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Changing climate reallocates the carbon debt of frequent-fire forests

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Abstract

Ongoing climate change will alter the carbon carrying capacity of forests as they adjust to climatic extremes and changing disturbance regimes. In frequent-fire forests, increasing drought frequency and severity are already causing widespread tree mortality events, which can exacerbate the carbon debt that has developed as a result of fire exclusion. Forest management techniques that reduce tree density and surface fuels decrease the risk of high-severity wildfire and may also limit drought-induced mortality by reducing competition. We used a long-term thinning and burning experiment in a mixed-conifer forest to investigate the effects of the 2012–2015 California drought on forest carbon dynamics in each treatment, including the carbon emissions from a second-entry prescribed fire that followed the drought. We assessed differences in carbon stability and tree survival across treatments, expecting that both carbon stability and survival probability would increase with increasing treatment intensity (decreasing basal area). Additionally, we analyzed the effects of drought- mortality on second-entry burn emissions and compared emissions for the first- and second-entry burns. We found a non-linear relationship between treatment intensity and carbon stability, which was in part driven by varying relationships between individual tree growing space and survival across treatments. Drought mortality increased dead tree and surface fuel carbon in all treatments, which contributed to higher second-entry burn emissions for two of the three burn treatments when compared to the first burn. Our findings suggest that restoration treatments will not serve as a panacea for ongoing climate change and that the carbon debt of these forests will become increasingly unstable as the carbon carrying capacity adjusts to severe drought events. Managing the carbon debt with prescribed fire will help reduce the risk of additional mortality from wildfire, but at an increasing carbon cost for forest management.

KEYWORDS

carbon carrying capacity, carbon stability, drought, dry conifer forest, forest management, high-severity wildfire, repeat fire

1 | INTRODUCTION

Forests are a substantial contributor to the terrestrial carbon (C) sink, but C uptake and stability are sensitive to anthropogenic and natural disturbances (Reichstein et al., 2013; Seidl, Schelhaas, Rammer, & Verkerk, 2014). The C carrying capacity of a forest—the amount of C capable of being stored by the ecosystem—is in part determined by the prevailing climate (Keith, Mackey, & Lindenmayer, 2009). However, the current climate has become increasingly non-stationary, with climatic extremes becoming more severe, frequent, and prolonged (AghaKouchak, Easterling, Hsu, Schubert, & Sorooshian, 2013; Cheng, AghaKouchak, Gilleland, & Katz, 2014). The other driver of C carrying capacity, prevailing natural disturbance regimes, has already been impacted by fire exclusion in historically frequent-fire forests and has increased the total C stored by these systems, but with greater risk of large-scale C loss from high-severity wildfire (Collins, Everett, & Stephens, 2011; Harris, Scholl, Young, Estes, & Taylor, 2019; Miller, Safford, Crimmins, & Thode, 2009). In these dry forest types, climate change is compounding risks to C stability through temperature-disturbance interactions, such as hotter droughts and increased vegetation flammability (Abatzoglou & Williams, 2016; Allen, Breshears, & McDowell, 2015). Restoring forest structure and surface fire in dry conifer forests can help stabilize forest C against loss from high-severity fire, but carry the C costs associated with management (Hurteau, North, Koch, & Hungate, 2019; Krofcheck, Hurteau, Scheller, & Loudermilk, 2017; North, Hurteau, & Innes, 2009; Stephens, Moghaddas, Hartsough, Moghaddas, & Clinton, 2009). While the contribution of forest restoration to stabilizing C against high-severity wildfire is well-supported, the effects of management on C stability during drought are unresolved (Voelker et al., 2019; Young et al., 2017).With ongoing climate change, the C costs of maintaining resistance to high-severity fire will depend of the sensitivity of the C carrying capacity to climatic extremes.

Historically, regular low- and mixed-severity wildfires modulated the amplitude of change of the live tree C stock in frequent-fire forests, stabilizing the C storage of these systems at large spatial scales over time (Hurteau, 2013). Wildfire interacted with topography, fuels, and weather to produce varying fire effects across the landscape (Hessburg et al., 2019). The resulting structural heterogeneity distributed C through different biomass pools (i.e., live trees, dead trees, surface fuels), which in turn, influenced the effects of subsequent wildfires (Perry et al., 2011). Furthermore, frequent burning maintained the distribution of C in fewer, large trees by consuming fine fuels and small trees that had accumulated during years of high productivity (Bonnicksen & Stone, 1981; Covington & Moore, 1994; North, Innes, & Zald, 2007). Over the past century, concerted efforts in the Western United States to exclude wildfire from dry conifer forests has increased tree density and surface fuels, causing total ecosystem C to surpass the C carrying capacity (Collins et al., 2011; Harris et al., 2019; Parsons & DeBenedetti, 1979; van Wagtendonk, 1985). The increase in total C above the carrying capacity produces a C debt to the atmosphere because the additional C stored in the system is less stable. The instability of the C debt is likely to compound under non-stationary climate as the C carrying capacity equilibrates to climatic extremes, such as severe droughts, which can transfer large amounts of live tree C to dead tree and surface fuel C. The effects of climate change, coupled with surface and ladder fuel accumulation, exacerbate the risk of further transfers of C from live trees to dead trees and substantial emissions of C to the atmosphere from high-severity wildfire (Liang, Hurteau, & Westerling, 2017; Miller et al., 2009; Westerling, Hidalgo, Cayan, & Swetnam, 2006).

