Disturbance history modulates how litter and herbaceous cover influence conifer regeneration after fire

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Abstract. Climate-driven increases in disturbance frequency and extent augment the potential for compounded disturbances. Drawing on well-studied forests that experienced successive disturbances, we asked: (1) how does post-fire cover of litter, herbaceous cover and bare ground vary between stands affected by combinations of blow-down, insect outbreak, and fire? (2) How do post-fire relationships between ground cover and conifer regeneration vary with recent disturbance history? We measured ground cover and conifer regeneration from 2003 to 2014 following stand-replacing fires in 2002. Burned stands were either blown down in 1997, affected by a 1940s *Dendroctonus rufipennis* (spruce beetle; SB) outbreak, or neither. Implementing mixed-effects models, we measured the relationships between pre-fire stand attributes (structural stage, canopy dominance and combination of disturbances) and post-fire ground cover and between post-fire ground cover and conifer regeneration. Fire-only stands had more litter and herbaceous cover post fire than other stands ($P < 0.05$). Fir regeneration increased with litter in stands that only burned, but decreased with litter in stands that were first blown down. Similarly, pine and fir regeneration increased with herbaceous cover after fire-only, but did the opposite in stands affected by the SB outbreak. Pre-fire legacies can modulate the effects of ground cover on plant regeneration.

Additional keywords: beetle outbreak, blow-down, compounded disturbance, facilitation, ground cover, post-fire regeneration, subalpine forest.

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Introduction

Disturbance behaviour and ecosystem response may be altered when disturbances of different types occur in overlapping areas over short time intervals (Paine *et al.* 1998). Such scenarios are termed disturbance interactions (Paine *et al.* 1998). For example, disturbance interactions can affect overall disturbance intensity (Kulakowski and Veblen 2007; Simard *et al.* 2011; Kulakowski and Jarvis 2013; Buma 2015) and/or post-disturbance development (Buma and Wessman 2011; Kulakowski *et al.* 2013; Buma *et al.* 2014; Buma 2015; Kulakowski and Veblen 2015), sometimes inhibiting species that are otherwise disturbance-adapted (Buma *et al.* 2013; Kulakowski *et al.* 2013; Enright *et al.* 2015; Harvey *et al.* 2016; Nelson *et al.* 2016). The frequency and severity of climatically driven disturbances are increasing in many ecosystems owing to climate change (Dale *et al.* 2001; Westerling *et al.* 2006; Allen 2007; Evangelista *et al.* 2011; Romme *et al.* 2011; Seidl and Rammer 2017). As disturbance frequency increases, disturbance interactions are expected to become more common than in the past (Seidl *et al.* 2017). The commonly used phrase 'compounded disturbances' assumes a compound effect of multiple overlapping disturbances. We use the term 'successive disturbances' to describe cases where such

an effect may exist; however, this does not necessarily imply that a compound effect does exist.

Compound effects between fires and other disturbances, including harvesting, grazing, hailstorms, insect outbreaks and hurricanes have been quantified in ecosystems ranging from temperate forest (Sibold *et al.* 2007; Carlson *et al.* 2017) to tropical dry forest (Cantarello *et al.* 2011), Mediterranean shrubland (Gower *et al.* 2015), subtropical pine savanna (Platt *et al.* 2002) and boreal forest (Krawchuk and Cumming 2009; James *et al.* 2011; Côté *et al.* 2013). Compound effects have been demonstrated to buffer against or increase vulnerability to subsequent disturbances (Cannon *et al.* 2017). Understanding divergent responses of ecosystems to altered disturbance regimes is a priority area for contemporary ecological research, because these responses will influence key drivers of global change and thus strongly affect ecosystem services and humanity (Turner 2010; Turner *et al.* 2013).

Much research on successive disturbances has been conducted in subalpine forests of the US Rocky Mountains, but most studies have focused on immediate effects, and especially on seedbanks of the dominant life form, trees. For example, interactions among wind disturbance, post-disturbance logging

and fire as well as interactions between bark beetle outbreak and fire have been shown to yield compound effects on the density and composition of post-fire tree regeneration (Kulakowski and Veblen 2002; Kulakowski and Veblen 2007; Buma and Wessman 2011; Buma and Wessman 2012; Kulakowski *et al.* 2013). Conifer regeneration was reduced in stands that burned shortly after being blown down, favouring *Populus tremuloides* (Michx.) that regenerate by clonal resprouting as well as seedling establishment (Kulakowski *et al.* 2013; Gill *et al.* 2017*a*). Evidence suggests that *Dendroctonus rufipennis* (spruce beetle; hereafter SB) outbreaks do not have as strong an influence on post-outbreak fire occurrence, extent, or severity as do climatic factors (Bebi *et al.* 2003; Kulakowski *et al.* 2003; Bigler *et al.* 2005; Andrus *et al.* 2016; Mietkiewicz and Kulakowski 2016), but may slightly affect post-fire seed availability (Harvey *et al.* 2013). Although compound effects on tree regeneration after successive disturbances have been documented, questions remain regarding the role of herbaceous plants and seedling microhabitat (e.g. bare ground, logs, litter) in these situations (Rumbaitis del Rio 2004), especially over more than a few years after disturbance. Disturbance interactions influence not only overstorey trees, but also understorey plant communities (Turner *et al.* 1999; Roberts 2004; Rumbaitis del Rio 2006). However, the possibility of compound effects on the understorey cascading down to tree establishment has not been explicitly examined.

