Crash and Burn: Forest Tornado Damage, Its Landscape Pattern, and Its Interaction with Fire

by

Jeffery B. Cannon

(Under the Direction of Chris J. Peterson)

Abstract

Forest disturbances from wind damage and fire are ubiquitous and have important ecological effects. Recent research in disturbance ecology emphasizes the potential for compounded disturbances to interact in unpredictable ways. Much of this research has focused on the possibility of wind damage to increase flammable fuel loads and lead to severe wildfires. However, there are many possible mechanisms by which wind damage and fire interact, including many where wind damage can lessen, or buffer, fire intensity or severity. This dissertation explores several themes surrounding wind–fire interaction mechanisms. In Chapter 1, I review available literature on theories and studies of forest disturbance by wind damage and fire and classify interaction mechanisms based on whether they act in synergy (amplifying) or whether they are antagonistic (buffering). The review emphasizes the importance of buffering effects especially during low-intensity fire and that both amplifying and buffering effects play a role in wind–fire interactions in a heterogeneous spatial mosaic. In chapter 2, I describe a field experiment simulating wind damage gaps from tornados and compare fuel characteristics and fire behavior in gaps and intact forest. The study shows that wind damage influences fuel loading, but also fuel arrangement—an important component of fuel continuity in prescribed fires. The study emphasizes that wind damage has the potential to increase fire intensity, but much of this effect is limited to areas directly within down tree crowns. In chapter 3, I examine the ecological effects of the combined disturbances from Chapter 2 on several vegetation parameters. The major results of this study show that interaction mechanisms vary by individual species leading to a heterogeneous mixture of amplifying and buffering effects following compounded disturbances. Despite the importance of landscape pattern on ecological processes, few studies address the landscape-scale distribution of tornado damage. In chapter 4, I describe a remote sensing methodology to measure tornado severity and landscape-scale characteristics of tornado damage. I also apply the methodology to test hypotheses about how tornados behave in rugged terrain. The remote sensing method presented could be used on multiple tornado tracks to generalize patterns of tornado damage at the landscape-scale.

Index words: amplifying effects, antagonism, buffering effects, compounded disturbances, disturbance interactions, fire, fire behavior, combustion characteristics, fuel arrangement, interaction mechanisms, landscape pattern, prescribed fire, remote sensing, synergism, topography, tornado damage, wind damage, wind disturbance

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Chapter 1

Introduction and Literature Review: Interactions Between Forest Disturbances from Wind and Fire[1]

[1]Cannon, J.B. and C.J. Peterson. To be submitted to *Ecology*

Abstract

Current research the interaction between disturbances emphasizes the potential for profound ecological effects that may occur when disturbances interact. However, much less attention has focused on the possibility of interactions to buffer ecological changes when disturbances co-occur. In this review, I classify and evaluate evidence for interactions between two common forest disturbances in the eastern U.S.—wind damage and fire—focusing on studies where forest wind damage precedes fire. Interaction mechanisms are classified according to how they influence ecosystem resistance to and resilience from subsequent disturbances and whether interactions have synergistic or antagonistic effects. Several important generalizations emerge from this classification of disturbance interactions. First, wind–fire interactions based on changes in fuel may vary with regional differences in climate or by severity of fire. Second, the potential for buffering interactions between wind damage and fire, may be more common when fire intensity is low. Third, amplifying and buffering effects may simultaneously or co-occur in a spatial mosaic in a given set of disturbances. Future studies on wind–fire interaction mechanisms that explicitly incorporate the effects of climate, fire severity, and disturbance heterogeneity will aid in understanding these ecologically important and ubiquitous disturbances.

Index words: blowdown, compounded disturbances, disturbance interactions, fire, interaction mechanisms, wind damage

1.1 Introduction

The process of successional change following single disturbances has long been studied by ecologists but the effects of multiple, or compounded disturbances have received less attention (Turner, 2010). Much of the current research on compounded disturbances suggests that initial disturbances can change ecosystems in ways that make a subsequent disturbance more probable, intense, or severe (Buma, 2015; Paine et al., 1998; Scheffer et al., 2001). For example, in many western U.S. forests, attack by the mountain pine beetle (*Dendroctonus ponderosae*) has led to widespread mortality of lodgepole pine (*Pinus contorta*) and may increase forest fuels, leading to intense fires (Amman and Schmitz, 1988). Disturbances may also interactively influence how ecosystems recover from disturbance. In general, disturbances are expected to reduce the resilience of ecosystems (*i.e.*, the tendency for an ecosystem to recover its previous state, Holling, 1973). Thus, when ecological communities are subjected to multiple disturbances, it is predicted that unanticipated "ecological surprises" may occur (Frelich and Reich, 1999; Paine et al., 1998). An ecological surprise is a long-term change in community composition caused by the interaction of two or more disturbances (Paine et al., 1998), an implicit consequence of reduced resilience.

Because unanticipated changes following compounded disturbances add uncertainty to ecological predictions, an understanding of interactions between common forest disturbances can inform ecosystem management following natural disturbances. This review focuses on the potential interactions between two disturbances common in the eastern United States—wind damage and fire. Wind damage and wildfire affect a combined forest area of over 2 million ha annually in the U.S. (Dale et al., 2001), and each disturbance has important ecological effects (Chambers et al., 2007; Peterson and Pickett, 1995; Turner et al., 1994). In addition to wildfires, prescribed fire is increasingly used for a variety of purposes including wildlife management (Main and Richardson, 2002), ecological restoration (Glitzenstein et al., 1995), and reduction of fuel hazards (Addington et al., 2015; Agee and Skinner, 2005). A total of 3.8 million ha were treated with prescribed fire in the U.S. in 2011 (Melvin, 2012).

Understanding the interaction between wind damage and fire is important because of the potential for severe wind damage to fuel intense wildfires (Myers and Van Lear, 1998). Wind damage has the potential to alter the behavior and effect of prescribed fire with important consequences for forest management (Cannon and Brewer, 2013; Cannon et al., 2014, Chapter 2, herein). In addition, frequent disturbance from tropical windstorms and fire has been hypothesized to be an important driver of the unique structure of longleaf pine (*Pinus palustris*) savannas (Gilliam et al., 2006; Myers and Van Lear, 1998). Unraveling the mechanisms by which disturbances interact is an important component of understanding how disturbances cause ecological change (Johnson and Miyanishi, 2007). Thus, the goals of this review are to (1) present a framework for classifying wind–fire interaction mechanisms based on the ecosystem reaction and direction of the interaction, and (2) present hypothesized mechanisms for the interactions along with evidence for these hypotheses.

1.2 Framework for Classifying Wind–Fire Disturbance Interactions

In a recent review, Buma (2015) outlined a useful framework for characterizing disturbance interactions based on which ecosystem reaction is affected. Some interactions alter ecosystem resistance to disturbance, and others alter resilience to disturbance. A single disturbance can increase or decrease the resistance of a system to a second disturbance (Buma, 2015; Simard et al., 2011). Wind damage may alter the probability, intensity, or severity of a subsequent fire. With respect to fire, the term intensity refers to the magnitude of energetic output from combustion (often measured as temperature or energy flux), while the term severity refers to measures of

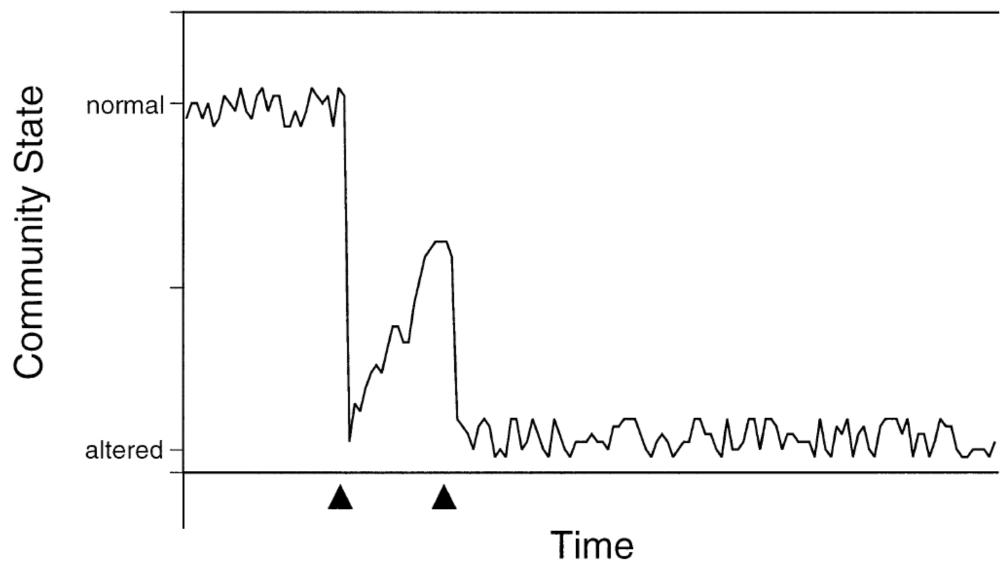

Figure 1.1: Schematic illustration of a community effected by two disturbances (arrows) in rapid succession, resulting in altered community state. From Paine et al. (1998)

biomass loss (often a measure of consumption or mortality, Keeley, 2009). Note that by this classification scheme, an increase or decrease of resistance to fire can include not only changes in resistance of the entire ecosystem to fire (*i.e.*, changes in probability or intensity of fire), but also changes in the resistance of individual organisms to mortality by fire (*i.e.*, changes in fire severity).

Disturbance interactions may also shift ecosystem succession or recovery by altering the resilience of a system to a second disturbance (Buma, 2015). That is, an initial disturbance may have ecological effects that alter the speed or trajectory of recovery following a subsequent disturbance (Figure 1.1; Paine et al., 1998). Thus, interactions between wind damage and fire may be classified according to whether a particular mechanism alters the impact of a subsequent fire (altered resistance), or the ecological response to a subsequent fire (altered resilience, Buma, 2015)

Disturbance interactions may also be classified on the basis of whether they cause the disturbances to act in synergy (Folt et al., 1999). Much of the current research on disturbance interactions focuses on the propensity for compounded disturbances to interact in a synergistic manner where the effect of the first disturbance increases the probability or severity of a subsequent disturbance (Kulakowski et al., 2013; Paine et al., 1998; Scheffer et al., 2001). Such synergistic effects can "amplify" the impact of a second disturbance (by decreasing resistance), and they may also shift ecosystem trajectories (by decreasing resilience). Dramatic amplifying interactions may have striking effects; but in a meta-analysis of 57 studies of compounded stressors on marine animals, Darling and Côté (2008) found that across studies, ecological responses to compounded stressors can include both amplifying effects as well as antagonistic, or "buffering" effects. In these cases, one disturbance can decrease the impact of a second disturbance (*i.e.*, increased resistance or resilience). As a terrestrial example, although it is generally thought that attack by mountain pine beetle outbreaks can increase the severity of wildfires by increasing fuel loads (Amman and Schmitz, 1988), disturbance by beetles may also reduce tree canopy density and decrease (or buffer) the severity of active crown fires in the short term (Simard et al., 2011). Thus, interactions between disturbances may also be classified along a spectrum of additivity, and may produce amplifying, buffering, or additive (*i.e.*, non-interactive) effects.

Although Buma (2015) recognized the occurrence of buffering effects, they were not explicitly included in his framework. In this review of wind–fire interaction mechanisms, I classify and discuss mechanisms of disturbance interactions along two axes: mechanism type and interaction additivity. Considering wind and fire: wind damage may alter the impact or response to subsequent fire (ie, altered resistance or resilience), and a given interaction direction may be amplifying or buffering, resulting in four distinct interaction categories (Table 1.1). The order in which disturbances occur can influence their effect and interaction (Fukami, 2001). Thus, in this review,

Table 1.1: Summary of proposed interaction mechanisms reported among studies of wind damage and fire arranged by mechanism types (altered resistance or resilience) and interaction direction (amplifying and buffering effects).

	Interaction Direction	
Mechanism Type	Amplifying Effects	Buffering Effects
Resistance	1) Increased temperature and decreased humidity within gaps (Matlack, 1993)	1) Reduction of leaf litter input (O'Brien et al., 2008)
Resistance	2) Fuel loading increases probability, intensity, or severity of fire (Myers and Van Lear, 1998; Liu et al., 2008; Urquhart, 2009; Kulakowski and Veblen, 2007)	2) Patchy fuel decreases fire continuity (Cannon and Brewer, 2013; Cannon et al., 2014)
Resistance	3) Hurricane increased fine fuels (cogongrass, *Imperata cylindrica* Holzmueller and Jose, 2012)	3) Potential increased survival on tip-up mounds (Chapter 3, herein)
Resistance	4) Hurricane reduces stem diameter/bark thickness (Wolfe et al., 2014)	
Resilience	1) Delayed regeneration after removal of adults (Liu et al., 2008; D'Amato et al., 2011; Buma and Wessman, 2011)	1) Greater sapling basal sprouting (Chapter 3, herein)
Resilience	2) Delayed regeneration after mortality of serotinous cones (Buma and Wessman, 2011)	2) Differential sapling sprouting useful for restoration (Cannon and Brewer, 2013)

I focus on mechanisms of interaction when wind damage precedes fire. Mechanisms of interaction when fire precedes wind damage are interesting in their own right (*e.g.*, Cannon et al., 2015; Matlack et al., 1993; Schulte and Mladenoff, 2005), and deserve separate discussion.

1.3 Mechanisms Altering Resistance to Fire

When wind damage of any severity affects a forest, several environmental changes take place that can influence the behavior of a subsequent fire. Pyne et al. (1996) summarizes the major factors influencing fire behavior which include fuel characteristics (*e.g.*, fuel type, size, and arrangement), weather (*e.g.*, temperature, humidity, and wind), and topography (*e.g.*, slope, elevation, and barriers). Wind damage has the potential to alter several of these factors. Blowdowns can increase loading of fine and coarse fuels (Busing et al., 2009; Holzmueller and Jose, 2012), alter fuel arrangement (Cannon et al., 2014), and decrease litter moisture (Matlack, 1993). Blowdowns can increase temperature (Denslow, 1980; Matlack, 1993; Schulz, 1960) and decrease humidity in gaps (Matlack, 1993). Such changes may be considered amplifying effects as they can make fire more likely or severe.

Conversely, other changes caused by wind damage potentially reduce the intensity, probability, or extent of subsequent fire, and are considered buffering effects. For example, wind damage can create micro-topography such as large pit and mound complexes formed when trees are uprooted (Sobhani et al., 2014; Ulanova, 2000) and an abundance of large downed woody debris (Busing et al., 2009). These legacies are typical of severe wind damage and could potentially act as barriers to the continuity of low-intensity fire (see Cannon et al., 2014). Thus, wind damage has the potential to both increase and decrease fire severity via amplifying or buffering mechanisms.

1.3.1 Amplifying Effects: Mechanisms Decreasing Ecosystem Resistance

Among amplifying mechanisms of wind–fire interactions, the most intuitive, and well-studied interaction mechanism involves wind damage that increases flammable fuel loads and the likelihood or severity of fire (Myers and Van Lear, 1998; Webb, 1958).

Two studies in coastal regions of the Gulf of Mexico and Caribbean Sea confirm that historically, fires frequently followed severe hurricane damage. Liu et al. (2008) examined lake sediment cores in a coastal lake in Alabama. Based on sediment deposits, in the past 1200 years, four major fires occurred near the focal lake: two of these fires were within 25 years of a major hurricane, one was within 50 years of a major hurricane, and one was arson related. In fact, minor charcoal peaks were associated with every major hurricane. Using similar methods, Urquhart (2009) examined sediment cores in a Nicaraguan coastal lagoon and discovered that in 1400 BC, a severe hurricane struck Nicaragua and was followed by multiple severe fires (Urquhart, 2009).

Reconstruction of forest disturbances in old growth forests in New Hampshire during the period from 1635 to 1938 revealed several blowdown and fire events (Foster, 1988). Foster documents three cases where wildfires followed severe hurricane or windstorms (wildfires occurred 2, 15, or 30 years after storms). Kulakowski and Veblen (2007) noted that forest disturbance history was a good predictor of fire severity based on remotely sensed fire severity data in a landscape-scale study of subalpine forests in northwestern Colorado. Forest stands that received a severe blowdown in 1997, also experienced severe wildfires in 2002. Johnson et al. (2013) modelled fire behavior following wind damage and fuel reduction treatments and found that fuel reduction treatments also reduced several aspects of fire intensity including flame length, reaction intensity, and rate of spread. This fuel removal study following wind damage suggests that high fuel loading is likely an important mechanism driving amplifying aspects of the wind–fire interaction.

In contrast to the previous studies documenting wildfires following severe blowdowns, two studies of fire regimes in the northeastern U.S. did not find co-occurrence of wind damage and fire. A study by Busby et al. (2008) used a compilation of historical and dendroecological records to reconstruct disturbance history for *Fa-*

gus-dominated forests of Naushon Island, Massachusetts. The authors found little evidence that fires occurred over the last 300+ years, despite the fact that the HURRECON model (Boose et al., 1994, 2001) identified 58 hurricanes affecting the study area since 1620.

Similarly, Schulte and Mladenoff (2005) characterized historical windthrow and fire regimes in northern Wisconsin using public land surveys to reconstruct the pre-Euroamerican forest composition and identify patches of forest affected by wind or fire. They found little evidence of co-occurrence of severe blowdown and fire disturbances, and suggested "such interactions were rare rather than inevitable, and likely dependent on historically important events, such as drought years." More interestingly, they found that wind and fire damage were geographically segregated in the study area, and suggested that in northern Wisconsin, short fire rotations in some areas maintained young forests, which are less susceptible to windthrow which tends to disproportionally affect larger diameter trees (Everham and Brokaw, 1996).

In addition to wind–fire interaction mechanisms that directly amplify fire intensity through increases in downed woody fuels, indirect mechanisms by which wind damage alters vegetation and leads to changes in fire intensity or severity have also been suggested. In an analysis relating occurrence of the aggressive and exotic cogongrass (*Imperata cylindrica*) within disturbed longleaf pine (*Pinus palustris*) forests of the Florida panhandle, Holzmueller and Jose (2011) noted that cogongrass was more likely to invade disturbed forest stands, such as those proximal to the path of Hurricane Ivan. In another study, these authors (2012) point out that presence of cogongrass can lead to increased fire intensity and severity in invaded areas. The increase in resources—especially light—following canopy removal could lead to the proliferation of species, such as grasses, which can alter the behavior of subsequent fires.

Wolfe et al. (2014) suggested another intriguing indirect wind–fire amplification mechanism operating via forest structure. Wind disturbance alters forest structure by removing larger trees (Everham and Brokaw, 1996) and initiating sprouting, leading to a reduction of mean stem diameter (Van Bloem et al., 2006). Bark thickness of stems is a major determinant of resistance to top-kill (aboveground mortality), and generally increases with stem diameter or tree size. Reduction of stem diameter and, by extension, bark thickness by wind damage may make forests more vulnerable to fire (Wolfe et al., 2014). In a Caribbean dry forest experiencing frequent hurricanes, Wolfe et al. (2014) found that only 5% of stems had a bark thickness that would provide a less than 50% probability of top-kill. Thus, wind damage can increase fire intensity or severity directly by increasing fuel inputs, but also indirectly through changes in species composition and forest structure.

1.3.2 Buffering Effects: Mechanisms Increasing Ecosystem Resistance

Although wind damage increases fuel loading in the largest size classes, wind damage has other effects that may buffer the intensity or severity of subsequent fire. Forest blowdown creates canopy gaps which are known to have reduced fuel input from leaf litter (or needle cast), interrupting an important component of fuel continuity in low-intensity fires (O'Brien et al., 2008). Although the amount of available fuel is an important determinant of fire intensity (Byram, 1959), other fuel properties such as fuel composition (*e.g.*, abundance of different fuel types or size classes), as well as fuel arrangement (*e.g.*, aggregation, continuity, or bulk density) can also influence fire behavior (Pyne et al., 1996). In severe wildfires, the amount of large woody debris may drive combustion, but in low-intensity surface fires, such as those typical of prescribed burns, larger fuel sizes (*e.g.*, $\geq$ 2.5 cm diameter) are often left unconsumed and combustion is driven by the abundance, composition, and arrangement of fine fuels (*e.g.*, Cannon et al., 2014).

Cannon et al. (2014, Chapter 2, herein) describe a field experiment simulating tornado damage via winching of trees. The authors characterized how experimental wind damage influenced fuel characteristics and intensity of a prescribed fire. Despite the large increase in fuel loading following experimental wind damage, the amount of consumable fuels (fine fuels, < 2.5 cm diameter) was not increased by simulated wind damage. Instead, simulated wind damage altered fuel spatial arrangement. Fuels in control plots were relatively evenly distributed, but in wind-damaged areas, fuels were patchily distributed (high fuel loads in some areas and low fuel loads in other areas). Fire intensity was greater in wind-damaged areas compared to control plots. However, the increase in fire intensity was only found within downed tree crowns. Outside of downed tree crowns, measures of fire intensity were consistently (though not significantly) lower than control plots (Figure 1.2). This pattern suggests that although wind damage may dramatically increase fuel loads in some areas (such as directly beneath downed tree crowns), it may lead to reductions in fuel abundance in other areas or disrupt fuel continuity during low-intensity fires.

Indeed, wind damage amplified fire intensity by concentrating fuel under down tree crowns, but other processes such as leaf litter reduction may play a role in reducing fire intensity in areas outside of downed crowns. This finding is intriguing because it suggests that, at least with low-intensity fires, disturbance interaction mechanisms can be simultaneously amplifying and buffering depending on how they alter fuel composition and continuity at fine scales. Cannon and Brewer (2013) report similar variation in temperature of prescribed fires that followed natural tornado damage in an oak–pine forest in northern Mississippi. They report similar mean fire temperatures between tornado damaged and intact plots (208 and 219 °C, respectively), but much greater temperature variability in tornado damaged plots (79–660 °C) compared to intact plots (163–288 °C), highlighting the potential for spatial variability in temperature and continuity in wind damaged forest stands.

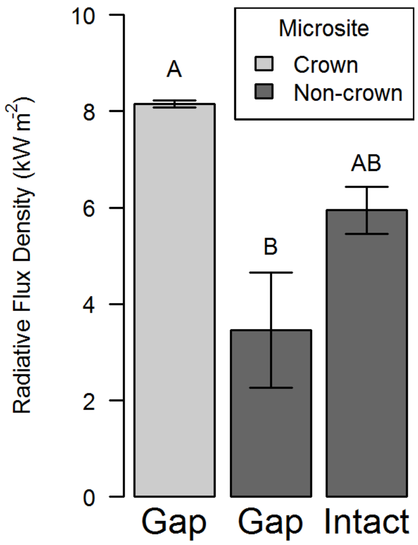

Figure 1.2: Prescribed fire intensity in forest gaps and intact stands. Error bars represent one standard error of the mean. Means sharing the same letter are not significantly different (Tukey's HSD, $P_{adj} < 0.05$). From Cannon et al. (2014, Chapter 2, herein)

For low-intensity fires, fine-scale fuel heterogeneity and fuel continuity are important drivers of fire behavior (Loudermilk et al., 2012). One prominent feature of forested areas following blowdown is the presence of large tip-up mounds formed when trees are uprooted, which have elevations of 0.5–2.5 m above the intact forest floor and host distinct vegetation and microclimate (Peterson et al., 1990; Ulanova, 2000). The elevation of plants on mounds can serve as refugia from herbivores (Krueger and Peterson, 2006). Seedlings established on mounds are at higher elevation than the surrounding forest floor, and may also be less vulnerable to subsequent fire.

Despite the fact that radiative energy from fire decreases dramatically with height above the flame plume (Cruz et al., 2011), seedlings established on mound microsites in our study (Chapter 3, herein) were not protected from fire. Height and size of tip-up mounds increases with tree diameter (Sobhani et al., 2014), so the refugia buffering mechanism may become more important in forests with larger trees and tip-up mounds, or in fires with lower intensity and flame height. Because fire behavior and effects are linked to fine scale distribution and continuity of fuels (Loudermilk et al., 2012), both amplifying and buffering effects of wind damage can occur in a heterogeneous spatial mosaic depending on how wind damage impacts fuel parameters such as fuel loading, continuity, and barriers.

Much research attention has focused on the interactions of wind damage and fire mediated through fuel, but fire resistance among individual trees has received less attention. Bark thickness and stem diameter are important predictors of resistance of individual trees to fire (Hare, 1965; Johnson and Miyanishi, 2007). Canopy-opening disturbances from wind damage increase resources, especially light, and release understory trees and saplings. It follows, then, that the release and rapid growth of stems following wind damage can allow individual stems to recruit to larger size classes, and become more likely to resist mortality from a subsequent fire. Through such a mechanism, wind damage may increase the resistance of individual stems to fire and results in a buffering effect. I know of no studies testing this hypothesis explicitly, however, Cannon and Brewer (2013) studied the effects of a prescribed fire executed two years following tornado damage. They found that larger saplings (basal diameter or height) were more likely to withstand damage from fire, and oak species were more likely to withstand fire relative to other species. Species that can respond rapidly to wind damage by allocating growth to dimensions that increase fire resistance (e.g, stem diameter or bark thickness) are expected to benefit from this mechanism more than other species. Because the mechanism depends on growth rates of individual stems and species, the magnitude and importance of this buffering mechanism could vary spatially depending on understory composition.

1.4 Mechanisms Altering Resilience to Disturbance

The manner in which an ecological community responds to and recovers from disturbance (*i.e.*, resilience) depends on ecological legacies such as remaining ecosystem structure, physical environment, and surviving organisms (Franklin et al., 2000). Disturbance interactions may delay recovery or alter succession of the post-disturbance community. Such changes may occur through removal of propagule sources such as reproductive adults, advance regeneration, or seed banks. Some models of compounded disturbances incorporate measures of cumulative severity through explicit measurement of total disturbance to canopy, understory, and soil (Roberts, 2007), or by calculation of a cumulative severity index based on the severity of component disturbances to various strata (Peterson and Leach, 2008). In these models, it is expected that increasing disturbance severity to canopy, understory, or soil results in delayed regeneration or altered successional trajectories at some threshold cumulative severity. Thus, removal or retention of propagules from various strata following disturbance may govern some mechanisms of interaction between wind damage and fire. Below, I review studies of combinations of wind and fire disturbances that demonstrate amplifying effects (those that decrease resilience), and those that demonstrate buffering effects (those that increase resilience).

1.4.1 Amplifying Effects: Mechanisms Decreasing Ecosystem Resilience

Examples of amplifying effects of wind damage and fire on ecosystem resilience typically focus on the negative effects of fire on regeneration from seed (Buma and Wessman, 2011; D'Amato et al., 2011; Liu et al., 2008). If severe wildfire causes mortality among reproducing adults, many biological legacies important for regeneration of the pre-disturbance community are removed. Such removal may delay regeneration of the pre-disturbance stand or lead to an alternative successional pathway (*e.g.*, "cusp catastrophe", Frelich and Reich, 1999). In the severe fires that followed historical hurricanes documented by Liu et al. (2008), the authors found, based on high-resolution pollen records, that *Pinus* populations decreased after hurricane damage and fires. In most cases, *Pinus* appeared to quickly rebound, except after two fire events. In these cases, the authors speculate that young trees were killed by fire before reaching sexual maturity, thus re-seeding and regeneration of the affected stands was delayed. Similarly, Urquhart (2009) noted that forest regeneration was delayed by repeated fires following catastrophic hurricanes.

In northern Wisconsin jack pine (*Pinus banksiana*) forests, D'Amato et al. (2011) documented that combinations of catastrophic blowdown (1999) and wildfires (2007) led to forest communities distinct from the individual disturbances. Regeneration in stands affected by blowdown and subsequent fire were dominated by quaking aspen (*Populus tremuloides*, which can sprout asexually), while those receiving only wildfires were dominated by jack pine (a fire-adapted species with serotinous cones, Burns and Honkala, 1990). The authors attribute the shift in composition and failure of jack pine regeneration on the short recovery time (approx. 8 years) between blowdown and wildfire, which precluded jack pine from reaching sexual maturity. Similarly, Frelich and Reich (1999) review case studies of disturbances and found shifts in forest composition following severe or compounded disturbances that impacted both the overstory as well as the understory regeneration.

Buma and Wessman (2011) examined regeneration following combinations of blowdown (1997) and wildfire (2002) in subalpine forests of Colorado. The authors also modelled fire characteristics and found that in stands with more severe wind damage, fire residence time and temperature increased, as did the duration of lethal seed temperature for lodgepole pine, (*Pinus contorta*, Buma and Wessman, 2011; Knapp and Anderson, 1980). They found that stands with severe wind damage were more

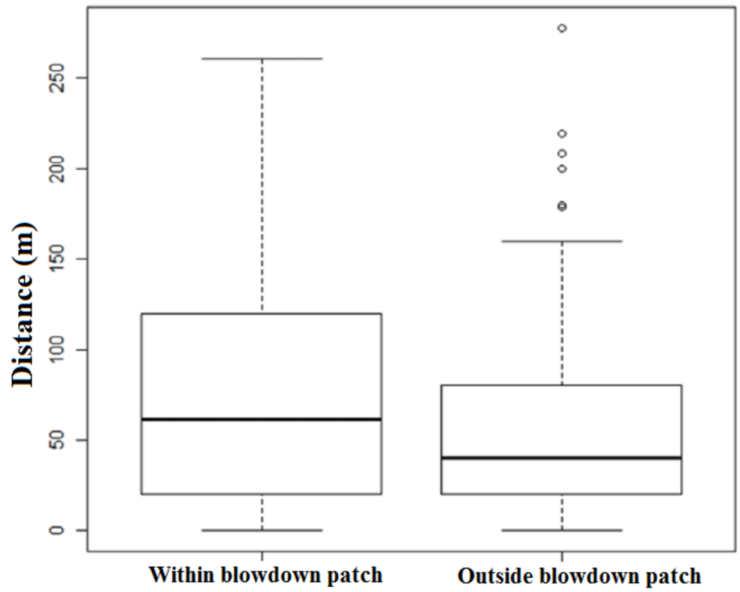

Figure 1.3: Boxplot of distances to lower burn severity (and, by extension, seed source) from random points in blowdown and intact patches. From Buma and Wessman (2011)

distant from potential seed sources (Figure 1.3). Furthermore, the authors found that regeneration was greatly reduced in stands receiving severe blowdown and fire, and attribute the differences to the increased seed mortality and isolation from seed sources (Buma and Wessman, 2011).

One important caveat is that for each of these examples of decreased resilience, the fire disturbance was also catastrophic and severe. As discussed in the next section, in cases of low intensity fire other interaction mechanisms that may have buffering rather than amplifying effects may dominate regeneration processes.

1.4.2 Buffering Effects: Mechanisms Increasing Ecosystem Resilience

Compared to amplifying effects, there are fewer examples of studies that demonstrate buffering effects, where wind damage increases ecosystem resilience. This disparity may be explained, in part, by the research focus on the combination of wind damage with severe wildfires. Wildfires are severe enough to remove significant biological legacies that are important for stand regeneration such as serotinous cones or surviving reproducing adults (Buma and Wessman, 2011; D'Amato et al., 2011; Liu et al., 2008; Urquhart, 2009). In contrast, following low-intensity fire, many biological legacies important for regeneration remain intact. Large juveniles and adult trees are frequently resistant to low-intensity fire (Hare, 1965); seedlings of longleaf pine (*Pinus palustris*) are famously resistant to fire in the grass stage (Burns and Honkala, 1990); and many woody species that are top-killed by fire have the ability to resprout rapidly by utilizing belowground carbohydrate reserves (Hodgkins, 1958; Robertson and Ostertag, 2009). Survival of propagules following low-itensity fire may poise these ecosystems for rapid recovery following compounded disturbances.

