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Large-diameter trees dominate snag and surface biomass following reintroduced fire

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Abstract

The reintroduction of fire to landscapes where it was once common is considered a priority to restore historical forest dynamics, including reducing tree density and decreasing levels of woody biomass on the forest floor. However, reintroducing fire causes tree mortality that can have unintended ecological outcomes related to woody biomass, with potential impacts to fuel accumulation, carbon sequestration, subsequent fire severity, and forest management. In this study, we examine the interplay between fire and carbon dynamics by asking how reintroduced fire impacts fuel accumulation, carbon sequestration, and subsequent fire severity potential. Beginning pre-fire, and continuing 6 years post-fire, we tracked all live, dead, and fallen trees ≥ 1 cm in diameter and mapped all pieces of deadwood (downed woody debris) originating from tree boles ≥ 10 cm diameter and ≥ 1 m in length in 25.6 ha of an *Abies concolor*/*Pinus lambertiana* forest in the central Sierra Nevada, California, USA. We also tracked surface fuels along 2240 m of planar transects pre-fire, immediately post-fire, and 6 years post-fire. Six years after moderate-severity fire, deadwood ≥ 10 cm diameter was 73 Mg ha^{-1} , comprised of 32 Mg ha^{-1} that persisted through fire and 41 Mg ha^{-1} of newly fallen wood (compared to 72 Mg ha^{-1} pre-fire). Woody surface fuel loading was spatially heterogeneous, with mass varying almost four orders of magnitude at the scale of $20 \text{ m} \times 20 \text{ m}$ quadrats (minimum, 0.1 Mg ha^{-1} ; mean, 73 Mg ha^{-1} ; maximum, 497 Mg ha^{-1}). Wood from large-diameter trees (≥ 60 cm diameter) comprised 57% of surface fuel in 2019, but was 75% of snag biomass, indicating high contributions to current and future fuel loading. Reintroduction of fire does not consume all large-diameter fuel and generates high levels of surface fuels ≥ 10 cm diameter within 6 years. Repeated fires are needed to reduce surface fuel loading.

Keywords: California Rim Fire, Fuel reduction, Sierra Nevada mixed-conifer, Smithsonian ForestGEO, Yosemite Forest Dynamics Plot, Yosemite National Park

Introduction

Reducing woody biomass fuel loads through reintroduction of fire is seen as an important step to decreasing future fire risk and increasing forest resilience in many ecosystems of western North America (Larson et al. 2013, Hessburg et al. 2015, Valliant et al. 2016). Forests where fire was once frequent have been reported to have higher tree densities, particularly of smaller and medium trees,

than was common prior to the 20th century (i.e., Becker and Lutz 2016, Levine et al. 2017, 2019). Although fire-induced mortality of smaller trees may be a desired outcome of reintroduced fire, one unintended consequence is the mortality of a relatively high proportion of smaller trees in addition to the medium and large-diameter trees surviving initial fire damage but succumbing to delayed fire effects (Furniss et al. 2019, 2020a). Because fire rarely consumes the boles of live trees, this pulse of delayed mortality can increase post-fire fuel levels by inputting additional biomass to snag and deadwood (down woody debris) pools (Fulé et al. 2004; Stephens 2004; Hyde et al.

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2012, Stenzel et al. 2019). Efforts to reduce these fuels through silvicultural treatment (i.e., salvage logging) have had mixed results, sometimes increasing fuel loads over the short term (i.e., Donato et al. 2006, Johnson et al. 2020a) and sometimes reducing subsequent fire severity (i.e., Povak et al. 2020).

First-entry fires following fire suppression may have substantially different impacts on forest structure, as compared to how frequent and relatively regular fires did historically (Johnstone et al. 2016). After decades without wildfire, fuel loads are higher than they would have been prior to fire exclusion, when regular fires burned surface fuels and thinned out young trees that served as ladder fuels (Harris and Taylor 2015). Consequently, first-entry fires can create patchy clumps of tree mortality (Kane et al. 2019) and higher overall fire severity compared to historical fire due to a more dense and complex fuel matrix (Harris and Taylor 2015, Kolden et al. 2017). This can give rise to distinct patterns of tree mortality (Grayson et al. 2017), post-fire demography (Varner et al. 2007), and large quantities of standing snags or deadwood pools (Miller and Urban 2000, Stephens 2004, Stephens and Moghaddas 2005, Grayson et al. 2019, Stenzel et al. 2019).

The explicit consideration of large-diameter fuels is essential because they represent a considerable portion of above-ground carbon stocks (Lutz et al. 2018a) and provide unique habitat structures that contribute to biodiversity of vertebrates and herbaceous plants (Taborska et al. 2015). Large-diameter deadwood can also significantly influence future fire behavior because of the high fire intensity they generate and their burn time longevity (Thaxton and Platt 2006). While coarse woody debris accumulation following fire may be estimated using snagfall models (e.g., Vanderwel et al. 2006, Passovoy and Fulé et al. 2006) and decomposition models (Hyde et al. 2011), the generalizability of these models is severely limited by variability in snagfall rates between species, sites, and fires. Additionally, existing studies have often sampled small areas or rely on small plots (1 m² to 1000 m²), making the examination of large diameter and long pieces of deadwood difficult (Lutz 2015). In some cases, this has led to the surprising conclusion of no post-fire increase in woody surface fuel loadings, and little deposition of large-diameter dead wood (Stalling et al. 2017).

Another challenge to quantifying impacts of reintroduced repeated fires into previously fire-excluded forests is a lack of unmanaged assessment stands, or highly characterized pre- and post-fire field data of the different biomass pools (Stephens 2004). Moreover, studies of large-diameter trees are generally only possible in primary forests, as secondary forests in western North America have generally not experienced enough time since harvest for significant numbers of trees to reach large diameters. Using a detailed census of trees and woody debris in a primary forest where a first-entry fire recently burned, our objective was to describe the

spatial variability of pools and fluxes of snags and deadwood through time. We use this dataset to answer the following questions related to carbon dynamics of post-fire forests:

