Snag-fall patterns following stand-replacing fire vary with stem characteristics and topography in subalpine forests of Greater Yellowstone

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ABSTRACT

Standing dead tree stems (snags) become abundant following disturbances like bark beetle outbreaks and stand-replacing fire. Snags are an important element of wildlife habitat, and when they eventually fall can injure or damage people and infrastructure and contribute to coarse wood and fuels accumulation. While species-specific and general trends in snag persistence following disturbance have been well-studied, less attention has been paid to how these patterns vary across broad topographical gradients. We studied the ca. 250,000 ha of fire-killed snags created by the extensive and severe 1988 Yellowstone fires in the Greater Yellowstone Ecosystem (Wyoming, USA) and asked: (1) What characteristics of individual tree stems contribute to the likelihood and mode of snag-fall? (2) How do snag-fall patterns vary across broad topographical gradients? In 2002 and 2003 (14–15 years postfire) we determined the abundance of standing snags vs. fallen stems to identify patterns of snag persistence in relation to stem characteristics and topography. In 2022 (34 years postfire), we sampled a separate set of plots to determine which, if any, trends identified 14–15 years postfire persisted for another two decades. Trends in snag persistence were species specific, with lodgepole pine (*Pinus contorta* var. *latifolia*) stems less likely to remain standing than either Engelmann spruce (*Picea engelmannii)*, Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), subalpine fir (*Abies lasiocarpa*), or whitebark pine (*Pinus albicaulis*). Across all species, larger snags and those dead at the time of fire remained standing longer than smaller snags and those alive at the time of fire. The mode of snag-fall (uprooted vs. snapped) also varied with stem characteristics and species identity. Greater proportions of snags (all species and sizes combined) remained standing at higher elevations and on steeper slopes, likely driven by soils, stem allometry, decay rates, wind patterns, and pre-fire stand composition. As the extent and frequency of large, severe fires increases in western subalpine forests, understanding snag dynamics and the ecology and management of both standing and fallen snags is increasingly important.

1. Introduction

High-severity forest fires create many standing dead tree stems (snags) that gradually fall over time. While standing, snags provide food for saproxylic bark beetles and roosting and nesting sites for numerous bird and bat species (Franklin et al., 1987, Chambers et al., 2002, Nappi and Drapeau, 2009, Tarbill et al., 2015). Once they fall, they add coarse wood to the forest floor, providing habitat for several animal species and contributing to soil development (Harmon et al., 1986, Waldien et al., 2006, Angers et al., 2012). However, fallen snags also add to the surface fuel load, obstruct or damage infrastructure, and can injure fire responders (Mortimer and Kane, 2004, Donato et al., 2013, Nelson et al., 2016, Dunn et al., 2019). With the frequency and extent of high-severity

wildfires increasing in recent decades and forecasted to continue (Westerling et al., 2011, Higuera et al., 2021, Turner et al., 2022), understanding the dynamics of snag-fall in coniferous forests of the western U.S. has become increasingly important for wildland management.

Previous studies of snag-fall have revealed both species-specific differences and general trends in snag persistence. For example, fire-created snags of ponderosa and Jeffrey pine (*Pinus ponderosa* Engelm. and *P. jeffreyi* Balf., respectively) typically fall sooner than snags of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) in part because of differences in bark thickness and decay resistance (Bull, 1983, Morrison and Raphael, 1993, Russell et al., 2006, Martinez et al., 2011, Ritchie et al., 2013, Grayson

et al., 2019). Shallowly rooted species often uproot before and after death (Smith et al., 1987, Frank, 1990, Taylor and MacLean, 2007), and even those with a taproot may be susceptible to uprooting (Angers et al., 2010). Beetle-killed snags of lodgepole pine may remain standing longer at high elevations and on protected aspects (Rhoades et al., 2020, Audley et al., 2021), and, across species, larger snags tend to remain standing longer than smaller snags following both insect outbreaks and wildfire (Lyon, 1977, Bull, 1983, Morrison and Raphael, 1993, Everett et al., 1999, Chambers and Mast 2005, Ritchie et al., 2013, Grayson et al., 2019). Despite this general understanding of drivers of snag persistence, less attention has been paid to landscape-level patterns of snag fall following stand-replacing fire and whether topographic variables (e.g., slope, aspect, and elevation) contribute to spatial variability in snag persistence.

The 1988 Yellowstone fires burned more than 250,000 ha of subalpine forest as high-severity fire in and around Yellowstone National Park (YNP; Wyoming, USA) and provide an opportunity to quantify postfire snag-fall in relation to species, stem characteristics, and topographic context. Previous studies have used two general approaches to characterize snag-fall. Most have been longitudinal/cohort studies based on measuring standing snags soon after a fire then tallying those snags over time to calculate snag-fall rates (e.g., Lyon, 1977, Morrison and Raphael, 1993, Russell et al., 2006, Ritchie et al., 2013, Grayson et al., 2019). A second approach, which we used in this study, is measuring the proportion of snags still standing at a single point in time and identifying relevant environmental predictors associated with variability in snag persistence. This second method does not quantify the rate of snag-fall but can reveal key differences in snag persistence across species, stem characteristics, and broad topographical gradients.