The influence of understorey vegetation on tree regeneration is context-sensitive (Callaway and Walker 1997; Bonnet *et al.* 2005). In subalpine forests, the presence of herbaceous cover often promotes conifer survivorship and seedling establishment by ameliorating conditions for germination and early growth (Feller 1998; Germino *et al.* 2002; Maher *et al.* 2005; Maher and Germino 2006), but can increase mortality rates when seedlings are surrounded by grasses without being protectively covered (Germino *et al.* 2002). Shrubs and other understorey flora may also compete with conifer seedlings (Conard and Radosevich 1982; Zhang *et al.* 2006) or facilitate their establishment (Rebertus *et al.* 1991), depending on biophysical context (Knapp *et al.* 2012), and the degree to which regeneration of tree species is facilitated by shrubs depends in part on abiotic heterogeneity (Gómez-Aparicio *et al.* 2005). Plant litter also influences tree regeneration through biogeochemical cycling and effects on surface temperature and flammability (Facelli and Pickett 1991; Xiong and Nilsson 1999; Sayer 2006; Li *et al.* 2014; Grootemaat *et al.* 2015; Dias *et al.* 2017). This myriad of context-dependent sensitivities makes clear that relationships between regenerating conifers and both seedling microhabitat (litter, logs, bare soil, etc.) and surrounding plant communities are complex and dynamic, yet they have not been studied comparatively across different combinations of successive disturbances. An increased understanding of the drivers of post-disturbance regeneration is needed, particularly following severe and compounded disturbances (Gill *et al.* 2017*b*). The context-sensitive relationships between ground cover and tree establishment represent one area that can be studied to improve our understanding of these drivers.

Here, we present a study of successive disturbances in subalpine forests to illuminate the potential for compound effects over a 14-year period through ground cover dynamics.

Given that ground cover can facilitate or inhibit conifer establishment depending on context, we aimed to answer two questions regarding the response of ground cover to successive disturbances and the relationship between ground cover and post-fire conifer regeneration density:

1. How do post-fire ground cover percentages of litter, herbaceous cover and bare ground vary between stands affected by single (i.e. fire only) *v.* successive (i.e. wind or SB outbreak, then fire) disturbances?
2. How do post-fire relationships between ground cover and regeneration of conifer trees vary in stands affected by single (i.e. fire only) *v.* successive (i.e. wind or SB outbreak, then fire) disturbances?

Study areas

Data were collected from permanent plots distributed across two subalpine forests of northern Colorado (Fig. 1). The 44-km^2 Headwaters of Big Creek study area lies in the northernmost unit of Routt National Forest and the Mount Zirkel Wilderness, ranging from 2400 to 3600 m above sea level. The climate is continental, and mean monthly temperatures since 1893 range from a minimum of $-17.1°C$ in January to a maximum of $28.1°C$ in July. Total mean annual precipitation is 60.2 cm, including 423 cm of snowfall (Western Regional Climate Center, http://www.wrcc.dri.edu/, accessed 9 January 2020). Upland forests in this region are underlain by coarse-textured soils consisting of glacial deposits and Precambrian crystalline parent material, while low-lying valleys are derived from poorly drained alluvial deposits (Snyder *et al.* 1987). Portions of this study area were burned by stand-replacing fires in 1879 and 1880 (Kulakowski and Veblen 2002, 2003), and are hereafter referred to as 'young' sites, as compared with other sites that are >200 years old.

The 46-km^2 North Fork of the White River study area is in north-western Colorado in the Flat Tops Wilderness and White River National Forest, ranging from 2450 to 3250 m above sea level. Parts of this area were also affected by severe fires in 1880, and by a severe outbreak of SB in the 1940s, which reached its peak in 1947 (Massey and Wygant 1954; Kulakowski *et al.* 2003). Mean monthly temperatures from 1948 to 2001 range from a minimum of $-13.9°C$ in January to a maximum of $27.2°C$ in July. Mean annual precipitation is 52.1 cm of rain, including 446.3 cm of snowfall (Western Regional Climate Center, http://www.wrcc.dri.edu/).

