DISTURBANCE INTERACTIONS IN SUBALPINE FORESTS, THEIR IMPACTS ON FOREST RESILIENCE, CARBON, AND FUTURE CARBON STORAGE UNDER A VARIETY OF MANAGEMENT AND CLIMATE CHANGE SCENARIOS

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Disturbance interactions in subalpine forests, their impacts on forest resilience, carbon, and future carbon storage under a variety of management and climate change scenarios

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ABSTRACT

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Disturbance interactions in subalpine forests, their impacts on forest resilience, carbon, and future carbon storage under a variety of management and climate change scenarios

Dissertation directed by Professor Carol Wessman

Forest disturbances are inevitable, and recovery from those disturbances (termed resilience) is required for the persistence of forests through time. Extraordinarily severe or compounding multiple disturbances may, however, exceed that resilience and shift the ecosystems into alternate regimes with potentially large implications for ecosystem structure and functioning. A compound disturbance event (wind, logging, and fire) in a Colorado subalpine forest was studied for the impact of the multiple disturbance events on disturbance characteristics, tree regeneration, and carbon stocks, an important ecosystem service provided by many forests. The regeneration was also grown using the Forest Vegetation Simulator to simulate the effects of climate change and various management/regeneration amounts on carbon stocks in the next century. Results indicate that the disturbances did interact in a mechanistic way, producing a novel disturbance with extreme burn times and temperatures. Regeneration was altered by this interaction, with the serotinous species (lodgepole pine) having reduced regeneration, whereas the seed dispersing species were relatively unaffected. Logging prior to the fire reduced this compound effect, supporting the conclusion that the interaction drove the differential regeneration. Carbon was additively affected by the disturbances, with more

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disturbances resulting in less carbon and charcoal on the plots. Given literature-derived decomposition rates, the interactions may result in a net loss of charcoal on the landscape over the entire fire return interval. Looking forward, carbon stocks recovered in the near-term despite the loss of conifers in many locations due to the influx of aspen. However, in the majority of the climate change scenarios large tree mortality near the end of the century reduced tree cover and carbon stocks. Aggressive planting of local species was not successful in maintaining tree/carbon stocks; only the establishment of non-local, more warm-climate adapted species maintained the forest. Overall, disturbance interactions create novel, interesting situations with implications for forest resilience, and result in an increase in heterogeneity across the landscape. Carbon is also affected by multiple disturbances. But the growing effects of climate change will likely overshadow the impacts of the disturbances and differential recovery in the next century.

DEDICATION

To Cole, without whom this would have been finished a year earlier.

(Just kidding!)

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CHAPTER 1

INTRODUCTION

FORESTS AND RESILIENCE

Forests are one of the most common ecosystem types on the planet. From tropical rainforests to the boreal, they exist from near-continuous stands of trees to sparsely scattered woodlands, spread over approximately 4.1 billion hectares (Lal 2005). And they persist for eons. Yet disturbances such as wildfire, windthrow, or flooding, are also common. For example, fires affect ~383 million hectares per year globally (all biomes), and release 2078 Tg C per year on average (Schultz *et al.* 2008). These events kill trees, clear the forest, and often leave little but charred soil. Yet forests recover. This is termed resilience – the ability of a system (in this case a forest) to be disturbed, yet recover to a qualitatively similar state. Historically, some ecological thinkers assumed systems were resilient (although they didn't use that terminology). For example, the Clementsian climax idea assumes that succession post-disturbance follows an orderly and predicable pathway to a similar ecosystem, which is determined by extrinsic and predictable factors such as topography, precipitation, and temperature. Given the existence of disturbance events, then, this view assumes resilience and an inevitable return to pre-disturbance conditions.

Two statements – from the same year, 1973 –show the importance of this often unstated assumption of resilience. First, Egerton (1973) summed up the previous assumptions of stability: "The balance of nature has been a background assumption in natural history since antiquity;" he then called into question the idea that nature is indeed "in balance." Rather than stability (either

permanent or cyclical), Egerton discusses the uneasy balance and potential for dramatic, permanent shifts in populations, communities, and ecosystems (although mainly in the context of animal populations and communities). Holling (1973) formalized this notion of instability, creating a conceptual framework that emphasized flexibility, disturbance, and recovery, but also the potential for non-recovery, regime shifts, and qualitatively different ecosystem states. Rather than stable systems, "resiliency is concerned with the probabilities of extinction" (Holling 1973). Ecosystems may be fairly stable when near their equilibrium, but when pushed far from equilibrium by a disturbance, a systems' recovery is not assured; rather, it depends on the combination of forces which caused the disturbance, the traits of the ecosystem itself, extrinsic factors such as climate, and other contingent variables.

The 1988 Yellowstone fires brought concerns about resilience to the fore. During a period of drought and high winds, and despite suppression efforts, over 250,000 ha of lodgepole pine forest were affected by the fires. Yet the burns were not the catastrophic events that some feared. Much of the landscape was in a good position for recovery. First, the majority of burned areas were within 50-200m of intact forest, providing ample reseeding opportunities from undisturbed portions of the forest (Turner *et al.* 2003). Second, lodgepole pine was the predominant pre-fire species, and because of its serotinous cones, it was able to recover rapidly in many places (although variable, Schoennagel *et al.* 2003). Aspen established in many areas of the burn as well (Romme *et al.* 1997). Heterogeneity was the rule for recovery, rather than the exception (Turner *et al.* 2003). This system has now been extensively studied, and it appears that some ecosystems are highly resilient to even the most seemingly catastrophic events.

many ecosystems, and many species in those systems are adapted and resilient to those disturbances accordingly.

Concern has risen, however, that if disturbances become more frequent they will overlap more often, and the combination may be greater than the sum of its parts. These are known as "compounding perturbations" or "interacting disturbances"- situations where the combination of effects are worse than any disturbance singly, and may overcome the resilience of a given system, pushing it into an alternate regime (Paine *et al.* 1998). In other words, while an ecosystem may be highly resilient to fire, disturbances prior to the fire may reduce that resilience, either through a reduction in seed source or alterations to the fire itself. The question of multiple disturbances – how they interact and what that means for ecosystem recovery – has been highlighted in several important papers in recent years (e.g. Turner 2010).

The question of resilience in forests also requires a consideration of climate change. Forests take centuries (in some cases) to develop, and so the timespan of forest recovery to current disturbances is directly influenced by future changes in climatic baselines. Resilience to a disturbance now may be a fairly moot point, if extirpation due to changing climates is expected in the next century. In addition, changes to disturbance regimes may further alter our expectations of ecosystem resilience.

In this dissertation, I explore those aspects of disturbance, resilience, and climate change. First, I look at the means by which disturbances can interact with each other, creating novel, new effects not expected from single disturbance events. I then explore the consequences of that interaction on forest tree species, and compare those responses to the resilience mechanisms of those species. Finally, I examine the effects on an important ecosystem characteristic, carbon

stocks, both currently (as a result of the compounding event), and in the future via growth projection modeling, taking into account different regrowth/management scenarios and climate scenarios.

THE STUDY AREA

The study area used in this work is ideally suited for studies of this kind. There are relatively few tree species, simplifying analyses. The species involved (Engelmann spruce, subalpine fir, lodgepole pine, and quaking aspen) all have differential resilience mechanisms, so the mechanistic effects of the compound disturbance events can be elucidated. The disturbance history allowed for a strong experimental design, a gradient approach that utilized salvage logging as an unintentional, but useful, experimental treatment. And finally, previous work in the area provided the necessary background to ask questions related to the emergent properties of compounding disturbance events and their effect on ecosystem recovery and carbon.

In 1997, the largest recorded forest blowdown in southern Rocky Mountain history hit the Park Range of northern Colorado. Winds in excess of 200-250 kph affected over 10,000 ha of subalpine forest (Meyers *et al.* 2003, Baker *et al.* 2002). Subsequent salvage logging throughout the blowdown area affected approximately 800 ha of severely blown down area. Then, in 2002, a large wildfire (the Mt Zirkel complex fire) burned over blowdown and salvage-blowdown alike, creating a complex mosaic of disturbance histories and severities (Fig. 1). None of these disturbances are particularly rare in isolation; their confluence (Fig. 2) allows us to ask questions related to the cumulative nature of disturbance interactions, their impact on ecosystem resilience, and the implications of that for the future.



Figure 1. Map of the blowdown and fire disturbances described in this study. The October 1997 blowdown (left) affected approximately 10,000 ha, mainly on the east facing slopes of the continental divide. Salvage logging was conducted in much of the high blowdown areas (~800 ha, not shown). The 2002 fire (right), called the Mt Zirkel Complex, burned around 12,500 ha of blown down, salvaged, and undisturbed forest.

QUESTIONS

In this dissertation, I explore several questions related to ecosystem characteristics and resilience in a compound disturbance environment.

- What do compound disturbance events look like? Are there mechanistic interactions between near-simultaneous disturbances that affect ecosystem resilience mechanisms (such as serotiny)?
- 2. Do different resilience mechanisms respond to compound disturbances in similar or differing ways?
- 3. How is ecosystem carbon balance affected by compound disturbances?
 - a. Is charcoal (or "black carbon") affected in similar ways? Do severe fires increase charcoal on the landscape?
- 4. What do the legacies of compound disturbances, both in terms of regeneration and initial carbon, mean for future carbon stocks? Will future ecosystem carbon stocks differ due to the compound disturbances?
 - a. Can management play a role in maintaining carbon stocks?
 - b. What is the relative influence of climate change on carbon?

The work presented here attempts to address these questions by studying the disturbance complex in the Routt National Forest in Colorado. It may be said that such an intersection of disturbances is a rare event, and so might be regarded as a "one-off." There is always the concern that disturbance events represent a sample size of one. Generalizations are always difficult from single case-studies, it is true. However, by framing the investigation in a resilience context, some of those single observation concerns are avoided. I can happily report that similar findings have since been reported in different ecosystems (e.g. D'Amato *et al.* 2011, Bradford *et al.* 2012, Brown and Johnstone 2012), with different species but similar resilience mechanisms and disturbances. This illustrates that similar phenomena may be observed across species and regions and provides some commonality between disturbance events despite geographic distance.

CHAPTER SUMMARY

<u>Chapter 1:</u> I explore the mechanistic nature of the interaction between the blowdown, logging, and fire disturbances, the consequences for the nature of the fire itself, and the implications of those interactions on the two resilience mechanisms of the system as a whole: Cone serotiny and seed dispersal. Resilience requires recovery, and the results indicate that postfire recovery is hampered due to the disturbance interaction. First, the fire appears to have been longer and somewhat hotter as a result of the blowdown+fire interaction; salvage logging partially ameliorated this interaction via a reduction in woody material prior to the fire. Regeneration surveys support this contention. Second, the required seed dispersal distance from unburned stands is larger in areas of blowdown+fire, indicating that influx of seed will be limited in areas that experienced blowdown and fire. These results have been published (Buma and Wessman 2011).

<u>Chapter 2:</u> I look at the individual species responses in more detail. As the modeling and initial analysis in Chapter 1 indicate, the serotinous species (lodgepole pine) was strongly influenced by pre-fire disturbance history, showing a significant trend of lower recruitment in areas of higher blowdown severity prior to the fire. Salvage logging increased lodgepole

regeneration densities, likely due to a decrease in woody material and the resultant decrease in fire intensity; ILocal and topographic factors were also important, but overshadowed by the disturbance interaction. The non-serotinous species, which rely on influx of seedlings from off-site to recolonize disturbed areas, were unaffected by the amount of blowdown prior to the fire. Instead, they appeared to be more structured by local and topographic variables. An analysis of the seedling ages indicates that recruitment is tapering off in recent years, which has long-lasting implications for forest structure and function. This chapter has been published (Buma and Wessman 2012).

<u>Chapter 3:</u> The story transitions to an exploration of the consequences of these disturbance interactions on an important ecosystem service, carbon (C) sequestration. Carbon stocks are of intense interest to many parties, from scientists to economists to law makers. Chapter 3 presents a detailed accounting of the current state of the landscape in terms of C stocks, and investigates the consequences of the interactions on a particular component of longterm C sequestration, charcoal. Charcoal is a fire-created spectrum of compounds with very high resistance to decay, and thus the potential to provide a long-lived carbon sink in fire affected ecosystems. While earlier chapters showed that three disturbances were less severe than two (in terms of the regenerating species and their densities), in terms of C stocks the disturbances each removed progressively more C from the system. Three disturbances had the lowest total C stocks (blowdown+logging+fire), with two disturbances slightly more (blowdown+fire), and a single fire disturbance showing the least reduction- although still substantial, around 60%. Reductions were primarily attributable to the massive loss of soil C through the combustion of the organic soil horizons, and the loss of C from living material and CWD. Charcoal showed a



Figure 2. Close-up view of the study area, showing the convergence of the 1997 blowdown and 2002 fire events. The northern portion of the Mt. Zirkel Complex was termed the Hinman fire, and was where the majority of the plots were located. Salvage logging was concentrated in the north central portion of the Hinman fire, as well as to the south (in unburned areas). Elevation ranges from approximately 2500-3300 meters.

similar pattern in terms of the disturbed treatments, but surprising results came from comparisons to control plots. While an increase in charcoal was observed after the fire, control plots were not significantly different. It appears that while the fire created charcoal, it also consumed the pre-existing charcoal, for little net increase. Given literature derived decomposition rates, fire-only areas will equal undisturbed plots in circa 350 years, whereas the blowdown+fire and blowdown+logging+fire histories may result in a net decrease in charcoal over the typical fire return interval. This is a very interesting wrinkle in the story of carbon post-fire, and further investigation is warranted.

Chapter 4: Current C is only part of the story, and the regeneration found in chapters 1 and 2 will start from the initial values found in chapter 3 to create a new ecosystem with its own carbon balance. The differences in species composition, and the associated developmental trajectories, have implications for C stocks into the future. Evidence from similar ecosystems indicates that these differing trajectories may last for centuries or longer (e.g. Lynch 1998). Paleoecological records from lake cores in the region indicate that these alternate regimes are stable in the face of repeat disturbances and resilient to variable climate (within historical bounds), although when regime shifts occur they tend to be rapid (Minckley et al. 2012). But of course, climate change is pushing climate norms outside historical ranges, and resilience to previous disturbance is no guarantee of resistance to future directional shifts in temperature and precipitation. Chapter 4 takes the results of three field seasons and projects them forward using the US Forest Service's growth model, the Forest Vegetation Simulator, under a variety of climate change projections and three management scenarios. Growth under the majority of climate change projections was severely curtailed, and mortality reached 100% in many model runs. Carbon stocks fell accordingly, and the resultant grassland had little C on site. These are

active landscapes, however, and so managerial actions intended to maintain C stocks were also modeled. A scenario of resilience-oriented management, where plantings took the form of augmenting local resilience (planting local species in areas where there was little natural regeneration), was simulated. It had little effect on long-term C stocks, as the local species showed a general lack of tolerance to simulated shifts in climate. More dramatic actions, specifically planting non-local species, were more successful in maintaining tree densities and C stocks. The implications and limitations of this approach are discussed as well, and this chapter raises important questions: Given the long lifespan of trees, adaptation and/or transformation needs to begin long before the climate demands it. Disturbances can be viewed as an opportunity, in that sense, given that they provide an opening for more climatically suitable species to established).