Increased availability of light following tornado damage presents the potential for wind damage to increase ecosystem resilience. Increased light availability from a canopy-opening disturbance such as wind damage may allow for rapid resprouting by understory vegetation, by increasing the growth rate of basal sprouts emerging from top-killed seedlings and saplings. In Chapter 3 (herein), I compared resprouting patterns of saplings following combinations of experimental wind damage and prescribed fire. Basal sprouts from plots receiving experimental wind damage one year before prescribed fire had greater biomass for a given sapling size relative to saplings in plots receiving only prescribed fire (Figure 1.4). This difference in sprout growth could have resulted from (1) increased light and soil resources following wind damage allowing faster growth rate of basal sprouts, (2) increased sapling allocation to belowground

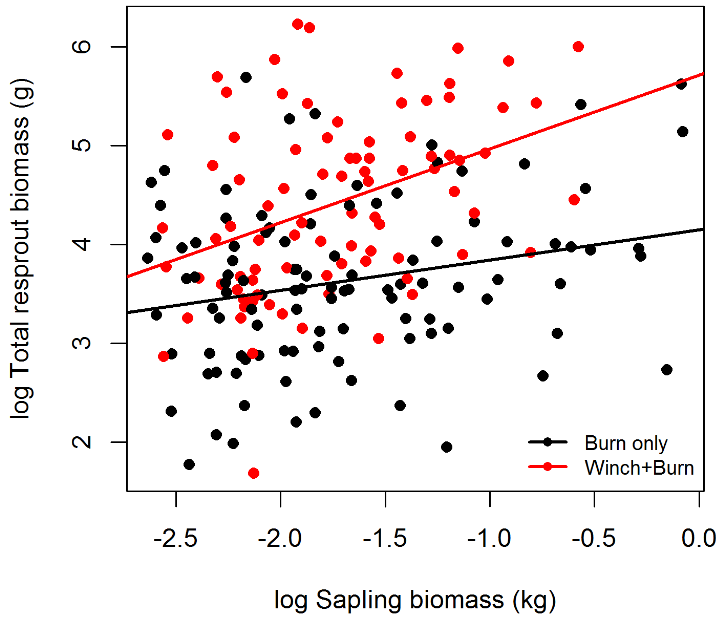

Figure 1.4: Relationship of biomass of top-killed saplings and the total biomass of basal sprouts from individual damaged saplings. Note both axes show log-transformed biomass. From Chapter 3, herein

reserves in the period between disturbances that allowed more rapid recovery, or (3) both mechanisms.

Species differ in their ability to resist disturbances such as wind damage or fire, and they also differ in how they respond to disturbance in terms of growth and reproduction (Bellingham et al., 1995; Batista and Platt, 2003). For example, Bellingham et al. (1995) outline a continuum of syndromes of damage and response to hurricane disturbance based on the differential ability of species to survive disturbance and their ability to recruit or reproduce following the disturbance. Species also differ in sprouting ability, sprouting growth rate, and allocation of carbohydrates to belowground reserves (Johnson et al., 2002; Robertson and Ostertag, 2009). Thus, any wind–fire mechanism dependent on life history traits such as survival, growth, or sprouting will vary between species. For example, in the context of a restoration experiment in northern Mississippi, Cannon and Brewer (2013) noted resprouting patterns following wind damage and fire differed following fire. As a group, species of upland oaks (*Quercus*) had larger resprouts relative to other species. The results of differential sprouting between species led to increased dominance by upland oaks, which were historically more common in the study area. The increased dominance of oaks was at the expense of more mesic species, which historically occupied lower slopes and has encroached upon ridges due to anthropogenic fire suppression (Nowacki and Abrams, 2008; Surrette et al., 2008). Sprouting responses after wind damage and fire can vary between individual species. Thus, the magnitude and importance of a particular disturbance interaction may vary in different portions of the same stand. Like resistance, mechanisms of resilience may also be spatially heterogeneous (Chapter 3, herein).

1.5 Discussion

Several important generalizations emerge from this classification regarding interactions between wind damage and fire with implications for future research. Intense wildfires following severe blowdowns depend on the coincidence of several factors such as available fuels, appropriate dry conditions, wind, and an ignition source (Pyne et al., 1996). Although wind damage certainly provides one of these factors (fuel), in order for severe fire to occur, the other factors related to climate and weather must also be met. In light of the considerable differences between climate and vegetation in areas where historical reconstructions of wind and fire has occurred (Gulf of Mexico region, Rocky Mountains, and the northeastern U.S.), the importance of wind–fire interaction mechanisms mediated through downed fuels likely vary with regional differences in climate. Future research examining landscape-scale wind damage and fire regimes which considers multiple regions, considers differences in disturbance severities, and explicitly incorporates climatic conditions may reveal the extent to which severe fires following wind damage are inevitable or dependent on climatic factors such as drought.

Second, current research on disturbance interactions focuses primarily on amplifying interactions, likely due to the potential for hazardous events such as wildfire (Myers and Van Lear, 1998). Only a few studies have identified mechanisms by which wind damage reduces the impacts of a subsequent fire such as reductions in fuel continuity (Cannon et al., 2014; O'Brien et al., 2008) or increased growth of basal sprouts (Cannon and Brewer, 2013, Chapter 3, herein). Interestingly, each buffering mechanism identified to-date seems to apply to low-intensity fires. Behavior of low-intensity fire is governed by heterogeneity of fuel at very fine-scales (< 1 m, Loudermilk et al., 2012), but such fine-scale sensitivity is likely absent in severe wildfires, where higher energy of combustion is available to overcome small-scale barriers or discontinuities in fuel.

A third important generalization from this review is that mechanisms producing amplifying and buffering effects can co-occur in the same disturbance event in a spatial mosaic. Although wind damage increases fuel loading and fire intensity in some areas such as downed tree crowns (Cannon et al., 2014, Chapter 2, herein), wind damage may reduce fire intensity outside of downed tree crowns through the creation of barriers and reduction in leaf litter inputs. Furthermore, resilience mechanisms may vary spatially in a heterogeneous manner. Sapling responses to fire such as basal sprouting, and the interaction between basal sprouting and increased light from wind damage differs by species (Cannon and Brewer, 2013). Thus, to the extent that species are heterogeneously distributed in the sapling layer, sprouting responses will also vary spatially, with some species such as oaks responding more rapidly to the combination of wind and fire than other disturbances. Such interactions between sprouting responses to wind and fire may add complexity to predicting future stand composition, but they may also be taken advantage of to achieve restoration objectives (Cannon and Brewer, 2013).

The association of catastrophic wind damage and severe fire is well-supported by historical studies, but not all disturbances from wind and fire are catastrophic. Even catastrophic wildfire produces a mosaic of patches of mixed severity (Turner et al., 1994). Similarly, wind disturbances such as tornado damage are extremely heterogeneous with patches of low-, medium-, and high-severity damage in roughly equal proportion (Chapter 4, herein). Thus, in reality, a continuum of disturbance severities exist for both wind damage and fire. Based on the previously reviewed studies, a variety of potential mechanisms govern interactions between wind damage and fire, and the nature and direction of the interactions likely differ between high-severity wildfire, and low-severity prescribed fire. Future research on interaction mechanisms which explicitly examines the heterogeneity of wind and fire disturbances will aid in understanding these ecologically important and ubiquitous disturbances.

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Chapter 2

The Influence of Experimental Wind Disturbance on Forest Fuels and Fire Characteristics[1]

[1]Cannon, J.B., J.J. O'Brien, E.L. Loudermilk, M.B. Dickinson, and C.J. Peterson. 2014. *Forest Ecology and Management* 330:294–303.

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Abstract

Current theory in disturbance ecology predicts that extreme disturbances in rapid succession can lead to dramatic changes in species composition or ecosystem processes due to interactions among disturbances. However, the extent to which less catastrophic, yet chronic, disturbances such as wind damage and fire interact is not well studied. In this study, I simulated wind-caused gaps in a *Pinus taeda* forest in the Piedmont of north-central Georgia using static winching of trees to examine how wind damage may alter fuel characteristics and the behavior of subsequent prescribed fire. I found that experimental wind disturbance increased levels of fine and coarse woody fuels (but not leaf litter), increased spatial heterogeneity of fuels, and led to more complete consumption of leaf litter. These patterns led to changes in fire behavior in experimental gap plots within areas of downed tree crowns where there were large increase in fire radiative flux density (kW m^{-2}) and its time integral, fire radiative energy density (MJ m^{-2}). These results suggest that wind disturbance may interact with fire not only through addition of fuel, but also through more subtle changes in fuel composition, consumption, and arrangement. More broadly, this study shows that disturbances can influence one another via a variety of mechanisms not all of which are immediately obvious. Understanding disturbance interactions can allow forest managers to make more informed decisions about how wind disturbance influences fuel heterogeneity, and how management processes, such as prescribed fire can interact with other prior wind disturbances to interactively shape plant communities.

Index words: disturbance interactions, fire behavior, fire combustion characteristics, fuel arrangement, wind disturbance

2.1 Introduction

2.1.1 Disturbance Interactions

Disturbances are important drivers of ecological change in many ecosystems. Consequently, their effects have been frequently examined. However, when ecosystems are subjected to multiple disturbances in rapid succession, current theory predicts that unanticipated "ecological surprises" such as non-linear changes in species composition may occur (Paine et al., 1998; Frelich and Reich, 1999; Scheffer et al., 2001). Paine et al. (1998) suggest that the ecological effect of disturbances in rapid succession may be multiplicative rather than additive. As an example, moderate severity forest disturbances that cause damage to either the overstory or understory can maintain pre-disturbance composition. However, when a more severe disturbance or disturbance combination affects both the understory and overstory, dramatic changes in forest composition occur (Frelich and Reich, 1999). Even so, most disturbances are not rare or catastrophic. In fact, there is a continuum of disturbance severity in most ecosystems; yet the interactions among these disturbances remain poorly understood (Turner, 2010). Here I investigate how two chronic and integral disturbances—wind disturbance and wildland prescribed fire—interact.

Prescribed burning is a commonly implemented forest management tool throughout the United States (*e.g.*, 3.8 million hectares of forest treated in 2011, Melvin, 2012), and wind damage from hurricanes, tornados, and other events is a particularly common forest disturbance, affecting a combined 1.65 million hectares in the U.S. annually (Dale et al., 2001). Understanding how these common and chronic disturbances interact can advance ecological understanding of disturbance interactions and inform forest management practices where wind disturbance and fire co-occur.

The most straightforward hypothesis of wind–fire interaction posits that wind disturbance to forests increases fuel loading, in turn increasing the likelihood or intensity of fire (Webb, 1958; Myers and Van Lear, 1998). Paleoecological studies corroborate the view that historically, fires frequently followed severe hurricane disturbance (Liu et al., 2008; Urquhart, 2009). Thus, wind disturbance such as hurricanes can increase the probability or extent of wildfire—likely due to increased surface fuel loads across large areas—but the interaction between wind and fire at the forest gap level is less understood. Smaller scale wind disturbance may affect fuel characteristics and the intensity and behavior of fire, which has a direct influence on individual plant mortality and regeneration (Whelan, 1995). In this study, I examine how wind disturbance at the gap level alters fuel availability and heterogeneity, and how these factors in turn influence fire combustion characteristics.

2.1.2 Effect of Wind Disturbance on Fuels and Fire Behavior

While fuel type, moisture, and wind speed all affect fire behavior, the amount of available fuel is a consistent determinant of fire intensity (Byram, 1959; Alexander, 1982; Whelan, 1995), and fire parameters such as radiative energy density increase with fuel consumption (Kremens et al., 2012). While it is known that small-scale changes in woody fuel such as downed tree branches can increase fuel loading and fire intensity, it is not known how larger-scale disturbances (such as multiple tree blowdown gaps) alters available fuels and alters fire behavior. Previous studies of blowdowns shed light on how wind disturbance may alter fuels such as woody debris and leaf litter. Studies in tropical, temperate, and boreal forests following wind disturbance have found marked increases in coarse woody debris, fine woody debris, and leaf litter, though these studies were not explicitly studying forest fuels (Whigham et al., 1991; Harmon et al., 1995; Busing et al., 2009; Bradford et al., 2012). Although wind disturbance can clearly increase woody fuels, it should also be noted that natural canopy gaps reduce leaf litter abundance, decreasing fuel availability and continuity for subsequent fires (O'Brien et al., 2008).

Fuels such as leaf litter, grass, and woody debris present on the forest floor are known to create fine-scale variation in fire behavior (Hiers et al., 2009; Mitchell et al., 2009; Thaxton and Platt, 2006; Loudermilk et al., 2012), including changes in radiant heat flux, fire intensity, rate of spread, and fire effects on vegetation recovery. Variation in fire intensity can in turn change the relative abundance of species and alter floristic composition during recovery (*e.g.*, Morrison, 2002; Wiggers et al., 2013). Determining the extent to which wind disturbance alters fire behavior is important for understanding how forests disturbed by wind and fire will recover from coupled disturbances. In this study, I examine how experimental wind disturbance can influence fuel characteristics and change aspects of fire combustion characteristics.

2.1.3 Research Questions and Hypotheses

I conducted a large-scale field experiment combining experimental wind disturbance with prescribed fire in a factorial design. I addressed the following research questions. (1) Does wind disturbance alter the forest fuel composition and distribution? (2) Do prescribed fire combustion characteristics differ between wind damaged and undamaged plots? I expected simulated wind gaps to increase the amount of fuel after the first year following disturbance. I also expected gaps to alter fuel composition such as an increase in woody fuels and herb-layer vegetation—particularly grasses. Conversely, I expected leaf litter mass to be lower due to decreased overstory inputs. Furthermore, I expected changes in spatial distribution of fuel loads across treatments. Finally, due to changes in fuel loading, composition, and aggregation, I hypothesized that fire radiation characteristics would be amplified in gaps, especially in areas of increased fuel load such as in tangles of downed tree crowns.

2.2 Methods

2.2.1 Study Site

The experiment was conducted at Piedmont National Wildlife Refuge (PNWR) in central Georgia. PNWR is composed of Piedmont forest burned approximately every three years, dominated by 80+ year old *Pinus taeda* trees with a mixed-hardwood sapling understory. For this experiment, I established six 1250 m^2 plots (Figure 2.1) in a forest stand that had received prescribed fires in 2004, 2006, and 2009 (Carl Schmidt, US Fish and Wildlife Service, personal communication). The selected plots had a standing tree ($>$ 10 cm dbh) basal area of 17 to 27 m^2 ha^{-1} and stand tree densities ranged from 140 to 570 stems ha^{-1}. Three plots were treated with simulated wind disturbance (Figure 2.1) and three were undamaged controls. In April 2013, one year following wind disturbance, all plots received a cool season prescribed fire.

2.2.2 Experimental Wind Disturbance and Fire

With a team of field helpers, I simulated wind damage gaps in three of the six plots (Figure 2.2) using static winching to manually pull down trees. Tension was applied to the target tree using nylon straps, a snatch block pulley, and a steel cable until the tree snapped or uprooted (for details see Peterson and Claassen, 2013). The winching gaps were designed to mimic a tornado gap by imposing realistic changes in forest structure and light levels. The largest trees were removed first until 80% of the basal area was removed. I winched the trees to fall northward—typical of tornado disturbance (Peterson, 2007), and winched between March and May—a time when significant tornado disturbance occurs in the area (Peterson, 2000). Though on the lower end of typical gap sizes created by moderate severity windstorms (*e.g.*, McNab et al., 2004), I chose to create 40 m diameter gaps (1250 m^2) as this was the maximum size possible with replication within the given size of the study area. Although I took

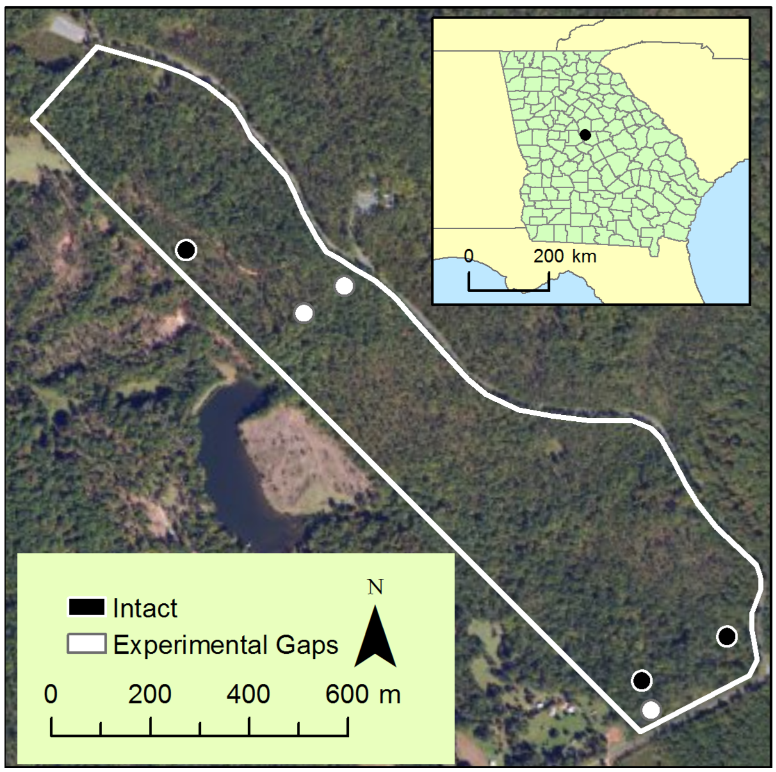

Figure 2.1: Map of study area within the Piedmont National Wildlife Refuge illustrating locations of six 1250 m^2 plots treated with experimental gaps (closed circles) or undamaged controls (open circles).

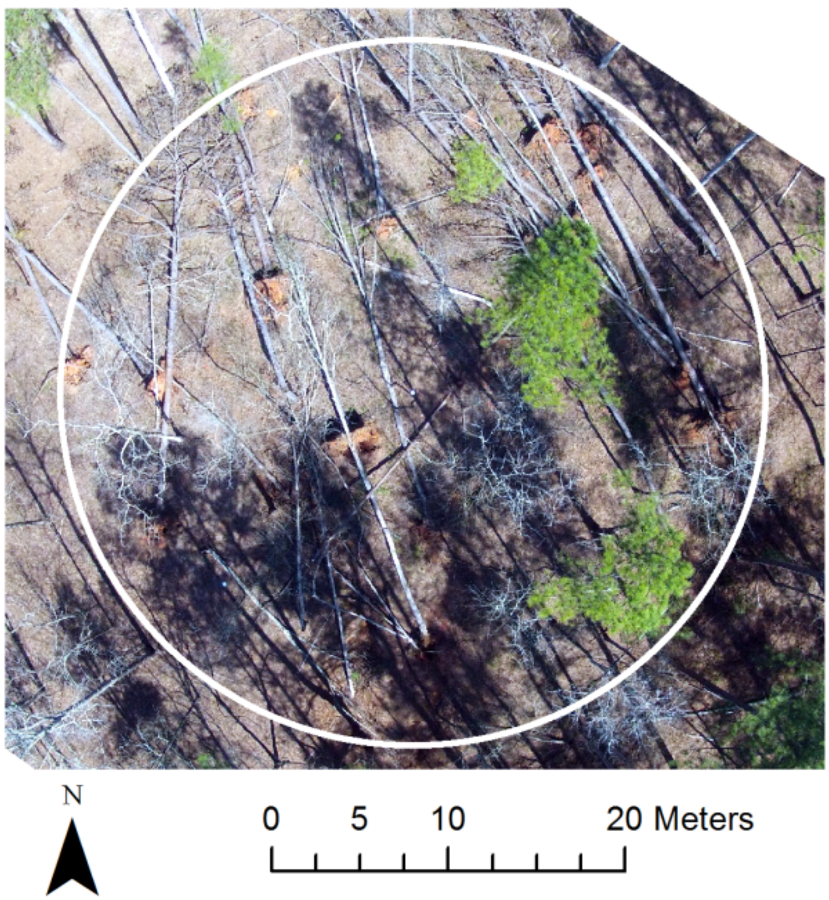

Figure 2.2: Aerial photograph of a plot that has received experimental wind damage. This plot is the northeastern most depicted in Figure 2.1. Photo courtesy of USDA Forest Service, Southern Research Station, Center for Forest Disturbance Science.

care to mimic many aspects of a natural windstorm, some events such as heavy rain and stripping of leaves by wind cannot be adequately simulated (Cooper-Ellis et al., 1999).

Approximately one year after winching, on 9 April 2013, the PNWR staff and US Forest Service volunteers implemented an experimental fire across the study area. Ambient air temperatures during the burn ranged from 26–27 °C; relative humidity decreased from 52–40% over the course of the fire. Flame lengths ranged from less than 0.5 m for backing fires to 2.5–3.5 m for heading fires.

2.2.3 Measuring Available Fuel and Residual Fuel

To examine how wind disturbance altered available fuel composition, I collected fuel samples from plots just prior to the prescribed burn. Within each plot, I sampled fuel from randomly placed 0.25 m^2 fuel sampling quadrats placed within each plot. I established 25 quadrats in each gap plot and 15 quadrats in each intact plot, because I expected more fuel variability in gap plots. Within each quadrat, I collected and sorted all leaf litter, grass, and cones, as well as woody debris, which was sorted according to fuel diameter—a proxy for drying time. The fuel classes included were 1-hour (0 – 0.6 cm), 10-hour (0.6 – 2.5), and 100-hour (2.5 – 7.6 cm, Fosberg, 1970). I included living vegetation < 0.6 cm in 1-hour fuels. I did not sample any living vegetation ≥ 0.6 cm (10-hour) or any woody debris > 7.6 cm (1000-hour) because they were not expected to combust in the prescribed fire. This expectation was supported from post-burn observations. The sampled fuel was oven-dried at 70 °C for 48 hours and weighed to the nearest 0.1 g. I measured residual fuels immediately following the prescribed burn in the same manner as pre-burn sampling in order to make inferences regarding the type and amount of fuel consumed.

2.2.4 Measuring Fire Radiation Characteristics

Measurements from dual-band radiometers allowed me to focus on differences in combustion characteristics at the scale of tree crowns. I report average and peak fire radiated flux density (FRFD, kW m^{-2}) and fire radiative energy density (FRED, kJ m^{-2}). FRFD is known to be linearly related to the rate of fuel consumption (Wooster et al., 2005; Freeborn et al., 2008), thus mean FRFD is linked to the mean rate of fuel consumption, peak FRFD is known to be linearly related to peak fuel consumption rate and Byram's fire intensity (W m^{-1}, Kremens et al., 2012), and FRED is known to be linearly related to fuel consumption (Wooster et al., 2005; Freeborn et al., 2008; Kremens et al., 2012). Each radiometer included two sensors with different band passes for which the ratio of outputs, through calibration against laboratory blackbody temperatures, determines FRFD (for analysis details see Kremens et al., 2010). FRFD is an average for the fractional area of the pixel that is above background levels (known as fire fractional area). FRFD measurements decline with height of deployment (because fire fractional area declines) and, thus, can only be compared among deployments that utilize the same sensor height. In contrast, time-integrated FRFD (*i.e.*, FRED) is not dependent on height of deployment as long as the integral spans the period from before fire arrival to the time at which radiation from the burned-over plot reaches an asymptote near background levels. The radiometers included a midwave infra-red (MW) and a longwave (LW) sensor. The MW sensor was built by Dexter Research (detector DR 2M) and has a calcium fluoride window with nominal bandpass of 0.15–12.5 μm and spectral transmission described by DC-6100-CaF2-U8. The LW sensor was built by Perkin Elmer (detector TPS334) and has a silica window with a nominal bandpass of 5–20 μm and spectral transmission described by DC-6188 5LWPSi - L1 (characterized by Dexter Research).

Specifically, the radiometer measurements allowed me to compare fire radiation characteristics within downed tree crowns in experimental gaps with radiation in both non-crown areas within experimental gaps and areas outside of gaps. Prior to burning, I deployed three radiometers in each plot (three gap and three intact plots). Each radiometer was mounted on 5.5 m posts to provide a nadir perspective with an approximate field of view of 47° (full angle) resulting in a field of view on the ground of approximately 18 m^2. In each intact plot, I suspended radiometers in randomly selected locations. In each gap plot, I suspended one radiometer over a randomly chosen downed tree crown and suspended two radiometers in randomly selected areas outside of a downed tree crown.

2.2.5 Statistical Analyses

Analysis of fuel data required special consideration because total fuel data was not normally distributed and required log-transformations in all tests of total fuel loading. However, analysis of individual fuel components (grasses, cones, etc.) required rank-based tests since these data contained many zeroes. To test whether winching increased total fuel, I used a one-tailed Welch t-test of log-transformed pre-burn total fuel data, as there was unequal sub-sampling in winched and control plots. To determine how winching altered pre-burn fuel composition, I used one-tailed Wilcoxon rank sum tests comparing amounts of individual fuel components in winched and control plots. To test whether more fuel was consumed in gap plots than in intact plots, I used two-way ANOVAs on the log-transformed total fuel data. I included treatment (gap, intact) and burn (before, after) as factors. A significant interaction would indicate differences in fuel consumption between treatments. Similarly, to evaluate whether consumption differed between various individual fuel components, I used two-way ANOVA followed by Tukey's HSD tests on ranked data because the fuel components data included many zeroes.

A simpler, more intuitive description of fuel composition (either before or after fire) is possible by adopting multivariate ordination techniques. While multivariate ordination is often used in ecology for the analysis of vegetation (McCune and Grace, 2002), it has also been adopted for other diverse purposes (*e.g.*, analysis of the microhabitats of fish, Grossman and Freeman, 1987). Multivariate ordination such as Principal Components Analysis (PCA) could be used to describe changes in fuel composition. This approach is analogous to familiar vegetation ordination, but abundances of fuel components (expressed as Mg ha^{-1}) are substituted for plant species abundances. To introduce this application, I performed PCA ordination of fuels before and after fires. I performed PCA using the **princomp** function for R version 3.0.0 (R Core Team, 2013). Fuel data was normalized using a z-transformation on each fuel type. The ordination was in two dimensions. After ordination, I calculated central ellipses representing the mean and standard deviation in 2-dimensional PCA space for each treatment combination.

To assess whether wind disturbance treatments or microsites (downed crown versus no-crown) had an effect on fire radiation characteristics, I used one-way ANOVAs to test for differences in average FRFD, peak FRFD, and FRED of each winching treatment and microsite combination, for a total of three levels: gap crowns, gap non-crowns, and intact non-crowns. The "crown" microsite was only located in gap plots and is represented by three replicates. The "non-crown" microsites were located in both gap and intact plots and are represented by four and seven replicates respectively, due to five radiometers failing to record data. I used Tukey's HSD tests to evaluate significant between treatment combinations.

2.2.6 Spatial Autocorrelation Analysis of Fuels

I measured the magnitude and significance of spatial autocorrelation or "clumping" of fuel loading using Moran's I analysis with the **spdep** package (Bivand, 2013) in R. I used total available fuels (excluding 100-hour fuels) and incorporated inverse distance weighting between fuel samples. To assess the range of spatial correlation and magnitude of spatial variability between treatments, I modeled the semivariance (spatial autocorrelation function) within treatments using Stanford Geostatistical Modeling Software (SGeMS v2.5b, Advanced Resources and Risk Technology, LLC, Stanford, CA, Remy et al., 2009). For each treatment, an isotropic exponential autocorrelation function (Goovaerts, 1997) was fit to the empirical semivariance using appropriate lag, nugget, sill, and range parameters (Table A.1). Semivariograms were created for three of the four time × treatment combinations (pre- and post-burn gap plots and post-burn intact plots), as no significant spatial autocorrelation was found in the pre-burn intact plots (see Moran's I in Results below).

2.3 Results

2.3.1 Effects of Wind Disturbance on Fuel Composition and Consumption

I found that total fuel loading was higher in gap plots than in intact plots (16.75 Mg ha^{-1} versus 14.15 Mg ha^{-1}, $t_{115.116} = 1.808$, $P = 0.037$). As the largest class of fuel (100-hour) showed no statistical or observational evidence of consumption, a characteristic of prescribed fires in the region, I omitted this fuel component in analyses of total fuels and included only the combustible fuels. Cones and 10-hour fuel also showed no significant consumption, but I included these fuels because both field observations as well as a consumption trend was evident (see below). When unburned fuels (100-hour) were excluded, the trend towards greater amount of fuel in the gap plots was not significant (14.51 Mg ha^{-1} versus 13.49 Mg ha^{-1}, $t_{107.830} = 0.880$, $P = 0.190$).

Although total available fuel did not differ between treatments, experimental gaps affected individual fuel components (Figure 2.3). Several fuel types were significantly higher in gap plots compared to intact plots, including grass ($W = 2067$, $P = 0.019$), 1-hour fuels (W = 2176, P = 0.004), and 100-hour fuels (W = 1943, P = 0.036). Woody fuel in the 10-hour class was marginally higher in gap plots compared to intact controls (W = 1983, P = 0.053). The amount of leaf litter and pine cones did not differ between gap and intact plots (W = 1525, P = 0.189 and W = 1714, P = 0.563, respectively).The prescribed fire consumed approximately 64% of the available fuel. Average available fuel decreased from 14.13 Mg ha^{-1} before the prescribed burn to 5.12 Mg ha^{-1} remaining after the burn ($F_{1,236}$ = 330.276, P << 0.001). However I did not detect a difference in overall fuel consumption between treatments ($F_{1,236}$ = 0.023, P = 0.880), and there was no treatment × burn interaction ($F_{1,236}$ = 0.904, P = 0.343), indicating that the overall pattern of fuel consumption did not differ between gap and intact plots.

Because the analysis of fuel totals can mask changes in individual fuel components, I also examined consumption patterns of component fuels. Several fuels showed a significant reduction after burning including leaf litter ($F_{1,236}$ = 521.003, P < 0.001), grass ($F_{1,236}$ = 120.839, P < 0.001), and 1-hour fuels ($F_{1,236}$ = 111.692, P < 0.001). It should be noted that grass was a small fraction of total fuel (1–2%). Other fuels showed no significant decrease after burning cones ($F_{1,236}$ = 0.551, P = 0.459), 10-hour ($F_{1,236}$ = 1.570, P = 0.211), or 100-hour fuels ($F_{1,236}$ = 0.846, P = 0.846. The two-way ANOVAs showed no significant interactions.

Using Tukey's HSD test, I found that although the amount of leaf litter was similar in gap and intact plots before the fire, leaf litter was lower in the gap plots after the fire (Figure 2.4A). This pattern indicates that more litter was consumed in the gap plots than in intact plots. Conversely, consumption of 1-hour fuels was higher in the intact plots (Figure 2.4D). These results indicate that leaf litter burned more completely in gap plots while 1-hour fuel burned more completely in intact plots.

