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Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience

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ABSTRACT

Disturbance interactions are of great interest in ecology due to their potential to cause non-linear, unexpected results. Increases in disturbance frequency and intensity as a result of climate change increase the need for better conceptual and mechanistic understanding of ecosystem response to compounded perturbations. Impacts on structural elements of ecosystems, such as tree species, are particularly important, as changes in these species' populations, frequencies, and distributions may influence landscape functioning for extended periods of time. This study investigated the impact of three overlapping disturbances common to western US forests (wind, logging, and fire) on three dominant tree species: Lodgepole pine, Engelmann spruce, and quaking aspen. Ninety-nine study plots were examined across a gradient of interaction severities from a 1997 blowdown, subsequent salvage logging, and a 2002 fire in a Rocky Mountain subalpine forest. Regeneration of dominant species was analyzed in the context of disturbance history and species-specific disturbance response strategies. Results indicated that species are differentially affected by disturbance interactions. Lodgepole pine is highly sensitive to both previous disturbances and their severities, whereas spruce and aspen are insensitive to disturbance history, although both showed higher recruitment levels in three-disturbance environments. Disturbance types, combinations, and specific resilience mechanisms appear to be more important than number of disturbances. Disturbance interactions were not necessarily additive, and in some cases, three disturbances were less severe than two. As a result of long-distance dispersal, aspen seems likely to greatly increase in dominance across the landscape. Species-specific responses are generalized through their individual response strategies, with specialized responses being less resilient to multiple disturbances than generic seed dispersal strategies. Differential responses by structural tree species will likely drive an increase in future landscape heterogeneity and potential decreases in future landscape resilience to fire.

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1. Introduction

Disturbances are important drivers of ecosystem structure and function, with legacies that shape landscape properties for long time periods. Extensive research has documented the various influences and consequences of disturbance events on a variety of ecosystems. However, the cumulative impact of multiple disturbances, or compounded perturbations, is a growing topic of concern. Multiple disturbances may result in ecosystem responses unpredictable from knowledge of the individual disturbances alone (Paine et al., 1998), potentially causing shifts between alternate stable regimes. Interactions between disturbances are among the most important foci of study in landscape and disturbance ecology (Turner, 2010). Future anthropogenic pressures and climate change are likely to increase disturbance frequency (Dale et al., 2001), resulting in higher probability of multiple disturbances impacting

a single location. Because forest ecosystem structure and functioning is in many ways driven by the composition of woody tree species (Ellison et al., 2005), the resilience of the tree component to multiple disturbances is of special interest. The resilience of these species will influence how the post-disturbance ecosystem will organize, and thus have long-term impacts on ecosystem structure and function (Holling, 1973; Gunderson, 2000; Beisner et al., 2003) and resilience to future disturbances (Eriksson, 2000).

Species response strategies are used to broaden the ecological relevance of individual disturbance studies, explain how disturbance can maintain biodiversity across a landscape, and generalize findings to other ecosystems (Lavorel et al., 1997; McIntyre et al., 1999). Fire responses have been grouped into general response strategies: invaders, evaders, endurers, avoiders, and resisters (Rowe, 1983). These classes can be considered the "method of resilience", the means to recover and maintain presence at a site over time, despite (or because of) disturbance. Invaders are opportunistic species which move into freshly disturbed areas. Evaders use specialized strategies to "get around" the disturbance; the

adult is usually killed, however seed stored in the soil, humus, or canopy, is able to immediately reestablish the population post-disturbance. Endurers utilize specialized tissues or resprouting mechanisms to recover once the aboveground portion of the plant is killed in the disturbance event. Avoiders are not considered disturbance-adapted, and are only found in areas late in succession. Resisters attempt to survive the disturbance itself, for example using thick bark to withstand fire-induced mortality. Species may present traits that fill one or more of these response strategies.

Rocky Mountain subalpine forests (2500–3200 m) are a useful ecosystem type for comparing the response of various species to multiple disturbances. While there is relatively low species diversity in terms of woody plants, the ecosystem displays a variety of disturbances (most commonly wind, fire, insects, and logging (Peet, 1981; Kulakowski and Veblen, 2007), disturbance response strategies (Cattelino et al., 1979), and successional pathways (Noble and Slatyer, 1980; Sibold et al., 2007). The response of individual species to compounded disturbances can be used to determine the applicability of the broad classes of Rowe (1983); furthermore those individual responses may highlight vulnerabilities of species/response strategies multiple disturbances and disturbance interactions. Potentially increasing rates of disturbance

(Dale et al., 2001) could heighten those vulnerabilities. Loss of individual species with particular resilience traits are of concern in an ecosystem context, as future resilience to disturbance is shaped by the species that successfully persisted after the last disturbance (Eriksson, 2000). By taking advantage of a natural experiment—three compounding disturbances of various severities—this study

Table 1
Dominant forest species in Colorado subalpine forest with their general fire response strategies and specific mechanisms for post-fire recruitment (McDonough, 1979; Noble and Ronco, 1978; Peet 1981; Lotan and Perry 1983; Veblen et al., 1991).

