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ARTICLE

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Snag decomposition following stand-replacing wildfires alters wildlife habitat use and surface woody fuels through time

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Abstract

High-severity wildfires create pulses of snags that serve a variety of functions as they decompose over time. Snag-related benefits (and hazards) are often linked to specific decomposition stages, but snag decomposition rates and pathways are not well understood in many forest types. We examined temporal patterns of snag decomposition, wildlife cavity creation, and surface woody fuel dynamics in dry coniferous forests of the interior Pacific Northwest region of North America by sampling 159 forest stands within a 39-year chronosequence of stand-replacing wildfires in dry coniferous forests dominated by ponderosa pine and Douglas-fir. We found that most snags broke or fell during the first 15 years after wildfire; small-diameter snags mostly broke off at or near ground level, while many large-diameter snags initially broke off above a height of 2 m and then remained standing for an extended period. Ponderosa pine and lodgepole pine snags fell earlier than Douglas-fir and true fir snags of comparable diameter classes. Wildlife cavities were most common in stands surveyed 8–20 years after fire and in snags with broken tops but were not limited to large diameter snags. Cavity snag diameters ranged from 17 to 98 cm, with 64% of cavity snags having diameters between 30 and 60 cm and 22% of cavity snags having diameters >60 cm. Surface woody fuels increased as snags broke and fell, reaching maximum levels in all size classes 15–20 years after fire. The percentage of large diameter rotten woody fuels increased steadily beginning about 15 years after fire, with implications for fuel management and subsequent wildfire behavior and severity. Our study supports the proposition that fire-killed snags represent a transient resource pulse in which the relative contribution of snags to different ecological functions varies with snag diameter, species, time since fire, and landscape position.

KEYWORDS
Abies, Douglas-fir, fuel succession, ponderosa pine, reburn, snag dynamics, snag longevity, wildlife cavities

INTRODUCTION

Wildfires and other disturbances generate pulses of dead trees that provide a wide range of social and ecological functions over time as they decompose (Bull et al., 1997; Harmon et al., 1986). Standing and fallen dead trees (hereafter, snags) provide shelter and feeding habitat for invertebrates and wildlife (Bull et al., 1997; Johnson & O'Neil, 2001), economic benefits (e.g., wood products) for humans (Campbell et al., 2016; Lowell et al., 2010; Prestemon et al., 2006), terrestrial carbon storage (Campbell et al., 2016; Harmon et al., 2020; Powers et al., 2013), and organic matter inputs to aquatic ecosystems (Bendix & Cowell, 2010) and forest soils (Harmon et al., 1986). Snag decomposition also generates surface woody fuels that can influence the intensity and severity of subsequent wildfires (Dunn & Bailey, 2012; Kulakowski & Veblen, 2007; Monsanto & Agee, 2008). Because they serve as resources for a variety of consumers, it may be useful to think of fire-generated snags as a disturbance-generated resource pulse (Ostfeld & Keesing, 2000; Yang et al., 2008).

Snag resource benefits are often linked to specific decomposition stages (Bull et al., 1997; Lowell et al., 2010), so the potential contribution of individual snags to wildlife habitat, wood products, carbon storage, or forest fuels depends on when a snag reaches the relevant stage of decomposition and how long it persists in that stage. Snag longevity and decomposition rates have been shown to differ among tree species, with snag height and diameter, and across environmental gradients, reflecting differences in initial wood properties, biological decay processes, and the frequency and intensity of physical disturbances (Dunn & Bailey, 2012; Everett et al., 1999; Grayson et al., 2019; Keen, 1955; Kimmey, 1955). Biological processes drive changes in wood strength and bulk density, as saprophytic fungi and bacteria break down sapwood, invertebrates bore through wood, and birds forage for invertebrates and excavate cavities for nests (Kimmey, 1955; Kimmey & Furniss, 1943; Lowell et al., 2010). Physical processes catalyze transitions from standing snags to downed coarse woody debris by breaking off branches and tops of snags (e.g., wind and ice storms) or toppling entire snags (e.g., wind or fire) as they are weakened by biological processes (Kimmey, 1955). Snag structural changes and wood decay also alter snag suitability for nesting habitat by primary cavity excavating (PCE) birds, which have been shown to prefer snags with broken tops (Lehmkuhl et al., 2003), and softer interior wood (Lorenz et al., 2015). Wood decay also alters fuel properties of standing and fallen snags (Brown et al., 2003; Monsanto & Agee, 2008).

Interior western U.S. forests have experienced significant increases in annual area burned, annual area burned at high severity, and high severity patch sizes in recent decades (Dennison et al., 2014; Parks & Abatzoglou, 2020; Westerling, 2016). Most of the increases in area burned and burn severity are associated with increasing numbers of large wildfires and "mega-fires" (Dennison et al., 2014). Following large wildfires, areas in which snags were once a scarce resource can have an abundance of snags, expanding opportunities for managing snag populations to achieve multiple objectives within burned landscapes (human safety, wildlife habitat, fuels, etc.). Improving our understanding of the sources of variability in snag decomposition patterns and rates will help forest managers align post-fire snag management priorities and activities with longer term forest restoration and management objectives and decide where and when to invest limited resources within burned landscapes.

In this study, we examined temporal patterns of snag decomposition, surface woody fuel dynamics, and cavity creation by PCE birds within a 39-year chronosequence of stand-replacing wildfires in dry ponderosa pine and Douglas-fir forests of the interior Pacific Northwest region of North America. These dry coniferous forests historically supported low- and mixed-severity fire regimes with mean fire return intervals less than 40 years (Agee, 1993; Everett et al., 2000), so woody fuels generated by one wildfire could influence future fire behavior and effects (Monsanto & Agee, 2008). Snags in these forests also provide foraging and nesting habitat for several species of PCE birds as well as secondary cavity nesters (Bull et al., 1997; Lorenz et al., 2015), so snag decomposition processes have important implications for wildlife habitat management. Based on prior studies, we hypothesized that (1) snag decomposition trajectories and rates would vary among tree species and with snag diameter; (2) surface woody fuel loadings would be temporally correlated with snag decomposition; and (3) wildlife cavities would be most common in broken, large diameter snags. We discuss the implications of our findings for managing snag resources after wildfire to meet multiple resource objectives.

METHODS

Study area

The study area encompasses most of the dry coniferous forest region in eastern Washington and Oregon (Figure 1). Dry coniferous forests typically occupy lower to middle elevation sites within the forested areas of the eastern Cascade Mountains, Blue Mountains, and Okanogan Highlands of Washington and Oregon. They are typically dominated by ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) but can also contain significant components of true firs

