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Long-term dead wood changes in a Sierra Nevada mixed conifer forest: Habitat and fire hazard implications

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ABSTRACT

Dead trees play an important role in forests, with snags and coarse woody debris (CWD) used by many bird and mammal species for nesting, resting, or foraging. However, too much dead wood can also contribute to extreme fire behavior. This tension between dead wood as habitat and dead wood as fuel has raised questions about appropriate quantities in fire-dependent forested ecosystems. Three plots installed in mixed conifer forest of the central Sierra Nevada in 1929 illustrate how amounts and sizes of dead wood have changed through time as a result of logging and fire exclusion. Diameter of snags was measured and CWD was mapped in the old-growth condition, prior to logging. Snags were re-measured in 2007 or 2008, and CWD was re-mapped in 2012. Snag density increased from 15.2 ha^{-1} in 1929 to 140.0 ha^{-1} in 2007/2008. However, average snag size declined, with 72% and 22% of snags classified as medium or large in 1929 and 2007/2008, respectively. Mechanisms of tree mortality also appear to have changed with greater mortality in smaller size classes, possibly as a result of higher live tree density. CWD volume, mass, and cover did not differ significantly between 1929 and 2012, with increased tree mortality and lack of periodic consumption by fire apparently compensating for the loss of inputs of large wood due to past logging. However, number of logs increased from 28 ha^{-1} to 76 ha^{-1} and average size declined substantially. Because larger-sized dead wood is preferred by many wildlife species, the current condition of more, smaller, and more decayed woody pieces may have a lower ratio of habitat value relative to potential fire hazard than it once did. Size, density, and stage of decomposition are therefore potentially better metrics for managing dead wood than mass and/or volume alone. To restore dead wood to conditions more like those found historically will require growing larger trees and reducing the inputs of dead wood from small and intermediate-sized trees. Fire, which preferentially consumes smaller and more rotten wood, would also help shift the balance to larger and less decayed pieces.

1. Introduction

Dead trees play an important role in forests, both when standing as snags or on the ground as course woody debris (CWD). A substantial proportion of the bird and mammal biota found in temperate forest ecosystems use snags for nesting, denning, roosting, resting, or foraging (Harmon et al., 1986). Holes excavated in snags house both primary cavity nesting birds as well as secondary cavity nesting species which use or enlarge existing cavities (Raphael and White, 1984). Bats roost under the loose bark of snags (Rabe et al., 1998) and flying squirrels frequently choose snags as nest trees (Meyer et al., 2005). Snags are also a source of food, with bark beetles and wood boring insects comprising an important part of the diet of woodpeckers and other bird species (Raphael and White, 1984). Snag size is an indicator of habitat potential, with use by cavity nesting bird species greatest in snags >38 cm diameter (Raphael and White, 1984; Morrison and Raphael, 1993). However, smaller snags are a valuable resource for foraging. Raphael and White (1984) found that birds preferred to forage on snags between 23 and 53 cm dbh, but smaller and larger snags were also used.

Most snags remain standing 5 years after tree death but then begin to rapidly fall between the 5th and 15th years (Keen, 1955). Larger diameter snags with higher amounts of heartwood generally fall more slowly than smaller trees with less heartwood (Keen, 1955). Rate of snag fall varies by species, with fir snags remaining upright longer, on average, than pine (Raphael and White, 1984; Morrison and Raphael, 1993; Ritchie et al., 2013). Once lying on the ground, CWD continues to provide habitat (Harmon et al., 1986). Many mammals and amphibians use CWD for shelter (Harmon et al., 1986; Bull and Heater, 2000; Butts and McComb, 2000; Ucitel et al., 2003), and volume of CWD was found

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to be correlated to forest arthropod community structure (Ferrenberg et al., 2006). CWD also plays a role in forest nutrient cycling, and although the proportion of total nutrients stored in logs is often relatively small (Harmon et al., 1986; Laiho and Prescott, 2004), decomposing logs are linked to increased microbial activity (Busse, 1994).

Dry dead wood is also combustible and too much can contribute to extreme fire behavior. While larger diameter dead wood loses moisture slowly, climate in the western US is characterized by long periods with relatively little precipitation, and both snags and CWD are generally readily consumed in wildfires. Burning snags can loft embers, and the common management practice prior to the 1970s was to fell snags in order to reduce fire hazard (Show and Kotok, 1924; Oliver, 2002). Once on the ground, dry dead wood provides a receptive surface for embers to ignite. The long burnout time and amount of heat released from combustion in large woody fuels can lead to torching and crown fire (Brown et al., 2003). Large numbers of snags and down logs are an issue for management or control of fire and safety of firefighting personnel working in proximity (Page et al., 2013). Concerns have also been raised about the negative effects to soil resources when excessive amounts of CWD are burned (Monsanto and Agee, 2008).

