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Future dominance by quaking aspen expected following short-interval, compounded disturbance interaction

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Abstract. The spatial overlap of multiple ecological disturbances in close succession has the capacity to alter trajectories of ecosystem recovery. Widespread bark beetle outbreaks and wildfire have affected many forests in western North America in the past two decades in areas of important habitat for native ungulates. Bark beetle outbreaks prior to fire may deplete seed supply of the host species, and differences in fire-related regeneration strategies among species may shift the species composition and structure of the initial forest trajectory. Subsequent browsing of postfire tree regeneration by large ungulates, such as elk (*Cervus canadensis*), may limit the capacity for regeneration to grow above the browse zone to form the next forest canopy. Five stand-replacing wildfires burned ~60,000 ha of subalpine forest that had previously been affected by severe (>90% mortality) outbreaks of spruce beetle (SB, *Dendroctonus rufipennis*) in Engelmann spruce (*Picea engelmannii*) in 2012–2013 in southwestern Colorado. Here we examine the drivers of variability in abundance of newly established conifer tree seedlings [spruce and subalpine fir (*Abies lasiocarpa*)] and resprouts of quaking aspen (*Populus tremuloides*) following the short-interval sequence of SB outbreaks and wildfire (2–8 yr between SB outbreak and fire) at sites where we previously reconstructed severities of SB and fire. We then examine the implications of ungulate browsing for forest recovery. We found that abundances of postfire spruce seedling establishment decreased substantially in areas of severe SB outbreak. Prolific aspen resprouting in stands with live aspen prior to fire will favor an initial postfire forest trajectory dominated by aspen. However, preferential browsing of postfire aspen resprouts by ungulates will likely slow the rate of canopy recovery but browsing is unlikely to alter the species composition of the future forest canopy. Collectively, our results show that SB outbreak prior to fire increases the vulnerability of spruce–fir forests to shifts in forest type (conifer to aspen) and physiognomic community type (conifer forest to non-forest). By identifying where compounded disturbance interactions are likely to limit recovery of forests or tree species, our findings are useful for developing adaptive management strategies in the context of warming climate and shifting disturbance regimes.

Key words: compounded disturbance; *Dendroctonus rufipennis*; disturbance interactions; fire ecology; Rocky Mountains; San Juan Mountains; subalpine zone; USA; wildfire.

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INTRODUCTION

In the context of climate change, a central challenge is to understand how climate-sensitive disturbances, such as wildfire and bark beetle

outbreaks, may drive ecological change (Turner 2010). There is a particular need to understand whether and when the spatial overlap of two or more ecological disturbances affecting the same site in close succession has the capacity to alter

trajectories of ecosystem recovery (Johnstone et al. 2016), a concept known as a compounded disturbance interaction (sensu Paine et al. 1998). Shifts in species composition and relative dominance (compositional resilience or recovery) or replacement of a forest by a non-forest community (physiognomic resilience or recovery; Andrus et al. 2020a) may occur if the prior disturbance modifies the occurrence, extent, or severity of the subsequent disturbance (i.e., linked disturbance interaction, sensu Simard et al. 2011). For example, high fuel loads on the forest floor from a large blowdown may result in higher burn severity (Kulakowski and Veblen 2007) and reduce the capacity for forest recovery (Buma and Wessman 2011). Or, in the absence of a modification of a subsequent disturbance by a previous disturbance, the potential for recovery may be reduced if a previous disturbance increases the proportion of individuals in a species population exposed to a subsequent disturbance—a concept termed interaction exposure effects by Shinoda and Akasaka (2020). For example, a reduction in the abundance of large trees due to a severe beetle outbreak would increase the relative abundance of small trees (Raffa et al. 2008), and thus, the proportion of the population exposed to ungulate browsing, potentially reducing the capacity for forest recovery. In this case, the pathway of processes explaining population resilience to a short-interval sequence of multiple disturbances may be more fully revealed by considering how a prior disturbance alters the proportion of a population exposed to a subsequent disturbance. Research examining pathways by which compounded disturbance interactions affect forest recovery is needed to anticipate future ecosystem dynamics (Turner 2010), resource management challenges (Vose et al. 2016, 2018), and consequences for ecosystem services (Thom and Seidl 2015).

Widespread bark beetle outbreaks (*Dendroctonus* spp.) and wildfire have affected many forests in western North America in the past two decades (2000 to present, Hicke et al. 2016, Vose et al. 2018, Sommerfeld et al. 2018) in areas of important habitat for native ungulates (Ivan et al. 2018). The potential for links between bark beetle outbreaks and subsequent wildfire activity has motivated many fire behavior modeling and retrospective studies under varying weather

conditions and time since bark beetle attack in coniferous forests of the U.S. Rocky Mountains (Kane et al. 2017, Hart and Preston 2020). However, far fewer studies address whether bark beetle outbreaks followed by fire produce compounded disturbance interactions, particularly in forest ecosystems without canopy seed banks (e.g., species other than lodgepole pine, *Pinus contorta*; Talucci et al. 2019). Even if bark beetle outbreaks do not increase the severity of wildfire, prior outbreaks may compromise resilience of the host tree population by reducing seed supply to support postfire seedling establishment (Harvey et al. 2013). Burned conifer forests also increase the relative abundance of juvenile trees, which may alter the exposure of some or all tree species to browsing by ungulates after fire. The extensive areas affected by wildfire and bark beetles, separately or overlapping spatially, within habitat for ungulates imply that negative effects of disturbance interactions on recovery mechanisms may have widespread implications.