Forest management to reduce the risk of fire-driven tree mortality can stabilize forest C but requires a reduction or redistribution of C through burning and mechanical thinning and regular C emissions from the reintroduction of frequent fire (Bennett, Aponte, Baker, & Tolhurst, 2014; Mitchell, Harmon, & O'Connell, 2009; North et al., 2009; Sorensen, Finkral, Kolb, & Huang, 2011). The reductions in tree density that are typically required to mitigate the risk of high-severity fire may also increase C stability during drought due to reduced water competition between trees. By increasing growing space and creating structural heterogeneity, reducing tree density can increase water availability, resulting in higher growth rates, stomatal conductance, and C assimilation compared to trees growing in unmanaged stands (Di Matteo, Nardi, & Fabbio, 2017; Giuggiola et al., 2016; Lechuga, Carraro, Viñegla, Carreira, & Linares, 2017). Additionally, recent evidence indicates that trees growing in a less competitive environment are more resilient to drought, exhibiting higher growth rates and lower mortality rates during drought events (Giuggiola, Bugmann, Zingg, Dobbertin, & Rigling, 2013; Sohn, Saha, & Bauhus, 2016; van Mantgem, Caprio, Stephenson, & Das, 2016; Vernon, Sherriff, van Mantgem, & Kane, 2018; Young et al., 2017). However, over the past decade hotter and more prolonged droughts have caused widespread tree mortality events and it is unclear if management to reduce competition will be sufficient to limit mortality during extreme droughts (Allen et al., 2015; Williams et al., 2013).

Widespread drought-related mortality can exacerbate the C debt of frequent-fire forests, with dead trees adding fuel that increases the risk of high-severity wildfire. The alteration of the C carrying capacity due to non-stationary climate, combined with disturbances such as fire, can act as a catalyst for substantial change (Liang et al., 2017), requiring C emissions from prescribed burning to maintain system-level resistance to high-severity wildfire (Stephens et al., 2018). Without subsequent burning, the increase in dead tree and surface fuel C that results from drought mortality will remain on the landscape, increasing the risk that drought and wildfire result in compounding live tree C loss. The reintroduction of fire in dry forests utilizes repeat burning to approximate the historic fire return interval, with the expectation that C emissions will decrease with each additional burn due to a reduction in available fuel. However, it is unclear how the sensitivity of the C carrying capacity to drought and the resulting reallocation of the C debt will influence the C cost of subsequent forest management.

In the Sierra Nevada of California, an extreme drought from 2012 to 2015 caused widespread tree mortality, especially in the southern part of the mountain range (Asner et al., 2016). We used a long-term experiment that implemented combinations of prescribed burning and mechanical thinning to quantify the effects of drought on the distribution of C as a function of treatment intensity and the C dynamics of a second-entry prescribed fire. We hypothesized that live tree C stability and survival during drought would vary by treatment, with treatments that had the largest reduction in basal area exhibiting the highest C stability due to reduced competition. We also hypothesized that second-entry burn emissions would be lower than the first-entry burn, with the expectation that the reduction of

C stocks after the initial treatments would result in less fuel available to burn. Finally, we hypothesized that the second-entry burn would reduce surface fuel C stocks back to predrought levels.

2 | MATERIALS AND METHODS

2.1 | Study site

This study was conducted at the Teakettle Experimental Forest (Teakettle), a 1,300 ha reserve of old-growth forest established in 1938. Teakettle is located 80 km east of Fresno, CA on the north fork of the Kings River at an elevation ranging from 1,900 to 2,600 m. The climate is Mediterranean, typical of the western Sierra Nevada, with an average precipitation of 125 cm that falls predominantly as snow between November and April (North et al., 2002). The site has no prior history of logging or known stand-replacing disturbance. For a complete site description, see North et al. (2002). Additionally, from 2012 to 2015 this area experienced a severe drought, with the driest 12-month period on record in California recorded during this event (Swain et al., 2014). The drought was characterized by precipitation deficits and high temperatures during both the wet and dry season (AghaKouchak, Cheng, Mazdiyasni, & Farahmand, 2014; Willams et al., 2015).

