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Dynamics of beetle-killed snags following mountain pine beetle outbreaks in lodgepole pine forests

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ABSTRACT

Snags (standing dead trees) are important components of forest ecosystems that, among other benefits, provide critical habitat for many species of wildlife, but also represent important safety concerns to firefighters, forest workers, and the public. We identified factors that influence the fall rates of lodgepole pines, *Pinus contorta* Dougl. ex Loud., killed by bark beetles during a severe regional-scale outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, that occurred in 2004–2012. Data were obtained during annual assessments (2010–2019) of a network of 107 0.081-ha circular plots installed in *P. contorta* forests in Colorado, Idaho, Montana, Utah and Wyoming, U.S. A total of 3789 *P. contorta* snags were monitored, and in each case we recorded, among other variables, the year the snag was created and the year the snag fell to the forest floor. Among snag age classes (i.e., number of years since tree death), the highest number of snags (1046) were 12 years since death (YSD), and those 13 and 14 YSD exhibited the lowest fall rates to date (<10%) despite being the oldest in our study. Snags 13 and 14 YSD were among the largest in diameter. Snag fall occurred in every snag age class from 1 to 14 YSD, with the greatest proportion of snag fall events occurring 4–8 YSD. By 2019, 24.7% (937) of snags fell to the forest floor. We modeled snag fall using a Cox's proportional-hazards model that included six covariates of interest: elevation (m), slope aspect (categorical, cardinal direction), slope (%), canopy cover (%), snag height (m), and snag height:dbh (m, diameter at 1.37 m in height). Slope aspect had the strongest influence on fall rates. Northern aspects, increased canopy cover, and taller snag heights decreased the probability of snag fall. Conversely, southern aspects and increased height:dbh ratios (i.e., taller, skinner snags) increased the probability of snag fall. The predicted half-life (i.e., the amount of time since death required for 50% of the snag population to fall to the forest floor) was ~16 YSD after which the function predicted a linear, ~0.04/year decline in snag survival probability 15–30 YSD. The observed longevity of *P. contorta* snags confers important ecological benefits for some wildlife, and may offer opportunities for extended periods of salvage. However, checking (cracks) rapidly occurred, and many snags 6 YSD and older had at least one check at 1.37 m and 5.5 m in height, which can negatively impact lumber recovery. The relatively slow snag fall rates observed in our study also lengthen concerns regarding hazard trees, human safety, and protection of critical infrastructure. The implications of these and other results to management of *P. contorta* forests are discussed.

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1. Introduction

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), colonizes at least 15 tree species in the western U.S. (Negrón and Fettig, 2014). Under endemic conditions, *D. ponderosae* often creates small gaps in the forest canopy by killing trees compromised by other agents. This differs, however, from patterns of tree mortality observed during *D. ponderosae* outbreaks when large numbers of trees may be killed in short periods of time, most notably in lodgepole pine, *Pinus contorta* Dougl. ex Loud., forests. Since 2000, ~10.3 million ha have been impacted by *D. ponderosae* in the western U.S. (Fettig et al., 2020). In most states in the Intermountain West, U.S., *D. ponderosae* populations rapidly increased in 2004; peaked in 2007–2009; and returned to endemic levels by 2012 (Audley et al., 2020; Fettig et al., 2020). Climatic changes, specifically increases in temperature and reductions in precipitation, have been implicated as important inciting factors (Bentz et al., 2010; Kolb et al., 2016), however, large areas of suitable host trees of susceptible size, age and density are required for an outbreak to develop (Fettig et al., 2007). Following these outbreaks, significant reductions in tree size and tree density, and significant increases in snag (standing dead tree) abundance were observed. In areas of heavy tree mortality, snag densities increased by >61-fold compared to background levels (from ~ 7.2 snags per ha; Bollenbacher et al., 2008; Audley et al., 2020).

Snags are important features of forested landscapes that provide nest and roost sites for cavity-nesting birds and bats (Scott et al., 1977; Raphael and White, 1984; Ohmann et al., 1994; Bull et al., 1997; Rabe et al., 1998; Saab et al., 2014). Snags also provide habitat for fungi, invertebrates, amphibians, reptiles and terrestrial mammals (Maser et al., 1978; Bull et al., 1997; Costello et al., 2013), and contribute to nutrient cycling. In Colorado, U.S., avian species richness increased substantially with time after a *D. ponderosae* outbreak in *P. contorta* forests, with changes in both snag abundance and understory vegetation likely contributing to the pattern (Latif et al., 2020). Janousek et al. (2019) reported that many avian species, particularly cavity nesters, use forests impacted by *D. ponderosae* outbreaks at higher rates for up to 10 years following outbreaks in Colorado, Idaho, Montana, and Wyoming, U.S. In British Columbia, Canada, woodpecker densities increased following a large-scale *D. ponderosae* outbreak, but annual fecundity (as indicated by clutch size and number of nestlings fledged) remained unchanged (Edworthy et al., 2011).

