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Reply to: Estimated tree longevity response to climate at risk of methodological bias

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REPLYING TO Salmon et al. *Communications Earth & Environment* https://doi.org/10.1038/s43247-026-03936-8 (2026)

Angove and Salmon[1] suggest that spatial biases in forest management and unquantified pith offsets in tree-ring width series may confound the climate-longevity relationships reported by Gao et al.[2]. We address these two main criticisms in turn below.

The claim that old-growth forests are unlikely to dominate the ITRDB because primary forests account for only 30% of global forest area[1] is conceptually and methodologically flawed. Primary and old-growth forests are not synonymous, making global primary forest area an invalid proxy for ITRDB composition. Furthermore, the ITRDB is not a random ecological survey. Dendrochronologists have historically targeted exceptionally long-lived trees at relatively unmanaged, environmentally limiting sites for climate reconstructions[3,4]. Consequently, the database is intentionally enriched in ancient trees from climate-limited habitats[5,6] rather than serving as an unrepresentative sample of old growth forests. This characteristic is precisely what is required to investigate the climatic drivers of longevity.

Angove and Salmon[1] also raise the issue that many tree-ring series were obtained from living trees. We agree that this is relevant, but its implications should be framed at the site level. We defined longevity as the 99th percentile of the age distribution within each site, not as the complete lifespan of individual trees. Therefore, the presence of living trees does not inherently introduce substantial bias into site-level longevity metrics. Such bias would become problematic primarily if the oldest age classes at a site were systematically truncated by forest management or other extrinsic mortality processes, and if this truncation covaried with climate in a spatially coherent manner.

Angove and Salmon[1] suggest the possible prevalence of managed forests in the ITRDB may artificially shorten tree longevity, thereby confounding the relationship between climate and longevity. We agree that forest management may alter stand age structure[7,8]. Our original analysis partly addressed anthropogenic influence through site screening and the inclusion of the Human Influence Index, which was negatively associated with longevity. We acknowledge, however, that these measures cannot fully resolve the effect of management legacies. Nevertheless, the evidence presented by Angove and Salmon[1] supports a more limited interpretation than the one they propose. In particular, the European analysis does not appear to support a general conclusion that site-level longevity differs consistently among all forest management regimes. The multiple comparisons reported in Fig. 1C[1] indicate that most management classes are not significantly different from one another. This suggests that management may contribute to variation in site-level longevity, but does not demonstrate that management regime is the dominant determinant.

Forest management can affect the persistence of very old trees, and we agree that management history may covary with climate, productivity, accessibility, and land-use history. However, we respectfully disagree that the greater longevity of trees in arid environments can be primarily attributed to lower human impact associated with limited forestry potential[1]. Low productivity does not necessarily imply low anthropogenic disturbance, as dryland forests are widely affected by grazing, fire, fuelwood harvesting, cultivation, and land degradation[9,10]. Moreover, the evidence presented by Angove and Salmon[1] does not demonstrate that management history is sufficient to replace the bioclimatic interpretation, particularly because growth rates and maximum longevity remain strongly conditioned by bioclimate[11]. We therefore regard management history as an important but unquantified source of variation that may complement, rather than invalidate, the observed association between aridity and greater tree longevity.

Angove and Salmon[1] point out that unquantified pith offsets can introduce uncertainty, particularly in our analysis of juvenile growth rates.

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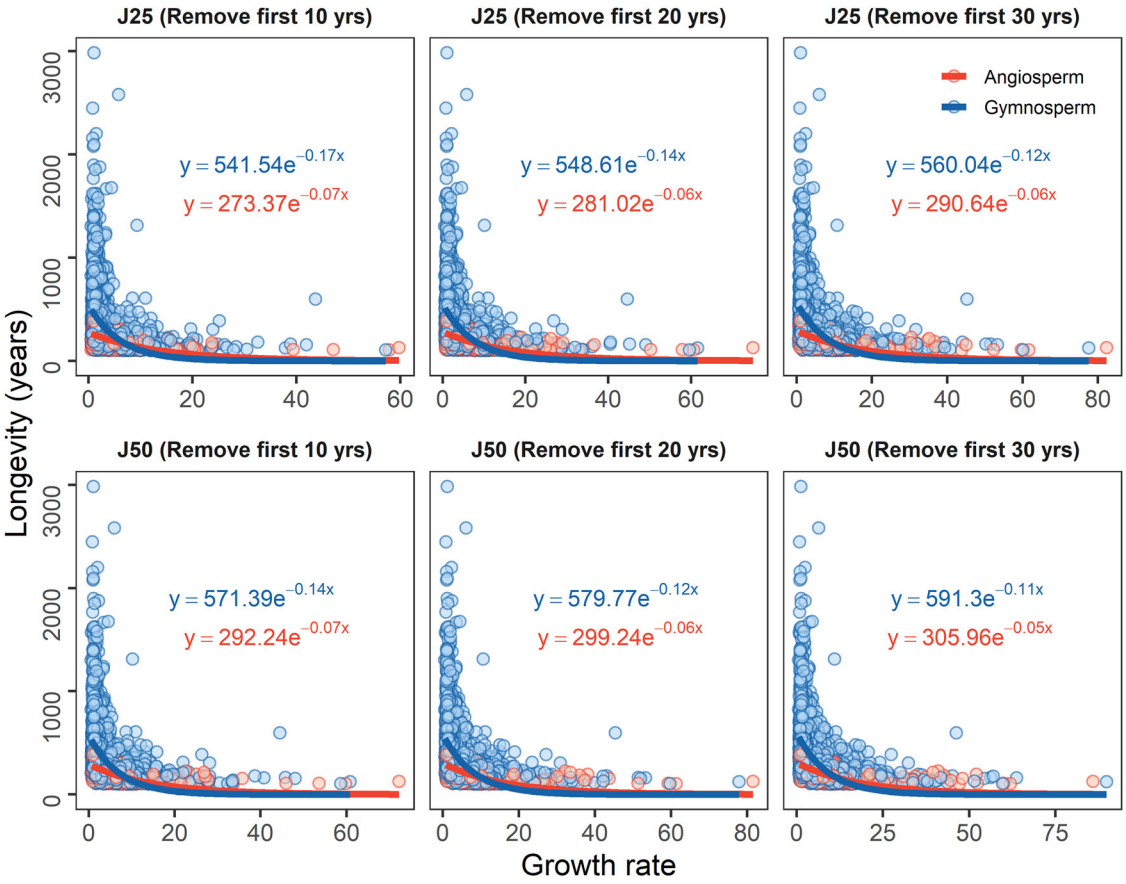