This tension between dead wood as habitat and dead wood as fuel has raised the question of how much wood is appropriate in fire-dependent forested ecosystems (Brown et al., 2003; Ucitel et al., 2003; Lehmkuhl et al., 2007; Scheller et al., 2011; Ritchie et al., 2013). Because wood is readily consumed by fire, one likely consequence of fire exclusion in unlogged forests where fire was historically frequent is an excess of coarse woody debris (Skinner, 2002). This is particularly true for heavily rotted wood, which is most readily consumed by fire (Kauffman and Martin, 1989; Skinner, 2002; Stephens and Moghaddas, 2005; Uzoh and Skinner, 2009). Historically, frequent fire would have likely resulted in rotten wood being maintained at relatively low levels (Stephens and Moghaddas, 2005). Conversely, in previously logged stands, past removals can influence future inputs of dead wood. Fewer large snags and logs may now be present in many areas because historical cutting typically targeted larger trees (Stephens, 2004; Stephens et al., 2007).

Information on appropriate quantities of snags and CWD, from which management targets are developed, can be gleaned from studies of historical forests, prior to logging and fire exclusion (Keen, 1929, 1955), or from contemporary reference stands with relatively intact fire regimes (Stephens, 2004; Stephens et al., 2007). Unfortunately, such records are scarce, and even what is available may not be applicable to the many different forest types of the western US where fire was historically common. In the absence of good reference information, Harrod et al. (1998) estimated historical snag density in dry ponderosa pine forests using historical size distributions of live trees and making assumptions about rates of snag creation and fall.

In this paper, I use re-measurement of historical plots installed in the old-growth condition in 1929 to evaluate how past logging and fire exclusion have influenced the dynamics of snags and downed wood over time.

2. Methods

2.1. Study area

Three large (3.9–4.4 ha) plots were established in 1929 in unlogged old-growth mixed conifer stands on the Stanislaus National Forest in the central Sierra Nevada (Fig. 1 in Knapp et al., 2013). Plots were located on a gentle NW slope in mixed conifer forest at elevations ranging from 1740 to 1805 m. The site is highly productive, with deep and well-drained loam to gravelly loam soils (Wintoner-Inville families complex) derived from granite or weathered from tuff breccia. Climate is Mediterranean, with the majority of the annual precipitation occurring during fall, winter, and spring, and more than half falling as snow. Fire was historically frequent in the study area, with a median return interval of 6 years (Knapp et al., 2013). The last fire occurred in 1889, 40 years prior to plot establishment. While some effects of fire exclusion were likely therefore already apparent in 1929, growth rate data from nearby plots (Stark, 1965) suggest that the majority of trees establishing due to the absence of fire would have been smaller than the minimum size cut-off used in this study (Knapp et al., 2013).

2.2. History

The 1929 plots were part of a network of "Methods of Cutting" plots established in different timber types and sites varying in productivity throughout national forests of California (Dunning, 1926), and are similar to plots established by U.S. Forest Service Research in other regions of the United States as early as 1909 (Moore et al., 2004). The three being studied here (hereafter designated as MC9, MC10 and MC11) were designed to "determine the growth rate and net growth, and to determine the rate of restocking after a light, a moderate and a heavy selection cutting" (Hasel et al., 1934). During the spring and early summer of 1929, locations of all trees within the plots with a diameter $\geqslant$9.1 cm at breast height were surveyed using a transit and steel tape according to instructions outlined by Dunning (1926). Species was noted, diameter at breast height (dbh) measured, and a stem map was produced (example shown in Fig. 2 of Knapp et al., 2013). Diameter of snags was only recorded for slightly more than half of MC11 and a portion of MC10, or approximately 33% of the total plot area. Because the methodology was consistent within these areas on the map, I assumed that some crews noted the diameter of snags and others did not, and that the values should be roughly representative of old-growth forest in the study area in 1929. Also mapped were large downed logs. Plots were then logged later the same year using three different methods. MC9 was marked for cutting according to standard USFS practice at the time ("USFS cut"), removing larger overstory trees of all species. MC10 was marked according to a "light economic selection" system, removing only the largest and highest value pines and leaving the other species. MC11 was marked with a "heavy cut", removing all merchantable trees (see Hasel et al., 1934; Knapp et al., 2013 for additional details). Tree data were again collected in the fall of 1929, after logging.

2.3. Tree/snag re-measurement

Digitized 1929 plot maps were registered to location using data from plot corners determined with a global positioning system (GPS) with external antenna and later differentially corrected to obtain sub-meter accuracy. Boundaries were marked at two chain (40.2 m) intervals with a section of metal pipe in 1929 and most of these markers were still present. In the summer of 2007 and 2008, a field crew re-mapped the plots, measuring the diameter at breast height (dbh) of all trees $\geqslant$ 10 cm, determining the status (dead or live), and noting the species (Knapp et al., 2013). I combined data for ponderosa and Jeffrey pine in the 2007/2008 census, because Jeffrey pine is uncommon (5% of "yellow pines" in 2007/2008), and was either not present in 1929, or the two species were not differentiated.