Species	Response strategy		Specific mechanisms	
	Primary	Secondary	Primary	Secondary
Aspen	Endurer	Invader	Lateral root resprouter	Seed (1+ km range)
Lodgepole pine	Evader	Invader	Serotinous cones	Seed (80 m range)
Engelmann spruce	Invader	Avoider	Seed (125 m range)	Advanced regeneration
Subalpine fir	Avoider	Invader	Advanced regeneration	Seed (100 m range)

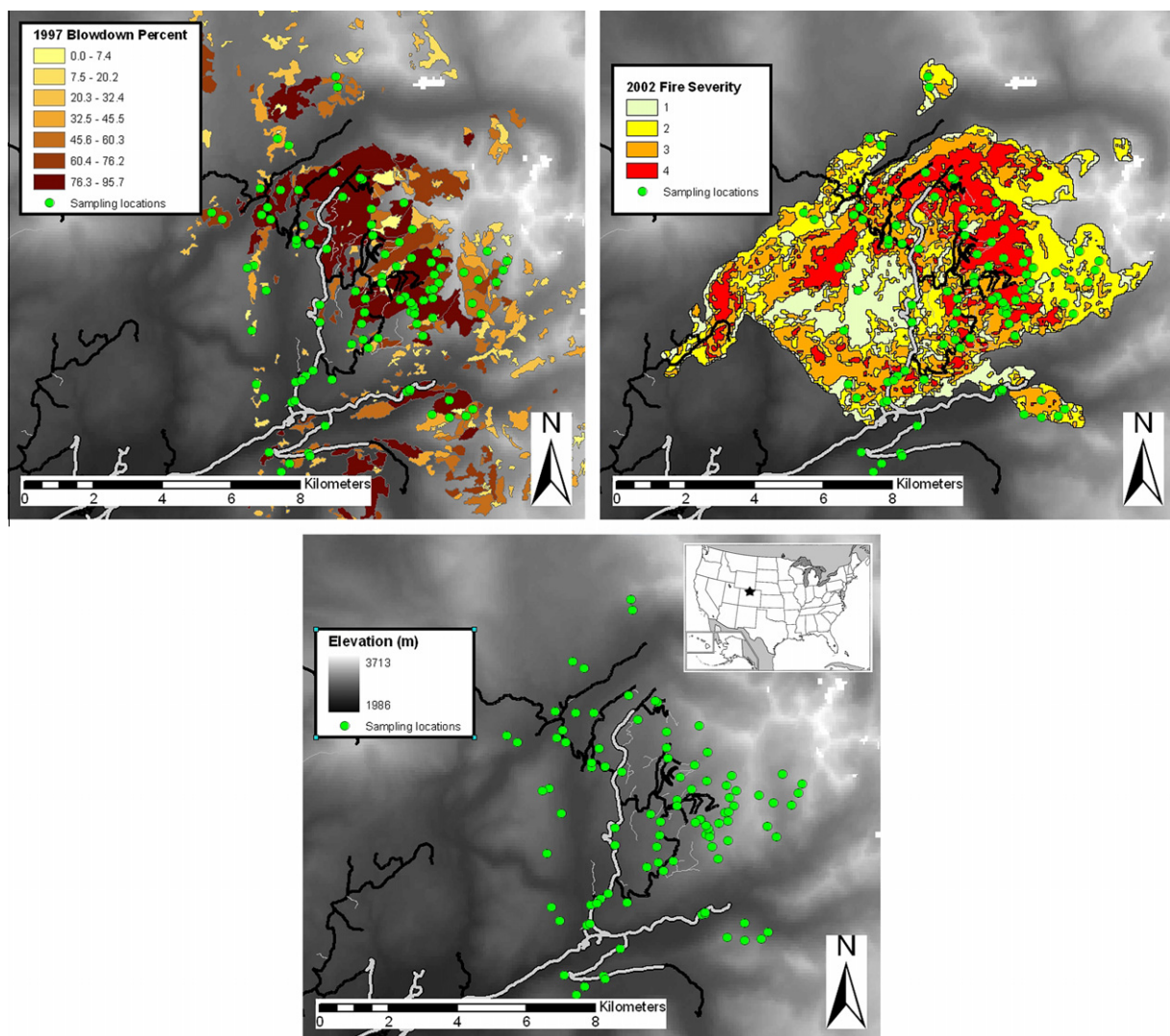**Fig. 1.** Map of blowdown, the surveyed portion of Mt. Zirkel complex burn, and elevation throughout the study area. 1997 blowdown severity, by percentage blowdown, fire severity (estimated by USFS dNBR mapping), sampling locations, and access roads are shown. Logging areas are scattered, small, and often unmapped and are thus omitted for clarity. Note that the blowdown area extends north and south off the map.

attempts to determine the importance of disturbance history to post-disturbance recovery of various tree species with different response strategies.

In the southern Rocky Mountains, the dominant subalpine species [Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*)] respond to individual disturbances in different ways (Table 1), and in most cases, recovery follows predictable patterns of succession (Clements, 1910; Peet, 1981; Veblen et al., 1991). If the tree species fail to recover, conversion to subalpine grasslands is possible (Stahelin, 1943; Lynch, 1998), which represents a major loss of biomass and a dramatic, long-term habitat conversion. If coniferous species fail to recover, but aspen resprouts or invades, stable, self-replacing aspen forests can form (Crawford et al., 1998) with corresponding changes in ecosystem functioning and services such as water supply (LaMalfa and Ryle, 2008). The adaptations and resilience mechanisms of these tree species are well described for singular disturbances; the response of the individual species to multiple disturbances, including anthropogenic disturbances, is not well-studied and given the ability of compounded perturbations to cause regime shifts (Paine et al., 1998) a better understanding of how these species respond is required.

