

## Disturbance interactions can impact resilience mechanisms of forests

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**Abstract.** Interactions between multiple disturbances are of special concern in ecology due to their potential for non-linear behavior and long-lasting legacies on landscape structure and function. If multiple disturbances overcome the ecological resilience of a system, alternate stable states are possible. Increases in the frequency and severity of disturbance events as a result of climate change heighten this concern. This study directly addresses the question of ecosystem resilience in the face of multiple disturbances. We investigated a gradient of disturbance interaction severities between two events in a subalpine forest, a 1997 windstorm (variable severity) and a 2002 wildfire (high-severity). A third disturbance, salvage logging of blowdown (1999–2001) prior to the fire, served as a de facto experimental treatment. Ninety-nine study plots were established across the disturbance gradient, including fire-only areas for a baseline fire response. Modeling indicated that the combination of two severe disturbances created novel conditions which exceeded the resilience mechanisms of the system. Modeled mean fire residence time and temperature (First Order Fire Effects Model, FOFEM), as well as mean distance to potential seed sources, increased as a result of the interaction. Regeneration 8 years post-fire was essentially absent in medium- to high-severity blowdown + fire plots, whereas low-severity blowdown + fire and fire-only areas showed strong regeneration. Blowdown + salvage + fire had significantly higher regeneration than areas of comparable blowdown, suggesting that fuel loading drove the interaction. CART analysis supported this hypothesis. Multiple disturbances have the potential to create surprising situations and reduce the resilience of an ecosystem. Differential recovery as a result of a “novel disturbance” created by compounding events will likely have long lasting legacies across the landscape.

**Key words:** compounded perturbations; fire ecology; forest disturbance; landscape dynamics; landscape ecology; multiple disturbance interactions; resilience mechanisms; subalpine.

**Received** 9 February 2011; revised 18 April 2011; accepted 4 May 2011; **published** 31 May 2011. Corresponding Editor: R. Gardner.

**Citation:** Buma, B., and C. A. Wessman. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2(5):art64. doi:10.1890/ES11-00038.1

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### INTRODUCTION

Disturbances at various spatial and temporal scales are common to terrestrial ecosystems (Pickett and White 1985, Turner 2010), which have evolved the capacity for recovery following disturbance. The ability of an ecosystem to experience a disturbance and recover to the same dominant cover (e.g., coniferous forest recover-

ing to coniferous forest) has been termed the “ecological resilience” of the system (Holling 1973, Gunderson 2000), referring to the amount and type of damage an ecosystem can endure while still reorganizing back to its original structural and functional identity. Our understanding of ecological response and recovery from various disturbances is integral to long-term projections, models, and resource manage-

ment. However much of our knowledge of landscape resilience, albeit sophisticated, is based on studies of singular disturbances (White 1979, Turner 2010). Concern regarding ecological surprises (i.e., non-additive effects) as a result of disturbance interactions, with potentially dramatic impacts on long-term ecosystem structure and functioning, is mounting (Paine et al. 1998, Darling and Côté 2008, Harley and Paine 2009); the likelihood of increasing disturbance frequencies resulting from climate change (Dale et al. 2001) heightens that concern.

Increased study of multiple disturbances and their interactions is important (Turner 2010), particularly when combinations of disturbances may exceed the ecological resilience of an ecosystem (Fig. 1). In the simplest case, it is conceivable that a disturbance of a high enough initial severity (e.g., number of trees killed or biomass lost) can overcome the ecological resilience of the ecosystem, which may result in a shift to an alternate stable state through the establishment of another dominant cover type (Turner et al. 1993, Beisner et al. 2003, Suding and Hobbs 2009). Resilience may also be exceeded through disturbance interactions (Paine et al. 1998). Compounded disturbances (multiple perturbations, in the same location, separated by less time than is required for recovery) can create a disturbance either of extraordinary severity or of novel characteristics. If the interaction results in a simple severity increase (e.g., two hurricanes which combine to destroy a given amount of trees; see C in Fig. 1), the cumulative effect may be equivalent to treating the disturbance combination as one large, infrequent disturbance (e.g., Turner et al. 1998). However, if the first disturbance alters the *characteristics* of the second disturbance, the combination thereof may be, in essence, a novel disturbance (see D in Fig. 1), likely to cause surprising results and potential non-linear ecosystem behavior as resistance and/or resilience mechanisms are exceeded (Paine et al. 1998).

A novel disturbance is defined as an event (e.g., fire or flood) which, when encountering conditions generated by a prior disturbance, impacts the ecosystem in a way it would not normally do were that event to happen in isolation; the cumulative impact is therefore the result of a true interaction, as opposed to two

isolated incidents. Ecosystem resilience mechanisms will likely be ill equipped to handle the new conditions. As in the case of large, infrequent disturbances (Turner et al. 1998, Romme et al. 1998), if the ecosystem's resilience is exceeded, recovery pathways may be unpredictable, resulting in increased landscape heterogeneity and formation of alternate stable cover types in areas of previously similar cover.