The mortality of dominant seed-producing trees of a host species or genus from bark beetle outbreaks may reduce chances for postfire regeneration of seed-obligate conifers (Raffa et al. 2008), which rely on in situ seed availability (serotinous species) or dispersal of seed from adjacent unburned patches (non-serotinous species) for postfire regeneration (Rowe 1983, Agee 1996). Substantial declines in the dominant seed-producing trees from a severe bark beetle outbreak (Andrus et al. 2020b) or large, stand-replacing patches that kill fire-sensitive species may sufficiently reduce seed supply or increase distance to seed source for one or more species, thereby limiting postfire establishment. Seed-obligate species unaffected by the outbreak and species that regenerate vegetatively (root suckering) following fire, such as quaking aspen (*Populus tremuloides* Michx.; Baker 1925), may represent a higher proportion of the postfire stems than would be expected if the stand had not experienced a bark beetle outbreak (Kulakowski et al. 2013). Success of seedling establishment and resprouts may also be affected by ungulates, such as elk (*Cervus canadensis*; Romme et al. 1995, Bailey and Whitham 2002), which can lower recruitment rates into the forest canopy after fire for decades by repeatedly removing the apical meristem (Seager et al. 2013, Rhodes et al.

2017). Given the complexity of interacting factors affecting postfire tree recovery, research that examines how prior (bark beetle) or subsequent (herbivory) disturbance affects the variability in abundance and success of postfire regeneration among species is essential to assessing the potential for compositional or physiognomic recovery.

Subalpine forests in the Rocky Mountains may be particularly vulnerable to compounded disturbance interaction effects, because they have limited capacity to resist bark beetle outbreaks (Raffa et al. 2008, Windmuller-Campione and Long 2015) or stand-replacing fire (Schoennagel et al. 2004, Sibold et al. 2006). Outbreaks of spruce beetle (SB, *Dendroctonus rufipennis* Kirby) in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) have affected vast areas of spruce and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests in the past two decades (Hicke et al. 2016), especially in the southern Rocky Mountains (Hart et al. 2017, Colorado State Forest Service 2018). Although prior studies in spruce–fir forests in the southern Rockies have documented, only modest or neutral effects of SB outbreaks on fire frequency (Bebi et al. 2003), extent (Bigler et al. 2005), and severity (Andrus et al. 2016), loss of seed sources from SB outbreaks may limit postfire spruce seedling establishment (Carlson et al. 2020). Vulnerability to slow or failed postfire recovery of spruce (and fir) is implied by the following species' traits: non-serotinous cones, infrequent cone production, and short-lived seedbanks (i.e., one-year viability; Alexander 1987, Buechling et al. 2016). In the absence of prior SB outbreak, spruce and fir seedling establishment and aspen resprouts can occur within the first decade following fire (Rebertus et al. 1991, Coop et al. 2010, Kulakowski et al. 2013, Gill et al. 2017). Because aspen and spruce recolonize burned areas at a higher rate than fir (Whipple and Dix 1979, Rebertus et al. 1991), the reduction of large spruce due to SB outbreaks prior to fire and browsing of aspen ramets by ungulates may have important implications for postfire recovery. To our knowledge, how postfire recovery is affected by fire shortly after a SB outbreak (~5 yr between outbreak and fire) and how ungulate herbivory effects recovery following these two disturbances has not previously been investigated.

Here we explore variability in subalpine forest recovery following a short-interval sequence of

bark beetle outbreaks, wildfire, and ungulate herbivory in southwestern Colorado. We resampled sites where we had previously reconstructed bark beetle and fire severity (Andrus et al. 2016) to investigate two questions: (1) How was initial postfire tree regeneration affected by bark beetle severity, pre-fire forest composition, and distance to forest patches surviving fire? (2) How was postfire regeneration success influenced by browsing by large ungulates? For research question 1, we expect the following: (1) The abundance of postfire aspen stems will be greater in stands with live pre-fire aspen, (2) abundance of postfire spruce establishment will be lower in areas with lower postoutbreak live spruce basal area due to lower seed availability, and (3) abundance of postfire conifer establishment will decrease with distance from nearest seed source. For research question 2, we expect (4) postfire stems of more palatable and abundant postfire species (aspen) will be browsed more frequently than less palatable and abundant postfire species (spruce and fir); consequently, ungulate browsing will slow the rate of recovery and tend to shift postfire trajectories away from aspen and toward conifer dominance.

METHODS

Study area

The study area consists of five lightning-ignited wildfires that burned (area burned >60,000 ha) through subalpine forests relatively unaffected (<10% mortality) to severely affected (90% mortality) by spruce beetle outbreak (1–8 yr from outbreak to time of fire) in 2012 or 2013 in southwestern Colorado (Table 1, Fig. 1). All plots were located in subalpine forests (2600–3500 m) dominated by Engelmann spruce and subalpine fir and containing variable amounts of aspen prior to the SB outbreak and fires. In lower subalpine forests, Douglas fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) are present at low abundances; however, lodgepole pine is not common in the study area. The subalpine zone is characterized by steep mountainous terrain, and a cool and moist climate; snowpack persists late into the spring (June) and summer monsoon rains occur from mid-July to September (Romme et al. 2009). Total annual precipitation ranges from 57 cm (East Fork fire) to 98 cm (West Fork

Table 1. Descriptions of five fires in southwestern Colorado, USA, the number of plots sampled in each fire (*n*), and the median (25th and 75th percentiles) density of postfire conifer establishment and aspen stems by species in each fire (number of new stems per ha).

