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Dynamics of coarse woody debris following wildfire in a mountain hemlock (*Tsuga mertensiana*) forest

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ABSTRACT

Coarse woody debris (CWD, comprised of snags and downed logs) is an important component of the structure and function of forest ecosystems, one which both influences the availability of fuel for wildfires and can be a result of wildfires. We studied snag persistence, and changes in mass of CWD in 10 years following a 1996 wildfire in mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) forest in the Cascade Range of Oregon, comparing unburned areas to areas with varying fire severity. Though mountain hemlock forest is a dominant type at high elevations in the Pacific Northwest, previous studies have not addressed the species. From studies of other conifers in western North America, we hypothesized that probability of snag persistence would be >75% 5 years and <50% 10 years after fire, and would increase with tree size. We modeled snag persistence on characteristics of the snags and the plots on which they occurred, using generalized mixed effects models. Probability of snag persistence was >75% 5 years after fire and increased with increasing tree diameter, as predicted. However, probability of persistence was >50% 10 years after fire. The cold climate, with a brief interval of optimal temperatures for decay organisms, probably contributed to prolonged snag persistence. Although probability of snag persistence remained high, estimated mass of snags declined and estimated mass of logs increased. Both breakage of snags and decreasing wood density due to advancing decay contributed to the decrease in estimated snag mass. Due to the nearly complete transformation of live trees to snags and the paucity of tree regeneration, we expect that patches of high fire severity will be effective barriers to the spread of crown fires for decades.

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1. Introduction

Coarse woody debris (CWD, comprised of snags and downed logs) is an important component of the structure and function of forest ecosystems, providing habitat for many non-vascular plants, invertebrates and vertebrates, facilitating nutrient cycling, storing moisture, and contributing to carbon sequestration (Harmon et al., 1986). The amount, sizes, and types of CWD also helps to determine the availability of fuel for wildfire (Agee, 1993). Wildfire, in turn, is an important process for creating snags and downed logs. The fate of snags created by fire has been studied for some types of coniferous forests in western North America (e.g. Chambers and Mast, 2005; Mitchell and Preisler, 1998; Morrison and Raphael, 1993; Russell et al., 2006), but not specifically for high-elevation forests of mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière).

Mountain hemlock occurs from the southern Sierra Nevada to south-central Alaska, commonly as a dominant or co-dominant component of late-successional forests (Tesky, 1992). Mountain hemlock occupies the highest forested elevations in the Cascade Range of the Pacific Northwest (Agee, 1993). Wildfire is the predominant large-scale disturbance of mountain hemlock forests in the Pacific Northwest; fires tend to be infrequent, and of high severity (Agee, 1993). Timber harvest has not been a major focus of management of mountain hemlock forests over much of the species' range, due to both inaccessibility and inclusion of many stands in national parks and wilderness areas (Tesch, 1995; Tesky, 1992).

Long-term observations of the persistence of coniferous snags in western North America have focused on pines (especially ponderosa (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) and lodgepole (*Pinus contorta* Douglas ex Loudon)), and includes studies of trees killed by fire (Chambers and Mast, 2005; Dahms, 1949; Harrington, 1996; Lyon, 1984; Morrison and Raphael,

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1993; Raphael and Morrison, 1987; Russell et al., 2006) and those killed by bark beetles (Keen, 1955; Mitchell and Preisler, 1998; Schmid et al., 1985). Persistence of snags of several species of true firs (genus *Abies*) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) has been the subject of fewer studies (Morrison and Raphael, 1993; Raphael and Morrison, 1987; Russell et al., 2006). In addition to direct, long-term observation of snags, relevant information has been obtained from chronosequence (Everett et al., 1999) and static life-table (Huggard, 1999) analyses. Although intensity (i.e., energy released during a fire) and severity (i.e., ecological effects) vary importantly within and between fire events (Agee, 1993; Gutsell and Johnson, 2007), very few long-term studies of snag persistence have assessed the effects of either fire intensity or fire severity.

We studied snag persistence, and changes in mass of snags and downed logs in the first 10 years following a 1996 wildfire in mountain hemlock forest in the Cascade Range of Oregon. Unlike most previous studies, we were able to take advantage of plots established prior to the fire (Acker et al., 1998), and were able to compare areas of contrasting fire severity (Gardner and Whitlock, 2001). We used the existing literature as the best available starting point for hypotheses, even though we recognized that the biological processes which influence snag persistence may occur more slowly at higher elevations (Lowell et al., 1992). We hypothesized that time would influence snag persistence, with at least 75% persisting for 5 years and less than 50% persisting for 10 years following the fire (Dahms, 1949; Harrington, 1996; Keen, 1955; Lyon, 1984; Mitchell and Preisler, 1998; Morrison and Raphael, 1993; Russell et al., 2006; Schmid et al., 1985). We hypothesized that larger snags would persist longer than smaller ones (Dahms, 1949; Everett et al., 1999; Keen, 1955; Mitchell and Preisler, 1998; Raphael and Morrison, 1987; Russell et al., 2006). We also hypothesized that greater fire severity would speed attrition of snags (Harrington, 1996; Huggard, 1999). Since species may differ in persistence due to differences in susceptibility to root or bole decay (Huggard, 1999; Russell et al., 2006), we investigated the effect of tree species. We also investigated whether or not snags persisted longer in areas with higher density of snags and live trees (Chambers and Mast, 2005; Russell et al., 2006).

We hypothesized temporal trends in mass of snags and downed logs corresponding to expected trends in snag persistence: little change in the first 6 years (date of the first repeat volumetric measurements) and a decrease in the mass of snags and an increase in the mass of downed logs 9 years after fire (date of the second repeat measurements). With respect to total CWD (the sum of snags and downed logs), we expected that though decomposition could begin relatively quickly (Janisch and Harmon, 2002), the time required for colonization by the insect vectors of decay fungi (Cline et al., 1980; Lowell et al., 1992) could slow the loss of mass. In addition, mass could be added by delayed mortality of fire-damaged trees (Lowell et al., 1992). Since it was unclear how these processes might balance one another, we hypothesized that the mass of total CWD would not change during the course of this study.