In addition to viewing these results as an interesting case study that tells us a bit about compound disturbances and forest resilience, they should also be viewed as an exploration of the consequences of regime shifts in a more general sense. The mechanistic nature explored in Chapter 1 is a method of thinking that should be applied to all disturbance interaction questions, from bark beetles altering fire risk (Will it burn hotter?) to the expected resilience of forests postbeetle+fire events (What will post-fire beetle-killed stands look like?). Chapter 2 illustrates that species-specific resilience mechanisms are important in the context of complex events. Chapters 3 and 4 raise important questions: To what extent should we attempt to restore ecosystem services (e.g. carbon storage) in a changing climate? Should we play a part in transforming systems to something more climatically suitable? If not, what are the implications for

communities that depend on specific ecosystem services? If yes, and given that forests take many decades to develop, when should we start?

CHAPTER 2

INTERACTIONS BETWEEN DISTURBANCES CAN CREATE "NOVEL DISTURBANCES" AND AFFECT FOREST RESILIENCE

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.

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 recovering 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 management. 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 Cote 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, Fig. 1:C), 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 (Fig. 1:D), 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.



Figure 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.

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 aboveground 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 the questions: (i) did blowdown legacies alter characteristics of the fire?; (ii) were forest resilience mechanisms detrimentally impacted by those new characteristics; and (iii) did the blowdown-fire combination reduce coniferous forest resilience and recovery?

Resilience mechanisms. The relevant fire-resilience mechanisms of the dominant conifer species are cone serotiny (*Pinus contorta* [lodgepole pine]) and seed dispersal (*Picea engelmannii* [Englemann 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 (\approx 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 ± 25 Mg/ha from 399 ± 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 machineryinduced 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 m² 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 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 nonparametric, 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

<u>Resilience Impacts</u>. 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 3, A), 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).



Figure 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 ± 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).

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, for fire-only areas it was 60 m (Fig 3, B). 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).

<u>Regeneration</u>. 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 p = -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 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 blowdown 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 (>7.62cm 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 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, <14mm 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.



Figure 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 (in terms of blowdown severity) error, bars are standard error. Classes are significantly different (Kruskal-Wallis test, p < 0.05).

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



log Conifer density (seedlings/ha)

Figure 5. Upper: 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: Back-transformed boxplots for each leaf to show residual variance.

(Buma and Wessman 2012). 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.* 1998, 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.

CHAPTER 3

DIFFERENTIAL SPECIES RESPONSES TO COMPOUNDED PERTURBATIONS AND IMPLICATIONS FOR LANDSCAPE HETEROGENEITY AND RESILIENCE

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 longdistance 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.

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

Site, Species Response Strategies, and Disturbance History: 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 1998) with corresponding changes in ecosystem functioning and services such as water supply (LaMalfa and Ryle 1998). 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 wellstudied 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.

Table 1. Dom	ninant fores	t species in C	olorado subalpine fore	st 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, and Veblen 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 (80m range)			
Engelmann spruce	Invader	Avoider	Seed (125 m range)	Advanced regeneration			
Subalpine fir	Avoider	Invader	Advanced regeneration	Seed (100m range)			

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 °C in July, with an average of 3.8 °C (Colorado Climate Center 2003).

<u>Objectives:</u> 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.

METHODS

Sampling Design: Disturbance interactions considered in this study were: 1) Fire only; 2) Blowdown + Fire (gradient of blowdown severities, from 5-95%); 3) Blowdown + Salvage Logging + Fire. Ninety-nine sites (15 x 15 meters) were surveyed in 2010, all in previously closed-canopy spruce-fir 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 1km (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 4.1.4 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.



Figure 1. Map of blowdown (upper left), the surveyed portion of Mt. Zirkel complex burn (upper right), and elevation throughout the study area (lower left). 1997 blowdown severity is shown by percentage blowdown and fire severity is by USFS dNBR estimation. Logging areas are scattered, small, and often unmapped and are thus omitted for clarity. Sampling points shown in green. Note that the blowdown area extends north and south off the map.

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).

1) TRASP =
$$(1 - \cos((\pi/180)(\text{aspect}-30)))/2$$

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 from 30 m 2002 Landsat imagery. Severity classification is ordinal, from 1 - 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 1991, Jenkins *et al.* 1998). Thus, the analyses were limited to lodgepole pine, Engelmann spruce, and quaking aspen.

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 (Breiman 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 (Breiman 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

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 15x15 meter 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 <i>et al.</i> 2002		
	Fire severity	dNBR (0-4)	2 - 4	USFS		
Topographic/Abiotic	Elevation †,‡,**	Meters	2516 - 3198	DEM		
	Aspect (TRASP) †	NA 0 - 1 DEM, Moisen an		DEM, Moisen and Frescino 2002		
	Slope †,**	Percent	3.9 - 27	DEM		
	Soil moisture [‡] ,**	Volumetric water	3.7 - 52.7	Sampled 3x at 5 random points on plot		
		content		$(n=15 \text{ points plot}^{-1})$		
Vegetation	Forb cover <i>‡</i> ,**	Percent cover	5.8 - 77.6	Ten 1m ² quadrats, mean		
	Rock cover	Percent cover	0 - 29.6	Ten 1m ² quadrats, mean		
	Graminoid cover	Percent cover	0 - 53	Ten 1m ² quadrats, mean		
	CWD cover	Percent cover	1.8 - 25.3	Ten 1m ² quadrats, mean		
	Bare ground ‡,**	Percent cover	0.2 - 63.2	Ten 1m ² quadrats, mean		
	Moss cover	Percent cover	0 - 44	Ten 1m ² quadrats, mean		
	Aspen density *,†,‡	Stems/m ²	0 - 1.51	Complete survey (15x15m plot)		
Spatial	Mean fire severity, 140m radius	dNBR (0 – 4)	0 - 4	USFS, analyzed in ArcMap (ESRI 2010)		

complexity and results in a reasonably generalizable tree (Qian 2010). Pseudo- r^2 values were calculated for each tree:

2) Pseudo $r^2 = 1 - (deviance_{pruned tree} - deviance_{inital data})$

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).

RESULTS

<u>Random Forest and CART analysis:</u> 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 3.1.3). The pseudo-r² 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-r² 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-r² value of 0.30 (0.33 unpruned).

<u>Trend Analysis and Salvage Logging Influence:</u> 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, ρ = -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 versus non-salvaged plots, although



Figure 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).

recruitment was marginally higher for spruce (spruce: H = 3.57, p = 0.06; aspen: H = 1.32, p > 0.05).

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.

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 ground inspection indicated that the 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 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 nonrandom 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.

Table 3. Modeling results and seedling count totals, significant relationships (p<0.05) in
bold. CART pseudo- r^2 calculated according to equation 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	CART pseudo r ²		Spearman's correlation			Kruskal Wallis	
	count	Pruned	Unpruned	S	ρ	р	Н	р
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

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.

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 five 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

five 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.

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 five 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 and the years immediately post-fire (and since) have been essentially average in terms of total precipitation, meaning aspen seeds could experience suitable conditions for establishment (Fig. 4). 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.



Figure 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.

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 fireinitiated 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.



Day of water year

Figure 4. Precipitation accumulation for each water year following the fire. Water years are defined as October 1 – September 31. Data is from the Lost Dog SNOTEL site, located within the burn perimeter. Data are available at the USDA Natural Resources Conservation Service webpage: http://www.wcc.nrcs.usda.gov/snow/

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 (in terms of species response), 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.

CHAPTER 4

DISTURBANCES, THEIR INTERACTIONS, AND CUMULATIVE EFFECTS ON CARBON AND CHARCOAL DYNAMICS IN FOREST ECOSYSTEMS.

ABSTRACT

Disturbances have a strong role in the carbon balance of many ecosystems, and the cycle of vegetation growth, disturbance, and recovery is very important in determining the net carbon balance of terrestrial biomes. Despite potentially large losses of carbon in disturbance events (due to combustion, decomposition, or other mechanisms), resilient systems can recover that balance to remain neutral over the disturbance return interval. Conversely, lack of recovery may initiate alternate regimes with a different carbon balance. Compound disturbances are phenomena of growing concern which can further impact ecosystems in novel ways, altering disturbance intensity, severity, and recovery trajectories. This research focuses on carbon stocks in a compound disturbance environment, with special attention on black carbon (charcoal). Black carbon is a potential source of long-term carbon sequestration, as it is very resistance to decomposition, formed in fires, and has numerous other benefits such as increasing soil fertility. This research focuses on a well-studied compound disturbance event (wind, logging, and fire) in a Colorado, USA subalpine forest that was extensively surveyed for impacts on carbon stocks, black carbon, and regeneration. All major pools were considered, including organic and mineral soil, and contrasted with neighboring undisturbed forests as a reference. The disturbances had an additive effect on carbon loss, with increasing numbers of disturbances resulting in progressively decreasing carbon/black carbon stocks. This is interpreted as resulting from substrate availability and fire intensity, and there was no significant difference between unburned and

burned plots in terms of total black carbon. Given literature-derived decay rates, it appears that high intensity fires may actually reduce net black carbon in these forests over the entire fire return interval, with additional disturbances compounding the loss. Overall, high intensity disturbances remove a large amount of carbon, and multiple disturbances compound this effect. Differences in regeneration have a small but significant difference on current carbon stocks, a difference that will likely get larger as time progresses due to differential species characteristics. Disturbances, and their interactions, will have long-lasting legacies for carbon, black carbon, and ecosystem structure and function.

INTRODUCTION

Disturbances have a strong role in the carbon balance of many ecosystems in the world, and it is vital to consider disturbances when calculating the carbon uptake and loss of terrestrial vegetation (Running 2008). Carbon balance is a fundamental characteristic of ecosystems, and important to global climate and circulation patterns. The disturbance and recovery of forests, which cover ~4.17 Mha globally and contain 1240 Pg C in the biomass and soil (Lal 2005), are particularly important to regional and global carbon budgets. However, disturbances are increasing (Dale *et al.* 2001), as are the potential for longer fire seasons (Westerling *et al.* 2006). In general, North America is expected to see increases in fire likelihood with increasing climatic shifts (Mortiz *et al.* 2012). Background tree mortality is increasing as well (van Mantgem *et al.* 2009). These increases in disturbance frequency and/or size distribution will result in increased amounts of overlapping disturbances, disturbance interactions, and an increased potential for "ecological surprises" (Paine *et al.* 1998), meaning shifts in regime, lack of recovery, or other results not expected from either disturbance alone.

Compound disturbances are useful study systems for two reasons. First, they present a means to identify specific mechanisms by which species level resilience is reduced or enhanced (Buma and Wessman 2012), which aids in determining under what future conditions forests are likely to be resilient (or not) to disturbance. They also provide a window into a future where disturbances are potentially more common (Dale *et al.* 2001, Westerling *et al.* 2006) and larger (e.g. fire: Holden *et al.* 2007). Larger fires would result in more overlap and short-interval fires, regardless of frequency, and short-interval fires are associated with regime shifts (Donato *et al.* 2009, D'Amato *et al.* 2011, Brown and Johnstone 2012) and carbon stock changes (Brown and
Johnstone 2011, Bradford *et al.* 2012). Therefore they are useful indicators of what future disturbance conditions may do to ecosystem structure, processes, and attributes.

If one considers disturbances as the destruction of biomass, then disturbances necessarily release some carbon via decomposition and the destruction process itself (e.g. combustion). However, regeneration can balance out that carbon loss via carbon fixation in regrowth. Over long timespans, then, ecosystems in equilibrium with their environment will be essentially carbon neutral (at large spatial scales), fluctuating around some carbon carrying capacity (Keith *et al.* 2010), through periods of carbon loss following disturbance and carbon uptake during recovery. Fires are one of the most common and destructive of natural disturbances, and strongly impact carbon cycling. On average, fires affect ~383 million hectares per year globally, and release 2078 Tg C per year (Schultz *et al.* 2008). Yet recovery from fire, to a similar ecosystem state with a similar pre-disturbance biomass, makes a burned landscape essentially carbon neutral, although it may be a protracted process (Kashian *et al.* 2006, Chapin *et al.* 2006). Biomass recovers as trees mature, stands infill, succession proceeds (Kashian *et al.* 2006), and as soils develop via inputs from growing biomass and decomposing disturbance legacies (Lal 2005).

If ecosystems have a common carbon "baseline," given their particular climate characteristics and disturbance regime (Keith *et al.* 2010), shifts in the ecosystem may result in a shift in the carbon balance. This shift in ecosystem type could be accomplished via changing disturbance regimes or compound disturbances (Buma and Wessman 2012). These species effects on carbon stocks may be realized through species-specific growth rates, densities, litter quality and soil effects (van Miegroet *et al.* 2005), or other factors. In addition, plant species respond differentially to climatic shifts, depending on their tolerance of precipitation shifts,

temperature increases, new pathogens arising from range shifts, and other factors. Disturbances catalyze species changes, as part of a typical successional process (i.e. forests regenerating over time, undergoing species compositional shifts from invader to shade tolerant species) or as part of a more long-term ecosystem shift as described previously. The carbon state of the landscape at a given point in time, then, reflects the species dynamics post-disturbance through the biomass accumulation process and the interaction of those species with the current climate.

There are several important carbon pools in post-disturbance and regenerating ecosystem carbon. Detrital pools (e.g. woody debris) are, for the most part, relatively rapidly degraded and released as CO₂. Regenerating carbon in living biomass will be maintained longer (at least until a subsequent disturbance), at which point some or all of it will be lost to the atmosphere or transferred to the detrital pool. Soil pools, both organic and mineral, are relatively slow to change and can hold large amounts of carbon, estimated at 1086 Pg globally (Lal 2005).



Figure 1. Map of the study area and location in the contiguous United States. Points show the location of sampling plots. Colors refer to disturbance history. All plots except controls were located in areas of high fire severity (see methods). While all plots were evaluated for carbon, only a subset had soil and charcoal/black carbon analysis, those are shown as circles, with the size corresponding to total carbon (including black carbon). BF sites marked with a white slash had less than 43 downed trees/ha prior to the fire, and so were not used in the categorical comparisons, although they were used in the gradient analysis. F = Fire only; BF = Blowdown + Fire; BLF = Blowdown + Logging + Fire; C = control.

There is a third carbon pool associated with fires that has a longer residence time, and is often considered extremely recalcitrant to degradation: Charcoal. Charcoal is a thermochemically reduced carbon material which is less vulnerable to abiotic and biotic decomposition, and some have hypothesized that charcoal may be a significant long-term carbon sink, potentially useful in efforts to counteract rising atmospheric CO₂ emissions (DeLuca and Aplet 2008, Lehmann et al. 2006). The global formation of charcoal is significant, estimated at 40-179 Tg/year (Schmidt and Noack 2000). Charcoal is not a single molecule; it exists as a continuum from lightly scorched biomass to pure carbon, such as graphite. Fire intensity and duration are key to the formation of charcoal (Forbes et al. 2006); as are fuel load/type/condition, weather conditions, and substrate heterogeneity (Schmidt and Noack 2000). Many have seen the potential for charcoal as a source of long-term carbon sequestration, but the scope of charcoal creation in a fire event is relatively unexplored, the extent to which charcoal may accrue on the landscape post-fire is relatively unknown, and charcoal contains a variety of carbon compounds, not all resistant to degradation. Resistance to decay is dependent upon the various organic compounds in the burned material (Forbes et al. 2006). The portion of charcoal that is resistant to decay, and therefore potentially a long-term carbon sink, is termed "black carbon," or BC. It is important to note that not all charcoal is BC, rather BC is a component of charcoal (or char), nor is BC a discrete subset of charcoal, as it also exists as a continuum of material. Likely the proportion of charcoal that is BC increases as one moves down the continuum from lightly scorched to graphite (Schmidt and Noack 2000). Throughout this paper the term "charcoal" will refer to the mass or volume of charred material that was measured in any given pool. The term "black carbon," or "BC," is used whenever referring to the subset of recalcitrant carbon inside that charcoal (as determined via chemo-thermal oxidation; see methods).

