

Disturbance interactions: characterization, prediction, and the potential for cascading effects

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Abstract. Disturbances are fundamental components of ecosystems and, in many cases, a dominant driver of ecosystem structure and function at multiple spatial and temporal scales. While the effect of any one disturbance may be relatively well understood, multiple interacting disturbances can cause unexpected disturbance behavior (e.g., larger extents), altered return likelihoods, or reduced ecosystem resilience and regime shifts. Given the long-lasting implications of such events, and the potential for changes in disturbance rates driven by climate change and increasing anthropogenic pressures, developing a broad conceptual understanding and some predictive ability regarding the likelihood of interactions between disturbances is crucial. Through a broad synthesis of the literature, and across multiple biomes, disturbance interactions are placed into a unified framework around the concept of changing ecosystem resistance (“linked interactions,” alterations to likelihood, extent, or severity) or ecosystem resilience (“compound interactions,” alterations to recovery time or trajectory). Understanding and predicting disturbance interactions requires disaggregating disturbances into their constituent legacies, identifying the mechanisms which drive disturbances behavior (or ecosystem recovery), and determining when and where those mechanisms might be altered by the legacies of prior disturbances. The potential for cascading effects is discussed, by which these interactions may extend the reach of anthropogenic or climate change-induced alterations to disturbances beyond what is currently anticipated. Finally, several avenues for future research are outlined, as suggested from the current literature (and areas in which that literature is lacking). These include the potential for cross-scale interactions and changing scale-driven limitations, further work on cascading effects, and the potential for cross-biome comparisons. Disturbance interactions have the potential to cause large, nonlinear, or unexpected changes in ecosystem structure and functioning; finding generality across these complex events is an important step in predicting their occurrence and understanding their significance.

Key words: compound interactions; disturbances; ecosystem structure; linked interactions; multiple disturbances; perturbations; recovery; resilience; resistance; synergistic relationships; vegetation.

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INTRODUCTION

Interactions between multiple disturbances are a major area of interest in ecology today as disturbance drivers (and as a result, disturbance

regimes) are being increasingly altered by climate change and increasing anthropogenic pressures. Feedbacks between post-disturbance conditions and subsequent disturbance events have the potential to drive unexpected or nonlinear

change in disturbance likelihood or characteristics, such as abnormally large extents or high frequencies. Furthermore, ecosystems already disturbed are likely less resilient (there is a greater chance of being replaced by a different ecosystem type; Holling 1973, Walker et al. 2004) to subsequent disturbances, should another even occur prior to recovery of the relevant resilience mechanisms (Paine et al. 1998). These disturbance interactions can be rapid, regime-shifting events which are unpredictable from knowledge of either disturbance alone—as a result, there is a need to study disturbance interactions as emergent phenomena, separate from studies of individual disturbance events and disturbance types. Numerous examples of these interacting disturbance events have been described in a variety of terrestrial, freshwater, and marine systems, such as altered rate and extent of subsequent disturbances (Kulakowski and Veblen 2007, James et al. 2011) and regime shifts with large and pervasive effects (e.g., Hughes 1994, Jasinski and Payette 2005, Buma and Wessman 2011). But the results of these events are not always synergistic nor necessarily intuitive. There are examples of positive interactions (e.g., increasing ecological severity as a result of two or more disturbances; Martone and Wasson 2008, Molinos and Donohue 2010, Brown and Johnstone 2012), but also minimal interaction (e.g., Valone 2003, Peterson and Leach 2008, Harvey et al. 2013) and even negative interactions (e.g., Veblen et al. 1994, Adjeroud et al. 2002, Simard et al. 2011, Kulakowski et al. 2012). Sometimes the effects of these interactions are counter-intuitive: Davies et al. (2009) found that restoring the historical disturbance regime led to increased invasive species establishment, whereas non-historical, multiple/interacting disturbance regime resisted invasion. In others studies, disturbance interactions did not lead to changes in mean response but altered variance about that mean (Fraterrigo and Rusak 2008), which may reduce system resilience in the future (Buma et al. 2013). This potential for the unexpected, from larger than expected fires to major shifts in coral reef landscapes, requires us to study and build predictive conceptual models to anticipate future interactive events.

SYNTHESIZING THE RESEARCH

The topic of disturbances is broad, encompassing such diverse events as wildfires, insect outbreaks, hurricanes, coral bleaching, and floods, but there is value in looking for generalities despite these differences (e.g., Frelich and Reich 1999, White and Jentsch 2001, Wilson et al. 2006, Peters et al. 2011). Many disturbances are rare relative to the timescales of human investigation, and it is only through synthetic approaches which cover multiple events and event types that generalities and idiosyncrasies can be described between and across events. Given that climate change and increasing anthropogenic pressures are rapidly altering disturbance drivers (such as heavy precipitation events and drought intensity), and subsequently disturbance frequency and characteristics (Dale et al. 2001), interactions may become more frequent.