Snags and the large amounts of downed woody debris that accumulate following abundant snag fall may also represent important safety concerns (Guyon et al., 2017) (Fig. 1). In more developed areas, snags pose legal liabilities as hazard trees to humans, homes and critical infrastructure, such as power lines and roadways (Mortimer and Kane, 2004). Furthermore, wildland firefighter safety may be negatively impacted. For example, firefighters may encounter increased difficulties in fireline construction and establishment of access, egress, and escape routes, and less predictable fire behavior in forests where large amounts of tree mortality have occurred due to *D. ponderosae* outbreaks (Jenkins et al., 2014). Runyon et al. (2020) reported that the soil disturbance created when *P. contorta* snags tip up and fall is prone to establishment and spread of invasive weeds, and that monitoring of these tip up sites could be a cost-effective and efficient tactic to limit invasions by weeds following *D. ponderosae* outbreaks. Snag longevity (defined as the number of years that a snag remains standing and represents the inverse of fall rate) influences how long snags are available for salvage as once a snag falls logistical concerns generally preempt use for many wood products at commercial scale. Several changes in wood quality occur in *P. contorta* snags over time that also affect salvage potential and lumber recovery (Plank, 1984; Lowell et al., 2010). The most important is an increase in the number and severity of checks attributed to declines in sapwood moisture content. As such, determination of factors that influence snag dynamics are important for addressing ecological, economic, social (human safety), and legal concerns.

Previous studies of beetle-killed snags have identified tree species and tree diameter, stand density, and site conditions as factors that influence snag longevity and spatial patterns (Hoffman et al., 2012; Chambers and Mast, 2014; Ganey et al., 2015; Rhoades et al., 2020), with half-lives of snags (i.e., the amount of time since death required for 50% of the snag population to fall to the forest floor) ranging from years to decades. Rhoades et al., (2020) reported 17% of *P. contorta* snags fell by ~ 12 years since death (YSD) following a *D. ponderosae* outbreak in north-central Colorado. In British Columbia, Lewis and Thompson (2011) reported negligible (<1%) fall rates for *P. contorta* snags 0–6

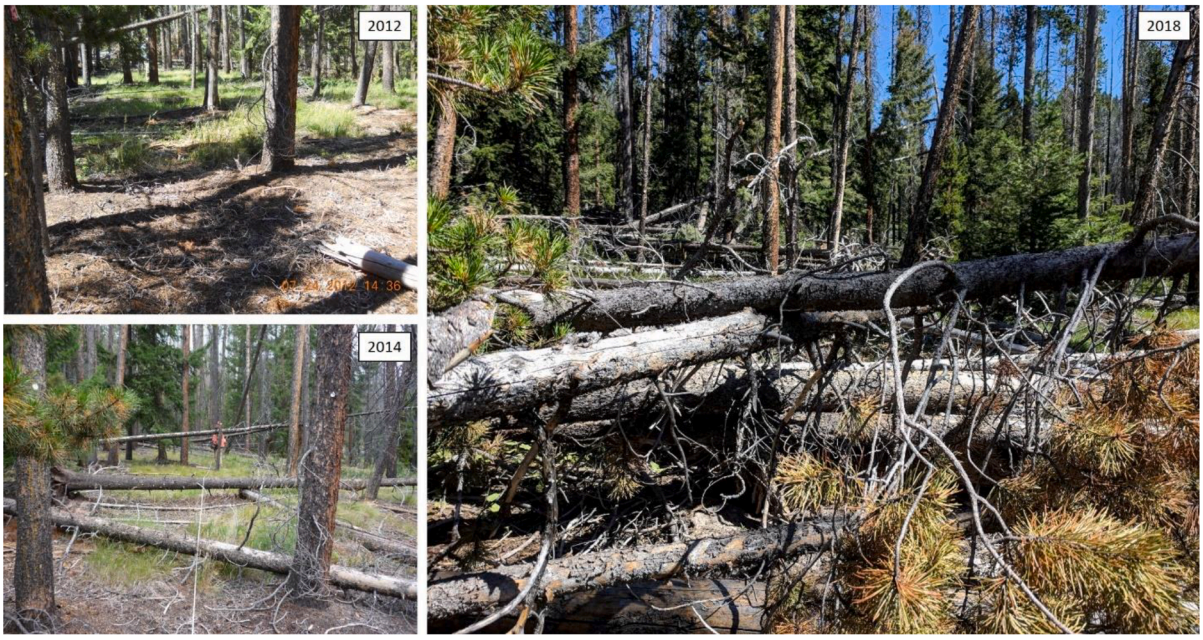

Fig. 1. Photos depicting snag fall on a plot on the Beaverhead-Deerlodge National Forest, Montana in July 2012, 2014 and 2018. Photos were taken in the same direction from the same point and represent what we consider to be an average depiction of change over time among plots. On this plot, most tree mortality occurred in 2006 (47.6% of total mortality) and 2007 (20%). Photo credits: J. Runyon, Rocky Mountain Research Station, USDA Forest Service.

YSD, and 28% for *P. contorta* snags 6–10 YSD.

During 2004–2019, we examined the causes and rates of tree mortality associated with *D. ponderosae* outbreaks in the Intermountain West based on a network of plots in Colorado, Idaho, Montana, Utah and Wyoming, U.S. The scope of our work encompasses areas where most of the tree mortality attributed to *D. ponderosae* in the U.S. occurred during this period (Fettig et al., 2020). The primary objective was to describe changes in forest conditions over time. Initial publications focused on responses of seedlings, saplings and trees (Audley et al., 2020) and of understory plants including invasive weeds (Runyon et al., 2020). Herein, we focus on the dynamics of *P. contorta* snags, including snag longevity, factors that influence snag longevity, and modeling of survival and hazard functions.

