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Commentary

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Imprints of climate stress on tree growth (the past as harbinger of the future): ecological stress memory in Tibetan Plateau juniper forests

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Time and history play fundamental roles on most ecological processes, but only recently have we been aware of the importance of antecedent conditions on shaping current responses of organisms and ecosystems [1]. This so-called ecological memory has been uncovered using ecological time series such as tree-ring data which have allowed us to quantify persistent or carryover effects (legacies) of past stressful events such as droughts [2–4]. For instance, conifers often show higher first-year drought legacies than hardwood tree species [5,6]. Such negative effects of cumulative drought stress determine long-term tree growth trends [7,8].

Therefore, tree growth patterns may contain information on past growing conditions and can be used as measures of ecological memory and proxies of post-drought recovery, i.e. resilience or the capacity to recover pre-drought growth levels [9]. Resilience growth indices have been widely used to assess post-drought responses [6,10]. However, they do not always consider the disturbance impact, the recovery rate and the post-drought climate conditions with respect to reference conditions [11].

Further research is needed to disentangle the ecological memory of trees using tree-ring series to forecast which forests would be more vulnerable to hotter droughts in terms of dieback and mortality [12]. Growth rate may decrease several decades prior to tree death, whereas inter-annual growth variability or year-to-year growth persistence (autocorrelation) may increase, but those signals vary among sites and species [4]. Therefore, more reliable measures of stress memory are needed to anticipate tree death and to measure how trees adjust or acclimate to drought by focusing on their recovery trajectories [13].

By studying a detailed tree-ring network of juniper forests across the Tibetan Plateau, Mu *et al*. [14] investigated the ecological stress memory (hereafter ESM) at annual to decadal scales. They quantified the growth decline and recovery rates during periods of severe growth depression, which occurred after previous stressing climate conditions (cold and dry spells). Mu *et al*. [14] concluded that trees could obtain ESM under antecedent stresses and show improved resistance to subsequent stress through enhanced post-stress recovery. Improved resistance to subsequent stress would be linked to slow recovery trajectories after antecedent stress, i.e. trees with slow post-stress recovery perform better and have higher resistance to subsequent stress than trees with rapid post-stress recovery. Their findings mean that a transitory growth depression after previous stressing events might lead to a long-term gain of ESM. In other words, a transitory growth drop triggered by climate stress might contribute to improve tree structural acclimation and resistance to subsequent environmental stresses on a long timescale [13]. Delayed recovery trajectories and slow recovery rates induced by moderate stress are more likely to provide ESM to trees by activating repair mechanisms and changing plant metabolism, while severe stress could damage tissues and impair tree functioning, reducing ESM. According to Mu *et al*. [14], fast post-recovery

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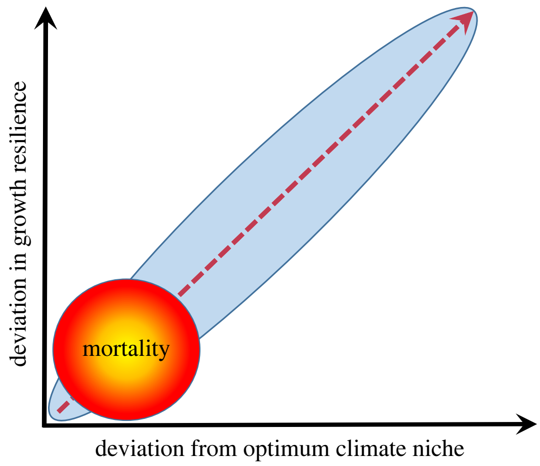

Figure 1. Relationships postulated between deviation from optimum climate conditions and deviation in growth resilience for particular forests or tree species. Mortality hotspots (red-yellow circle), with abnormally high mortality rates, could be observed in sites or periods with stress climate conditions (e.g. droughts) and low growth resilience.

rates might reflect preferential carbon allocation to rebuild damaged xylem tissue at the expense of reduction investment in defence, making trees more susceptible to recurrent stresses. Therefore, Mu *et al*. [14] suggest risk-taking strategies involving fast recovery after stress might lead to impending dieback and tree death, indicating high vulnerability, whereas slow post-stress recovery rates are linked to ESM and portend improved resistance.

As acknowledged by the authors, these ideas should be further tested considering longer series of tree-ring data and more species and bioclimate types. This would allow better framing of the relationships between ESM and post-stress recovery rate. The link between post stress growth depression and climate stress needs elucidating and understanding further by considering droughts of different severity, timing and duration. It is also questionable that adjustments related to ESM can be maintained for long periods since they are costly, so they could be useless if the frequency of severe climate events is low. However, if climate warming leads to more frequent and intense droughts, the ESM might become a relevant adjustment mechanism. An elevated frequency of severe droughts could lead to growth decline, forest dieback and tree death caused by accumulated damage [15]. It could be speculated that forests or trees showing a low growth resilience under harsh climate conditions deviating from the community's or species' optimum climate niche (e.g. dry conditions) could show the highest mortality rate (figure 1). Such mortality hotspots or foci, characterized by abnormally high mortality rates triggered by climate stress, could be mapped or even forecasted using climate and tree growth data [16,17].

Data accessibility. This article has no additional data.

Authors' contributions. J.J.C.: conceptualization, funding acquisition, investigation, methodology, resources, validation, visualization, writing—original draft, writing—review and editing.

Conflict of interest declaration. I declare I have no competing interests.

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