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Snagfall the first decade after severe bark beetle infestation of high-elevation forests in Colorado, USA

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Abstract. The persistence and fall rate of snags (standing dead trees) generated during bark beetle outbreaks have consequences for the behavior, effects, and suppression of potential wildfires, hazard tree and timber salvage operations, wildlife habitat, and numerous ecosystem processes. However, post-beetle snagfall dynamics are poorly understood in most forest types. We tagged standing live and dead lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*), including beetle-killed pine snags following the peak of a recent mountain pine bark beetle outbreak in watersheds at the Fraser Experimental Forest in northcentral Colorado and sampled snagfall 10 and 12 years later. Bark beetle attacks began in 2003, peaked by 2006, and killed 78% of overstory lodgepole pine in 133 plots distributed across a range of stand and site conditions. Of those snags, only 17% fell between 2007 and 2018. Most snags broke at ground level, due to butt rot, and were oriented downhill. In contrast, snags that tipped up or snapped off above the ground were oriented with the prevailing winds. Equal numbers of snags fell singly and in multiple-tree groups, and equal numbers remained elevated rather than in contact with the ground. Lodgepole pine snagfall was 1.6-times higher on steep slopes (>40%) where dead pine density was higher, compared to flatter sites. Based on our findings and previous research, we estimate that one-half the beetle-killed lodgepole pine in high-elevation forests such as those at Fraser may fall within 15–20 yr of beetle infestation, but that some pine snags are likely to persist for decades longer. Post-outbreak snagfall dynamics create a multiple-decade legacy of bark beetle outbreaks that will persist longer in high-elevation compared to lower-elevation forests.

Key words: Dendroctonus ponderosae; *forest disturbance; insect outbreak; lodgepole pine; mountain pine beetle; subalpine forest; windthrow.*

Introduction

Recent mountain pine beetle (*Dendroctonus ponderosae*) outbreaks have caused one of the most dramatic changes in forest condition in western North American forests in more than a century. This widespread disturbance has been attributed to regional increases in air temperature and drought and changes in forest structure (Bentz 2009, Chapman et al. 2012, Creeden et al. 2014). The outbreaks affected lodgepole pine (*Pinus contorta* var. *latifolia*) forests from Colorado to British Columbia (Kurz et al. 2008, Raffa et al. 2008) and resulted in tree mortality in excess of 75% in many forests (Klutsch et al. 2009, Collins et al. 2011, Diskin et al. 2011). The severity and extent of mortality prompted efforts to salvage dead timber, reduce canopy fuels, and regenerate new forests (Collins et al. 2012, Pelz et al. 2015). Post-outbreak harvesting aims to remove standing dead trees before snagfall reduces timber value, complicates site access, and exacerbates potential wildfire effects and suppression efforts (Page et al. 2013, Jenkins et al. 2014). There is also growing safety concern associated with snagfall along forest trails and in campgrounds, reflecting increased awareness of wind-related tree damage and fatalities (Schmidlin 2009).

Snagfall alters forest structure and supplies downed wood that has important effects on ecosystem processes and plant and animal community dynamics (Harmon et al. 1986, Edburg et al. 2012, Saab et al. 2013, Buettel et al. 2017). Canopy openings created by snagfall gaps influence seedling regeneration and the growth of residual trees (Stuart et al. 1989, Vodde et al. 2010, Pelz et al. 2018), shrubs (Pec et al. 2015), and herbaceous plants. The high carbon and low nutrient content of downed wood create a long-term source of soil C and sink for soil nitrogen (Busse 1994, Kurz et al. 2008). Combustion of fallen logs can generate high temperatures that

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penetrate soil profiles (Busse et al. 2013) and have lasting effects on belowground resources (Tinker and Knight 2000, Rhoades et al. 2004). Unlike the highly visible "red-needle phase" that typically lasts for 3–5 yr, due to their slow decomposition, beetle-killed logs can persist for decades to more than a century in high-elevation forests (Fahey 1983, Brown et al. 1998, Kueppers et al. 2004).

Studies of previous beetle outbreaks have identified tree species and diameter, stand density, and site conditions as factors that influence snagfall rates and spatial patterns (Keen 1955, Hoffman et al. 2012, Chambers and Mast 2014, Ganey et al. 2015). Sapwood decay and breakage at the base of the tree are typical of most beetle and fire-killed snags (Harvey 1986, Lewis and Thompson 2011, Oberle et al. 2018, Grayson et al. 2019) as opposed to tip-up mounds or stem breakage. Smaller diameter pines have proportionally more sapwood area and generally fall sooner than larger trees (Landram et al. 2002, Russell et al. 2006, Chambers and Mast 2014, Ganey et al. 2015). Snag persistence varies widely among studies, and findings from ponderosa pine (Keen 1955, Schmid et al. 1985, Hoffman et al. 2012) or low-elevation lodgepole sites (Bull 1983, Mitchell and Preisler 1998, Landram et al. 2002) may not adequately represent snagfall rates for high-elevation lodgepole forests typical of much of the Southern Rockies.

Our objectives were to quantify the spatial and temporal variability of lodgepole pine snagfall across a range of forest conditions typical of high-elevation forests affected by severe bark beetle outbreak. We inventoried snagfall in 2016 and 2018, roughly a decade after the 2006 peak of pine bark beetle attacks in subalpine forests of northcentral Colorado, and compared the relative importance of site (aspect, slope, elevation) and stand conditions (tree diameter, stand density, and species composition) on post-bark beetle snagfall in managed and old-growth forests. We also documented the directional patterns of snagfall relative to prevailing wind direction, site topography, and snagfall type. This work helps identify conditions that favor higher snagfall and improves estimates of snag persistence after severe beetle outbreaks in high-elevation forests.

Methods

Site description and study areas

The Fraser Experimental Forest (FEF) lies west of Denver and the Continental Divide on the western edge of Colorado's Front Range (Fig. 1). Fraser has long cold winters and short cool summers; mean annual air temperature is 0.6°C with January and July average temperatures of −10° and 12.2°C, respectively (FEF, *unpublished 1976–2005 data*). As recorded throughout Colorado (Lukas et al. 2014), daily minimum temperatures at FEF have increased during the past 30 yr (FEF, *unpublished data*). Total annual precipitation averages 750 mm, primarily as snowfall. Soils are typically skeletal, sandy loam Dystric and Typic Cryochrepts (Alstatt and Miles 1983); subsurface soils contain 20–30% gravel and 30–50% cobble-sized materials.

