two areas [4]. In addition, the Basu treeline was 220 m higher in elevation than the Langkazi treeline, increasing the difference in temperature and probably influencing water use efficiency [42]. The similar distribution of tree-ring widths before and after the 1850s in the isolated trees suggested that the growth of these trees did not receive benefits from the climate warming (Figure 3). On the one hand, the steady and slow growth rates in the isolated trees may be a trade-off between resource allocation to above or below ground biomass for hydraulic safety and growth efficiency [43,44]. On the other hand, moisture supply was found to be a major factor limiting the radial growth of trees at these two treelines [4] and other treelines in the Himalaya [45]; therefore, the isolated trees kept slow growth rates even when the climate became warming.

4.2. Comparison of Tree-Ring Widths in Isolated and Non-Isolated Trees in Their Common Growth Period

The higher growth variability in isolated trees than non-isolated trees suggested that trees experiencing the LIA developed the ability to adjust their growth rate for survival and, consequently, became more sensitive to environmental changes [46,47] (Figure 4). This difference in sensitivity might be related to the number and intensity of disturbances that the isolated trees experienced in the past [6,48–50]. Survival in adversity can be regarded as an intuitive indicator of vitality, thus these isolated trees are symbols of strong vitality and might have played a role in facilitating treeline formation after the LIA at the current position [51].

4.3. Fluctuations in the Growth Synchronicity among Trees

The fluctuation of GLK values suggested that the growth-limiting factors changed their strength through time (Figure 5). When the growth of different trees was strongly limited by a single environmental factor, the tree-ring widths would show the same year-to-year change among different trees; when different factors were in play influencing tree growth, the consistency of tree-ring variation among trees would decrease [29]. We found that values of high GLK corresponded to the low growth rate of trees in some intervals, such as the 1740s, 1780s, and mid-1810s to mid-1820s at the Basu treeline and in the early 1810s at the Langkazi treeline (Figure 5). This observation suggests that environmental stresses might enhance synchronicity in tree growth. However, this pattern was not observed in other periods of time, suggesting that mechanisms regulating the growth synchronicity is much more complicated than the growth-limiting factor [52]. Recent studies of treeline trees showed that climate–growth association might change in different climate backgrounds [53]. The changing climate–growth response also affects the relationships between growth synchronicity and growth rates of trees. In addition,

the pattern of changes in GLK and growth rate of trees was different between the two treelines, suggesting that local factors (such as windstorms and insect infestation) were in play [54,55].

We found that there were small trees growing in the vicinity of the isolated trees. These small trees are likely the offspring of the previously colonized isolated trees since few other potential parent trees grow within a radius of ten meters of the isolated trees. Our previous work reported that treeline trees have a facilitation effect to disperse seeds and to promote the survival and growth of young trees [56]. Therefore, it is particularly urgent to protect the isolated trees to ensure sufficient seed source for the regenerations of these alpine treelines.

In this study, we only studied the growth characteristics in the isolated trees that survived severe stressful conditions and strong disturbances in the past. Tree rings of dead trees were not available, thus limiting our ability to assess the actual position of the highest trees and to test the threshold of resilience to stresses and disturbances. More studies should be conducted to identify the physiological mechanisms of isolated trees to adapt to cold conditions in the LIA and to the future climate warming [57].

5. Conclusions

Our results demonstrated that the isolated trees growing above the two Tibetan Plateau treelines developed the ability to adapt to harsh conditions in the LIA. Such ability includes reducing the growth rate at a young age and taking different growth strategies in different trees to cope with diverse environmental stresses and disturbances. Relative to non-isolated trees growing in the treelines after the LIA, the old and isolated trees kept a slow growth rate and high sensitivity to maintain a high level of resilience to environmental change. These isolated trees might have posed a facilitative effect in the sustainability and dynamics of the treelines after the LIA. Our findings shed light on growth plasticity of the isolated trees growing above treelines. Such knowledge is essential for understanding treeline tree growth in a changing climate and is useful for forest managers to predict treeline dynamics in the future.

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