Here, we used two complementary datasets to determine the patterns and drivers of snag-fall following stand-replacing fire in the conifer-dominated subalpine forests of Greater Yellowstone. In 2002 and 2003, we sampled tree stems in YNP that had been killed by the 1988 fires (14 or 15 years earlier), distinguishing between those that had fallen since the fires and those still standing. We asked: (1) What characteristics of individual tree stems contribute to the likelihood and mode of snag-fall? (2) How do snag-fall patterns vary across broad topographical gradients? In 2022, we also recorded standing and downed stems in a new set of stands that regenerated after the 1988 fires to determine what predictors of snag-fall at 14–15 years postfire remained important after 34 years. We hypothesized that the proportion of fire-killed stems still standing would be greater for lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm. Ex S. Watson) than for subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) owing to its heavier root system and greater total root length (Eis, 1970), but comparable to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) and whitebark pine (*Pinus albicaulis* Englem.) which possess deep root systems (Horton, 1958, McMinn, 1963, Arno and Hoff, 1989, Hermann and Lavender, 1990). Across all species, we hypothesized that the proportion of stems still standing would be greater for larger than smaller stems owing to greater root and stem mass (Mitchell and Preisler, 1998, Landram et al., 2002, Lewis and Thompson, 2011), and that trees dead at the time of fire would be less likely to remain standing than those alive at the time of fire because of advanced stem and root decay. For stems that had fallen, we hypothesized that the proportion of those fallen via uprooting vs. snapping would be driven by species-specific root morphology and decay rates, with lodgepole pine more likely to fall via stem-snapping than Engelmann spruce and subalpine fir for those reasons outlined above. Finally, at the landscape level, we hypothesized that the proportion of snags still standing in each stand would increase with elevation and on shallow sloped, leeward aspects due to slower decay rates and protection from prevailing winds (Harvey, 1986, Everett et al., 1999, Brown et al., 1998, Kueppers et al., 2004, Rhoades et al., 2020, Audley et al., 2021).

2. Materials and methods

2.1. Study area

Yellowstone National Park occupies ca. 9000 km^2 in northwestern Wyoming and adjacent Montana and Idaho. Coniferous forests dominated by lodgepole pine cover approximately 80% of the park. Less abundant conifer species include Engelmann spruce, subalpine fir, and whitebark pine at higher elevations and Douglas-fir at lower elevations. Most soils are dry and infertile and underlain by substrates of rhyolite and tuff, although somewhat less dry and infertile soils are also found on andesitic substrates and detrital deposits (Despain, 1990). The climate is characterized by cold, snowy winters and dry, mild summers; mean January and July temperatures (1981–2010) were −17.1 °C and 22 °C, respectively, with mean annual precipitation of 581 mm, falling mostly as snow in winter (Lake Yellowstone, Wyoming, station #485345; Western Regional Climate Center, 2021).

2.2. Site selection

Sites sampled in 2002–03 were selected using a stratified random sampling design based on aspect and slope. We created a 4x3 factorial design using the four cardinal aspects – north (325°-45°), east (45°-135°), south (135°-225°), and west (225°-325°) – and three grades of slope – gentle (0-5°), moderate (6-15°), and steep (>15°). The broad, gentle plateaus of YNP mean that much of the landscape burned as stand-replacing fire in 1988 was not very steep, so steeper slope categories were uncommon in this study. Thirty-meter digital elevation models (DEMs) were used to create these aspect and slope layers, which were clipped to the 1988 burned area using fire perimeter maps. Sampling sites (n = 131; Fig. 1) were then randomly selected from each factorial category while spanning the elevational gradient within the 1988 fires (Table 1). Data layers were obtained from the National Park Service Spatial Analysis Center (https://public-nps.opendata.arcgis.com) and processed in ArcGIS.

Plots sampled in 2022 were part of a separate study of vascular plant communities and aboveground carbon stocks in areas where tree regeneration following the 1988 Yellowstone fires was poor (Kiel and Turner, 2022). Plots (n = 55; Fig. 1) were stratified by elevation (above and below 2500 m) and distance to seed source (<90 m and > 120 m), and were separated by at least 250 m to reduce spatial auto-correlation. Among plots, slope did not exceed 20° and aspect varied (Table 1). All sampled stands across all years burned at high severity in 1988 with 100% tree mortality.

2.3. Field sampling

In 2002–03, three 4x50 m belt transects were established 25 m apart within each plot. All dead trees > 7.5 cm diameter at breast height (DBH) and currently rooted or determined to have been rooted at the time of the 1988 fires were tallied within each belt transect. Downed wood that had fallen prior to the fires was not measured for this study; such wood was recognizable from advanced decay stages or charcoal on stumps or tipped-up roots. For each stem in each transect, we recorded species identity, DBH, whether it was standing or fallen, and – for fallen stems – whether it was broken along the stem or uprooted. We measured slope and aspect in the field and recorded the geographic coordinates (northing and easting in Universal Transverse Mercator) of the midpoint of each middle transect using a global positioning system. Elevation was determined subsequently from a DEM.