The forests at FEF are a mix of lodgepole pine, subalpine fir (*Abies lasiocarpa*), and Englemann spruce (*Picea engelmannii*), and part of the temperate steppe mountain ecoregion that extends from New Mexico to southern Canada (Bailey 1998). Lodgepole pine dominates lower-elevation and south-aspect stands (Huckaby and Moir 1998) and stands that regenerate after timber harvesting or wildfire. Mixed-species conifer forests occupy valley bottom and north-facing slopes and extend to treeline (3,300–3,500 m); fir and spruce dominance increases with elevation and stand age. Bark beetles were detected at FEF in 2003 in lodgepole pine trees attacked in 2002 and epidemic levels of beetle emergence were measured in various locations across the research area the following year (Tishmack et al. 2004). Beetle activity and tree mortality peaked around 2006 both at FEF and elsewhere in northern Colorado (Collins et al. 2011, Diskin et al. 2011, Chapman et al. 2012, Meddens and Hicke 2014).

The four watersheds included in this analysis (Fig. 1) represent two paired watershed studies designed to quantify the effects of forest management on vegetation and hydrology. Harvesting of the Fool Creek–East Saint Louis Creek study occurred between 1954 and 1956. Approximately one-half of the forested portion of the Fool Creek watershed was cleared in strip cuts; East Saint Louis Creek watershed was not logged. Harvesting of the Deadhorse Creek–Lexen Creek study was conducted between 1977 and 1984. Approximately 30% of the forested portion of the Deadhorse Creek watershed was cleared in circular and irregular clear cuts; the Lexen Creek watershed was not harvested. The East Saint Louis and Lexen Creek watersheds represent old-growth forest conditions and the two managed watersheds (Fool and Deadhorse Creek) contain a mixture of old- and second-growth forest (Mixed Age).

Sampling and analysis

In 2007, we established 133, 10 m radius plots distributed throughout FEF's snow sampling network in old-growth (East Saint Louis and Lexen) and mixed-age (Fool and Deadhorse) watersheds. All standing trees were tagged, species and status (live/dead) were noted, and diameter at 1.4 m height (dbh) measured. The year of death for pines trees attacked during 2007 and the previous 4 yr was assigned according to general patterns of foliar color and senescence and pitch tube condition (Safranyik and Carroll 2006). Specifically, current-year beetle-killed pines had boring dust, and soft pitch tubes. Previous-year snags had red needles, larval galleries, drier pitch tubes, exit holes and blue-stained wood. Older snags lost an increasing proportion of red needles. Peak bark beetle activity occurred in 2005 and 2006

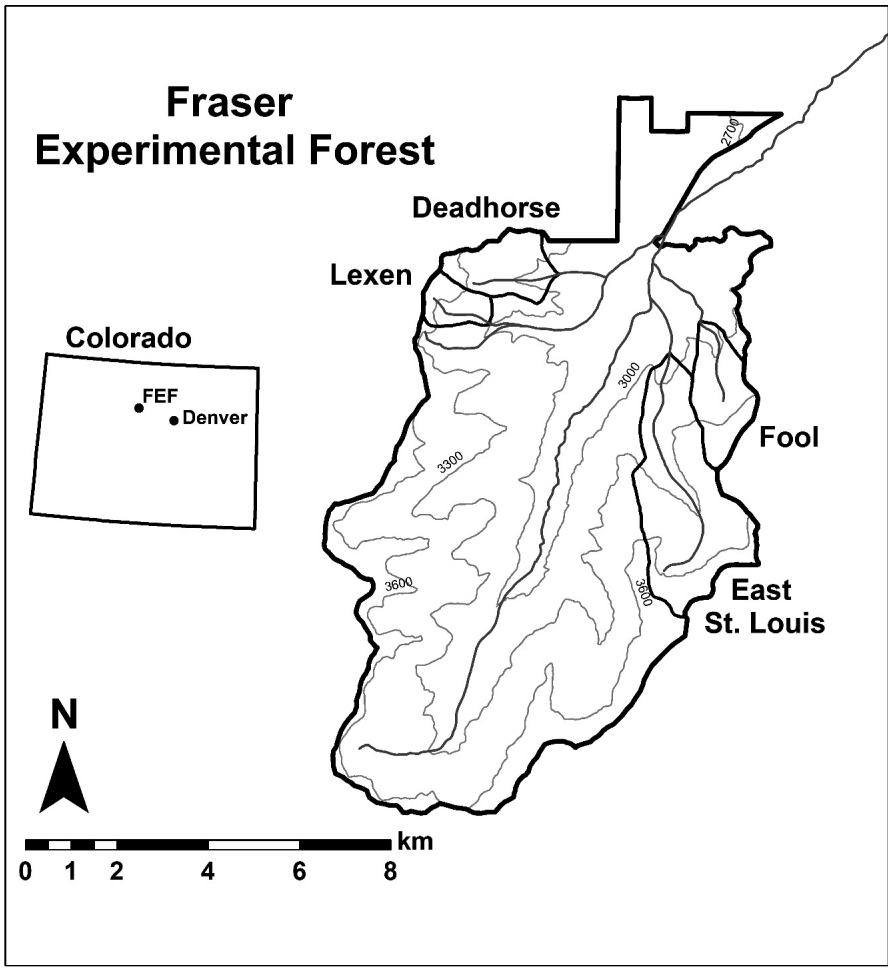

FIG. 1. Watersheds containing long-term snagfall, forest structure, and snow measurement plots at the U.S. Forest Service Fraser Experimental Forest, Colorado, USA (FEF). Solid black lines outline watershed boundaries of old-growth (East Saint Louis, Lexen) and mixed-age (Fool, Deadhorse) watersheds. Dark gray lines denote streams and light gray lines are 300-m contour intervals above sea level.

when 80% all beetle attacks occurred. We re-inventoried standing and fallen overstory (≥10 cm diameter) and understory trees (>2.5 and <10 cm diameter) in 2016 and 2018, 10 and 12 years after most of the overstory pines were attacked. Year of death was unknown for fir and spruce. Trees that died after 2007 were excluded from the snagfall assessment.

