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INVITED REVIEW

Limits to post-fire vegetation recovery under climate change

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Abstract

Record-breaking fire seasons in many regions across the globe raise important questions about plant community responses to shifting fire regimes (i.e., changing fire frequency, severity and seasonality). Here, we examine the impacts of climate-driven shifts in fire regimes on vegetation communities, and likely responses to fire coinciding with severe drought, heatwaves and/or insect outbreaks. We present scenario-based conceptual models on how overlapping disturbance events and shifting fire regimes interact differently to limit post-fire resprouting and recruitment capacity. We demonstrate that, although many communities will remain resilient to changing fire regimes in the short-term, longer-term changes to vegetation structure, demography and species composition are likely, with a range of subsequent effects on ecosystem function. Resprouting species are likely to be most resilient to changing fire regimes. However, even these species are susceptible if exposed to repeated short-interval fire in combination with other stressors. Post-fire recruitment is highly vulnerable to increased fire frequency, particularly as climatic limitations on propagule availability intensify. Prediction of community responses to fire under climate change will be greatly improved by addressing knowledge gaps on how overlapping disturbances and climate change-induced shifts in fire regime affect post-fire resprouting, recruitment, growth rates, and species-level adaptation capacity.

KEYWORDS

climate change, germination, heat stress, herbivory, mortality, obligate seeding, resprouting, wildfire

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1 | INTRODUCTION

In 2019–20, a series of mega-fires burnt an estimated 21% of the total temperate forest biome in Australia (Boer, Resco de Dios, & Bradstock, 2020). These fires, termed the 'Black Summer' fires, more than doubled the estimated area burnt in a single fire season in eastern Australia (Nolan et al., 2020), and resulted in an unprecedented extent of high severity fire (Collins et al., 2021) in the modern fire management record. These fires coincided with record low rainfall and high temperatures (Bureau of Meteorology, 2019). Similar fire seasons have also occurred in many other regions globally in recent years, including North America (Kirchmeier-Young, Gillett, Zwiers, Cannon, & Anslow, 2019; Williams et al., 2019), South America (Bowman et al., 2019) and the Mediterranean (Turco et al., 2019). These types of extreme fire seasons raise important questions about the capacity of ecological communities to respond to climate-driven changes in fire regimes.

Many plant species and ecological communities are well-adapted to local historical fire regimes, broadly defined as the frequency, severity, seasonality and extent of fire (Gill, 1975; Turner, 2010; Whelan, 1995). Shifts in local fire regimes can test the resistance and resilience of species and communities to fire (Karavani et al., 2018). At the same time as fire regimes are changing, climate change is affecting other abiotic and biotic disturbances, such as drought, heatwaves and insect outbreaks. Since wildfires typically coincide with drought and elevated temperatures, (Dowdy & Mills, 2012; Nolan et al., 2020; Pook, 1986), climate change driven increases in these abiotic disturbances (Hoegh-Guldberg et al., 2018; Kirono, Round, Heady, Chiew, & Osbrough, 2020) are expected to coincide with increases in wildfire frequency, severity and extent. Climate change effects on biotic disturbances, such as insect outbreaks, are more difficult to predict, and are likely to be both positive and negative (Pureswaran, Roques, & Battisti, 2018). Here, we explore the overlapping and often antagonistic influence of these disturbances with changing fire regimes.

Under climate change, woody plant extinction is likely to increase through a phenomenon termed 'interval squeeze', whereby climate-driven changes in population demographics, disturbances and biotic stressors combine with increased fire frequency to increase post-fire mortality and reduce recruitment (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015). Yet, the combined effect of these disturbances on plant communities remains one of the largest uncertainties in modelling ecosystem responses to fire under a changing climate. This uncertainty arises because mechanistic and modelling studies have largely focused on single stressors; for example, quantifying plant mortality following fire (Michaletz & Johnson, 2007), quantifying impacts of fire severity and frequency on tree mortality (Bennett et al., 2016), or identifying thresholds of drought stress that lead to mortality (Choat et al., 2018). Further, field-based studies on post-fire mortality and recruitment have necessarily been limited in scope by focusing on individual fire events and/or regions.

In this review, we summarize the suite of mechanisms involved in plant or population level responses to fire, and then examine how climate-driven shifts in fire regime, combined with other abiotic and biotic disturbances, can affect post-fire vegetation recovery. We begin by outlining the different plant responses to fire. We then separately examine two key post-fire responses that facilitate vegetation recovery, namely resprouting and fire stimulated recruitment. To distil the complexity of these interacting mechanisms, we present them as conceptual models (Figures 1 and 2). With respect to resprouting, we explain how plant persistence depends on the impacts of fire on plant structure and resources, such as non-structural carbohydrate reserves and bud banks (Figure 1a). We then outline how overlapping disturbances (additional fires, drought, herbivory, etc.) affect resprouting and may lead to resprouting failure (Figure 1b). With respect to post-fire recruitment, we first examine the different recruitment mechanisms (seed release, flowering and germination) in isolation (Figure 2a), and then examine the likely impacts of different disturbances in combination with changes in fire regimes (Figure 2b). While we illustrate our review with literature primarily from Australian temperate and mediterranean ecosystems, in particular forests, the mechanisms governing plant and community responses to fire that we discuss here are applicable to many ecosystems globally.