The dominant tree species that comprise Teakettle's mixed-conifer forest type are white fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr), incense-cedar (*Calocedrus decurrens* (Torr.) Florin), sugar pine (*Pinus lambertiana* Dougl.) and Jeffrey Pine (*Pinus jeffreyi* Grev. & Balf., Rundel, Parson, & Gordon, 1988). Red fir (*Abies magnifica* A. Murr.) and California black oak (*Quercus kelloggii* Newberry) are also found at the site but at lower densities (North et al., 2007). The mean fire return interval at Teakettle was 17.3 years prior to the last known fire, which occurred in 1865 (North, Hurteau, Fiegener, & Barbour, 2005). The past 155 years have been a period of fire exclusion. A reconstruction of the fire-maintained structure of this forest found that it was characterized by a low density (67 trees/ha) of large trees (quadratic mean diameter 49.5 cm), with Jeffrey pine and sugar pine accounting for 48.9% of the trees (North et al., 2007). After fire exclusion, substantial establishment of shade-tolerant white fir and incense-cedar occurred, which was coincident with years of high precipitation (North et al., 2005). These establishment events resulted in higher tree densities (469 tree/ha) dominated by white fir (67.6%, North et al., 2007). Prior to treatment, white fir, incense-cedar, and red fir comprised approximately 84% of the basal area at Teakettle, while sugar pine and Jeffrey pine comprised 14%.

2.2 | Treatments and data collection

Within the mixed-conifer forest type at Teakettle, 18 permanent 4 ha treatment units were established in 1998. Using a full-factorial design, treatments consisted of two levels of prescribed burning (Burn and Unburned) and three levels of thinning (No Thin, Understory Thin and Overstory Thin) for a total of six treatments. Each treatment was replicated across three treatment units (Figure S1). Understory thinning removed trees between 25 and 76 cm diameter at breast height (DBH) while retaining at least 40% canopy cover, following the prescription guidelines outlined in Verner et al. (1992). Overstory thinning removed trees greater than 25 cm DBH while retaining 22 evenly spaced large diameter (>100 cm) trees per hectare (TPH). All cut trees were removed from the site. The understory thinning reduced stem densities from a pretreatment mean of 469 TPH to a posttreatment mean of 239.5 TPH, reducing the mean basal area by 15.2 m^2/ha. The overstory thinning posttreatment mean was 150.3 TPH (pretreatment mean of 469 TPH) and the mean basal area was reduced by 33.7 m^2/ha (North et al., 2007). The treatments that included thinning and burning were thinned in 2000 and burned in 2001 and the thin-only treatments were thinned in 2001. The prescribed burn was applied in late-October 2001 after the first major fall rain. In 2002, the overstory thin treatments were planted with 2-year-old container stock, accounting for less than 3% of total regeneration in these plots. A second-entry prescribed burn was implemented in the burn plots during the fall of 2017, to approximate the fire return interval for the site.

Prior to treatment, all trees were mapped, tagged, and measured, and sampling gridpoints were established within all 18 treatment units. Gridpoints for two of the three treatment replicates were established on a 50 m grid with nine points per treatment unit. One replicate was selected for intensive sampling and used a 25 m grid with 49 points per treatment unit. Surface fuels were measured using a modified planar-intercept method, with three 15 m transects measured at nine gridpoints within each treatment unit, to quantify 1, 10, 100, and 1,000 hr fuel loads and litter depths (Brown, 1974). Fuel classifications are based on the amount of time it takes for a fuel to respond to changes in atmospheric moisture. The 1,000 hr fuels are referred to as coarse woody debris (CWD) and 1, 10, and 100 hr fuels are collectively referred to as fine woody debris (FWD). Percent cover of shrub species was visually estimated using a 10 m^2 circular plot at each gridpoint. Tree measurements and fuel surveys occurred pretreatment (1999–2001), posttreatment (2002–2004), 10 years posttreatment (2011 and 2012), 15 years posttreatment (2016 and 2017), and post-second-entry burn (2018 and 2019). Additionally, large trees greater than 75 cm DBH were measured in 2008. All saplings that had grown to greater than 5 cm in diameter were added to the tree dataset during each remeasure. For each mapped tree, DBH, species, status, and decay class (Maser, Anderson, Cromack, Williams, & Martin, 1979) were recorded. For changes in status, it was noted whether the tree transitioned from live to dead, from standing to dead on the ground, was consumed during the burn, or was cut.

2.3 | Carbon calculations

We partitioned the C stock into the following biomass pools: live tree and dead tree (snag) biomass, CWD, FWD, and litter. To calculate live tree and snag biomass, we used genus-specific allometric equations from Jenkins, Chojnacky, Heath, and Birdsey (2003). Litter biomass was calculated using the coefficients from van Wagtendonk, Benedict, and Sydoriak (1998), assuming a C concentration of 37% (Smith & Heath, 2002). CWD and FWD biomass were calculated following Brown (1974). Biomass of CWD varies by decay class and was quantified following Harmon, Cromack, and Smith (1987). CWD and FWD calculations were converted to megagrams per hectare using the equation outlined in van Wagtendonk, Benedict, and Sydoriak (1996). Shrub biomass was quantified using a site-specific relationship between percent cover and biomass (Hurteau & North, 2008) and assumed a C concentration of 49% (Campbell, Alberti, Martin, & Law, 2009). Prescribed fire emissions were calculated using the pre- and postburn C stock values.

