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

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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

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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

Table 1
Definition of disturbance interaction terms.

Terminology	Definition
Disturbance	relatively discrete event that disrupts the biological and physical environment resulting in a loss of biomass
Disturbance Interaction	two or more relatively discrete events that spatially overlap during a relatively short time frame that alter the biological and physical characteristics of an ecosystem
Interaction Linkage	degree to which one disturbance influences the incidence or extent of another disturbance
Neutral Interaction	incidence of an initial disturbance does not influence the incidence or extent of a subsequent disturbance
Facilitated Interaction	incidence of initial disturbance increases or promotes the incidence or extent of a subsequent disturbance
Impeded Interaction	incidence of initial disturbance decreases or limits the incidence or extent of a subsequent disturbance
Interaction Intensity	influence of the initial disturbance on the intensity of the subsequent disturbance
Maintained Intensity	intensity of the initial disturbance does not influence the intensity of the subsequent disturbance
Amplified Intensity	intensity of the initial disturbance increases the intensity of the subsequent disturbance
Reduced Intensity	intensity of the initial disturbance decreases the intensity of the subsequent disturbance
Interaction Effect	collective effect of the initial and subsequent disturbances
Additive Effect	interaction between two disturbances that results in an effect that is equivalent to the summation of disturbances individually
Synergistic Effect	interaction between two disturbances that results in an effect that is greater than the summation of disturbances individually
Antagonistic Effect	interaction between two disturbances that results in an effect that is less than the summation of disturbances individually
Ecosystem Response	longer-term, persistent response to one or more disturbances
Resilient Interaction	disturbance interaction that does not have a negative effect on recovery or cause a shift in the community state
Compounded Interaction	disturbance interaction that has a negative effect on recovery and shifts the community trajectory
Resistant Interaction	disturbance interaction that withstands change

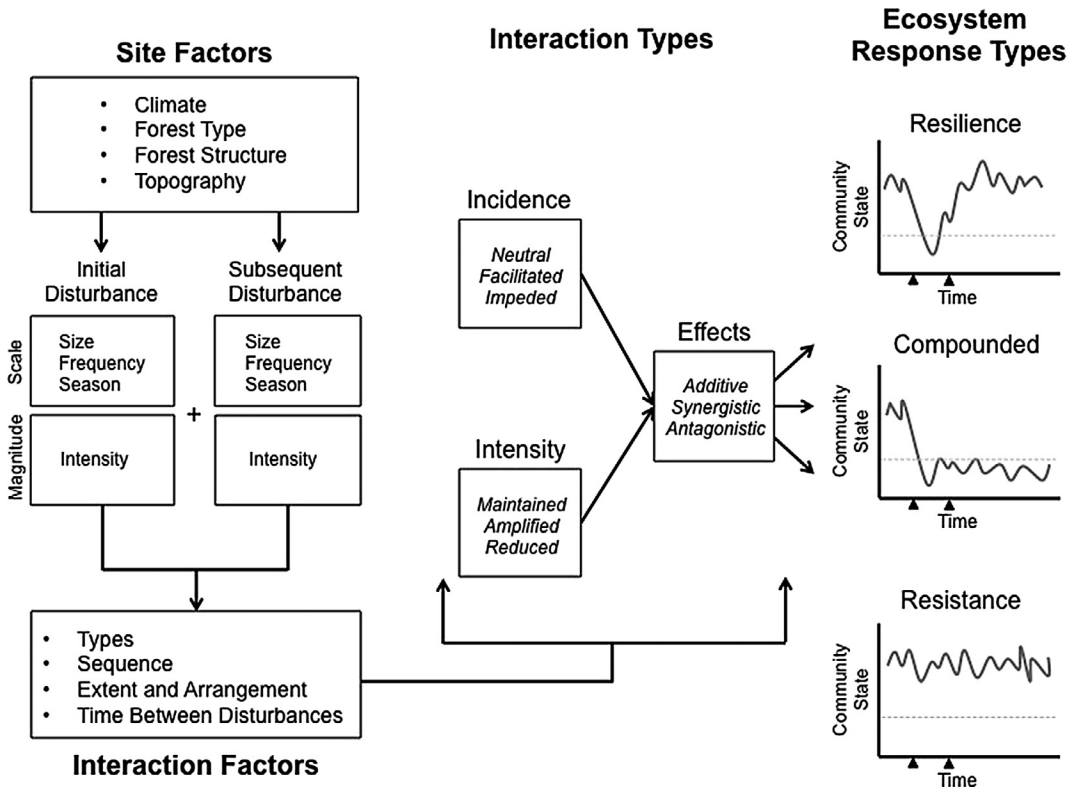


Fig. 1. A conceptual diagram on the mechanisms and patterns of disturbance interactions. The three panels under the ecosystem response type denote discrete disturbances with triangles, and the dashed line represents the threshold characterizing an altered state. Definitions of interaction and ecosystem response types are provided in Table 1.

ecosystem responses (Fig. 1). The initial and subsequent disturbances will be separately driven by individual site and disturbance factors but will also be influenced by factors associated with the interaction. Individually, disturbance characteristics in forested ecosystems will reflect the site characteristics that typically include climate, forest structure and composition, soils, and topography. These site conditions will affect the incidence, frequency, extent, intensity and effects of each disturbance. However, the subsequent disturbance will be influenced by the characteristics of the initial disturbance as well as the time between disturbances, the type of disturbances involved, and sequence of interaction (e.g., fire-bark beetle or bark beetle-fire interaction).

The incidence of disturbance interactions reflects the probability of occurrence and the spatial and temporal distribution of each disturbance type. Spatial controls that relate to the likelihood of disturbances interacting are partially driven by the extent (i.e. area and shape) of each disturbance. In instances where disturbances are large, the probability of interaction with other disturbances increases with size. However, disturbances that are non-randomly distributed in space and time (e.g., fire, bark beetle attacks) may result in either an increase or decrease in the likelihood of interaction. If two disturbances have high spatial specificity (i.e. occurrence is dependent on certain conditions) in their distribution and these conditions are similar, then there is

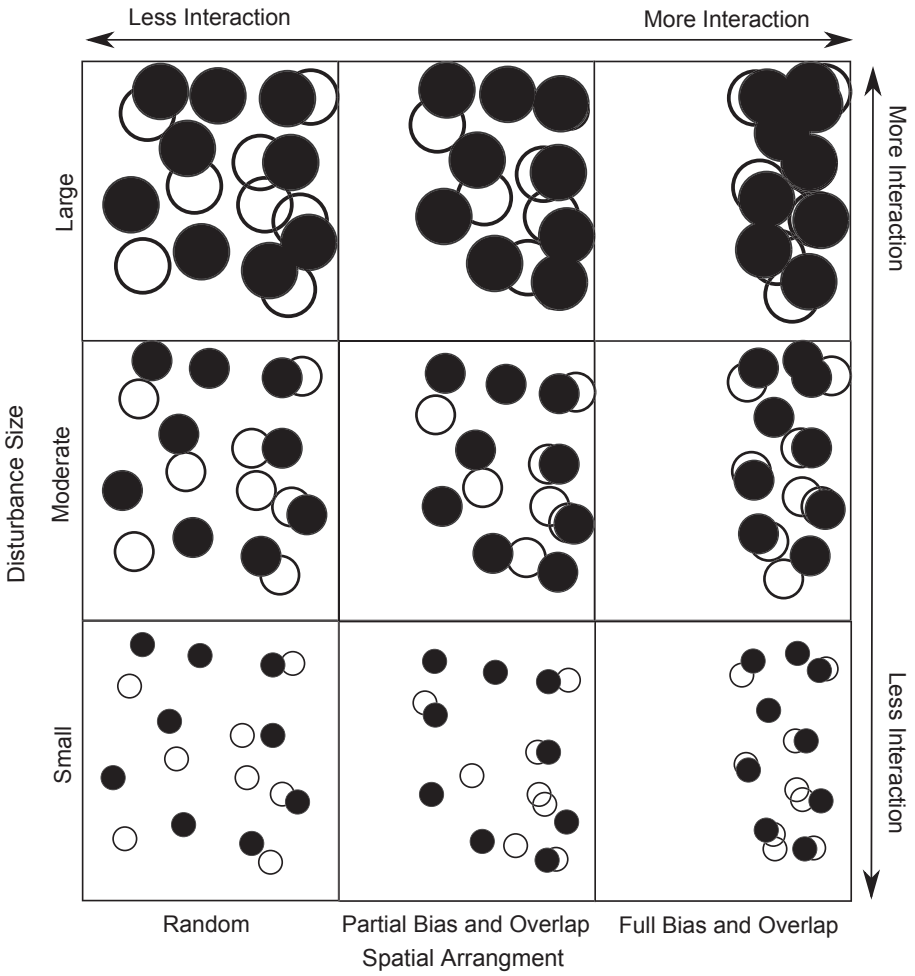


Fig. 2. Hypothetical relationship of increasing disturbance size along differing spatial arrangements and the potential influence on the probability of interaction. This example assumes that both disturbances (dark circles = disturbance A and light circles = disturbance B) share similar spatial specificity. Specificity refers to the range of conditions suitable for the occurrence of a disturbance. Incidences of disturbance interactions are more common as the size and shared specificity of the disturbances increase.

a greater likelihood that these disturbances will interact as the size of one or both disturbances increases (Fig. 2). For example, the incidence of drought and fire often occur in similar areas (albeit at different extents), thus there is a greater likelihood for interaction between these two disturbance types. Conversely, if the two disturbances have low spatial specificity or differ in the conditions that promote their occurrence, then there would be a much lower chance of interaction. High frequency disturbances will also contribute to an increased potential for interaction independent of the size of disturbances. Furthermore, if disturbances are non-randomly distributed in time, and disturbances are similar in their temporal specificity (occur during the same year), then the probability of interaction will increase (Fig. 3). The incidence of disturbance interactions will also depend on the linkage between disturbances, or in other words, how much the presence of one disturbance promotes or limits the presence of another disturbance (Table 1). Types of incidence interactions include neutral interactions, facilitated interactions, and impeded interactions (Fig.4a). Facilitated and impeded interactions would constitute two different types of linked interactions (*sensu* Simard et al., 2011).