Although multiple disturbances and their interactions have received considerable attention in recent years, the topic has seen study for some time (e.g., Jimenez et al. 1985, Turner 1988), sometimes emphasizing their importance in driving observed landscape pattern (e.g., Noble and Slatyer 1980), sometimes dismissing them as relatively unimportant (stated in memorable fashion: "...when there are multiple disturbances it is unlikely that they are so perverse as to combine intelligently to drive an ecosystem to destruction..."; Goh 1975). The attention has increased in recent years with the recognition that disturbance interactions can lead to unexpected, rapid, and nonlinear change (Paine et al. 1998, Turner 2010). There are examples from a variety of systems, but they are scattered throughout the literature, isolated in context, not interpreted in a common way, and conducted on various aspects of "overlapping disturbances," "multiple disturbances," "repeat disturbances," and "short-interval disturbances," among other terms. While the lack of a common conceptual framework presents challenges, it also provides a wide spectrum of biomes, approaches, and study designs that present an opportunity for synthesis between and across systems. This paper is an attempt to synthesize the disturbance interaction literature from a variety of fields, find commonalities, and identify emerging trends and research areas. It is not

meant as a complete review of the available literature on multiple disturbances, though the hope is that by presenting a common conceptual framework, it will facilitate future reviews and meta-analyses.

Broadly, disturbances result in some disruption to resources (Pickett and White 1985), minimal structure (Pickett et al. 1989), a loss in biomass (Grime 1979), or a suppression of natural dynamics (Rykiel 1985), depending on the scope/scale of investigation and operational definition of the study. These events may be relatively common occurrences, such as migratory grazers which occasionally revisit a patch of grass, or infrequent events such as major hurricanes. Natural disturbances, frequent or severe, are integral parts of an ecosystem regime (the suite of biotic components, abiotic processes, and disturbance dynamics which characterize an ecosystem). In all cases, disturbances result in functional, structural, biological, and biogeochemical legacies (Pickett and White 1985, Turner et al. 1993, Peters et al. 2011, McLauchlan et al. 2014, Seidl et al. 2014), a template left on the ecosystem with which a subsequent disturbance may interact in some fashion. These legacies take the form of altered functioning (e.g., rapid growth of surviving individuals, altered nutrient cycling), dead material, residual (e.g., survivors) and regenerating individuals and communities, and unique spatial patterns in cover types, ranging from undisturbed to highly disrupted. These legacies may decline as detritus decays and structures converge on their pre-disturbance state, but while they persist there is the potential for alterations to subsequent disturbance events. Interactions emerge from those legacies, often structural or spatial (e.g., altered fuel loading), but also biological (e.g., altered community structure, acclimatization of survivors) or environmental (e.g., water temperature). Specifically, interactions develop when legacies are functionally connected to a subsequent disturbance event, either in terms of disturbance drivers or recovery mechanisms.

TYPES OF INTERACTIONS

Across the published literature, there are two broad and non-mutually exclusive ways that an initial disturbance may drive an interaction: by altering the inherent resistance or the resilience of

the system to a subsequent disturbance (to put it another way, the *impact of* and/or *response to* that event). Resistance is the ability of an ecosystem to avoid a perturbation given a set of disturbance drivers (Walker et al. 2004). Disturbance legacies that alter resistance, by increasing or decreasing the likelihood of the subsequent disturbance, its spatial extent (likelihood at a location), intensity, or severity can drive an interaction; this type of interaction is termed a “linked disturbance” (Simard et al. 2011). The term “linked” implies a spatial and/or temporal aspect to the relationship, whereby changes in the spatial/temporal scale or intensity of a disturbance is affected by the legacies of a previous disturbance. Several studies have described linked disturbances. For example, long-term linkages between pest outbreaks and fire likelihood alter disturbance probability, with effects dependent on species, stand structure, and fuels (altering fire probability, Bigler et al. 2005; altering pest outbreak likelihood, Kulakowski and Jarvis 2013). Other examples include hurricanes reducing the incidence of coral bleaching by lowering water temperatures (Manzello et al. 2007), and stand replacing forest disturbances reducing the likelihood of bark beetle outbreaks by reducing host tree availability (Veblen et al. 1994, Kulakowski et al. 2012). The direction of effect—additive, synergistic, or negative—is a function of how legacies interact with disturbance drivers in the future, and the duration of potential linked events is directly related to the time legacies are a significant feature of the ecosystem—extremely transient in the hurricane example, but longer lived in the bark beetle example.

The second way disturbances may interact would be by altering the resilience of the ecosystem to subsequent disturbance. In this case, the interaction makes recovery (in sense of recovering to a similar state and function, Holling 1973) from the subsequent event more or less likely, or alters the speed of recovery. Paine et al. (1998) explored this potential, describing such interactions as “ecological surprises.” These interactions have also been observed in diverse systems, such as species which benefit from multiple disturbance events due to reduced resilience of competitors (e.g., clonal bamboo: Gagnon and Platt 2008; *Fagus* dominated forests in New England: Busby et al. 2008),

forests with differing post-fire recovery patterns depending on prior disturbance history (e.g., Girard et al. 2009, Uriarte et al. 2009, Kulakowski et al. 2013), and grass systems, which are more resistant to invasion in a non-historical, interacting disturbance situation (Davies et al. 2009). This type of interaction is termed a “compound disturbance” (Paine et al. 1998, Buma and Wessman 2011, Simard et al. 2011), implying that from the individual elements (the disturbance events), a new phenomenon is created. This new disturbance, sometimes referred to as a “novel disturbance” (e.g., Buma and Wessman 2011, Sturtevant et al. 2014), has the potential to reduce system resilience by creating conditions outside the species tolerances and the capacity of resilience mechanisms to successfully recover.