This work explores the consequences of a well-studied compound disturbance event (wind, logging, and fire) which led to differential species recovery and successional trajectories. It focuses on current carbon and BC pools, and explores the implications of the differential regeneration on future carbon dynamics. The following hypotheses are explored:

H₁: Multiple disturbances prior to the fire lead to alterations in post-fire tree species.

 H_{1a} : Increasing the number of disturbances will lead to species better adapted to relatively harsher post-fire conditions.

H₂: Increasing the number of disturbances prior to the fire lead to decreasing C stocks postfire.

H₃: Increasing disturbance magnitude (multiple events) will alter BC stocks (post-fire).

 H_{3a} : BC will increase with increasing blowdown severity prior to the fire, due to increasing modeled fire duration (modeling results in Buma and Wessman 2011).

 H_{3b} : BC will decrease with increasing blowdown severity due to consumption of charcoal *en mass* during the fire event and reduction in biomass pre-fire.

METHODS

The study area is in north central Colorado, USA, in the subalpine forests of the Park Range north of Steamboat Springs (Fig. 1), ranging from 2500-3300m ASL and dominated by a mix of *Picea engelmannii* (Engelmann spruce), *Abies lasiocarpa* (subalpine fir), *Pinus contorta* (lodgepole pine), and *Populus tremuloides* (quaking aspen). *P. engelmannii* and *A. lasiocarpa* compose the dominant overstory in undisturbed areas, with *P. contorta* a more prominent

member at slightly lower elevations and in many post-burned areas. *P. tremuloides* is typically a successional species, although it can form stable, self-replacing stands if *P. engelmannii* or *A. lasiocarpa* do not establish in the understory.

A series of large, severe disturbances hit the area from 1997-2002. In October 1997, an early season blizzard and windstorm impacted approximately 10,000 ha of forest on the western slopes of the Park Range, the largest blowdown in recorded southern Rocky Mountain history with wind speeds estimated over 200 kph (Baker et al. 2002, Meyers et al. 2003). After the blowdown, salvage logging was conducted on approximately 935 ha of the high severity blowdown areas, primarily with tractor and cables, and had deleterious effects on the postblowdown regenerating forest and understory (Rumbaitis-del Rio 2006). Finally, in 2002, a large wildfire burned through portions of the undisturbed forest, the blown down area, and the logged blowdown landscape. The Mt. Zirkel Complex fire (12,500 ha) burned during one of the worst regional droughts on record. The fire was more likely to be high severity in areas of blowdown, whereas other disturbances present (logging and insect mortality) had no effect on estimated burn severity (Kulakowski and Veblen 2007). The blowdown-fire and blowdownlogging-fire interactions had an impact on modeled fire intensity metrics (burn temperature and burn time increased with increasing blowdown prior to fire) and post-fire conifer resilience (Buma and Wessman 2011).

To investigate the impacts of compound disturbances on carbon stocks on regenerating C pools, detrital C pools, and BC pools, various disturbance histories were surveyed. A total of 56 plots (each 15x15m) were organized according to their disturbance history: Undisturbed (control), fire-only, blowdown+fire, and blowdown+logging+fire. To control for variation in fire severity, all plots (except the controls) were located in areas of severe fire, which met three

conditions: complete aboveground mortality, no surviving individuals within 100m, and complete organic soil consumption. The first condition ensured all plots started from a similar successional state. The second controlled for the influence of residual stands on seedling density and species (see Buma and Wessman 2011 for further discussion on this point). The third condition meant that soil pools were comparable between burned plots, and that the organic soil layers were not driving differences between disturbed plots.

Disturbance Histories: Fire-only plots had no recorded history of prior blowdown or logging. The blowdown+fire treatment were limited to areas that saw more than 50% of the trees blown down in the 1997 event to provide distinction between it and the fire-only treatment. Because percentages do not lend themselves to mechanistic interpretations (due to variance in stand density), this was converted to 43 blown downed trees/ha, which is the 50th percentile of blowdown observed over all plots (see Baker *et al.* 2002 for the blowdown severity map). This group was used for the treatment-level comparisons. The entire gradient (and a larger sample), from 0 downed to 74 downed (the max observed) was used for the blowdown severity, and all had the majority of their downed woody debris removed prior to the fire. Control plots were also investigated to determine the baseline and the net change in carbon/BC on the landscape as a result of the disturbances, relative to pre-fire conditions.

Final tallies were: Fire only ("F"; n=14), Blowdown+Fire ("BF"; n= 10; all greater than 43 downed trees/ha prior to fire), Blowdown+Logging+Fire ("BLF"; n=8), and control plots ("C"; n=10). For the gradient analyses of BC, 38 plots of varying pre-fire blowdown severity were analyzed. Some of these plots overlap with the F group (e.g. 0 downed/ha) and BF group (those above 43 downed/ha). This equates to 56 unique plots for soil carbon/BC.

TOTAL CARBON METHODOLOGY

The following carbon pools were considered (detailed methodology below): Living tree species, living coarse roots, dead standing trees, dead coarse roots, coarse woody debris (CWD), herbaceous and graminoid cover, organic soil carbon (control plots only), and mineral soil carbon (10cm depth). BC methodology is explained separately.

Living trees: All living trees were counted on each plot. Seedlings shorter than 1.5m were measured for height. This represents the entirety of the living trees on all the disturbed plots. Trees above 1.5m on the control plots were measured for height (via a Haglöf digital clinometer) and diameter at breast height (DBH). Biomass was calculated via allometrics from Jenkins *et al.* (2003) using the USFS growth model, the Forest Vegetation Simulator (FVS) with the Fires and Fuels Extension (FVS-FFE; Rebain 2010), and assuming 50% carbon by mass.

Living coarse roots: Living root biomass was obtained via the same allometric equations from Jenkins *et al.* 2003.

Dead standing trees: In the disturbed plots, all standing dead ("snags") trees were measured for DBH and height. Biomass was calculated using allometrics from Kozak *et al.* (1969), which uses species specific tapering equations to calculate volume, after adjusting DBH for the absence of bark by adding in species and size-specific bark thicknesses using FVS allometrics. Volume of broken snags was calculated by projecting an unbroken height via Robinson and Wycoff (2004), and then integrating up to the broken height via the tapering equations. Leaning snag volume was calculated via the projected height and measured DBH, rather than their recorded height. To obtain biomass from the volume, 50% carbon by mass and 405 kg/m³ wood was assumed (Harmon and Sexton 1996).

Dead coarse roots: It was not practical to gain a direct estimate of dead roots based on the field survey, because many of the snags had fallen, been broken, or removed via the salvage logging, causing difficulties in determining what should contribute to the dead coarse root pool. FVS methods were used to calculate coarse roots for the control plots, and then all of those roots were passed to the dead coarse root detrital pool (as a result of the fire). The mean of the control plots coarse roots was assigned to the disturbed plots as the initial dead coarse root biomass. This is a conservative move which reduces the variance between the treatments. Because the plots were measured nine years after the fire, the estimated biomass was decayed according to the FVS Central Rockies root decay rate of 4.25%/year for 9 years.

<u>CWD</u>: Two 21.2m Brown's transects (Brown 1974) were used to estimate CWD at each plot using standard methodology.

<u>Forb and graminoid cover</u>: Ten 1m² quadrats were randomly located in each plot. For each quadrat, percent cover of forbs and graminoids were estimated. Mean cover of each was calculated for each plot. To determine biomass, 21 1m² samples of continuous forb cover, and 22 of continuous graminoid cover, were destructively sampled down to ground level. All biomass in the square meter was clipped, dried, massed, and subsamples of each were run on a Carlo Erba 1108 CHN analyzer (CE1108) to determine percent C. This percent C and the average grams/m² were used to calculate carbon present in the forb and graminoid cover (independently) for each plot, based on the means of the percent cover survey.

<u>Organic soil carbon:</u> Since the burned sites had no organic soil, sampling for this pool was limited to control plots. Five soil cores were taken to determine bulk density of the organic horizon (fine and coarse fraction density were calculated separately). Samples were chilled until

they could be dried at 105° C/24 hours and weighed. Bulk density measurements are in Appendix 4-1. Five additional cores were taken from the surface to the organic-mineral soil interface. Each core was homogenized in the field and a subsample taken. Samples were chilled until they could be dried in the lab (60° C/24 hours). Each core was sieved through a 2mm mesh to separate the fine and coarse fractions. The organic fine fraction (O_{FF}) was ground and analyzed for percent carbon on the CE1108. The organic coarse fraction (O_{CF}) was sorted into charcoal, woody material, and rocks. Woody material was assumed to be 50% C. Charcoal was ground and run on the CE1108 to determine percent C (see "Charcoal methodology" section). The relative proportion of each was then multiplied by the coarse fraction bulk density and mean depth of the organic layer to determine areal C.

<u>Mineral soil carbon:</u> Ten 10cm deep cores were randomly located and extracted from each plot. Each core was homogenized and a subsample was taken to the lab. Storing, drying, and sieving were the same as the organic soil methods. Mineral soil fine fraction (M_{FF}) areal carbon was calculated using fine bulk density measurements from Rumbaitis-del Rio (2004), which are from a subset of the sites used in this study. The mineral soil coarse fraction (M_{CF}) was sorted into charcoal, woody material, and rocks. Woody material was assumed to be 50% C. The charcoal was ground and run on the CE1108 to determine percent C. The relative proportion of each (coarse charcoal and woody material) was then multiplied by the bulk density of the M_{CF} (Rumbaitis-del Rio 2004) to determine the contribution of carbon in the coarse fraction. Bulk densities available in Appendix 4-1.

CHARCOAL AND BC METHODOLOGY

Each charcoal and BC pool was considered separately. Soil charcoal consists of fine fraction char (<2mm) and coarse fraction char (>2mm), in the mineral soil (all plots) and the organic soil (control plots only). Non-soil charcoal consists of charred material remaining on dead CWD and on dead snags. As noted above, not all charcoal can be considered BC. So the calculations were slightly different, using different percent carbon totals. Charcoal percent C was calculated by grinding coarse charcoal fragments and analyzing on the CE1108; this percent was used in total C calculations, BC was determined via digestions (described below).

<u>Fine soil charcoal and BC (<2mm):</u> Charcoal in the fine soil fraction was included in the total soil carbon percent from analysis of the dried and ground soils on the CE1108. Many methodologies exist for estimating BC in soils. Because of the diverse nature of charcoal compounds, and their continuum nature, each method quantifies different portions of the continuum (Hammes *et al.* 2007). Ideally, digestion proceeds from the least recalcitrant portions of the charring continuum (unaltered wood) to the highly recalcitrant end, graphite. The digestion procedure leaves some portion of *more* recalcitrant C (e.g. BC) than was initially in the digester. Standardization between studies and methods is accomplished by use of a common reference char (described in Hammes *et al.* 2008, available for order at www.geo.uzh.ch/phys/bc). By digesting the reference char, and quantifying the BC, results can be compared between studies (see Hammes *et al.* 2007 for example).

After processing the soil as described previously, the KMD methodology for BC determination was used (Kurth *et al.* 2006), which utilizes a combination of hydrogen peroxide, weak nitric acid, and heat to chemically digest the charcoal. The KMD method has been shown to be effective at the expected concentrations of C and BC, in similar soils (Kurth *et al.* 2006), and in other post-fire environments (Pingree *et al.* 2012). In addition, it is relatively simple,

facilitating the large amount of samples run in this study (~750 digestions). The percent C of the post-digestion material was determined via the CE1108. The percent was adjusted based on the mass lost in the digestion, to avoid an upward bias due to loss of non-C material in the digestion (Pingree *et al.* 2012). Total fine char was then calculated via the bulk densities, as described earlier. The methods were the same for the mineral and organic fine fractions. Methodological parameters, including incubation times, temperatures, mass loss correction, and the results of the reference char tests, can be found in Appendix 4-2.

<u>Coarse soil charcoal and BC (>2mm):</u> All coarse fraction soils were sorted, as above. A subset of the charred fraction was ground and run on the CE1108 to determine total percent C of the coarse charcoal. Because charcoal fragments may still contain less BC than total carbon, 14 subsamples of the coarse fragments were ground and digested using the KMD methods as before. This percent BC was used to calculate BC totals, whereas the total percent carbon (undigested) was used when calculating total carbon. The coarse fraction (charcoal or charcoal-converted-to-BC) of each soil sample (10 per plot) was massed and converted to grams C, which was then converted to areal C or areal BC based on the coarse bulk density as described above. The methods were the same for the mineral and organic soils. See Appendix 4-2 for further methodological details.

<u>Non-soil charcoal and BC</u>: Charcoal on CWD was quantified using methods from Donato *et al.* (2009). In essence, this is calculating a "rind" of charcoal around the uncharred inner part of the debris. Briefly, as part of the standard Brown's lines methodology (1974), charcoal is noted if the piece being measured is charred at the point the transect crosses the line (for 2.54 cm diameter pieces and larger, smaller pieces were assumed to be 100% charred). The depth of the charcoal is measured, and the relative proportion of charred vs. uncharred wood is

calculated using allometric equations from Donato *et al.* (2009). The volume of char is converted to Mg/ha C by assuming 405 kg/m² initial wood density (Harmon and Sexton 1996), 70% mass loss upon burning, and 75% C in the remaining mass (Donato *et al.* 2009). The proportion of the circumference that was charred was also noted, as many pieces were not charred all the way around, and the estimates were adjusted accordingly. CWD BC was calculated with a different C percentage, determined from the previous digestions of charcoal collected as part of the coarse soil methods.

For snag BC, there is no standard methodology. The methods used in this study are as follows: For all snags on the plot, the presence of char at breast height was tallied. If char existed, its depth, proportion of the circumference, and height was noted. Height was calculated in the same way as for living trees. The "rind" method was used here as well. Total volume was calculated according to the methods presented above. Adjusting for the depth, height, and proportion of char gave the volume of the inner, uncharred core of the snag. The difference was the char volume, which was then converted into Mg/ha C using the same coefficients as the CWD char and converted to BC totals using the same percent C as CWD.

STATISTICAL METHODS

Comparisons between all treatments were conducted via the Kruskal-Wallis rank sum test. If a treatment effect was found, pairwise comparisons between burned treatments (to determine any effect of compounding disturbances) were conducted with Wilcoxon rank sum tests, unless otherwise noted. Significance was set at p < 0.05, and the Holm method for adjusting p-value calculation was used to guard against Type I errors (H₁ and H₂) when appropriate. To investigate the relationship between compound disturbances and BC, and the

potential for increasing fire intensity (as modeled, see Buma and Wessman 2011) to alter longterm BC stocks, the pre-fire blowdown severity (downed trees/ha) was compared to total plotscale BC using quadratic linear regression (H₃). A quadratic regression was used to accommodate the potentially confounding effects of driving BC formation/consumption (H_{3a & b}) at different points on the interaction continuum.