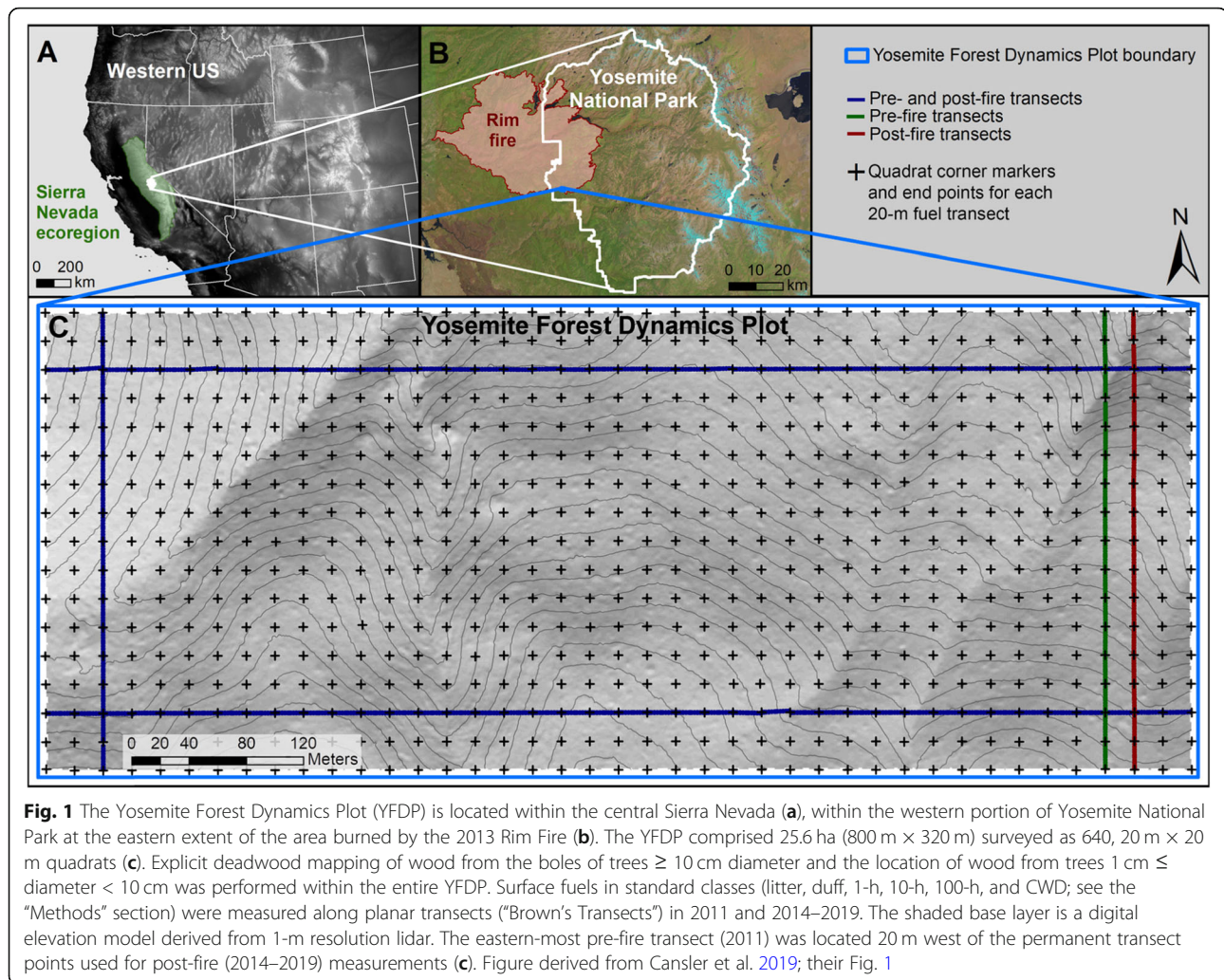
- 1) Following fire, what are the temporal dynamics of woody biomass pools in trees, snags, and deadwood?
- 2) What is the proportion of snags and deadwood represented by large-diameter trees, and how rapidly does the large-diameter surface fuel component accumulate after fire?

Materials and methods

Description of study site

The study took place within the Yosemite Forest Dynamics Plot (YFDP; Lutz et al. 2012, 2013) a single 25.6 ha plot located between 1774 m and 1911 m elevation in the *Abies concolor*/*Pinus lambertiana* vegetation zone in Yosemite National Park, California, USA (Yosemite) (van Wagtenonk et al. 2020, Fig. 1). The principal overstory tree species by basal area are *Pinus lambertiana*, *Abies concolor*, and *Calocedrus decurrens* with small populations of *Pseudotsuga menziesii*, *Abies magnifica*, and *Pinus ponderosa*. Important angiosperm species include *Quercus kelloggii* and *Cornus nuttallii*. Species richness of woody plants reaching 1 cm diameter at breast height (DBH) is 24 (see Lutz et al. 2012 for full species lists). Prior to Euro-American settlement, the fire return interval at the YFDP was 29.5 years (Barth et al. 2015) with a fire exclusion period spanning 113 years between 1899 and 2013, for a fire return interval departure of about four (Odion and Hanson 2006). Prior to Euro-American settlement, fires in the *Abies concolor*/*Pinus lambertiana* zone burned at mixed severities, with only small patches of high-severity fire (Scholl and Taylor 2010).

The YFDP was burned in an unmanaged backfire ignited to retard the advance of the 2013 Rim Fire (for details, see Lutz et al. 2017 for fire weather, Blomdahl et al. 2017 for unburned surface area, Cansler et al. 2019 for fuel consumption, and Stavros et al. 2016 for remote sensing data). Previous to this, the YFDP had not experienced fire since 1899 (Barth et al. 2015). Cansler et al. (2019) calculated the pre-fire coarse woody debris in the YFDP was 72 Mg ha⁻¹. Fire behavior was of moderate intensity with most trees experiencing canopy and bole scorch, but few trees experiencing much canopy and bole combustion. One-year post-fire (initial) fire mortality (initial; 2014) was 71% of stems and 13% of basal area (Furniss et al. 2019, 2020a), with extended mortality (2015–2019) rising to 86% of stems and 47% of basal area (Furniss et al. 2020b). The intentional backburn ignition and the dry conditions produced fire effects in the YFDP similar to recent fires within the broader Yosemite landscape (van Wagtenonk and Lutz 2007, Lutz et al. 2009b) in contrast to the larger proportion of the unmanaged



Rim Fire that burned outside Yosemite with higher-than-normal severity (Lydersen et al. 2014, Kane et al. 2015). The post-fire period coincided with a multi-year drought which increased delayed mortality (Furniss et al. 2020b).

Data collection

Within the YFDP, all trees ≥ 1 cm DBH and all snags ≥ 10 cm DBH were identified, measured, mapped, and tagged in 2009–2010 according to the protocols of the Smithsonian Forest Global Earth Observatory network (ForestGEO; Anderson-Teixeira et al. 2015, Lutz 2015). The Smithsonian ForestGEO is a global network of 70 spatially explicit plots using the same field and data protocols (Anderson-Teixeira et al. 2015). The YFDP was partitioned into 640 20 m × 20 m quadrats, with corners surveyed by total stations. All trees, snags, and logs in the entire 25.6 ha area were originally referenced to the surveyed grid. Subsequent to plot establishment, and prior to fire, each of the 34,866 original trees and 2735 snags in the YFDP (see Table S1 for demographic data)

was visited each year (2011–2013) to check for mortality and snagfall (new recruitment was also recorded), with the 2013 survey resulting in a comprehensive stem map of pre-fire trees and snags. We remeasured the diameter of all trees and snags in 2014 and of trees again in 2019. We measured the diameter and height of each newly dead tree in every year (2011–2019).

