

Long-term dynamics and characteristics of snags created for wildlife habitat



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ABSTRACT

Snags provide essential habitat for numerous organisms and are therefore critical to the long-term maintenance of forest biodiversity. Resource managers often use snag creation to mitigate the purposeful removal of snags at the time of harvest, but information regarding how created snags change over long timescales (> 20 y) is absent from the literature. In this study, we evaluated the extent to which characteristics of large (> 30 cm diameter at breast height [DBH]) Douglas-fir (*Pseudotsuga menziesii*) snags created by topping had changed after 25–27 y. We also tested whether different harvest treatments and snag configurations influenced present-day snag characteristics. Of 690 snags created in 1989–1991, 91% remained standing during contemporary surveys and 65% remained unbroken along the bole. Although most snags were standing, we detected increased bark loss and breaking along the bole relative to prior surveys conducted on the same pool of snags. Although snag characteristics were not strongly influenced by snag configuration, we found that snags in one harvest treatment (group selection) experienced less bark loss and had lower evidence of use by cavity-nesting birds (as measured by total cavity cover) relative to snags created with clearcut and two-story harvest treatments. Our results indicate that Douglas-fir snags created by topping can remain standing for long time-periods (≥ 25 y) in managed forests, and that the influence of harvest treatment on decay patterns and subsequent use by wildlife is an important consideration when intentionally creating snags for wildlife habitat.

1. Introduction

Standing dead trees, or snags, are important ecological structures that can be formed naturally through the actions of fire, wind, insects, and fungi (Morrison and Raphael, 1993; Rose et al., 2001). Snags play a crucial role in forest health by storing terrestrial carbon and contributing to soil development as snags decompose (Harmon et al., 1986; Rose et al., 2001; Angers et al., 2012). In addition, they enhance biodiversity by providing nesting and foraging habitat for many species of insects, amphibians, birds, and mammals during their transition from a living tree to a snag (Thomas, 1979; Harmon et al., 1986; Newton, 1994; Rose et al., 2001; Seibold et al., 2016). For example, decay in living trees and snags creates pockets of rot that provide critical nesting and roosting habitat for species that require cavities (e.g., woodpeckers) and areas under loose bark (e.g., bats, Brown Creeper [*Certhia americana*]; Harmon et al., 1986; Franklin et al., 1987; Chambers et al., 2002; Bunnell, 2013; Geelyne et al., 2016). As snag decay progresses, parts of the snag begin to break and fall to the ground and become downed wood, providing additional shelter and feeding substrates for many species of insects, amphibians, and mammals (Franklin et al., 1987; Duane, 2001; Manning and Edge, 2004; Rose et al., 2001;

Waldien et al., 2006; Kluber, 2007; Kilgo and Vukovich, 2014).

Despite their ecological significance, snags are often removed during timber harvest because of their commercial value and to comply with safety regulations (McComb et al., 1993; Kroll et al., 2012). Therefore, decades of intensive forest management practices, such as clearcutting and fire suppression, have resulted in a reduction in the number of snags within managed forest landscapes (Cline et al., 1980; Swanson and Franklin, 1992; Wilhere, 2003). A reduction in snags can reduce native biodiversity by degrading or eliminating habitat (Hane et al., 2012). Therefore, intentional creation of snags, which is typically undertaken at the time of harvest, has been implemented to mitigate loss of wildlife habitat in managed forests (Bull and Partridge, 1986).

The amount of time that created snags remain standing and the rate at which snags decay are critical for determining their useful lifespan as wildlife habitat, and snag lifespan can be influenced by the density of residual live trees and the configuration of snags following harvest. Direct exposure to environmental factors, such as solar radiation, precipitation, and wind can cause rapid changes in moisture content of wood within snags, in turn influencing bark and wood retention. Therefore, greater residual live tree density around snags may decrease breaking rates and increase bark and wood retention by protecting

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snags from environmental factors (Harmon et al., 1986). Whether snags are retained in clusters or scattered throughout a harvest unit may also affect their decay rate; clustered snags may promote greater insect colonization and subsequent mineralization of wood and colonization by fungi, bacteria and other invertebrates (Chamberlin, 1918; Angers et al., 2012). The presence of insects can also attract additional species such as woodpeckers, which further contribute to snag decay through fragmentation of wood during their foraging and excavating activities (Harmon et al., 1986) and can facilitate the establishment of fungi (Jusino et al., 2016). Although wildlife use of snags tends to increase with snag age (Schreiber and DeCalesta, 1992; Chambers et al., 1997; Hallett et al., 2001; Walter and Maguire, 2005; Arnett et al., 2010), information is lacking about how long snags persist, and how harvest type and snag configuration may influence snag characteristics that are important for wildlife. Nevertheless, this information is critical for resource managers who are charged with creating snags as a form of habitat mitigation for snag-associated wildlife species within managed forest landscapes (Kroll et al., 2012).

