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Climate Change Effects on Interacting Disturbances in Forest Ecosystems

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Abstract

Drought, wildfire, wind, insects, and pathogens can interact across space and time to shape forest ecosystems. Although subdisciplines in ecology have long studied individual disturbances, their interactions remain poorly understood, particularly under climate change. Further, inconsistent terminology used to describe these interactions compounds this gap. To address this challenge, we first develop a unifying framework and then review the literature to synthesize climate change effects on the seven classes of forest disturbance interactions. Climate change alters the impacts of disturbance interactions by shifting (*a*) the characteristics of disturbances and (*b*) the effects of interactions when they occur. Many studies document amplifying effects of climate change, and disturbance interactions governed by nonlinearities and positive feedbacks can be particularly transformative in forest ecosystems. In some cases, however, climate change can dampen outcomes of disturbance interactions, which may buffer forests from disturbance impacts. Critically, climate change is expected to increase the frequency of ecosystem transitions worldwide by amplifying the outcomes of complex interactions, particularly coupled feedbacks and network effects. Although there is strong evidence that climate change is modifying some disturbance interactions, they remain an important, yet understudied frontier in ecology.

INTRODUCTION

Wildfires, storms, droughts, insects, and pathogens are key drivers of change and renewal in forest ecosystems. These disturbances—defined as discrete events in forests that unfold over relatively short timescales (Pickett & White 1985)—can reshape forest structure and function across scales, with impacts lasting decades to centuries (Thom et al. 2017, Yue et al. 2016) and extending from individual trees to subcontinents (Cooke et al. 2021, Senf & Seidl 2018). Because disturbances can be hazardous to human health and wellbeing, they have attracted public and scientific attention, leading to subfields including wildfire science, forest pathology, and forest entomology. This compartmentalization, however, constrains insights into how disturbances interact (Sturtevant & Fortin 2021), limiting our ability to anticipate their impacts, particularly in response to anthropogenic warming. An integrated understanding of disturbance interactions is therefore essential for predicting their impacts on forest ecosystems and guiding management under climate change (Buma 2015, Seidl et al. 2017).

Although disturbance interactions are an important component of disturbance regimes (Jentsch et al. 2022), they are often understudied due to logistical and conceptual challenges (Cobb 2022, Turner 2010). Many disturbances are relatively rare and difficult to predict (Dale et al. 1998, Marlon et al. 2012)—therefore, their interactions are even rarer (Turner 2010). As a result, interaction studies are often retrospective and limited by sample size, which can bias our understanding of their effects (Fisher et al. 2008). Moreover, the complexity and diversity of disturbance interactions make it difficult to isolate distinct effects, leading to inconsistent terminology (Buma 2015, Burton et al. 2020, Kane et al. 2017, Sturtevant & Fortin 2021). Building a unified conceptual framework of disturbance interactions is critical for advancing theory and improving predictions of ecosystem responses (Buma 2015, Seidl et al. 2017).

Climate change is increasingly linked to shifts in the frequency, severity, seasonality, and spatial extent of disturbances (Cook et al. 2018, Dudney et al. 2021, Seidl et al. 2011, Weed et al. 2013). Higher temperatures have doubled the extent of fire in the western US (Abatzoglou & Williams 2016), increased fire severity in Canada (Wang et al. 2025), and incited unprecedented insect outbreaks across North America and Europe (Bentz et al. 2010, Hlásny et al. 2021). Climate change is also causing range shifts of disturbance agents, including insects and pathogens (Battisti et al. 2005, Dudney et al. 2021), which can lead to novel disturbance interactions in forests that are naive to their impacts (Turner & Seidl 2023). As climate change shifts the likelihood and impacts of individual disturbance events, it also influences their interactions (Keane et al. 2015, Seidl et al. 2017). How climate change is reshaping the many distinct classes of forest disturbance interactions, however, remains poorly understood.

Here we synthesize the current understanding of the effects of climate change on interactions among forest disturbances. First, we develop a framework for classifying disturbance interactions, unifying conceptual ideas from subdisciplines in ecology. Second, we describe how climate change is altering disturbance interactions through two primary pathways. Then, we apply these frameworks to a literature review. We focus on how climate change is altering seven classes of disturbance interactions that involve fire, wind, drought, lethal pathogens, and primary insects (i.e., insects that can kill healthy trees). Finally, we identify knowledge gaps for future research and evaluate the implications of shifting disturbance interactions for forest health and resilience.

SEVEN CLASSES OF DISTURBANCE INTERACTIONS

Clarifying Terminology to Understand Climate Change Effects

Disturbances can interact across space and time to affect forest structure, function, and resilience, as well as characteristics of individual disturbances and disturbance regimes (Burton et al. 2020, Sturtevant & Fortin 2021). To classify disturbance interactions requires clarifying how many different types of disturbances are involved, the mechanisms that cause effects, and the outcomes of interest (e.g., tree mortality or the severity of a disturbance) (Buma 2015). One disturbance event can affect the probability of a different disturbance (the outcome) by changing forest structure (the mechanism)—an example of a linked effect (**Table 1**). For instance, fire can shift the probability of a mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak (the outcome) by increasing the vulnerability of fire-damaged trees to attack (the mechanism) (Powell & Raffa 2011).

Given the complexity of disturbance interactions, definitions describing their effects are highly variable (Burton et al. 2020, Flores & Staal 2022, Kleinman et al. 2019, Sturtevant & Fortin 2021) (**Supplemental Table 1**). For example, compound disturbances have been defined as combinations of disturbance events that threaten forest resilience (Buma & Wessman 2011, Kleinman et al. 2019), while others define them statistically as additive effects (i.e., no interaction effect) (Dudney et al. 2020), synergistic effects (Simard et al. 2011), or "multiplicative effects, not additive" (Paine et al. 1998, p. 537). Here we use compound disturbance as a general term that describes when multiple disturbances lead to intensified impacts on forest ecosystems, e.g., when two disturbances cause higher levels of mortality relative to one disturbance. Compound effects can result from a single type of disturbance that occurs multiple times (e.g., multiple wildfires impacting the same forest patch) or different types of disturbances (e.g., wind and bark beetles) that impact forest metrics, which include tree mortality, species richness, and mechanisms of resilience. If these compound effects are quantified using statistical models, the magnitude of the sum of the additive and/or interaction effects from multiple disturbances would exceed the effect of any single disturbance. This includes cases where interaction effects dampen the outcome of additive effects, but the sum of the additive and interaction effects still exceeds the effects of a single disturbance.

Additionally, multiple frameworks have been developed to classify disturbance interactions (Buma 2015, Burton et al. 2020, Cannon et al. 2017, Flores & Staal 2022, Kane et al. 2017, Sturtevant & Fortin 2021). Some frameworks focus on how disturbances can affect the likelihood or characteristics of one or more subsequent disturbances (Burton et al. 2020). Other frameworks focus on describing how different disturbance interactions shift forest resilience (Buma 2015, Cannon et al. 2017) or how additive, antagonistic, or synergistic disturbance interactions shift forest metrics (Kane et al. 2017). To reconcile these differences—which is critical to understand the impacts of climate change—we build on this body of work using directed acyclic diagrams (DAGs) (Huntington-Klein 2021). DAGs help formalize the web of causal relationships among disturbances and their mechanisms (**Table 1**).

We use disturbance interactions as an umbrella term for the many classes of effects whereby disturbances affect themselves (e.g., through feedbacks) or other types of disturbances or jointly affect forest conditions. We identify seven classes of disturbance interactions: (*a*) linked effects, (*b*) additive effects, (*c*) disturbance cascades, (*d*) interaction effects, (*e*) self-feedbacks, (*f*) coupled feedbacks, and (*g*) disturbance networks (**Table 1**). The adjective cross-scale can be a modifier for all seven classes of disturbance interactions if the disturbances cause effects at different spatial or temporal scales (Kullman 2002, Peters et al. 2004). For example, the linked effect of drought on tree disease is often cross-scale (e.g., regional drought—short term—can affect tree disease—long term—at the local scale). In the following sections, we further distinguish these classes of

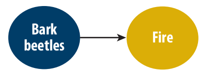
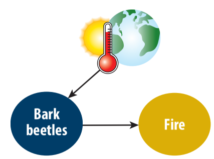
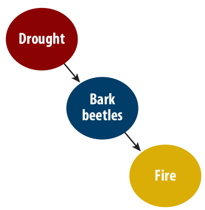
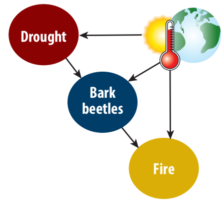
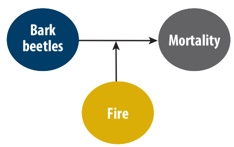
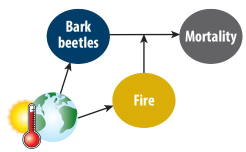
Outcome: the measured response variable (i.e., the dependent variable of interest), which can be a forest metric or a disturbance characteristic (e.g., frequency, spatial area, severity)