In the year immediately following fire (2014) and the subsequent five years (2015–2019), each main bole of newly fallen stems or portions of stems (i.e., broken tops) originating from trees ≥ 10 cm DBH was mapped and assessed for decay class according to Smithsonian ForestGEO deadwood protocols (Janík et al. 2018). Snags and deadwood were divided into five decay classes according to the following definitions:

Class 1—for snags; freshly dead (0–5 years for many species); branches of 3rd order are present; the full height of stem is present unless there was damage prior to the mortality event or caused during the mortality event; fully barked (usually ≥ 80% of stem surface);

usually trees that died from suppression, bark beetle outbreak (coniferous), fungal infection (broadleaved), or those killed but not burned by fire. The species is still recognizable. For deadwood; freshly fallen tree (usually windthrow or a basal rot); texture—wood intact; branches of 2nd order are attached; fully barked (usually $\geq 80\%$ of stem surface); species is still recognizable.

Class 2—for snags; branches of the first order are present; full tree height unless there was damage prior to or during the mortality event; partly barked (usually $< 80\%$ of stem surface; broadleaved trees should be still fully barked); the species can usually still be identified. For deadwood; texture—wood intact to partly hard or soft; branches of the first order are partly attached; partly barked; the species can usually still be identified.

Class 3—for snags; only short basal rests of main branches; full height unless there was damage prior to the mortality event; bark missing or absent (usually $\leq 20\%$ of stem surface) in the case of coniferous species. For deadwood; texture—wood hard but in large pieces; the wood is not compact any more along the entire stem length with the core or outer mantle subjected to rot. The genus can often be recognized, but species identification is difficult.

Class 4—for snags; no branches or small basal rests; height $\leq 80\%$ of even height curve (according to DBH); bark missing or absent (usually $\leq 20\%$ of stem surface) in the case of coniferous species; for deadwood; texture—wood chunks small, soft, and blocky; the wood is not compact and the cross section is either elliptical or circular.

Class 5—for snags; stumps or short snags; the wood is at a stage of advanced rot. For deadwood; the wood is at a stage of advanced rot; texture—wood chunks soft and powdery; deadwood no longer has a cylindrical shape; the species cannot be identified anymore, a kick into a stem results in stem breakage.

Deadwood was tracked in two ways, depending on tree diameter. For trees ≥ 10 cm diameter at the previous measurement, each piece of the main bole ≥ 1 m long was mapped separately, and pieces shorter than 1 m were ocularly combined with adjacent pieces. For each piece, length and diameter at both ends were measured, as was its location (see Janík et al. 2018 for measurement details). Trees were considered to be fully “fallen” if the remaining stump height was < 1.37 m high; otherwise, deadwood was mapped as the “broken top” of a standing snag. Additionally, woody debris originating from main stems that was present pre-fire and persisted through the fire at a diameter ≥ 10 cm was mapped and assessed for decay class. For trees $1 \text{ cm} \leq \text{DBH} < 10 \text{ cm}$, the year of snagfall was recorded, but these smaller stems were not mapped and were assumed to have fallen as a single piece.

Volume and biomass calculations

The biomass of live trees was calculated using the biomass equations of Chojnacky et al. (2014). For snags that had died relatively recently (decay class 1 or 2) and were still intact (first-order branches present, bark intact, and top diameter ≤ 10 cm), biomass was estimated with the equations of Chojnacky et al. (2014) and corrected with the species- and decay-class-specific relative density factors of Harmon et al. (2008), or if available, using the data of Cousins et al. (2015). For snags that were either in a more advanced state of decay or were not intact, their biomass was estimated by modeling their volume as a conic frustum and using the species- and decay-class-specific absolute density values provided by Harmon et al. (2008) or, if available, Cousins et al. (2015).

For individual pieces of wood on the ground, we calculated volume from their physical dimensions, assuming their shape was a conic frustum. Biomass was calculated for the entire originating tree using the equations of Chojnacky et al. (2014) and attributed to specific pieces that fell from that tree by weighting a piece according to its volume as a proportion of the total volume of the tree, including any remaining standing volume. Biomass was then corrected for decay class using the relative density factors of Harmon et al. (2008). When no values were obtainable for a species, we used values for the most closely related species with the most similar wood characteristics (i.e., specific gravity; Chojnacky et al. 2014). For pieces that could not be identified, we used an average density value calculated by proportionally weighting the identified pieces from the data set. For unknown snags, density values were 0.40 g cm^{-3} for decay class 1, 0.35 g cm^{-3} for decay class 2, 0.29 g cm^{-3} for decay class 3, 0.23 g cm^{-3} for decay class 4, and 0.18 g cm^{-3} for decay class 5. For unknown deadwood, density values were 0.36 g cm^{-3} for decay class 1, 0.28 g cm^{-3} for decay class 2, 0.14 g cm^{-3} for decay class 3, 0.14 g cm^{-3} for decay class 4, and 0.13 g cm^{-3} for decay class 5.

Preliminary analysis of woody debris following the 2019 remeasurement showed little change in decay class and wood dimensions in the years since fire. We therefore calculated deadwood volume and biomass in 2014–2019 using the values recorded when trees and snags fell into the deadwood pool. We calculated mean values of volume and biomass of deadwood for the entire YFDP and for each of the 640 $20 \text{ m} \times 20 \text{ m}$ quadrats in the YFDP. This enabled us to calculate the variability in fuel accumulation at the spatial grain of $20 \text{ m} \times 20 \text{ m}$. For calculating wood in each $20 \text{ m} \times 20 \text{ m}$ quadrat, pieces of wood that lay in multiple quadrats were split along quadrat boundaries and counted as virtual fragments that were contained within each quadrat. Pieces ≤ 10 cm diameter were assumed to be wholly within the quadrat that contained the rooting location of the originating tree. We also assessed the directionality of the largest

portion of fallen trees from the deadwood endpoint locations.

In addition to the explicit mapping, we installed 2240 m of planar transects (Brown's transects, Fig. 1) pre-fire (2011) consisting of 112, 20-m transects (Brown 1974). Transect locations were selected to be 40 m from the edge of the YFDP so that trees contributing to deposition of debris would be within the YFDP (Fig. 1). We measured surface fuels in four size classes (1 h; less than 0.25 in. (0.64 cm) in diameter, 10 h; between 0.25 in. and 1 in. (between 0.64 cm and 2.54 cm) in diameter, 100 h; 1 in. to 3 in. (2.54 cm to 7.62 cm) in diameter, and 1000 h; greater than 3 in. (7.62 cm) in diameter) as well as litter and duff at ten points on each transect (odd meters from 1 m to 19 m). These transects, running between the permanent quadrat markers, were resampled post-fire (2014–2019). We calculated fuel loading and extrapolated to the plot scale by the methods of Brown (1974) as implemented by Cansler et al. (2019).

We calculated the time dependency of surface fuels by dividing the fallen pieces into diameter classes (1 cm \leq DBH < 10 cm, 10 cm \leq DBH < 60 cm, \geq 60 cm, and all diameters together) and examined the fall rate from the

existing years of data in terms of stems and biomass (*sensu* Lutz and Halpern 2006). We assessed biomass pools of live trees, portions of dead trees that were still standing, and deadwood by these diameter classes.

All calculations were performed in R version 3.6.2 (R Core Team 2020) using packages rgdal version 1.4-8 (Bivand et al. 2019), rgeos version 0.5-2 (Bivand and Rundel 2019), sp version 1.3-2 (Pebesma and Bivand 2005), and sf version 0.8-1 (Pebesma 2018).