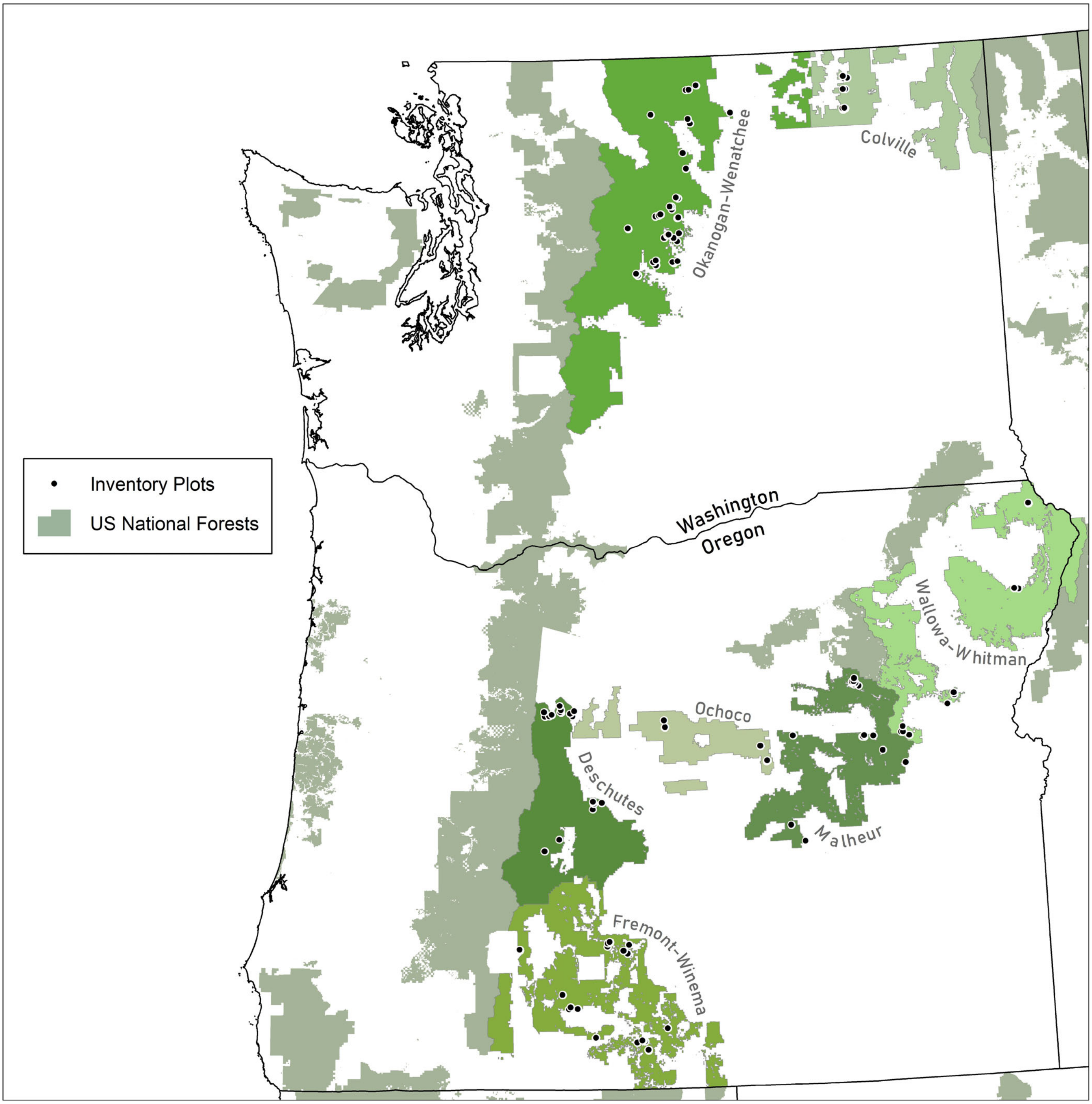

FIGURE 1 Study site locations in dry coniferous forests of eastern Washington and Oregon, USA.

(*Abies grandis* (Douglas ex D. Don) Lindl., *A. concolor* (Gord. & Glend.) Lindl. ex Hildebr., *A. lasiocarpa* (Hook.) Nutt., or *A. magnifica* A. Murray bis), other pines (*P. contorta* Dougl. ex. Loud., *P. lambertiana* Dougl., or *P. monticola* Dougl. ex D. Don), junipers (*Juniperus occidentalis* Hook.), or larches (*Larix occidentalis* Nutt.).

Topography and soils vary considerably among the dry coniferous forests of Washington and Oregon. Topography ranges from deeply dissected mountainous terrain to relatively flat plateaus. Dry coniferous forests typically occur at elevations of 200–1000 m above sea level in eastern Washington State but can be found at elevations up to 1800 m in central Oregon. Soils also vary considerably, but are typically well drained, poorly developed, and derived from some combination of igneous or metamorphic bedrock, glacial till (or outwash sediments), pumice (particularly in Oregon), and volcanic ash.

Climate varies across elevational and latitudinal gradients within the study region but generally features warm, dry summers, and cold, wet winters. Mean annual precipitation varies from a low of about 35 cm per year in some ponderosa pine forests to over 100 cm per year in some mixed-conifer forests. Most of the dry forests in this study support a persistent winter snowpack, ranging from one to several months in duration. Warm summer temperatures and low summer precipitation produce extended dry periods each year, routinely producing weather and fuel moisture conditions that favor summer wildfires.

Wildfires in this region are therefore limited primarily by ignitions, active fire suppression efforts, and fuel continuity on the landscape (e.g., roads and recently burned areas). Historically, these forests burned in mostly low- and mixed-severity wildfires; mean fire return interval estimates are highly variable but generally range between 5 and 45 years (Agee, 1993; Everett et al., 2000; Johnston et al., 2016; Wright & Agee, 2004).

Data collection

We used a chronosequence approach to study temporal patterns of snag decomposition following severe wildfires in dry coniferous forests of eastern Washington and Oregon. From the population of wildfires that burned at mixed or high severity between 1970 and 2007, we selected 55 wildfires that provided good spatial coverage of the geographic region and a wide range of fire years (time since fire). For each wildfire, we used fire perimeter maps and site visits to select forest stands for sampling. Stand selection criteria included high stand-level burn severity (minimum 95% overstory tree mortality), a significant proportion of overstory Douglas-fir or ponderosa pine trees, no post-fire logging, no subsequent wildfires, and no other post-fire restoration or fuel reduction treatments (e.g., prescribed burning) that would significantly alter snag condition or downed woody debris.

We selected 159 stands for field sampling (Figure 1), with the goal of representing a broad range of fire ages and pre-fire stand structural conditions (different species and size distributions); we therefore have a representative, but nonrandom, sample of stands. Most of the stands had burned less than 25 years prior to sampling. Our study included only nine stands from three wildfires that burned between 1970 and 1983, because there were fewer wildfires during this period and much of the area burned at high severity during that period had been subjected to logging or fuel treatments after wildfire and were therefore unsuitable for this study.

Sampling plots

Within each selected stand, we established one circular sampling plot for surveying snags and surface woody fuels by subjectively selecting a "representative" point in the interior of the stand and then locating the plot center using a randomly selected offset distance of 0–25 m in a random direction. The base sample plot radius (typically 18–25 m) was chosen in the field to provide a sample size of 40–80 snags and to capture the structural complexity of the pre-fire stand; we therefore sampled more trees in stands with high structural and species diversity than in even-aged, single-species stands. To better balance the species and size distribution of surveyed snags at each site, we also extended the base plot area for sampling large snags (>45 cm dbh) by a factor of up to four (double the base plot radius) if fewer than 20 snags of a locally abundant species were sampled in the base plot radius; however, we sampled only under-represented species-size groups in the extended plot area.

Snag status and cavity presence

For each snag within a sample plot that was assessed to have been a living tree at the time of the fire and had a dbh ≥ 15 cm, we recorded the species, status, and dbh. We recorded snag status as standing (≥2 m tall) or fallen (<2 m tall). For "standing" snags, we noted whether the snag top condition was broken or intact and assigned the snag to one of three decay classes (sensu Parks et al., 1997). Snags in class 1 were recently dead and retained most branches and bark; snags in class 2 had shed many branches and often had broken tops but had mostly solid bole wood; and snags in class 3 ("soft snags") had broken tops, soft bole wood, and little or no bark. For "fallen" snags, we located the stump (<2 m tall snag) or root mass (uprooted snag) and then measured the diameter at the (estimated) former breast height location and assigned a decay class (1–3) like that used for standing snags (Parks et al., 1997).

We also noted the presence or absence of wildlife cavities in standing snags but did not attempt to measure cavity dimensions or assess occupancy. Field crews identified wildlife cavities based on published images and descriptions (Bull et al., 1997) and field training by an experienced wildlife biologist (John F. Lehmkuhl, Research Wildlife Biologist, USDA Forest Service). We did not look for or record wildlife cavities in fallen snags.

We characterized pre-fire overstory stand structure for each plot by calculating stand density and basal area from snags (standing or fallen) measured within the base plot radius. We also recorded the slope, aspect, elevation, and geographic location for each plot.