In northern Colorado, an early season blizzard (October 1997) with extreme winds resulted in ~10,000 ha of forest blowdown along the western slope of the Park Range. Areas of fallen trees ranged from patches of low (~5%) to high severity (near 100% mortality of overstory trees, Lindemann and Baker, 2001). Following the blowdown, salvage logging commenced within the Routt National Forest. Between 1999 and 2001, approximately 900 ha were salvaged. In the summer of 2002, during an extreme drought, the Mt. Zirkel Fire Complex ignited, burning from July to September and consuming around 12,000 ha of forest, some of which had experienced blowdown or blowdown and salvage logging (Kulakowski and Veblen, 2007). This created a mosaic of disturbance histories in a natural, semi-factorial design, allowing for the differentiation of disturbances and their singular and interactive effects on the ecology of the subalpine forest (study area centered around lat: 40.82, long: −106.73; Fig. 1). The area receives approximately 1000 mm of precipitation annually, mostly as snow (NRCS/Snotel, 2010). Temperatures range from means of −9.6 °C in January to 16.6 °CC in July, with an average of 3.8 °C (Colorado Climate Center, 2003).

The objectives of this study were to identify factors related to tree recovery (or non-recovery) after a multiple disturbance event (blowdown, salvage logging, and fire), determine if disturbance history/severity was an important factor in recruitment, and relate responses to multiple disturbances to species-specific response strategies. Lodgepole pine typically recruits strongly post-fire via cone serotiny (Lotan and Perry, 1983); we hypothesize that the presence of pre-fire blowdown will reduce recruitment via increased burn times/temperatures, and salvage logging may ameliorate this effect somewhat via reduced fuel loading (Buma and Wessman, 2011). In contrast, we expect that the response strategies which depend on seeding from off-site (Engelmann spruce, subalpine fir, aspen) will remain neutral in their response to blowdown + fire vs. fire alone.

2. Methods

2.1. Sampling design

Disturbance interactions considered in this study were: (1) Fire only; (2) Blowdown + Fire (gradient of blowdown severities, from 5% to 95%); (3) Blowdown + Salvage Logging + Fire. Ninety-nine sites (15 × 15 m) were surveyed in 2010, all in previously closed-canopy conifer forest, with lodgepole as a significant canopy component (United States Forest Service (USFS) mapping and general observations, 1999–2010). To reduce the potential influence of pseudo-replication in disturbance-based studies, a gradient analysis was used (Wiens and Parker, 1995), minimizing the impact of non-random distribution of disturbance-related factors in recovery analyses (Parker and Wiens, 2005). Sampling was designed to maximize the resolution of the disturbance interactions. All plots experienced high-severity fire. The prior disturbance (1997 blowdown) was sampled along its entire gradient, from zero (fire-only, $n = 6$) to near 100% blowdown (total along gradient, $n = 82$). An additional 11 plots were located in areas that were salvage logged prior to the fire, with varying degrees of blowdown severity (66–92%). Blowdown severity is taken from maps by Baker et al. (2002). By minimizing variability in the fire severity (complete aboveground mortality and organic soil consumption at all plots), differences in recovery could be ascribed to either disturbance interactions (rather than simple increases in cumulative mortality or residual survivors) or environmental variables (e.g. topography). To limit variability in the influx of seed, only sites at least 100 m from any green tree were considered; this is the approximate distance at which spruce and fir seed supply level off to a steady, low amount (Noble and Ronco, 1978). Aspen can seed over 1 km (Burns and Honkala, 1990), so all sites were assumed to be available for aspen recruitment. Plots were located in pairs separated by 75 m, with at least 500 m between pairs. This sampling design (random clustered) is recommended by Fortin et al. (1989) for determining landscape-scale structure in similar analyses.

At each plot, all conifer species were counted and recorded by species, height, and basal diameter; number of whirls were counted to determine ages. Several seedlings were destructively sampled for age confirmation. Aspen clones were counted and recorded by height. Because young aspen grow several shoots before assuming a tree-form, evaluation of a "single aspen" can be difficult. A clump of aspen shoots was considered a single individual if all the shoots emerged from the ground within ~10 cm of each other. While this can be somewhat subjective, it was rarely an issue; most aspen was well differentiated. Approximately 20 aspen were excavated (entire root system) to confirm they were not regenerating from suckers; only one was found to have suckered off a neighboring shoot. Aspen trunks, even when almost completely consumed by fire, are easily differentiable from conifer remains. No aspens were present in the overstory prior to the fire on or near any plot, thus all aspen were likely new recruits (see Section 4.4 for further discussion).

To determine the influence of substrate and other vegetation on recruitment, percent cover was estimated for several cover types. Percent cover (to 2% resolution) of rocks, forbs, graminoids, bare ground, woody debris, and moss was visually estimated using ten 1 m² quadrats randomly located throughout the plot. It was not expected that any particular forb or graminoid species has a differential impact on seedling regeneration, thus they were treated as functional groups.

Topographic variables were considered using 30 m USGS digital elevation maps (DEM). Plot elevation and slope were calculated using bilinear interpolation. Aspect was transformed to a radiation index (TRASP) using Moisen and Frescino (2002).

$$TRASP = (1 - \cos((\pi/180)(aspect - 30)))/2 \qquad (1)$$

TRASP assigns 0 to NNE aspects (typically wettest) to 1 on SSW aspects (typically driest). Soil moisture (volumetric water content) was measured using a hand-held probe at 10 random locations per site.