Results

Immediately pre-fire (May 2013), there were 34,193 trees and 4045 snags present. Of those, 408 trees and 273 snags were completely consumed by fire (no visible remains). An additional 2528 trees and 1680 snags had \geq 75% consumption, but were still identifiable (Tables 1, S1). Fully 82% of the fire-consumed trees were \leq 5 cm DBH; thus, they contributed minimally to consumed biomass. By 2019, there were 7069 live stems: 4853 that survived the fire and the following years of drought and 2216 net post-fire recruits (for demographic details, see Table S1). Net of consumption and snagfall, there were 13,304 remaining snags, with 20,820 trees on the ground in 2019 (Fig. 2, Table S1, Figs. S1–S8).

Table 1 Evolution of surface fuel immediately following fire (2014) and in the 5 years following in the 25.6-ha Yosemite Forest Dynamics Plot. The Rim Fire of 2013 directly consumed 12% of trees \leq 10 cm DBH, but very few trees \geq 10 cm DBH (0.5%). Most fire-killed trees and snags that persisted through the fire fell in subsequent years. For yearly progression of trees, snags, deadwood, recruitment, mortality, and snagfall, see Table S1

	Diameter class	Year						Total	Per ha
		2014	2015	2016	2017	2018	2019		
Snags consumed by fire [†]	1 cm \leq DBH < 10 cm	664	-	-	-	-	-	664	25.9
	\geq 10 cm DBH	1289	-	-	-	-	-	1289	50.3
Live trees consumed by fire [†]	1 cm \leq DBH < 10 cm	2863	-	-	-	-	-	2863	111.8
	\geq 10 cm DBH	73	-	-	-	-	-	73	2.8
Newly fallen trees and snags [‡]	1 cm \leq DBH < 10 cm	491	897	2043	3891	3468	3317	14,107	551.0
	\geq 10 cm DBH	354	303	563	1485	1087	1481	5273	206.0
206.0									
New pieces of deadwood*	1 cm \leq DBH < 10 cm	492	897	2043	3894	3472	3322	14,120	551.6
	\geq 10 cm DBH	428	351	625	2138	2218	2715	8475	331.0
	Persisted through fire	1352	-	-	-	-	-	1352	52.8
Deadwood volume (m ³)	1 cm \leq DBH < 10 cm	1.60	3.56	10.82	22.78	17.94	22.36	79.06	3.09
	\geq 10 cm DBH	376.48	50.46	59.61	287.68	559.54	503.85	1837.62	71.78
	Persisted through fire	2048.20	-	-	-	-	-	2048.20	80.01
	Total	2426.28	54.02	70.43	310.46	577.48	526.21	3964.88	154.88
Deadwood biomass (Mg)	1 cm \leq DBH < 10 cm	0.44	0.96	2.63	5.82	4.72	6.03	20.60	0.80
	\geq 10 cm DBH	276.94	43.00	37.16	154.83	253.94	272.03	1037.90	40.54
	Persisted through fire	808.67	-	-	-	-	-	808.67	31.59
	Total	1086.05	43.96	39.79	160.65	258.66	278.06	1867.17	72.94

[†]Less than 25% of original bole remaining in 2014

[‡]Trees and snags that fell during or after fire with the remaining stump < 1.37 m tall

*Explicitly mapped pieces of wood \geq 10 cm diameter and \geq 1 m long and non-mapped pieces of wood from trees 1 \leq DBH \leq 10 cm, with those smaller trees assumed to have fallen as one piece (see the "Methods" section)

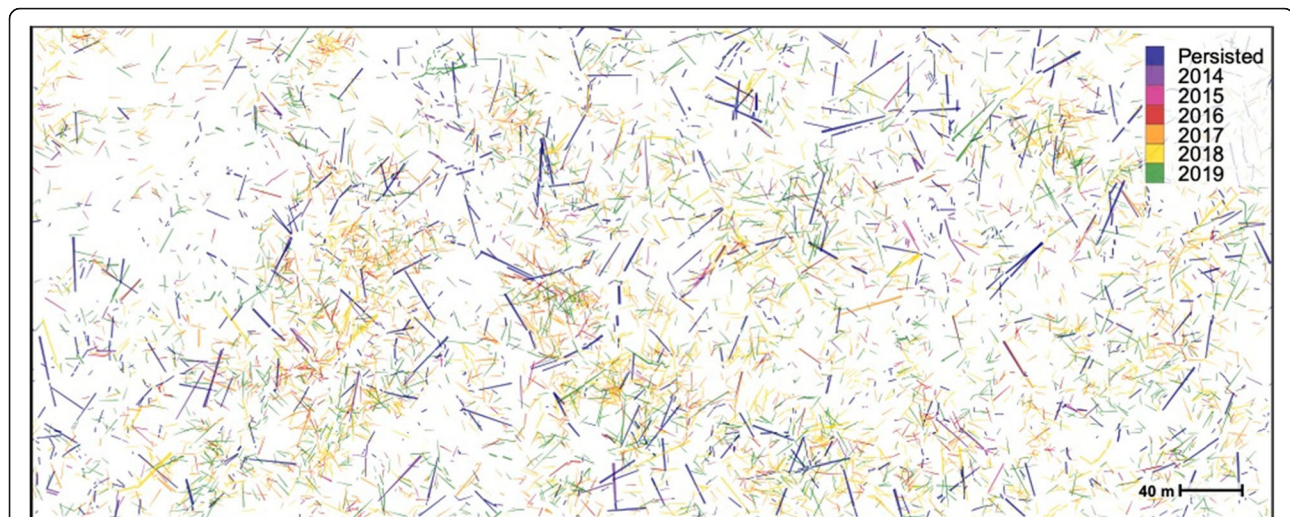


Fig. 2 The 9827 pieces of coarse woody debris ≥ 10 cm diameter in the 25.6-ha (800 m \times 320 m) Yosemite Forest Dynamics Plot as of 2019 showing the year of snagfall and also those pieces of deadwood that were present pre-fire and that persisted through the fire ("Persisted"). For individual figures of woody debris accumulation by species and year, see Supplemental Figures S1–S8

The accumulated wood volume and biomass (2019) in each of the 640, 20 m \times 20 m quadrats varied by more than three orders of magnitude (Figs. 3, S9). Biomass (minimum, 0.1 Mg ha⁻¹; mean, 73 Mg ha⁻¹; maximum, 497 Mg ha⁻¹), tracked volume (minimum, 0.2 m³ ha⁻¹; mean 153 m³ ha⁻¹; maximum, 1103 m³ ha⁻¹), but larger pieces generally had lower density due to their more advanced decay. Neither all deadwood nor large deadwood indicated strong directionality, but both showed slight trends in direction of fall (Fig. 4). The southwesterly bias in large deadwood reflects the direction of the Mono Wind event of 30 November 2011, which caused widespread windthrow throughout some parts of the Sierra Nevada (USFS 2012) and toppled numerous large-diameter trees within the YFDP (Lutz 2015). The northeasterly bias among all trees ≥ 10 cm DBH is likely due to much of the YFDP having north and northeast facing aspects.

