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A review and classification of interactions between forest disturbance from wind and fire

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ABSTRACT

Current research on interactions between ecological disturbances emphasizes the potential for greatly enhanced ecological effects that may occur when disturbances interact. Much less attention has focused on the possibility of disturbance interactions that buffer ecological change. In this review, we discuss and classify evidence for interactions between two forest disturbances common in eastern North America—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 synthesis of disturbance interactions. First, buffering interactions between wind damage and fire may be more important when fire intensity is low. Second, wind–fire interactions related to changes in fuel may vary with climatic conditions, with regional differences, and with intensity or severity of individual disturbances. Third, both amplifying and buffering effects may co-occur in a spatial mosaic through a variety of interaction mechanisms. In this respect, the concept of ecosystem response to multiple disturbances parallels that of classical models of successional pathways. It is useful to conceptualize ecosystem response to compounded disturbances as a diverse collection of individual, co-occurring mechanisms of interaction rather than considering multiple disturbances to be wholly amplifying or wholly buffering. Future studies on wind–fire disturbances that explicitly examine mechanisms of interactions and the factors that govern them will aid in understanding these ecologically important and ubiquitous forest disturbances.

1. Introduction

The process of successional change following single disturbances has long been studied by ecologists (e.g., Cowles, 1899) but the effects of multiple, or compounded disturbances have received less attention (Turner, 2010). Much of the recent research on compounded disturbances suggests that initial disturbances can alter ecosystems in ways that make subsequent disturbances more probable, intense, or severe (Buma, 2015; Paine et al., 1998; Scheffer et al., 2001). For example, disturbances result in altered ecosystem structure and function and leave behind important biological legacies (Franklin et al., 2000, 2007) that can change the manner in which an ecosystem is impacted by or recovers from subsequent disturbances (Buma, 2015; Frelich and Reich, 1999; Paine et al., 1998). Thus, disturbances may interactively impact the resilience of ecosystems to subsequent disturbances (i.e., the recovery of an ecosystem to its previous state following disturbance; Calow, 1999).

Because unanticipated responses following compounded disturbances add uncertainty to ecological predictions of disturbance effects and ecosystem recovery (Frelich and Reich, 1999; Paine et al., 1998), an understanding of the potential mechanisms of interactions between common forest disturbances can inform models of ecosystem change and forest management following natural disturbances. This review focuses on classifying and evaluating evidence for interactions between two common disturbances 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 widespread (3.8 million ha treated in 2011, Melvin, 2012) and is used for a variety of management purposes including wildlife management (Main and Richardson, 2002), ecological

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restoration (Brewer et al., 2015; North et al., 2007) and reduction of hazardous fuels (Agee and Skinner, 2005; Fulé et al., 2012).

Understanding interactions between wind damage and fire is important due to 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 (Brewer, 2016; Buma and Wessman, 2011; Cannon and Brewer, 2013; Cannon, 2015; Cannon et al., 2014). 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*) savannahs (Gilliam et al., 2006; Myers and Van Lear, 1998). Unravelling the mechanisms by which these disturbances interact is an important component of a mechanistic understanding of 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 interaction type and direction of the interaction and (2) present hypothesized mechanisms for the interactions along with available evidence for these hypotheses.

2. Framework for classifying wind–fire disturbance interactions

In a recent review, Buma (2015) outlined a framework for characterizing disturbance interactions based on how legacies of an initial disturbance drive interactions with subsequent disturbances. We build on this framework as a classification scheme to review mechanisms of interactions between forest wind damage and fire, and we add a second axis for classification based on the whether the interaction is synergistic or antagonistic. Disturbance interaction mechanisms can be classified into two types based on whether the mechanism alters the resistance or resilience of an ecosystem to a subsequent disturbance. Disturbance legacies may either increase or decrease ecosystem *resistance to* a second disturbance (Buma, 2015; Simard et al., 2011). For example, hurricane damage may increase surface fuels and increase the probability, intensity or severity (*sensu* Keeley, 2009) of a subsequent wildfire (Myers and Van Lear, 1998). Disturbance legacies may alter ecosystem *resilience* to a second disturbance by creating legacies that alter the speed or trajectory of recovery following a subsequent disturbance. (Fig. 1; Buma, 2015; Paine et al., 1998). Wind damage may reduce adult density and seed availability, causing delayed recovery following fire (Buma and Wessman, 2011). 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).

A second axis on which to classify interactions is based on whether the disturbances act in synergy (Folt et al., 1999). Disturbance interaction studies often emphasize that compounded disturbances interact in a synergistic manner where the effect of the first disturbance

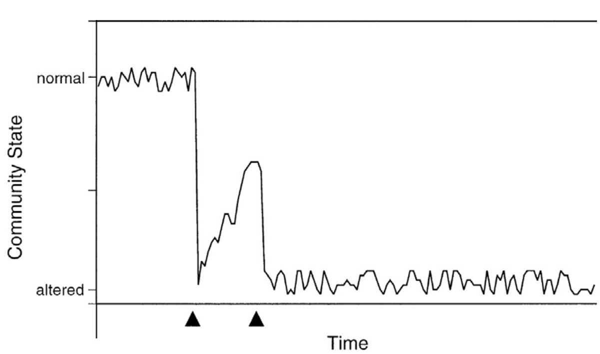

Fig. 1. Schematic illustration of a community affected by two disturbances (arrows) in rapid succession, resulting in altered community state.
Figure from Paine et al. (1998)