Fire severity was taken from a USFS map created post-burn using the dNBR index (difference normalized burn ratio) derived

Table 2
Predictive variables in modeling and disturbance history analyses. All measured variables are shown, as well as the abbreviations seen in the CART analyses (Fig. 2). All variables were input into random forest model for important variable identification. All field-sampled variables come from individual 15 × 15 m plots. Response variables (densities of lodgepole pine, Engelmann spruce, subalpine fir, and quaking aspen) were also measured on each plot and are a complete census. *, Only considered in spruce and lodgepole models. Variables identified by random forest analysis and input into CART model; †, lodgepole pine; ‡, Engelmann spruce; **, aspen.

Variable class	Variable	Units	Range	Source
Disturbance history	Salvage logging	NA	Yes/no	USFS communication, site evaluation
	Blowdown density[†]	Downed trees ha^{-1}	0–75.125	Baker et al. (2002)
	Fire severity	dNBR (0–4)	2–4	USFS
Topographic/abiotic	Elevation[†,‡,**]	Meters	2516–3198	DEM
	Aspect[†]	NA	0–1	DEM, Moisen and Frescino (2002)
	Slope[†,**]	Percent	3.9–27	DEM
	Soil moisture[‡,**]	Volumetric water content	3.7–52.7	Sampled 3× at five random points on plot (n = 15 points plot^{-1})
Vegetation	Forb cover[‡,**]	Percent cover	5.8–77.6	Ten 1 m^2 quadrats, mean
	Rock cover	Percent cover	0–29.6	Ten 1 m^2 quadrats, mean
	Graminoid cover	Percent cover	0–53	Ten 1 m^2 quadrats, mean
	CWD cover	Percent cover	1.8–25.3	Ten 1 m^2 quadrats, mean
	Bare ground[‡,**]	Percent cover	0.2–63.2	Ten 1 m^2 quadrats, mean
	Moss cover	Percent cover	0–44	Ten 1 m^2 quadrats, mean
	Aspen density[*,†,‡]	Stems/m^2	0–1.51	Complete survey (15 × 15 m plot)
Spatial	Mean fire severity, 140 m radius	dNBR (0–4)	0–4	USFS, analyzed in ArcMap ESRI (2010)

from 30 m 2002 Landsat imagery. Severity classification is ordinal, from 1 to 4, 1 being light burn, with no crown scorch, to 4 which is complete mortality. Zero indicates no fire. All 99 sites were checked in the field; only one was incorrectly classified; this site was not included in the analysis. To determine neighborhood fire severity for each site, a 140 m radius plot was created around each field plot using ArcMap (ESRI, 2010) and the mean severity (0–4) within that radius was recorded. A distance of 140 m represents the upper limit of reliable conifer seed dispersal (Alexander, 1987; Lotan and Perry, 1983). All considered variables listed in Table 2.

While subalpine fir is common in the understory and overstory of a mature subalpine forest, in the fire-recovery areas it was not present in enough numbers for quantitative analysis. In addition, subalpine fir is not generally a post-fire colonizer, and recruitment is quite variable post-disturbance (10–150 years, Veblen et al., 1991; Jenkins et al., 1998). Thus, the analyses were limited to lodgepole pine, Engelmann spruce, and quaking aspen.

2.2. Analysis

Recovery from disturbance is a complex process and typically fails to meet several assumptions of parametric statistical techniques (Wiens and Parker, 1995; Parker and Wiens, 2005). To address those concerns, a combination of random forests and regression trees (CART) were used. While CART is useful in identifying complex and non-linear interactions between variables (Moisen and Frescino, 2002), it has the potential to find false minima, as it is a greedy algorithm. To avoid this pitfall, random forests were first used to identify the most relevant variables. Random forests (Brieman, 2001) utilize an ensemble approach to regression trees, using a subset of predictors and data points multiple times, and aggregating the results. While this avoids the potential for false minima and creates a powerful model for prediction, it makes interpretation of variable interactions difficult. To combine the two methods, random forests (n = 5000 trees) were used to identify the five most explanatory variables for each individual species, and those variables were used in CART tree construction (Brieman et al., 1984). As a secondary means to avoid over fitting, a 10-fold cross-validation process was conducted, with the tree size giving the smallest error recorded for each run. The average tree size was used to prune the original tree (from the complete dataset). This tends to minimize complexity and results in a reasonably generalizable tree (Qian, 2010). Pseudo-r^2 values were calculated for each tree:

$$\text{Pseudo } r^2 = 1 - (\text{deviance}_{\text{pruned tree}} - \text{deviance}_{\text{initial data}}) \qquad (2)$$

Using the pruned deviance is conservative, as the random forest approach already grants a degree of generalizability. Pseudo-r^2 values are also reported for the initial trees for comparison.

As a second test of the influence of prior disturbance severity on post-fire recovery, post-fire densities of each species were regressed against blowdown severity using Spearman's rank correlations. Logging plots (n = 11) were excluded from this analysis because the amount of residual biomass prior to the fire was unknown. To assess differences between regeneration in salvage-logged and unlogged plots, the data was subset to ensure comparable groups. Only plots with 60 downed trees ha^{-1} and above were considered (the lowest severity observed in salvage areas) and only plots below 2992 m elevation were considered (the highest elevation observed in salvage areas). Aspect, elevation, fire severity, and blowdown severity did not differ significantly between salvaged and unsalvaged plots (unpaired t-tests, $p > 0.05$). This resulted in 11 salvage-logging plots and 14 non-salvage plots for comparison. Kruskal–Wallis tests were used to compare median recruitment for each species in salvage vs. unsalvaged areas. All analyses were conducted in R (R Project for Statistical Computing, 2008).

