



Climate change and altered fire regimes: impacts on plant populations, species, and ecosystems in both hemispheres

Brian J. Harvey · Neal J. Enright

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Abstract Extreme fire seasons in both hemispheres in 2019 and 2020 have highlighted the strong link between climate warming and altered fire regimes. While shifts in fire regimes alone can drive profound changes in plant populations, communities, and ecosystems, the direct effects of warming climate conditions can impose added stress on key demographic processes prior to and immediately following fire. Altered survival-, growth-, and reproductive- rates in periods between fires, coupled with post-fire recruitment failure from increasingly stressful environmental conditions (including both heatwave and drought) can pose serious threats for conservation in fire-adapted ecosystems worldwide, raising concerns of ecosystem conversion and state change. In this special issue, a collection of 11 papers from fire-prone ecosystems in both hemispheres documents key insights into how changes are unfolding—and mechanisms underpinning such changes—across a diverse range of species and ecosystems. Here, we synthesize this work that uses latitudinal observational surveys, experiments, and simulation modeling to understand how climate warming and altered fire regimes

are reshaping our planet. We place these studies in the context of broader advances, and highlight additional research directions to uncover how altered fire regimes, fires interacting with other disturbances, and pre-and post-fire demographic processes can erode resilience in a warming climate.

Keywords Resilience · Fire interval · Serotiny · Global warming · Resprouting · Post-fire recruitment · Seed production · Self-replacement

Introduction

Climate warming and associated increases in disturbance activity are driving profound shifts in terrestrial ecosystems worldwide. For example, direct effects of climate warming are increasing drought-related stress in forests, leading to widespread increases in tree mortality across all forested continents (Allen et al. 2010, 2015). In many areas, warmer and drier conditions are also associated with decreases in tree recruitment (e.g., Andrus et al. 2018), which are particularly important following severe disturbance (Coop et al. 2020). In addition to the direct effects of climate on ecosystems, many disturbances are highly climate-sensitive (Seidl et al. 2017), and thus climate change can indirectly affect resilience by altering disturbance regimes to the point where they are no longer aligned with disturbance-adapted traits of dominant plants (Johnstone et al. 2016). Fire is among

B. J. Harvey (✉)
School of Environmental and Forest Sciences, University
of Washington, Seattle, WA, USA
e-mail: bjharvey@uw.edu

N. J. Enright
Environmental and Conservation Sciences, Murdoch
University, Perth, WA, Australia

the most climate-sensitive disturbances, as warming is associated with longer wildfire seasons (Jolly et al. 2015), increases in area burned (Westerling 2016), and greater burn severity (Parks and Abatzoglou 2020; Collins et al. 2021a)—all key dimensions of fire regimes that are changing and require better understanding (McLauchlan et al. 2020). Fire activity is expected to increase well into the twenty-first century, even as prior fires reduce fuels and impose constraints on burned area (Abatzoglou et al. 2021)—though current trends of increasing burn severity (e.g., plant mortality or organic material consumed) may attenuate and reverse as vegetation and fuel structures change (Parks et al. 2016). Collectively, the direct effects of climate warming on plant populations and communities, coupled with the indirect effects of climate warming on altered fire regimes, have raised concern worldwide for the resilience and conservation of terrestrial ecosystems (Millar and Stephenson 2015).

Concerns about rapidly changing ecosystems in a warmer and more fire-prone future have catalyzed development of multiple frameworks conceptualizing resilience to fire (e.g., capacity to experience fire without shifting to an alternative state; cf. Walker et al. 2004). Fire-prone ecosystems that are adapted to severe fire via obligate seeding after fire-caused plant death may be particularly at risk of eroding resilience, and have therefore been the focus of several recent conceptual advances. For example, the interval squeeze presents a framework to test how shortened intervals between severe fires and both pre- and post-fire shifts in climate can erode resilience of terrestrial ecosystems to fire (Enright et al. 2015). Johnstone et al. (2016) build on earlier concepts of biological legacies (Franklin et al. 2000), differentiating legacies into material (e.g., physical structures) and information (e.g., life-history traits) legacies that if misaligned with dimensions of climate space and fire regimes, can catalyze loss of resilience as ecosystems depart a safe operating space (Johnstone et al. 2016). This special issue presents 11 studies that test many of the dimensions presented in these and other frameworks (e.g., Hessburg et al. 2019; McLauchlan et al. 2020)—using complementary approaches in observational, experimental, and simulation modeling studies to better understand the mechanisms of resilience in the face of climate warming and increasing fire. We organize our synthesis of this work along four themes

where these studies expand on, or provide insights into, mechanisms identified in existing frameworks of resilience to fire. We close by presenting a series of new research directions that could further explore these themes and contribute understanding of additional mechanisms to build on existing frameworks.