Fire	Area burned (ha)	Fire year	Elevation (m)	Severity (%)			No. plots	Postfire stem density(no./ha)		
				High	Mod./Low	Unburned		Fir	Spruce	Aspen
Papoose	22,400	2013	3105 (3305–2884)	76	17	7	16	0 (0, 0)	0 (0, 0)	7100 (3325, 9690)
West Fork	25,700	2013	3090 (3490–2611)	73	19	7	13	0 (0, 0)	0 (0, 0)	0 (0, 2600)
Windy Pass	1,400	2013	3222 (3256–3150)	33	56	11	5	0 (0, 0)	0 (0, 0)	0 (0, 0)
East Fork	450	2013	3319 (3481–3099)	52	33	15	5	1778 (717, 2621)	2296 (1595, 2795)	1113 (102, 2683)
Little Sands	10,000	2012	2831 (2911–2792)	22	55	23	7	0 (0, 0)	0 (0, 200)	5200 (4200, 7175)

Notes: Area burned is from GeoMAC (USGS 2014). High severity (%) is the percentage of each fire where tree mortality was estimated at 100%, moderate/low severity is estimated at >0% but <100%, and unburned did not burn (estimated from field calibration of Relative differenced Normalized Burn Ratio [RdNBR] data, see Appendix S1). Elevation is mean and range.

Complex; 1950–2018; PRISM 2019). Average annual temperatures are 1.8°C (West Fork Complex) to 2.8°C (East Fork fire; 1950–2018, PRISM 2019) with temperatures reaching an average monthly maximum of 19.6°–21.9°C in July and minimum of –14.1° to –13.1°C in January (1950–2019, PRISM 2019). Temperatures increased by about 1°C from 1975 to 2012 in the subalpine zone (Kelsey et al. 2018).

The SB outbreak initiated in about 2005 in the eastern San Juan Mountains and by 2013 had affected ~270,000 ha in this area (Fig. 1; USDA 2018). When the fires burned, most beetle-killed Engelmann spruce had been dead for approximately 5 yr, as evidenced by the absence of a majority of needles and the presence of most fine branches and bark (Andrus et al. 2016). Severity of the SB outbreak varied within and among fires with the highest SB severity in the West Fork Complex fires (median plot basal area infested, 96%; range, 9–100%) and much lower severity in the Little Sands fire (median plot basal area infested, 34%; range, 0–100%) and East Fork fire (median plot basal area infested, 0%; range, 0–86%; Andrus et al. 2016). In the West Fork Complex, the majority of the burned area did not include any surviving trees (Table 1), though there was considerable heterogeneity in fire severity (Appendix S1: Fig. S1). The fires burned in remote areas with minimal suppression efforts, and sampling was

conducted in areas without evidence of active suppression (firelines or chainsaw activity) or replanting (USFS 2019).

Sampling design

In summer 2014, we reconstructed stand structure and composition prior to the SB outbreak, following the SB outbreak but prior to the fire, and after the fire in 143 randomly located plots (0.04 ha) >100 m from the fire perimeter (Andrus et al. 2016). Following well-established methods detailed in similar studies (e.g., Harvey et al. 2013), we assessed pre-fire spruce beetle severity by removing the bark from dead trees to examine the cambium for evidence of *Dendroctonus* activity or when cambium was burned, inferring prior *Dendroctonus* activity based on depth of charring. In summer 2019, we relocated and surveyed pre-fire and postfire live stems (seedlings and ramets) in 45 plots where SB outbreak and fire severity were previously reconstructed. Original plot locations were not marked, but a GPS unit with an accuracy of ±5 m was used to relocate plot centers. Plots for the current study were selected to include a range of SB outbreak and fire severities and pre-fire stand compositions (with and without aspen). Sampling for the current study was conducted 6 yr after the West Fork Complex and East Fork Fire and 7 yr after the Little Sands Fire. Plot aspect (°), slope (°), elevation (m), and geographic position (UTMs)