In the 2016 and 2018 inventories, we recorded the azimuth of each tagged, fallen snag, and noted the apparent cause of fall (Fig. 2) as follows: (1) butt rot, breakage at or below ground level with visual evidence of wood decay, few attached roots and no soil mound; (2) tip up: tree bole remains attached to exposed roots and soil mound; (3) bole snap: tree remains rooted with physical breakage >1 m above the ground surface. We also recorded whether trees fell singly or in multiple-tree groups, and whether fallen snags remained elevated or were in contact with the ground (i.e., >75% of bole length). Multiple-tree groups included clusters that fell in unison and single trees that toppled into others. We were unable to assign a cause of death to the understory conifers and as such, we documented snagfall since 2007, but did not estimate snag longevity.

We evaluated how the density (trees/ha) of fallen snags varied with tree diameter and the aspect, slope, elevation, tree density, and species composition of the study plots. The proportion of fallen snags in 2016 and 2018 were compared to the number of snags tagged in 2007. Slope aspect (°) and gradient (%) were calculated from a digital elevation model for a 9 × 9 m area centered on each plot center using geospatial software (ArcGIS Desktop, V. 10.3.1; Environmental Systems Research Institute, Redlands, California, USA). We evaluated whether snagfall orientation related more closely to site aspect or the direction of prevailing winds. Prevailing wind speed and direction for FEF were measured at 10-min intervals from 2010 through 2016, 3 m above the ground in an alpine landscape (3,639 m).

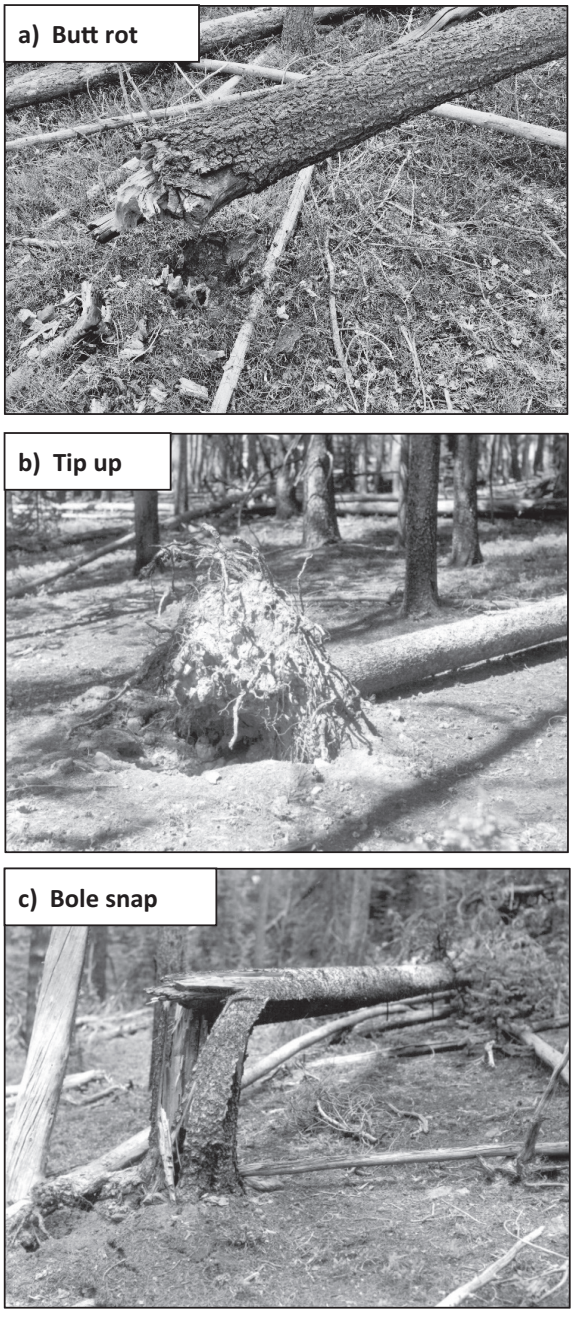

FIG. 2. Causes of snagfall classified at the Fraser Experimental Forest. (a) Butt rot: breakage at or below ground level with visual evidence of wood decay, few attached roots, and no exposed soil mound. (b) Tip up: tree bole remains attached to exposed roots and soil mound. (c) Bole snap: tree remains rooted with physical breakage >1 m above the ground surface.

We used one-way analysis of variance ($\alpha = 0.05$; SPSS; IBM, Armonk, New York, USA) to evaluate site conditions (elevation and slope) among watersheds, stand structure and snag fall among steep (>40%) and flatter slopes, and tree diameters among snagfall types. Levene's statistic and Shapiro-Wilk test were used to evaluate homogeneity of variance and normality, respectively, and data were log transformed as necessary. We used linear regression analysis to examine the relationship between total lodgepole pine stand density and pine snagfall (SPSS). We summarized prevailing wind and snagfall direction using circular statistics on angular orientation data that does not designate zero, high, or low values (NCSS V 19.0.1; NCSS LLC, Kaysville, Utah, USA; Mardia and Jupp 2000). Mean direction (theta) and dispersion (circular standard deviation) means were tested using the Watson-Williams statistic. We determined whether mean snagfall directions among snagfall causes or species were significantly different from random radial distribution using Watson U2 test at $P < 0.001$.

RESULTS

Site and stand conditions

Overall, the study plots averaged 3,122 m elevation and had 32% slope, with elevation spanning from 2,908 to 3,309 m (Table 1) and slopes from 4% to 66%. One-quarter of the plots were on steep ground (e.g., >40%) that would be inaccessible to ground-based logging operations. Plots faced all cardinal directions and were oriented northeast (60.3°) on average. The mean slope aspect differed among the two watershed pairs (Fig. 1); East Saint Louis and Fool Creek were both oriented north, and Lexen and Deadhorse faced east.

The conifer species comprised similar proportions of total overstory stand density in general (lodgepole pine, 35%; subalpine fir, 39%; Engelmann spruce, 26%; Table 2), though pine represented 50–97% of the overstory trees in 45% of the plots. In 2007, 78% of overstory pine were beetle killed, equivalent to 28% of the total forest overstory. Snags comprised 86% of pine overstory (≥10 cm diameter) in old-growth, compared to 67% in mixed-age watersheds.