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 shift ecosystem trajectories (by decreasing resilience). Dramatic amplifying interactions such as those cases outlined by Paine et al. (1998) 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, where one disturbance decreases the impact of a second disturbance (i.e., increased resistance or resilience). Such findings highlight the importance of a more comprehensive view of disturbance interactions that includes buffering effects. Early hypotheses of insect outbreak–fire interactions suggested that mountain pine beetle outbreaks can increase the severity of wildfires by increasing fuel loads (Amman and Schmitz, 1988). However, a growing body of recent research finds little evidence that insect outbreaks impact fire extent (Flower et al., 2014; Hart et al., 2015; Meigs et al., 2015), and increases in fire severity may be short-lived (Harvey et al., 2014a). In fact, some insect outbreaks may even reduce fire likelihood (Meigs et al., 2015) or severity (Harvey et al., 2014a). Thus, interactions between disturbances may be classified along a spectrum of additivity, and may produce amplifying or buffering effects. As we argue below, the latter may be more common with low-severity fire when coarse fuels are not consumed (e.g., Cannon et al., 2014). Although Buma (2015) recognized the occurrence of buffering effects, they were not emphasized in the framework, though they may be common in some systems (Darling and Côté, 2008).

In this review of wind–fire interactions, we classify and discuss mechanisms of disturbance interactions along two axes: interaction type and interaction direction. (Table 1). Disturbance legacies are temporally dynamic—some legacies are ephemeral (e.g., changes in surface fuel structure) while others endure (e.g., changes in forest structure), thus it is crucial to consider that the time elapsed between disturbances may govern which mechanisms drive interaction processes (Buma, 2015). Temporal dynamics following disturbances may differ dramatically depending on the disturbance type, climatic conditions, or ecological system under consideration. For example, interactions between insect outbreaks and fire are, in part, driven by the time elapsed between disturbances. Outbreaks of mountain pine beetle have been shown to increase fire severity in the years immediately following outbreaks (green tree/red-stage, < 3 years) and may have a negative effect on fire severity under extreme conditions in later stages (gray-stage, 3–15 years; Harvey et al., 2014a). Similarly, the interactions between wind damage and fire may also be driven, in part, by fuel temporal dynamics (i.e., decomposition of downed fuels and vegetation response). In this review, we emphasize the diversity of interaction mechanisms that exist along gradients of interaction direction and interaction types. However, a paucity of studies of interacting wind and fire disturbances make generalizations of how dominant interaction mechanisms may differ through time tenuous. Though not explicitly integrated into the current framework, relevant aspects of temporal dynamics of disturbance interactions are discussed as appropriate. Although the order in which disturbances occur can influence their effect and interaction (Fukami, 2001), we focus on mechanisms of interaction when wind damage precedes fire. Mechanisms of interaction when fire precedes wind damage (e.g., Cannon et al., 2015; Matlack et al., 1993; Platt et al., 2002; Schulte and Mladenoff, 2005) warrant separate discussion.

3. Mechanisms altering resistance to fire

The major factors influencing fire behavior include fuel characteristics (e.g., fuel type, size and arrangement; Mitchell et al. 2009), weather (e.g., temperature, humidity and wind), and topography (e.g., slope, aspect and barriers; Pyne, Andrews & Laven 1996) Wind damage

Table 1
Summary of proposed interaction mechanisms reported among studies of wind damage and fire arranged by mechanism type (altered resistance or resilience) and interaction direction (amplifying or buffering effects).

Interaction type	Interaction direction: Amplifying effects (Synergisms)	Interaction direction: Buffering effects (Antagonisms)
Wind damage alters impact of fire (Resistance)	1. Increased temperature and decreased humidity within gaps (Matlack, 1993) 2. Fuel loading increases probability, intensity or severity of fire (Kulakowski and Veblen, 2007; Liu et al., 2008; Myers and Van Lear, 1998; Urquhart, 2009) 3. Pyrophilic species increased (*Imperata cylindrica;* Holzmueller and Jose, 2012) 4. Reduction of stem diameter and bark thickness (Wolfe et al., 2014)	1. Reduction of leaf litter input disrupts fuel continuity (O'Brien et al., 2008; Ross et al., 2009) 2. Patchy fuel decreases fire intensity outside tree crowns (spatially variable, Cannon and Brewer, 2013; Cannon et al., 2014) 3. Accelerated succession to less flammable plant communities (Holzmueller et al., 2012; Nowacki and Abrams, 2008) 4. Potentially increased survival on tip-up mounds (fire refugia, Cannon, 2015) 5. Increased sapling growth in wind damage plots may confer resistance to top-kill (Cannon and Brewer 2013)
Wind damage alters response to fire (Resilience)	1. Delayed regeneration after removal of adults (Buma and Wessman, 2011; D'Amato et al., 2011; Liu et al., 2008; Urquhart, 2009) 2. Delayed regeneration after mortality of serotinous cones (Buma and Wessman, 2011)	1. Greater sapling basal sprouting permits accelerated recovery (Cannon, 2015) 2. Differential species responses useful for restoration (Brewer, 2016; Cannon and Brewer, 2013)

has the potential to create disturbance legacies impacting several fuel characteristics and microclimate conditions in ways that may either increase or decrease the probability, intensity, or severity of fire.