Forests in both study areas are dominated by *Pinus contorta*, *Populus tremuloides*, *Picea engelmannii* and *Abies lasiocarpa*. *Picea engelmannii* and *A. lasiocarpa* are shade-tolerant species but can be found in post-fire subalpine environments (under no canopy), albeit in lower densities than under closed canopies. *Pinus contorta* regenerate in high numbers following fire through serotiny, but establish through non-serotinous seed as well. *Pinus contorta* are shade-intolerant and common after stand-replacing fires. In October 1997, ~10.3 km^2 of the Headwaters of Big Creek study area was blown down in a severe windstorm. In 1999–2000, we reconstructed the history of fires, SB outbreaks and wind disturbance from ~1700 to 2000 in both study areas (Kulakowski and Veblen 2002; Kulakowski *et al.* 2003). Subsequently, large parts of both study areas burned in
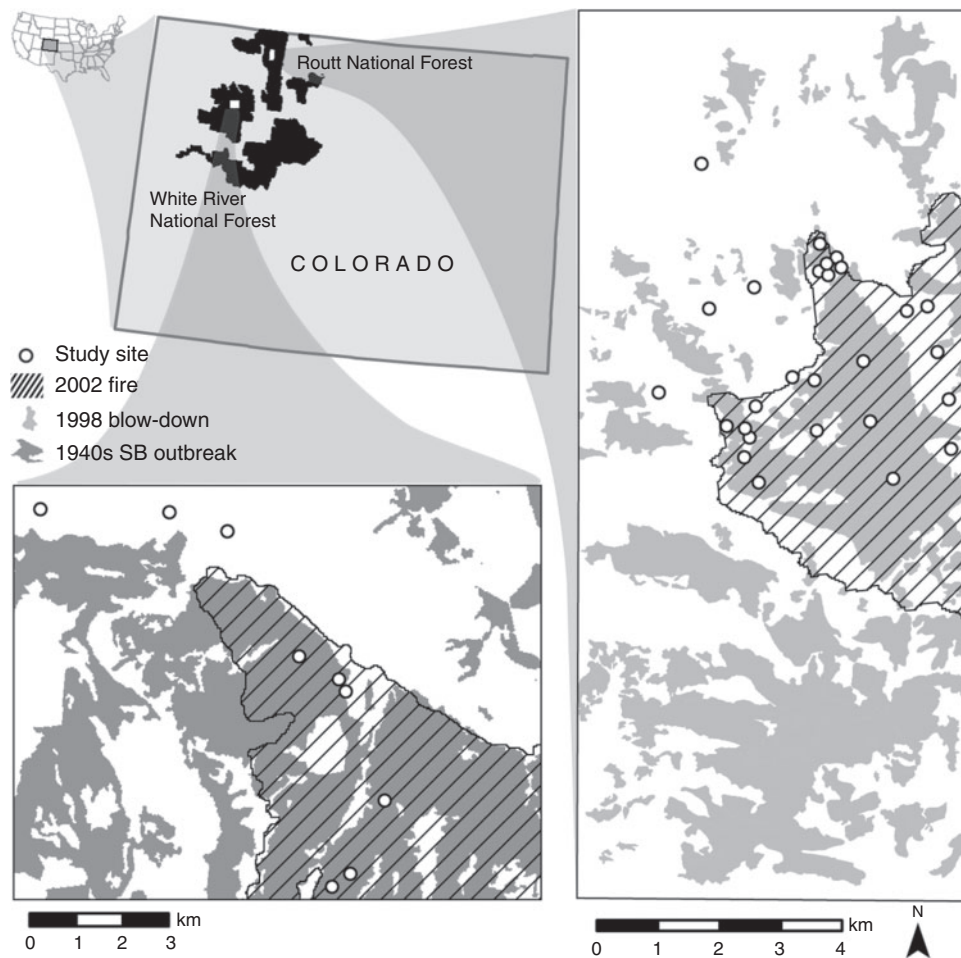
Fig. 1. We established permanent plots in 20 conifer stands that had burned severely in 2002 across the study areas, and in seven conifer stands that had not burned, blown down or experienced 1940s spruce beetle (SB) outbreaks (Kulakowski *et al.* 2013). Five of the seven control stands were subsequently affected by beetle outbreaks. Sites were randomly located by pre-fire stand canopy dominance (*Pinus contorta* or *Picea engelmannii–Abies lasiocarpa*), pre-fire stand structural stage (stands that originated in the 1880s or >200-year-old stands), and combination of recent disturbance (2002 fire-only, 'F'; 1940s SB outbreak followed by 2002 fire, 'SBF'; 1997 wind blow-down followed by 2002 fire, 'WF').

high-severity fires in 2002, including stands that had been affected by the 1940s SB outbreak, 1997 blow-down, or neither.

Materials and methods

Data collection

In 2003, we established 900 2 × 1-m permanent plots in 20 conifer stands that had burned severely in 2002 across the study areas, and 225 2 × 1-m permanent plots in seven conifer stands that had not burned, blown down or experienced a 1940s SB outbreak (Kulakowski *et al.* 2013). Five of these seven control stands were subsequently affected by SB and/or *Dendroctonus ponderosae* (mountain pine beetle; hereafter MPB). All sites were located based on a stratified random design (see Kulakowski *et al.* 2013) by pre-fire stand canopy dominance (*Pinus contorta* and *Picea engelmannii–Abies lasiocarpa*), pre-fire stand structural stage (stands that originated in the 1880s

and >200-year-old stands), and combination of recent disturbance (2002 fire-only, hereafter 'F'; 1940s SB outbreak followed by 2002 fire, 'SBF'; 1997 wind blow-down followed by 2002 fire, 'WF'). All blown-down sites were located in areas of high severity (>50% downed) according to US Forest Service aerial detection surveys. All burned sites were located in patches of high-severity (stand-replacing) fire. Pre-fire dominance was categorised as *P. contorta* if that species made up >40% of canopy trees and *P. engelmannii–A. lasiocarpa* if those species made up >90% of canopy trees.

In each plot in the years 2003, 2004, 2005, 2010 and 2014–15, percentages of six ground cover categories and counts of all seedlings (height ≤140 cm) of each conifer species were recorded. Proportions of bare ground, litter (dead plant material <4 cm in diameter, including charcoal, and decomposed duff), herbaceous cover, shrubs, live trees and logs were each recorded for each plot as one of six interval categories ranging from 0 to 5

(<1, 1–5, 6–25, 26–50, 51–75 and >75% respectively). Saplings (height >140 cm), which were not present until after 2005, were counted in 2 × 10-m macroplots in which three of the smaller permanent plots were nested. Sites of different categories were interspersed to the degree possible given the natural spatial arrangement of disturbances, species dominance and age structure. WF sites and SBF sites were geographically separate from each other, but replicate sites of each were interspersed with F sites to the degree possible. Total regeneration densities in nested 2 × 10-m microplots were estimated by adding seedling densities to the sapling density that was recorded at the 2 × 10-m macroplot level surrounding each microplot. Plots were grouped for analysis according to pre-fire structural stage (~120 *v.* >200 years old) and recent disturbance history (F, WF or SBF). Equal numbers of stands (and plots) of each age and dominance category were within each category of disturbance combination, with the exception of SBF stands, for which there are no young stands owing to SB preferences for older stands ($n = 180$ plots for each of five categories). All reported seedlings and saplings established after the 2002 fires. Site was accounted for as a random effect in our models. All regeneration data were expressed as number of stems per hectare.

Analysis

Using *R* package lmerTest 2.0–33, we created two sets of mixed-effects analysis of variance models to measure not only the effects of stand age, canopy dominance and disturbance combination on post-disturbance ground cover, but also the effects of post-disturbance ground cover on regeneration density of each conifer species.