The intensity of interaction represents the impacts of an initial disturbance on the subsequent disturbance (Table 1). The intensity of interaction will depend on the site-level factors that contribute to the intensity of the initial disturbance. In addition to the overall impacts of intensity of both the initial and subsequent disturbance, the spatial arrangement and patch dynamics will also influence the interaction intensity. For instance, we could imagine two separate scenarios where the initial disturbance intensity has a similar overall level of intensity, but the distribution of patches across a landscape are different. All else being equal, the intensity of the subsequent disturbance would likely differ if the arrangement of intensity levels of the initial disturbance were distributed in many smaller, evenly distributed patches compared to fewer large patches. The spatial arrangement and patch-size distribution of intensity for each disturbance will also be important for the effects of the interactions (e.g., severity).

Three general types of intensity interactions may result: maintained interactions; amplified interactions; and reduced interactions (Fig. 4b). Maintained interactions reflect a condition where the intensity of the initial disturbance does not positively or negatively influence the intensity of the subsequent disturbance. Amplified interactions result when the subsequent disturbance is increased by the conditions created by the initial disturbance. Conversely, reduced interactions occur when the intensity of the subsequent disturbance is lowered due to the conditions created by the initial disturbance.

Disturbance interaction effects broadly refer to the direct and indirect impacts from the two disturbances on forest ecosystems (Table 1). The impacts of disturbance interactions (i.e. interaction effects) on tree mortality in forests likely depend on a combination of site-level characteristics, disturbance characteristics, and interaction characteristics. Site-level characteristics include local climate, topography, soils, and forest structure and composition that will collectively influence the characteristics of each disturbance alone and in combination with other disturbances. Disturbance interactions will also have separate characteristics that will affect tree mortality such as the type, sequence, spatial and temporal specificity, and time between disturbances. While tree mortality is provided as a focal example of an interaction effect in this paper, there are many others effects (e.g., regeneration, soil nutrients) that also need to be considered and each of these effects may respond individually or in association with one

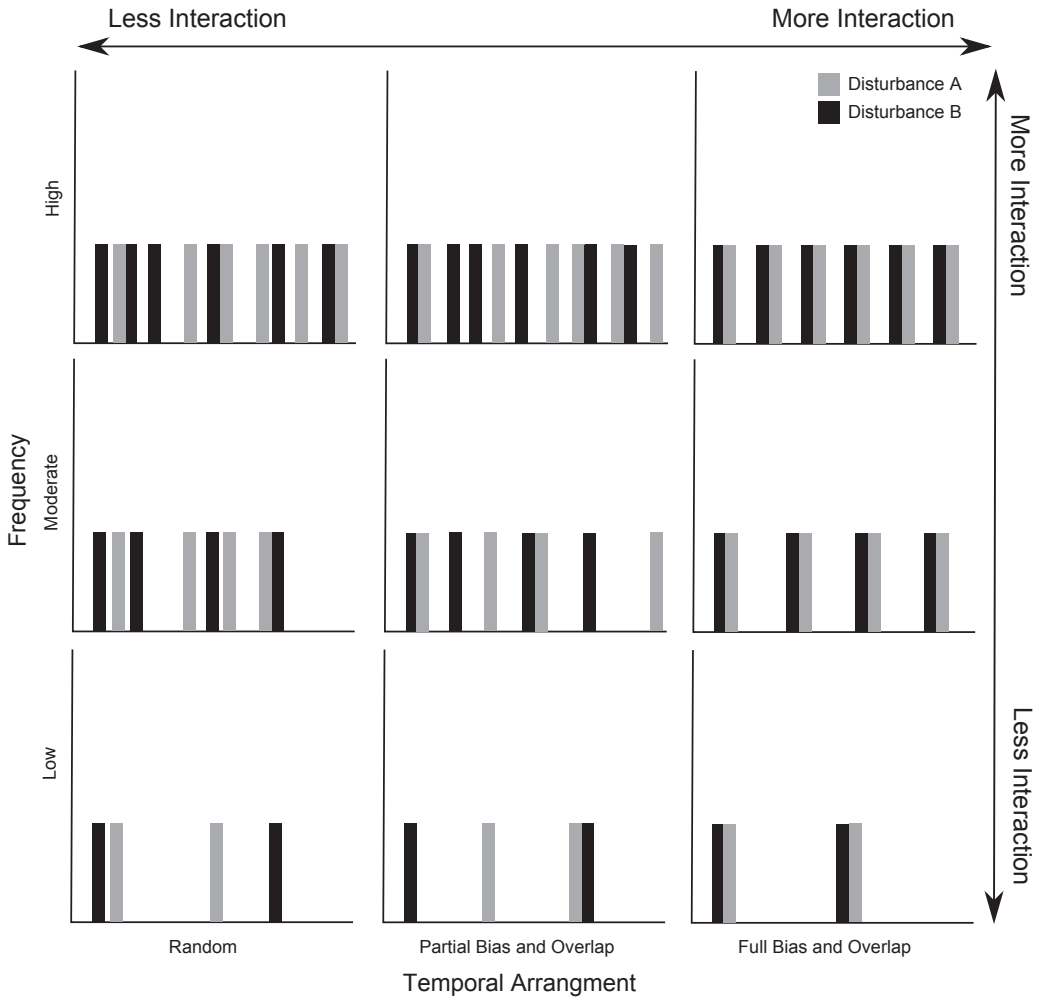


Fig. 3. Hypothetical relationship of increasing disturbance occurrence (presence/absence) along differing frequencies (low, moderate, and high) and temporal arrangements (specificity) for two disturbance types (disturbance A = gray bars and disturbance B = black bars). Specificity refers to the range of conditions suitable for the occurrence of a disturbance. Instances where the two disturbances are side-by-side indicate the presence of an interaction. Incidences of disturbance interactions are more common as the frequency increases and temporal specificity of the two disturbances overlap.

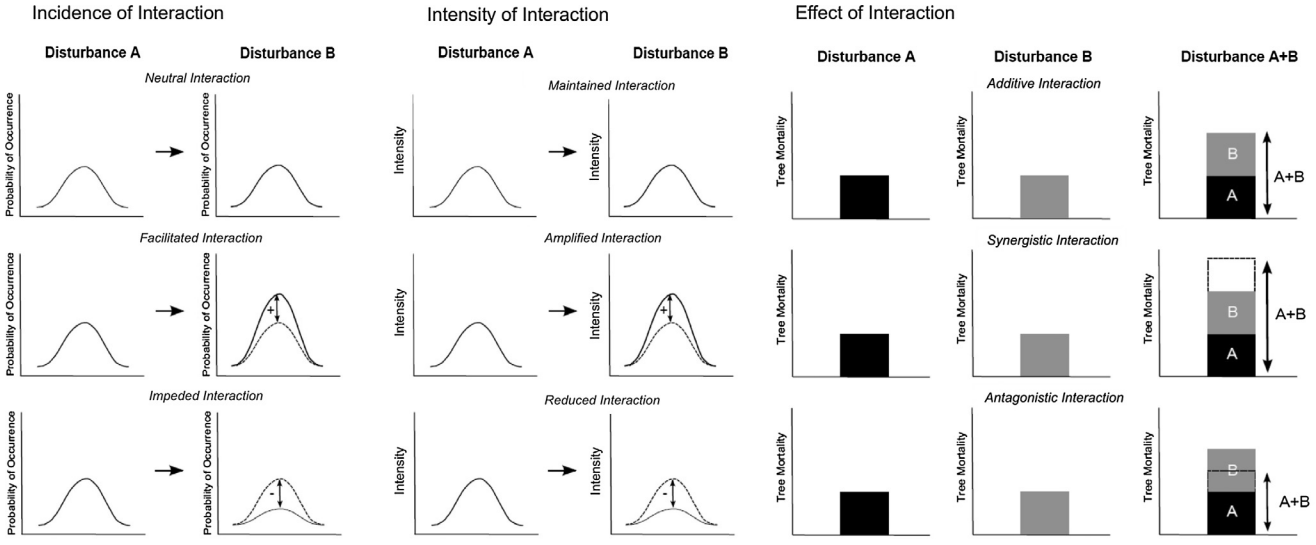


Fig. 4. Simplified description of potential two-way disturbance interaction types based on: (a) incidence of interaction; (b) intensity of interaction; and (c) effects of interaction.

another.

There are three possible patterns of disturbance interaction effects: additive, synergistic, and antagonistic (Fig. 4c). Additive effects of disturbance interactions result when two disturbances occur, but the first disturbance does not increase or decrease the effects (e.g., tree mortality) of the subsequent disturbance. A synergistic effect may result when the initial disturbance promotes conditions that exacerbate the effects of the subsequent disturbance. Conversely, antagonistic effects result when the presence of the initial disturbance reduces tree mortality of the subsequent disturbance, which may be related to the intensity of the initial disturbance or the time between disturbances.

The collective effects of disturbance interactions will promote

conditions (i.e. disturbance legacies) that determine the longer-term response of the ecosystem (Fig. 1). The response of the ecosystem will vary widely and the cause of this variation could arise from a range of combinations of interaction types, though some are clearly not mutually exclusive. Similar to the incidence, intensity, and effects of interactions, there are three possible ecosystem responses to disturbance interactions: resilient, compounded, and resistant interactions (Table 1). Resilient interactions represent ecosystems that rapidly recover from the effects of interaction. Compounded interactions result when the ecosystem response is unable to recover to the previous baseline and results in an altered community state. Resistant interactions occur when the interaction results in a condition that inhibits change in the ecosystem and the community state is largely unchanged. While there may be clear patterns of interaction (incidence, intensity, and effects) that promote these ecosystem response types, multiple combinations of these interaction types will likely be determined by the resultant legacies of the interaction.