2. Study area

The study was conducted in the Torrey-Charlton Research Natural Area (TCRNA) on the crest of the Cascade Range in central Oregon, at approximately 43°46′ north latitude and 121°59′ west longitude. TCRNA is on the Willamette and Deschutes National Forests, at an elevation of approximately 1700 m. The topography consists mostly of gentle, west-facing slopes (Salix Associates, 1998). Soils in the portion of TCRNA we studied are derived from volcanic ash, pumice, and glacial till, with ash and pumice in the thin surface layers. Soils are excessively drained and are classified

as Typic Cryorthents (Legard and Meyer, 1973, 1990). The higher portions of the Cascade Range have snowy winters, persistent, deep snowpacks, and brief, cool and dry summers (Jackson, 1985). At the nearby Irish Taylor Snotel site (43°48′, 121°45′, 1689 m elevation; USDA NRCS, 2011), between 1997 and 2006 the average annual precipitation was 169 cm, with snow cover beginning by mid-November and lasting until at least mid-June in most years. The average mean minimum temperature in January was −7.3 °C, the average mean maximum temperature in July was 22.1 °C. Vegetation of the area is mostly forest dominated by mountain hemlock, with an understory of grouse huckleberry (*Vaccinium scoparium* Leib. ex Coville) and a sparse herbaceous layer (Salix Associates, 1998).

In August, 1996 much of TCRNA was burned by the Charlton Fire, a lightning-caused fire which covered over 3700 ha (Gardner and Whitlock, 2001; Salix Associates, 1998). Fire severity varied spatially, with the majority of the area within the burn experiencing >95% tree mortality (Gardner and Whitlock, 2001) (Fig. 1).

3. Methods

3.1. Data collection

We collected information from 12 plots to investigate dynamics of CWD. The plots represented three replicates of the following four classes, in increasing order of fire severity:

(1) Unburned (>90% surviving trees).
(2) Partial mortality (>10% and <90% surviving trees).
(3) High mortality (<10% surviving trees), tree crowns scorched by the fire.
(4) High mortality (<10% surviving trees), tree crowns consumed by the fire.

We used existing permanent plots to the extent possible. Of the 20 plots established in Torrey-Charlton Research Natural Area in 1976, several were excluded from the post-fire study either due to missing center stakes in 1997, or excessive tree mortality due to *Phellinus weirii* (Murr.) Gilb. root-rot. Among the remaining plots, five were in the unburned category; three were chosen at random for the post-fire study. One of the existing plots was in the partial mortality category, and two each were in the high mortality categories (i.e., crowns scorched and crowns consumed). For five of the eight previously-established plots used in this study, all trees >5 cm dbh (diameter at breast height, 1.37 m) had been tagged and measured at 5-year intervals prior to the fire.

To complete the sample of three plots per fire-severity category, we used a fire-severity map created from post-fire aerial photographs (and informed by low-level flights over the area shortly after the fire) (Fig. 1). We randomly selected polygons of the appropriate fire severity in the general vicinity of the existing plots. Plots were established at random locations within these patches after confirming on the ground that the patches matched the mapped fire-severity category.

All 12 of the plots were circular, 17.84 m in radius, not corrected for slope (nominally 0.1 ha each). Slope on the plots ranged from 1% to 20%, with a median of 8%.

All snags and live trees ⩾5 cm dbh were tagged (if not previously tagged or if the tag burned off) and measured. The following items were recorded for all snags in 1997: (1) species; (2) dbh; (3) position (standing with crown, main stem broken, crushed but still rooted, uprooted); (4) crown condition (consumed, scorched, dead with no apparent scorch, or live); (5) decay class (using the five-stage system of Maser et al., 1988); and (6) scorch height, recorded
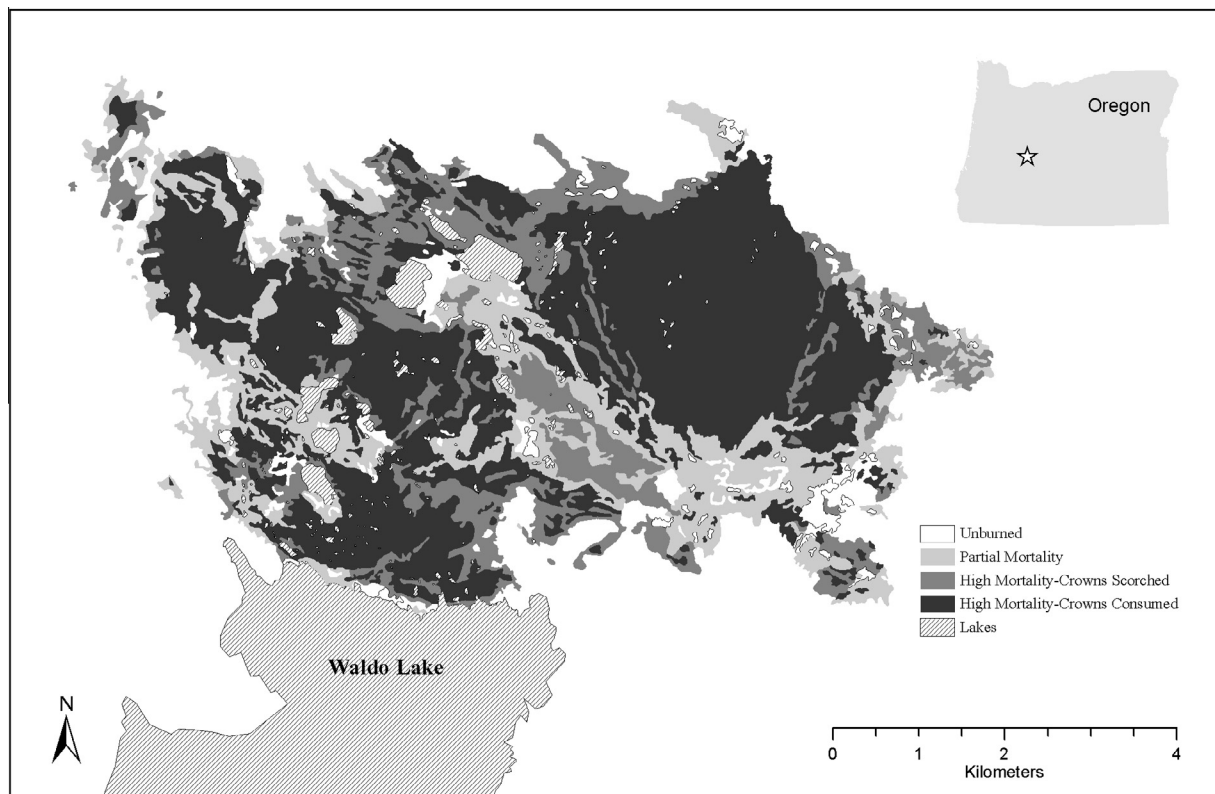
Fig. 1. Location of the study area in the central Cascade Range of Oregon, including the 1996 Charlton Fire.