In the first set of mixed-effects models, each model included a ground cover category (bare ground, litter, herbaceous, shrub or logs) as the response variable and structural stage, pre-disturbance canopy dominance, and combination of disturbances (F, WF or SBF) as fixed-effect explanatory variables. Year, site and plot-nested-within-site ($n = 900$) were included as random-effects explanatory variables in each model. Each category of stand age and disturbance history held $n = 180$ plots. Ground-cover dynamics are plotted in Fig. 2. Distributions of ground-cover categories after fire are given in Fig. 3.

The second set of mixed-effects models tested the regeneration density of *A. lasiocarpa*, *P. engelmannii*, or *P. contorta* as a function of structural stage, pre-disturbance canopy dominance, combination of disturbances (F, WF, or SBF), ground cover percentages (bare, litter, and herbaceous) and the interactions of each ground cover percentage with combination of disturbance. Year, site and plot-nested-within-site ($n = 900$) were included as random-effects explanatory variables in each model. Each category of stand age and disturbance history held $n = 180$ plots.

For all models, the correlation between fixed effects rarely exceeded $r > 0.200$ and never exceeded $r > 0.378$. To explore model interaction terms, scatterplots of single-year conifer regeneration and ground cover were generated in *R* (see Figs. S1–S5 available as Supplementary Material to this paper).

Results

Each ground cover type varied with at least one combination of disturbance, even when it did not vary significantly with other contextual factors (pre-fire structural stage and canopy dominance). Logs, litter and shrubs were each sensitive to both SBF and WF combinations (Table 1). Burned stands that were not beetle-affected or blown down (F stands) exhibited fewer logs and more post-fire litter and shrubs than stands that experienced either combination of multiple disturbances (Table 1). However, these stands had only moderate change in litter cover over time (Fig. 2*a* and *b*), whereas stands affected by multiple disturbances saw sharp declines in litter initially, followed by a gradual increase (Fig. 2*c*, *d* and *e*). When wind blow-down preceded fire (WF), more post-fire ground area was bare (Table 1, Fig. 2*a–d*, Fig. 3). When SB outbreak preceded fire (SBF), average post-fire herbaceous cover increased to 26–50% cover in the first 3 years, as opposed to F stands where average herbaceous cover was slower to recover and did not exceed 25% (Table 1, Fig. 2*a*, *e*, Fig. 3). Overall, ground-cover patterns were highly sensitive to successive disturbances (Fig. 3).

Picea engelmannii regeneration density was significantly influenced by stand structural stage at the time of disturbance (higher densities in younger stands), but not by disturbance combination or ground cover (Table 2). Furthermore, interaction terms in this model were insignificant, meaning that the relationships between *P. engelmannii* and ground cover were not different given differences in structural stage, dominance, or number of disturbances.

However, the directionality of relationships between ground cover and *Pinus contorta* and *Abies lasiocarpa* regeneration densities depended on combination of disturbances, not on pre-fire structural stage and canopy dominance. Litter cover and herbaceous vegetation each exhibited significant relationships with *P. contorta* and *A. lasiocarpa* regeneration densities (Tables 3–4), but these relationships were sensitive to successive (though not individual) disturbances (Figs. S1–S4). Maximum regeneration densities of *P. contorta* and *A. lasiocarpa* were observed under moderately low levels of litter and herbaceous cover (most frequently 6–25% cover, and consistently <50%; Figs. S1–S4). In F plots, regeneration was positively correlated with both litter and herbaceous cover (Tables 3–4), but when fire was preceded by blow-down or SB outbreak, regeneration became uncorrelated (Table 3) or even negatively correlated with these ground cover types (Table 4). A summary of how the strength and directionality of these correlations vary with disturbance combination is provided in Table 5. Plots with >50% litter in 2003 exhibited greater conifer densities than those with lower litter cover after fire only, but when blow-down preceded fire, plots with >50% litter cover in 2003 had much less dense conifer regeneration than plots with less litter (Fig. S6). Similarly, conifer densities were relatively high in plots with >25% herbaceous cover by 2005, unless SB outbreak preceded fire – then the opposite became true (Fig. S7).