In this study, our goal was to quantify characteristics of snags that were intentionally created in 1989–1991 as part of a long-term silvicultural experiment at Oregon State University (i.e., College of Forestry Integrated Research Project; Maguire and Chambers, 2005). Snags were created at the time of harvest in one of three harvest treatments (group selection: uneven-aged with 33% tree volume removed in patches, two-story: even-aged with 75% tree volume removed uniformly, clearcut: even-aged with all tree volume removed except for 1.3 live trees/ha) and one of two spatial configurations (clustered, scattered), both of which were applied at the stand level (Chambers et al., 1997). Our objectives were to (1) test whether experimental harvest treatment and snag configuration influenced persistence of created snags, (2) quantify how current-day snag characteristics related to decay were influenced by harvest treatment and snag configuration, and (3) incorporate historic data from the same pool of snags to document changes in characteristics and use by cavity-nesting birds across a ≥ 25 -y period.

Experimental harvest treatments in our study differed in the amount of basal area removed, so we hypothesized that greater harvest intensity would result in greater levels of decay, as tree density is thought to influence decay rate (Garber et al., 2005; Harmon et al., 1986; Seibold et al., 2016). Based on findings from previous surveys conducted on the same snags (Chambers et al., 1997; Walter and Maguire, 2005), we also hypothesized that snags created in the clearcut and two-story treatments would receive more cumulative use by birds over time than those in the group selection treatment, as measured by the extent of cavity cover. We defined cavity cover as the cumulative area on the snag bole that comprised of nesting, foraging, and natural cavities because (1) many snags in our study were extensively decayed, making it impossible to distinguish between cavity types, and (2) it is possible that some cavities on created snags began as one cavity type (e.g., nesting) but were expanded to become a different cavity type (e.g., foraging) during the lifetime of the snag. With respect to snag configuration, we hypothesized that snags created in clusters would experience greater use than scattered snags because snag proximity may increase foraging efficiency for birds. Under this assumption, we expected snags to have greater external decay resulting from foraging activity and greater cavity cover within the clustered configuration, relative to snags in the scattered configuration. Given the influence of foraging on snag decay, we also predicted that snags created in clusters would have greater fall rates, break along the bole faster, and have more bark lost than scattered snags (Harmon et al., 1986; Jusino et al., 2016; Lorenz et al., 2015). Alternatively, snags created in clusters may be more protected from wind than snags that are scattered and may therefore be less likely to fall or break due to wind damage. As the first to quantify the decay process of created snags in managed forests across ≥ 25 y, our study provides a critical step in understanding the implications of a widespread management technique for creating wildlife habitat that is commonly used within working forest landscapes.

2. Methods

2.1. Site description

Our study sites were located within Oregon State University's McDonald-Dunn Research Forest (123°15'W, 44°35'N) near Corvallis, Oregon on the lower east slope of the Coast Range. The original study design comprised 30 stands (5–18 ha each) dominated by Douglas-fir (*Pseudotsuga menziesii*) that had regenerated naturally after harvest. These stands included two understory plant association types: hazel (*Corylus cornuta* var. *californica*)/brome (*Bromus vulgaris*) and vine maple (*Acer circinatum*)/salal (*Gaultheria shallon*; Franklin and Dyrness 1973). Dominant trees on stands were 45–150 y old at the time of harvest treatments were applied and snag creation took place (see below), and stands were similar in plant species composition among treatments prior to harvest (Chambers, 1996). Mean density of live conifers was approximately 540 trees/ha, live hardwood tree density averaged 165 trees/ha, and natural snag (i.e., snags formed naturally without tree topping) density averaged < 1.9 snags/ha (Chambers, 1996). At the time of our research (2015–2016), natural snag densities varied relative to harvest treatment: group selection treatment: 10.6 snags/ha (SE ± 1.9 , $n = 16$ stands), two-story treatment: 6.4 snags/ha (SE ± 2.2 , $n = 7$ stands), clearcut treatment: 13.3 snags/ha (SE ± 5.1 , $n = 3$ stands; Barry, 2017).

2.2. Study design

Our study consisted of a randomized, complete block design with three study blocks, with each block harvested in a separate year (i.e., Lewisburg block in 1989, Peavy block in 1990, Dunn block in 1991) and planted the spring following harvest. Each block contained $n = 10$ stands in which snags were created at the time of harvest. Individual stands within each block were assigned randomly to one of three harvest treatments and one of two snag configurations. The harvest treatments and snag configurations were intended to mimic variations in natural disturbance patterns and test the effects of operational alternatives to traditional clearcutting on a range of ecological responses (Chambers et al., 1999). Experimental harvest treatments included (1) group selection, which represented localized, low intensity disturbance and resulted in 33% of the tree volume removed in 0.2 ha patches; (2) two-story, which represented evenly distributed moderate disturbance and resulted in 75% of the tree volume removed uniformly; and clearcut, which represented high intensity, stand-replacing disturbance and resulted in all tree volume removed except for 1.3 live trees/ha. All stands were replanted with Douglas-fir seedlings at a density of 625–865 trees/ha, depending on harvest treatment, and received herbicide applications 2–5 y after harvest to control competing vegetation (Chambers et al., 1997).

At the time stands were harvested, snags were created in either a clustered configuration with 3–5 discrete groups within each stand, or scattered uniformly throughout each stand. In both configurations, mean density of created snags was equal at the stand scale (3.8 snags/ha). When available, natural snags were included in clusters of created snags (Chambers et al., 1997). Snags were created throughout each stand except for the group selection treatment, where the small size of the harvested patches constrained snag creation to unharvested areas (Maguire and Chambers, 2005). All snags were created by topping live Douglas-fir trees with a chainsaw at a mean height of 17 m (minimum: 15 m) and a mean diameter at breast height (DBH) of 75 cm (range: 33–198 cm). Each snag was marked with a uniquely marked aluminum tag, allowing us to document changes in individual snags across time. Due to modification of treatments in some stands over time, only 26 of the 30 original stands were available for our study (group selection: $n = 16$, two-story: $n = 5$, clearcut: $n = 5$).