RESULTS

<u>Living trees:</u> Differences in disturbance history caused significant differences in total stem density, including trees (>1.5m) and seedlings (<1.5m) (Fig. 2). Control plots had significantly more stems, dominated by an abundant *A. lasiocarpa* understory. Total *P. engelmannii* seedlings were also significantly higher than the burned plots. Among the burned plots, F and BLF were not significantly different in terms of overall seedling densities, although there was great variability. BF plots had significantly lower total seedlings compared to the BLF plots (p < 0.05) and moderately less than F plots (p = 0.09), driven by significantly lower *P. tremuloides* densities than BLF plots and significantly less *P. contorta* densities compared to F and BLF plots.

<u>Living tree carbon</u>: Control plots had significantly higher aboveground live carbon in trees than in disturbed plots; little total carbon is currently found in living trees in the disturbed areas. BLF plots had significantly higher carbon than BF treatments. Figure 3 has a summary of the major pools, and a detailed account is in Table 1.

<u>Living coarse roots</u>: Similar to the aboveground tree C, control plots had significantly more C in this pool than all the disturbed plots, and BLF plots had significantly higher than BF plots.

<u>Snags:</u> There was no significant difference between C and F plots. BF plots were significantly lower than C and F, and BLF the lowest of all the treatments.



Figure 2. Stem density for each disturbance history (no minimum size, all established individuals counted). Differences between the burned histories, especially in terms of conifer species, can be seen. Note that the control plots are dominated by fir, but the basal area of the stand was dominated by a few large *P. engelmannii*, with ample *A. lasiocarpa* understory. Two *Pseudotsuga menziesii* in control plots not shown. F = Fire; BF = Blowdown + Fire; BLF = Blowdown + Logging + Fire; C = Control

<u>Dead coarse roots</u>: Control plots had 4.21 Mg/ha C in dead coarse roots. For the other plots, a value of 14.9 Mg/ha was assigned (sum of living and dead coarse roots in control plots, and after decaying from 2002 to 2012). This was significantly more than the control plots dead total.

<u>CWD:</u> BLF plots had the lowest CWD levels, as a result of the salvage logging removal. F and BF plots were not significantly different. Mean CWD carbon in C plots was higher, on average, than the disturbed plots, but not significantly higher than F and BF.

<u>Forb and graminoid cover:</u> Forbs contained 42.5% C, with 179.1 g/m² dry weight. Graminoids contained 43.0% C, with 164 g/m² dry weight. Combined with the percent cover measurements, there was no significant difference between any of the treatments.

<u>Organic soil</u>: Coarse fraction charcoal contained 56.7% carbon. The organic soil contained 22.44 Mg/ha C in the control plots, split between the fine (19.51 Mg/ha, SD = 8.69) and the coarse (2.93 Mg/ha, SD = 1.56) fractions.

<u>Mineral Soil</u>: There were no significant differences between total mineral soil C for any of the treatments (p=0.06), or between fine or coarse subsets. On average, F plots contained 30.84 Mg/ha fine (SD = 10.80) and 5.43 Mg/ha coarse C (SD = 3.05), BF plots 33.15 Mg/ha fine (SD = 9.29) and 5.30 Mg/ha coarse C (SD = 3.69), BLF plots 24.24 Mg/ha fine (SD = 5.85) and 6.61 Mg/ha coarse C (SD = 5.80), and C plots 31.95 fine (SD = 9.81) and 5.58 Mg/ha coarse C (SD = 2.59).

BC Results (Table 2)

Digesting the coarse charcoal resulted in a BC proportion of 38.6%. Therefore the calculations for quantifying charcoal C as described above (which assume 75% C in charcoal, and were used for the numbers in Table 1) were modified, and BC calculations assume that charcoal is 38.6% BC. Detailed results and the reference char digestions are in Appendix 4-2. Treatment comparisons are in Fig. 4. There was a significant, although weak, linear relationship between total carbon and BC (p = 0.04, $r^2 = 0.08$), with BC increasing as total carbon increased, regardless of the number of disturbances (Fig. 5).

<u>CWD BC:</u> No BC was found on CWD in control sites. Burned plots were not significantly different. However, BF had consistently more BC than the other burned treatments, marginally significant (vs. F, p = 0.12; vs. BF, p = 0.055).

Snag char: Although many snags were charred, the total BC was small. There was no significant difference between the treatments.

 M_{FF} char: There was significantly less BC in the M_{FF} in control plots when compared to F and BF plots, although not when compared to BLF. BF and BLF plots were not significantly less than F plots when compared directly.

 $\underline{M_{CF} \text{ char}}$: There were no significant differences between M_{CF} averages regardless of treatment.

 O_{FF} and O_{CF} char: Control plots contained, on average 1.29 Mg/ha BC in the fine portion of the organic horizons, and 0.27 Mg/ha BC in the coarse fraction. The burned plots had no organic soil as a result of the fire, and so this pool did not exist on in those disturbance histories.

<u>Relationship between compound disturbances and charcoal</u>: There were no significant differences between disturbance history and total BC (Table 2), although the general trend was decreasing BC with increasing disturbances (Fig. 4). To test for significance, the gradient of prefire blowdown severities (downed trees/ha) was regressed against total BC (Fig. 6). While the mean decreased (Fig. 4), there was no significant relationship (p > 0.05, F and BF plots only). High plot level variability was found all along the gradient (see Appendix 4-3 for plot-level results and blowdown severity contrast).

Table 1. Pool totals for overall carbon. Mean C Mg/ha (standard deviation in parentheses). Number of plots in each treatment												
shown, each plot contained 10 individual samples. Superscript refers to significance groupings. Carbon totals associated with the												
same superscript are not significantly different. *includes fine and coarse fractions, see text for individual totals. **see methods.												
Disturbance History	Aboveground Living Trees	Living Coarse Roots	Snags	Dead Coarse Roots**	CWD	Forb/Graminoid	Organic Soil*	Mineral Soil*	Mean Total C			
Fire only (F) (n = 14)	0.09 (0.10) ^{1,2}	$0.32 \\ (0.37)^{1,2}$	$(13.96)^1$	$14.9 \\ (0)^1$	19.36 (15.57) ¹	$0.37 (0.18)^1$	0	36.28 (12.30) ¹	89.94 (25.31) ¹			
Blowdown+Fire (BF) (n = 10)	$0.03 (0.02)^1$	$\begin{array}{c} 0.14 \\ \left(0.08 ight)^1 \end{array}$	6.41 (9.36) ²	$14.9 \\ (0)^1$	20.75 $(11.38)^{1}$	$0.26 (0.07)^1$	0	38.45 (12.25) ¹	80.94 (27.35) ¹			
Blowdown+Logging+Fire (BLF) (n = 8)	$0.13 (0.10)^2$	$0.56 \\ (0.46)^2$	$0.14 \\ (0.35)^3$	$14.9 \\ (0)^1$	7.62 (8.56) ²	$0.29 (0.08)^1$	0	30.85 $(9.82)^1$	54.49 (12.56) ²			
Control (C) (n = 10)	80.74 (58.43) ³	(17.81) $(12.22)^3$	$(17.34)^{1}$	4.21 (3.31) ²	34.70 (18.35) ¹	$0.35 (0.14)^1$	22.44 (8.95)	37.53 (9.64) ¹	215.12 (71.28) ³			

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Table 2. Black C pools (mean Mg/ha, standard deviation in parentheses). Significance groupings shown via superscript numbers. *Wilcoxan test performed between pools with some BC only. Organic soil was not present on any disturbed site. No char was present on CWD or snags in control sites.

Disturbance History	CWD*	Snag*	Mineral soil (fine)	Mineral Soil (coarse)	Organic Soil (fine)	Organic Soil (coarse)	Total BC
Fire only (F) (n = 14)	$\begin{array}{c} 0.22 \\ (0.22)^1 \end{array}$	$\begin{array}{c} 0.01 \\ (0.05)^{1} \end{array}$	$6.13(1.75)^1$	$0.87 (0.93)^1$	0	0	7.24 (1.97) ¹
Blowdown+Fire (BF) (n = 10)	$\begin{array}{c} 0.39 \\ (0.22)^1 \end{array}$	$\begin{array}{c} 0.01 \\ (0.03)^1 \end{array}$	$5.66(1.77)^1$	0.92 (0.56) ¹	0	0	6.98 (2.00) ¹
Blowdown+Logging+Fire (BLF) (n = 8)	$0.20 \\ (0.12)^1$	0 (0)	4.59 (1.14) ^{1,2}	1.46 (1.37) ¹	0	0	6.26 (2.22) ¹
Control (C) (n = 10)	0 (0)	0 (0)	$3.49(0.84)^2$	0.90 (0.85) ¹	1.29 (0.66)	0.27 (0.32)	5.96 (1.95) ¹

DISCUSSION

<u>Total carbon</u>: Increasing layers of disturbances produced progressively less total C stocks. Fire plots saw \approx 58% decrease in C stocks relative to the control plots, in large part due to the complete loss of the soil organic layer. A similar study of compound disturbances and carbon in the southern boreal forests saw less of a reduction (approx. 30%, Bradford *et al.* 2012). However, their results only considered the top 10cm of soil, whereas the results presented here consider the entirety of the organic soil layer, whatever depth, and the top 10cm of the mineral soil. This could account for the discrepancy, as could differences in fire intensity or initial conditions. Other studies in the boreal (e.g. Lynch *et al.* 2004, Clark *et al.* 1998, and Czimczik *et al.* 2003, summarized in Forbes *et al.* 2006) showed losses approaching 50%. BF plots contained lower carbon than F plots, indicating that the blowdown-fire combination produced a more intense disturbance (in terms of C stocks), as suggested by modeling results showing higher temperatures and longer fire residence times (Buma and Wessman 2011).

Other pools were relatively similar. The BLF plots had the lowest C (a 75% reduction compared to control plots) as a result of salvage logging operations which directly removed woody material. There was also lower M_{FF} C in the BLF plots, which was partially balanced by increased coarse fraction C, although it was highly variable (Fig. 3). This could be a result of woody material incorporated into the soil during salvage logging operations (Morliengo-Bredlau 2009). While there was significantly more living tree biomass in BLF plots compared to the other burned plots, resulting from heavy aspen establishment (Fig. 2), it contributed relatively little to the overall C totals.



Figure 3: Carbon pool sizes for each disturbance history, and total. Soil and dead material (snag and CWD) dominate the disturbed stands, although increasing layers of disturbance result in decreasing totals. Undisturbed stands are a mix of living and dead, with significantly more total C. Forbs and graminoids not shown, as they were a small pool and not significantly different between the plots. F = Fire; BF = Blowdown + Fire; BLF = Blowdown + Logging + Fire; C = Control



Figure 4: Charcoal distribution between the disturbance histories by components, and total. Decreasing soil charcoal (mineral fine +coarse) with increasing layers of disturbance (within the burned area) is apparent. Control plot charcoal in the organic layer is an important component, but does not balance out lower char in the other pools, and controls have the lowest total char. F = Fire; BF = Blowdown + Fire; BLF = Blowdown + Logging + Fire; C = Control Overall, the differences in current total C stocks were driven first by the disturbances – all disturbed plots had less carbon than control plots – and increasing number of disturbances resulted in less total C on the plots. This was mainly apparent in the CWD/snag pools. Lower C in these pools as a result of increased fire intensity (in BF plots) and as a result of human extraction (BLF plots) resulted in net lower C stocks compared to just fire. As the detrital material decays, however, these differences will eventually be overshadowed by the relative contribution of the regenerating trees.

<u>Black Carbon</u>: Increasing disturbances lowered total BC, similar to total C. The hypotheses of decreasing BC were supported, although not significantly so – the only significant differences in BC were found between F and BF vs. control plots in the mineral soil pool, and total BC was not significantly different between disturbance histories.

The total post-fire BC was not significantly higher than unburned plots (Table 2, Fig. 4), although a trend of decreasing BC with increasing layers of disturbances is apparent. This suggests a balance between formation of BC, combustion of old BC, and decomposition. BC is formed during incomplete oxidation of woody biomass, and so should vary according to substrate availability and fire intensity. In terms of substrate (meaning biomass available to burn prior to the fire, and so available for conversion to BC), although the relationship between BC and total C was significant in the burned plots, it was weak (p < 0.05, $r^2 = 0.07$; Fig. 5). Lower levels of BC in the BLF plots, however, support the substrate limitation mechanism. In terms of fire intensity, Kane *et al.* (2010) found higher levels of mineral soil BC on south facing slopes with less organic soil, which they interpreted to result from higher bulk densities on southern slopes due to increased moisture. This could not be investigated directly in this study, as the organic layer was

completely combusted. There was no relationship between soil organic horizon thickness and total BC in our control sites (p > 0.05, linear regression, log_{10} transformed), nor total BC and aspect (p > 0.05, linear regression) as in Kane *et al.* (2010), however this could result from more intense fires typical of subalpine forests completely consuming the organic layer. High intensity fires were also associated with less BC in Oregon (Pingree *et al.* 2012) in the upper layers of the mineral soil, although they found increases in the organic layers post-fire. The trend towards lower levels in BF sites compared to F sites (Fig. 4), where BF sites were more intense (higher temperatures, longer duration; Buma and Wessman 2011), also support this hypothesis. Because all plots in this study were high severity fire, the relatively small increase over the control plots suggests that, while some BC was formed, it was mostly balanced by consumption of BC, especially in the BF plots. The logging plots support this combined substrate/consumption hypothesis – they experienced high severity fire without large amounts of pre-fire carbon (the substrate for post-fire BC) and consequently retained the lowest BC of the disturbed plots (Fig. 4).

The relative lack of differences between burned and unburned plots (in terms of BC) has interesting connotations for long-term BC dynamics. Because BC levels were only slightly elevated above control plots, decay could be extremely slow and yet not produce an appreciable on-site carbon sink; instead, a long fire return interval might result in a net loss of charcoal due to decay (relative to the unburned plots). For example, based on BC turnover time calculations from Harden *et al.* (2000) for similarly cold and acidic boreal soils (low estimate of 1111 years, high estimate of 2000 years), BC levels in the fire plots would decay to levels observed in unburned forests in ~225-400 years. This is similar to decay rate estimates by Singh *et al.* (2012), which give an estimate of approximately 325 years for return to pre-fire levels.

Estimating time since the previous fire to confirm this is not feasible in the post-fire plots, but work done in the unburned, adjacent watershed suggests that these mature spruce-fir stands (disturbed and undisturbed) were on the order of 300-400 years at the time of fire (Kulakowski and Veblen 2002). Given that the typical fire return interval in these forests is quite long (a compilation of fire rotation periods in N. Colorado reports estimates from 175 – 521 years, Baker 2009), this suggests that intense fires do not increase plot-level BC levels (on the plot) over the entire fire rotation period, but rather maintain it over multiple events. Multiple disturbances further reduced plot level BC: On the BF plots (~175-325 years of decay to equal unburned plots, using Harden *et al.* 2000 rates) likely through increased consumption of pre-existing BC, and ~50-100 years to decay to control plots for the BLF plots. Thus a loss of plot-level BC (over the entire disturbance return interval) may result from the multiple disturbances.

Net BC formation: These results highlight the need to quantify net BC creation, rather than simple BC amounts, post-fire. If only pre-fire C stocks (via the controls) and post-fire BC (fire-only plots, to eliminate compound disturbance effects) are compared, the percentage of combusted carbon-to-BC is approximately 6% (125.18 Mg/ha carbon lost due to the fire, 7.24 Mg/ha charcoal in burned plots). Considering only net increase in BC, subtracting out the BC already present on the unburned plots, the number drops to 1% (1.28 Mg/ha difference in BC). This is slightly lower than the studies presented by the Forbes *et al.* (2006) synthesis, which reports a range of 1.5-3.1% of consumed carbon being converted to BC in comparable settings. This could be due to the high fire intensity in this study. Further work on less severe fire scenarios is needed to determine the relative balance between BC formation and consumption. Although rare in these ecosystems, less intense fires may produce more BC, especially fires which do not eliminate the organic soil. This study found substantially more mineral soil BC (in

the unburned plots) than a recent study in the region (Licata and Sanford 2012) which used similar lab methodology; however the lack of BC standards (such as those from Hammes *et al.* 2008) in that study precludes direct comparison. Quantifying soil BC under various fire regimes and fire conditions which may result from climate change should be conducted as well.