Discussion

Our findings suggest that disturbances interact to influence post-fire ground cover patterns, which in turn may affect post-fire tree regeneration. In stands that burned at high severity but were not preceded by another recent disturbance (F), ground cover and its relationship with conifer seedling establishment were consistent
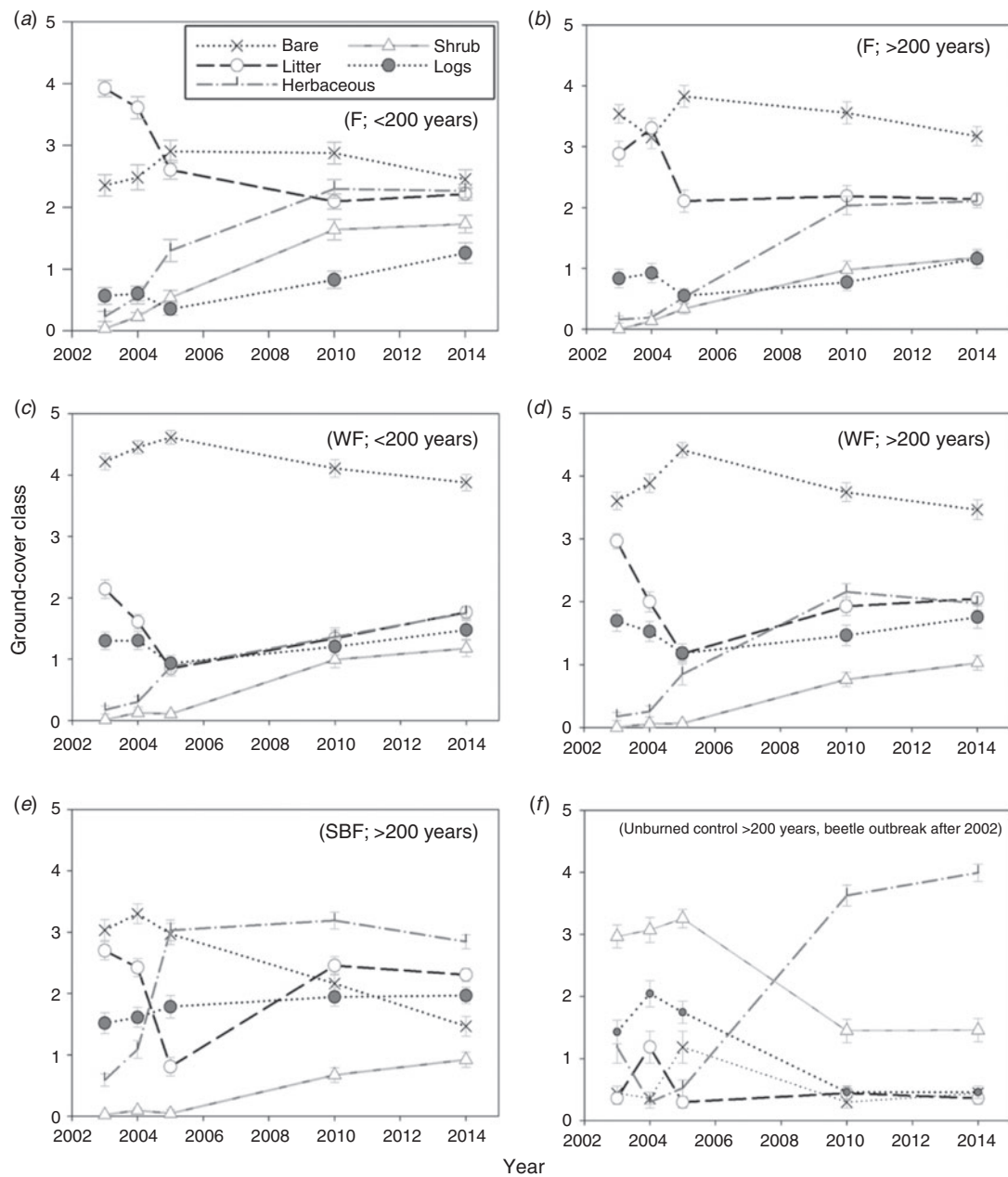
Fig. 2. Five categories of ground cover (bare ground, litter, herbaceous, shrubs and logs) in *Pinus contorta* and mixed *Picea engelmannii–Abies lasiocarpa* stands from 2003 to 2014 (mean ± s.e.). F (fire-only) stands burned in 2002, but had no recent preceding disturbance (*a* and *b*; *n* = 180 each). WF (wind blow-down and fire) stands were blown down in 1997 and burned in 2002 (*c* and *d*; *n* = 180 each). SBF (spruce beetle and fire) stands underwent 1940s SB outbreak and burned in 2002 (*e*; *n* = 180). Panel (*f*) shows control stands that did not burn, but underwent outbreaks of SB and/or Mountain Pine Beetle (MPB) that began after 2002 (*n* = 180). Each panel in the figure represents data from an equal number of plots dominated by *P. contorta* as *P. engelmannii–A. lasiocarpa*.

with expectations in post-fire subalpine forest ecosystems (small amounts of litter and herbaceous cover that ameliorate conditions for conifer establishment; Knapp and Smith 1982; Maher and Germino 2006). However, our data suggest that successive disturbances filtered ground-cover patterns and inverted the effect of ground cover to inhibit post-fire conifer regeneration.

Successive disturbances yielded differences in post-fire ground cover. We did not explicitly test for potential mechanisms behind differences in ground cover. The arrangement of fuels in blown-down stands may cause longer burn times (Buma and Wessman 2011) and thus presumably lead to increased proportions of bare ground after fire. One potential explanation for the observed differences in beetle-affected stands is that increased
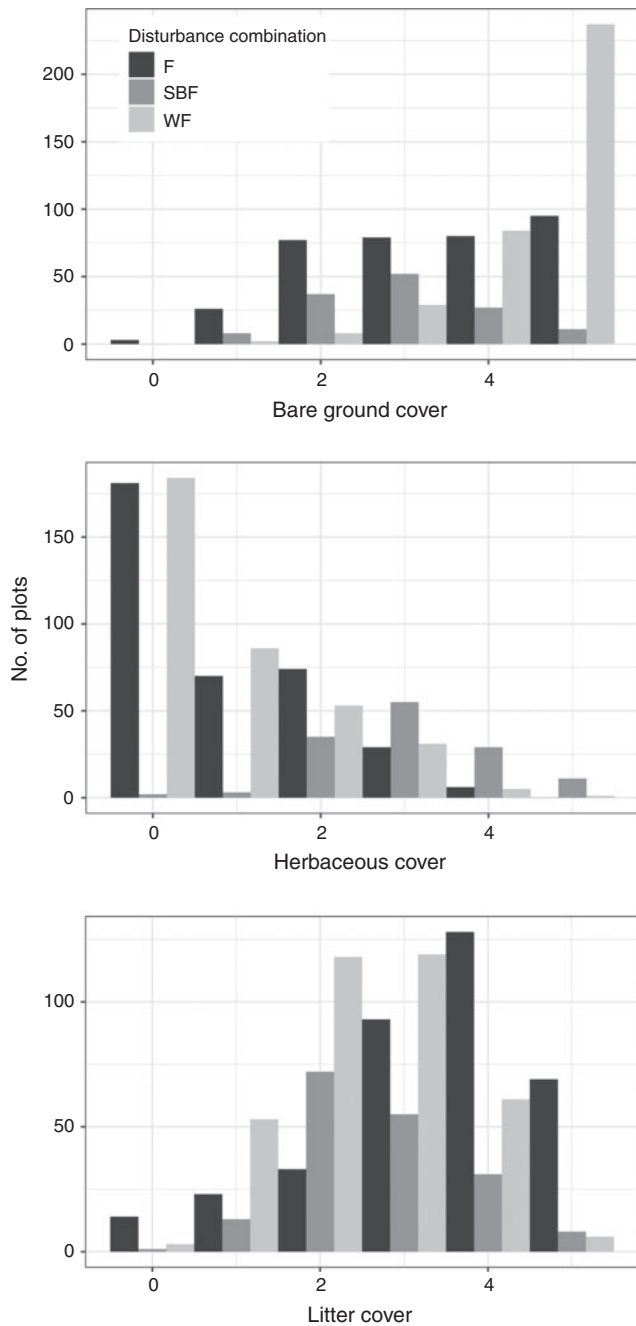
Fig. 3. Histograms of bare ground herbaceous, and litter cover in plots across categories of single and multiple successive disturbances. F = 2002 fire only (*n* = 360). WF = 1997 wind blow-down and 2002 fire (*n* = 360). SBF = 1940s spruce beetle outbreak and 2002 fire (*n* = 180). Bare ground cover interval categories range from 0 to 5 (<1, 1–5, 6–25, 26–50, 51–75 and >75% respectively).