3.1. Amplifying effects: mechanisms decreasing ecosystem resistance to fire

One of the more conspicuous legacies of severe wind disturbance is mortality of adult trees and abundance of potentially combustible coarse and fine woody debris transferred to the forest floor (Busing et al., 2009; Everham and Brokaw, 1996; Holzmueller and Jose, 2012). The potential for wind damage to increase the probability, intensity or severity of fire through increased fuel loading is the most intuitive and well-documented interaction mechanism between these disturbances (Myers and Van Lear, 1998; Webb, 1958). Two studies in coastal regions of the Gulf of Mexico and Caribbean Sea confirm that historically, severe wildfires 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, evidence of wildfire (minor charcoal peaks) were associated with every major hurricane. Using a similar approach, 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).

Co-occurrence of wind damage and fire does not provide evidence that wind damage alters the intensity or severity of fire; however, co-occurrence may lend support to the concept of wind damage and fire interacting as linked disturbances (Buma, 2015). Studies of contemporary disturbance regimes, including a reconstruction of forest disturbances in old growth forests in New Hampshire during the period from 1635 to 1938 revealed the co-occurrence of 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). In a landscape-scale study of subalpine forests in northwestern Colorado, Kulakowski and Veblen (2007) noted that forest disturbance history was a good predictor of fire severity based on remotely sensed fire severity data, finding that forested stands that received severe blowdown in 1997 also experienced severe wildfires in 2002. Johnson et al. (2013) modeled fire behavior following forest wind damage followed by fuel reduction treatments and found that fuel reduction treatments reduced several aspects of modeled wildfire 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.

Other reconstructions of contemporary disturbance regimes also include anecdotal evidence of co-occurrence of severe wind and wildfire. In a dendrochronological reconstruction of forests of the Great Lakes region, Frelich and Lorimer (1991) support the claim by Stearns (1949) that fires rarely affect undisturbed forest and instead occur in areas with recent disturbance such as logging activity or wind disturbance. Canham and Loucks (1984) used General Land Office (GLO) survey records to reconstruct catastrophic windthrow during the presettlement period (1834–1873) in Wisconsin. The authors point out that personal notes of surveyors include descriptions of major forest fires in extensive areas of windthrown forests. However, Whitney (1986) points out that quantitative estimates of co-occurrence of fire and other disturbances is difficult to ascertain from GLO surveys because legacies or other evidence of previous forest disturbances may have become obscured to surveyors by subsequent fires. Other anecdotal support for the linkage of wind and fire disturbances comes from Martin et al. (2011).

In a survey of stands that burned during a 2005 escaped fire in cloud forests of the Dominican Republic, the authors note that four of six extensively burned stands surveyed displayed evidence of fuel accumulation because of previous hurricane disturbance.

It is clear that wind damage increases overall surface fuel loading, especially among coarse fuels, but legacies of wind disturbance includes other changes to fuel structure such as altered spatial arrangement of surface fuels. Cannon et al. (2014) found that experimental wind damage led to higher prescribed fire intensity in areas such as downed tree crowns where fuels were highly aggregated, leading to localized patches of higher intensity fire relative to areas outside of downed tree crowns. It should be noted that outside of downed tree crowns, some fire characteristics were decreased by wind damage, indicating that both amplifying and buffering can co-occur, as discussed in the following sections.

The previous studies each emphasize increased fuel loading and arrangement as important wind disturbance legacies that produce amplifying interactions with fire. Wind disturbance has additional legacies that affect fire behavior via direct and indirect effects on fuels. Forest blowdowns create canopy openings that can lead to increased air temperature and decreased humidity in gaps (Denslow, 1980; Matlack, 1993; Schulz, 1960). Such changes to the abiotic microenvironment can accelerate fuel drying and lead to fuel beds with greater fuel availability and lower fuel moisture relative to closed canopy stands. In addition, indirect mechanisms whereby wind damage alters vegetation and leads to changes in fire intensity severity have been documented. 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 pyrophilic species, such as warm-season grasses, which alter fuel beds and the behavior of subsequent fires. Wind disturbance and its resulting biotic and abiotic legacies can alter fuel beds via increasing fuel loading, aggregation and availability. Each of these changes has the potential to facilitate fire ignition and spread and to increase the intensity of fire (Pyne et al., 1996).