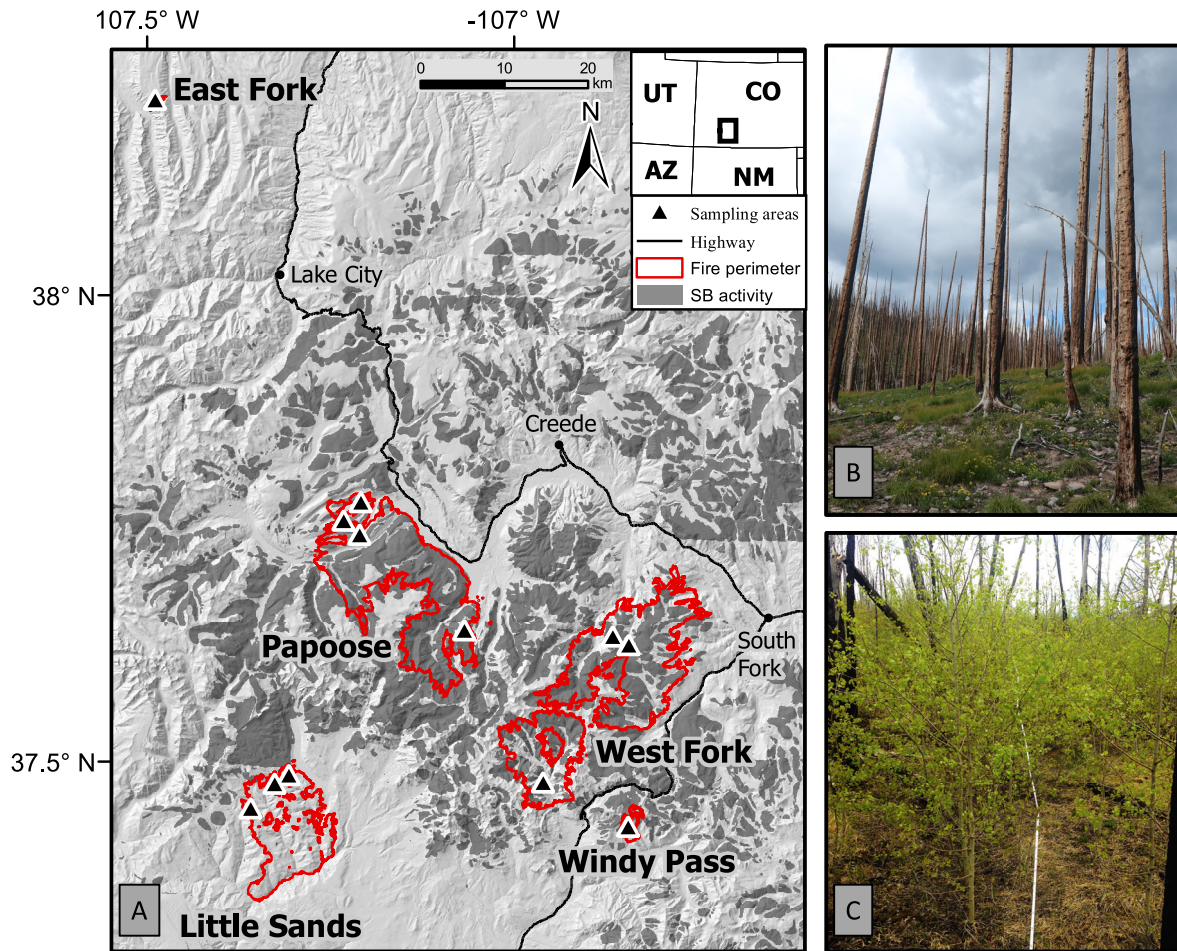


Fig. 1. (A) Study area map illustrating sampling areas (collections of plots, $n = 5\text{--}16$ per triangle) and spruce bark beetle activity from 1995 to 2013 (dark gray) and the perimeter of the five subalpine fires in the southern Rocky Mountains, USA. Photographs show (B) example of very low abundances of postfire establishment following high-severity bark beetle outbreak and high-severity fire, and (C) abundant aspen resprouts and no post-fire conifer establishment following high-severity bark beetle outbreak and high-severity fire. In (A), SB activity spatial data are from the USDA Aerial Detection Survey (USDA 2018) and fire data are from GeoMAC (USGS 2014). All fires burned in summer 2013, except the Little Sands Fire which burned in 2012. Photo credit: R. Andrus.

from Andrus et al. (2016) were confirmed in the field in summer 2019.

In each relocated plot, we surveyed pre-fire and postfire juveniles (conifer seedlings and aspen ramets >5 cm height and <4 cm dbh) as well as surviving trees (>4 cm dbh) in two 2×50 m transects located at plot center. The azimuth of the first transect was selected at random, and the second transect was perpendicular to the first. We used bud scar counts and seedling size (all postfire conifer establishment

<20 cm tall) to determine whether conifer seedlings established pre-fire ($>6\text{--}7$ yr old) or postfire ($<6\text{--}7$ yr old; Urza and Sibold 2013). Conifer seedlings <5 cm tall were not surveyed because mortality rates are $>95\%$ (Kueppers et al. 2017). We assumed the majority of aspen stems in burned areas were ramets, though we acknowledge a small portion of aspen stems in burned areas may have originated from seed. For conifer and aspen juveniles (separately), we surveyed a minimum of 2×25 m on the first transect. If

conifer or aspen juvenile density was <1 stems per 1 m^2 in the first 25 m of transect 1, we surveyed an additional 25 m until we surveyed >50 stems. Aspen stems were sampled separately from conifers, because they regenerate asexually in dense clusters. For each live individual encountered, we recorded species, height (cm), and a browse rating. Ungulate browsing of the apical meristem (i.e., leader) has an important effect on recruitment into the canopy (Rhodes et al. 2017), so we created two browse rating categories: (1) light, $<10\%$ browsed, apical meristem not browsed and (2) heavy, $11\text{--}100\%$ browsed, apical meristem browsed.

We recorded Euclidean distance from plot center to the nearest postfire live seed tree with current or past year cones present on or beneath the tree for each conifer species with seedlings in each plot and the distance to nearest pre-fire live aspen (TruPulse 200 Rangefinder). If distance to nearest conspecific adult exceeded 200 m, we measured the Euclidean distance from plot center to the nearest conspecific adult (typically unburned edge with many adults) identified in pre-fire (2010) NAIP imagery (1-m resolution) in Google Earth (Aerial Photography Field Office 2016).

Analytical methods

Postoutbreak and pre-fire forest types.—To understand how pre-fire forest composition affects initial forest trajectories following SB outbreaks and wildfire, we classified each stand into one of two stand types based on the proximity to nearest pre-fire live aspen. Postfire aspen stem density decreased substantially when pre-fire live aspen were >100 m from plot center (Appendix S2: Fig. S1), and thus, we defined pre-fire stand types as (1) conifer (spruce–fir, plot center >100 m from pre-fire live aspen) or (2) conifer–aspen (plot center <100 m from pre-fire live aspen).