Linked and compound effects are not mutually exclusive and can emerge from the same events, although the proximate mechanism will be different. For example, an interaction which increases the spatial extent of a subsequent disturbance (a linked disturbance) may also impact resilience if the primary mechanism governing post-disturbance recovery is seed from outside the disturbed area. In the subalpine forests of Colorado, a blowdown altered the spatial distribution of subsequent severe fire (Kulakowski and Veblen 2007) via changes in fuel structure (Fig. 1). This event also impacted the primary resilience mechanism of several tree species present (serotiny and seed dispersal from unburned edges) resulting in altered post-fire successional trajectories, a compound disturbance (Buma and Wessman 2012), driven by two mechanisms—the large, high severity blowdown+fire patches reduced the ability of seed to disperse into the entirety of the burned areas and higher burn intensities and longer burn durations due to fuel bed compaction vertically consumed serotinous cones. The proximate mechanisms for the linked and compound effects differed, though the ultimate cause (the blowdown preceding the fire) was the same.

In sum, disturbance interactions can be grouped into two broad categories, those altering ecosystem resistance (linked disturbances, affecting likelihood, extent, or severity) and those altering ecosystem resilience (compound disturbances, affecting recovery); these interactions can be additive, synergistic, or negative.

When do they matter?

There is ample evidence that disturbance interactions have played, and continue to play, an important role in landscape heterogeneity across a variety of biomes. For example, disturbance regimes are strongly influenced by linked disturbance interactions, often through a series of negative feedbacks (Noble and Slatyer 1980, Veblen et al. 1994): A fire removes live biomass from a forest, which is a driver of pest populations, thus raising the resistance of a forest to insect disturbance. We therefore see a negative interaction between fire events and subsequent insect disturbance likelihood, the effect of which disappears with time. These interactions may be asymmetrical: the converse (insects influencing fire) is not necessarily equivalent, current hypotheses related to the question of insect mortality and changing forest resistance to fire (e.g., altered likelihood, extent, or severity of a subsequent fire) indicate a short period of decreased resistance to active crown fire followed by a longer period of increased resistance (Simard et al. 2011, but see Jolly et al. 2012a). In contrast, high frequency disturbance regimes may be driven by positive linked disturbance interactions. When seen over long time scales, linked disturbances, as a series of mechanistic feedbacks, can shape disturbance regimes, particularly in places where feedbacks between legacies and recovering vegetation affect disturbance likelihood, such as in fuel-limited fire regimes.

Compound disturbances have occurred historically as well; Liu et al. (2008) describe a hurricane-fire interaction cycle along the Gulf of Mexico; earlier work suggests this compound relationship is responsible for presettlement vegetation patterns across broad regions of the American South (Myers and van Lear 1998). Child et al. (2010) propose that the interaction of two disturbances (fire and herbivory) at multiple spatial scales promotes the coexistence of alternate stable states in savanna ecosystems. Fine scale heterogeneity formed by tipup mounds from a blown down Eucalyptus forest drives post-fire successional trajectory at the meter scale by altering competition for post-fire resources (Florentine et al. 2008). Similarly, fire and grazing alters spatiotemporal patterns in grasslands in a different fashion than grazing or fire alone,