Despite the importance of these potential interactions, investigation is difficult due to the lack of suitable study areas at the proper scale. This study takes advantage of a recent combination of disturbances that created a natural gradient in interaction severities as well as a de facto experimental treatment. We examined a subalpine forest in the Southern Rocky Mountains that experienced catastrophic disturbances (wind, salvage logging and fire) within the span of 5 years. All the areas investigated experienced severe, stand-replacing fire as the last disturbance in the sequence, with complete above-ground mortality and consumption of the organic soil. Thus, because the fire essentially "reset the landscape" through complete mortality, any adverse impacts on resilience mechanisms as a result of the disturbance interactions could be attributed to novel disturbance characteristics, rather than simple increases in cumulative mortality (e.g., "D," not "C," in Fig. 1). If there was no interaction between the fire and the preceding disturbances, then all areas would be expected to resemble fire-only areas (in terms of forest recovery). If, however, the combination of disturbances detrimentally impacted forest resilience mechanisms, regeneration should be reduced or absent in areas that experienced severe disturbances prior to the fire. Historically, subalpine forests are adapted to large, infrequent stand-replacing fires (Peet 2000, Veblen 2000). Because subalpine forests can assume alternate successional trajectories in the absence of coniferous regeneration (which then further hinder conifer establishment), lack of coniferous seedlings signifies, in essence, the loss of resilience. We considered these questions: (1) Did blow-down legacies alter characteristics of the fire? (2) Were forest resilience mechanisms detrimentally impacted by those new characteristics? (3) Did the blowdown-fire combination reduce coniferous forest resilience and recovery?

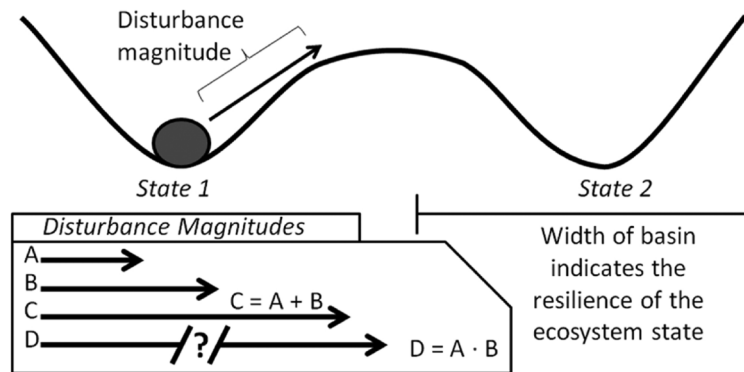


Fig. 1. Multiple disturbances in a resilience context. The ecosystem is represented as the grey ball. Potential stable states are indicated as basins. If two disturbances (A and B) of differing magnitudes impact the same location, their impact could be a cumulative increase in magnitude (C), which would push the ecosystem further from its stable state and potentially to another basin of attraction (State 2). If the disturbances interact (D), the results may be unpredictable, depending on the interaction and its impact on the resilience mechanisms of the ecosystem.

*Resilience mechanisms.*—The relevant fire-resilience mechanisms of the dominant conifer species are cone serotiny (*Pinus contorta* [lodgepole pine]) and seed dispersal (*Picea engelmannii* [Engelmann spruce] and *Abies lasiocarpa* [subalpine fir]). In a typical subalpine crown fire, fire is sustained in an individual tree canopy for 20–30 seconds (Despain et al. 1996), enough to trigger seed release from the serotinous cones. An increase in fire residence time or absolute temperature can consume cones and seeds, and has been an observed cause for lack of regeneration under burned slash piles (Lotan and Perry 1983 and references therein). *P. engelmannii* and *A. lasiocarpa* rely on seeding from off-site to repopulate following a stand-replacing disturbance (Alexander 1987). Both have relatively short dispersal distances, with few seeds reaching more than 100 m for either species (Noble and Ronco 1978). Non-serotinous *P. contorta* may also seed from off-site, but its dispersal distance is less than either *P. engelmannii* or *A. lasiocarpa*, and therefore is impacted in the same fashion.

## METHODS

### Site

In October 1997, a severe windstorm was associated with an early season blizzard in the Routt National Forest of northern Colorado (40°46' N, 106°46' W). The subalpine forest

(dominated by *A. lasiocarpa* and *P. engelmannii*, with *P. contorta* and *Populus tremuloides* [trembling aspen]) experienced the largest blowdown (>10,000 ha) in Southern Rocky Mountain recorded history (Baker et al. 2002). Some areas of high severity blowdown (≈900 ha) were salvage logged (1999–2001). In 2002, lightning ignited a stand-replacing fire that burned a substantial portion of the blowdown, salvaged blowdown, and surrounding forests. Sampling was conducted along a gradient of blowdown-fire interaction severities, in fire-only areas to establish a baseline fire response, and in burned salvage-logged areas. Sampling in salvage areas functioned as a de facto experimental treatment reducing the blowdown severity (in terms of fuel loads) while preserving the blowdown severity in terms of mortality. All sites experienced severe fire (complete aboveground mortality and organic soil consumption), isolating the interactions between the disturbances as opposed to simple increases in cumulative mortality.