Live pines comprised only 8% of total overstory density. The relative abundance of live pines was higher in the mixed-age watersheds, especially for understory trees, where density was three times more than in the old-growth watersheds. Subalpine fir was the most abundant component of the residual live overstory (50%) and understory (65%). In general, the density of live spruce was intermediate between pine and fir, though the post-outbreak proportion of spruce increased to 42% of the live overstory density.

Snagfall patterns

Overall, 519 snags tagged in 2007 fell by 2018. Of those, 71% were overstory trees and 56% were beetle-killed lodgepole pine (Table 2). On average, 17% of overstory pine snags fell since 2007 (Fig. 3a). There was no snagfall for trees infested 9 yr prior to the 2016 survey, and the proportion of snags remaining decreased slightly with time since death (Fig. 3b). The proportion of

Table 1. Characteristics of research watersheds at the Fraser Experimental Forest, Colorado, USA.

Watershed	No. plots	Elevation (m)			Slope (%)			Aspect (°)		
		Mean	Min	Max	Mean	Min	Max	Mean direction (Theta)	Circular SD	Watson's U2
East Saint Louis	32	3,094 a	2,908	3,246	32	9	57	349.7 a	74.5	0.0024
Fool	31	3,091 a	2,938	3,262	28	16	47	5.8 a	66.1	0.0001
Lexen	36	3,220 b	3,129	3,309	34	4	66	125.8 b	57.0	<0.0001
Deadhorse	34	3,084 a	2,874	3,208	34	10	49	90.4 b	82.9	0.0074
Significance†		<0.001			NS			<0.001‡		

Notes: Measurements of 10 m radius permanent snow course plots in adjacent watershed pairs. Mean direction of plots within watersheds was determined to be nonrandom based on Watson's U2 analysis of circular data. Different letters denote significant differences among watershed means at the $\alpha = 0.05$ level. Min, minimum; max, maximum.
† One-way ANOVA.
‡ Watson-Williams F test.

remaining snags was uniform among the year of death cohorts at the time of the 2018 survey. Overstory pine snagfall density was significantly higher in old-growth compared to mixed-age watersheds (63 vs. 34 trees/ha), corresponding to the higher proportional density of dead pine. The proportions of overstory fir and spruce snagfall (29% and 27%) were both higher than for beetle-killed pine (Fig. 3a). Overstory snagfall increased during the latter period (2016–2018) for spruce and pine but remained constant for fir. Between 2016 and 2018, the fall rate was 2.4%, 3.1%, and 4.6% annually for fir, pine, and spruce overstory snags, respectively, and was roughly double that for understory snags (data not shown).

Overall, butt rot accounted for more than one-half of overstory snagfall (53%) across the three species (Table 3) and was the most abundant cause of understory snagfall. Tip ups represented a third of the overstory snagfall but were the most common cause for understory subalpine fir. Bole breakage was uncommon. Snagfall cause was unrelated to tree diameter ($P > 0.05$), though the diameter of fallen overstory snags differed among the conifer species (Table 3). Mean diameters of standing pine snags were larger than those that fell (27.5 vs. 25.4 cm dbh, $P = 0.002$), but the size of standing and fallen fir and spruce snags were similar.

Equal numbers of snags fell to the ground as remained elevated (data not shown). Fir and spruce snags that reached the ground had significantly larger diameters than those that remained elevated. Diameter had no effect on how fallen overstory pine were situated, though understory pines that fell to the ground were smaller than those that remained elevated. Similar numbers of overstory pine trees fell singly and in multiple-tree groups (99 vs. 100). More overstory fir fell singly and they had significantly larger diameter than those that fell in multiple-tree groups (23 vs. 19 cm, $P = 0.02$).

Factors contributing to snagfall

Stand conditions.—Pine snagfall increased with total lodgepole density ($r^2 = 0.41$; $P < 0.001$); pine density explained 46% and 30% of snagfall variability in old-growth and mixed-age stands (Fig. 4). Linear analysis through 2018 estimated that 14 pines fell per 100 in old-growth compared to 8 per 100 in mixed-age stands. The proportion of stand density composed of lodgepole explained 35% of pine snagfall and the density of dead lodgepole explained 16%. Neither the combined density of all three conifers or the density of their snags explained pine snagfall. In general, snagfall was twice as high in old-growth compared to mixed-age stands (Table 2). High rates of pine snagfall (e.g., >150 trees/ha) occurred in 28% of old-growth but only 7% of mixed-age plots. Total overstory density was marginally higher in the old-growth plots ($P = 0.1$), but neither the density or proportional abundance of lodgepole differed among the watershed classes.

Site factors.—Overstory pine snagfall was correlated with slope gradient ($P = 0.001$), though it explained only 7% of snagfall variation. Pine snagfall was 1.6 times higher on slopes above 40% (Fig. 5), reflecting the increase in pine snag density relative to flatter slopes. Plots with the highest pine snagfall rates (>150 trees/ha) were located on significantly steeper slopes than those with lower fall rates (39% vs. 31% slope; $P = 0.008$).

The prevailing winds at FEF are from the west (280°) with a range in monthly mean azimuth of 262° in May and 292° in January. Winds in excess of 25 m/s, known to uproot trees in mountain environments (Csillery et al. 2017, Gregow et al. 2017), represented the 99.5th and 99.9th percentile of 10-minute maximum and mean wind speeds (2010–2016). Wind gusts >14 m/s (50 km/h) represented the 87th percentile of FEF wind data and these had significantly more northerly direction (298.2°) than slower gusts (279.3°; Fig. 6a).

The mean snagfall direction was 84.6° (Fig. 6b), which represented a nonrandom orientation (Watson's U2 $P < 0.0001$). More than one-half the overstory trees (54%) fell within a 135° radial zone bracketing the mean wind gust heading (110°, Fig. 6a). Orientations of spruce, pine, and fir snagfall averaged 73.0°, 82.3°, and 94.4°, respectively. Spruce snagfalls were oriented

TABLE 2. Tree density (trees/ha) in 10 m radius plots within research watersheds at the Fraser Experimental Forest, Colorado.