3. Patterns and mechanisms of fire-disturbance interactions and effects

3.1. Fire-drought interactions

Reduced precipitation is the hallmark of drought, but high temperatures lead to increased evapotranspiration so that drought is often measured by changes in vapor pressure deficit (Williams et al., 2013) or climatic water deficit (Stephenson, 1998). These conditions are often associated with reduced tree vigor or elevated tree mortality, but the level of impact will depend on the intensity and duration of drought as well as the species' physiological mechanisms to withstand drought (McDowell, 2011). Drought may cause tree mortality directly (Adams et al., 2009) or indirectly by making trees more vulnerable to insects or other pathogens (Weed et al., 2013). Indeed, high temperatures and associated drought stress have been linked to increased 'background' tree mortality (van Mantgem and Stephenson, 2007). Recent observations have shown that the co-occurrence of reduced precipitation and high temperatures is associated with massive forest die-back, where > 80% of trees within a stand can be killed (Breshears et al., 2005; Allen et al., 2010).

Numerous recent observations have shown that warmer, drier conditions overlap with greater forest fire frequency and size (Westerling et al., 2006; Littell et al., 2009; Dillon et al., 2011). It is likely that drought leads to facilitated interactions with fire by altering fire weather conditions (drought conditions reduce dead fuel moisture which increases available fuel and fireline intensity), which is modified by interactions with other site-level controls (Fried et al., 2008; Abatzoglou and Williams, 2016; Littell et al., 2016). Increases in the extent and frequency of both drought and fire and the facilitated interaction between the two disturbances suggest that the area of drought and fire interactions should also be increasing.

Synergistic effects of drought on fire may arise from increased fuel loading from drought-related needle cast, branch abscission, and proximal drought-induced tree mortality (Carnicer et al., 2011) that can increase fire intensity and the amount of fire injury, leading to increased post-fire tree mortality (Ryan and Reinhardt, 1988). The influence of exclusively drought-induced tree mortality on changes in fuel characteristics and microclimate has not been directly investigated; however, changes will likely be similar to bark beetle-induced tree mortality (see Hicke et al., 2012 and bark beetle-fire interaction subsection below).

An additional consequence of drought may be an increasing sensitivity of individual trees to fire, which may differ from the vulnerability of trees to drought in the post-fire landscape. A recent study of post-fire conifer mortality suggested high pre-fire climatic water deficit exacerbated the effects of fire-caused injuries (crown scorch and char height), but failed to find significant effects of post-fire drought stress (van Mantgem et al., 2013). In unburned stands, diminished tree growth is indicative of environmental stress and is predictive of tree mortality, particularly for conifers (Cailleret et al., 2017). Likewise, there are reports that show slow growing trees to die more readily following fire (van Mantgem et al., 2003; Nesmith et al., 2015). These results are supported by studies of tree physiology, which have demonstrated that heat from fire may cause embolisms and deformation of xylem elements in the stem and crown (Kavanagh et al., 2010; Michaletz et al., 2012; West et al., 2016). If the xylem is already under high tension due to drought stress, fire-caused loss of function may be promoted. It is also possible that following fire, xylem repair mechanisms may be compromised with continuing drought (Anderegg et al., 2013). These studies imply that chronic or acute drought stress may increase fire severity, as measured by post-fire tree mortality, independent of changes that affect fire intensity.

The sequence of drought and fire may have opposing effects on tree mortality. It is possible that mortality caused by fire may thin forest stands sufficiently so that surviving trees may have more resources available and therefore are more likely to resist subsequent drought stress (D'Amato et al., 2013; Bradford and Bell, 2017; Young et al., 2017). In a study examining low severity prescribed fires in lower elevation conifer forests in California, van Mantgem et al. (2016) found reduced tree mortality during drought compared to unburned areas and the effectiveness of fire did not decrease with time since fire. However, a clear and consistent relationship between stand density and drought mortality has not been observed across different sites of the same species (Clifford et al., 2013; Dorman et al., 2015; Meddens et al., 2015; Carnwath and Nelson, 2016), indicating other site-level factors (e.g., soil nutrients, drought severity) may also need to be considered.

3.2. Fire-bark beetle interactions

Fire-bark beetle interactions involve the incidence of bark beetle attacks on trees in association with fire. More specifically, we refer to bark beetles as those species in the family Curculionidae (subfamily Scolytidae) (e.g., *Dendroctonus* spp., *Ips* spp., and *Scolytus* spp.) that are endemic at low levels but are also well known to cause large-scale mortality in susceptible tree hosts during outbreaks (Bentz et al., 2010). However, it is important to point out that bark beetle species differ in their ability to kill trees and vary in response to many factors (e.g., fire, drought, tree characteristics, stand structure and composition) that are highlighted by species-specific hazard rating systems and other models (e.g., Negrón, 1998; Shore et al., 2000). Individually, bark beetle outbreaks and fire disturbances vary widely in size among and within ecosystems (Chapman et al., 2012; Meddens and Hicke, 2014), but both are often spatially widespread where they occur (Raffa et al., 2008; Aukema et al., 2010; Meddens et al., 2012; Meddens and Hicke, 2014). Increases in the incidence of bark beetle and fire interactions may result where both have large extents in a given area, but the incidence of interaction will be neutral because the presence of bark beetle-killed stands alone does not increase or decrease the probability of fire. Most observational studies support neutral interactions between bark beetles and fire occurrence, (Berg et al., 2006; Kulakowski and Jarvis, 2011; Kulakowski et al., 2012; Black et al., 2013; Hart et al., 2015; Meigs et al., 2015). These findings were confirmed in a study spanning the western U.S. where bark beetle outbreaks did not contribute to increases in fire size and climate was a more important driver (Mietkiewicz and Kulakowski, 2016). Conversely, Kulakowski et al. (2003) found that spruce forests with high bark beetle mortality were less likely to experience a surface fire compared to low bark beetle mortality areas.

The incidence, intensity, and effects of bark beetle and fire interactions are dependent on the influence of time between disturbances and bark beetle outbreak intensity on fire behavior. Facilitated interactions may result where bark beetle attacks are recent and severe enough to provide more available fuels that may increase the likelihood

of a crown fire (Brown, 1975). For instance, recent bark beetle outbreaks that result in sufficient dead marcescent foliage of low moisture content (i.e., "red stage") may increase crown fire ignition (Jolly et al., 2012b, 2012a; Page et al., 2012, 2013). As time-since-outbreak increases, the senescence of dead foliage (i.e., "gray stage", 3–7 years) reduces the potential for crown ignition and perhaps canopy spread due to lower canopy bulk density (Klutsch et al., 2011; Harvey et al., 2013). While the "gray stage" likely reduces the possibility for a facilitated interaction due to a lower crown fire potential, underlying surface fuels (accumulated senesced litter plus pre-outbreak fuels) may simultaneously become more flammable (Simard et al., 2011). Surface fuels beneath dead trees can have lower fuel moisture due to greater exposure to solar radiation and wind, thus potentially increasing the probability of ignition and transition to a crown fire.

While much of the research supports neutral interactions between bark beetle and fire, some studies have detected facilitated interactions under certain time between disturbances and bark beetle outbreak levels. Bigler et al. (2005) found that stands that had a bark beetle attack 60 yrs prior to fire were twice as likely to experience a high severity fire. Similarly, Lynch et al. (2006) found that older (16–19 years between disturbances) bark beetle attacked lodgepole pine stands (*Pinus contorta* var. *latifolia*) resulted in an 11% increased probability of fire compared to more recently (5–8 years between disturbances) attacked stands, possibly due to regrowth of vegetation that increased surface fuel loading and continuity. A recent study of spruce forests in Alaska found an area where the bark beetle outbreak size was relatively small and the outbreak duration lasted between two and three years had an increased likelihood of burning (Hansen et al., 2016). The incidence of crown fire will also depend on the intensity of the bark beetle outbreak. Turner et al. (1999) reported that lodgepole pine stands with intermediate levels of bark beetle mortality had a greater incidence of crown fire (i.e. intensity).

Regardless of the impact on fire incidence, increased fuel loads from bark beetle attack have the potential to alter fire behavior and severity (Hicke et al., 2012; Jenkins et al., 2014). Model projection studies that utilize field-based data to inform potential fire behavior subsequent to a bark beetle attack have been conducted for Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), lodgepole pine, and Engelmann spruce (*Picea engelmannii*) forests in the Intermountain West (Jenkins et al., 2008), Rocky Mountains (Simard et al., 2011; Schoennagel et al., 2012; Perrakis et al., 2014; Hoffman et al., 2015), and central Oregon and Idaho (Hoffman et al., 2012). In each of these studies, changes in fuel loading and availability caused by bark beetle outbreaks resulted in increased potential fire behavior compared to unattacked or "endemic" stands. Jenkins et al. (2008) and Schoennagel et al. (2012) found that recently attacked stands (i.e., red stage) could result in increased fire behavior. However, Simard et al. (2011) concluded that such changes in potential fire behavior were not supported, though limitations in the assumptions and modeling approaches have been highlighted by others (Jolly et al., 2012a; Moran and Cochrane, 2012). Hoffman et al. (2015) used a more advanced physics-based fire modeling approach that accounted for changes in wind patterns and found that recent, higher intensity bark beetle outbreaks could result in increased rate of fire spread. These modeled results are also consistent with observations of increased rate of fire spread from wildfire and experimental fires in recent (< 5 yrs) bark-beetle affected stands (Perrakis et al., 2014).

Observational studies have also increased our understanding of fire-bark beetle interaction effects on tree mortality, often assessed through remote sensing estimates of fire severity based on vegetation change. Harvey et al. (2013) found that bark beetle outbreaks in Douglas-fir forests in the Middle Rocky Mountain ecoregion were not associated with subsequent increases in fire severity. A similar lack of association was found in higher elevation spruce-fir forests in southwestern Colorado under moderate or extreme fire weather conditions (Andrus et al., 2016). Another study examining mountain pine beetle (*Dendroctonus ponderosae*) attacked stands from the Pacific Northwest showed that fire severity did not increase in recently attacked stands relative to uninfected stands and that severity decreased with time since beetle outbreak (Meigs et al., 2016). Although these trends are not uniform across forest type and regions, other studies in lodgepole pine forests of the Rocky Mountains have shown increases in fire severity following bark beetle outbreaks, depending on the time between disturbances and moderate burning conditions (Harvey et al., 2014a, 2014b).

