




Forest recovery following extreme drought in California, USA: natural patterns and effects of pre-drought management

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Abstract. Rising temperatures and more frequent and severe droughts are driving increases in tree mortality in forests around the globe. However, in many cases, the likely trajectories of forest recovery following drought-related mortality are poorly understood. In many fire-suppressed western U.S. forests, management is applied to reverse densification and restore natural forest structure and species composition, but it is unclear how such management affects post-mortality recovery. We addressed these uncertainties by examining forest stands that experienced mortality during the severe drought of 2012–2016 in California, USA. We surveyed post-drought vegetation along a gradient of overstory mortality severity in paired treated (mechanically thinned or prescribed-burned) and untreated areas in the Sierra Nevada. Treatment substantially reduced tree density, particularly in smaller tree size classes, and these effects persisted through severe drought-related overstory mortality. However, even in treated areas with severe mortality (>67% basal area mortality), the combined density of residual (surviving) trees (mean 44 trees/ha) and saplings (mean 189 saplings/ha) frequently (86% of plots) fell within or exceeded the natural range of variation (NRV) of tree density, suggesting little need for reforestation intervention to increase density. Residual tree densities in untreated high-mortality plots were significantly higher (mean 192 trees/ha and 506 saplings/ha), and 96% of these plots met or exceeded the NRV. Treatment disproportionately removed shade-tolerant conifer species, while mortality in the drought event was concentrated in pines (*Pinus ponderosa* and *P. lambertiana*); as a consequence, the residual trees, saplings, and seedlings in treated areas, particularly those that had experienced moderate or high drought-related mortality, were more heavily dominated by broadleaf (“hardwood”) trees (particularly *Quercus kelloggii* and *Q. chrysolepis*). In contrast, residual trees and regeneration in untreated stands were heavily dominated by shade-tolerant conifer species (*Abies concolor* and *Calocedrus decurrens*), suggesting a need for future treatment. Because increased dominance of hardwoods brings benefits for plant and animal diversity and stand resilience, the ecological advantages of mechanical thinning and prescribed fire treatments may, depending on the management perspective, extend even to stands that ultimately experience high drought-related mortality following treatment.

Key words: California; drought; forest; mixed conifer forest; mortality; oak; pine; recovery; regeneration; resilience; Sierra Nevada.

INTRODUCTION

Climate is an important driver of the distribution, structure, and species composition of forests (Holdridge 1947, Stephenson 1998). Thus, changes in climate and associated variability in weather (e.g., more extreme and

or frequent droughts) have the potential to drive forest change. Indeed, recent droughts have triggered substantial shifts in many forested sites globally (Allen et al. 2010). In the short term, the most visible impact of drought on forests is often an increase in tree mortality, leading to reduced density of one or more species. These changes sometimes lead to shifts in species dominance (Beckage et al. 2008) and contraction of forest margins (Allen and Breshears 1998). In the longer term, recruitment of new trees may compensate for mortality and

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reduce the magnitude of change (Millar et al. 2007, Collins et al. 2011, Redmond and Barger 2013); in other cases, recruitment—or lack thereof—may lead to further divergence from historical conditions (Veblen et al. 1991, Suarez and Kitzberger 2008, Kayes and Tinker 2012, Vilà-Cabrera et al. 2013, Ibáñez et al. 2017). These changes may be exacerbated by the fact that mortality can modify wildfire behavior via changes in fuel loading (Harvey et al. 2014). Thus, to predict the longer-term impacts of drought, it is essential to understand how drought affects both mortality and recruitment.

In many cases, forest regeneration following drought mortality is relatively abundant (Suarez and Kitzberger 2008, Kayes and Tinker 2012). While regeneration often contains “new regeneration,” or seedlings that recruit following the mortality event, another important component is the “advance regeneration” comprised of seedlings and saplings that were present in the understory prior to the mortality event (e.g., Veblen et al. 1991). The species composition of advance regeneration cohorts often differs substantially from the forest overstory (e.g., by being more heavily dominated by shade-tolerant species that recruited in the understory) (Veblen et al. 1991, Astrup et al. 2008, Collins et al. 2011, Kayes and Tinker 2012), highlighting that even when regeneration is strong, it may drive a post-drought shift in species composition from the pre-drought condition.

In forests of the western United States, as in many forests globally, management over the past century has shifted forest structure and species composition dramatically away from historical conditions. A case study for such change is the yellow pine and mixed-conifer forests of California’s Sierra Nevada, where a century of fire suppression has resulted in forest densification as well as increased dominance of shade-tolerant and fire-intolerant tree species that recruit in the understory in the absence of disturbance (Stephens et al. 2015, Safford and Stevens 2017). Dense stands are known to be more susceptible to mortality during droughts (Young et al. 2017, Restaino et al. 2019), suggesting a potential for stand density reduction treatments (i.e., mechanical thinning, prescribed burning, or managed wildfire) to ameliorate future drought impacts (Fettig et al. 2007). While density reduction has been shown to reduce drought-related mortality of overstory trees (Restaino et al. 2019), no work to our knowledge has evaluated how density reduction prior to drought affects post-drought recovery (e.g., new and advance regeneration and other stand attributes that may influence future trajectories).

During the four years from 2012 to 2016, California experienced a drought so extreme that it was likely unprecedented in the previous 1,200 years or more, at least in the central and southern parts of the state (Robeson 2015). The drought triggered dramatic increases in tree mortality, especially in the southern Sierra Nevada, where (1) precipitation is normally low relative to other forested areas of the state and (2) the drought was especially severe in terms of the proportional reduction in

precipitation (Young et al. 2017, Fettig et al. 2019). Mortality of medium and large pines (diameter at breast height >25 cm) approached 100% in many sites (Fettig et al. 2019), especially in relatively arid sites with high tree densities (Restaino et al. 2019), and often occurred in large contiguous areas (>4 km²) (Young et al. 2017). The density of tree regeneration (seedlings and saplings) following mortality was generally very high, far greater than necessary for replacement of overstory trees that experienced mortality (Fettig et al. 2019). However, in contrast to the overstory prior to mortality, tree regeneration was heavily dominated by shade-tolerant conifers (especially incense cedar [*Calocedrus decurrens*]) (Fettig et al. 2019), much like it is in fire-suppressed stands in the absence of drought (Safford and Stevens 2017).

Modern yellow pine and mixed-conifer (YPMC) forests in California diverge dramatically from historical conditions, due primarily to human management (Dolanc et al. 2014a,b, Safford and Stevens 2017). There is substantial interest in restoring YPMC forest conditions to align more closely with their historical or “natural” range of variation (Landres et al. 1999), as these conditions are assumed to represent a more resilient state and are more likely to ensure that important management goals can be met (Safford et al. 2012a,b). In addition to reducing mortality associated with drought (Restaino et al. 2019) and reversing changes in stand structure associated with fire suppression (Stephens and Moghaddas 2005), forest density reduction treatments can increase the proportion of fire- and drought-adapted species in the regenerating vegetation (Zald et al. 2008) and increase resistance and resilience to wildfire (Agee and Skinner 2005, Stevens et al. 2014, Kalies and Yocom Kent 2016), thus facilitating the restoration of natural fire regimes. Density reduction treatments, which include mechanical thinning, prescribed fire, and/or managed wildfire (i.e., wildfires managed for resource objectives), can also reintroduce spatial heterogeneity in stand structure (Knapp et al. 2017) and provide a wider range of habitats for biota (White et al. 2013, Roberts et al. 2015, Stevens et al. 2015), thus increasing biodiversity on the landscape and reducing the potential for large-scale, synchronous losses from fire, drought, insects, or disease (North et al. 2009). In Sierra Nevada YPMC forests, density reduction treatments intended to move stand structure and composition closer to their natural ranges of variation are commonly referred to as “restoration treatments” (North 2012), which distinguishes them from other forms of density reduction such as overstory harvest. In this work, we focus only on density reduction applied as a restoration treatment.

While restoration treatments in YPMC forests generally seek to reduce the density of non-pine tree species in smaller size classes, mortality during the recent California drought disproportionately reduced the density of large pines, suggesting the effects of drought mortality were not aligned with management objectives. However, the post-mortality stand conditions and potential recovery

trajectories, and the extent to which they are affected by pre-drought restoration treatments, are not well understood. A better understanding of post-drought conditions and recovery trajectories would enable assessment of whether management actions (e.g., tree planting or density reduction) may be required to meet specific management goals following drought-related mortality. In this contribution, we evaluate how extreme drought and pre-drought density reduction treatments (and their combination) altered stand conditions and potential recovery trajectories in YPMC forests.

METHODS

Study region

We evaluated post-drought stand conditions in yellow pine and mixed-conifer forests in the central and southern Sierra Nevada of California, USA (Fig. 1). These forests are dominated by relatively fire-tolerant, shade-intolerant pines (ponderosa pine [*Pinus ponderosa*], Jeffrey pine [*P. jeffreyi*], and sugar pine [*P. lambertiana*]) and relatively fire-intolerant, shade-tolerant white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*), with greater dominance of the shade-tolerant species in cooler, wetter areas and at higher elevations and latitudes (Safford and Stevens 2017). There is also an important hardwood component, composed primarily of black oak (*Quercus kelloggii*) and canyon live oak (*Q. chrysolepis*), particularly in areas of lower moisture availability (Safford and Stevens 2017). While conifers and hardwoods in this system can reproduce via seed, hardwoods can additionally resprout from the root crown following top kill (which can occur, for example, due to fire or mechanical thinning) (Plumb and Gomez 1983).