In 2022, the abundance of snags 34 years after the 1988 fires was tallied from four photos taken in cardinal directions from the center of each 30x30 m plot (n = 55). Each snag was classified as either dead or alive at the time of the fire based on presence of charring on the stem, but species identity and DBH could not be determined. Only snags within the 30x30 m plot were included, and the location of each snag
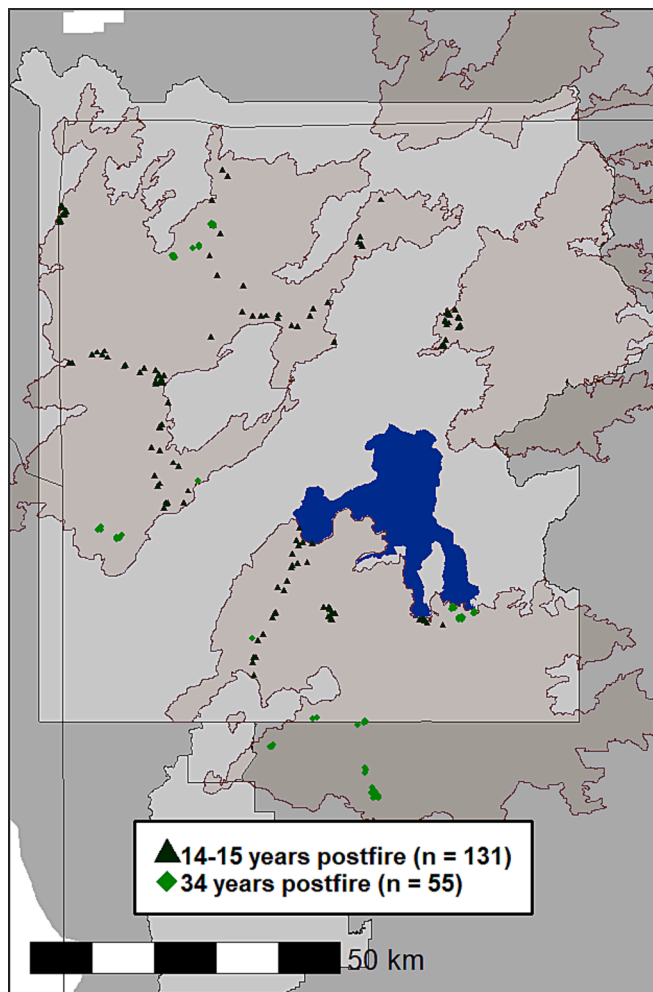
Fig. 1. Location of plots sampled 14–15 years (*n* = 131; dark green triangles) and 34 years (*n* = 55; light green diamonds) after the 1988 Yellowstone fires (brown outline and shading) within the Greater Yellowstone Ecosystem (dark grey) centered over Yellowstone and Grand Teton National Parks (light grey).

Table 1
Topographic characteristics used in generalized linear modeling of snag-fall patterns across the area burned as stand-replacing fire in the 1988 Yellowstone fires either 14–15 years or 34 years postfire.

Topographic characteristic	Year	Minimum	Maximum	Mean (±SE)	Median
Elevation (m)	2002–03	2034	2686	2328 (14)	2336
	2022	2237	2801	2525 (20)	2554
Slope (°)	2002–03	1	31	11.2 (0.8)	9
	2022	0	18.2	7.5 (0.6)	7.2
Cosine-transformed aspect	2002–03	0	2	1.0 (0.1)	1.7
	2022	0	2	0.9 (0.1)	0.8

inside or outside of the plot was verified with Google Earth imagery. To determine the proportion of all stems killed in 1988 still standing at 34 years postfire, the number of fallen stems was counted in each plot using Google Earth imagery. Charring could not be determined reliably for fallen stems using Google Earth imagery, so identification as alive or dead at the time of fire was only done for standing snags. Despite high-quality imagery, our method may underestimate the number of fallen stems 34 years after the 1988 fires.

2.4. Analysis

To answer question one, we fit logistic mixed effects models with a logit link to identify stem-level drivers of (i) snag persistence and (ii) modes of snag-fall across species. In our first model, we predicted whether a given stem had fallen or remained standing 14–15 years postfire, with 'fallen' set as the reference (i.e., predicting drivers of a given stem remaining standing). Potential predictors included whether the stem was dead at the time of fire (with stems alive at the time of the fire set as the reference to predict the likelihood of standing for dead stems), stem DBH, species identity (with lodgepole pine as the reference to predict each species' likelihood of standing relative to lodgepole pine), and stem status- and species-by-DBH interactions. In our second model, we predicted whether fallen stems were more likely to have fallen via uprooting or snapping at the base, with snapping set as the reference (i.e., predicting drivers of stems fallen via uprooting). Potential predictors included whether the stem was dead at the time of the fire, stem DBH, and species identity, with the same categories set as reference as above. Only lodgepole pine, subalpine fir, and Engelmann spruce were included in the latter model due to low replication for Douglas-fir and whitebark pine. Diameter at breast height as a continuous predictor was *z*-transformed prior to analysis. Site was included as a random effect in both models but was not interpreted as an ecologically relevant predictor. Overdispersion of model residuals was tested for using the DHARMa package (Hartig, 2022), with neither model overdispersed.