Fire regimes and their changing nature

One focal thematic area in forecasting how climate warming is affecting ecosystems is building a mechanistic understanding of fire regimes and how they are changing over space and time. For example, combined with changes in ignition patterns and land management following colonization and subsequent exclusion of Indigenous fire use (Kimmerer and Lake 2001), warming climate increases the likelihood of crossing of thresholds that control many aspects (e.g., size, frequency, severity) of fire regimes (Pausas and Keeley 2021). Historical and contemporary fire regimes have been thoroughly explored in some regions (e.g., North America and Australia), yet many fire-prone locations have yet to receive the same level of attention—leaving major geographic gaps in understanding the nature of some fire regimes. Franco et al. (2022; this issue) explore drivers of burn severity in *Araucaria* forests in Patagonia—an ecosystem that has intermixed fire-prone shrubland and fire-inhibiting forests. By testing relationships across scales ranging from individual trees to broader landscapes, they demonstrate an important dimension of understanding the Andean montane fire regime—scale-dependent effects on burn severity. Strong local-scale constraints on burn severity that are dictated by fire-resistant traits of dominant trees (in this case *Araucaria araucana*) can be overridden by broad-scale drivers such as extreme weather, and support findings in other systems (e.g., Belote et al. 2015). In addition to characterizing drivers of burn severity to continue building fundamental understanding of fire regimes, such findings contribute insight into how fires can catalyze positive feedbacks between vegetation mosaics and burn severity via varying levels of flammability and sensitivity to fire (Paritsis et al. 2015; Tepley et al. 2018). Future work that incorporates the landscape patterns of burn severity (e.g., Cansler and McKenzie 2014; Harvey et al. 2016b) and interactions among multiple fires (Parks et al. 2014; Harvey et al. 2016a; Collins et al. 2021b) could build on this

mechanistic understanding of burn severity (Franco et al. 2022) to further understanding and tracking of fire regimes as they change in ecosystems around the globe (Prichard et al. 2017).

Demographic mechanisms underpinning resilience to fire

A relatively understudied dimension of how warming climate and altered fire regimes can erode resilience is the demographic processes underpinning population persistence and post-fire recovery (Davis et al. 2018). For example, severe fire recurring over a short interval can lead to local post-fire regeneration failure for serotinous trees if the time between fires is insufficient to recover the canopy seedbank (i.e., immaturity risk, sensu Keeley et al. 1999). While outcomes of this phenomenon have been observed following short-interval fires across different ecosystems (Brown and Johnstone 2012; Turner et al. 2019; Whitman et al. 2019), the demographic parameters (e.g., plant growth, survival, fecundity) that drive outcomes are less well understood. Quantifying cone or seed abundance across a range of conditions pre-fire requires dedicated data to be collected across individuals and populations, necessitating much more time than is possible in many typical vegetation surveys. Further, understanding how reproductive traits such as seed dormancy that support demographic parameters can change over evolutionary time scales is an important dimension of understanding adaptive capacity in the face of rapid climate change.

In ecosystems characterized by stand-replacing fires, tracking demographic parameters and how they change over the inter-fire period is critical for understanding subsequent post-fire outcomes. Recent work in subalpine forests of North America has quantified cone production on individual trees in old-growth (i.e., several centuries after fire) (Andrus et al. 2020) and young post-fire (Turner et al. 2007) stands. Incredibly valuable insights are born of such rigorous cone measurements across large populations of established trees, though they present a snapshot in time of reproductive capacity if a disturbance were to occur, leaving the temporal development of this critical stage less well understood. In this issue, (Agne et al. 2022) present data on cone abundance across a chronosequence of past stand-replacing fire across most of the geographic distribution for knobcone

pine (*Pinus attenuata*) and bishop pine (*Pinus muricata*) on the west coast of the USA. These two serotinous species are adapted to a stand-replacing fire regime and demonstrate tremendous resilience to fire (Harvey and Holzman 2014; Reilly et al. 2019), but given their short fire-return-intervals relative to other serotinous conifer forests in North America, are an ideal setting to test how immaturity risk varies with fire interval (Keeley et al. 1999). Taking a chronosequence approach allows for identifying the period of time where immaturity risk is greatest (very high < 10 years since fire and moderate 10–20 years since fire in this case), and how drought-related mortality in inter-fire periods can lengthen the period of immaturity risk (Agne et al. 2022).