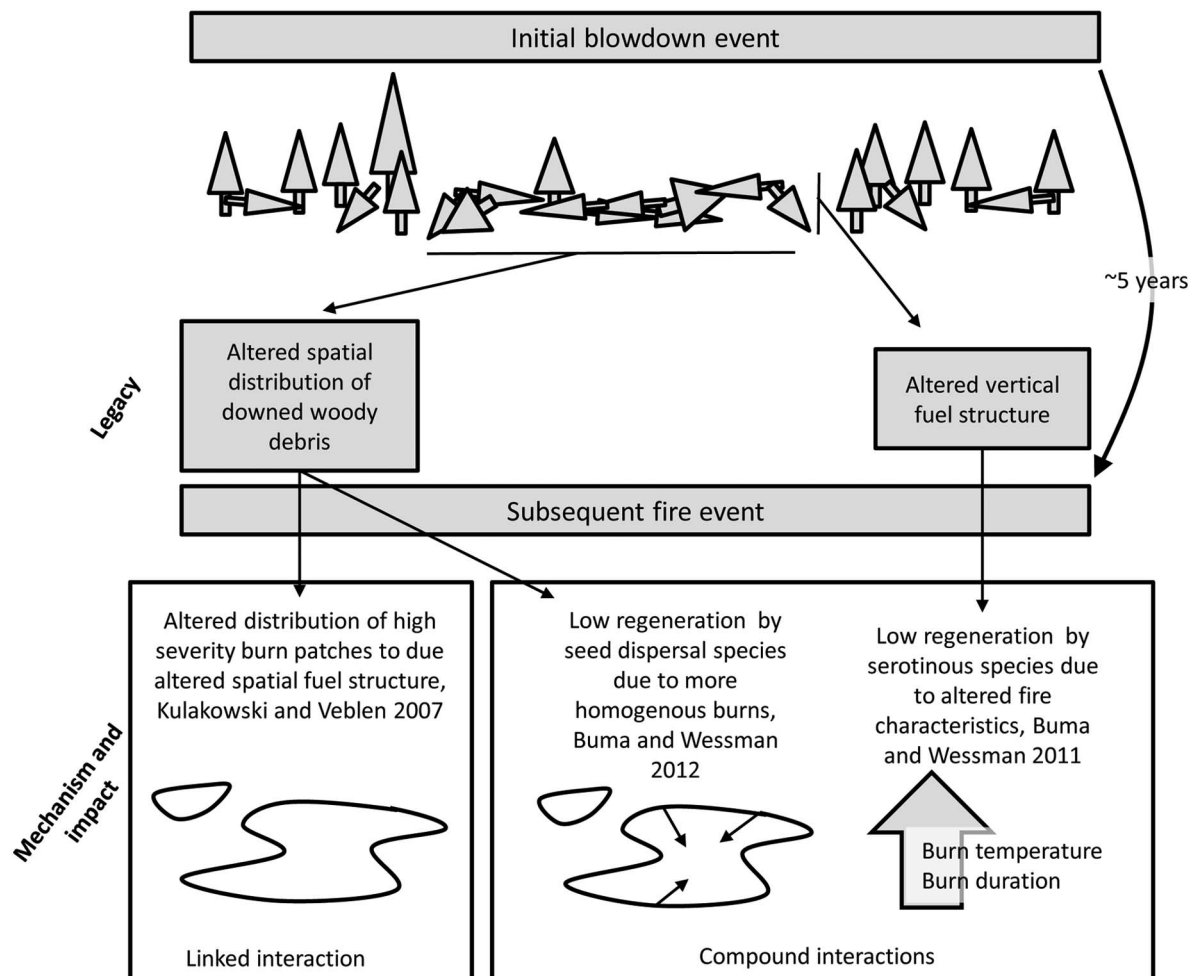


Fig. 1. Example of linked and compound interactions driven by two different mechanisms. The spatial distribution of high severity burns was affected by the previous disturbance (a linked interaction), which also influenced post-fire resilience via seed dispersal (a compound interaction). Another effect of the blowdown, altered vertical fuel structure, influenced a different post-fire resilience mechanism, serotiny, by altering burn times and temperatures.

changing structure and functioning at the patch scale (Collins and Smith 2006). In some cases, compound events may be the way in which certain populations are maintained on a landscape, such as knobcone pine (*Pinus attenuata*) populations in the California and Oregon coast range. These populations benefit from very short interval fires (relative to the mean fire return interval for the region) which promote knobcone regeneration (via a rapid development of its serotinous seedbank) and reduce populations of nonserotinous tree species (Donato et al. 2009, Buma et al. 2013). In another case, Newbery et al.

(2004) explore the potential for repeat disturbances in maintaining and growing tropical forest tree populations. In all cases, the resilience of the system is altered due to the interaction, to the benefit of some species and the detriment of others.

Variability in disturbance intensity and occurrence (e.g., patchy fire) is of itself an important attribute of disturbance events (Turner et al. 1993). Alterations to variability are a useful tool for diagnosing the spatiotemporal response of ecosystems to disturbance and trends in disturbance driven change (Fraterrigo and Rusak

2008). Disturbance interactions have the potential to alter that variability, which may feedback into functional responses (e.g., ecosystem level biogeochemical cycling rates; McLauchlan et al. 2014). Compound disturbances may homogenize neighboring patches (e.g., Brown and Johnstone 2012). At the landscape scale, however, those small homogenous patches may increase heterogeneity in cover types (Buma and Wessman 2012), and the spatial patterns resulting from those interactions may themselves constitute a mechanism for interaction with future disturbances (Sturtevant et al. 2014). For example, spatially mediated interactions between fire resilience, species level flammability, and fire spread may drive smaller fire extents in Alaskan boreal forests relative to climate projections which do not consider spatial legacies (Johnstone et al. 2011), and the effects of spatial configuration and interactions between repeat fires has been proposed as a mechanism for the maintenance of forest-savannah systems (Schertzer et al. 2015).

One can hypothesize that the significance of these spatial interactions will be highest in disturbance regimes characterized by infectious or contagious disturbance processes, where spatial structure has a strong effect on disturbance spread, such as fire or, to a lesser extent, insect outbreaks; in the case of relatively non-contagious disturbances, such as ice storms in temperate forests, there is little potential for spatially-mediated linked interactions. Finally, to the extent that resilience mechanisms are spatially dependent, as is the case with seed dispersing species, any linked disturbance which alters spatial pattern (e.g., larger extent) may have a compound effect, although there is likely a threshold response which is dependent on the seed dispersal distance of the species under consideration.

In sum, disturbance interactions do cause important changes to ecosystem functioning and drive long-term disturbance regimes (in terms of mean return intervals, mean size, etc.). There is also evidence that compounding disturbance interactions have partially shaped landscape heterogeneity at broad scales, by altering recovery from historical disturbance events. Changes to average disturbance characteristics, such as mean return interval, are important, but

alterations to disturbance variability are equally important (Buma et al. 2013). Finally, there is not a general trend of decreased resistance or resilience; there are as many examples of interactive effects which increase resistance as cause unexpected regime shifts.

Disaggregating disturbances and predicting interactions

Disturbance interactions are mediated by the mechanistic interplay between disturbance drivers (e.g., high winds), mechanisms of ecosystem resistance or resilience (e.g., rooting strength), and the legacies left by the previous disturbance. Therefore potential interactions can be identified by isolating the mechanistic drivers of disturbance likelihood or intensity (linked disturbances) or the drivers of resilience (compound disturbances) and comparing them to the legacies left by prior disturbances. These mechanisms are the point of action whereby an interaction can take place, and are unique to each disturbance event both in terms of the drivers and the legacies they leave (Peters et al. 2011). The consideration of scale is crucial, as different drivers act at different scales. In some cases fine scale variation in species type or structure may drive differential interactions (Bigler et al. 2005, Cannon et al. 2014), but broader scale drivers, such as weather, may overwhelm mechanistic limitations at finer scales (Peters et al. 2007, Westerling et al. 2011).

