Forest Density and the Future of Sierra Nevada Legacy Pines

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Large, fire-adapted pines in the Sierra Nevada face compounding threats from competition, drought, bark beetles, and high-severity wildfire, all of which are worsened by the dense, shade-tolerant stands that have developed under a century of fire exclusion. Research shows that reducing stand density improves the water availability, defensive capacity, growth, and fire survivability of retained legacy trees (large, old, fire-adapted pines that have survived prior disturbance regimes and disproportionately support biodiversity and forest resilience). This review briefly summarizes that evidence and places it in the context of the North Yuba Landscape Resilience Project.

Over the last century, fire exclusion and the logging of large pines have transformed Sierra Nevada forests. Multiple studies comparing historical forest inventories to current conditions have found that forests in the Sierra Nevada are now roughly two to four times denser than they were historically (Scholl & Taylor 2010; Collins et al. 2011; Knapp et al. 2013; Stephens et al. 2015). Much of this increase is in shade-tolerant, fire-intolerant species, especially white fir, Douglas-fir, and incense cedar, which historically were kept in check by frequent, low-intensity fire. Today's forests have much higher tree densities, a shift in species dominance from pine to fir, lower density of large trees, and higher canopy cover (Stephens et al. 2015). In the North Yuba watershed specifically, true fir types more than doubled in extent across the broader Sierra between 1945 and 1993, from roughly 842,000 to 2,197,000 acres. Beardsley (1999) attributed this 2.6-fold increase to fire exclusion and the loss of pines. At the same time, the largest trees have been disproportionately lost. Across California, large trees (≥ 61 cm dbh; ≥ 24 inches dbh) have declined substantially since the 1930s. In the Sierra Nevada highlands specifically, large tree density dropped by roughly 50%, from 64.3 to 28.0 trees per hectare (McIntyre et al. 2015).The upper Yuba River watershed specifically shows a deficit of late-development (i.e., large tree) forest across all major cover types relative to historical range of variability (McGarigal et al. 2018; USDA Forest Service 2023). The forest now has too many small trees and too few large ones.

Wildfire Severity

Dense stands of shade-tolerant trees create continuous fuel ladders from the forest floor to the canopy. When wildfire arrives, these conditions can turn what would historically have been a low-intensity surface fire into crown fire capable of killing large, fire-adapted trees. A recent meta-analysis of 40 fuel treatment studies across western U.S. conifer forests found overwhelming evidence that combining thinning with prescribed fire or pile burning reduced subsequent wildfire severity by 62-72% on average (Davis et al. 2024).

The 2020 Creek Fire in the southern Sierra Nevada illustrated what happens without intervention. The largest factors driving extreme fire behavior were dead biomass from the

2012-2016 drought and high live tree densities from fire exclusion, while weather during the fire's greatest growth was largely within normal ranges (Stephens et al. 2022).

Competition for Water

In dense stands, trees compete for water from a shared, finite soil moisture pool. During drought, chronic water stress can directly impair tree physiology and weaken defenses against secondary mortality agents (Kolb et al. 2007; Fettig et al. 2019). Using thousands of repeatedly measured Forest Inventory and Analysis plots across the western U.S., Bradford et al. (2022) modeled that a 50% reduction in stand basal area (the cross-sectional area of all tree trunks measured at breast height – a standard measure of stand crowding) could reduce drought-driven ponderosa pine mortality by 20-80%. Basal area also interacts with temperature and soil moisture, such that competition multiplies drought stress. The effect is strongest in the densest stands and during the hottest droughts (Bradford & Bell 2017; Bradford et al. 2022). Climate models project that high-temperature extremes will increase across the western U.S. through the 21st century, making these "hotter droughts" more frequent and more severe (Allen et al. 2015). Currently, density reduction is one of the few management tools available to buffer forests against this trend.

Young et al. (2023) tested this directly in the Sierra Nevada, comparing paired treated and untreated stands across a precipitation gradient through the 2012-2016 drought. On wetter sites (those receiving more than 1100 mm of normal annual precipitation), ponderosa pine in untreated stands lost more than 15% of expected growth during the drought, while trees in adjacent treated stands held at or near their long-term trend. The growth benefit was weaker on the driest sites and in the largest trees (>65 cm dbh), though density reduction still reduced mortality across the full gradient. Much of the North Yuba watershed falls within the wetter end of that gradient.

