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Snag persistence rates and patterns following mountain pine beetle epidemic in the Elkhorn Mountains, Montana, USA

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A B S T R A C T

Bark beetle (*Dendroctonus* spp.) epidemics generate snags, providing nesting and foraging opportunities for woodpeckers and other disturbance-associated wildlife. Forest managers need to know how long snags persist to include wildlife habitat conservation in their objectives, but published studies of snag persistence following disturbance under-represent beetle-killed forest. We analyzed snag persistence rates in relation to environmental covariates following a mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the Elkhorn Mountains (Montana, U.S.A.) over a 6-year study period (2010–2015). We evaluated hypothesized relationships with topography, local tree density, and snag characteristics. Consistent with our hypotheses, we found snags with greater diameter at breast height (DBH), younger snags, and broken-top snags persisted relatively long. Also consistent with our hypotheses, snags located in areas of relatively rugged topography and greater tree densities persisted longer. Moreover, we estimated a diameter-height ratio ≥ 4.8 cm $\times$ m^{-1} as a useful threshold for distinguishing broken-top snags likely to persist longer than other snags. Greater snag persistence on north-facing slopes and on topographic high points were inconsistent with our hypotheses, suggesting these conditions may be less useful for understanding snag dynamics. Our study contributes to general knowledge capable of helping managers identify snags most likely to persist and thereby provide extended habitat value for nesting woodpeckers.

1. Introduction

Snags provide critical habitat features for many forest vertebrate species (Raphael and White, 1984; Bull et al., 1997a; Martin and Eadie, 1999; Saab et al., 2014). In particular, woodpeckers (Picidae) use snags for both nesting and foraging, and other species subsequently use cavities initially excavated by nesting woodpeckers (e.g., Martin and Eadie, 1999; Drever et al., 2008). Large-scale disturbances, such as wildfire and bark beetle (Curculionidae) epidemics, generate numerous snags that provide nesting and foraging opportunities for many woodpeckers in lower elevation dry forests of western North America. Human activities in these forests impact habitat for woodpeckers both by altering the timing and frequency of disturbance and by impacting snag resources following disturbance (e.g., Russell et al., 2006; Saab et al., 2009; Saab et al., 2011; Audley et al., 2021). Given these various impacts and the importance of woodpeckers for other species, management plans for recently disturbed forests commonly include habitat conservation objectives (United States Department of Agriculture (USDA), 2012).

In disturbed forests, salvage logging can diminish woodpecker habitat. Salvage logging provides economic and safety benefits by obtaining lumber value and removing hazardous snags along areas of concentrated human traffic such as roads (e.g., Audley et al., 2021). Snag removal, however, negatively impacts wildlife habitat (Lindenmayer and Noss, 2006). Several studies examine habitat and snag use patterns by woodpeckers, which are needed to identify habitat for conservation (Hutto and Gallo, 2006; Saab et al., 2007, 2009, 2011; Vierling et al., 2008). Snag persistence studies following large-scale disturbance are also needed to help forest managers identify snags likely to provide maximum habitat value for as long as possible (Russell et al., 2006; Saab et al., 2014; Audley et al., 2021).

Wildfire and bark beetle disturbance generate opportunities and conflicts for woodpecker habitat needs and salvage logging. The ecological processes influencing habitats generated by these disturbance types overlap somewhat but also differ substantially. Both increase snag densities, but wildfire affects all trees whereas bark beetles are host-tree specific. Additionally, wildfire initially reduces understory vegetation, but frequently and shortly after benefits understory growth by opening the canopy and stimulating nutrient cycling (e.g., Certini, 2005). In

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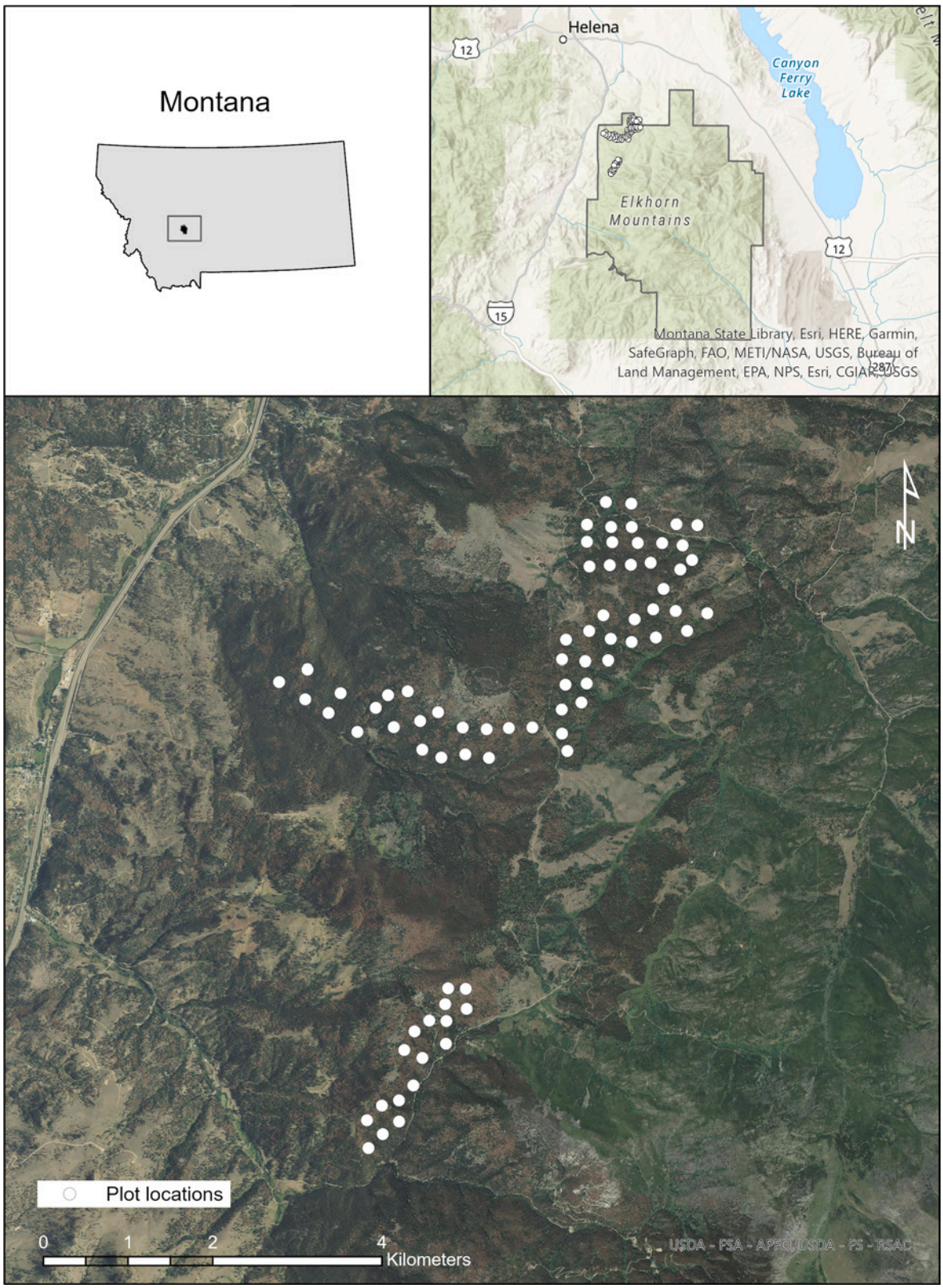