Beyond characterizing the temporal window of immaturity risk, how the period of immaturity risk varies spatially—and additional drivers of seed abundance other than ontogeny—are critical factors for identifying locations and contexts at particular risk from fire-catalyzed loss of resilience. By modeling the regional distribution of the juvenile (i.e., reproductively immature) period for a wide range of serotinous obligate seeding species across southwestern Australia, Gosper et al. (2022; this issue) contribute an important spatial dimension to understanding immaturity risk (Keeley et al. 1999). Importantly, they demonstrate that the juvenile period is predicted to continue lengthening with further climate warming, extending the period of immaturity risk even if fire-return-intervals remain constant. Beyond time required to maturity, many other factors underpin reproductive capacity between stand-replacing fires—yet such factors are often assumed to remain stable and dependable. For example, pollination by wind or insects is a key requisite for cone/seed production, but relative to ontological factors contributing to seed production, is poorly accounted for in most fire-prone ecosystems. Using simulation modeling, Souto-Veiga et al. (2022; this issue) test how the decrease in pollination success observed in ecosystems worldwide might interact with other better-represented drivers in the interval squeeze (Enright et al. 2015). In serotinous *Banksia hookeriana* shrublands of SW Australia, they demonstrate how declining pollination success can qualitatively increase the likelihood of immaturity risk, as pollination limitation for flowering serotinous species can erode the inter-fire seed accumulation rate. The findings by Souto-Veiga

et al. (2022) raise important questions about how widespread this phenomenon may be in other systems where different modes of pollination could alter mechanisms of resilience to fire.

Demographic mechanisms underpinning resilience are also important to understand on evolutionary time scales. For a trait such as serotiny, the variability in space across the range of a species, as well as variability through time, may have critical consequences for alignment or misalignment of adaptations with current and future climate and fire regimes (Johnstone et al. 2016). Ladd et al. (2022; this issue) demonstrate how variability in the fire regime—a key driver in variability in serotiny—differs across island populations and moisture gradients on the mainland of SW Australia, across the range of the serotinous native cypress pine, *Callitris preissii*. Serotiny level is greater in drier mainland locations with more regular fire than in wetter mainland and island populations where fire intervals are more variable and less predictable. Similar gradients of moisture across coastal and inland areas have been related to variation in serotiny in pines on the west coast of North America (Millar 1986a, 1986b) and demonstrate critical spatial dimensions to fire adaptations within a species. Lamont (2022; this issue) explores pathways of how three classes of fire-adapted traits—fire resistance, fire-stimulated dormancy release, and rapid post-fire growth—are guided by different combinations of climate, associated fire regimes, and post-fire growing conditions. Using this historical lens through evolutionary time scales is especially relevant when considering the pace of climate and fire regime change in the twenty-first century (Pausas and Keeley 2021). The conclusions by Lamont (2022) about the mismatch between the times required for adaptation or mitigation vs the accelerating rate of global change have important implications for biodiversity conservation worldwide.

Post-fire conditions as an important filter on response to fire

In addition to climate-driven changes to fire regimes and effects on key pre-fire demographic parameters that govern post-fire seed availability, environmental conditions after fire at different scales are an important filter for vegetation response. Observational (Enright et al. 2014; Harvey et al. 2016c; Tepley

et al. 2017; Stevens-Rumann et al. 2018), experimental (Hansen and Turner 2019), and modeling (Davis et al. 2019; Turner et al. 2022) work demonstrates the strong direct effects of climate on post-fire tree and shrub species seedling establishment. However, fewer studies have examined the role of post-fire vegetation dynamics between tree seedlings and shrubs/herbs (e.g., Harvey and Holzman 2014; Tepley et al. 2018; Werner et al. 2019), or focused more directly on the response of the plant community as a whole following fire (e.g., Brodie et al. 2021).