Maximum snagfall by number of trees peaked 3 years post-fire. The probability that dead trees would fall changed over time and varied among size classes, with smaller stems exhibiting a higher probability of falling earlier (Fig. 5). From 2014 to 2019, most pieces of deadwood remained at decomposition class 1 or class 2. Overall fuel loading in 2019 was very similar to the 2013, pre-fire level; litter (measured by Brown's transects) generally recovered to pre-fire levels, although new duff formation was still essentially zero (duff persisted in the approximately 5% of the surface that was unburned). Importantly, biomass of coarse woody debris in 2019 was almost the same as 2013 (Figs. 6, 7). Wood from large-diameter trees (≥ 60 cm diameter) comprised 57% of surface fuel in 2019 and was 75% of snag biomass (Fig. 7).

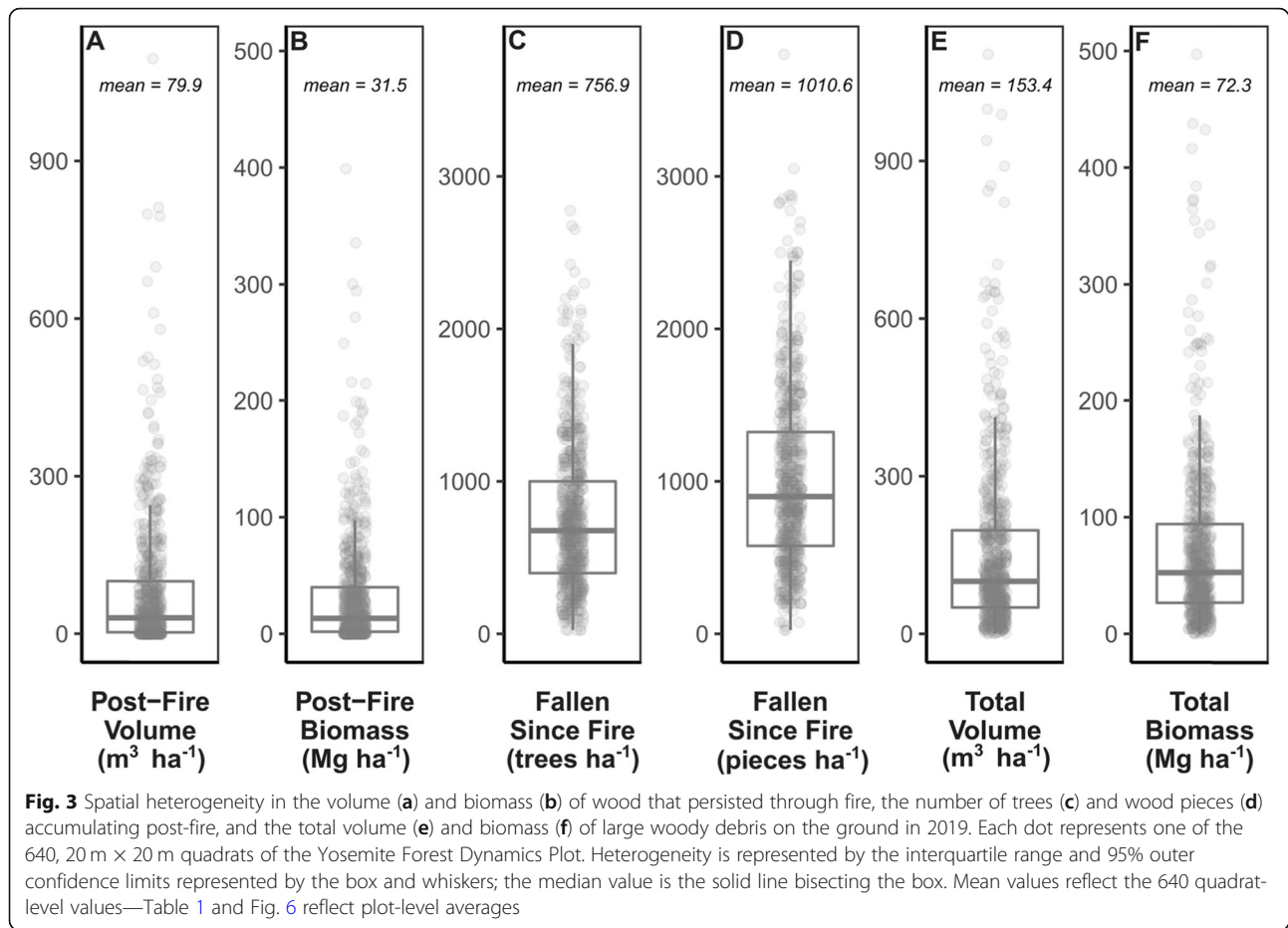
Discussion

A notable characteristic of Sierra Nevada forests is their potential to include large-diameter trees. These trees

generate high levels of large-diameter fuel in sometimes long sections (Figs. 2, 6). Furthermore, Sierra Nevada forests have a heterogeneous structure in terms of the presence of small- and large-diameter trees, snags, and deadwood at multiple scales, which is at least partly due to spatial and temporal heterogeneity in fire behavior and effects (Jerónimo et al. 2019, 2020). This fire-induced heterogeneity depends on the structural heterogeneity associated with spatial variation in large-diameter trees (Furniss et al. 2020b) and large-diameter deadwood (Lutz et al. 2009a, Lutz et al. 2013, Kane et al. 2014). The formation dynamics of deadwood, in turn, inherently depend on the fire frequency and the ability of trees to reach large diameters prior to mortality. In the *Abies concolor*/*Pinus lambertiana* zone, the prevalence of large pieces of deadwood, both of those that persist through fire and post-fire inputs, reinforces the ecological significance of large-diameter trees, even beyond their death (Hyde et al. 2011, Lutz et al. 2018a).