Drivers of postfire regeneration density.—To test factors affecting postfire conifer establishment (conifer model) and aspen stem abundance (number per hectare; aspen model), we constructed zero-inflated generalized linear models with a negative binomial distribution (ZINB; pscl package in R; Zeileis et al. 2008). Zero-inflated models were necessary to account for the high abundance of plots with zero postfire stems (score test for zero inflation for aspen model and

conifer model, $P < 0.001$; van den Broek 1995). The negative binomial error structure accounted for significant overdispersion in Poisson models (Smith et al. 2009). In the aspen model and conifer model, we tested three predictor variables in the zero and count models (one additional variable in the conifer model); predictor variables varied with primary regeneration mode of each tree species (seed vs. resprouting). For predictor variables, we tested (1) distance to seed source to account for proximity to available seed (conifer model) or distance to nearest postoutbreak, pre-fire (hereafter, pre-fire) live aspen to account for proximity to roots for resprouting (aspen model). To account for seed quantity (conifer model) or root quantity (aspen model), we tested (2) pre-fire conspecific live basal area in the plot. In the conifer model, pre-fire conspecific basal area of spruce significantly decreased with spruce basal area killed by SB (spearman $\rho = -0.74$, $P < 0.001$). We chose to include conspecific basal area rather than spruce beetle severity (%), because it is a better indicator of spruce seed availability for postfire spruce establishment and incorporates much of the variability that would be explained by spruce beetle severity. To examine variability in regeneration abundance with soil moisture, we used the Topographic Wetness Index (TWI; Beven and Kirby 1979), which integrates water inputs from upslope areas and water loss due to local slope. In the conifer model only, we also included species to account for differences between spruce and fir (see Appendix S2: Table S1 for further description of predictors). ZINB models were trimmed by dropping individual predictor variables from a full model with all potential predictors and comparing nested models with a likelihood ratio test (lmtest package in R, Zeileis and Hothorn 2002). Prior to model construction, all predictor variables were standardized to allow comparison of model coefficients. Residuals for both models were checked (Smith et al. 2009). We used pseudo r^2 (coefficient of determination based on the likelihood ratio test in MuMIn package in R; Bartoń 2018) to quantify the variability explained by each ZINB model, because true model R^2 values for generalized linear models are not available.

Comparing ungulate herbivory by juvenile height class and species.—Preferential browsing of one or

more tree species within the browse zone (<200 cm tall; max. browsing height for elk) can have important effects on forest recovery dynamics (Rhodes et al. 2017, Andrus et al. 2020a). Consequently, we examined the proportion of postfire stems heavily browsed by plot for each species. Using a non-parametric, one-way Mann–Whitney U test ($\alpha = 0.05$), we statistically compared whether the proportion of heavily browsed aspen was greater than fir and spruce (which are expected to be less palatable) for post-fire stems <200 cm tall. We also examined the variability in postfire aspen stems (5–200 cm tall) heavily browsed by height.

RESULTS

Variability in postfire aspen stems and conifer establishment

Conifer seedling establishment and stem density of aspen resprouts after fire varied with pre-fire stand composition (Table 2). Relative to the high densities of aspen ramets (median 6475 per ha) in stands with live aspen prior to fire (conifer–aspen forest type), the density of post-fire conifer establishment was very low (spruce and fir: median 0 seedlings/ha) in both pre-fire stand types (Table 2) and most fires (4 of 5, Table 1). Postfire stems of all species were absent (i.e., 0 individuals/ha) in 74% of pre-fire conifer stands, whereas all stands in conifer–aspen forest type contained some postfire stems (median individuals for all species, 6662 per ha). Postfire conifer establishment was consistently low across forest types with postfire conifer establishment absent in >80% of sampled stands. Among conifers, postfire spruce establishment was more abundant than fir establishment (Table 1). Few adult trees (>4 cm dbh) survived the fire (Appendix S1: Table S1) and low abundances of conifer juveniles (<4 cm dbh) that established prior to the fire were present along the unburned forest edge (Appendix S1: Table S2).

The absence (zero model) and abundance (count model) of postfire aspen stems and conifer establishment was affected by the distance to nearest conspecific adult (mature postfire live conifer or pre-fire live aspen) and pre-fire conspecific basal area (Table 3). For aspen, we found that both presence and abundance of postfire stems significantly decreased with distance to

Table 2. Median (and 25th and 75th percentiles) density of postfire stem density (number per ha establishing or resprouting after fire) in two pre-fire forest types.

Pre-fire forest type	No. plots	Postfire stem density (no./ha)			
		Fir	Spruce	Aspen	All species
Conifer	19	0 (0, 0)	0 (0, 0)	0 (0, 0)	0 (0, 100)
Conifer–aspen	26	0 (0, 0)	0 (0, 0)	6475 (4473, 8853)	6662 (4675, 8853)

Note: Conifer stands include subalpine fir and Engelmann spruce.

nearest pre-fire live aspen. While a likelihood ratio test suggested pre-fire live aspen basal area (slight positive effect) did not statistically improve model fit ($P = 0.236$), we retained it in the full model because it improved residual diagnostics. The abundance of aspen stems decreased substantially when the nearest aspen adult was >100 m away (Appendix S1: Fig. S1). For conifers, lower pre-fire conspecific basal area (indicator of seed availability at the unburned forest edge and the severity of the spruce beetle outbreak) decreased the chances of seedling presence (zero model, Table 2). Spruce seedling establishment was only found where postoutbreak spruce basal area was >20 m²/ha (i.e., areas with low SB severity; Appendix S2: Fig. S1). When conspecifics were present, conifer establishment decreased with distance to nearest post-fire live conspecific adult (count model, Table 2). No postfire conifer establishment was found >100 m from the nearest postfire live conspecific adult (Appendix S2: Fig. S2). Spruce and fir did not differ in these relationships (likelihood ratio test of nested model with species, $P = 0.15$). TWI had no effect on abundance of aspen stems or conifer establishment. The aspen model explained 66% of the variance and the conifer model explained 28% of the variance (pseudo R^2). To account for differences in climate among fires that may influence postfire establishment patterns, we examined temporal variability in water year and summer drought indices and found that they were similar among all fires (Appendix S2: Fig. S1), though climate is warmer and drier in the East Fork fire (see *Methods*).