When the sequence of disturbances is reversed, the occurrence of fire often leads to a facilitated interaction because fire-injured trees can be weakened sufficiently to encourage bark beetle attack (Thomas and Agee, 1986; McHugh and Kolb, 2003; Hood and Bentz, 2007; Breece et al., 2008; Hood et al., 2010). This is typically attributed to the potential for bark beetles to detect volatiles emitted by fire-damaged trees (Kelsey and Joseph, 2003) and reduced resin flow in trees with greater crown scorch (Wallin et al., 2003). However, in areas that experience fires severe enough to kill most or all large live trees that would otherwise be susceptible to attack, the incidence of interaction is impeded (Veblen et al., 1994; Kulakowski et al. 2003; Kulakowski and Veblen, 2006), though Kulakowski et al. (2012) found that the strength of this relationship diminished during more recent outbreaks (e.g., 2000–2010) in lodgepole pine forests of Colorado.

The incidence and intensity of bark beetle attack following fire will vary widely depending on a number of factors including: the timing and proximity of fire with bark beetle emergence, bark beetle species and population levels, the degree of damage and number of susceptible trees, and post-fire weather impact on beetles and tree vigor (Gibson and Negrón, 2009 and references therein). In ponderosa pine (*Pinus ponderosa*) forests of northern Arizona, the response of bark beetle attack following prescribed fire varied depending on both the amount of damage, timing of fire, and the bark beetle species present (McHugh et al., 2003). Bark beetles that are typically less aggressive had a greater response than more aggressive bark beetle species. Yet, when this disturbance interaction is facilitated it often leads to a synergistic effect on bark beetle-caused tree mortality when compared to adjacent unburned areas (Schwilk et al., 2006). Powell et al. (2012) found that post-fire beetle attack on lodgepole pine in the Greater Yellowstone area was more common for moderately injured trees and at higher population levels of mountain pine beetle. While bark beetle-caused mortality is often elevated after fire, the magnitude of bark beetle attack decreases rapidly with time since fire (Davis et al., 2012). The inability of bark beetles to reach outbreak levels is likely related to the reduced availability of weakened trees and some evidence suggests that areas that have experienced a previous fire are less prone to bark beetle attack (Bebi et al., 2003; Kulakowski et al., 2016). Additionally, studies in ponderosa pine forests that had experienced low severity fires had greater resin flow (Feeney et al., 1998; Perrakis and Agee, 2006) and more resin duct defenses (Hood et al., 2015, 2016) compared to long-unburned forests. Increased allocation to resin defense has been shown to reduce bark beetle attack and mortality in many pine forest types (Kane and Kolb, 2010; Ferrenberg et al., 2014; Hood and Sala, 2015).

3.3. Fire-pathogen interactions

Forest disease emerges as an interaction between tree hosts and pathogens under suitable environmental conditions. Increased warming will likely alter diseases through individual and combined effects on the host, pathogen, and environment resulting in some pathogens expanding and others contracting (Sturrock et al., 2011; Altizer et al., 2013; and references therein). Both native and non-native fungal pathogens occur throughout a variety of fire-prone forested ecosystems, with many non-native pathogens rapidly increasing in their incidence across North America (Aukema et al., 2010).

While the evidence for increasing fire frequency and size is mounting in many landscapes (Dennison et al., 2014; Abatzoglou and Williams, 2016), the effects on native pathogens are much less certain

Table 2
Suggested research needs related to fire-disturbance interactions.

Interaction Type	Interaction Category	Research Needs
Drought-Fire		
	Incidence	Determine the extent and temporal trends of drought and fire interactions
		Quantify the influence of drought-induce mortality on fuel loading and availability over time
	Intensity	Develop better methods to assess intensity of drought and fire
	Tree mortality effects	Directly observe fire behavior following drought-induced tree mortality
		Further examine the role of drought in predisposing trees to fire-related mortality
		Incorporate direct and indirect effects of drought in post-fire tree mortality models
Bark beetle-Fire		
	Incidence	Determine the extent and temporal trends of bark beetle-fire interactions
		Further examine the thresholds for facilitated interactions
		Examine bark beetle-fire interactions in historically low severity fire regime forests
	Intensity	Directly observe fire behavior following bark beetle-induced tree mortality to better determine mechanisms for synergistic effects
	Tree mortality effects	Acquire additional information on the role of fire in promoting tree resistance to bark beetle attack
Pathogen-Fire		
	Incidence	Determine the extent and temporal trends of pathogen-fire interactions
		Quantify the extent of native pathogen outbreaks
		Quantify the influence of pathogen-induce mortality on fuel loading and availability over time
		Examine more incidences of potential pathogen-fire interactions
	Intensity	Directly observe fire behavior following pathogen-induced tree mortality
	Tree mortality effects	Determine the thresholds for pathogen-fire interactions
		Examine the influence of sequence on pathogen-fire interactions

and make generalizations on the incidence of interaction challenging. Disease effects can range widely from the death of individual leaves to extensive swaths of forest (Burdon et al., 1989; Gilbert, 2002). The scale of effect is relevant in that small, isolated attacks will likely result in fewer interactions with fire. In contrast, pathogens that are more rapidly or continuously dispersed will likely result in more interactions with fire. A further complicating case is “staggered” disease effects, where individuals or small patches die in spatially heterogeneous ways (Meentemeyer et al., 2012). However, in most cases the incidence of interaction will be neutral, unless the pathogen alters fuel moisture sufficiently to increase the probability of ignition.

Disease-related tree mortality can, in turn, change the structure or composition of fuels (Cobb et al., 2012), that can subsequently influence fire behavior and effects. There are two important temporal components of pathogen impacts on fuels that vary among tree diseases. First, pathogens may initiate tree mortality at varying rates, with either acute effects aggregated through time, or chronic effects with a lower incidence of disease-related mortality at a given time. Second, the progression of fuel recruitment from pathogen-related mortality can occur at different rates depending on the duration and number of stages in the disease epidemic. For example, several wilt-like pathogens (e.g., *Phytophthora ramorum* in the western USA, which causes sudden oak death) cause short-term leaf death followed by delayed marcescence of killed foliage. This phenomenon of attached dead leaves with correspondingly low fuel moisture (Kuljian and Varner, 2010) has been implicated in increased torching, firebrand generation, and spot fires for tanoak, *Notholithocarpus densiflorus,* (Metz et al., 2011; Kuljian and Varner, 2013; Metz et al., 2013) and coast live oak, *Quercus agrifolia,* (Shaw et al., 2017) in coastal forests of California. Following eventual leaf senescence, branches and stems fall and increase surface fuels in proportion to the amount of basal area affected by the pathogen, which has been shown to increase modeled surface fire behavior (Valachovic et al., 2011; Forrestel et al., 2015; Shaw et al., 2017). As mentioned for bark beetles above, the phase or temporal stage of disease impacts coincident with fire occurrence is critical for the strength of the interaction and magnitude of the disturbance interaction effects (Kuljian and Varner, 2010; Metz et al., 2011, 2013). *Phytophthora ramorum* tends to initiate high tree mortality within a few years of pathogen establishment, but the rate at which dead leaves are cast, snags fragment or fall, and fuels decompose, will depend on the community composition of the stand, hosts killed, and environmental variation among infected stands (Cobb et al., 2012). Other pathogens may be more continuous producers of woody fuels such as the native root rot pathogens *Heterobasidion annosum* or *Armillaria mellea* in the western U.S., which slowly spread from tree to tree and initiate tree mortality over a longer period. The prevalence or impact of these pathogens can change suddenly in response to management decisions (e.g., tree-felling) with long-lasting changes to forest structure (Slaughter and Rizzo, 1999). That dead trees are recruited to the surface woody fuelbed is common across most tree-killing pathogens, although the rate and amount of this recruitment have undergone little study for most pathogens.

For those pathogens that influence fuel loading and fire behavior, synergistic interaction effects on tree mortality have been demonstrated. The effects of these interacting disturbances go beyond the host species and can affect neighboring species. In coastal California forests, sudden oak death-killed tanoak caused substantially greater post-fire mortality for the co-occurring iconic coast redwood, *Sequoia sempervirens*, a species that experiences minimal pathogen impacts and had lower mortality in burned areas free of the disease (Metz et al., 2013). The interaction of fire and disease also led to higher landing rates of ambrosia beetles compared to areas with either fire or disease, and this could herald further elevated tree mortality in susceptible species (Beh et al., 2014).

When the disturbance interaction sequence is reversed, the influence of fire on subsequent disease dynamics depends on the changes fire makes to hosts, pathogen, and the environmental conditions. Fires can also affect the incidence of diseases, reducing pathogens in some cases (e.g., the relationship between fire and *Scirrhia acicola* in *Pinus palustris* of the southeastern USA; Grelen, 1983), weakening trees sufficiently to promote infection and spread in other cases (Parker et al., 2006), or disproportionately killing species that play major roles in the epidemiology of the disease and thereby suppress pathogen in the post-fire landscape (Beh et al., 2012). In some cases fire (e.g., lower intensity fires) can impose selective tree mortality because certain species and genotypes differ in their vulnerability to disturbance and thus can serve to alter species composition and structure that can impede or hasten the subsequent disturbance, but this effect likely declines with time since fire.

4. Areas for further research inquiry

Altered disturbances related to climate changes are evident and the impact of these changes on disturbance interactions is of increasing interest to researchers and managers (Turner, 2010; Buma, 2015). Our

review of fire-disturbance interactions highlights the major findings on the topic, but research gaps on the incidence, intensity, and effects of these interactions are evident (Table 2). Regardless of the fire-disturbance interaction type, we consistently noted that more information is needed on the spatial and temporal drivers of these disturbances individually and their propensity to interact. While it is logical to think that the increased frequency of individual disturbance types should yield increased interactions, the degree to which disturbance interactions are relatively rare occurrences is also not well understood. Our findings suggest studies that examine the trends in the frequency and extent of interactions over time are warranted.