2. Materials and methods

2.1. Study area and data collection

A detailed description of study sites and data collection methods can be found in Audley et al. (2020). In brief, a network of 125 0.081-ha circular plots was established across Colorado, Idaho, Montana, Utah, and Wyoming ($n = 25$ per state) in 2010. However, 15 plots were lost to high-severity wildfires in Idaho, and three plots were lost to tree cutting in Wyoming. These 18 plots were excluded from our analyses ($N = 107$). For inclusion in the network, plots were required to be >50% *P. contorta* by basal area, and to contain a minimum of 10 *P. contorta* > 13.9 cm dbh with evidence of at least two of these trees being colonized and/or killed by *D. ponderosae* within the last three years. Plots meeting these criteria were randomly selected in groups of five, with ≥ 100 m separating plots within each group. Groups within each state were separated by > 1.6 km (mean distance ± SEM = 23.4 ± 3.0 km). Following plot establishment, all trees ≥ 7.62 cm diameter at breast height (dbh, 1.37 m in height) were tagged and the species, dbh, total height, status (live or dead), causal agent of mortality (when applicable), and year of death (when applicable) were recorded. For trees that died prior to plot establishment in 2010, year of death was estimated based on the color of faded needles in the crown and degree of needle and twig retention (i.e., 1 year prior, > 90% retention of yellow and/or red needles; 2 years prior, ≥ 50–90% retention of red needles; 3 years prior, < 50% retention of red needles; 4 years prior, no needle retention but small and large (5–7.62 cm diameter) twigs remain; 5 years prior, only large twigs remain; 6 years prior, both small and large twigs no longer remain) (Audley et al., 2020). For purposes of this study, we focused only on *P. contorta* snags killed by bark beetles, which represented 74.2% of all tree deaths observed (all tree species and causes; Audley et al., 2020). Plots were surveyed annually through 2019, and the status (standing or fallen) of each snag was updated annually. The year of snag fall was attributed to the year of discovery during surveys executed in summer (June-September). Snags were only considered fallen when broken below 1.37 m in height or tipped over (i.e., with some roots and soil intact). In 2014, we also recorded the presence or absence of checks (cracks > 7 mm in width, the thickness of a #2 pencil) on the boles of snags at 1.37 m and 5.5 m in height based on ocular estimates from the ground. In some cases, an individual check was long enough to be recorded at both 1.37 m and 5.5 m in height.

Elevation, slope, and slope aspect were measured for each plot and attributed to each individual snag within the plot. Slope aspects were measured in degrees and converted to cardinal directions (N = 316–45°, E = 46–135°, S = 136–225°, W = 226–315°) and treated as a categorical variable in our models. In addition, latitude was determined for each cluster of five plots within each state. Finally, tree density (number of live trees/ha) and canopy cover (%) were calculated for each plot. Canopy cover was measured at plot center and at 4.5, 9, and 13.5 m from plot center along three fuels transects (Audley et al., 2020), resulting in 10 measurements per plot. The 10 measurements in each plot were averaged to determine mean canopy cover per plot. A summary of covariates of interest is provided in Table 1.

2.2. Pinus contorta snag fall rate modeling

We modeled the fall rate of *P. contorta* snags killed by bark beetles by fitting a Cox's proportional-hazards model to the data. We selected the Cox's proportional-hazards model for its ability to measure the effect of multiple factors (covariates) on survival (snag longevity) simultaneously, while not being constrained to a parametric probability distribution (Cox, 1972; Harden and Kropko, 2018). The model is specifically expressed by the hazard function ($h(t)$):

$$h(t) = h_0(t) x \exp(b_1 x_{1p} + b_2 x_{2p} + \cdots + b_p x_p) \quad (1)$$

where t = survival time; h_0 = the baseline hazard (value when all $x_i = 0$); b_i = covariate coefficients measuring the effect size of each covariate; and x_i = covariates (explanatory variables). Covariates of interest were informed from prior snag fall modeling efforts (*see* Mitchell and Preisler, 1998; Parish et al., 2010; Rhoades et al., 2020) and included: elevation (m), latitude (°), slope aspect (categorical, N,S,E,W), slope (%), tree density (number of live trees/ha), canopy cover (%), snag dbh (cm), snag height (m), and snag height (m):dbh (m). Cox's proportional-hazards models were fit to the data using the coxph() function. Final model selection was informed by likelihood-ratio testing and concordance levels. The assumption of proportionality was assessed via inspections of residuals and proportionality tests using the cox.zph() function (Grambsch and Therneau, 1994; Bradburn et al., 2003). Kaplan-Meier estimates were also fit to the survival object for each covariate individually for visual inspections. Numerical covariates were stratified by median values and categorical covariates were stratified by category for inspection (Rickert, 2017).

We were interested in predicting *P. contorta* snag longevity beyond the observation window (i.e., the maximum YSD of snags in our study was 14). To achieve this goal, we simulated survival times based on the Cox's proportional-hazards model using the sim.survdata() function (Harden and Kropko, 2018; Kropko and Harden, 2020). This approach utilizes the covariate coefficients (hazard ratios, which provide the effect size for each covariate) from the fit model and allows the modeler to set the number of observations (N), time limit (T), and final censoring rate (censor; i.e., the expected probability of survival at T) (Kropko and Harden, 2020). Simulations were generated using parameters: N = 10000, T = 30 years, and censor = 0.01. Time limit (T) and censor values were informed from previous modeling efforts of snag dynamics following *D. ponderosae* outbreaks in central Oregon, U.S. where 90% of *P. contorta* snags fell by 12–14 YSD (Mitchell and Preisler, 1998); in northeast Utah where 77% of *P. contorta* snags fell by 20 YSD (Page and Jenkins, 2007); and in northern Colorado where all *P. contorta* snags fell by 30 YSD (J. Negrón, unpublished data). All analyses were conducted using R statistical software (3.6.3) in RStudio (1.2.5033) using the survival and coxed packages (R Core Team, 2020).

Table 1
Descriptive statistics for covariates of interest for modeling *Pinus contorta* snag fall rates in the Intermountain West, U.S.

