



# Threshold responses of juniper tree growth and regeneration to climate warming and drought stress at alpine treeline

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Alpine treelines are suitable monitors of ecosystem responses to climate warming (Körner 1998). In general, the alpine treeline position is considered to be largely controlled by temperature (Harsch et al. 2009). Since high-elevation areas have shown a rapid warming rate (Yao et al. 2019), a growth enhancement and upward treeline shifts are expected. However, moisture could mediate the sensitivity of treeline shifts to climate warming in the twenty-first century (Lu et al. 2021) and treeline responses to temperature could be lower than predicted by warming trends (Camarero et al. 2021). Increasing drought stress due to climate warming has caused widespread forest dieback and growth decline (Babst et al. 2019; Brodribb et al. 2020). Global warming may further have profound implications on alpine treelines through a reduction of soil moisture causing a decrease in growth and an increase in mortality rates. For example, tree growth could become less dependent on temperature changes at warmer and drier alpine treelines (Liang et al. 2019; Elliott et al. 2021; Camarero et al. 2021). Such threshold responses are keys for effectively understanding and forecasting alpine treeline dynamics; however, few studies have captured the tipping points or change thresholds in the relationships between temperature and tree growth and regeneration at alpine treelines (Huang et al. 2019a; Du et al. 2020).

Zhang et al. (2021, this issue) focused on a threshold response of juniper tree (*Juniperus przewalskii* Kom.) growth and recruitment to drought stress related to climatic warming at alpine treelines located in the eastern Qilian Mountains, northeastern Tibetan Plateau, a region characterized by continental and dry conditions. They found

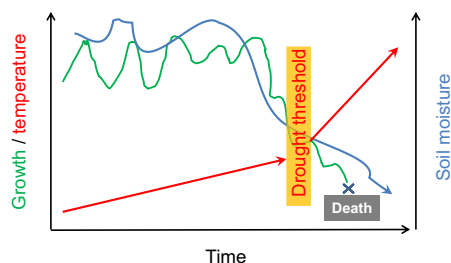
that juniper recruitment increased until the 1940s, and then rapidly declined after the 1970s. Mortality of saplings increased during the period 1959–1999 and reached a peak in 2000–2004 as climate warmed and dried. In addition, the radial growth of adult trees became less responsive to climate warming since 1988. These findings suggest age-dependent vulnerability to climate stress in the alpine treeline and illustrate the performance of tree population dynamics after passing climatic thresholds, providing fundamental knowledge for modeling alpine treeline dynamics.

Increasing mortality risk of tree regeneration may threaten the stability of high-elevation forests and treelines in the study area. First, current drought stress significantly limits juniper and Qinghai spruce (*Picea crassifolia*) growth in this area (Shao et al. 2010; Yang et al. 2014; Zhang et al. 2015). This is translated into higher frequency of missing rings as climate warming induces water shortage at the alpine treeline (Liang et al. 2016). Second, field survey data indicate increasing tree mortality and growth suppression since the 1940s and 1950s, simultaneously with the rapid temperature increase (Liang et al. 2016; Wang et al. 2018). Zhang et al. (2021) illustrated a higher vulnerability of saplings than adult trees in response to drought stress at the alpine treeline. As climate warming proceeds, drought stress may exceed the physiological threshold of sapling survival recruited at the treeline during wetter periods (Fig. 1). It is likely that old trees were more capable of adapting to drying, because their more developed root systems allowed them to access to deeper soil moisture pools. This idea might be tested by analyzing H and O isotopes in soil and xylem water at tree-line (Huang et al. 2019b; Wang et al. 2020). As a result, the higher resilience of old trees may allow them to be less coupled with changes in temperature (Camarero et al. 2021). Forest dieback and growth decline at treeline are concerning phenomena since mountain forest ecosystems provide substantial ecological and climatological benefits to society. Given a rapid climate warming in the future,

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**Fig. 1** Theoretical process of how increasing drought stress associated with climate warming may lead to increasing mortality of saplings and trees at the alpine treeline once a drought lethal threshold is surpassed. The *green line* shows the ring-width series of a dying tree

the low recruitment and high mortality of saplings may lead juniper treelines to local dieback and retraction on the northeastern Tibetan Plateau.

There is increasing interest in the development of tools to predict forest dieback and tree mortality from drought stress (Trugman et al. 2021). A better scientific understanding of the biology needed to develop those tools would allow identifying threshold responses of alpine treelines to climate warming and drought stress as already pointed out on the Tibetan Plateau (Lu et al. 2019). Dendroecology has offered a clear insight into long-term drought effects on growth and recruitment processes (e.g., Camarero et al. 2015; Xu et al. 2017). Tree-ring studies may also be applied to reconstruct and identify climate thresholds affecting treeline dynamics at inter- and intra-annual scales. For instance, it was found that both temperature and precipitation requirements should be met to start spring cambial cell division at dry juniper treelines on the northeastern Tibetan Plateau (Ren et al. 2018). A mismatch between the temperature and soil moisture thresholds for the onset of xylogenesis may increase treeline vulnerability in semi-arid areas under forecasted warmer and drier conditions. Thus, long-term monitoring of xylogenesis may provide a better understanding of the threshold responses of treelines to climatic change. Therefore, an integration of retrospective (dendroecology) and onsite monitoring methods (e.g., xylogenesis, plot surveys) at different temporal scales may further improve our understandings on the tipping points of tree growth and regeneration at the alpine treeline in response to climate. Last but not least, the research by Zhang et al. (2021) also called for a pressing need for sustainable forest management in cold, semi-arid biomes such as the northeastern Tibetan Plateau.

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## Declarations

**Conflict of interest** The authors declare no competing interests.

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