Fig. 1. Study area and plots ($n = 75$) located within the Elkhorns Wildlife Management Unit, Helena National Forest, Montana, U.S.A., where pine (*Pinus* spp.) snags were monitored following the 2008 mountain pine beetle (*Dendroctonus ponderosae*) epidemic.

contrast, bark beetles only attack trees, which often benefits understory vegetation, although these benefits arise over a more extended period following onset of disturbance (>6 years; Stone and Wolfe, 1996; Page and Jenkins, 2007; Jenkins et al., 2008). Habitats generated by wildfire and bark beetle epidemics attract many of the same woodpecker species but differ for two species in particular. Black-backed woodpeckers (*Picoides arcticus*) tend to favor burned forests, where they specialize on consuming larvae of wood-boring beetles (Buprestidae and

Table 1
Number of pine trees that were tagged and monitored by status and species in the Elkhorns Wildlife Management Unit, Helena National Forest, Montana, U.S.A. Pine species monitored were ponderosa pine (*Pinus ponderosa*) and lodgepole pine (*P. contorta*). Tagged individuals were first measured before mountain pine beetle epidemic (2002–2003), and then re-measured post-epidemic (2010–2015). Parenthetic values are the percent of the total by species in each status class (live, snag, fallen). The total number of snags represented in each year (row 2–7 sums) do not exactly match the original sample (row 1 sum) due to a small number of missed status checks and lost tags.

Year	Ponderosa pine *n* (%)			Lodgepole pine *n* (%)		
	live	snag	fallen	live	snag	fallen
2002–2003	1103 (100)	0 (0)	0 (0)	185 (100)	0 (0)	0 (0)
2010	95 (9)	988 (90)	1 (0)	4 (2)	172 (93)	4 (2)
2011	9 (1)	1060 (96)	33 (3)	4 (2)	170 (92)	11 (6)
2012	2 (0)	1017 (92)	84 (8)	2 (1)	162 (88)	21 (11)
2013	2 (0)	932 (84)	169 (15)	1 (1)	152 (82)	32 (17)
2014	0 (0)	811 (74)	290 (26)	1 (1)	134 (72)	50 (27)
2015	0 (0)	660 (60)	440 (40)	0 (0)	114 (62)	69 (37)

Cerambycidae) (Tremblay et al., 2020a); whereas American three-toed woodpeckers (*P. dorsalis*) associate more with beetle-killed forests where they specialize on the feeding of bark-beetle larvae (Tremblay et al., 2020). Of the few studies measuring post-disturbance snag persistence, a majority focus on burned forests (Everett et al., 1999; Chambers and Mast, 2005; Russell et al., 2006; Angers et al., 2011; Ritchie et al., 2013; Grayson et al., 2019) whereas fewer examine snag dynamics in beetle-killed forests (Mitchell and Preisler, 1998; Lewis and Hartley, 2006; Rhoades et al., 2020). Additionally, only a subset of these studies measure environmental relationships with snag persistence potentially useful for informing salvage logging prescriptions (Russell et al., 2006; Chambers and Mast, 2014; Grayson et al., 2019; Rhoades et al., 2020).

We studied snag persistence following a mountain pine beetle (*Dendroctonus ponderosae*) epidemic in a dry mixed conifer forest in Montana, U.S.A. We estimated snag persistence rates and covariate relationships while accounting for additional spatial and temporal heterogeneity using hierarchical modeling. We considered covariates describing topography, local tree density, and snag characteristics hypothesized in the literature as potentially important factors influencing snag persistence. We used our results to inform post-disturbance snag dynamics in the context of forest management with considerations for woodpecker habitat conservation.

2. Materials and methods

2.1. Study area

We monitored snags following a mountain pine beetle (MPB) epidemic in the Elkhorns Wildlife Management Unit of the Helena National Forest, Montana, U.S.A. (1,500 m to 1,700 m elevation; 46°46′ N, 111°91′W). The epidemic killed ~ 90% of ponderosa (*Pinus ponderosa*) and lodgepole (*P. contorta*) pine trees over > 445,000 ha in 2006–2010 (Crabb and Stoner, 2011). Annual pine tree mortality was highest in 2008 and declined in subsequent years. Prior to the epidemic, the canopy was dominated by ponderosa pine, Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine. Predominant understory plant species included snowberry (*Symphoricarpos albus)*, Oregon grape (*Berberis repens*), and kinnickinnick (*Arctostaphylos uva-ursi*).

We originally established study units and plots to monitor forest bird community responses to prescribed fire. Elevation at study plots ranged 1446–1740 m. Pre-treatment monitoring and vegetation measurements occurred in 2002–2006, but litigation prevented treatment implementation and data collection was suspended. Meanwhile a mountain pine beetle infestation began in the Helena National Forest during 2006, peaked in 2008, and continued through 2009–2011, when beetle-caused tree mortality declined as the epidemic slowed. The MPB epidemic provided an opportunity to study both bird responses (Mosher et al., 2019; Saab et al., 2019) and snag persistence (this study).

