Forest Ecology and Management 405 (2017) 188–199

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. Forests

Jeffrey M. Kane[a,*], J. Morgan Varner[b], Margaret R. Metz[c], Phillip J. van Mantgem[d]

[a] Department of Forestry & Wildland Resources, Humboldt State University, One Harpst Street, Arcata, CA 95521, USA
[b] Pacific Wildland Fire Sciences Laboratory, United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Seattle, WA 98103, USA
[c] Department of Biology, Lewis & Clark College, Portland, OR 97219, USA
[d] Redwood Field Station, United States Geological Survey, Arcata, CA 99521, USA

ARTICLE INFO

Keywords:
Bark beetles
Climate change
Compounded disturbances
Disturbance interactions
Drought
Forest pathogens
Wildland fire

ABSTRACT

Increasing evidence that pervasive warming trends are altering disturbance regimes and their interactions with fire has generated substantial interest and debate over the implications of these changes. Previous work has primarily focused on conditions that promote non-additive interactions of linked and compounded disturbances, but the spectrum of potential interaction patterns has not been fully considered. Here we develop and define terminology, expand on the existing conceptual framework and review the patterns and mechanisms of disturbance interactions with a focus on interactions between fire and other forest disturbances and a specific emphasis on resulting tree mortality. The types of interactions reflect the positive, negative, or neutral responses to the incidence, intensity, and effects of the interaction. These types of interactions are not always mutually exclusive, but can be distinct. The collective effect of the interactions will determine the longer-term ecosystem response that can result in a resistant, resilient, or compounded interaction. Our review indicates that the interactions of drought, bark beetles, or pathogens with fire often result in neutral or maintained interactions that do not negatively or positively influence the incidence or intensity following fire. The effect of these disturbance interactions on tree mortality ranged from antagonistic (reduced mortality compared to individual disturbances) to synergistic (greater mortality compared to individual disturbances) within and among disturbance interaction types but often resulted in additive effects (mortality is consistent with the summation of the two disturbances). Synergistic effects on tree mortality have been observed when the severity of the initial disturbance is moderate to high and time between disturbances is relatively short. When the sequence of disturbance interaction is reversed (e.g., fire precedes other disturbances) the conditions can generally promote impeded interactions (lower incidence of interaction), reduced interactions (lower intensity of interaction), and antagonistic interactions (lower tree mortality). While recent research on fire-disturbance interactions has increased over the last decade and provided important insights, more research that identifies the specific thresholds of incidence, intensity, and effects of interaction by region and forest type are needed to better assist management solutions that promote desired outcomes in rapidly changing ecosystems.

1. Introduction

Disturbances regulate and influence the structure and processes of forests over a wide span of temporal and spatial scales (Pickett and White, 1985), but many disturbance regimes have been substantially altered over the past few decades due to anthropogenic changes. Fire is one of the most widespread and important ecological disturbances across many biomes (Bowman et al., 2011). Over the past few decades rising temperatures and drier conditions have been associated with the increased frequency and size of fires in many regions (Flannigan et al., 2009; Abatzoglou and Williams, 2016; Westerling, 2016). Areas where fire is common are often prone to other disturbance types, many of which are also increasing, such as drought (Cook et al., 2015; Diffenbaugh et al., 2015) and large-scale bark beetle outbreaks (Raffa et al., 2008; Bentz et al., 2016). Of additional concern is the increased prevalence of novel disturbances (e.g., non-native tree killing insects and pathogens) and their impacts on forested ecosystems (Rizzo and Garbelotto, 2003; Aukema et al., 2010; Kolb et al., 2016). The increased occurrence of these disturbances individually has prompted substantial interest from ecologists and managers about the impacts of disturbance interactions (Turner, 2010).

Disturbance interactions have been documented in many

* Corresponding author.
E-mail address: jkane@humboldt.edu (J.M. Kane).

http://dx.doi.org/10.1016/j.foreco.2017.09.037
Received 2 April 2017; Received in revised form 24 August 2017; Accepted 15 September 2017
Available online 21 September 2017

ecosystems but were largely descriptive in earlier works (e.g., Brown, 1975; Knight, 1987; Paine et al., 1998). Quantitative research on the topic has increased in the past few decades, highlighting the complex patterns and mechanisms regarding the incidence and effects of disturbance interactions (e.g., Veblen et al., 1994; Bebi et al., 2003; Bigler et al., 2005; Allen, 2007). The varied responses observed likely reflect differences in the circumstances and conditions of interactions that may be directly and indirectly exacerbated by climate change (McKenzie et al., 2008). While the literature on disturbance interactions is rapidly expanding and frameworks for communicating the commonalities of these events are being developed (e.g., (McKenzie et al., 2008; Buma, 2015), advancement of the topic is still hindered by inconsistent terminology, contrasting approaches, and conflicting results. In fact, the term *disturbance interaction* has had numerous phrases applied to the same phenomenon, such as "overlapping disturbances", "multiple disturbances", "repeat disturbances", "stress complexes", and "short-interval disturbances", to name a few (Buma, 2015). This suite of limitations likely has contributed to scientific debate on the prevalence and impacts of disturbance interactions (Simard et al., 2011; Jolly et al., 2012a).