2.3. Contemporary characteristics of created snags

During January–March 2016, we revisited all individually marked created Douglas-fir snags ($n = 731$) to assess their status (i.e., fallen or standing). From this total, 41 snags lacked historic measurements that were used as covariates in our model to assess influence of harvest treatment and configuration on snag characteristics (see below), resulting in $n = 690$ snags available for analyses. We considered a snag to be standing if it was ≥ 2.5 m in height. For every snag we found standing, we also recorded whether it had broken along its bole. We classified a snag as broken by the appearance of an uneven top which contrasted sharply with the smooth, even top that all snags had at the time of creation. Of the pool of snags that were still standing, we selected a random subset ($n = 238$) divided evenly among the three harvest treatments to quantify three additional characteristics by a single observer (AMB). For each snag, we estimated bark cover as the percent of the bole covered by bark (to the nearest 5%). We categorized snags as having peeling bark (as a binary variable) when bark was partially detached from ≥ 1 m² of the bole. To measure the cumulative use of snags by cavity-excavating birds we estimated cavity cover as the extent of all cavities observed on the bole (to the nearest 10%); we did not include bark that was missing due to wood deterioration and lacked holes. We described a cavity as any excavation or depression in the snag that resulted from a nesting or foraging attempt or from a natural occurrence such as limb loss or fungal decay. Cavities may be used for multiple ecologically relevant functions over time (e.g., a nesting cavity may become a foraging area), so the origin of each cavity was difficult to determine with certainty. Thus, we did not attempt to distinguish between nesting, foraging, and natural cavities but instead combined them into a single estimate of cavity cover. This provided use with a relative estimate of snag use under the assumption that a greater amount of cavity cover represented greater cumulative use of snags by cavity-nesting birds. To calibrate cavity cover estimates, we first calculated cavity cover from digital photographs taken on a subset of created snags and used this to compare with visual estimates taken in the field on the same subset of snags before data collection began. We then used photographs with cavity cover calculated in this manner as a visual reference during data collection to improve the accuracy of our estimates. We used two variables that were measured during surveys in 1990–1991 (i.e., snag DBH and ground slope) in our statistical models. Snag DBH was measured at 1.4 m above ground height on all snags, and ground slope was measured as the slope of the ground averaged from 20 m upslope and down-slope from each snag (Chambers et al., 1997).

2.4. Long-term patterns of snag decay

Initial characteristics of created snags were documented approximately three months after each block was harvested in 1990–1991 (Chambers et al., 1997). Created snags were revisited at four points in time (1995, 2001, 2008, and 2016) and data from those visits were used to provide a longitudinal assessment of snag characteristics (Chambers et al., 1997; Walter and Maguire, 2005; Huff and Bailey, 2009). To assess changes in snag characteristics over time, we compared contemporary snag characteristics from our surveys (i.e., proportion standing, proportion with a broken bole, extent of bark cover, and extent of bark peeling) to data from previous reports (i.e., Chambers et al., 1997; Huff and Bailey, 2009; Walter and Maguire, 2005; hereafter, historic data). We note that prior studies (Chambers et al., 1997; Walter and Maguire, 2005) reported the number of cavities observed on each snag, but this was not feasible during contemporary surveys because decay in the intervening years did not allow for a strict delineation of some cavities. In turn, this prevented us from making direct comparisons of the number of historic and contemporary cavities on created snags.

2.5. Statistical methods

We used a mixed linear modeling approach in the R (v3.3.1) statistical environment to quantify treatment and time-specific variation in snag characteristics. We used the ‘lme4’ package to construct generalized linear mixed models with a binomial distribution and a logit link to examine the proportion of snags standing, the proportion of snags broken, and the proportion of snags with peeling bark. We constructed linear mixed models to test for differences in contemporary estimates of mean bark cover and mean cavity cover among harvest treatments and between snag configurations. All models included harvest treatment (3 levels: group selection, two-story, clearcut), snag configuration (2 levels: clustered, scattered), a treatment \times configuration interaction, and study block as fixed effects; stand as a random effect; and snag DBH and ground slope as covariates. Both DBH and slope covariate data were obtained at the time of snag creation and were included in models because they are associated with Douglas-fir snag persistence (Huff and Bailey, 2009). We log-transformed mean bark cover and mean cavity cover to adhere with assumptions of normality and equal variance, and back-transformed results for interpretation; we found no evidence of overdispersion in our models. We used Tukey adjustments for all models with multiple comparisons, and we report least-squares marginal means for effect sizes and their associated 95% confidence intervals (CIs) with covariates set to their mean value.

To assess how snag characteristics changed over time, we compared historic data to contemporary data collected during the current study. We compared the proportion of snags that had fallen, the proportion of snags broken, and bark cover across all 4 time periods and we also compared contemporary estimates of the proportion of snags with peeling bark to estimates taken in 2001 using descriptive statistics.