Table 2
Covariates considered in analysis of snag persistence following a mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the Elkhorns Wildlife Management Unit, Helena National Forest, Montana, U.S.A.

Covariate (abbrev.)	*k*	Type	Description	Predicted relationship with persistence
Surface Area Ratio (SAR)	1	remote-sensed, plot level	index of topographic roughness. Surface area divided by planimetric area within 50 m radius neighborhood.	negative
Aspect (CASP, SASP)	2	remote-sensed, plot level	orientation of slope for plots with > 2% slope. Separated into sine- and cosine-transformed components prior to analysis (50 m radius neighborhood mean)	negative on west-facing slopes (direction of prevailing winds)
topographic position index (TP)	1	remote-sensed, plot level	elevation minus mean elevation within 200-m radius circle (50 m radius neighborhood mean)	negative
Tree density (TD)	1	field-collected, plot level	Number of trees and snags (height > 1.4 m) standing within 20 × 200-m plot	positive
Snag diameter (DBH)	1	field-collected, snag level	Diameter at breast (1.4 m) height (cm)	positive
Diameter-height ratio (DHR)	1	field-collected, snag level	Snag diameter (DBH) divided by height (cm × m^{-1})	positive
Snag species (SPP)	1	field-collected, snag level	Species (0 = ponderosa pine, 1 = lodgepole pine)	none
Years since mortality index (YSMI)	1	time-varying	Number of years since active monitoring began for a given snag. Monitoring was initiated in 2010 ($YSMI_{2010} = 0$) for 92% of snags and in 2011–2015 remaining snags.	negative

2.2. Field surveys

We monitored snags at 75 plots distributed across 4 133–269 ha study units (17–20 plots per unit; Fig. 1). Each plot consisted of 2 100-m perpendicular belt transects centered on a point located randomly within study unit boundaries. Plots were spaced ≥ 180 m from each other. Study units and plots were established to study prescribed fire effects on bird populations, communities, and habitats. In conjunction with bird habitat measurements, we measured all large live trees ≥ 23 cm DBH (diameter at 1.4 m above ground) within 3 m of transect centerlines in 2002–2003. We then returned in 2010 to re-measure and mark each tree with a uniquely numbered tag (verifying identity based on DBH, height, species, and location within plots) and initiated annual

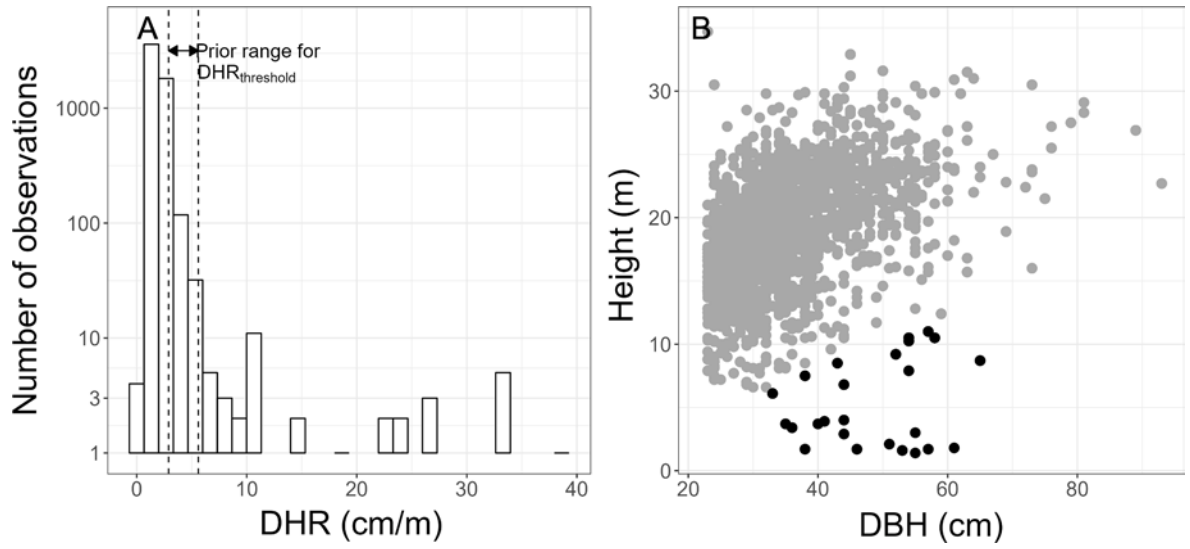

Fig. 2. Distribution of annual observations of tagged snags along diameter-height ratio (DHR) gradient (A) and with respect to diameter at breast height (DBH) and height (B) in the Elkhorns Wildlife Management Unit, Helena National Forest, Montana, U.S.A. Panel A also shows the prior distribution for estimating a threshold distinguishing higher-DHR snags with greater persistence from lower-DHR snags that persisted at lower rates. Panel B distinguishes observations above (black) versus below (gray) the posterior median estimate for the DHR threshold (4.796 cm × m^{-1}).

Table 3
Parameter estimates for pine snag persistence model following a mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the Elkhorns Wildlife Management Unit, Helena National Forest, Montana (for full variable names and descriptions, see Table 2). Except for YSMI and SPP, covariates were standardized (*z*-scored) prior to model fitting. P_{period} = estimated persistence at average conditions (mean covariate values) for 2010–2015 at an average plot, a low-persistence plot (2.5th percentile), and a high-persistence plot (97.5th percentile).