As a simplified example, landslides are a major disturbance agent in Pacific Northwest temperate rainforests. Through empirical work (Swanston 1974, Swanston 1997) the primary drivers of landslide likelihood (and resistance to sliding) have been identified: The mass of the soil via gravity (promoting sliding), resisted by friction on the sliding surface, soil cohesion, and rooting strength (resisting sliding). Because the counter-acting effects of soil mass (both gravitationally and frictionally, as mediated through slope) are much larger than forces created by rooting strength and soil cohesion, those resistance mechanisms are only important in terms of slope stability on steeper slopes, where friction is finely balanced against gravity (Swanston 1997). Of all these terms, there is little that other types of disturbance can do in terms of altering soil mass, soil cohesion, or altering slope, but vegetation

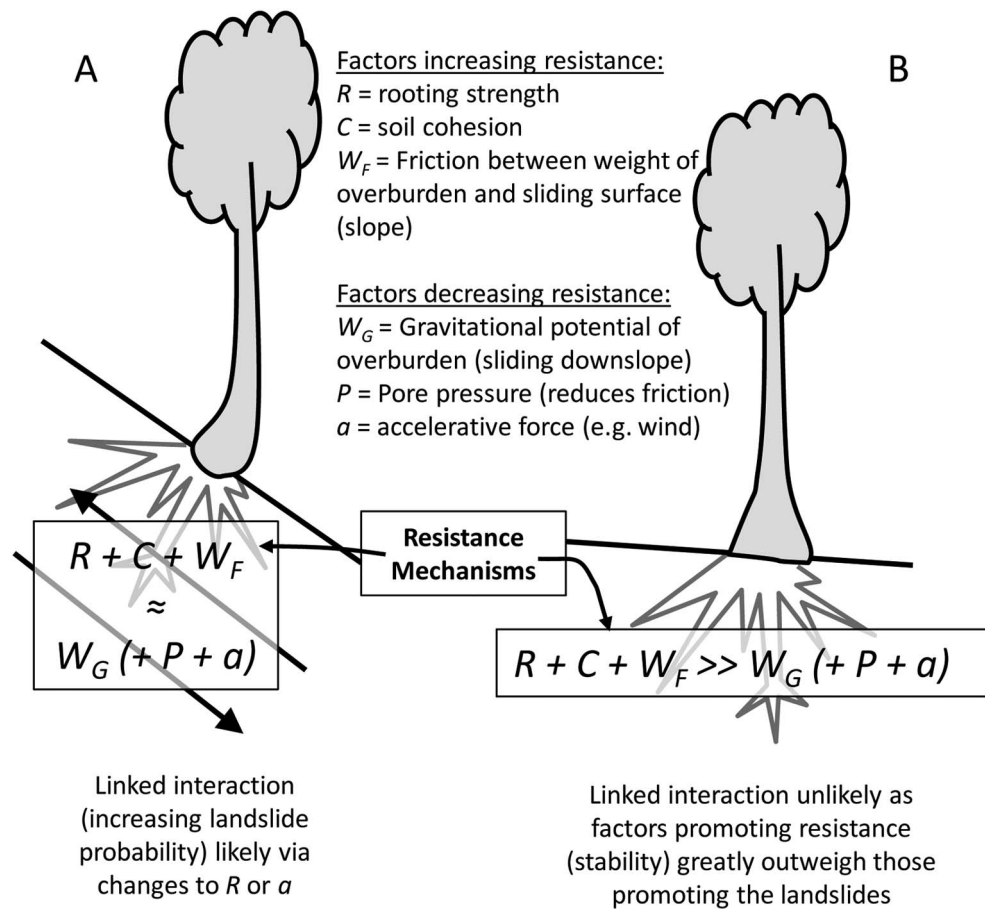


Fig. 2. Potential for interactions depend on the relative importance of resistance or resilience mechanisms which can be influenced by other disturbances. When forces resisting sliding are delicately balanced against forces promoting sliding (A), any change (e.g., through wind induced mortality or physical acceleration) can increase sliding likelihood, a linked interaction. In contrast, when factors resisting sliding far outweigh factors promoting sliding (such as on shallow slopes where W_F far outweighs W_G), there is little potential for disturbances to interact.

mortality can reduce rooting strength. Thus, a linked relationship is only expected on steeper slopes where root strength is a significant factor in stability, and that is what has been observed in the region: Exposure to high, mortality-causing winds increases landslide likelihood (a linked interaction) but only on steep slopes where rooting strength is a crucial factor in slope stability (Fig. 2). No interaction between wind and slide susceptibility is seen on shallow slopes, where rooting strength is not a primary factor in resistance to landslides (Buma and Johnson 2015). Similar to work in fire systems (e.g., Harvey et al. 2014a), the resistance to sliding

can also be reduced by weather (in the form of heavy rains, a driver operating at a broader scale), which reduces friction by increasing pore pressure. Knowledge of these interactions allows for a refinement of disturbance susceptibility maps (Buma and Johnson 2015), important for ecological understanding as well as civic and local planning (e.g., Camarero et al. 2011).