3. Results

3.1. Contemporary characteristics of created snags

Across all treatments, 91% of all created snags were still standing and 65% of standing snags remained intact (i.e., were unbroken) ≥ 25 y after creation. The mean height of standing snags was 15.9 m (95% CI: 15.4, 16.5), indicating that standing snags lost very little of their tops since the time of creation. All snags that had fallen were found to have broken near their base, and no fallen snags showed evidence of having been uprooted. We detected effects of harvest treatment on both the proportion of snags that were standing ($X^2 = 7.12$, $P = 0.03$; Fig. 1a) and the proportion of snags that broke ($X^2 = 6.46$, $P = 0.04$; Fig. 2a). The odds of a created snag remaining standing in the group selection treatment were 2.7 \times greater (\pm 95% CI: 1.1, 6.4; $z = 2.7$, $P = 0.02$) than in the clearcut treatment. In contrast, we did not detect a difference between the proportion of snags standing in the two-story treatment compared with either the group selection (odds ratio [OR] = 1.7 \pm 95% CI: 0.7, 4.1; $z = 1.4$, $P = 0.34$) or the clearcut treatment (OR = 1.6 \pm 95% CI: 0.6, 4.3; $z = 1.1$, $P = 0.52$). The odds of a created snag being broken in the two-story treatment were 1.9 \times greater (\pm 95% CI: 1.1, 3.2; $z = 2.9$, $P = 0.01$) than in the group selection treatment; however, there were similar proportions of snags broken when comparing between the clearcut treatment and either the two-story (OR = 1.8 \pm 95% CI: 0.9, 3.4; $z = -2.0$, $P = 0.11$) or the group selection treatments (OR = 0.9 \pm 95% CI: 0.5, 1.6; $z = 0.34$, $P = 0.94$). In contrast to an effect of harvest treatment, we did not detect an effect of snag configuration on either the proportion of snags standing ($X^2 = 0.02$, $P = 0.88$; Fig. 1b) or on the proportion that broke ($X^2 = 0.09$, $P = 0.77$; Fig. 2b). We also note that we detected an effect of DBH on whether a snag was standing ($X^2 = 19.30$, $P < 0.001$) or had broken ($X^2 = 33.47$, $P < 0.001$), but did not detect an effect of slope on either measure ($X^2 = 0.95$, $P = 0.33$; $X^2 = 1.01$, $P = 0.32$, respectively).

For the created snags for which we quantified additional

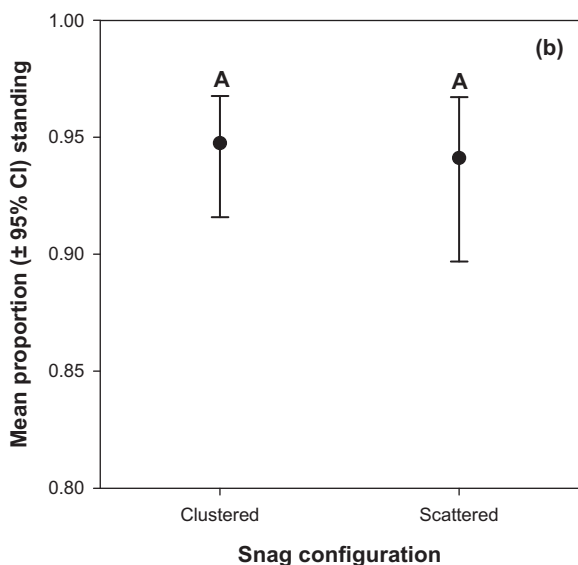
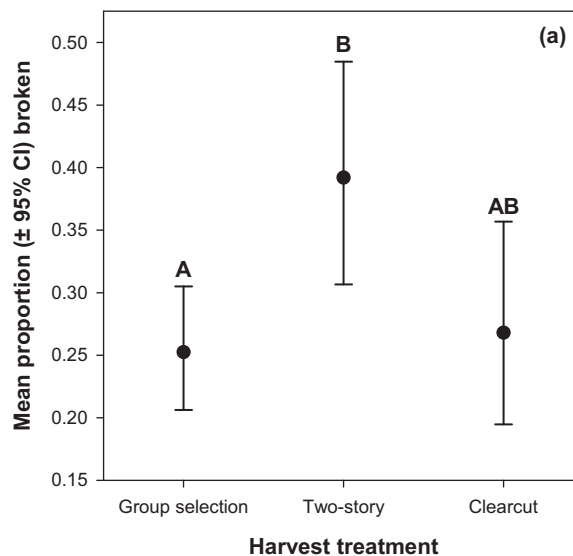
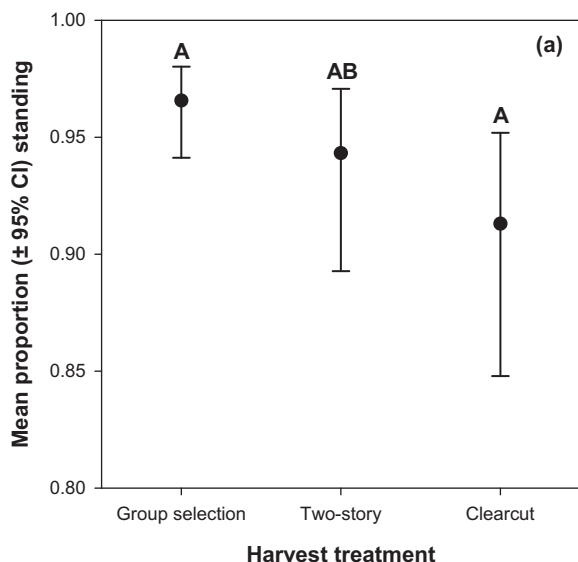