as a percent of (estimated) intact tree height, (from base of tree to highest point of continuous scorch).

In subsequent years we recorded position and decay class. Snags were measured every year until 2006. Stems which were up-rooted or broken below breast height were defined as no longer part of the population of snags.

Volumetric measurements of snags and downed wood were obtained in 1997, 2002, and 2005, and converted to mass using values of wood density pertaining to the species and decay class, following the methods of Harmon and Sexton (1996). For intact snags, we measured dbh and length; for broken snags the top diameter was also measured or estimated. For downed logs, we measured the diameter at both ends and the midpoint and the length. We also recorded whether or not the piece was hollow, and recorded dimensions of the void space for hollow pieces.

3.2. Statistical analysis

We modeled the persistence of snags as a function of characteristics of both the snags and the plots on which they occurred, using logistic regression. To test hypotheses concerning temporal patterns of snag persistence, we used simulation to generate confidence intervals around model predictions (see below for details). We included in the analysis of persistence only those snags present in 1997; most of the burned plots had no or few surviving trees which could have succumbed in later years (see Section 4.1). We used analysis of variance (ANOVA) to test hypotheses concerning changes in mass of snags and downed logs.

We used generalized mixed effects models to carry out logistic regression of snag persistence. Mixed effects models are appropriate when predictors include factors for which the particular levels are of interest (e.g., dbh, species), and factors for which the particular values are not inherently meaningful, but rather the degree of variability is of interest (e.g., plots) (Bolker et al., 2008). The former

are referred to as "fixed effects," while the latter are referred to as "random effects." We used the *glmer*( ) function in the *lme4* R library to implement the models (Bates and Maechler, 2009).

To assess the effect of time on snag persistence, we assigned an age to each snag at each measurement. For the majority of the snags, age was assigned as the number of years since the fire; these trees had been observed as alive in 1996 or evidently had live crowns at the time of the fire. For the 9% of the snag population which either occurred on unburned plots or were evidently dead prior to the fire, we estimated age using published data on the range of time required for Douglas-fir snags of different sizes to attain different stages of decay (Maser et al., 1988). Decay is likely to be slower at the higher elevations where mountain hemlock is found, so this method may underestimate snag age. However, any other approach to estimating age for the snags for which death was not related to fire is likely to require a host of untestable assumptions.

We found that indicators of fire intensity for individual snags (crown condition, scorch height) were confounded with the fire-severity classes assigned to the plots. Thus, we elected not to include the fire intensity indicators in the models we tested. Since decay class was used to estimate the ages of some of the snags we also omitted that variable from the models.

We selected models by starting with all fixed effects in the model and fitting varying levels of random effects (Zuur et al., 2009). We compared performance among these models using Akaike's Information Criteria (AIC; Bolker et al., 2008), using the model with all fixed and random effects ("full model") as the standard for comparison (Burnham and Anderson, 2010). The full model contained fixed effects for snag age, dbh, tree species, fire severity (implemented as dummy variables for the various levels), total stems (snags plus live trees) on the plot, and the interaction between fire severity and snag age. The full model contained random effects for the intercept associated with each plot, and the

change to the age slope and the dbh slope associated with each plot. After selecting the proper number of random effects, we determined the significance of the fixed effects from results of individual *t*-test in the model output. We then generated a final model by eliminating non-significant fixed effects.

To improve usefulness of predictions at the intercepts, we centered values of quantitative predictors before fitting models. For dbh and tree density, the respective median was subtracted; for age, we subtracted 10. Thus, predictions at the intercepts represent average results for a 10-year-old snag with median dbh on a plot with median stem density.

Although we hypothesized that snag persistence may vary between species, the preponderance of mountain hemlock in our dataset (see Section 4.1) limited the probability of detecting this effect. For this reason we fit models to a reduced dataset with only mountain hemlock, in addition to the full dataset. For the full dataset, species other than mountain hemlock were combined into one category due to small sample sizes and imbalance among fire-severity classes.