The study area experiences a Mediterranean climate with cool, wet winters and warm, dry summers. Due to a century of fire suppression, the historic fire regime of frequent, low- to moderate-severity fires has been replaced with one of infrequent and often stand-replacing fires, and contemporary forests are much denser and more heavily dominated by shade-tolerant conifer species than they were before Euro-American settlement (Safford and Stevens 2017; also see *Introduction*). The four-year drought between 2012 and 2016 brought roughly 50–60% of normal precipitation throughout the region (Fig. 1) and above-average temperatures (Young et al. 2017). While YPMC forests cover a broad geographic area within the Sierra Nevada, they are sufficiently consistent in structure, composition, and function such that ecological assessments and management strategies often apply to the full geographic extent of the forest type (e.g., North et al. 2009, Safford and Stevens 2017).

Data collection

In 2017, we collected plot data at 10 paired sites (treated vs. untreated) in the Sierra Nevada, California, from

the Eldorado National Forest (NF) in the north (centroid 38.66° N, 120.46° W) to the Sierra NF in the south (37.03° N, 119.29° W; Fig. 1), and including the Stanislaus NF, nearby Bureau of Land Management (BLM) land, and Yosemite National Park. Sites were selected such that suitable treated and untreated areas occurred adjacent to one another. Treated areas had received mechanical thinning and/or burning (either prescribed fire or pile burning) with the goal of reducing stand density (especially in the smaller size classes) and surface fuels. Treated stands were selected to meet the following conditions: (1) treatments involved multiple mechanical and/or burn treatments intended to serve as restoration treatments (e.g., by prioritizing density reduction of smaller trees and/or shade-tolerant species and retention of large trees and/or shade-intolerant pines); (2) the treatments were completed after the year 2000 (i.e., within the time period representing the historical mean fire return interval in these forests; Van de Water and Safford 2011); and (3) the treated area was a minimum of 4 ha. Sites were located on lands administered by the United States Forest Service (USFS), National Park Service, and Bureau of Land Management.

At each site, we established 14–16 plots (6–8 in treated stands and 6–8 in untreated stands), for a total of 157 plots. Plots were randomly placed in areas dominated or codominated by pine (prior to recent mortality); where mortality exceeded pre-drought background levels of 7 trees/ha (as indicated by USFS Aerial Detection Survey data; U.S. Forest Service 2015); which were >50 m from roads, skid trails, and large canopy gaps associated with unproductive sites or recent disturbance (e.g., hazard tree removal or stand-replacing wildfire); which were not located in developing tree plantations; and which contained three or more live and/or recently dead trees. Plots in untreated stands were located 50–1,000 m from plots in treated stands and were selected to be comparable to plots in the paired treated stand with respect to slope, aspect, and successional stage. We visually evaluated the successional stage of each plot (or site) by noting the general size class (diameter and height) of the dominant and codominant trees in the stand. Due to their proximity, paired treated and untreated plots had similar historical treatments and therefore were at similar successional stages. All plots were ≥ 50 m apart. Across all 157 study plots, elevations ranged from 912 m to 1,677 m above sea level, and normal annual precipitation (1981–2010 mean; PRISM Climate Group 2018) ranged from 830 to 1,270 mm, with the higher precipitation values generally at the more northern sites (Fig. 1).

At each sampling location, we established a circular plot with a 12.6 m radius (500 m²; 0.05 ha). For each tree >7.6 cm diameter at breast height (DBH) (hereafter referred to as “trees”), we recorded species, DBH, and status (live, recently dead, and long dead). We considered trees retaining at least some needles as recently dead (i.e., mortality potentially attributable to the 2012–2016 drought). We assumed dead trees with no needles

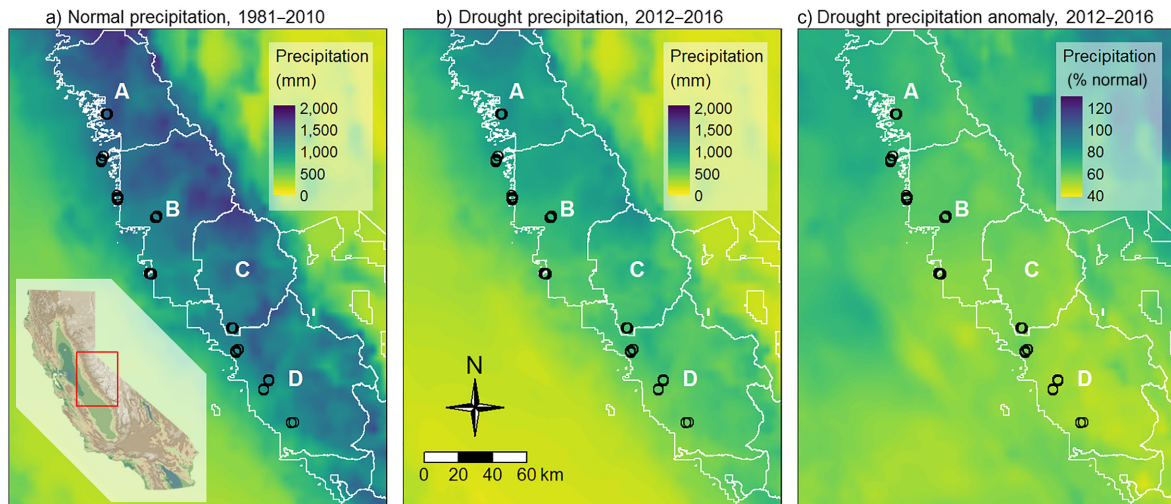


FIG. 1. Location of study sites (black circles) relative to spatial variation in (a) normal annual precipitation during the period from 1981 to 2010, (b) mean annual precipitation during recent California drought (i.e., the water years ending in 2012 through 2016), and (c) mean precipitation anomaly during the drought. White outlines indicate National Forest and National Park boundaries, with units represented by letters: A, Eldorado National Forest; B, Stanislaus National Forest; C, Yosemite National Park; D, Sierra National Forest. The inset map in the left panel shows the location of the study region within the state of California. Figure reprinted from Restaino et al. (2019).

(generally along with other signs of advanced decay including fragmented bark and absence of small branches) had died prior to the drought (Keen 1929, sensu Egan et al. 2010). We additionally counted the number of “saplings” (stems > 1.4 m tall but ≤ 7.6 cm DBH) by species and status (live or dead). Within a subplot with a 4.37 m radius centered on the same point, we counted the number of “seedlings” (stems ≤ 1.4 m tall, including germinants and resprouting hardwood stems) by species and status. Given seedling growth rates and the relatively short period between mortality and plot survey, seedlings may have recruited prior to the drought (advance regeneration) or following the drought (new regeneration), though based on qualitative assessment in the field, we expect most seedlings represented advance regeneration. The majority of saplings also likely recruited prior to the drought.

We quantified fuel loading in each plot using Brown’s fuels transects (Brown 1974). We tallied 1-h (diameter < 6.4 mm) and 10-h (diameter ≥ 6.4 mm and < 25.4 mm) fuels along the outer 3.3 m of four separate plot radii in the four cardinal directions, we tallied 100-h (≥ 25.4 and < 76.2 mm) fuels along the outer 7.6 m of the four radii, and we tallied and measured sound and rotten coarse woody debris (CWD, or 1,000-h fuels; diameter ≥ 7.6 cm) along the entire 12.6 m length of the four radii. We computed total fuel load as the sum of the estimated mass of 1-, 10-, and 100-h fuels and CWD following Brown (1974). We additionally estimated the potential biomass of fuel in recently dead standing trees (snags) using the DBH-based allometric equations presented by Kaye et al. (2005) (sensu Sorensen et al. 2011). We included biomass in stem wood and branches but

excluded stem bark and foliage. We assumed all tree species followed similar allometric relationships as ponderosa pine, for which the equations we used were developed. These calculations were intended to provide rough estimates, and we do not analyze the values statistically or draw inferences regarding the effects of treatment on snag biomass.

Finally, we visually estimated absolute percent cover of each 12.6 m radius plot by live overstory tree canopy and by shrubs, and we identified the shrub species with the greatest cover in each plot. During training and regularly throughout the field season, crew members calibrated their cover estimates against one another in an effort to maintain consistency. All plot measurements were collected in the summer of 2017, with the exception of overstory tree cover and shrub cover, which were recorded in the summer of 2016.

Derivation of natural range of variation (NRV) reference values

To provide context for stand conditions following restoration treatments and/or drought, we characterized natural ranges of variation in stand attributes (tree and snag basal area, tree density, tree size-class distribution, tree species composition, overstory cover, shrub cover, and fuel loading), mostly relying on data in Safford and Stevens (2017), but adding newer studies where available, where such studies used empirical evidence or historical records to infer stand conditions in YPMC forests in the California Floristic Province during the first half of the 20th century or prior (i.e., after relatively little time, if any, following initiation of fire suppression). From each

study evaluating any given stand attribute (Appendix S1: Tables S1–S8, Fig. S1), we extracted a value (or more than one value if the study quantified multiple YPMC forest types) and then computed the group mean and interquartile range (25th to 75th percentiles).