Previous studies have identified two types of disturbance interactions, "linked" and "compounded" interactions. A linked interaction has been defined as when the presence of one disturbance changes the extent, severity, or probability of occurrence (Simard et al., 2011). A compounded disturbance interaction (*sensu* Paine et al., 1998) occurs when two disturbances occur within a relatively short time interval and results in an alteration in the community trajectory, or reduces the rate of recovery. Buma (2015) expanded the framework on disturbance interactions by connecting them with other concepts regarding disturbance legacies (Franklin et al., 2000; Johnstone et al., 2016) and ecosystem resilience (Holling, 1973; Gunderson, 2000) and identified potential conditions that may promote cascading effects. This review highlighted the need to disaggregate disturbance legacies into their constituent parts to determine whether they would foster ecosystem resistance and resilience or lead to unexpected or undesired outcomes.

While the conceptual framework on disturbance interactions has expanded, some of the terminology and identified patterns used to describe disturbance interactions have not been consistently applied or do not encompass the full spectrum of outcomes. For example, the definition of a "linked interaction" has been used to describe when the initial disturbance increases or decreases the occurrence or extent of the subsequent disturbance as well as the amplified effect of interaction (e.g., severity). The incidence or extent of an interaction may be independent of the intensity or severity of a disturbance. Thus, separating these characteristics should enable better identification of the mechanisms that result in altered effects or responses to disturbance interactions. Additionally, it is unclear that a synergistic effect must be present for a compounded disturbance interaction to occur, though this is often implied or stated directly. The longer-term response of an ecosystem will reflect the collective impacts of the immediate effects, the resultant disturbance legacies, and conditions present following the interaction. Conversely, instances where a synergistic effect is detected may not lead to longer-term impacts on resistance or resilience. Further advances in the conceptual framework could employ clearer terminology that better represents the full spectrum of disturbance interaction patterns and mechanisms.

Much of the existing research on disturbance interactions in forests has focused on tree mortality likely because many of the disturbances individually have led to elevated rates of tree mortality. Recent temperature increases have been experimentally and empirically associated with increased tree mortality across many regions and species (Adams et al., 2009; van Mantgem et al., 2009; Allen et al., 2010; Young et al., 2017). Recent increases in fire-caused tree mortality, as measured by fire severity, have been demonstrated; however, evidence supporting this trend has been mixed (Miller et al., 2009; Dillon et al., 2011; Miller et al., 2012; Mallek et al., 2013). Often in close association with rising temperatures, tree mortality resulting from bark beetle attacks has also been substantial over the past two decades (Raffa et al., 2008; Bentz et al., 2010). Increased tree mortality events can alter fuel characteristics and microclimate that can influence the incidence, intensity, and effects of fire (Hicke et al., 2012) that may lead to longer-term and possibly unique impacts to ecosystems.

Disturbances and their interactions are of particular concern because they can serve as catalysts that may promote novel ecosystems (communities that have not previously occurred in a biome; Hobbs et al., 2006) and other unexpected outcomes (also referred to as "ecological surprises" *sensu* Paine et al., 1998). Incidences of disturbance interactions may more rapidly effect ecosystems than direct climate-related changes alone (McKenzie et al., 2008). In forest and woodland ecosystems, these unexpected outcomes may be primarily mediated through substantial tree mortality, especially if it disproportionally occurs in foundation species that are essential to maintaining the structure and function of ecosystems (Ellison et al., 2005). Substantial loss or maintained loss of tree cover resulting from disturbance interactions may also promote cascading effects (Buma, 2015) through changing disturbance legacies (Johnstone et al., 2016), disrupting ecosystem resilience (Buma and Wessman, 2011), and altering carbon dynamics (Bowman et al., 2014; Buma et al., 2014).

Here we examine the potential patterns and mechanisms leading to interactions between fire and other disturbances (hereafter, fire-disturbance interactions). We focus our efforts on a subset of two-way interactions between fire and drought, bark beetles, or fungal pathogens, placing specific emphasis on forest ecosystems and the effects on tree mortality. More specifically, the objectives of this review are to: (1) refine terminology and expand the conceptual framework to more broadly characterize disturbance interactions; (2) identify recurrent patterns and mechanisms that influence the incidence, intensity, and tree mortality effects of fire-disturbance interactions based on published research; and (3) identify research gaps in our understanding of altered disturbance regimes and interactions in the context of a changing climate. Our review is limited to a subset of fire-disturbance interactions in forests of the western U.S. and it is not meant to be a comprehensive synthesis on the topic. Rather our intention with this paper is to expand some of the concepts on the patterns and mechanisms of disturbance interactions in fire-prone forests to provoke the advancement of research into the consequences of disturbance interactions.

2. Characterizing disturbance interactions: definitions, patterns, and types

Disturbances have been defined in many different ways, but here they are referred to as the occurrence of a relatively discrete event that disrupts the biological and physical environment resulting in a loss of biomass (Grime, 1979; Pickett and White, 1985; Table 1). Individually, disturbances can vary widely in their impact to ecosystems and, thus similarly, the interaction of two or more disturbances will vary widely as well (Paine et al., 1998). To encompass this range of impact, we broadly define disturbance interactions as areas that have experienced two or more relatively discrete, spatially overlapping disturbances during a relatively short time frame that alter the biological and physical environment. This definition differs from other uses of disturbance interactions, which often focus on interactions that result in non-linear or synergistic effects. However, somewhat akin to species interactions, the effects of disturbance interactions can be positive, negative, or neutral and will likely have a spectrum of possible outcomes. Broadening this definition can serve to improve our ability to characterize and communicate the patterns and types of disturbance interactions present and improve our understanding of their longer-term impacts.

Characterizing the patterns and mechanisms of disturbance interactions requires information on the incidence, extent, intensity, and effects of these interactions and their influence on longer-term