Bark Beetle Vulnerability

Bark beetles are the proximal killer of most large pines during drought. Dense stands worsen the problem in two ways. Trees weakened by competition produce less defensive resin, and closely spaced host trees allow beetle populations to build and spread to outbreak levels. The 2012-2016 California drought killed an estimated 129 million trees (Restaino et al. 2019). Mortality continued past the formal drought period, and by 2018, the USFS aerial detection surveys had recorded over 147 million dead trees in the Sierra Nevada since 2010 (Axelson et al. 2019). Detailed plot surveys across four central and southern Sierra Nevada national forests found that nearly half of all trees died during the peak of the drought (2014-2017), with ponderosa pine suffering the heaviest losses. About 89% of the largest ponderosa pines were killed, primarily by western pine beetle, and tree mortality was positively correlated with stand density (Fettig et al. 2019). This vulnerability is concentrated in large trees. Across the Sierra Nevada, Stovall et al. (2019) found that large trees died at twice the rate of small trees during this drought, with tree height being the single strongest predictor of mortality. Drone-based surveys of over 450,000 trees across the same region revealed an acute interaction between tree size and climate, with larger ponderosa pines amplifying mortality rates at hotter, drier sites but not at cooler, wetter ones (Koontz et al. 2021). Across six Sierra Nevada national forests, Restaino et al. (2019) found that ponderosa pine mortality was significantly lower in previously thinned stands. Pine mortality was also positively related to the density of nearby medium-to-large pine trees, especially in drier areas, suggesting that the abundance of neighboring host trees was an important driver of beetle attack success.

Direct physiological evidence comes from long-term experiments at the Gus Pearson Natural Area in Arizona, where thinning and burning around pre-settlement-age ponderosa pines increased resin flow by more than threefold, increased soil water content, and improved growth compared with untreated controls (Feeney et al. 1998). A seven-year follow-up found that most beneficial effects on physiology and growth persisted (Wallin et al. 2004; reviewed in Kolb et al. 2007). Resin flow is a direct measure of a tree's capacity to defend against bark beetle attack. These findings suggest that even centuries-old trees can mount stronger defenses when competition is reduced.

Accelerated Background Mortality

Even in the absence of drought or wildfire, high stand density accelerates the death of large trees. At the Teakettle Experimental Forest in the southern Sierra Nevada, researchers mapped over 30,000 trees and found that mortality was significantly higher than expected for large-diameter trees (>100 cm dbh) across most major conifer species (Jeffrey pine excepted), and that overall mortality was higher in areas of high stand density and lower in areas of low stand density (Smith et al. 2005). Across 76 long-term monitoring plots in old-growth forests throughout the western U.S., van Mantgem et al. (2009) found that background tree mortality rates have been increasing rapidly, with doubling periods of 17 to 29 years depending on region. The increases were pervasive across elevations, tree sizes, and genera, and were likely driven by regional warming and increasing water deficits. Large trees in dense, fire-suppressed stands face compounding threats from competition, warming climate, insects, and pathogens, even without an acute drought or fire event.

The same pattern shows up beyond the Sierra Nevada. Lindenmayer et al. (2012) documented a global decline in large old trees, noting that in Yosemite National Park, the density of the largest trees declined by 24% between the 1930s and 1990s (citing Lutz et al. 2009). These declines were associated with increasing climatic water deficit, a trend that density reduction can help mitigate by reducing competition for limited soil moisture (Bradford et al. 2022). Where large trees do persist, fire suppression has allowed extensive ingrowth that increases competitive pressure and makes them more susceptible to severe fire, drought, and insects (Collins et al. 2011; Knapp et al. 2013; North et al. 2022).

Management Implications

The research supports targeted, stand-level density reduction rather than broad-scale logging. Treatments focus on removing specific shade-tolerant trees (primarily large white fir, Douglas-fir, and incense cedar) that compete directly with legacy fire-adapted pines. Stand-level thinning, not just localized cutting around individual trees, can meaningfully improve growth and survival of old pines (Hood et al. 2018).

The evidence that legacy trees respond positively to density reduction is strong. Kolb et al. (2007) found that thinning of neighboring trees increases water and carbon uptake of old ponderosa pines within one year, with radial growth increases persisting for up to two decades. Hood et al. (2018) documented that growth of legacy ponderosa and Jeffrey pines in northeastern California increased immediately after stand-level thinning and was sustained for 15 years, with soil moisture remaining elevated for five years post-treatment. Even old trees that have experienced decades of competitive stress can respond, though the response tends to be slower and less dramatic in the largest, oldest individuals than in younger trees (Kolb et al. 2007; Zald et al. 2022).

Our research in the North Yuba watershed found that all common diameter limit scenarios imposed on thinning operations produce similar improvements in stand density, but they differ substantially in species composition. The current 30-inch diameter limit retains all large shade-tolerant conifers, leaving stands still dominated by shade-tolerant species (primarily white fir) in basal area. When the diameter limit is raised to 40 inches for shade-tolerant species, treatments shift stands towards a more pine-dominant composition associated with greater resilience to fire, drought, and insects (Safford & Stevens 2017). Research in similar mixed-conifer forests in eastern Oregon came to the same conclusion. Johnston et al. (2021) found that diameter limits on cutting prevented restoration of historical species composition because they retained an overabundance of large shade-tolerant trees that were not present historically.

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