Of the published studies on disturbance interactions to date, almost all have not directly observed or quantified measures of fire behavior (i.e. intensity) in these disturbance interactions. Existing studies have either relied on modeled fire behavior or burn severity observations (but see Perrakis et al., 2014). While these approaches are informative, similar fire severity patterns can result from differing fire behavior patterns. For instance, high severity fires can result from either a high intensity surface fire that scorches the tree sufficiently to cause mortality or through a crown fire that actively consumes the crown. However, use of satellite-derived estimates of fire intensity have been well correlated with fire severity measures (Smith and Wooster, 2005; Heward et al., 2013) and hold promise for quantifying fire intensity for interactions of disturbances with fire. Future research would benefit from more studies that directly examine fire behavior to determine the mechanisms of fire-disturbance interactions.

As we have highlighted, there are many instances where disturbance interactions have resulted in unexpected effects on tree mortality. However, the impacts of these altered disturbance interactions are highly variable and dependent on many factors related to the individual disturbance types and the circumstances in which they interact. A better understanding of the patterns, mechanisms, and impacts of disturbance interactions is essential to determine ecosystem response and the appropriate management strategies needed before, during, and after fires. Information on the role of severity of the initial disturbance and the influence of time between disturbances has recently increased but there is a continued need for more long-term studies of drought, beetles, pathogens and other disturbances across a broader range of fire-prone ecosystems that explicitly examine disturbance effects in the context of fire. This line of research could include quantifying fuel quality, abundance, and composition and changes to these conditions because of drought, beetle attack or forest disease. In particular, there is a need to determine the thresholds at which facilitated incidences and synergistic effects occur by climatic region and forest type.

Further elucidation of the patterns, mechanisms, and effects of fire-disturbance interactions will be largely reliant on interdisciplinary collaborations across multiple scales that work to increase our understanding of this complex topic. As instances of these fire-disturbance interactions occur across the landscape, we should continue to use these events as natural experiments to address these research gaps, but also increase our understanding of how each of these disturbances change fuels and micro-climate prior to the interaction with fire. Our review also indicates that, where possible, experimental or manipulative approaches are needed to better understand disturbance interactions, as suggested by others (Foster et al., 2016).

We focused our review on examples from the western U.S., which may limit broad applicability to other regions. Most continents are also experiencing increased fire activity, drought, and other disturbances and the impacts of these interactions have (Seidl et al., 2017). While the summary of studies presented here may be more broadly representative, our findings will most directly apply to other temperate, moisture-limited, and fire-prone regions. Yet, western U.S. forests are also unique in some regards. For instance, much of this region has experienced a relatively distinct history of fire exclusion for over a century that is not common to other fire-prone areas. In addition, the western U.S. represents a relatively large expansive forested area that may increase the potential for the incidence of disturbance interactions that may not be as prevalent in other regions (e.g., Europe). Future research may examine how broadly the incidence, intensity, and effects of disturbance interactions in the western U.S. inform other biomes and regions, and vice versa.

In this review, we only focused on two-way fire-disturbance interactions, however, often times three or more disturbances (e.g., drought/bark beetle/fire interactions) can be involved (Allen, 2007; Kulakowski and Veblen, 2007; Sibold et al., 2007; Allen et al., 2015). Focusing on the multiple disturbances and circumstances in specific forest types and regions may be a more approachable way to understand these higher-order interactions (e.g., McKenzie et al., 2008). Further insights can be made through mechanistic, process-based modeling (Butler and Dickinson, 2010; Loehman et al., 2016) that can assess potential effects and develop testable hypotheses that will ultimately provide us with a better understanding of how multiple disturbances influence forest dynamics. The data requirements for such models can be daunting, but this work will highlight future research needs and identify areas where generalizations are possible.

The broader impacts of changes in fire-disturbance interactions clearly extend beyond tree mortality. Incorporating research that focuses on the consequences of altered disturbance interactions regimes on regeneration, ecosystem trajectories, ecosystem services, and biosphere-atmosphere interactions will be necessary. As most model projections indicate continued warming with more varied precipitation, not only will these changes affect disturbances individually but they will also affect how these disturbances interact. Without a more comprehensive understanding the impacts of changes to disturbance interactions, the effectiveness of policy and management decisions may be diminished.

5. Conclusions

Increased temperatures and greater incidences of many historically common and novel disturbances can have profound effects on their interactions with fire. Existing research suggests that in most cases increases in disturbances that cause elevated tree mortality do not seem to increase the probability of fire (i.e. neutral interactions), and that fire weather conditions are often a major overriding driver. However, disturbances that result in tree mortality sufficient to increase surface fine-fuel loading and lower fuel moisture enough can increase the probability of ignition. Even still, where changes in surface fuel load and availability do not increase the probability of a surface fire, changes in crown fuel characteristics can promote greater incidences of crown fire when ignitions occur. Clear and consistent evidence of increased crown fire initiation is lacking across disturbance interaction types, but tended to occur when under moderate to high intensity of the first disturbance or low to moderate fire weather conditions.

Our review indicates that where these disturbance interactions occur the interaction effect on tree mortality is much more varied, often resulting in simple additive effects. Still, there are circumstances where the interaction between other disturbances and fire has resulted in synergistic effects (greater mortality than either disturbance alone). In these instances the severity of the initial disturbance is moderate to high and time between disturbances is relatively short. A prolonged or severe drought that reduces tree vigor sufficiently may promote a synergistic effect of greater tree mortality during a subsequent fire. When the sequence of disturbance interaction is reversed (e.g., fire precedes other disturbances) most evidence suggests that the incidence and effects of interaction will be reduced (impeded interactions and antagonistic interaction effects). For example, when a preceding fire sufficiently reduces competition and removes weakened trees, a subsequent drought or bark beetle outbreak may result in lower mortality when compared to a bark beetle outbreak without an initial fire in the area.

Recent research on fire-disturbance interactions has contributed to our broader understanding on the topic, yet numerous research gaps

persist. Future studies could focus on developing forest type and region-specific thresholds that can have unexpected impacts. This information can then be used to inform broader impacts on biodiversity, ecosystem function, ecosystem services, and bio-climatic feedbacks. Further information that examines the mechanisms and thresholds of disturbance interaction incidences and effects will help facilitate appropriate policies and management strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.037.

References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113, 11770–11775. http://dx.doi.org/10.1073/pnas.1607171113.

Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. 106, 7063–7066.

Allen, C.D., 2007. Interactions across spatial scales among forest dieback, fire, and erosion in northern New Mexico landscapes. Ecosystems 10, 797–808. http://dx.doi.org/10.1007/s10021-007-9057-4.

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, art129.

C.D. Allen A.K. Macalady H. Chenchouni D. Bachelet N. McDowell M. Vennetier T. Kitzberger A. Rigling D.D. Breshears E.H. Hogg P. Gonzalez R. Fensham Z. Zhang J. Castro N. Demidova J.-H. Lim G. Allard S.W. Running A. Semerci N. Cobb 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests For. Ecol. Manag. 259 660–684 10.1016/j.foreco.2009.09.001.

Altizer, S., Ostfeld, R.S., Johnson, P.T.J., Kutz, S., Harvell, C.D., 2013. Climate change and infectious diseases: from evidence to a predictive framework. Science 341, 514–519. http://dx.doi.org/10.1126/science.1239401.

Anderegg, W.R.L., Plavcová, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A., Field, C.B., 2013. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. Glob. Change Biol. 19, 1188–1196. http://dx.doi.org/10.1111/gcb.12100.

Andrus, R.A., Veblen, T.T., Harvey, B.J., Hart, S.J., 2016. Fire severity unaffected by spruce beetle outbreak in spruce-fir forests in southwestern Colorado. Ecol. Appl. 26, 700–711.

Aukema, J.E., McCullough, D.G., Von Holle, B., Liebhold, A.M., Britton, K., Frankel, S.J., 2010. Historical accumulation of nonindigenous forest pests in the continental United States. BioScience 60, 886–897. http://dx.doi.org/10.1525/bio.2010.60.11.5.

Bebi, P., Kulakowski, D., Veblen, T.T., 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology 84, 362–371.

Beh, M.M., Metz, M.R., Frangioso, K.M., Rizzo, D.M., 2012. The key host for an invasive forest pathogen also facilitates the pathogen's survival of wildfire in California forests. New Phytol. 196, 1145–1154. http://dx.doi.org/10.1111/j.1469-8137.2012.04352.x.

Beh, M.M., Metz, M.R., Seybold, S.J., Rizzo, D.M., 2014. The novel interaction between Phytophthora ramorum and wildfire elicits elevated ambrosia beetle landing rates on tanoak, Notholithocarpus densiflorus. For. Ecol. Manag. 318, 21–33. http://dx.doi.org/10.1016/j.foreco.2014.01.007.

Bentz, B.J., Hood, S.A., Hansen, E.M., Vandygriff, J.C., Mock, K.E., 2016. Defense traits in the long-lived Great Basin bristlecone pine and resistance to the native herbivore mountain pine beetle. New Phytol. http://dx.doi.org/10.1111/nph.14191.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60, 602–613. http://dx.doi.org/10.1525/bio.2010.60.8.6.

Berg, E.E., David Henry, J., Fastie, C.L., De Volder, A.D., Matsuoka, S.M., 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. For. Ecol. Manag. 227, 219–232. http://dx.doi.org/10.1016/j.foreco.2006.02.038.

Bigler, C., Kulakowski, D., Veblen, T.T., 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology 86, 3018–3029.

Black, S.H., Kulakowski, D., Noon, B.R., DellaSala, D.A., 2013. Do bark beetle outbreaks increase wildfire risks in the central U.S. Rocky Mountains? Implications from recent research. Nat. Areas J. 33, 59–65. http://dx.doi.org/10.3375/043.033.0107.

Bowman, D.M.J.S., Balch, J., Artaxo, P., Bond, W.J., Cochrane, M.A., D'Antonio, C.M., DeFries, R., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Mack, M., Moritz, M.A., Pyne, S., Roos, C.I., Scott, A.C., Sodhi, N.S., Swetnam, T.W., 2011. The human dimension of fire regimes on Earth: the human dimension of fire regimes on Earth. J. Biogeogr. 38, 2223–2236. http://dx.doi.org/10.1111/j.1365-2699.2011.02595.x.