2 | OVERVIEW OF PLANT RESPONSES TO FIRE

There are a range of plant responses to fire that ensure persistence or recruitment, which are tightly linked to fire regime attributes. Fire-resistant species are those that can survive fire without resprouting new foliage, that is, the fire causes little damage to them (Midgley, Kruger, & Skelton, 2011). Consequently, fire-resistant traits provide an advantage in low intensity surface fire regimes, where fire induces limited canopy defoliation, and where fire survival may be achieved through a combination of plant height and protection of meristematic tissues and the cambium (Midgley et al., 2011).

Resprouting is a key plant functional trait that enables plants to persist following disturbances (Bond & Midgley, 2001). Post-fire resprouting occurs when meristematic tissues, specifically buds, are protected from fire (Clarke et al., 2013). Resprouting can occur: (a) belowground, from roots and rhizomes; (b) basally, from buds located at or belowground, for example, from lignotubers; (c) epicormically, from stems and branches; and (d) apically, from the apical meristem (Clarke et al., 2013; Figure 3). Belowground and basal resprouting is more widespread than aerial resprouting (i.e., epicormic, apical); with the latter predominantly occurring in arborescent life forms (Clarke et al., 2013; Pausas & Keeley, 2017). Resprouting is considered an expensive strategy in terms of allocation to belowground roots and/or storage organs and protection of bud banks. Consequently, resprouting species may predominate at productive sites (Knox & Clarke, 2005; Pausas et al., 2016; Pausas & Bradstock, 2007), although converse relationships between resprouting and productivity have also been observed (Hammill, Penman, & Bradstock, 2016).

Seed germination following fire is a common post-fire recruitment strategy. For species with fire-cued seed germination, seeds can either be stored in the soil or on the plant in woody structures (Figure 3e).

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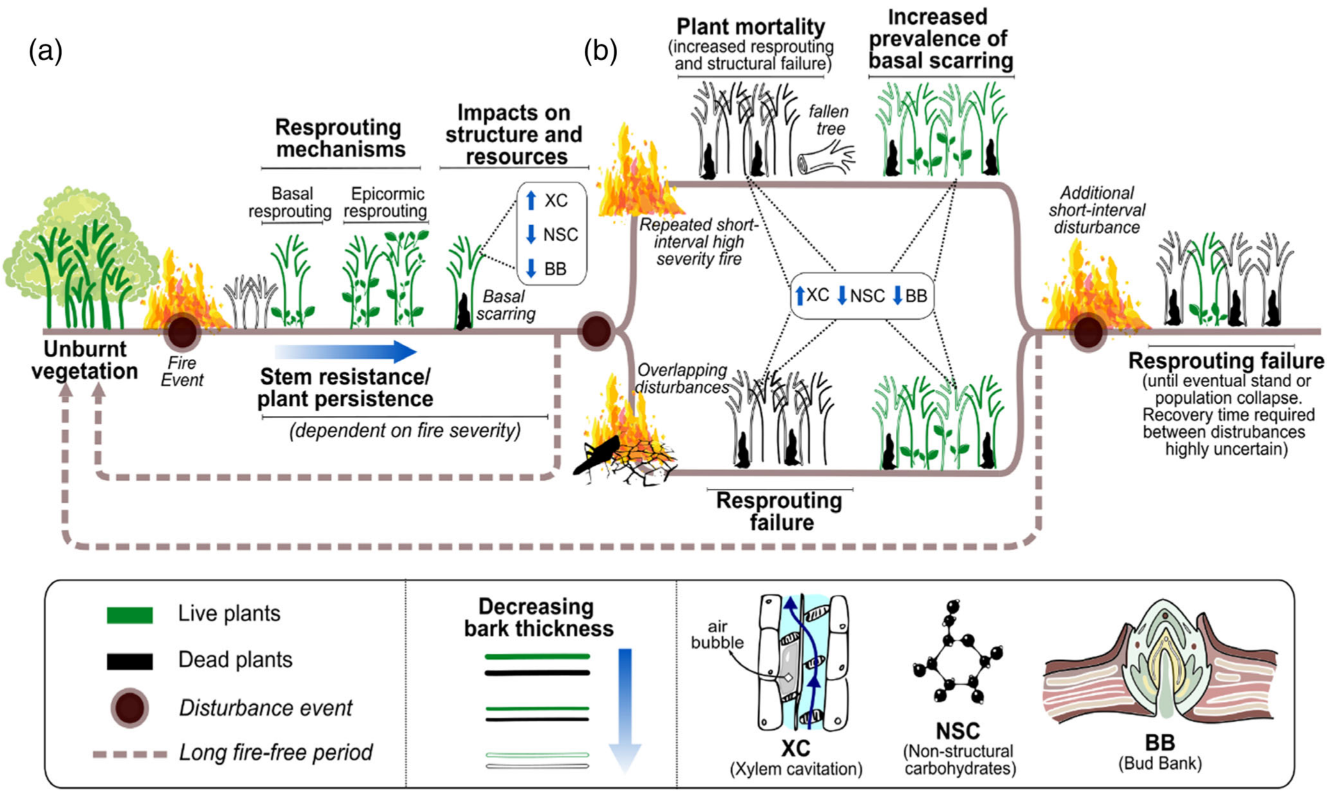

FIGURE 1 (a) Overview of mechanisms involved in post-fire recovery via resprouting under (a) historical fire regimes; and (b) changing fire regimes and overlapping disturbances due to climate change. Also illustrated are population transitions (brown lines). Moving from left to right (solid lines), the figure illustrates (i) the range of resprouting responses and structural and physiological changes to trees following a single fire event; (ii) responses following either a repeated short-interval fire event or overlapping disturbance events (i.e., when other abiotic or biotic disturbances, such as insect outbreak or drought, coincide with fire); and (iii) eventual stand collapse following repeated short-interval disturbance events. The dashed lines indicate population recovery trajectories in the absence of repeated disturbances

Serotiny, the extended storage of plant-stored seeds which are released after fire, is observed to occur in lower productivity sites compared to soil-storage of seeds, as a strategy to limit predation on seeds (Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). Species that only recover from fire via fire-cued seed release and/or germination are termed 'post-fire obligate seeders' (Prior & Bowman, 2020), whereas species that recover from fire via both seeding and resprouting are termed 'facultative resprouters' (Clarke et al., 2015). Another recruitment strategy is fire-cued flowering (Lamont & Downes, 2011; Figure 3f).