The first two axes in the PCA explained 58.5% of the fitted variation in fuel abundances (37.6% and 20.9%, respectively). The two-axis ordination (Figure 2.5)

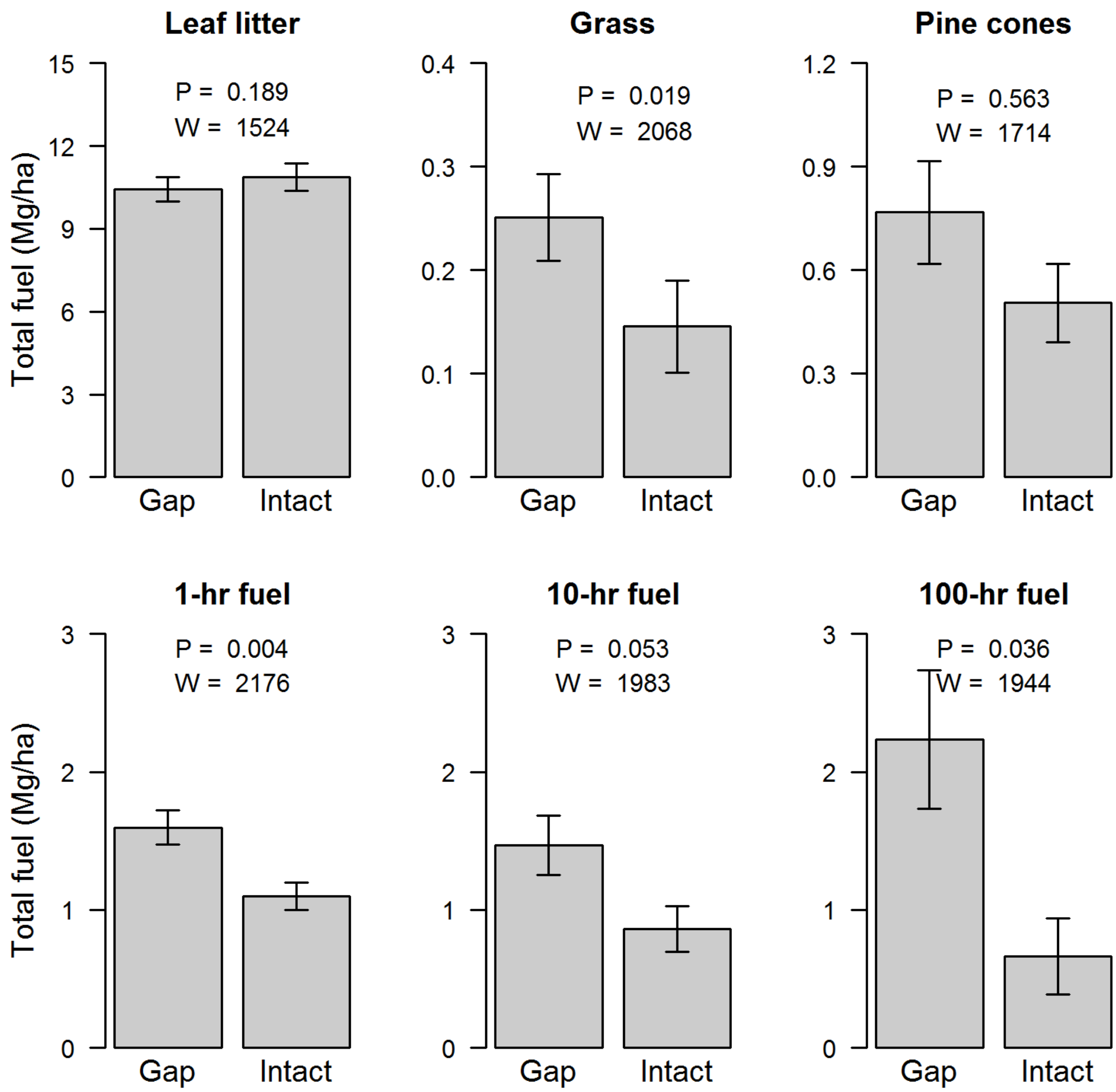

Figure 2.3: Mean mass of forest floor fuels following simulated tornado damage. P-values represent the result of one-tailed Mann–Whitney U-tests comparing fuel mass in experimental gap (G) and intact (I) plots. Error bars represent one standard deviation of the mean.

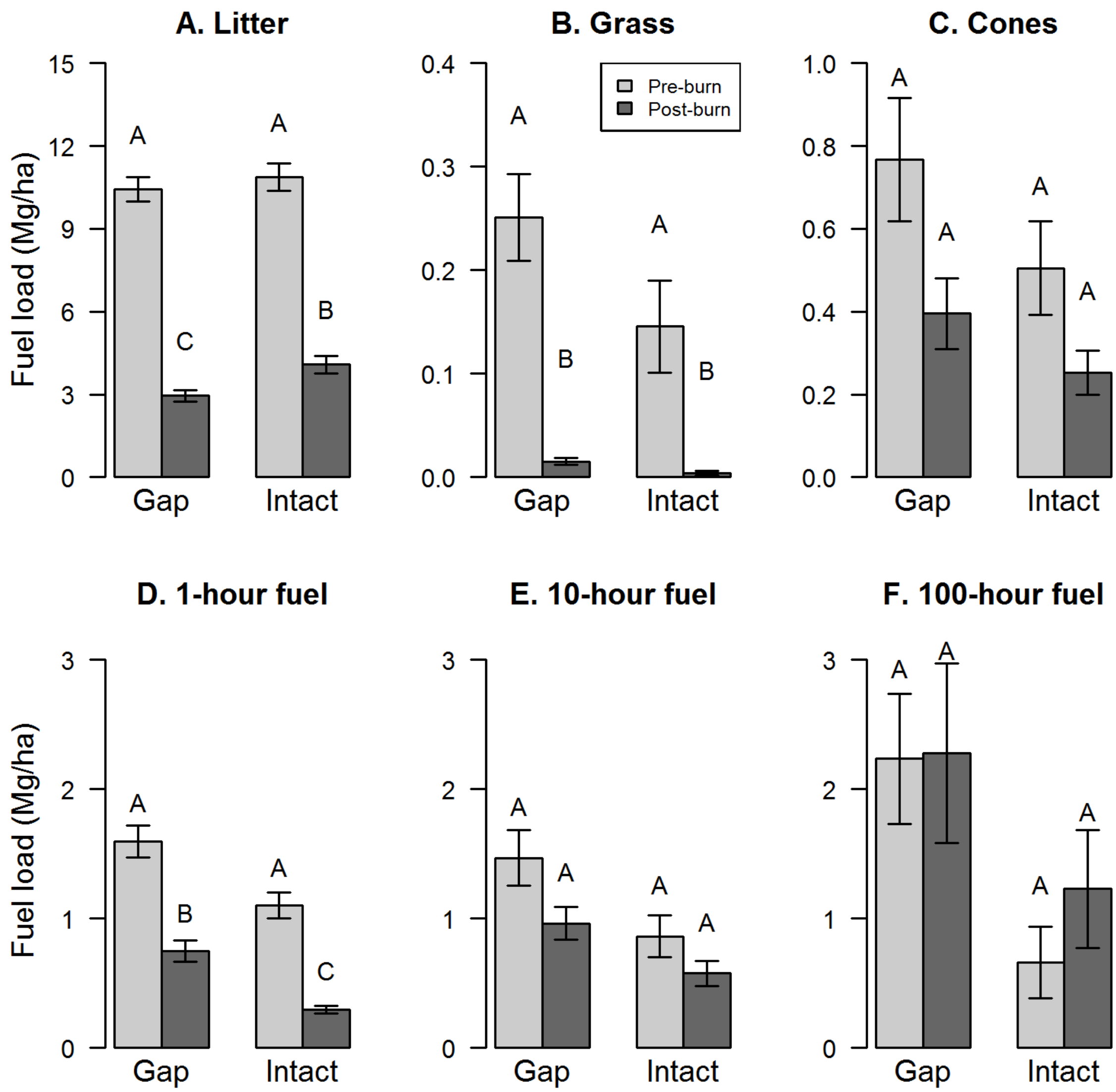

Figure 2.4: Mean mass of forest floor fuels comparing experimental gap (G) and intact (I) plots before and after burning. Within each graph, means sharing the same letter are not significantly different (Tukey's HSD, $P_{adj} < 0.05$.) Error bars represent one standard error of the mean.

gives an overview of overall changes in fuel composition, and plainly illustrates several important points. First, the large scatter present in pre-burn plots compared to post-burn plots demonstrates the reduction in fuel variability after fire in both treatments. Second, the larger scatter in gap plots both before and after fire relative to intact plots illustrates the greater variability of fuel composition in gap plots. Third, the pre-burn plots are shifted to the right along the x-axis relative to post-burn plots. Because this axis is strongly correlated to leaf litter and 1-hour fuels, this indicates that fine fuels such as litter and 1-hour fuels exhibited the greatest reduction during burning, and are likely responsible for fire continuity.

2.3.2 Spatial Structure of Fuel Loading

Fuel loadings showed significant spatial autocorrelation within the gap plots both before (Moran's I = 0.075, P = 0.002) and after burning (Moran's I = 0.076, P = 0.002). No significant spatial structure was found in intact plots before burning (Moran's I = 0.022, P = 0.183), but there was significant spatial structure in the post-burn intact plots (Moran's I = 0.313, P $<$ 0.001). Furthermore, Moran's I values for the post-burn control plots were closer to zero than any treatment plots, illustrating a more even distribution of fuel loads in control plots. The semivariance was smaller after the fire (post-burn treatments) simply because of the reduction in fuel loads after the fire. The range (distance) of spatial variability was similar (8–11 m) between the three treatments.

2.3.3 Fire Radiation Characteristics

In general, FRFD and FRED were greater in crown microsites and lowest in non-crown microsites in gap plots. Furthermore, intact plots generally showed intermediate levels of the three measured radiation characteristics (Figure 2.6). Mean FRFD (related to mean rate of fuel consumption; Wooster et al., 2005, Freeborn et al., 2008) differed

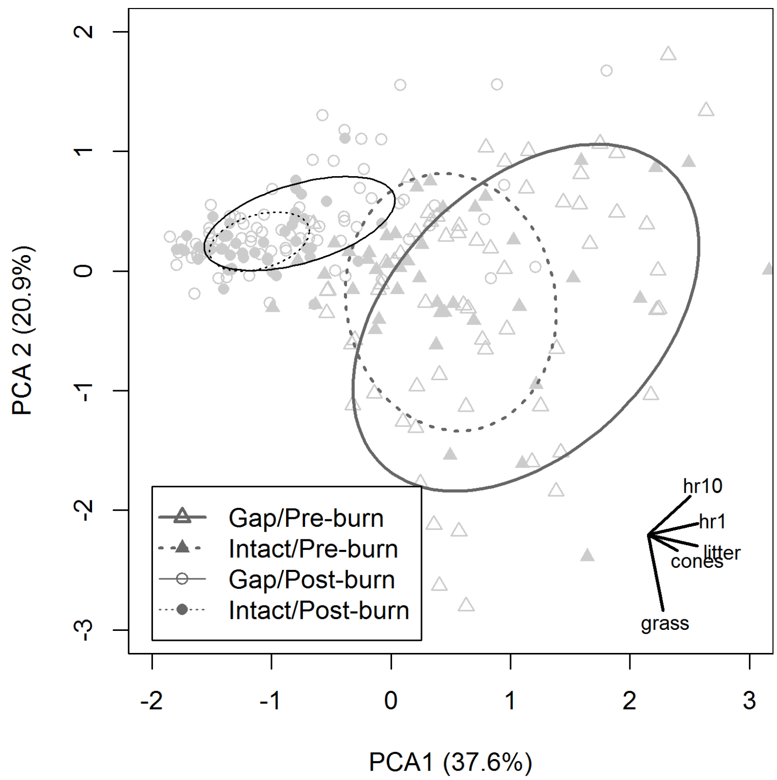

Figure 2.5: Principal Components Analysis ordination of fuel composition of experimental gap treatment and intact control plots before and after prescribed burning. Ellipses represent the standard deviation of the mean axis scores for each treatment combination. Inset arrows represent partial correlation vectors, which are proportional in length to the partial correlation of the associated fuel component with each axis.

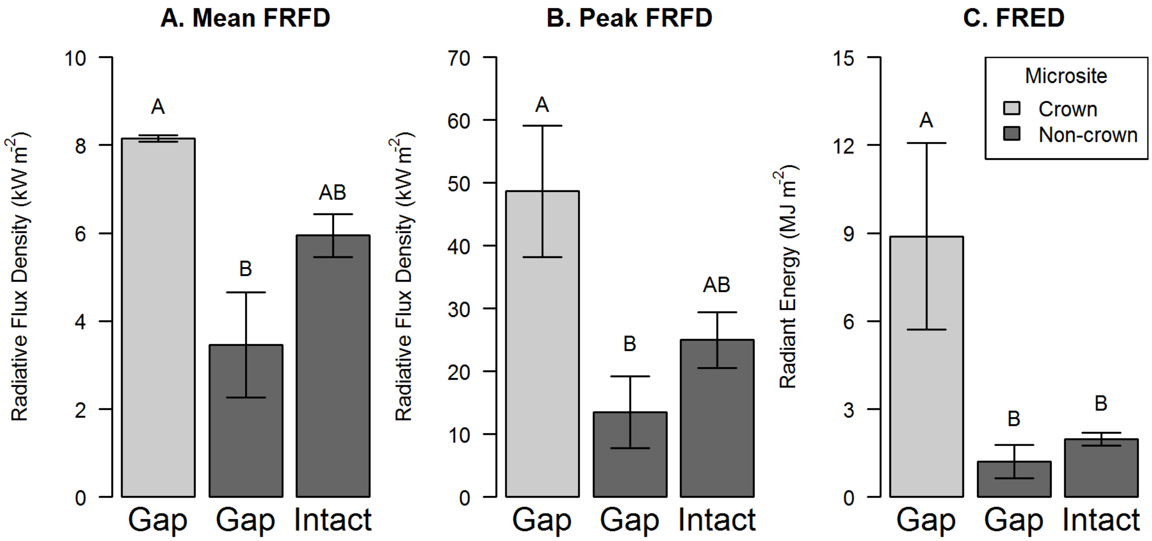

Figure 2.6: Measures of fire radiation characteristics including (A) mean fire radiative flux density (FRFD; kW m^{-2}), (B) peak fire radiative flux density (FRFD; kW m^{-2}), and (C) fire radiative energy density (FRED; MJ m^{-2}) in both gap and intact plots. Gap plots contain both crown and non-crown microsites. Error bars represent one standard error of the mean. Within each graph, means sharing the same letter are not significantly different (Tukey's HSD, $P_{adj} < 0.05$.)

significantly between treatment combinations ($F_{2,10} = 8.929$, $P = 0.006$). Mean FRFD was greatest in crown microsites of gap plots (8.2 kW m^{-2}), lowest in non-crown microsites of gap plots (3.5 kW m^{-2}), and intermediate in intact plots (5.9 kW m^{-2}; Figure 2.6A). Tukey's HSD test indicated that crown microsites had higher mean FRFD relative to non-crown microsites in gap plots ($P_{adj} = 0.005$), but intact plots were not significantly different from either crown or non-crown microsites in gap plots ($P_{adj} = 0.094$ and $P_{adj} = 0.058$, respectively).

In the same fashion, peak FRFD (proportional to peak fuel consumption rate and fire intensity; Kremens et al., 2012) differed significantly between treatment combinations ($F_{2,10} = 5.864$, $P = 0.021$). Peak FRFD was greatest in crown microsites of gap plots (48.6 kW m^{-2}), lowest in non-crown microsites of gap plots (13.5 kW m^{-2}), and intermediate in intact plots (24.9 kW m^{-2}; Figure 2.6B). Tukey's HSD test indicated that crown microsites had higher peak FRFD relative to non-crown microsites in gap plots ($P_{adj} = 0.019$), but intact plots were not significantly different from either crown or non-crown microsites in gap plots ($P_{adj} = 0.059$ and $P_{adj} = 0.436$, respectively).

Lastly, FRED (related to fuel consumption, Wooster et al., 2005; Freeborn et al., 2008; Kremens et al., 2012) differed significantly between treatment combinations ($F_{2,10} = 9.187$, $P = 0.005$). As with the other combustion characteristics, FRED was greatest in crown microsites of gap plots (8.9 MJ m^{-2}), lowest in non-crown microsites of gap plots (1.2 MJ m^{-2}), and intermediate in intact plots (2.0 MJ m^{-2}; Figure 2.6C). Tukey's HSD test indicated that crown microsites had higher FRED relative to both non-crown microsites in gap plots ($P_{adj} = 0.010$) and in intact plots ($P_{adj} = 0.007$). However, FRED did not differ significantly between non-crown gap plots and intact plots ($P_{adj} = 0.900$).

2.4 Discussion

The results of this study indicate that small-scale wind disturbance may alter aspects of gap-level fire characteristics. These results suggest that the mechanism by which wind disturbance alters fire combustion characteristics is more nuanced than a simple addition of fuel (*e.g.*, Myers and Van Lear, 1998). Plots receiving experimental wind disturbance had altered fuel composition and spatial distribution without a corresponding increase in available fuels compared to controls. These changes in fuel characteristics led to fires with higher energy released and altered fuel consumption patterns in treatment plots.

2.4.1 Fuel Loading, Composition, and Consumption

The increase in fuel loading caused by winching in this study was not surprising. Several studies have documented increased fuel loading after hurricane or windthrow (Whigham et al., 1991; Harmon et al., 1995; Busing et al., 2009; Bradford et al., 2012). In this study, simulated wind disturbance substantially increased coarse woody fuels such as 100-hour fuels (Figure 2.3). Although unmeasured, 1000-hour fuels (> 7.6 cm diameter) such as downed tree boles dramatically increased after winching (Figure 2.2).

Despite increases in 100- and 1000-hour fuels, the prescribed fire did not consume these large fuels, likely due to the low intensity of the prescribed fire. Among finer fuels, loading was similar between gap and intact plots. Thus, the observed changes in fire characteristics in gap plots cannot be explained by a simple increase in fuel loading. It appears that more subtle changes in fuel characteristics such as changes in the composition, consumption, and physical arrangement of the fuel may have led to changes in combustion patterns in gap plots. In this study, I found that loading of available fuels was unchanged from winching treatments. While the longest time lag fuels (100- and 1000-hour) were not consumed during this prescribed burn, these larger fuels could combust during a wildfire that occurred after sufficient drying such as during a drought (Fosberg, 1970). I hypothesize that in conditions which lead to combustion of larger fuels, the patterns shown here would be accentuated.

Although I found no differences in available fuel loading, the composition of fuel differed between simulated gap openings and the intact forest. Gap openings created by winching had increased representation of grasses, as well as increases in woody fuels (including 1- and 100-hour fuels and a marginal increase in 10-hour fuels; Figure 2.3). Analysis of residual fuels indicated that leaf litter was more thoroughly consumed in gaps while grasses and 1-hour fuels were more thoroughly consumed in intact plots (Figure 2.4). The PCA ordination comparing fuel composition of treated plots before and after experimental wind disturbance (Figure 2.5) illustrated several important changes in fuel characteristics such as differences in variability between gap and intact plots as well as changes in fuel composition before and after burning.

2.4.2 Spatial Structure of Fuel Loading

The spatial analysis of fuel loads illustrated how wind disturbance can create a more clumped distribution of fuel loadings across an area, even if fuel loads are similar. This discrepancy in spatial structure of fuel loads between treatments may explain differences in consumption of particular fuel types (*e.g.*, litter, grasses). More heterogeneous fuel loadings were likely created by the concentration of fuels in areas such as within downed tree crowns.

Fuels were spatially heterogeneous after burns in both gap and intact plots. This patchy burn structure has been found within similar southeastern ecosystems where fuels and fire behavior vary at very fine-scales (within just a few meters) and throughout the forest matrix with various disturbance patterns (Hiers et al., 2009; Loudermilk et al., 2012; Thaxton and Platt, 2006). The downed trees in gap plots created more spatial variability in consumption, however, than the intact forest, likely a product of less fuel continuity and fire spread potential. Ultimately, spatial connectivity of various fuel characteristics affects fire behavior and consumption patterns at various scales and is not necessarily driven by overall fuel loadings.

2.4.3 Combustion Characteristics

Closely linked to the spatial structure of fuels, I found that fire radiation characteristics were greatly altered in gap plots compared to intact plots. Each of the three measured radiation characteristics (mean FRFD, peak FRFD, and FRED) was higher within downed crowns in gap plots and consistently lower in gap plots outside of tree crowns. When comparing the non-crown portions of gap with intact plots, there were no significant differences though non-crown portions of gap plots had significantly lower measures of all three combustion characteristics. These results make clear that extreme fire behavior is localized within downed crowns where fuels are aggregated. Furthermore, I found consistent (though not significant) reductions in fire radiation in non-crown microsites of gap plots. These results suggest that although wind disturbance likely amplifies fire intensity within downed crowns, wind disturbance may lead to somewhat muted fire behavior outside of downed crowns. Thus, to understand how wind disturbance influences fire behavior, it is important to consider the spatial structure of fuels created by wind disturbance which can be influenced by factors such as forest density, wind disturbance severity, as well as the size and degree of overlap of downed tree crowns.

One criticism of this approach of measuring combustion characteristics using radiometers is that the measured radiative energy is that a small fraction of the total combustion energy density released from fire—the largest fraction actually coming from convective heat which is difficult to measure. An integrated heat budget (Kremens et al., 2012) and measurements of stationary (Wooster et al., 2005; Freeborn et al., 2008) and spreading flames (Kremens et al., 2012) suggests that radiation from flame fronts accounts for some fraction of total heat dissipation from combustion and that fraction is on the order of 15% as measured from the nadir perspective. Recent laboratory measurements suggest that fire radiated fraction varied from 8–15% as fuel moisture content varied from 25% to 0% (Smith et al., 2013). This is a large range that would not likely be encountered either within a given wildland fire or among fires. Differences among fuel types are also expected (Smith et al., 2013). Data from spreading fires in 8 × 8 m plots indicated that fire radiated fraction varied by a standard deviation of 3% among plots (Kremens et al., 2012) as litter moisture in these plots varied from 8–14% of dry weight.

For the experiment at PNWR, I was not able to measure fuel moisture before the prescribed fire for this experiment but several lines of reasoning suggest that the moisture content of consumed fuels was similar between gaps and intact stands and, thus fire radiated fraction can be assumed to be reasonably constant among gap and non-gap areas. First, the prescribed fire was applied to all plots under consistent weather on the same day and fuel composition varied modestly. Second, data from a related study (Chapter 3, herein) shows that the total biomass of the dominant seedlings (*Pinus taeda* and *Liquidambar styraciflua*) were relatively similar in gap (23.1 g m^{-2}) and intact plots (29.3 g m^{-2}) so differences in moisture of live fuels is not expected. Grass biomass was higher in gaps, but grasses were cured during these late dormant-season fires. Finally, intact stands had relatively low basal areas (basal area 17 to 27 m^2 ha^{-1}; mean canopy openness in intact plots was 16.6%), reducing potential differences in fuel drying rates between gaps, where increased wind and solar radiation would be expected. As such, I expect that any effect of variation in fuel moisture and, thus, radiated fraction, between gap and intact plots would be modest. If fuels were more moist in intact plots, the differences were not enough to obscure the results that in non-crown microsites of gap plots, all three descriptors of fire radiation were lower than in intact plots (Figure 2.6), supporting a conclusion that fuel consumption was also lower in non-crown gap plots than in intact plots.

Although most of the energy dissipated from flame fronts is from convection (Kremens et al., 2012), convection is difficult to measure even at a single point much less over wide areas as can be done for radiation. Given that radiative fraction can be expected to fall within reasonable bounds within a given fire and given that the instruments are sensitive to radiation from even low-intensity flame fronts (Kremens et al., 2012), it is justifiable to assume that dual-band radiometer measurements of FRFD are proportional to combustion rates, peak FRFD is proportional to fireline intensity, and FRED is proportional to fuel consumption.

One final caveat regarding the radiometer measurements should be noted. Due to the extremely high combustion rates within downed crowns in gap plots two of the radiometer sensors in those microsites saturated at the highest flux measurement of 59.1 MJ m^{-2}. However, because fire radiative flux density is recorded at a rate of 1 Hz, and because the period of saturation was brief, less than 0.02% of the readings from each of the two radiometers were saturated. Saturation in the radiometers leads to underestimates of measured fire radiation. Because the saturated radiometers measurements were in the downed crowns, the conclusion that measured fire combustion rates and totals were highest in those sites is conservative.

2.5 Conclusions and Management Implications

This research further supports the concept of the "ecology of fuels" (Mitchell et al., 2009), where understanding fire effects within a system requires understanding of how fuels link fire behavior and vegetation response. This study demonstrates how relatively small areas of downed trees create highly heterogeneous fuels and increased fire radiation and (by inference) fire intensity and fuel consumption in localized areas. Because the intensity of fire is linked to plant mortality at both small and large spatial scales (*e.g.*, Wiggers et al., 2013; Keeley, 2009, respectively), the largest ecological effects of fire on changes in recruitment patterns may be in localized areas of overstory disturbance, where downed trees created patches of higher than average intensity and consumption. In this study, wind disturbance altered several fire radiation characteristics in localized areas. However, because litter input could be reduced following the removal of trees from the canopy, (O'Brien et al., 2008), subsequent fires in these plots are expected to be less intense due to lower fuel continuity. Thus the interaction between wind and fire depends on the both the spatial distribution, order, and the timing of disturbances.

This study sheds light on the mechanisms of interaction between two common forest disturbances—wind disturbance and prescribed fire. Like more extreme disturbances, forest gap-level wind disturbance can interact synergistically with fire to create the potential for more intense fires than possible without prior wind disturbance. The observed interaction between wind disturbance and fire is more complex than a simple addition of fuel as has been hypothesized in previous research. Rather, wind disturbance can increase fire intensity and heterogeneity through changes in fuel composition, consumption, and spatial distribution.

Several temporal and spatial aspects of the wind–fire interaction warrant further exploration. In this study, wind disturbance influenced the combustion characteristics of a prescribed fire one year after the experimental wind disturbance. However, this interaction could change if the time between disturbances increases and processes such as fuel decomposition and deposition alter fuel composition further. Moreover, because vegetation recovery can depend on the type and severity of disturbance, plant communities may also differ between intact plots and gap plots, especially around areas with extreme fire behavior such as downed crowns. Research addressing this question is presented in a parallel study in Chapter 3. In some cases, using a prescribed fire following a wind disturbance may be an opportunity for managers to favor specialist rather than generalist plant communities compared to salvage logging after wind disturbance (Cannon and Brewer, 2013; Brewer et al., 2012). For example, Cannon and Brewer (2013) describe how utilizing prescribed fire following wind disturbance may help restore dwindling upland oak communities in Mississippi. With a better understanding of how disturbances interactively affect forest recovery, managers can make more informed decisions on how to manage wind-disturbed forests.

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Chapter 3

Interactions Between Wind and Fire Disturbance in Forests: Competing Amplifying and Buffering Effects[1]

[1]Cannon, J.B., and C.J. Peterson. To be submitted to *Forest Ecology and Management*

Abstract

Recent studies of ecological disturbance highlight the profound impact that compounded perturbations can have on communities. Wind damage and prescribed fire are common forest disturbances and have important ecological effects. One of the most well studied mechanisms by which forest wind damage and fire interact is that wind damage increases flammable fuels, leading to intense fire and dramatic ecological change. Such striking amplifying interactions are often the focus of studies of compounded disturbance. However, the extent to which wind and fire disturbances may interact in a way that buffers, or reduces, the magnitude of ecological change has been less well studied. In this study, I winched trees to simulate wind damage in experimental plots and crossed this treatment with prescribed fire. This design allowed me to examine how multiple measures of forest regeneration respond to combinations of disturbance by wind damage and prescribed fire. I also tested for evidence of two specific mechanisms of disturbance interaction that are expected to buffer the cumulative ecological impact. Overall, treatment combinations of winching and burning produced interactive effects on sapling structure, composition, and richness. However, individual vegetation strata (seedlings versus saplings), and individual species responded differently to disturbance combinations depending on factors such as size or life history characteristics. Significant interactions included a combination of amplifying effects (*e.g.*, dramatic growth and establishment of *Rhus copallinum*) as well as buffering effects (*e.g.*, buffered changes in abundance and biomass of *Acer rubrum*). The results of this study highlight the need for a mechanistic understanding of disturbance interactions that accounts for the variable responses of species to disturbance. Such variable responses may lead to a heterogeneous mixture of amplifying and buffering effects following compounded disturbances.

Index words: amplifying effects, antagonism, buffering effects, compounded disturbance, prescribed fire, synergism, wind damage

3.1 Introduction

Disturbances are an important driver of ecological processes in communities, and recent disturbance studies highlight the profound impact that compounded disturbances can have on ecological communities, particularly when ecosystems are affected by multiple disturbances in rapid succession. Current theory predicts that when ecosystems are subjected to multiple disturbances, unanticipated "ecological surprises" such as non-linear changes in species composition may occur (Paine et al., 1998; Frelich and Reich, 1999; Scheffer et al., 2001). Paine et al. (1998) suggest that the ecological effect of disturbances in rapid succession may be multiplicative rather than additive, leading to drastic changes in ecosystem structure, composition, or diversity. For example, five years following a severe blowdown in a subalpine forest in Colorado, an intense fire followed and shifted composition from mixed-conifer forests to a forest dominated by trembling aspen (*Populus tremuloides*, Buma and Wessman, 2011). Unlike stand-replacing wildfires, many types of disturbances are neither rare nor catastrophic, and the interactions among these common disturbances remain poorly understood (Turner, 2010).

In this study, I focus on the potential for interactions between two disturbances common to eastern U.S. forests—wind damage and fire. Forest disturbance from wind damage is widespread, affecting an estimated 1.65 million ha of forest annually in the U.S. (Dale et al., 2001), and it can have profound impacts on patterns of regeneration (Peterson and Pickett, 1995), carbon cycling (Chambers et al., 2007; Dahal et al., 2014), and maintenance of tree and herb diversity (Beatty, 1984; Ulanova, 2000). Likewise, prescribed fire is a commonly used forest management tool in both eastern and western U.S. forests with 3.8 million ha treated in 2011 (Melvin, 2012). Prescribed fires are used to manage wildlife resources (*e.g.*, Main and Richardson, 2002), rare ecosystems (*e.g.*, Glitzenstein et al., 1995), and to reduce wildfire hazard (*e.g.*, Agee and Skinner, 2005; Addington et al., 2015).

3.1.1 Disturbance Interactions between Wind Damage and Fire

Fuels mediate one of the most well studied mechanisms by which wind and fire disturbances interact. Myers and Van Lear (1998) hypothesized that hurricane damage to forests can considerably increase fuel loading and lead to an increased probability or severity of a subsequent fire. Long-term retrospective studies have confirmed that historically severe wildfires have often followed severe hurricanes (Liu et al., 2008), and they have even found evidence that intense post-hurricane wildfire can delay forest regeneration, based on pollen record data (Urquhart, 2009). Kulakowski and Veblen (2007) documented that subalpine forest stands in Colorado that experienced a wind event in 1997 burned more severely than other stands during a 2002 wildfire. Reconstruction of forest disturbances to old growth forests in New Hampshire during the period from 1635 to 1938 revealed several blowdown and fire events (Foster, 1988). Foster documents Foster (1988) three cases where wildfires followed severe hurricane or windstorms (wildfires occurred 2, 15, or 30 years after storms). Each of these examples point toward wind disturbance having a synergistic or "amplifying" effect on subsequent fires.

It should be noted that although wind can lead to catastrophic fires, the linkage is not inevitable. Other studies reconstructing forest disturbances have found no such co-occurrence between wind damage and severe fires. Oliver and Stephens (1977) found evidence of two hurricanes impacting forests in Massachusetts; although they found evidence of charcoal, they did not report catastrophic forest fires. In a reconstruction of disturbance to montane forests in North Carolina, Lorimer (1980) found evidence for several sizable blowdowns but no evidence of damage from fire. Busby et al. (2008) reconstructed disturbance history in coastal forests of Massachusetts and found little evidence of fire despite frequent impacts from hurricanes.

Synergistic interactions between disturbances are not inevitable, yet the current paradigm for compounded disturbances focuses mostly on amplifying interactions between disturbances (Paine et al., 1998; Frelich and Reich, 1999; Scheffer et al., 2001). Due to the hazardous nature of extreme wildfires, it is not surprising that research on wind–fire interaction mechanisms has such an emphasis. Although amplifying effects between disturbances may be striking, some disturbance studies may also interact in an antagonistic or "buffering" manner. In a meta-analysis of 57 studies of compounded stressors on marine animals, Darling and Côté (2008) found that across studies, ecological responses to compounded stressors in experimental marine systems can vary from those that are additive to non-additive (amplifying or buffering) effects. In forest disturbances, mechanisms where one disturbance decreases the intensity or severity of a subsequent disturbance (buffering effects) may prove to be common if examined explicitly. For example, although mountain pine beetle outbreaks are generally thought to increase the severity of wildfires (Amman and Schmitz, 1988), beetle disturbance can also reduce the severity of active crown fires in the short term by thinning tree canopy density (Simard et al., 2011). Likewise, investigation of responses to combinations of wind damage and fire may reveal interactions that have buffering rather than amplifying effects.