Table 1. Mixed-effects model results: ground cover and contextual factors

Each ground-cover category was tested as a function of structural stage, pre-disturbance canopy dominance and combination of disturbances (as fixed-effect variables). Year, site and plot-nested-within-site were included as random-effects variables. *, significance at the 95% level. SB, spruce beetle

Category	Factor	Coefficient	*t* value	*P* value
Logs	Structural stage	−0.204	−1.639	0.122
	Dominance	0.134	1.202	0.248
	Pre-fire SB outbreak	0.835	5.059	<0.001*
	Pre-fire blow-down	0.601	4.819	<0.001*
Litter	Structural stage	−0.057	−0.297	0.771
	Dominance	0.138	0.805	0.435
	Pre-fire SB outbreak	−0.552	−2.177	0.046*
	Pre-fire blow-down	−0.924	−4.823	<0.001*
Shrubs	Structural stage	0.206	3.250	0.005*
	Dominance	0.089	1.578	0.135
	Pre-fire SB outbreak	−0.220	−2.624	0.019*
	Pre-fire blow-down	−0.248	−3.917	0.001*
Herbaceous	Structural stage	0.071	0.431	0.672
	Dominance	−0.231	−1.567	0.138
	Pre-fire SB outbreak	0.962	4.419	<0.001*
	Pre-fire blow-down	−0.180	−1.093	0.291
Bare	Structural stage	−0.200	−0.835	0.417
	Dominance	−0.064	−0.298	0.770
	Pre-fire SB outbreak	−0.537	−1.690	0.112
	Pre-fire blow-down	1.011	4.208	<0.001*

Table 2. Mixed-effects model results for *Picea engelmannii*

Picea engelmannii regeneration density as a function of structural stage, pre-disturbance canopy dominance, combination of disturbances, ground cover percentages (bare, litter and herbaceous) and interaction terms (italicised). Year, site and plot-nested-within-site were included as random-effects variables. *, significance at the 95% level. SB, spruce beetle

Factor or interaction term	Coefficient	*t* value	*P* value
Structural stage	70.729	2.586	0.020*
Dominance	−4.106	−0.171	0.867
Pre-fire SB outbreak	−116.528	−0.706	0.480
Pre-fire blow-down	−192.961	−1.285	0.199
Litter cover	−9.157	−0.506	0.613
Herbaceous cover	23.193	1.429	0.154
Bare ground	−27.108	−1.550	0.121
Pre-fire SB : Litter	9.899	0.338	0.736
Pre-fire blow-down : Litter	24.835	0.992	0.321
Pre-fire SB : Herbaceous	−34.862	−1.433	0.152
Pre-fire blow-down : Herbaceous	−31.150	−1.505	0.132
Pre-fire SB : Bare	30.312	1.083	0.279
Pre-fire blow-down : Bare	29.890	1.133	0.257

pre-fire herbaceous productivity during a beetle outbreak (Pec *et al.* 2015) allows increased resprouting shortly after fire (Turner *et al.* 1997). This is consistent with data from our plots in unburned sites that were affected by SB and MPB outbreaks during the study period (Fig. 2*f*). Regardless of the underlying mechanism behind these differences, we found that they depend

on combinations of disturbances, and that they may influence seedling establishment differentially, as described below.

Significant relationships exist between post-fire ground cover and conifer regeneration densities by species, but these relationships are sensitive to prior, successive disturbances. In stands that were blown down before burning, the positive

Table 3. Mixed-effects model results for *Abies lasiocarpa*

Abies lasiocarpa regeneration density as a function of structural stage, predisturbance canopy dominance, combination of disturbances, ground cover percentages (bare, litter and herbaceous) and interaction terms (italicised). Year, site and plot-nested-within-site were included as random-effects variables. *, significance at the 95% level. SB, spruce beetle

Factor or interaction term	Coefficient	*t* value	*P* value
Structural stage	138.941	1.709	0.108
Dominance	−66.894	−0.923	0.371
Pre-fire SB outbreak	−263.726	−1.177	0.240
Pre-fire blow-down	−231.763	−1.167	0.244
Litter cover	−54.826	−2.533	0.011*
Herbaceous cover	17.675	0.881	0.378
Bare ground	−1.338	−0.060	0.952
Pre-fire SB : Litter	82.061	2.325	0.020*
Pre-fire blow-down : Litter	76.630	2.551	0.011*
Pre-fire SB : Herbaceous	−29.883	−1.015	0.310
Pre-fire blow-down : Herbaceous	−3.028	−0.121	0.904
Pre-fire SB : Bare	6.461	0.185	0.853
Pre-fire blow-down : Bare	−18.566	−0.557	0.578