For species without any of the above adaptations to fire, persistence may still be possible in post-fire environments via dispersal from nearby unburnt stands or from fire refugia. Fire refugia are locations that experience less severe and/or less frequent fire than the surrounding landscape (Krawchuk et al., 2020). However, this method of persistence is limited by the inherent dispersal capacity of the species as well as the spatial configuration of the fire refugia (Thomson, Moles, Auld, & Kingsford, 2011).

Invariably, vegetation communities are often identified by the post-fire response of the dominant or most easily-identified vegetation – such as an overstorey comprised of resprouting trees – however, many vegetation communities support species with a mix of post-fire responses. For example, across eucalypt forests, approximately 50% of species are facultative resprouters, 21% are obligate resprouters and 27% are obligate seeders (P. J. Clarke et al., 2015). For simplicity, in the following sections we will consider each of the post-fire responses individually, recognising that each of these responses may co-occur within a single vegetation community.

3 | POST-FIRE RESPROUTING

3.1 | Mechanisms impacting post-fire recovery of resprouting plants

We consider resprouting as a continuum ranging from belowground resprouting to aerial resprouting from the upper branches of trees, with plant resistance/persistence following fire increasing along this continuum (Figure 1a). Mechanisms contributing to post-fire mortality include changes to both plant structure and access to resources. Plant structural changes include physical damage to stems and roots and consumption of bark during fire. Changes to resources include

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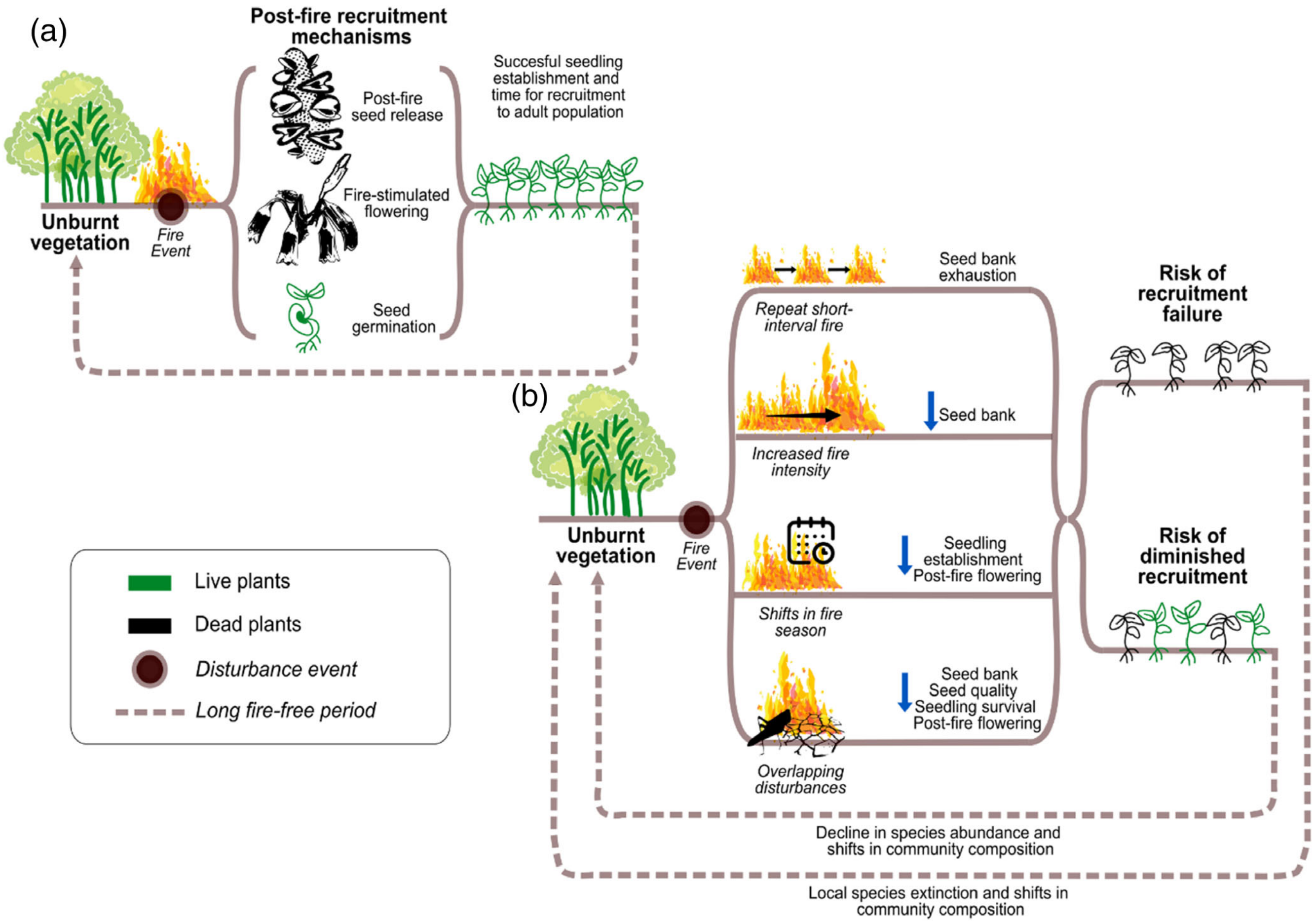

FIGURE 2 Overview of mechanisms involved in post-fire recovery via seed recruitment under (a) usual fire regimes; and (b) changing fire regimes due to climate change. The figure also gives an overview of population transitions (brown lines). The dashed lines indicate population recovery trajectories in the absence of disturbance [Colour figure can be viewed at wileyonlinelibrary.com]

hydraulic limitations due to xylem cavitation, depletion of non-structural carbohydrates and depletion of bud-banks.