To test our hypotheses concerning temporal patterns of snag persistence, it was necessary to use a simulation approach to generate confidence intervals around model predictions (Gelman and Hill, 2007). We used the R function *sim*() to generate random values for model parameters based on their means and variances, using a multivariate normal distribution (Gelman and Hill, 2007). The hypotheses concerning temporal patterns of snag persistence are one-sided, so they need to be evaluated against one-sided confidence limits. In particular, we compared the hypothesis of at least 75% persistence after 5 years to a lower confidence limit on probability of survival; we compared the hypothesis of <50% persistence after 10 years to an upper confidence limit. We set α to 0.05 (95% confidence limits). We obtained 1000 simulations for each fire-severity group, for an average plot (random plot effects set to zero), and a snag of average dbh on a plot of average stem density. The lower 95% confidence limit is the 50th of the 1000 simulated values, in order; the upper 95% confidence limit is the 950th of the 1000 ordered values. To illustrate predicted relationships between snag persistence, dbh, and fire-severity class, we also used the simulation approach to generate medians and two-sided 95% confidence intervals for snags on average plots with average stem density and dbh values representing selected points along the overall dbh-distribution for all snags (5%, 25%, 50%, 75%, and 95% quantiles).

Inasmuch as the probability of persistence of snags 10 years after the fire was greater than we hypothesized (see Section 4.2), we took advantage of the models we developed to ask when probability of persistence would drop below the level we predicted for year 10 (i.e., 50%). This approach required extrapolation beyond the range of most of the observed snag ages; we mitigated the resulting uncertainty somewhat by generating predictions only for the central values (medians) of dbh and density of snags and live trees (Wonnacott and Wonnacott, 1977).

To assess changes in mass of snags and downed logs we used the differences within plots over time as the basic response variable. For each plot, the snag mass in 1997 was subtracted from the snag mass in 2002 and in 2005, and the same was done for mass of downed logs. We used these difference variables in analysis of variance (ANOVA) to determine if there were differences among the fire-severity levels. To assess whether residuals met the assumption of normality, we inspected them graphically using quantile–quantile plots (QQ-plots) and applied the Shapiro–Wilks test (Crawley, 2007). To determine which fire-severity classes differed from one another, we used Tukey's test of Honest Significant Differences (Crawley, 2007). Since we did not find significant differences between burned classes (see Section 4.3), we addressed our overall hypotheses concerning changes in snag and log mass

by combining data across all burned severity classes and applying *t*-tests. We also investigated whether or not changes in snag mass on the burned plots could have been due to breakage of boles and/or advancing decay (and hence decreasing wood density, Harmon and Sexton, 1996).

4. Results

4.1. Snag population

The snag population on the plots 1 year after the fire (initial observations) numbered 662. Snags were most abundant in the high mortality—crowns consumed plots, and least abundant in the unburned plots (Table 1). On individual plots, density of snags ranged from 40 to 1290 per hectare (on burned plots, 440–1290 per hectare). Most snags were mountain hemlock (75%), with smaller amounts of Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes, 17%), lodgepole pine (5%), stems too decayed to assign a species (1%), and western white pine (*Pinus monticola* Douglas ex D. Don, 1%). In all severity classes, on average mountain hemlock accounted for the majority of snags within plots (Table 1). There was only one plot in which mountain hemlock was not the most abundant species among snags (one of the high mortality—crowns consumed plots, in which Pacific silver fir accounted for 78% of the snags). Snags tended to be larger in the burned plots than the unburned plots; among burned plots, snags tended to be larger in the high mortality—crowns scorched plots than in the other two severity classes (Table 1). The number of live trees on plots in 1997 ranged from zero to 2050 per ha. On the unburned plots, there were more than 1000 live trees per ha on average; there were no live trees on the high mortality—crowns consumed plots (Table 1). The proportion of the initial snag population still standing 10 years after the fire ranged from 28% to 84% for individual plots (Table 1). The average was lower for unburned plots than in any of the sets of burned plots. However, to assess the relative contributions of snag size, fire severity and other factors on snag persistence required the analysis in the following section.

4.2. Snag persistence

For the full dataset (*n* = 6620), the full model with all random effects was the most plausible of the alternatives we compared (Table A1). Thus, plots differed from one another in a random fashion with respect to intercept, the age slope, and the dbh slope.

Age, fire severity, dbh, and total stems all were significant fixed effects (Table 2). Probability of persistence decreased with age and total stems and increased with dbh. The largest decrease in probability of persistence among fire-severity classes was for the high mortality – crowns scorched plots, followed by plots with partial mortality. Since the interaction between fire-severity class and snag age was not significant, differences between fire-severity classes in probability of snag persistence are not predicted to change over time. Thus, average probability of persistence for snags on consumed plots was greater than the average probability of persistence on scorched plots for the same dbh and total number of stems, irrespective of snag age. The effect of species was also not significant.

For the data set with mountain hemlock only (*n* = 4970), the model with a random intercept and a random slope for dbh was the most plausible of the alternatives (Table A2). The full model with all random effects was nearly as plausible as the selected model (i.e., ratio of Akaike weights = 1.2, Burnham and Anderson, 2010).

All of the fixed effects were significant in this model (Table 3). As for the full data set, probability of persistence decreased with

Table 1

Attributes of the initial populations of snags and live trees, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Density of snags (ha⁻¹)	Percentage of mountain hemlock in snag population	Median dbh of snags (cm)	Density of live trees (ha⁻¹)	Percentage of snags standing at year 10
Unburned	147 ± 74 (40–290)	92 ± 8 (76–100)	17.3 ± 7.8 (7.9–32.8)	1263 ± 506 (320–2050)	47 ± 11 (28–64)
Partial	600 ± 110 (440–810)	79 ± 19 (42–99)	27.0 ± 11.2 (10.8–48.4)	347 ± 244 (50–830)	63 ± 16 (31–84)
Scorched	470 ± 10 (450–480)	95 ± 3 (91–100)	37.7 ± 4.2 (29.8–44.2)	20 ± 15 (0–50)	79 ± 4 (71–83)
Consumed	990 ± 159 (750–1290)	68 ± 27 (17–95)	22.3 ± 3.6 (20.7–29.2)	0 ± 0 (0–0)	67 ± 8 (52–77)

Note: Values are means ± standard errors, with ranges in parentheses.

Table 2

Parameter estimates for fixed effects from the most parsimonious model fit to the full dataset ($n = 6620$).