Covariate	Mean ± SEM	Range
Elevation (m)	2434 ± 37	1919–2991
Slope (%)	16 ± 1	1–40
Latitude (°)	43.1 ± 0.04	40.6–46.2
Years since death (yr)	10.5 ± 0.04	1–14
Dbh (cm)	22.5 ± 0.11	7.6–72.1
Height (m)	16.0 ± 0.07	1.1–30.2
Height (m):dbh (m)	75.1 ± 0.37	8.7–272.7
Numbers of live trees/ha	1233.2 ± 63.3	296.5–4163.6
Canopy cover (%)	42.7 ± 0.34	0–100

3. Results and discussion

3.1. *Pinus contorta* snag fall

A total of 3789 *P. contorta* snags were monitored during this study, of which 90.2%, 5.8% and 4.0% were killed by *D. ponderosae*, pine engraver, *Ips pini* (Say), and *Pityogenes knechteli* Swaine/*Pityopthorus confertus* Swaine, respectively. Snags averaged 22.5 ± 0.1 cm dbh and 16.0 ± 0.1 m tall (Table 1). Snag ages ranged from 1 to 14 YSD in 2019. The highest number of snags (1046) were 12 YSD as across our network of plots tree mortality peaked in 2007 in all states except Colorado (2009) (Fig. 2 in Audley et al., 2020). By 2019, only 24.7% (937) of snags fell to the forest floor with the highest proportions observed for snags 4 and 7 YSD. Snags 4–8 YSD experienced > 50% fall (maximum = 73.8% at 7 YSD) whereas no other snag age class experienced > 40% snag fall except for 1 YSD (Fig. 2). It is not readily apparent from these data why a greater proportion of snags fell within these age classes. Kruskal-Wallis rank sum testing revealed significant differences in mean elevation ($\chi^2 = 153.5$, df = 13, $P < 0.001$), slope ($\chi^2 = 84.9$, df = 13, $P < 0.001$) and aspect ($\chi^2 = 49.8$, df = 13, $P < 0.001$), however, *post-hoc* multiple means comparisons did not reveal differences consistent with snag fall patterns. Differences in mean dbh by YSD classes ($\chi^2 = 172.8$, df = 13, $P < 0.001$) revealed a pattern more consistent with snag fall proportion by YSD as snags 4–8 YSD had smaller diameters than those 10–12 YSD. Tree size has been shown to influence fall rates (Parish et al., 2010; Lewis and Thompson, 2011; Rhoades et al., 2020; also *see* below).

The ages and proportions of snags that fell in our study are in general agreement with the limited data available from studies in north-central Colorado (Rhoades et al., 2020) and northeast Utah (Page and Jenkins, 2007), but differ substantially from those from a study in central Oregon (Mitchell and Preisler, 1998). Mitchell and Preisler (1998) found the half-lives of *P. contorta* killed by *D. ponderosae* in central Oregon were 8 and 9 years in thinned and unthinned stands, respectively (Mitchell and Preisler, 1998). In unthinned stands, 90% of snags fell to the forest floor by 14 YSD (Mitchell and Preisler, 1998). However, Mitchell and Preisler's results contrast with Harvey (1986) who reported that only 25% of *P. contorta* killed by *D. ponderosae* fell after 11 YSD in northeast Oregon. Our results are more consistent with snag fall rates reported from northeast Oregon.

The Cox's proportional-hazards model fit to these data included six of the covariates of interest: elevation, slope aspect, slope, canopy cover, snag height, and snag height:dbh. A likelihood ratio test (223.1 on 8 df, $P < 0.001$) and a concordance value of 0.651 suggested good fit and the proportional hazards assumption was satisfied ($\chi^2 = 11.7$, df = 8, $P = 0.16$). The survival function from the fit model (Fig. 3) indicated a gradual decline in *P. contorta* snag survival over time. In fact, the probability of a snag remaining standing (surviving) exceeded 60% even at 14 YSD. Influence of each of the covariates included in the model are described in Table 2 and in a forest plot (Fig. 4). Exponentiated coefficients > 1.0 indicated a negative influence on snag survival while those < 1.0 indicated a positive influence. In other words, as covariates with a negative influence increase in value, the probability of a snag remaining standing decreases and *vice versa*. Coefficient values of 1.0 are considered neutral. Interestingly, two of the covariates significant in the model (elevation and canopy cover) had almost neutral coefficients (Table 2, Fig. 4). Also of note, two covariates not significant in the model (slope and height:dbh, Table 2) were retained as likelihood ratio testing indicated removal of these two covariates resulted in a worse log-likelihood score.

Slope aspect was strongly correlated with snag fall rates (Fig. 4). The probability of snag fall was lower on northern facing aspects and was greater on southern facing aspects. In fact, southern facing aspects were the most important predictor for elevated fall rates in the model. Of note, there was a considerable amount of variability in the hazard ratio (i.e., effect size) for each of the aspect covariates (Fig. 4). Slope aspect has largely been ignored in previous modeling efforts of *P. contorta* snag dynamics (e.g., Mitchell and Preisler, 1998; Parish et al., 2010; Rhoades et al., 2020), despite temperature within a stand, particularly in the understory, being suggested as an important factor influencing fall rates. For example, Mitchell and Preisler (1998) attributed differences in fall rates between *P. contorta* snags in thinned and unthinned stands to higher rates of bole decay by sap-rot fungi at the base of snags in thinned stands due to higher levels of solar radiation and heat accumulation (and not to differences in wind conditions), which increased snag fall rates in thinned stands. Higher levels of solar radiation and heat accumulation generally occur on southern aspects in western U.S. forests (e.g., Hayes, 1941; Berryman et al., 2015) and similarly likely explain the increased fall rates on southern aspects due to enhanced growth of sap-rot and other wood decay fungi (Donnelly et al., 1990). It follows that increased snag longevity on northern slopes reflects cooler temperatures and