One location of key interest for where post-fire conditions and vegetation dynamics may inhibit or promote ecosystem change is in transition zones (e.g., forest—grassland boundaries). Combining observational and experimental approaches, Brehaut and Brown (2022; this issue) test how wildfire might catalyze poleward expansion of the boreal forest (*Picea glauca*) in Yukon, Canada as the climate warms—which may be a potential outcome in a warmer and more fire-prone future (Batllori et al. 2017). Although fires create opportunities for forest expansion into tundra ecosystems, competition from tundra shrubs and more extreme microclimate conditions post-fire imposed constraints on *Picea glauca* establishment even when tree seed was available. Collectively, these factors limited post-fire expansion of forest into tundra (Brehaut and Brown 2022). The effects of post-fire community dynamics (Harvey and Holzman 2014; Werner et al. 2019) and/or microsite conditions created by fire (Hoecker et al. 2020; Wolf et al. 2021) are emerging as an important, yet less understood dimension of how ecosystem conversions may unfold with future climate warming (HilleRisLambers et al. 2013).

In forests and shrublands, the broader plant community response to fire and climate has received less attention than myriad studies about the dominant woody vegetation (trees in forests and shrubs in shrubland); however, a much wider range of plant traits are represented across entire communities. Further, post-fire early seral plant communities may be sensitive indicators of change, often comprise much of the biodiversity in many fire-prone ecosystems (Swanson et al. 2011; Harvey and Holzman 2014), and contain many culturally important plants that were fostered by Indigenous burning practices for millennia (Kimmerer and Lake 2001). Across the range of conditions that burned in the

uncharacteristically severe 2014 wildfire season in the boreal forests of NW Canada, Dawe et al. (2022; this issue) tracked post-fire trajectories of the entire plant community over 5 years. Widespread differences between pre- and post-fire plant communities and tree species dominance, while somewhat expected via successional dynamics, may also be important early indicators of shifts toward dominance by post-fire vegetation communities better adapted to a warmer and drier future (Dawe et al. 2022). Beyond being an indicator of change, post-fire plant communities can also contribute to important feedback mechanisms that can accelerate changes to fire regimes (Tepley et al. 2018). For example, in Chile, *Araucaria-Nothofagus* forests that experienced high-severity fire were characterized by post-fire plant communities dominated by resprouting species and more flammable taxa than present pre-fire (Arroyo-Vargas et al. 2022; this issue). Such feedbacks of severe fire begetting more flammable post-fire vegetation are especially important to understand as climate constraints to fire are lessened in a warmer future, and can enable better forecasting of where disturbance interactions may hasten ecosystem transitions (Lindenmayer et al. 2011; Tepley et al. 2018).

Interacting drivers and compound responses

In addition to increasing disturbance activity generally as climate warms, multiple disturbances can also interact mechanistically and/or produce synergistic effects on ecosystems (Burton et al. 2020). For example, one disturbance can alter the likelihood, size, or intensity/severity of a subsequent disturbance—a process termed *linked* disturbance interactions (Simard et al. 2011). With fires, linked interactions are often negative over short intervals as one fire removes key necessary ingredients (i.e., fuel) for subsequent fires (Parks et al. 2015; Harvey et al. 2016a; Prichard et al. 2017; Collins et al. 2021b), however positive links have also been observed (Lindenmayer et al. 2011; Tepley et al. 2018). Whether or not two disturbances are linked, if coupled closely in time, they can produce *compound* disturbance effects on ecosystem response if the mechanisms of resilience to disturbance have not fully recovered by the time of subsequent disturbances (Paine et al. 1998). Obligate seeding species are particularly vulnerable to compound disturbance

effects when two fires occur in quick succession (Turner et al. 2019) or fire occurs soon after a biotic disturbance such as bark beetle outbreak (Harvey et al. 2013)—two contexts where the first disturbance removes much of the necessary seed source required for tree establishment following a subsequent fire.