It is important to note that, throughout this paper, we use our NRV estimates as reference points or “benchmarks” rather than as management targets, as we acknowledge that management goals and/or changing abiotic conditions may dictate other targets. We identify all sources used to derive NRV values in Tables S1–S8 (Appendix S1) and map those that can be mapped (Appendix S1: Fig. S1).

Analysis

We performed all analysis in R version 3.5.0 (R Core Team 2018). For most analyses, we divided plots into three categories based on proportional basal area mortality of trees > 7.6 cm DBH (basal area of recently dead trees divided by the total basal area of live and recently dead trees): low (<33%; 91 plots), moderate (\geq 33% and <67%; 28 plots), and high (\geq 67%; 38 plots; Table 1). For analyses of species composition, we grouped species into three functional groups: pines (which are relatively shade intolerant and recruit in gaps, often following disturbance; Safford and Stevens 2017), shade-tolerant conifers (specifically, white fir and incense cedar, which can recruit in both shaded and open conditions; Safford and Stevens 2017), and hardwood trees (primarily black oak and canyon live oak). Although our plots span a relatively broad latitudinal gradient, there are no clear trends in stand structure and composition among our plots along this gradient, and variation among subregions is generally as great as variation within them (Appendix S1: Fig. S2). While there is a latitudinal gradient in mortality severity within our study region (potentially driven by a climate gradient; Restaino et al. 2019), we group our plots by mortality severity rather than by geographic location because (1) we wish to describe broad-scale patterns in post-mortality recovery and (2) mortality severity is likely

a more relevant covariate for managers and ecologists than is geographic subregion.

To visualize patterns, we computed mean and standard errors of relevant plot metrics across all plots in each mortality severity category. As the only exception, we visualized sapling mortality (%) by summing the number of live and recently dead saplings across all plots in each category (e.g., low-mortality treated, low-mortality untreated). We did this to avoid averaging across plots with differing numbers of trees (thus giving equal weight to, e.g., a plot with 10 trees as one with 50 trees), but as a consequence, we do not have standard errors to report for sapling mortality. However, our statistical analysis does provide metrics of confidence in the effect of treatment.

We statistically tested for an effect of treatment on stand attributes (e.g., tree densities, species relative abundance, and percent cover) as well as sapling mortality (based on counts of observed live and dead saplings) by fitting Bayesian hierarchical (mixed-effect) models using Hamiltonian Monte Carlo in Stan (Gelman et al. 2015) via the R package brms (Bürkner 2017). We performed the analysis at the plot level, with one value of each response variable (e.g., seedling density) per plot. We fit models to predict a given response variable using only an intercept and a categorical (yes/no) variable for treatment, and we allowed these two parameters to vary by mortality severity category (low, moderate, and high). We modeled basal area and fuel loading using a gamma distribution with a log link, density (stems per unit area) using a Poisson distribution with a log link, mortality using a binomial distribution with a logit link (with the response modeled as the number of recently dead saplings out of the total number of saplings), size distribution (percent of trees in low, medium, and large size classes) using a binomial distribution with a logit link (with the response modeled as the number of trees of the focal size class out of the total number of trees), and cover and proportion (e.g., relative abundance) using a beta distribution with a logit link.

We computed 95% credible intervals (CIs) for the model-fitted intercept and treatment effect for each of the three mortality severity categories (groups),

TABLE 1. Number of study plots in each National Forest (NF) or National Park (NP), by mortality severity and treated status.

National Forest or Park	Low mortality		Moderate mortality		High mortality		Total
	Untreated	Treated	Untreated	Treated	Untreated	Treated	
Eldorado NF	6	8	1	0	1	0	
Stanislaus NF	18	21	6	7	9	3	64
Yosemite NP	6	3	1	1	1	2	14
Sierra NF	15	14	4	8	13	9	63
Total	45	46	12	16	24	14	157

Notes: Plots on Bureau of Land Management land just outside the Stanislaus NF were classified as Stanislaus NF plots for the purposes of this table. The forests and park are arranged from north (Eldorado NF) to south (Sierra NF). Plots are categorized based on the extent of drought-associated overstory mortality: low (0–33% basal area mortality), moderate (33–67% basal area mortality), or high (67–100% basal area mortality).

incorporating both the overall fixed effects and group-level effects. We interpret a treatment effect for which the 95% CI excludes zero as a “significant” effect but acknowledge that there is no categorical difference between effects for which the CI excludes zero and those for which the CI slightly overlaps zero (McElreath 2016).

RESULTS

Distribution of mortality severity across the study region

Across the study region, the majority or plurality of plots experienced low drought-related mortality (<33% mortality by basal area; Table 1). However, the percentage of plots experiencing high mortality (>67% mortality by basal area) increased progressively southward, from 6% on the Eldorado NF to 19% on the Stanislaus NF, 21% in Yosemite NP, and 35% on the Sierra NF (Table 1). Among high-mortality plots, the majority (63%) were untreated, while among low- and moderate-mortality plots, the modest majority (52%) were treated (Table 1).

Residual tree structure

Post-drought (i.e., 2017) stand basal area (BA) of all trees > 7.6 cm DBH was substantially lower than pre-drought basal area in most plot categories. Across the 38 plots experiencing high mortality (>67% BA mortality; 24% of all plots), live BA remaining following the drought averaged 4.6–8.0 m²/ha, roughly 15% of pre-drought BA (Fig. 2). Pre-drought BA was marginally or significantly lower in treated stands than in untreated stands, and this pattern persisted following mortality (Fig. 2; Appendix S1: Table S9). Prior to drought, BA in untreated stands exceeded our NRV estimate, while BA in treated stands fell very near to or within the NRV estimate (Fig. 2; Appendix S1: Table S1). Following the drought, mean BA in moderate mortality stands fell within or near our NRV estimate for both treated and untreated stands, but BA in high-mortality stands was well below NRV, especially in treated stands (Fig. 2).

Tree density (number of stems per hectare of all trees > 7.6 cm DBH) was also substantially lower following drought. In the stands experiencing greatest mortality, mean post-drought tree density was 23–48% of pre-drought density, depending on whether the stand was treated (Fig. 3). Treated stands were significantly and substantially less dense (<40% of the density of treated stands, on average), and, as with BA, this pattern persisted following mortality (Fig. 3; Appendix S1: Table S9). In the areas experiencing greatest mortality, mean tree density fell to 44 trees per hectare (TPH) in treated stands vs. 192 TPH in untreated stands (Fig. 3). As with BA, treatment moved pre-drought density to within or near our NRV estimate (Fig. 3; Appendix S1: Table S2). For the treated stands experiencing low and

moderate mortality, mean tree density (both pre- and post-drought) fell near to or within our estimate of the NRV, whereas mean tree density in untreated stands (both pre- and post-drought) was more than double the upper limit of the NRV (Fig. 3). In stands experiencing the highest mortality, post-drought mean TPH in untreated stands was within the NRV, whereas the very low mean density in treated stands (44 TPH) was substantially below our NRV estimate.

Drought mortality led to a disproportionate loss of trees in larger size classes (Fig. 4). Relative to the average pre-drought stand, the stands experiencing highest mortality lost 57% of trees with DBH < 50 cm (434 TPH pre-drought to 149 TPH post-drought), whereas they lost 97% of trees with DBH ≥ 50 cm (73 TPH to 2 TPH; Fig. 4). As a consequence, the relative abundance of small trees (relative to larger trees) increased significantly and substantially (Appendix S1: Table S10). Treatment had the opposite effect; nearly all of the density reduction was due to loss of trees with DBH < 50 cm, producing a more even (less small tree-dominated) distribution of pre-drought tree sizes (Fig. 4; Appendix S1: Table S10). This effect was significant and persisted through drought mortality; treated stands had a greater proportional representation of larger trees both prior to and following drought than did untreated stands (Appendix S1: Table S10). Nonetheless, stands remained more heavily dominated by the small size classes (Fig. 4; Appendix S1: Table S10).

The size-class distribution of YPMC and similar forest types under reference conditions (frequent low-severity fire; low cover; unlogged; dominance of large, fire-tolerant trees) is relatively flat or even hump-shaped (Safford and Stevens 2017; Fig. 4; Appendix S1: Table S3). As expected, the untreated pre-drought stands (and low-mortality post-drought stands) in our study showed a reverse J-shaped curve that is characteristic of undisturbed forests dominated by small and medium-sized shade-tolerant trees (Fig. 4). Moderate and high-mortality stands lost most of their large trees, and the size-class distribution was far from our NRV estimate. Treated stands showed a much flatter distribution of size classes that much more closely resembled the NRV distribution (though still with somewhat higher density in the smaller size classes). As with untreated stands, moderate and high drought mortality depleted the large size classes, but the proportional representation of large trees was still much greater in the treated than untreated stands, especially after drought (Appendix S1: Table S10).