Compound disturbance: multiple disturbances that result in intensified impacts on forest ecosystems; in statistical models, the magnitude of the sum of additive and/or interaction effects from multiple disturbances exceeds the effects of any single disturbance

Forest metrics: quantitative measurements of forest attributes, including tree density, mortality, richness, and remotely sensed productivity indices

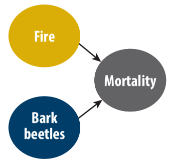
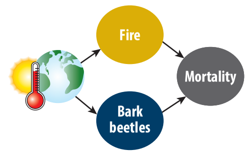
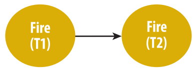
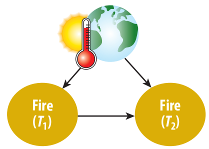
Supplemental Material >

Table 1 Seven classes of disturbance interactions under climate change

Classification	Definition[a]	Similar terms[b]	DAG example[c]	DAG example description[d]	Climate change effects[e]	Climate change example description[f]
Linked effects	One disturbance (e.g., MPB) has an effect on a different disturbance type (e.g., fire), which can include direct and indirect effects but not feedbacks.	Interaction linkage Cross-scale interactions Direct/indirect interactions		MPB outbreaks can increase the probability of high-severity fire if certain conditions are met.		Under climate change, increases in MPB outbreaks can elevate the risk of high-severity fire through the positive linked effect of MPB on fire.
Disturbance cascades	A sequence of three or more linked disturbances, whereby one disturbance type alters the likelihood or characteristics of two or more subsequent disturbance types (feedbacks not included)	Cascading effects Trophic interactions Chains of disturbances		Drought incites bark beetle outbreaks, which changes the risk of high-severity fire.		Climate change increases drought severity, which can increase bark beetles and fire via cascading effects (climate change can also directly affect bark beetles and fire, which can further amplify outcomes).
Interaction effects	The effect of one disturbance on an outcome variable (e.g., a forest metric or third disturbance) depends on the level of another disturbance.	Synergistic effects Compound disturbances Antagonistic effects		The effect of MPB on tree mortality partially depends on the level of fire damage (i.e., fire severity).		Climate change can affect the characteristics of fire and MPB outbreaks, which shifts the outcome of their interaction effects on tree mortality.

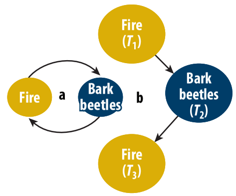
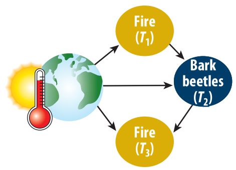
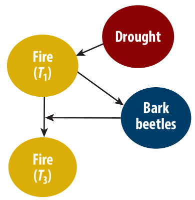
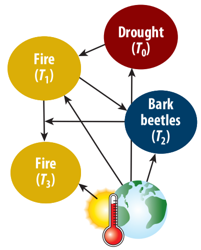
(*Continued*)

Table 1 *(Continued)*

Classification	Definition[a]	Similar terms[b]	DAG example[c]	DAG example description[d]	Climate change effects[e]	Climate change example description[f]
Additive effects	The effects of two or more independent disturbances (e.g., drought and fire) sum to affect a forest metric or third disturbance.	Unlinked disturbances Compound disturbances		Fire and MPB both have positive effects on tree mortality, leading to greater mortality (their sum) when both disturbances occur.		Climate change can increase fire frequency and bark beetle outbreaks, which can amplify their additive effects on tree mortality.
Self-feedbacks	Cyclical effects of one disturbance type that emerge within the same disturbance event or over time (e.g., disturbance effects on forests at Time 1 cause a feedback on the same type of disturbance at Time 2).	Cross-scale feedbacks Disturbance loops		A fire that burns at time 1 can affect the likelihood or characteristics of a subsequent fire through impacts on forests.		Climate change can affect fire behavior at time 1, which can shift the likelihood or characteristics of a subsequent fire (that is also affected by climate change).

(Continued)

Table 1 (*Continued*)

Classification	Definition[a]	Similar terms[b]	DAG example[c]	DAG example description[d]	Climate change effects[e]	Climate change example description[f]
Coupled feedbacks	Cyclical effects that involve two different types of disturbances that modify the likelihood or characteristics of one or both disturbances over time	Cross-scale feedbacks Disturbance loops		(*a*) Coupled feedbacks between fire and bark beetles can be positive or negative (i.e., on subsequent fires), depending on timing; (*b*) they can be estimated as a sequence of effects.		Climate change can alter disturbances that have coupled feedbacks with other disturbances, changing the likelihood or characteristics of the affected disturbances.
Disturbance networks	Multiple classes of disturbance interactions that can form a complex structure of effects; networks can include linked effects, interaction effects, feedbacks, and disturbance cascades.	Network structure Network of interactions		The relationship between drought, fire, and MPB is probably best described as a network of linked, cascading, and feedback effects.		Climate change can affect disturbances within a network, changing the likelihood or characteristics of the affected disturbances and/or forest metrics.

Abbreviations: DAG, directed acyclic graph; MPB, mountain pine beetle.

[a]A brief definition of each class of disturbance interaction.

[b]Related terms used in the literature that describe similar but not necessarily identical concepts (see **Supplemental Table 1**).

[c]A DAG illustrating a representative example of each disturbance interaction. Arrows depict directional effects—the arrow extends from the explanatory variable to point to the outcome variable. Arrows that bisect other arrows represent statistical interaction effects. The circles represent disturbance-related variables, including tree mortality or disturbances characteristics (e.g., "bark beetles" could represent the severity of a bark beetle outbreak; "fire" could represent the frequency of fire).

[d]A summary of the DAG clarifying the modeled relationships.

[e]A DAG showing how climate change can influence the interacting disturbances (e.g., by shifting their characteristics, which alters the outcomes of disturbance interactions). These outcomes include tree mortality or subsequent disturbance events.

[f]A brief description of how climate change can affect the interacting disturbances. Note: all DAGs show only climate change effects via Pathway 1 (see **Figure 2**).

Supplemental Material

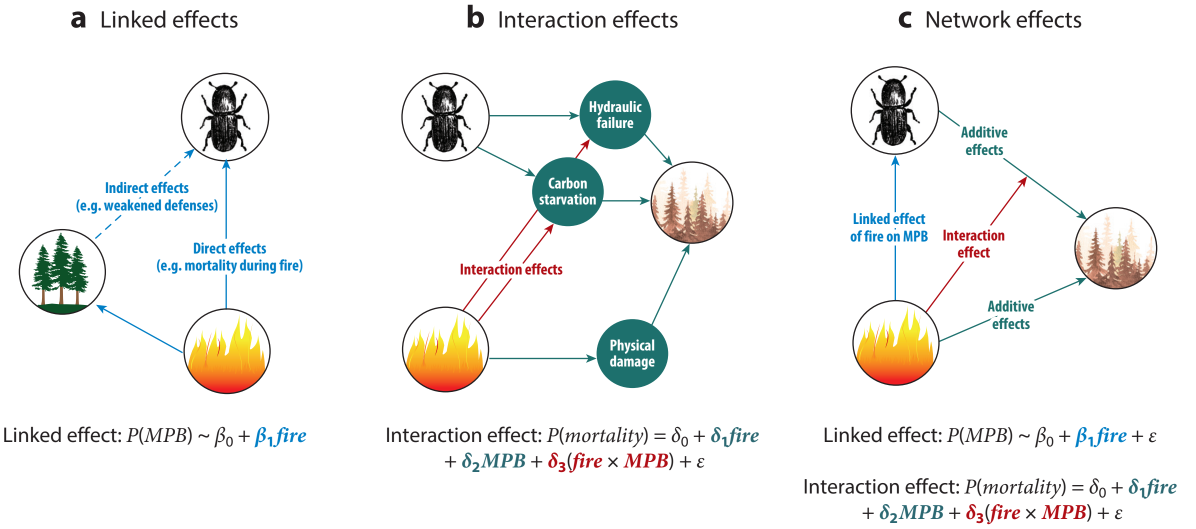


Figure 1

Differences between linked and interaction effects. (*a*) Example mechanisms associated with linked fire–MPB effects. These mechanisms can be estimated separately or implicitly included in a model estimating the aggregate effect of fire (e.g., fire severity, occurrence) on MPB attacks using the linked effect equation. Arrows represent directional effects from the explanatory variable to the outcome variable (e.g., *solid arrows* represent direct fire effects; *dashed arrows* represent indirect fire effects). (*b*) Example mechanisms of the interaction effect between fire and MPB on tree mortality. The probability of an individual tree dying is largely governed by hydraulic failure, carbon starvation, and physical impact (e.g., combustion, scorching). The DAG shows how fire can increase the lethality of MPB attacks through shared mechanisms (*red arrows* affecting the primary mechanisms of MPB-induced tree mortality). As a result, MPB effects on tree mortality can vary with fire severity. (*c*) A disturbance network of linked, additive, and interaction effects. Although the linked effect changes MPB attacks (*blue arrow*), the interaction effect equation does not include this linked effect, only the additive and interaction effects when these disturbances cooccur in space (see **Figure 3**), thereby forming a network of effects. The colors of the terms in the equations map on to the arrows in the DAG. Abbreviations: β, coefficients in the linked effect model; δ, coefficients in the interaction effects model; ε, error; DAG, directed acyclic diagram; MPB, mountain pine beetle; P, probability.

disturbance interactions and review the literature to examine how climate change is altering these distinct relationships. Although climate change is often considered a persistent or press disturbance (Bender et al. 1984), our framework focuses on how it alters the relationships among other types of disturbances (**Table 1**).