Fig. 1. Mean proportion (± 95% CI) of created snags that were standing within each (a) harvest treatment (group selection: n = 368, two-story: n = 165, clearcut: n = 157) and (b) snag configuration (clustered: n = 398, scattered: n = 292) when measured 25–27 y after creation. Point estimates that do not share the same letter are considered to be statistically different from each other ($P < 0.05$).

characteristics (n = 238), we found that snags in treatments that experienced greater levels of harvest intensity and were subjected to an open environment (i.e., two-story and clearcut) were generally more similar to each other than to those created under lower harvest intensity and where snags remained under a closed canopy (i.e., group selection treatment; Table 1). We detected an effect of harvest treatment on bark cover ($F_{2,18} = 28.35$, $P < 0.001$), bark peeling ($\chi^2 = 38.27$, $P < 0.001$), and cavity cover ($F_{2,18} = 10.30$, $P = 0.01$). Created snags in the group selection treatment typically exhibited less bark loss and bark peeling and had less cavity cover than snags in either the two-story or clearcut treatments. Mean bark cover in the group selection treatment was 1.4× greater (± 95% CI: 1.2, 1.6; $t = 5.15$; $P < 0.001$) than in the clearcut treatment and 1.2× greater (± 95% CI: 1.0, 1.4; $t = 2.93$, $P = 0.02$) than in the two-story treatment. When compared to the group selection treatment, the odds of a snag with peeling bark were 14.5× greater (± 95% CI = 5.0, 41.8; $z = 5.92$, $P < 0.001$) in the clearcut and 9.0× greater (± 95% CI: 3.1, 25.9;

Fig. 2. Mean proportion (± 95% CI) of created snags that were broken within each (a) harvest treatment (group selection: n = 368, two-story: n = 165, clearcut: n = 157) and (b) snag configuration (clustered: n = 398, scattered: n = 292) when measured 25–27 y after creation. Point estimates that do not share the same letter are considered to be statistically different from each other ($P < 0.05$).

$z = 4.86$, $P < 0.001$) in the two-story treatment. Although all created snags contained cavities, mean cavity cover was 1.4× greater in both the clearcut (± 95% CI: 1.1, 1.9; $t = 2.65$; $P = 0.03$) and the two story (± 95% CI: 1.0, 1.9; $t = 2.46$; $P = 0.04$) treatments relative to the group selection treatment.

We did not detect an effect of snag configuration on bark cover (OR = 1.1 ± 95% CI: 0.9, 1.4; $t = 1.67$, $P = 0.15$) or cavity cover (OR = 1.1 ± 95% CI: 0.8, 1.4; $t = 0.44$, $P = 0.68$), but we did detect an effect on bark peeling ($\chi^2 = 5.90$, $P = 0.02$). Snags in a clustered configuration were 2.6× more likely (± 95% CI: 1.2, 5.6; $z = 2.54$; $P = 0.01$) to have bark peeling than in a scattered configuration. We also detected an effect of DBH on bark cover ($\chi^2 = 8.36$, $P = 0.003$), bark peeling ($\chi^2 = 5.04$, $P = 0.03$), and cavity cover ($\chi^2 = 24.47$, $P < 0.001$). In contrast, we did not detect an effect of slope on bark cover ($\chi^2 = 0.02$, $P = 0.89$), bark peeling ($\chi^2 = 0.07$, $P = 0.81$), or cavity cover ($\chi^2 = 0.17$, $P = 0.68$).

Table 1

Snag characteristics (i.e., mean bark cover, proportion of snags with peeling bark, mean cavity cover) measured on intentionally created snags relative to experimental harvest treatments 25–27 y after creation. See text for detailed definitions of snag characteristics.

Harvest treatment	n	Mean bark cover (± 95% CI)	Snags with peeling bark (± 95% CI)	Mean cavity cover (± 95% CI)
Group Selection	73	99.1% (86.5, 113.4)	16.7% (9.1, 28.7)	9.8% (7.7, 12.5)
Two-story	69	81.1% (70.6, 93.4)	64.4% (51.0, 75.8)	13.7% (10.2, 18.3)
Clearcut	96	71.1% (62.4, 81.0)	74.4% (63.7, 82.8)	13.9% (10.4, 18.5)

3.2. Long-term patterns of snag decay

Fall rate of created snags increased over time, with the greatest increase between 2008 and 2016. No snags fell within the first 4–6 y after creation, and only a single snag had fallen by 2001, 10–12 y after creation. By 2008, 99.5% of the snags were still standing although that decreased to 91% by 2016. Similarly, no standing snags had broken within the first 4–6 y after creation, and only 1 had broken by 2001. The percentage of standing snags that were broken was still low (3%) in 2008, but increased markedly to 27% in 2016. Finally, the rate of bark loss also advanced with time since creation. The percent of snags with bark peeling away from the bole increased from 8% in 2001 to 54% in 2016. Although bark cover on snags remained high (97%) in 2001, it had decreased to 82% across treatments by 2016. The percentage of snags that contained evidence of cavities increased from 88% in 2001 to 100% in 2016.