Parameter	Posterior estimates		
	median	2.5 %-ile	97.5 %-ile
$\overline{\beta_0}$	3.756	3.476	4.052
$SD(\beta_0)$	0.589	0.428	0.790
β_{SAR}*	0.221	0.015	0.423
β_{SASP}	−0.097	−0.289	0.086
β_{CASP}*	0.222	0.026	0.423
β_{TP}*	0.176	0.000	0.355
β_{TD}	0.084	−0.090	0.262
β_{YSMI}*	−0.608	−0.691	−0.531
β_{SPP}*	0.417	0.000	0.845
β_{dbh}*	0.184	0.072	0.299
β_{DHR}*	2.573	0.781	5.889
$DHR_{threshold}$ [a]	1.656	1.417	1.957
$P_{period,average}$	0.599	0.543	0.651
$P_{period,low}$	0.244	0.136	0.348
$P_{period,high}$	0.843	0.784	0.897

*statistically supported covariate relationships (Bayesian $p > 0.95$ or $p < 0.05$).
[a]The unstandardized posterior median estimate for $DHR_{threshold}$ = 4.986 (95% BCI: 4.563, 5.515) cm × m^{-1}.

monitoring of marked individuals, most of which were killed (i.e., no green needles) but remained standing when we began monitoring (Table 1). We focused on monitoring relatively large snags (DBH ≥ 23 cm) because these are typically the minimum diameter for nesting woodpeckers (e.g., Bull et al., 1997b; Saab et al., 2019). We recorded species, height (m; measured with a laser hypsometer or clinometer), and DBH in 2002–2003. After tagging and recording initial status (live, snag, or fallen) in 2010, we revisited individuals and recorded their status once each year in 2011–2015, i.e., from 2 to 7 years after the peak in beetle-caused tree mortality. We considered a snag fallen when uprooted, broken to a height < 1.4 m, or when oriented ≤ 45° from the ground. We also recorded new heights each year whenever changes occurred, and thus tracked heights for snags that broke above 1.4 m but remained standing (i.e., broken-top snags).

Although we tagged and monitored both live trees and snags, most pine trees had died by 2010 when we initiated active monitoring (Table 1). Pine snags were relatively rare prior to the epidemic and all tagged individuals were verified alive prior to the epidemic (2002–2003), so we assumed all tagged pine snags monitored in this study were killed by MPB.

2.3. Environmental data and snag characteristics

We compiled remotely sensed and field-measured variables describing characteristics of plots and individual snags hypothesized to influence snag standing rates (Table 2; e.g., Russell et al., 2006; Hollenbeck et al., 2013; Chambers and Mast, 2014; Rhoades et al., 2020). In general, we expected snag persistence to vary with snag structural integrity and exposure to wind, a major proximate agent of snag falls. We expected less exposure to wind and therefore predicted higher persistence rates for snags in plots with rough terrain, negative topographic position (i.e., plot elevation below the mean elevation for a 200-m neighborhood centered on the plot), and greater tree density (see Table 2 for predictions). We counted all trees within 10 m of belt transect centerlines (tagged and untagged; note the greater 20 m plot width for counting trees here compared to the narrower 6 m width for tagging and monitoring individual snags described above) twice during the post-epidemic study period (2010 and 2012), and scaled counts as the number of trees and snags per ha for each plot to represent densities. We also expected lower snag persistence rates for plots with west-facing slopes because winds were predominantly westerly at our study area.

Structural integrity increases with snag diameter (DBH), so we predicted persistence would relate positively with DBH (Table 2). We expected taller snags to be more prone to wind. Taller snags tend to also have larger diameter trunks (height correlates positively with DBH; Temesgen and Gadow, 2004), but broken-top snags deviate from the typical DBH-height relationship. We expected elevated persistence rates for larger-diameter but shorter broken-top snags compared to relatively intact snags. We did not reliably record top condition (broken or intact) in the field, so we relied on DBH-height ratios (DHR; Table 2) to distinguish broken-top snags aberrant DHR values from the remainder of the population. Specifically, we designed our analysis to estimate an optimal DHR threshold for distinguishing broken-top (higher DHR) from intact (lower DHR) snags differing in persistence rates (described further