Residual tree species composition

Drought and treatment also substantially affected tree species composition. In terms of both basal area and tree counts, in the stands that experienced high mortality, pines moved from being dominant (69% of BA and 52% of trees in untreated stands) to being a minor

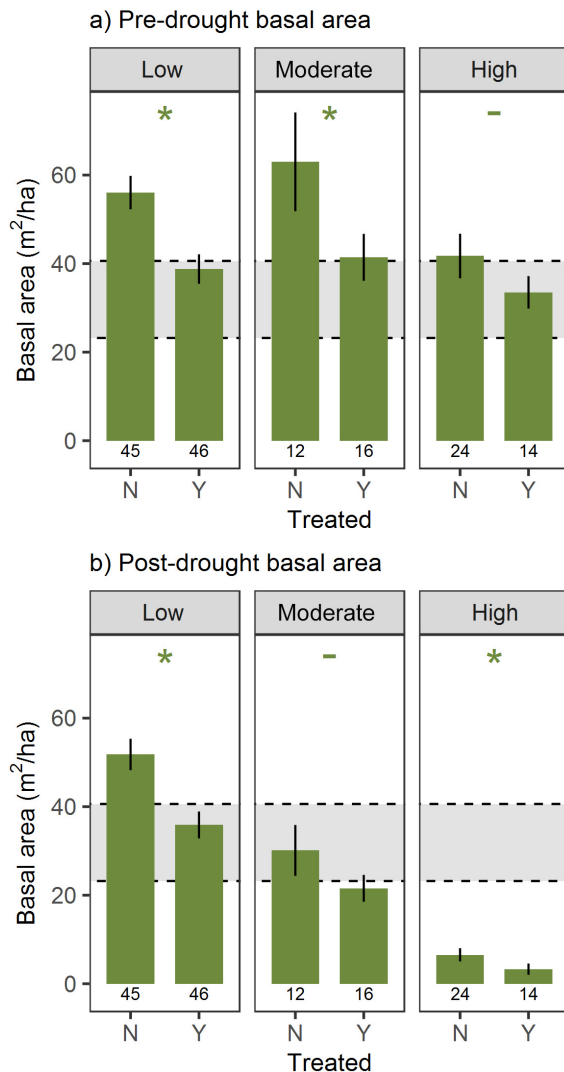


FIG. 2. Basal area of live trees >7.6 cm DBH in treated (Y) and untreated (N) stands (a) before the drought and (b) following drought-induced mortality. Stands are categorized based on the extent of overstory mortality they ultimately experienced: low (0–33% basal area mortality), moderate (33–67% basal area mortality), or high (67–100% basal area mortality). Error bars depict \pm SE around the mean. An asterisk above a pair of bars indicates a significant difference (see Methods) in basal area between treated and untreated plots; a dash indicates no significant difference. The gray shaded band reflects the natural range of variation of basal area for yellow pine and mixed-conifer stands in the California Floristic Province (see Methods). The numbers beneath the bars indicate the number of study plots in each category. The plotted values reflect the contribution of all tree species, including conifers and hardwoods.

component (10% of BA and 16% of trees in untreated stands); the disproportionate loss of pines led to dramatic increases in the relative abundance of shade-tolerant conifers (from 26% to 61% by BA and 40% to 62% by tree count in untreated stands) and of hardwoods (from 4% to 27% by BA and 9% to 22% by tree count in

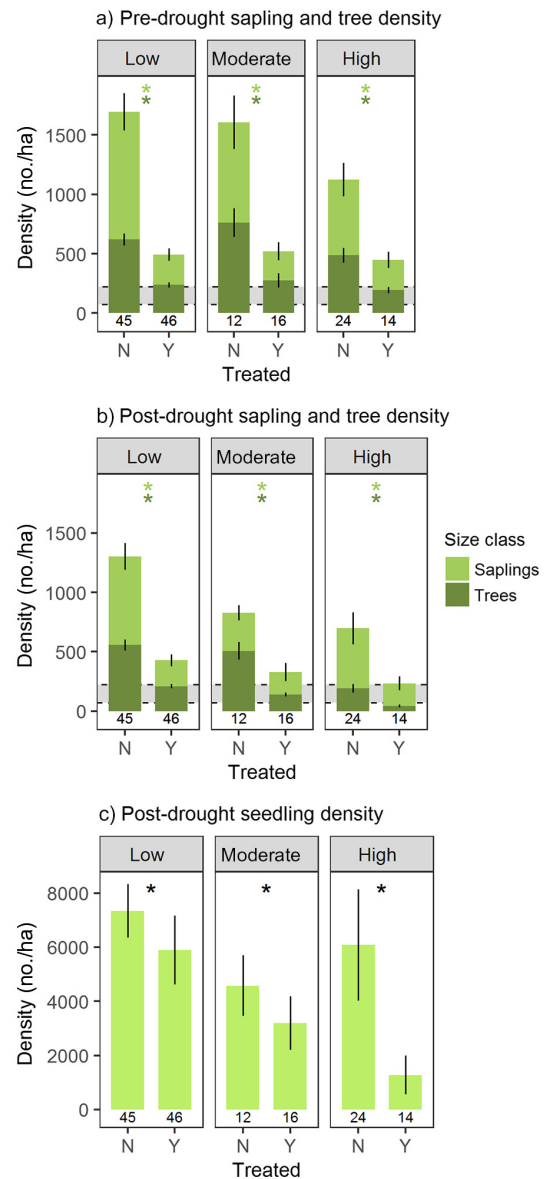


FIG. 3. Tree, sapling, and seedling density in treated (Y) and untreated (N) stands (a) before and (b, c) following the drought. Stands are categorized based on the extent of overstory mortality they ultimately experienced: low (0–33% basal area mortality), moderate (33–67% basal area mortality), or high (67–100% basal area mortality). Error bars depict \pm SE (separately for each size class). An asterisk above a pair of bars indicates a significant difference (see Methods) in density between treated and untreated plots (in panels a and b, the top row of symbols reflects significance for saplings, and the bottom row reflects significance for trees). The gray shaded band reflects the natural range of variation of tree density for yellow pine and mixed-conifer stands in the California Floristic Province (see Methods). The numbers beneath the bars indicate the number of study plots in each category. Seedlings are <1.4 m tall and include germinants as well as hardwood resprouts, saplings are \geq 1.4 m tall and \leq 7.6 cm DBH, and trees are \geq 1.4 m tall and >7.6 cm DBH. The plotted values reflect the contribution of all tree species, including conifers and hardwoods.

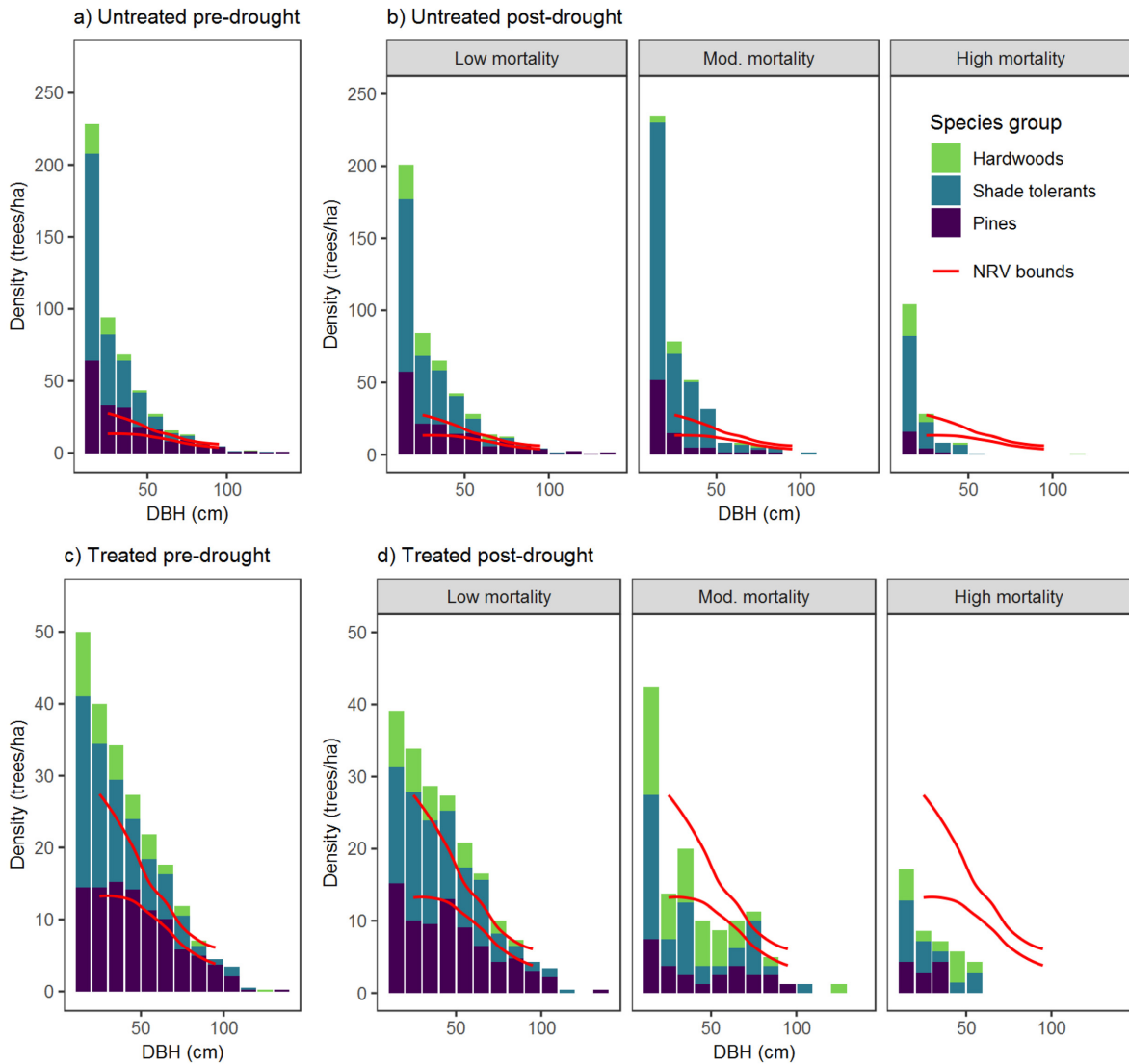


FIG. 4. Size distribution of (a and c) pre-drought and (b and d) post-drought live trees in both (a and b) treated and (c and d) untreated stands. Note the difference in the y-axis scale between top (untreated) and bottom (treated) panels. The red lines depict the upper and lower bounds of our approximated historical reference size distribution for yellow pine and mixed-conifer (YPMC) forests (see *Methods*). NRV: natural range of variation.

untreated stands). In stands that experienced moderate mortality, shade-tolerant trees were the dominant species group (by both BA and tree count), and drought mortality resulted in even greater relative abundance of these species (Fig. 5). Drought mortality drove very similar compositional shifts in treated stands (Fig. 5).