Effect of ungulate herbivory on postfire regeneration.—Ungulates heavily browsed 23.3%

of all postfire stems (conifer establishment 5–20 cm and aspen stems 5–200 cm) in the browse zone and 17.6% (median, range 0–100%) of postfire stems (<200 cm) across all plots (Fig. 2; Appendix S2: Fig. S3). However, browsing varied by species (Fig. 2A) and stem height (aspen only, Fig. 2B). Aspen stems (median, 16.8%) were heavily browsed more frequently than fir (0%; Mann–Whitney $W = 206$, $P < 0.001$) or spruce (0%; Mann–Whitney $W = 88$, $P = 0.004$; Fig. 2A). The proportion of aspen heavily browsed was greatest at ~80 cm, and individuals shorter and taller were heavily browsed less frequently (Fig. 2B). Most aspen stems (63%) were <100 cm tall, and 93% was shorter than the browse zone (2 m; Fig. 2B; Appendix S2: Table S4).

DISCUSSION

The abundance and composition of postfire tree regeneration were strongly shaped by pre-fire stand composition and effects of the prior bark beetle outbreaks on seed availability following five stand-replacing wildfires that burned 60,000 ha in subalpine forest in the southern

Rocky Mountains. As expected, very low abundances of postfire Engelmann spruce seedling establishment were observed in areas experiencing severe SB outbreaks prior to wildfire. Prolific aspen resprouting in stands with pre-fire live aspen will favor postfire aspen dominance for at least the next several decades. Low abundances of conifer establishment and high abundances of aspen stems are emerging as a common response to compounded disturbances in subalpine forests in the southern Rocky Mountains (Buma and Wessman 2011, Kulakowski et al. 2013, Gill et al. 2017). Preferential browsing of aspen stems will likely slow the rate of canopy recovery rather than alter the species composition of the future forest canopy in our study area. Overall, the

Table 3. Zero-inflated negative binomial model results for absence (zero model) and abundance (count model) of postfire aspen stems (aspen model) and conifer seedling establishment (conifer model).

Model	Predictor	Beta	SE	z	P
Aspen model					
Count model	Intercept	6.911	0.3019	22.89	<0.001
	Distance	-3.038	0.523	-5.81	<0.001
	Conspecific BA	0.145	0.122	1.18	0.236
Zero model	Intercept	-0.187	0.650	-0.28	0.774
	Distance	4.108	1.272	3.23	0.001
Conifer model					
Count model	Intercept	5.440	0.363	15.00	<0.001
	Distance	-5.864	1.162	-5.05	<0.001
Zero model	Intercept	2.512	0.457	5.50	<0.001
	Conspecific BA	-1.344	0.413	-3.25	0.001

Notes: Predictor variables for both the zero and count models included: (1) Distance (Distance) to nearest postfire live adult tree (conifer model) or postoutbreak, pre-fire live adult aspen (aspen model) and (2) postoutbreak, pre-fire conspecific basal area (conspecific BA). Conspecific basal area was lower in areas with higher spruce beetle severity (see *Methods*). Model results are standardized beta coefficients, standard error (SE), z score, and P value. Bold P -values indicate statistically significant effects ($P < 0.05$).

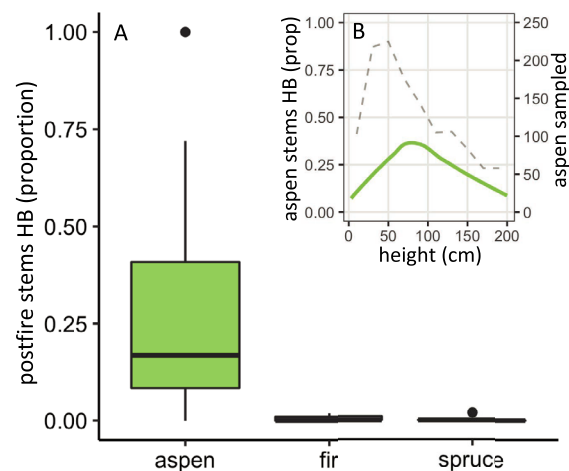


Fig. 2. Proportion of postfire stems 5–200 cm heavily browsed (HB, >10% foliage and apical meristem browsed) by (A) plot for subalpine fir, Engelmann spruce, and aspen and (B) height (cm) for all aspen stems (green line, $n = 1275$). In (A), proportion is computed as number of postfire stems heavily browsed by species divided by total number of postfire stems by plot for stems shorter than the maximum browsing height (200 cm). (B) Proportions are displayed using a loess smoother (smoothing window, 0.75 cm), and dashed gray line is the number of aspens sampled in 20 cm bins. In the boxplots (A), the thick horizontal line within the box is the median, and the lower and upper hinges represent the interquartile range (IQR; 25th–75th percentiles) of the distribution. The whiskers extend ± 1.5 times the IQR to form the limit for outliers (black dots).

mechanisms by which prior disturbances have affected recovery following subsequent disturbances appear to be consistent with Shinoda and Akasaka's (2020) concept of interaction exposure effects of multiple disturbances.