3. Results

3.1. Random forest and CART analysis

Random forest analyses identified different predictive variables for each species. The best predictor of post-fire lodgepole regeneration was blowdown severity, followed by (descending order of importance) elevation, slope, aspect, and aspen density. For spruce, identified variables were the mean cover percent of forbs, aspen density, mean cover of bare soil, mean moisture, and elevation. For aspen, mean moisture, mean cover of bare soil, slope, mean cover of forbs, and elevation were identified (Table 2). These variables were used in the CART analysis.

Lodgepole pine had a different response compared to spruce and aspen, which were similar (Fig. 2). Lodgepole recruitment was strongly structured by the severity of the pre-fire blowdown, with generally lower levels of recruitment found above 20 downed trees ha^{-1} prior to the fire. Southerly aspects (indicated by a higher TRASP value) were also favorable to regeneration in areas of low blowdown, although it is unclear if this was due to actual recruitment effects or pre-fire species composition differences (see Section 4.1). The
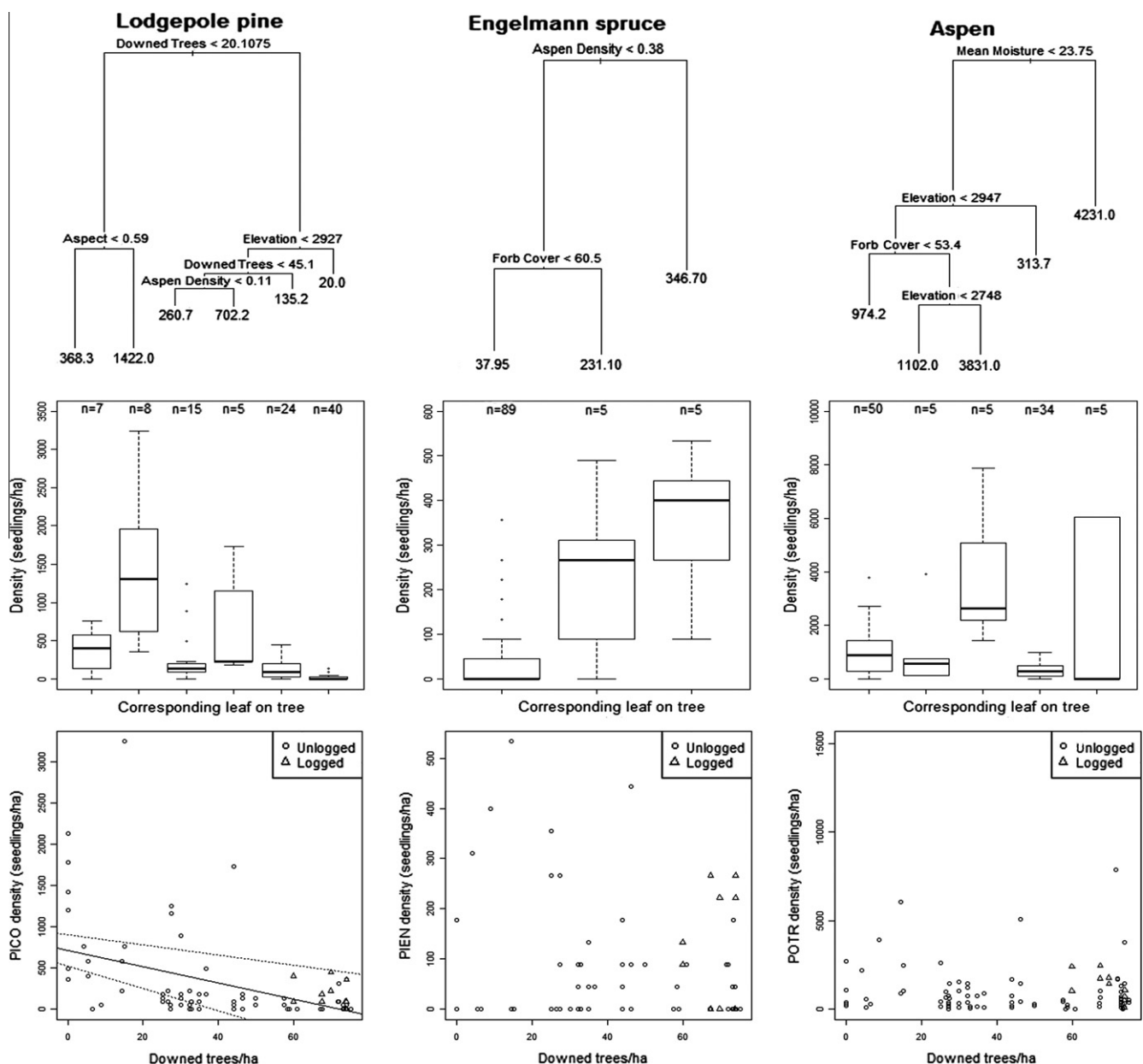
Fig. 2. CART and blowdown severity vs. seedling density. Top row: Pruned regression tree analysis, for each species, showing the significant predictive variables in rank of importance. If the condition at each branch is satisfied, move to the left. If not, move to the right. Each leaf of the regression tree (terminal node) is identified with the mean seedling density of that node. Middle row: Boxplot displaying the variance in each leaf; sample size refers to the number of plots partitioned into each leaf. Each box is directly below the leaf it represents. Note that scales differ between plots. Bottom row: Relationship between the number of downed trees ha^{-1} prior to the fire (any species) and individual seedling densities (post-fire) for both logged and unlogged plots (note that salvaged plots had reduced fuel loading prior to the fire (Buma and Wessman, 2011), pre-salvage loadings are shown). Only the relationship between lodgepole pine seedlings and blowdown severity was significant ($p < 0.05$, 95% confidence interval shown); lodgepole pine also had significant differences between logged and unlogged plots ($p < 0.05$).