The Difference Between Linked Effects and Interaction Effects

The diverse uses of the term interactions in ecology can lead to conflation with interaction effects as defined in statistics (**Figure 1**). Ecology broadly examines interactions among organisms and their environment (Wootton 1994), and these processes can be described using various mathematical models. In statistics, interaction effects quantify whether the effect of one variable depends on the level of another (Côté et al. 2016). Interaction effects are estimated using interaction terms in statistical models [e.g., $\beta_3(X \times Z)$, where β_3 is the interaction coefficient and X and Z are the interacting variables] (Talucci & Krawchuk 2019), gradient studies, or factorial experiments (Buma & Wessman 2011, Gomez-Gallego et al. 2022).

In the disturbance ecology literature, linked, additive, and interaction effects can be difficult to distinguish because they often influence each other and sometimes share the same mechanisms (**Figure 1**). Effects are linked if one disturbance alters the likelihood or characteristics of another disturbance (**Figure 1*a***; **Table 1**) (Buma 2015). Additive effects occur when multiple disturbances independently influence a third variable, i.e., their combined impact equals the sum of their individual effects (**Figure 1*c***; **Table 1**) (Burton et al. 2020). Disturbance interaction effects occur when two or more disturbances affect a shared outcome variable in a nonadditive way—i.e., the effect of one disturbance varies based on the level of another disturbance (**Figure 1*b***). The outcome variable can be a forest metric (e.g., tree mortality, stand structure) or another disturbance (e.g., drought and wind can interact to affect fire). When linked, additive, or interaction effects cooccur in a forest, they can form a disturbance network that requires complex modeling approaches to quantify (**Figure 1*c***).

Amplifying effect: when climate change increases the outcomes of disturbance interactions relative to the outcome in the absence of climate change

Dampening effect: when climate change decreases the outcomes of disturbance interactions relative to the outcome in the absence of climate change

HOW CLIMATE CHANGE ALTERS DISTURBANCE INTERACTIONS

Outcomes of Disturbance Interactions Can Be Amplified or Dampened

Although much of the literature focuses on the amplifying effects of climate change (Dollinger et al. 2024, Kane et al. 2017, Seidl et al. 2011), dampening effects also occur, leading to complex shifts in disturbance events and forest ecosystems (Seidl et al. 2017, Sommerfeld et al. 2021, Turner et al. 2022). Climate change has an amplifying effect when it increases the magnitude of the outcome of a disturbance interaction relative to a counterfactual state of the world without climate change. For example, more frequent drought under climate change can increase the number of bark beetle outbreaks (an amplified outcome) (Raffa et al. 2008). In contrast, climate change has a dampening effect when it reduces the magnitude of an outcome compared to the absence of climate change. Drought can suppress pathogen prevalence in some regions (Desprez-Loustau et al. 2006, Sturrock et al. 2011); therefore, more frequent drought under climate change can dampen tree disease (the outcome). The attribution of amplified and dampened outcomes to anthropogenic climate change requires multiple steps (Dudney et al. 2025); as a result, climate change effects are often inferred rather than directly quantified (but see Abatzoglou & Williams 2016, Dudney et al. 2021, Parks & Abatzoglou 2020, Williams et al. 2019).

Two Pathways by Which Climate Change Alters the Outcomes of Disturbance Interactions

Climate change alters the outcomes of disturbance interactions through two pathways: (*a*) by shifting the characteristics of disturbances and (*b*) by modifying the effects of disturbances when they occur (**Figure 2**). The first pathway describes how climate change can shift the location, timing, and intensity of the disturbance(s) causing the effects (i.e., the explanatory variable), which can lead to amplified or dampened outcomes (**Figure 1*a*,*b***). For example, climate change is increasing drought frequency in semiarid regions (Cook et al. 2018). This shift can lead to increases in disease prevalence in energy-limited, subalpine forests (Dudney et al. 2023). Drought in energy-limited forests can lengthen the growing season (van Mantgem et al. 2023), which extends the infection window for white pine blister rust (WPBR)—a lethal tree disease caused by *Cronartium ribicola* (Dudney et al. 2021, Sturrock et al. 2011) (**Figure 1*b***). Thus, climate change amplifies the outcomes of this linked effect by changing the characteristics of drought.

The second pathway describes how climate change can alter the underlying disturbance relationship itself, measurable as a change in effect size (the coefficient) or the functional form of the relationship (**Figure 2*c*,*d***). For example, climate change can flip the drought–disease linked effect in montane forests from positive to negative in some pathosystems (**Figure 2*d***). As climate change increases water limitation in historically energy-limited forests (Denissen et al. 2022), trees can become more drought stressed and close their stomata during the infection window for WPBR, dampening disease prevalence under climate change (Dudney et al. 2021). These two pathways highlight the fact that climate change can shift the outcomes of any disturbance interactions not

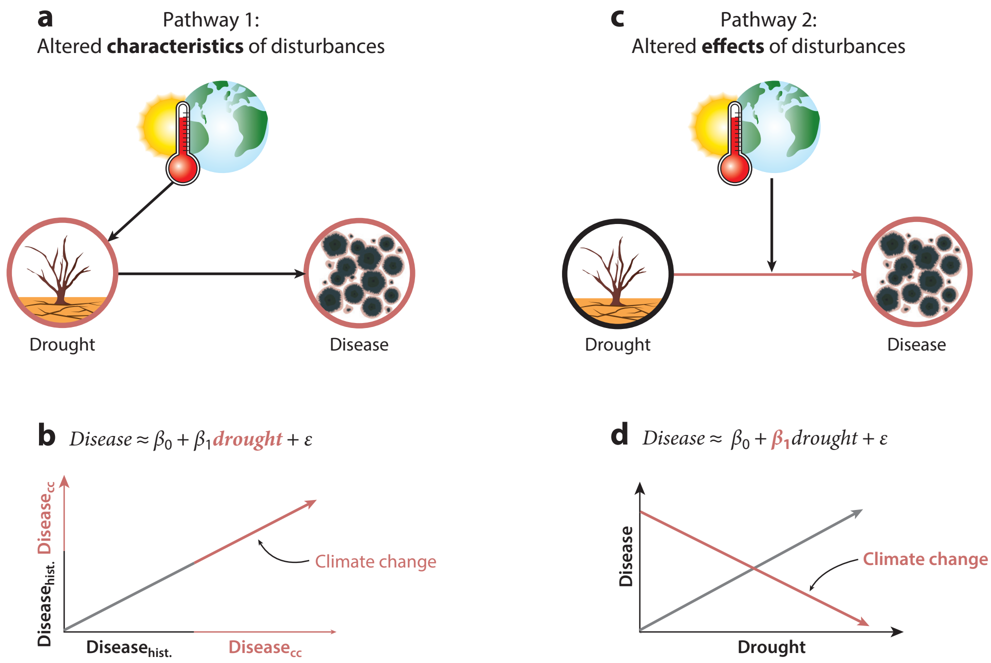


Figure 2

Two pathways by which climate change alters drought–disease linked effects. (*a*) Pathway 1: In high elevation, subalpine forests, drought increases tree disease prevalence (e.g., white pine blister rust; *black arrow from drought to disease*). Climate change can shift drought characteristics, including the frequency and severity, which alters disease outcomes (*pink circles* illustrate climate change effects). Note that the arrows do not change color because the effects are not changing; only the outcomes are changing (e.g., climate change is shifting the characteristics of drought—the first outcome—which is changing disease prevalence—the second outcome). (*b*) This climate change–induced shift can be estimated by the equation $Disease \approx \beta_0 + \beta_1$drought; the pink text indicates that the characteristics of drought have changed. Thus, disease prevalence increases (*pink line*) relative to the historical prevalence (*gray line*). (*c*) Pathway 2: Climate change can also modify the effects of drought on disease measured by changes in the effect size and/or direction. This change in the *effect* of drought on disease—note that the black arrow has changed to pink—also shifts disease prevalence (*pink circle*). (*d*) As aridity increases in high-elevation systems, the linked effect (*gray line*) can become negative (*pink line*) because water limitation contracts the window of infection. Thus, climate change shifts the causal effect of drought on disease prevalence (*pink coefficient*) from positive to negative. Pathways 1 and 2 both lead to changes in disease outcomes under climate change and can cooccur, particularly at large spatial scales. Abbreviations: β, represents the different coefficients in the linked effect model; ε, error; cc, with climate change; hist., historical.