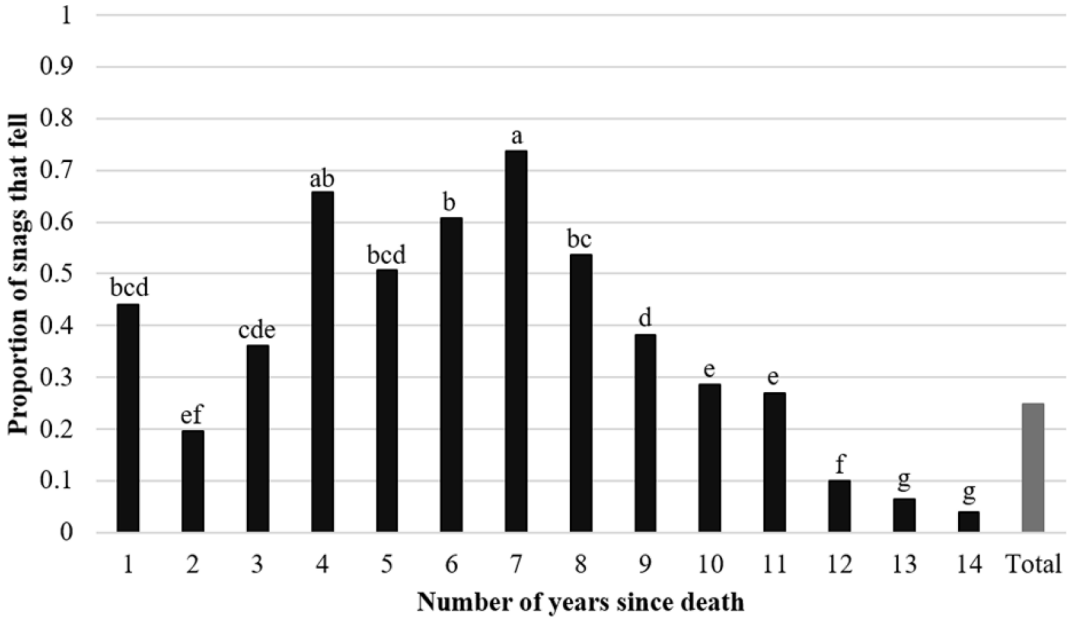

Fig. 2. Proportion of *Pinus contorta* snags within each years since death (YSD) class that have fallen. Means followed by the same letter are not significantly different ($P > 0.05$). About 24.7% of all snags (right bar, Total) fell by 2019.

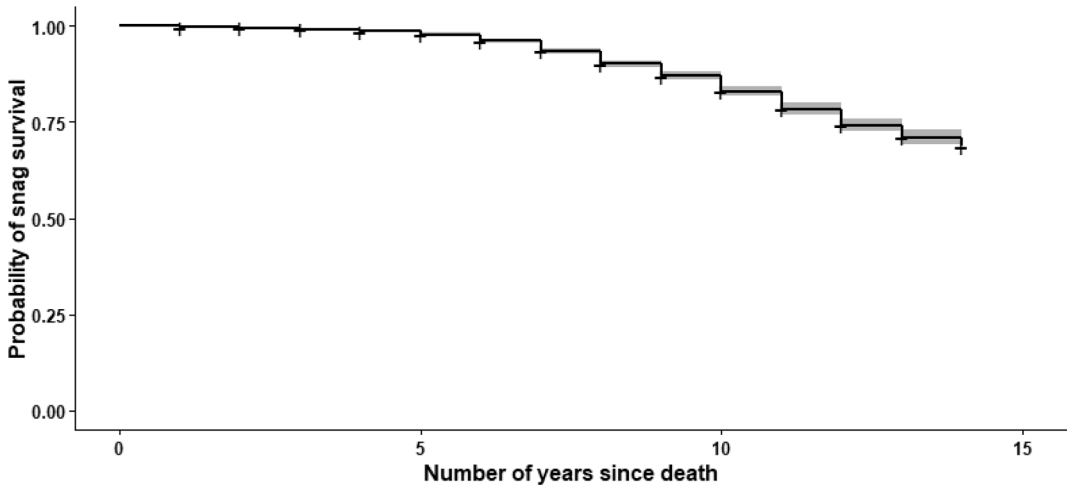

Fig. 3. Survival function from a Cox's proportional-hazards model describing the probability that *Pinus contorta* snags remain standing (i.e., "survive") based on individual snag and plot level characteristics. Final model selection was informed by likelihood-ratio testing and concordance levels. The assumption of proportionality was assessed via inspections of residuals and proportionality testing (cox.zph() fuction). Modeling was done using the coxph() function in the survival package with R statistical software (3.6.3) in RStudio (1.2.5033).

Table 2
Covariates, with corresponding coefficients, *z*-scores, and *P*-values included in the Cox's proportional-hazards model for *Pinus contorta* snag fall rates in the Intermountain West, U.S.