Table 4. Mixed-effects model results for *Pinus contorta*

Pinus contorta regeneration density as a function of structural stage, predisturbance canopy dominance, combination of disturbances, ground cover percentages (bare, litter and herbaceous) and interactions terms (italicised). Year, site and plot-nested-within-site were included as random-effects variables. Significance at the 95% level (*). SB, spruce beetle

Factor or interaction term	Coefficient	*t* value	*P* value
Structural stage	961.81	1.453	0.167
Dominance	−746.81	−1.262	0.226
Pre-fire SB outbreak	−1205.26	−1.120	0.271
Pre-fire blow-down	−1652.91	−1.883	0.066
Litter cover	−198.93	−2.879	0.004*
Herbaceous cover	242.35	3.691	<0.001*
Bare ground	−181.67	−2.562	0.010*
Pre-fire SB : Litter	294.86	2.621	0.009*
Pre-fire blow-down : Litter	328.54	3.435	<0.001*
Pre-fire SB : Herbaceous	−295.06	−3.144	0.002*
Pre-fire blow-down : Herbaceous	−178.48	−2.240	0.025*
Pre-fire SB : Bare	131.55	1.180	0.238
Pre-fire blow-down : Bare	120.80	1.137	0.255

Table 5. Summary of ground cover-conifer establishment relationships

The relationships between ground cover (litter and herbaceous) and conifer regeneration density (*Abies lasiocarpa* and *Pinus contorta*) were positive, negative, or insignificant depending on combination of recent disturbances. F, fire only; WF, wind blow-down, then fire; SBF, spruce beetle outbreak, then fire

Context	Ground cover type	Relationship with *A. lasiocarpa*	Relationship with *P. contorta*
F	Litter	Positive	Positive
	Herbaceous	Positive	Positive
WF	Litter	Not significant	Negative
	Herbaceous	Not significant	Positive
SBF	Litter	Not significant	Positive
	Herbaceous	Negative	Negative

majority of *A. lasiocarpa* and *P. engelmannii* seedlings in this region occur most frequently on thin layers of litter substrate (Knapp and Smith 1982). It follows that while small amounts of litter (as opposed to bare ground) may facilitate conifer establishment, abundant and/or deep litter may be inhibitive (Fig. S1).

Just as the relationship between litter and conifer regeneration was context-dependent, the relationship between herbaceous cover and conifer regeneration was reversed if blow-down or SB outbreak preceded fire. Fire-only (F) plots tended to have positive relationships between regeneration densities of each conifer species and herbaceous cover, which predominantly remained under 25% in most cases and rarely exceeded 50% (Fig. 3, see also Fig. S2). When blow-down preceded fire, this positive relationship held for *Pinus contorta* but not *Abies lasiocarpa* or *Picea engelmannii*. WF plots had post-fire herbaceous cover levels at the low end of the spectrum (i.e. predominantly under 25%; Fig. 3, Fig. S2), perhaps owing to increased fire intensity (Buma and Wessman 2011). It may be that a positive relationship remains at play, but herbaceous vegetation was so sparse that it had no detectable effect on conifer regeneration at these sites. In SBF plots, herbaceous cover was high and conifer densities were low. Stands affected by SB are at the high end of the distribution of herbaceous cover (Fig. 3), possibly owing to increased pre-fire herbaceous cover (Fig. 2f) and post-fire resprouting. Even in stands associated with high serotiny (i.e. greater pre-fire densities of younger lodgepole pine; Figs. S5–S6), *P. contorta* regeneration decreased as herbaceous cover reached its peak, indicating that whereas a moderate amount of herbaceous cover may facilitate conifer seedling establishment, very high herbaceous cover (i.e. 26–50% cover or more) may reduce conifer regeneration owing to competition (e.g. Germino *et al.* 2002). Both *P. contorta* and *A. lasiocarpa* exhibited sensitivity to herbaceous cover (and litter cover). Germino *et al.* (2002) found that the relationship between grasses and *P. engelmannii* and *A. lasiocarpa* regeneration shifts from facilitative to competitive when grasses surround but do not (protectively) cover tree seedlings. Our findings also support the view that relationships between subalpine plant species may typically be competitive, yet become facilitative under harsher conditions (Choler *et al.* 2001).

relationship between litter and conifer regeneration density was negated and even reversed. Differences in the observed temporal trends in litter cover at single- *v.* multiple-disturbance sites (Fig. 2) lead us to believe that litter qualities that we did not measure (e.g. composition, depth, percentage charcoal, grain size, whether fuels were living or dead at time of fire; Dias *et al.* 2017) at these sites may have been fundamentally different than at fire-only sites. Alternatively (or additionally), the observed relationships between conifer densities and litter cover may suggest that thresholds of suitability for establishment exist based on litter quantity rather than quality. Further research is required to identify the underlying mechanism(s) behind the varying effect of litter cover on conifer regeneration. The

We measured increased herbaceous cover in unburned sites that were affected by beetle outbreak during our study period (Fig. 2*f*), suggesting that very high pre-fire herbaceous cover may have characterised SBF sites before they burned. At such sites, competition for conifer establishment would be high there amid abundant herbaceous plants that regenerate vegetatively after fire. However, we did not measure species-level abundance of grasses; thus, we cannot compare vegetative regeneration potential to confirm this theory given the data available. Unfortunately, the inclusion of species-level data for ground cover was beyond the scope of this study, and thus plant traits that may indicate whether an herbaceous species facilitated or competed with conifer regeneration cannot be explored without additional data collection.