Regeneration abundance and composition following bark beetles and fire

The very low abundance of spruce seedlings and dominance of aspen regeneration in stands previously dominated by spruce is evidence that severe SB outbreaks prior to fire can result in shifts in species composition and vegetation type (i.e., compounded disturbance effects). Previous studies have documented strong resilience of spruce following high-severity fire via abundant establishment of new seedlings (Rebertus et al. 1991, Coop et al. 2010) and following SB outbreaks via release of subcanopy populations (Veblen et al., 1991, Andrus et al. 2020a) in the southern Rocky Mountains when these disturbance events are separated by many decades. However, the combined loss of spruce seed sources from SB (as indicated by conspecific basal area in our study) and fire in the present study lead to no postfire spruce seedling establishment in many stands (80% of stands) and high abundances of aspen in stands with pre-fire live aspen (100% of stands). This result is consistent with the findings from a similar study focused on one of the fires we studied (Carlson et al. 2020). In stands with low levels of spruce mortality (<10% spruce basal area mortality from SB), we found much higher abundances of post-fire spruce seedling establishment (conifer establishment >2000 seedlings per hectare) that greatly exceeded desired management stocking levels (370 conifer seedlings per hectare; USDA 2017). By examining regeneration patterns across a gradient of SB outbreak severity, we show that reduced spruce seed sources increased the exposure of the spruce population to failed postfire recovery (Shinoda and Akasaka 2020) instead of any effect of the SB outbreak on fire severity.

Differences in fire-related regeneration traits among subalpine tree species help explain the variability in abundance and composition of postfire regeneration. The capacity for extensive aspen root systems to survive fire and resprout vegetatively, even in stands with very low abundances (one individual) of pre-fire live aspen

(Baker 1925, Peet 1981), gives aspen a distinct advantage over conifers in the initial phase of postfire forest recovery. Consistent with postfire studies of seed-obligate species in spruce–fir forests (Coop et al. 2010) and other high elevation forests (Harvey et al. 2016), seed availability was an important limitation for postfire conifer establishment in our study. Conifer seedling establishment occurred with sufficient seed availability on the unburned forest edge (as indicated by pre-fire conspecific live basal area), and conifer abundance declined with increasing distance to seed supply. Conifer establishment was absent at distances greater than 100 m from seed trees, which is a distance where substantial declines in seedling abundance for wind-dispersed conifers following fire are often observed (Kemp et al. 2015). Very limited conifer establishment is expected to persist for decades because spruce juveniles will likely require decades to reach reproductive maturity (Andrus et al. 2020b), years of high seed production are infrequent for spruce and fir (every 2–5 yr; Alexander 1987, Buechling et al. 2016), and climate conditions suitable for spruce and fir establishment are becoming increasingly less frequent (Andrus et al. 2018).

Warmer and drier conditions are increasingly implicated as a key driver of low abundances of postfire conifer establishment following fire in dry forests especially at lower elevations (e.g., Welch et al. 2016, Davis et al. 2019, Rodman et al. 2019a), but variability in postfire spruce establishment appears to be better explained by the effect of SB outbreak severity on seed availability in our study of subalpine forests. Across all fires, postfire climate conditions (2013–2018) were generally unfavorable for spruce (and fir) seedling establishment as summer and water year moisture availability were below average (1950–2018; Kueppers et al. 2017, Andrus et al. 2018). Young spruce and fir seedlings have very high rates of mortality from climatic and topographic effects on moisture (typically >99% mortality after 4 yr; Kueppers et al. 2017), and survival and thus our detection of seedlings was most likely affected by postfire climate in some capacity. However, we observed the highest abundances of spruce establishment in the fire in the driest geographic location (East Fork fire) during relatively unfavorable years for establishment. Higher

abundances of postfire spruce establishment in areas relatively unaffected by SB outbreaks and scarce spruce establishment in areas severely affected by SB outbreak suggest that the effect of the SB outbreak on seed availability is likely a key contributor to failed postfire spruce establishment, a finding also reported by Carlson et al. 2020 for the West Fork Fire.

Scarce fir seedling establishment in many of the same areas where spruce establishment also failed may be explained by multiple factors. Years of abundant cone production for subalpine fir tend to be less frequent than for spruce (Alexander 1987), resulting in multi-year intervals of insufficient seed supply for fir. Fir, a more shade-tolerant species, typically establishes at much lower abundances than spruce and sometimes a multi-decadal lag occurs following fire (Veblen 1986, Aplet et al. 1988, Rebertus et al. 1991). In our study, fir seed availability was likely low at the unburned forest edge (median fir basal area <7 m²/ha; Andrus et al. 2020b) and fir in some areas may have been affected by western balsam bark beetle (WBBB, *Dryocoetes confusus*; Andrus et al. 2020a). Additionally, larger fir seeds may disperse shorter distances than spruce seed and postfire seedbeds (e.g., bare mineral soil) and microsite conditions (i.e., no shade) are generally considered unsuitable for fir establishment (Knapp and Smith 1982, Alexander 1987). However, further research is needed to determine whether failed postfire conifer establishment in the West Fork Complex fires is the result of limited seed delivery and/or unsuitable site or climate conditions.