3.1.1 | Impacts on structures: Basal scarring and physical damage to roots

Trees that survive fire may suffer cambium necrosis of part of the stem base, which is referred to as 'basal scarring' (Figure 4). Cambium necrosis exposes heartwood to decay and fire. Over time, the excavation of heartwood will compromise the structural integrity of stems, increasing the likelihood of collapse during subsequent disturbances (Figures 1 and 4, Whitford & Williams, 2001; Gibbons, Cunningham, & Lindenmayer, 2008). The presence of basal scarring can substantially increase the probability of topkill, that is, death of aboveground biomass (e.g., +20%; Collins, 2020; Collins, Bradstock, Tasker, & Whelan, 2012), and the likelihood of mortality by causing tree collapse (Bowman & Kirkpatrick, 1986; Collins, 2020). The nature and size of basal scarring required to cause tree hollow formation has not been well studied, nor has the role of bark type in susceptibility to basal scarring. Basal scarring is, however, more likely to be prevalent in larger trees, which are typically older and have therefore had increased exposure to fire (Collins, 2020; Collins et al., 2012; Parnaby, Lunney, Shannon, & Fleming, 2010).

Any physical damage to roots may decrease structural stability of the plant or affect access to water and nutrients. There are very few studies of fire impacts on roots, although studies from boreal Scots pine forests and semi-arid sagebrush shrubland in western USA indicate that fire can reduce fine root biomass, particularly under prolonged smouldering combustion driven by large biomass accumulation (Hood, Varner, van Mantgem, & Cansler, 2018; Rau, Johnson, Chambers, Blank, & Lucchesi, 2009; Smirnova, Bergeron, Brais, & Granstrom, 2008). However, most surface and canopy wildfires often exert a limited impact on roots as soil is an excellent thermal insulator (Resco de Dios, 2020).

3.1.2 | Impacts on structures: Damage to bud banks

A requirement for stem and branch survival is that the buds and cambium are sufficiently protected from high temperatures during fire (Clarke et al., 2013; Figure 1). Bark thickness is a key trait determining

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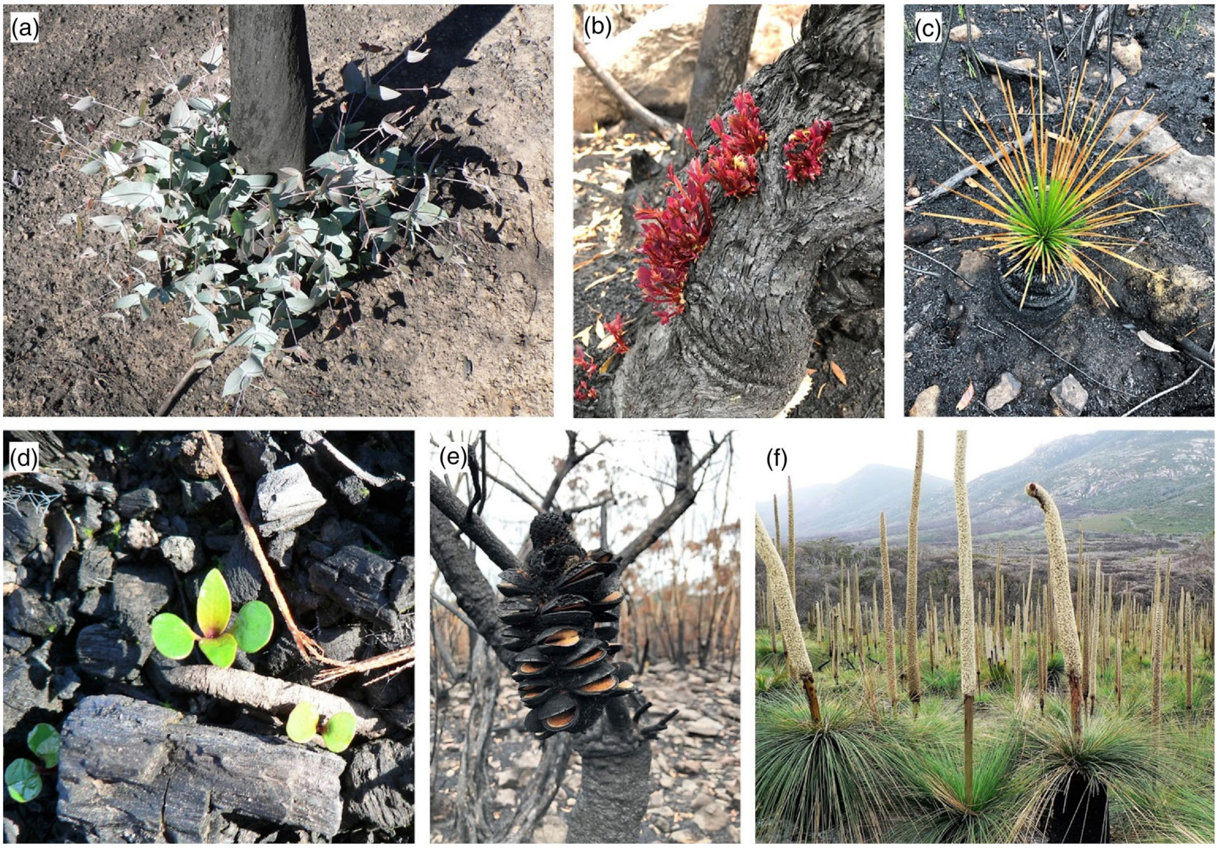
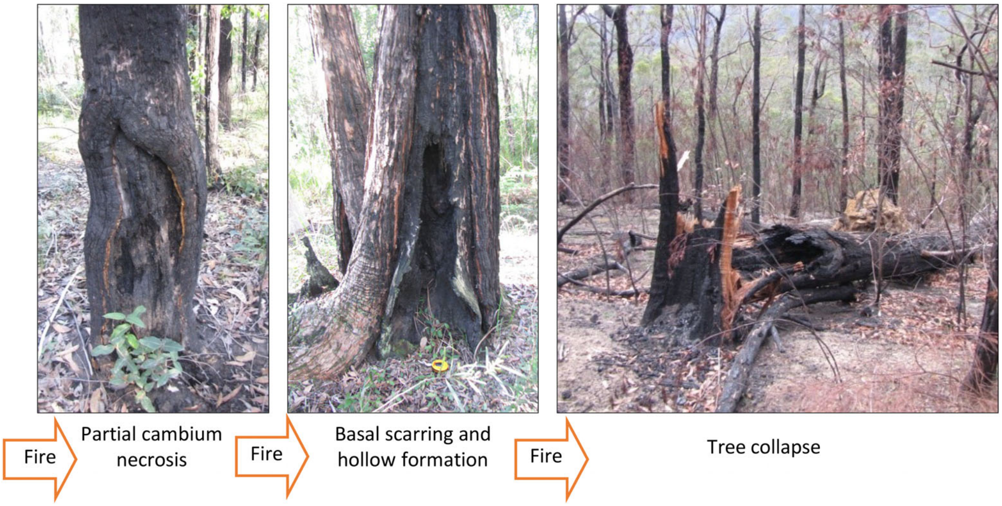