Surface woody fuels

To assess changes in surface woody fuels over time, we surveyed surface fuels on each plot using at least three

20-m fuel transects (Brown, 1974). We sampled fuels using three transects per plot on 126 plots and seven transects per plot on 33 additional plots. We tallied transect intercepts with fine woody fuels (0.1–2.5 cm diameter) on the first 2-m segment of each transect and medium woody fuels (2.6–7.6 cm diameter) on the first 3-m segment of each transect. We recorded transect intercepts with large woody fuels (>7.6 cm diameter) individually, noting the diameter and decay condition (sound or rotten) at the point of intersection with the transect tape. We converted woody fuel counts from individual transects fuel mass estimates (in megagrams per hectare) using formulae provided by Brown (1974) and then averaged values across all transects within each plot to develop plot-level fuel mass estimates.

Data analysis

We limited our analysis to the six most common snag species in our dataset: ponderosa pine (*P. ponderosa*), Douglas-fir (*P. menziesii*), grand fir (*A. grandis*), white fir (*Abies concolor*), lodgepole pine (*Pinus contorta*), and western larch (*L. occidentalis*). We combined western larch and Douglas-fir snags into a Douglas-fir species group and combined grand fir and white fir into a true fir species group for data analyses after preliminary analyses showed highly similar responses among the paired species. The paired species have also previously been found to have similar wood strength and elasticity properties (Forest Products Laboratory, 1999). We therefore report results for the resulting four species groups, hereafter ponderosa pine, Douglas-fir, true fir, and lodgepole pine.

Snag, log, and cavity dynamics

We assessed species group and diameter effects on post-fire snag decomposition over time using generalized linear mixed models with binomial response variables (true or false) and the logit link function. We developed separate models for the following response variables: (1) snag status (standing or fallen), (2) standing snag top condition (whole or broken), (3) standing snag in decay class 2 or 3, (4) standing snag in decay class 3, (5) fallen snag in decay class 3 (rotten), and (6) wildlife cavity present. Models were developed using the SAS GLIMMIX procedure (SAS Institute) using maximum likelihood estimation based on the Laplace approximation and the Kenward–Roger correction for denominator degrees of freedom.

Models included predictor variables at both the snag (within-plots) and stand (among-plots) levels. Within individual plots, we modeled responses as functions of species group (a categorical variable), snag diameter (a continuous, linear variable), and a species-diameter interaction term. We modeled variability in the intercept, species, and diameter effects among plots as functions of time since fire (in years) and random plot effects. We used natural cubic splines with three or four internal knots to model responses to time since fire. We developed final models for each response through a backward-elimination procedure, starting with the full model and removing the least-significant fixed effects individually (based on Type 3 tests, removing higher order effects first) until all remaining fixed effects were statistically significant ($p < 0.05$) or could not be removed without increasing the corrected Akaike information criterion ($\mathrm{AIC_c}$, Burnham & Anderson, 2002).

We first developed the snag status (standing or fallen) model using the full snag dataset. We then split the dataset by snag status and developed conditional probability models for the remaining response variables using only the standing (top condition, standing snag decay class, and cavity presence responses) or fallen (fallen snag decay class response) snag observations. We then calculated joint probability models by multiplying the conditional model probability estimates by the associated snag status probability estimates. For example, the snag top conditional model estimates the probability of a snag having a broken top, given that it was standing at the time of sampling. From this, we develop a joint probability model estimating the probability a snag would be standing and have a broken top at different times since fire by multiplying the conditional probability estimate for a standing snag having a broken top by the probability estimate for a snag remaining standing.

Fuel dynamics

We analyzed changes in surface fuel loadings and downed coarse woody debris with time since fire using linear mixed-effects models. Response variables included small (<2.6 cm diameter), medium (2.6–7.6 cm), large (7.7–20.0 cm), and very large (>20 cm) woody fuels, with separate models developed for total fuel and rotten-only fuel for the large and very large fuel size classes. We used square root transformations on the response variables after preliminary analysis indicated strong non-normality of model residuals without transformation. The full statistical models for each response included time since fire (in years), pre-fire stand basal area (in square meters per hectare), and their interaction as fixed effects and wildfire as a random effect (allowing for potential correlations among plots or stands burned in the same fire). As with the snag models, we used a natural cubic spline to model the effects of time since fire and linear terms to model the effects of stand basal area and mean temperature. Fuel models were implemented using the SAS GLIMMIX procedure using restricted maximum likelihood estimation and the Kenward–Roger correction for denominator degrees of freedom.

RESULTS

We sampled 8395 fire-generated snags, including 2738 ponderosa pine (*P. ponderosa*), 3563 Douglas-fir (*P. menziesii*), 1293 true fir (*Abies* spp.), 456 lodgepole pine (*P. contorta*), and 184 western larch (*L. occidentalis*) snags for this study (Table 1). Snag diameters were heavily skewed toward the smaller size classes, as we surveyed 4086 snags in the 15–29.9 cm diameter class, compared to only 777 snags in the 60 cm and larger diameter class (Figure 2). Proportional representation of ponderosa pine in the sample increased with snag diameter, from 28% of snags in the smallest diameter class to 55% of snags in the largest diameter class. Douglas-fir snags were well represented across all diameter classes (35%–47% of snags), while proportional representation of true firs declined from 11% in the smallest diameter class to only 7% in the largest diameter class.

Snag dynamics

Time since wildfire significantly influenced the probability of snags remaining standing (persisting) and the probability of a standing snag having a broken top (Figure 3). The probability of a snag remaining standing at a height of 2 m or more declined over time following a descending sigmoidal curve, with few snags falling in the first 2–5 years after fire, many snags falling in the next 10–15 years, and then few snags falling per year during the last 20–25 years (Figure 3). Similarly, the probability of a standing snag having a broken top increased over time, with the tops of most standing snags remaining intact during the first 2–5 years after fire, but then breaking over the following 10–15 years. Most snags either fell or broke within the first 15 years after fire.

Snag diameter and species both influenced the probability of snag persistence and top breakage through time (Figure 3). Large diameter snags persisted (remained standing) longer than small-diameter snags on average for all species except lodgepole pine. Douglas-fir and true fir snags persisted longer on average than ponderosa pine and lodgepole pine snags when controlling for snag diameter (Figure 3). Estimated median post-fire persistence times for small-diameter snags (15–30 cm dbh) ranged from 6 to 7 years for lodgepole and ponderosa pine snags to 10–11 years for true fir and Douglas-fir snags (Figure 3). Estimated median persistence times for very large diameter snags (>60 cm dbh) ranged from 17 years for ponderosa pine snags to more than 40 years for Douglas-fir snags (Figure 3). Estimated median persistence times for very large diameter true fir snags also exceeded 30 years but are less reliable because we sampled very few large true fir snags on older sites. Snag breakage patterns largely mirrored snag persistence patterns. Small diameter snags retained their tops longer than larger diameter snags, and small diameter Douglas-fir and true fir snags retained their tops longer than small diameter ponderosa pine snags (Figure 3). Broken tops were uncommon in lodgepole pine

TABLE 1 Dead tree counts and conditions, by species, including total trees sampled, standing dead trees (snags), standing dead with broken tops, and standing dead with wildlife cavities.