To answer question two, we used generalized linear modeling to identify plot-level drivers of the proportion of dead stems still standing at 14–15 years postfire and to determine whether those drivers persist at 34 years postfire. Potential predictors at 14–15 years included the proportion of stems that were lodgepole pine, elevation (m), slope (°), cosine-transformed aspect (with 0 = southwest, 2 = northeast; Beers et al., 1966), and stand density (stems ha⁻¹). Model residuals were overdispersed, so a negative binomial distribution was used. Potential predictors at 34 years included all the above predictors except the proportion of stems that were lodgepole pine as species could not be identified. Predictors were *z*-transformed prior to analysis to allow comparison of the effect sizes across coefficient estimates. All statistical modeling was done using the lme4 (Bates et al., 2015) package and all analyses and data visualization were conducted in R (R Core Team 2023).

3. Results

Nearly 7400 stems were tallied across plots sampled in 2002–03. Of these, ~70% were lodgepole pine, ~80% were alive at the time of the 1988 fires, and ~25% were still standing 14–15 years postfire (Table 2). Comparatively, nearly 1250 stems were tallied in 2022, of which ~15% were still standing. Of those still standing in 2022, only ~40% were alive at the time of the fires.

A given stem was more likely to have remained standing at 14–15 years postfire if it was dead at the time of the fire; had a larger DBH; or was a subalpine fir, whitebark pine, Engelmann spruce, or Douglas-fir rather than lodgepole pine (Fig. 2). Stems were more likely to have fallen if they were less than 40 cm DBH (Fig. 3a). Stem DBH interacted with whether it was dead or alive at the time of the fire, with the probability of standing increasing more quickly with increasing DBH for stems that were alive rather than dead at the time of fire (Fig. 3b). The influence of DBH also varied among species, with the probability of standing increasing more gradually for Engelmann spruce stems than for other conifers (e.g., lodgepole pine; Fig. 3c).

Fallen stems at 14–15 years postfire were more likely to have fallen via stem-snapping if they were dead at the time of the fire but were more likely to have fallen via uprooting if they were larger or were subalpine fir or Engelmann spruce instead of lodgepole pine (Fig. 4). At the stand level, a greater proportion of stems remained standing at higher

Table 2
Number of stems tallied by species as well as the number of those stems either alive at the time of fire or still standing after the 1988 Yellowstone fires. For those that had fallen, the number of uprooted stems were tallied. PICO: lodgepole pine; ABLA: subalpine fir; PIEN: Engelmann spruce; PIAL: whitebark pine; PSME: Douglas-fir. Rows containing data from 2002–03 are shaded grey.

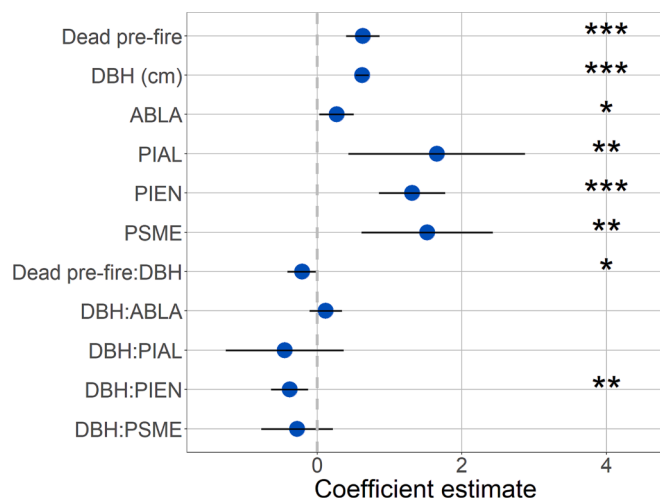| Stem characteristic	Year	PICO	ABLA	PIEN	PIAL	PSME	Unidentified stems	Total
Standing	2002-03	1308	202	115	43	25	195	1888
	2022	-	-	-	-	-	-	180
Uprooted (if fallen)	2002-03	1315	495	88	0	7	77	1982
	2022	-	-	-	-	-	-	-
Alive at time of fire	2002-03	4662	924	225	42	47	86	5986
	2022	-	-	-	-	-	-	72
Total	2002-03	5329	953	230	48	48	791	7399
	2022	-	-	-	-	-	-	1258

Fig. 2. Coefficient estimates of predictors of snag persistence (i.e., whether a given dead stem is or is not standing) 14–15 years after the 1988 Yellowstone fires. Positive coefficients are more likely to be standing and negative coefficients are more likely to be fallen. A given stem is more likely to be standing 14–15 years after the 1988 Yellowstone fires if: it was dead at the time of fire; had a larger DBH; or was a subalpine fir (ABLA), whitebark pine (PIAL), Engelmann spruce (PIEN), or Douglas-fir (PSME) relative to lodgepole pine (PICO). Significant interactions were visualized below. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

elevations and on steeper slopes 14–15 years postfire (Fig. 5a). The positive relationship of proportion standing with elevation persisted 34 years postfire ($F_{1,53} = 6.28, p = 0.015$), though the final model explained relatively little of the variation across plots ($R^2_{adj} = 0.09$; Fig. 5b).