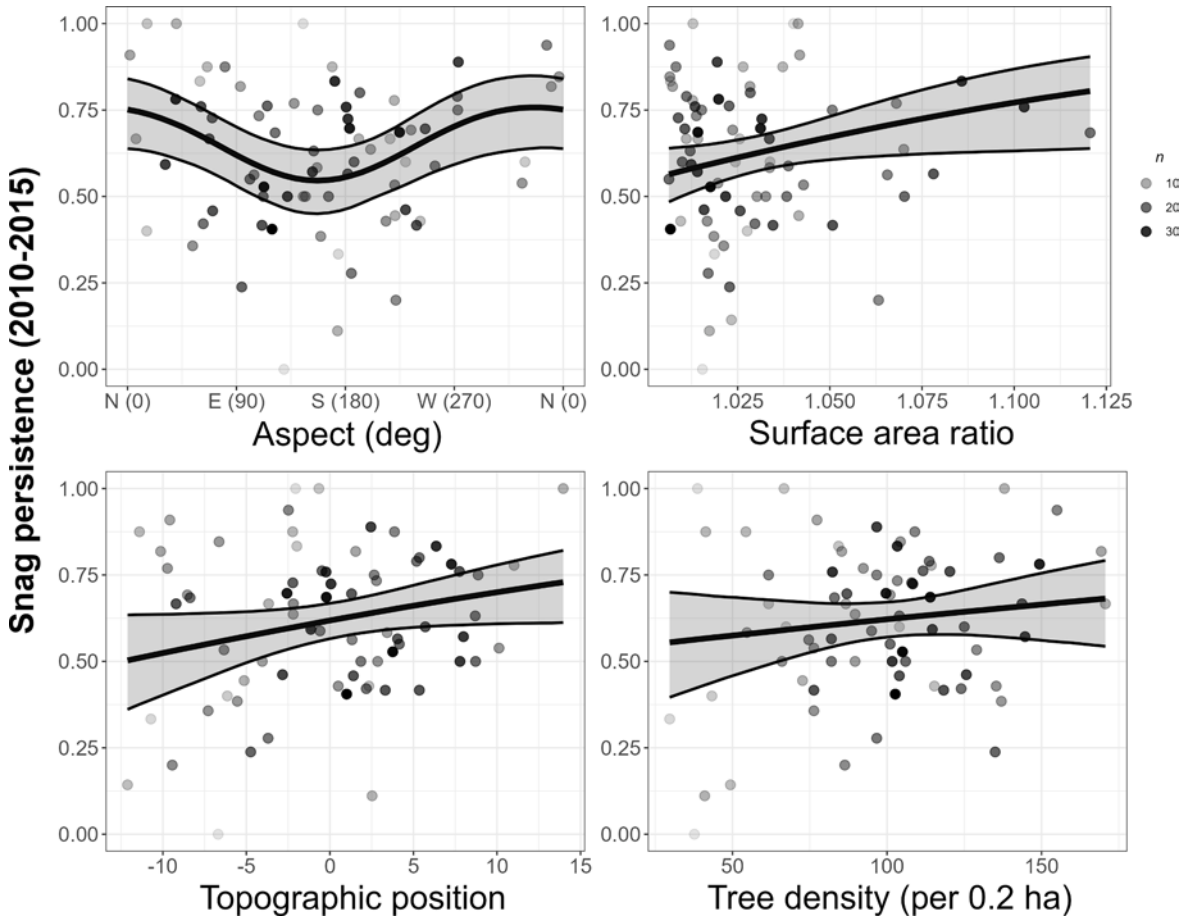

Fig. 3. Snag persistence in relation to plot characteristics following mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the Elkhorns Wildlife Management Unit, Helena National Forest, Montana, U.S.A., from 2 to 7 years after the peak of beetle-caused tree mortality. Lines and error bands represent posterior median and 95% credible predictions for persistence over the 6-year study period. Dots represent plot-level observations of the proportion of snags that persisted, with shading representing sample size (the number of snags monitored).

below). Finally, we expected structural integrity to decline with progression of the decay process, and so persistence rates to decline with years since mortality. Because active monitoring began in 2010, two years after peak tree mortality, we did not know the exact timing of mortality for most snags, so we used the number of years since initiating monitoring to approximately index years since mortality. Thus, we assigned years since mortality index (YSMI) = 0 to most snags when first recorded in 2010 ($n = 1160$) and YSMI = 0 to remaining snags ($n = 100$) when first observed (i.e., year following tree mortality).

2.4. Data analysis

We analyzed annual snag persistence rates using a hierarchical survival model. Our data described a binomial outcome (persistent = 1, fallen = 0) for each status check following year-long observation intervals. We related the annual probability of persistence with covariates using a logit-link function. Snags were nested within plots, so persistence probability was subject to a plot-specific random effect along with covariate relationships. Our model described relationships with 9 covariates (Table 2):

$$logit(P_{ijt}) = \beta_{0,j} + \beta_{SAR} \times SAR_j + \beta_{SASP} \times SASP_j + \beta_{CASP} \times CASP_j + \beta_{TP} \times TP_j + \beta_{TD} \times TD_j + \beta_{Age} \times Age_t + \beta_{SPP} \times SPP_i + \beta_{DBH} \times DBH_i + \beta_{DHR} \times \frac{max(0, DHR_i - DHR_{threshold})}{DHR_i - DHR_{threshold}}$$

wherein P_{ijt} is the annual persistence probability for snag i in plot j during year t, $\beta_{0,j}$ is the intercept subject to a plot-specific normal random effect, β_{DHR} is a threshold effect of diameter-height ratio (DHR), $DHR_{threshold}$ is the threshold above which β_{DHR} is applied, and remaining β are logit-linear effects of all other covariates (Table 2). Covariates were at most moderately correlated with each other (max $|r| = 0.39$).

We modeled DHR's relationship with snag persistence as a threshold effect to estimate the difference in persistence probability between two distinct classes of snags: 1) broken-top snags with aberrantly high DHR values versus 2) relatively intact snags. We were interested in distinguishing these two categories primarily in so far as they differed in persistence sufficiently to inform habitat conservation. Therefore, we considered both the distribution of DHR values and snag persistence to identify a useful threshold. We first identified a range of values corresponding with a natural break in the DHR distribution (Fig. 2A). We then estimated the $DHR_{threshold}$ parameter (see above model) using a prior distribution describing this range of values *Uniform*[2.9, 5.6]. Threshold values within this range distinguished 0.8–5.1% of the highest DHR values in our data (Fig. 2A).

We assessed statistical support for covariate relationships using Bayesian *p*-values, where p = the proportion of posterior estimates that were greater than or equal to zero. We considered low ($p > 0.95$) or high ($p < 0.05$) values to indicate statistical support.

We estimated period snag persistence probability for 2010–2015 under average conditions (mean values for all covariates) to compare with other studies and inform management. We estimated period snag persistence as the product of annual probabilities: $P_{period} = \prod_t^T P_t$, where year t = 2010, …, 2015. To represent spatial heterogeneity in