Two studies in this issue explore different dimensions of how disturbance interactions can catalyze profound changes to ecosystems. Lindenmayer et al. (2022; this issue) build on an earlier conceptual model of ‘landscape traps’ (Lindenmayer et al. 2011), whereby positive links between fires can lead to ecosystem collapse. Specifically, young post-fire vegetation recovering from fire is more flammable than older unburned forest, leading to a greater likelihood of subsequent stand-replacing fire in the mountain and alpine ash forests of SE Australia. Adding significantly to the risk of forest conversion after fire is the reinforcing effect of increasing area and continuity of this highly flammable young post-fire vegetation, and increasing immaturity risk. While the effects of post-fire drought on obligate seeding species have been documented in many forests (Enright et al. 2014; Harvey et al. 2016c; Tepley et al. 2017; Stevens-Rumann et al. 2018), resprouting species have been less fully explored, and are generally expected to be more buffered from compound disturbance effects, or even benefit from disturbances occurring in rapid succession (Kulakowski et al. 2013). Bendall et al. (2022; this issue) investigated the interactive effects of drought and fire on net post-fire density of juveniles (i.e. surviving resprouts plus new seedling recruits) in wet versus dry eucalypt forests, eastern Australia. They found that severe drought increased juvenile mortality by up to 15% and was a more important driver of change than was frequency and severity of recent fire. Further, while overall juvenile numbers declined after severe drought in wet eucalypt forest sites, they increased in dry forest sites, potentially reflecting differences in competitive interactions and in the various drivers of seed availability at the time of fire. They concluded that, although shifts in stand attributes were not occurring quickly, further climate change to a more drought- and fire-prone future may pose a threat to persistence of these forest types.

Conclusions and future directions

Continued climate warming and associated increases in fire activity are likely to profoundly affect the resilience of plant populations, communities, and ecosystems worldwide. The collection of studies in this special issue highlights many dimensions of how these changes are already unfolding across continents in both hemispheres, and identifies key mechanisms that underpin these changes now and into the future. Some changes will arise from climate-driven alterations to different dimensions of fire regimes, such as increases in severity that are governed by the combination of fire behavior and fire-adaptive (or sensitive) plant traits (Franco et al. 2022). Other changes will emerge when shifting fire regimes interact with key demographic and community dynamics pre-fire (Agne et al. 2022; Gosper et al. 2022; Souto-Veiga et al. 2022) and post-fire (Arroyo-Vargas et al. 2022; Dawe et al. 2022; Brehaut and Brown 2022); some occurring over evolutionary time scales (Lamont 2022; Ladd et al. 2022). Finally, some changes will

emerge as surprising outcomes from disturbances interacting in a linked (Lindenmayer et al. 2022) or compound (Bendall et al. 2022) manner. The findings in these studies also highlight new dimensions that expand on existing conceptual frameworks (e.g., Enright et al. 2015; Johnstone et al. 2016) to build further insight into mechanisms of ecosystem change in a warmer and more fire-prone future (Fig. 1). Here, we explore some of those future directions, focusing specifically on the four main dimensions of the studies that comprise this special issue.

Demographic processes during inter-fire periods

Species that store mature seeds in various structures can routinely build the available seedbank from near zero immediately following fire to levels sufficient to support resilience to fire after some time (Agne et al. 2022). However, temporal variability (specifically reduction) in seed production during inter-fire periods (Redmond et al. 2016; LaMontagne et al. 2021) via masting, and untimely cone opening and subsequent

Dimensions of fire- and climate-driven ecosystem change

Demographic mechanisms

Agne et al.; Gosper et al.;
Ladd et al.; Lamont; Souto-
Veiga et al. (this issue)

Fire regimes

Franco et al. (this issue)

Disturbance interactions

Bendall et al.; Lindenmayer
et al. (this issue)

Post-fire climate and stress

Arroyo-Vargas et al.;
Brehaut and Brown; Dawe
et al. (this issue)

Future research areas to expand on existing frameworks

Demographic processes during inter-fire periods:

- **Seed dormancy, masting, and leakage**
- **Pollinator population dynamics and pollination success**
- **Growth and reproductive compensation within populations**

Changing fire frequency interacting w/ severity, spatial patterns, and seasonality:

- **Spatial patterns of fires and effects on nearby seed availability**
- **Fire severity, especially extreme high severity and loss of biological legacies**
- **Shifts in seasonality of fires and interaction with reproductive mechanisms**

Interactions between fire and other disturbances:

- **Effects of biotic disturbance (insect and pathogen outbreaks) on fire severity**
- **Potential compound effects if biotic disturbances erode seed sources**
- **Novel disturbance interactions with pathogens or anthropogenic disturbance**

Altered post-fire outcomes in shifting climate:

- **Fire-catalyzed increase in post-fire environmental stress**
- **Shifting interactions (competition, facilitation) on post-fire stress gradients**
- **Feedbacks with post-fire vegetation and future fire likelihood**