4. Discussion

4.1. Contemporary characteristics of created snags

Our study found that the great majority of Douglas-fir snags created by topping remained standing ≥ 25 y after they were created. The size of the snags in our study (mean DBH = 75 cm) likely enhanced their persistence because large diameter natural Douglas-fir snags can remain standing for > 100 y in the Oregon Coast Range (Cline et al., 1980). In addition, Douglas-fir snags may remain standing longer than other tree species due in part to their higher ratio of heartwood to sapwood, which has higher resistance to fungi and thus greater resistance to decay (Kimmey and Furniss, 1943; Harmon et al., 1986; Hallett et al., 2001). Furthermore, all created snags had indications of use by birds over time, perhaps because topped snags receive more use by birds than snags created through girdling within 4–7 y since creation (Hallett et al., 2001). Taken together, this suggests that both tree species and method of creation are important considerations for determining longevity and usefulness of created snags, and that topped Douglas-fir trees serve as useful habitat features for cavity-nesting birds within managed forests.

Although the proportion of created snags that were still standing during the course of our study was high, we did find that silvicultural practices (e.g., harvest treatment at time of creation) had a strong influence on the propensity to break and current-day bark characteristics. The greater levels of bark loss in treatments with fewer live trees retained at harvest may have resulted from changes in microclimatic conditions that were induced by a reduction in canopy cover and surrounding tree densities, which are typically more variable in open stands (Harmon et al., 1986; Garber et al., 2005). For example, snags in the two-story and clearcut treatments were less protected and subjected to more extreme fluctuations in moisture and temperature than those in the group selection treatments. This may have led to greater decay rates via enhanced stress to wood cells, in turn increasing breaking and bark detachment from the bole of the snag (Harmon et al., 1986). In contrast, snags in the group selection treatment have experienced a more stable environment with dampened fluctuations in moisture and temperature within the matrix of mature forest canopy, ultimately leading to lower rates of decay we observed in our study.

Harvest treatment also influenced cumulative use of snags over time by cavity-nesting birds, as indicated by the extent of cavity cover. Previous surveys conducted on the same pool of snags in 1995 and 2001 (Chambers et al., 1997; Walter and Maguire, 2005) were concordant to the findings from our study, with the highest estimates of bird-formed cavities and more direct observations of nesting and foraging by cavity-nesting birds in the two-story and clearcut treatments. These two treatments may have historically provided better habitat for some woodpecker species, such as the Northern Flicker (*Colaptes auratus*), that select open stands with lower live tree densities for nesting (Aitken et al., 2002; Elchuk, et al., 2003; Walter and Maguire, 2005; Warren et al., 2005). Snags created in more open treatments may have also initially provided better foraging resources than snags in group selection stands. Indeed, a recent study found that species richness of saproxylic beetles was higher in dead wood in open forest plots compared with closed forest plots (Seibold et al., 2016). If increases in wood-boring beetles did occur in more open treatments in our study, it could have attracted species that use snags as foraging substrates (e.g., woodpeckers; Spring, 1965; Harmon et al., 1986) and led to greater areas of cavity creation and use. Foraging and nesting by woodpeckers may have further contributed to the contemporary differences in snag characteristics we observed by changing the structure of snags as they drilled through bark and sapwood to obtain food and create nesting cavities (Bull et al., 1983). In the process of excavating, woodpeckers can directly expose heartwood to fungi and other decay organisms (Jusino et al., 2016), thereby accelerating physical and biological snag decay in the historically more open treatments. Although we were unable to distinguish between the effects of the microclimate and bird use on snag decay, this should be an important focus of other studies as they are both likely to contribute to the patterns we found.

The minimal effect that we observed of spatial configuration on nearly all snag characteristics measured is consistent with previous work (Chambers et al., 1997; Walter and Maguire, 2005; Arnett et al., 2010; Hane et al., 2012); the lone exception was the proportion of snags that contained peeling bark. Clustered snags may be more likely to attract beetles or decomposer organisms that accelerate decay and cause sapwood to break down more quickly (Chamberlin, 1918; Angers et al., 2012; Seibold et al., 2016), and the activity of these organisms can often lead to a greater propensity for bark to peel away from created snags. An increase in insect density on clustered snags may also attract more foraging birds, such as woodpeckers, that drill for prey (Raphael and White, 1984), resulting in a similar effect on snag decay and subsequent bark integrity. However, we did not detect any differences in cavity cover or bark cover between snag configurations, so the differences in bark integrity we detected are likely due to some other factor(s). To the best of our knowledge, there are no similar studies that have examined the effect of spatial configuration on characteristics of created snags, so this topic warrants further exploration.