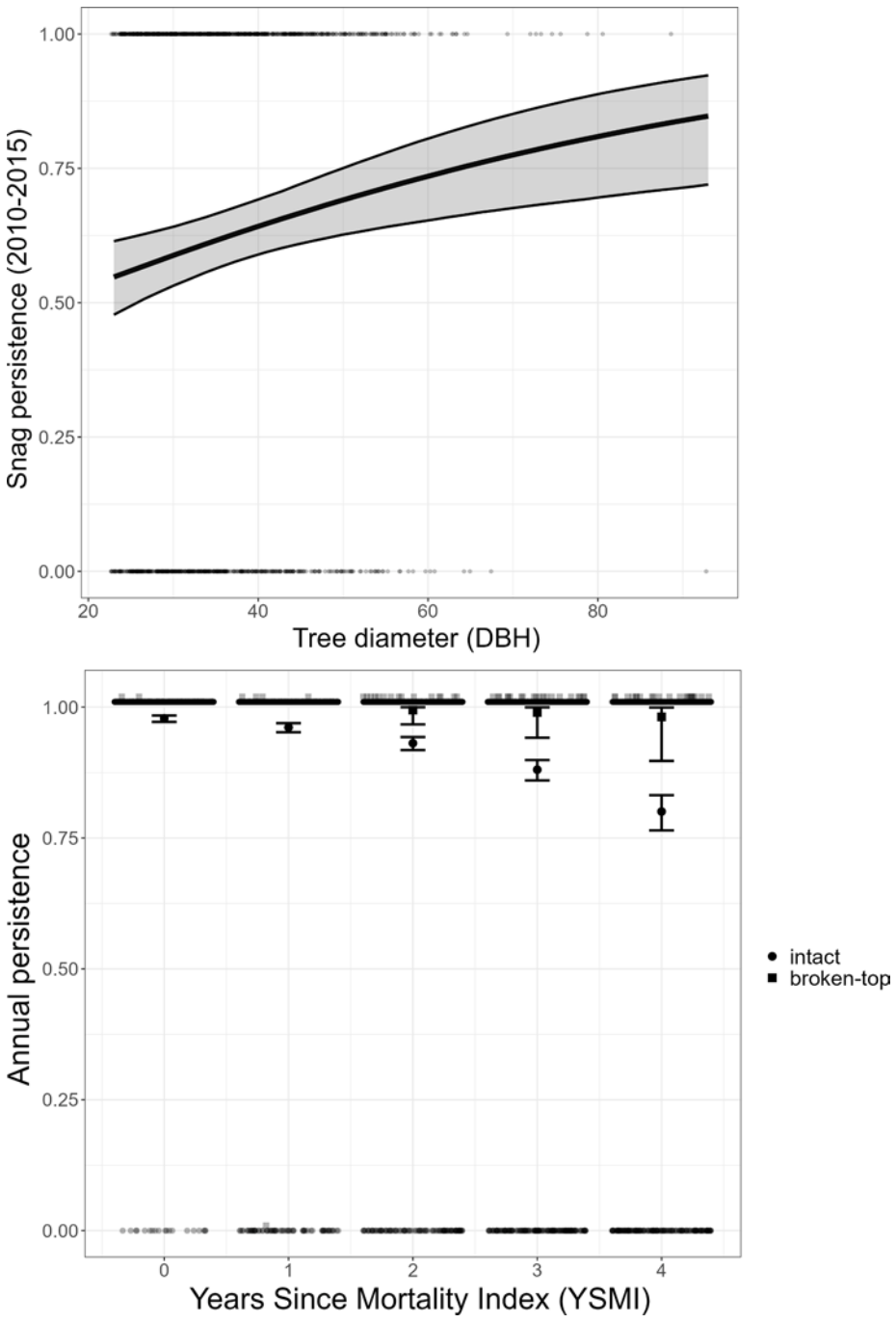

Fig. 4. Snag persistence in relation to snag characteristics following mountain pine beetle (*Dendroctonus ponderosae*) epidemic in the Elkhorns Wildlife Management Unit, Helena National Forest, Montana, U.S.A., from 2 to 7 years after the peak of beetle-caused tree mortality. In the top panel, lines and error bands represent posterior median and 95% credible predictions for persistence over a 6-year study period in relation to snag diameter (DBH). In the bottom panel, dots and error bars represent posterior median and 95% credible predictions for annual persistence in relation to years since mortality index (YSMI). Dots at the top and bottom of each panel represent snag-specific observations (1 = persistent, 0 = fallen) across the study period (top panel) or annually (bottom panel).

persistence probabilities, we estimated period snag persistence for an average plot ($logit(P_{t,average}) = \overline{\beta_0} + \beta_{Age} \times Age_t$), a low-persistence plot ($logit(P_{t,low}) = \overline{\beta_0} - 1.96 \times SD(\beta_0) + \beta_{Age} \times Age_t$), and a high-persistence plot ($logit(P_{t,high}) = \overline{\beta_0} - 1.96 \times SD(\beta_0) + \beta_{Age} \times Age_t$, where $\overline{\beta_0}$ and $SD(\beta_0)$ are the estimated mean and standard deviation, respectively, for the plot-specific normal random effect).

We fitted our model using JAGS v. 4.2 (Plummer, 2003) programmed from R (R Core Team, 2013; Su and Yajima, 2014). We standardized (subtracted mean and divided by the standard deviation) all covariates except SPP and YSMI prior to analysis. We used independent non-informative priors for all covariate effects ($\beta \sim Uniform$[-10, 10]), and hierarchically structured priors for the random plot effect ($\beta_{0_j} \sim Normal[\overline{\beta_0}, SD(\beta_0)]$, with priors of $\overline{\beta_0} \sim Uniform[-10, 10]$ and $SD(\beta_0) \sim Uniform[0, 10]$). We sampled posterior parameter distributions with 2 parallel MCMC chains of length 10,000 *it*, burn-in 2,000 *it*, and no thinning, resulting in $n_{\text{effective}} \geq 500$ and $\widehat{R} \leq 1.1$ for all parameters (Gelman and Hill, 2007). We examined model goodness-of-fit using posterior predictive testing (Appendix S1; Gelman and Hill, 2007).

3. Results

Of 1399 pine trees tagged in 2002–2003, 1288 (92%) were confirmed dead post-epidemic (Table 1). We estimated and modeled persistence for 1260 of these snags, i.e., those that stood at some point in 2010–2014, resulting in a dataset consisting of 5598 year-long observation intervals, during which we recorded 482 snag fall events (i.e., 38% of monitored snags fell). Goodness-of-fit testing indicated the

Table A1
Bayesian *p*-values assessing goodness-of-fit each plot in each year.