2.4. Coarse woody debris

The original numerical data for downed logs could not be relocated and the number and size of logs was therefore reconstructed from the 1929 plot maps. All features, including logs, were drawn to scale as described in the plot establishment guide (Dunning, 1926), and log cover was estimated from these same maps in early data summaries (Hasel et al., 1934). Furthermore, dimensions of the largest downed logs were fully consistent with diameter and height of the largest live trees in the stand. For each log, diameter at the largest end, smallest end, and length was quantified using a Velmex measuring table with digital readout (accuracy ± 0.01 mm) (Velmex Inc., Bloomfield, NY 14469, USA) and converted to actual size using the mapped scale of 2.54 cm (1 in.) = 9.1 m (30 ft). The large end of all but two logs was >26 cm, and the number of logs increased substantially once in the 29–31 cm range. I therefore estimated that the size cut-off for the 1929 log mapping was 30 cm (>11.6 in.). This was also a commonly used threshold in live tree data collection at the time. I assumed measurement error was the cause for the few values below this size threshold. Proportion of logs remaining intact after logging was estimated visually by overlaying a 1935 map of the same plots also showing the downed wood, onto the 1929 maps.

The same size criteria were used to quantify downed logs within the three MC plots in the field in August 2012, measuring large and small end diameter for all logs ⩾30 cm at their widest point. Small end diameter was measured down to a minimum of 10 cm. Log lengths were also measured from end to end (or to the point at which the log diameter dropped below 10 cm). I considered broken segments to be one log if the broken segments were obviously from the same tree and the distance between segments on the ground was <30 cm. Logs were mapped by measuring the distance and determining the azimuth of the large end from the nearest previously mapped and tagged tree. The compass direction that each log was laying on the ground was also noted. Species of the log was determined from bark and wood characteristics (except that Jeffrey pine was lumped with ponderosa pine), and state of log decay was categorized as either sound or rotten, based on whether the log wood could be dented with a kick.

2.5. Data analyses

A road was built in the 1970s that bisected the north-eastern corner of MC11 and the area to the north of the road was thinned in 2006, removing approximately 0.7 ha from the plot. Therefore, all comparisons among years used only the portion of the plot remaining unaffected at the time of the 2007–2012 data collection. For CWD, I used bulk density values from van Wagtendonk et al. (1996) to calculate mass. For the 1929 data, I calculated specific gravity as the weighted average of stand wood volume by species, and assumed all logs were sound. The majority of logs in systems with frequent fire are typically sound because rotten logs are much more readily consumed by fire (Kauffman and Martin, 1989; Uzoh and Skinner, 2009). Nevertheless, log mass in 1929 may be slightly over-estimated to the extent that logs were rotten.

I compared total snag density, snag density by species, and all CWD variables among the three MC plots and among measurement intervals (1929 pre-logging, 1929-post-logging, and 2007/2008 for snag variables; 1929 pre-logging and 2012 for CWD variables), using a repeated measures design in SAS PROC MIXED with plot ($n = 3$) considered a random effect and time ($n = 2$ or 3, depending on the variable) a fixed effect. To account for heterogeneity of variance among measurement times, I specified the time intervals as separate groups in the covariance structure. I used the Tukey's HSD test to for all pairwise comparisons between measurement times.

3. Results

3.1. Snags

Density of snags in 2007/2008 (140.0 ha^{-1}) was nearly an order of magnitude greater than in the old-growth condition in 1929 (15.2 ha^{-1}) (Table 1). The increase over the 1929 density was statistically significant for white fir, incense cedar, sugar pine, and total snag density. The proportion of snags by species was similar in 1929 and 2007/2008, with white fir comprising somewhat more than half of the total in both time periods. The proportional increase in density of white fir and incense cedar snags was highest in MC10, where the 1929 logging treatment did not target the large trees of these two species. Another major difference between time periods was the decline in snag size. In 1929, 72% of snags were classified as medium (38.1–76.1 cm (15–30 in.)) or large (>76.1 cm (30 in.)), based on a limited sample. In 2007/2008, only 22% of snags were classified as medium or large. Change was even more dramatic when considering only the largest snag size category, with the percentage dropping from 23% in 1929 to 4% in 2007/2008. (Note that snag size categories are based on values frequently used to define snag quality for wildlife management.)

Snags comprised 4% of all standing trees >10 cm in the unlogged condition in 1929 (Table 2). By 2007/2008, 16% of the standing trees were dead. Substantial differences existed among species, with the increase over time statistically significant for white fir and sugar pine (Table 2). Over 37% of standing sugar pine trees and 18% of the standing white fir trees were dead in the 2007/2008 census, compared with 8% of the incense cedar trees.

Contemporary snag density was the lowest in MC11 (Table 3), which was logged the most heavily in 1929. This plot also

Table 1
Snag density (stems >10 cm dbh) by species within three "Methods of Cutting" plots prior to logging in 1929, and in 2007 or 2008, 78+ years after logging. Plot 9 was logged using a USFS preferred marking system, plot 10 was logged using a light economic selection system where mainly the largest pines were removed, and plot 11 was logged using a heavy cutting system, similar to common practice on privately owned timber lands at the time. Numbers followed by different letters are significantly different at $P = 0.05$.