	Estimate	Std. error	z Value	P-value for z
Intercept	2.89	0.42	6.90	5.39×10^{-12}
Age	−0.45	0.05	−8.50	$<2 \times 10^{-16}$
Partial mortality	−1.40	0.32	−4.31	1.62×10^{-5}
Scorched[a]	−1.74	0.44	−3.96	7.55×10^{-5}
Consumed[b]	−1.09	0.33	−3.29	0.000992
Dbh	0.16	0.03	5.56	2.65×10^{-8}
Total stems on plot	−0.01	0.002	−3.57	0.000351

[a] Dummy variable representing the fire-severity class high mortality with tree crowns scorched.

[b] Dummy variable representing the fire-severity class high mortality with tree crowns consumed.

Table 3

Parameter estimates for fixed effects from the most parsimonious model fit to the dataset with mountain hemlock only ($n = 4970$).

	Estimate	Std. error	z Value	P-value for z
Intercept	3.65	0.41	8.98	$<2 \times 10^{-16}$
Age	−0.33	0.04	−7.61	2.80×10^{-14}
Partial mortality	−2.54	0.37	−6.95	3.74×10^{-12}
Scorched[a]	−2.89	0.44	−6.52	7.11×10^{-11}
Consumed[b]	−2.63	0.37	−7.05	1.85×10^{-12}
Dbh	0.16	0.03	5.47	4.47×10^{-8}
Total stems on plot	−0.01	0.003	−4.01	6.03×10^{-5}
Interaction of age and partial mortality	−0.21	0.06	−3.35	0.000798
Interaction of age and scorched	−0.23	0.08	−2.86	0.004190
Interaction of age and consumed	−0.50	0.09	−5.79	7.11×10^{-9}

[a] Dummy variable representing the fire-severity class high mortality with tree crowns scorched.

[b] Dummy variable representing the fire-severity class high mortality with tree crowns consumed.
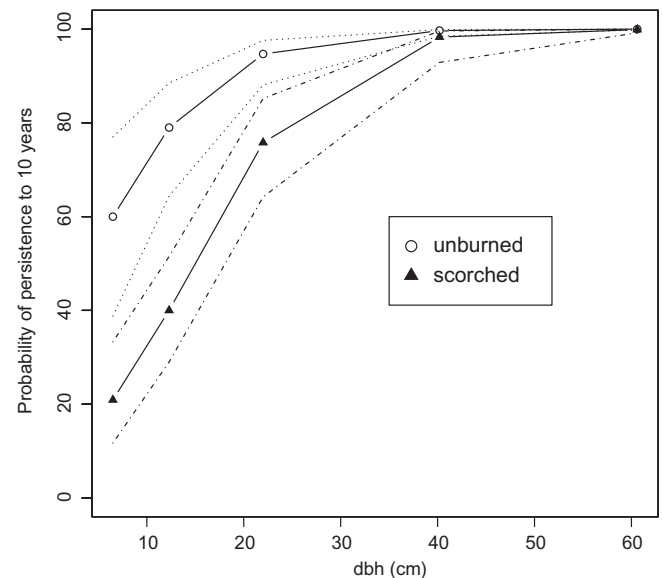

Fig. 2. Predicted probability of persistence to 10 years for snags on unburned and high mortality—crowns scorched plots, based on the model developed from the full data set. Solid lines represent median probability of persistence; broken lines represent lower and upper 95% confidence intervals. Dbh values indicated by symbols represent selected quantiles of the dbh distribution of all snags (5%, 25%, 50%, 75%, and 95% quantiles). Results for plots with partial mortality and high mortality—crowns consumed are intermediate between the two displayed fire-severity classes.

age and total stems and increased with dbh. The largest decrease in probability of persistence among fire-severity classes was for plots with complete mortality and crowns scorched; unlike the model for the full data set the smallest decrease in probability of persistence was for plots with partial mortality. In addition, the interaction between snag age and fire-severity class was significant; with greater snag age, the decrease in predicted persistence on plots with high mortality—crowns consumed was greater than for the other fire-severity classes.

For both the full data set and the data set with mountain hemlock only, the predicted probability of persistence of an "average" snag (i.e., a snag of median dbh on a plot of median density of snags and live trees) for 5 years was high for all fire-severity classes (i.e., the lower, one-sided 95% confidence interval was >94–99%). This is consistent with our hypothesis. The probability of persistence was lower at age 10, with the upper, 95% confidence interval ranging from 84% to 97% for the full data set and 78% to 99% for the data

set with mountain hemlock only. Thus, the predicted probability of snag persistence for 10 years was greater than the value of <50% which we hypothesized.

Persistence of the very smallest snags for 10 years was unlikely in burned areas (Fig. 2). The median probability of persistence for snags with dbh of 6.5 cm in plots with high mortality—crowns scorched was 21% (27% and 34% for partial mortality and high mortality—crowns consumed, data not shown in Fig. 2). In unburned areas, persistence of the very smallest snags was about as likely as attrition (median probability of persistence was 60%). Persistence of snags of median size (22 cm) to age 10 was likely on burned and unburned areas (median probability of persistence ranges from 76% to 95%). Persistence of larger snags for 10 years after tree death was very likely on both burned and unburned areas (e.g., median probability of persistence for snags 40.2 cm dbh (75th percentile) ranges from 98% to 100%).