2.4 | Analyses

All statistical analyses were conducted in R Version 3.6.3 (R Core Team, 2020). To assess the effects of the thinning and burning on C stability during the 2012–2015 drought, we used a binomial logistic regression to analyze the probability of tree survival during the drought period using growing space, treatment, and tree size as predictor variables. Growing space in meters squared was calculated for each tree using Voronoi polygons. Additionally, we calculated a C stability metric for each treatment following the temporal stability calculation described in Tilman, Reich, and Knops (2006). For our stability calculation, we calculated total C (Mg C/ha) of all live trees greater than 75 cm DBH in each treatment for 2008, 2011, and 2017. Large trees were used since they contribute the largest proportion of C to the live tree C pool. Immediate posttreatment C totals were excluded from our calculation to avoid capturing treatment-related mortality from the initial treatments. To calculate the temporal stability of live tree C during the drought period, we divided the mean C value for the time period by the standard deviation of the residuals for each treatment. Smaller values indicate low carbon stability, or a high degree of variation when compared to the mean. We then used linear regression to determine whether posttreatment basal area (measured in 2004), a proxy for treatment intensity, was a significant predictor of the C stability metric. We tested for linearity, normality, and homogeneity to ensure assumptions of a parametric regression were met. To analyze treatment differences for each C pool (live trees, snags, CWD, FWD, litter, and total C) through time, we conducted a repeated measures ANOVA using the nlme package and the multcomp and lsmeans packages for Tukey's post hoc tests (Hothorn, Bretz, & Westfall, 2008; Lenth, 2016; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2020). Because shrub C is the smallest pool (<0.09% of total carbon), it did not experience significant changes through time and was excluded from analyses and results. To assess the transition of dead tree C to surface fuel C, we used binomial logistic regression to analyze the probability of snag fall during the drought period. For this analysis, we only included trees that died during the drought, using treatment and DBH as predictor variables.

To evaluate treatment differences in emissions during the second-entry burn, we used ANOVA. Additionally, we used a binomial logistic regression to analyze the probability of snag consumption during the first and second burn using treatment and decay class as predictor variables. To determine the effects of the second-entry burn on the C stocks, we used a two sample t test to compare each C pool before and after the burn across all burn treatments. For litter, FWD, and CWD we used 2018 as the postburn year and for live and dead trees we used 2019 as the postburn year to capture burn-related mortality. To compare total surface fuel C across all measure years, we used ANOVA. We tested for normality using the Shapiro–Wilk test and for homoscedasticity using Bartlett's test prior to running ANOVA. For all ANOVAs, the data were log-transformed if assumptions were not met. For all logistic regressions, we tested the linearity of the logit and for multicollinearity (VIF threshold = 3) using the package car (Fox & Weisberg, 2019). All figures were created using ggplot2 and formatted using the ggsci, ggpubr and data.table packages (Dowle & Srinivasan, 2019; Kassambara, 2020; Wickham, 2016; Xiao, 2018).

3 | RESULTS

3.1 | The effects of treatments on carbon stability and drought survival

C stability and tree survival during the drought period varied by treatment. Growing space was a significant predictor of tree survival ($p < .001$), with the likelihood of survival increasing with growing space (Figure 1). However, this trend varied by treatment with the probability of survival decreasing with increasing growing space for small (<25 cm DBH) and medium (25 cm < DBH <75 cm DBH) sized trees in the Burn/Understory and Burn/Overstory Thin treatments (Figure 1). The temporal stability of large tree C also varied by treatment, with the highest stability in the Overstory Thin, Burn Only and Burn/Understory Thin treatments and the lowest stability in the Burn/Overstory Thin treatment (Figure 2). Posttreatment basal area was not a strong predictor of C stability during the drought period ($p = .1$, $r^2 = .16$).