Treatment resulted in significant and substantial reductions in the dominance of shade-tolerant trees, especially in terms of tree counts (but also in some cases in terms of BA; Fig. 5). Prior to drought mortality, relative abundance of shade-tolerant trees (based on counts) was 58%, 67%, and 40% (in stands that ultimately experienced low, moderate, and high severity mortality, respectively) in untreated stands, and 40%, 50%, and

16% in treated stands. Our estimated NRV for shade-tolerant relative abundance is 21–36% of stems (Appendix S1: Table S4); thus, treatment generally brought stands much closer to the NRV (Fig. 5). The reduction in shade-tolerant abundance with treatment remained significant following mortality in all mortality severity classes. Decreases in shade-tolerant tree abundance achieved via treatment were associated with increased relative abundance of pines and, in most cases, hardwoods (Fig. 5). Nonetheless, in treated stands following mortality, pine relative abundance for trees, saplings, and seedlings remained well below the NRV of 45–56% (Appendix S1: Table S4), and hardwood relative abundance was often at or above the high extreme of the

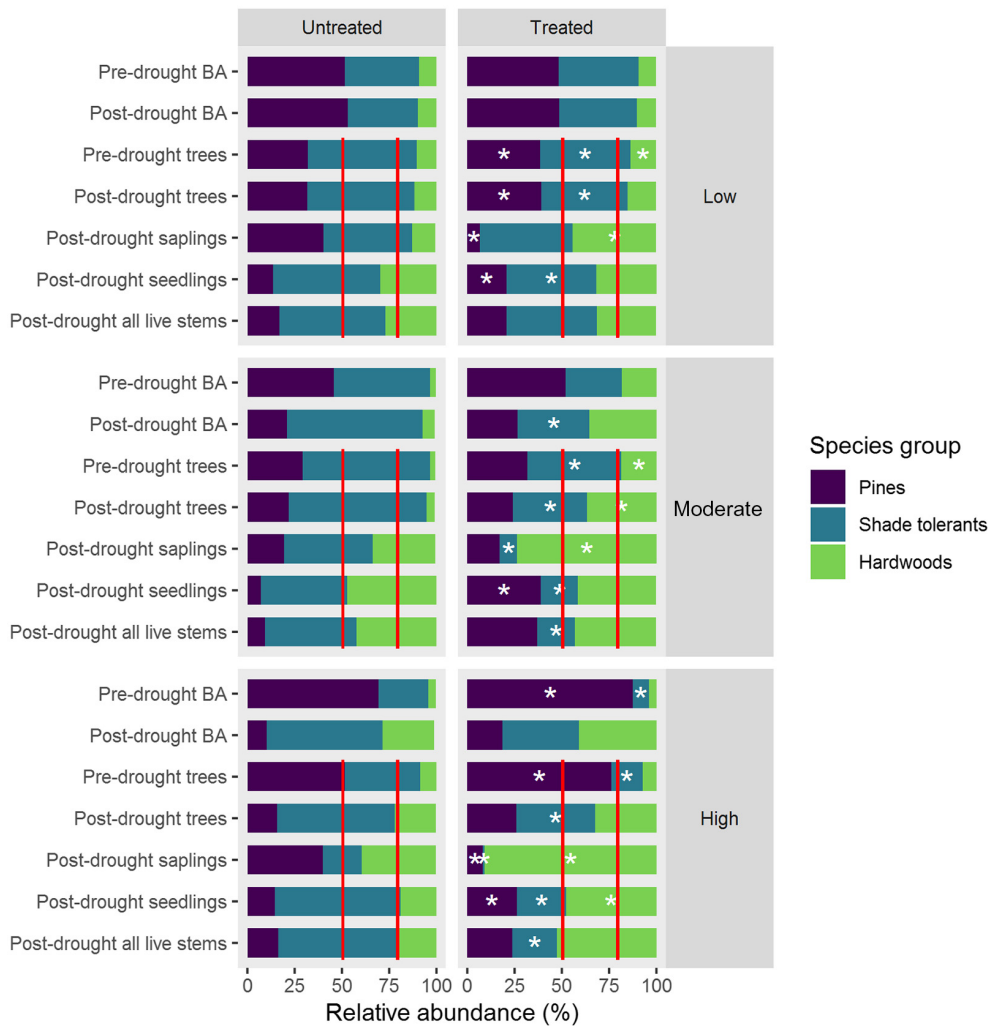


Fig. 5. Relative abundance by species functional group in the study plots, with plots categorized based on treated status and mortality severity. Rows reflect different metrics of species composition. The two BA (basal area) metrics reflect only trees (stems ≥ 1.4 m tall and >7.6 cm DBH). Seedlings are <1.4 m tall and include germinants and resprouting hardwood stems, saplings are ≥ 1.4 m tall and ≤ 7.6 cm DBH, and trees are >1.4 m tall and >7.6 cm DBH. In the “Treated” category, an asterisk reflects a significant change relative to untreated stands ($P \leq 0.05$). Vertical red lines represent NRV estimates of mean pine (left line) and pine + shade tolerant (right line) relative abundance in central and southern Sierra Nevada YPMC forests (see Appendix S1: Table S4). Absolute abundances by species group are shown in Appendix S1: Fig. S3.

NRV (32%) (Fig. 5). Treatment and drought-associated mortality influenced species composition in opposite directions (the former disproportionately reducing shade-tolerant abundance and the latter disproportionately reducing pine abundance). However, their net effect, in stands that ultimately experienced high mortality, was to reduce the relative abundance of pines (from 52% of trees to 26%) while not substantially affecting the relative abundance of shade-tolerant trees (40% of trees vs. 42%; Fig. 5). The reduction in pine abundance was compensated by a substantial increase in the relative abundance of hardwoods (from 9% of trees to 32%). A similar increase in hardwood abundance occurred in stands experiencing moderate mortality, though in those

stands, the net effect of treatment and mortality was to reduce the dominance of shade-tolerant trees rather than pines (Fig. 5).

Regeneration environment

Live overstory tree canopy cover following drought decreased with increasing mortality severity (Fig. 6a). Among the areas experiencing lowest mortality, treated stands had significantly lower canopy cover than untreated stands. The effect of treatment persisted through severe mortality: among the areas experiencing highest mortality, treated stands again had significantly lower canopy cover (Fig. 6a; Appendix S1: Table S9). In