only by altering the characteristics of disturbances but also by modifying the fundamental relationship between two or more disturbances. Further, both of these climate change effects can cooccur in a system, which complicates predictions of climate change impacts. Differentiating these two pathways, however, is critical for deepening our understanding of climate change effects on disturbance interactions and the corresponding impacts on forest ecosystems. In the following sections, we use this framework to illustrate how climate change is altering the outcomes of seven classes of disturbance interactions.

CLIMATE CHANGE IS RESHAPING LINKED EFFECTS

Linked effects occur when one disturbance affects the characteristics of another, such as bark beetles shifting fire behavior (**Table 1**). These interactions can have profound consequences for forests, biodiversity, air quality, infrastructure, and human well-being (Seidl et al. 2017, Turner

2010). Thus, climate change–induced shifts in linked effects threaten forests and societies worldwide (Seidl et al. 2017). More frequent and severe droughts in the western United States, for instance, are shifting fire behavior, increasing fire frequency, extent, and severity (Williams et al. 2019, 2023). Given the current and projected impacts of many different types of disturbances (Millar & Stephenson 2015), understanding how their associated linked effects will also change is critical for managing and sustaining forests. Here our review highlights that climate change is amplifying the outcomes of linked effects worldwide via both Pathway 1 and Pathway 2 (**Figure 2**). However, dampened outcomes also occur, and lagged and nonlinear linked effects underscore that climate-driven changes are temporally dynamic and can destabilize or sometimes buffer forests from disturbance impacts.

Climate Change Is Amplifying Outcomes of Linked Effects Worldwide

Our review suggests that amplified outcomes of linked disturbances via Pathway 1 (**Figure 2*a*,*b***) are the most commonly reported climate change impacts on disturbance interactions globally (Brando et al. 2014, Hernández-Duarte et al. 2024, Zhao et al. 2024). For example, increases in the frequency and spatial extent of fire, drought, bark beetles, and disease (Cook et al. 2018, Hicke et al. 2016, Simler-Williamson et al. 2019, Zhao et al. 2024) elevate the probability that these disturbances overlap and interact under climate change (**Figure 2*a***). Higher frequencies of (*a*) spruce budworm outbreaks, (*b*) root pathogen infections, and (*c*) low-severity fire due to climate change can increase windthrow severity, the amplified outcome of the three distinct linked effects (Honkaniemi et al. 2017, Silvério et al. 2019, Taylor & MacLean 2009). Increases in windstorms in Europe are also expected to amplify bark beetle outbreaks (Seidl & Rammer 2017) because windthrown trees are less defensible against attacks by bark beetle (e.g., *Ips typographus*) (Lehmanski et al. 2024, Marini et al. 2017). This body of research on linked effects provides the strongest evidence that anthropogenic emissions are amplifying the outcomes of disturbance interactions (Brando et al. 2014, Dudney et al. 2021, Koontz et al. 2021, Parks & Abatzoglou 2020, Raffa et al. 2008, Seidl et al. 2017, Williams et al. 2019), which threatens forests worldwide.

Stronger Linked Effects Can Cause Major Shifts in Disturbance Regimes

Climate change can modify the strength or direction of linked effects, which fundamentally changes the relationship between two disturbances (**Figure 2*c*,*d***). For example, bark beetle outbreaks in cooler, wetter subalpine forests may not have a strong effect on subsequent fire behavior due to higher average fuel moisture relative to water-limited forests (Resco de Dios et al. 2021, Romualdi et al. 2023). As climate change increases aridity in subalpine forests (Denissen et al. 2022), however, this linked effect may be strengthened (Harvey et al. 2014a, Moriarty et al. 2019, Romualdi et al. 2023). In forests naive to linked disturbances (i.e., historically these effects did not occur), increases in the magnitude of positive linked effects may pose greater risks to long-term persistence (Wong & Daniels 2017). Few studies, however, distinguish between climate-driven shifts in the causal effects and changes in the spatiotemporal dynamics of disturbances, even though both shift the outcomes of linked effects. Making this distinction can improve our understanding of how climate change is modifying linked disturbances, and it can help identify areas likely to experience the most negative impacts under climate change.

Dampened Outcomes of Linked Effects Under Climate Change

Dampening effects on linked disturbances typically occur when climate change shifts the frequency, occurrence, or intensity of a disturbance, which can decrease the outcomes of their linked effects. For example, as warming shifts disturbances in space, including pathogens and insects (Bebber 2015), the outcomes of their linked effects are likely to be dampened at the trailing edge (Pathway 1). There are many examples in the literature that help illustrate how dampened linked effects can buffer forests from disturbance impacts under climate change (Cannon et al. 2017, 2019). For example, climate change–induced increases in stand-replacing fires or bark beetle outbreaks in temperate forests can result in dampened outcomes of windthrow severity, as these impacted stands are often less susceptible to windfall (Dobor et al. 2020, Kulakowski & Veblen 2002). Similarly, although wildfire is often associated with increased drought impacts (Young et al. 2019), increases in the frequency of low-severity fire can mitigate drought impacts by reducing competition (Knapp et al. 2021). Interestingly, the positive linked effect of drought on bark beetles can also be dampened under climate change because in some regions, chronically stressed trees provide insufficient nutritional resources, leading to reduced beetle development and host acceptance (Kolb et al. 2016, Raffa et al. 2008). Although warming often amplifies outcomes, dampening effects underscore that climate impacts are more complex and nuanced than they might initially appear.

Nonlinear Linked Effects Lead to Multidirectional Effects Under Climate Change

Some linked effects are nonlinear, meaning changes in one disturbance can trigger disproportionate or potentially unexpected responses in another. These often surprising outcomes can arise from complex relationships, such as bifurcation points or parabolic, sigmoidal, and exponential functional forms. The linked effect of fire on bark beetle outbreaks, for example, can be parabolically nonlinear: Low- to moderate-severity fire can increase the probability of a bark beetle attack by compromising host defenses (Bernal et al. 2023, Hood et al. 2015, Kulakowski & Jarvis 2013, Powell & Raffa 2011), while high-severity fire can incinerate the majority of suitable hosts, resulting in a negative linked effect (Cannon et al. 2019, Seidl et al. 2016). This nonlinear relationship suggests that climate change effects on bark beetle–fire linked effects are multidirectional. As fire severity increases under climate change (Parks & Abatzoglou 2020), some regions are likely to experience elevated bark beetle attacks, while others may experience declines due to fewer host trees.

Drought–disease effects can also be nonlinear, leading to both amplified and dampened outcomes under climate change. Because many fungal pathogens require moisture for germination and initial infection, drought effects on pathogens are often negative (Desprez-Loustau et al. 2006, Jactel et al. 2012, Kolb et al. 2016)—and moderated by the timing of drought (Caldeira 2019, Hossain et al. 2019). In subalpine, energy-limited forests, however, drought can increase the prevalence of tree disease (Dudney et al. 2021, 2023) (**Figure 2**). Additionally, resistance to *Heterobasidion annosum* on Norway spruce (*Picea abies*) is greatest at moderate drought severity (Lindberg & Johansson 1992). These studies illustrate that climate change impacts on linked drought–disease disturbances are multidirectional and highly variable in some pathosystems.

Lagged Linked Effects Moderate Outcomes Under Climate Change

Lagged effects capture important temporal dynamics of many linked disturbances (Sturtevant & Fortin 2021). Some disturbances can affect other disturbances concurrently, while other linked effects operate over years, even decades (Buma 2015, Hood 2020). These time-delayed, legacy effects can shift the direction or strength of linked effects over time, complicating prediction under climate change. Fire's effect on disease prevalence, for example, can initially be negative because it removes hosts and incinerates spores and infections (Beh et al. 2012, Cobb 2022). Over time, however, the effect of fire on disease becomes positive, particularly if host species recruit at higher frequencies and become infected (Simler-Williamson et al. 2021). The direction of MPB–fire linked effects can also change over time, from positive (Wayman & Safford 2021) to negative (Meigs et al. 2015) to no effect (Harvey et al. 2013), in part due to time-dependent decomposition, which changes fuel profiles (Hicke et al. 2012). Thus, identifying and quantifying lagged effects is essential for understanding and forecasting how climate change will reshape linked disturbances.