FIGURE 3 Examples of post-fire resprouting and recruitment, all photos taken in south-eastern Australian ecosystems: (a) basal resprouting in *Eucalyptus* sp.; (b) epicormic resprouting in *Angophora* sp.; (c) apical re-growth in *Xanthorrhoea* sp.; (d) seedling germination in *Eucalyptus* sp.; (e) serotinous cone in *Banksia* sp.; and (f) post-fire flowering in *Xanthorrhoea* sp. Photo credits: R. Nolan [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Conceptual overview of the process of basal scarring and tree collapse from repeated fires. Photo credits: L. Collins [Colour figure can be viewed at wileyonlinelibrary.com]



stem survival during fire, with thicker bark providing greater insulation (Wesolowski, Adams, & Pfautsch, 2014), reducing the likelihood of stem and branch mortality (Lawes, Adie, Russell-Smith, Murphy, & Midgley, 2011). Fire regimes were thought to account for much of the variation in bark thickness globally (Pausas, 2015), but recent studies highlight that supporting metabolism and additional processes may also play an important role (Resco de Dios, 2020; Rosell, 2019).

Bark thickness develops with stem size and age, hence the likelihood of topkill decreases with stem size for many eucalypt species (Collins, 2020; Fairman, Bennett, & Nitschke, 2019). The position of

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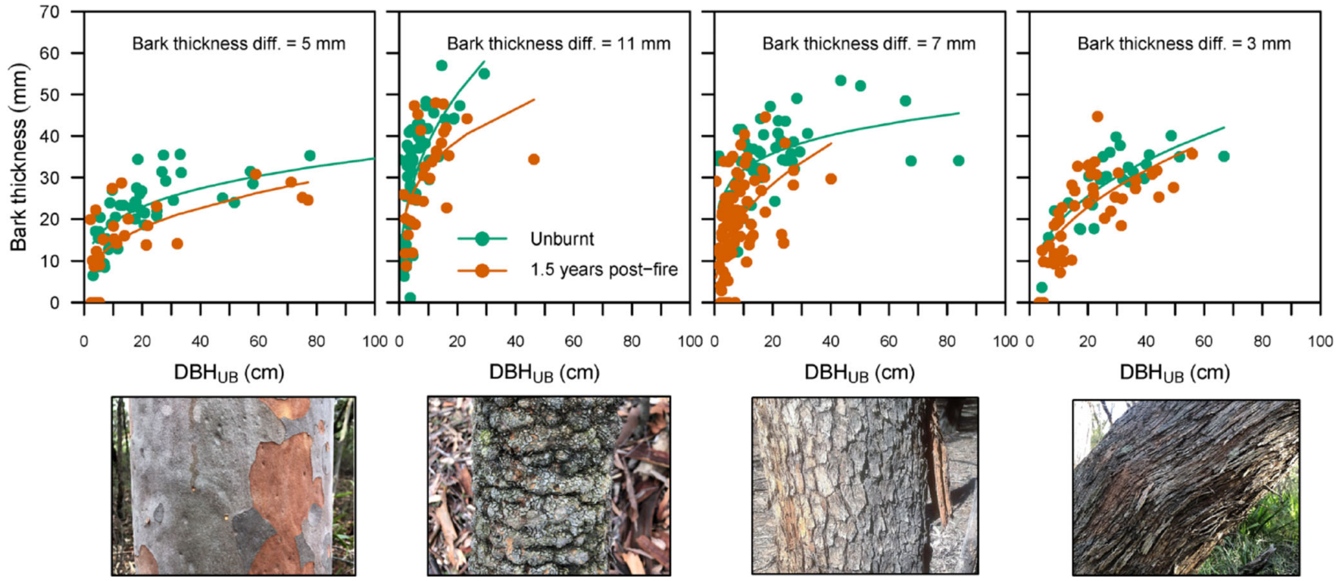
buds relative to the bark surface determines the degree of insulation, with higher resprouting success being observed for species with buds deeply embedded beneath the bark surface, such as eucalypts (Charles-Dominique, Beckett, Midgley, & Bond, 2015). Canopy height can also protect buds and tissues in the upper stems and branches, though adequate insulation is still required to facilitate stem survival (Clarke et al., 2013).