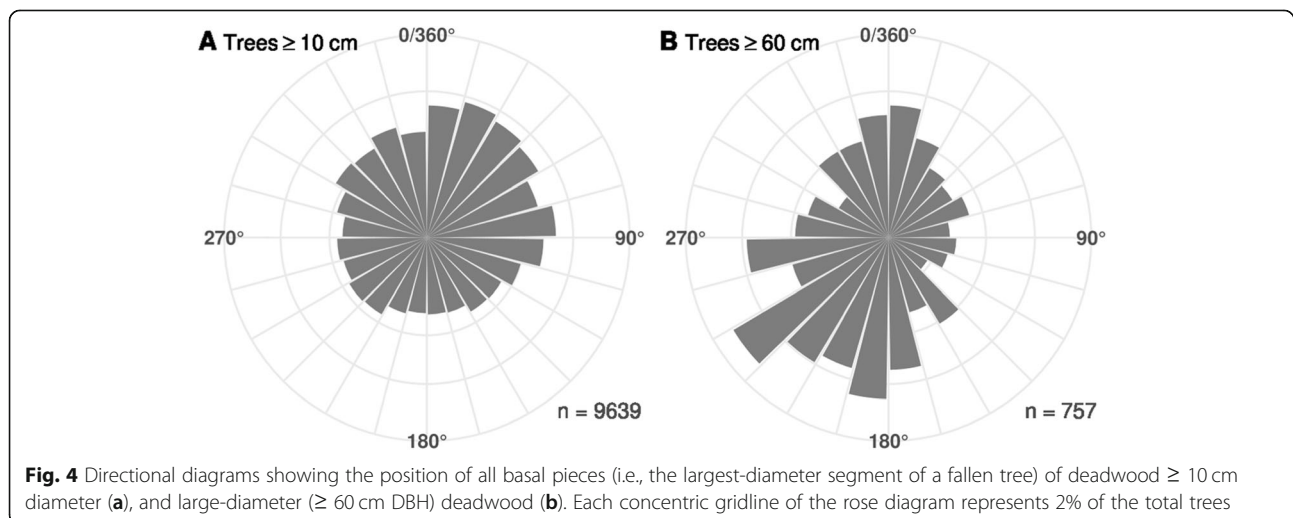
To our knowledge, this study is the first-ever spatially explicit analysis of snag and deadwood dynamics after fire conducted at this spatial scale (25.6 ha) and including this range of diameter classes (1 cm \leq diameter < 201 cm). The time trends, and, importantly, the variation around the means (Fig. 2) are important data for landscape-scale accumulation of fuel. These data could be of particular value to provide a baseline dataset to predict how other carbon dynamics and woody debris in ecosystems may respond to fire, especially if those ecosystems are experiencing higher fire frequencies due to shifts in fire regimes (Smith et al. 2016).

Variation in pre-fire forest structure and site conditions can determine accumulation of large-diameter fuel following fire (Cansler et al. 2019, Lutz et al. 2018b). In



the intervals between fire, deadwood decays at various rates depending on landscape position (Privetiv et al. 2018), and directly contributes to biodiversity by providing a substrate (Taborska et al. 2015) and modifying the local environment (Vrška et al. 2015). Areas remaining unburned within fire perimeters (Kolden et al. 2015, Meddens et al. 2018), due

either to low pre-fire fuel loads, low connectivity, or wet landscape positions (Kolden et al. 2012), can function as refugia for small-statured trees (Blomdahl et al. 2019a) and other elements of the biota (Roberts et al. 2008, Blomdahl et al. 2019b); such refugia can also serve as areas where fuel accumulates between fires which, in turn, impacts



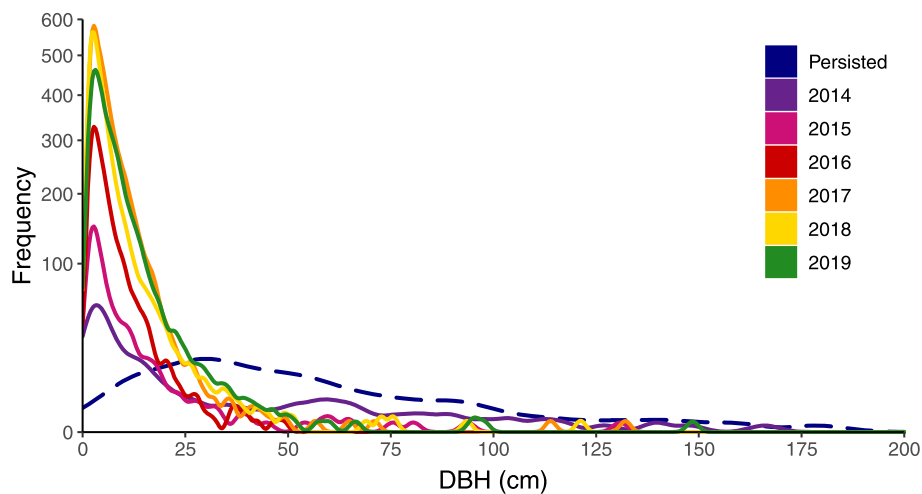


Fig. 5 Diameter distribution of each piece of fallen trees (remaining stump < 1.37 m high) from 2014–2019 in the Yosemite Forest Dynamics Plot, as well as the post-fire diameter distribution of those pieces that persisted through the Rim Fire. Trees < 10 cm DBH were considered to have fallen as a single piece; wood from trees ≥ 10 cm DBH was mapped explicitly by piece. Colors correspond to those in Fig. 1. Curves are based on the raw diameters smoothed with a Gaussian density kernel. The square-root transformation of the y-axis shows the low frequency but cumulative effects of large-diameter inputs