3.2 | The effects of drought on carbon distribution

The drought resulted in large decreases in live tree C (−48 ± 26 Mg/ha) and substantial increases in dead tree (45 ± 27 Mg/ha) and CWD (10 ± 4 Mg/ha) C across all treatments (Figure 3; Figure S2; Table S1). Additionally, total surface fuel C (CWD, FWD, and litter) was significantly higher in 2017 than 2011 (Figure 4a, $p = .043$). We found significant differences in live tree C decreases ($p < .01$) and dead tree C increases ($p < .01$) between treatments, but not between the increases in surface fuel C pools (CWD: $p = .87$; FWD: $p = .93$; Litter: $p = .82$). Snag fall during the drought period also varied by treatment, with The Burn/Understory Thin and Burn/

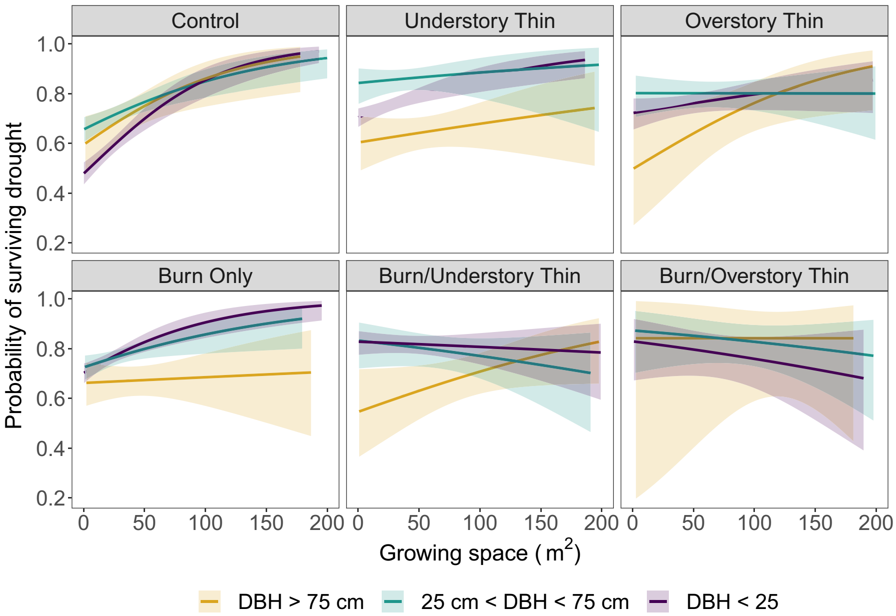

FIGURE 1 Binomial logistic regression of the probability of tree survival during the drought period (measure years 2011–2017) by tree size (diameter at breast height) and growing space. Shading represents 95% confidence intervals. Trees with a growing space greater than 200 m^2 were omitted (~3% of trees) from the figure but were included in the analysis. Growing space ranged from 0.1 to 1,500 m^2 [Colour figure can be viewed at wileyonlinelibrary.com]

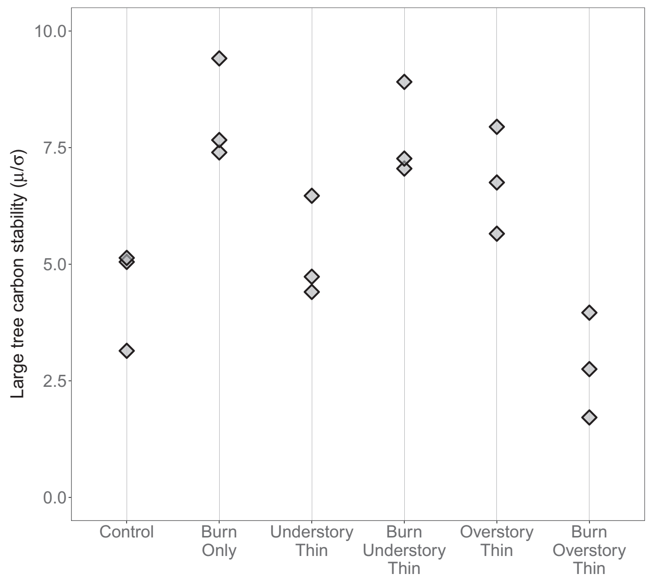

FIGURE 2 Temporal carbon stability of live trees (>75 cm diameter at breast height) during the drought period (measure years 2008–2017). Temporal carbon stability was calculated by dividing the mean live tree C value for a treatment replicate by the standard deviation of the residuals. Treatments are ordered left to right by increasing treatment intensity (decreasing posttreatment basal area). Each symbol represents the carbon stability value calculated for each treatment replicate. Low stability values indicate high temporal variation in relation to the mean. High stability values indicate low temporal variation in relation to the mean

Overstory Thin treatments having a higher probability of snag fall than the Burn Only, Understory Thin and Control treatments (Figure S3, $p < .05$). While all treatments had the highest probability of snag fall among small diameter snags, the Burn/Understory Thin treatment had a higher probability of snag fall among larger diameter snags compared to other treatments (Figure S3). This treatment also had the largest proportion of snag C becoming CWD, with 15% of the C that transitioned from live to dead during the drought becoming surface fuel by 2017.