Species Differences and Implications: Significant differences were found between disturbance histories, as well as between disturbed and undisturbed plots. The reasons for these differences have been explored mechanistically in Buma and Wessman (2011, 2012). At this in point in time the contribution of the differential regeneration to carbon is minor (Table 1), but significant differences already exist. Going forward, these differences may grow via three mechanisms: Different growth rates, future disturbances, climate change. *P. tremuloides* is very fast growing, and thus the C recovery period may be shorter in plots with extensive *P. tremuloides* establishment, not only due to simple differences in seedling densities but also due to rapid C fixation. However, the litter of *P. tremuloides* is more rapidly degraded and may be more mobile, increasing losses due to leaching relative to conifer or graminoid cover types (van Miergroet *et al.* 2005). In addition, climate change may alter C fixation rates even in the absence of disturbance (Hu *et al.* 2010).



Figure 5. Total carbon vs. total BC in disturbed plots, to explore the potential for substrate (biomass available) correlation with total BC. Relationship is significant but with very low predictive ability (p < 0.05, $r^2 = 0.07$). Total carbon considers all pools. F = Fire; BF = Blowdown + Fire; BLF = Blowdown + Logging + Fire. Note that the BF classification includes the entire blowdown gradient (see methods).



Downed trees/ha, prior to fire

Figure 6. Relationship between compound disturbance severity and total BC, with mean undisturbed (control) plot BC included for comparison. There was no significant relationship (quadratic linear regression) between increasing blowdown severity prior to the fire and total plot-level BC.

In terms of potential future disturbances (which no long-term study should fail to consider), there are important differences. Control plots likely have the highest chance of burning in the near future, due to higher biomass; a disturbance will happen eventually, and regeneration will play a role similar to what it is now playing in the disturbed plots. The differences in species establishment in the disturbed plots will likely cause differences in the future as well. The burned plots themselves are unlikely to burn for a time due to low biomass, although reburns are possible with compounding impacts on forest resilience (e.g. Brown *et al.* 2012). As the vegetation develops, differential flammability will develop. *P. tremuloides* is relatively less flammable, often used as a fire break in forest and fire planning (e.g. Fechner and Barrows 1976). The conifers, by contrast, are more likely to burn in fire events, and so disturbance history specific effects may develop in terms of future disturbances. This is also likely true for insect disturbances.

Occurring concurrently with these dynamics is climate change. Mortality rates are rising across the US West (van Mantgem *et al.* 2009), but climate change, and its attendant mortality (regardless of proximate cause) affects species differentially. Thus disturbances which favor regeneration of certain species, such as aspen, may have different effects in terms of future C stocks by virtue of differences in the effects of climate change on the regenerating species. In the same vein, the lack of disturbance on the control plots means, barring a future disturbance, the species currently dominating the plots will be the ones responding to changing conditions. In this case, the regenerating post-fire plots were dominated by *P. tremuloides* in most cases, especially in the BLF plots. In fire-only plots (F), *P. contorta* was also significant. Both species are adapted towards more xeric conditions often found post-disturbance, compared to *A. lasiocarpa* and, to some extent, *P. engelmannii*. To the extent that climate change will warm and

dry the western US, conditions may come to more reflect post-disturbance conditions, and favor those species. It can be hypothesized, then, that currently disturbed landscapes may support higher C densities near the end of the century due to species shifts (relative to undisturbed plots), from more mesic species to the typically more xeric post-disturbance species assemblages (Buma and Wessman, *in revision*). At the species level, disturbances may facilitate shifts to a more adaptable landscape (e.g. Sykes and Prentice 1996), at least in these ecosystems. Other species-specific considerations, however, such as the link between drought conditions and sudden aspen decline (Worrall *et al.* 2010), are of concern as well and must further be investigated, both in terms of the mechanisms of decline within the trees and the climatic modeling which would make prediction of such declines possible.

LIMITATIONS

As with all post-disturbance studies, several caveats exist. First of all, disturbance ecology is often an opportunistic field, and consideration of single event analysis, potential spatial autocorrelation, and other spatial effects must be considered. The design here was intended to avoid these problems where possible, by using a gradient approach when appropriate (Parker and Weins 2005), using a nested design with plot pairs isolated from each other (Buma and Wessman 2011), and only using published information on pre-fire conditions, as opposed to on-site reconstructions. All sites were located >100m from intact stands (in the disturbed area) to limit the influence of residuals on seeding densities. USFS mapping and observations made on site identified all plots as closed-canopy, mature conifer forest prior to the blowdown. This makes the assumption that initial differences between sites were minimal and that burned sites were similar to the control sites (prior to the disturbances). The study also brings together several datasets, including USFS Burn Severity Mapping program data (www.mtbs.gov),

published data on the blowdown severity (e.g. Baker et al. 2002), and several methods for quantifying C and charcoal stocks. While the charred CWD methodology has been published (Donato *et al.* 2009), there is no information on quantifying charcoal on standing snags. The methodology used here is comprehensive, in that all snags were measured, although it does likely contain some bias; the method assumes a constant depth of char to the maximal char height, when in reality the charcoal likely decreases in depth up to the max height. So the methods likely bias the amounts high, but as the snag charcoal was an extremely small pool, correction would only make that small pool smaller. Surficial losses of BC cannot be quantified, although experimental burning suggests it is minimal, at least initially (Lynch et al. 2004). The sites were located in areas of minimal slope, limiting erosion (there was no relationship between BC totals and slope). Convective loss to the atmosphere cannot be quantified either, although the synthesis of Forbes et al. (2006) indicates that it is likely less than 20% of the total produced, the remainder of which enter the soils. It seems likely that lower intensity fire would result in higher post-fire BC levels because of retention of organic soils and less atmospheric losses, but this remains to be investigated. Second, if we assume that the control plots, at the time of their last fire (e.g. 300 years before present), also underwent similar loss processes, then the comparisons with control plots still hold, and we can conclude that at the plot level, net BC increase is minimal, nine-years post. Scale is also an issue. A 225 m² plot encompasses substantial variation in terms of downed wood, standing dead, and other detritus. Variation in charcoal, if driven by those local factors more than the disturbance-scale factors tested, would be quite high within plots. Appendix 4-3 contains plot-scale variation in mineral soil BC.

CONCLUSIONS

Compound disturbances have impacts on carbon stocks via two primary mechanisms: By altering the magnitude of the cumulative event (in terms of intensity and severity) and by affecting the resilience of the constituent species. Mechanistically, BF plots likely experienced higher fire intensity (Buma and Wessman 2011), reducing total carbon. The logging reduced C through mechanical removal, and while it likely decreased the relative impact of the blowdown + fire combination, fire intensity was still likely higher than fire-only plots (Buma and Wessman 2011). BC appears to have been similarly affected, with the contrasting effects of formation and consumption conspiring to reduce BC levels in the compound disturbance plots, to the extent that BLF plots had very little increase in BC over the unburned plots despite the fire. Given decay rates from the literature, high intensity fire appears may maintain BC in this ecosystem over the entire fire-return interval, but multiple disturbances could result in a net loss over that time period. Further refinement of BC decay estimates, and investigations into BC totals in less intense burned areas (e.g. areas without complete organic soil loss), are needed. Another impact of the compound disturbance event was differential recovery of the tree species, which will influence C stocks via growth rate, litter quality, susceptibility to future disturbances, and vulnerability to climate-change induced mortality. Going forward, the multiple disturbances and their interactions will continue to have an influence on ecosystem structure, function, and carbon characteristics.

Compound disturbances are an important area of study given their potentially large effects (Paine *et al.* 1998, Turner 2010). The results presented here indicate that compound events do substantially impact current carbon stocks, additively reducing total carbon after the final disturbance. Ample regeneration suggests that carbon stocks could recover, although climate change, mediated through the differential recovery observed, may alter rates or final

states. BC, at the plot level, is not likely to play a major role in plot-level carbon sequestration. While it does constitute an appreciable fraction of the total carbon, the lack of net increase from control to burned plots indicates recalcitrant carbon stocks are not substantially increased via fire, at least at this fire severity and in these forests. In sum, current differences in carbon stocks are driven by aspects of the compounding disturbances, but longer term differences will likely be driven by differential species-level resilience to the compound disturbance event.

CHAPTER 5

THE EFFECTS OF DIFFERENTIAL REGENERATION AND CLIMATE CHANGE ON POST-DISTURBANCE CARBON STOCKS IN THE NEXT CENTURY

ABSTRACT

Ecosystems and ecosystem services are subjected to both disturbances (e.g. fire) and shifting climatic conditions resulting from anthropogenic drivers. Resistance and resilience to these perturbations are of prime interest to researchers and land managers. I explore how differential resilience to forest fire, differing establishment scenarios, and a shifting climate are expressed in terms of both species composition and an important ecosystem service, carbon sequestration. Modeling shows that while initial conifer resilience (defined as seedling density post-fire) does not drive carbon stock resilience, future climate exerts a strong influence on carbon stocks. Active, adaptation-oriented management, which includes establishment of non-local species, maintained forest structure and carbon stocks under most future climate projections. While this preserves the presence of a forest, it does not preserve the presence of a given forest species or forest type. In a sense, disturbances are opportunities that enable more climatically-adapted species/communities to establish, although the complexities of assisted migration and novel ecosystems remain.

INTRODUCTION

Ecosystems, and the services they provide, will experience two types of perturbations in the future: discrete disturbances such as fire and the slower change imposed by shifting climatic regimes. Disturbances are inevitable in the majority of forests around the world. Continuation of a forest in any given location through multiple cycles of disturbances is contingent upon ecosystem resilience: the recovery of the system to a similar state (Holling 1973). This may be rapid, depending on initial post-disturbance establishment (Brown and Johnstone 2012) or protracted through early and late successional stages. In either case, if the ecosystem recovers, it can be considered resilient. In the future, however, recovery will take place in an era of changing temperatures, precipitation, and disturbance regimes. Consequently, any long-term projection of ecosystem recovery must take those factors into account. Disturbances are expected to increase across a wide range of forest ecosystems (e.g. Dale et al. 2001, Flannigan et al. 2009) and may trigger shifts in species ranges (e.g. Johnstone and Chapin 2003) or eliminate forests all together (Brown and Johnstone 2012). Interactions between multiple disturbances may cause novel disturbance characteristics (Buma and Wessman 2011), differential recovery (D'Amato et al. 2011, Brown and Johnstone 2012), and/or regime shifts (Paine et al. 1998). Given the potential for disturbances to cause such large changes in ecosystem character, and the likely increasing rates of disturbance, it is important to investigate their impact on ecosystems and their properties going forward.

In addition to changes in disturbance regimes, climate change may move many ecosystems outside of their climatic tolerances, requiring extensive dispersal to maintain equilibrium with climate; for example, Loarie *et al.* (2009) estimate a mean rate of temperature movement (the required movement distance to maintain the same mean temperature) of 0.42
km/year under the IPCC's A1B emission scenario (rapid growth, balanced energy sources; See Table 1). This may mean greater susceptibility to disturbances, increased mortality, and/or decreased recruitment, with the end result being (1) an altered, but mostly original community, or (2) ecosystem replacement (complete or partial) with either an analogous community from a different climatic zone or a novel assemblage of species – these are two extremes of the response continuum. Thus, in the context of a disturbed landscape, land managers need to identify desired outcomes under changing climates and act appropriately; taking no action (passive management), fostering current system resilience, or actively responding to changing climatic conditions (similar to Millar *et al.* 2007). In this paper, the outcomes of those post-disturbance management strategies were investigated in the context of carbon storage.

Carbon storage in ecosystems is related to local climate (Davidson and Janssens 2006), species composition and structure (Wessman *et al.* 2004), soil characteristics (Lal 2005) and disturbance history (Brown and Johnstone 2011), among other factors. Forests in particular sequester a large amount of carbon in biomass and soils (1086 Pg globally, Lal 2005). They do not sequester that carbon in perpetuity, however; disturbances and mortality return a portion of that carbon to the atmosphere through either combustion (direct carbon emissions, usually as CO₂) or through the resultant decomposition of the killed biomass. Yet if the forest recovers to a similar structure and density, the total carbon exchange will be neutral over the time period of recovery (Kashian *et al.* 2006). This recovery may be fairly rapid; regenerating vegetation may quickly take up enough carbon to offset decomposition. Investigation in Canadian lodgepole pine forests with heavy insect infestations found that even high mortality stands were a carbon sink during the growing season within a few years (Brown *et al.* 2010). This was attributed to the understory vegetation rapidly fixing carbon in response to the newly available resources

freed up by the death of the overstory trees (Bowler *et al.* 2012). Given that the system recovers to a similar state, it is likely that carbon stocks will recover as well. Changing ecosystem states, however, may have large impacts on total carbon stocks due to fundamental changes in plant structure, density, and soil inputs. For example, woody plant encroachment may have a strong effect on the carbon balance of the landscape, mainly through the increase in plant biomass (Wessman *et al.* 2004), although the magnitude of change depends upon moisture and other factors. In other cases, regimes may change without a concurrent shift in carbon stocks.

Those questions are investigated here. Using a forest growth simulator supported by extensive field measurements in disturbed forest landscapes, carbon stock recovery was simulated in the context of a changing climate and various regeneration/management scenarios. The pre-disturbance ecosystem was coniferous subalpine forest; the post-disturbance recovery is highly heterogeneous – in some areas, coniferous domination, in others, deciduous or graminoid. This heterogeneity is followed through the coming century and total ecosystem carbon (non-mineral soil) was simulated to determine the relative influence of disturbance history/regeneration, management, and climate change on forest carbon stocks.

METHODS

Site and Plot Design: A combination of disturbances (blowdown, logging, fire) in the subalpine forest of the Park Range in northern Colorado, USA, resulted in a spectrum of post-fire recovery rates and trajectories in a subalpine spruce-fir forest (Buma and Wessman 2011, 2012). The forest (approx. 2700-3300 m ASL) is comprised of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lsiocarpa*), lodgepole pine (*Pinus contorta*), and quaking aspen (*Populus tremuloides*). Precipitation averages approximately 1000 mm a year, mostly as snow (NRCS)

2010). The blowdown (October 1997, approx. 10,000 ha, Baker *et al.* 2002) left a mosaic of severities, from zero to near 100% blowdown. Salvage logging, conducted post-blowdown (1998-2001), took place on approximately 900 ha. In the summer of 2002, the Mt. Zirkel fire complex burned approximately 12,500 ha of undisturbed, blown-down, and salvage logged forest. The blowdown altered fire severity (Kulakowski and Veblen 2007), as well as postfire recovery (Buma and Wessman 2012).