Effects of ungulate herbivory on forest recovery following bark beetle outbreaks and fire

Ungulate browsing is affecting the success of postfire forest recovery, primarily for the more abundant and palatable postfire species, aspen. Postfire conifer establishment was relatively unaffected by browsing in our study. In neighboring subalpine forests affected by bark beetle outbreaks only (Andrus et al. 2020a), much higher proportions of juveniles (~55%, <4 cm dbh), including conifers, were heavily browsed. Lower rates of browsing on conifers in the present study may reflect their short stature (<20 cm tall) as postfire aspen stems below this height were also browsed much less frequently. Given

the very low abundances of postfire conifer establishment in stands severely affected by SB outbreaks, forest physiognomy recovery is contingent on the successful recruitment of aspen into the forest canopy. Here we found 93% of aspen stems were still vulnerable to browsing (i.e., <200 cm tall) six to seven years postfire. However, the rates of browsing on aspen apical meristems in our study (median across plots, 17%) were below 30%, which has been proposed as the critical threshold for successful recruitment of aspen sprouts into the canopy (Rhodes and St. Clair 2018). Thus, ungulate browsing may slow the rate of canopy recovery, but the future forest canopy is likely to be dominated by aspen in sites where aspen was present prior to fire. The stand-replacing fires increased the relative abundance of juvenile trees and the overall proportions of trees susceptible to ungulate browsing (i.e., exposure disturbance interaction, Shinoda and Akasaka 2020), which in turn affects the rate and trajectory of forest recovery.

Implications of expected increases in bark beetle outbreaks and wildfire for management of subalpine forests

Adapting forests to uncertainty in the outcomes of environmental change is a key challenge for natural resource scientists and managers (Millar and Stephenson 2015, Vose et al. 2018, Halofsky et al. 2018). Appropriately addressing these challenges requires robust scientific knowledge of ecological systems and consideration of societal values as well as the time scales under which the dynamics of these systems operate (Higuera et al. 2019). Continued warming and more extreme droughts are anticipated to further increase the area affected by bark beetles and wildfire activity in the next several decades (Raffa et al. 2008, Temperli et al. 2015, Abatzoglou and Williams 2016).

By identifying when initial postfire trajectories following bark beetle outbreaks may indicate potential shifts in tree species composition and loss of forest cover, our results improve understanding of the dynamics of subalpine ecological systems and help inform where and when management action may be needed. Greater area affected by the spatial overlap of bark beetle outbreaks and fire may result in forest cover loss for

non-serotinous, seed-obligate species with short-term seed viability, such as Engelmann spruce and subalpine fir (present study, Kulakowski et al. 2013). Very low densities of postfire spruce establishment in areas severely affected by spruce beetle and greater distances from seed sources indicates that management action to promote recovery of spruce, such as planting in areas with a high chance for success (cooler, wetter locations), may be necessary if the goal is to maintain spruce populations or forest cover in areas that burned. Indeed, postfire planting of spruce is already occurring in some locations within the West Fork Complex (USFS 2019). However, the slow nature of subalpine forest recovery following disturbance (Rodman et al. 2019b) and shifting climate space for subalpine species as climate warms (Bell et al. 2014) implies that management action to support postfire compositional recovery of spruce may be a short-term fix, particularly in marginal sites (e.g., lower elevation, drier sites). If the goal is to maintain forest cover, strategies that facilitate movement of species (e.g., assisted migration) suitable to current and future climate and disturbance regimes may be preferred (Millar et al. 2007). However, the risks of such management interventions need further study (Hill and Ex 2020) and the remote location of spruce–fir forest in designated wilderness boundaries often precludes the use of management equipment and strategies.

Apparent increases in forest cover for species that reproduce vegetatively (aspen) from fire may be critical to maintaining forest cover. Negative feedbacks between aspen forest and subsequent disturbance (fire, bark beetles, or blowdown) may reduce future forest vulnerability to disturbance in subalpine forests (Veblen et al. 2001, Baker et al. 2002, Bigler et al. 2005, Shinneman et al. 2013). Alternatively, the potential for aspen forest cover to increase following disturbance may be offset by its shrinking suitable habitat under climate warming (Rehfeldt et al. 2009) and the susceptibility of aspen to climate-caused die-off (Anderegg et al. 2012). Complex interactions and feedbacks among disturbances, vegetation, and climate create significant uncertainty about the response to disturbance interactions and the future distribution and composition of subalpine forests.

CONCLUSION

Our study contributes to the broader understanding of complex ecosystem responses to disturbance interactions and is relevant to resource management challenges. Shifts in forest composition (conifer to aspen) and vegetation type (conifer forest to non-forest) resulted from the independent effects of the SB outbreak and fire on tree populations whereas recovery pathways reflected exposure effects of multiple disturbances. Even if a prior disturbance does not directly affect or modify the behavior and effects of a subsequent disturbance, disturbance-caused changes in the abundance and size structures of tree populations significantly altered the rate and pathways of forest recovery. The SB outbreak prior to fire and large distances to seed sources following stand-replacing fire appears to have severely limited spruce seed availability for postfire spruce establishment. Abundant aspen resprouts signals an important shift in tree species composition and illustrates the legacy of pre-disturbance tree species composition for postdisturbance forest recovery. The additional effect of browsing of aspen by large ungulates will likely slow forest recovery rather than alter the composition of the future forest canopy. Initial postfire trajectories created by compounded beetle–fire interactions imply that greater area affected by these two disturbances will likely reduce forest cover, creating heterogeneity in ecosystem composition and structure in subalpine ecosystems. By identifying pathways by which multiple disturbances affect forest resilience, our findings inform natural resource managers understanding of conditions that are limiting postfire seedling establishment and success.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3345/full>