Tree species	Trees surveyed	Standing dead	Standing, broken	Standing, cavity
Pseudotsuga menziesii (Mirb.) Franco	3563	2316	1155	38
Pinus ponderosa Lawson & C. Lawson	2738	1488	574	42
Abies grandis (Douglas ex D. Don) Lindl.	752	452	187	5
Pinus contorta Douglas ex Loudon	456	116	12	0
Abies concolor (Gord. & Glend.) Lindl. ex Hildebr.	305	75	67	8
Larix occidentalis Nutt.	184	111	38	0
Abies magnifica A. Murray bis	174	63	22	0
Abies lasiocarpa (Hook.) Nutt.	62	56	8	0
Calocedrus decurrens (Torr.) Florin	59	55	4	2
Picea engelmannii Parry ex Engelm.	50	44	0	0
Juniperus sp.	39	21	1	0
Other species	13	8	4	1
Totals	8395	4805	2072	96

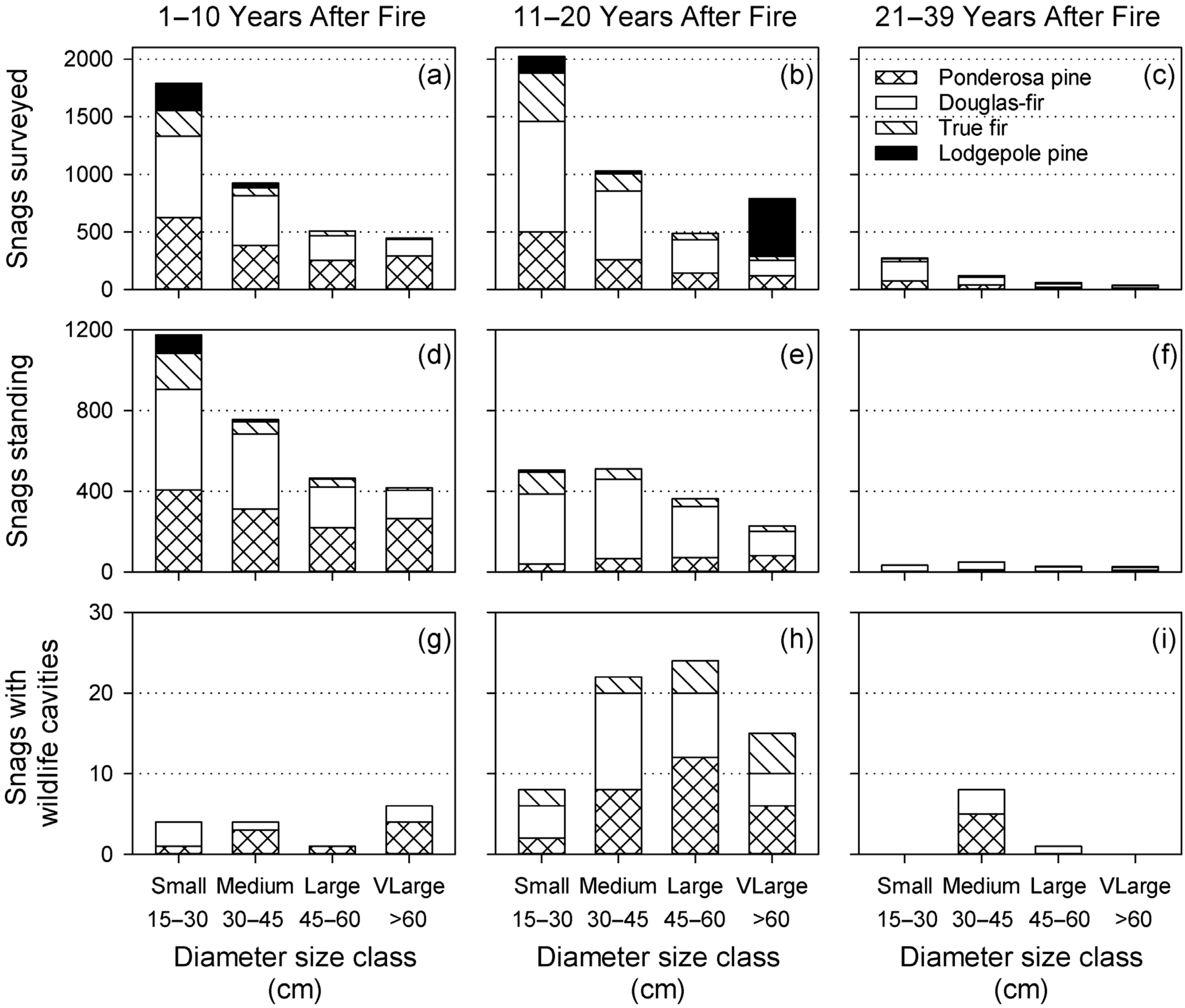

FIGURE 2 Counts of snags surveyed for this study, by time since fire (in years), diameter class, and species. Rows show counts for all snags (a–c), standing snags (d–f), and standing snags with cavities (g–i). Columns show counts for the first decade (a, d, g), second decade (b, e, h), and third and fourth decades (c, f, i) after stand-replacing wildfire. Stacked bars show counts, by species, for the small, medium, large, and very large snag diameter size classes.

snags as only 12 out of 116 standing lodgepole pine snags surveyed had broken tops.

Standing and fallen snag wood decay conditions also changed over time, as measured by decay class. Most standing snags reached decay class 2 during the first decade after fire, largely mimicking the temporal patterns of snag breakage (Figure 4). Snag transitions from decay class 2 to decay class 3 (soft snags) began in the second decade after fire and increased gradually so that about 50% of standing snags were soft snags (decay class 3) by 30 years after fire (Figure 4). Most fallen snags were recorded as being in decay class 2 or 3 at the time of sampling, but the proportion of soft fallen snags (decay class 3) increased steadily between 15 and 30 years after fire (Figure 4).

Snag species and diameter had less effect on snag transitions to decay class 3 than on snag fall and top breakage. Species and diameter showed weak, but statistically significant, effects on the odds of a fallen snag being in decay class 3 but did not significantly influence the odds of a standing snag being in class 3. Fallen true fir snags reached decay class 3 faster, on average, than fallen ponderosa pine and Douglas-fir snags, particularly in the largest diameter classes (Figure 4). Diameter influenced the odds of fallen Douglas-fir and true fir snags being in decay class 3, with large diameter fallen snags transitioning to decay class 3 earlier than small diameter fallen snags but diameter had no discernable effect on fallen ponderosa pine snags.