3.3 | Second-entry burn emissions, consumption, and effects on carbon stocks

We had hypothesized that second-entry burn emissions would be lower than the initial burn due to the reductions in stand density and surface fuel loads from the initial treatments. However, we found that second-entry burn emissions increased slightly in the Burn Only (39.8–42.8 Mg/ha) and Burn/Understory Thin (33.4–54.4 Mg/ha) treatments when compared to the first-entry burn, while emissions from the Burn/Overstory Thin treatment decreased (34.0–18.5 Mg/ha, Figure 4b). Second-entry burn emissions were significantly different between the Burn/Understory Thin and Burn/Overstory Thin treatments ($p = .028$). The second-entry burn was characterized by higher emissions from the dead tree and CWD C pools for the Burn Only treatment (Dead Tree = 4.7 ± 25 Mg/ha, CWD = 1.1 ± 9.9 Mg/ha) and Burn/Understory Thin treatment (Dead Tree = 9.7 ± 10.3 Mg/ha, CWD = 6.2 ± 9.9 Mg/ha) when compared to the first burn. Surface fuel C consumption during the second-entry burn resulted in significant reductions in litter and CWD ($p < .01$) and postburn surface fuel levels that were statistically similar to predrought levels (Figure 4a, $p = .93$). The second-entry burn did not result in significant reductions to the live tree or FWD C pools (Figure S2; Figure 4a, $p > .05$). Additionally, the probability of snag consumption was higher in the second-entry burn than the first-entry burn ($p < .001$), with a higher probability of consumption for smaller diameter snags and snags of higher decay classes. While snag consumption was higher, it did not significantly reduce the dead tree C pool ($p = .65$) due to the substantial increases in dead tree C from drought-mortality (Figure S2). Furthermore, consumption of large diameter, decay class 5 snags was highest in the Burn/Understory Thin and Burn/Overstory Thin treatments (Figure S4).

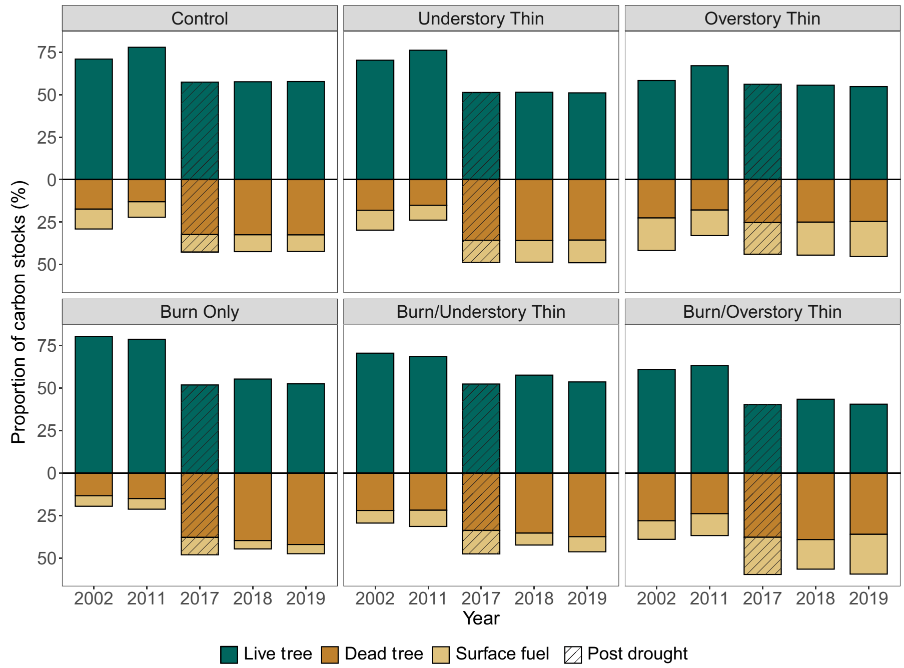

FIGURE 3 The proportion of carbon in the live tree, dead tree, and surface fuel carbon pools for each measure year. Hash marks (2017) indicate the first measure year after the 2012–2015 drought. Post-second-entry burn measurements occurred in 2018 and 2019 [Colour figure can be viewed at wileyonlinelibrary.com]