During fire, some of the protective bark on plants is consumed (Nolan et al., 2020; Volkova & Weston, 2013). This reduction in bark thickness reduces the insulation capacity of bark, thereby increasing vulnerability of stems to cambium necrosis from subsequent fire (Figures 1 and 5; Wesolowski et al., 2014; Gill & Ashton, 1968; Catry et al., 2012). However, it is unclear whether the partial loss of bark is sufficient to increase mortality rates of large eucalypts, owing to their deeply embedded buds (Charles-Dominique et al., 2015). Further, the length of time required for recovery of that bark is largely unknown, due to limited data on bark growth rates. Bark consumption is dependent on fire intensity and season of burn, which may be a function of seasonal variation in bark moisture content affecting bark combustion (Chatto, Bell, & Kellas, 2003).

Another hypothesized cause of resprouting failure following short interval fires is bud-bank limitation (Figure 1), which represents a reduction in the number of buds available to resprout (Enright, Fontaine, Westcott, Lade, & Miller, 2011). In a study on resprouting shrubs in south-west Australia, Bell and Pate (1996) observed bud bank exhaustion after experimental clipping. However, the frequency of the clipping in that experiment (6 months or less) is unlikely to replicate naturally-occurring fire frequencies. Resprouting failure has also been attributed to a lack of buds following long fire intervals (Enright et al., 2011). However, these declines in resprouting may be a function of plant age, rather than fire interval, with declines in bud-banks observed with plant age or size (Hodgkinson, 1998; Holland, 1969). Thus, while there is some evidence of bud-bank exhaustion affecting resprouting, further studies are required that replicate the impact of realistic increases in fire frequency.

3.1.3 | Impacts on resources: Stored carbohydrates and hydraulic limitations

As fire frequency increases and fires increasingly coincide with other disturbances, such as severe drought, it has been hypothesized that resprouting species may reach the limits of their capacity to resprout (Karavani et al., 2018; Figure 1, Fairman, Nitschke, & Bennett, 2016; Resco de Dios, 2020). This phenomenon has been termed 'resprouting exhaustion syndrome' (Karavani et al., 2018). Resprouting exhaustion has largely been attributed to depleted carbohydrate reserves. There is some indirect evidence for carbohydrate limitation driving resprouting exhaustion from observations of declines in root and stem starch reserves following a resprouting event (Bowen & Pate, 1993; Smith, Arndt, Miller, Kasel, & Bennett, 2018). While temporary declines in starch are to be expected, a complete consumption of starch reserves has only seldom been documented. That is, while limited carbohydrate concentrations may impact resprouting capacity, direct evidence for this phenomenon is still scarce.



Angophora costata
(Smooth, gum bark)

Banksia serrata
(cork-like bark)

Corymbia gummifera
(rough, tessellated bark)

Eucalyptus sieberi
(stringybark – rough, compact bark)

FIGURE 5 Power regressions of bark thickness as a function of stem size (diameter at breast height under bark, DBH$_{UB}$) illustrating a trend of thinner bark in recently burnt trees. Recently burnt trees were subject to canopy fire 1.5 years prior to measurement, while unburnt trees had not been burnt for at least 10 years prior to measurement. Also presented are the difference in bark thickness between burnt and unburnt trees when DBH$_{UB}$ is 20 cm. Data collected from dry sclerophyll forest in eastern Australia (Nolan, Rahmani, et al., 2020) [Colour figure can be viewed at wileyonlinelibrary.com]

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Few mechanistic studies on the role of carbohydrate reserves in limiting resprouting capacity have been conducted to date. An exception is a study by Resco de Dios et al. (2020), where resprouting was affected by low concentrations of stored non-structural carbohydrates, but only in a species with high leaf construction costs in combination with large losses of hydraulic conductance. In this case, the depletion in stored reserves was driven by a protracted drought, indicating how intense droughts may pre-condition post-fire responses. Similarly, in a study on the Mediterranean shrub *Erica australis*, Cruz, Perez, and Moreno (2003) observed that resprouting was not correlated with carbohydrate reserves, but rather soil nutrients and water availability. Thus, resprouting failure is likely to be driven by a combination of carbohydrate and hydraulic limitations (Figure 6), further modulated by soil nutrients. There is growing evidence that high intensity fires can cause xylem embolism and subsequently trigger tree mortality in resprouting and non-resprouting species (Bär, Nardini, & Mayr, 2018; Ducrey, Duhoux, Huc, & Rigolot, 1996; Kavanagh, Dickinson, & Bova, 2010; Michaletz, Johnson, & Tyree, 2012; West, Nel, Bond, & Midgley, 2016). Furthermore, fire-induced cavitation may show carry-over effects that increase the vulnerability of a plant to drought in the years after the fire (Karavani et al., 2018). However, to date the role of fire intensity in triggering xylem embolism in resprouters has not been explicitly examined.