The extrapolations beyond age 10 suggest that attrition of fire-caused snags in mountain hemlock forest is only slightly slower than observed in other types of coniferous forest in western North America (Figs. 3 and 4). The details of predicted attrition beyond the first 10 years depend on whether the model includes or excludes tree species other than mountain hemlock. For the model with all species, probability of persistence falls
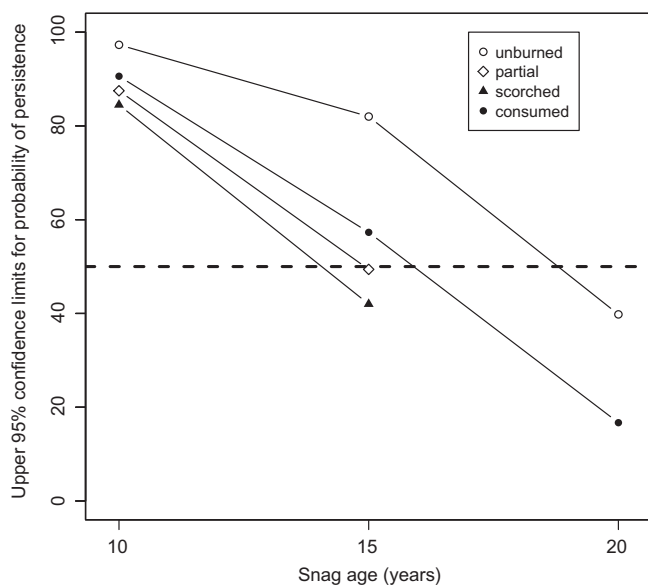
Fig. 3. Predicted number of years required for probability of snag persistence to fall below 50% by fire-severity class, based on the model developed from the full data set. Points represent the upper 95% confidence interval for persistence of a snag of median dbh on a plot of median density of snags and live trees. The dashed line indicates an upper 95% CI of 50%.

Fig. 4. Predicted number of years required for probability of snag persistence to fall below 50% by fire-severity class, based on the model developed from the data set with mountain hemlock only. Points represent the upper 95% confidence interval for persistence of a snag of median dbh on a plot of median density of snags and live trees. The dashed line indicates an upper 95% CI of 50%.
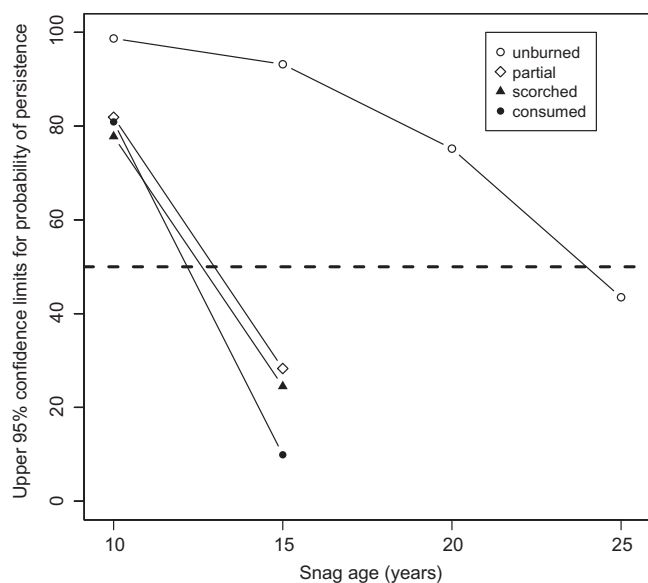
Table 4

Initial mass of snags, downed logs, and total CWD, averaged over plots within each fire-severity class (unburned, partial mortality, high mortality with tree crowns scorched, and high mortality with tree crowns consumed).

Fire-severity	Snags (Mg/ha)	Logs (Mg/ha)	Total CWD (Mg/ha)
Unburned	6 ± 3 (3–12)	44 ± 13 (18–61)	50 ± 15 (20–64)
Partial	184 ± 82 (31–312)	13 ± 8 (3–28)	197 ± 75 (59–315)
Scorched	284 ± 40 (223–360)	17 ± 3 (13–22)	301 ± 39 (238–373)
Consumed	198 ± 21 (158–228)	13 ± 8 (2–29)	211 ± 25 (160–236)

Note: Values are means ± standard errors, with ranges in parentheses.

Table 5

Results of *t*-tests for changes in mass of snags and logs over measurement intervals, all burned plots combined.

Variable	Null hypothesis	Mean change (Mg/ha)	Standard error	*p*-Value of *t*-test
Change in snag mass, 1997–2002	No decrease	−36.4	9.3	0.002
Change in log mass, 1997–2002	No increase	4.5	2.0	0.03
Change in total CWD mass, 1997–2002	No change	−32.0	9.7	0.01
Change in snag mass, 1997–2005	No decrease	−96.7	18.7	0.0004
Change in log mass, 1997–2005	No increase	66.8	12.1	0.0003
Change in total CWD mass, 1997–2005	No change	−30.0	19.5	0.16

below 50% by 15 years for the partial mortality and high mortality—crowns scorched severity classes (Fig. 3). For the high mortality—crowns consumed severity class, probability of persistence falls below 50% between 15 and 20 years. For the model with mountain hemlock only, probability of persistence falls below 50% by 15 years for all the severity classes (other than unburned) (Fig. 4).

4.3. Changes in mass of snags and logs

Immediately following the wildfire, the unburned and burned plots exhibited contrasting patterns of types and amounts of CWD (Table 4). In the unburned plots, downed logs comprised most of the CWD, whereas in the burned plots most of the coarse wood was in the form of snags. The burned plots contained more total CWD than the unburned plots, with the largest quantity on average in the high mortality—crowns scorched fire-severity class (Table 4).

In the comparison of changes in CWD by fire-severity class, only the changes in log mass over the longer interval (1997–2005) were significant ($p = 0.04$). The only pairwise comparison which was significant was high mortality—crowns scorched versus unburned (mean difference = 99.1 Mg/ha, 95% confidence interval 6.4–191.9, $p = 0.04$).

For changes in CWD among the combined burned plots, results confirmed our hypotheses for the longer interval, but contradicted our hypotheses for the shorter interval (Table 5). Snag mass decreased significantly and log mass increased significantly from 1997 to 2002. For the longer interval, both the decrease of snag mass and the increase of log mass were larger than the changes for the shorter interval, and they were also significant. Total CWD decreased a similar amount over both intervals. The decrease was significant for the shorter interval; for the longer interval, the variability between plots was greater and the decrease was not significant. The decrease averaged 14% of the initial mass for the longer interval.