Generally, if the limiting factor governing resistance or resilience to disturbance can be influenced by another disturbance, a relationship is possible. Similar to a limiting reagent in chemistry, identification of specific mechanisms and what disturbance legacies may alter those

mechanisms is useful in identifying potential interactions. This requires “disaggregating” a disturbance event (Peters et al. 2011) into its constituent drivers and legacies, which are then analyzed for their mechanistic impact on future disturbance likelihood, characteristics, or the resilience of the system. Conceptually, Fig. 2 should be seen as an example of how one would disaggregate and diagram these opposing mechanisms as a first step in exploring the potential for disturbance interactions and their likely effects. Forces opposing an event are compared to forces promoting an event, and their relative strengths compared. Then, the potential for other disturbances to alter those forces is evaluated; if the relative strength of those forces varies spatially (as in the landslide example), then variation as a function of topography or location must be considered. Experimental data is useful in determining the relative strength of drivers, and associated change in those drivers post-disturbance (e.g., Cannon et al. 2014), and GIS has proven useful in predicting linked and compound disturbance relationships spatially, when changes in those drivers can be mapped (e.g., sudden oak death, Dillon et al. 2013).

The near universal constant across disturbance interaction studies is the need to elucidate mechanisms of interactions and their spatiotemporal scale of effect. In most cases, an interaction between a prior disturbance legacy and a mechanism for either resistance (e.g., fine fuel loading, Donato et al. 2006) or resilience (e.g., serotiny; Buma and Wessman 2011, Brown and Johnstone 2012), are explicitly identified and evaluated. In contrast, apparent interactions which have garnered attention because of their assumed mechanistic relationship have not necessarily been supported empirically. For example, the potential relationship between mountain pine beetle (MPB) and fire likelihood, with postulated mechanisms such as reduced fuel moisture in the dead canopy, has generated intense debate, mainly centered around intensity and behavior (e.g., active crown fire vs. surface fire), with implications for severity (Simard et al. 2011, Jolly et al. 2012a, Jenkins et al. 2014). But rather than fuel moisture limiting fire severity in lodgepole pine forest burns, the limiting factor is often attributed to burning conditions (weather) during the fire (Turner et al. 2003, Harvey et al.

2014a). Thus limited interactions between MPB and fire severity would be expected at the landscape scale, as the dominant driver of fire severity at broad extents (daily weather) is not modified by MPB attack. In contrast, tree or patch scale fire behavior may be altered (Jolly et al. 2012b), and other types of disturbance (e.g., severe ground fires, Donato et al. 2013) may interact in different ways. Some interactions may manifest more when an external driver is actually stronger, such as when extreme burning conditions can cause gray-stage outbreaks to burn at higher severity, presumably because dry and windy conditions are needed to sustain severe fire in coarse dead fuels (Harvey et al. 2014b). Work should continue to determine if cross-scale interactions (such as patch scale interactions feeding back into landscape scale patterns, or weather driving interactive effects) may alter previously observed relationships (see *Research Directions*).

It is important, then, to consider the possibility of interactive effects as long as legacies left by a previous disturbance are present and can interact mechanistically with the drivers limiting or promoting a subsequent disturbance (or that disturbances' severity). A focus on mechanisms driving resistance or resilience at the particular scale and time of interest serves to scope research efforts towards interactions which are likely significant.

CASCADING EFFECTS

Climate change is causing alterations to disturbance likelihood, intensity, and extent throughout the world (Dale et al. 2001, van Mantgem et al. 2009). Some of those effects are relatively straightforward; for example, a reduction in precipitation and an increase in temperature will likely result in increased fire frequency in the American West (Westerling et al. 2006). These trends continue to be a concern and an important object of study. An interesting aspect of disturbance interactions is the potential to extend the reach of climate change and anthropogenic pressures by causing “cascading effects.” These are emergent phenomena where a disturbance interaction can extend the impacts of a driver for one disturbance into another disturbance type (Fig. 3).