Because sampling within disturbances necessarily invokes some spatial autocorrelation and pseudoreplication (Wiens and Parker 1995), we used a gradient analysis to minimize the impact of inherent assumptions of recovery in disturbed areas (Parker and Wiens 2005). Blowdown patches were stratified into five classes according to the percent downed trees due to the 1997 windstorm (1–19%, 20–39%, 40–59%, 60–79%,

80–100%). Percent down, as opposed to the number of down trees per hectare, was used for simplicity in organization of the field campaign; the two are highly correlated ( $r^2 = 0.78$ ,  $p < 0.05$ ). The number of downed trees/ha was used in the majority of analyses because it represents the mechanistic aspect of the blowdown/fire interaction. Both the percent down and number of downed trees/ha were taken from published maps (Baker et al. 2002). Ten sites, each consisting of two paired plots, were randomly located in each class using ArcMap (ESRI 2009), with a minimum of 500 m spacing between sites ( $n = 50$ ). Fire-only plots had been previously established (Rumbaitis-del Rio 2006), and one additional fire-only plot was added in this study ( $n = 6$ ). In salvage logged plots ( $n = 11$ ), fuel loadings prior to the fire were reduced to  $139 \pm 25$  Mg/ha from  $399 \pm 58$  Mg/ha in severe blowdown areas (Rumbaitis-del Rio 2004), roughly corresponding to 20% blowdown (Fig. 2). While there were other pre-fire ecological impacts as a result of the salvage (Rumbaitis-del Rio 2004, 2006), biogeochemical and soil characteristics recovered rapidly (Morliengo-Bredlau 2009). Differences between salvage and blowdown in advanced regeneration, from machinery-induced mortality, were eliminated by the fire; all regeneration started from a common point.

At each site, two plots were located 75 m apart, following the random cluster design recommended for spatial phenomena (Fortin et al. 1989). To eliminate variability in seed supply and control the influence of disturbance residuals, only plots  $>100$  m from the nearest live tree were retained. Given the limited dispersal distances of the conifers, 75 m between paired plots was assumed to be enough to consider both sites independent in terms of seed supply. The 100 m requirement reduced the viable plot count to 99; however, a good representation of all blowdown severities remained.

At each plot, percent cover of several functional groups was measured (aspen, bare soil, coarse woody debris (CWD), forb, graminoid, rock, and moss) using ten randomly-placed  $1 \text{ m}^2$  quadrats; soil moisture was measured at 10 random points. Means for each were calculated and used in analyses. All conifer seedlings were counted and measured for height and basal diameter; internodes were counted for aging

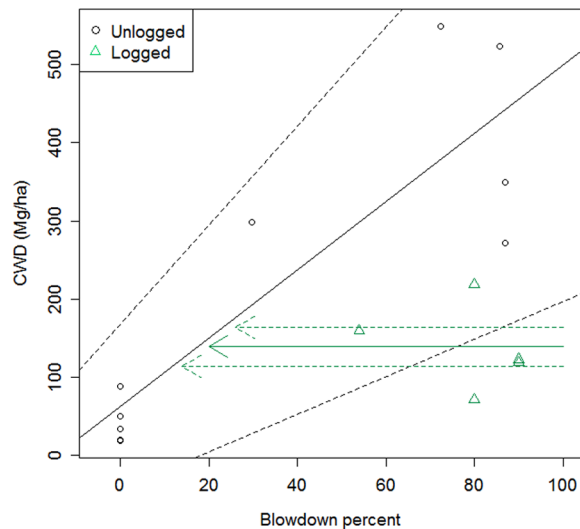


Fig. 2. Salvage logging reduction of pre-fire fuel loads and their relation to blowdown severity. Areas which were unlogged prior to the fire are represented by black circles, black line represents linear regression ( $r^2 = 0.77$ ,  $F = 26.2$ ,  $p < 0.05$ ) and 95% confidence intervals for unlogged plots only. The trend shows increasing fuel loading with increased blowdown severities. Green triangles are CWD in logged plots. Salvage logging reduced fuel loads in high severity blowdown to levels similar to 20% down, representing a de facto experimental treatment. Lines are the mean and standard error ( $139 \pm 25$  Mg/ha) and demonstrate the relationship between the fuel reduction and equivalent blowdown severity. Data on prefire fuel loadings from Rumbaitis-del Rio (2004).

purposes.

The First Order Fire Effects Model (FOFEM) was used to simulate burn times and temperatures based on fuel loadings (Reinhardt 2003). FOFEM uses physical and empirical methods to model fire temperatures and soil heating, among other first-order effects using factors including weather, fuel moisture and fuel decay state. Model runs were initiated using data on pre-fire fuel loadings and decay status (Rumbaitis-del Rio 2004) at a variety of blowdown severities. For the other variables, the defaults defined as Interior West/high fire-danger weather were used with the slash burn sub-model. Calculation of burn time was limited to 1000 minutes due to constraints of the program. Fire temperatures and burn times were modeled for the surface of



the mineral soil without a duff layer. While the exclusion of duff from consideration may cause the fire to appear hotter than it actually was, removal served to standardize the soil exposure, and was deemed an equitable means of comparison between fuel loadings (Brown et al. 2003) since the relative change in fire characteristics along the interaction gradient was the phenomenon of interest.