pseudo-r^2 value for the lodgepole regression tree was 0.56 (0.65 unpruned). Engelmann spruce was positively correlated with the presence of aspen and forbs. Pseudo-r^2 for spruce was 0.36 (0.48 unpruned). Aspen recruitment was best explained by moisture levels, followed by elevation and forb cover. Aspen had the poorest fit, with a pseudo-r^2 value of 0.30 (0.33 unpruned).

Table 3
Modeling results and seedling count totals, significant relationships ($p < 0.05$) in bold. CART pseudo-r^2 calculated according to Eq. (2). To test a relationship between blowdown severity (downed trees ha^{-1}) and seedling density, Spearman's rank correlations were calculated (salvage plots excluded, total $n = 88$). To test difference between salvaged and non-salvaged densities, Kruskal Wallis tests were performed (only plots below 2993 m elevation and above 60 downed trees ha^{-1} included, total $n = 25$).

Species	Total count	CART pseudo-r^2		Spearman's correlation			Kruskal Wallis	
		Pruned	Unpruned	S	ρ	p	H	p
Lodgepole pine	572	0.56	0.65	**180123**	**−0.58**	**≈0**	**6.66**	**≈0**
Engelmann spruce	124	0.36	0.48	124528	−0.10	0.37	3.57	0.06
Aspen	2038	0.30	0.33	129203	−0.14	0.20	1.32	0.2

3.2. Trend analysis and salvage logging influence

Lodgepole was the only species to have a significant relationship with pre-fire blowdown levels and recruitment (Table 3), with seedling densities declining as pre-fire blowdown severity increased (Spearman's correlation test, $S = 180123$, $\rho = -0.58$, $p \approx 0$). Spruce and aspen recruitment did not show any significant correlation with pre-fire blowdown severity ($p > 0.05$). Kruskal–Wallis tests used to determine any difference in recruitment on salvage-logged vs. non-salvage logged plots showed significantly higher recruitment for lodgepole ($H = 6.66$, $p \approx 0$) in salvaged plots. Engelmann spruce and aspen recruitment were not significantly higher in salvaged vs. non-salvaged plots, although recruitment was marginally higher for spruce (spruce: $H = 3.57$, $p = 0.06$; aspen: $H = 1.32$, $p > 0.05$).

4. Discussion

The disturbance interactions investigated had differential impacts on individual tree species, with corresponding effects on densities of seedlings and implications for future landscape heterogeneity. Compounded disturbances are not necessarily additive or synergistic; a three-disturbance system may be less severe than a two-disturbance system.

4.1. Limitations of results

Any conclusions are tempered by several difficulties in the study design resulting from the non-random nature of disturbances. These difficulties are not fatal, and are inevitable in disturbance ecology (Wiens and Parker, 1995). Chief among them was the lack of knowledge of pre-fire stand composition. Due to the intensity of the fire, it was impossible to differentiate dead coniferous species. A previous USFS survey, and personal observations, indicated that all plots were spruce–fir dominant with lodgepole subdominant, and lodgepole are present throughout the intact spruce–fir forest around the burned area (personal observations). The gradient analysis advocated by Parker and Wiens (2005), the statistical approach (random forests and CART) and the large sample size attempted to compensate for the missing information and potential co-linearity. The influence of aspect may be a partial reflection of differences in stand composition, as lodgepole may be more successful on drier, south-facing slopes (Lotan and Perry, 1983). Another potential source of unaddressed variability in the lodgepole analysis is cone serotiny, which may vary between

Fig. 3. Histogram of conifer ages and aspen heights. Conifer ages were estimated by counting whirls and destructively sampling a subset of individuals to confirm the validity of that approach. Both species show a dramatic tapering of establishment after a peak approximately 3 years post-fire. Aspen are difficult to age, and so height is shown as a proxy. Relatively few small aspen were seen, and the height graph implies a pulse of recruitment for that species as well.

stands as a function of age and elevation (Schoennagel et al., 2003). Higher elevation stands, however, are typically less variable (Tinker et al., 1994). It can be assumed that enough serotinous cones were present in all stands to provide ample seeds because lodgepole pine regeneration was seen at all elevations and since seed dispersal distances are quite low for lodgepole. Further, the low variability seen in high-blowdown/high-fire sites indicates that the blowdown-fire interaction is the major driver of the observed variation in lodgepole densities. While these complexities temper the results, they are an inherent part of any disturbance study and mainly spring from the fact that disturbances are singular events with non-random distributions. This study was conducted 8 years post-fire, and recruitment may continue. However, recruitment rates have fallen dramatically (Fig. 3) and any additional recruitment is unlikely to substantially alter the patterns observed, although the possibility of substantial further recruitment cannot be discounted.