Critical transition: broadly defined as an abrupt shift in productivity or species composition that persists for an extended period of time

Despite their importance, few empirical studies test how climate change is altering lagged effects. Changes in disturbance timing, frequency, and severity can shift forest recovery trajectories (Buma 2015, Steel et al. 2022), however, suggesting that lagged effects may become increasingly disrupted. For example, higher fire frequency can protract forest recovery (Coop et al. 2020), which may dampen the likelihood of subsequent disturbances, including bark beetles, disease, or windfall (Simler et al. 2018). Additionally, the direct effects of climate change on forests can disrupt lagged effects. Higher aridity can accelerate wood decomposition (Allison et al. 2010), which may shorten the window during which disturbance-driven tree mortality can affect other disturbances (Fettig et al. 2022). These examples highlight that as climate change alters decomposition, recovery rates, and disturbance characteristics, it can reshape lagged linked effects, which complicates prediction under climate change.

PARSING THE COMPLEXITY OF DISTURBANCE INTERACTION EFFECTS UNDER CLIMATE CHANGE

While linked effects describe how one disturbance alters another disturbance's characteristics, interaction effects quantify dependencies between disturbances—i.e., whether the *effect* of one disturbance depends on the level of another disturbance (**Figure 1*c***; **Table 1**). These dependencies can stem from resource limitation, threshold dynamics, or shared effects (e.g., both disturbances affect tree regeneration via the same mechanisms) (Abella 2018, Anderegg et al. 2015, Côté et al. 2016, Gomez-Gallego et al. 2022). Disturbance interactions are classified as synergistic when the combined effects are greater in magnitude than the sum of the additive effects, antagonistic when the magnitude is less than the additive sum, and additive when the interaction effect is zero (**Figure 3*b***) (Côté et al. 2016, Kane et al. 2017). All of these disturbance interactions, however, can lead to compounding effects if the outcome is greater than the effect of any individual disturbance.

Below we describe how climate change is amplifying and dampening the outcomes of additive and interaction effects via Pathways 1 and 2 (**Figure 2**). In some regions, increases in the frequency, severity, and spatial overlap of disturbances have amplified the outcomes of additive effects and synergistic interactions (Pathway 1) (Abella 2018, Stephenson et al. 2019, Walden et al. 2023), which erodes forest resilience by increasing the magnitude of their impacts relative to historical conditions. Antagonisms, however, can sometimes buffer forests by reducing the net amplification of disturbances under climate change (Homet et al. 2019). In a few examples, climate change has reduced the spatial overlap, severity, or frequency of disturbances, which has dampened the outcomes of additive and interaction effects (Dudney et al. 2021, Itter et al. 2019). Additionally, climate can modify interaction effects (Pathway 2), shifting not only the magnitude but sometimes the direction of the effects (Csilléry et al. 2017, Stevens-Rumann et al. 2018). These changes underscore that interaction effects will become increasingly consequential for forests, driving novel disturbance dynamics and in some cases inciting critical transitions (Scheffer et al. 2012).

Cooccurring Disturbances Can Have Big Impacts Even if They Do Not Interact

Multiple disturbance effects can be additive—independent—because the disturbances do not sufficiently overlap in time or space to result in an interaction (Burton et al. 2020, Kane et al. 2017). Additive effects can also occur where disturbances sufficiently overlap but context dependencies,

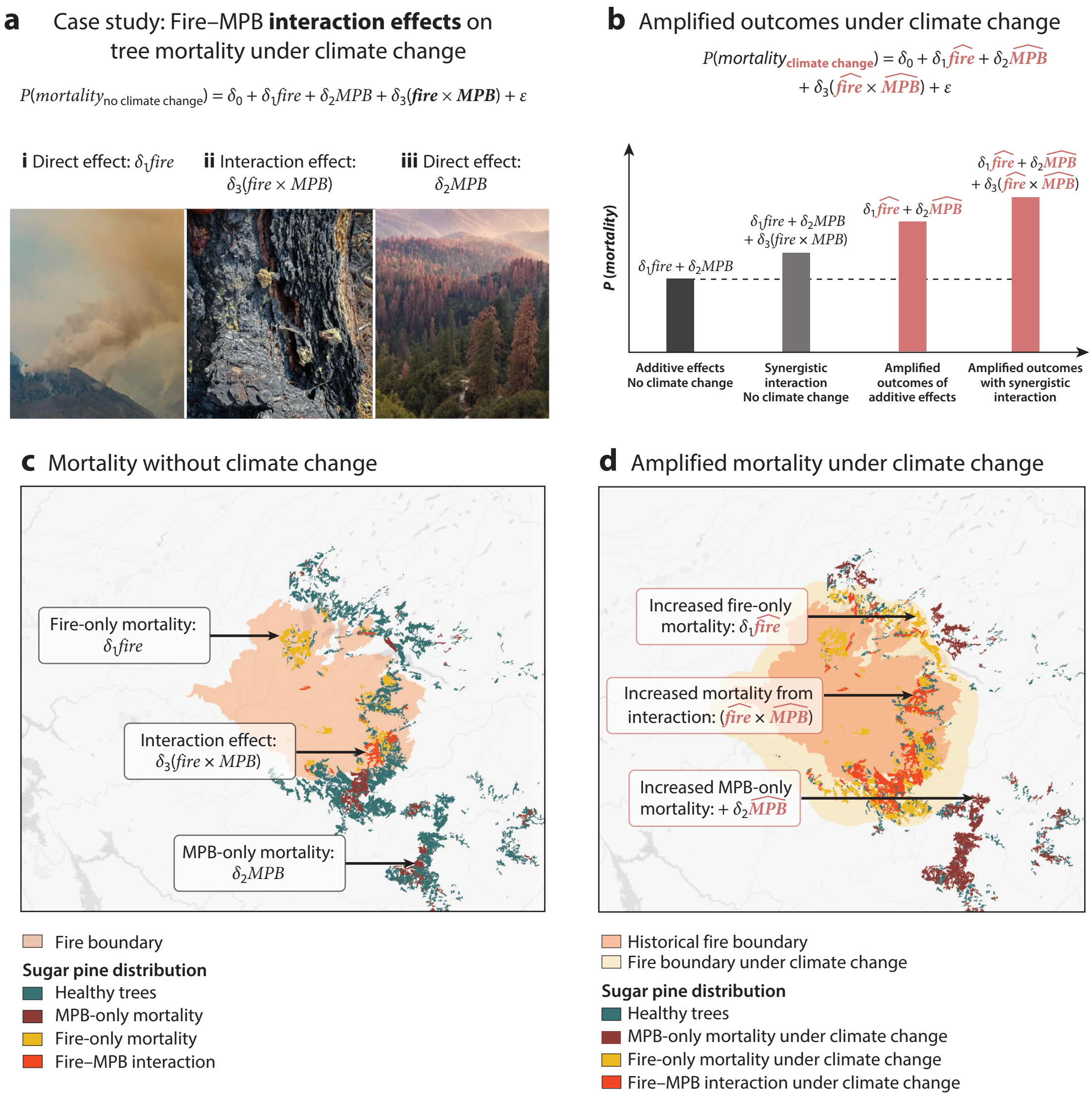


Figure 3

Conceptual case study: fire–MPB effects on tree mortality under climate change. (*a*) In the absence of climate change, fire and MPB can interact to shift tree mortality in the Sierra Nevada. The images show (*i*) wildfire-only mortality, (*ii*) mortality from the interaction effect (char on stem with MPB pitch tubes), and (*iii*) MPB-only mortality. The equation is the reference model quantifying the additive and synergistic interaction effects of fire and MPB on tree mortality in the absence of climate change. (*b*) Amplified outcomes of tree mortality under climate change. Here climate change increases the extent of fire and MPB attacks, leading to amplified outcomes (i.e., higher mortality) of the additive effects (*first pink bar*) and both the additive and interaction effects (*highest pink bar*). The dashed line shows the reference probability of mortality (additive effects only) in the absence of climate change; the gray bar shows mortality with a fire–MPB interaction effect. (*c*) Fire (*yellow*) and MPB attack (*maroon*) can interact to amplify tree mortality when they cooccur in space (*red areas within the pink fire footprint*). (*d*) Under climate change, the extent of fire (*pink*) and MPB outbreaks (*maroon*) increases, leading to a net amplification of tree mortality from their additive and synergistic interaction effects. Photos provided by J. Dudney. Abbreviations: δ, coefficients in the interaction effects model; ε, error; MPB, mountain pine beetle; P, probability.

