



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



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ARTICLE INFO

Keywords:

Blowdown
Compounded disturbances
Disturbance interactions
Fire
Interaction mechanisms
Wind damage

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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<http://dx.doi.org/10.1016/j.foreco.2017.07.035>

Received 30 May 2017; Received in revised form 19 July 2017; Accepted 21 July 2017
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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 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

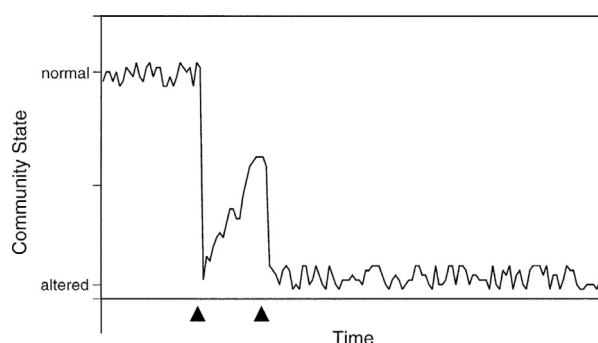


Fig. 1. Schematic illustration of a community affected by two disturbances (arrows) in rapid succession, resulting in altered community state.

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

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