Table 1. GCM and emission scenarios used in the simulations.					
Abbreviation	Group	SRES Scenario	Description	Name	
CGCM3	Canadian	A2	Heterogeneous world, rapidly increasing population, production oriented	CGCM3 A2	
CGCM3	Climate	A1B	Homogenizing world, rapid growth, balanced energy sources	CGCM3 A1B	
CGCM3	and Analysis	B2	Heterogeneous world, slowly increasing population, more environmentally friendly	CGCM B2	
GFDL A2	Geophysical Fluid	A2	Heterogeneous world, rapidly increasing population, production oriented	GFDL A2	
GFDL B1	Dynamics Laboratory	B1	Rapid growth, global problem solving, service and information economy emphasis	GFDL B1	
HAD A2	Hadley A2		Heterogeneous world, rapidly increasing population, production oriented	HAD A2	
HAD B2	Prediction and Research	B2	Heterogeneous world, slowly increasing population, more environmentally friendly	HAD B2	

112 15x15m plots were censused for post-fire regeneration of woody plant species and woody debris. These plots were stratified according to their disturbance history (Fig. 1): no/low blowdown and fire (0-20 downed trees/ha; n = 27), medium blowdown/fire (20-55 downed trees/ha; n = 41), areas of high blowdown/fire (55+ downed trees/ha; n = 33), and logged

blowdown/fire (55+ downed trees/ha and prior logging; n = 11). Standing dead was measured on a subset of plots (no/low = 22 plots; medium = 8 plots; high = 10 plots; logged = 8 plots). This grouping scheme corresponds with decreasing conifer regeneration (as measured by seedling densities, Fig. 1 middle). At each plot, seedlings (<150cm) were counted and measured for height and coarse woody debris (CWD) was estimated via methods from Brown (1974). All standing dead (snags) were measured for their diameter at breast height (DBH) and height. To compare recovering carbon stocks to undisturbed forests, 10 additional plots were established within undisturbed spruce-fir forests. The same measurements were conducted, with species, DBH and height recorded for all trees.

Model: Carbon dynamics were modeled in the USDA Forest Vegetation Simulator (FVS) for 100 years (2010-2109) using the carbon sub-model contained in the Fires and Fuels extension (FVS-FFE, Rebain 2010) and the climate extension module (FVS-Climate, Crookston *et al.* 2010). FVS is a well-known forest simulator often used for carbon and disturbance modeling (e.g. Hurteau and North 2009), and is setup for different geographical regions; the Central Rockies variant was used here. FVS was chosen due to its direct applicability to land management decisions. Growth occurs based on species-specific relationships between local climate/topography and the local community (e.g. crown closure, tree density), and was calibrated according to DBH and height allometric relationships. Mortality occurs via two processes, background mortality (species and size specific probabilities) and density-dependent mortality, which is species specific and determined based on stand density and species shade tolerance. Regeneration is user specified, and so was implemented according to the management strategies described below. Each plot was grown independently. Elevation was obtained from

the USGS national elevation dataset with a resolution of 30m. Aspect and slope were calculated from this dataset using ArcMap (ESRI 2010).



Figure 1. Groupings for the model based on disturbance severity (number of downed trees/ha with or without salvage logging; all sites experienced fire), and their corresponding initial carbon totals (top, Mg/ha C), conifer seedling densities (middle, total conifer stems/ha), and aspen seedling densities (bottom, total stems/ha). Total C includes above and belowground live C, belowground dead C, CWD, snags, and grass/forb layer. Organic soil was not present at the beginning of the simulation period, and so is not included in this initial data. Mineral soil excluded.

Live seedlings were input into the model and their total C was calculated according to Jenkins *et al.* (2003). Field estimated CWD was used to initialize downed debris loads; FVS-FFE allometrics were used to calculate C in initial snags (based on field survey). Because species could not be determined for the burned snags, all snags were considered Engelmann spruce, the dominant species in unburned stands. Forest floor (e.g. duff) and shrub/herb layers were calculated using Smith and Heath (2002) via FVS-FFE and based on canopy cover percent, age, and dominant tree species.

The initial amount of dead coarse roots could not be determined for each plot because it was impossible to determine pre-fire tree sizes and densities with any certainty. In addition, logging removed the majority of the tree boles and some stumps, so their coarse roots would be unaccounted for if stumps or snags were used to initialize belowground dead coarse roots. Instead, the mean belowground coarse root carbon totals (live and dead) from the undisturbed plots were used to initialize all the burned plots. This assumes that the burned plots were compositionally similar to the control plots, and is a conservative move, reducing the variability between the treatments. This initial value was decayed for eight years to match the initial time since fire, and that value was used as the initial dead coarse root C for all disturbed plots. Root decay was set at the Central Rockies variant default of 4.25%/year. Movement between pools and decay (e.g. standing dead to CWD occurs as snags decay and fall) is calculated according to species-specific rates found in Rebain (2010) and references therein. Mineral soil dynamics are not simulated in FVS. Carbon estimates are calculated every year for the simulation period, and are the sum of living tree biomass (above and belowground), dead trees (standing and fallen), dead roots, the herbaceous layer and the organic soil.

Regeneration/Management Scenarios: Estimating future establishment is difficult, and so this study bracketed potential establishment by looking at the endpoints – no (further) future establishment, and two scenarios for future establishment – heavy establishment of local species (resilience-oriented) and heavy establishment of climatically suitable tree species, local or not (adaptation-oriented). These two scenarios parallel the actions proposed by Millar *et al.* (2007) for forest management responses to climate change. The *no action* scenario explores the effect of differing resilience on long-term carbon stocks, without human intervention or further establishment. The plots are modeled using only seedling densities observed in the field.

The *resilience* scenario attempts to simulate a high-resilience situation, bolstering current seedling levels by establishing Engelmann spruce (990 trees/ha (400 trees/acre), standard planting density, USFS *personal communication*; 0.3m average height) whenever the tree densities fell below 40% of optimal (full stocking, defined via USFS defaults, Rebain 2010). Engelmann spruce can survive planting on the open, bare mineral soil found in the plots (Alexander 1988). The no action and resilience scenarios can also be considered as bracketing potential natural recovery, from no further establishment to prolific recovery of the local forest.

The *adaptation* scenario allowed establishment of any central Rockies tree species. The species in the adaptation scenario were chosen based on what would survive the best based on climatic conditions at the time (full listing of the species is in Appendix 5-1). This option simulates management oriented towards maintenance of a *forest*, rather than maintenance of a *specific* forest. This should provide better continuity in forest-specific (as opposed to species-specific) ecosystem services, such as snow interception and carbon stocks. The four most adapted species, as determined by the FVS-Climate model (below), are established in each plot in the same fashion as spruce in the resilience scenario.

Growth: FVS-Climate modifies growth in the context of three global climate models (GCMs) and four emission scenarios, for a total of seven GCM/scenario combinations which cover a range of severities of projected climate changes (Table 1). The climate model incorporates the change in 35 climate variables from 2010 to 2110, and alters tree growth, mortality, and site carrying capacity based on species-specific climatic variables from survey sites throughout the western US (n= 45,000, modeled via Random Forests) and genetic effects. Full details are available in Crookston *et al.* (2010) and based on methodology from Rehfeldt *et al.* (2009); climate/suitability maps can be found at http://forest.moscowfsl.wsu.edu/climate/. Each plot was run from 2010 to 2109 under each climate scenario. Because FVS is a deterministic model, estimating uncertainty requires an extra step. To generate means and confidence distributions which better describe the variability in sampling, each group was bootstrapped 1000 times (random sampling, n = group size, with replacement). The final mean and 5/95% quantiles were calculated from that 1000 sample population. Carbon totals were simulated for each management and climate scenario.

Carbon budgets are sensitive to the model used (Melson *et al.* 2011), however the main purpose of this study is comparison *between* resilience levels and management choices, rather than absolute prediction, and the results should be viewed as such. For the most severe climate change scenario, GFDL A2 ("severe" in terms of its effect on the species present in the plots), the total live trees/ha was followed to explore the consequences on forest persistence in addition to total C stocks. Table 3. Modeled carbon outputs for each climate and management scenario for the midpoint (2060) and final year (2109) in the projections. Values represent the median plot level totals (non-soil pools), over all disturbance histories. 5% and 95% percentile values are from the bootstrapped distribution to give an estimate of variability. Totals are quite similar for 2060, but diverge for many of the projections by 2109.

		Projection Year 2060		Projection Year 2109			
		(Mg/ha C)		(Mg/ha C)			
Climate	Management	Median	5%	95%	Median	5%	95%
model	Scenario						
A1B	No Plant	82.9	55.9	118.2	82.1	53.9	114.1
CGCM3 A2	No Plant	82.4	55.9	118.9	69.6	46.6	99.0
CGCM3 B1	No Plant	81.4	55.3	118.1	147.8	106.8	214.1
GFDL A2	No Plant	57.1	34.0	101.9	31.3	11.7	61.8
GFDL B1	No Plant	79.9	55.2	116.8	119.2	58.9	158.4
HAD A2	No Plant	73.9	53.8	118.5	44.9	24.8	80.0
HAD B2	No Plant	77.0	55.0	116.7	71.4	43.3	101.8
CGCM3 A1B	Plant Spruce	83.3	60.1	121.0	82.6	55.5	115.3
CGCM3 A2	Plant Spruce	83.3	60.8	124.8	71.2	48.5	100.9
CGCM3 B1	Plant Spruce	82.4	60.5	119.4	152.5	119.5	210.0
GFDL A2	Plant Spruce	59.8	34.4	103.8	32.3	12.4	64.1
GFDL B1	Plant Spruce	80.1	58.7	120.8	118.6	59.4	158.3
HAD A2	Plant Spruce	75.0	53.9	121.1	45.7	25.6	79.0
HAD B2	Plant Spruce	77.3	58.6	119.0	71.4	43.2	102.4
CGCM3 A1B	Adaptation	97.9	75.0	141.4	115.1	80.4	152.6
CGCM3 A2	Adaptation	97.4	75.3	139.2	99.2	64.1	136.9
CGCM3 B1	Adaptation	95.7	76.9	140.8	210.6	169.6	241.5
GFDL A2	Adaptation	74.5	46.9	122.2	40.8	18.0	69.6
GFDL B1	Adaptation	93.9	73.3	136.9	159.4	87.6	204.4
HAD A2	Adaptation	91.2	69.6	138.0	68.1	36.0	102.2
HAD B2	Adaptation	94.4	78.6	143.4	99.3	63.0	136.9



Figure 2. Carbon stocks for each disturbance history group, undisturbed plots, and three model/emission scenarios (CGCM3 B1, CGCM3 A1B, and GFDL A2). Differences in categories (low, medium, high, and salvaged) reflect the different initial densities of the current species related to their fire resilience, their longevity under the different scenarios, and how much flexibility that afforded to the plantings. The effect of differing resilience levels is found in the spread of projections within each graph, the question of differences between management scenarios are addressed by comparison between columns, differing climate scenarios are on different rows. Lines show each resilience grouping bootstrapped 1000x, dotted lines represent the 5%/95% quantiles. Each line was smoothed with a 10 year moving average.





Each group was significantly different in terms of initial non-soil C as a result of their

disturbance history (Table 2). The groups also had different levels of conifer establishment,

according to their disturbance history (Fig. 1, middle), with all pairwise comparisons

significantly different except the medium and logged groups (Wilcoxon rank sum test, p < 0.05).

Aspen establishment was abundant in all groups and highly variable (Fig. 1, bottom; Table 2).

and standard deviation (in parentheses). Significance groupings denoted by superscripts (pairwise Wilcoxon rank sum test, Holm correction). Groups were significantly different in terms of initial carbon and conifers (except for the medium and logged groups); aspen was more variable.					
Group	Non-soil Carbon (Mg/ha)	Conifer (seedlings/ha)	Aspen (seedlings/ha)		
Low	68.6 (16.9) ¹	$1052 (875)^1$	1484 (1702) ^{1,2}		
Medium	94.7 $(23.4)^2$	$336(390)^2$	709 (928) ^{1,2}		
High	52.7 (18.6) ³	88 (207) ³	795 (1451) ¹		
Logged	$\overline{24.6}$ (8.3) ⁴	$283(209)^2$	$2570 (4226)^2$		

<u>Near term</u>: Carbon stocks began to recover after a period of negative carbon balance (yearly loss) due to decomposition (Fig 2) and the source-to-sink conversion predicted by Kashian *et al.* (2006) was produced. Despite the fact that conifer regeneration essentially failed as a result of the compound disturbance interaction in the high interaction group (averaging 88 seedlings/ha), aspen appears to have offset the loss of coniferous tree species. The logged site, which started with substantially lower C than the other histories as a result of CWD/snag removal, grew equal to the other groups within approximately 40 years (Fig. 2); logged plots also saw the highest aspen seedling densities, at 2570 seedlings/ha on average (Table 2). In the end, the differential conifer resilience observed had little effect on C stocks.

Long term: In terms of management strategies, there was no long-term difference between no-action and resilience-oriented management. The adaptation-oriented approach diverged from the other strategies around 2060, and large differences appeared by the end for some climate scenarios (Table 3). Low emission projections (CGCM3 B1 and GFDL B1) maintained climates mostly hospitable to current species, and carbon stocks continued to recover under the projected climate regime regardless of managerial strategy, although the adaptation approach did have higher C stocks (Fig. 2, top row; Table 3). For the other climate scenarios, current species were unable to survive in the projected climate, and high rates of mortality reduced tree levels and carbon stocks. Differences between the no-action and resilience scenarios were slight, and by the end of the simulation were minimal; the adaptation plan had consistently higher C stocks, although the magnitude of the difference depended upon the climate scenario (Fig. 3; note that this combines the disturbance histories into single management scenarios, which makes the assumption that the plots are essentially interchangeable. Given their rapid convergence (e.g. Fig. 2) this seems valid, but the figure should be interpreted with this caveat in mind.) The forest type transitioned, however, from a spruce/fir/lodgepole/aspen community to oak/juniper/pinion pine dominated woodland (Fig 4).

<u>Tree densities:</u> Disturbance history had no influence on final tree densities (Table 4), however they were much higher in the adaptation-oriented scenario than in the no-action and resilience-oriented approaches, both of which had zero live trees at the end of the simulation period (Fig. 5). Tree numbers were slightly declining in the adaptation scenario, likely due to

natural thinning. This is also likely responsible for the leveling off and even slight reductions in carbon stocks as the forest moved into a more open woodland configuration (Fig. 2).

The complete model outputs can be found in Appendix 5-1 (species composition and relative contribution to total C in the adaptation scenarios, as in Fig. 4) and Appendix 5-2 (total C for all scenarios, as in Fig. 2).

DISCUSSION

Broadly speaking, differences in coniferous resilience had minimal effect on carbon stocks, as shown by the convergence of the disturbed groups (Fig. 2). In the near term, the establishment of aspen more than compensated for any loss of coniferous species, to the point where plots with zero coniferous seedlings were similar in terms of total carbon stocks to areas with ample regeneration. So while the aspen forest will be different in many other respects (e.g. forage, understory composition, phenology), carbon stocks should recover more or less similarly across the groups in the near to mid-term due to the aspen. This parallels the results of Kashian *et al.* (2006), who hypothesized that differences in resilience (measured by post-fire recruitment rates) would cause changes in carbon stocks initially but those levels converged as forests developed (however that study did not simulate growth/mortality changes due to climate). The rapid growth of aspen (relative to the conifer species) appears to have accelerated that process, and further infilling and establishment may hasten that recovery, at least in the near term.