4. Discussion

Landscape variability in snag persistence affects wildlife habitat quality, coarse wood and fuels accumulation, and hazard tree abundance and distribution. The 1988 Yellowstone fires burned over 250,000 ha of subalpine forest as stand-replacing fire, leaving millions of snags to decay and fall over time. Our study identified stem characteristics and topographic factors as important drivers of snag-fall patterns after stand-replacing fire in these conifer-dominated subalpine forests. While some hypotheses were supported by our findings, such as the persistence of larger stems and snags at higher elevations, others were not. In particular, lodgepole pine was less likely to have remained standing than every other species, important given stands sampled at 14–15 years postfire were ca. 70% lodgepole pine. Snag persistence on steeper slopes suggested that much of the gentle, undulating plateaus of YNP experienced relatively high rates of snag-fall within 15 years

postfire. Snags at higher elevations were also more likely to remain standing (Fig. 6), important given much of YNP's infrastructure is concentrated at relatively low elevations. Snag persistence owing to stem characteristics and topographic factors may contribute to localized, prolonged aboveground carbon storage given slower decay rates of standing vs. fallen stems.

4.1. Stem characteristics influenced snag persistence and modes of snag-fall

Whitebark pine, Engelmann spruce, subalpine fir, and Douglas-fir were each more likely to have remained standing than lodgepole pine 14–15 years postfire despite differences in wood density and root morphology that would suggest the opposite trend. However, stems of subalpine fir and Engelmann spruce, when they did fall, were more likely to fall via uprooting than snapping along the stem. These species possess shallower root systems than lodgepole pine (Eis, 1970) which may contribute to their propensity to uproot and fall even if it may not influence their likelihood of falling. Further, lodgepole pine often have greater height-diameter ratios (Wheeler and Critchfield, 1985), which can increase rates of snag-fall (Ganey and Vojta, 2005). Elsewhere, snags of Engelmann spruce may persist for decades after disturbance, with 27% of stems still standing 48 years after spruce bark beetle (*Dendroctonus rufipennis*) outbreaks in Utah and Colorado (Schmid and Hinds, 1974) and some fire-killed spruce stems persisting as snags for up to 80 years (Everett et al., 1999). However, comparably slow rates of lodgepole pine snag-fall have been observed following mountain pine beetle (*Dendroctonus ponderosae*) attack (Rhoades et al., 2020). These findings were limited to high-elevation subalpine forests (2900–3300 m), and inclusion of lower elevation forests that exhibit higher rates of lodgepole pine snag-fall following mountain pine beetle outbreaks (Bull, 1983, Mitchell and Preisler, 1998, Landram et al., 2002) may weaken or reverse this trend. Indeed, our sampling 14–15 years postfire spanned ca. 650 m in elevation, suggesting our species-specific findings may be more representative of subalpine forests generally and highlighting the importance of sampling widely across environmental gradients.

Stem size also influenced both the likelihood of snag persistence and mode of snag-fall. The longer persistence of larger versus smaller snags has been observed previously following forest disturbance (Lyon, 1977, Bull, 1983, Everett et al., 1999, Ritchie et al., 2013, Grayson et al., 2019) which may contribute to the species-specific snag persistence patterns we observed. Subalpine fir and lodgepole pine stems were the smallest across species and within 2.5 cm mean DBH of one another, whereas the DBH of Douglas-fir, whitebark pine, and Engelmann spruce stems were > 6.5 cm larger than lodgepole pine and were more likely to remain standing (Table A1). Larger stems of lodgepole pine were still more likely to have remained standing than smaller stems 14–15 years postfire (Fig. 3), suggesting DBH both alone and in conjunction with species identity influenced postfire snag persistence and mode of snag-fall.

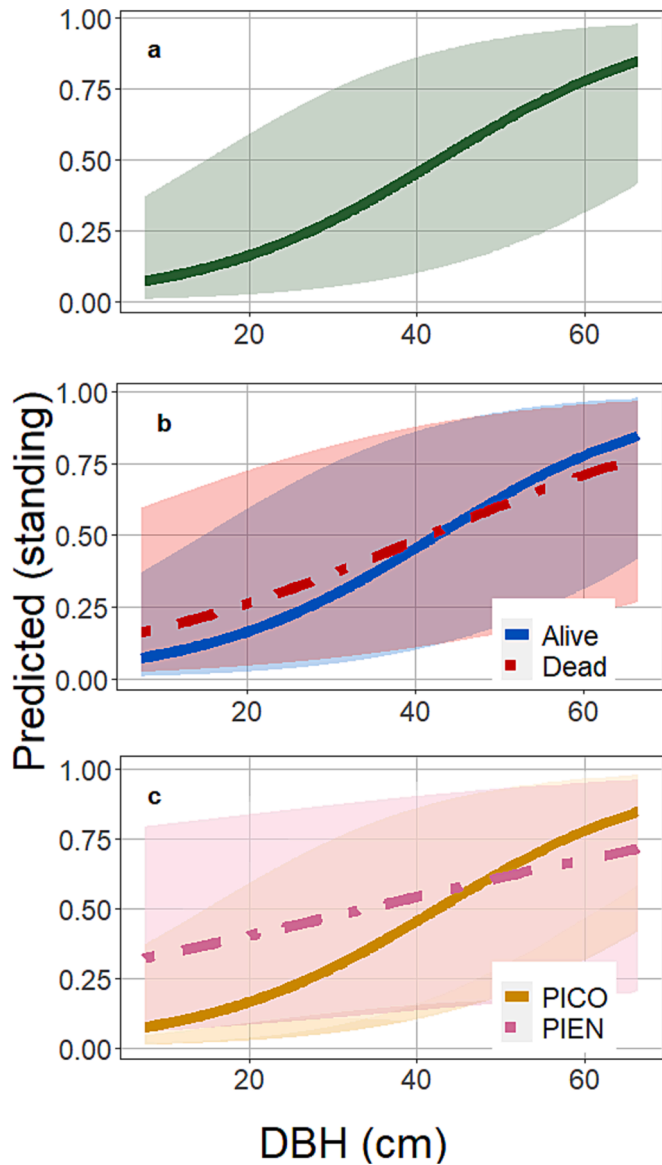Counter to our expectations, stems dead at the time of the 1988 fires