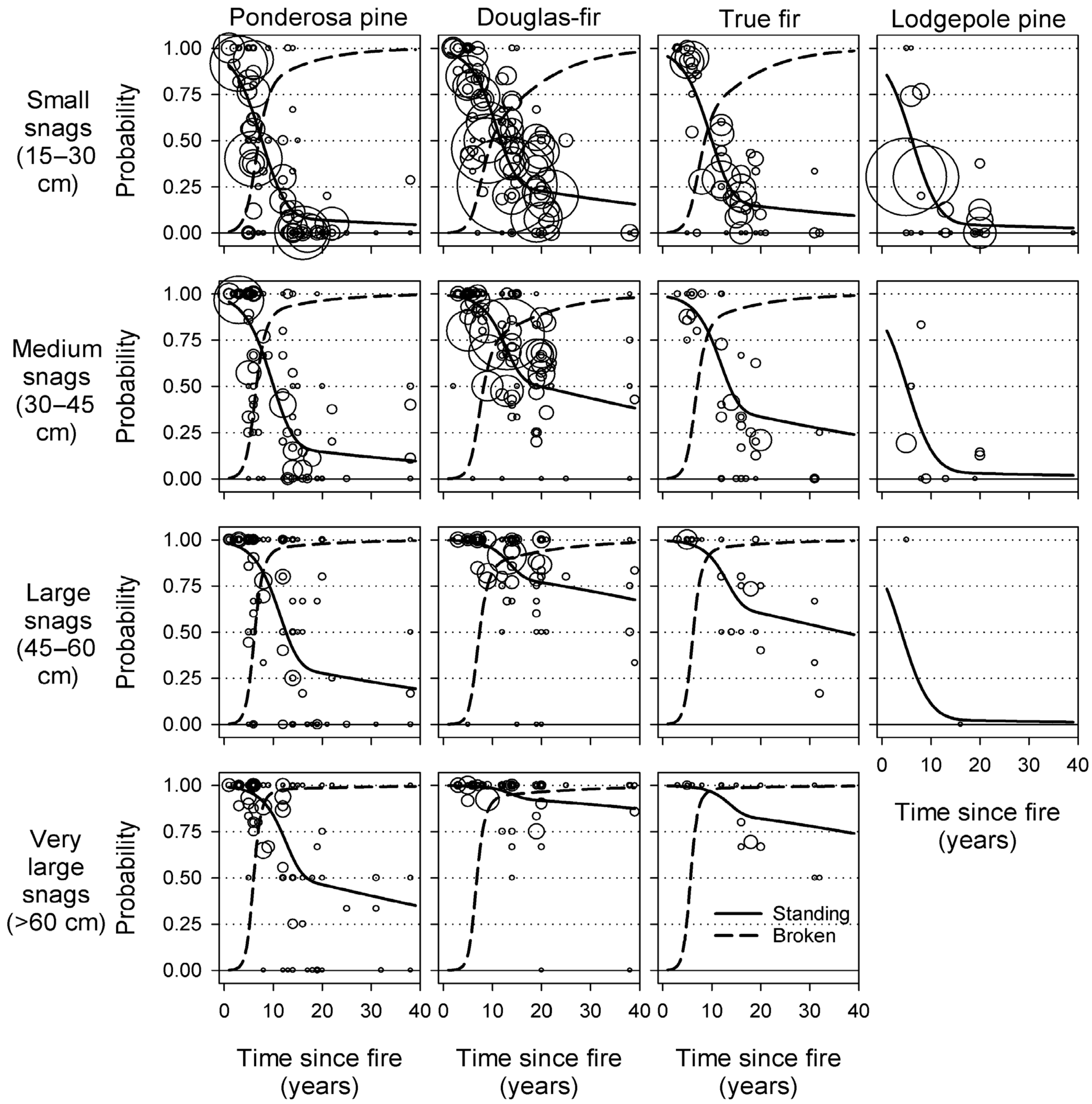

FIGURE 3 Changes in snag condition with increasing time since wildfire. Observed data (circles) and expected values from statistical models (lines) are presented by species (columns) and snag diameter class (rows). For each species and diameter class combination, graph panes show the proportion of snags standing by site (circles, scaled by sample size), the modeled probabilities of snags remaining standing (solid line), and the modeled probability of snags having broken tops (dashed line) as a function of time since fire, in years.

Wildlife cavity dynamics

Wildlife cavities—indicating current or previous use by PCE species—were present in only a small percentage of standing snags (2.3% or 96 of 4092 snags) surveyed for wildlife cavities (Table 1). Standing snags with cavities included 42 ponderosa pines, 38 Douglas-firs, 8 white firs, 5 grand firs, 2 incense-cedars, and 1 quaking aspen (Table 1). No cavities were found in lodgepole pine or western larch snags. Cavity snag diameters ranged from 17 to 98 cm, with 64% of cavity snags having diameters between 30 and 60 cm and 22% of cavity snags having diameters greater than 60 cm. Most of the cavity snags had broken tops (89%) and were in decay class 2 (76%) at the time they were surveyed. Cavity snags were found at only 53 of the

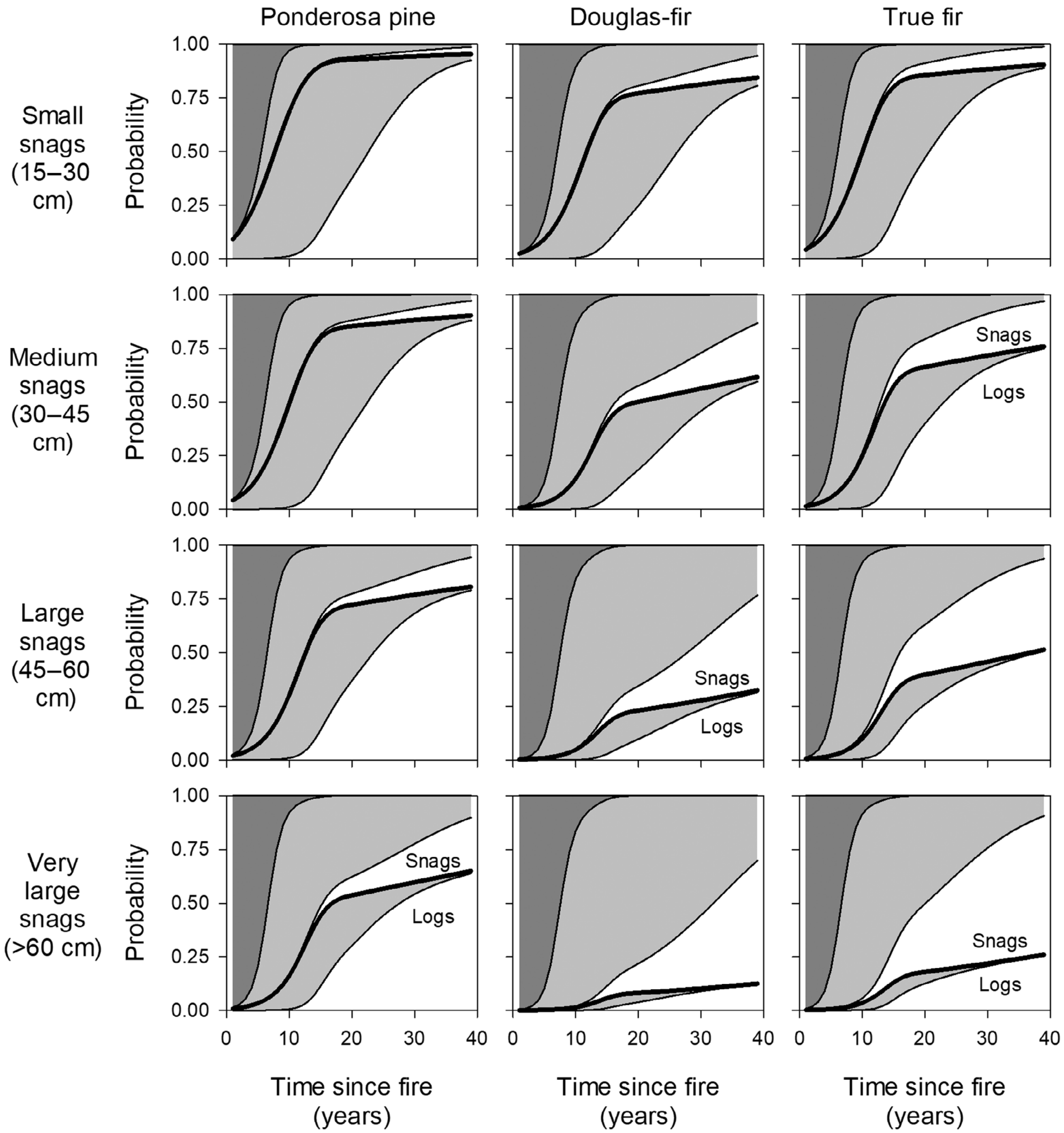

FIGURE 4 Snag and log decay class transitions by species, diameter class, and time since fire. Heavy black line represents the probability a snag has fallen. Shaded areas within graph panes show the expected proportion of snags in five conditions, standing in decay class 1 (dark gray), standing in decay class 2 (light gray above line), standing in decay class 3 (white above line), fallen in decay class 1 or 2 (light gray below line), and fallen in decay class 3 (white below line), during the first 40 years after stand-replacing wildfire.

126 sampling sites (42%), with individual sites hosting up to 5 cavity snags.

The probability of finding a cavity in a standing snag varied significantly with time since fire, snag diameter, snag species, and snag top condition. Cavity snags were most frequently found on sites surveyed during the second decade after wildfire (11–20 years), regardless of snag species or diameter (Figure 2). The probability of a standing snag containing a cavity was very low immediately after fire, reached a maximum 15–20 years after fire, and then declined slowly beyond 20 years. The probability of cavity presence in a standing snag increased significantly with snag diameter and was significantly higher for ponderosa pine snags than for Douglas-fir and true fir snags of the same diameter. Snags with broken tops were 4–5 times as likely to have a cavity as snags with intact tops.

Diameter effects carried over to the joint probability of a snag remaining standing and having a wildlife cavity at a given time since fire, but species effects were reduced (Figure 5). Large diameter snags persisted longer and had a greater individual probability of becoming cavity snags, whereas small diameter snags tended to fall early and were less likely to be selected by cavity nesters if they remained standing (Figure 5). The estimated probability of a snag remaining standing and having a cavity peaked at 8%–12% for very large diameter snags, 5%–6% for large diameter snags, 2%–3% for medium diameter snags, and 0.8%–1.0% for small diameter snags. Species differences were reduced in the joint probabilities, as standing ponderosa pine snags were more likely to have a cavity but Douglas-fir and true fir snags were more likely to remain standing (Figures 3 and 5), particularly in the larger size classes.