Plot	Year	*Abies concolor*	*Calocedrus decurrens*	*Pinus lambertiana*	*Pinus ponderosa*	Unknown species	Total
		Trees ha^{-1}					
9	1929 pre-logging	5.0	3.0	0.5	0.7	0	9.2
9	1929 post-logging	5.0	3.0	0.5	0.7	0	9.2
9	2008	90.5	35.1	29.4	5.0	0.1	160.8
10	1929 pre-logging	8.0	1.5	1.0	0.3	1.0	11.8
10	1929 post-logging	6.9	1.0	0.5	0.3	0	8.8
10	2008	104.1	22.6	34.6	1.3	0	163.2
11	1929 pre-logging	11.2	5.2	6.8	1.4	0	24.7
11	1929 post-logging	5.5	2.5	1.9	1.1	0	11.0
11	2007	56.0	16.1	22.8	2.7	0	99.7
All plots	1929 pre-logging	8.1^{a}	3.2^{a}	2.8^{a}	0.8^{a}	0.3	15.2^{a}
All plots	1929 post-logging	5.8^{a}	2.2^{a}	1.0^{a}	0.7^{a}	0	9.7^{a}
All plots	2007/2008	83.5^{b}	24.6^{b}	28.9^{b}	$3.0a^{a}$	0	140.0^{b}

Table 2
Average percentage of all standing trees >10 cm dbh by species in three "Methods of Cutting" plots that were snags, in the old-growth condition in 1929 and in 2007 or 2008, 78+ years after logging.

Plot	Year	*Abies concolor*	*Calocedrus decurrens*	*Pinus lambertiana*	*Pinus ponderosa*	All species (incl. unknowns)
9	1929	3.4	2.9	1.0	4.5	2.9
9	2008	18.1	9.6	41.1	10.3	16.3
10	1929	4.8	1.9	2.0	3.7	3.5
10	2008	20.0	9.1	39.9	8.9	18.7
11	1929	4.2	6.3	8.4	9.8	5.6
11	2007	15.5	5.3	31.4	8.7	12.7
All plots	1929	4.1	3.7	3.8	6.0	4.0
All plots	2007/2008	18.2	8.0	37.5	9.3	15.9
	P	*<0.001*	*0.089*	*<0.001*	*0.170*	*0.004*

Table 3
Snag density and basal area by size class in three "Methods of Cutting" plots in 2007 and 2008, 78+ years after logging using three different methods.

Plot	Logging treatment	Year	Size class (cm)					
			Small 10–38.1	Medium 38.2–76.1	Large ⩾76.2	Small 10–38.1	Medium 38.2–76.1	Large ⩾76.2
			Snags ha^{-1}			BA ha^{-1}		
9	USFS cut	2008	133.3	23.1	3.4	4.4	4.8	2.1
10	Light economic	2008	128.2	21.3	13.1	5.1	5.1	10.1
11	Heavy	2007	70.7	25.2	1.6	2.5	5.4	0.9

contained the fewest large (>76.1 cm) snags (1.7 ha^{-1}). MC10, which was logged the lightest and where large fir and cedar were not cut in 1929 contained far more large snags (13.1 ha^{-1}) (Table 3). The density of large snags in MC9 was intermediate (3.9 ha^{-1}). The majority of the snag basal area was in the large size category in MC10, and in the medium size category in both MC 9 and MC11. Percentage of the total (live plus dead) basal area composed of snags was 14% in MC9, 21% in MC 10, and 11% in MC11.

3.2. Coarse woody debris

Log volume, log mass, log surface area, and log cover did not differ significantly between the old-growth condition in 1929 and 2012, eighty-three years after logging (Table 4). However, the number of logs increased significantly and the average size of the logs declined significantly over time (Fig. 1, Table 4). An average of 28 logs ha^{-1} was recorded in 1929 and 76 logs ha^{-1} in 2012 (Table 4). Average size of the large end of logs declined from 83.9 cm (33.0 in.) in 1929 to 47.8 cm (18.8 in.) in 2012. Log surface area to volume ratio increased significantly over time (Table 4). The increase in log number over time resulted in a reduction in the minimum distance between logs. One indicator of this difference that relates directly to potential fire behavior is the density of intersecting logs, which averaged 2.2 ha^{-1} in 1929 and 12.2 ha^{-1} in 2012 ($P < 0.001$).

A visual comparison between pre and post-logging maps indicated that approximately 30% of logs were either moved or destroyed by the logging. Of the remaining 70%, approximately 10% were still either wholly or partially intact in 2012, based on overlapping location. In 2012, 63% of logs and 59% of the volume, respectively, were classified as rotten wood. The percentage of rotten wood by volume ranged from 71% for white fir to 41% for incense cedar. The pine species were intermediate (51% of volume rotten).

4. Discussion

Amount and composition of dead wood is related to disturbance history as well as forest composition and productivity. These factors vary by geographic locale, which can complicate comparisons among studies or between contemporary data and the historical literature. In this study, the same plots were evaluated over time and experienced the same fire regime, making it easier to elucidate the cause of long-term changes and attribute differences to variation in management.

Table 4
Coarse woody debris measures within three "Methods of Cutting" plots prior to logging in 1929, and in 2012, 83 years after logging by three different methods. Average log diameter is for the large end.