3.1.2 Potential Buffering Effects of Wind–Fire Interactions

Studies explicitly investigating potential buffering effects (or antagonisms) of wind–fire interactions are sparse. Although catastrophic windthrow is linked to severe wildfire in historical studies (*e.g.*, Urquhart, 2009), this interaction may differ when wind damage is followed by low-intensity prescribed fire. Although wind damage causes increases in large woody debris (Busing et al., 2009), these larger logs and branches are often not available for combustion owing to their size, as well as cooler temperatures and other constraints of cool-season prescribed fires (Cannon et al., 2014). Large fuels produced by wind damage have the potential to disrupt fuel continuity and decrease prescribed fire severity or extent. Second, considering only available small-diameter fuels, wind damage can create patchy fuel conditions without an actual increase in available fuels (Chapter 2, herein, Cannon et al., 2014). Although fuel loadings increase in some areas following wind damage, fuel loads may decrease in other areas, potentially disrupting fuel continuity (Cannon et al., 2014). Thus, wind damage has the potential to both increase fire intensity in some areas and disrupt fuel continuity in others suggesting that a mosaic of amplifying and buffering effects likely characterizes wind–prescribed fire interactions. Furthermore, individual species are expected to respond individualistically to wind damage, fire, or a combination of disturbance according to species-specific life history traits and structural characteristics. Thus, vegetation responses may consist of a heterogeneous mix of amplifying and buffering effects, even when overall compositional change after disturbance is amplifying.

Apart from interactions involving fuel, other mechanisms for wind–fire interactions remain unclear. In this study, I also test how wind damage and fire may produce buffering effects through other mechanisms—one involving treefall mound microsites, and a second involving resprouting. First, one prominent feature of forested areas following blowdown is the presence of large tip-up mounds formed when trees are uprooted. Mound microsites are elevated above the intact forest floor and often have a distinct microclimate and vegetation (Beatty, 1984; Ulanova, 2000; Peterson et al., 1990). The micro-elevation of plants on mounds can serve as refugia from herbivores (Krueger and Peterson, 2006). Similarly, because radiative energy from fire decreases dramatically with height above the flame plume (Cruz et al., 2011), mound microsites may also protect established plants from prescribed fire—an example of a buffering effect. Second, prescribed fire frequently girdles or "top-kills" the above ground portions of many hardwoods, but a number of hardwood species can recover rapidly following fire through basal sprouting, made possible by utilizing belowground carbohydrate reserves (Hodgkins, 1958; Robertson and Ostertag, 2009). Sprouting patterns after fire may differ when prescribed fire is preceded by a canopy-opening disturbance such as windthrow. Increased light availability, for example, may allow rapid resprouting and faster recovery and increasing resilience following fire—another potential buffering effect.

3.1.3 Objectives and Hypotheses

In this study, I winched trees to simulate wind damage in experimental plots and crossed this treatment with prescribed fire. This design allowed me to examine how forest regeneration responds to combinations of disturbance by wind damage and prescribed fire. I examined several measures of vegetation structure, composition, and species richness to evaluate whether the responses of vegetation characteristics to disturbance tends to show evidence of amplifying effects, buffering effects, or a combination of effects. Second, I evaluated evidence for two specific mechanisms of wind–fire interactions, testing whether (1) seedlings established on mounds are less vulnerable to fire, and (2) whether basal resprouting after fire is more rapid when burning is preceded by wind damage.

3.2 Methods

3.2.1 Study Site

This experiment was conducted at Piedmont National Wildlife Refuge (PNWR) in central Georgia. PNWR is composed of Piedmont forest burned approximately every three years, dominated by 80+ year old *Pinus taeda* trees (70% of basal area) with a mixed-hardwood sapling understory consisting of *Liquidambar styraciflua* and *Acer rubrum* (making up over 70% of the sapling understory stems). The seedling layer (stems < 1.37 m) is dominated by *Pinus taeda*, which made up over 50% of woody seedlings. For this experiment, I established twelve 1250 m^2 plots (Figure 3.1) in a forest stand that previously received prescribed fires in 2004, 2006, and 2009 (Carl Schmidt, US Fish and Wildlife Service, personal communication). The selected plots had a standing tree (> 5 cm dbh) basal area of 17 to 34 m^2 ha^{-1} and stand tree densities ranged from 130 to 580 stems ha^{-1}.

In 2012, six of the twelve plots were treated with simulated wind disturbance (leaving six as unwinched controls). One year later, the winching treatments were crossed with a cool season prescribed fire—half in each of the simulated wind disturbance treatments. This resulted in a 2 × 2 factorial design with four combinations of simulated wind damage and fire: control plots, winch only plots, burn only plots, and winch+burn plots, each with three replicates (Figure 3.1).

3.2.2 Experimental Winching and Fire

In spring 2012, with a team of field helpers, I simulated wind damage in six of the twelve plots (Figure 3.1 and Figure 3.2) using static winching to manually pull down trees. Briefly, tension was applied to the target tree using nylon straps, a snatch block pulley, and a steel cable until the tree snapped or uprooted (for details see Cannon et al., 2014, 2015). The winching gaps were designed to mimic a severe tornado gap by imposing realistic changes in forest structure and light levels. The largest trees were removed first until 80% of the basal area was removed. I winched the trees to fall northward—typical of tornado disturbance (Peterson, 2007), and winched between March and May—a time when significant tornado disturbance occurs in the area (Peterson, 2000). Though on the lower end of typical gap sizes created by moderate severity windstorms (*e.g.*, McNab et al., 2004), I chose to create 40 m diameter gaps (1250 m^2) as this was the maximum size possible with replication within the given size of the study area. Although I took care to mimic many aspects of a natural

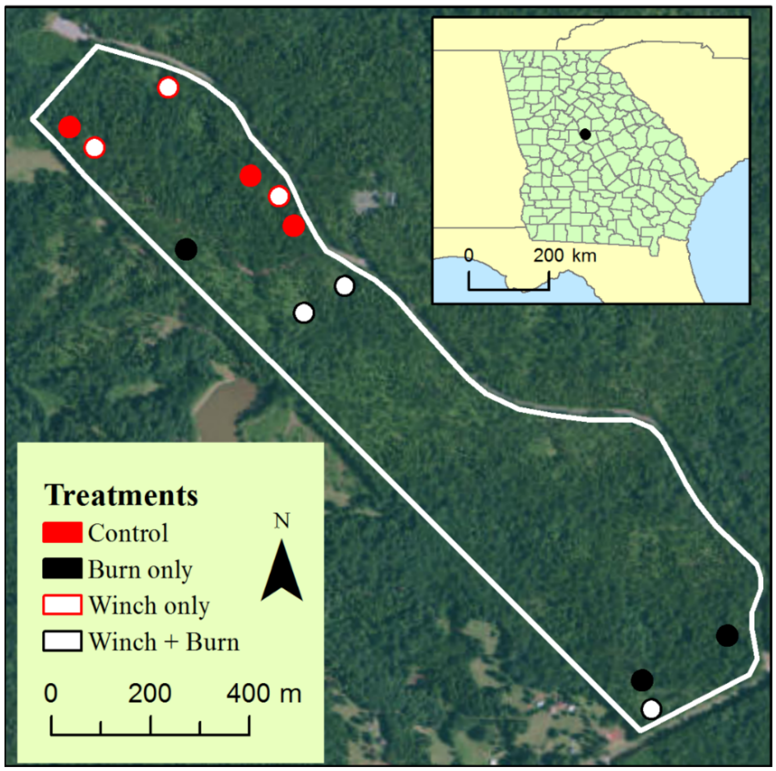

Figure 3.1: Map of study area within the Piedmont National Wildlife Refuge illustrating locations of twelve 1250 m^2 plots treated with winching (open circles) or undamaged controls (closed circles). Color of plots represents whether plots were burned (black circles) or unburned (red circles)

windstorm, some natural windstorm effects such as heavy rain and stripping of leaves by wind cannot be adequately simulated (Cooper-Ellis et al., 1999).

Approximately one year after winching, on 9 April 2013, the PNWR staff and US Forest Service volunteers implemented an experimental fire in half of the study plots (Figure 3.2). Ambient air temperatures during the burn ranged from 26–27 °C; relative humidity decreased from 52–40% over the course of the fire. Flame lengths ranged from less than 0.5 m for backing fires to 2.5–3.5 m for heading fires. Further details on fuel conditions and fire characteristics can be found in Chapter 2, herein, and Cannon et al. (2014).

3.2.3 Vegetation Sampling

Within each of the twelve 1250 m^2 plots, I established smaller vegetation plots to sample sapling and seedling composition. I established eight 9-m^2 sapling quadrats at random locations within each plot prior to winching, for a total of 96 sapling quadrats. In each sapling plot, I tagged and monitored each living woody plant ($\geq$ 1.37 m), identified it to species, and measured the height, diameter at breast height (dbh), and diameter at root collar (drc). Saplings were monitored from 2011–2014, and thus included a pre-disturbance survey (2011), a survey between winching and fire disturbances (2012), and two post-fire surveys (2013–2014). Similarly, I established four 1-m^2 seedling quadrats within each plot. In seedling plots, I tagged and identified all woody vegetation $<$ 1.37 m to species and measured plant height. Seedlings were monitored from 2011–2013, and thus included a pre-disturbance survey (2011), a survey between winching and fire disturbances (2012), and one post-fire survey (2013). Each seedling quadrat was nested within one of the sapling quadrats for a total of 48 seedling quadrats. The vegetation survey information was used to create a database of 1173 saplings and 1234 seedlings that were present in plots during at

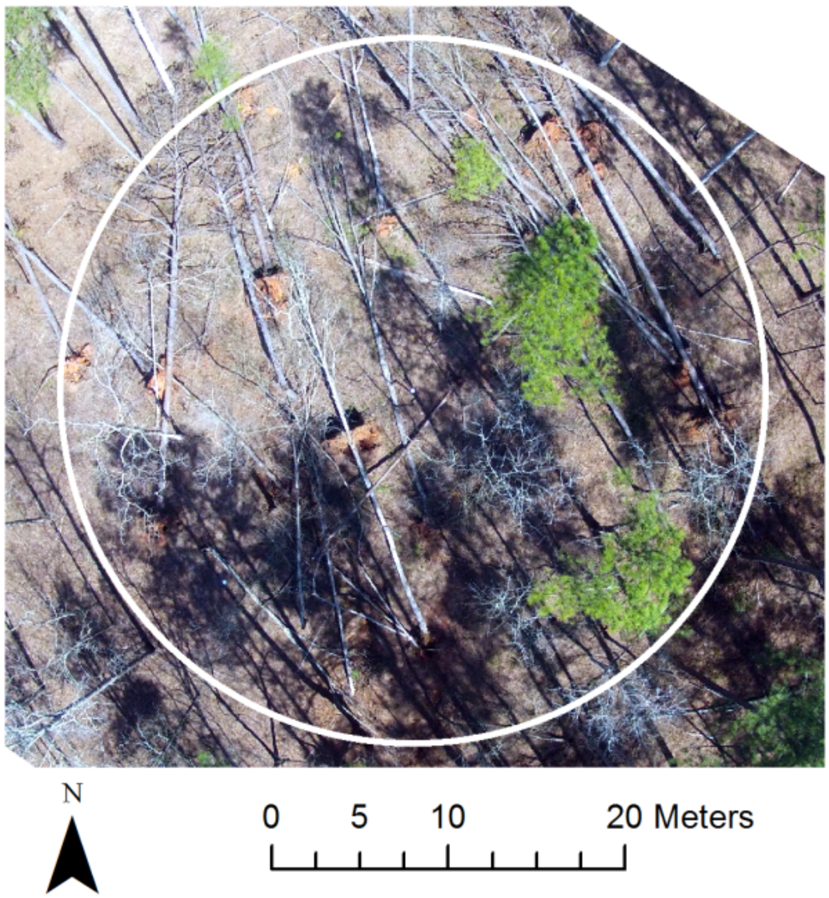

Figure 3.2: Aerial photograph of a plot that has received experimental wind gaps. This plot is the northern most winch+burn plot depicted in Figure 3.1. Photo courtesy of USDA Forest Service, Southern Research Station, Center for Forest Disturbance Science.

least one sampling period, which was used to calculate changes in vegetation density, structure, and composition over the course of the study.

In order to examine changes in plant density as well as biomass, I derived allometric equations for 3 major sapling species (*Liquidambar styraciflua*, *Acer rubrum*, and *Rhus copallinum*) and 2 major seedling species across the size ranges exhibited at the site (*Pinus taeda*, and *Liquidambar styraciflua*). For saplings, allometry was based on height, dbh, and drc; for seedlings, allometry was based on height only. I estimated biomass of the remaining species of saplings and seedlings by deriving allometric parameters from data pooled from the dominant species (See Appendix B for complete details and allometric parameters). Allometric equations were used to estimate the biomass of individual saplings and seedlings over the course of the study in order to complement measures of vegetation composition and structure.

In addition to the sampling above which focuses on exploring interactive effects on overall vegetation structure, composition, and richness, I also collected data to test for evidence of two specific buffering mechanisms. In order to test whether seedlings perched on tip-up mounds following winching were less vulnerable to mortality by fire, I surveyed woody vegetation established on tip-up mounds following winching disturbance in fall 2013. The survey included 8 tip-up mounds within burned plots and 14 tip-up mounds within unburned plots for a total of 153 seedlings on mounds in burned plots and 94 seedlings on mounds in unburned plots. On each mound, I tagged all seedlings, measured seedling height, and seedling elevation from ground level. Following the April 2013 fire, I re-surveyed tagged vegetation to note survival or mortality from fire. Data on survival of seedlings perched on mounds was combined with seedling survival data in vegetation quadrats away from mounds in order to contrast patterns of mortality on tip-up mounds with "intact" areas. The seedling data gathered from winched plots (described above) was used for this purpose. Seedlings monitored from intact areas consisted of 176 seedlings from burned areas and 239 seedlings from unburned areas.

I also explored a second potential buffering mechanism to determine whether basal sprouting from fire-damaged saplings differed between burned-only plots and winch+burn plots. To test this hypothesis, I measured incidence of basal sprouting from fire-damaged saplings in the year following winching (2013) for saplings present prior to the prescribed fire ($n = 299$). For each fire-damaged sapling, I noted the number of basal sprouts (if any) occurring at the base of each sapling, as well as the height of each sprout, allowing the comparison of sprouting patterns from fire-damaged saplings in burn-only plots and winch+burn plots.

3.2.4 Statistical Analyses

This study takes two approaches to explore the nature of disturbance interactions between wind damage and fire. In the first approach, I use ordination and multi- and univariate analysis of variance (MANOVA and ANOVA) techniques to examine overall changes in several vegetation community parameters such as structure, composition, and diversity to determine whether there is statistical evidence for interactive effects, and use univariate tests to determine whether specific vegetation responses show evidence of amplifying or buffering effects. In the second approach, I test for evidence of specific interaction mechanisms to evaluate evidence for buffering effects.

3.2.5 Relative Occurrence of Amplifying and Buffering Effects

In order to explore whether winching and burning interactively changed overall vegetation composition, I visualized vegetation composition for seedlings and saplings separately using ordination by Non-metric multi-dimensional scaling (NMS). I used the vegetation survey data to build species by vegetation plot matrices for each year surveyed. The species matrices for saplings consisted of the estimated biomass of 27 species for 96 vegetation plots over 4 years (resulting in 384 composition points in ordination space). To create the ordination I used the **metaMDS** function in the **vegan** package in R. I applied a $\log(x + 1)$ transformation to sapling biomasses to examine relative changes in recruitment and biomass over time. Because sapling biomasses were zero-inflated, I added 1 to the total biomass of each species to each vegetation plot to allow calculation of Bray–Curtis distances between each sample. I used NMS ordination to reduce dimensionality to two axes, and ordination stress was minimized using 200 random starts. I averaged NMS axis scores for each treatment and year combination. To compare the overall magnitude of community change in the four treatment combinations, I measured the Euclidean distance in ordination space between the 2011 and 2014 points for each treatment. I repeated the above steps to create an NMS ordination for seedlings. The species matrices for seedlings consisted of the biomass of 21 species for 48 vegetation plots over 3 years (resulting in 144 points plotted in ordination space). I averaged NMS ordination axis scores for seedlings by treatment and year combinations and measured Euclidean distances in ordination space between 2011 and 2013 points for each treatment.

To evaluate whether winching and burning exhibited interactive (winch $\times$ burn) effects on vegetation structure, composition, and diversity, I created a dataset of changes in vegetation structure, composition, and diversity for both saplings and seedlings. Response variables are listed in Table 3.1. The data set included changes in vegetation characteristics from each sapling or seedling quadrat including structural characteristics (Δ density, Δ biomass, Δ mean vegetation height, and survival after fire), composition characteristics (Δ density and Δ biomass of dominant species, and Δ density and Δ biomass of all other species), and a measure of diversity (Δ species richness). I used multivariate analysis of variance (MANOVA) to test for significant winch $\times$ burn interactions among sapling structure or composition variables separately, and used analysis of variance (ANOVA) to test for significant winch $\times$ burn interaction effects on changes in sapling richness. I repeated parallel analyses for seedlings. The vegetation data came from 96 sapling plots and 48 seedlings plots from the four treatment combinations. The data contained changes in response variable (Table 3.1) from the start and end-points of observation (2011–2014 for saplings, and 2011–2013 for seedlings). For saplings, the dominant species included were *Liquidambar styraciflua*, *Acer rubrum*, and *Rhus copallinum*. For seedlings, the dominant species included were *Pinus taeda*, *Liquidambar styraciflua*, and *Acer rubrum*, as these were the dominant species from the study. Table 3.1 below contains a summary of the variables used in each analysis. Where indicated in Table 3.1, data from start and end points were $\log(x + 1)$ transformed before calculating differences in order to examine relative changes and more accurately model relative changes in growth for each variable.

Table 3.1: Vegetation response variables included in MANOVA and ANOVA analyses

Vegetation Characteristic	Saplings (2011–2014)	Seedlings (2011–2013)
Structure	Δlog total sapling density (m^{-2})	Δlog total seedling density (m^{-2})
	Δlog total sapling biomass (kg m^{-2})	Δlog total seedling biomass (g m^{-2})
	Δ log mean sapling height (m)	Δlog mean seedling height (mm)
	Sapling survival after fire (%)	Seedling survival after fire (%)
Composition	Δlog sapling density by species (kg m^{-2})	Δlog seedling density by species (g m^{-2})
	L. styraciflua	*P. taeda*
	A. rubrum	*L. styraciflua*
	R. copallinum	*A. rubrum*
	All other saplings	All other seedlings
	Δlog sapling biomass by species (kg m^{-2})	Δlog seedling biomass by species (g m^{-2})
	L. styraciflua	*P. taeda*
	A. rubrum	*L. styraciflua*
	R. copallinum	*A. rubrum*
	All other saplings	All other seedlings
Richness	Δsapling richness (m^{-2})	Δseedling richness (m^{-2})

For each MANOVA or ANOVA with a significant winch $\times$ burn interaction, I classified the interaction coefficient for each individual response variable as either amplifying or buffering to quantify the relative occurrence of each interaction type. In the case of wind followed by fire, an interaction between winching and fire implies that the presence of winching alters the effect of fire. Thus, I classified amplifying effects as those where the additional effect of the interaction affected the response variable in the same direction as the burn—amplifying the burning effect. To illustrate, if burning reduced biomass (*i.e.*, negative burn coefficient), and winching amplified this effect (*i.e.*, negative interaction coefficient), the burn and interaction coefficients are in the same direction, so amplification occurred. In ANOVA terminology, amplification occurs when the interaction coefficient is the same sign as the burn coefficient. Conversely, buffering effects are those where the additional effect of the interaction is opposite of the effect of burning. With respect to ANOVA coefficients, buffering occurs when the interaction coefficient has the opposite sign as the burning coefficient.

The previous analyses revealed that sapling structure, composition, and richness were each interactively effected by winching and burning. In order to determine which individual responses were driving interactive effects, I used univariate ANOVAs to test specific interactive effects of the 13 component variables of wind damage and fire on sapling structure, composition, and diversity (variables listed on left-hand side of Table 3.1). Because 13 hypotheses were tested, I used a Bonferroni correction, considering only those tests with a P-value < 0.0038 as significant to maintain an overall α level of 0.05 for this family of tests.

3.2.6 Testing Specific Buffering Mechanisms

In order to test whether seedlings established on elevated portions of mounds in burned areas had higher survival, I used a multiple logistic regression with survival of an individual seedling as the response variable. The main effects included in the model were seedling location (tip-up mound vs. intact soil), burn treatment (burned vs. unburned), elevation of a seedling relative to the ground (m), and height of a seedling prior to fire (mm). To test whether mounds buffered seedlings from mortality by fire, and whether this buffering was due to elevation, I included a location × treatment interaction as well as an elevation × treatment interaction.

To test whether patterns of survival and resprouting differed between fire-damaged saplings in burned-only plots versus those in winched and burned plots, I tabulated the number of saplings top-killed (*i.e.*, damaged and resprouting) and the number of saplings killed (*i.e.*, not resprouting 1 year following fire) for both burned-only plots and winch+burn plots. I tested for differences in occurrence of resprouting using a χ^2 test. Among saplings that were resprouting (n = 192), I tested whether saplings in winch+burn areas exhibited greater resprouting productivity using a regression analysis with sprout biomass as the response variable. Explanatory factors included in the analysis were sapling biomass, winch treatment, and biomass × winch interaction. Measures of sapling and resprout biomass were log-transformed so that regression residuals were normally distributed.

3.3 Results

3.3.1 Interactive Effects on Overall Vegetation Structure, Composition, and Richness

For both seedlings and saplings, the treatment combination of experimental winching plus fire exhibited the greatest change in ordination space (Figure 3.3). The ordination revealed that sapling composition in control plots and winched-only plots changed moderately, with an approximately 0.15 unit change in ordination space (Figure 3.3B). Additionally, control plots and winched-only treatments followed sim-

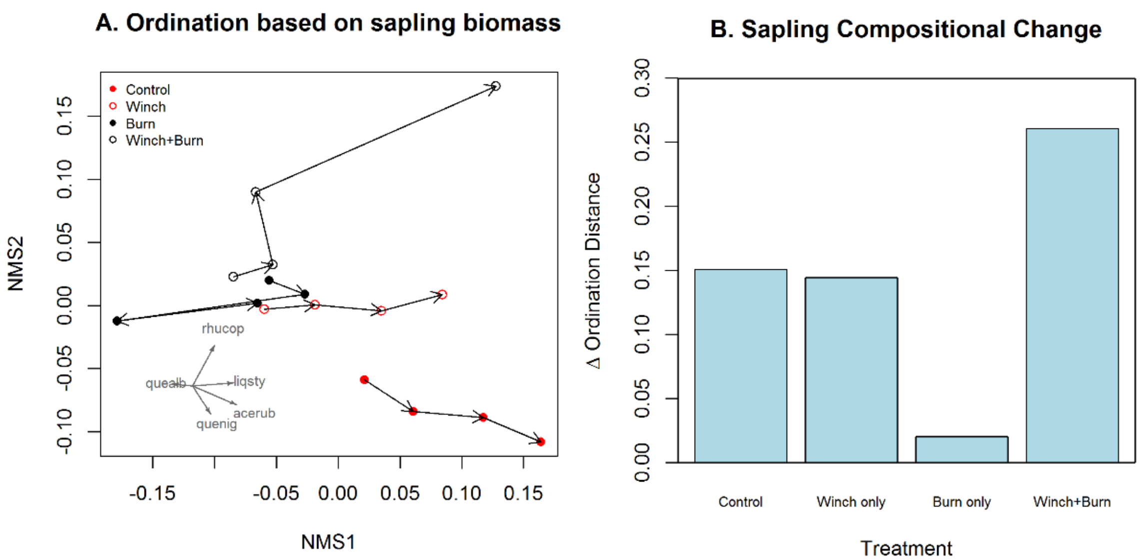

Figure 3.3: (A) Ordination of sapling composition using non-metric multi-dimensional scaling based on sapling biomass. Species loading arrows in bottom-left corner show the five strongest correlations with NMS axes 1 and 2 (rhucop = *Rhus copallinum*, liqsty = *Liquidambar styraciflua*, acerub = *Acer rubrum*, quenig = *Quercus nigra*, and quealb = *Quercus alba*). (B) Estimated compositional change index for seedlings based on Euclidean distance between start and end points (2011–2014) of sapling composition from A.

ilar trajectories, shifting to the region of ordination space indicative of species such as *Acer rubrum* and *Liquidambar styraciflua* (Figure 3.3A). Sapling composition in burned plots was more constrained, with only a 0.02 unit change in composition. Compositionally, the winch+burn treatment shifted sapling composition most dramatically with a 0.26 unit change in ordination space. Unlike winching alone, when winching was combined with fire, sapling composition shifted toward the region of ordination space indicative of species such as *Rhus copallinum*.

For seedlings, compositional change in control plots was minor (0.01 units) relative to plots receiving winching and/or burning treatments (Figure 3.4). Winching alone and burning alone each altered species composition in ordination space to a

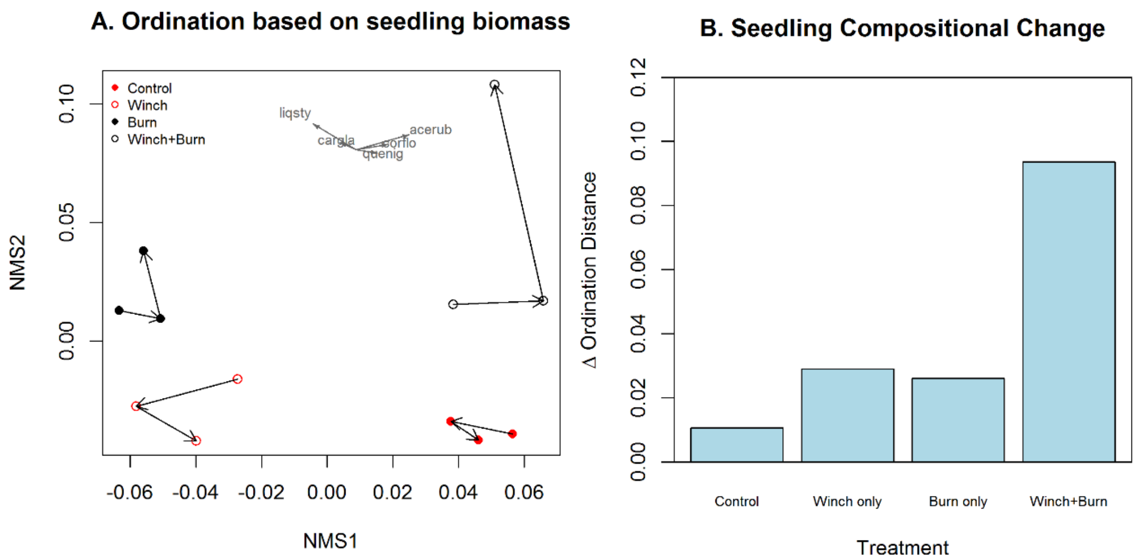

Figure 3.4: (A) Ordination of seedling composition using non-metric multidimensional scaling based on seedling biomass. Species loading arrows at the top show the five strongest correlations with NMS axes 1 and 2 (acerub = *Acer rubrum*, corflo = *Cornus florida*, quenig = *Quercus nigra*, cargla = *Carya glabra*, and liqsty = *Liquidambar styraciflua*). (B) Estimated compositional change index for seedlings based on Euclidean distance between start and end points (2011–2013) of seedling composition from A.

Table 3.2: MANOVA and ANOVA results showing significance tests for the winch × burn interaction for the six sapling and seedling characteristics investigated.
* Results from sapling and seedling richness are from ANOVA with exact F-values and results from remaining variables are from MANOVA with approximated F-ratios

Response	Pillai	F-ratio*	df	P-value
Sapling Structure	0.23893	4.5521*	4,58	0.00289
Sapling Composition	0.30376	4.6355*	8,85	0.00010
Sapling Richness	-	9.4167	1,92	0.00283
Seedling Structure	0.16363	2.0054*	4,41	0.11171
Seedling Composition	0.16757	0.9310*	8,37	0.50293
Seedling Richness	-	1.0722	1,44	0.30611

similar degree, with shifts of 0.29 and 0.26 ordination units, respectively. The shift in seedling composition in winch+burn plots was greater than the sum of change in either treatments separately, with a 0.94 unit shift in ordination space (Figure 3.4B).

The MANOVA and ANOVA results testing for significant winch × burn interactions among vegetation characteristics suggest that winching and burning had a mixture of buffering and amplifying effects on the vegetation structure, composition, and richness of saplings and seedlings (Table 3.2). Interactive effects of winching and burning were evident for sapling structure (P = 0.0029), composition (P = 0.0001), and richness (P = 0.0028). Interactive effects of winching and burning on seedlings were not evident for seedling structure (P = 0.1117), composition (P = 0.5029) or richness (P = 0.3061). Among the vegetation responses with significant winch × fire interactions (sapling structure, composition, and diversity), I examined the coefficients for burning and winch × burn interaction to classify the interactions of 13 variables in Table 3.1 as amplifying or buffering.

Among the vegetation characteristics exhibiting significant interaction effects from the previous analyses (Sapling structure, composition, richness, Table 3.2), I used univariate ANOVA tests to examine which individual vegetation responses exhibited significant winching × burn interactive effects. Using a corrected α-level of 0.0038 to correct for multiple significance tests, six of the thirteen sapling response variables exhibited significant winch $\times$ burn interactive effects (See Appendix C, Table C.1, and C.2). Four response variables exhibited significant buffering interactions and two showed significant amplifying interactions. Variables showing buffering effects were Δ sapling density (P = 0.0008; Figure 3.5A), Δ sapling richness (P = 0.0028; Figure 3.5B), Δ *Acer rubrum* sapling density (P = 0.0004; Figure 3.5C), and Δ *Acer rubrum* sapling biomass (P < 0.0001; Figure 3.5D). Sapling density increased in both control plots and winch-only plots. Burning prevented such an increase except when burning was combined with winching, where sapling density increased (Figure 3.5A). In a similar pattern, sapling richness increased in both control and winched-only plots over the course of the study (Figure 3.5B). In burned plots, sapling species richness decreased slightly, however, burned plots that were also winched exhibited the highest increase in sapling richness (Figure 3.5B). In control plots, *Acer rubrum* density increased greatly over the course of the study. However, recruitment of *Acer rubrum* saplings was much lower after burning, with nearly no change in biomass. Similar to burning, winched-only plots displayed only a small increase in *Acer rubrum* biomass. Despite that winching and burning mostly prevented *Acer rubrum* recruitment or growth relative to controls, the combination of winching and burning produced a moderate increase in *Acer rubrum* biomass over the course of the study (Figure 3.5C). This pattern was echoed in the response of *Acer rubrum* biomass (Figure 3.5D). This analysis showed that Δ *Rhus copallinum* sapling density and biomass each exhibited significant amplifying effects (each P = 0.0005). Control plots, burned plots, and winched-only plots exhibited very small increases in *R. copallinum* density (Figure 3.5E) or biomass (Figure 3.5F). However, when winching was combined with burning, *R. copallinum* density and biomass each rose much greater compared to control plots and plots with only one disturbance.