4.2. Long-term patterns of snag decay

When historic data are considered (Chambers et al., 1997; Walter and Maguire, 2005; Huff and Bailey, 2009), it is evident that the rate of breaking and bark loss on snags across all harvest treatments was initially slow and increased markedly in the second decade since creation. Between 17–19 y (Huff and Bailey, 2009) and 25–27 y (this study) after

snags were created, breaking and bark peeling had increased substantially across all harvest treatments. Breaking and bark loss are external characteristics that have been commonly used to describe more advanced stages of snag decay, and our findings match other studies of natural Douglas-fir snags in our region which have reported extensive breaking and bark loss when snags were between 19 and 50 y old (Cline et al., 1980). Whereas breaking and bark loss may be important factors in the availability and selection of habitat by wildlife (Bunnell, 2013; Chambers et al., 2002; Franklin et al., 1987; Geleynse et al., 2016; Harmon et al., 1986; Rose et al., 2001), external characteristics of snags have been shown to be poorly correlated with internal decay (Schepps et al., 1999). Thus, future studies should seek to combine measurements of internal wood hardness with external characteristic of created snags to better understand how external characteristics relate to snag decay, which was not possible in our study because of safety considerations. Although we were unable to assess changes in cavity cover over time, we note that current-day estimates of cavity cover did not exceed 60% (Barry, 2017), suggesting that snags may not remain standing above this threshold, perhaps due to structural instability caused by removing structural components of snags.

4.3. Conclusions and management implications

Although most of the snags we examined were still standing ≥ 25 y after creation, snags had an increased rate of breaking and experienced changes in characteristics that appear to be associated with advanced decay. Because snags created in treatments with greater harvest intensity exhibited greater likelihood of falling and more bark loss, forest managers whose goal is wildlife habitat creation may consider leaving some live trees at the time of snag creation to provide long-term habitat features for snag-dependent species. If snags created under a mature forest matrix have greater persistence and experience lower rates of decay than snags created in the open, as was the case in our study, then they may represent important structures that can be used by wildlife across long timescales. A critical but unanswered question is the extent to which created snags are used by cavity-nesting birds for foraging and nesting after ≥ 25 y. The increased rate of breaking and bark loss that we observed in the open treatments suggests that the usefulness of these snags for some cavity-nesting birds, such as woodpeckers, may decline through time. Nevertheless, some species use snags in later stages of decay, so they may benefit from snags containing greater decay in managed stands that result from a combination of different harvest treatments.

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References

Aitken, K.E.H., Aitken, K.E.H., Wiebe, K.L., Wiebe, K.L., Martin, K., Martin, K., 2002. Nest-site reuse patterns for a cavity-nesting bird community in interior British Columbia. *Auk* 119, 391–402.

Angers, V.A., Drapeau, P., Bergeron, Y., 2012. Mineralization rates and factors influencing snag decay in four North American boreal tree species. *Can. J. For. Res.* 42, 157–166.

Arnett, E.B., Kroll, A.J., Duke, S.D., 2010. Avian foraging and nesting use of created snags in intensively-managed forests of western Oregon, USA. *For. Ecol. Manage.* 260, 1773–1779.

Barry, A.M., 2017. Created snag dynamics and influence on cavity-nesting bird communities over 25 years in Western Oregon. Masters thesis Oregon State University.

Bull, E.L., Partridge, A.D., 1986. Methods of killing trees for use by cavity nesters. *Wildl. Soc. Bull.* 14, 142–146.

Bunnell, F.L., 2013. Sustaining cavity-using species: patterns of cavity use and implications to forest management. ISRN For. 1–33 Article ID 457698.

Chamberlin, W., 1918. Bark-beetles infesting the Douglas fir. *Oregon Agric. Exp. Station Bull.* 147, 1–40.

Chambers, C., Carrigan, T., Sabin, T., Tappeiner, J., McComb, W., 1997. Use of artificially created Douglas-fir snags by cavity-nesting birds. *West. J. Appl. For.* 12, 93–97.

Chambers, C.L., 1996. Response of terrestrial vertebrates to three silvicultural treatments in the Central Oregon Coast Range. Ph.D. thesis Oregon State University.

Chambers, C.L., McComb, W.C., Tappeiner, J.C., 1999. Breeding bird responses to three silvicultural treatments in the Oregon coast range. *Ecol. Appl.* 9, 171–185.

Chambers, C.L., Alm, V., Sliders, M.S., Rabe, M., 2002. Use of artificial roosts by forest-dwelling bats in Northern Arizona. *Wildl. Soc. Bull.* 30 (2002), 1085–1091.

Cline, S.P., Berg, A.B., Wight, H.M., 1980. Snag characteristics and dynamics in Douglas-Fir forests, Western Oregon. *J. Wildlife Manage.* 44, 773–786.

Duane, M., 2001. Response of wood-boring beetles (Coleoptera: Buprestidae, Cerambycidae) to prescribed understorey burning in mixed-conifer stands in Southwestern Oregon. Masters thesis Oregon State University.

Elchuk, C.L., Wiebe, K.L., Wiebe, E., 2003. Home-range size of Northern Flickers (*Colaptes auratus*) in relation to habitat and parental attributes. *Can. J. Zool.* 81, 954–961.

Franklin, J.F., Shugart, H.H., Harmon, M.E., 1987. Tree death as an ecological process: the causes, consequences, and variability of tree mortality. *Bioscience* 37, 550–556.

Garber, S.M., Brown, J.P., Wilson, D.S., Maguire, D.A., Heath, L.S., 2005. Snag longevity under alternative silvicultural regimes in mixed-species forests of central Maine. *Can. J. For. Res.* 35, 787–796.