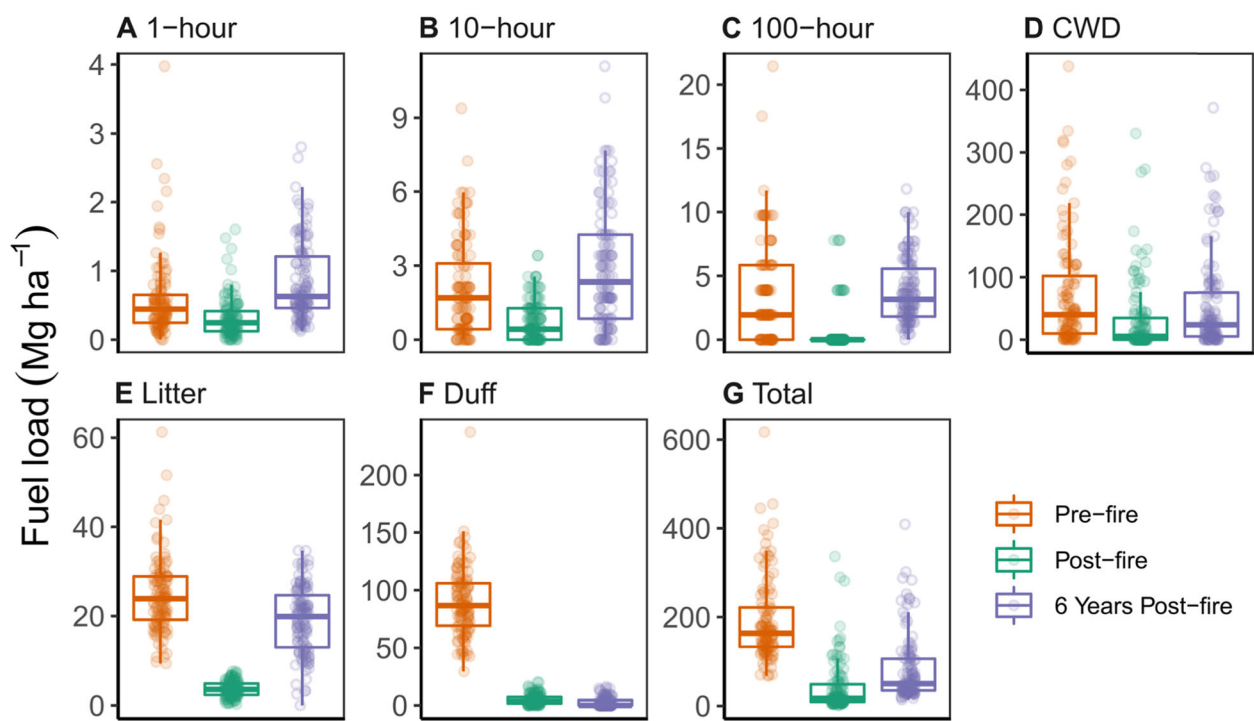
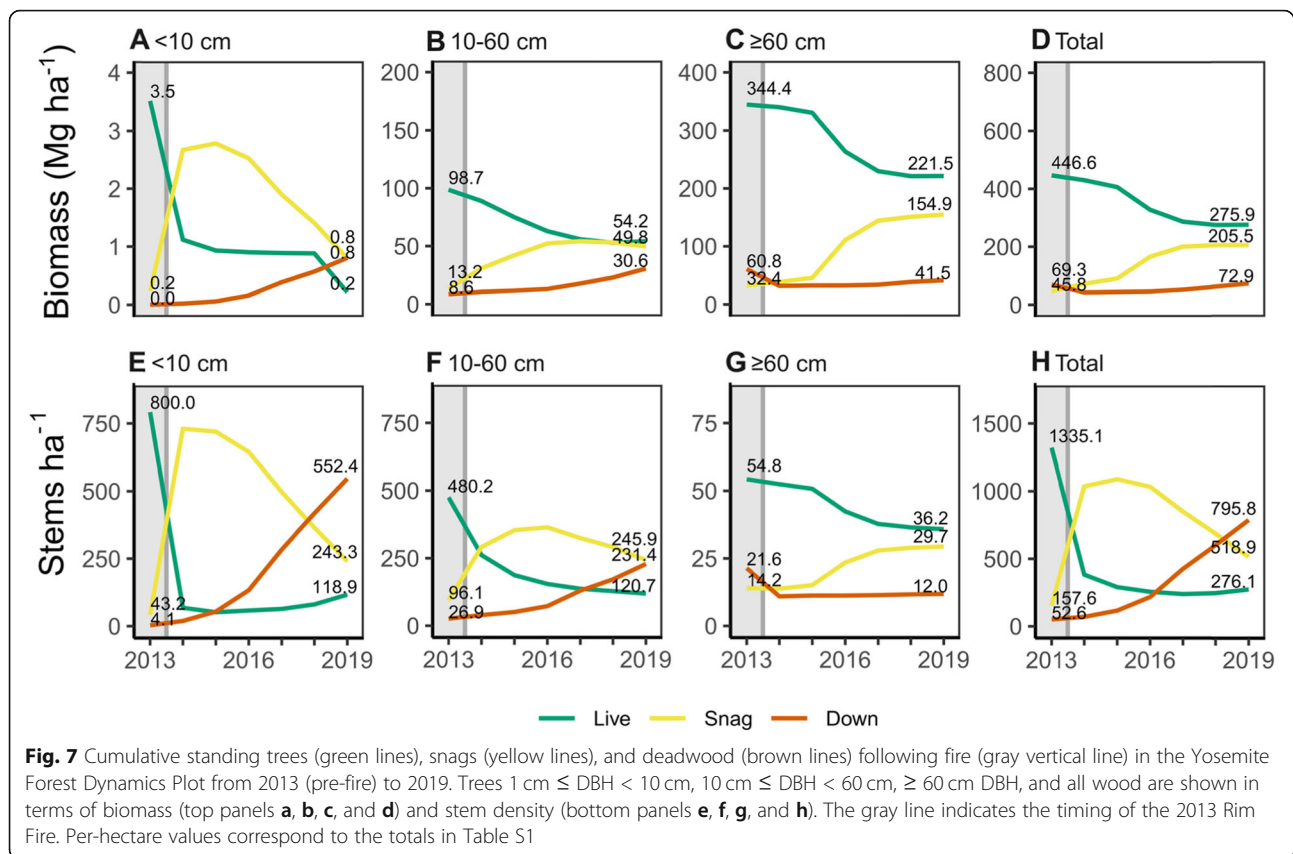


Fig. 6 Fuel loading for the Yosemite Forest Dynamics Plot as determined by 112, 20-m Brown's transects (2240 m total) in 2011, pre-fire and after a century of fire exclusion, in 2014, immediately post-fire, and in 2019, 6 years post-fire. Heterogeneity in fuel loading among transects is represented by the interquartile range and 95% outer confidence limits represented by the box and whiskers; the median value is the solid line bisecting the box. Brown's transect data was used to survey all surface fuel pools; other figures display only those fuels above the 1000-h diameter threshold. CWD, coarse woody debris (≥ 7.62 cm diameter)



ecosystem vulnerability and future heterogeneity of fire behavior and effects (Vaillant et al. 2016, Kolden et al. 2017).

Rapid post-fire fuel accumulation, particularly from small-diameter tree mortality, suggests that repeated burns may be necessary to return historical ecological processes and to bolster resilience to future fire (Stevens et al. 2014). We show that 2013 (pre-fire) and 2019 (post-fire) surface fuels were virtually indistinguishable in total amount due to a net balance of fuels consumed during the fire and fuels accumulated post-fire, reflecting high fire-related mortality rates expected following fire exclusion (Varner et al. 2007). The exception to this was the duff layer, which had not begun to accumulate again by 2019. The Rim Fire caused widespread tree and shrub mortality, dramatically reducing ladder fuels and canopy bulk density. Although surface fuel loads in our study site have returned to pre-fire levels, the composition of fuels is distinct (more fine fuels, similar amount of deadwood, lower shrub cover, and canopy fuels [Fig. 5]). The different fuel structure that has emerged will influence the intensity of repeat burns, though it is difficult to predict the directionality of this relationship (and will depend greatly on fire weather and fuel moisture levels). Future fires will be necessary to return surface fuels to the pre-suppression levels that facilitated frequent, low-severity fire in this forest (Larson et al. 2013), but these fires may still pose a risk to the remaining live trees, particularly those

in the large-diameter cohort (Lutz et al. 2018) that were damaged in the Rim Fire or to newer cohorts that have not yet developed morphological protections (Smith et al. 2017, Steady et al. 2019). Smoldering of large logs contributes to large-diameter tree mortality by creating large wounds (i.e., catfaces), causing mechanical failure in previous fire scars (Furniss et al. 2019), and scalding shallow subsurface roots (as with duff smoldering *sensu* Varner et al. 2009).

Broader multi-agent interactions mediated the delayed mortality processes that contributed to the rapid accumulation of large-diameter deadwood following fire (Furniss et al. 2020b). Importantly, coarse woody debris accumulated later than finer fuels due to specific mortality and fragmentation processes affecting the largest diameter class of trees (Furniss et al. 2020b), indicated by field observations including (1) saprophytic rot entering fire-killed portions of live trees, contributing eventually to structural failure; (2) windthrow or stem breakage of trees made structurally unstable by the fire itself (i.e., large cat faces, reduced heartwood); and (3) fire-increased bark beetle activity (such as by *Dendroctonus valens* LeConte). However, these processes often resulted in fragmented wood (i.e., branches and treetops) rather than whole snagfall and thus contributed less to the accumulation of large-diameter fuels than did rot- and fire-related collapse. In future fires, the presence

and relative abundances of biotic agents along with observed fire severity will likely determine delayed mortality rates and further coarse woody debris accumulation (i.e., Hood et al. 2018).