In contrast to studies documenting wildfires following severe blowdowns, two reconstructions of fire regimes in the northeastern U.S. did not find co-occurrence of wind damage and fire, underscoring that synergistic interactions between severe wind damage and fire are not inevitable. A study by Busby et al. (2008) used a compilation of historical and dendroecological records to reconstruct disturbance history for *Fagus*-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. Several factors such as lack of fire spread from the mainland, or variation in ignition patterns or fire regimes on islands (Bergeron, 1991) may account for the lack of amplifying interactions in some cases. 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 argued that wind–fire interactions were rare and likely dependent on events such as droughts. Interestingly, the authors 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 of small diameter trees, which are less susceptible to windthrow than forests composed of larger diameter trees (Everham and Brokaw, 1996). Exceptions to amplifying effects between wind damage demonstrate that synergistic interactions are not inevitable and highlight that feedbacks with climatic factors such as ignition patterns and weather conditions play an important role in mediating disturbance interactions.

Other important legacies of wind disturbance include changes in forest structure (e.g., distribution of tree sizes), which increases forest vulnerability to fire (Wolfe et al., 2014). Wind disturbance alters forest structure by removing larger trees and often initiating basal sprouting (Everham and Brokaw, 1996), 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 by fire (aboveground mortality) and generally increase with stem diameter or tree size. Reduction of mean stem diameter and, by extension, mean bark thickness by wind damage may make forests more vulnerable to fire (Wolfe et al., 2014). In the short term, wind damage can increase fire intensity or severity directly by increasing fuel inputs, but also indirectly through changes in species composition and forest structure.

3.2. Buffering effects: mechanisms increasing ecosystem resistance to fire

In contrast to amplifying effects, some legacies resulting from wind disturbance may instead reduce the intensity, probability or extent of subsequent fire. For example, forest blowdown creates canopy gaps which are known to have reduced fuel input from leaf litter, interrupting an important component of fuel continuity in low-intensity fires (O'Brien et al., 2008). Similarly, Ross et al. (2009) described a wind-–fire interaction mechanism whereby storm surge indirectly impacts fire spread. In pine forests of the Florida Keys, frequent surface fires prevent succession to hardwood forests. However, wind damage and hurricane storm surge to pine stands eliminate many salt-sensitive species—many of which are crucial producers of fine fuels necessary to carry frequent fires.

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) also influence fire behavior (Pyne et al., 1996). In intense wildfires, the amount of large woody debris may drive combustion, but in low-intensity surface fires, such as those more typical of prescribed burns, larger fuel particles (e.g., 2.5 cm diameter) can be left unconsumed and combustion is instead driven by the composition and arrangement of fine fuels (e.g., Cannon et al., 2014).

Cannon et al. (2014) found that experimental wind damage did not increase the loading of consumable fine fuels, (< 2.5 cm diameter), but instead altered spatial arrangement of consumable fine fuels. Fine fuels in control plots were more evenly distributed, whereas in wind-damaged areas, fine fuels were patchily distributed (with high fuel loads in some areas and low fuel loads in other areas). Consequently, fire intensity metrics were greater in experimental wind-damaged areas compared to control plots, but the increase in fire intensity was limited to portions of simulated gaps within downed tree crowns. Outside of downed tree crowns, measures of fire intensity were consistently lower than control plots (Fig. 2). This pattern suggests that wind damage can dramatically increase fuel loads in some areas (such as directly beneath downed tree crowns), and lead to reductions in fuel abundance in other areas—potentially disrupting fuel continuity during low-intensity fires. This finding is intriguing because it suggests that, at least with low-intensity fires, disturbance legacies can simultaneously lead to both amplifying and buffering interactions with fire by altering fuel composition and continuity depending on the scale observed. Cannon and Brewer (2013) report similar variation in intensity 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 (mean = 208 °C) and intact plots (mean = 219 °C), but much greater temperature variability in tornado damaged plots (range = 79–660 °C) compared to intact plots (range = 163–288 °C), highlighting the potential for spatial variability in fire characteristics in

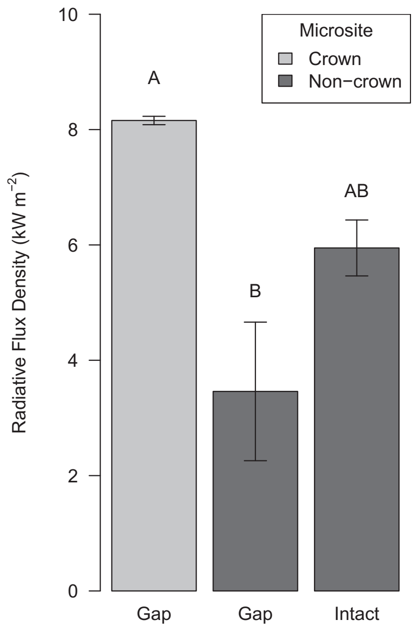

Fig. 2. Prescribed fire mean intensity in forest gaps and intact stands. Error bars represent one standard error of the mean. Means sharing the same letter are not significantly different (Tukey's HSD, $P_{adj} < 0.05$).
Figure from Cannon et al. (2014)

wind damaged forest stands.