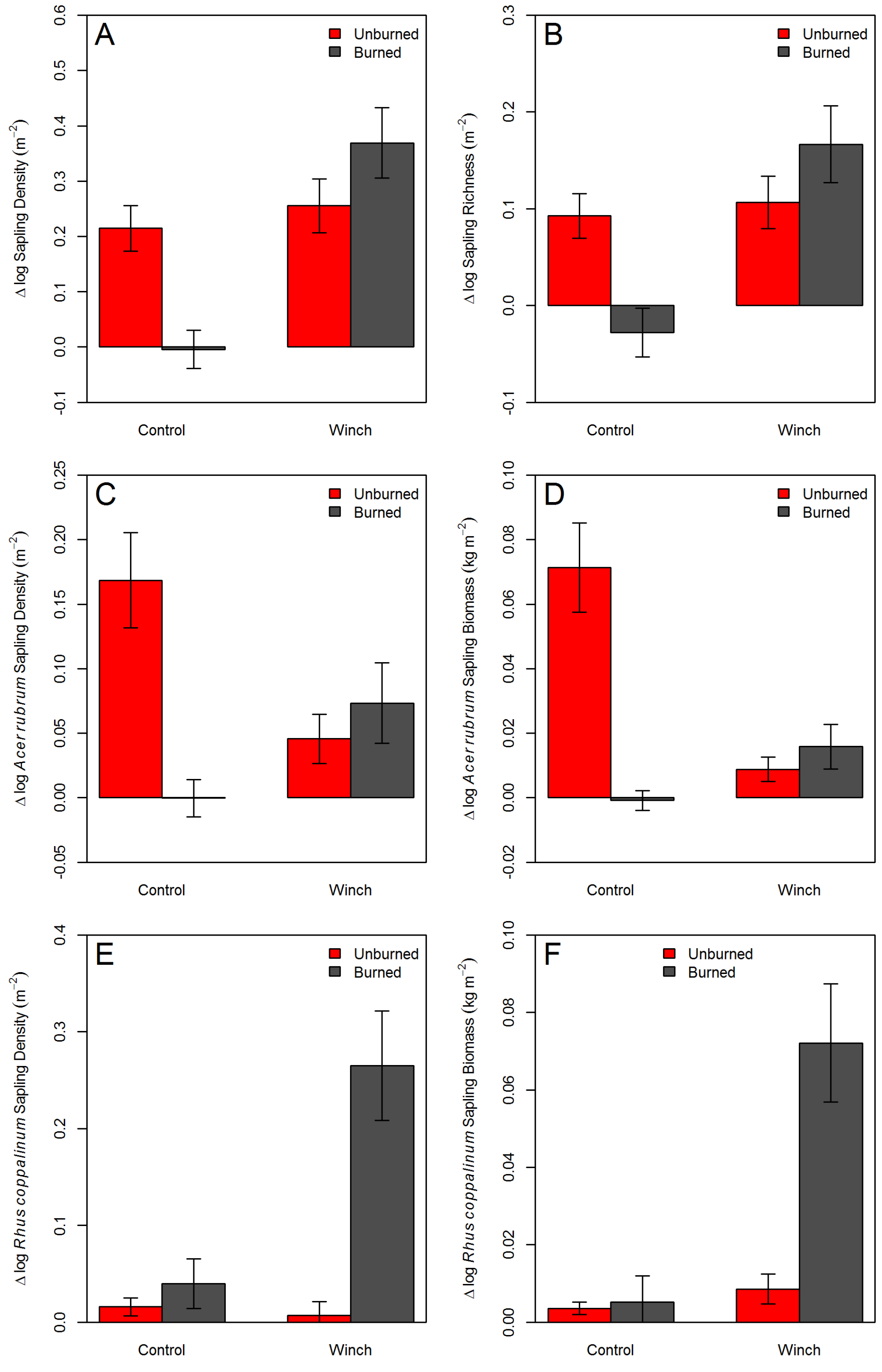

Figure 3.5: Vegetation response variables showing interactive effects of winching and burning. Significant buffering interactions were found for Δ sapling density (A), Δ sapling richness (B), Δ *Acer rubrum* sapling density (C), Δ *Acer rubrum* sapling biomass (D). Both Δ *Rhus copallinum* sapling density (E) and biomass (F) exhibited significant amplifying effects. Error bars represent mean ± 1 s.e.

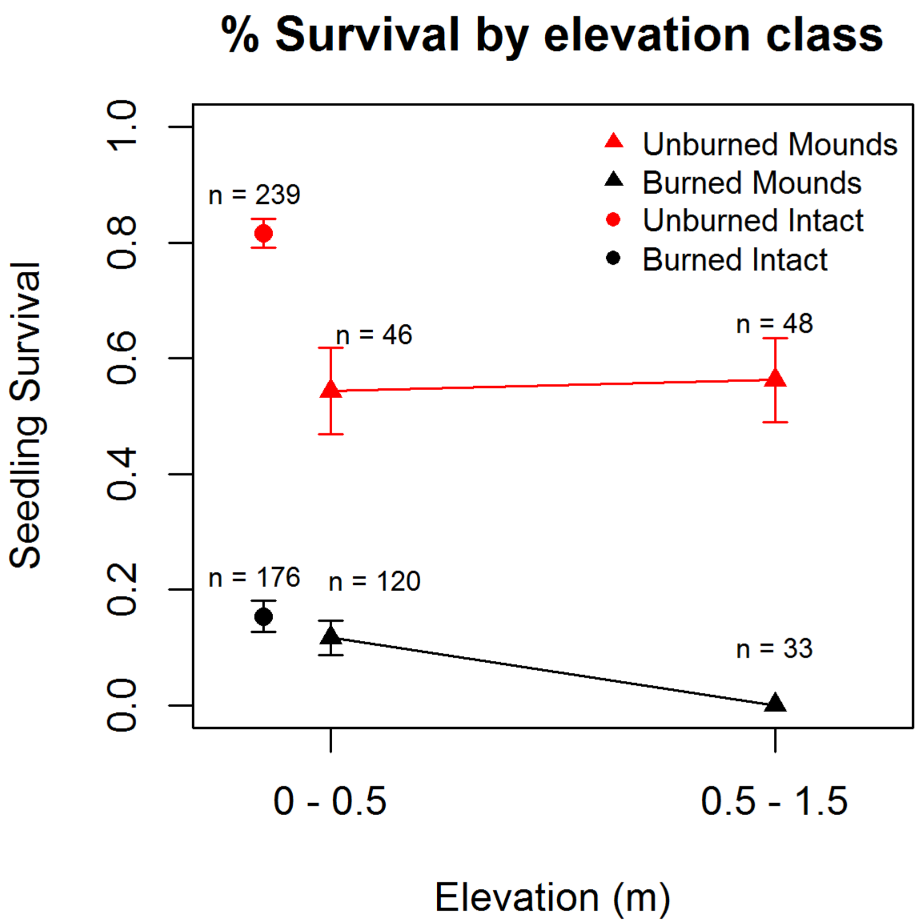

Figure 3.6: Mean seedling survival for burned (black) and unburned (red) seedlings on tip-up mounds (▲) and intact soil (●). Seedlings on tip-up mounds are classified by elevation class to illustrate effect of elevation on seedlings. Error bars represent one standard error of mean survival (coded as 0 or 1). Note that survival of high elevation seedlings on burned mounds was 0%, thus no error bars are displayed for this treatment combination.

3.3.2 Specific Buffering Mechanisms

Regarding increased survival of seedlings on mounds, the logistic multivariate regression revealed that seedling survival was lower in burned areas (12.5%) compared to unburned areas (74.2%, $P < 0.0001$). Although seedling survival was not lower on mound microsites overall ($P = 0.1660$), a significant microsite × treatment interaction indicated that survival on mounds was reduced in unburned areas, but not in burned areas ($P = 0.0053$). In unburned areas, seedling survival was 81.6% on intact microsites, but only 55.3% on mounds. However, seedling survival was more similar on intact and mound microsites in burned areas (15.3% vs 9.1%, respectively). Seedling survival decreased with elevation on mounds ($P = 0.0299$), and a significant elevation × treatment interaction indicated that this effect was more pronounced in burned sites ($P = 0.0400$, Figure 3.6). For example, on unburned mounds, seedling survival was relatively similar on low elevations (54.3%, ≤ 0.5 m) compared to high elevations (56.2%, > 0.5 m). However, on burned mounds, seedling survival was higher on low elevations (11.7%) than on high elevations (0%). Seedling survival was not significantly correlated with the covariate seedling height ($P = 0.0578$).

There were no differences in the proportion of saplings with basal sprouts between burned and unburned areas. The proportion of sprouting saplings was approximately equal in both treatments with 83% of saplings sprouting in burned-only plots (106 of 127), and 84% resprouting in winch+burn plots (86 of 102, χ^2=0.301, $P = 0.8622$). The regression analysis revealed that biomass of sprouts increased with the biomass of associated saplings ($P = 0.0148$), and sprout biomass was greater for a given sapling size in winch+burn plots relative to burn-only plots ($P = 0.0002$, Figure 3.7). In general, sprout biomasses from top-killed saplings in winch+burn plots were 2 to 3× greater than sprouts from burn-only saplings of a similar size. Furthermore, there was a marginally significant sapling biomass × winching interaction, indicating that

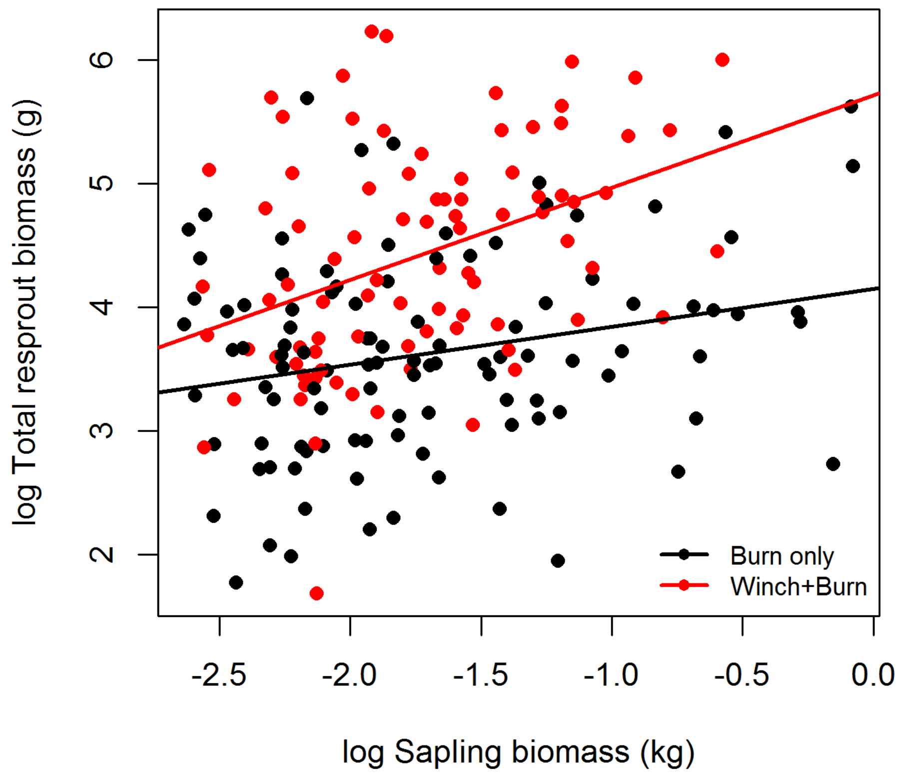

Figure 3.7: Relationship of sapling biomass of top-killed saplings and the total biomass of basal sprouts from individual damaged saplings, displaying higher resprout biomass for a given sapling size in winch+burn plots relative to burn-only plots. Note both axes show log-transformed biomass.

sprout biomass may increase to a greater degree with sapling size in winch+burn plots compared to burn-only plots (P = 0.0517).

3.4 Discussion

3.4.1 Occurrence of Amplifying and Buffering Effects

Overall, the results of this study support the notion that compounded disturbances can have interactive effects, where the combination of disturbances produces an outcome that is qualitatively different from—and not easily predicted by—the individual disturbances. However, in contrast to the focus on synergistic or amplifying effects emphasized by Paine et al. (1998), and other researchers, the results of this study are more consistent with the idea that ecological responses from tornado damage and prescribed fire result from a combination of both synergistic (or "amplifying") effects, and several antagonistic (or "buffering") effects. In this sense, these findings align more closely with those of Darling and Côté (2008) who found that only 35% of experiments showed amplifying effects, 42% showed buffering effects, and 23% showed no interactive effects. In our study, we characterized a number of vegetation responses to disturbance, and also found a heterogeneous mixture of additive, amplifying, and buffering effects.

Based on the NMS ordination showing changes in sapling and seedling composition over the course of the study, overall composition of seedlings and saplings shifted in an amplified or synergistic manner (*i.e.*, more than additive) with more change in species composition than expected from the individual disturbances (Figure 3.3 and Figure 3.4). When winching was combined with burning, compositional change was greater than expected from the effects of individual disturbances, and winch+burn plots shifted strongly to ordination space indicative of dominance by *Rhus copallinum* and *Liquidambar styraciflua* (Figure 3.3). For seedlings, compositional shifts were small in most treatments (control, winching-only, and burning-only), but much larger in the winch+burn treatment (Figure 3.4), similarly exhibiting an amplifying effect of experimental wind damage and fire on seedling composition. On the surface, this finding seems to support that compounded or cumulative disturbances can alter the successional trajectories of ecological communities, as has been the conclusion of other studies of combined disturbances (Buma and Wessman, 2011; Frelich and Reich, 1999; Paine et al., 1998). However, to better understand and predict the consequences of disturbance effects, it is also important to examine changes in specific ecological responses to disturbance combinations. Changes in individual variables such as vegetation structure, composition, and diversity may be masked by only examining overall changes.

In our study, despite amplifying changes in overall species composition, the analyses of vegetation structure, composition, and richness indicated that interactive effects of experimental wind damage and fire were numerous and varied, including both amplifying and buffering effects. These analyses examined individual changes in vegetation structure (density, biomass, height, and survival), composition (density and biomass change in major species), and species richness. Although no significant interactive effects of winching and burning were detected for seedling characteristics, interactive effects were found for sapling structure, composition, and richness. When examined individually, six specific characteristics showed significant interactive effects, four of these demonstrating buffering effects, and two demonstrating amplifying effects.

The meta-analysis of compounded disturbances on marine animals by Darling and Côté (2008) highlights that disturbance interactions range across a spectrum from buffering, to additive, to amplifying effects. Their study found a variety of interaction types across taxa, stressor type, and life-history stages. However, none of these factors were significant predictors of interaction direction (amplifying versus buffering), as interaction direction and strength varied considerably between studies (Darling and Côté, 2008). In light of these findings, it seems reasonable that our study, which includes multiple species and two life-history stages (seedlings and saplings), will also display considerable variation in interaction directions and strengths and strengths across species and life-history stages.

In our study, both Δ sapling density and Δ sapling richness exhibited buffering effects. Sapling density increased over the course of the study for each treatment except the burn-only treatment (Figure 3.5A) in which 100% of saplings were damaged by fire. Although most of saplings (83%) were able to recover through basal sprouting, some had not reached sapling height by the time of the final sapling survey in 2014. In contrast, growth of sprouts from top-killed saplings in winch+burn plots was more rapid (see sprouting discussion below). This effect is considered buffering because winching before prescribed burning increased resilience and resprouting of saplings such that sapling density was more similar to control plots than to burn-only plots.

The buffering effect on density and biomass of *Acer rubrum* saplings differs from those found in other disturbance combination studies. For example, D'Amato et al. (2011) found that sapling densities were greatly reduced following blowdown and fire because the blowdown removed adult jack pine (*Pinus banksiana*), and fewer propagules were available when the fire occurred 8 years later. However, such amplifying effects should not apply to our study of low-intensity prescribed fire where sapling survival was very high (83%), because sapling abundance does not rely on seed source.

Much of the increase in sapling density in winch+burn sites can be attributed to the increased representation by *Rhus copallinum*, which accounted for 54% of the increased sapling density in that treatment. In other treatments, recruitment of *Rhus copallinum* was low (ranging from 3%–80% increases), but was much higher in winch+burn plots ($>$ 800% increase). The pattern of changes in sapling richness closely mirrors that of change in total sapling density with little change in burn-only plots, moderate increases in control and winch-only plots, and the greatest increases in winch+burn plots (Figure 3.5B). *Rhus copallinum* likely played a role in increasing sapling richness in winch+burn plots, as it was the species most commonly recorded in the 2014 survey that was not present at the beginning of the experiment.

Acer rubrum was responsible for two additional buffering effects, where density and biomass showed buffering effects. *Acer rubrum* is generally classified as shade tolerant, but also sprouts prolifically following damage to the main stem (Burns and Honkala, 1990). In undisturbed control plots, *Acer rubrum* sapling density and biomass each increased dramatically, but this increase was completely prevented by burning (Figure 3.5C and Figure 3.5D). However, when winching was combined with burning, both *Acer rubrum* density and biomass increased, thus the growth prevention by burning alone was reversed when winching and burning were combined.

Brose and Van Lear (1998) examined regeneration of *Acer rubrum* following the combination of a canopy-opening disturbance (shelterwood harvest removing 50% of overstory basal area) followed two years later by a prescribed fire. In their study, advance regeneration of *Acer rubrum* was greatly reduced following disturbance combinations, especially for summer burns. By contrast, in our study, prescribed fire greatly reduced *A. rubrum* regeneration relative to controls, but this effect was lessened when combined with canopy opening wind damage. One explanation for this difference may lie in the size of *A. rubrum* saplings during the time of study. In this study, saplings included those woody plants $\geq$ 1.37 m, and prior to prescribed fire, *A. rubrum* saplings were larger (mean height, 1.76 m $\pm$ 0.35) than those in the study of Brose and van Lear (1.25 m $\pm$ 0.8). The smaller *A. rubrum* saplings in the Brose and van Lear study may have made them more vulnerable to disturbance from fire. This discrepancy in the interaction direction for *A. rubrum* saplings highlights that even when comparing similar sets of disturbances in similar systems, disturbance effects and interactions may differ greatly depending on the severity of the individual disturbances as well as the life-history stage of organisms involved.

In this study, saplings of *Rhus copallinum* showed a synergistic, or amplified, response to winching and burning combinations. In the control, burn-only, and winch-only treatments, *R. copallinum* density and biomass increased. However, when winching and burning were combined, density and biomass of *R. copallinum* increased dramatically (Figure 3.5E and Figure 3.5F). Although this increase in abundance of *Rhus* is striking, the amplified response of this species is not altogether surprising. Unlike the shade-tolerant *A. rubrum*, *Rhus copallinum* is a fast-growing and short-lived early pioneer shrub species (Duncan and Duncan, 1988). Fire can stimulate the root crown of *Rhus copallinum* to sprout following top-kill (Taylor and Herndon, 1981), as well as stimulate the germination of seeds by scarification (Cain and Shelton, 2003)

One inference that can be made from the large increase in *Rhus copallinum* is that generalist reproductive strategies may be more likely to exhibit greater recovery and resilience following compounded disturbances than specialist strategies. The generalist reproductive strategy of *Rhus* includes increased growth in response to light, resprouting after damage from fire, as well as increased seed germination following fire. Other studies also emphasize that generalist reproductive strategies may drive community shifts following compounded disturbances. For example, quaking aspen (*Populus tremuloides*) can regenerate by seed as well as through asexual sprouting. Consequently, following combined blowdown and fire disturbance (D'Amato et al., 2011), aspen regeneration was more prevalent than jack pine (*Pinus banksiana*) which relies on a specialist strategy (serotinous cones) that is sensitive to removal of adults following blowdown. Parallel findings have been demonstrated between quaking aspen and lodgepole pine (*Pinus contorta*) which also relies on serotinous cones for reproduction (Buma and Wessman, 2012).

3.4.2 Specific Interaction Mechanisms

The analyses that examine individual disturbance mechanisms further highlight that both buffering and amplifying effects characterize the interaction between experimental wind damage and prescribed fire. I expected that seedlings in winched plots established on high portions of mound microsites would be protected from prescribed fire. However, the opposite pattern was found. In burned areas, seedling survival was actually higher on low portions of mounds (12%), but dropped to 0% survival on the highest portions of mounds (Figure 3.6). The elevation of seedlings on tip-up mounds can make them inaccessible to some browsing herbivores such as white-tailed deer (Krueger and Peterson, 2006), but an analagous interaction may differ with tip-up mounds and prescribed fire. In a study characterizing energetic parameters of prescribed fires, Cruz et al. (2011) found that radiosity is greatly reduced with the height of the fire plume. Size of tip-up mounds typically increase with tree size (Sobhani et al., 2014), yet the highest mounds in our study (1.5 m) were not high enough to protect seedlings from fire. In addition, it is possible that at upper portions of mounds seedlings may be exposed to fire while also being vulnerable to increased erosion, as soil dynamics can differ in various positions of pit–mound complexes (Peterson et al., 1990).

Lastly, although we found that saplings in both burn-only and winch+burn plots were equally likely to resprout, saplings in winch+burn plots showed significantly greater sprouting rates relative to burn-only plots (Figure 3.7). Because prescribed fire greatly reduced sapling density in our study, faster growth of basal resprouts acts as a buffering mechanism allowing more rapid recovery of saplings following fire. Faster growth in basal sprouts in winched plots following fire could simply be the result of increased light and decreased competition with adult trees for soil resources. However, many hardwood saplings often have substantial underground carbohydrate reserves (Hodgkins, 1958; Robertson and Ostertag, 2009). Many oaks (*Quercus* spp.), for example, are known for higher investment of photosynthate into belowground tissues, compared to other hardwood species, which allows rapid sprouting following fire (Johnson et al., 2002). High light availability in winched plots may allow increased investment in belowground tissues of some saplings prior to fire that allow more rapid regrowth and recovery following fire. Cannon and Brewer (2013) hypothesized that such a mechanism may have increased representation by oak species relative to other hardwoods following a prescribed fire applied two-years after natural tornado damage.

3.4.3 Conclusion

In this study, individual vegetation strata (seedlings versus saplings), and individual species responded differently to disturbance combinations depending on factors such as size or life history. Such individualistic responses to disturbances led to a combination of amplifying and buffering effects being identified in our study. I identified one amplifying effect which led to prolific establishment and growth of the pioneer species *Rhus copallinum*, and a second potential amplifying effect leading to increased vulnerability of seedlings established on tip-up mounds. Conversely, the study identified multiple buffering effects whereby the combination of wind damage and fire caused changes more similar to those found in control plots than in burn-only plots, including changes in sapling density, *Acer rubrum* abundance and biomass, and sapling species richness. Interestingly, amplifying effects in one response variable can drive buffering effects in another. For example, abundance and biomass of *Rhus copallinum* was greatest in winch+burn plots and, in part, drove increased species richness in those plots. Thus, the establishment of *R. copallinum* helped to buffer the reduction in species richness in winch+burn plots that typically occurred in burn-only plots.

Undoubtedly, severe windthrow by hurricanes, for example, can amplify wildfire intensity and induce dramatic changes in vegetation composition (*e.g.*, Urquhart, 2009). Yet, disturbance interactions may differ when the disturbances are of lower severity. Foster et al. (1997) argue that many of the ecological impacts usually attributed to the severe 1938 New England Hurricane were instead caused by the disturbance of widespread salvage logging that was used to remove downed timber and was widespread in areas affected by the hurricane. However, the effects of windthrow and salvage logging do not always have detrimental effects. Peterson and Leach (2008) examined the cumulative effects of windthrow and salvage logging across a range of severities and found no evidence of interactive or threshold effects. Thus, they argue that the dramatic amplifying disturbance interactions that may occur when windthrow and logging severities are high (*e.g.*, Foster et al., 1997), may be less important when disturbance combinations are of lower severity. Similarly, the amplifying disturbance interactions that occur when wind damage is followed by severe wildfire likely differs in cases of lower-severity fire.

By design, prescribed fires are of a much lower intensity than wildfires. Studies of windthrow prior to low-intensity, prescribed fires highlight the significance of buffering effects of windthrow $\times$ fire (Cannon et al., 2014, Chapter 2, herein;). Thus, the interactive effects of wind damage and fire likely depend on the severity of the disturbances occurring. It is important to note that the severity of a single wildfire can be extremely heterogeneous with some areas burning with high intensity, and other areas with low intensity (Turner et al., 1994). Forest wind damage from tornadoes (Chapter 4, herein; Peterson et al., 2016), can likewise have strong heterogeneity with areas of high, moderate, and low severity blowdown. Thus, when wind damage and fire interact in forests a range of severities of each disturbance are likely to co-occur and interact. If the interaction between disturbances depends on the severity of the disturbances, then a complex mixture of different interaction mechanisms are expected to occur when two heterogeneous disturbances co-occur. The interaction between wind damage and prescribed fire in this study could not be adequately described as simply “synergistic” or “antagonistic”. Rather, competing and related interactions—both amplifying and buffering—were characteristic of the interaction between wind damage and low-intensity prescribed fire. A mechanistic understanding of the various potential interactions can help predict how disturbance interactions can drive ecological processes at the landscape scale.

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Chapter 4

Landscape-scale Patterns of Forest Tornado Damage in Mountainous Terrain[1]

[1] Cannon, J.B., J. Hepinstall-Cymerman, C.M. Godfrey, and C.J. Peterson. To be submitted to *Landscape Ecology*

Abstract

Natural disturbances such as windstorms can have important effects on forest regeneration, diversity, and carbon cycling. Measuring landscape patterns created by forest disturbances is important because of their influence on forest ecological processes such as colonization and recovery. This study demonstrates an objective procedure for estimating tornado damage severity in forests using aerial photographs. Here I apply the method to characterize landscape patterns of damage severity from two April 2011 tornados that struck the Chattahoochee National Forest (CNF) in northern Georgia and the Great Smoky Mountains (GSM) National Park in southeast Tennessee. The 64-km CNF track damaged 1712 ha (>25% severity), while the 26-km GSM track damaged 1407 ha. Gap sizes exhibited a negative exponential distribution with many small gaps and few, very large gaps. Mean gap sizes averaged 0.57 and 1.02 ha with maximum gap sizes of 208 and 498 ha, respectively, within the CNF and GSM tracks. Within a patch, damage became less severe and more dissected in the patch periphery. Patch size increased but patch number decreased with damage severity. Lastly, I found evidence that tornado behavior interacted with topographic features such as ridges. Tornado damage severity declined as tornados ascended ridges and increased as they descended ridges. My results indicate that remotely sensed data can be used to assess patterns of tornado damage severity at the landscape-scale.

INDEX WORDS: blowdown, landscape pattern, remote sensing, topography, tornado damage

4.1 Introduction

Natural disturbances such as hurricanes, floods, fires, insect outbreaks, and tornadoes affect nearly every forested ecosystem and can create large, disturbed forest gaps (Lorimer, 1980; Canham and Loucks, 1984). Disturbance from wind damage is widespread, effecting an estimated 1.65 million ha of forest annually in the U.S. (Dale et al., 2001). In April 2011, the largest tornado outbreak ever recorded in the U.S. spawned over 200 confirmed tornadoes over four days (NOAA, 2011). Extreme forms of wind damage from tornadoes and hurricanes drive many ecological processes in forests such as regeneration patterns (Peterson and Pickett 1995) and impact regional carbon cycling (Dahal et al., 2014; Chambers et al., 2007). At smaller scales, the uprooting of trees characteristic of wind damage can create pit-and-mound microsites, which maintain tree and herb diversity (Beatty, 1984; Ulanova, 2000), alter patterns of herbivory (Krueger and Peterson, 2006), and influence soil respiration (Millikin and Bowden, 1996).

Natural disturbance regimes are typically defined by the type of disturbance, magnitude, spatial factors (*e.g.*, area, shape, and spatial distribution), and temporal factors (*e.g.*, duration and frequency, Pickett and White, 1985; White and Jentsch, 2001). Disturbance regime factors such as frequency and regional distribution are only measurable by considering multiple disturbance events (Canham and Loucks, 1984; White and Jentsch, 2001). However, other aspects of a disturbance regime, such as the extent, damage distribution, and spatial patterns of damage can be characterized at the level of individual disturbances. Spatial patterns of forest damage include attributes such as typical gap size, shape, and spatial arrangement of gaps—each of which can have particular ecological effects. Forest gap size can influence seedling establishment, growth, and influence species diversity of the regenerating stand (Gray and Spies, 1996; Schnitzer and Carson, 2001). Moreover, the spatial pattern or arrangement of gaps (also called gap structure or configuration) can influence ecological processes. For example, a complex mosaic of burned and intact areas resulted from the 1988 Yellowstone National Park wildfires. This heterogeneous mosaic hastened forest recovery because most burned patches were within 50–200 m of intact or lightly burned stands allowing for rapid seedling dispersal (Turner et al., 2003).

Typical gap sizes are well-characterized for some natural disturbances such as gaps created by individual tree death (Runkle, 1982). Several studies also shed light on the extent, gap size, and severity of certain windstorms including hurricanes (Foster and Boose, 1992), thunderstorms (Webb, 1989; Waldron and Ruel, 2014), and straight-line winds (Nowacki and Kramer, 1998; Lindemann and Baker, 2001). Despite the frequency and ubiquity of tornados in the eastern United States, little is known about the landscape patterns tornadoes create. Although two remote sensing studies report on the extent of damage from particular tornados (Yuan et al., 2002; Wilkinson and Crosby, 2010), these studies do not report important landscape patterns created by tornados such as the distribution of and typical gap size, severity of damage within gaps, or gap configuration (Foster et al., 1998). Characterizing these spatial components of tornado disturbances complements parallel work after hurricanes, thunderstorms, and straight-line winds, and fills a major gap in our knowledge of the wind disturbance regime. Documenting the extent, severity, and spatial arrangement of damage to forests from tornados will contribute to a better understanding of the range of variability of tornado impacts on forests (Vaillancourt et al., 2009) as well their ecological significance. Diffenbaugh et al. (2013) report that climate change scenarios predict future tornado frequency to increase, suggesting that the importance of forest disturbance from tornados will increase. Understanding current tornado damage patterns is important for predicting future changes in forest disturbance regimes.

Studying patterns of tornado damage can also increase meteorological understanding of tornados, as tornado damage patterns may be useful for indirectly studying and classifying tornado behavior (*e.g.*, Beck and Dotzek, 2010). Because of limited accessibility and visibility in rugged terrain, Doppler radar is rarely used in mountainous, forested regions, thereby limiting knowledge about how variables such as tornado intensity responds to topographic changes such as elevation, slope, and aspect (Bluestein, 2000) and how that variability governs forest damage severity. Analyses that relate tornado damage severity to topographic variation may provide valuable meteorological information about how tornadoes behave in mountainous terrain. In this study, I demonstrate how mapping tornado damage can be used for testing hypotheses of how topographic features such as valleys and ridges influence tornado behavior and realized severity.

4.1.1 Study Objectives and Overview

Of over 200 confirmed tornadoes were spawned during the April 2011 outbreak, one damaged parts of the Chattahoochee National Forest (CNF) in northern Georgia, and another struck the Great Smoky Mountains National Park (GSM) in eastern Tennessee. Using digital aerial photographs, I mapped damage severity from each storm track, and used the maps to characterize landscape-scale patterns of tornado damage. Despite the apparent linear pattern of tornadoes (Foster et al., 1998), I expected tornado damage to be highly variable with respect to damage severity distribution, gap size, and gap shape. Next, I used the severity map to test three specific hypotheses relating forest damage severity to topographic features. Some anecdotal evidence suggests that tornados intensify as they travel along valley bottoms as the valley width narrows (hypothesis 1). Additional anecdotal evidence suggests that tornadoes "skip" the leeward hillsides as they pass over ridges (hypothesis 2). Meteorological research suggests that tornados may weaken when ascending slopes and strengthen when descending slopes (hypothesis 3) based on simulation models (Lewellen, 2012). This idea has been supported by radar evidence from three tornado tracks (Lyza and

Knupp, 2014). Thus, I expected tornadoes to interact with physiographic features such as valleys and ridges, which may be important predictors of damage severity.

4.2 Methods

Three months after tornado damage, aerial photographs (3-band true color, 20 cm resolution) were taken of each tornado track and then ortho-rectified using a 10 m digital elevation model (U.S. Geological Survey, 2015). I developed a map of damage severity along the tornado path by estimating severity from aerial photographs using supervised classification and verified the classification using k-fold cross-verification of training plots. I validated the photographic classification by comparing estimated damage severity to damage severity measured from ground-truth plots. The spatial patterns of tornado damage at each site were characterized by calculating several landscape metrics using Fragstats v4.0 (McGarigal et al., 2012) including patch number, size, shape, and spatial configuration. Lastly, I explored how topographic variables influence tornado damage severity using overlay analyses in specific pysiographic settings such as valleys and ridges.

4.2.1 Damage Classification and Verification of Aerial Photographs

To determine the damage severity from aerial photographs, I classified each photograph into damage categories using supervised classification. To train the classification, 400 m^2 training plots were distributed across the extent of each tornado track. The plots were stratified so that half were in completely unaffected areas (margins of the photograph), and half were concentrated near the damaged portions of the photographs (Figure 4.1A). I distributed approximately 1200 training plots over the CNF track (approximately 64 km long) and 670 plots over the GSM track (approximately

26 km long), corresponding to an areal coverage of 0.5% of each track. Each training plot was classified visually at a consistent scale (1:8,000) according to expert opinion (CJ Peterson, examples shown in Figure 4.1B). Training plots were visually classified according to the estimated percentage of basal area (BA) down using the following categories: undamaged (0% BA down), low (1–25% BA down), medium (26–50% BA down), high (51–75% BA down), and very high (76–100%).