Bowman, D.M.J.S., French, B.J., Prior, L.D., 2014. Have plants evolved to self-immolate? Front. Plant Sci. 5. http://dx.doi.org/10.3389/fpls.2014.00590.

Bradford, J.B., Bell, D.M., 2017. A window of opportunity for climate-change adaptation: easing tree mortality by reducing forest basal area. Front. Ecol. Environ. 15, 11–17. http://dx.doi.org/10.1002/fee.1445.

Breece, C.R., Kolb, T.E., Dickson, B.G., McMillin, J.D., Clancy, K.M., 2008. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. For. Ecol. Manag. 255, 119–128. http://dx.doi.org/10.1016/j.foreco.2007.08.026.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. U. S. A. 102, 15144–15148 other.

Brown, J.K., 1975. Fire cycles and community dynamics in lodgepole pine forests. In: Baumgartner, D. (Ed.), Management of Lodgepole Pine Ecosystems: Symposium Proceedings. Washington State University Cooperative Extension Service, Pullman, Washington, USA, pp. 429–456.

Buma, B., 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. Ecosphere 6, art70. http://dx.doi.org/10.1890/ES15-00058.1.

Buma, B., Poore, R.E., Wessman, C.A., 2014. Disturbances, their interactions, and cumulative effects on carbon and charcoal stocks in a forested ecosystem. Ecosystems 17, 947–959. http://dx.doi.org/10.1007/s10021-014-9770-8.

Buma, B., Wessman, C.A., 2011. Disturbance interactions can impact resilience mechanisms of forests. Ecosphere 2, art64. http://dx.doi.org/10.1890/ES11-00038.1.

Burdon, J.J., Jarosz, A., Kirby, G., 1989. Pattern and patchiness in plant-pathogen interactions-Causes and consequences. Annu. Rev. Ecol. Syst. 20, 119–136.

Butler, B.W., Dickinson, M.B., 2010. Tree injury and mortality in fires: developing process-based models. Fire Ecol. 6, 55–79. http://dx.doi.org/10.4996/fireecology.0601055.

Cailleret, M., Jansen, S., Robert, E.M.R., Desoto, L., Aakala, T., Antos, J.A., Beikircher, B., Bigler, C., Bugmann, H., Caccianiga, M., Čada, V., Camarero, J.J., Cherubini, P., Cochard, H., Coyea, M.R., Čufar, K., Das, A.J., Davi, H., Delzon, S., Dorman, M., Gea-Izquierdo, G., Gillner, S., Haavik, L.J., Hartmann, H., Hereş, A.-M., Hultine, K.R., Janda, P., Kane, J.M., Kharuk, V.I., Kitzberger, T., Klein, T., Kramer, K., Lens, F., Levanic, T., Linares Calderon, J.C., Lloret, F., Lobo-Do-Vale, R., Lombardi, F., López Rodríguez, R., Mäkinen, H., Mayr, S., Mészáros, I., Metsaranta, J.M., Minunno, F., Oberhuber, W., Papadopoulos, A., Peltoniemi, M., Petritan, A.M., Rohner, B., Sangüesa-Barreda, G., Sarris, D., Smith, J.M., Stan, A.B., Sterck, F., Stojanović, D.B., Suarez, M.L., Svoboda, M., Tognetti, R., Torres-Ruiz, J.M., Trotsiuk, V., Villalba, R., Vodde, F., Westwood, A.R., Wyckoff, P.H., Zafirov, N., Martínez-Vilalta, J., 2017. A synthesis of radial growth patterns preceding tree mortality. Glob. Change Biol. 23, 1675–1690. http://dx.doi.org/10.1111/gcb.13535.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., Penuelas, J., 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proc. Natl. Acad. Sci. 108, 1474–1478. http://dx.doi.org/10.1073/pnas.1010070108.

Carnwath, G.C., Nelson, C.R., 2016. The effect of competition on responses to drought and interannual climate variability of a dominant conifer tree of western North America. J. Ecol. 104, 1421–1431. http://dx.doi.org/10.1111/1365-2745.12604.

Chapman, T.B., Veblen, T.T., Schoennagel, T., 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93, 2175–2185.

Clifford, M.J., Royer, P.D., Cobb, N.S., Breshears, D.D., Ford, P.L., 2013. Precipitation thresholds and drought-induced tree die-off: insights from patterns of *Pinus edulis* mortality along an environmental stress gradient. New Phytol. 200, 413–421. http://dx.doi.org/10.1111/nph.12362.

Cobb, R.C., Chan, M.N., Meentemeyer, R.K., Rizzo, D.M., 2012. Common factors drive disease and coarse woody debris dynamics in forests impacted by sudden oak death. Ecosystems 15, 242–255. http://dx.doi.org/10.1007/s10021-011-9506-y.

Cook, B.I., Ault, T.R., Smerdon, J.E., 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Sci. Adv. 1http://dx.doi.org/10.1126/sciadv.1400082. e1400082–e1400082.

D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecol. Appl. 23, 1735–1742.

Davis, R.S., Hood, S., Bentz, B.J., 2012. Fire-injured ponderosa pine provide a pulsed resource for bark beetles. Can. J. For. Res. 42, 2022–2036. http://dx.doi.org/10.1139/x2012-147.

Dennison, P.E., Brewer, S.C., Arnold, J.D., Moritz, M.A., 2014. Large wildfire trends in the western United States, 1984–2011. Geophys. Res. Lett. 41, 2928–2933. http://dx.doi.org/10.1002/2014GL059576.

Diffenbaugh, N.S., Swain, D.L., Touma, D., 2015. Anthropogenic warming has increased drought risk in California. Proc. Natl. Acad. Sci. 112, 3931–3936. http://dx.doi.org/10.1073/pnas.1422385112.

Dillon, G.K., Holden, Z.A., Morgan, P., Crimmins, M.A., Heyerdahl, E.K., Luce, C.H., 2011. Both topography and climate affected forest and woodland burn severity in two regions of the western US, 1984 to 2006. Ecosphere 2, art130. http://dx.doi.org/10.1890/ES11-00271.1.

Dorman, M., Svoray, T., Perevolotsky, A., Moshe, Y., Sarris, D., 2015. What determines tree mortality in dry environments? a multi-perspective approach. Ecol. Appl. 25, 1054–1071.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N.L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and

dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486.
Feeney, S.R., Kolb, T.E., Covington, W.W., Wagner, M.R., 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Can. J. For. Res. 28, 1295–1306.
Ferrenberg, S., Kane, J.M., Mitton, J.B., 2014. Resin duct characteristics associated with tree resistance to bark beetles across lodgepole and limber pines. Oecologia 174, 1283–1292. http://dx.doi.org/10.1007/s00442-013-2841-2.
Flannigan, M.D., Krawchuk, M.A., de Groot, W.J., Wotton, B.M., Gowman, L.M., 2009. Implications of changing climate for global wildland fire. Int. J. Wildland Fire 18, 483. http://dx.doi.org/10.1071/WF08187.
Forrestel, A.B., Ramage, B.S., Moody, T., Moritz, M.A., Stephens, S.L., 2015. Disease, fuels and potential fire behavior: Impacts of Sudden Oak Death in two coastal California forest types. For. Ecol. Manag. 348, 23–30. http://dx.doi.org/10.1016/j.foreco.2015.03.024.
Foster, C.N., Sato, C.F., Lindenmayer, D.B., 2016. Integrating theory into disturbance interaction experiments to better inform ecosystem management. Glob. Change Biol. 22, 1325–1335.
Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity. Conservation 1, 8–17.
Fried, J.S., Gilless, J.K., Riley, W.J., Moody, T.J., Simon de Blas, C., Hayhoe, K., Moritz, M., Stephens, S., Torn, M., 2008. Predicting the effect of climate change on wildfire behavior and initial attack success. Clim. Change 87, 251–264. http://dx.doi.org/10.1007/s10584-007-9360-2.
Gibson, K., Negrón, J.F., 2009. Fire and bark beetle interactions. In: Hayes, J.L., Lundquist, J.E. (Eds.). The Western Bark Beetle Research Group: A Unique Collaboration with Forest Health Protection: Proceedings of a Symposium at the 2007 Society of American Foresters Conference. USDA Forest Service Pacific Northwest Research Station, Portland, Oregon, USA, pp. 51–69.
Gilbert, G.S., 2002. Evolutionary ecology of plant diseases in natural ecosystems. Annu. Rev. Phytopathol. 40, 13–43. http://dx.doi.org/10.1146/annurev.phyto.40.021202.110417.
Grelen, H.E., 1983. May burning favors survival and early height growth of longleaf pine seedlings. South. J. Appl. For. 7, 16–20.
Grime, J.P., 1979. Plant Strategies and Vegetation Processes. Wiley, New York, New York, USA.
Gunderson, L.H., 2000. Ecological resilience—in theory and application. Annu. Rev. Ecol. Syst. 31, 425–439.
Hansen, W.D., Chapin, F.S., Naughton, H.T., Rupp, T.S., Verbyla, D., 2016. Forest-landscape structure mediates effects of a spruce bark beetle (Dendroctonus rufipennis) outbreak on subsequent likelihood of burning in Alaskan boreal forest. For. Ecol. Manag. 369, 38–46. http://dx.doi.org/10.1016/j.foreco.2016.03.036.
Hart, S.J., Schoennagel, T., Veblen, T.T., Chapman, T.B., 2015. Area burned in the western United States is unaffected by recent mountain pine beetle outbreaks. Proc. Natl. Acad. Sci. 112, 4375–4380. http://dx.doi.org/10.1073/pnas.1424037112.
Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. Ecol. Appl. 24, 1608–1625.
Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G., 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. Ecology 94, 2475–2486.
Harvey, B.J., Donato, D.C., Turner, M.G., 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. Proc. Natl. Acad. Sci. http://dx.doi.org/10.1073/pnas.1411346111.
Heward, H., Smith, A.M.S., Roy, D.P., Tinkham, W.T., Hoffman, C.M., Morgan, P., Lannom, K.O., 2013. Is burn severity related to fire intensity? Observations from landscape scale remote sensing. Int. J. Wildl. Fire 22, 910. http://dx.doi.org/10.1071/WF12087.
Hicke, J.A., Johnson, M.C., Hayes, J.L., Preisler, H.K., 2012. Effects of bark beetle-caused tree mortality on wildfire. For. Ecol. Manag. 271, 81–90. http://dx.doi.org/10.1016/j.foreco.2012.02.005.
Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vila, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Glob. Ecol. Biogeogr. 15, 1–7. http://dx.doi.org/10.1111/j.1466-822X.2006.00212.x.
Hoffman, C., Morgan, P., Mell, W., Parsons, R., Strand, E.K., Cook, S., 2012. Numerical simulation of crown fire hazard immediately after bark beetle-caused mortality in lodgepole pine forests. For. Sci. 58, 178–188. http://dx.doi.org/10.5849/forsci.10-137.
Hoffman, C.M., Linn, R., Parsons, R., Sieg, C., Winterkamp, J., 2015. Modeling spatial and temporal dynamics of wind flow and potential fire behavior following a mountain pine beetle outbreak in a lodgepole pine forest. Agric. For. Meteorol. 204, 79–93.
Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1–23.
Hood, S., Bentz, B., 2007. Predicting postfire Douglas-fir beetle attacks and tree mortality in the northern Rocky Mountains. Can. J. For. Res. 37, 1058–1069. http://dx.doi.org/10.1139/X06-313.
Hood, S., Sala, A., 2015. Ponderosa pine resin defenses and growth: metrics matter. Tree Physiol. 35, 1223–1235. http://dx.doi.org/10.1093/treephys/tpv098.
Hood, S., Sala, A., Heyerdahl, E.K., Boutin, M., 2015. Low-severity fire increases tree defense against bark beetle attacks. Ecology 96, 1846–1855.
Hood, S.M., Baker, S., Sala, A., 2016. Fortifying the forest: thinning and burning increase resistance to a bark beetle outbreak and promote forest resilience. Ecol. Appl. http://dx.doi.org/10.1002/eap.1363.
Hood, S.M., Smith, S.L., Cluck, D.R., 2010. Predicting mortality for five California conifers following wildfire. For. Ecol. Manag. 260, 750–762. http://dx.doi.org/10.1016/j.foreco.2010.05.033.
Jenkins, M.J., Hebertson, E., Page, W., Jorgensen, C.A., 2008. Bark beetles, fuels, fires and implications for forest management in the Intermountain West. For. Ecol. Manag. 254, 16–34. http://dx.doi.org/10.1016/j.foreco.2007.09.045.
Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., Bentz, B.J., 2014. Interactions among the Mountain Pine Beetle, fires, and fuels. For. Sci. 60, 489–501. http://dx.doi.org/10.5849/forsci.13-017.
Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E., Mack, M.C., Meentemeyer, R.K., Metz, M.R., Perry, G.L., Schoennagel, T., Turner, M.G., 2016. Changing disturbance regimes, ecological memory, and forest resilience. Front. Ecol. Environ. 14, 369–378. http://dx.doi.org/10.1002/fee.1311.
Jolly, W.M., Parsons, R., Varner, J.M., Butler, B.W., Ryan, K.C., Gucker, C.L., 2012a. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. Ecology 93, 941–946.
Jolly, W.M., Parsons, R.A., Hadlow, A.M., Cohn, G.M., McAllister, S.S., Popp, J.B., Hubbard, R.M., Negron, J.F., 2012b. Relationships between moisture, chemistry, and ignition of Pinus contorta needles during the early stages of mountain pine beetle attack. For. Ecol. Manag. 269, 52–59. http://dx.doi.org/10.1016/j.foreco.2011.12.022.
Kane, J.M., Kolb, T.E., 2010. Importance of resin ducts in reducing ponderosa pine mortality from bark beetle attack. Oecologia 164, 601–609. http://dx.doi.org/10.1007/s00442-010-1683-4.
Kavanagh, K.L., Dickinson, M.B., Bova, A.S., 2010. A way forward for fire-caused tree mortality prediction: modeling a physiological consequence of fire. Fire Ecol. 6, 80–94. http://dx.doi.org/10.4996/fireecology.0601080.
Kelsey, R.G., Joseph, G., 2003. Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can. J. For. Res. 33, 870–884. http://dx.doi.org/10.1139/x03-007.
Klutsch, J.G., Battaglia, M.A., West, D.R., Costello, S.L., Negron, J.F., 2011. Evaluating potential fire behavior in lodgepole pine-dominated forests after a mountain pine beetle epidemic in north-central Colorado. West. J. Appl. For. 26, 101–109.
Knight, D.H., 1987. Parasites, lightning, and the vegetation mosaic in wilderness landscapes. In: Landscape Heterogeneity and Disturbance. Springer, pp. 59–83.
Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., Weed, A.S., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. For. Ecol. Manag. 380, 321–334. http://dx.doi.org/10.1016/j.foreco.2016.04.051.
Kulakowski, D., Jarvis, D., 2011. The influence of mountain pine beetle outbreaks and drought on severe wildfires in northwestern Colorado and southern Wyoming: A look at the past century. For. Ecol. Manag. 262, 1686–1696. http://dx.doi.org/10.1016/j.foreco.2011.07.016.
Kulakowski, D., Jarvis, D., Veblen, T.T., Smith, J., 2012. Stand-replacing fires reduce susceptibility of lodgepole pine to mountain pine beetle outbreaks in Colorado: stand-replacing fires reduce susceptibility to beetle outbreaks. J. Biogeogr. 39, 2052–2060. http://dx.doi.org/10.1111/j.1365-2699.2012.02748.x.
Kulakowski, D., Veblen, T.T., 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88, 759–769.
Kulakowski, D., Veblen, T.T., 2006. The effects of fires on susceptibility of subalpine forests to a 19th century spruce beetle outbreak in western Colorado. Can. J. For. Res. 36, 2974–2982.
Kulakowski, D., Veblen, T.T., Bebi, P., 2016. Fire severity controlled susceptibility to a 1940s spruce beetle outbreak in Colorado, USA. PLoS One 11, e0158138.
Kulakowski, D., Veblen, T.T., Bebi, P., 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regimes of a subalpine forest in Colorado. J. Biogeogr. 30, 1445–1456.
Kuljian, H., Varner, J.M., 2013. Foliar consumption across a sudden oak death chronosequence in laboratory fires. Fire Ecol. 9, 33–44. http://dx.doi.org/10.4996/fireecology.0903033.
Kuljian, H., Varner, J.M., 2010. The effects of sudden oak death on foliar moisture content and crown fire potential in tanoak. For. Ecol. Manag. 259, 2103–2110. http://dx.doi.org/10.1016/j.foreco.2010.02.022.
Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western US ecoprovinces, 1916–2003. Ecol. Appl. 19, 1003–1021.
Littell, J.S., Peterson, D.L., Riley, K.L., Liu, Y., Luce, C.H., 2016. A review of the relationships between drought and forest fire in the United States. Glob. Change Biol. http://dx.doi.org/10.1111/gcb.13275.
Loehman, R.A., Keane, R.E., Holsinger, L.M., Wu, Z., 2016. Interactions of landscape disturbances and climate change dictate ecological pattern and process: spatial modeling of wildfire, insect, and disease dynamics under future climates. Landsc. Ecol. 1–13. http://dx.doi.org/10.1007/s10980-016-0414-6.
Lynch, H.J., Renkin, R.A., Crabtree, R.L., Moorcroft, P.R., 2006. The influence of previous mountain pine beetle (Dendroctonus ponderosae) activity on the 1988 Yellowstone Fires. Ecosystems 9, 1318–1327. http://dx.doi.org/10.1007/s10021-006-0173-3.
Mallek, C., Safford, H., Viers, J., Miller, J., 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. Ecosphere 4, art153.
McDowell, N.G., 2011. Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiol. 155, 1051–1059. http://dx.doi.org/10.1104/pp.110.170704.
McHugh, C.W., Kolb, T.E., 2003. Ponderosa pine mortality following fire in northern Arizona. Int. J. Wildland Fire 12, 7–22. http://dx.doi.org/10.1071/WF02054.
McHugh, C.W., Kolb, T.E., Wilson, J.L., 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environ. Entomol. 32, 510–522.
McKenzie, D., Peterson, D.L., Littell, J.J., 2008. Chapter 15 Global Warming and Stress Complexes in Forests of Western North America. In: Developments in Environmental Science. Elsevier, pp. 319–337. 10.1016/S1474-8177(08)00015-6.
Meddens, A.J., Hicke, J.A., Ferguson, C.A., 2012. Spatiotemporal patterns of observed bark beetle-caused tree mortality in British Columbia and the western United States. Ecol. Appl. 22, 1876–1891.
Meddens, A.J.H., Hicke, J.A., 2014. Spatial and temporal patterns of Landsat-based detection of tree mortality caused by a mountain pine beetle outbreak in Colorado, USA. For. Ecol. Manag. 322, 78–88. http://dx.doi.org/10.1016/j.foreco.2014.02.037.
Meddens, A.J.H., Hicke, J.A., Macalady, A.K., Buotte, P.C., Cowles, T.R., Allen, C.D., 2015. Patterns and causes of observed piñon pine mortality in the southwestern United States. New Phytol. 206, 91–97. http://dx.doi.org/10.1111/nph.13193.