A map of burn severity was used to estimate distance to the edge of high-severity burned areas for the spatial scale analysis and neighborhood burn severity. The 30 m resolution map was created by the US Forest Service using the dNBR index (differenced Normalized Burn Ratio) and is ordinal, from 1–4, 1 being extremely light burn, with no crown scorch, to 4 which is high severity/complete mortality. Only one location was found to be incorrectly classified during the field survey, so the map was assumed accurate for the purposes of the neighborhood and spatial analysis. For the neighborhood severity index, 140 m radius plots were placed around each field plot in ArcMap, and the mean burn severity class (0–4) was calculated. To measure differences in required seed dispersal distances between blowdown/fire and fire only areas, 100 random points were placed using ArcMap in high-severity burned areas which experienced blowdown prior to the fire, and 100 in areas which did not. Euclidean distance to the nearest lower burn severity (class 1–3 or unburned) was recorded for each point.

CART (classification and regression tree) techniques were used to identify key variables and breakpoints structuring seedling recovery across the burned landscape. CART splits the dataset at binary breakpoints to reduce model variance. These techniques are a common non-parametric, non-linear way to analyze continuous data that exhibit complex interactions and potential threshold-like effects (Qian 2010). CART uses a “greedy algorithm” and is therefore susceptible to mistakes whereby a split is chosen to maximize the current node variance reduction but does not ultimately lead to the best model. In addition, CART can overfit models, where variance is reduced to near nil at the cost of reduced generalization. Cross-validation is used to avoid this difficulty and choose the optimal model size. However, because cross-validation

uses a random subset of the data, results can vary from run to run. Despite these difficulties, CART is extremely useful in identifying non-linear relationships in datasets and is a recognized method for identifying important predictor variables (Qian 2010); it performs well using both modeled and actual data for forest ecosystems (Moisen and Frescino 2002). In creating the trees, the R (2008) software package “rpart” was used, which closely follows procedures from Brieman et al. (1984). Cross-validation was run 10 times on the dataset, and the size of the tree with the least residual variance was recorded; the size getting the most “votes” overall (majority rule) was used to prune the original tree. Conifer density values were log transformed before CART analysis according to the recommendations of Qian (2010); 0.5 was added to plots with zero seedlings for log transformation. The tree was used to determine important structuring variables and boxplots of residuals were used to identify areas with high variability.

## RESULTS

### *Resilience impacts*

Results indicated that the blowdown-fire interaction negatively impacted both resilience mechanisms (cone serotiny and seed dispersal) through increased burn times and increased seed dispersal distances (Fig. 3). Modeled sustained temperature times and modeled maximum temperatures increased with increasing blowdown severity (Fig. 3A), using pre-fire fuel loading data from Rumbaitis-del Rio (2004). Linear regressions on the model results indicated that there was a small upward trend in temperatures experienced at the mineral soil level. Burn times increased substantially, from 0.5–2 hours above lethal levels to 15+ hours for two temperature thresholds, 60°C (live tissue death) and 75°C (*P. contorta* seed destruction, Knapp and Anderson 1980). All trends were significant ( $p < 0.05$ ).

The presence of blowdown also appeared to influence the size of the high fire-severity patches, increasing required seed dispersal distances for regeneration. Areas which experienced both blowdown and fire were on average further from the edge of the high fire-severity patch; mean distance to edge for areas that experienced both blowdown (any severity) and fire was 77 m,