Understanding snag and wood dynamics is critically important for evaluating the tradeoffs and effects of possible post-fire management actions such as salvage logging or reforestation planting on a host of key concerns (Graham et al. 1994), including future wildfire potential (Johnson et al. 2020), wildlife habitat conservation and development (Schaedel et al. 2017), distribution of shrubs and forbs (Halpern and Lutz 2013), forest recruitment, forest carbon sequestration, and CO₂ emissions from fire (Stenzel et al. 2019).

The study demonstrates the ecological processes that govern future fire risk; small diameter stems rapidly contribute to an increasing fuel load, whereas the larger boles (which are the focus of salvage logging) fall at a lower rate that may be delayed 1–6 years following fire. Experimental and simulation studies demonstrate short-term increases but long-term decreases in woody surface fuel loadings in salvage-logged post-fire conifer forests compared to untreated controls (McIver and Ottmar 2007, Dunn and Bailey 2015, McIver and Ottmar 2018, Johnson et al. 2020). However, a second fire or reburn can erase salvage logging treatment effects on standing and down woody fuel loadings (McIver and Ottmar 2018) and override salvage logging effects on fire risk, suggesting that in landscapes conducive to a regime of frequent surface fires, timely re-introduction of repeated fires may be the most effective restoration post-fire management strategy (Larson et al. 2013).

This study is particularly relevant to identify methods for quantifying fire-induced movement of sequestered carbon from the live tree carbon pool to the deadwood carbon pool (Stenzel et al. 2019). With the exception of surface fuels, leaves, and fine branches that are completely consumed, fire does not rapidly release much carbon from larger woody structures directly into the atmosphere (Table 1). Fire and fire-mediated biotic or physical agents can kill live trees, but it takes many years for decay microbes to cycle that carbon into atmospheric CO₂ and soil carbon pools. This is particularly true regarding carbon stored in large-diameter trees, where the majority of aboveground forest carbon is found (Stephenson et al. 2014, Lutz et al. 2018). For example, 62 years after clear-cut harvest and broadcast burning, large-diameter legacy wood originating from the pre-harvest stand still accounted for 45% of aboveground woody detritus stocks in a long-term replicated forest development experiment (Schaedel et al. 2017). While newly created snags and fallen surface fuels will burn during future fires, any pieces that are not completely consumed will become charred, which can increase the carbon residence in these systems (DeLuca et al. 2008,

Brewer et al. 2013, Santin et al. 2015, Ward et al. 2017). The low-consumption rate and long retention times of large logs facilitates the continued conversion of biomass by soil microbes into recalcitrant forms of soil organic matter, which constitutes the largest and longest-lived carbon pool in temperate forests (Lal 2005, Averill et al. 2014), provided soil incorporation occurs faster than other removal mechanisms like erosion and repeated fires (Tinkham et al. 2016). As such, carbon stored within large-diameter trees is at least partially retained following fire-induced mortality and accumulation as coarse woody debris.

Conclusions

The consequences of a first-entry burn in areas where fire has long been excluded are starting to be understood, with broad implications for landscape and resource management. In this forest, the Rim Fire consumed 61% of the total deadwood ≥ 10 cm diameter existing pre-fire, but post-fire accumulation of coarse wood ≥ 10 cm diameter contributed 41 Mg ha⁻¹, replacing the pre-fire loadings of coarse fuels within 6 years. Total pre-fire surface fuels of all classes as measured by planar transects (and after 113 years of fire exclusion) were 192 Mg ha⁻¹ and 6 years post-fire total surface fuels were 83 Mg ha⁻¹ (Fig. 6), a difference due primarily to the slow development of the thick duff layer that was present pre-fire. The high biomass in large-diameter snags (154.9 Mg ha⁻¹; Fig. 7) suggests that these large-diameter structures will continue to contribute to surface fuels for many years. Repeated fires will be necessary to restore the pre-European settlement ecological dynamics of this forest by reducing these fuels to a level where subsequent fire will not have the potential to burn at high intensity and effect widespread large tree mortality. More broadly, these findings suggest that adequately dealing with the structural and demographic consequences of fire deficit in fire-excluded dry forests is a multi-stage process that merits further observation and experimentation.

Supplementary information

Supplementary information accompanies this paper at <https://doi.org/10.1186/s13717-020-00243-8>.

Additional file 1: Table S1. Yearly totals of trees, snags, and deadwood for the Yosemite Forest Dynamics Plot including recruitment, two different categories of mortality (transitions of trees to the snag pool and transitions of trees directly to the surface deadwood pool) and snagfall (transition of a snag to the surface deadwood pool). Dead trees ≥ 1.37 m tall are classified as snags. Dead trees with a remaining stump height < 1.37 m tall are classed as deadwood. **Fig. S1.** Deadwood ≥ 10 cm diameter from 2013 and earlier that persisted through fire in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S2.** New deadwood ≥ 10 cm diameter from 2014 in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE –

Quercus kelloggii, UNKN – Unknown. **Fig. S3.** New deadwood ≥ 10 cm diameter from 2015 in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S4.** New deadwood ≥ 10 cm diameter from 2016 in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S5.** New deadwood ≥ 10 cm diameter from 2017 in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S6.** New deadwood ≥ 10 cm diameter from 2018 in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S7.** New deadwood ≥ 10 cm diameter from 2019 in the Yosemite Forest Dynamics Plot. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S8.** Cumulative deadwood ≥ 10 cm diameter in the Yosemite Forest Dynamics Plot in 2019, six years following fire. ABCO – *Abies concolor*, ABMA – *Abies magnifica*, CADE – *Calocedrus decurrens*, CONU – *Cornus nuttallii*, PILA – *Pinus lambertiana*, PSME – *Pseudotsuga menziesii*, QUKE – *Quercus kelloggii*, UNKN – Unknown. **Fig. S9.** Spatial variation of surface fuel biomass (≥ 10 cm diameter) in the Yosemite Forest Dynamics Plot at 20 m \times 20 m grain. Locally high levels of biomass persisted through the 2013 Rim Fire (A), contributing 43% of total surface fuels ≥ 10 cm diameter present in 2019 (B).

Abbreviations

DBH: Diameter at breast height, 1.37 m above the pre-fire forest surface; Mg ha⁻¹: Megagrams per hectare, approximately equal to 0.45 tons per acre; YFDP: Yosemite Forest Dynamics Plot

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Authors' contributions

JAL conceived the study. JAL, CAC, and SS performed analyses. JAL, SS, TJF, SJG, MES, and AJL collected data. All authors contributed to writing and editing the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

All data necessary to recreate analyses is available from the corresponding author.

Ethics approval and consent to participate

Not applicable

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Competing interests

The authors declare no competing interests.

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