Woody fuel dynamics

Surface woody fuel loadings varied significantly with time since fire and, for the larger diameter classes, with pre-fire stand basal area. Surface woody fuels were highly variable among sites but, on average, were lowest shortly after fire, rose to maximum levels 10–20 years after fire, and then declined slowly over the next two decades (Figure 6). Temporal patterns differed little among the fuel diameter size classes, though expected values peaked slightly earlier for small diameter fuels (14 years after fire) than for large diameter fuels (16 years after fire). Within the large and very large diameter fuel groups, the rotten fuel fraction was very low immediately after fire and then increased steadily over time, particularly during the period 20–40 years after fire (Figure 6). Surface woody fuel loads were positively correlated with pre-fire stand basal area across all diameter size classes, but the basal area effect was not significant for small diameter fuels. For plots surveyed less than 15 years after fire, we also found significant positive correlations between surface woody fuel loadings and the square root of the density and basal area of broken and fallen snags, with correlation coefficients ranging from 0.37 and 0.34 for small diameter (<2.6 cm) fuels to 0.71 and 0.57 for large diameter (7.7–20.0 cm) fuels (Figure 6).

DISCUSSION

As total annual forest area burned in wildland fires has increased in recent decades, the area burned at moderate to high severity has also increased, greatly increasing the

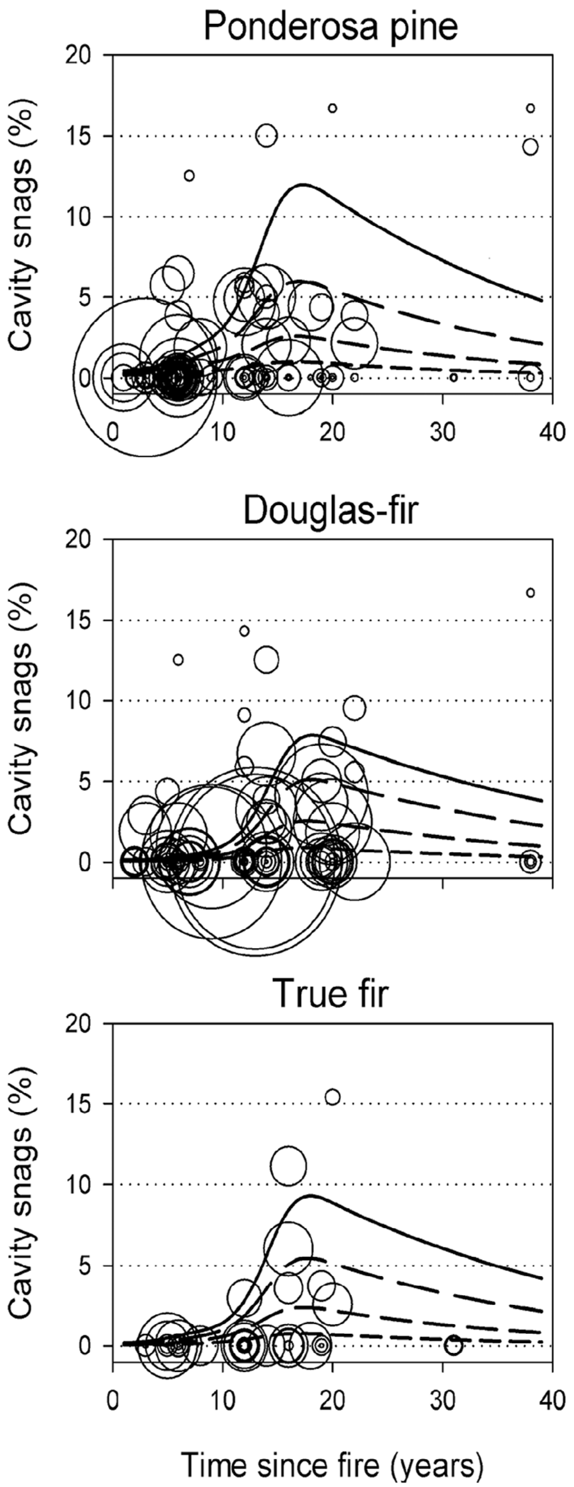

FIGURE 5 Temporal changes in observed and predicted percentages of snags that are standing and have at least one cavity, by tree species. Circles show the observed percentage of standing snags that had a cavity for each site at which the species was present, with circle diameters scaled to indicate relative abundance. Lines show changes over time in expected probabilities that a snag will remain standing and have a cavity for very large snags (>60 cm dbh; solid), large snags (45–60 cm dbh; long dashes), medium snags (30–45 cm dbh; medium dashes), and small snags (15–30 cm; short dashes).