Covariate	Coefficient	Exp. (coef.)*	95% conf. interval	*z*	*P*
Elevation	−0.0009109	0.9991	0.9989–0.9993	−8.755	**<0.001**
Aspect E	Reference	na	na	na	na
Aspect N	−0.3496503	0.7049	0.5814–0.8547	−3.558	**<0.001**
Aspect S	0.2032215	1.2253	1.0439–1.4383	2.485	**0.013**
Aspect W	0.1800356	1.1973	0.9747–1.4707	1.716	0.086
Slope	−0.0036845	0.9963	0.9898–1.0029	−1.098	0.272
Canopy cover	−0.0096615	0.9904	0.9870–0.9938	−5.511	**<0.001**
Height	−0.0556201	0.9459	0.9303–0.9617	−6.57	**<0.001**
Height:dbh	0.0543556	1.0559	0.7493–1.4878	0.311	0.756

* Exponentiated coefficients.

reduced growth rates of sap-rot and other wood decay fungi. Northern slopes also had more live trees/ha and greater canopy cover than southern slopes (mean ± SEM): 1605.8 ± 26.9 versus 1369.9 ± 17.9 trees/ha ($\chi^2 = 16.3$, df = 1, $P < 0.001$) and 48.3 ± 0.7 versus 37.3 ± 0.6% cover ($\chi 2 = 111.8$, df = 1, $P < 0.001$), which may have had some influence (*see* below).

Snag height also influenced fall rates with taller snags having greater longevity (Fig. 4). However, unlike in other studies in Oregon, Colorado, and British Columbia (Mitchell and Preisler, 1998; Lewis and Thompson, 2011; Rhoades et al., 2020), dbh had no influence on snag fall rates in our study. This may be attributed to *P. contorta* snags in our study generally being of larger dbh (most ≥ 17.5 cm, Audley et al., 2020), and to the limited differences in dbh that occurred among YSD classes (mean ± SEM; range = 16.3 ± 1.0 to 23.5 ± 0.2 cm dbh for 2 and 12 YSD, respectively) although significant differences were observed ($\chi^2 = 172.8$, df = 13, $P < 0.001$). Even though dbh did not prove to be a significant explanatory covariate, the influence of snag height is likely

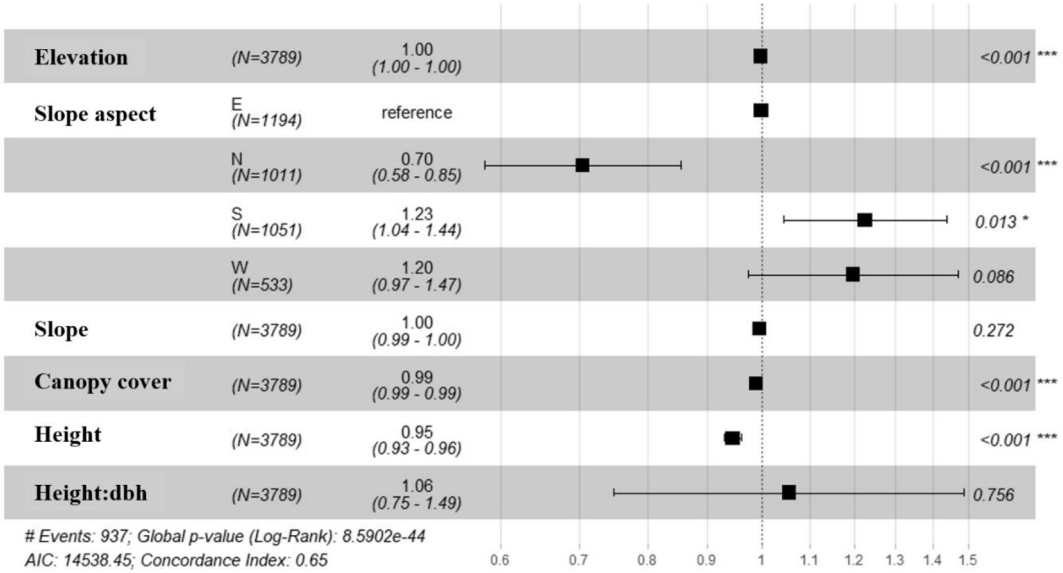

Fig. 4. Forest plot depicting covariate influences on *Pinus contorta* snag survival from a fit Cox's proportional-hazards model. Hazard ratios (black boxes) that are < 1.0 indicate that as the value of the covariate increases, the probability of a snag surviving (not falling) increases. The opposite is true of hazard ratios that are > 1.0. Values of 1.0 have a neutral influence. Bars around hazard ratios represent 95% confidence intervals.

representative of the same underlying principle supported by previous investigations of snag longevity – that larger snags remain longer (Parish et al., 2010; Lewis and Thompson, 2011; Rhoades et al., 2020). This is further supported by the negative influence of snag height:dbh on snag longevity. While not a statistically significant covariate in the model (Fig. 4, Table 2), the hazard ratio of 1.06 indicates that as height:dbh increases in value (i.e., taller, skinner snags) the less likely a snag remains standing. It appears that the influence of height:dbh was variable across most of the observed ratios. In other words, we observed snags falling and remaining standing across much of the height:dbh spectrum. This is reflected in the wide 95% confidence interval (Fig. 4).

Canopy cover explained snag fall rates better than tree density (live trees/ha) and was significant in our final model (Table 2; Fig. 4). Interestingly, the hazard ratio for canopy cover was just below neutral (0.99), indicating that as canopy cover increases the probability of snag fall decreases, though only slightly. Rhoades et al. (2020) reported increased snag fall rates as the density of *P. contorta* increased in north-central Colorado, but this differs from results of Mitchell and Preisler (1998) in central Oregon who found snags fell ~2 years later in unthinned stands compared to thinned stands. Although temperatures were not measured in our study, the moderating influence of tree cover on surface temperature is well documented (e.g., Ziter et al., 2019) and likely provides a better correlate for surface temperature than number of trees/ha, as trees vary in size and the amount of canopy cover provided. As canopy cover decreases, surface temperature increases (Redding et al., 2003) increasing growth of sap-rot and other decay fungi at the base of snags (Donnelly et al., 1990). It appears that as more light penetrates the canopy *P. contorta* snag longevity decreases.