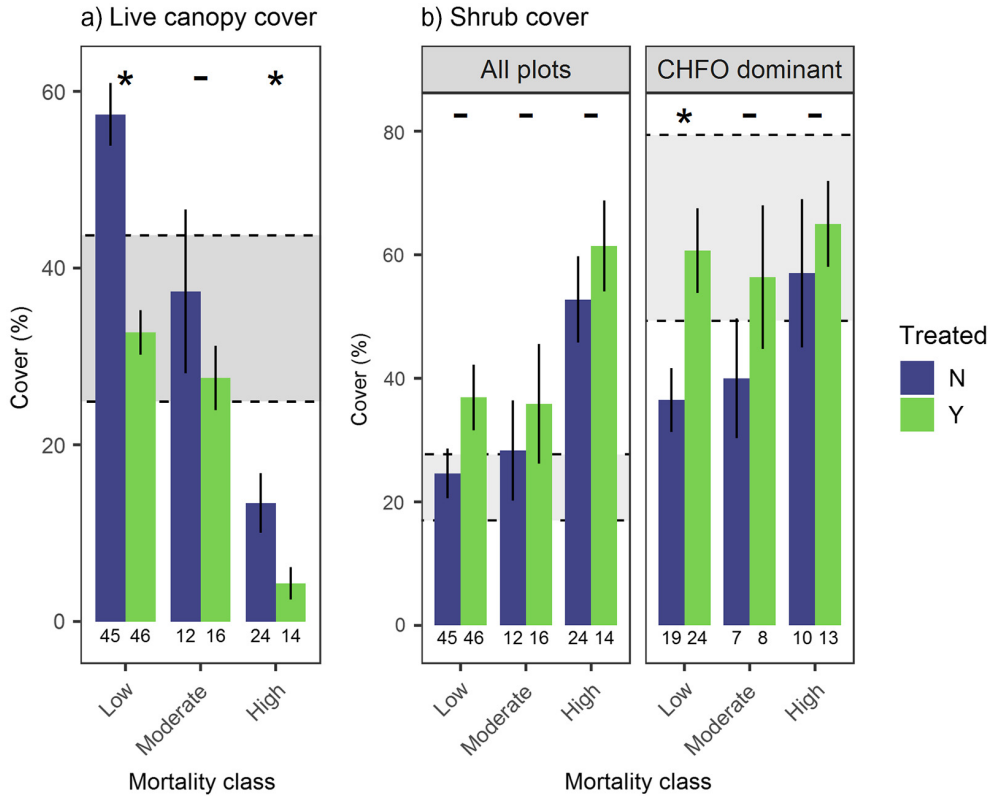


FIG. 6. Biotic characteristics of the post-mortality regeneration environment. Error bars depict \pm SE. An asterisk above a pair of bars indicates a significant difference in cover between treated and untreated plots (see Methods); a dash indicates no significant difference. The gray shaded bands reflect the natural range of variation of shrub and live canopy cover in YPMC stands. Shrub cover data (panel b) are summarized two ways: the first (left) uses data from all study plots and also depicts the natural range of variation based on all available data; the second (right) depicts data specifically for plots in which shrub cover was dominated by *Chamaebatia foliolosa* (CHFO) and depicts the natural range of variation specifically for areas dominated by *C. foliolosa*. The numbers below the bars indicate the number of plots in each classification (i.e., all plots, and plots with shrub cover dominated by *C. foliolosa*).

the areas experiencing lowest mortality, untreated stands supported very high canopy cover (mean 57%); canopy cover in our treated plots on the other hand (mean 33%) was within our estimate of NRV (Appendix S1: Table S5; Fig. 6a). Following moderate drought mortality, both treated and untreated stands fell within the NRV estimate. In contrast, in untreated stands experiencing high mortality, canopy cover (mean 10%) fell well below the NRV, and in treated areas, mean canopy cover was even lower (2%; Fig. 6a).

Treated areas had marginally greater shrub cover than untreated areas across all mortality severities (Fig. 6b), but this effect was not significant. Under low and moderate levels of drought mortality, untreated stands supported shrub cover that was within or very near our NRV estimate of 17–28% (Appendix S1: Table S6a; Fig. 6b), while treated stands were somewhat above NRV. Areas experiencing high mortality had substantially higher shrub cover (mean 53% in untreated stands and 61% in treated stands). In many of these plots the dominant shrub species was bear clover

(*Chamaebatia foliolosa*), a low subshrub that provides high levels of ground cover in some drier sites often dominated by ponderosa pine. Nonetheless, these values are well within NRV (Fig. 6b), as shrub cover values in excess of 50% are common in reference stands where the dominant shrub species is bear clover (Appendix S1: Table S6b).

The post-drought basal area of snags (i.e., standing dead trees that died during or prior to the drought) was, not surprisingly, greatest in areas experiencing moderate and high mortality (mean 26–53 m²/ha, depending on mortality severity and treated status). Snag basal area was lower in treated stands, but this difference was not significant (Fig. 7b; Appendix S1: Table S9). Areas experiencing low mortality had substantially lower snag basal area (mean 12–15 m²/ha). However, all snag BA values, regardless of mortality severity and treated status, were far higher than our estimate of NRV (Appendix S1: Table S8); in fact, snag BA values were roughly 7–80 times greater than the upper limit of our NRV estimate.

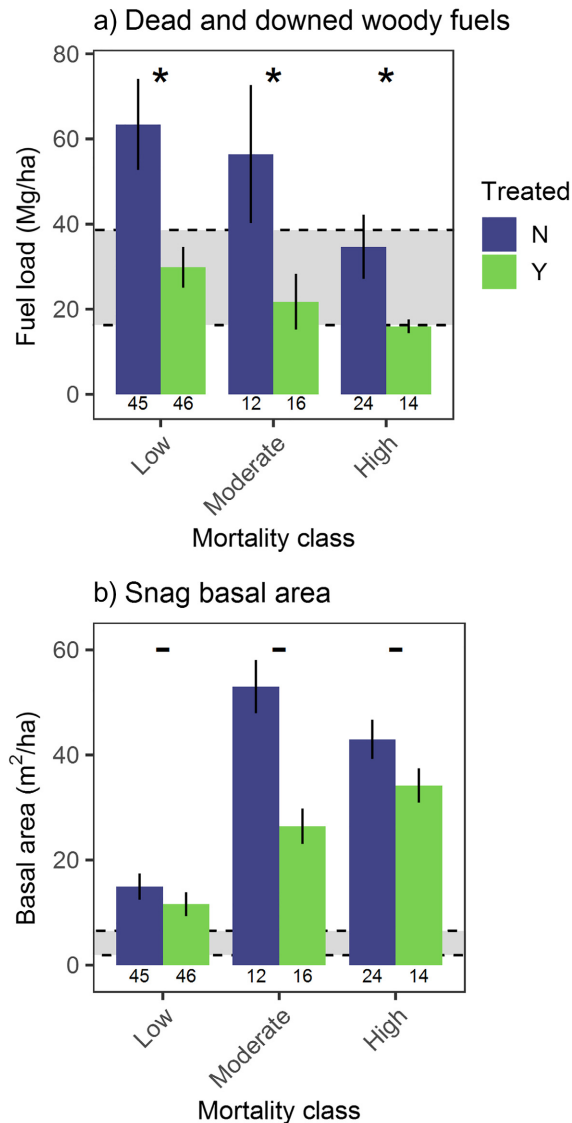


FIG. 7. Fuel and snag loads in the study plots. Error bars depict \pm SE. Stands are categorized based on the extent of drought-associated overstory mortality they experienced: low (0–33% basal area mortality), moderate (33–67% basal area mortality), or high (67–100% basal area mortality). The gray shaded bands reflect the natural range of variation of fuel and snag loads for yellow pine and mixed-conifer stands in the California Floristic Province. The numbers beneath the bars indicate the number of study plots in each category. An asterisk above a pair of bars indicates a significant difference in (a) fuel load or (b) basal area between treated and untreated plots (see Methods); a dash indicates no significant difference.

Surface fuel loads decreased marginally with increasing mortality severity, and fuel load was significantly and substantially reduced by treatment in all three mortality classes (e.g., from 35 to 16 Mg/ha in high-mortality stands; Fig. 7a; Appendix S1: Table S9). In areas with low or moderate mortality, mean surface fuel load in untreated stands was far above our estimate of the

NRV (Fig. 7a; Appendix S1: Table S7). However, surface fuel loads in treated plots (regardless of mortality severity), as well as loads in untreated plots in areas experiencing high mortality, were within or very near the NRV. In high-mortality areas, the estimated fuel loads (biomass) contributed by recently dead (drought-associated) snags were approximately 5–10 times greater than surface fuel loads (mean snag fuel load estimate 176 Mg/ha in untreated plots and 163 Mg/ha in treated plots). In contrast, in low-mortality areas, estimated snag fuel loads were much lower than in high-mortality areas and roughly two to three times greater than surface fuel loads (mean snag fuel load estimate 25 Mg/ha in untreated plots and 34 Mg/ha in treated plots).

Tree regeneration

Mean post-drought densities of seedlings (trees < 1.4 m height; we use the term “seedlings” to include both germinants and resprouts) ranged from 1,274 to 7,344 seedlings/ha (median 250 to 5,002 seedlings/ha), depending on mortality severity and treatment status (Fig. 3c). Among untreated stands, there was no clear relationship between overstory mortality severity and seedling density, but among treated stands, there was a clear decline in seedling density with increasing mortality (Fig. 3c). In all mortality severity categories, treated stands had significantly fewer seedlings than untreated stands (Fig. 3c; Appendix S1: Table S9). Seedlings were generally dominated by shade-tolerant species (or codominated by shade-tolerant species and hardwoods in moderate-severity mortality areas), though in treated stands experiencing moderate or high mortality, seedlings were dominated by hardwoods (in high-mortality areas) or codominated by hardwoods and pines (in moderate-mortality areas; Fig. 5).

Mean post-drought densities of saplings (trees \geq 1.4 m height but <7.6 cm DBH) were lower than seedling densities, ranging from 189 to 745 saplings/ha, depending on mortality severity and treatment status. Sapling density did not appear to vary consistently with overstory mortality severity, but it was significantly and substantially reduced by treatment (e.g., from mean 506 to 189 saplings/ha in high-mortality areas; Fig. 3b; Appendix S1: Table S9). In untreated stands, saplings were dominated by shade-tolerant species, except in high-mortality areas, where they were codominated by pines and hardwoods (Fig. 5). Hardwood dominance was significantly and substantially greater in treated stands than untreated stands across all mortality classes. In treated stands, saplings were either codominated by shade-tolerant trees and hardwoods (in low-mortality areas) or dominated outright by hardwoods (in moderate and high-mortality areas; Fig. 5, Appendix S1: Table S9). In these areas, absolute densities of pine saplings were very low (e.g., mean 34 saplings/ha in treated low-mortality areas and 11 saplings/ha in treated high-mortality areas; Appendix S1: Fig. S3). When all post-drought live stems (seedlings, saplings, and trees) are considered together,

hardwoods were the most abundant species in treated stands in areas that experienced moderate or high mortality; in contrast, shade-tolerant species dominated untreated stands (in all mortality severity classes).