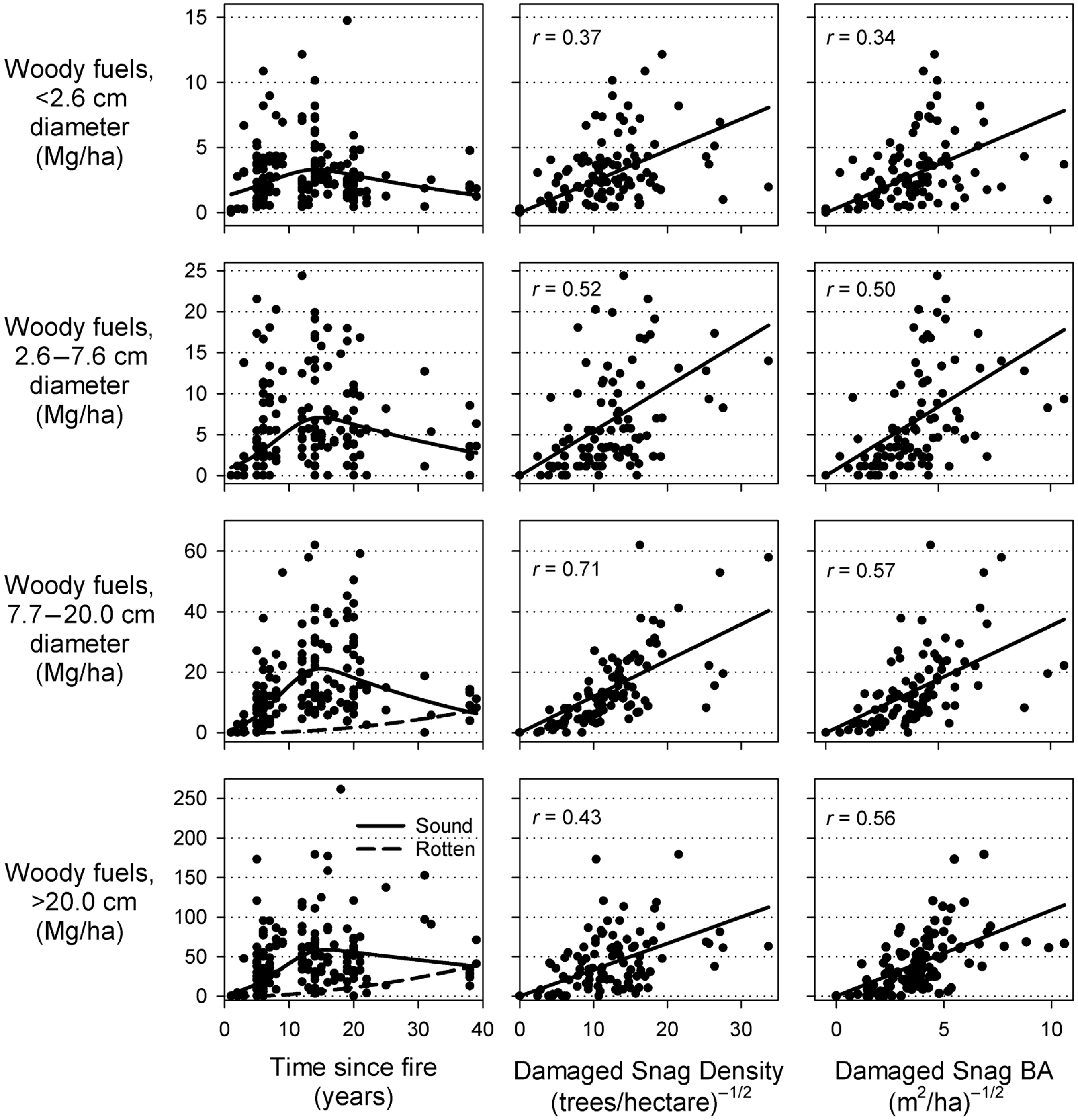

FIGURE 6 Effects of time since fire and stand structural changes on surface woody fuel loads, by diameter size class. Scatter plots (filled circles) show mean estimated surface woody fuel loadings (in megagrams per hectare) at each study site for small diameter (<2.6 cm), medium diameter (2.6–7.6 cm), large diameter (7.7–20.0 cm), and very large diameter (>20.0 cm) fuels. In the left column, solid lines show changes in expected values with increasing time since fire based on statistical models for a stand with pre-fire basal area of 30 m^2/ha, which is between the median (26 m^2/ha) and mean (33 m^2/ha) stand basal area estimates for stands in this study, and dashed lines show expected values for the rotten component of large and very large diameter fuels. The center and right columns of graphs show relationships between surface woody fuel loads and the square root of the density (center column) and basal area (right column) of damaged snags (fallen or broken top) for sites surveyed less than 15 years after fire.

abundance of fire-killed snags within forest landscapes of western North America (Cansler & McKenzie, 2014; Singleton et al., 2019; Westerling, 2016). Moderate- and high-severity wildfires convert forest biomass that has accumulated in trees over decades to centuries into dead wood in snags, creating a pulse of increased resources for organisms and processes that depend on coarse woody debris (e.g., fungi, wood borers, fire). They also generate losses in ecosystem services like timber values and carbon sequestration; those losses may be realized immediately or gradually over time as snags decompose (Campbell et al., 2016; Halema et al., 2018; Kimmey, 1955; Prestemon et al., 2006). This study showed that snag decomposition rates and trajectories vary among tree species and snag diameter classes, thereby altering the timing and magnitude of snag contributions to different habitat functions, disturbance processes, and ecosystem services.

Snag dynamics

Fire-generated snags attract sapwood-feeding and wood-boring insects that invade snags shortly after fire and persist for several years (Costello et al., 2011). Sapwood-feeding insects use snags as habitat (feeding and shelter) but also promote wood decay by facilitating the entry of decay fungi spores (Parker et al., 2006). Decay fungi reduce wood strength as they first spread through the sapwood and then the more decay-resistant heartwood, making snags more susceptible to breaking under stress from high winds or heavy ice or snow loads (Kimmey, 1955; Lowell et al., 2010). Wood-boring insect larvae serve as prey for woodpeckers, which also contribute to snag decomposition and wood decay as they create holes that serve as entry points for fungal spores and spread fungal spores as they forage among snags (Farris et al., 2004). Important factors regulating initial wood decay and snag breakage rates include the proportions of bole cross-sectional area in sapwood and heartwood, bark thickness (important for wood moisture retention), species differences in wood chemistry and decay resistance, and snag diameter (Eslyn & Highley, 1976; Kimmey, 1955; Lowell et al., 2010).

These biological processes help explain the patterns of snag decomposition we observed during the first 40 years following stand-replacing wildfire. Snags exhibited only minor structural changes during the first 2–5 years after fire as insects and fungi were becoming established within snags. Snag and stand structure then changed rapidly over the following 10–15 years as wood decay and physical stressors caused most snags to break off at or above the soil surface and deposit coarse woody debris on the forest floor. Snags broke and fell at a slower rate over the remaining years covered by our study, while wood decay progressed to advanced stages, as physical stressors were reduced following breakage (e.g., less wind interception). Within this common temporal pattern of snag decomposition, snag species and diameter significantly influenced decomposition rates and whether snag stems initially broke off near the soil surface and fell or broke off higher up and left the lower stem standing as a broken snag.

Similar temporal phases of snag decomposition have been reported for snags generated by fires and insect activity for dry coniferous forests (Bull, 1983; Keen, 1955; Kimmey, 1955), maritime forests (Parish et al., 2010), and boreal forests (Angers et al., 2010) of North America. Previous studies have reported minimal ponderosa pine snag fall during the first 2–5 years after wildfire followed by rapid snag fall and top breakage during the subsequent decade (Bull, 1983; Chambers & Mast, 2005; Keen, 1955; Kimmey, 1955). Everett et al. (1999) reported that ponderosa pine and Douglas-fir snags reached soft snag status 15–25 years after fire. Previous studies have also found that ponderosa pine snags decomposed faster than Douglas-fir and true fir snags and that large-diameter snags persist longer than small-diameter snags (Dunn & Bailey, 2012; Everett et al., 1999; Keen, 1955; Kimmey, 1955).

Variability in bark thickness, sapwood-heartwood ratios, and wood strength among tree species can explain much of the species and size effects we observed on snag decomposition through time. Thin-barked lodgepole pine snags and small diameter snags of all species mostly broke off near their base and fell during the first 10–15 years after fire, likely because wood decay weakened the snags primarily near or below the soil surface where adequate moisture was available. Large Douglas-fir snags likely persist longer than large ponderosa pine snags because they have lower proportions of sapwood in their lower stems (Kimmey, 1955; Lowell et al., 2010) and because their wood has higher elasticity, initial strength, and resistance to decay than the other species in this study (Eslyn & Highley, 1976; Forest Products Laboratory, 1999). These mechanisms also help explain tops breaking off larger diameter snags within the first decade after fire, as heartwood strengthens the lower stem and drying retards decay in the upper stem, but the middle of the stem decays and weakens owing to a combination of intermediate bark thickness and a high ratio of sapwood to heartwood (Lowell et al., 2010).

Cavity snag dynamics

Consistent with prior studies, we found that PCE species preferred nesting in moderate and large diameter ponderosa pine and Douglas-fir snags with broken tops (Bull, 1983; Chambers & Mast, 2005; Ganey & Vojta, 2004; Lehmkuhl et al., 2003). Contrary to our original hypothesis, however, we found cavities in snags spanning a broad range of diameters and several tree species. Some of this diversity in cavity snag characteristics may be due to differing preferences among PCE species (Bull et al., 1986). It also seems likely, though, that PCE species are flexible in their nesting requirements and select cavity snags based on the "best available" standing snag of acceptable size and wood hardness within a desired location (Lorenz et al., 2015). Site characteristics, like slope aspect or distance to unburned forest edge, may also be important for nest snag selection and breeding success (Nappi & Drapeau, 2009; Stillman et al., 2019) but were not assessed in this study.

Time since fire also influences snag usage by PCEs. Previous studies in ponderosa pine and Douglas-fir forests of western North America have reported cavity creation in snags as early as 3–8 years after fire (Bull, 1983; Chambers & Mast, 2005) but Lehmkuhl et al. (2003) found very few cavity snags in stands surveyed less than 20 years after wildfire. Most of the cavity snags found in this study were in stands sampled during the second decade after fire, when most of the standing snags had broken tops and, we presume, sapwood had decayed sufficiently to facilitate cavity excavation. Proportions of standing snags with cavities also peaked during the second decade after fire and declined thereafter, suggesting that loss of cavity snags to further snag breakage or snag fall exceeded new cavity creation beginning sometime in the third decade after fire. Unfortunately, our study design does not allow us to determine to what extent cavity creation continues into the third and fourth decades after fire. Many of the cavity snags we observed during that period may have simply persisted after cavities were excavated during the first two decades after fire. Longitudinal studies of cavity excavation and snag decomposition, perhaps beginning 10 or more years after wildfire, would be helpful for better defining the length of the snag cavity creation phase, the PCE species excavating the cavities, and the mechanisms by which cavities (or cavity snags) are lost.