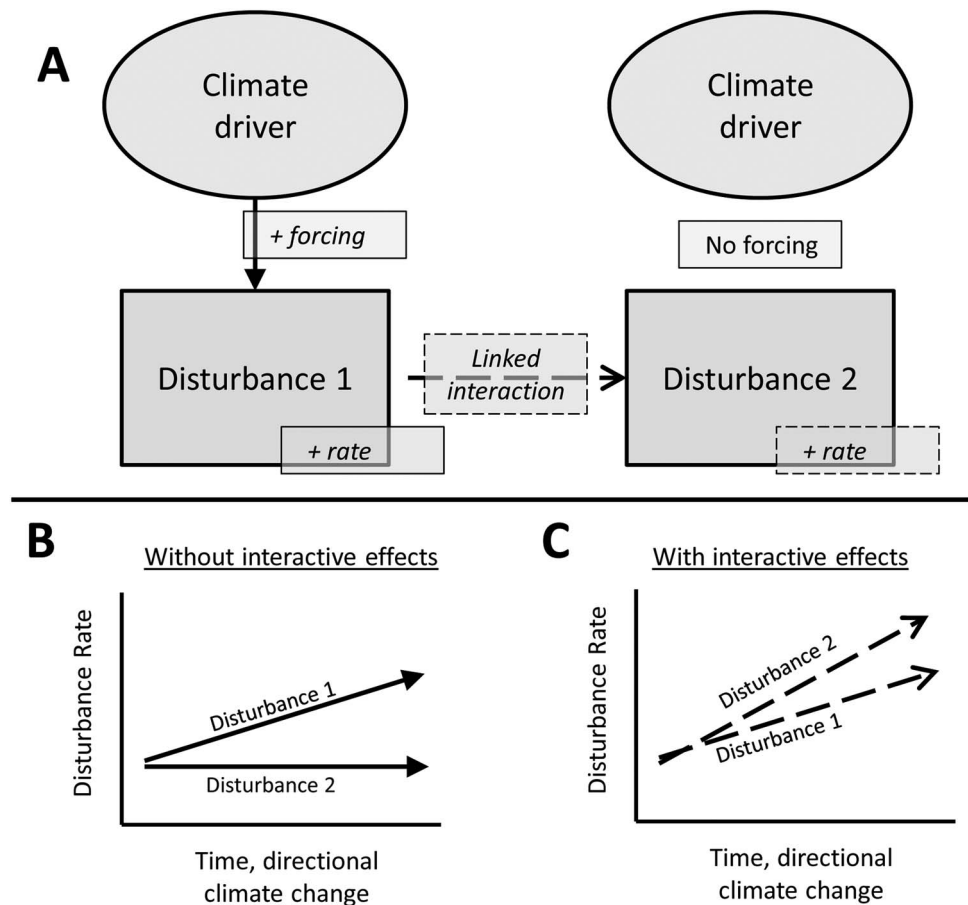


Fig. 3. Cascading effects of disturbance interactions. (A) Cascading effects can occur when one disturbance type is altered by an external driver, such as directional climate change or increasing anthropogenic presence. This predictably leads to an increase in associated disturbances. Without an interaction, rate of disturbance increases are limited to disturbance types directly affected by that driver (B). But through interactive effects, increases in disturbance types unrelated to the affected driver may also occur (C).

Disturbance interactions have the potential to change the impact of and response to non-climate affected disturbances via these cascading effects. For example, while the effects of an increasing population and warming climate on fire are expected to be significant, climate changes' effect on wind disturbances is less clear (potentially less frequent, more severe storms with high variability, Knutson et al. 2010). Yet wind events may become more damaging even without a significant change in storm characteristics due to cascading interactions. Platt et al. (2002) observed that fires during the wet season in Florida, USA, did not alter the likelihood of snapping trees during subsequent hurricanes; in other words

there was no linked relationship between wet-season fires and the resistance of the forest to wind. However, dry season fires, typically anthropogenic in origin, did lower the resistance of the trees to subsequent hurricane and post-hurricane mortality. There is a linked disturbance relationship: fires increased the likelihood of a wind-driven disturbance, despite no change in the wind regime itself. Change in the dry season fire regime in the future, either anthropogenic or due to climate change, will therefore be expected to decrease the resistance of the forest to wind disturbance. To put it another way, storms may become more damaging to forests even without a change in the storms themselves due to this

interaction.

In the context of global environmental change and increasing anthropogenic pressures, directional shifts in disturbance drivers are likely (Dale et al. 2001). Disturbance interactions, via cascading effects, may extend the reach of altered disturbance dynamics from the relatively predictable (increases in fire due to warming/drying in some regions, Moritz et al. 2012) to the previously unexpected, such as increase in blowdown as a result of alterations to the fire regime (Platt et al. 2002). We are only beginning to explore and examine these interactions, but given the substantial impacts on direct disturbance drivers from climate change (e.g., Moritz et al. 2012), any potential for an expansion of those effects is important to consider.

IMPLICATIONS AND APPLICATIONS TO OTHER SYSTEMS

The conceptual tool of disaggregating disturbances into their constituent mechanisms and exploring potential interactions (as in Fig. 2) leads to some implications and generalized hypotheses. Linked and compound interactions are likely most significant in systems where disturbance characteristics are either (1) dependent on some aspect of the biotic environment, such as mean tree size for insect/pest outbreak likelihood, or (2) dependent on abiotic conditions controlled by the biotic environment, like fine soil moisture which varies as a function of canopy cover. Thus these interactions are partially tied to the development rate of the system post-disturbance and the degree to which disturbances are externally vs. internally controlled; for example, in locations where disturbance frequency is unrelated to the biotic environment, we would expect to see less linked interactions. A test of the importance of these interactions would be examining the relationship between ecosystem development rate and disturbance characteristics (e.g., disturbance frequency for linked interactions) or heterogeneity in cover types (for compound interactions).

The conceptual relationship described in Fig. 3 emerges when considering these disaggregated, mechanistic disturbance drivers (as in Fig. 2) in a non-stationary climatic context. This becomes useful when considering (1) locations where

some disturbances are climate sensitive (e.g., some of their drivers are related to climate change) but some are not or (2) locations where all disturbances are climate sensitive, but expected to change (individually) at different rates. Because linked and compound relationships can extend beyond those disturbance directly influenced by climate, the need to disaggregate disturbance drivers and disturbance legacies into their mechanistic components is necessary to understanding how these interactions, via cascading effects, will increase or inhibit disturbance-driven change.