Fig. 1 | Effects of artificial early-ring truncation on the relationships between juvenile growth and longevity. J25 juvenile 25-year, J50 juvenile 50-year. Curves represent fitted negative exponential regressions.

We agree that pith offset can affect estimates of juvenile growth. While missing pith and hollow trunks undoubtedly lead to age underestimation, as already noted in our original paper, we remain cautious about the quantitative reconstruction of pith offset proposed by Angove and Salmon[1]. Their estimates rely on model-based extrapolation rather than direct measurements of the distance to the pith and may be particularly uncertain for long-lived trees, in which prolonged juvenile suppression is common and unlikely to be reconstructed reliably using simple exponential or linear models.

To quantify the potential effect of missing early rings, we performed an artificial left-truncation sensitivity analysis by removing the first 10, 20 and 30 years from each detrended tree-ring width series and refitting the negative exponential regressions between growth rate and longevity. In all truncation scenarios, the slope parameter b remained negative (Fig. 1). In gymnosperms, b changed from −0.17 to −0.14 and −0.12 for the juvenile 25-year growth rate, and from −0.14 to −0.12 and −0.11 for the juvenile 50-year growth rate. In angiosperms, the reduction was smaller, with b changing only from −0.07 to −0.06 and from −0.07 to −0.05 for the juvenile 25-year and 50-year growth rate. Thus, the simulated loss of early rings slightly weakened the fitted relationship but did not reverse or eliminate it.

This interpretation is consistent with a previous study[12], which reported a stronger juvenile growth-lifespan trade-off in the more rigorously screened NFI-Quebec dataset than in the corresponding ITRDB subset of the same species (mean $b = -0.25$ versus −0.10; paired $t = 2.49$, $p = 0.047$, $n = 7$ species). This comparison suggests that pith offset in ITRDB data is more likely to lead to an underestimation of the relationship than to generate it artificially. We therefore conclude that pith offset may reduce the estimated magnitude of juvenile growth-longevity trade-offs, but it does not invalidate the negative association itself. Instead, it is more likely to make our estimates conservative.

The trade-off between slow growth across life stages and increased longevity is a widely recognized ecological principle, consistently documented in dendrochronological studies[13–16]. Our main finding of a negative association between growth rates and longevity is not solely dependent on the juvenile growth rate at 25 or 50 years. Crucially, our analysis demonstrated a strong negative exponential relationship between the mean growth rate over the entire lifespan and tree longevity. The mean growth rate is a statistic that is far more robust to pith offset errors than juvenile growth. Even if the true first year of growth is shifted by decades, the average tree-ring width across centuries or even millennia remains a reliable indicator of the tree's overall metabolic pace.

In conclusion, although the ITRDB is not perfect, it remains a uniquely valuable archive for examining broad-scale patterns of tree growth and longevity. The issues raised by Angove and Salmon[1], including forest management history, incomplete metadata, and pith-offset uncertainty, may affect estimates of longevity and juvenile growth and should be treated as meaningful sources of uncertainty. We therefore support improved reporting standards and cautious data use. Nevertheless, these uncertainties do not invalidate the use of the ITRDB for testing global ecological hypotheses. Our sensitivity analyses indicate that simulated loss of early rings weakens but does not eliminate the negative growth–longevity relationship, suggesting a bias toward conservative estimates rather than the artificial generation of this relationship. Our results should be interpreted as robust broad-scale associations among aridity, slower growth, and greater observed site-level longevity.

Data availability

The raw tree-ring width data are accessible on the International Tree-Ring Data Bank (https://www.ncei.noaa.gov/products/paleoclimatology/tree-ring).

Code availability

The codes used in this study have been deposited in Figshare and are accessible at https://doi.org/10.6084/m9.figshare.29436140.

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Author contributions

J.G. and K.F. designed the study; J.G. performed the data analyses, produced the figures, and led the writing. J.G., K.F., J.M.C., J.L., S.R., D.C., H.W.L., J.J.C., J. E., N.K.D., T.F.A. and Z.G. contributed to the interpretation of the results and the writing of the paper.

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Competing interests

The authors declare no competing interests.

Additional information

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