The proportion of standing snags with intact boles on the burned plots declined over time, with an especially large drop between 2002 and 2005 (i.e., 85% intact in 1997, 74% in 2002, and 24% in 2005). Decay class 1 (the least-decayed stage) was the most common on burned plots in 1997, accounting for 78% of snags. In subsequent measurements, snags in decay class 1 accounted for just under 1/3 of the total (31% in both 2002 and 2005), while snags in decay class 2 were the most common (43% in 2002 and 65% in 2005). The proportion of snags in decay class 3 declined between 2002 and 2005 (from 26% to 4%), presumably due to attrition.

5. Discussion

5.1. Snag persistence

In the mountain hemlock forest we studied, the effects of time since wildfire and tree size on snag persistence were evident, though not entirely in the manner we hypothesized. As expected, attrition of snags was not likely for the first 5 years after wildfire, and the probability of persistence increased with snag size. Contrary to our expectations, probability of persistence was also high for the first 10 years after wildfire. Only among the smallest of snags was attrition clearly more likely than persistence by 10 years after fire (Fig. 2).

The slower than predicted attrition of snags we observed may be due to the relatively cold climate of the study site. Fungi borne on bark beetles, wood borers and other insects are one of the main causes of deterioration of fire-killed trees (Lowell et al., 1992). Wood-decay fungi can be active at temperatures as low as 4 °C, but optimum temperatures for wood decay are 20 °C or higher (Harmon et al., 1986; Lowell et al., 1992). Insects are also directly influenced by temperature (Furniss and Carolin, 1980). For example, ambrosia beetles (e.g., *Gnathotrichus* spp. and *Trypodendron* spp.), which commonly attack recently-killed trees, helping to spread decay fungi, only fly when air temperatures are ≥16 °C for several hours (Daterman and Overhulser, 2002). During the course of our study, the mean maximum air temperature at the Irish-Taylor Snotel was >20 °C in July and August every year, and only once in any other month; mean maximum air temperature was ≥16 °C for 3 months in most years (USDA NRCS, 2011). Thus the season for deterioration of snags due to the combined action of insects and fungi was brief.

The effects of fire severity on persistence of snags were commingled with differences among tree species in persistence, even though species was not a significant predictor in and of itself. When we included all species in the analysis (i.e., mountain hemlock versus all other species combined), the greatest probability of persistence among burned areas, all else being equal, was in the high mortality—crowns consumed severity class, followed by partial mortality. Since the interaction between fire severity and age was not significant, the model predicted that among burned areas, the probability of persistence would continue to be greatest in the high mortality—crowns consumed severity class over time. When we included only mountain hemlock, however, the relative probability of persistence changed, with the greatest probability of persistence among burned areas in the partial mortality severity class, followed by high mortality—crowns consumed. The interaction between fire severity and age was significant, with the strongest interaction applying to the high mortality—crowns consumed severity class. The implication of this model is that at some point beyond 10 years after fire, the probability of snag persistence will be lowest in the high mortality—crowns consumed severity class, all else being equal.

Differences in morphology among tree species may help explain the differences between the two models of snag persistence. In particular, both Pacific silver fir and lodgepole pine have relatively thin bark, which contributes to their tendency to succumb to wildfire (Anderson, 2003; Cope, 1992). Mountain hemlock, by contrast, has relatively thick bark, and tends to succumb to fire due to damage to crowns or roots (Tesky, 1992). Thin-barked species tend to dry quickly after wildfire, inhibiting the insects and fungi which contribute to wood decay and hence attrition of snags (Everett et al., 1999; Flanagan et al., 2002). With the thin-barked species included, predicted probability of snag persistence is greatest for the highest fire severity, which is consistent with inhibition of decay in dehydrated boles. Without these species, probability of attrition is predicted to eventually be greatest where fire severity was highest.

Density of snags and live trees was a significant predictor of probability of snag persistence, whether or not species other than mountain hemlock were included in the analysis. For both models, the effect was much smaller than the other predictors. The direction of the effect was the opposite of previous studies (Chambers and Mast, 2005; Russell et al., 2006), with a decreased probability of persistence corresponding to a greater density of snags and trees. For fire-killed ponderosa pines in northern Arizona, Chambers and Mast (2005) speculated that higher surrounding basal area of snags and live trees contributed to snag persistence by blocking the wind. Given that our study area slopes toward the prevailing winter winds (Jackson, 1985), it may be that in plots with many stems, falling snags striking other snags out-weighs attenuation of wind.

The influence of the predictors on snag persistence was not uniform across our study area, as evidenced by the large number of significant random effects. Tree species composition may contribute to this spatial heterogeneity. In particular, the second-most-abundant species, Pacific silver fir, occurred in only three plots, one of which accounted for 89% of the snags of that species. In addition, there may have been heterogeneity of fire effects within the severity classes we used that related to persistence of snags. For example, Miller and Keen (1960) indicate that some snags are "charred and 'case-hardened' by fire," and persist longer than other snags. We did observe indurated surfaces of snags in some, but not all, plots, especially where extreme fire behavior resulted in removal of bark during the fire and where Pacific silver fir was abundant. We have not yet found a practical method of measuring this characteristic; however, it is an important area for further research.

5.2. Changes in mass of CWD

The total amount of CWD in the unburned plots in our study was small compared to other mature and old-growth coniferous forests in the Pacific Northwest. Among the 56 mature and old-growth locations reported by Harmon et al. (1986) and Smithwick et al. (2002), only 11% had lower total mass of CWD than the unburned plots. Those locations represent the relatively arid and unproductive end of the spectrum of forests in the region, dominated by lodgepole pine, ponderosa pine, or Douglas-fir (Franklin and Dyrness, 1988). The unburned plots were unusual in the preponderance of downed logs; the ratio of snag mass to log mass was lower in only 5% of the locations reported by Harmon et al. (1986) and Smithwick et al. (2002).