One conspicuous legacy of forested areas following blowdown is the presence of large tip-up mounds formed when trees are uprooted which may play a role in wind–fire interactions. Mounds typically have elevations 0.5–2.5 m above the forest floor, persist for decades, and host distinct vegetation and microclimate (Beatty, 1984; Peterson et al., 1990; Sobhani et al., 2014; Ulanova, 2000). The elevation of plants on mounds can serve as refugia from herbivores (Krueger and Peterson, 2006). Analogously, seedlings established on tip-up mounds are at a higher elevation than the surrounding forest floor, and may be less exposed to subsequent fire. This hypothesis has been tested in one study combining experimental wind damage and prescribed fire (Cannon, 2015). Cannon (2015) compared survival of seedlings on tip-up mounds to those on intact soil in both burned and unburned stands and suggested that mounds have harsher microclimate conditions less conducive to seedling survival, but they may contribute to seedling survival during fire. It should be noted that Cannon (2015) also noted high soil instability on the highest portions of mounds (0.5–1.5 m) where seedling survival was 0% in burned areas. Soil instability is typical of newly created tip-up mounds (Peterson et al., 1990), and the benefit of reduced mortality from fire may be offset in some cases by instability of mound microsites, especially when wind and fire disturbances occur in quick succession (i.e., < 2 years). Height and size of tip-up mounds increases with tree diameter (Sobhani et al., 2014), thus 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 length.

Wind damage may reduce the likelihood, intensity, or severity of fire through changes in forest composition and structure. Wind damage severity can alter the structure or composition of forests via preferential mortality of overstory rather than understory trees or via species-specific mortality (Everham and Brokaw, 1996). Through preferential mortality of early-seral species, disturbances such as wind damage can lead to accelerated succession if late-seral species dominate the understory stratum (e.g., Abrams and Nowacki, 1992; Holzmueller et al., 2012). Nowacki and Abrams (2008) coined the term 'mesophication' to describe the process whereby fire suppression facilitates succession of fire-frequent forests to less flammable systems dominated by mesic species. Similarly, wind damage could lead accelerate changes in tree communities that sustain a less flammable fuel bed (e.g., *Acer* spp.), reducing the potential likelihood or intensity of fire (Abrams and Nowacki, 1992; Holzmueller et al., 2012).

Much research has focused on the interactions of wind damage and fire mediated through fuel, but interacting effects at the scale of 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). As discussed above, structural changes following wind disturbance may create stands with lower mean diameter and bark thickness that are temporarily more vulnerable to fire in the short-term (Wolfe et al., 2014). However, legacies of canopy-opening disturbances increase resources, especially light, and release understory trees and saplings from competition. The rapid growth of stems or sprouts following wind damage allows individual stems to recruit to larger size classes—becoming more likely to resist mortality from subsequent fire. As the time elapsed between disturbances increases, this effect may become more important. We know of no studies testing this hypothesis explicitly; however, Cannon and Brewer (2013) studied the effects of a prescribed fire 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. Following wind damage that snaps trees, species can vary widely in resprouting responses (Peterson and Pickett, 1991). Because the mechanism depends on resource allocation and physical characteristics of individual species (e.g., rates of stem diameter growth or bark thickness), the magnitude and importance of this buffering mechanism can vary spatially and temporally in a given pair of disturbances depending on the composition of the regenerating understory.

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; Johnstone et al., 2015). Disturbance interactions may delay recovery or alter succession of the post-disturbance vegetation 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, we review studies of combinations of wind and fire disturbances that demonstrate amplifying effects (i.e., those that decrease resilience) and those that demonstrate buffering effects (i.e., those that increase resilience).

4.1. Amplifying effects: mechanisms decreasing ecosystem resilience after fire

Examples of amplifying interactive 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). Removal of seed sources 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, that *Pinus* populations decreased after hurricane damage and fires. In most cases, *Pinus* appeared to quickly rebound, except in two cases where the authors speculate that young trees were killed by fire before reaching sexual maturity, thus reseeding and regeneration of the affected stands was delayed. In northern Wisconsin jack pine (*Pinus banksiana*) forests, D'Amato et al. (2011) documented combinations of catastrophic blowdown (1999) and wildfires (2007) that 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 sprout asexually), while those receiving only wildfires were dominated by jack pine which reproduce via serotinous cones (Burns and Honkala, 1990). The authors attribute the shift in composition and failure of jack pine regeneration to the short recovery time (approximately 8 years) between blowdown and wildfire, which precluded jack pine from reaching sexual maturity and providing seed source to the post-fire stand. Similarly, Frelich and Reich (1999) review 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 modeled fire characteristics and found that in stands with severe wind damage, fire residence time and temperature increased, as did the duration of lethal seed temperature for lodgepole pine, (Buma and Wessman, 2011; *Pinus contorta*, Knapp and Anderson, 1980). Stands with severe wind damage were more distant from potential seed sources relative to intact stands and regeneration was greatly reduced in stands receiving severe blowdown and fire (Fig. 3). The authors attribute the differences to increased seed mortality and isolation from seed sources in wind-damaged stands (Buma and Wessman, 2011).

Research following the severe 1988 wildfires in lodgepole pine forests of Yellowstone National Park revealed that the heterogeneous pattern of wildfire helped ameliorate seed source limitation and recovery following fire (Turner et al., 2003, 1994). Complex landscape patterns of damage have been found following wind damage from hurricanes (Chambers et al., 2007) and tornadoes (Cannon et al., 2016) which may likewise facilitate forest recovery. Thus, delayed regeneration following combined wind damage and fire is surprising and contrasts with what may be expected following either wind or fire disturbances individually.