including unshared mechanisms or resources, eliminate the possibility of an interaction effect. In the Appalachian Mountains, for instance, wind, drought, and the invasive hemlock woolly adelgid (*Adelges tsugae*) jointly contributed to unprecedented forest mortality, but they did not interact due, in part, to unshared resources (Abella 2018). Similarly, the invasive disease WPBR occurs more frequently in smaller-stemmed trees in lower elevation forests, while at higher elevations, the disease is prevalent across many size classes (Dudney et al. 2020). Because mountain pine beetle (MPB) typically prefers larger-stemmed individuals (Bockino & Tinker 2012, Negrón 2020), this size-dependent preference (i.e., an example of unshared resources) can result in some studies reporting additive effects, while other studies report interaction effects (Bockino & Tinker 2012, Dudney et al. 2020, van Mantgem et al. 2004). Regardless of whether they interact, amplification of MPB and WPBR impacts under climate change can cause rapid white pine decline (Dudney et al. 2020, van Mantgem et al. 2004). Because most forest ecosystems experience impacts from multiple disturbances (Gauthier et al. 2015, Gora & Esquivel-Muelbert 2021, Seidl et al. 2017), increases in the outcomes of their additive effects under climate change represent a global threat to forests.

Synergisms Erode or Bolster Forest Resilience Under Climate Change

Synergisms can emerge from nonlinear dynamics, particularly when disturbances share drivers (i.e., mechanisms) that amplify impacts (Metz et al. 2013). Fire and drought, for example, can both limit seedling recruitment by reducing soil moisture and increasing heat loading (Boag et al. 2020, Stevens-Rumann et al. 2022). When fire and drought overlap, their combined effects can be greater than their additive effects because aridity effects on vegetation often scale nonlinearly (Sasaki et al. 2023). Synergisms can also arise when disturbances jointly affect ecological processes governed by threshold dynamics, such as tree mortality and pathogenicity (**Figure 1*b***). Drought can reduce carbon uptake and hydraulic function, which increases the probability of mortality and flammability (Adams et al. 2017, Choat et al. 2012). When fire burns through a drought-stressed forest, mortality is more likely because of shared mechanisms that can push trees over mortality thresholds: (*a*) Drought and fire jointly increase the likelihood of carbon starvation and hydraulic failure (**Figure 1*b***), and (*b*) drought can increase flammability, thereby increasing the fire's lethality (Cansler et al. 2024, van Mantgem et al. 2013).

When disturbances interact synergistically (Paine et al. 1998, Walden et al. 2023) (**Figure 3**), climate change can further amplify their outcomes via Pathway 1 (changes in disturbance characteristics). Although synergistic effects of multiple disturbances on tree mortality are well documented (Cansler et al. 2024, Nardi et al. 2022, van Mantgem et al. 2013), few studies explicitly quantify or predict outcomes under climate change. Limited empirical evidence suggests that the outcomes of synergistic effects on mortality can be amplified under climate change if the severity, frequency, or extent of the individual disturbances increases (**Figures 2*a*** and **3*b*,*d***). Projected increases in drought frequency in Europe, for instance, are expected to amplify tree mortality due to the additive and synergistic effects of drought and European spruce bark beetle (Temperli et al. 2015). Increased drought severity under climate change (Mann & Gleick 2015) led to higher rates of tree mortality from drought–pathogen (Dudney et al. 2021) and drought–bark beetle (Koontz et al. 2021, Stephenson et al. 2019) interaction effects. Additionally, as climate change alters the spatial overlap of disturbances (Bebber 2015, Ramsfield et al. 2016), novel synergistic effects may emerge, which will be challenging to anticipate and manage.

Amplified outcomes of synergistic interactions will also impact forest regeneration, growth, and diversity—key mechanisms that underpin resilience to disturbances (Falk et al. 2022, Salesa et al. 2024, Shive et al. 2018). As climate change increases the frequency and severity of fire, drought, bark beetles, and pathogens in many regions (Bebber 2015, Lafferty 2009, Raffa et al.

2008, Williams et al. 2023), their synergistic interaction effects on forest regeneration and composition are increasingly documented (Hansen et al. 2018, Harvey et al. 2016, Salesa et al. 2024, Steel et al. 2022, Stevens-Rumann et al. 2022). In Australia's Northern Jarrah Forest, for example, increased fire and drought frequency have amplified recruitment failure (Walden et al. 2023). Though less common, fire and insect outbreaks can interact synergistically to reduce recruitment (Kulakowski & Veblen 2015), which has been found in montane Douglas-fir forests (Harvey et al. 2013). Additionally, fire and disease can interact to reduce the survival of resprouting trees, particularly following high intensity fires (Simler et al. 2018). These processes can erode structural and compositional diversity, leading to shifts in forest resilience (Johnstone et al. 2016). Despite their significant ecological impacts, however, few studies explicitly quantify how climate change is shifting the likelihood or impacts of these effects.

Perhaps paradoxically, synergisms can also increase the capacity of ecosystems to adapt to emerging novel climatic conditions (Millar & Stephenson 2015), ultimately facilitating ecosystem resilience in some systems. For example, increased drought and spruce beetle outbreaks accelerate mortality in Engelmann spruce, favoring more drought-tolerant species such as Douglas fir and ponderosa pine under projected climate scenarios (Temperli et al. 2015). Similarly, varying drought tolerance among tree species and slower regeneration of loblolly pine following high-severity fire may shift forest composition toward more drought-resistant oaks (Cooper et al. 2017). However, because the rate of climate change can quickly outpace the adaptive capacity of forest ecosystems, major shifts in forest composition, including critical transitions, are expected to become increasingly common (Armstrong McKay et al. 2022, Phillips et al. 2024).

Antagonisms Sometimes Mitigate the Impacts of Climate Change

Antagonistic interaction effects are more likely to emerge when a disturbance incites resistance (i.e., cross-tolerance) (Zhou & Wang 2023) or reduces the availability of resources required for a second disturbance's effect (i.e., biological negation) (Cannon et al. 2017). For example, fire can damage and kill trees that would otherwise experience mortality from bark beetles, which dampens the effect of bark beetles on tree mortality via biological negation (Fettig et al. 2010). Similarly, low-severity fire can induce resin defense in ponderosa pine, reducing the lethality of bark beetle attacks, thereby lowering the probability of mortality relative to their additive effects—an example of cross-tolerance (Hood et al. 2015). Although cross-tolerance and biological negation are key mechanisms of disturbance antagonisms, their strength and prevalence remain poorly understood in systems affected by multiple disturbances (Cannon et al. 2017).

Increases in the likelihood of antagonistic interactions (via Pathway 1 in **Figure 2*a*,*b***) may play an underappreciated role in sustaining forest resilience under climate change (Zhou & Wang 2023). Antagonisms can buffer the amplifying effects of climate change on individual disturbances by reducing tree mortality, promoting regeneration, and bolstering forest resilience. For example, droughts are expected to intensify in the Mediterranean Basin (Guiot & Cramer 2016). The corresponding reductions in soil moisture can limit pathogen effects (via biological negation) and favor seedling establishment (Homet et al. 2019). Similarly, as warming amplifies drought and biotic agent impacts, their additive effects on tree growth can be partially offset if the biotic agents decrease water demand (i.e., incite cross-tolerance), dampening the effects of drought on tree mortality (Balducci et al. 2020, Itter et al. 2019). In some contexts, increases in fire frequency under climate change can dampen the additive effects of fire and drought on mature tree mortality by reducing evapotranspiration (Norlen et al. 2024). If climate change effects on at least one of the antagonistic disturbances are negative, it can further buffer compounding disturbances. Hotter temperatures, for instance, can negatively impact insects and pathogens occurring close to their thermal limits (Bebber et al. 2013, Sturrock et al. 2011), which can dampen the impacts of their compounding effects. These antagonistic effects are likely location and disturbance-agent specific, however, and more research is needed to understand the strength of these mitigating effects.

Stronger Interaction Effects Threaten Forests Naive to Their Impacts

If climate acts as a moderator—affecting whether and how two disturbances interact to affect a third variable—then warming can change the strength of interaction effects (Pathway 2 in **Figure 2**). For example, in subalpine forests where conditions are cooler and wetter, bark beetle outbreaks and fire did not interact to reduce tree regeneration due to intact seed banks and a favorable postdisturbance climate (Harvey et al. 2014b). In contrast, in lower elevation forests, bark beetles and fire contributed to synergistic declines in tree regeneration (Harvey et al. 2013), suggesting a climate-dependent shift in interaction outcomes. As climate change continues to alter temperature and moisture regimes, these three-way interactions—where climate modifies interaction effects—may become increasingly common and ecologically consequential.