Plot	Logging treatment	Year	Logs ha^{-1}	Ave. diam. (cm)	Linear length (m ha^{-1})	Log cover (%)	Surface area (m^2)	Volume (m^3 ha^{-1})	SA:V ratio	Log mass (Mg ha^{-1})
9	USFS cut	1929	13.9	98.0	180.0	1.43	448.0	100.4	4.46	37.9
9	USFS cut	2012	68.4	44.5	562.0	1.90	597.5	59.5	10.04	19.8
10	Light Economic	1929	20.9	86.5	252.2	1.89	592.3	125.2	4.73	47.3
10	Light Economic	2012	99.5	51.9	759.4	3.26	1027.3	131.9	7.79	43.0
11	Heavy	1929	50.0	67.3	378.8	2.53	796.2	148.6	5.36	56.1
11	Heavy	2012	60.8	47.1	522.8	1.87	589.0	63.4	9.29	20.7
All plots		1929	28.3	85.7	270.3	1.97	619.9	127.6	4.85	47.1
All plots		2012	76.2	47.8	614.7	2.34	737.9	84.9	9.04	27.8
		P	*0.042*	*0.019*	*0.021*	*0.548*	*0.543*	*0.201*	*0.004*	*0.105*

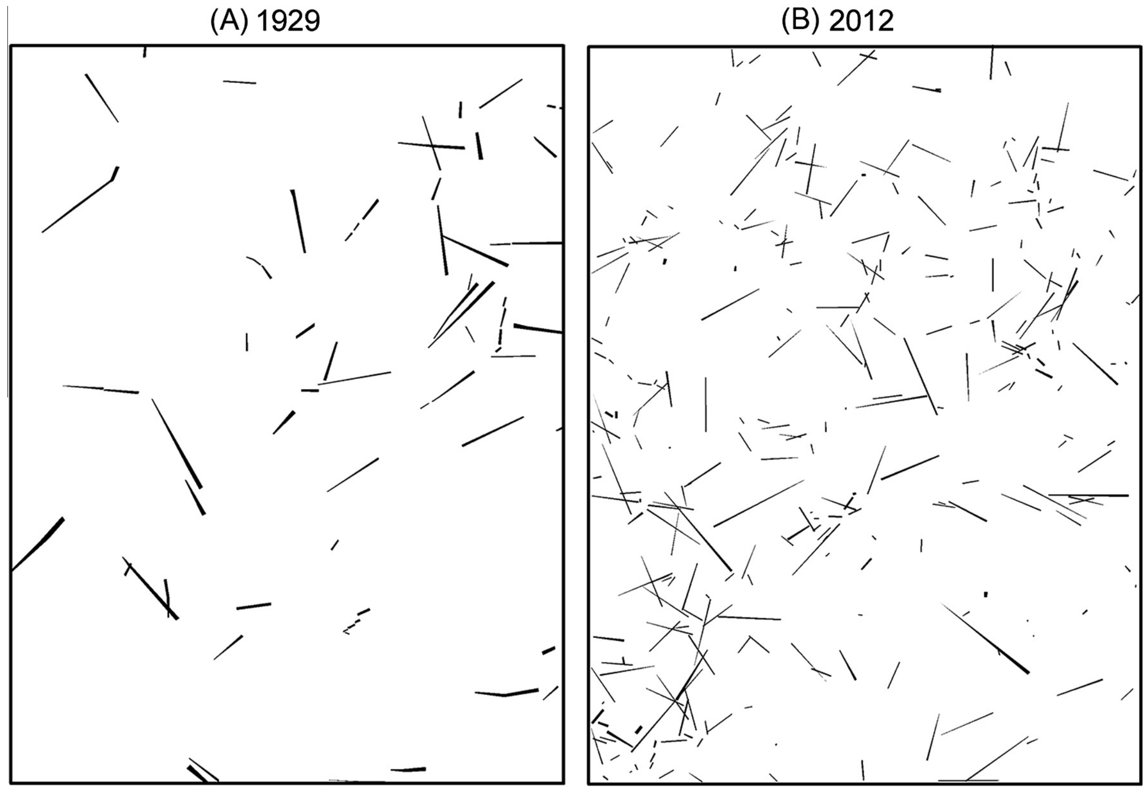

Fig. 1. Downed logs in methods of cutting plot 9 (MC9) in (A) 1929, prior to logging, and (B) 2012, eighty-three years after logging and continued fire exclusion.

4.1. Snag dynamics over time

Snags are a valued ecological resource and subject to management targets in western conifer forests, yet little is known about historical abundance and how snag characteristics have changed over time. The density and size of snags is dependent on the density and size distribution of live trees, as well as mechanisms of mortality. Any logging that reduces stand density and alters the tree size distribution will influence future snag recruitment and size. Increasing forest density as a result of fire exclusion can also alter snag density if greater tree density leads to more tree deaths. In addition, in the absence of fire, more snags might be expected to remain standing longer because fire typically consumes a substantial proportion (Horton and Mannan, 1988; Stephens and Moghaddas, 2005; Bagne et al., 2008). However, the lack of fire also removes one mechanism of tree mortality (Harmon, 2002).

Historical estimates of snag numbers or estimates from forests with an intact natural fire regime and prior to manipulation of forest structure through logging are rare (e.g. Taylor, 2010), but important for developing restoration targets for management. In extensive surveys of ponderosa pine forest in NE California completed in the 1920s and 1930s, Keen (1929, 1955) reported snag densities ranging from 2.7 to 19.5 ha^{-1} (mean = 9.9 ha^{-1}), which is similar to the 13.8 snags ha^{-1} found in 1929 in this study when using the same minimum snag size cut-off. The 1929 snag density was somewhat higher than found in contemporary surveys of unlogged stands in the Sierra San Pedro Mártir (SSPM) in northwestern Mexico, where the fire regime is still largely intact (Savage, 1997; Stephens, 2004), but lower than the 69 conifer snags ha^{-1} recorded in an old-growth reference forest in the southern Cascades of California that experienced five fires in the 20th century (Taylor (2010).