Plot	Bayesian *p*				
	2011	2012	2013	2014	2015
1	0.042*	0.2	0.306	0.464	0.014*
2	0.065	0.122	0.199	0.224	0.269
3	0.047*	0.086	0.149	0.24	0.373
4	0.338	0.291	0.365	0.691	0.146
5	0.111	0.189	0.07	0.757	0.746
6	0.244	0.4	0.106	0.392	0.894
7	0.096	0.188	0.311	0.452	0.304
8	0.093	0.01*	0.834	0.276	0.184
9	0.313	0.511	0.219	0.062	0.88
10	0.458	0.061	0.791	0.528	0.635
11	0.166	0.282	0.21	0.953*	0.559
12	0.315	0.339	0.861	0.066	0.836
13	0.087	0.14	0.242	0.207	0.774
14	0.129	0.378	0.487	0.633	0.244
15	0.092	0.191	0.298	0.281	0.526
16	0.094	0.205	0.338	0.349	0.838
17	0.051	0.852	0.805	0.556	0.156
18	0.455	0.656	0.329	0.02*	0.866
19	0.518	0.003*	0.276	0.639	0.985*
20	0.486	0.073	0.822	0.205	0.934
21	0.073	0.125	0.206	0.32	0.462
22	0.358	0.589	0.299	0.525	0.109
23	0.071	0.114	0.544	0.811	0.774
24	0	0.054	0.085	0*	0
25	0.487	0.575	0.367	0.218	0.156
26	0.369	0.168	0.038*	0.651	0.796
27	0.112	0.221	0.273	0.171	0.428
28	0.298	0.454	0.201	0.575	0.275
29	0.172	0.296	0.419	0.541	0.93
30	0.179	0.294	0.443	0.299	0.473
31	0.091	0.195	0.309	0.056	0.873
32	0.053	0.09	0.147	0.221	0.29
33	0.273	0.331	0.878	0.26	0.503
34	0.486	0.072	0.577	0.605	0.815
35	0.299	0.545	0.051	0.706	0.255
36	0.223	0.368	0.54	0.414	0.211
37	0.477	0.352	0.26	0.414	0.546
38	0.659	0.603	0.285	0.029*	0.941
39	0.409	0.594	0.084	0.447	0.177
40	0.061	0.115	0.993*	0.964*	0.298
41	0.312	0.486	0.309	0.046*	0.603
42	0.4	0.59	0.074	0.158	0.559
43	0.265	0.296	0.868	0.846	0.033*
44	0.214	0.193	0.846	0.417	0.649
45	0.29	0.45	0.103	0.903	0.129
46	0.565	0.428	0.389	0.589	0.196
47	0.204	0.341	0.525	0.703	0.07
48	0.128	0.926	0.32	0.879	0.766
49	0.405	0.572	0.217	0.642	0.067
50	0.384	0.578	0.62	0.406	0.441
51	0.147	0.209	0.922	0.864	0.798
52	0.309	0.482	0.341	0.876	0.04*
53	0.274	0.352	0.108	0.585	0.872
54	0.585	0.127	0.079	0.816	0.443
55	0.267	0.93	0.413	0.908	0.039*
56	0.054	0.227	0.982*	0.536	0.569
57	0.43	0.238	0.707	0.54	0.237
58	0.208	0.331	0.314	0.364	0.23
59	0.149	0.965*	0.324	0.963*	0.881
60	0.529	0.084	0.78	0.26	0.24
61	0.174	0.957*	0.903	0.86	0.133
62	0.207	0.208	0.382	0.54	0.957*
63	0.22	0.345	0.524	0.24	0.479
64	0.553	0.091	0.971*	0.345	0.13
65	0.169	0.361	0.31	0.425	0.439
66	0.259	0.431	0.909	0.158	0.27
67	0.479	0.632	0.015*	0.95	0.901
68	0.242	0.923	0.296	0.106	0.989*
69	0.418	0.013*	0.318	0.812	0.966*
70	0.196	0.303	0.449	0.014*	0.609
71	0.254	0.399	0.269	0.125	0.95
72	0.13	0.281	0.341	0.122	0.902
73	0.581	0.261	0.444	0.379	0.103
74	0.342	0.553	0.002*	0.369	0.945
75	0.279	0.539	0.252	0.183	0.242

*indicates evidence for poor fit.

persistence model provided a reasonable fit to the data (Appendix S1).

We found statistical support for 3 plot-level and 4 snag-level covariate relationships, while accounting for substantial variation in snag persistence rates among plots (Table 3). Mean persistence rates estimated for an average plot in 2010–2015 varied between ~ 50–75% among conditions measured by covariates (Fig. 3), and persistence varied additionally among plots (Table 3, Fig. 3). We found greater snag persistence at plots on north-facing slopes, with more trees, and with greater topographic ruggedness (SAR; Fig. 3). Snag persistence also tended to be greater in plots with greater topographic position (Fig. 3), although statistical support for this relationship was weak (Table 3). Persistence declined with YSMI and was greater for a subset of snags with large diameter-height ratios, likely indicating broken-top snags (Fig. 4). We estimated a lower period persistence rate for ponderosa pine snags (median [95% BCI] = 0.61 [0.554, 0.661]) compared to lodgepole pine (0.715 [0.611, 0.8]; for statistical support, see Table 3). The lower persistence rate translates to a shorter expected mean persistence time for ponderosa pine (10.1 [8.5, 12.1] years) compared to lodgepole pine snags (14.9 [10.2, 22.4] years; persistence time = -5/log[persistence rate]).

The median estimated DHR threshold for distinguishing broken-top snags associated with higher persistence rates from relatively intact snags with lower persistence rates was 4.683 cm × m^{-1}. This threshold distinguished 63 observations of 24 snags, of which 22 snags (92%) persisted through 2015 (Fig. 2B, 4). All but two of these snags were relatively intact (DHR < 4.796 cm × m^{-1}) in 2010 and subsequently broke but retained sufficient height to be considered persistent (≥1.4 m; Fig. 4).

4. Discussion

Relationships of snag persistence with topographic ruggedness and snag characteristics (YSMI, DBH, and top condition) were statistically supported and consistent with our predictions. Although not as strongly supported, the direction of the estimated relationship with local tree density (TD) was also consistent with our predictions. Tree density measurements strictly represented spatial variation among plots, whereas measurements centered on individual snags might have captured additional within-plot and inter-annual variability to inform a more precise estimate of this relationship. In contrast, relationships with topographic aspect and position were inconsistent with our predictions, suggesting potential unreliability and lack of generality in how these factors influence snag persistence. In addition to covariate relationships with snag persistence, our model described substantial spatial heterogeneity in annual persistence probabilities among study plots.

Support for some predicted relationships with environmental features and snag characteristics contribute to evidence for wind exposure, structural integrity, and decay as central drivers of snag persistence. Decayed snags with poor structural integrity are most susceptible to falling, and wind can catalyze toppling of susceptible snags. Rugged topography and relatively dense forest stands may shelter snags from wind events (Russell et al., 2006; Waldron et al., 2013). Large-diameter snags, particularly broken-top snags with lower centers of gravity, will tend to persist longest. Finally, snags become increasingly likely to fall as they age and become more decayed. Although lodgepole snags persisted longer than ponderosa pine snags in our study, our sample size for lodgepole pine snags was relatively small and we had no *a priori*

hypothesis for a species-specific difference in persistence. We therefore consider this relationship exploratory and would require a better understanding of underlying mechanisms before drawing general inference. Nevertheless, positive relationships of DBH and DHR with snag persistence here were consistent with relationships reported by Audley et al. (2021) following mountain pine beetle outbreaks in lodgepole pine forests, suggesting shared mechanisms for ponderosa and lodgepole pine snag persistence.