The resolution of photographs was reduced from 20 cm to 4 m using the Aggregate tool in ArcMap on each of three bands to average reflectance values and reduce the influence of shadows and produce a better spatial representation of wind damage. Supervised classification in ArcMap (ESRI, 2011) was used to classify each pixel in the photographs. The classification process is illustrated in Figure 4.1C–E. Briefly, the classification uses the spectral signature of training plots within each class to classify the remaining pixels using, in this case, maximum likelihood classification. For example, undamaged areas of the photograph were identifiable by a range of green pixels indicating intact canopy, while heavily damaged areas were identifiable by brown/red pixels indicating fallen tree trunks and exposed soil. Each pixel in the photographs was assigned to the category of the training plot that it most closely matched. The procedure classified each 16 m^2 pixel into one of the five damage classes (Figure 4.1D). Finally, the midpoint damage severity was assigned to each pixel (undamaged = 0%, low = 12.5%, medium = 37.5%, high = 62.5%, and very high = 87.5%) and blocks of twenty-five 16 m^2 pixels were averaged into 400 m^2 non-overlapping blocks resulting in estimates of tornado damage being standardized to the maximum of 87.5% (Figure 4.1E). The standardization translated classified pixels into a continuous estimate of damage severity and resulted in a continuous estimate of damage severity (0–100%) at a resolution of 20 m.

The classification described above was combined with an approach that allowed for the use of k-fold internal cross-verification of the classification. For each track,

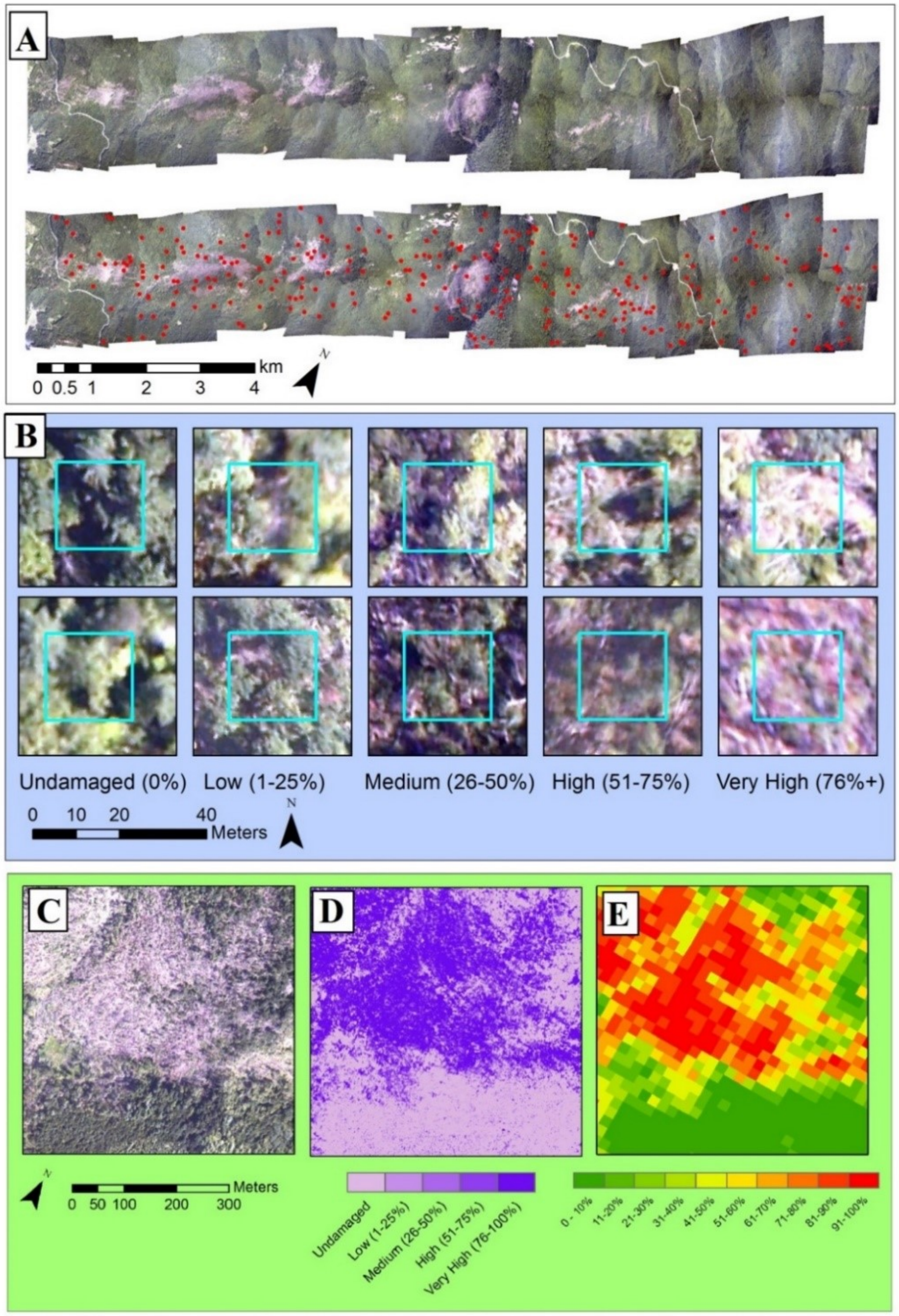

Figure 4.1: (A) Aerial photograph of tornado damaged area in the Chattahoochee National Forest and stratified random placement of training plots (red dots) across the photograph used for the classification. This particular composite photograph includes roughly 25% of the CNF track length. (B) Examples of training plots overlaid on the imagery used in the classification. Each plot was visually assigned to one of five damage categories. (C) Representative damage image. (D) Classification of the damaged area shown in C. (E) Estimate of tornado damage calculated by averaging 25 pixels in 400 m^2 blocks from the classification shown in D.

I classified the photograph as above using a subset (80%) of the training plots and withholding a smaller subset (20%) to internally verify each classification. For each track, the classification was repeated five times withholding a different set of training plots for verification in each instance. This resulted in five estimates of damage severity for each track that were averaged together to produce a single estimate of damage severity.

I conducted an out-of-sample validation of remotely sensed damaged classing using field plots. At the CNF site, I collected ground measurements of the percentage of basal area down in thirty-eight 400 m^2 ground plots. Similarly, I measured basal area down in thirty-four 400 m^2 ground plots at GSM. To validate the damage severity map, ground measurements of damage severity were related to those estimated by the classification of each tornado track in the corresponding area of the photograph using simple linear regressions separately for each site. Because the training plots were categorical (*e.g.*, low damage = 1–25%), and the classification produced a continuous estimate of damage severity (*e.g.*, 12%), I used fuzzy class boundaries of $\pm$ 10% to evaluate whether training plots were accurately classified.

I used the resulting damage severity map to estimate the area of land affected by each tornado by calculating the amount of land receiving $> 25\%$ and $> 50\%$ damage severity. To place the affected area into context, I compared the area affected from the CNF and GSM tornados to other recorded tornados. The National Weather Service Storm Prediction Center Severe Weather Database reports estimated lengths and widths of all recorded tornados from 1950–2014. Using the length and width dimensions from recorded storms, I estimated the typical area affected by tornados assuming tornado tracks were rectangular (when average tornado path width was reported, pre-1995) or rhomboidal (when maximum path width was reported, post-1995). I then compared the area affected by the CNF and GSM tornado tracks to the distribution of the area affected by historical EF-3 and EF-4 tornados.

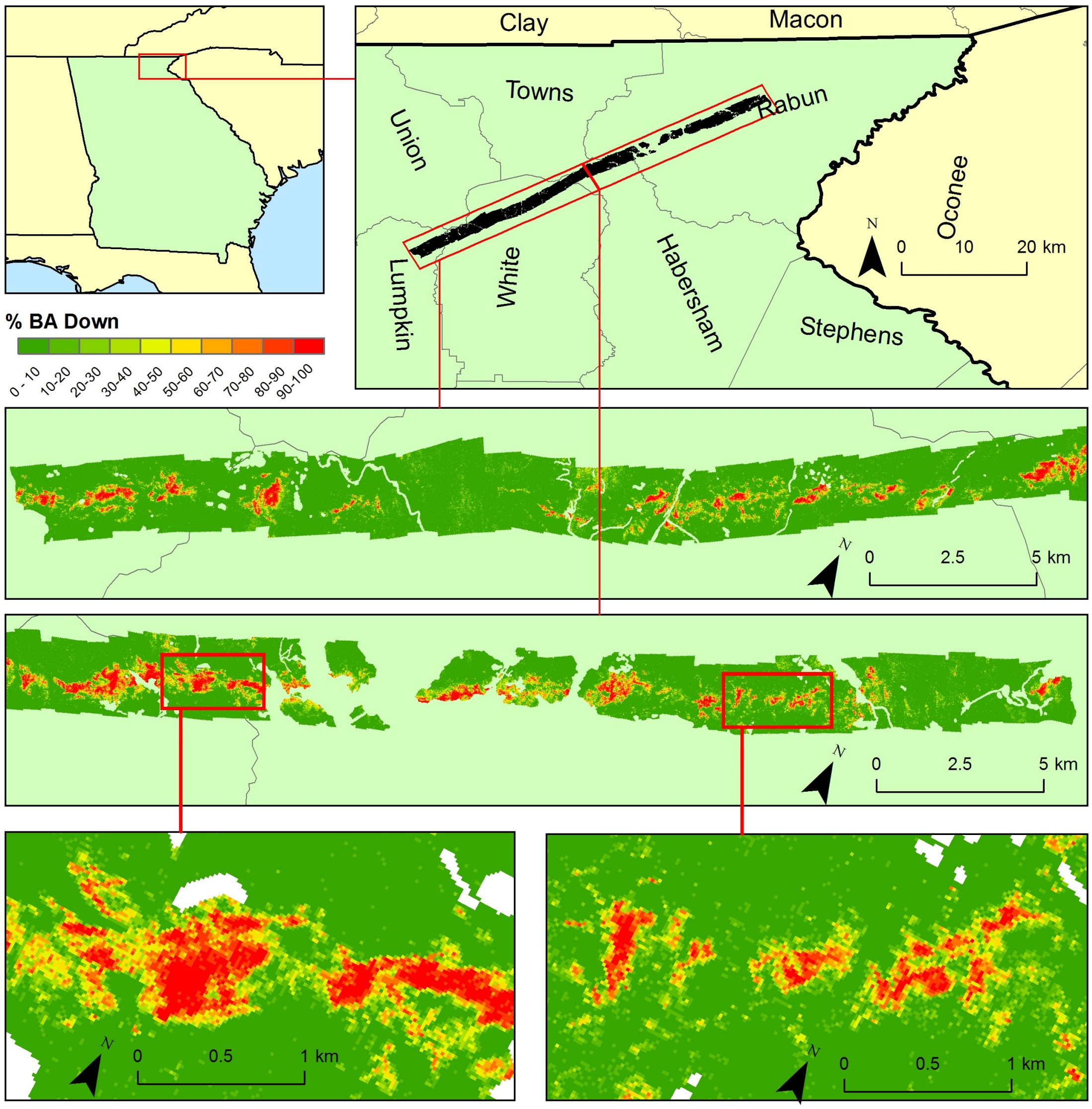

Figure 4.2: Map of tornado damage severity from April 2011 tornado that struck the Chattahoochee National Forest in northeastern GA. Note lower four insets are rotated 28 degrees clockwise. Lowest two insets compare clusters of damaged patches in subsets of each tornado track. Areas missing from maps represent areas not included in the flyover, or areas of non-forest (lakes, streams, roads, wildlife cuttings, etc.)

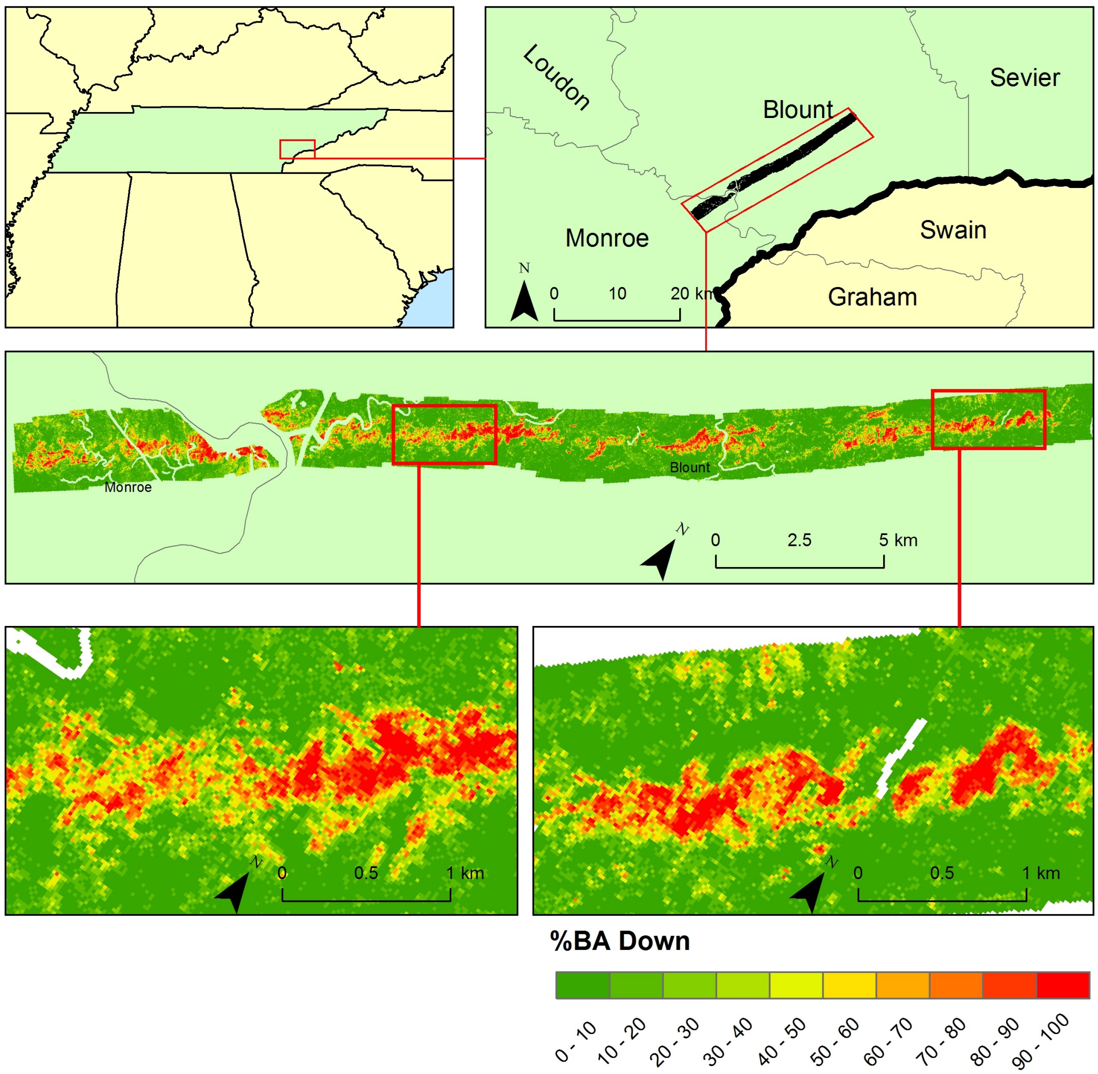

Figure 4.3: Map of tornado damage severity from April 2011 tornado that struck the Great Smoky Mountains National Park in eastern TN. Note lower four insets are rotated 35 degrees clockwise. Lowest two insets compare clusters of damaged patches in subsets of each tornado track. Areas missing from maps represent areas not included in the flyover, or areas of non-forest (lakes, streams, roads, wildlife cuttings, etc.).

4.2.2 Analysis of Landscape Pattern

The final damage map consisted of a continuous variable ranging from 0–100% basal area down (See Figure 4.2 and Figure 4.3). To facilitate the use of Fragstats v4.0 (McGarigal et al., 2012) software and to allow comparison of results to other studies, I reclassified the damage severity map into four categories: low (10–25%), medium (26–50%), high (51–75%), and very high (76–100%). To characterize the pattern of damage in the blowdown area, I measured various spatial metrics within each class. Therefore, I chose landscape metrics that would characterize the most important components of landscape heterogeneity without redundancy (Li and Reynolds, 1994). The metrics calculated within each damage class included (1) the number of patches, (2) mean size of patches, (3) mean patch shape index ($S_i = \frac{0.25P_i}{\sqrt{a_i}}$), where S_i is the shape index of patch i, P_i is the perimeter (m) of patch i, and a_i is the area (m^2) of patch i, and (4) mean edge-to-edge distance to the nearest patch of the same type (nearest neighbor distance), a measure of patch aggregation. Mean patch shape index is a measure of shape complexity based on perimeter and area. Shape complexity ranges from one (for a simple square) to infinity, increasing as patch shape becomes more irregular and complex (McGarigal et al., 2012). To measure gap size distribution, I analyzed damaged patches in a binary manner, considering continuous areas with >10% damage as gaps and areas $\leq$ 10% damage severity as non-gaps in order to measure gap size distribution.

4.2.3 Topographic Influence on Tornado Damage Severity

To examine how topographic features such as valleys and ridges influence tornado damage severity, I used overlay analyses within the context of a geographic information system to test three hypotheses of tornado behavior in rugged terrain. Each analysis below utilizes a 30 m digital elevation model overlaid with the tornado path to relate changes in topography (elevation or slope) to changes in damage severity in particular physiographic settings such as valleys and ridges.

Hypothesis 1: Tornado severity increases when valley width narrows

In order to examine whether tornado severity increased in areas where a tornado passed through narrow portions of a valley, I identified portions of each tornado track where the tornado path travelled through a valley bottom and delineated each valley along the ridges parallel to the tornado path. I divided each valley bottom into 100-m segments and measured the valley width for each segment (Figure 4.4A). I included any valleys where the path length was at least 300 m, resulting in six valleys identified in the CNF track and four at the GSM site (See Table D.1 for details). Within each valley segment, I calculated the mean tornado damage severity within x meters from the tornado track, where x is equal to the narrowest portion of each valley to maintain comparisons between segments of a constant area (Figure 4.4B). To determine whether changes in valley width were correlated to changes in damage severity, I calculated the Δ valley width and Δ severity between adjacent segments and related the measurements using simple linear regression, pooling data for all valley segments.

Hypothesis 2: Tornado severity decreases on rear aspects of ridges

For areas where the tornado ascended upslope perpendicular to a ridge and subsequently descended downslope, I compared whether front slope aspects received higher damage than rear aspects to test the hypothesis that tornados skip rear aspects of ridges. I identified portions of each tornado track where the tornado path travelled perpendicular to a ridge and delineated each ridge, placing adjacent 150 $\times$ 150 m sampling plots on front and rear aspects of each ridge (Figure 4.4C). I included all

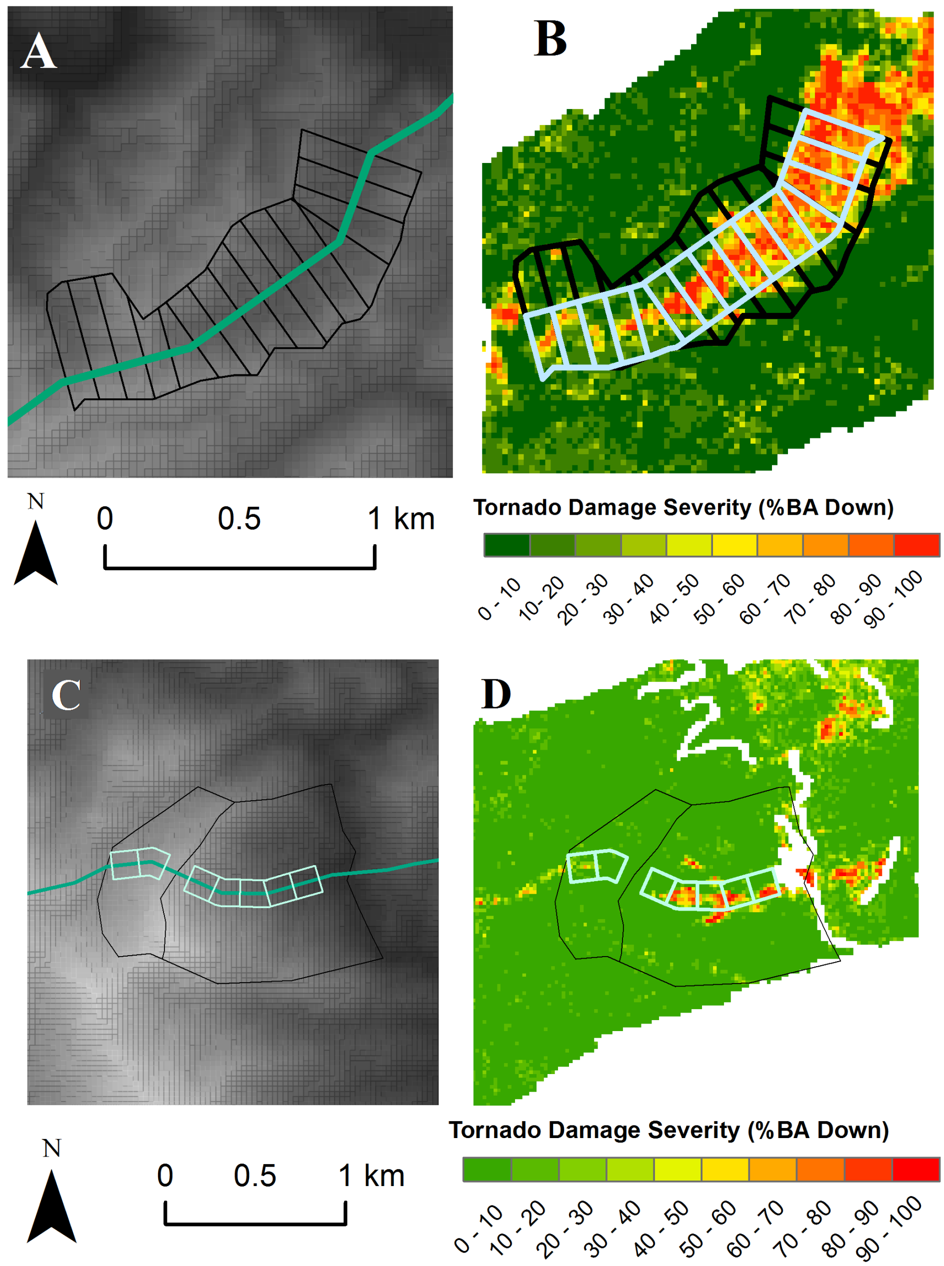

Figure 4.4: (A) Portion of GSM tornado track where tornado path (blue line) passed through valley bottom showing the outline of adjacent ridges and transects for measuring valley width. (B) Same portion of GSM track as in A with map of severity overlaid showing sampling areas (light rectangles). (C) Portion of GSM tornado track where tornado path passed through valley bottom showing the outline of adjacent ridges and transects for measuring valley width. (D) Same portion of GSM track as in A with map of severity overlaid showing sampling areas (light rectangles). White areas in D represent roads, streams, or other non-forest where damage severity was not estimated.

ridges with front and rear slope aspects at least 150 m long (from minimum elevation to maximum elevation) to allow the placement of at least one sampling plot on each ridge aspect. The sample included 10 ridges from the CNF track and 6 from the GSM track (See Table D.2 for details). To aid in the identification of ridges running perpendicular to the tornado track, I calculated an exposure index for each pixel on the digital elevation model [cos(slope direction − tornado path direction − 180)]. This index contrasted the front and rear aspects of ridges—with front aspects having large values (+1), and rear facing aspects to have low values (-1)—allowing ridges perpendicular to the tornado path to be easily identified (Figure D.1). I calculated the mean tornado damage severity in regions contained within subplots for front and rear aspects of each ridge (Figure 4.4D), pooling severity data for subplots on a given aspect. I used a one-tailed paired t-test to test the hypothesis that tornado damage severity was greater on front-facing ridge aspects than rear-facing ridge aspects.

Hypothesis 3: Tornado severity decreases upslope and increases downslope

To test whether tornado damage diminishes as tornados ascend slopes and increases while moving downslope, I correlated elevation changes along ridges to changes in damage severity. I used data from the same set of ridges as in the previous hypothesis (Table D.2), however, for each subplot, I calculated Δ elevation and Δ severity between adjacent subplots for each aspect on each ridge, and related the measurements using simple linear regression. A positive value of Δ elevation represents portions of the track where the tornado is moving upslope, and negative values represent downslope portions. Because Δ elevation and Δ severity require at least two subplots to calculate a difference, I only included ridges that contained at least two subplots on both front and rear aspects, resulting in 9 ridges being included in the analysis (all from CNF track which exhibits broad, gradually sloping ridges, Table D.2, Figure D.2). Finally, to examine whether the slope of ridges may influence the strength of the effect of Δ elevation on Δ severity, I used simple linear regressions between the two variables to obtain the regression coefficient of each relationship, and modelled these coefficients against the slope of individual ridges using simple linear regression.

4.3 Results

4.3.1 Verification of Aerial Photograph Classification

Internal verification comparing visual classification of the aerial photographs to the resulting severity map showed that the photographs were classified with overall accuracies of 93.4% for CNF and 88.5% for GSM (Table D.3 and Table D.4, respectively). Producer accuracies for CNF ranged from 78–95% and from 77–88% for GSM. User accuracies ranged from 80–100% for CNF and from 76–100% for GSM. In general, accuracies were highest for the higher and lower severity classes and lowest for the intermediate severity classes. Ground-truth measurements of damage severity were significantly correlated to the corresponding estimates from the severity map for both CNF ($P < 0.001$, $r = 0.775$) and GSM ($P < 0.001$, $r = 0.640$). The aerial photograph classification produced estimates of damage severity illustrated in Figure 4.2 and Figure 4.3.

4.3.2 Tornado Damage Extent

The CNF tornado track produced considerable damage with 1003 ha receiving damage greater than 50% severity over the 64 km length of the track. An area of 1712 ha was damaged with a severity greater than 25%, and an area of 2914 ha with a severity greater than 10%. The GSM tornado damaged 743 ha with greater than 50% severity over the 26 km track, damaged an area of 1407 ha with a severity greater than 25%, and damaged an area of 2678 ha with a severity greater than 10%. In Figure 4.5, the amount of land area affected by each tornado in damage class bins of 10% is illustrated (see also Table D.5).

The analysis of historical tornados showed that damage extent for EF-3 and EF-4 tornados was highly skewed, with estimates of damage for EF-3 tornados ranging from 0 to 29,000 ha with a mean of 797 ha and a median of 235 ha. Damage extent from EF-4 rated tornados ranged from 0 to 33,813 ha with a mean of 2201 ha and a median of 830 ha in damaged area (See Table D.6 for details). The 1712 ha damaged (>25 %) by the CNF tornado places it at the 89th percentile among EF-3 tornados. Similarly, these estimates place the GSM tornado (1407 ha, >25% damage) at the 63rd percentile among historical EF-4 tornados.

As expected, the tornado damage was extremely heterogeneous across the landscape. Each tornado exhibited similar patterns of severity distribution with a large amount of minor damage (10–20% severity) and roughly equal amounts of land area distributed among the higher levels of damage severity (30–100%; Figure 4.5).

4.3.3 Landscape Patterns of Tornado Damage and Gap Size Distribution

Considering landscape metrics of patch number, size, shape, and arrangement together suggests that tornado damage is distributed in a dissolved bull's-eye pattern (Figure 4.6). Overall, the number of patches decreased as damage severity increased (Figure 4.7A,E; Table D.7 and Table D.8). Conversely, the size of patches increased with damage severity (Figure 4.7B,F; Table D.7 and Table D.8). For CNF, patch shape was simpler in the highest and lowest damage severity classes, but more complex in patches with intermediate damage severity (Figure 4.7C, Table D.7). However, no clear pattern between patch severity and shape was detected for GSM (Figure 4.7G, Table D.8). Finally, the analysis showed that distance between like patches increased significantly with damage severity class from about 53 m between patches in the lower

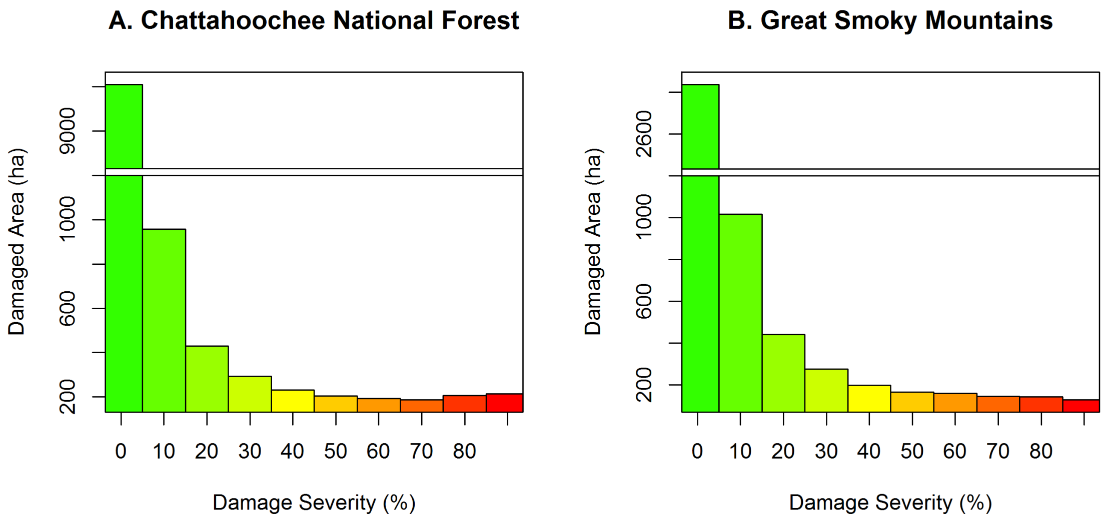

Figure 4.5: Distribution of damage severity extent for (A) Chattahoochee National Forest and (B) Great Smokey Mountains tornado tracks. Note break in y-axes at 1200 ha.

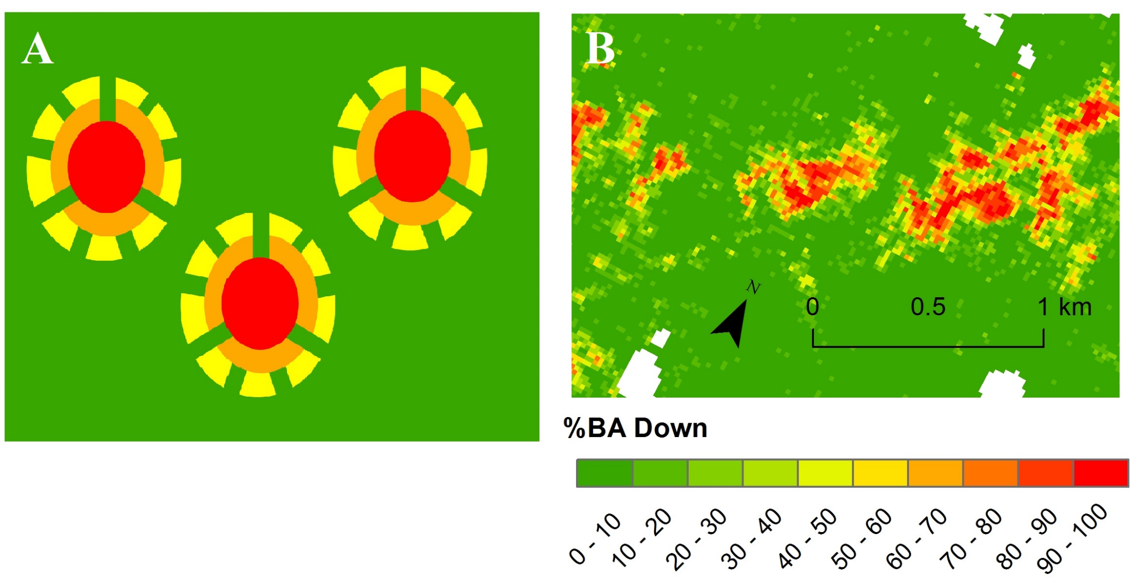

Figure 4.6: (A) Schematic diagram representing three dissolved bull's-eyes, the proposed landscape pattern created by tornado damage. (B) An approximately 2 km portion of the Chattahoochee National Forest tornado track showing actual tornado gaps in bull's-eye pattern.

damage severity class to 72 m between patches in the highest damage severity class at CNF (Figure 4.7D, Table D.7) and from 46 m to 71 m at GSM (Figure 4.7H, Table D.8).