	Lodgepole pine					Subalpine fir					Engelmann spruce					Sum of conifers				
	Standing		Fallen			Standing		Fallen			Standing		Fallen			Standing		Fallen		
Watershed	Live	Dead	Live	Dead	Total	Live	Dead	Live	Dead	Total	Live	Dead	Live	Dead	Total	Live	Dead	Live	Dead	Total
Overstory																				
Old growth	98	319	0	64	481	202	58	0	19	278	261	40	0	18	318	561	417	0	100	1,078
East Saint Louis	20	256	0	63	339	319	110	0	35	464	205	50	1	12	268	545	416	1	111	1,072
Lexen	168	185	0	39	392	405	20	0	11	435	224	24	0	6	254	797	228	0	56	1,081
Mixed age	44	170	0	28	242	285	63	0	37	384	180	30	0	17	227	508	263	0	81	853
Fool	331	931	0	194	1,456	1,210	250	0	102	1,562	869	143	1	53	1,066	2,411	1,323	1	349	4,084
Deadhorse	80	233	0	49	361	302	64	0	26	392	216	36	0	13	266	598	333	0	88	1,019
Sum of watershed	98	319	0	64	481	202	58	0	19	278	261	40	0	18	318	561	417	0	100	1,078
Mean of watersheds	20	256	0	63	339	319	110	0	35	464	205	50	1	12	268	545	416	1	111	1,072
Understory																				
Old growth	119	44	0	13	176	475	106	0	44	626	457	9	1	11	477	1,051	159	1	68	1,279
East Saint Louis	4	4	0	2	11	703	86	0	14	803	164	12	0	3	179	871	103	0	19	992
Lexen	545	68	2	24	639	1,256	50	3	9	1,318	411	7	1	4	423	2,211	125	6	37	2,380
Mixed age	75	8	0	4	87	771	56	0	15	842	164	11	0	3	178	1,010	76	0	22	1,107
Fool	744	124	2	42	912	3,205	299	3	82	3,589	1,195	40	2	21	1,257	5,144	463	7	145	5,758
Deadhorse	176	30	0	10	216	794	75	1	20	890	292	10	0	5	307	1,262	115	2	35	1,414
Sum of watershed	119	44	0	13	176	475	106	0	44	626	457	9	1	11	477	1,051	159	1	68	1,279
Mean of watersheds	4	4	0	2	11	703	86	0	14	803	164	12	0	3	179	871	103	0	19	992

Notes: Data are means and sums for overstory (>10 cm DBH) and understory (>2.5 and <10 cm DBH) trees. Snagfall density based on 2018 resampling of trees tagged in 2007.

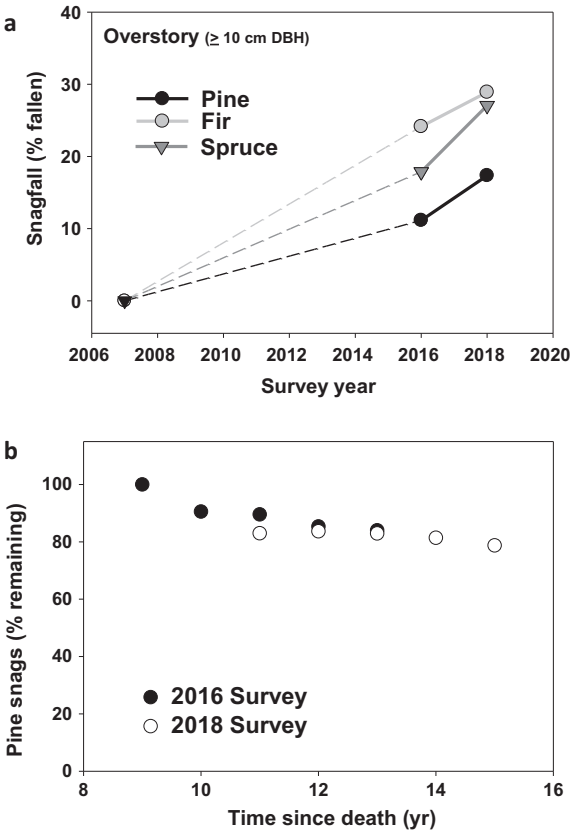

FIG. 3. (a) Snagfall of overstory (>10 cm diameter) trees measured in 2016 and 2018 at the Fraser Experimental Forest. Data are snagfall since 2007 (%) within 10 m radius plots (n = 133). Fall of live trees was minor (e.g., <3 trees per species per size class). Beetle attacks on pine peaked during 2005 and 2006. The date of tree mortality was unknown for spruce and fir. (b) The proportion of overstory lodgepole pine snags remaining for individual "year of death" cohorts (2003–2007) classified during initial sampling in 2007 and surveyed in 2016 and 2018.

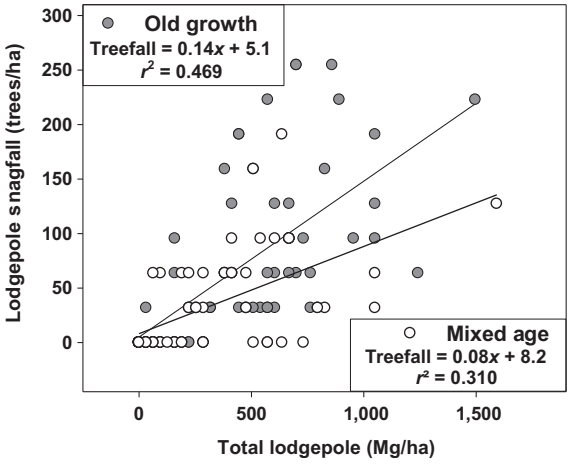

FIG. 4. Linear relation between total overstory lodgepole pine and lodgepole pine snagfall between 2007 and 2018 in old-growth and mixed-age stands at the Fraser Experimental Forest.

significantly more to the north than fir snagfalls (P = 0.04). Orientation varied among snagfall causes for pine and spruce (P = 0.0014), but not fir. Regardless of the cause, fir snagfalls aligned with the prevailing wind gusts. For pine and spruce, mean snagfall direction from butt rot was 64.0°, which differed from the direction of tip ups (94.6°; P = 0.004) and snapped boles (101.3°; P = 0.003). The direction of butt rot snagfalls was correlated with slope aspect (r = 0.189; P = 0.025) for pine and spruce, and they fell significantly north of the prevailing wind gusts (e.g., 110°; P < 0.001). In contrast, tipped and snapped snagfalls of these species were aligned with the prevailing gusts. Orientation did not differ between single or multiple stem snagfalls or between those that reached the ground compared to elevated snags.