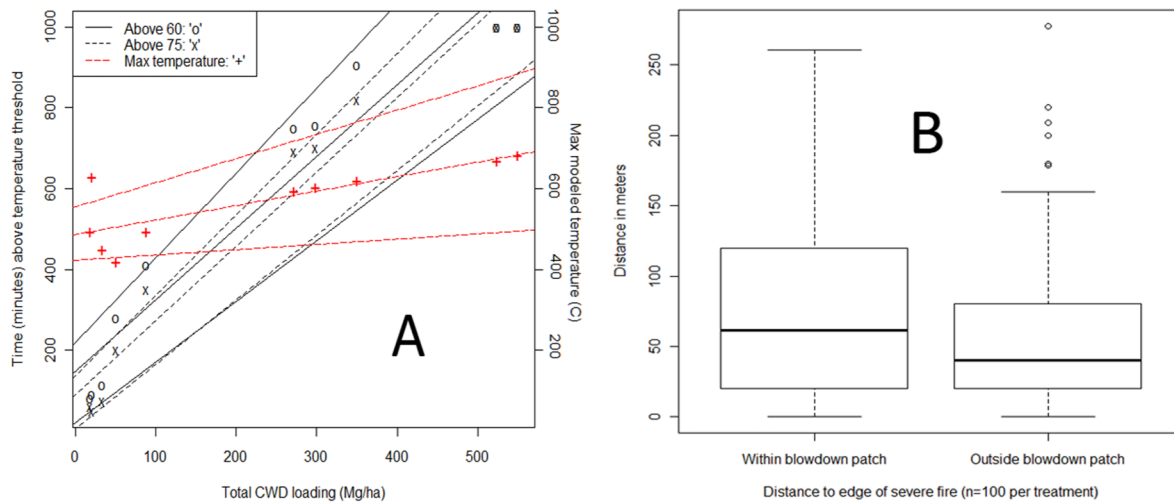


Fig. 3. Results of the compounding disturbances on individual resilience mechanisms. (A) FOFEM model results for burn times (above 60° and 75°C) and max temperatures, with confidence intervals. Fuel load characteristics (e.g., CWD loadings, fine woody debris loadings, decay classifications) from Rumbaitis-del Rio (2004); scale roughly corresponds to 0–100% down (0–500 Mg/ha). Results show dramatic increase in fire residence times and slight increase in max temperatures, both as experienced at mineral soil surface (all relationships significant  $p < 0.05$ ). (B) Boxplot of distances (meters) to lower burn severity for random points ( $n = 100$  per class) in class 4 fire areas experiencing blowdown or not experiencing blowdown. Difference is significant (unpaired t-test,  $t = 2.05$ ,  $p < 0.05$ ), demonstrating that areas blown down prior to high-severity fire are typically further from potential seed sources.

for fire-only areas it was 60 m (Fig. 3B). Considerable variance existed in distance of the sampled points to less severe fire, as evidenced by the wide spread in the boxplots, a result of the varied sizes of the blown down and burned patches. Also, points were randomly assigned in class 4 fire pixels from the Forest Service classification, which could have resulted in points located within extremely small or one pixel “patches” of severe burn. Despite the variance, the difference was significant (Euclidean distance, unpaired t-test,  $t = 2.05$ ,  $p < 0.05$ ).

### Regeneration

Results indicated that blowdown severity did have a detrimental impact on actual conifer seedling regeneration following the fire (Fig. 4), with little regeneration found in areas with higher numbers of downed trees/ha prior to the fire. In low-severity blowdown (less than  $\approx 20$  downed trees/ha), regeneration densities were comparable to fire-only areas, indicating the resilience of the forest was not seriously impacted. Above  $\approx 20$  downed trees/ha, regeneration

was severely reduced on almost all plots; above  $\approx 60$  downed trees/ha, coniferous regeneration was basically absent. These trends were significant after removing the influence of elevation, aspect, and slope via a linear model and analyzing the residuals (“partialling out”), showing that conifer regeneration decreased as blowdown severity increased (logged plots excluded, Spearman’s  $\rho = -0.30$ ,  $p < 0.05$ ). If disturbance interactions had no impact on the resilience of the ecosystem, no trend would be apparent (i.e., all blowdown severities would appear similar in terms of post-fire seedling densities). Plots which experienced salvage logging after high-severity blowdown exhibited significantly higher post-fire regeneration (mean = 262 seedlings/ha) than comparable blowdown severities without logging (mean = 65 seedlings/ha). Salvage plots were compared to non-salvaged sites with greater than 60 downed trees/ha prior to fire (Fig. 4), as that was the minimum observed blowdown severity that had been salvaged (Kruskal Wallis test,  $X^2 = 10.725$ ,  $p < 0.05$ ). Because the original blowdown map had an error