I measured gap size distribution considering any continuous areas with > 10% damage severity as gaps and other areas as non-gap matrix (Figure 4.8). Mean gap sizes ($\pm$ 1 s.e.) for CNF and GSM were 0.568 $\pm$ 0.092 and 1.015 $\pm$ 0.316 ha, respectively. Owing to the very large number of very small gaps, minimum and median gap sizes for CNF and GSM were each 0.04 ha. The three largest gaps for CNF were 154, 159, and 207 ha; the three largest gaps for GSM were 338, 347, and 498 ha.

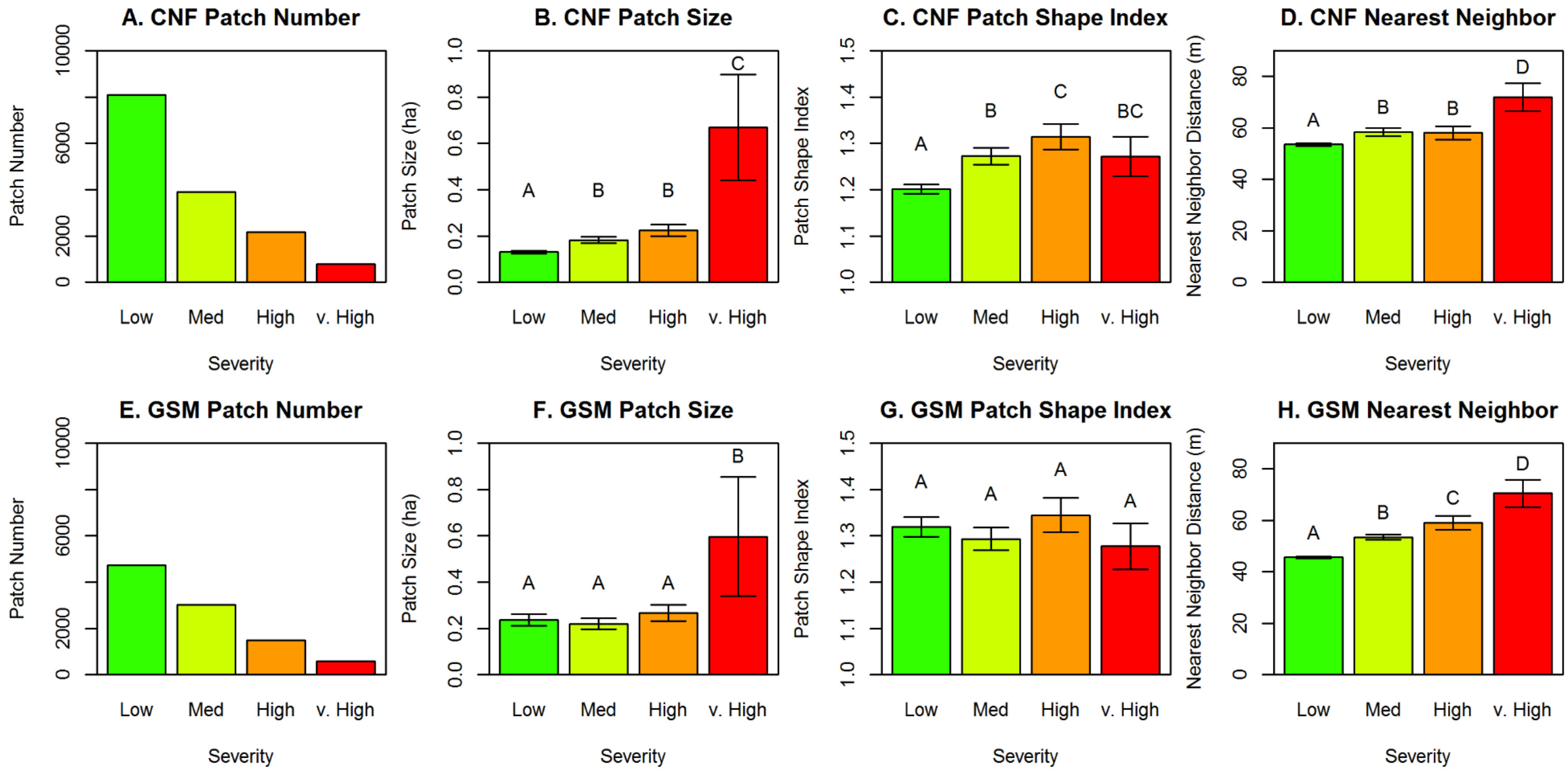

Figure 4.7: Patch-based metrics by each damage severity class (low, medium, high, and very high) for CNF (A–D) and GSM (E–F). Number of patches (A, E). Mean patch size (B, F). Mean patch shape index (C, G). Mean nearest neighbor distance (D, H). Error bars represent ± 2 standard errors of the mean metric.

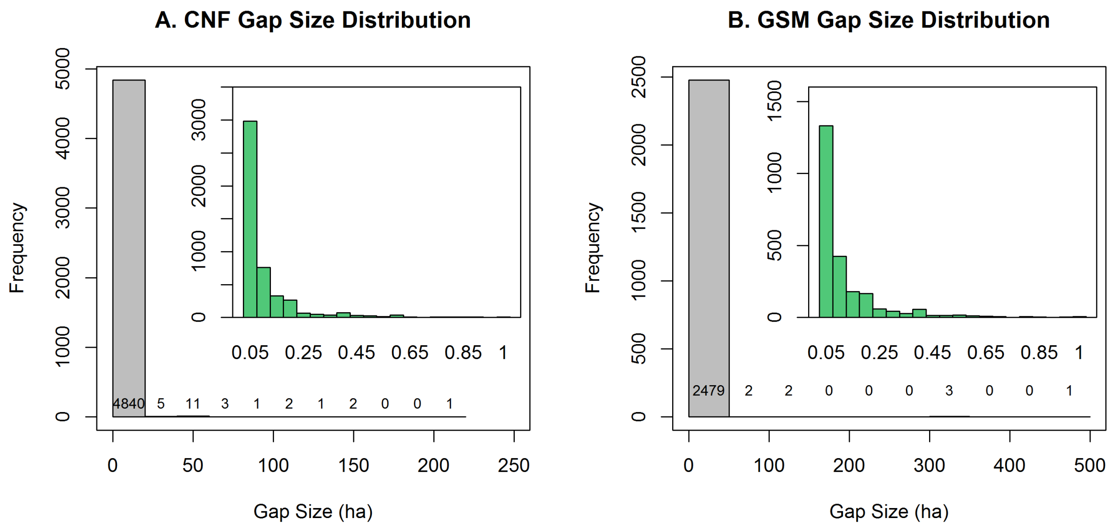

Figure 4.8: Histogram of gap size distribution of (A) CNF and (B) GSM tornado tracks illustrating negative exponential distribution of patch size. Because most gaps (99.5%) were $\leq$ 1 ha, insets in A and B show histogram for gaps $\leq$ 1 ha. Note the changes in the y- and x-axes between panels A and B.

4.3.4 Effects of Topography on Damage Severity

Overall, tornado severity did not increase when valleys narrowed (hypothesis 1). Based on simple linear regression, there was no relationship between changes in valley width and changes in tornado damage severity (Figure 4.9A, $R^2 < 0.001$, df = 90, P = 0.864). In fact, for individual valleys, the relationship between changes in valley width and damage severity was highly variable, ranging from a negative relationship (*e.g.*, CNF-1 in Figure D.3) to a positive relationship (*e.g.*, CNF-6 in Figure D.3). There was also no evidence that rear aspects of ridges traversed by tornados were sheltered from damage. Tornado damage was slightly higher on front ridge aspects (40.3%) than rear ridge aspects (32.6%, Figure 4.9B), but the difference was not significant (paired one-tailed t = -0.215, df = 9, P = 0.417).

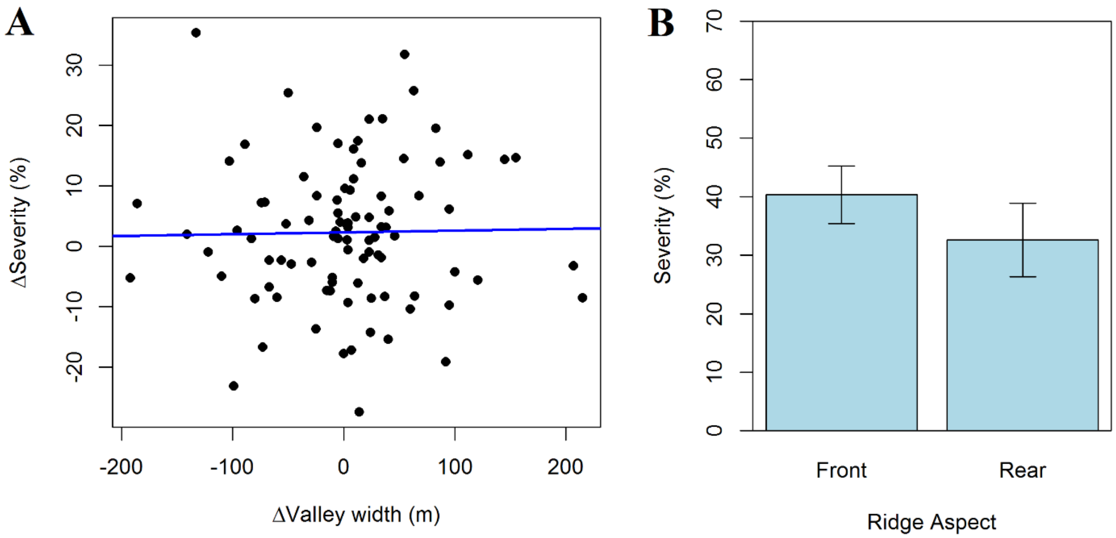

Figure 4.9: (A) Scatterplot illustrating relationship between changes in valley width and changes in tornado damage severity. Δ Severity as a percentage point ($R^2 < 0.001$; P = 0.864). (B) Mean damage severity of front and rear aspects of ridges traversed by a tornado at CNF and GSM (Paired *t*-test, P = 0.4173)

Tornado damage severity decreased with increases in elevation (Figure 4.10A, $R^2 = 0.143$, P = 0.001). In Figure 4.10, note that positive values of Δ Elevation represent subplots where the tornado traversed upslope and negative values represent subplots where tornados traversed downslope. Decreases in damage severity were typical when the tornado moved upslope while increases in tornado damage severity were typical when the tornado moved downslope. The overall regression coefficient of -0.21 indicates that increases of elevation of 100 m result in decreases in damage severity by approximately 21 percentage points, while 100 m decreases in elevation result in 21 percentage point increases in damage severity. The relationship between Δ elevation and Δ severity was consistently negative for each of the nine individual ridges examined, with regression coefficients ranging from strongly negative (-0.82) to weakly negative (-0.03) with a mean coefficient of -0.34 (Figure D.4). Further,

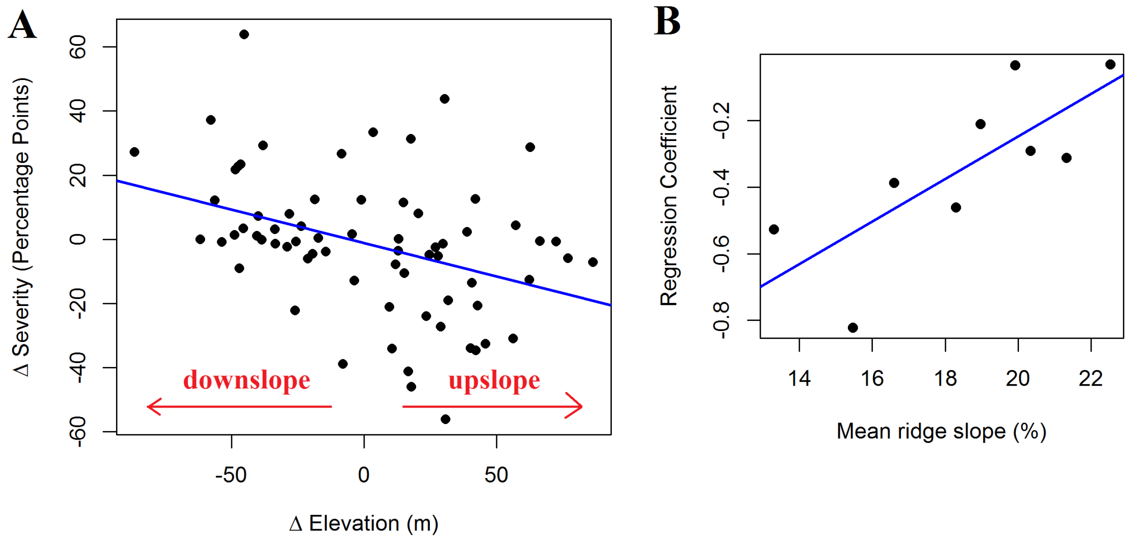

Figure 4.10: (A) Scatterplot illustrating relationship between changes in elevation and changes in tornado damage severity ($R^2 = 0.143$, $P = 0.001$). Note that negative values of Δ elevation represent portions of the tornado track where the tornado traversed downslope while positive values represents portions of the track where the tornado traversed upslope. (B) Linear regression illustrating the relationship between the mean slope of a ridge and the regression coefficient of Δ elevation versus Δ severity ($R^2 = 0.51$, $P = 0.018$). Lower regression coefficients indicate stronger effect of elevation.

the effect of elevation was greater on ridges with shallower slopes relative to steeper slopes (Figure 4.10B, $R^2 = 0.51$, $P = 0.018$).

4.4 Discussion

4.4.1 Tornado Extent

The potential area affected by a tornado is highly variable, but it is correlated with the intensity of the tornado (Brooks, 2004). I estimate that the area affected by the CNF (EF-3) and GSM (EF-4) tornados rank in the 89th percentile and 63rd percentile, respectively, among tornados of the same Fujita-scale rating (Table D.6). Wilkinson and Crosby (2010) estimated the area affected by an April 2010 EF-4 tornado that struck Mississippi, finding that nearly 16,768 ha received at least "light" damage, corresponding to the 99th percentile among EF-4 tornados.

Although there are recognized limitations of EF-scale ratings, and reports of path lengths (Doswell and Burgess, 1988), the length and width data from the Storm Prediction Center remains the best resource for understanding the extent of previous tornados. While track lengths and widths as reported by the National Weather Service can be used to calculate a very rough estimate of the areal extent of forest damage, it is problematic to use such an estimate when considering ecological processes for several reasons. First, such an areal calculation gives no indication of the level of damage severity the forest sustained (*i.e.*, the proportion of trees downed). Second, the estimated area does not consider heterogeneous damage severity within tornado tracks, which was considerable in this study (Figure 4.5).

The technique described here to remotely map tornado damage to forests from aerial photographs provides a straightforward and relatively objective method to map tornado extent as well as damage severity within a given track at a fine scale. Thus, I recommend adoption of this method in closed canopied forests, such as those in the eastern U.S., for making detailed measurements of tornado extent while explicitly incorporating the extreme spatial heterogeneity often present in tornado damage.

However large, the amount of forested area damaged by a single tornado is minute compared to the area affected by larger, infrequent natural disturbances such as the Mt. St. Helens eruption, the 1938 New England Hurricane, or the Yellowstone wildfires (Turner et al., 1994; Foster et al., 1998). However, the cumulative effect of hundreds of tornadoes during a tornado outbreak can affect a much larger spatial extent. The tornado outbreak of April 2011 produced over 200 detected tornadoes. In fact, large tornado outbreaks are quite common. According to the National Weather Service (2012), notable destructive or violent tornado outbreaks occurred five times during the 1990s, five times during the 2000s, and four times since 2010. Moreover, an estimated 1,300 tornadoes occur in the U.S. each year (Storm Prediction Center, 2012). Consequently, the cumulative effect of thousands of tornadoes may impact a substantial fraction of the area impacted by infrequent—though more dramatic—disturbances. Preliminary research suggests that tornadoes may damage as much as 300,000 ha of forest annually—an area nearly that of Rhode Island (CJ Peterson, JB Cannon, and LJ Snyder, unpublished data).

4.4.2 Landscape Patterns of Tornado Damage

One interesting result from the analysis of landscape pattern created by this tornado is the description of a putative pattern that may be characteristic of tornado damage. The results of the patch analysis are consistent with a dissolved bull's-eye pattern (Figure 4.6). In this pattern, a central area with severe damage is nested within less severely damaged patches that become broken-up, or dissolve, away from the center of the damaged area. The dissolved bull's-eye pattern is consistent with the positive correlation of patch size and severity, as well as the negative correlation of patch number and severity. A similar size–severity correlation among forest gaps was also found in non-tornadic wind by Peterson et al. (2013). Lastly, adjacent damaged areas shaped like a bull's-eye create the dispersion pattern seen in Figure 4.7D and Figure 4.7H with low damaged severity areas with short nearest neighbor distances and high severity areas dispersed with much longer neighbor distances.

Comparing specific values of landscape metrics across studies can be problematic because aspects of image processing may vary with differences in image interpretation, minimum patch size recognized, resolution of severity classes, and the spatial resolution of data (Turner, 2001). Therefore, one should be cautious drawing strong conclusions between studies with differing methodologies. Nevertheless, patterns of tornado damage are best placed in context by cautious comparison with other disturbances.

Damage severity from these tornados was extremely heterogeneous, and although there was a large amount of land area exhibiting minor damage (10-20%), approximately equal amounts of land area was affected by medium to higher (30%+) levels of damage severity (Figure 4.5). Heterogeneous damage with approximately equal amounts of land in each of the higher damage severity classes may be a general characteristic of some natural disturbances such as tornados. The fact that low-severity patches are small and numerous while high-severity patches are large and few (Figure 4.7 and Figure 4.7B) may result in the relatively uniform distribution seen in Figure 4.5.

A pattern with relatively even distribution of forested area among damage severity categories was found with the Yellowstone fires (Turner et al., 1993). Canham et al. (2001) observed that only a relatively small portion of land area received "catastrophic" damage from separate derecho blowdown events that struck the Adirondack Mountains and northern Wisconsin (Canham and Loucks, 1984), but the study does not report area affected by intermediate levels of damage severity. A heterogeneous pattern of damage from tornados contrasts with that from other types of disturbances that exhibit damage patterns with damaged areas concentrated in the most severe classes such as the 1938 New England hurricane (Foster and Boose, 1992) and a barrier-induced downslope wind event in the Rocky Mountains (Lindemann and Baker, 2001). A greater meteorological understanding of different types of windthrow and how they interact with topography may shed light on variation among damage patterns created by wind disturbances.

4.4.3 Gap Size Distribution

Gap sizes exhibited a negative exponential distribution with numerous very small gaps and few, very large gaps. Several studies of windstorms report gap size distributions skewed toward small gaps including hurricanes (Foster and Boose, 1992; McNab et al., 2004; Xi et al., 2008), thunderstorm winds (Evans et al., 2007), blowdowns (Rebertus and Meier, 2001), and downslope wind events (Lindemann and Baker, 2001). Thus, the negative exponential distribution of gap size may prove to be a general property of windstorms. A mechanism explaining this pattern may be related to the fact that in many windstorms including tornados, wind severity is low over much of the affected areas and only a small fraction of the area is affected by winds of high intensity. In areas experiencing low-intensity winds, small gaps may be created when only the most vulnerable trees are damaged such as the largest trees (Peterson, 2000), those with fungal rot (Matlack et al., 1993), or those previously fire-scarred (Cannon et al., 2015). Such a pattern would create small, low severity gaps over a large area. However, in a few areas, extreme winds may overcome differences in vulnerability (Peterson, 2000; Canham and Loucks, 1984; Canham et al., 2001) resulting in more complete windthrow of trees and thus, larger gap sizes in a smaller portion of the affected area. A positive correlation between damage severity and gap size (Peterson et al., 2013), combined with a negative correlation between gap size and gap number may result in a relatively even distribution of damage severity across a blowdown.

In this study, gap sizes at CNF and GSM averaged 0.6 and 1.0 ha, respectively, which were most similar to those reported from Hurricane Opal damage to the Bent Creek Watershed (gap sizes of 0.6 ha in basin and 0.9 ha in highlands, McNab et al., 2004). Gap sizes from these tornado tracks were also similar to those reported from blowdowns in the Missouri Ozarks (mean gap size 0.8 ha, estimated from Fig. 1 in Rebertus and Meier, 2001), and those reported from Hurricane Fran (0.01–1.1 ha, Xi et al., 2008; Busing et al., 2009) although it should be noted these analyses were conducted at the stand-scale and used a stricter concept of gap size (Runkle, 1982) rather than a threshold damage severity level, resulting in smaller gaps. Gap sizes in this study were much smaller than those gaps formed from the 1938 New England hurricane (estimated mean gap size is 3.5 ha, Fig. 6 in Foster and Boose, 1992), and a Pennsylvania windstorm (mean gap size 4.78 ha, Evans et al., 2007). They were also much smaller than from a downslope wind event in the Rocky Mountains (mean 25.2 ha Lindemann and Baker, 2001).

The small and irregularly shaped gaps in this study starkly contrast with the gaps from the downslope wind event study (Lindemann and Baker, 2001), which were larger and had simpler shapes. These differences in damage pattern could arise from differences between the wind disturbances themselves or from differences in vegetation between the regions. For example, gaps in the temperate Southern Appalachians may be more diffuse and irregular owing to the differences in windfirmness among the diverse trees, while gaps in the less-diverse subalpine forests of the Rocky Mountains may be larger and uniform. It is also possible that stronger topographic variation in the Rocky Mountains could "break-up" tornado wind fields resulting in many smaller gaps.

Although neither mechanism is explicitly supported by the Lindemann and Baker (2001) study, it is difficult to reject either hypothesis with the pattern from a single disturbance. Such difficulties illustrate the problems generalizing from studies of individual disturbances, each using disparate methodologies. This study utilized an objective classification procedure, whereas the hurricane study used ground plots to estimate damage, and the downslope wind event study utilized manual delineation of patches from aerial photographs. Thus, it is recommended that future landscape-scale studies utilize a common methodology such as the one herein, which is both objective and large in spatial extent to allow comparison and generalization between studies.

4.4.4 Topographic Influences on Tornado Severity

Lastly, this study demonstrates that topography influences tornado damage severity in physiographic settings. In several instances along tornados appeared to be channeled along valley bottoms. However, I found no evidence that changes in valley width led to increased damage severity in narrowing valleys (Figure 4.9A). Furthermore, this analysis did not find that the rear aspects of ridges are protected from wind damage when a tornado passes over a ridge (Figure 4.9B).

This analysis did support the hypothesis that tornado severity diminishes as tornados travelled uphill and strengthens on downhill aspects of ridges (Figure 4.10A), and the effect was stronger in shallow slopes (Figure 4.10B). Such upslope/downslope effects appear to be a relatively common occurrence and similar effects have been reported using simulation models of tornadoes (Lewellen, 2012) and from radar evidence from three tornado tracks (Lyza and Knupp, 2014). Analysis of tornado damage to forests informs tornado behavior in complex terrain, where accessibility, visibility, and availability of radar data are often limited. There is growing awareness among the meteorological community of the utility of remotely sensed forest damage as important data sources for tornado intensity.

In these analyses of the effect of topography on tornado severity, I specified particular hypothetical tornado behaviors (ie, "skipping" over ridges) and tested for evidence for them in specific topographic settings (ridges or valleys). This approach allowed the examination of specific tornado behaviors, and differs somewhat from previous analyses (Foster and Boose, 1992, *e.g.,*) in which specific topographic variables (slope, elevation, and aspect) or combinations of topographic variables ("exposure") are correlated with damage severity at a large scale. For hurricanes, the scale of the storm dwarfs individual topographic features such as ridges. But for tornados, the size of a tornado is more similar to the scale of individual ridges, thus a smaller-scale approach is necessary for analyzing topographic effects of tornados. To illustrate, if easterly winds from a hurricane damage two similar, adjacent hills, the exposed (eastern) aspect of each hill will likely be damaged while the leeward (western) aspect will likely be sheltered, and they will likely be damaged in a similar manner. However, in the same setting, a tornado may cross on the western side of one hill and the eastern side of the other. Thus, the windward and leeward sides of a tornado track cannot be defined at a landscape-scale, and must instead be defined and examined individually because the size of the tornado phenomenon is similar in scale to the size of the topography effecting it. This approach confirmed one purported behavior of tornados and may be useful for examining and testing additional hypotheses regarding how tornados move through complex terrain.

Previous landscape-scale studies of other types of windstorms have revealed general patterns of the effects of topography. The fact that topography influences wind damage severity is well established for hurricanes. Higher slope wind exposure resulted in higher damage from the 1938 New England Hurricane, Hurricane Hugo (Foster and Boose, 1992; Boose et al., 1994), Hurricane Opal (McNab et al., 2004), Hurricane Fran (Xi et al., 2008), and Hurricanes Charley, Katrina, Rita, Gustav, and Yasi (Negrón-Juárez et al., 2014). In some of these studies, other topographic factors have been correlated with higher hurricane damage severity, though not consistently. For example, Xi et al. (2008) found the greatest damage on ridge tops and valley bottoms, while McNab et al. (2004) found the greatest damage at low elevation with less damage on ridges. The effects of topography on other types of windstorms is even less consistent. Lindemann and Baker (2002) found that exposed, east-facing slopes were most vulnerable from a downslope wind event in the Rocky Mountains when winds traveling eastward damaged leeward slopes. Rebertus and Meier (2001) also found that leeward slopes were more heavily damaged from a blowdown in the Missouri Ozarks. While Lindemann and Baker (2002) found that flatter and shallow slopes had the highest level of damage, Evans et al. (2007) found that areas with higher slope variability had experienced the greatest damage after a windstorm in Pennsylvania.

Unlike hurricanes, there is a paucity of studies on topographic influences on non-hurricane, non-tornado blowdowns, and even fewer studies on how tornado damage interacts with topography. Replicate studies using a similar methodology are needed in order to make stronger generalizations on the potential interactions between windstorms and topography. This study comparing two tornados is a step toward this goal, and it presents an objective methodology to apply toward future tornado studies.

4.4.5 Conclusion

Supervised classification offers an objective methodology to remotely measure tornado damage severity at a large scale. Such estimates allow characterization of landscape-scale patterns of tornado damage. Using this method, I found that tornadoes are extremely heterogeneous with roughly equal proportions of high-, medium- and low-severity patches. In line with other types of wind damage, gap sizes resulting from tornado damage exhibit a negative exponential distribution with many small gaps and a few very large gaps. Lastly, tornado damage has complex interactions with topography which can be explored using remote sensing methods.

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Chapter 5

Conclusions

The major findings of this dissertation emphasize several themes regarding the heterogeneity of forest disturbance from tornados, fire, and the interactions between these disturbances.

An important and well-studied interaction between wind damage and fire in forests, is the potential for wind damage to increase fuel and lead to intense and severe wildfires. Because of the potential for disturbances to behave synergistically and drastically alter ecological communities, much of the current research on wind–fire interactions focuses on such synergistic mechanisms. However, in a review of studies on wind–fire interactions (Chapter 1), I discuss antagonistic interactions, or "buffering effects," where wind damage decreases the intensity or severity of fire, which may also play a role in wind–fire interactions. In fact, because low-intensity fires respond strongly to fuel heterogeneity, and because they leave many plant propagates intact, low-intensity fires may be more likely to exhibit buffering effects than severe wildfires. Although synergistic or "amplifying" interactions between the disturbances may be a cause for alarm in some ecosystems, an understanding of buffering mechanisms, including how, when, and to what extent they operate, will inform a basic understanding and management of disturbed forest ecosystems.

A second contribution of this dissertation to the field of forest disturbance ecology is an examination of how wind damage alters fuel conditions and the behavior of prescribed fire. It is well-known that wind damage increases fuel loads (especially large coarse fuels from downed tree boles). In Chapter 2, I explore how wind damage alters fine fuels which are more important to continuity and behavior of low-intensity prescribed fire. One of the major findings of this study is that wind damage can lead to very intense fire. However, much of this effect is limited to downed tree crowns. Outside of downed tree crowns, damage from tornado damage may actually decrease fire intensity. Wind damage leads to patchy fuel distributions across a forest stand, with large masses of fuels in some areas (such as beneath downed tree crowns), and lower masses in areas outside of crowns. Previous studies of wind–fire interactions focus on increases in fuel loads (especially coarse fuels). This study expands the focus of wind–fire interactions to focus, not only on fuel loading, but also on other fuel factors such as composition and arrangement, which may have strong effects on fire intensity and continuity.

A third important aspect of this dissertation is that when examining the interaction between wind damage and prescribed fire, it is clear that both amplification and buffering processes play a role in vegetation responses to the disturbances. In Chapter 3, I describe how wind and fire interactively effect several vegetation parameters such as sapling densities, species richness, or changes in biomass of specific species. Some of these interactive effects were buffering and some were amplifying, and many of these differences could be explained by species-specific differences in responses to disturbances. An important implication of this finding is that combinations of disturbances will rarely interact *either* synergistically *or* antagonistically. Instead, ecosystem responses to compounded disturbances will be a heterogeneous combination of both kinds of interactions because individual species respond differently to combinations of disturbance depending on differences in life-history characteristics.

The second and third chapters of this dissertation explored how a particular level of simulated tornado damage (80% severity) influenced the spatial heterogeneity of fuels, fire behavior, and vegetation response. However, tornado damage severity itself is spatially heterogeneous. Unlike other large forest disturbances such as hurricanes and fires, little is known about the landscape-scale patterns of tornado damage. In Chapter 4, I describe a methodology to remotely measure tornado damage severity, and characterize landscape-scale patterns of tornado damage. Some of the main findings are that (1) tornadoes are extremely heterogeneous with roughly equal proportions of high-, medium- and low-severity patches. In line with other types of wind damage, gap sizes resulting from tornado damage exhibit a negative exponential distribution with many small gaps and a few very large gaps. Lastly, tornado damage has complex interactions with topography which can be explored using remote sensing methods.

Overall, this dissertation highlights the complex linkages between tornado severity, fire behavior, and individual species responses to disturbance. These studies shed light on how tornado damage interactively influences prescribed fire, and how together wind damage and fire have the capacity to interactively influence vegetation. Both tornado damage and prescribed fire are spatially heterogeneous, and it follows that interactions between these disturbances are also variable and spatially complex. However, studies that improve our understanding of mechanisms of these interactions will help unravel this complexity and inform a basic understanding of how these ubiquitous and important disturbances interact.

Appendix A

Supplemental Table for Chapter 2

Table A.1: Parameters for modeling the exponential semivariograms of total fuel (Mg ha-1) in SGeMS (Remy et al., 2009) within treatments including, numbers of lags, lag separation distance, lag tolerance distance, sill, and range distance. The nugget was zero for all models. There was no spatial autocorrelation found within the intact:pre-burn plots.

Treatment combination	No. of lags	Lag separation (m)	Lag tolerance (m)	Sill (Mg ha^{-1})	Range (m)
Gap:pre-burn	10	4	2	27	10
Gap:post-burn	10	2	1	7.5	8.2
Intact:pre-burn	NA	NA	NA	NA	NA
Intact:post-burn	10	5	2.2	4	11

Appendix B

Allometric Equations for Dominant Sapling and Seedling Species at Piedmont National Wildlife Refuge

B.1 Background

I developed allometric equations for dominant sapling and seedling species at Piedmont National Wildlife Refuge (PNWR) in order to interpret changes in sapling and seedling density and size in terms of biomass. My survey of saplings included all woody vegetation ≥ 1.37 m, and seedlings included all woody vegetation < 1.37 m, regardless of age, and often included small basal sprouts from established saplings. At the time of initial vegetation sampling (2011, pre-winching disturbance), the most common sapling species included *Liquidambar styraciflua* (43%), *Acer rubrum* (29%), and *Rhus copallinum* (15%)—together accounting for 87% of all saplings. In 2011, common seedling species were *Pinus taeda* (54%) and *Liquidambar styraciflua* (8%).