TABLE 3. Frequency of snagfall by cause between 2007 and 2018 at the Fraser Experimental Forest.

	Lodgepole pine			Subalpine fir			Engelmann spruce		
Type	No.	%	DBH (cm)	No.	%	DBH (cm)	No.	%	DBH (cm)
Overstory (≥10 cm DBH)									
Butt rot	108	53.2	24.4 a	56	51.4	21.8 a	31	54.4	29.2 b
Tip up	66	32.5	26.1 b	35	32.1	19.0 a	16	28.1	27.1 b
Bole snap	29	14.3	27.6	18	16.5	23.1	10	17.5	29.6
Total	203		25.4 b	109		21.1 a	57		28.7 c
Understory (<10 cm DBH)									
Butt rot	26	57.8	5.1	30	33.7	5.5	13	56.5	6.3
Tip up	12	26.7	5.5	44	49.4	5.7	9	39.1	6.8
Bole snap	7	15.6	5.2	15	16.9	5.8	1	4.3	4.2
Total	45		5.2	89		5.6	23		6.4

Notes: Data are total numbers (No.), relative proportion (%), and mean tree diameter (DBH; at 1.4 m height) by species and size class. For individual and total snagfall cause classes, letters denote differences among species' diameter based on Tukey's adjusted pairwise means test at α = 0.05.

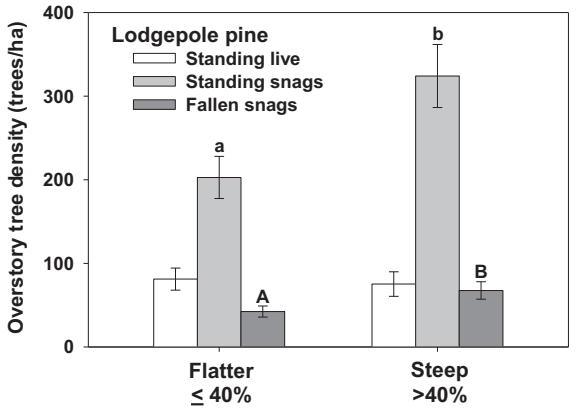

FIG. 5. Mean density and standard error bars for standing and fallen overstory lodgepole pine on steep (>40% slope, $n = 33$) and flatter (≤40%, $n = 100$) plots. Within the standing and fallen classes, different letters indicate significant differences among the means of steep and flatter slope plots at $\alpha < 0.05$.

DISCUSSION

Persistence of beetle-killed pine snags

Recent mountain pine beetle outbreaks initiated a period of dramatic change that will have prolonged consequences for North American forests (Raffa et al. 2008, Edburg et al. 2012). Bark beetles killed 78% of overstory lodgepole pines throughout the headwater forests at FEF, similar to mortality levels observed elsewhere in Colorado (Klutsch et al. 2009, Chapman et al. 2012, Collins et al. 2012, Meddens and Hicke 2014). Snagfall removed only 17% of beetle-killed lodgepole from the overstory between 2007 and 2018 (Fig. 3a), indicating slower snag dynamics than observed in lower elevation forests (Fig. 7).

Though post-bark beetle snagfall varies between species and sites (Fig. 7), most studies report a 3–5-yr lag followed by a period of significant snagfall and a leveling off after 80–90% of snags have fallen (Keen 1955, Mitchell and Preisler 1998, Page and Jenkins 2007). At FEF, we found that 11.1% of beetle-killed snags fell within 10 yr of the peak infestation with an additional 6.2% falling during the next 2 yr (Figs. 3a and 7). Assuming an initial 5-yr lag, annual snagfall at FEF averaged 2.2% between 2011 and 2016 and 3.1% between 2016 and 2018. Snagfall averaged 4.2% annually at a high-elevation site in eastern Oregon after an initial 5-yr lag (Harvey 1986); this resulted in 25% snagfall of the beetle-killed pines over 11 yr (Table 4, Fig. 7). In interior British Columbia, few snags fell during an 8-yr lag (Lewis and Thompson 2011), and the bulk fell 10–18 yr after peak infestation (Lewis and Hartley 2006). At a high-elevation site in eastern Utah, 33% of lodgepole snags remained standing 20 yr after beetle infestation (Page and Jenkins 2007). In contrast to high-elevation sites, snagfall averaged 10% annually in lower-elevation, beetle-killed lodgepole in Central Oregon and left only 10% of the snags standing after 14 yr (Mitchell and Preisler 1998). In general, in ponderosa pine stands, one-half of the snags fell within 5–10 yr of beetle infestation, resulting in 10% of snags standing after 10–20 or more years (Keen 1955, Schmid et al. 1985, Hoffman et al. 2012, Chambers and Mast 2014, Hansen et al. 2015).

Contributors to snagfall

Most of the snags we tallied at Fraser fell due to butt rot (53%), similar to findings in beetle-killed pine stands elsewhere (Keen 1955, Schmid et al. 1985, Mitchell and Preisler 1998, Lewis and Thompson 2011). All the beetle-killed lodgepole snags broke at ground level at a lower elevation site in central Oregon, (Mitchell and Preisler 1998) and 71% of conifer snags broke at the ground after California wildfires (Grayson et al. 2019). Site microenvironment and soil water content may explain variation in snagfall. Snagfall on loamy soils with higher moisture-holding capacity was higher than on coarser, drier, pumice soils (Keen 1955), though the opposite has been observed elsewhere (Lewis and Thompson 2011). Butt rot snags at FEF fell predominantly in the direction of the slope-aspect. Studies of other species document that snagfall orientation is highly variable but that it is often concentrated downhill (Rentch 2010, Oberle et al. 2016).

The slow snagfall we documented at FEF agrees with observations from other cold, high-elevation sites and differs from observations from warmer, lower elevations (Table 4, Fig. 7). Wood decay is slow in lodgepole pine forests (Harvey 1986), especially in high-elevation sites where coarse wood can persist for a century (Brown et al. 1998, Kueppers et al. 2004). After initial checking (formation of longitudinal cracks), wood deterioration proceeds slowly in beetle-killed lodgepole snags (Harvey 1986, Lewis and Thompson 2011) and they may remain standing (Page and Jenkins 2007) and retain commercial value for decades (Tegethoff et al. 1977). About one-half of the snags we tallied at FEF remained elevated above the ground where decay will be inhibited further (Fahey 1983, Busse 1994, Brown et al. 1998).