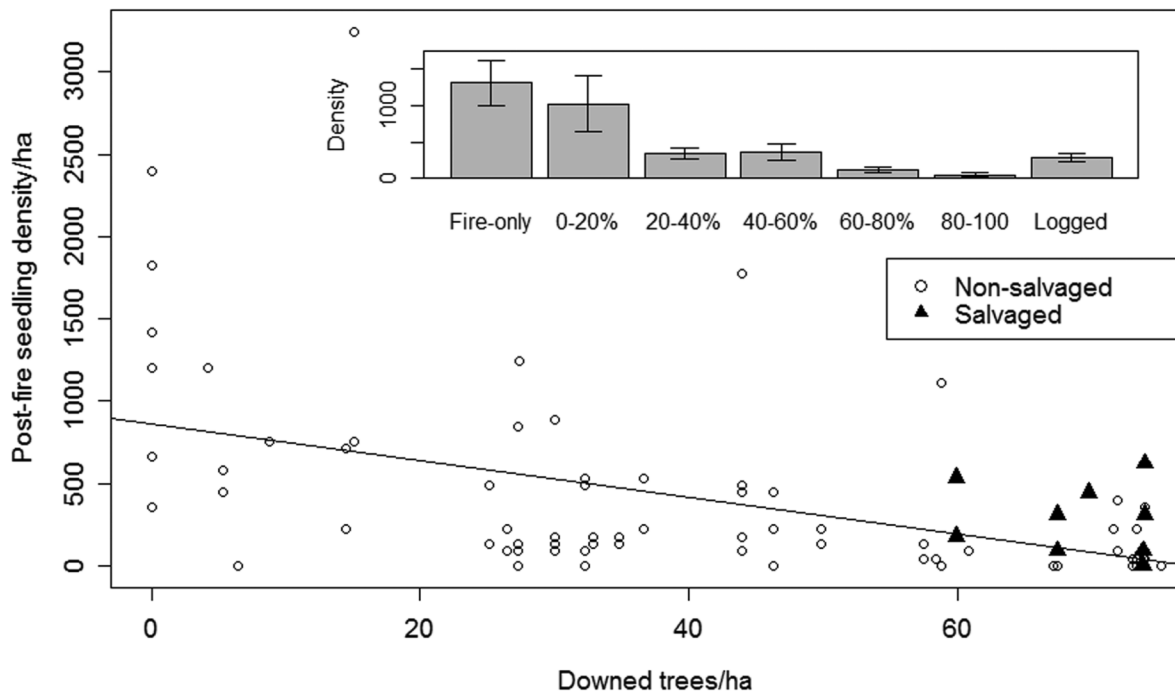


Fig. 4. Results of regeneration survey. As blowdown severity increased (measured by downed trees/ha), the resultant fire was more ecologically severe, assessed via recruitment (conifer seedling density (seedlings/ha), all species). Trend line is significant ( $p < 0.05$ ) after removal of topographic effects and does not include salvage logged plots. Salvage logged plots show significantly higher conifer density than comparable non-salvaged plots ( $p < 0.05$ , only plots  $>60$  downed trees/ha considered). Inset: Same data transformed to percent down classes (Fire only, 20% increments, and salvage logged) to account for potential measurement error, bars are standard error. Classes are significantly different (Kruskal-Wallis test,  $p < 0.05$ ).

rate of approximately 9% (Baker et al. 2002), means in the 20% class groupings were also compared (Fig. 4, inset) to account for potential measurement error; results were still significant (Kruskal Wallis test:  $X^2 = 27.6$ ,  $p < 0.05$ ).

CART analysis confirmed that while several variables contribute to recovery (or lack thereof), the best explanatory variable was the number of downed trees/ha prior to the fire (Fig. 5). The split that reduced the most variance was around 64 downed trees/ha (approximately equivalent to 55–80% canopy mortality). Above that amount, elevation became a significant factor, as well as neighborhood burn severity. Of the 14 plots experiencing high-severity blowdown, high elevation, and high neighborhood fire severity, only two showed any coniferous regeneration, although all groups experiencing  $>64$  downed trees/ha prior to the fire had a number of plots with no conifer regeneration. At lower blow-

down severities, slope and graminoids became significant explanatory variables. Overall, plots with little or no blowdown showed the strongest regeneration, as expected.

## DISCUSSION

### *Impacts of disturbance interactions on resilience mechanisms*

The legacy of increased coarse woody debris left by the blowdown led to unique behavior of the stand-replacing fire which followed 5 years later. Modeled fire burn times increased dramatically with increasing blowdown severity. This was due to the increase in CWD ( $>7.62$  cm diameter), which tends to hold heat and smolder for considerable amounts of time. In another study in this region, high blowdown severity was strongly spatially correlated with high fire severity (Kulakowski and Veblen 2007). As