The inverting of ground cover–conifer regeneration relationships appears to be at play across conifer stands of different composition and structural stage and arises in different forms in SBF *v.* WF sites. Temporally, these mechanisms are at play for decades at least. After more than half a century, the effect of SB outbreak on the abundance of understorey herbaceous cover was sufficiently strong that emergent phenomena were perceptible in post-fire regeneration. The observed effect of blow-down and fire on ground cover may be related to fundamental changes in litter. Although blow-down preceded fire by only 5 years, coarse woody debris (abundant after blow-down) in subalpine forests remains for decades or longer and slows litter decomposition significantly (Remsburg and Turner 2006), so this effect too may be long-enduring. Altered ground-cover patterns such as those identified after interacting disturbances in the present study have important implications for seedling establishment (Facelli and Pickett 1991; Messier *et al.* 1998; Nilsson and Wardle 2005; Dias *et al.* 2017). The directionality of these implications may depend on disturbance context (Maher *et al.* 2005; Vandenberghe *et al.* 2008).

Although the current study does not definitively identify underlying mechanisms, it is evident that successive disturbances alter not only herbaceous plants, but also can influence conifers via the relationship between herbaceous cover and conifer seedling establishment. This effect may be associated with ephemeral factors, such as the convergence of climate and disturbance, or more enduring, such as the abundance of herbaceous cover, quality of herbaceous cover, or presence of mycorrhizae. Further research is needed to identify the operative mechanism behind the shifting influence of herbaceous vegetation on post-fire conifer seedling establishment.

We recognise that possible confounding factors may be at play. For example, we did not measure edaphic characteristics, herbivory (Vandenberghe *et al.* 2008), seed supply (Harvey *et al.* 2013), herbaceous species composition (e.g. abundance of N-fixers) or other important factors that can interact with the combination of disturbances to drive differences in herbaceous cover and conifer density. Additionally, our plots were constrained to White River and Routt National Forests, and the degree to which they represent trends across a broader region has not been tested here. Future research should address these potential influences.

Implications

Carlson *et al.* (2017) found that although an SB outbreak does not affect fire severity in *P. engelmannii–A. lasiocarpa* forest in

southern Colorado, the combination does result in a compound effect on post-fire regeneration. Harvey *et al.* (2013) found that reduced seed sources surrounding beetle outbreak contributed to decreased post-fire regeneration. Our findings suggest that post-fire conifer regeneration is inhibited through a compound effect of SB and fire on the relationship between herbaceous vegetation and tree seedling establishment, further denoting only a second-order relationship with fire behaviour.

The rapid combination of blow-down and fire has been shown to significantly reduce conifer regeneration and make long-term regeneration trajectories unpredictable (Kulakowski *et al.* 2013; Gill *et al.* 2017*b*). The compound effects of multiple disturbances on regeneration have been attributed to direct linkages between blow-down and fire as the arrangement of fuels alters fire behaviour and intensity (Buma and Wessman 2011) and is thereby likely to affect post-fire seed abundance (Harvey *et al.* 2013). The present study supports the notion that compound effects on forest response via ground cover may also be at play.

To fully understand how disturbance interactions affect post-disturbance development, it is not enough to focus only on seed demography of dominant lifeforms, but is also essential to examine how compound effects may influence community structure and seedling microhabitat (Turner and Dale 1998) over many years. The present study demonstrates that disturbance interactions influence not only dominant tree species, but also dynamic, community-level relationships (i.e. relationships between trees, shrubs and herbaceous vegetation) and seedling microhabitat conditions (i.e. logs, litter and bare ground) that are important to ecosystem trajectories. Although more direct compound effects may be apparent on the seed availability of dominant life forms, the ability of these species to regenerate depends also on biophysical context (e.g. competition and facilitation). Such relationships are key to determining the resilience of systems as they respond to disturbance (Montoya and Raffaelli 2010; Gill *et al.* 2017*b*). Although changes to community-level relationships under climate change are complex, they are nonetheless key to ecological forecasting, management and conservation efforts (Agrawal *et al.* 2007).

Summary and conclusions

Compounded disturbances can alter patterns of ground cover. In turn, these ground-cover patterns can affect conifer regeneration. When fire was preceded by blow-down, post-fire litter cover was lower and cover of bare ground was higher compared with sites affected only by fire. This may be explained by higher-intensity burning and fine fuel consumption at the forest floor where coarse fuels (blown-down tree stems) were dense. Under these conditions, post-fire litter no longer exhibited a positive relationship with *Pinus contorta* and *Abies lasiocarpa* regeneration, possibly owing to differences in litter quantity, quality, or both. This is supported by the contrasting relationships of ground cover with conifer densities between sites that were blown down and burned *v.* comparable sites that were only burned.

When fire was preceded by the 1940s SB outbreak, post-fire herbaceous cover was higher compared with sites in which fire was not preceded by beetle outbreak. Similarly, unburned sites

affected by beetle outbreaks exhibited substantial increases in herbaceous cover. Whereas a moderate amount of herbaceous cover may ameliorate conditions for regeneration, as is consistent with our observations at fire-only sites, the large amounts of post-fire herbaceous cover associated with SB outbreaks and subsequent fire appear to reduce *P. contorta* and *Picea engelmannii* regeneration.

Together, these context-sensitive relationships between ground cover and conifer regeneration may signify an underappreciated pathway by which compound effects arise after interacting disturbances. A first disturbance may affect not only the behaviour of a second disturbance and subsequent propagule availability, but also the competitive and facilitative context under which regeneration occurs. The sensitivity of tree regeneration to ground-cover patterns is dynamic and known to be context-dependent across ecosystem types. Fundamental changes to these relationships should be explicitly considered when intervals between disturbances are atypically brief relative to the recent past. Measuring these relationships over many years strengthens confidence and reveals new insights that cannot be learned from observations taken at only a single point in time.

Conflicts of interest

The authors of this manuscript declare no conflicts of interest.

Acknowledgements

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