Episodic snagfall is commonly associated with strong local wind events (Keen 1955, Schmid et al. 1985), though we found no evidence of extensive blow down at FEF. However, 47% of pine snags were associated with tip ups or stem breakage and these snags were aligned with the prevailing winds. Multiple- and single-tree snagfalls were equally abundant at FEF, but the multiple-tree events were twice as likely to be associated with tip-up mounds. Elsewhere in Colorado, individual windstorms downed more than one-half of beetle-killed ponderosa snags (Schmid et al. 1985). Windspeeds sufficient to damage live trees (e.g., 25–30 m/s; Mayer 1987) are common at FEF and those known to cause stem breakage

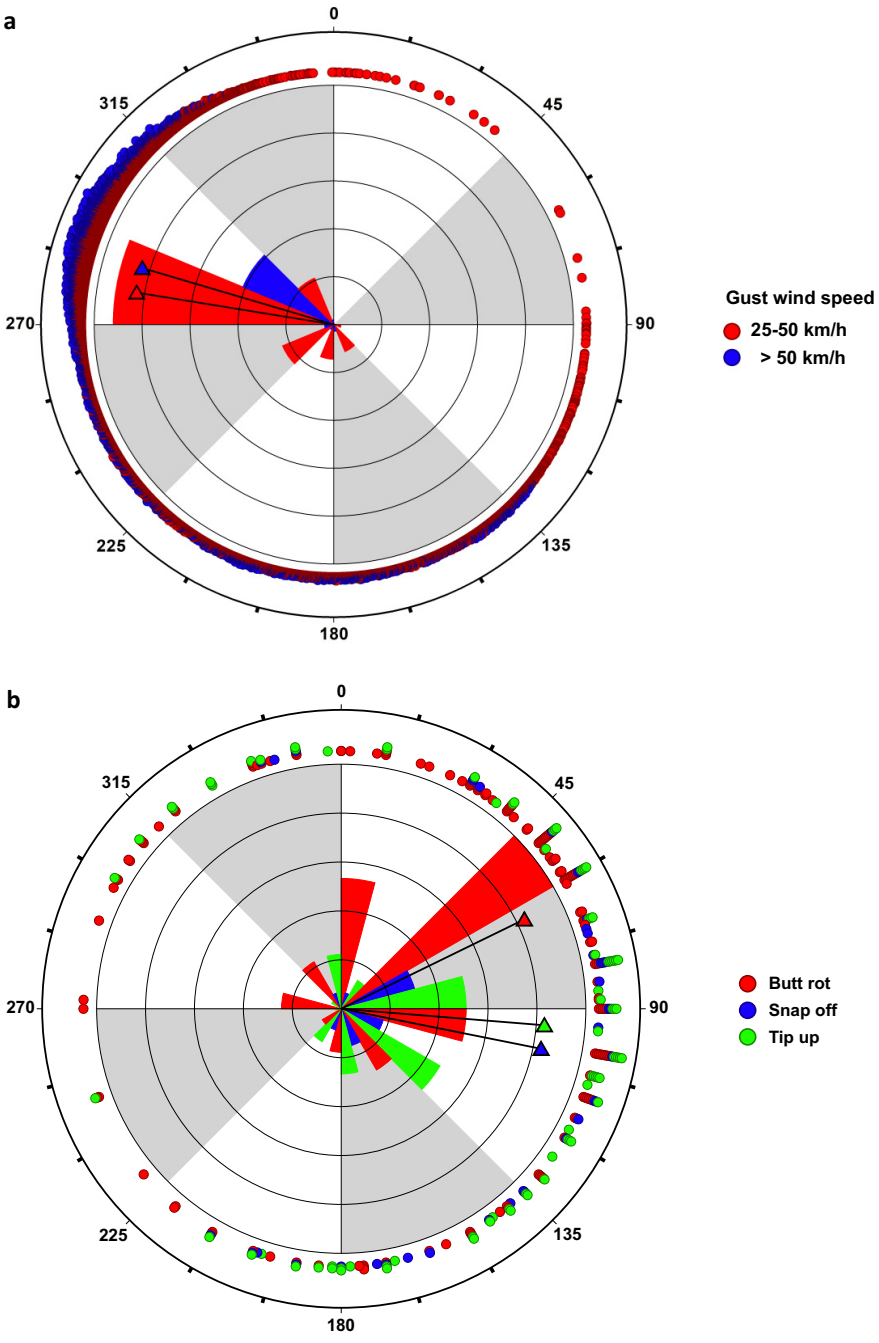

FIG. 6. (a) Wind gust and (b) snagfall direction at the Fraser Experimental Forest. Wind gusts were measured at 3,639 m elevation in an alpine landscape throughout 2011. Colored circles show the azimuth of wind gusts (a) measured at 10-minute intervals and the colored triangles show the mean azimuth. Colored wedges denote the number of observations per radial zone. All the mean directions were significantly different from a random radial distribution (Watson U2 $P < 0.001$). Mean gust directions differed at $P < 0.001$. Mean wind direction for 2011 was equal to the 5-yr mean. Colored circles show the azimuth of individual pine and spruce snagfalls (b) and the colored triangles show the mean azimuth by snagfall cause between 2007 and 2018. The colored wedges tally the numbers of trees by snagfall cause within each radial zone. Fir snagfall orientation did not differ by cause. The mean directions were significantly different from a random radial distribution (Watson U2 $P < 0.001$).

(42 m/s; Gregow et al. 2017) occurred during the study period. Gray-phase (needle-free) lodgepole resist wind damage during the first decade after infestation, though wind-related snagfall may become more prevalent if wind speeds increase as snagfall and basal decay progresses (Schmid et al. 1985, Ciftci et al. 2014).