4.2. Lodgepole pine response

Lodgepole pine regeneration appeared to be strongly driven by prior disturbances and their severities. Seed in serotinous cones remains viable for decades in dead trees (Aoki et al., 2011), and so were viable at the time of the fire. The dominant factor structuring lodgepole recruitment was the density of downed trees prior to the fire. At high blowdown severities, little variation in seedling densities was seen, bolstering support for the argument that disturbance history, and not pre-fire species composition variability, was controlling the response. The presence of salvage logging prior to the fire increased levels of lodgepole regeneration. This is likely due to a decrease in fire duration as a result of CWD removal (Buma and Wessman, 2011).

Abiotic conditions created by the logging may have increased recruitment success for all species as well (compared to high-severity blowdown that was unsalvaged). Soil carbon was significantly increased in salvage-logged sites compared to non-salvaged sites; probably a result of the incorporation of woody debris into the soil (Morliengo-Bredlau, 2009). An increase in soil organic matter may raise the available water capacity of the soil (Hudson, 1994), in turn increasing the survival chances of recruits. Volumetric water content in logged plots was higher, although not significantly so, than comparable non-logged plots (10.9% vs. 7.5%, unpaired t-test, $p > 0.05$). The variability introduced by sampling moisture over several weeks and the inherent spatial variability in recovery potentially contribute to the lack of significance.

4.3. Engelmann spruce response

Engelmann spruce regeneration increased with increasing aspen density, likely a function of environmental stress mitigation and site quality. Aspen seedlings, which are characteristically shrub-like initially, provide shade for spruce seedlings, which are inhibited by full sunlight, especially at high elevations (Alexander, 1984). They also function to trap snow in the winter. Engelmann spruce seedlings are very dependent on adequate moisture for the first 5 years of life (Alexander, 1984), and increases in snow depth due to aspen recruitment may translate into higher soil moisture in the summer. In terms of site quality, aspen typically grow in wetter soils (McDonough, 1979; Burns and Honkala, 1990, see also Fig. 2). This abiotic factor could thus favor both aspen and spruce, resulting in higher densities of both species in wetter areas. Soil moisture itself was not a predictive variable for spruce densities; this could be a result of the time span over which sampling occurred. Approximately 5 weeks were required to sample all the sites, and therefore sampling order could have contributed to the variability in measured soil moisture values.
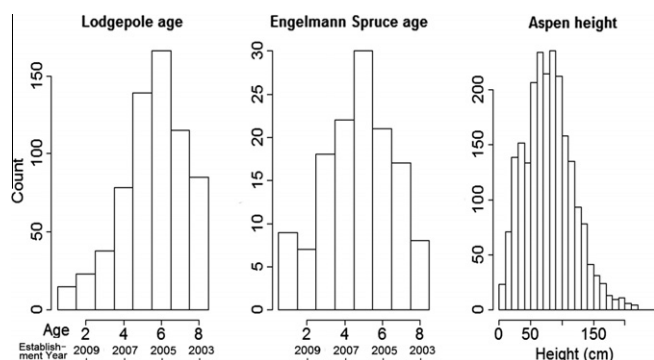
Disturbance history was not a factor in spruce recruitment in either the CART or statistical analysis.

4.4. Aspen response

Soil moisture was the dominant driver of aspen recruitment. The relationship with soil moisture was evident despite the variability introduced by sampling moisture over 5 weeks. The association of higher aspen densities with higher forb cover could also reflect this relationship between site quality and aspen recruitment. Blowdown severity did not influence post-fire recovery, as expected from an invading strategy. While aspen recruitment from seed is often considered a rare event, actual evidence is conflicting, with several studies showing no aspen establishment and several showing strong establishment (Howard, 1996). Evidence of aspen recruiting from seed has been found throughout the North American West (Williams and Johnston, 1984; Kay, 1993; Romme et al., 1997; Quinn and Wu, 2001). The common belief that aspen does not reproduce from seed is based on exacting seed bed requirements, and the necessity that the seedbed remain adequately moist for a long-time period during germination and establishment (McDonough, 1979). Conditions required for establishment of seedlings (exposed mineral soil, consistent soil moisture; DeByle and Winokur, 1985) were likely met after this fire. The Routt National Forest is one of the wetter places in the southern Rocky Mountains, receiving approximately 1000 mm of precipitation per year (USDA Natural Resources Conservation Service: http://www.wcc.nrcs.usda.gov/snow/). While some of the counted individuals are likely suckers from nearby seedlings, it seems reasonable to assume that the majority of individuals counted were from seed, given that all but one of the excavations were confirmed seedlings and likely favorable establishment conditions.