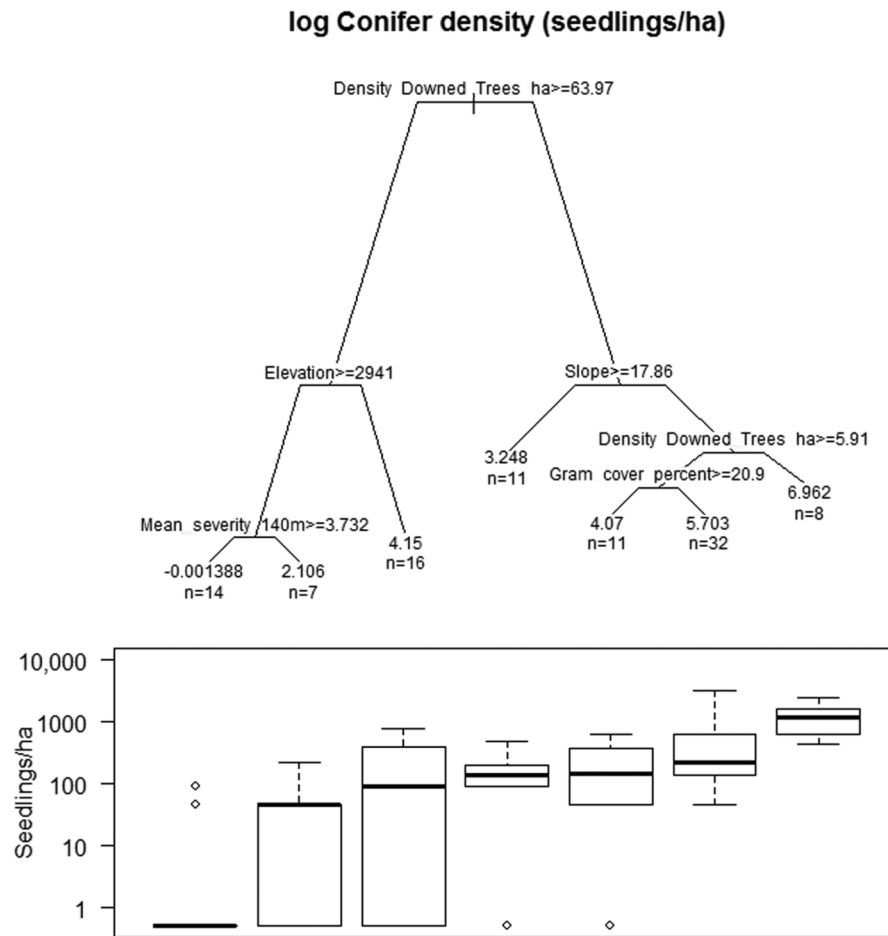


Fig. 5. Upper panel: CART analysis of conifer density. On tree, if condition is satisfied (e.g., if the density/ha of downed trees is greater than 63.97) proceed left on the tree. Length of vertical connectors indicate the relative amount of variance explained by that split. Results indicate that the dominant driver of conifer recruitment post-fire is previous disturbance severity (1997 blowdown, number of downed trees/ha). At high elevations, the mean burn severity within 140 meters is an important predictor. At lower blowdown severities, slope and graminoid cover (percent) are important factors. Number of plots in each “leaf” indicated, value is the log of the mean for that leaf. Lower panel: Back-transformed boxplots for each leaf to show residual variance (log scale).

demonstrated by the salvage logging treatment in this study, this interaction was mainly driven by the CWD loading and likely resulted in the consumption of *P. contorta* cones, reducing regeneration rates (Fig. 4). High severity fire alone does not typically consume serotinous cones in tree crowns (Despain et al. 1996) and the lack of deep soil charring (for example, <14 mm in the highest burn class surveyed post-1988 Yellowstone fires, Turner et al. 1999) indicates low duration burns (Neary 1999). The weaker increase in modeled maximum temperature (Fig.

3) is likely due to the relative lack of difference in fine woody fuels between fire-only and high blowdown plots. These “flashy” fuels burn quickly, and hot, but do not sustain combustion for long amounts of time. It appears that the CWD from the blowdown interacted with the fire to create a fire with novel characteristics, particularly in terms of burn time spent above lethal temperatures for *P. contorta* seeds.

Extent of the fire also increased significantly, hindering seed dispersal into severely blowdown and burned areas. While distance-to-edge means



for both patch types are within the dispersal distances of the coniferous species, it should be noted that there were many small, high fire severity patches. The differences in means seems to reflect the large interior of blowdown/burn patches which outweighed the many small but high fire severity patches in both disturbance histories. Also, seed totals drop rapidly with distance (Noble and Ronco 1978), and so a mean increase of 17 m may represent a large loss in seed volume. As a result, adequate seed dispersal into the blowdown/burn is less likely than burn-only areas.

#### *Implications of exceeding resilience*

A disturbance (or multiple disturbances) that exceeds the resilience of an ecosystem implies potential non-recovery and ecosystem shift (Gunderson 2000, Beisner et al. 2003). Forest ecosystems are characterized by long turnover times of dominant organisms and protracted periods of slow change, thus it is difficult to demonstrate a true change in the dominant cover. Dramatic changes to forest ecosystems may result from disturbance events (Frelich and Reich 1998), and some studies have shown shifts in cover types as a result of multiple disturbances/stressors (Jasinski and Payette 2005, Johnstone et al. 2010). Several studies have demonstrated alternate stable states exist in the Rocky Mountain subalpine. Conifer seedlings may aid in the establishment of future seedlings (through shading of grasses or eventual overtopping of *P. tremuloides*; Stahelin 1943, Nyland 1998), but both *P. tremuloides* stands (Crawford et al. 1998) and grasslands (Schauer et al. 1998, Lynch 1998) can effectively exclude seedlings. *P. tremuloides* is potentially self-replacing indicating long-term dominance (Crawford et al. 1998); *P. tremuloides* seedlings are prevalent within the burned area, and seedling densities are insensitive to the compounding effects of the blowdown/burn (B. Buma, unpublished data). Subalpine grasslands, likely created through disturbances, have also been documented as stable for millennia (Fall 1997, Lynch 1998). Therefore, the lack of conifer seedlings at a plot signals a *potential* switch from conifer domination to *P. tremuloides* or grassland domination, and the presence of ample seedlings signals that the coniferous ecosystem will likely regain control (in the resilience sense) of the site,

regardless of current grass cover or *P. tremuloides* densities. While it is possible that continued recruitment may raise seedling density levels, it is unlikely to be substantial. Post-fire seedling establishment in subalpine forests is accomplished rapidly from local seed sources (Peet 1981, Jenkins et al. 1997, Antos and Parish 2002). Aging of the seedlings surveyed via node counts indicates that recruitment rates have dropped dramatically on all three coniferous species, which all peaked three to four years post-fire. As a result of the exhaustion of local seed sources and large distances to intact trees, areas of high-severity blowdown + fire may convert to a different cover type (Nyland 1998), altering ecosystem services, habitat, and species composition.