B.2 Methods

In order to estimate allometric parameters of dominant sapling species, I collected individuals of *L. styraciflua* (n = 23), *A. rubrum* (n = 23), and *R. copallinum* (n = 18) covering the range of sizes found in vegetation surveys (*i.e.*, 1.37 – 4.5 m). I measured sapling height, dbh, drc *in situ* before collection. For each individual, I dried plants in a drying oven for 72 hours at 70 °C, before measuring total biomass of each sapling to the nearest 1 g.

For each sapling species, I developed allometric equations (1) for instances when only sapling height was available (*i.e.*, dbh and drc measurements were missing) and (2) for instances where height, dbh, and drc were all measured. This allowed application of allometric equations to field-collected data even when data on dbh and/or drc were missing. Allometric equations for saplings took the following form:

$$\log(biomass) = a \cdot \log(h) + i \tag{B.1}$$

$$\log(biomass) = a \cdot \log(h) + b \cdot dbh + c \cdot drc + i \tag{B.2}$$

where *biomass* is measured in kg, h is the sapling height (in m), and *dbh* and *drc* represent sapling diameter at breast height and diameter at root collar, respectively (both in mm).

I also developed an allometric equation with species combined, pooling all allometric data to develop equations to estimate biomass of non-dominant species. Although biomass estimates for one species derived from data that is not species-specific should be interpreted with caution, in general, I found high overlap of allometric regressions among species.

Measurement of seedling biomass was similar to that of saplings. I collected individuals of *P. taeda* (n = 35) and *L. styraciflua* (n = 19). Seedlings were collected

Table B.1: Allometry for dominant sapling species at PNWR based on height. Allometric equation takes the form of log(biomass, kg) = $a\cdot$ height, m + i

Species	a	i	R^2	n	Ht. range (m)
Liquidambar styraciflua	2.292481	-3.11575	0.938	23	1.39–6.30
Acer rubrum	2.702125	-3.65651	0.855	23	1.48–4.70
Rhus copallinum	2.453585	-3.52699	0.839	18	1.40–4.08
Species combined	2.503843	-3.45145	0.876	64	1.39–6.30

across a range of heights mirroring those observed from vegetation surveys and included *P. taeda* from 34–389 mm in height, and *L. styraciflua* with heights ranging from 94–1386 mm. For each of these seedling species, I developed allometric equations based on seedling height using the following form:

$$\log(biomass) = a \cdot \log(h) + i \tag{B.3}$$

where biomass is measured in g, and h is the seedling height in mm.

B.3 Allometry results

Here, I report allometric coefficients for three sapling species and two seedling species collected from PNWR. In general, allometric equations showed strong relationships between biomass and size parameters with R^2 values between 0.84–0.94 for saplings and R^2 values between 0.95–0.98 for seedlings (Figure B.1 and Figure B.2). For sapling allometric equations, inclusion of diameter measurements (dbh and drc) increased R^2 values and lower AIC-scores relative to equations that did not include diameter measurements. Thus, when diameter data was available for saplings, equations from Table B.1 were used. When diameter data was not available, equations from Table B.2 were applied. Allometric parameters for seedlings are shown in Table B.3.

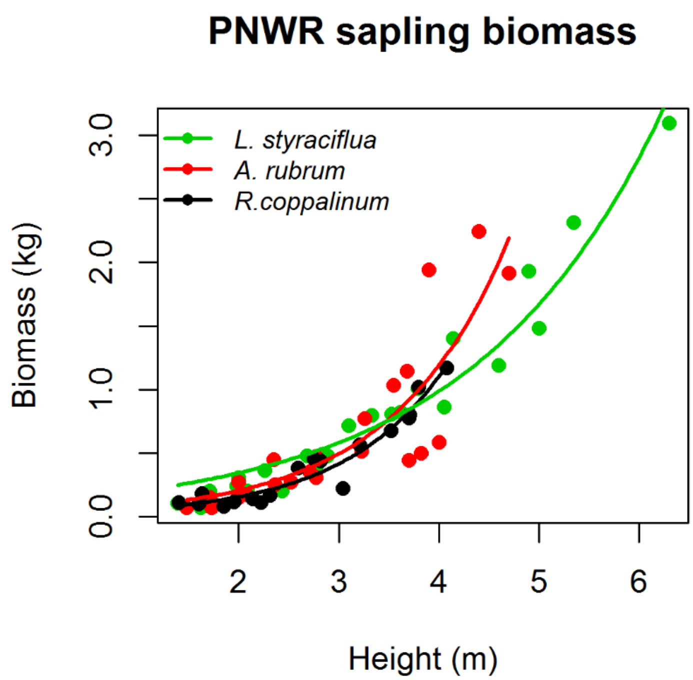

Figure B.1: Relationship between biomass and height for three dominant sapling species at PNWR

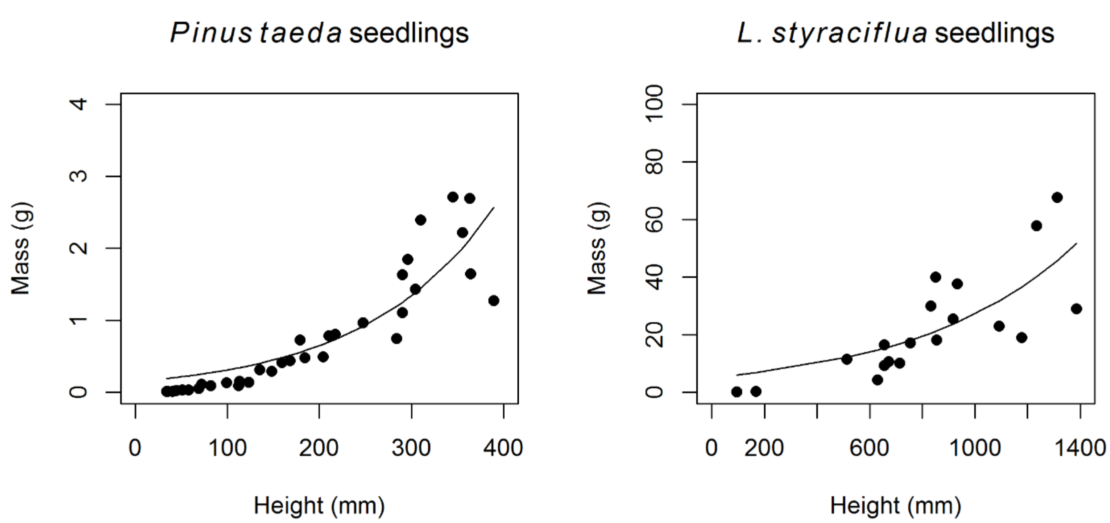

Figure B.2: Relationship between biomass and height for two dominant seedling species at PNWR.

Table B.2: Allometry for dominant sapling species at PNWR based on height, dbh, and drc. Equation takes the form of log(biomass, kg) = $a\cdot$ height, m + $b \cdot dbh$, mm + $c \cdot drc$, mm + i,

Species	a	b	c	i	R^2	n	Ht. range (m)
L. styraciflua	1.1421	-0.0106	0.0523	-3.3264	0.967	18	1.40–4.08
A. rubrum	0.8664	0.00915	0.0640	-3.5952	0.980	23	1.48–4.70
R. copallinum	0.2263	0.06502	0.0442	-3.3486	0.953	23	1.39–6.30
Species combined	1.2284	-0.0137	0.0606	-3.5661	0.953	64	1.39–6.30

Table B.3: Allometry for dominant seedling species at PNWR based on height. Allometric equation takes the form of log(biomass, g) = $a\cdot$log(height, mm) + i

Species	a	i	R^2	n	Ht. range (mm)
Pinus taeda	2.127835	-11.779836	0.979	35	94–1386
Liquidambar styraciflua	2.133832	-11.421012	0.973	19	34–389
Species combined	2.259503	-12.366988	0.977	54	34–1386

Appendix C

Supplemental Tables for Chapter 3

Table C.1: MANOVA or ANOVA coefficients from sapling characteristics with significant overall winch $\times$ burn interaction effects. All reported coefficients come from MANOVA coefficients from tests of sapling structure and composition, except Δ sapling richness, which was a univariate test. All tests were classified into potential interaction types based on sign of coefficients. See Methods for details (liqsty = *Liquidambar styraciflua*, acerub = *Acer rubrum*, rhucop = *Rhus copallinum*).

Response Variable	**Intercept**	**Winch**	**Burn**	**Winch$\times$Burn**	**Interaction Type**
Δsapling density	0.275	0.011	-0.316	0.424	Buffering
Δsapling mass	0.200	0.166	-0.213	-0.013	Amplifying
Δsapling size	0.142	0.035	-0.155	0.052	Buffering
sapling survival	0.983	-0.060	-0.984	0.060	Buffering
Δliqsty sapling density	0.007	0.031	-0.009	-0.007	Amplifying
Δacerub sapling density	0.169	-0.123	-0.169	0.197	Buffering
Δrhucop sapling density	0.016	-0.009	0.024	0.234	Amplifying
Δall other sapling density	0.114	0.125	-0.177	0.063	Buffering
Δliqsty sapling mass	0.060	0.108	-0.063	-0.081	Amplifying
Δacerub sapling mass	0.071	-0.063	-0.072	0.079	Buffering
Δrhucop sapling mass	0.004	0.005	0.002	0.062	Amplifying
Δall other sapling mass	0.023	0.045	-0.031	-0.013	Amplifying
Δsapling richness	0.093	0.014	-0.120	0.181	Buffering

Table C.2: Univariate ANOVA results of individual sapling response variables. Tests with significant winch $\times$ burn interaction effects ($\alpha = 0.0038$, see Methods details) were classified as Amplfiying or Buffering effects (liqsty = *Liquidambar styraciflua*, acerub = *Acer rubrum*, rhucop = *Rhus copallinum*).

Response Variable	**Winch**	**Burn**	**Winch×Burn**	**Interaction**
Δ sapling density	<0.0001	0.2757	0.0008	Buffering
Δ sapling biomass	0.0001	<0.0001	0.5446	ns
Δ sapling size	0.0339	0.0002	0.0972	ns
sapling survival	<0.0001	<0.0001	0.1073	ns
Δ liqsty sapling density	0.1846	0.5707	0.8772	ns
Δ acerub sapling density	0.3642	0.0104	0.0004	Buffering
Δ rhucop sapling density	0.0012	<0.0001	0.0005	Amplifying
Δ other sapling density	0.0001	0.0003	0.4165	ns
Δ liqsty sapling biomass	0.0094	0.0001	0.1127	ns
Δ acerub sapling biomass	0.0006	0.0001	<0.0001	Buffering
Δ rhucop sapling biomass	0.0001	0.0003	0.0005	Amplifying
Δ other sapling biomass	0.0002	0.0015	0.5663	ns
Δ sapling richness	0.0006	0.3090	0.0028	Buffering

Appendix D

Supplemental Material for Chapter 4

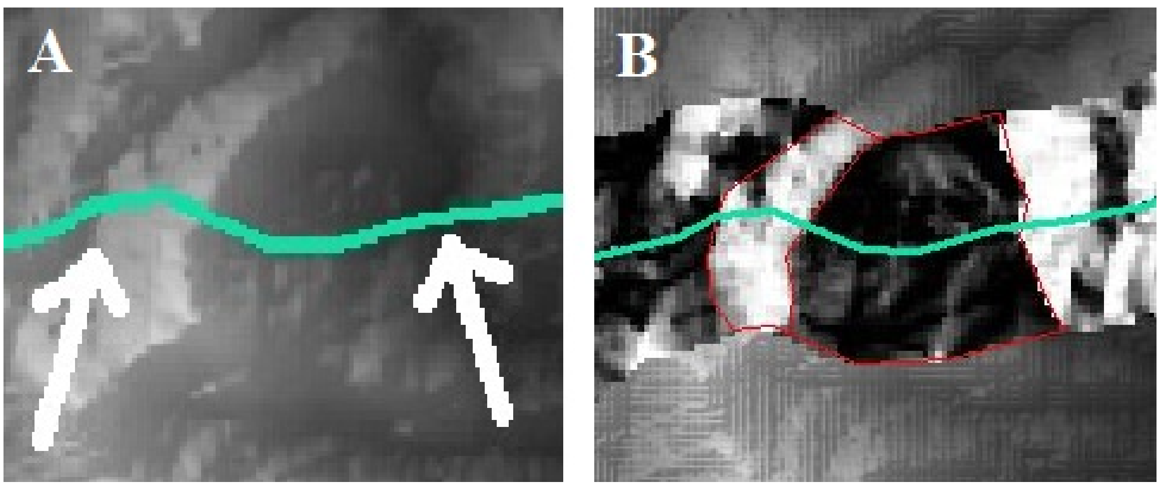

Figure D.1: (A) Portion of the GSM tornado track where tornado path passed perpendicular over a ridge. (B) Same portion of tornado track as panel A with overlay of tornado exposure index which highlights slope aspects facing the direction opposite of the tornado (white), and slope aspects facing in the same direction as the tornado path (black), allowing identification of ridges parallel to the tornado path.

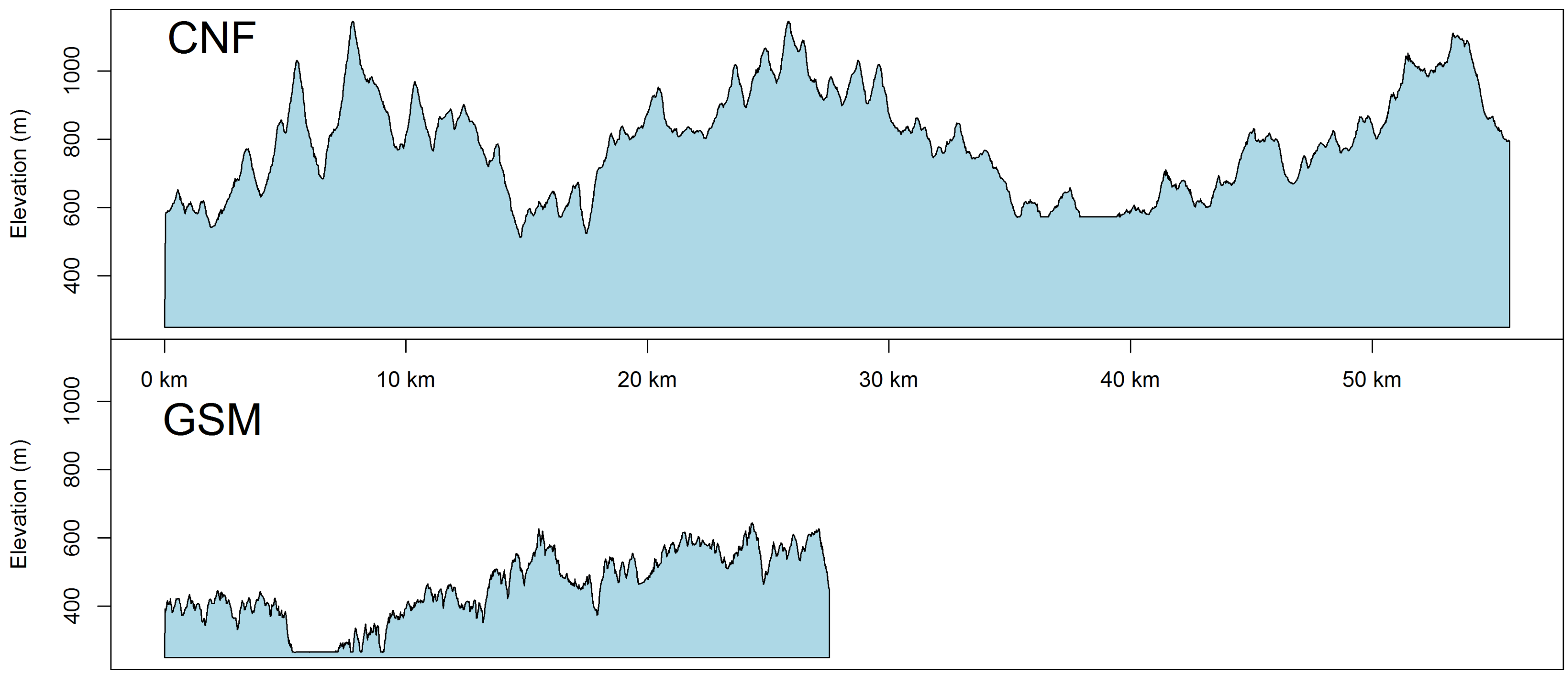

Figure D.2: Elevation profiles along tornado path for (A) Chattahoochee National Forest (CNF), and (B) Great Smoky Mountains National Park (GSM). Note that the CNF track has a larger range of elevations with higher peaks and lower valleys relative to GSM. However, ridges and valleys at CNF are gradually sloping while those at GSM are steeply sloping

Table D.1: Summary of valleys examined for topographic analysis at CNF and GSM tracks

Valley	No. of Transects	Valley length (m)	Mean slope (%)
CNF-1	14	1916	13.9
CNF-2	8	999	14
CNF-3	9	899	14.1
CNF-4	6	600	10.1
CNF-5	9	897	21.8
CNF-6	8	800	13.3
GSM-1	6	620	36.2
GSM-2	13	1519	43.3
GSM-3	17	1987	38
GSM-4	12	1222	40.9
Total	102		

Table D.2: Summary of ridges examined for CNF and GSM tracks

	No. of segments		**Elevation (m)**			**Slope**
Ridge	Front	Rear	Min.	Max.	Range	%
CNF-1	2	2	581	614	33	15
CNF-2	9	11	691	1127	436	20
CNF-3	2	6	528	750	222	17
CNF-4	3	5	825	945	120	14
CNF-5	8	3	812	1009	197	16
CNF-6	5	4	905	1062	157	20
CNF-7	3	3	992	1126	134	22
CNF-8	2	1	933	967	34	14
CNF-9	4	2	914	1018	104	19
CNF-10	3	3	896	1006	110	18
GSM-6	1	1	428	435	7	51
GSM-9	1	1	387	390	3	43
GSM-10	2	1	485	536	51	44
GSM-12	1	1	493	520	27	44
GSM-13	1	1	593	599	6	37
GSM-15	1	2	567	601	34	36

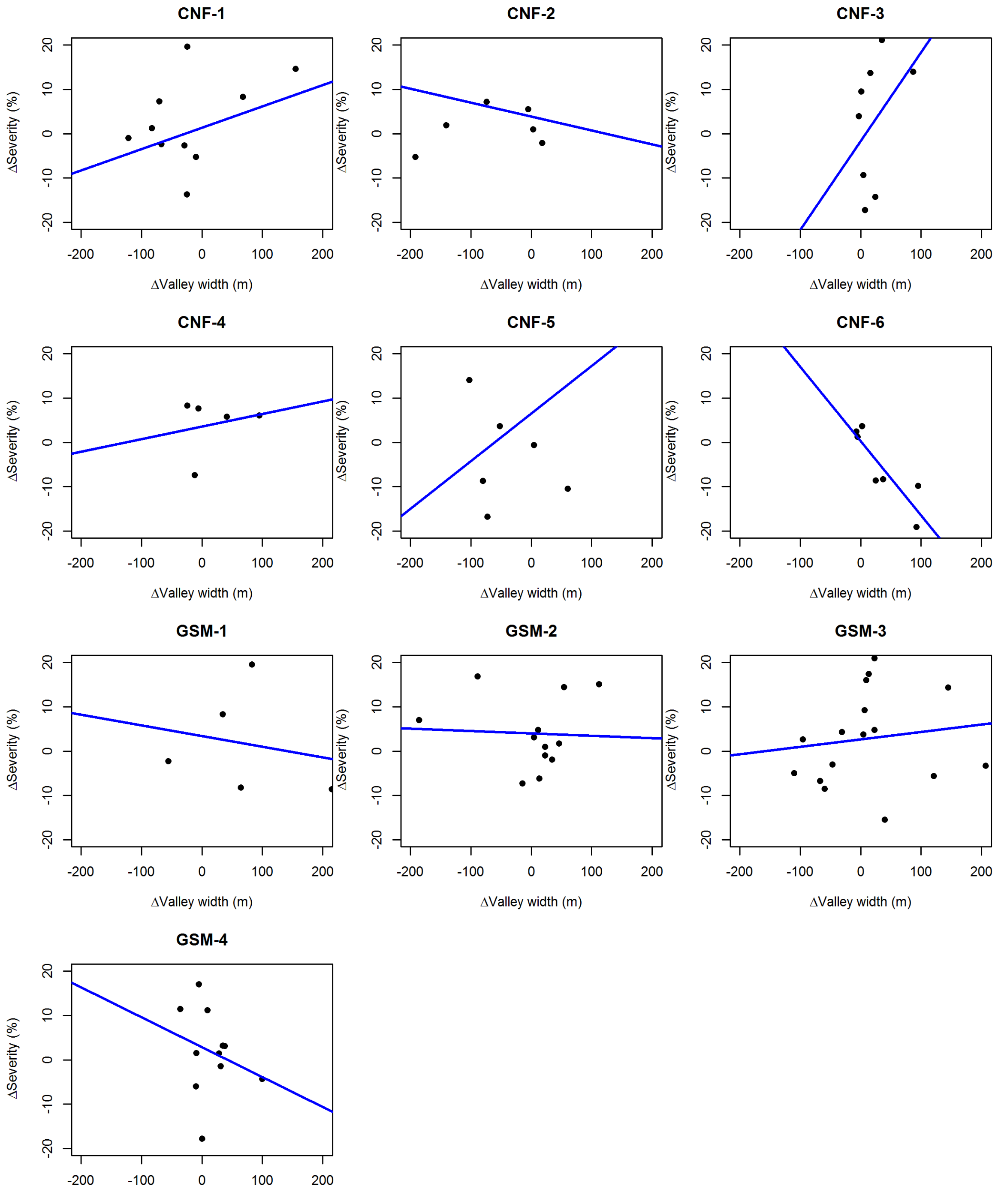

Figure D.3: Relationship between Δ Valley width and Δ Severity for ten valleys at CNF and GSM. Slope coefficients (in order) are CNF 1 = 0.05, CNF 2 = -0.03, CNF 3 = 0.20, CNF 4 = 0.03, CNF 5 = 0.11, CNF 6 = -0.17, GSM 1 = -0.02, GSM 2 = -0.01, GSM 3 = 0.02, and GSM 4 = -0.07.

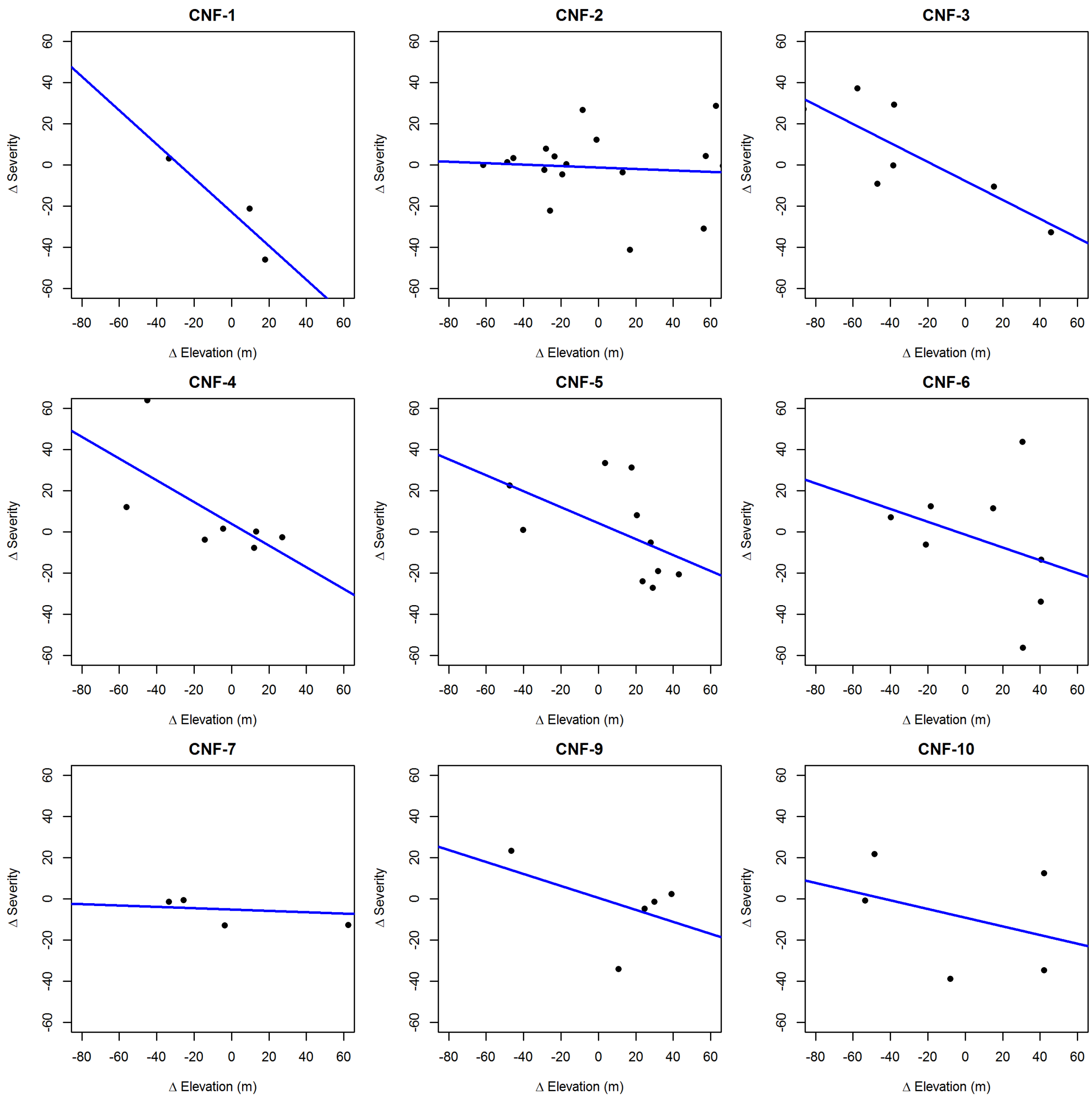

Figure D.4: Relationship between Δ Elevation and Δ Severity for each of nine individual ridges at CNF. Slope coefficients (in order) are CNF-1 = -0.82, CNF-2 = -0.03, CNF-3 = -0.46, CNF-4 = -0.53, CNF-5 = -0.39, CNF 6 = 0.31, CNF-7 = -0.03, CNF-9 = -0.29, and CNF-10 = -0.21.

Table D.3: Confusion matrix for classification using fuzzy matching for Chattahoochee National Forest tornado track. Values in each cell represent the number of training reference plots classified into a particular damage severity level. Cells with two values represent the number of reference plots within ± 10% of the correct damage class, and the number of plots outside of the ± 10% range, respectively. Accuracies were calculated using fuzzy matching counting plots with ± 10% of the correct class as correctly classified

	Reference Classification						**Accuracy**	
Map Classification	*Und.*	*Low*	*Med.*	*High*	*V. High*	Total	Producer	User
Undamaged (0–1%)	346	16,0	0	0	0	362	95.3%	100%
Low (1–25%)	367,24	134	19,11	2	0	557	95.2%	93.4%
Medium (26–50%)	11	27,5	49	17,4	3	116	78.0%	80.2%
High (51–75%)	0	4	17,8	47	16,2	94	92.9%	85.1%
Very High (76–100%)	0	0	5	15,0	57	77	93.6%	93.5%
Total	748	186	109	85	78	1206	Overall:	93.4%

Table D.4: Confusion matrix for classification using fuzzy matching for Great Smoky Mountains National Park tornado track. Fuzzy matching and accuracy assessment details same as in Table D.3

	Reference Classification						**Accuracy**	
Map Classification	*Und.*	*Low*	*Med.*	*High*	*V. High*	Total	Producer	User
Undamaged (0–1%)	54	4,0	0	0	0	58	88.4%	100%
Low (1–25%)	204,21	121	18,13	2	0	379	96.1%	90.2%
Medium (26–50%)	11	21,4	40	15,7	2	100	76.7%	76.0%
High (51–75%)	2	2	8,2	36	9,6	65	0.877	81.5%
Very High (76–100%)	0	0	5	13,0	47	65	87.5%	92.3%
Total	292	152	86	73	64	667	Overall:	88.5%

Table D.5: Land area affected by various levels of damage severity in bins of 5% for CNF and GSM tracks.

Damage Severity	**CNF Track (EF-3)**		**GSM Track (EF-4)**	
	Area (ha)	Area (%)	Area (ha)	Area (%)
0-5 %	7876	65	1748	31.7
5-10 %	1334	11	1090	19.8
10-15 %	606	5.0	633	11.5
15-20 %	350	2.9	384	7.0
20-25 %	246	2.0	254	4.6
25-30 %	184	1.5	188	3.4
30-35 %	156	1.3	151	2.7
35-40 %	138	1.1	126	2.3
40-45 %	120	1.0	103	1.9
45-50 %	111	0.9	96	1.7
50-55 %	104	0.9	85	1.5
55-60 %	100	0.8	80	1.5
60-65 %	97	0.8	81	1.5
65-70 %	96	0.8	79	1.4
70-75 %	91	0.8	73	1.3
75-80 %	96	0.8	73	1.3
80-85 %	99	0.8	72	1.3
85-90 %	107	0.9	71	1.3
90-95 %	115	1.0	74	1.3
95-100 %	98	0.8	55	1.0

Table D.6: Distribution of estimated area affected (ha) by EF-3 and EF-4 tornados using NOAA's estimated path lengths and widths. See Discussion for details and assumptions.

Estimated land area affected (ha)		
Percentile	EF-3	EF-4
0	0	0
5	1	24
10	7	56
15	15	116
20	29	185
25	45	254
30	66	336
35	96	486
40	132	596
45	184	736
50	235	830
55	294	1001
60	388	1219
65	508	1497
70	618	1876
75	804	2512
80	984	2978
85	1301	3992
90	1860	5286
95	3258	9110
100	29060	33813

Table D.7: Summary of landscape metrics from CNF tornado track summarized into four damage classes

Patch area and number

Class	Total area affected, ha	Number
10–25%	1,051 (9.9%)	8099
26–50%	709.0 (5.8%)	3894
51–75%	488.4 (4.1%)	2170
76–100%	516.0 (4.3%)	771

Patch size (ha)

Class	Mean patch size (± se)
10–25%	0.130 ± 0.0033
26–50%	0.182 ± 0.0069
51–75%	0.225 ± 0.0123
76–100%	0.669 ± 0.1147

Patch Shape (unitless)

Class	Mean shape index (± se)
10–25%	1.20 ± 0.0050
26–50%	1.27 ± 0.0092
51–75%	1.31 ± 0.0138
76–100%	1.27 ± 0.0212

Distance to Nearest Neighbor (m)

Class	Mean distance (± se)
10–25%	53.6 ± 0.30
26–50%	58.3 ± 0.79
51–75%	59.1 ± 1.30
76–100%	72.0 ± 2.69

Table D.8: Summary of landscape metrics from GSM tornado track summarized into four damage classes.

Patch area and number

Class	Total area affected, ha	Number
10–25%	1,271 (23.1%)	4729
26–50%	664 (12.0%)	3021
51–75%	398 (7.2%)	1492
76–100%	345 (6.2%)	579

Patch size (ha)

Class	Mean patch size (± se)
10–25%	0.236 ± 0.0123
26–50%	0.220 ± 0.0116
51–75%	0.266 ± 0.0178
76–100%	0.597 ± 0.1286

Patch Shape (unitless)

Class	Mean shape index (± se)
10–25%	1.32 ± 0.0106
26–50%	1.29 ± 0.0122
51–75%	1.35 ± 0.0184
76–100%	1.28 ± 0.0251

Distance to Nearest Neighbor (m)

Class	Mean distance (± se)
10–25%	45.6 ± 0.18
26–50%	53.5 ± 0.51
51–75%	59.1 ± 1.38
76–100%	70.5 ± 2.66