The 2007/2008 snag densities in this study (79 years after logging, and following over a century of fire exclusion) were similar to numbers reported for other non-old growth forests in Oregon and Washington (Spies et al., 1988), but approximately three times greater than densities found by Stephens and Moghaddas (2005) in the north-central Sierra Nevada (104.5 ha^{-1} versus 35.7 ha^{-1} for snags >15 cm dbh). Density of snags in our study was also more than double values reported by Ganey (1999) in two National Forests in Arizona (68.4 vs 29.0 for snags >20 cmin two National Forests in Arizonadbh). Differences in snag density both among reference sites and among previously logged sites where fire has been excluded could be attributed to variation in productivity, stage of stand development, as well as timing of the surveys relative to the latest mortality-causing event, such as wildfire or bark beetle outbreak.

The dramatic increase in number of snags I report, corresponding to the increase in live tree density between 1929 and 2007/2008 is similar to findings from contemporary comparisons between forests where fire has been allowed to spread and forests where fire has been excluded. Savage (1997) found over five times fewer snags in the SSPM in Mexico, which has a near intact fire regime, than in the San Bernardino Mountains of southern California, where fires have been actively suppressed for over 90 years. Forests in the two areas have a nearly identical tree species composition, but the forests in the San Bernardino Mountains were approximately twice as dense. As in our study, this added tree density was thought to be largely the result of fire exclusion. The change in the percentage of standing trees that were dead (4.0% and 15.9% in 1929 and 2007/2008, respectively), was also almost identical to the difference in percentage of dead standing trees noted between the SSPM and the San Bernardino Mountains (4.3% and 14.5%, respectively).

Instead of a preponderance of medium and large snags noted in 1929, snags are on average much smaller today. The observed shift in snag size may be due, in part, to the logging-produced deficit of larger trees relative to historic old-growth condition (Knapp et al., 2013), but also suggests that dominant mechanisms of tree mortality have changed over time. In the absence of fire, tree density has increased dramatically (Knapp et al., 2013), and greater mortality is now seen among small and intermediate trees, presumably as a result of competition for resources and suppression of smaller statured individuals (Fiedler and Morgan, 2002; Smith et al., 2005). Rates of mortality are generally highest in the stem-exclusion phase of succession – higher than in old-growth stands (Harmon, 2002). In a stand age chronosequence, snag density was noted to peak at 81–100 years (Smith et al., 2008), similar to the time since logging in this study. Mortality has been shown to be correlated with forest density or basal area in other studies (Ferrell et al., 1994; Dolph et al., 1995; Savage, 1997; Fiedler and Morgan, 2002; Ritchie et al., 2008), but changing climate could also be playing a role (van Mantgem and Stephenson, 2007). Density may amplify the effects of drought, with stress predisposing trees to attack by bark beetles (Guarin and Taylor, 2005). Additionally, in this study, a greater proportion of the standing sugar pine were dead compared to any of the other tree species, and much of this mortality appears to be the result of an introduced pathogen - blister rust (*Cronartium rubicola* J.C. Fisch.). Blister rust was first introduced to North America around 1910 and is not thought to have reached the central Sierra Nevada until the 1940s (Smith, 1996). Smaller trees are most susceptible to the stem cankers that kill sugar pine (van Mantgem et al., 2004).

While birds will forage on smaller snags, larger snags are believed to provide the best habitat (Raphael and White, 1984; Morrison and Raphael, 1993). Cavities are more likely to be excavated in larger snags (Saab et al., 2009), and larger snags are also potentially preferred by mammals. For example, resting habitat of the fisher contained more large snags (and higher snag basal area) compared to random sites (Purcell et al., 2009). Larger snags also have more heartwood and remain standing for a longer period of time (Keen, 1955; Ritchie et al., 2013). The current preponderance of snags of small size is similar to that noted by Ganey (1999) and Barbour et al. (2002) for conifer forests in Arizona, and northern California, respectively.

4.2. Coarse woody debris dynamics over time

Because fire consumes downed wood, old-growth forests where fire has been excluded are thought to now contain higher levels of CWD than they would have with a natural fire regime (Skinner, 2002; Stephens, 2004). Indeed, contemporary CWD mass values reported from studies of old-growth stands without recent fire (Knapp et al., 2005; Innes et al., 2006) were greater than values found in the MC plots in 1929. However, volume and mass of CWD in this study actually showed a declining trend between 1929 and 2012 (the difference was not statistically significant), presumably because the effects of the 1929 logging more than cancelled out the effects of fire exclusion. The legacy of logging on CWD is readily seen when comparing the three logging treatments. MC10, which was logged the lightest, contained approximately double the log cover, volume and mass of MC9 and M11. Many of the larger white fir left standing in MC10 had died and fallen to the ground by 2012. This source of large wood was not present in the two more heavily logged plots. While the amount of dead wood added because of the mortality of smaller trees increased substantially over time in all plots as well, smaller diameter material contributes far less to volume and mass metrics.