Fig. 3. The predicted likelihood of a given stem still standing 14–15 years after the 1988 Yellowstone fires. Shaded regions are 95% confidence intervals. (a) Stems with greater diameter at breast height (DBH) were more likely to remain standing by 14–15 years postfire. (b) DBH interacted with whether the stem was alive or dead at the time of the fire to influence the probability of standing, which increased more steeply for stems alive at the time of fire than those dead at the time of fire with increasing DBH. (c) DBH also interacted with species identity to influence the probability of standing, which increased more gradually for Engelmann spruce (PIEN) than lodgepole pine (PICO) with increasing DBH.
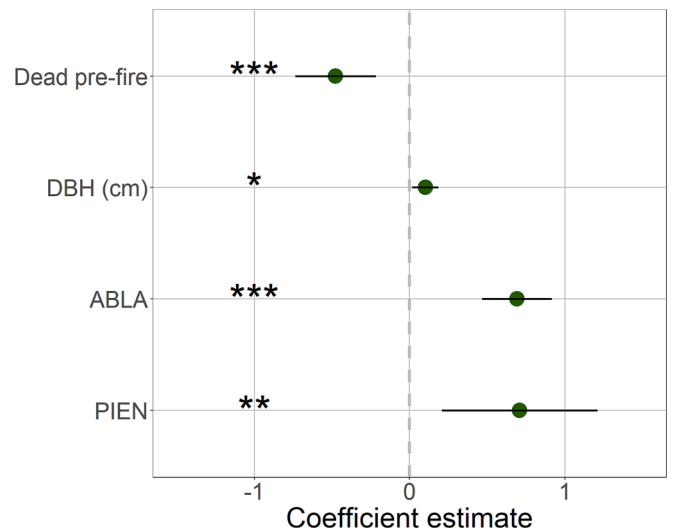

Fig. 4. Coefficient estimates of snag fall type (uprooting or stem-snapping) for fallen stems 14–15 years after the 1988 Yellowstone fires. Positive coefficients are more likely to have fallen via uprooting and negative coefficients are more likely to have fallen via stem-snapping. Stems dead at the time of fire were more likely to have fallen via snapping whereas larger trees and subalpine fir (ABLA) and Engelmann spruce (PIEN) were more likely (relative to lodgepole pine) to fall via uprooting. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

were more likely to have remained standing 14–15 years postfire, and by 34 years postfire made up 60% (108) of the remaining snags. Stems dead at the time of fire in subalpine forests are subject to deep charring unlike those living at the time of fire (Donato et al., 2009, Talucci and Kraw-chuk, 2019). This may slow stem decomposition (DeLuca and Aplet, 2008, Donato et al., 2009) and contribute to case hardening. However, charring of stems that were dead at the time of the fire may also weaken stems, and snag height can decline with time since fire (Ritchie et al., 2013). If stems dead at the time of fire were more susceptible to re-ductions in height than uncharred stems while still maintaining vertical material, this may lower the height-diameter ratio and increase snag persistence (Ganey and Vojta, 2005). Whether this was the case for the snags in our study is not known, but further research on snag height
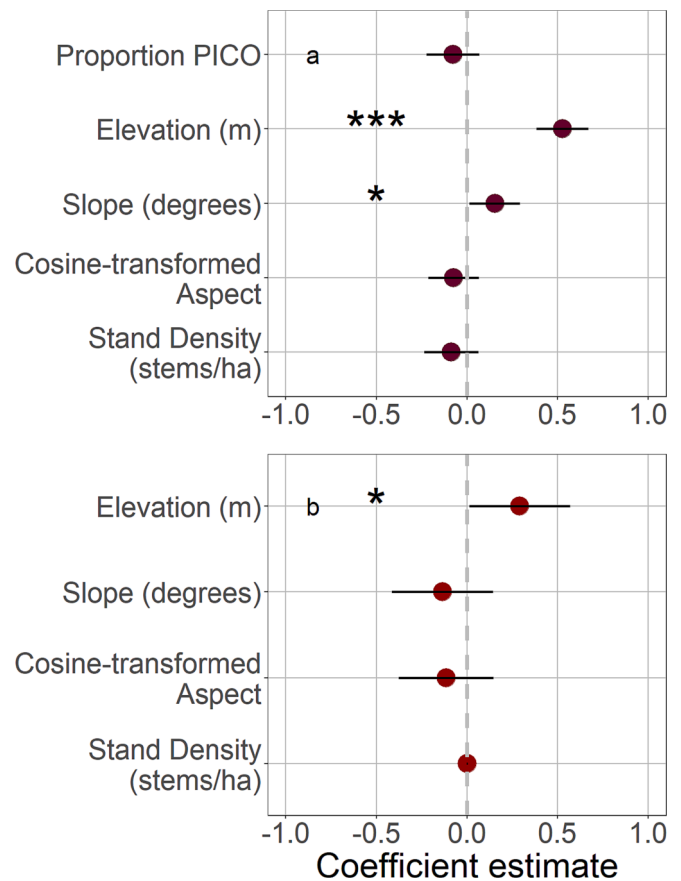