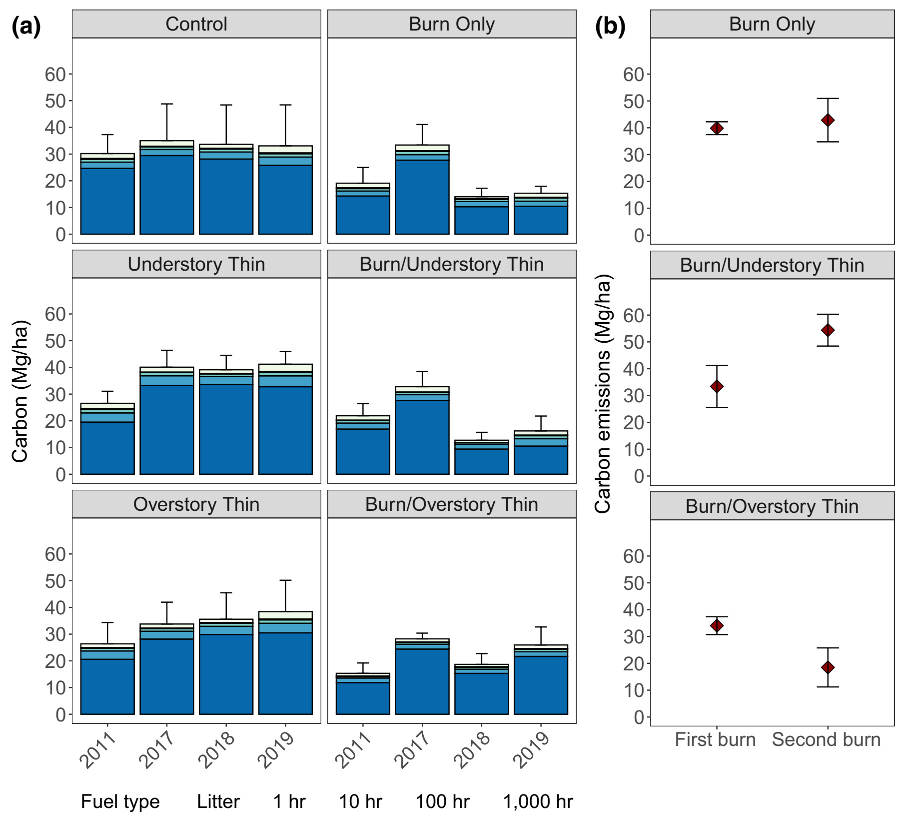

FIGURE 4 (a) Surface fuel carbon for each treatment before the drought (2011), after the drought (2017) and after the second-entry burn (2018 and 2019). Thousand hour fuels are referred to as coarse woody debris (CWD) and 1, 10, and 100 hr fuels are collectively referred to as fine woody debris (FWD). Total surface fuel C was significantly higher in 2017 than 2011 when considering all treatments ($p = .043$). Error bars represent standard error. (b) Carbon emissions from the first- and second-entry burn for each burn treatment. Error bars represent standard error [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Changes in prevailing climate and disturbance regimes are altering the C carrying capacity of fire-prone forests (Anderegg et al., 2015; Millar & Stephenson, 2015; Nolan et al., 2019; Seidl et al., 2014). While the efficacy of forest treatments to reduce the risk of high severity wildfire is well-established (Agee & Skinner, 2005), the effectiveness of these treatments at promoting C stability during drought and the C dynamics of subsequent management is not as well studied. We had hypothesized that live tree C stability under drought would increase with increasing treatment intensity. While we found that C stability and tree survival during drought varied by treatment, this relationship was non-linear (Figures 1 and 2). Furthermore, while the magnitude of live tree C loss during drought also varied by treatment (Figure S2), our results suggest that these treatments will not serve as a panacea for the effects of ongoing climate change, with all treatments experiencing a substantial redistribution of live tree C into dead tree and surface fuel pools (Figure 3).

While the redistribution of C across different biomass pools was ubiquitous, treatments that involved thinning reduced stand density and increased growing space, which influenced the probability of tree survival during drought (Figure 1). This result was likely due to reduced competition for soil moisture which alleviated water stress during the drought period (Giuggiola et al., 2013). Because drought often disproportionately affects large trees, their loss can have a significant impact on the distribution and storage of C in drought affected ecosystems (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; da Costa et al., 2010; Yang et al., 2018). As a result, the Overstory Thin and Burn/Understory Thin treatments which increased the probability of large tree survival exhibited higher C stability values during the drought (Figures 1 and 2). However, we did find that the probability of tree survival decreased with increasing growing space for medium sized trees (DBH between 25 and 75 cm) in the Overstory Thin, Burn/Understory Thin and Burn/Overstory Thin treatments and for small trees (<25 cm) in the Burn/Understory Thin and Burn/Overstory Thin treatments. One potential explanation for this result is that the reduction in stand density resulted in a postthinning growth release and associated increase in biomass which could not be supported during a prolonged drought period (Brown, Murphy, Fanson, & Tolsma, 2019; D'Amato, Bradford, Fraver, & Palik, 2013; Hood, Cluck, Jones, & Pinnell, 2018). This "structural overshoot" may become a significant source of tree mortality in thinned stands if annual oscillations in precipitation become more pronounced under changing climate conditions (Goulden & Bales, 2019; Jump et al., 2017).