As with the standing snags, the major difference over time has been in the size of the CWD. Today's CWD volume and mass is comprised of many more but smaller pieces of wood. While the finding is consistent with the snag density and size distribution data, a portion of the difference in log density and average size could be due to variation in what was counted as a log between measurement times. No written documentation of the minimum size cut-off used for logs in 1929 has been found, so it was estimated from hand-drawn maps. However, because most logs at that time were medium to large (based on both the maps and the distribution of snag sizes, which eventually become CWD), small differences in the minimum size cut-off would likely have had little effect on the outcome. In addition, our decision to consider logs lying >30 cm apart as separate may have inflated the number slightly, because some pieces undoubtedly originated from the same tree. For example, approximately 9% fewer logs would have been counted in the 1929 data if all sections apparently originating from the same fallen tree/snag (based on visual examination of the maps) were considered as one. Breakage and separation upon falling may have been more prevalent in the 2012 data, because more snags were fir and the average snag was smaller. Fir snags tend of stay standing longer than pine (Ritchie et al., 2013) and then fall in a highly decayed state and in sections. Smaller decayed snags also often break into pieces on impact. While both the minimum size cut-off and separation criteria for counting logs may have influenced the numbers slightly, the effect on the outcome was likely relatively minor, and would not come close to explaining the nearly 3-fold increase in log number between 1929 and 2012. Volume and mass measurements are less sensitive to variations in choice of minimum diameter cut-off, because the majority of CWD volume and mass are contained within the larger pieces.

While numerous terrestrial vertebrate and invertebrate species use CWD for cover, movement, or food (Harmon et al., 1986), strength of associations between abundance and CWD measures vary. Red-backed voles (*Clethrionomys gapperi*) have been shown to use CWD at a greater rate than expected based on availability (Ucitel et al., 2003; Thomson et al., 2009), and Goodwin and Hungerford (1979) reported a strong positive relationship between density of deer mice (*Peromyscus maniculatus*) and cover of downed wood. Several studies have reported the strongest associations to occur in stands with relatively low overall abundance of decayed CWD and other structures that provide cover (Bowman et al., 2000; Ucitel et al., 2003). In other forest types and for other vertebrates, the relationship with CWD is weak to non-existent (Bowman et al., 2000; Owens et al., 2008). It is possible that many wildlife species use CWD when available, but find cover in alternate structures, if not. In addition, because CWD is consumed by fire, small mammals in forests where fire was historically frequent may not have evolved to rely on CWD (Owens et al., 2008). For species that use CWD, the influence of size is not clear, with studies reporting both a preference for larger logs (Hayes and Cross, 1987), or small and medium sized logs (Thomson et al., 2009). One potential benefit of large CWD is that it lasts longer (Harmon et al., 1986).

4.3. Management implications

4.3.1. Management targets for dead wood

Raphael and White (1984) predicted that snag densities of >8.6 ha^{-1} (diameter not specified) would be required to maximize populations of snag-using species. Raphael and Morrison (1987) speculated based on a 1978–1983 survey in the Sierra Nevada that snag density was more than enough to meet wildlife needs, but a follow-up survey in 1988 showed a decline in the rate of recruitment of medium to large (>38 cm) snags, demonstrating that the episodic nature of snag recruitment due to climate or disturbance events requires consideration (Morrison and Raphael, 1993). Current guides for management on National Forest Service lands in the Sierra Nevada require 10 snags ha^{-1} >38 cm diameter (USDA Forest Service, 2004). In 1929, the MC plots contained an average of 10.9 ha^{-1} snags >38.1 cm, which is very close to this management target. Even though logging reduced the density of medium to large trees, density of such snags in 2008 (29.2 ha^{-1} >38 cm dbh) was still nearly three times greater than current management target. The two plots logged the heaviest (MC9 and MC11) contained only slightly fewer medium and large snags (26.5 ha^{-1} and 26.8 ha^{-1}, respectively) than MC10 (35.1 ha^{-1}), which was logged the lightest and where all large fir and cedar were left uncut. The two most heavily logged plots did contain far fewer snags in the largest size category (>76.2 cm dbh).

If wildlife of mixed conifer forests are limited by the presence of snags >38 cm dbh, forests in the study area and other similar forests should have plenty of snags, relative to the numbers that were once present in this forest and relative to management targets for wildlife on Sierra Nevada FS lands. For downed wood, general guidelines emphasize retention in the largest size classes (USDA Forest Service, 2004). Unfortunately, in forests such as those in this study, the presence of medium to large standing and down wood is also accompanied by a considerable quantity of small sized standing and downed wood. Less productive second-growth forests where growth of trees to larger sizes is slower are likely to have less large wood than found in this study, and may still be in deficit.