A growing number of studies provide empirical support for climate-mediated shifts in interaction effects. For example, Stevens-Rumann et al. (2018) found that the interaction between postfire water deficit and average climate significantly influenced tree regeneration in the twentieth century, but this relationship weakened or disappeared after 2000, suggesting that climate change can dampen synergistic effects of drought and fire. Similarly, Csilléry et al. (2017) showed that the interaction between drought and wind disturbances on tree mortality varied along an aridity gradient in Europe: In more arid sites, the two disturbances acted synergistically to increase mortality, whereas in less arid areas, their effects were antagonistic or additive. These results demonstrate that climate change not only shifts the magnitude but also the direction (sign) of disturbance interaction effects, and studies that assume static interaction effects may mischaracterize climate change impacts.

Climate-driven increases in the strength of interaction effects (Pathway 2) are especially concerning because they represent fundamentally novel interactions compared to those historically experienced by forests. These novel interactions, however, may increasingly threaten forests worldwide (Turner & Seidl 2023). As aridity increases in high-elevation and high-latitude forests—where regeneration is often slower—it may strengthen synergistic interactions between insects and pathogens on tree mortality (Bockino & Tinker 2012) or between fire and insects on regeneration (Harvey et al. 2013). These changes in synergistic effects via Pathway 2 may have disproportionately large consequences for forest resilience.

Climate Change Impacts on Interaction Effects Are Difficult to Quantify Due to Statistical Challenges

Interaction effects are typically much more challenging to estimate than additive effects due to statistical complexities (Côté et al. 2016). In a balanced experiment, for example, estimating a two-way interaction with the same precision as the main effects can require 16 times the sample size (Gelman et al. 2020). Because many disturbance events are relatively infrequent and difficult to manipulate, field experiments that can achieve these high replication requirements are relatively rare. Similarly, observational studies—which are often retrospective—seldomly provide the statistical power needed to confidently make claims about disturbance interaction effects (but see Buma & Wessman 2011, Csilléry et al. 2017, Fettig et al. 2010, Homet et al. 2019, Knapp et al. 2021, Stephenson et al. 2019, Stevens-Rumann et al. 2018). Further, to quantify how climate change is modifying interaction effects via Pathway 2 requires estimating a three-way interaction effect, which is even more challenging. The identification of the causal effects of individual disturbances, as well as their interaction effects, on forest metrics is often highly data intensive and represents

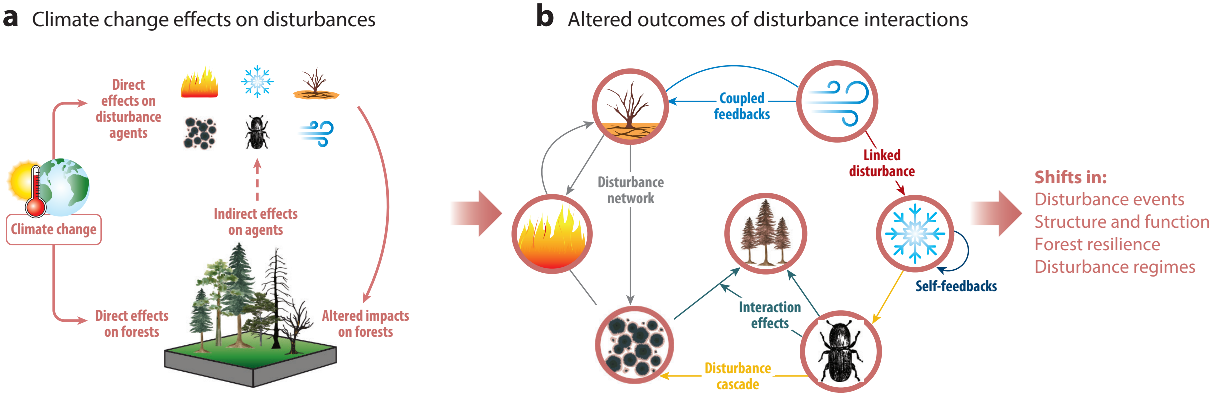


Figure 4

Climate change effects on interacting forest disturbances. (*a*) Climate change can alter forest disturbances via two primary mechanisms: (①) direct effects on disturbance agents and (②) indirect effects on agents mediated by shifts in forest conditions (e.g., declines in host density, increased water limitation). For example, warming can increase lightning strikes (Romps et al. 2014)—direct effects—and reduce fuel moisture (Jolly et al. 2015)—indirect effects. Both of these mechanisms increase ignition rates under climate change, altering fire frequency, as well as the impacts of fire on tree mortality. (*b*) These altered disturbances (*pink circles*) shift the outcomes—as well as the complex structures—of disturbance interactions via Pathway 1 (in **Figure 2**). The combination of altered disturbances (*a*) and altered outcomes of disturbance interactions (*b*) shifts disturbance events, forest structure and function, forest resilience, and disturbance regimes. Colored arrows highlight different classes of disturbance interactions. For simplicity, panel *b* shows only changes in the characteristics of disturbances (Pathway 1 in **Figure 2**), not changes in the effects of disturbance interactions that are directly moderated by climate change (Pathway 2 in **Figure 2**).

an important scientific frontier. These statistical challenges may bias the literature toward easily detectable, strong interaction effects, limiting our understanding of how multiple disturbances affect forest health under climate change.

AN UNDERSTUDIED FRONTIER: COMPLEX DISTURBANCE INTERACTIONS

Linked and interacting effects are often components of network effects that can produce much larger impacts on forest structure and composition (Flores & Staal 2022). A central challenge is that most studies focus on simpler interactions. As a result, the effects of complex disturbance interactions, such as network effects, coupled feedbacks, and disturbance cascades (**Figure 4**; **Table 1**), are poorly understood (Burton et al. 2020, Flores & Staal 2022), particularly under climate change. Conceptually, climate change will amplify or dampen their outcomes by shifting the location, timing, and intensity of disturbances (Pathway 1) and shifting the strength or direction of disturbance effects (Pathway 2) within a feedback loop, cascade, or network. Both Pathways 1 and 2 can restructure and complexify feedbacks and disturbance networks (**Figure 4**). Although empirical studies of complex interactions are relatively limited and focus primarily on feedbacks involving fire, wind, and a subset of bark beetle species, we highlight key examples illustrating how climate change can alter these complex effects—buffering some forests from disturbance impacts while pushing others over critical thresholds.

Amplified Positive Feedbacks Destabilize Mechanisms of Resilience and Can Accelerate Climate Change

Many disturbances create self-feedbacks or coupled feedbacks by altering vegetation, agent behavior, or environmental conditions in ways that promote subsequent disturbances (**Figure 4**;

Table 1). Amplified outcomes of feedbacks under climate change can rapidly shift forest structure and composition, threatening forests worldwide (Raffa et al. 2008, Wunderling et al. 2022). Wildfire, for example, is moving into higher elevations, which can feed back to increase fire frequency at specific timescales (Camac et al. 2017). This amplified outcome (i.e., more fire) not only alters historical fire regimes but may be particularly impactful in forests that historically experienced very low frequencies of wildfire (Van de Water & Safford 2011). Similarly, wind can increase the spread and severity of wildfire, which can in turn intensify wind and then fire—a positive, coupled feedback that emerges at short timescales (Peters et al. 2004). Positive self-feedbacks and coupled feedbacks are often considered destabilizing because they can lead to much greater impacts on forests and disturbance characteristics than the initial effects (e.g., a linked effect or the combination of linked and interaction effects) and are important drivers of ecosystem transitions (Scheffer et al. 2012, Seidl et al. 2017).

Amplified outcomes of positive feedbacks under climate change are particularly concerning because they can overwhelm forest resistance and recovery mechanisms. For example, the 2012–2016 hotter drought in California precipitated extensive outbreaks of western pine beetle, as water limitation undermined ponderosa pine resistance mechanisms, amplifying outcomes of density-dependent feedbacks (Koontz et al. 2021). Positive feedbacks can also occur between wind and pathogens because strong winds cause root breakage, which facilitates pathogen infection and reduces resistance to subsequent wind events (Cobb & Metz 2017). Given predicted increases in wind disturbances in some regions (Chemke et al. 2022), these positive feedbacks may become more prevalent in the future (Pathway 1 in **Figure 2**), causing higher mortality relative to outcomes in the absence of climate change. Further, drought–fire coupled feedbacks, which can cause critical transitions, are becoming more common in the Amazon (Balch et al. 2015), Piñon–juniper woodlands (Phillips et al. 2024), and mixed conifer forests (Steel et al. 2022). Perhaps even more concerning, however, are the amplified outcomes of disturbance feedbacks with the atmosphere—as warming increases the frequency of fire and bark beetle outbreaks, CO_2 emissions rise, which can accelerate warming (Kurz et al. 2008, Walker et al. 2019).