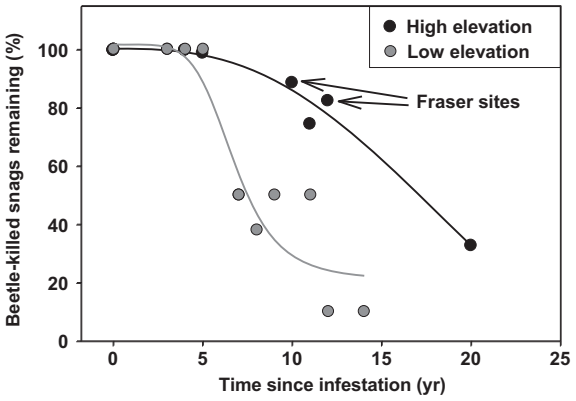

FIG. 7. Snagfall in higher (black) and lower (gray) elevation, beetle-infested, lodgepole pine forests. References and climate data for the cited data are listed in Table 4. Year since infestation at FEF is based on the peak of beetle activity in 2006. Arrows identify 2016 and 2018 resampling events at FEF.

Pine snagfall in old-growth stands was twice that of mixed-age stands (Table 2). Plots with high pine snagfall (Fig. 4, >150 trees/ha) had 2.5 times higher pine density than plots with lower snagfall and few of those plots occurred in the mixed-age forests. Mean diameter of overstory pine was statistically higher in old-growth compared to mixed-age plots (26.6 vs. 22.6 cm) and fall rate is typically less for larger snags (Mitchell and Preisler 1998, Landram et al. 2002) due to the greater volume of rot-resistant heartwood (Lewis and Thompson 2011). Nonetheless, we found that historic harvesting reduced post-beetle snagfall compared to old-growth stands due to changes in species dominance and tree size.

Implications of snag dynamics

Overstory mortality and snagfall create canopy gaps that alter forest floor conditions and influence post-outbreak responses. Previous studies of beetle-killed stands at FEF showed that seedling establishment and conifer growth increased with the degree of overstory tree mortality (Rhoades et al. 2017, Pelz et al. 2018). The single- and multiple-tree snagfalls we observed will create varying opening sizes likely to prompt distinct vegetation patterns. Similar findings have been documented for shrub growth after bark beetles in lodgepole stands in west central Alberta, Canada (Pec et al. 2015). Pit and mound topography from historic windthrow events are present but not common at FEF (C. Rhoades, *personal observation*) and elsewhere in northern Colorado (Baker et al. 2002). We found tip-up mounds on 32% of the pine snagfalls and similar proportion of overstory fir and spruce. These features create microsites that favor seedling establishment by exposing mineral soil seed beds within high-light environments (Simon et al. 2011). Live treefall was extremely rare during this study, but it and tip-up formation may become more frequent if wind speeds increase as snagfall progresses.

This study provides new insights regarding lodgepole pine snag dynamics and refines expectations regarding post-outbreak ecological conditions and commercial opportunities after severe bark beetle outbreaks in high-elevation forests. At Fraser, 17% of beetle-killed snags fell during the decade since the peak of the outbreak. Based on observations at FEF and other high-elevation lodgepole ecosystems, we estimate that one-half of the beetle-killed trees will fall within about 15–20 yr after the peak of the outbreak (Fig. 7). A period of significant snagfall, consisting of ~5% y^{-1}, is expected to continue for more than 15 yr after the initial lag period. Studies of lower-elevation lodgepole forests document snag half-life of 7.5–10 yr and a period of rapid snagfall concentrated during a 5-yr period (Fig. 7).

Our findings suggest that the influence of beetle outbreaks on snag dynamics will have ecological and

TABLE 4. Mean annual climatic conditions for beetle-killed lodgepole pine snagfall study sites.

Site	Region	Elevation (m)	Mean precipitation (mm)	Temperature (°C)			Study citation
				Min	Mean	Max	
Fraser Experimental Forest	N Colorado	3,122	750	−6.6	1.2	9.4	This study
Ashley NF	NE Utah	2,861	649	−4.9	2.3	9.5	Page and Jenkins (2007)
Anthony Lakes	E Oregon	2,250	941	−2.7	2.7	8.1	Harvey (1986)
Upper Elevation Average		2,744	780	−4.7	2.1	9.0	
Deschutes NF	Central Oregon	1,976	830	−1.0	5.7	12.4	Mitchell and Preisler (1998)
Modoc Lassen NFs	NE California	1,874	952	0.3	7.2	14.0	Landram et al. (2002)
Starkey Experimental Forest	NE Oregon	1,392	636	0.5	6.6	12.6	Bull (1983)
Lower Elevation Average		1,747	806	−0.1	6.5	13.0	

Notes: Higher and lower elevation sites correspond to the faster and slower snagfall patterns in Figure 7. NF, National Forest; N, northern; NE, northeastern; E, eastern.

commercial consequences in high-elevation forests lasting more than two decades. Based on previous work in lodgepole and ponderosa pine, it seems likely that 10–20% of beetle-killed snags (Keen 1955, Hoffman et al. 2012, Chambers and Mast 2014), equivalent to 28–56 standing snags/ha could persist for years to decades longer in FEF forests; this agrees with snag densities documented in uncut forests elsewhere in the interior Rocky Mountains (Harris 1999). The long-term fate of the beetle-killed lodgepole snags will require future monitoring, though 10% of beetle-killed ponderosa lasted for 25 yr and some stood for at least 40 yr (Keen 1955), so it is likely that relatively decay-resistant lodgepole will remain standing longer in these high-elevation sites. These snags represent a substantial reduction (7–14 Mg/ha) in the 50–70 Mg/ha input of large diameter surface fuel expected from post-beetle snagfall (Brown et al. 2003, Page and Jenkins 2007, Klutsch et al. 2009, Collins et al. 2012). The prevalence of butt rot in these snags and the abundance of new tree seedlings (Collins et al. 2011) both complicate logging of gray-phase stands, though the standing snags retain some value for saw timber and biomass (Tegethoff et al. 1977, Lewis and Thompson 2011). Striking a balance between managing fuel loads, harvesting timber, and conserving habitat value and disturbance legacies associated with post-beetle snags represents a significant land management challenge (Brown et al. 2003, Hutto 2006, Lindenmayer and Noss 2006, Buettel et al. 2017), and one that will become more complex if projected climatic changes alter wood decay and snagfall (Oberle et al. 2018).

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Data Availability

Data are available from the USDA Forest Service Research Data Archive at https://doi.org/10.2737/rds-2019-0048