3.2 | Impacts of shifts in fire regimes on resprouting

Research to date indicates that resprouting species are typically resilient to frequent, low intensity fires (Bennett, Aponte, Tolhurst, Löw, & Baker, 2013; Guinto, House, Xu, & Saffigna, 1999; Watson, French, & Collins, 2020). There is also mounting evidence that resprouting species can also remain resilient in response to repeated crown fires (Collins, 2020; Fairman et al., 2019; Williams, Cook, Gill, & Moore, 1999). Thus, resprouting species are likely to persist under increasing fire intensities. However, there may be demographic shifts (Figure 1b). For example, in forest trees, small trees are most vulnerable to high fire severity, and complete loss of these plants can occur in extreme cases (Bennett et al., 2016). Large trees generally maintain high rates of resprouting, even after repeat high severity fires (Collins, 2020; Fairman et al., 2019; Williams et al., 1999). However, large trees may be vulnerable to increased fire frequency, which increases the prevalence of cambium damage, leading to eventual tree collapse or mortality (Fairman, Bennett, Tupper, & Nitschke, 2017).

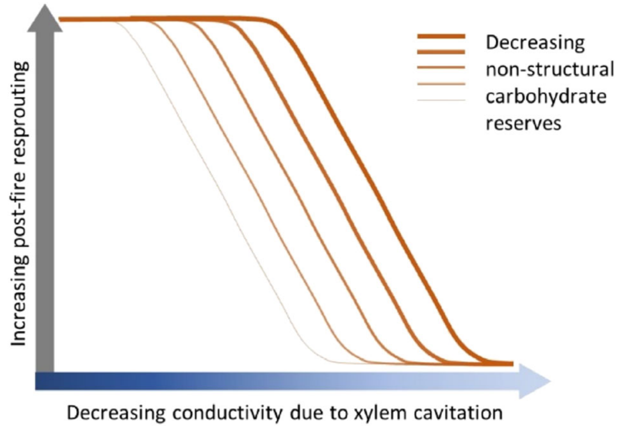

FIGURE 6 Hypothesized probability of resprouting exhaustion, due to carbohydrate and water limitations. As non-structural carbohydrate reserves are depleted, and xylem cavitation increases, resprouting is expected to decline. Several processes, such as shading or protracted water scarcity, could deplete non-structural carbohydrate stores and induce eventual carbon starvation. This conceptual model is derived from studies on resprouting failure, xylem embolism and carbohydrate depletion in chaparral shrubland (Pratt et al., 2014) and *Quercus* spp. (Resco de Dios et al., 2020) [Colour figure can be viewed at wileyonlinelibrary.com]

Shifts in the timing of fires may indirectly affect resprouting success by influencing fire intensity. For example, fires in tropical savannas become more intense as the dry season progresses, owing to the senescence and desiccation of grass fuels (Williams et al., 1999). Consequently, rates of topkill in juvenile size classes are often greater during late-season fires compared to early-season fires (Werner & Franklin, 2010; Williams et al., 1999).

3.3 | Impacts of overlapping disturbances on post-fire resprouting

3.3.1 | Drought

An increase in drought and associated heatwaves with climate change is already resulting in an increase in forest mortality and canopy die-off events globally (Allen, Breshears, & Mcdowell, 2015; Breshears et al., 2021; Ciais et al., 2005). For example, prior to and during the Black Summer fires in eastern Australia in 2019–20, there were widespread observations of canopy die-off (Figure 7; De Kauwe et al., 2020; Nolan et al., 2021). If a drought is severe enough to trigger plant mortality in resprouting species, and there is additional mortality following fire, then there will be higher rates of overall plant mortality when severe drought precedes fire. Similarly, when severe drought follows fire, there is likely to be higher rates of overall plant mortality (Pratt et al., 2014).

3.3.2 | Heatwaves and heat stress

Heatwaves are rapidly increasing in intensity, duration and frequency, including a longer heatwave season (Hoegh-Guldberg et al., 2018). Heat stress, when coupled with drought stress, increases plant mortality before fire (Allen et al., 2010; Teskey et al., 2015) and may also potentially increase the damage sustained to living plants during a fire. Drought stress causes stomata to close, increasing leaf temperatures and therefore leaf level tissue damage and mortality (Teskey et al., 2015), but heat stress itself can also cause leaf damage (French, Jansens, Ashcroft, Ecroyd, & Robinson, 2019). Damaged and dead

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FIGURE 7 Images of eucalypt woodland in south-eastern Australia during severe drought in 2019–20, illustrating understorey and tree canopy die-off. Photo credits: R. Nolan [Colour figure can be viewed at wileyonlinelibrary.com]

leaves may increase fire intensity, thereby increasing the risk of post-fire mortality (Nolan, Blackman, et al., 2020).