Considering saplings and larger trees together (as both size classes are likely to contribute to future overstory density given suitable conditions), stem densities ranged from 233 to 1,301 stems/ha, mostly well above the NRV of adult tree density of roughly 132–234 trees/ha. As the one exception, the plot category with the lowest mean sapling + larger tree density (treated stands in high-mortality areas), mean density (233 trees/ha) was at the upper limit of our NRV estimate, and across this plot category, 86% of plots (12 of 14) had a density exceeding the lower end of the NRV estimate (132 trees/ha; Table 2). The combined tree and sapling density of pines, specifically, in this plot category was particularly low (19 stems/ha; Appendix S1: Fig. S3). In contrast, among plots experiencing low and moderate mortality (<66% basal area mortality), regardless of treated status, mean density of residual trees and saplings alone was sufficient to substantially exceed the NRV of tree density (Fig. 3b), and few individual plots fell below the minimum NRV threshold (Table 2). Most plots (83–100%) had sufficient tree stems to meet U.S. Forest Service stocking criteria for yellow pine forests (USDA 1989), with the exception of the treated plots in the high-mortality class, among which 57% met the criteria (Table 2).

Sapling mortality (i.e., the proportion of saplings that were dead in plots of a given overstory mortality severity and treated status) ranged from 14% in low-mortality, treated plots to 62% in moderate-mortality, untreated plots (Appendix S1: Fig. S4). There was no clear relationship between sapling mortality and overstory mortality severity; however, in both low- and moderate-overstory mortality areas, sapling mortality was significantly lower in treated stands. Notably, in high overstory mortality areas, sapling mortality averaged only 21–26%, despite the fact that overstory mortality in these plots was >67% (by basal area).

DISCUSSION

Drought and treatment effects on overstory stand structure

Density reduction treatments generally moved stand structure metrics (density, BA, and diameter distribution) closer to the NRV, and they remained so even following moderate drought mortality, suggesting that the ecological benefits of treatments (North et al. 2009, North 2012, Stevens et al. 2014) can persist even following notable mortality events. However, in the treated areas experiencing high mortality (>67% BA mortality), tree basal area and density values fell well below NRV, and farther from it than in untreated

TABLE 2. Percentage of plots in each category (treated status and mortality class) exceeding a specified density threshold.

Mortality class	Percentage of plots with density above. . .			
	73 stems/ha	223 stems/ha	371 stems/ha	494 stems/ha
Trees and saplings				
Untreated				
Low	100	98	–	–
Moderate	100	100	–	–
High	96	67	–	–
Treated				
Low	98	63	–	–
Moderate	100	44	–	–
High	86	43	–	–
Trees, saplings, and seedlings				
Untreated				
Low	100	100	98	98
Moderate	100	100	100	100
High	96	83	83	83
Treated				
Low	98	98	98	89
Moderate	100	94	94	94
High	86	71	57	43

Notes: The threshold of 73 stems/ha reflects the approximate lower limit of the natural range of variation (NRV) for tree density, the threshold of 223 stems/ha reflects the approximate upper limit, and the thresholds of 371 and 494 stems/ha (150 and 200 stems/acre) reflect the U.S. Forest Service silvicultural goal for regenerating conifer seedlings (excludes hardwood stems) following stand-replacing disturbance in ponderosa pine and mixed-conifer forests, respectively, in the Pacific Southwest region (USDA 1989). Dashes in the table indicate values that are not relevant (i.e., stem counts that do not include seedlings compared against the USFS seedling regeneration goals). “Trees and saplings” include all individuals ≥ 1.4 m tall.

stands (Figs. 2 and 3). This raises a conundrum: treatment is often seen as an effective means of reducing future drought-related mortality (Egan et al. 2010, van Mantgem et al. 2016, Restaino et al. 2019), but if post-treatment mortality is unusually high, it may also lead to unacceptably low stand densities, depending on the management objectives.

We see several reasons why low post-treatment, post-mortality overstory basal areas and densities should not overly concern managers. First, the effect of treatment in reducing the unnaturally high densities of the smallest diameter trees, one of its primary objectives (North et al. 2009), persists even following high mortality (Fig. 4). Second, due to the abundance of advance regeneration, even most treated high-mortality areas show strong potential for recovery following drought (see *Recovery of stand density*). Third, lower densities may confer greater resistance and resilience to increasing aridity and drought stress expected in the future (Millar and Stephenson 2015, Restaino et al. 2019). Fourth, given the fact that treatment is known to reduce the severity of overstory mortality (Restaino et al. 2019), the areas that were treated but still experienced high mortality may be in the harshest sites, and thus even if they had not been treated, they may have experienced similar BA and density losses. Indeed, most of the treated, high-mortality plots were on the Sierra National Forest (Table 1), where conditions are normally the driest and where drought intensity was the greatest (Fig. 1). Finally, our NRV estimates are means and percentiles derived from multiple studies (Safford and Stevens 2017), but the full range of values for any forest characteristic follows a distribution. If overstory tree basal area and density on the landscape follow a distribution approximating a normal curve, then the low mean values we recorded for basal area and density in the high-mortality treated plots still fall less than two standard deviations from the NRV mean.

Post-drought recovery of stand density

Despite the extremely high mortality of overstory trees in many areas, most stands had relatively abundant regeneration (Fig. 3; Table 2), sufficient to recover tree densities within the natural range of variation of YPMC forests, assuming conditions remain suitable for the young trees to survive and grow. Recovery of NRV density in the majority of plots appears likely even when considering only the residual adult trees and the saplings (Table 2). These individuals are relatively large (>1.4 m height) and well established and therefore likely to survive, particularly given the relatively open growing conditions (i.e., reduced aboveground and belowground competition) following severe mortality.

Although shrub cover in high-mortality plots was relatively high on average (mean approximately 60%), the advanced regeneration saplings are mostly taller than the shrub canopy (data not shown) and will not suffer the heavy light and resource competition that shrubs

pose for post-disturbance seedlings (Lauvaux et al. 2016). Nonetheless, high shrub cover may slow sapling growth due to belowground competition (Lanini and Radosevich 1986), and some management to control shrub biomass may help to speed forest recovery in high-mortality areas. High shrub cover will almost certainly reduce the growth and survival of seedlings, particularly of shade-intolerant pines (Wagner et al. 1989), potentially driving longer-term shifts toward shade-tolerant species dominance (Lauvaux et al. 2016). In high-mortality plots, much of the shrub cover was provided by bear clover, an extremely strong competitor with conifer seedlings despite its low stature (Tappeiner and Helms 1971, McDonald and Everest 1996). Where bear clover is present in areas of high drought mortality, seedling survival and future recruitment may be notably reduced (Tappeiner and Helms 1971), making recovery even more dependent on the advance regeneration saplings. In this regard, pre-drought treatment may slow post-drought conifer recovery because it involves removing the saplings that would otherwise contribute to advance regeneration. Nonetheless, shrub cover values in areas dominated by bear clover were largely within the NRV (Fig. 6b). Occasional patches dominated by bear clover, as opposed to conifers, were likely present in the historical reference condition (see next paragraph).

Despite the apparently strong potential for recovery in most areas that we observed and which has been reported elsewhere (Fettig et al. 2019), we did find that regeneration was weakest in treated areas experiencing high mortality, where 14% of plots had insufficient residual tree and sapling densities to meet the low end of the NRV for tree density (Table 2). Forest managers may wish to augment these “deficient” conifer stem densities with artificial regeneration (likely of pines, the most depauperate post-drought species group relative to NRV) to move stand density closer to NRV. However, a small percentage of lower-density sites may be acceptable to managers given that yellow pine and mixed-conifer forests historically were spatially heterogeneous and frequently included low-density stands as well as openings dominated by shrubs rather than trees (Safford and Stevens 2017), including some relatively open stands containing a high cover (40–80%) of bear clover (Collins et al. 2015, Stephens et al. 2015). We bounded our NRV estimates at the 25th and 75th percentiles of reported values, but tree densities outside this range are not necessarily “unnatural.” The proportion of a given area requiring supplemental planting would be greater if managers wished to achieve stand densities consistently *above* the NRV (Table 2) or assumed high mortality of the advance regeneration. This is particularly true in treated areas, which is intuitive given that treatments are generally intended to move (decrease) stand density toward its NRV.

The relatively high tree and sapling densities in plots experiencing low and moderate drought-related mortality (<67% BA mortality), as well as in some high-

mortality plots, suggest that future density reduction treatments will be required relatively soon if managers wish to keep stand density near the NRV. Indeed, even among untreated moderate-mortality stands, mean density of trees, alone, far exceeded the NRV, demonstrating that even 33–67% (“moderate”) mortality by basal area does not provide sufficient density reduction in the modern forest. This is largely because the basal area loss due to mortality was concentrated in large trees (which contribute disproportionately to BA), due to the tendency of bark beetles, the primary mortality agents in this drought event, to preferentially attack large pines (Furniss and Carolin 1977; Fig. 4). This finding highlights the fact that the effect of drought mortality mediated by insect outbreaks is often the reverse of the effect of density reduction treatments (including wildfire) in that drought mortality disproportionately affects the large trees that managers generally wish to retain, while leaving the smaller trees they usually wish to remove (North et al. 2009, Restaino et al. 2019).