#### *Limitations of study methods*

Fire occurrence is essentially unpredictable in time and space, and experimentation on this scale is impossible. Therefore, “natural experiments” are the best means to understand disturbance interactions and resilience over the landscape. However, this requires some reliance on modeling. Model results are based on a subset of plots for which pre-fire fuel data existed and should be interpreted in a relative sense (e.g., increased blowdown severity resulted in longer-lived fires) rather than as explicit numerical predictions. The number of salvage logged plots was somewhat low ( $n = 11$ ) and at relatively lower elevations, as a result of the selection criteria (see Methods) and a lack of known salvage logged areas. Finally, several different datasets were used in this investigation: previously published maps (Baker et al. 2002), pre-fire data (Rumbaitis-del Rio 2004), and USFS products and models (Reinhardt 2003), as well as extensive survey work by the authors. While this allows for large-scale synthesis, it should be recognized that these datasets were created independently and at different scales.

A potential factor not addressed is differential cone serotiny or stand composition prior to the fire. Unfortunately, these data are not available and cannot be reliably determined post-fire. Elevation and topography may influence fire frequency, and thus stand age (Romme and Knight 1981). Similarly, serotiny can change with stand age and elevation (Schoennagel et al. 2003).

However, because all blowdown severity classes were sampled across all elevations, the potential influence of stand age, stand composition, and serotiny differences were accounted for as well as possible. The gradient analysis and large sample size ( $n = 99$ ) also reduced problems associated with studying non-randomly distributed phenomena such as disturbances (Parker and Wiens 2005). Finally, while the inclusion of these data would allow refinement on the relative contributions of the serotinous/seed dispersal resilience strategies to the observed conifer densities, all regeneration would follow one of those pathways, and so while the absence of those data increases the unexplained variance, it does not undermine the conclusions.

## CONCLUSIONS

The objective of this study was to determine if disturbance history in a subalpine forest influenced the characteristics of a subsequent disturbance and if that influence/interaction created a novel disturbance with characteristics and effects significantly different from what would be expected from the final disturbance alone (fire-only). Modeling indicates that the combination of severe blowdown and fire created an uncharacteristically long-lived fire; GIS analyses demonstrate an increase in patch size of areas experiencing both severe blowdown and fire (thus requiring long distances for seed dispersal) in contrast to fire alone. These two characteristics directly impact the two major fire resilience mechanisms of the coniferous subalpine forest, cone serotiny and seed dispersal. As a result, increasing blowdown severity prior to the fire is significantly correlated with decreasing coniferous regeneration, whereas recruitment in fire-only areas was relatively strong. The lack of recruitment in areas where non-typical fire characteristics resulted from the disturbance interactions indicates that those resilience mechanisms were detrimentally affected. Higher regeneration densities in salvage logged treatments further support these conclusions. Due to the ability of alternate cover types to exclude future seedling establishment (e.g., thick litter layers in *P. tremuloides* stands, moisture competition in subalpine grasslands), substantial future recruitment is unlikely, leading to long-term changes in

the spatial heterogeneity of regional composition and function.

While the outcome of disturbance interactions may be hard to predict without extensive knowledge of the individual systems, the disturbance characteristics, and their temporal order, some potential interactions can be imagined. The current bark beetle epidemic in Canada and the western US is resulting in millions of hectares of dead *P. contorta* forests. These trees will eventually fall, creating fuel loadings similar to the blowdown, at a large spatial extent. In fire-prone ecosystems, this could result in a similar interaction as described here. In the boreal forests of Canada, a strong correlation between insect outbreaks, fire, and subsequent long-term forest loss has been demonstrated in a historical study (Jasinski and Payette 2005), however mechanisms for the direct interaction are lacking. This study presents one potential means by which insects and fire could interact to produce long-lasting compositional change.

Multiple, interacting disturbances have the capacity to create novel situations with potential impacts on ecosystem resilience. Subalpine forests can show high resilience to severe, stand-replacing fires alone (Turner et al. 2003), indicated by the fire-only plots in our study. However, interacting disturbances can lead to a surprising lack of resilience, creating an event of extraordinary magnitude and may cause shifts to alternate stable states. It is conceivable that other disturbances, especially those with structural effects, could also interact with unusually dramatic and long-term consequences (e.g., Kulakowski et al. 2003, Bigler et al. 2005, Sibold et al. 2007). Because many ecosystems are adapted to the disturbances common to their biome, compounding disturbances that create atypical conditions may impact them in unique and surprising ways, potentially exceeding ecosystem resilience. Multiple, interacting disturbances may not only increase the magnitude of the cumulative event but also result in novel disturbance conditions for which ecosystem resilience is either inadequate or unprepared, resulting in dramatic and persistent changes in landscape structure and function.

## ACKNOWLEDGMENTS

We thank C. Rumbaitis-del Rio for early contribu-

tions, as well as A. Markovitz, R. Gonzalez, G. Dillehay, and A. Nelson for field help, and two anonymous reviewers for comments on the manuscript. This work was supported by the University of Colorado Cooperative Institute for Research in Environmental Sciences (CIRES), a CIRES Graduate Student Fellowship to B. Buma, and funds from CU's Department of Ecology and Evolutionary Biology.

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