4.3.2. Balancing habitat and fire hazard

While the importance of woody detritus to the ecological health of many forested ecosystems is undeniable, it is also recognized that in seasonally dry forests a balance is necessary so that excessive fire hazard does not result (Brown and See, 1981; Brown et al., 2003; Lehmkuhl et al., 2007). A substantial proportion of lighting-ignited fires start in snags (Komarek, 1968). Burning snags, particularly ones that are highly decayed, are also a prolific source of embers that propagate spot fires, contributing to rapid fire spread (Barrows, 1951). In addition, the instability and unpredictability of burning snags are a serious safety issue for fire management personnel (Page et al., 2013). While a greater proportion of the dead wood biomass in coniferous forests is typically found in CWD than in snags (Harmon et al., 1986), consumption of both standing snags and CWD increases fire-line intensity, contributing to extreme fire behavior and more severe fire effects (Page et al., 2013). With CWD, Brown et al. (2003) speculated that an optimum quantity for warm and dry ponderosa pine and Douglas fir forest types of the western U.S. that would provide for wildlife, nutrients and other ecological benefits, without contributing to excessive risk of an uncharacteristically severe wildfire, would fall within the range of 11.2–44.8 Mg ha^{-1} (5–20 tons ac^{-1}), with the higher fuel loading acceptable if the CWD was comprised of larger pieces. While these numbers may or may not be fully applicable to the more productive mixed conifer forests of this study, it is interesting to note that fuel loading calculated from the 1929 MC plot maps actually exceeded the acceptable management range by a small amount, while the quantity measured in 2012 was approximately in the middle of this range.

The long-term comparisons in this study illustrate why changes to CWD that have implications for future fire behavior are inadequately captured by the mass or volume metrics often used to quantify fuel loads or define optimum wildlife habitat. For example, I noted a downward trend in both CWD mass and volume over time (due to high variance and low sample size, the difference was not statistically significant), even though the number of logs increased substantially and the average size of the logs decreased. With the lower abundance on the 1929 maps, most logs were isolated and not touching other logs. A sound log by itself is often not completely consumed in a fire because the relatively low surface area to volume ratio results in insufficient surface combustion to heat the interior of the log. The addition of logs through 2012 reduced the minimum distance between logs, and many more logs now intersect or cross in "jackpots". Heat transfer from adjacent burning logs compensates for the low SAV ratio and allows for more prolonged combustion (Albini and Reinhardt, 1997; de Souza Costa and Sandberg, 2004), producing pockets of higher intensity fire. In this study, the 270% increase in log density over time translated into a 550% increase in the density of crossing logs, despite the smaller average log size. In addition, smaller logs dry more readily with the onset of summer and have a higher SAV ratio, both of which increase the likelihood of complete consumption (Brown et al., 1991).

The highly decayed state of CWD in many forests where fire has been excluded for long periods exacerbates many of these potential fire behavior issues. For example, upon combustion, decomposed wood produces more heat per gram than sound wood, apparently as a result of the higher lignin content (Hyde et al., 2011). The cracked nature of decayed wood also increases the surface area to volume ratio (Means et al., 1985; Hyde et al., 2011) and aids drying, contributing to more complete consumption (Stephens and Moghaddas, 2005; Uzoh and Skinner, 2009). The more complete consumption and longer burnout time can result in substantial soil heating (Monsanto and Agee, 2008), particularly at the intersection of one or more logs (Brown et al., 2003). Rotten wood also requires less energy to ignite (Stockstad, 1979; Susott, 1982) and therefore provides a receptive surface for embers. Highly decayed snags are more likely to be ignited by embers (Stephens, 2004). This makes rotten wood an important contributor to rapid fire spread through spotting. It is unlikely that historical forests with a regime of frequent fire would have accumulated as much material in this stage of decay, because rotten wood is readily consumed by fire, and several cycles of fire would have been expected during the decades long decomposition phase (Uzoh and Skinner, 2009). Regardless, some highly decayed CWD was likely still present, escaping burning due to spatial discontinuities in the historical fuel bed (Stephens et al., 2007).

Our findings illustrate the need to consider size and decay class, in addition to quantity and mass or volume, when managing for dead wood. In addition, simply managing for a quantity of larger snags and larger CWD is also inadequate, because the amount of smaller dead wood, which contributes more to fire intensity relative to habitat value, also needs to be factored in (Brown et al., 2003). Providing for a number of snags and/or logs per unit area within an acceptable management range, and either adjusting the numbers based on the amount of smaller diameter dead wood also present (Brown et al., 2003), or maximizing the ratio of larger to smaller structures might be one way of maintaining the habitat value without causing undue fire hazard.

Forest management increasingly emphasizes structural complexity and spatial and temporal variation (North et al., 2009), and heterogeneity in dead wood abundance and size would be one outcome and also an indicator of a healthy ecosystem. Thus targets or management ranges for snags and CWD cannot and should not be met in every stand (Stephens, 2004). In addition, as noted by Harmon (2002), dead wood is a dynamic entity, with live stand structure, snags and CWD intimately intertwined. For the long-term management of dead wood, these relationships need to be recognized and planned for in every phase of forest development. To restore dead wood to conditions more like those found historically will require growing larger trees and reducing the rate at which smaller and intermediate sized dead wood accumulates. Maintaining a lower overall tree density in at least some areas, through mechanical thinning or fire, would be one means of reducing mortality of small- and intermediate sized-trees. The options may be more limited with sugar pine, which is experiencing high mortality in especially the smaller tree sizes, due to introduced blister rust. For snags that have fallen and transitioned to CWD, fire, which preferentially consumes smaller and more rotten wood, should help shift the balance to larger and less rotten pieces.

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