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Commentary

Forests of the future: the importance of tree seedling research in understanding forest response to anthropogenic climate change

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This scientific commentary refers to “Ability of seedlings to survive heat and drought portends future demographic challenges for five southwestern US conifers” by Crockett & Hurteau (https://doi.org/10.1093/treephys/tpad136).

What will future forests look like and what properties will they have? This question is, in some sense, a simple one; future forest composition and structure will be shaped by the seedlings and saplings currently inhabiting the forest floor. Part of future forest composition will come from old trees that manage to outlive their peers, but, at some point, new trees will grow into and replace the current canopy. Adult trees are important to forest succession because they determine seed input and understory microenvironmental conditions, but seedling and sapling recruitment dynamics are what will determine the ecosystem processes and ecosystem services of tomorrow.

Climate change is projected to have many (primarily negative) impacts on both how forests are structured and the ecosystem services they provide. While many mainstream news headlines focus on how climate change is affecting and will continue to affect mature canopy trees, it is equally important to understand how climate change will impact tree recruitment—the process by which seeds germinate into seedlings, seedlings grow into saplings and, if all goes well, saplings mature into canopy trees. Because trees are not immortal (although see discussion in Piovesan and Biondi 2021), it is important that we not only understand how and why adult trees die, but also that we understand the drivers of tree recruitment that will shape the next generation of canopy trees (Ibáñez et al. 2017) and the services they provide as a cohesive ecosystem.

This is particularly dire within the context of climate change because younger age classes are the most vulnerable to climate change (Niinemets 2010) and also the most likely to experience nonrandom mortality (Green et al. 2014). That is, while adult trees can rely on deep rooting structures and carbon reserves to withstand climate change-related stress (Niinemets 2010), seedlings and saplings are more likely to die when faced with adverse conditions. And just like adult trees, seedlings of different species have been shown to have different resilience and resistance to climate change-related stress (Lee and Ibáñez 2021*a*, 2021*b*). If some species are prevented from recruiting into the canopy, the structure and composition of future forests may be substantially different from what they are today.

It is with this in mind that Crockett and Hurteau (2024) designed their recent study published in *Tree Physiology*. The authors investigated how short-term drought and extreme heat events affect seedling survival for five conifer species native to the southwest USA. Species ranged from xeric species (i.e. those that inhabit drier, lower-elevation regions; *Pinus edulis* and *Pinus ponderosa*), to more mesic species (*Pseudotsuga menziesii*, *Picea engelmannii* and *Abies concolor*) that inhabit cooler, moister and higher-elevation areas. The authors tested the ability of seedlings of each species to survive different combinations of drought and heat and then used climate change projections to forecast changes to seedling survival across their ranges.

The authors' results are in line with their hypotheses and with previous literature. The xeric species that already inhabit warmer, drier regions of the US southwest were able to tolerate hotter and drier conditions better than the three mesic species. This is consistent with previous research showing that warm-adapted species (Teskey et al. 2015) as well as warm-adapted populations of the same species (Marias et al. 2016) have traits better suited to withstand drought and bounce back from extreme drought events. Note that this is not necessarily the case for trees accustomed to warm and wet conditions, which were recently projected to be the most negatively affected by climate change-related drought events (Heilmayr et al. 2023). Alone, these findings would suggest that tree species

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in warmer and drier regions will be better able to withstand future climate change-related disturbances in the American southwest.

However, Crockett and Hurteau's findings generated novel insights by accounting for differences in future climate change exposure. Using climate change projections for the end of the current century (2080–2099) in combination with parameters from their seedling survival experiments, the authors found that mesic species were likely to maintain their current performance better than the xeric species. This was generally because the cooler, wetter regions these species inhabit will experience less overall change in temperature and water availability. That is, although mesic species are more vulnerable to drought compared with xeric species, they also currently inhabit regions that are predicted to experience relatively less negative environmental change over the coming decades. It is important to note that the asynchrony of vulnerable species and vulnerable regions is not likely to be the same across all ecosystems or across broad latitudinal gradients (Boisvert-Marsh et al. 2019), and there are systems other than the desert southwest to which Crockett and Hurteau's results may not apply. For example, boreal systems are comprised of several tree species that are vulnerable to climate change and are expected to experience large shifts in abiotic conditions in the near future (Price et al. 2013). Thus, future work should focus on understanding the generalizability (or lack thereof) of Crockett and Hurteau's work before extrapolating to other systems.