Our results suggest that some environmental features thought important may not consistently relate with underlying drivers of persistence. Although prevailing winds were westerly in our study area, snags on west-facing slopes were not notably more susceptible to falling (*contra* Peltola, 2006; Angers et al., 2011; Buettel et al., 2017). Similarly, snags that remained standing 9 years after a beetle outbreak in Arizona were on west-facing slopes, possibly an influence of cooler temperatures and moister conditions (Chambers and Mast 2014). Snags on south-facing slopes were most prone to falling, perhaps because those slopes experienced higher temperatures, potentially facilitating more rapid fungal decay and faster fall rates (cf. Lonsdale et al., 2008; Hararuk et al., 2020). Mortality caused by bark beetles is also associated with "stress zones" such as hotter and drier south-facing slopes (Negrón et al., 2009). These stresses interact to create greater susceptibility to bark beetles (Fettig et al., 2007).

Snags located on relative highpoints (i.e., positive values for topographic position index) were less prone to falling in contrast with our predictions and those of others (Ganey et al., 2021). Correlations among environmental features may confound observed relationships, leading to unexpected patterns for particular locations or datasets. Topographic slope in our data was strongly correlated with ruggedness ($r = 0.98$, $n = 75$ plots), leading us to exclude slope as a covariate from our analysis. Consequently, we could not test the generality of negative relationships of snag persistence with slope reported by others (e.g., Audley et al., 2021). Such peculiarities in topography may also explain the unexpected positive relationship with topographic position.

Observed variation in persistence rates among study plots suggest potential avenues for improving predictive models of snag persistence. Observed variation may reflect heterogeneity in important environmental or snag covariates missed by our model. Potential covariates identified by others but unavailable for this study include soil characteristics, temperature, and forest CO_2 emissions (Everett et al., 1999; Hararuk et al., 2020). Covariates included in our model may also imperfectly quantify fundamental drivers of persistence, such as wind, structural integrity, and decay. Inclusion of direct measurements of these drivers as covariates might improve model predictions, but intensive sampling likely needed to obtain such data may reduce model utility for informing management.

4.1. Management implications

Despite potential limitations in generality, our model combined with avian habitat selection studies has potential to inform habitat conservation following MPB epidemic. Larger-diameter snags are valuable because they are most likely to persist and are most useful for cavity-nesting birds and bats (Chiroptera) (e.g., Raphael and White, 1984; Zarnowitz and Manuwal, 1985; Gibbs et al., 1993; Rabe et al., 1998; Saab et al., 2009; Chambers and Mast, 2014), whereas both large and small diameter snags are used for foraging by birds. Additionally, broken-top snags generally persist longer than other snags, providing extended nesting and roosting habitat value (e.g., Campos et al., 2020). Broken-top trees prior to disturbances are attractive to woodpeckers immediately following fire and bark-beetle outbreaks, likely because of established decay and ease of cavity excavation in broken-top snags (Hutto, 1995; Spiering and Knight, 2005; Saab et al., 2009; Campos et al., 2020).

Our model provides a useful criterion for distinguishing broken-top snags likely to persist longer than other snags (DHR $\gtrsim$ 4.8). Longer-term snag monitoring could inform predictive modeling by identifying which snags break in this manner to further inform their retention. Retaining snags within denser and relatively continuous patches on west-facing slopes may also promote longer persistence (e.g., Russell et al., 2006; Angers et al., 2010; Ganey et al., 2021). Topography clearly plays a role in determining persistence rates, although additional study is likely needed to identify general relationships with particular components of topography capable of informing management, for example influence of topography on microclimates and temperatures, and subsequent snag fall rates (i.e. warmer temperatures increase snag fall rates; Oberle et al., 2018).

Post-disturbance forest management would be best informed by general patterns capable of predicting snag persistence rates across sites. Consistent with our findings, large diameter ponderosa pine snags on west-facing slopes persisted the longest after a beetle outbreak and were found as the most valuable snags for wildlife in Arizona (Chambers and Mast 2014). Other post-MPB snag longevity studies defined persistence differently from ours and targeted different snag sizes and species for economic rather than conservation objectives (Mitchell and Preisler, 1998; Lewis and Hartley, 2006; Rhoades et al., 2020). Longer studies will be important to comprehensively quantify and understand processes underlying snag persistence. Additionally, to the extent that topography, wind, and decay influence snag persistence across green, burned, and beetle-infested forests, our study combined with others of snags under various conditions will inform general knowledge.

CRediT authorship contribution statement

Quresh S. Latif: Formal analysis, Writing – original draft. **Jonathan G. Dudley:** Investigation, Supervision, Writing – review & editing. **Matthew A. Dresser:** Investigation, Writing – review & editing. **Denise Pengeroth:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing. **Victoria A. Saab:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

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.

Data availability

Data will be made available on request.

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Appendix A. Posterior predictive evaluation of model goodness-of-fit.

We used posterior predictive tests to evaluate model goodness-of-fit (GOF), i.e., the ability of the model to replicate data resembling those to which it was fitted. Following Gelman et al. (2004, p. 162), we compared scalar summary values for data drawn from the posterior predictive distribution, $T(y^{rep})$, to those for observed data, $T(y)$. For each test quantity, T, we generated a Bayesian p-value, $p = [T(y^{rep}) \geq T(y)|\theta]$,

where θ represents estimated model parameters and extreme values ($p > 0.95$ or $p < 0.05$) indicated evidence for lack of fit. We assessed GOF using deviance ($T = -2 \times$ log-likelihood) as an omnibus test quantity. We also conducted targeted GOF assessments, for which $T =$ the observed persistence rate for each plot in each year sampled ($n = 371$; no snags were present during 2 years at one plot).

Posterior predictive GOF test results indicated adequate model fit. We found no evidence for lack of fit with respect to overall deviance ($p = 0.457$). Additionally, Bayesian p-values for targeted tests suggested lack of fit for only 29 (7.8%) of plot × year occasions (Table S1).

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Appendix Table A1

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