Given the paucity of surviving trees and the abundance of snags on burned plots, the fire converted most of the mass of trees to CWD. The total mass of CWD on burned plots is somewhat less than the live mass reported for forests in the area by Boone et al. (1988)(i.e., about 200–300 Mg/ha average total mass for burned plots versus 315 Mg/ha for live trees reported by Boone et al.). However, total mass of CWD on the burned plots is greater than the amount reported by Boone et al. for patches killed by *P. weirii* root-rot (i.e., about 160 Mg/ha).

The similarity among the various fire-severity classes with respect to changes in mass of CWD is consistent with the relatively small differences in rates of snag attrition (see for example Fig. 4) and the considerable spatial heterogeneity represented as random effects in the analysis of snag persistence. There was considerable variation among plots with respect to both decreases of snag mass and increases of log mass; however, the

variability did not correspond to variation in fire severity as we defined it.

Changes in mass of snags and downed logs were detectable on burned plots more quickly following the fire than we hypothesized based on the expected timing of attrition of snags. The analysis of snag persistence indicates that this was not due to rapid attrition of snags. The earlier than expected decrease in snag mass was due in part to both breakage of boles and the advancing decay of standing snags. Density of dead wood decreases as decay progresses (Harmon and Sexton, 1996), so mass of snags can decrease over time without a decrease in the number of snags.

5.3. Management implications

This study provides a foundation from which to further enhance understanding of dynamics of CWD in high-elevation coniferous forests by extending the duration of observations, encompassing additional processes, and expanding the ecological scope. Though wildfire can promptly produce an abundance of resources for species dependent on snags and downed logs, in the longer-term fires can lead to a local lack of these resources (Everett et al., 1999). In the first 10 years after wildfire, we observed a high probability of persistence for the larger snags which are of greater use to wildlife. However, tree seedling recruitment may be very slow in mountain hemlock forest (Boone et al., 1988), so many decades will be required to compare rates of snag recruitment and snag fall. Similarly, mass and carbon loss have been measured for one to several decades after disturbance (Harmon et al., 1990; Law et al., 2004), so the small decline in total CWD mass we observed is just the beginning of a much longer process. Tree regeneration, which will help determine future rates of snag recruitment and carbon sequestration, is the most important additional process to include. It will also be important to directly measure changes in wood density as CWD ages, to improve upon the accuracy of mass estimates produced by assigning wood density based on decay class. The contrast between thick- and thin-barked tree species is a key ecological attribute to emphasize in future studies of effects of wildfire in high-elevation forests.

Our observations indicate that the pulse of mountain hemlock snags created by fire can be expected to provide habitat for at least a decade. For cavity-nesting birds, it is likely to represent foraging, rather than nesting habitat, inasmuch as most snags exhibited limited decay (i.e., decay classes 1 and 2; Bull et al., 1997; Everett et al., 1999). The pulse of snags may also indirectly ameliorate extreme habitat conditions for conifer regeneration following fire. In the absence of tree cover, the soil at our study area in mid-summer may reach lethal temperatures for tree seedlings (Boone et al., 1988). Downed logs resulting from breakage of the snags are likely to create some shaded microsites for seedlings (Harmon et al., 1986).

Our results suggest that the phase of carbon loss to the atmosphere following fire may be more protracted in mountain hemlock forest than for forests at lower elevations. The time course of decay of CWD generated by stand-replacing disturbance is one of the determinants of how long forests are net sources of carbon (Janisch and Harmon, 2002). Assuming that decay of CWD can be described by a negative exponential function, a 14% decline in 9 years represents a decomposition rate of 1.6%, lower than the 2.5–3% reported by Janisch and Harmon (2002) for forests of Douglas-fir and western hemlock. We observed only sparse tree regeneration in the first decade, so it is likely that the change in carbon

storage during this interval was dominated by decomposition of CWD.

We expect that burned areas similar to our high-mortality plots function as effective barriers to the spread of wildfire. The infrequent fires in mountain hemlock forests tend to be crown fires, driven by wind and carried by lichens and foliage in tree canopies (Agee, 1993; Gifford Pinchot National Forest, 1997; Tesky, 1992). The nearly complete transformation of live trees to snags and the paucity of tree regeneration suggest the high-mortality areas will be likely to inhibit fire spread for some number of decades to come. Until forest becomes established in high-mortality areas, fire spread will probably be determined by the distribution of patches of partial mortality, and the density of live trees within those patches.

Acknowledgements

Appendix A.

Results of model selection process for generalized mixed effects models of snag persistence (see Tables A1 and A2).

Table A1
Model selection results for the full data set (n = 6620) with varying random effects.

Model	AIC	K	ΔAIC	w_i
Random intercept + age and dbh slope	2921.1	17	0	1
Random intercept + dbh slope	2977	14	55.9	7.3×10^{-13}
Random intercept + age slope	3003.5	14	82.4	1.3×10^{-18}
Random intercept only	3077.5	12	156.4	1.1×10^{-34}

Note: K is the bias-correction factor (or number of estimable parameters), and w_i is the Akaike weight for the model (Burnham and Anderson, 2010).

Table A2
Model selection results for the data set with mountain hemlock only (n = 4970) with varying random effects.

Model	AIC	K	ΔAIC	w_i
Random intercept + dbh slope	1776.3	13	0	0.55
Random intercept + age and dbh slope	1776.7	16	0.4	0.45
Random intercept + age slope	1854.2	13	77.9	6.7×10^{-18}
Random intercept only	1861.8	11	85.5	1.5×10^{-18}

Note: K is the bias-correction factor (or number of estimable parameters), and w_i is the Akaike weight for the model (Burnham and Anderson, 2010).

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