Figure 4. Species proportions for aboveground carbon stocks for one climate scenario (GFDL A2), the adaptation management action, and the four resilience categories. These correspond to the bottom right graph in Fig. 2. Abbreviations: GO, Gambel oak; UJ, Utah juniper; PI, Common pinyon; RM, Rocky Mountain juniper; ASP, Quaking aspen; LP, Lodgepole pine; AF, Subalpine fir; ES, Engelmann spruce; LM, Limber pine; BS, Blue spruce; DF, Douglas fir; OJ, Oneseed juniper; PM, Singleleaf pinyon. Note that all species listed are modeled as present, although their contribution may be difficult to see in the graph. The remainder of the climate/management outputs are found in Appendix 5-1.

In the long-term, C stocks were more responsive to the climate scenario than their initial conditions. The majority of the GCM/emission scenarios modeled resulted in climatic conditions outside the range of the current suite of species, which overwhelmed any signal of the differential response to the disturbances. Planting of spruce increased carbon stocks in the midterm (20-50 years) by filling in low density plots, but was not successful in the longer term (50+ years) as the modeled climate conditions moved outside spruce's expected tolerance. Large-scale climate related mortality has been observed; for example, sudden aspen decline (SAD), the large scale dieoff of aspen stands in the southern Rockies, has been tied to climate drivers (moisture stress/hydraulic failure, Worrall *et al.* 2010, Anderegg *et al.* 2011). To the extent that these drivers become more common, further dieoffs (as simulated here) may become more likely. In any case, rapid die-offs are certainly possible, and must be considered in any long-term planning.

Allowing for species shifts (Fig. 4) resulted in higher carbon stocks and maintained tree cover (Fig. 3 & 5). These species are certainly different in many important respects, but could provide many of the same ecosystem services going forward (i.e. snow capture, soil temperature regulation). Even in the most severe change scenarios (e.g. GFDL A2), tree species were still viable, albeit at a low density, resulting in low standing carbon stocks (Fig 2, bottom row).

The control plots further illustrate this point. The control plots were comprised primarily of spruce and fir, two species which were quickly extirpated in many of the climate scenarios. In many of the simulations, the control plots were very similar to the disturbed plots by the end of the period due to mortality of the spruce and fir. Interestingly, the control plots were often lower in the adaptation-oriented scenarios, lagging behind the disturbed plots in terms of carbon stocks (Fig. 2, Appendix 5-2). This is likely due to the lack of opportunity for alternate species

establishment, which required a minimum number of stems on the plots before planting could commence. This would likely reflect reality to a degree, in that competition from living trees may inhibit the establishment of non-local species. The disturbance facilitated their establishment by eliminating that competition.

This suggests the hypothesis that perhaps disturbances may set up more climatically suitable species – species more tolerant of the hot and dry post-disturbance environments – facilitating natural adaptation towards warmer and dryer climates, in the near-term at least. In this study, the lower magnitude climate change scenarios showed higher C in the disturbed plots than the undisturbed plots (at the end of the simulated period; CGCM3 B1 and GFDL B1), as did the majority of the adaptation-oriented simulations. Modeling results in Scandinavia (Sykes and Prentice 1996) also demonstrated that more disturbances facilitated faster adaptation to changing climates, assuming no dispersal limitations. This exercise made a similar assumption by relying on managerial actions to get suitable species to the area. There are dispersal limitations in reality, however. Given the rapidity of expected temperature shifts, populations will need to migrate very quickly (Loarie *et al.* 2009). Naturally migrating populations will require not only the ability to move that distance, but also time to reach maturity after each dispersal event and the opportunity to establish. Although some of the species found near the end of the adaptive scenario are found locally (Gambel oak, Rocky Mountain juniper), others not (based on distribution maps from Little 1971, available at: http://esp.cr.usgs.gov/data/little/). The extent to which disturbances do facilitate the transition to more climatically suitable species assemblages will be limited by the dispersal ability of those species themselves, and the community dynamics that are setup by the assemblage of establishing species.

Post-disturbance management strategies must aim at a moving target while also hedging bets, since the variation between climate scenarios is quite large and species suitable in 50-100 years are not necessarily suitable now. A hybrid approach to post-disturbance forest management is likely the most reasonable – planting currently viable species en masse (using more climate appropriate provenances where possible, e.g. Rehfeldt et al. 1999), but also providing for "seed islands" of species which may be viable in the future and who cannot be expected to migrate naturally. These seed islands would provide critical information on how a changing forest would affect other aspects of the forest such as the understory and herbivores (e.g. Chapin et al. 2007), needed before any mass transplanting should commence, and potentially provide seed to replace the current species as the increasingly inhospitable climate and future disturbances remove them. There are valid concerns about this strategy, which essentially amounts to assisted migration, and they should be considered (McLachlan et al. 2007). The way bioclimatic tolerances are defined and variance in those models should be considered (Mbogga et al. 2010), as well as the potential for runaway invasions and other detrimental effects. Local knowledge and skills will be needed to establish species in currently non-hospitable climates. However, the risks of inaction must also be considered, and they may be outweighed by the risks associated with facilitated adaptation (e.g. Gray *et al.* 2011). The seedling supply is available in many areas, and in some cases, nurseries are working with geneticists to develop more appropriate genotypes for future conditions (Tepe and Meretsky 2011). In any case, climatic adaptation, facilitated by humans or not, is inevitable. Whether adaptation occurs naturally, subject to those dispersal limitations discussed earlier, or is facilitated via planting is a matter of policy, and should consider the extent to which specific ecosystems and ecosystem services are desirable or irreplaceable.



Looking further, resilience to future disturbances should also be considered (Solomon and Freer-Smith 2007). This study looks at the effect of subalpine conifer resilience to a fire now (and did not simulate future disturbance events); what about a fire in 2050? Further work needs to explore some potentially contrasting effects of climate change on future fire behavior, and from there, future fire resilience. Fire weather is almost universally expected to increase in western North America (Moritz *et al.* 2012). Severity (in terms of post-fire regeneration) is more difficult to forecast, but is likely dependent upon species composition and the relative proportion of fire-adapted species. The increase in tree mortality expected to result from climate change (e.g. SAD) may result in less spatially continuous fuel loading, which may alter fire behavior and severity as well. Combinations of models of future forest dynamics like those presented here need to be further integrated with models of future fire likelihood, which are often statistical and do not consider feedbacks with vegetation (e.g. Westerling *et al.* 2011). This would extend the range of planning options to not only look at a single ecosystem service, but also the value of different management options to potential future events.

Table 4. Numbers of live trees/hectare (GFDL A2 climate model) for the adaptation-oriented				
management scenario for the year 2100. Each group was bootstrapped 1000x, the 5%/95%				
percentiles are reported. Groups are not significantly different.				
Treatment	Mean	5%	95%	
Low	938	889	987	
Medium	956	909	1004	
High	917	872	966	
Logged	925	816	1033	

LIMITATIONS: As in all studies which explore non-analog conditions (such as future climate), questions arise about the models ability to handle projections which are inherently extrapolations. Bioclimatic envelope-based models are prime examples. Bioclimatic envelopes make several assumptions, including the lack of biotic interactions, the lack of local adaptation,

and the exclusion of dispersal limitations in terms of the current range of species (Hampe *et al.* 2004). However, when used appropriately, they are still useful for baseline estimates of general future change (Pearson and Dawson 2004, Lawler *et al.* 2009). It should be noted that these GCM projections involve the mean temperature, precipitation, etc., whereas in some cases distributions and survivorship may be better described by climatic variability, such as extreme cold weather events, which are relatively infrequent but may have a disproportionate influence of distributions, and are not yet modeled in GCMs.

Another limitation regards the role of mortality in climate change models. The mechanistic nature of climate-induced mortality is still under investigation, with several nonexclusive means by which the trees may be killed, such as hydraulic failure due to xylem cavitation/collapse, carbon starvation, biotic attack, and the interaction between these and other stressors (Hartmann 2011, McDowell et al. 2011). This is an active area of research, and it is likely that the relative contribution of these mechanistic factors are species dependent, varying on several factors including stomatal behavior, rooting depth, and relative growth. One could argue that these mechanistic causes for mortality are built into bioclimatic envelopes, especially for ecosystems strongly structured by abiotic constraints. However, current distributions may not reflect the actual physiological bounds of a species in historical time, either. For example, Minckley et al. (2012) have recorded stable coniferous ecosystems despite variation in climate over a 6000 year period in lake cores approximately 100 km from the study area, indicating that lodgepole (specifically) is resilient to somewhat variable disturbance and climate regimes over long time periods. Tree mortality needs to be further explored and the models validated by experiment, especially given other factors which may alter or partially ameliorate the effects of climate change (e.g. CO₂ fertilization) or complex interactions between a changing climate,

changing tree vigor, and biotic disturbances such as bark beetles. The model used here increases probabilistic mortality when the climate shifts out of that observed for a given species. There is some verification of this methodology in the region (sudden aspen decline, Worrall *et al.* 2010), and the majority of research agrees that mortality will rise (McDowell *et al.* 2011). This supports the conclusion that active management will be required to maintain tree cover if natural dispersal of more climatically appropriate species proves insufficient.

Finally, future establishment is an unknown. The scenarios used here bracket the possibilities – either no future establishment or prolific establishment, both with local and more climatically suitable species. Results should be interpreted with this in mind.

CONCLUSIONS

Disturbances can be seen as opportunities for adaptation. They allow for new species to establish, and (potentially) reset the community to something that is more in tune with the current climate. For this system, the importance of differing resilience to C stocks appears to be relatively minor due to the rapid growth of aspen. In the long term, concerns of forest type and its influence on C stocks are outweighed by the larger implications of climate change.

Maintaining natural system dynamics (no action) may have an ecological of philosophical appeal for some. However, an approach that preserves the structural system (e.g. a forest) may, in some cases, better sustain critical or desired ecosystem services even if it requires direct intervention – although a cost/benefit analysis would be needed to judge the suitability of any specific project. In the resilience parlance, this is an example of adaptive transformation; the social system transforms the ecological system to maintain resilience in the face of climatic change, using disturbances as windows of opportunity to move the system into a more adaptive

state. There are drastic transformations at the community level, but at the structural level, resilience is maintained. The tools of restoration ecology, which have been long developed both professionally and academically, will certainly be of use in conjunction with silvicultural techniques to both plan and establish communities resilient to emerging conditions (e.g. Tepe and Meretsky 2011, Seidl *et al.* 2011).

This is a place-based analysis, one concrete example of a broader issue. It brings an important reference point to discussions on resilience and climate change - these results are grounded in actual plots, at an actual place, and simulated for that place. A look at climate projections shows that this degree of change is not unusual throughout the globe, so while this example is place-specific, the generalities it explores are not. Resilience of ecosystems is not guaranteed, nor is the background climate on which that resilience plays out. Timely action is needed and has already been explored in some parts of the globe (Seidl *et al.* 2011). Species ranges are moving, often faster than the species themselves can disperse (Loarie *et al.* 2009). Ecosystems, and ecosystem services they provide, may see their resilience to specific disturbances undermined by a changing climate.

CHAPTER 6

CONCLUSIONS AND FURTHER RESEARCH

The phenomenon of compound disturbances is an important unknown in ecology, as disturbance rates are expected to increase in many places due to climate change and as human pressures becomes more widespread (Paine *et al.* 1998, Dale *et al.* 2001, Turner 2010). First, they represent potential unknowns, "novel" conditions which are difficult to predict and for which ecosystems may have little native resilience. Second, disturbance frequencies are being altered by climate change and anthropogenic activities, potentially increasing the chances of multiple disturbances affecting the same place in a short period of time. Finally, they can have long term implications for landscape structure and function, especially in slow-cycling ecosystems such as subalpine forests. This dissertation has explored compound disturbances via a substantial field campaign, a "natural experiment," laboratory work, modeling, and statistical analyses. The results illustrate several aspects of disturbance interactions: Their mechanistic basis, their implications for stand growth and structure (Fig. 1).

INTERACTIONS AND RESILIENCE

The blowdown (1997), salvage logging (1998-2001), and fire (2002) in the Routt National Forest interacted to create a disturbance with novel characteristics, one that would not have been in the absence of the interaction. This is explored in Chapter 2, where fire behavior modeling is used to explore the consequences of the interaction in terms of fire temperature, residence time, and spatial extent. Those novel characteristics directly impacted the resilience

mechanisms of some of the species on the landscape, and have important consequences for this ecosystem; lodgepole pine, the primary post-fire coniferous species, is nearly absent post-fire in areas that experienced these interacting disturbances. Not only was the landscape more prone to high magnitude fire as a result of the blowdown (as reported in Kulakowski and Veblen 2007), it was less resilient. The salvage logging provided an interesting nuance. Higher conifer recruitment was observed in the salvage logged areas, likely due to decreased fire intensity and duration. Salvage logging has a contentious history; work in the Routt conducted before the fire indicated that salvaging was detrimental to recovery (Rumbaitis del Rio 2006). The situation postfire is more complex. That salvage logging apparently reduced fire intensity and severity (in terms of conifer regeneration) is an interesting twist. Of course, one cannot know if a fire will occur ahead of time, and some research suggests salvage logging may increase fire likelihood (Donato *et al.* 2006) in addition to damaging recovery. Any commentary on salvage logging based on these results must consider the likelihood of fires in a given location, and weigh that against the damage caused in the absence of a fire.



Figure 1. Overall diagram of the disturbance history of the Routt NF study area, the general successional trajectories, and selected results. Arrows indicate direction of change relative to either the reference treatment (fire-only; seedling resilience and climate modeling) or to undisturbed plots (carbon and BC stocks). *: Indicates differences between the treatments. †: No differences in treatments overall, but significant differences in individual pools.

CONSEQUENCES FOR CARBON

The consequences of altered forest resilience depend on the characteristics of the forest one is interested in. This dissertation has taken on the topic of carbon with an in-depth investigation into where the landscape stands now, post-compound disturbance event, and where it might go in the future. Current stocks were progressively lowered as a result of the compound disturbance, with more disturbances resulting in increased losses. This is perhaps not surprising, as the blowdown+fire interaction caused higher intensity burning and the logging removed material manually (and we do not know the removed carbons' ultimate fate). A full accounting requires considering the decay rate of the salvaged wood (potentially quite long, if placed inside houses, for example) and the emissions creating during the salvage operations.

The exploration of black carbon (BC) produced surprising results. If considered over the entire fire return interval (which, although variable, is typically long), this intensity of fire does not appear to raise BC stocks, and potentially lowers it, based on literature-derived decomposition rates (Chapter 4). BC decomposition is an ongoing field of research, and a much better understanding of the thermodynamics of BC decay and fluvial export are required before definitive statements can be made (Davidson and Janssens 2006, Singh *et al.* 2012). Lower severity portions of these fires are an important consideration – areas of complete mortality but not complete organic soil consumption, and areas of partial mortality. These areas comprise a substantial part of these fire events (30-55% of the Mt. Zirkel fire complex, depending on how low severity is quantified), and given the lower fire intensities, lower mortality, and less soil combustion, they may comprise a disproportionally important part of the post-fire carbon stocks.

It appears, at this point, that the compound disturbance event resulted in a fundamentally different landscape, one with more heterogeneity in cover type, a mosaic of regeneration which bears the mark of the prior disturbance history, and with important differences in total carbon and BC. Some areas are starting with an aspen overstory and a strong coniferous understory, but many areas are starting with no coniferous presence at all. Some areas have no tree individuals and an expanding carpet of graminoids (predominantly *Carex geyeri*; unpublished data). There are potential feedback mechanisms that will maintain the alternate stable regimes (a thick litter layer in aspen preventing conifer establishment, fierce competition from grass species preventing any tree establishment at all), but only time will tell. It is impossible to rule out convergent succession over the long term, which will only be tested via turnover and self-replacement of the longest-lived species in the system (Connell and Sousa 1983). In the near term (e.g. a century), however, we can be fairly confident in concluding that heterogeneity has increased, conifers have decreased, and there is a stronger deciduous presence as a result of the compounding disturbance.