Wind may also play a role in snag longevity. Rhoades et al. (2020) reported that the stems of nearly half of fallen snags in their study were aligned with the prevailing wind direction, suggesting that wind may have been a contributing factor in snag failure. Mitchell and Preisler (1998) also considered increased wind speeds in thinned stands, as compared to unthinned stands, as a possible explanation for decreased snag longevity in thinned stands. Yet in both studies, the authors concluded that increased growth of sap-rot and other wood decay fungi was equally, if not more importantly, contributing to snag fall. Although not statistically significant, higher snag fall rates tended to occur on western aspects (Fig. 3). While our plot network represents a large geographic area of complex topography, prevailing winds are generally from the southwest and west (Western Regional Climate Center, 2016).

The hazard ratio for elevation was neutral (Table 2, Fig. 4) despite being significant in our model suggesting that there was not a clear relationship between elevation and snag fall. Conversely, Rhoades et al. (2020) reported slower rates of snag fall at high elevations compared to low elevations when comparing the fall rates they observed in north-central Colorado with those from several other studies including Harvey (1986), Mitchell and Preisler (1998) and Page and Jenkins (2007), among others. It may be that the large latitudinal gradient of our study (40.6–46.2°) mitigated the influence of elevation, as mean plot elevation decreased with latitude in our study (Audley et al., 2020).

3.2. Simulated Pinus contorta snag fall

To predict snag fall rates beyond 14 YSD (maximum YSD in our study) a survival curve was generated from 10000 simulated observations (Fig. 5). The shape of the first 14 YSD of the simulated survival function differed from that of the survival function fit to the observed data predominantly during 6–12 YSD (Figs. 2 and 4). Simulated data predicted a sharp decline in survival probability for snags 6–7 YSD. Survival probability decreased from just below 1.0 to approximately 0.68, followed by a plateau until 12 YSD (Fig. 5). Conversely, the survival function fit to the observed data shows a more gradual decline, not reaching the 0.75 probability threshold until ~12 YSD (Fig. 3). From the simulated survival function, we found the predicted half-life of beetle-killed *P. contorta* snags was ~16 YSD. After which, the function predicts a linear ~0.04/year decline in snag survival probability 15–30 YSD. Our model predicts that ~37% of snags will remain at 20 YSD (Fig. 5), which agrees with data based on stand reconstructions from the Ashley National Forest in northeast Utah where 33% of *P. contorta* snags

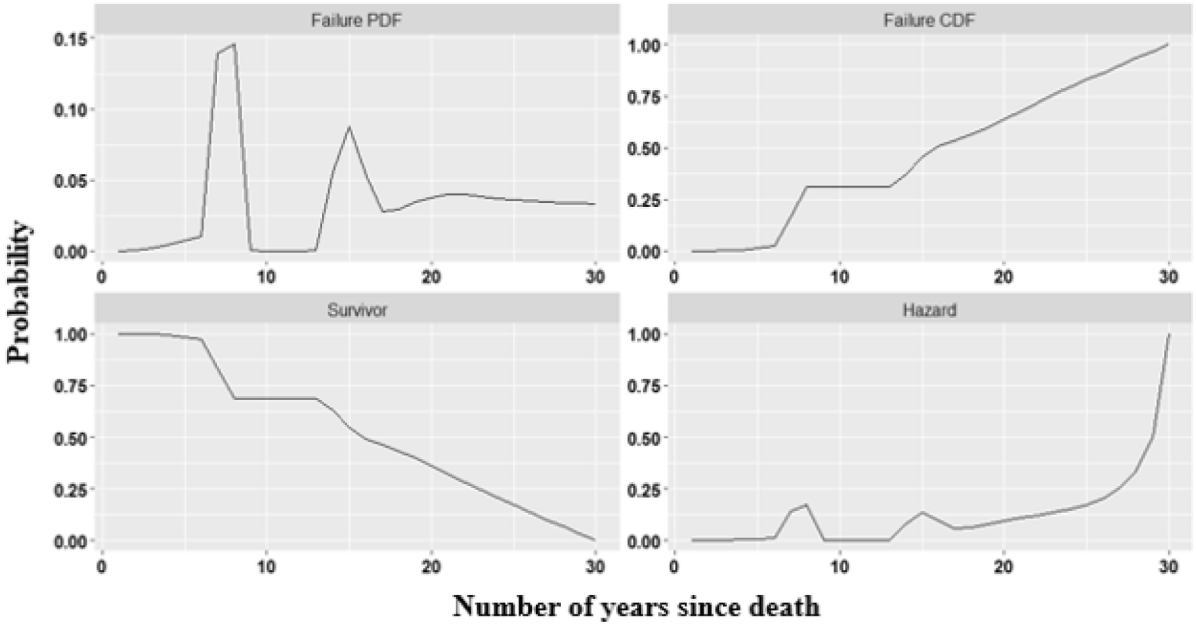

Fig. 5. Baseline functions for *Pinus contorta* snag simulated data. Data were simulated from the Cox's proportional-hazards model covariate coefficients (hazard ratios). A total of 10000 observations were generated. A final censoring rate of 0.01 after 30 years (snag age, YSD) was used and based on previous modeling efforts of *P. contorta* snag dynamics from the literature. Resulting baseline functions include the probability density function (PDF), cumulative distribution function (CDF), survival function, and hazard function. The PDF and CDF describe the probabilities drawn from for generating the random data points. The survival function describes the probability a snag remains standing and the hazard function describes the probability of failure (i.e., a snag falling) for a given time point. Data were simulated using the sim.survdata() function from the coxed package using R statistical software (3.6.3) in RStudio (1.2.5033).

remained at 20 YSD following a different (earlier) *D. ponderosae* outbreak (Page and Jenkins, 2007).