RESEARCH DIRECTIONS

Disturbance interactions continue to be an important area of study due to their potential to cause nonlinear responses in ecosystems, from larger than expected blowdowns to significant changes in recovery trajectories which can shape regional landscape structure. This synthesis has examined the broad categories of disturbance interactions, builds on the body of literature around disturbance legacies (e.g., Peters et al. 2011), and extends the discussion into multiple disturbance events, disaggregation and limiting drivers, cascades, and the potential for regime shifts that result. Moving forward, there are several avenues of study suggested by current research:

1. Cross-scale interactions: The majority of disturbance interaction literature focuses on mechanisms operating at similar spatial scales, such as the interaction between fuel loading, fire intensity, and serotiny (Buma and Wessman 2011) or sedimentation and herbivory on coral reefs (Jones et al. 2004). There is less work on cross-scale interactions which drive disturbance likelihood, despite their importance for disturbance events (Peters et al. 2007), residual community composition and patterning (e.g., Burton et al. 2014), and subsequent resilience (Reyer et al. 2015). Fine-scale limitations on disturbance likelihood, such as fine fuel loading, may be removed by broader scale shifts in climate, in which case mechanistic interactions between disturbance legacies may become less important relative to

Table 1. Additional studies of disturbance interactions.

Disturbances	Method	Summary/Author
Coral reefs		
Coral bleaching, sedimentation, and starfish outbreak	Observation	The combination of bleaching, sedimentation, and a starfish outbreak precipitated a phase shift in coral cover (reduction in coral), exceeding the resilience of the system. Jones et al. (2004)
Bleaching, cyclone, bleaching	Observation	Bleaching followed by cyclone decreased coral cover, but a subsequent bleaching event caused little mortality, likely because of acclimatization and/or genetic adaptation. Adjeroud et al. (2002)
Hurricanes and coral bleaching	Observation	Hurricanes cool sea temperatures and alleviate thermal stress, lowering the likelihood of a coral bleaching event despite regionally high ocean temperatures. Manzello et al. (2007)
Grasslands		
Grazing and fire	Observation	Grazing can alter likelihood of fire in savannah systems, which may partially drive the bimodal distribution of forests and savannahs in the tropics. Archibald et al. (2005), Staver et al. (2011)
Simulated flooding, sedimentation, rapid nutrient influx, and grazing.	Mesocosm experiment	Effects were additive or synergistic, with resilience reduced with increasing stressors; loss of species due to the disturbances facilitated invasive species establishment. Kercher and Zedler (2004)
Fire, wind, and drought	Conceptual	Drought and wind increased likelihood of fire, which maintained native bamboo species historically. Gagnon (2009)

broader scale drivers, which would further alter anticipated disturbance events and regimes (e.g., subalpine systems: Harvey et al. 2014a; Mediterranean systems: Pausas and Paula 2012). Modelling studies are especially useful in exploring these complex interactions (e.g., Westerling et al. 2011, Templerli et al. 2013).

2. Cascading effects: Disturbance interaction research typically focuses on direct drivers of likelihood, such as increased fine fuel loading and fire likelihood (Donato et al. 2006). However, cascading effects are relatively indirect, and are rarely explored. It is, in effect, taking disturbance projections one step further in time and exploring the mechanistic implications of legacies created by future disturbances (and disturbance regimes) in the context of other potential disturbances. This requires disaggregation of the drivers of disturbance and the resistance/resilience mechanisms of the ecosystem to determine when and where legacies may drive unexpected changes in disturbance characteristics.

3. Links between biomes: Much of the disturbance interaction literature is focused on forested ecosystems and fire, yet substantial bodies of work also exist in the grassland and coral reef literature (for examples, see Table 1), among others. However, little work compares disturbance interactions across biomes, despite the potential for the useful analogies that have informed other aspects of ecology, such as biodiversity patterns (e.g., Connell 1978). A few interesting examples do exist (e.g., tropical forests and coral reef responses to hurricanes, Lugo et al. 2000), but the potential outside the tropics remains relatively unexplored. Partially this results from a lack of common vocabulary, which hinders discovering similar research in unfamiliar fields, or a lack of focus on common mechanisms (Peters et al. 2011). Intentionally seeking cross-biome comparisons, where common mechanisms of resistance or resilience (e.g., structural complexity, as in tropical rainforests and coral reefs) may occur, would be a useful step in generalizing ecosystem response to

multiple, interacting (and potentially changing) disturbance regimes.

CONCLUSIONS

Disturbance interactions are important phenomena of study because they expose hidden dynamics in ecosystems and have potentially dramatic effects on future disturbance likelihood and landscape resilience. A common framework is useful because it allows for synthesis across a variety of linked and compound systems, and also because it will allow for identification of systems where interactions may be intuitively expected, but are not observed. These “null” systems are as important as further study of known interacting systems in developing generalized hypotheses within disturbance ecology and across biomes. Linked and compound interactions have the potential to drive disturbance behavior not only beyond historical norms, but also in unexpected directions due to cascading effects. Disturbance frequencies may be altered through interactions, as well as through the direct effects of climate and anthropogenic pressures; impacts may be more or less severe as a result. A better understanding of the potential for interactions between disturbances is necessary, as is further exploration of cross-scale interactions and cross-biome comparisons. Interactions between multiple disturbances, mediated mechanistically by legacies, are important phenomena acting at multiple spatial and temporal scales. This generalized method for description and understanding will aid in their characterization and further study.

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