CLIMATE CHANGE

Any hypotheses about recovering forests run quickly into the reality of a changing climate. The rapidly shifting climate (Loarie *et al.* 2009) means that a multi-century successional perspective is not necessarily applicable. Most climate models project an environment outside the historical range of these tree populations, and in some cases outside the range these species experience anywhere. Colorado is near the southern extent of many of these species distributions, and so range loss will likely occur here first. (It should be noted that even in these worst-case scenarios, individual trees and groups of trees may survive in hollows and protected, mesic areas. But they will likely cease to be an important functional component on

the landscape.) For most scenarios, only through the active establishment of new species was a forest cover and substantive carbon stocks maintained. The majority of the species in this simulation are not present in the study area, although scattered Rocky Mountain juniper and Douglas-fir individuals can be found. The major players in the simulations, Gambel oak (*Quercus gambelii*), Utah juniper (*Juniperus osteosperma*) and Pinyon pine (*Pinus edulis*), would need either migrate or be intentionally introduced through management. According to USGS species distribution maps (available at: http://esp.cr.usgs.gov/data/atlas/little/), the nearest Utah juniper population is approximately 65 km to the west, and there is a pinyon pine population 100 km to the south. Both are small and isolated (Fig. 2). Gambel oak is nearby, at lower elevation. It is also important to note that the species chosen were considered optimal (out of the regional species pool), whereas natural adaptation will likely create a mix of better suited, but not necessarily optimal, species as a function of their migration abilities. So extensive natural dispersal, or human-facilitated movement, may be necessary to maintain a forest, or at least the forest type envisioned in this project.

MOVING FORWARD

Climate change puts the resilience of the subalpine forest (or lack thereof) into a different perspective. Rather than just focusing on landscape resilience to disturbances now, it is worth taking a large perspective and think about how differential landscape resilience *sets up* forests for climate change.

Considering the large climatic changes expected over just the next century, it is prudent to consider how the results presented here will play out over the long term. A resilient system now may not be well suited for expected future climatic conditions. To put it another way,

disturbances are an opportunity for ecosystem re-equilibration with the climatic environment. If the recovering system is better adapted to projected future climate conditions, then perhaps these events which exceed the resilience of the system should be seen as opportunities. For example, Colorado (and much of the American West) is expected to get significantly warmer (Ray *et al.* 2008), and although precipitation changes are still uncertain, increased temperature will drive increased evapotranspiration and likely result in drier environments. If disturbances trigger shifts to more xeric tolerant species assemblages, e.g. more (future) climatically appropriate species, then they could be considered adaptive processes. From one perspective, adaptation will happen regardless, even if that means a large loss of forest cover. So whether that adaptation occurs naturally via dispersal (in which case the result may or may not be structurally similar) or via human intervention is an important consideration for land managers.



Figure 2. Three candidate species for future forests in the study area, *Q. gambelii, P. edulis* and *J. osteosperma*. They may have potential to offset loss of native species (due to climate change) in terms of forest cover and partial carbon storage. Current distribution shown.

FURTHER RESEARCH

The confluence of events in the Routt National Forest (and excellent supporting research) provided the opportunity to take a mechanistic look at disturbance interactions and their impact on resilience and one specific ecosystem service, carbon storage. Additional work should follow the development of this ecosystem, focusing on any additional recruitment (which may serve to reduce differences) and potential mechanisms for maintenance of these differences, such as the establishment of sedges and grasses which inhibit any further establishment. Beyond these stand level dynamics, several other avenues for further research have been suggested.

- Interactions: What disturbances interact to produce novel, new disturbance conditions? Blowdown/logging/fire interactions explored here have direct relevance to hurricane/fire areas, but what about deadfall from mountain pine beetle infestations? Will these disturbances rates increase/decrease as a result of climate change or increasing anthropogenic pressures?
- Resilience: Will those interactions directly affect the resilience mechanisms of the ecosystem? At what levels do these interactions matter in a qualitative fashion? Will successional trajectories be altered as a result?
- 3. Carbon stocks and other ecosystem services: Are the fates of other ecosystem services tied to ecosystem resilience? When and where should assisted migration and direct manipulation of species assemblages for the purposes of ecosystem service preservation be tested and implemented?
- 4. Adaptation: How might currently disturbed areas fare relative to undisturbed areas under various climate change scenarios? Are early successional species more appropriate for

expected conditions? Might disturbances setup more climatically suitable species assemblages, and if not, can (or should) humans facilitate that transition?

Through this dissertation, I have explored compound disturbances and their implications for one ecosystem service, carbon storage. This work has produced excellent insights into how disturbances interact to create novel disturbance characteristics, affect species resilience, and alter subalpine forest composition – and raised interesting further questions. The current forest landscape is, in some ways, at a transition point – from a time where successional dynamics were predictable, if protracted, to a period where a changing climate is moving faster than the forest dynamics themselves. Rather than resetting succession and maintaining a mosaic of stand ages and compositions across the landscape, perhaps they are better viewed as catalysts for climate adaptation for ecosystems going forward.

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Appendix 4

Appendix 4-1: Bulk Density measurements

Disturbed Areas: Each of the disturbed treatments (F, BF, BLF) used bulk density measurements developed from Rumbaitis del Rio (2004 and unpublished data), who used a subset of these sites. These bulk densities were used for all the plots.

F: Fine soil bulk density was 0.82 g/cm³; coarse soil bulk density was 0.14 g/cm³.

BF: Fine soil bulk density was 0.93 g/cm³; coarse soil bulk density was 0.14 g/cm³.

BLF: Fine soil bulk density was 0.87 g/cm³; coarse soil bulk density was 0.23 g/cm³.

Control Areas: Fine and coarse bulk densities were calculated for each individual plot, using five subsamples at each plot. A core of known volume (10cm depth) was extracted at each plot, organic and mineral soils were split at the mineral horizon, and the depth of each layer recorded. Volumes for each were then calculated. Mass was determined after drying at 100° for 24 hours. The mean mineral fine soil bulk density was 0.66 g/cm^3 (SD 0.17); the mean mineral coarse bulk density was 0.12 g/cm^3 (SD 0.15 g/cm^3). The mean organic soil fine bulk density was 0.18 g/cm^3 (SD 0.04) and the mean organic soil coarse bulk density was 0.02 g/cm^3 (SD 0.01). The individual bulk density measurements for each plot were calculated, so each control plot used those individual bulk density estimates rather than the mean.

Appendix 4-2: Digestion parameters for the black carbon analysis and reference char information

Methods follow Kurth *et al.* (2006), a hydrogen peroxide-weak nitric acid chemical digestion method.

Fine Soil (<2mm); mineral and organic soils (control only)

<u>Sample Preparation</u>: Soil samples were ground on a roller mill for 24 hours (or longer, if necessary). Each plot consisted of 10 random samples for mineral soil BC, 5 for organic soil (control plots only); a 10 mg subsample was removed for total carbon analysis from each homogenized subsample. The 10th sample had three 10 mg subsamples removed to ensure proper grinding and homogenization. The subsample(s) were run on the Carlo Erba 1108 elemental analyzer for total carbon.

<u>Digestion</u>: To determine recalcitrant carbon (BC), a 1 g subsample was taken from each ground sample. This sample was placed in large digestion tube in a Labconco block digester with 20 mL 30% H₂O₂ and 10 ml 1M nitric acid. The sample was held at 95-97° C for 20 hours. Tubes were covered lightly with foil. Tubes were swirled lightly to ensure full mixing. The majority of soils were then vacuum pumped through a #2 filter to extract the majority of the H₂O₂/ nitric acid mixture, and dried at 60° for 24 hours. This method is much faster than gravity filtration; however it results in some loss of digested material. The lost material was collected for a subsample of digestions and tested to ensure that there was no bias in carbon percentages resulting from this loss. While there was no bias in percent carbon of the digested material that resulted from this method, the mass lost in the digestion could not be determined for samples processed in this way.

Mass Loss calibration:

Mass loss of non-carbon materials must be considered to get accurate BC percentages in *undigested* soils. Not considering mass loss would bias the percentages higher, as the mass multiplier would be artificially low. Calculating mass loss for each sample, however, is prohibitively time consuming for the ~750 digestions run in this study. So, we built a regression model to predict mass loss based on pre and post carbon percentages, which could then be applied to the entire dataset.

A subset was analyzed for mass loss to create this model. After digestion, the contents of 128 mineral soil samples and 32 organic soil samples were gravity filtered through Whatman #2 filter paper, taking care to ensure all material in the flask deposited on the filter paper. The solids were dried 24 hours at 60° , and massed. Mass loss was calculated as pre-digestion dry weight – post-digestion dry weight.

Loss was well predicted via a linear regression ($p \approx 0, r^2 = 0.95$; Fig. 4-1). To satisfy the assumptions of a standard linear regression, the data points were separated into mineral and organic soils for analysis. For mineral soil, the best predictive equation was found as:

Percent mass loss =
$$\Delta C * 2.58 + 0.10$$
; p ≈ 0 , r² = 0.58

Where ΔC is: Pre-digestion percent C – post-digestion percent C. Residuals were normally distributed about zero.

For organic soil:

Percent mass loss =
$$\Delta C * 2.61 + 0.10$$
; p ≈ 0 , r² = 0.91

Residuals were normally distributed about zero.

Post-digestion mass for the unknown soils was then calculated by:

*Post digestion mass (estimated) = Pre digestion mass * percent mass loss*

Determining percentage BC: The final percentage BC is calculated via:

 $Percent BC in sample = \frac{Percent C post-digestion * post-digestion mass}{Pre-digestion mass}$

Where post-digestion mass is either measured or modeled. Once the percentage BC was determined, the total BC was calculated via the same bulk density measurements as for total carbon (see Methods and Appendix 4-1).

Coarse Soil (>2mm); mineral and organic soils (control only)

Coarse BC methodologies are described in the methods. Briefly, the soil coarse fraction (>2mm) was sorted and massed to determine mass C, and converted to mass/area via the coarse bulk density measurements in Appendix 4-1. 23 subsamples of these coarse charcoal "chunks" were hand ground using a mortar and pestle. Subsamples came from the entire spectrum of sites: 4 C, 4 F, 4 BLF, and 2 BF. For total carbon calculations, 10 mg of each of these ground charcoal samples were run on the CE1108 for percent C. For BC, the subsamples were digested (in an identical fashion to the fine soil) and analyzed.

Coarse charcoal in the soil was found to be 56.7% C (undigested, range 33.4-72.9%, n=23) and 38.6% BC (post-digestion, range 16.1-65.6%, n=11), after correction for mass loss.

These percentages were used in conjunction with the bulk density measurements (see Methods and Appendix 4-1) to calculate total C and BC in the coarse fraction.

Reference Chars

Percent carbon from the reference chars (see Hammes *et al.* 2008 for chemical description and ordering information) are reported here (Fig. 4-2). Three levels of analyses are shown: Undigested, digested, and digested with adjustment for mass loss. This will allow for cross comparison between studies at multiple steps in the digestion process.

Grass results (mean): 58% C undigested; 51% digested; 42.7% adjusted for mass loss Wood results (mean): 72% C undigested; 54% digested; 44.4% adjusted for mass loss





Appendix 4-3: Plot level black char (mineral soil only)

Plot level variation in mineral soil BC (fine and coarse) for all plots. Each plot is 15x15m, but extrapolated to Mg/ha to facilitate comparison to main text and other studies.



Figure 4-3. Plot level variation in mineral soil charcoal, organized by disturbance history. Each boxplot represents 10 digestions/plot. BF plots are annotated with their pre-fire blowdown severity (red line, right axis). The vertical line denotes the severity cutoff for the categorical comparisons; BF plots to the right of the line were used for those tests (see methods). Opaque boxes are fine soil char, transparent (and lower) boxes are coarse fraction char. Organic soil BC in control plots not shown. One high data point cutoff to create a more visible scale. Colors organized by disturbance history for clarity.

Appendix 5

Appendix 5-1: Species composition and contribution to total C

Species composition and contribution to total C for each management and climate scenario. Each management/establishment scenario is presented for each climate simulated. The graphs show the percentage of aboveground live carbon contributed by each species. For the total carbon, see Appendix 5-2.

Page Numbers:Species listing: 161Adaptation oriented scenario: 162 - 168Resilience oriented scenario: 169 - 175No action scenario: 176 - 182

Adaptation oriented scenarios. This plan allowed for the establishment of local and non-local

species (Table A5-1), native to the southern Rocky Mountains.

Table A5-1. Species included in the adaptation model. Note other species were available for planting, only those actually planted at some point are shown here. Abbreviations correspond to the species proportion graphs shown in the following pages. If a species is listed on a particular graph, it was included in that simulation, although the proportions may be too minor to see.

Abbreviation	Common Name	Scientific Name
GO	Gambel oak	Quercus gambelii
UJ	Utah juniper	Juniperus osteosperma
PI	Common pinyon	Pinus edulis
RM	Rocky Mountain juniper	Juniperus scopulorum
ASP	Quaking aspen	Populus tremuloides
LP	Lodgepole pine	Pinus contorta
AF	Subalpine fir	Abies lasiocarpa
ES	Engelmann spruce	Picea engelmannii
LM	Limber pine	Pinus flexilis
BS	Blue spruce	Picea pungens
DF	Douglas fir	Pseudotsuga menziesii
OJ	Oneseed juniper	Juniperus monosperma
PM	Singleleaf pinyon	Pinus monophylla



Adaptation oriented scenario



Adaptation oriented scenario



Adaptation oriented scenario



Adaptation oriented scenario



Adaptation oriented scenario



Adaptation oriented scenario



Adaptation oriented scenario

Resilience oriented scenarios



Resilience oriented scenario



Resilience oriented scenario



Resilience oriented scenario


Resilience oriented scenario



Resilience oriented scenario



Resilience oriented scenario



Resilience oriented scenario

No action scenarios



No action scenario



No action scenario



No action scenario



No action scenario



No action scenario



No action scenario



No action scenario

Appendix 5-2: Total C projections for each climate and establishment scenario

Complete projections for each climate and management scenario (years: 2010 - 2109). The results are presented as 10 year average, hence the first 10 years are missing.

No action plan simulates the growth of the current regeneration, with no further establishment. The resilience oriented management plan supplements the current natural regeneration with establishment of Engelmann spruce, a local species, and thus simulates a high-resilience (either naturally or via planting) situation. The adaptation oriented plan simulates the establishment of whatever species in the species list (Table A5-1) is most climatically suitable at the time. This simulates either the natural migration of the most climatically suitable species or direct management to adapt to climate change in this post-disturbance environment.

<u>Page Numbers</u> No action plan: 184 - 190 Resilience oriented scenario: 191 - 197 Adaptation oriented scenario: 198 - 204



No additional establishment

(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



No additional establishment



No additional establishment

Year (bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



No additional establishment

No additional establishment



(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



No additional establishment

(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



No additional establishment

Resilience Oriented Management



Spruce establishment





(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)





Adaptation oriented management



Adaptive management; any establishment



Adaptive management; any establishment



Adaptive management; any establishment

(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



Adaptive management; any establishment



Adaptive management; any establishment

(bootstrapped (n=1,000), 10 year moving average; mean & 5%/95% percentiles)



Adaptive management; any establishment



Adaptive management; any establishment