The hazard function for the simulated data predicted a low (near zero) probability of failure for snags 1–15 YSD, with the exception of two spikes. The first occurred 5–9 YSD, with the peak at ~7 YSD (Fig. 5). Similarly, we observed a peak in the proportion of snags that fell 7 YSD (Fig. 2). A second peak occurred at ~15 YSD, however, unlike with the first spike, the predicted probability of failure did not return to near zero (Fig. 5). The simulated hazard function then follows an approximately exponential increase in the probability of snag failure beginning at ~20 YSD.

3.3. Checking

As wood dries, it initially releases free water not bound in cells until it reaches the fiber saturation point, and then begins to lose water bound to the cellulose molecules in the cell walls. As water is drawn from the cell walls shrinking occurs causing checks to develop in the wood. Chow and Obermajer (2007) reported the average moisture content of sapwood in live *P. contorta* was ~140% but drops to 28–34% within a few years of tree death. In our study, snags < 1 YSD (i.e., trees that died the year assessments for checks were made) had no checks (Table 3). However, the proportion of snags with checks rapidly increased with YSD, and many snags 6 YSD or older had at least one check (Table 3). Similarly, Magnussen and Harrison (2008) reported the proportion of *P. contorta* snags without checks declines sharply at a rate of ~25% per year after 1 YSD in British Columbia. Lewis and Hartley (2006) reported the depth of checks was greatest at ~1.37 m in height where the effect of moisture absorption from the ground disappeared.

Sap-rot and other decay fungi and wood boring insects may also affect wood quality in *P. contorta* snags (Lewis and Hartley, 2006; Lewis and Thompson, 2011). Our anecdotal observations of wood decay were negligible and localized to the base of snags, where moisture content is highest (Lewis and Hartley, 2006; Chow and Obermajer, 2007). This is why most *P. contorta* snags fail (break) at the root collar (Rhoades et al., 2020), which we also observed in our study. Bluestain fungi are inoculated into *P. contorta* upon colonization by *D. ponderosae* and other species of bark beetles. While this causes blue pigmentation of the wood, it does not affect snag longevity or suitability of the wood for service as structural lumber (Lum et al., 2006). Within 1 YSD, blue-stained wood volumes reach maximum levels due to rapid declines in sapwood moisture content (Kim et al., 2008).

4. Conclusions

Beetle-killed snags in *P. contorta* forests in the Intermountain West can last for several decades following *D. ponderosae* outbreaks. Our modeling suggests, barring stochastic events such as windstorms and wildfire, ~50% will last 16 years (YSD) and ~ 25% will last 22 years (Fig. 5). Such snag longevity confers important wildlife benefits and may offer opportunities for salvage years after a *D. ponderosae* outbreak has occurred (Figs. 2 and 5). However, checking rapidly occurs in *P. contorta* snags, and by 6 YSD most snags are likely to have at least one check which can negatively impact lumber recovery for certain wood products (Plank, 1984; Table 3). At the same time, the relatively slow snag fall rates observed in our study will likely lengthen concerns regarding hazard trees, human safety, and protection of critical infrastructure.

Snag fall occurred in every snag age class, with the highest proportions occurring at 4 and 7 YSD (Fig. 2). Among snag age classes, the highest number of snags are 12 YSD, which agrees with peak levels of tree mortality attributed to *D. ponderosae* in 2007 (Fig. 2 in Audley et al., 2020). Snags 13 and 14 YSD exhibited the lowest fall rates (<10%, Fig. 2). As an outbreak develops, *D. ponderosae* initially colonizes and kills the largest *P. contorta* (Shepherd, 1966; Rasmussen, 1972), with progressively smaller *P. contorta* being colonized over time (Klein et al., 1978) as the proportion of larger trees declines. Snags 12–14 YSD were created during the beginning and peak of the *D. ponderosae* outbreak, and as a result are larger than snags < 12 YSD (mean ± SEM; snags 12–14 YSD = 23.0 ± 0.2 cm dbh, snags < 12 YSD = 22.0 ± 0.2 cm dbh; $\chi^2 = 16.3$, $df = 1$, $P < 0.001$). At the same time, these snags are the most desirable for wildlife and salvage, but perhaps exhibit greater safety concerns in sites where forest users or critical infrastructure could be impacted due simply to their larger sizes. In conclusion, there is less concern with *P. contorta* snag failures during the first several years following a *D. ponderosae* outbreak (Fig. 1, 2012) as the snags created during this time tend to last the longest (Fig. 2). However, failures can happen 1 YSD and *P. contorta* snags in recreational areas and other high-use sites should be mitigated promptly (Guyon et al., 2017). Overall, managers should expect reduced longevities for smaller snags, snags on southern slope aspects, and snags in stands of reduced canopy cover. The latter suggests that the severity of a *D. ponderosae* outbreak (e.g., based on canopy cover loss) directly influences *P. contorta* snag fall rates, with higher severities (tree losses) resulting in lower snag longevities. The effect is most likely mediated through enhanced solar radiation and surface heat accumulation that influence the growth rate of sap-rot and other decay fungi at the base of snags.

Table 3
Percentage of *Pinus contorta* snags with at least one check at 1.37 m and 5.5 m in height in *P. contorta* forests in the Intermountain West, U.S.

Years since death (YSD)	1.37 m	5.5 m
<1	0%	0%
1–2	27.9%	18.6%
3–5	59.7%	49.2%
≥ 6	65.7%	59.9%

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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