Fig. 5. Z-transformed coefficient estimates of multiple environmental predictor variables on the proportion of stems still standing in each plot either (a) 14–15 years after the 1988 Yellowstone fires (n = 131) or (b) 34 years after the 1988 Yellowstone fires (n = 55). The proportion of standing snags 14–15 years postfire increased with elevation and slope but increased only with elevation by 34 years postfire. * $p < 0.05$, *** $p < 0.001$.
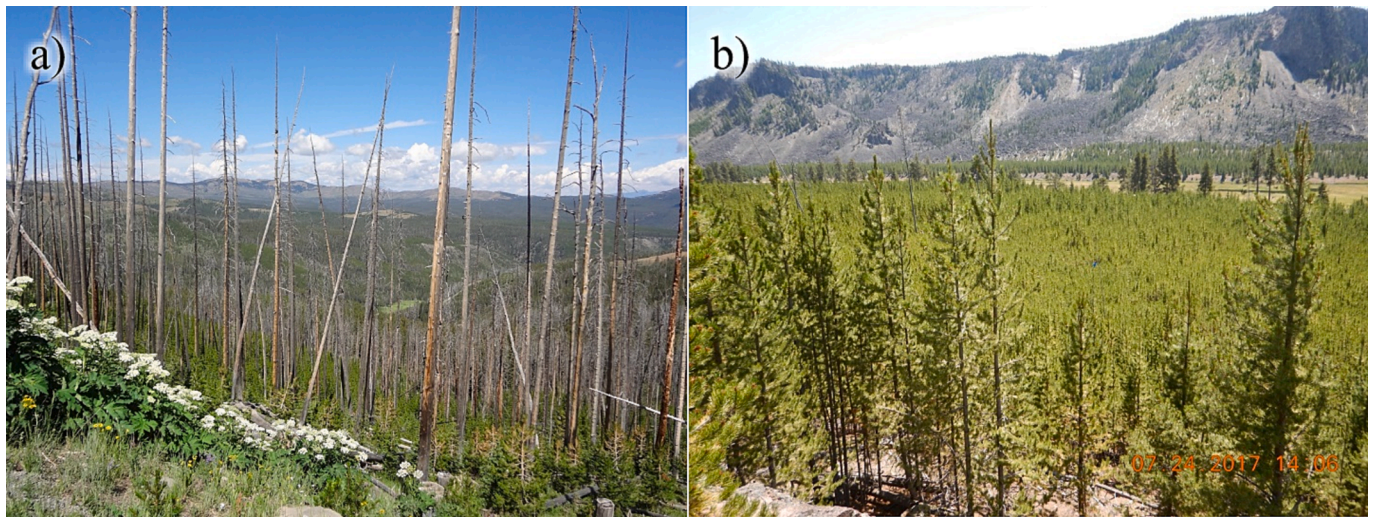
Fig. 6. Photos taken in 2017 of two areas recovering from the 1988 Yellowstone fires in Yellowstone National Park, USA. (a) Looking into the burn scar from the 1988 Yellowstone fires from the Grand Loop Road through Dunraven Pass (~2650 m asl) illustrating the extent of snag persistence at high elevations. (b) View of recovering forest following the 1988 Yellowstone fires from the West Entrance Road along the Madison River (~2070 m asl) illustrating the lack of snag persistence at low elevations. Photos by Monica G. Turner.

attrition, its variability with other stem and topographical characteristics, and its influence on stem persistence is warranted. Stems dead at the time of fire were also more likely to fall via snapping rather than uprooting. Charring often results in loss of wood mass (Donato et al., 2009) which could make charred stems relatively lighter than uncharred stems of comparable size, making them less likely to fall via uprooting.