Relatively few case studies of forest recovery following wind damage and fire are available, thus two important caveats should be noted. First, in each of the cases cited above, fire disturbance was catastrophic and severe. As discussed in the next section, in cases of low-intensity fire regeneration processes may be dominated by interaction mechanisms that have buffering rather than amplifying effects. Second, among the contemporary examples cited in this section, the disturbances occurred in relatively rapid succession (5–8 years, Buma and Wessman, 2011; D'Amato et al., 2011). As time between disturbances increases, the expected interactions may change. For example, limitation of seed sources may become less severe as wind-damaged stands recover over time.

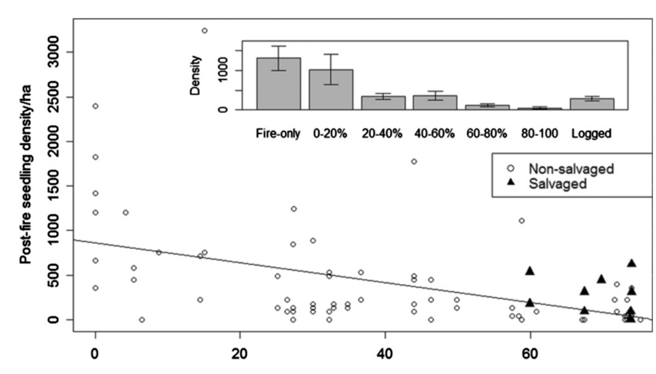

Fig. 3. Following wind damage and subsequent wildfire in a Colorado conifer forest, post-fire seedling decreased with increasing wind damage severity.
Figure from Buma and Wessman (2011)

4.2. Buffering effects: mechanisms increasing ecosystem resilience after fire

While studies demonstrating amplifying effects on forest resilience are limited, studies of buffering effects, where wind damage increases ecosystem resilience after fire are even more limited. This disparity may be explained, in part, by the research focus on the combinations of wind and severe fire rather than wind and low-intensity fire. Intense wildfires are often severe enough to remove significant biological legacies that are important for resilience such as advance regeneration 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 resilience 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). Many woody species that are top-killed by fire have the ability to resprout rapidly by utilizing belowground carbohydrate reserves (Hodgkins, 1958; Johnson et al., 2002; Robertson and Ostertag, 2009). Higher survival of propagules following low-intensity fire may poise stands for rapid recovery following compounded disturbances.

Propagules surviving low-intensity fire may interact with legacies of previous wind damage in a way that enhances ecosystem resilience. Increased availability of light and other resources following a canopy-opening disturbance may facilitate rapid regrowth of understory vegetation, by enhancing the growth rate of basal sprouts emerging from top-killed seedlings and saplings. In an experiment combining canopy thinning followed by multiple prescribed fires, Iverson et al. (2008) found that increase in canopy openness prior to fires enhanced competitiveness of oak regeneration. Cannon (2015) compared resprouting patterns of top-killed saplings following combinations of experimental wind damage and prescribed fire. Basal sprout biomass in plots receiving both experimental wind damage and prescribed fire (one year apart) was greater than in plots receiving prescribed fire only (Fig. 4). This enhanced growth of sprouts in plots receiving both disturbances could have resulted from (1) increased light and soil resources following wind damage allowing faster growth of sprouts, (2) increased sapling allocation to belowground reserves during the period between disturbances, which could allow more rapid resprouting, or (3) both

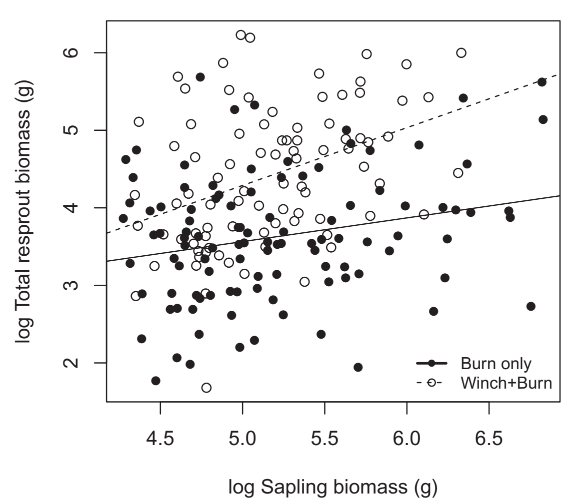

Fig. 4. Relationship of biomass of top-killed saplings and the total biomass of basal sprouts from individual damaged saplings. Note both axes show log-transformed biomass.
Figure from Cannon (2015)

mechanisms. Note that the Wolfe et al. (2014) study described above found that reductions in stem diameter can decrease stand resistance to fire, however canopy opening disturbances increase resources and may also increase resilience of stands to fire via faster growth of surviving post-fire regeneration.

