AMPLIFYING RESILIENCE TO DROUGHT IN THE LAKE TAHOE BASIN

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Land managers are at a critical moment in how to best manage resources for adaptation and uncertainty. In particular, the selection of seed and source material, either local or non-local, for restoration, has become a fundamental and much-debated decision for resource and land managers. Given the scale of ecosystem disturbance and wildland loss, there is an urgent need to procure native seed across taxonomic groups, to secure the diversity and local adaptation in wild populations. This article will discuss how reforestation strategies using the progeny of local and diverse sugar pine "survivors" can promote forest resiliency to changing climatic conditions.

NATURAL SELECTION PLAYING OUT OVER CONTEMPORARY TIMESCALES

Five years of drought and bark beetle outbreaks from 2012-16 killed more than 126 million trees in California and 72,000 in the Lake Tahoe Basin. This drought resulted in significant mountain pine beetle–mediated mortality in sugar pine (*Pinus lambertiana*) populations on the north shore of the basin. Despite high levels of sugar pine mortality, numerous sugar pine trees survived.

Natural selection is the process through which the environment and genetics determine which individuals survive better than others. Present-day sugar pine

Sugar pine mortality on a south-facing slope in Tahoe Vista, CA.
Photograph by California Department of Forestry and Fire Protection

Mountain pine beetle trapped in a pitch tube.
Photograph by Patricia Maloney

trees face intense selection pressures including severe drought, climate-driven outbreaks of bark beetles, and infection by an invasive forest pathogen.

Bark beetles such as the mountain pine beetle preferentially attack drought-stressed trees. Mountain pine beetles in particular have been a significant cause of tree mortality, both historically (Evenden, 1944; Perkins and Swetnam, 1996; Taylor et al., 2006; and Brunelle et al., 2008) and currently, with the severity of outbreaks reaching unprecedented levels in recent years (Paz-Kagan et al. 2017, Fettig et al. 2019). Mountain pine beetle hosts such as sugar pine have evolved both physical and chemical defense strategies. Host defense chemistry represents the primary chemical defense mechanism against bark beetle attack, but can also attract beetles to host trees and signal a tree's vulnerability (Seybold et al., 2000; Raffa et al., 2005; Seybold et al., 2006; and Kelsey et al., 2014).

In 2016, we compared 100 sugar pines that had survived the 2012–16 drought with 100 sugar pine trees that had succumbed to bark beetle attack. We retrospectively analyzed the trees' water-use efficiency over the last 90 years, and found that the sugar pine trees that were more water efficient, and thus better adapted to drought, had survived the mountain pine beetle outbreak in the Lake Tahoe Basin. In contrast, sugar pines killed by mountain pine beetles had used water less efficiently and were most susceptible to beetle attack.

Such selective events are playing out over contemporary (e.g., present-day) timescales (Hendry 2017) and include wildfires, insect outbreaks, invasion by plants and pests, and severe and prolonged droughts like the 2012–16 drought described above. Many of these selective events yield survivors across taxonomic groups and within individual species. Webster et al. (2017) argue that land managers need to take a "more comprehensive" view of species adaptation and ecological reorganization, which includes how species acclimate and evolve in response to environmental change through natural selection.

Lacking this broader perspective, researchers have focused too much attention and funding on predicting range shifts and prescribing "assisted migration," a conservation management tool and a strategy fraught with risky unknowns, and the likelihood of negative consequences. These species distribution models (SDMs) often forecast the loss of suitable bioclimatic habitats and major range shifts (Wiens et al., 2009), yet have significant uncertainties and limitations including the assumptions associated with them (Javeline et al. 2015, Webster et al. 2017, Breed et al. 2018, Bradley et al. 2020). Importantly, these models lack eco-evolutionary mechanisms and data on species demographics, dispersal, genetic variation, and heritability of traits, and fine-scale topoclimatic features that could influence survival.

The flora and fauna of California have been experiencing fluctuations in climate, species interactions, and disturbance events for millennia; some of these fluctuations are becoming far greater and more extensive, but species are likely still evolving and adapting to current selective pressures, and hence natural "survivors" emerge.