4.2. Stand-level snag-fall varied across topographic gradients

Elevation and slope were important drivers of snag persistence in the decades following stand-replacing fire, with elevation having twice as strong an effect at 14–15 years postfire and remaining important 34 years postfire. Snag persistence at higher elevations has also been found in beetle-killed lodgepole pine forests (Bull, 1983, Harvey, 1986, Mitchell and Priesler, 1998, Landram et al., 2002, Rhoades et al., 2020). Variable snag persistence with elevation is likely related to a combination of climate, soil, pre-fire forest composition, and species-specific differences in stem characteristics and decay rates. Wood decay rates are slower at colder, high elevations (Brown et al., 1998, Kueppers et al., 2004, Acker et al., 2013), and in Greater Yellowstone, andesite-derived soils at higher elevations are finer-textured than rhyolite-derived soils at lower elevations (Despain, 1990). Large Engelmann spruce and white-bark pine are also more abundant at higher elevations (Despain, 1990), and high-elevation forests were generally older at the time of the 1988 fires (Schoennagel et al., 2003, Tinker et al., 2003), which together may contribute to greater snag persistence. Height-diameter ratios are also important for snag persistence (Navratil, 1995, Ganey and Vojta, 2005), and tree height often declines with elevation (Cuevas, 2003, Mayor et al., 2017). However, our study sites were not close to treeline, and variability in snag persistence with elevation is likely explained more by differences in forest composition and decay rates than reduced tree height driven by colder climatic conditions.

Snag persistence was also greater on steeper slopes 14–15 years postfire. This finding contrasts with those of Everett et al. (1999) of greater snag persistence on flat and moderate slopes but is consistent with recent findings in dry mixed conifer and subalpine forests following mountain pine beetle outbreaks (Rhoades et al., 2020, Latif et al., 2023). Complex terrain may slow wind speeds (Wood and Mason 1993), reducing pressure on snags compared with those on flatter terrain. Large snag-fall events are often associated with strong wind events (Keen, 1955), so moderation of winds on steeper slopes may promote snag

persistence. Further, windthrow appears to be most common on upper leeward slopes owing to laminar wind flow (Buck, 1964, Jane, 1986), and greater force is needed to overturn trees in the upslope than downslope direction on steep slopes (Nicoll et al., 2005). Other topographical characteristics, such as topographical exposure (Chapman, 2000) and local concavity, likely play important roles in snag persistence and should be further investigated. Root morphology may also vary with slope, with larger first-order lateral roots and greater total root volume for a given stem DBH on steeper slopes (Di Iorio et al., 2005) and root asymmetry on steeper slopes also likely to increase persistence (Sundström and Keane, 1999, Nicoll et al., 2006). Such root characteristics that contribute to live tree longevity on steep slopes can also contribute to snag persistence following mortality.

4.3. Management implications and conclusions

Understanding patterns of snag-fall may be increasingly important for wildland management as the extent and severity of wildfires continues to increase with climate change. Cavity-nesting birds benefit from postfire snags, but falling snags can injure people and damage infrastructure (Huggard, 1999). Fire-killed trees in proximity to homes, transportation corridors, powerlines, and other infrastructure are typically removed before they fall. Our analysis of species-specific and spatial patterns of standing vs. fallen fire-killed snags suggests possible priorities for removing hazard trees. Small to medium-sized snags at lower elevations may be among the first to fall and could be prioritized for removal near infrastructure for human safety. In contrast, large stems, especially those of Engelmann spruce, Douglas-fir, subalpine fir, and whitebark pine, and stems on steeper slopes and at higher elevations, are likely to persist for a longer time. Indeed, it may be desirable to retain or even protect large snags of all species where safe to do so for the benefit of cavity nesting birds and other wildlife (Harmon 1986), as large snag abundance positively correlates with Northern Spotted Owl (*Strix occidentalis cuarina*) habitat selection (Irwin et al., 2020), marten (*Martes americana*) den sites (Ruggiero et al., 1998), and feeding and nesting opportunities for several woodpecker species (Haggard and Gaines, 2001, Lehmkuhl et al., 2003, Hutto, 2006).

Though the removal of hazard trees may be a management priority, dead and downed wood of all sizes plays an important ecological role following forest disturbance generally (Leverkus et al., 2020) and wildfire in subalpine forests specifically. For example, litter

decomposition and nitrogen cycling processes in Yellowstone's burned forests vary with microsite position (i.e., whether beneath a log or not; Remsburg and Turner, 2006, Metzger et al., 2008), and piles of fallen logs may inhibit movement of large mammals or create refuges from herbivory or predation (Ripple and Larsen, 2001, Forester et al., 2007). Because of slow wood decomposition rates in this environment, especially of stems not in contact with the soil and at higher elevations (Brown et al., 1998), great quantities of large coarse wood will persist in the 1988-burned forests for many decades to come and may influence the likelihood of future forest fires (Nelson et al., 2016).

Changes to climate and fire regimes in subalpine forests may alter future landscape-level snag-fall patterns and dynamics. Most forests that burned in 1988 had not been burned previously for 100 – 300 years, but recent fires have reburned young forests < 30 years after the previous fire, well before young trees were of sufficient size to become persistent postfire snags. Such short fire-return intervals may become the norm by the end of this century (Westerling et al., 2011), driving both reduced postfire tree regeneration (Turner et al., 2019, Braziunas et al., 2023) and smaller tree sizes of those that do reburn. As such, it is possible that the extensive tracts of large, fire-killed snags that subsequently fall to create persistent piles of coarse dead wood may become less common in many western subalpine forests as changes to climate and fire activity continue.

Author contributions

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 are deposited with the Environmental Data Initiative (EDI) repository: https://doi.org/10.6073/pasta/7cdc34a8ad703f82d8fe43b3e521f02f.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121485.

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