Just as species differ in their ability to resist disturbances such as wind damage or fire, they differ in response to disturbance in terms of growth and reproduction (Batista and Platt, 2003; Bellingham et al., 1995). Bellingham et al. (1995) outlined a continuum of syndromes of resistance and resilience to hurricane disturbance based on species-specific differences in basal sprouting ability, sprouting growth rate and allocation of carbohydrates to belowground reserves (Johnson et al., 2002; Robertson and Ostertag, 2009). Any wind–fire interaction mechanism dependent on life history traits such as survival, growth or sprouting will vary among species. Due to species-specific disturbance responses, interactive effects are also expected to vary in a species-specific manner. For example, Cannon and Brewer (2013) noted resprouting patterns differed among species following wind damage and fire. Species of upland oaks (*Quercus*) had larger basal resprouts relative to other woody species. The results of differential resistance between species led to increased dominance by upland oaks, at the expense of more mesic species. The initial size advantage of resistant species or rapidly resprouting species following disturbances can be exaggerated if size asymmetry leads to competitive suppression as documented following wind and fire by Brewer (2015). The differential responses to wind and fire disturbance favored those species that were historically present (Nowacki and Abrams, 2008; Surrette et al., 2008), thus variable interactive effects may have restoration applications. As above with mechanisms of resistance (e.g., Cannon et al., 2014), mechanisms of resilience can exhibit variability in a spatially heterogeneous manner.

5. Discussion

From this classification of interactions between wind damage and fire, several generalizations emerge. First, the interactive effect of wind and fire disturbances can vary depending on the intensity or severity of the disturbances themselves. Severe wind damage combined with intense fire can lead to amplifying effects via increases in available fuels (Liu et al., 2008; Myers and Van Lear, 1998; Urquhart, 2009). However, wind damage may actually decrease the intensity or continuity of fire (a buffering effect) when fire intensity is low, as with prescribed fire (Cannon et al., 2014). Research on disturbance interactions to date primarily emphasizes amplifying interactions—likely due to the concern over hazardous events such as severe wildfire. 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; Cannon, 2015). Interestingly, each buffering mechanism identified to date is most applicable to low-intensity fire. One explanation for increased buffering interactions with wind damage and low-intensity fires is that behavior of low-intensity fire is governed by heterogeneity of fuel at very fine-scales (< 1 m, Loudermilk et al. 2012). Because wind damage alters fuel heterogeneity at fine-scales, legacies of wind damage such as reduced litter input (O'Brien et al., 2008), or increased fuel breaks (Cannon et al., 2014) may reduce intensity or continuity of low-intensity fire. 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. Such findings parallel those in forests following insect outbreaks. For example, beetle outbreak severity amplified the effects of subsequent wildfire under extreme weather conditions, whereas under moderate weather conditions, no such interactions were evident. These findings suggest that coarse fuels resulting from high severity beetle outbreak became available for combustion under extreme weather conditions allowing for high severity fire (Harvey et al., 2014b).

A second generalization that can be drawn from the preceding classification is the potential importance for region and climate to govern disturbance interactions. Intense wildfires following severe blowdowns depend on the coincidence of several conditions such as available fuels, low fuel moisture, high wind speeds and an ignition source (Pyne et al., 1996). Wind damage enhances one of these prerequisites (dead woody fuel); however, other climatic conditions must be met for severe fire to occur. In light of the considerable differences in climate and vegetation in areas where historical reconstructions of wind and fire have 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. In dry climates such as the western U.S., the surfeit of course woody debris following wind damage may more rapidly become available to combustion and persist for a longer period of time relative to mesic climates of the eastern U.S. (Harmon et al., 1986). Such differences in the dynamics of fuel availability may govern whether the wind–fire interactions are amplifying or buffering, and how wind and fire interact as the time between disturbances increases. Predictions of warmer and drier climatic conditions (IPCC, 2014), coupled with predictions of more intense and severe wind and fire disturbances (Diffenbaugh et al., 2013; Webster et al., 2005; Westerling et al., 2011), imply an increase in the frequency of amplifying wind–fire interactions (Dale et al., 2001). Future research on wind–fire interactions comparing multiple events may be useful to explore how frequency and in what settings these interactions occur. In addition, further research exploring how factors such as the time between disturbances, disturbance severity, and climatic conditions govern dominant interaction mechanisms will allow a better understanding of the potential ecological effects of such interactions.

A third important generalization from this review of wind–fire interactions is that mechanisms producing amplifying and buffering effects can co-occur in the same disturbance event in a spatial mosaic (Fig. 5). Mechanisms of species resistance to wind and fire can vary spatially (Cannon et al., 2014). Resilience mechanisms also 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). Such interactions between sprouting responses to wind and fire may add complexity to predicting future stand composition, but they may also be leveraged to achieve restoration objectives (Brewer, 2016; 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. Instead, the intensity and severity of wind damage and fire are extremely heterogeneous with a mosaic of patches of mixed severity (Cannon et al., 2016; Chambers et al., 2007; Turner et al., 1994). When fire follows wind disturbance, a wide range of fire severities may overlap with a wide range of wind severities in a complex spatial mosaic, creating opportunities for a multitude of interaction mechanisms—both amplifying and buffering—to co-occur in a single set of interacting disturbances that vary across space and time.