Meentemeyer, R.K., Haas, S.E., Václavík, T., 2012. Landscape epidemiology of emerging infectious diseases in natural and human-altered ecosystems. Annu. Rev. Phytopathol. 50, 379–402. http://dx.doi.org/10.1146/annurev-phyto-081211-172938.
Meigs, G.W., Campbell, J.L., Zald, H.S., Bailey, J.D., Shaw, D.C., Kennedy, R.E., 2015. Does wildfire likelihood increase following insect outbreaks in conifer forests? Ecosphere 6, 1–24.
Meigs, G.W., Zald, H.S.J., Campbell, J.L., Keeton, W.S., Kennedy, R.E., 2016. Do insect outbreaks reduce the severity of subsequent forest fires? Environ. Res. Lett. 11, 045008. http://dx.doi.org/10.1088/1748-9326/11/4/045008.
Metz, M.R., Frangioso, K.M., Meentemeyer, R.K., Rizzo, D.M., 2011. Interacting disturbances: wildfire severity affected by stage of forest disease invasion. Ecol. Appl. 21, 313–320.
Metz, M.R., Varner, J.M., Frangioso, K.M., Meentemeyer, R.K., Rizzo, D.M., 2013. Unexpected redwood mortality from synergies between wildfire and an emerging infectious disease. Ecology 94, 2152–2159.
Michaletz, S.T., Johnson, E.A., Tyree, M.T., 2012. Moving beyond the cambium necrosis hypothesis of post-fire tree mortality: cavitation and deformation of xylem in forest fires. New Phytol. 194, 254–263. http://dx.doi.org/10.1111/j.1469-8137.2011.04021.x.
Mietkiewicz, N., Kulakowski, D., 2016. Relative importance of climate and mountain pine beetle outbreaks on the occurrence of large wildfires in the western USA. Ecol. Appl. 26, 2523–2535.
Miller, J.D., Safford, H.D., Crimmins, M., Thode, A.E., 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. Ecosystems 12, 16–32. http://dx.doi.org/10.1007/s10021-008-9201-9.
Miller, J.D., Skinner, C.N., Safford, H.D., Knapp, E.E., Ramirez, C.M., 2012. Trends and causes of severity, size, and number of fires in northwestern California, USA. Ecol. Appl. 22, 184–203.
Moran, C.J., Cochrane, M.A., 2012. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Comment. Ecology 93, 939–941.
Negrón, J.F., 1998. Probability of infestation and extent of mortality associated with the Douglas-fir beetle in the Colorado Front Range. For. Ecol. Manag. 107, 71–85.
Nesmith, J.C.B., Das, A.J., O'Hara, K.L., van Mantgem, P.J., 2015. The influence of prefire tree growth and crown condition on postfire mortality of sugar pine following prescribed fire in Sequoia National Park. Can. J. For. Res. 45, 910–919. http://dx.doi.org/10.1139/cjfr-2014-0449.
Page, W.G., Jenkins, M.J., Alexander, M.E., 2013. Foliar moisture content variations in lodgepole pine over the diurnal cycle during the red stage of mountain pine beetle attack. Environ. Model. Softw. 49, 98–102. http://dx.doi.org/10.1016/j.envsoft.2013.08.001.
Page, W.G., Jenkins, M.J., Runyon, J.B., 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. Can. J. For. Res. 42, 1631–1647. http://dx.doi.org/10.1139/x2012-094.
Paine, R.T., Tegner, M.J., Johnson, E.A., 1998. Compounded perturbations yield ecological surprises. Ecosystems 1, 535–545.
Parker, T.J., Clancy, K.M., Mathiasen, R.L., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric. For. Entomol. 8, 167–189.
Perrakis, D.D., Agee, J.K., 2006. Seasonal fire effects on mixed-conifer forest structure and ponderosa pine resin properties. Can. J. For. Res. 36, 238–254. http://dx.doi.org/10.1139/x05-212.
Perrakis, D.D.B., Lanoville, R.A., Taylor, S.W., Hicks, D., 2014. Modeling wildfire spread in mountain pine beetle-affected forest stands, British Columbia. Canada. Fire Ecol. 10, 10–35. http://dx.doi.org/10.4996/fireecology.1002010.
Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press Inc., Orlando, FL.
Powell, E.N., Townsend, P.A., Raffa, K.F., 2012. Wildfire provide refuge from local extinction but is an unlikely diver of outbreaks by mountain pine beetle. Ecol. Monogr. 82, 69–84.
Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517.
Rizzo, D.M., Garbelotto, M., 2003. Sudden oak death: endangering California and Oregon forest ecosystems. Front. Ecol. Environ. 1, 197–204.
Ryan, K.C., Reinhardt, E.D., 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. 18, 1291–1297.
Schoennagel, T., Veblen, T.T., Negron, J.F., Smith, J.M., 2012. Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA. PLoS ONE 7, e30002. http://dx.doi.org/10.1371/journal.pone.0030002.
Schwilk, D.W., Knapp, E.E., Ferrenberg, S.M., Keeley, J.E., Caprio, A.C., 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For. Ecol. Manag. 232, 36–45. http://dx.doi.org/10.1016/j.foreco.2006.05.036.
Seidl, R., Thom, D., Kautz, M., Martin-Benito, D., Peltoniemi, M., Vacchiano, G., Wild, J., Ascoli, D., Petr, M., Honkaniemi, J., Lexer, M.J., Trotsiuk, V., Mairota, P., Svoboda, M., Fabrika, M., Nagel, T.A., Reyer, C.P.O., 2017. Forest disturbances under climate change. Nat. Clim. Change 7, 395–402. http://dx.doi.org/10.1038/nclimate3303.
Shaw, D.C., Woolley, T., Kelsey, R.G., McPherson, B.A., Westlind, D., Wood, D.L., Peterson, E.K., 2017. Surface fuels in recent Phytophthora ramorum created gaps and adjacent intact Quercus agrifolia forests, East Bay Regional Parks, California, USA. For. Ecol. Manag. 384, 331–338. http://dx.doi.org/10.1016/j.foreco.2016.11.011.
Shore, T.L., Safranyik, L., Lemieux, J.P., 2000. Susceptibility of lodgepole pine stands to the mountain pine beetle: testing of a rating system. Can. J. For. Res. 30, 44–49.
Sibold, J.S., Veblen, T.T., Chipko, K., Lawson, L., Mathis, E., Scott, J., 2007. Influences of secondary disturbances on lodgepole pine stand development in Rocky Mountain National Park. Ecol. Appl. 17, 1638–1655.
Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G., 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? Ecol. Monogr. 81, 3–24.
Slaughter, G.W., Rizzo, D.M., 1999. Past forest management promoted root disease in Yosemite Valley. Calif. Agric. 53, 17–24.
Smith, A.M.S., Wooster, M.J., 2005. Remote classification of head and backfire types from MODIS fire radiative power and smoke plume observations. Int. J. Wildl. Fire 14, 249–254.
Stephenson, N., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. 25, 855–870.
Sturrock, R.N., Frankel, S.J., Brown, A.V., Hennon, P.E., Kliejunas, J.T., Lewis, K.J., Worrall, J.J., Woods, A.J., 2011. Climate change and forest diseases: Climate change and forest diseases. Plant Pathol. 60, 133–149. http://dx.doi.org/10.1111/j.1365-3059.2010.02406.x.
Thomas, T.L., Agee, J.K., 1986. Prescribed fire effects on mixed conifer forest structure at Crater Lake. Oregon. Can. J. For. Res. 16, 1082–1087.
Turner, M.G., 2010. Disturbance and landscape dynamics in a changing world. Ecology 91, 2833–2849.
Turner, M.G., Romme, W.H., Gardner, R.H., 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int. J. Wildl. Fire 9, 21–36.
Valachovic, Y.S., Lee, C.A., Scanlon, H., Varner, J.M., Glebocki, R., Graham, B.D., Rizzo, D.M., 2011. Sudden oak death-caused changes to surface fuel loading and potential fire behavior in Douglas-fir-tanoak forests. For. Ecol. Manag. 261, 1973–1986. http://dx.doi.org/10.1016/j.foreco.2011.02.024.
van Mantgem, P.J., Caprio, A.C., Stephenson, N.L., Das, A.J., 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? Fire Ecol. 12, 13–25.
van Mantgem, P.J., Nesmith, J.C.B., Keifer, M., Knapp, E.E., Flint, A., Flint, L., 2013. Climatic stress increases forest fire severity across the western United States. Ecol. Lett. 16, 1151–1156. http://dx.doi.org/10.1111/ele.12151.
van Mantgem, P.J., Stephenson, N.L., 2007. Apparent climatically induced increase of tree mortality rates in a temperate forest. Ecol. Lett. 10, 909–916. http://dx.doi.org/10.1111/j.1461-0248.2007.01080.x.
van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524. http://dx.doi.org/10.1126/science.1165000.
van Mantgem, P.J., Stephenson, N.L., Mutch, L.S., Johnson, V.G., Esperanza, A.M., Parsons, D.J., 2003. Growth rate predicts mortality of Abies concolor in both burned and unburned stands. Can. J. For. Res. 33, 1029–1038. http://dx.doi.org/10.1139/x03-019.
Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reid, M., Villalba, R., 1994. Disturbance regime and disturbance interactions in a rocky mountain subalpine forest. J. Ecol. 82, 125. http://dx.doi.org/10.2307/2261392.
Wallin, K.F., Kolb, T.E., Skov, K.R., Wagner, M.R., 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environ. Entomol. 32, 652–661. http://dx.doi.org/10.1603/0046-225X-32.3.652.
Weed, A.S., Ayres, M.P., Hicke, J.A., 2013. Consequences of climate change for biotic disturbances in North American forests. Ecol. Monogr. 83, 441–470.
West, A.G., Nel, J.A., Bond, W.J., Midgley, J.J., 2016. Experimental evidence for heat plume-induced cavitation and xylem deformation as a mechanism of rapid post-fire tree mortality. New Phytol. 211, 828–838. http://dx.doi.org/10.1111/nph.13979.
Westerling, A.L., 2016. Increasing western US forest wildfire activity: sensitivity to changes in the timing of spring. Philos. Trans. R. Soc. B Biol. Sci. 371, 20150178. http://dx.doi.org/10.1098/rstb.2015.0178.
Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science 313, 940–943. http://dx.doi.org/10.1126/science.1128834.
Williams, P.A., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Change 3, 292–297. http://dx.doi.org/10.1038/nclimate1693.
Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20, 78–86. http://dx.doi.org/10.1111/ele.12711.