Shifts in species composition

Drought and treatment triggered dramatic shifts in the species composition of overstory trees and regeneration. The disproportionate mortality of pines during the drought led to increased dominance of the overstory by shade-tolerant species and hardwoods. Disproportionate reduction in pine density is frequently observed in modern YPMC forests (Fettig et al. 2019, Restaino et al. 2019), and it is explained by the unnaturally high densities of modern stands. High densities predispose pines to attack by bark beetles (*Dendroctonus* spp.), which experience enhanced attack success when pines are drought-stressed and grow in close proximity (Fettig et al. 2007).

In contrast to drought, treatment seeks to disproportionately remove shade-tolerant trees, which have successfully recruited as a result of fire suppression. Thus, when combining treatment (disproportionate reduction of shade-tolerant trees) with the mortality in this drought event (disproportionate reduction of pines), the net effect is a substantial increase in the relative abundance of hardwoods. This effect is even more pronounced in saplings, likely because fuel treatments target conifer saplings (Agee and Skinner 2005, Schwilk et al. 2009), and hardwoods, if top-killed (e.g., by prescribed fire), have the ability to resprout from the root crown (Plumb and Gomez 1983). Usually, a given top-killed hardwood develops many resprouting stems surrounding the original stem(s); over time, the resprouting stems self-thin to one or a few stems that form the mature tree (Fryer 2007). The clonal origin of resprouts may constrain the potential for hardwood populations to adapt to changing conditions in situ (Schreiber et al. 2013), particularly relative to conifer species that exclusively reproduce sexually. The high relative abundance of hardwood saplings that we observed in high-mortality, treated areas may partially reflect numerous stems

resprouting from a smaller number of hardwood individuals top-killed by treatment. To the extent that this is the case, we may expect the relative abundance of hardwood saplings to decline somewhat (and thus the relative abundance of pines and shade-tolerant conifers to increase) as the stems self-thin to become mature trees. However, the fact that the absolute abundance of hardwood sapling stems was lower following treatment in high-mortality areas (Appendix S1: Fig. S3) suggests that the increase in relative abundance that we observed is not primarily driven by a temporary flush of resprouting stems.

Conditions in the Sierra Nevada are expected to become increasingly challenging, with more frequent drought and wildfire (Westerling et al. 2011, Wang et al. 2017). Shifts toward hardwood dominance may reflect effective reorganization given these new conditions, as the primary hardwood species in our study area, black oak and canyon live oak, are more resistant to outbreak-type insect attack than conifers, are more resilient to high intensity fire (due to their ability to resprout), and are less flammable and thus act to reduce fire severity (Pausas et al. 2004, Safford et al. 2012b, Safford and Stevens 2017). Indeed, several studies in the Sierra Nevada observe or predict increases in hardwood dominance as a consequence of changing climate and disturbance regimes (Lenihan et al. 2008, McIntyre et al. 2015, Liang et al. 2017). In addition to their importance in conferring resistance and resilience to drought and disturbance, oaks are valued for their benefits for wildlife, their important cultural significance to Native Americans, and their contribution to plant and fungal biodiversity (Thornburgh 1990, Long et al. 2016, 2017).

If managers wish for conifers to return to dominance rapidly following high mortality, they may need to plant them, particularly in high-mortality areas that had received density reduction treatments, where hardwood saplings far outnumbered conifer saplings and nearly did among seedlings as well (Fig. 5; Appendix S1: Fig. S3). While hardwood tree and sapling stem density averaged 130 stems/ha in these areas, conifer tree and sapling stem density averaged 33 stems/ha (Appendix S1: Fig. S3). These low densities suggest that species-specific planting (as opposed to removal) is necessary to move toward NRV.

Even if establishment of hardwood dominance is allowed (or facilitated) in the longer term given limited natural disturbance or management, shade-tolerant conifer species may again become dominant, as evidenced by the very high relative abundance of shade-tolerant species we observed among the seedlings in untreated stands (Fig. 5), consistent with other observations in this system (Fettig et al. 2019). Therefore, management to reduce the abundance of shade-tolerant species may be necessary in the future (as well as the present), especially in untreated stands, in the absence of future disturbance (e.g., under continued fire suppression). Although seedlings in untreated stands were dominated by shade-

tolerant species, future species dominance depends not only on relative seedling species abundances but also on relative growth and survival rates. Restoration treatments and/or drought-related mortality, by creating open canopy conditions, can disproportionately favor growth and survival of disturbance-adapted and/or shade-intolerant species such as pines and hardwoods (Zald et al. 2008, Pelz et al. 2018).

Fuels and snags

Fuel loads are important to consider when evaluating potential stand development trajectories, as wildfire can cause high mortality in young stands, potentially leading to longer-term regeneration failure even when regeneration is initially strong. In this regard, post-mortality stand development has a substantial advantage in treated areas, where dead, downed fuel loads are significantly and substantially lower relative to untreated areas (Fig. 7a). Treatment, particularly prescribed fire, likely removed much of the downed fuels present prior to mortality, which otherwise would have largely persisted following the mortality event. The general decline in fuel load with increasing mortality severity (Fig. 7a) may reflect the fact that higher-mortality sites are generally more arid (Young et al. 2017, Restaino et al. 2019) and thus produce fuel more slowly. Regeneration in these sites may therefore be at somewhat lower risk of wildfire, at least prior to snag fall.

Snag loading can also substantially affect future stand trajectories as (1) snags and branches will eventually contribute to downed fuel load when they fall, potentially fomenting large areas of high severity burning (Stephens et al. 2018); (2) when snag density is extremely high (as in many of our plots), a substantial proportion of seedlings, saplings, and small trees are at risk of being crushed or covered by falling snags; and (3) the safety risk of falling snags and operational constraints of fallen snags (i.e., logs) reduces the potential for future active stand management and fire management. These effects are greatly magnified by the exceptionally high post-drought snag densities observed in our study (i.e., approximately 7–80 times greater than NRV) and the fact that the fuel present in drought-associated snags is roughly two to ten times greater than surface fuel loads, depending on mortality severity and treated status. Given that rapid removal of snags was not feasible due to operational constraints, the likely best option for addressing high fuel loads is the use of managed wildfire under low and moderate burning conditions (North et al. 2009).

Drought mortality does not serve as a restoration treatment

Because drought-related mortality has the effect of reducing stand density, one may ask whether the mortality event served as a “natural” restoration treatment.

Drought mortality on its own did result in some limited shifts toward NRV conditions, for example in overall basal area in moderate-mortality areas (Fig. 2) and in tree density in high-mortality plots (Fig. 3). However, for the most part, the effects of drought mortality on untreated YPMC forest stands were either ineffective in restoring NRV conditions or resulted in even greater departure from NRV. For example, untreated low and moderate drought mortality plots continued to support very high tree densities (Fig. 3); tree size-class distributions in untreated stands after the drought event supported high positive departures in small trees and high negative departures in large trees in all mortality scenarios (Fig. 4); mortality drove increases in the relative abundance of shade-tolerant conifers to values even farther above our NRV estimate (while pine relative abundance decreased to far below it; Fig. 5); and snag basal areas were >10 times higher than our NRV estimate and were particularly high in moderate and high-mortality stands (Fig. 7b). In contrast to drought-related mortality, density reduction treatments moved nearly all metrics closer to or within our NRV estimates (Figs. 2–7), suggesting they are more effective as restoration treatments.

Conclusions and management implications

We have shown that many of the intended effects of treatment (e.g., removal of small trees, shade-tolerant species, and surface fuels) appear to persist even following severe mortality. Thus, application of prescribed fire and/or mechanical thinning may be effective for achieving management goals whether or not treated areas ultimately experience high mortality. Although treated areas that experience high mortality have relatively low overstory live tree densities, we found that they show relatively strong potential for rapid recovery of overstory density within or above the NRV (Fig. 3). From a tree density perspective, supplemental tree planting appears unnecessary across the majority of high-mortality area (Table 2), but if dominance of conifers specifically (as opposed to hardwoods) is desired in the short term, planting them may be necessary, particularly in treated stands given the low densities of conifers observed there (Appendix S1: Fig. S3). Given that fuel loads will increase as dead branches and snags fall, stand recovery in high-mortality areas will likely depend on (1) using prescribed fire or managed wildfire under low and moderate burning conditions to reduce fuel loads (North et al. 2009) and/or (2) preventing the landscape from burning under severe fire weather conditions for at least a few decades.

Treated, high-mortality areas are more likely (relative to untreated and/or lower-mortality areas) to become dominated by hardwood species (Fig. 5), an outcome that may confer greater resistance and resilience to increasingly harsh future conditions while supporting biodiversity and cultural values. In contrast, untreated

areas experiencing high mortality became significantly enriched in disturbance-sensitive, shade-tolerant, conifer species, suggesting that management to shift dominance toward more disturbance-adapted pines and hardwoods (such as species-specific thinning and/or planting) may be required to promote future resilience. Because pre-drought treatment also substantially reduces surface fuel loading (even following severe mortality; Fig. 7), it reduces the probability that a post-mortality landscape might experience severe wildfire that would kill regenerating trees and thus prolong or preclude effective post-drought recovery. The effectiveness of stand density reduction treatment in reducing the probability of severe drought-related mortality in the first place (Restaino et al. 2019) further suggests that treatment may become increasingly important in a future with more extreme droughts.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2002/full>

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: <https://doi.org/10.25338/b8tk5p>