The distinction between species that are vulnerable to climate change stress and regions that will experience stronger or weaker changes in environmental conditions is an important one with respect to species conservation questions. In part, it highlights the need to consider prioritizing the conservation of landscapes in addition to the conservation of individual species or communities, a sentiment echoed by recent work arguing for the preservation of geodiversity as a means of preserving biodiversity (Schrodt et al. 2019; Read et al. 2020). The distinction also serves to better contextualize remaining questions about how to best manage our forests in preparation for ongoing climate change. Should land managers and conservation practitioners prioritize limited resources to the conservation of xeric forests that are closer to the edge of habitable conditions or to the mesic forests that will likely avoid the brunt of climate change stress until the tail end of this century? In which parts of the American southwest will we see the largest limitation to seedling recruitment and in which parts will we continue to see successful recruitment in remnant populations? At what point, if any, will recruitment limitations become the overriding limitation to stability and persistence of southwestern forests (as opposed to patterns of adult tree die-off)?

Negative climate change effects in these forests are also likely to differently affect human populations. For example, indigenous peoples in the American southwest that disproportionately rely on ecosystem services provided by these forests may also be proportionally more vulnerable to disruptions due to climate change and could be at high risk for climate change-related stress (Voggesser et al. 2013; Magargal et al. 2023). How do we make decisions that simultaneously protect the health of nature as well as the health of people?

An important facet of this paper is the controlled, experimental nature of the authors' work. Tree seedlings were grown in individual cones and potting mix in incubators, providing an excellent understanding of physiological limits. However, the flip side of using growth chambers is the loss of countless confounding variables that tree seedlings experience in the natural environment. These include edaphic qualities like nutrient availability, soil texture and soil microbial communities (including symbionts and pathogens), as well as biotic interactions with surrounding plants (Schaffer-Morrison and Zak 2023). Prior work comparing incubator and greenhouse experiments to observational studies has shown a mix of similar trends and marked differences in results (Wolkovich et al. 2012; Kambach et al. 2019). For this reason, it is important that future work on seedling response to climate change includes field-based observational studies in addition to controlled greenhouse and/or incubator experiments to contextualize findings.

Importantly, Crockett and Hurteau's work leaves unanswered questions related to seedling performance in field settings. Microenvironmental conditions experienced by juvenile trees in forests will be affected by environmental heterogeneity and altered by biotic interactions with surrounding organisms. For example, Dobrowski et al. (2015) found that canopy trees can ameliorate some negative climate change impacts on tree seedling performance. Transplanting seedlings into different tree communities or areas within a community that have different average environmental conditions could be an important next step in experimentally assessing how these dynamics shape tree recruitment.

Another important unanswered question is whether and how variation in tree seedling performance will translate to canopy tree recruitment and to community-level stability. Seedling survival is only one component of tree recruitment, and previous research indicates that processes like seed production, germination success and intermediate sapling recruitment success will be just as important to determining what future forests look like (Ibáñez et al. 2017). Therefore, while mesic species seedling survival may not be at immediate risk from climate change, persistence in their current range may still be negatively affected in the short term by reductions in seed production and seedling germination. Seedlings cannot survive if they do not recruit into the forest floor in the first place.

Despite these limitations, the work presented here by Crockett and Hurteau represents an important step toward gaining a better understanding of what future forests in the American southwest will look like. Because tree seedlings represent the future of a forest, information from their study will help land managers and conservation practitioners make decisions about how best to manage their forests in the face of climate change. Future work should keep in mind lessons from Crockett and Hurteau's study—that climate change results are dependent not only on species-level performance but also on system-level susceptibility to climate change—while continuing to explore how other biotic and abiotic processes shape the forests of tomorrow.

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Data availability

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