4.5. Implications of differential species responses

Long-term changes in species composition across the landscape are likely due to the differential response of these structurally important species to the rapid sequence of multiple disturbances. Aspen will likely increase in dominance; in areas with no conifer species present and far from potential conifer seed sources, long-term aspen dominance is likely (Morgan, 1969; Crawford et al., 1998). Lodgepole representation may decrease; while often considered a fire-dependent species due to its serotinous cones and relative shade intolerance, this blowdown-fire interaction may surprisingly result in less lodgepole at the landscape scale. Other research has observed a similar elimination of fire-dependent conifers (Johnstone and Chapin, 2006) after multiple disturbances in a short time period (fire + fire), and interactions of this sort may be important in maintaining alternate states across the landscape. There is evidence that increased fire severity in post-blowdown areas maintains alternate landscape regimes (American southeast, Myers and van Lear, 1998), although it is unknown as to the prevalence of this interaction in the subalpine ecosystem. It has been hypothesized that fire-initiated lodgepole stands can facilitate the later establishment of spruce and fir (Stahelin, 1943) through amelioration of harsh abiotic conditions. Thus, areas with sparse lodgepole pine may experience slowed recovery to a spruce–fir forest (which existed previously), or not recover at all, although the association of spruce with aspen may fill that role. Even in areas which recover to spruce–fir forests, if few lodgepole are present the consequences for resilience to future fire may be important. Remnant species can provide important resilience functions (Eriksson, 2000), and the serotinous nature of lodgepole, coupled with its potentially facultative role for spruce and fir (Stahelin, 1943), may provide important resilience benefits to future fire events. At the landscape scale, however, the increased prevalence of aspen may

provide fire breaks and lower landscape susceptibility to fire (Johnstone et al., 2010). Aspen is less likely to burn and may disrupt fire spread (Fechner and Barrows, 1976), and resists blowdown in wind events (Lindemann and Baker, 2001). The increase in spatial heterogeneity of species composition will therefore likely have varied impacts on future forest resilience to a variety of disturbances, in addition to current ecosystem functioning.

Salvage logging often does more harm than good (Lindenmayer et al., 2004). In this area it was highly detrimental to the ecosystem prior to the fire, especially in regards to the advanced regeneration strategy of Engelmann spruce and subalpine fir (Rumbaitis-del Rio, 2006), and while it appears that salvaging did ameliorate some impacts of the subsequent fire, it cannot be assumed that all salvage logged areas will burn. The limited sample size ($n = 11$ salvaged plots) also precludes any strong conclusions from the increase in regeneration in salvaged plots. However, limited fuel loading may increase resilience of lodgepole to fire through a reduction in burn times, which lead to a decrease in serotinous cone consumption (Buma and Wessman, 2011). Further research on the interaction between logging and subsequent fire is needed, especially in the context of resilience mechanisms that may be more successful in a lower fuel load environment (e.g. serotinous cones). Other issues, such as road construction and increased human traffic post-logging, both ecologically damaging, must also be considered. Management decisions should anticipate future disturbances, and deliberate ecological consequences in addition to economic incentives (Lindenmayer et al., 2004).

There may be some generality in species responses to multiple disturbances depending on their particular disturbance strategies, with disturbance-specialized species exhibiting more unexpected/non-linear behavior when confronted with multiple, interacting disturbances. Lodgepole pine, the evader, shows a surprising lack of resilience to fire in areas of high severity blowdown despite serotinous cones, and lacking an efficient seed dispersal mechanism may be lost in areas experiencing both disturbances at high levels (likely due to an increase in fire residence time, Buma and Wessman, 2011). Aspen was found in high densities due to invasion via seed, however its endure strategy would have been overcome by the severe fire. While high severity fire (consumption of organic soil) is not atypical in subalpine fires, the blowdown/fire combination increased the proportion of area experiencing a high severity burn (Kulakowski and Veblen, 2007). Spruce was not significantly influenced by disturbance history, likely because it relies solely on an invader strategy, and thus only the severity and spatial scale (e.g. distance from seed source) of the final disturbance matters (Buma and Wessman, 2011). Overall, species exhibiting invader characteristics are likely insensitive to potential disturbance interactions because of their lack of disturbance-response specificity, in contrast to more "adapted" species (Johnstone and Chapin, 2006), although interactions which affect recruitment success (e.g. edaphic effects) may be important. In this case, few biologically significant soil impacts were seen (Morliengo-Bredlau, 2009). More specialized responses exhibited by the evaders and endurers (cone serotiny and resprouting), and especially those that rely on a specific disturbance type (e.g. fire), may be more likely to exhibit unexpected responses to multiple disturbances as their specialization becomes more a liability than an evolutionary advantage. The response flexibility provided by a simple seed dispersal strategy may confer resilience to complex, interacting disturbances.

5. Conclusions

Disturbances are complex events, whether natural or human caused. Depending on the ecosystem in question and the species

involved, multiple disturbances may have compounding effects, although the cumulative impact is dependent on species-specific response strategies and characteristics. Disturbance types, their interactions, and species resilience mechanisms may be more important than the number of disturbances. In this case, three disturbances were less severe than two disturbances for lodgepole pine (the evader); for others, the number of disturbances was irrelevant (the invaders). Disturbances which occur before the ecosystem has recovered from previous disturbances must be studied (Paine et al., 1998); with climate change and increasing anthropogenic pressures will come increasing disturbance frequency (Dale et al., 2001) and the need to understand disturbance interactions is paramount (Turner, 2010). This study illuminates ways in which disturbance interactions differentially impact major structural species, which may have impacts on ecosystem services such as water yield, wildlife habitat, and carbon sequestration. Landscape-scale changes in species composition may influence future landscape resistance and resilience to disturbances. Multiple disturbances are not necessarily additive nor synergistic, and a combination which was initially highly negative in terms of ecosystem damage (blowdown/logging, Rumbaitis-del Rio, 2006) appears in a more nuanced light when an additional disturbance is imposed (blowdown/logging/fire). Response to multiple, interacting disturbances varies on a species by species basis, with long term implications for both cover and resilience to future disturbances.

Acknowledgments

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