The probability of tree survival was also influenced by whether a tree was attacked by bark beetles during the drought period (Steel et al., 2020). Susceptibility to beetle infestation varies with stand density, species assemblage, and tree size, and bark beetle attack can be higher in trees that have experienced prescribed fire (Maloney et al., 2008; Pile, Meyer, Rojas, Roe, & Smith, 2019; Schwilk, Knapp, Ferrenberg, Keeley, & Caprio, 2006; Steel et al., 2020). This relationship between prescribed fire and bark beetle susceptibility may explain the low C stability value observed in the Burn/Overstory Thin treatment (Figure 2), with bark beetles killing larger trees which have a greater proportional representation in this treatment. This treatment also exhibited a negative relationship between growing space and survival probability (Figure 1), which may be due to bark beetle infestation increasing mortality rates despite increases in growing space.

The widespread drought-related mortality that occurred in the southern Sierra Nevada may, in part, has been a function of the high biomass present in these fire-excluded forests (van Mantgem et al., 2016; Young et al., 2017). However, our treatments that had significantly lower live tree biomass and still experienced substantial drought-mortality suggest that we should expect additional reductions in live tree C as the C carrying capacity is influenced by ongoing climate change (Figure S2). The increase in fuel loading from these mortality events redistributes the C debt in fire-prone forests, which has implications for the C cost and C dynamics of subsequent management activities. The hypothesis for the second-entry burn at Teakettle, barring the occurrence of an extreme drought, was that emissions would be lower relative to the first, because the first-entry burn consumed a build-up of FWD and litter that had accumulated with over a century of fire exclusion. However, we found that the drought's reallocation of the C debt resulted in slight increases in emissions for both the Burn Only and Burn/Understory Thin treatments. These increases were driven by increased consumption of snag and CWD carbon, the C pools that experienced the largest increases from drought-related mortality (Figures 3 and 4a). The Burn/Overstory thin treatment did meet our expectation of reduced emissions from the second-entry burn, likely due to this treatment experiencing the largest reduction in standing biomass during the initial treatment. Furthermore, burn-related mortality reduced tree density beyond that of the Overstory Thin treatment. This substantial reduction in standing biomass may also explain the low C stability metric calculated for this treatment, with low live tree C averages for each treatment replicate contributing to the low stability values. Interactions between the overstory canopy, fuel moisture, and the understory plant response may explain some of the consumption differences between treatments. For example, thinning and overstory mortality results in a more open canopy which reduces fuel moisture as higher amounts of solar radiation reach the forest floor (Cawson, Duff, Tolhurst, Baillie, & Penman, 2017; Ma, Concilio, Oakley, North, & Chen, 2010). This could contribute to our finding that the probability of snag consumption was highest in the Burn/Understory Thin and Burn/Overstory Thin treatments for large diameter, decay class 5 snags (Figure S4). Furthermore, in the Burn/Overstory Thin treatment, a significant increase in shrub cover in the 16 years following treatment implementation (Goodwin, North, Zald, & Hurteau, 2018), may have limited the spread of prescribed fire. While the C dynamics of the second-entry burn were largely influenced by the drought's redistribution of C, the differences between which C pools were consumed in each treatment were likely influenced by the initial treatment's alteration of the fuel structure and light environment (Innes, North, & Williamson, 2006; Ma et al., 2010).

While second-entry burn emissions were higher than expected in two of the burn treatments due to drought-related fuel inputs, the burn successfully dealt with a portion of the C debt (Figure 4a; Figure S2). The second-entry burn returned surface fuels in the burn treatments back to predrought levels. However, in the unburned plots, surface fuel C levels remained high, which can elevate the risk of high-severity wildfire (Figure 4a). Managing the increased dead tree and surface fuels associated with drought-induced mortality is necessary to limit the potential for "mass fire" (Stephens et al., 2018). As our work demonstrates, repeat prescribed fire that approximates the historic fire return interval of frequent-fire forests can reduce the wildfire risk associated with drought-related fuel inputs. However, this will come at the cost of additional C emissions to the atmosphere and the expectation that emissions will decrease with each subsequent burn may no longer hold with ongoing climate change.

As the climate continues to change, we can also expect associated changes in the C carrying capacity of forests (Liang et al., 2017).

Our results indicate that dry conifer forests may experience a reduction in their C carrying capacity, evident by the loss of live tree C across all treatments as the C carrying capacity equilibrated to a prolonged drought event. This reduction in the C carrying capacity from drought-induced mortality exacerbates the C debt that has already accrued from fire exclusion pushing frequent-fire forests beyond their historic C carrying capacity. Our results demonstrate that forest restoration can increase C stability in the face of extreme drought but is unlikely to make forests completely resilient to non-stationary climate. As extreme climatic events continue to cause changes in the distribution of C throughout dry conifer forests, managing fire to maintain this ecosystem process will be central to mitigating the risk of large, catastrophic wildfires and managing the increasing instability of the C debt.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in "Supporting data for changing climate reallocates the carbon debt of frequent-fire forests" at https://doi.org/10.5061/dryad.7pvmcvdqn.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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