Geleynse, D.M., Nol, E., Burke, D.M., Elliott, K.A., 2016. Brown Creeper (*Certhia americana*) demographic response to hardwood forests managed under the selection system. *Can. J. For. Res.* 46, 499–507.

Hallett, J.G., Lopez, T., O'Connell, M.A., Borysewicz, M.A., 2001. Decay dynamics and avian use of artificially created snags. *Northwest Sci.* 75, 378–386.

Hane, M.E., Kroll, A.J., Johnson, J.R., Rochelle, M., Arnett, E.B., 2012. Experimental effects of structural enrichment on avian nest survival. *For. Ecol. Manage.* 282, 167–174.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., et al., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 1–436.

Huff, T.D., Bailey, J.D., 2009. Longevity and dynamics of fatally and nonfatally topped Douglas-fir in the Coast Range of Oregon. *Can. J. For. Res.* 39, 2224–2233.

Jusino, M.A., Lindner, D.L., Banik, M.T., Rose, K.R., Walters, J.R., 2016. Experimental evidence of a symbiosis between red-cockaded woodpeckers and fungi. *Proc. R. Soc. B: Biol. Sci.* 283, 20160106.

Kilgo, J.C., Vukovich, M.A., 2014. Can snag creation benefit a primary cavity nester: response to an experimental pulse in snag abundance. *Biol. Cons.* 171, 21–28.

Kimmey, J.W., Furniss, R.L., 1943. Deterioration of Fire-killed Douglas-fir. USDA Tech. Bull. Washington, D.C.

Kluber, M., 2007. Terrestrial amphibian distribution, habitat associations and downed wood temperature profiles in managed headwater forests with riparian buffers in the Oregon Coast Range. Masters thesis Oregon State University.

Kroll, A.J., Lacki, M.J., Arnett, E.B., 2012. Research needs to support management and conservation of cavity-dependent birds and bats on forested landscapes in the Pacific Northwest. *West. J. Appl. For.* 27, 128–136.

Lorenz, T.J., Vierling, K.T., Johnson, T.R., Fischer, P.C., 2015. The role of wood hardness in limiting nest site selection in avian cavity excavators. *Ecol. Appl.* 25, 1016–1033.

Maguire, C., Chambers, C., 2005. College of Forestry Integrated Research Project: Ecological and Socioeconomic Responses to Alternative Silvicultural Treatments. Oregon State University, Corvallis.

Manning, J.A., Edge, W.D., 2004. Small mammal survival and downed wood at multiple scales in managed forests. *J. Mammal.* 85, 87–96.

McComb, B.W.C., Spies, T.A., Emmingham, W.H., 1993. Douglas-fir forests: managing for timber and mature-forest habitat. *J. For.* 91, 31–42.

Morrison, M.L., Raphael, M.G., 1993. Modeling the dynamics of snags. *Ecol. Appl.* 3, 322–330.

Newton, I., 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biol. Cons.* 70, 265–276.

Raphael, M.G., White, M., 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. *Wildlife Monogr.* 86, 3–66.

Rose, C.L., Marcot, B.G., Mellen, T.K., Ohmann, J.L., Waddell, K.L., Lindley, D.L., Schreiber, B., 2001. Decaying Wood in Pacific Northwest Forests: Concepts and Tools for Habitat Management. Wildlife-habitat Relationships in Oregon and Washington. Oregon State University Press, Corvallis.

Schepps, J., Lohr, S., Martin, T.E., 1999. Does tree hardness influence nest-tree selection by primary cavity nesters? *Auk* 166 (3), 658–665.

Schreiber, B., DeCalesta, D., 1992. The relationship between cavity-nesting birds and snags on clearcuts in western Oregon. *For. Ecol. Manage.* 50, 299–316.

Seibold, S., Bassler, C., Brandl, R., Buche, B., Szallies, A., Thorn, S., et al., 2016. Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. *J. Appl. Ecol.* 53, 934–943.

Spring, B.L.W., 1965. Climbing and pecking adaptations in some North American woodpeckers. *Condor* 67, 457–488.

Swanson, F.J., Franklin, J.F., 1992. New forestry principles from ecosystem analysis of

- Pacific Northwest forests. *Ecol. Appl.* 2, 262–274.
- Thomas, J.W., 1979. *Wildlife Habitats in Managed Forests: the Blue Mountains of Oregon and Washington*, vol. 553. U.S. Department of Agriculture.
- Waldien, D.L., Hayes, J.P., Huso, M.M.P., 2006. Use of downed wood by Townsend's chipmunks (*Tamias townsendii*) in Western Oregon. *J. Mammal.* 87, 454–460.
- Walter, S.T., Maguire, C.C., 2005. Snags, cavity-nesting birds, and silvicultural treatments in western Oregon. *J. Wildlife Manage.* 69, 1578–1591.
- Warren, T.L., Betts, M.G., Diamond, A.W., Forbes, G.J., 2005. The influence of local habitat and landscape composition on cavity-nesting birds in a forested mosaic. *For. Ecol. Manage.* 214, 331–343.
- Wilhere, G.F., 2003. Simulations of snag dynamics in an industrial Douglas-fir forest. *For. Ecol. Manage.* 174, 521–539.