LOCAL AND GENETICALLY DIVERSE SEED SOURCES FOR RESTORATION

Common garden studies are used to evaluate important plant traits (e.g., phenology, water-use efficiency, resource allocation, defense chemistry, disease

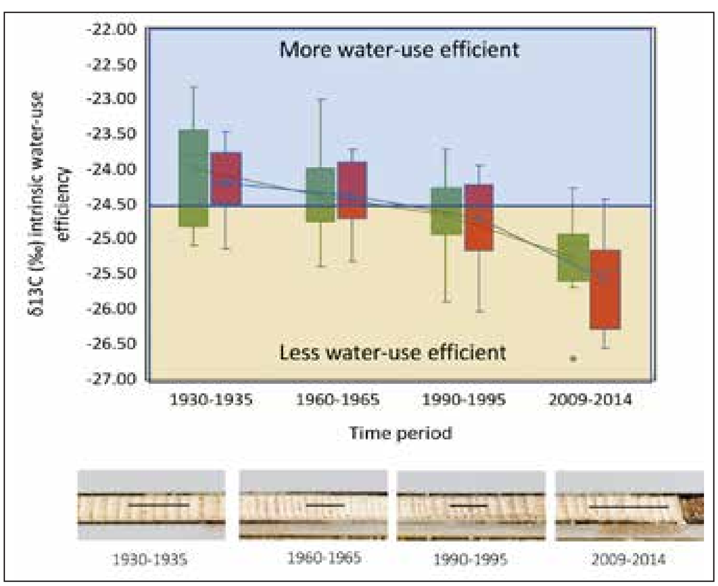
Sugar pine seedlings at the UC Davis Tahoe City Field Station.
Photograph by Kat Kerlin, UC Davis

resistance, etc.) to estimate quantitative genetic parameters, including heritability and population differentiation, which allows one to assess the ability of "local" populations to respond to selection pressures. Our lab, in collaboration with others, found that in sugar pines, ecologically relevant traits such as water use are correlated not only with climate, but with soil and geography. Such correlations are one type of evidence for local adaptation.

Common garden studies linked with comprehensive environmental databases can provide a perspective on evolutionary potential that can better inform gene conservation activities such as seed collection, seed-banking, and restoration. In 2017, for example, we collected seed from 100 local and diverse drought "survivors" from the Lake Tahoe Basin to use in reforestation. We used the information from Maloney et al. (submitted) to guide restoration strategies for sugar pine reforestation for mountain pine beetle outbreak recovery and to facilitate regeneration in high mountain pine beetle-impacted areas in the Lake Tahoe Basin.

Moving forward, our lab will be studying important plant traits of the 100 surviving "mother trees" of sugar pine from the Lake Tahoe Basin. We want to determine, through a common garden study, if these "survivors" carry genes and hence plant traits (e.g., water-use efficiency, plant defense chemistry to bark beetles, phenology, and resource partitioning) that will allow them to be more resilient to future drought and bark beetle outbreaks. To address the drought–bark beetle interaction, we will conduct a drought stress experiment in which a control group will receive regular water and other trees will receive no water to mimic drought. We will evaluate water-use efficiency and plant defense chemistry at the start and end of the experiment. Pre- and post-analyses will allow us to identify mechanisms underlying the trees' varied responses to drought and bark beetle pressure—an important interaction that remains largely unexplored.

Our current data suggests that resource managers need to take a more spatially nuanced view of gene conservation activities such as seed collection strategies, reforestation, and seed-banking, as we have done, within the Lake Tahoe Basin. This may also apply to other regions of California, and help to guide the development of new seed source selection strategies for land managers.



Box and whisker plots of intrinsic water use efficiency from 1930-35, 1960-65, 1990-95, and 2009-2014 from live (green) and mountain pine beetle-killed (red) sugar pine trees in the Lake Tahoe Basin.

Map of collection sites for sugar pines around the Lake Tahoe Basin.
Credits: Patricia Maloney

CONCLUSIONS

Our ecological and genetic studies with sugar pine and other five-needled white pines provide valuable information regarding seed source material for restoration and reforestation. Thus far, the work provides strong evidence that using local and diverse seed sources can promote forest resiliency and provide a form of "insurance" against climate change. California is a biodiversity hotspot, and given the scale and extent of threats to native plant populations, there is an urgent need to procure native genetic material across taxonomic groups to secure the diversity and local adaptation in wild populations. We are at a tipping point, facing an unprecedented loss of California wildlands and all the associated ecosystem services they provide. Collections from extant plant populations and individuals that have proved to be resilient to anthropogenic and natural stressors should be prioritized for seed collection. Novel restoration strategies guided by a better understanding of how native plants evolve in response to selective pressures such as drought and pest outbreaks hold the potential to increase not only the pace and scale of ecosystem restoration, but to amplify population resiliency to contemporary pressures and stressors.

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