The Buffering Effects of Negative Feedbacks Under Climate Change

Positive feedbacks can be replaced by negative feedbacks and vice versa, leading to complex temporal disturbance dynamics. Negative self-feedbacks and coupled feedbacks typically arise from disturbance-induced changes in vegetation, environmental conditions, and density-dependent processes that disrupt the conditions required for subsequent disturbances. These negative feedbacks are often considered stabilizing because they can dampen the likelihood of a subsequent disturbance (Hart et al. 2019, Howe et al. 2024, Sommerfeld et al. 2021). Under climate change, however, these stabilizing effects are shifting, which can both provide a buffer and increase forest vulnerability to disturbance impacts.

Under climate change, shifts in disturbance characteristics can increase the frequency of negative feedbacks in a forest, which can further dampen the likelihood or severity of a subsequent disturbance. Elevated disease virulence under climate change (Gomez-Gallego et al. 2022) can cause hosts to die more quickly, thereby suppressing disease prevalence in some regions (Dudney et al. 2021, Singh et al. 2023). Similarly, severe bark beetle outbreaks can incite negative density-dependence feedbacks during and following an outbreak (i.e., declines in host availability) (Koontz et al. 2021, Raffa et al. 2008, Wallin & Raffa 2004), which can limit bark beetle reproduction for a longer period of time under climate change. Further, increases in wind severity and/or bark beetle outbreaks under climate change can dampen the likelihood of subsequent mortality from wind and bark beetle (*I. typographus*) because both disturbances reduce the number of Norway spruce on the landscape (Sommerfeld et al. 2021, Temperli et al. 2013). Thus, as climate change increases the severity and frequency of disturbances, it can amplify the outcomes of both positive and negative feedbacks, leading to complex shifts in disturbance characteristics and forest ecosystems (**Figure 4**).

Although negative feedbacks may initially bolster resilience under climate change, important context dependencies and network effects (see the next section) can weaken their efficacy, threatening forest resilience in the long term. For example, wildfire is associated with negative self-feedbacks that can reduce the probability of a subsequent high severity fire in the Amazon (Balch et al. 2008), Australia's eucalyptus forests (Weston et al. 2022), Canada's boreal forests (Hart et al. 2019), and California's mixed conifer forests (Tubbesing et al. 2019). These buffering effects, however, can simultaneously increase forest vulnerability to other climate change impacts that may not be part of the feedback loop. Increased frequency and spatial overlap of the same or different types of disturbances due to exogenous factors, for instance, can increase the likelihood of forest transitions (Hart et al. 2019).

Disturbance Networks May Be an Overlooked Driver of Critical Transitions

Many disturbance interactions are components of nested or more complex structures of effects, referred to as disturbance networks (**Table 1**) (Burton et al. 2020). Different types of interactions—e.g., linked, cascading, and feedback effects—often interact across scales, and their combined impacts can accelerate change, in some cases pushing forests across critical thresholds (Flores & Staal 2022). In the Amazon, three distinct structures of nested feedbacks that emerge following multiple disturbances best describe critical transitions from an intact rainforest to white-sand savanna, open canopy, or degraded forest (Flores et al. 2024). Fire and drought, for example, generate nested feedbacks that shift fire frequency, seed limitation, and soil erosion, transitioning rainforests to white-sand savannas (Flores et al. 2024). Although disturbance networks are much harder to quantify empirically, they are likely to be important drivers of critical transitions in many systems that experience multiple disturbances. In fact, as climate change shifts the strength and characteristics of disturbances—particularly changing the frequency of overlapping disturbances—network effects may become increasingly impactful in forested regions worldwide (Burton et al. 2020, Flores et al. 2024, Flores & Staal 2022).

Disrupted Cascades Can Lead to Multidirectional Impacts on Forests

Disturbance cascades are also recognized as important drivers of forest change (Buma 2015, Burton et al. 2020). Drought, for example, can incite bark beetle outbreaks through a linked effect (Fettig et al. 2019), which in turn can shift fire behavior (Wayman & Safford 2021), creating a disturbance cascade: drought → bark beetles → fire. Similarly, pathogen infections by *Heterobasidion* root rot can increase tree susceptibility to windthrow, which facilitates outbreaks of the European spruce bark beetle *I. typographus* (Honkaniemi et al. 2018). Climate change is likely to be a major disrupter of disturbance cascades, amplifying some outcomes while dampening others. Increased drought stress, for example, can suppresses fungal pathogens that require moist conditions to reproduce (Sturrock et al. 2011), which can dampen the outcomes of linked disease–bark beetle effects (Bockino & Tinker 2012). Hotter drought followed by increased fire frequency can reduce *Phytophthora ramorum*, thereby dampening disease prevalence (Burgess et al. 2017, Simler-Williamson et al. 2021). These patterns underscore the need to understand how climate change alters disturbance cascades, as shifts in their strength and outcomes are likely to impact forest resilience in a warming world.

CONCLUSION

As climate change shifts the characteristics of forest disturbances, their interactions are also changing. Most disturbance interactions are influenced by climate, and many are tightly coupled with climate extremes. Thus, anthropogenic climate change is disrupting and modifying disturbance interactions globally. As climate change increases the frequency and extent of disturbances, there will be more opportunities for disturbance interactions to occur, including complex effects like coupled feedbacks and network effects. The increased frequency and impacts of complex interactions are particularly concerning, as they are likely to be important drivers of critical transitions. There is some evidence, however, that climate change can dampen outcomes of disturbance interactions—particularly those associated with antagonisms and negative linked effects or feedback effects—which may buffer some forests from climate change impacts. Because most forests are affected by multiple disturbances that can drive rapid change, shifts in their interactions will have profound impacts on forest ecosystems worldwide.

SUMMARY POINTS

1. More consistent use of terminology will improve our understanding of disturbance interactions and the impacts of climate change.
2. We should expect ecological surprises (i.e., outcomes that are difficult to predict) under climate change due to understudied disturbance interactions, as well as rarely quantified nonlinear and feedback effects.
3. Disturbance interactions are increasingly important to understand as climate change alters their spatiotemporal dynamics in many regions. Disturbance interactions, however, remain understudied partly due to a regional research bias that emphasizes North American and European systems.
4. Amplified outcomes of disturbance interactions threaten forest ecosystems worldwide; long-term outcomes, however, are difficult to predict due to complex feedbacks and network effects.
5. Some disturbance interactions not only buffer forests from climate change impacts but can enhance adaptive capacity by increasing tolerance to subsequent disturbances; the buffering capacity of negative feedbacks and antagonistic interactions, however, may weaken as disturbances increasingly overlap under climate change.
6. Although complex interaction effects remain poorly studied, they are likely key drivers of ecosystem transitions under climate change.
7. Even small shifts in disturbance characteristics caused by climate change can trigger substantial changes in subsequent disturbances, particularly when disturbances are governed by positive feedbacks or nonlinearities.

FUTURE ISSUES

1. More long-term studies and applications of complex and novel modeling approaches will improve our understanding of disturbance interactions.

2. Clarifying the role of network effects on forest mortality and tipping points is critical for predicting and managing climate change impacts.
3. Determining which disturbance pairings are most likely to produce antagonistic or synergistic effects and identifying causal interaction effects are important to fill knowledge gaps.
4. Context dependencies can lead to conflicting results for the same disturbance pairings. Quantifying how moderating variables, including tree density, tree size, forest type, or various climate variables, alter the effects of disturbance interactions will help clarify these relationships, as well as climate change impacts.
5. Few studies have identified or attributed changes in disturbance interactions to climate change; more attribution-focused research is essential to determine how much recent warming has impacted outcomes of forest disturbance interactions.
6. Most studies focus on changes in aridity or temperature, while the effects of changes in other climate variables, including snowpack, wind patterns, atmospheric rivers, or climate variability are rarely documented, limiting our understanding of climate change impacts on disturbance interactions.
7. Developing a safe operating space for forests experiencing shifting disturbance interactions will help prioritize management interventions.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

AUTHOR CONTRIBUTIONS

Author contributions are defined using the Contributor Roles Taxonomy (CRediT; **https://credit.niso.org/**). Conceptualization: J.D., J.E., B.J.H., R.S.; literature review: J.D., J.E., B.J.H., R.S.; project leadership: J.D.; visualization: J.D.; writing—original draft: J.D., J.E., B.J.H., R.S. writing—review and editing: J.D., J.E., B.J.H., R.S.

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