In managing snag populations after wildfire, our study suggests that a strategy that focuses on retaining snag patches containing a broad range of snag diameters (>30 cm dbh) and multiple species could be more beneficial for PCE species than a strategy that focuses primarily on large diameter snags. Diversity in snag diameters and species may promote diversity in PCE species owing to different nesting requirements (Bull et al., 1986). Snag diversity may also expand the temporal window during which snags suitable for cavity excavators are present in a patch, as species and diameter influence snag decomposition and wood decay rates.

Our study also suggests that snag usage for foraging and nesting by PCE species may be partially decoupled in time. Most of the cavity snags we observed were in older (6–22 years since fire) stands. Bark beetle and borer activity is much diminished during this period relative to earlier periods (Boulanger & Sirois, 2007; Covert-Bratland et al., 2006). So, although PCE species excavate cavities in these older stands, they are likely foraging on alternative prey species or in nearby stands more recently affected by fire or insect disturbances (Covert-Bratland et al., 2006; Dudley et al., 2012). This supports the idea that snag patches close to unburned forest patches may be more beneficial for primary and secondary cavity nesters than those in the interior of large areas of stand-replacing fire (Steel et al., 2022).

Woody fuel dynamics and potential reburn severity

As expected, we found that surface woody fuel loadings tracked temporal patterns of snag decomposition and were positively correlated with fallen and broken snag density or basal area. Surface woody fuels increased rapidly as snags broke and fell during the first 15 years after wildfire. Temporal patterns of surface woody fuel accumulations were very similar among fuel size classes, suggesting that snag decomposition events like snag fall and top breakage influence surface woody fuel loads more than early loss of smaller branches from mostly intact snags. Although total woody fuel loads remained stable or declined after 20 years, observed increases in the rotten component of large-diameter woody fuels from 15 to 40 years after fire are important for subsequent wildfire severity and potential human impacts because large diameter rotten fuels ignite more easily, burn longer and more completely, promote greater soil heating, and generate more smoke through smoldering combustion than large diameter solid fuels (Brown et al., 2003; Covington & Sackett, 1984; Hyde et al., 2011; Monsanto & Agee, 2008).

Post-fire surface woody fuel accumulation and decay over time help explain the wide range of severity responses observed when sequential wildfires interact. Previous wildfires have been shown to inhibit the spread of subsequent wildfires (Collins et al., 2009; Parks et al., 2015), reduce the severity of subsequent wildfires (Parks et al., 2014; Prichard et al., 2017), or increase the severity of subsequent wildfires (Brown et al., 2003; Lydersen et al., 2019), with prior wildfire severity, fire weather, time since fire, and vegetation type being important factors influencing subsequent wildfire severity (Coppoletta et al., 2016; Parks et al., 2014; Prichard et al., 2020). Understanding these different interaction responses and their drivers is important for reducing future wildfire hazards through post-fire fuel management.

Past fires (wild or prescribed) inhibit the spread of subsequent wildfires by disrupting horizontal continuity of surface fuels (Harvey et al., 2016; Parks et al., 2015). Surface fuels are typically very low and discontinuous following wildfire and must be replenished by a combination of understory vegetation recovery (litter and biomass), deposition of scorched leaves, and decomposition of fire-killed shrubs and trees before fire can carry through a previously burned area. Understory vegetation can recover in as little as a year in some grass-dominated communities but can take much longer in other communities and climates (Fornwalt & Kaufmann, 2013; Peterson et al., 2009), so this period of fire inhibition can vary considerably among forest types. Given sufficient fine fuels to facilitate fire spread, potential fire intensity and severity increases with deposition and decay of surface woody fuels from decomposing snags.

Wildfires and prescribed fires promote low-severity burns in subsequent wildfires if they reduce fuel loads, at least in the short term, by consuming more surface fuels than they generate (Harvey et al., 2016; Parks et al., 2014). This negative feedback on subsequent fire severity declines over time as woody fuels accumulate through snag decomposition or new tree and shrub growth and mortality (Harvey et al., 2016; Prichard & Kennedy, 2014). Negative feedbacks of wild or prescribed fire on subsequent fire severity can persist for 20 years or longer in western forests (Parks et al., 2014).

High-severity wildfires promote future high-severity wildfires by generating large pulses of surface woody fuels over time that promote future high fire intensity, long fire residence times, and high burn severity with respect to both vegetation and soils under favorable fuel moisture and fire weather conditions (Brown et al., 2003; Lydersen et al., 2019). Based on snag decomposition, fuel deposition, and fuel decay patterns observed in this study, high-severity reburns are most likely to occur during the third and fourth decades after wildfire. However, extremely low fuel moisture and fire weather conditions can produce high-severity wildfires even in areas with low to moderate surface fuel levels (Prichard et al., 2020), so earlier high-severity reburns can and do occur.

Active fuel management may be needed or desired after higher severity wildfires to limit the magnitude of post-fire woody fuel pulses and associated future wildfire behavior and effects, with prescribed fire and post-fire logging being two of the most common management options. Prescribed fire is commonly used for ecological restoration of and fuel reduction in dry coniferous forests and can be highly effective for reducing total surface fuels and spatial continuity of fuels (Stephens et al., 2009), making it a potentially effective tool for managing post-fire fuels by periodically burning woody fuels before they accumulate to hazardous levels. However, management use of prescribed fire is often limited by funding, favorable fuel moisture and weather conditions, work force availability, and air quality concerns, so using prescribed fire to manage post-fire fuels in regenerating forests may limit its use in mature forests. Prescribed fires in regenerating forests can also damage or kill seedlings and saplings and accelerate snag fall rates (Battaglia et al., 2009; Harrod et al., 2009; Peterson et al., 2007), so its use may conflict with other resource management objectives. Further studies of prescribed fire effects on fuels, snags, and trees in young regenerating stands would be helpful to better understand the resource tradeoffs involved in this approach and to develop metrics for deciding where and when prescribed fires can best be used for managing fuels in young forests.

Post-fire logging provides an alternative (though often controversial) approach to managing fuels after high-severity wildfires. Post-fire logging reduces surface woody fuels over time and alters the timing of the fire-generated fuel pulse by removing large-diameter wood and depositing small-diameter fuels on the soil surface (Donato et al., 2013; Peterson et al., 2015; Ritchie et al., 2013). Logging recently killed trees increases surface woody fuels relative to unlogged areas during the first 5–10 years after wildfire if logging slash is not adequately treated (Donato et al., 2013) but then reduces woody fuels over longer time frames, particularly large-diameter sound and rotten fuels (Peterson et al., 2015; Ritchie et al., 2013). Reducing fuels early in the post-fire recovery process may also increase management options for using prescribed fire to treat residual fuels, maintain low surface fuel levels, and modify overstory canopy fuels as new forest stands develop.

CONCLUSIONS

Consistent with our first two hypotheses, we found that snag decomposition trajectories and rates varied among snag species and diameter classes and that surface woody fuel loadings are temporally correlated with snag density and decomposition stages. Our third hypothesis was partially supported in that wildlife cavities were found at a higher rate in larger diameter snags than in smaller diameter snags, given that snag tops were broken. However, we found that very large-diameter snags (dbh > 60 cm) accounted for only 22% of cavity snags, while 64% of cavity snags had diameters between 30 and 60 cm, suggesting that snag species and diameter parameters for cavity snags can be quite broad so long as snags are large enough and are sufficiently decayed to facilitate cavity excavation.

Our study also generally supports the proposition that fire-generated snags represent a transient resource pulse in which the relative contribution of snags to different ecological functions varies with snag diameter, species, time since fire, and landscape position. Small-diameter snags typically fall rapidly and contribute primarily to downed coarse woody debris and fuel for future fires. Larger snags with broken tops often remain standing longer, providing a growth substrate for decay fungi and bacteria and providing foraging and nesting habitat for a variety of different invertebrate and wildlife species. Fallen snags continue to serve as wildlife habitat, generate duff for forest soils, and serve as fuels for subsequent fires.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Peterson et al., 2023) are available from the USDA Forest Service Research Data Archive: https://doi.org/10.2737/RDS-2023-0037.

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