5.1. Conclusions and management implications

Our classification has parallels to an observation described in the seminal Pickett et al. (1987) paper on hierarchies of successional causes. Those authors pointed out that the classical successional mechanisms of facilitation, tolerance, and inhibition proposed by Connell and Slatyer (1977) are not monolithic descriptors of an entire successional pathway, but instead operate concurrently and idiosyncratically in the turnover between various pairs of species in a spatial mosaic. Similarly, we suggest that wind–fire interactions may have both synergistic and antagonistic interactions within the same disturbed patch or stand, and that such variable interactions occur in a spatial mosaic

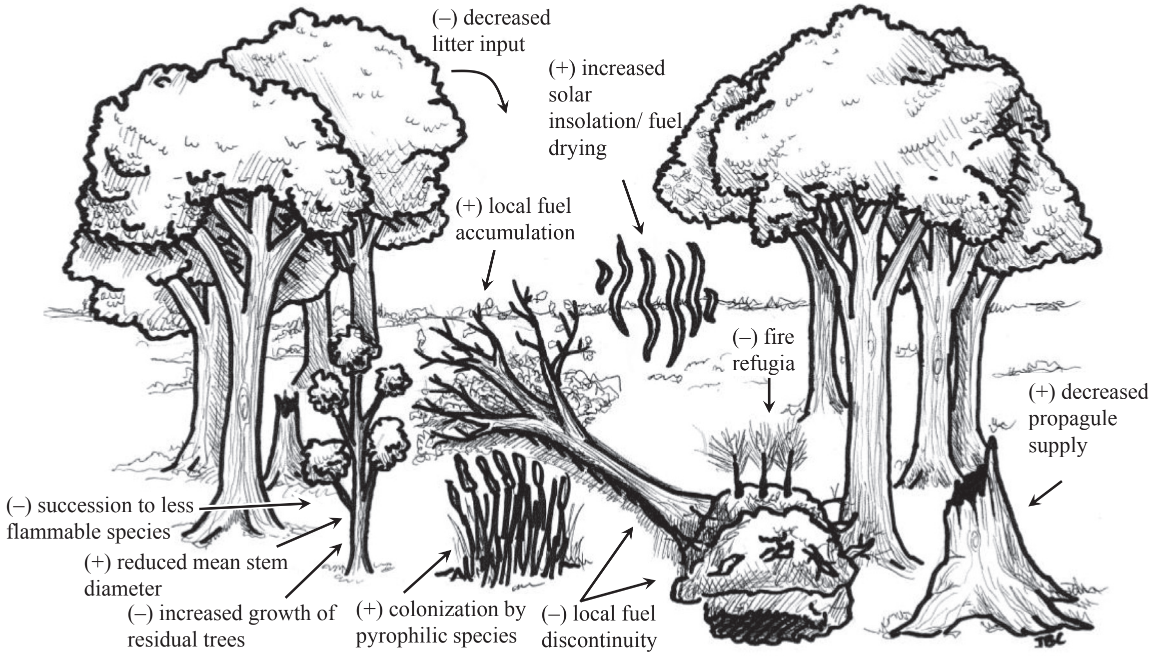

Fig. 5. Schematic diagram of potential mechanisms of interaction between forest wind damage and fire including both amplifying (+) and buffering (–) effects illustrating the potential for co-occurrence of multiple mechanisms in a spatial mosaic. See Table 1 and text for details and references.

that varies over time. A variety of potential mechanisms govern interactions between wind damage and fire, and the type and direction of the interaction mechanisms likely depends on a host of complex factors such as local severity of the disturbances, time between disturbances, climatic conditions, physiographic setting, heterogeneity of fuels and individualistic species responses. Thus, it may be more useful to conceptualize disturbance interactions as a diverse collection of individual, co-occurring interaction mechanisms rather than considering a set of interacting disturbances to be wholly amplifying or wholly buffering (Fig. 5).

This review of wind–fire interactions can inform potential management responses following wind damage. In many cases, land managers are compelled to remove merchantable timber resulting from catastrophic wind damage in order to reduce the risk of insect outbreaks or wildfire (Lindenmayer and Noss, 2006), yet these actions can inhibit regeneration in the short term (Royo et al., 2016; Zenner et al., 2007), alter understory composition (Brewer et al., 2012; Cannon and Brewer, 2013), and alter nutrient cycling (Cooper–Ellis et al., 1999). A better understanding of how wind damage alters fire probability, intensity, and severity can inform decisions on the type of management intervention necessary (e.g., salvage logging or prescribed fire) to mitigate risk to forest resources. Understanding the various mechanisms of wind damage and fire may allow managers to make predictions of how combinations of management actions may impact forested systems. In addition, knowledge of individualistic species responses to combinations wind–fire interactions may allow restoration practitioners to capitalize on wind damage as a restoration opportunity (Brewer, 2016; Cannon and Brewer, 2013), especially in systems where forest thinning and prescribed fire are important restoration tools such as mesic eastern U.S. forests (Nowacki and Abrams, 2008) or western U.S. ponderosa pine forests. Future research on interaction mechanisms which explicitly examines specific mechanisms of interactions between wind damage and fire and characterization of the conditions under which particular interactions govern stand dynamics such as climatic and temporal factors will aid in understanding these ecologically important and ubiquitous disturbances.

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