Fig. 1 Four key dimensions of how fire and climate warming are altering ecosystems in the papers comprising this special issue (left column), and corresponding future research

directions for additional insights in these dimensions that can expand on existing conceptual frameworks (e.g., Enright et al. 2015; Johnstone et al. 2016) (right column)

seed release/leakage, can affect seedbanks during this critical window of time. Understanding the mechanisms that deplete the seedbank, once formed, are an important additional dimension of exploration. When post-fire populations are sparse, plants can produce more cones/seeds per individual, potentially buffering otherwise slower seedbank accumulation assumed from the number of mature plants alone (Turner et al. 2007; Agne et al. 2022). However, the limits to these compensatory responses (e.g., a single tree is fixed in one location and can only produce so many cones) may not fully make up for lower numbers of cones/seeds that would be present with a larger population of mature individuals. Seed production in fire-adapted structures that depends on pollinators (Souto-Veiga et al. 2022) may be drastically impacted by declines in pollinating animals (Potts et al. 2010)—highlighting the importance of exploring this mechanism further. In sum, there remains myriad dimensions of mechanisms underpinning the buildup and depletion of seedbanks in inter-fire periods that require additional exploration.

Altered post-fire outcomes in a shifting climate

Post-fire, a critical demographic parameter often of focal interest is the recruitment and survival of young seedlings (Stevens-Rumann et al. 2018; Davis et al. 2018, 2019). Short-interval fires that are followed by drought can quickly erode resilience via compounding effects of successive fires and stressful environmental conditions (Whitman et al. 2019). However, fires themselves can add compounding environmental changes (via consumption of moisture-retaining litter or shade-producing above-ground structures), thereby affecting seedling mortality (Hoecker et al. 2020; Wolf et al. 2021). Disentangling how post-fire vegetation dynamics are affected by external drivers (e.g., broad-scale drought) vs. fire-induced changes in local microclimate is a key research frontier. Further, contrasting outcomes of post-fire interactions among plant species may shift in a warming climate—with important implications for ecosystem transitions (Brehaut and Brown 2022). For example, in some contexts, post-fire dominance by flammable woody shrubs can lead to decreased dominance of trees via competition (Harvey and Holzman 2014) or feedbacks to future fires (Tepley et al. 2018; Arroyo-Vargas et al. 2022), whereas in other contexts shrubs

can facilitate tree establishment under harsh post-fire climate conditions (Werner et al. 2019). How competitive vs facilitate outcomes vary along stress gradients has been explored in many contexts (Maestre et al. 2009), and incorporation into post-fire studies could add important insight into shifting post-fire plant community dynamics in the future.

Changing fire frequency interacting with severity, spatial patterns, and seasonality

Increasing fire frequency can erode seed availability for seed banking species (Keeley et al. 1999; Buma et al. 2013; Agne et al. 2022). However the spatial patterns of fires set the distance to seed sources dispersing from elsewhere (Kemp et al. 2016; Harvey et al. 2016b; Collins et al. 2017; Tepley et al. 2017). This spatial dimension to changing fire frequency has recently highlighted how the amount of seed in surrounding unburned areas may be eroding with increasing disturbance activity (Gill et al. 2022). In addition, increased fire severity locally can remove seed sources and erode additional key legacies (e.g., woody carbon) via extreme burn severity that is only recently beginning to be better understood (Turner et al. 2019; Saberi et al. 2022). Finally, the seasonal timing of fires has gained attention as a key focus area of understanding how fire regime change can affect plant populations (Miller et al. 2019), and continued work on this dimension could uncover how more subtle or finer resolution changes to fire regimes may alter resilience. Collectively, these examples highlight key research gaps about how severity, seasonality, and size/spatial dimensions of fire regimes may interact with frequency to erode resilience to fire.

Interactions between fire and other disturbances

Other disturbances that occur in inter fire periods can constrain post-fire responses in several ways that are not fully understood. For example, prior disturbances can amplify or dampen the severity of fire (Kane et al. 2017), which alone can erode resilience to fire if severity is so great that it consumes seed sources (e.g., blowdown followed by fire, Buma and Wessman 2012). However, pre-fire disturbances can also reduce seed availability by killing large, seed-producing individuals, eroding the capacity to respond to fire well before the fire event occurs (Harvey et al. 2013).

Finally, novel interactions between fire and disturbances such as non-native plant pathogen or insect outbreaks (e.g., Simler et al. 2018) will be increasingly important to track and forecast as global travel and trade continue in the Anthropocene. Building a mechanistic understanding about how other disturbances interact with fire to erode key biological legacies remains a key area of needed research (Johnstone et al. 2016; Kane et al. 2017).

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