Irrespective of drought, plant physiological responses to heat stress require a range of mechanisms to protect against protein denaturation, rebuild damaged proteins and maintain the integrity of cell membranes (Wahid, Gelani, Ashraf, & Foolad, 2007). Upregulation of heat shock proteins and isoprenes, which are commonly synthesized in response to heat stress in many species, including eucalypts, represent the diversion of stored photosynthates and other compounds from growth (including re-sprouting) and reproduction (Bita & Gerats, 2013; Teskey et al., 2015). For example, many crop studies have demonstrated reduced flowering, and subsequently reduced yields, following heat stress (Bita & Gerats, 2013). Increasing frequency of heat stress events potentially compounds the problem. The time between heat stress events required for photosynthetic tissue recovery varies from hours to days (Curtis, Knight, Petrou, & Leigh, 2014; Karim, Fracheboud, & Stamp, 1999), likely complicated by the presence of accompanying stressors and the health of the plant to begin with. However, recovery of non-structural carbohydrate reserves and plant biomass may take much longer. More research on between-stress intervals under combined heat and drought stress is crucial to understanding vegetation resilience and ability to re-sprout after fire.

3.3.3 | Insect outbreaks

Insect outbreaks post-fire can have negative impacts on the recovery of resprouting plants. However, these impacts are likely to be dependent on other factors. For example, resprouting exhaustion due to insect herbivory has been observed in eucalypts in agricultural landscapes (Crombie & Milburn, 1988; Landsberg, 1983). For these trees, it is hypothesized that resprouting foliage following canopy die-back due to drought is more vulnerable to insect infestation, with new foliage repeatedly attacked by insects until eventual tree death (Landsberg, 1983). Evidence from *Abies concolor–Pinus lambertiana* forest in California indicates that post-fire biotic processes, including bark beetles and pathogens, may disproportionately drive mortality in medium to large sized trees in the years following fire (Furniss, Larson, Kane, & Lutz, 2020), indicating variation in vulnerability to post-fire biotic processes with tree size.

4 | POST-FIRE RECRUITMENT

4.1 | Mechanisms underpinning post-fire recruitment

All plant species in fire-prone regions depend on some level of recruitment post-fire, in order to replace individuals that have suffered mortality (Clarke et al., 2015). Here, we discuss the mechanisms that underpin post-fire recruitment, including fire stimulated seed release, seed germination and flowering, which is of relevance for both obligate seeding and facultative resprouting species (i.e., species that exhibit both post-fire resprouting and recruitment).

4.1.1 | Post-fire seed release

Seed release from serotinous cones is usually triggered when heat from fire causes death of the supporting stem and/or degradation of the binding resin (Lamont, He, & Yan, 2019). Serotiny occurs in temperate and mediterranean ecosystems, including Australia, North America, the Mediterranean Basin, and South Africa (Lamont, Pausas, He, Witkowski, & Hanley, 2020). Since seed release is dependent on heat for some species (pyriscent species, sensu Lamont, Lemaitre, Cowling, & Enright, 1991), but can happen upon death of the supporting stem in others, it can therefore also occur in the absence of fire giving rise to questions regarding risk spreading strategies among different species (Lamont et al., 2019). For example, opening of *Allocasuarina* and *Hakea* cones may occur when individuals are subject to drought, whereas many *Banksia* species require fire-related high temperatures for follicles to open (Espelta, Arnan, & Rodrigo, 2011). However, the rate of seed release varies with the

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temperature the cones are exposed to, with lower temperatures producing slower seed release. Furthermore, the length of time seeds are held in the canopy seed bank can influence the rate at which seeds are released from open follicles, with species with long seed retention times producing slower rates of seed release following fire (Clarke, Knox, & Butler, 2010). Very recent work has also questioned the size of the available seed bank that is actually retained by serotinous species in long unburnt sites. Whelan and Ayre (2020) found in a long-term longitudinal study that seed banks of the serotinous shrub *Banksia spinulosa* maintained a relatively small seed bank, even after more than 20 years. Regeneration was dependent on seeds produced in just a few years prior to the fire event, with predation from birds (cockatoos) and insects causing most of the seed bank decline.

4.1.2 | Post-fire germination and seedling establishment

The generation of dormancy-breaking and germination cues, primarily heat shock, smoke and their interaction, is essential for the recruitment of many species, with some maintaining a greater level of dependence on fire cues than others (i.e., obligated to fire cues; Ooi, Denham, Santana, & Auld, 2014; Collette & Ooi, 2017). Temperature thresholds required to break seed dormancy varies across species. For example, in Australian fire-prone ecosystems, temperatures required to break seed dormancy can vary from 40°C to 100°C (Ooi et al., 2014). The mechanisms underlying this variation in temperature thresholds are not well studied. However, there is growing evidence that seed size is negatively correlated with temperature thresholds (Ooi et al., 2014). Higher temperature thresholds in smaller seeded species are hypothesised to be a function of these seeds being buried at shallow soil depths, and therefore being exposed to higher temperatures during fire than larger seeds, buried deeper within soil (Ooi et al., 2014). In addition to heat cues, smoke-cued seed germination has also been observed in a large number of species from across Australia and many fire-prone regions around the world (Keeley & Pausas, 2018).

A number of active compounds have been identified as stimulating germination from either smoke, or charred wood (Keeley & Pausas, 2018), with the most well-known including a butenolide (karrikinolide) and glyceronitrile (Flematti, Ghisalberti, Dixon, & Trengove, 2004). Like serotiny, where some species are obligated to heat for cone opening (pyriscent as opposed to simply stem death) there appears to be a gradient of heat and smoke sensitivity. Some species are obligated to fire cues (at least when seeds are fresh), while others have germination increased by them (Collette & Ooi, 2021; Ooi et al., 2014). Unlike serotiny, it is currently unknown how factors such as drought or plant age may directly affect dormancy breaking and germination cues (e.g. via transgenerational plasticity). However, indirect effects, such as increases in soil temperature from a warming climate may have a large potential to affect species reliant on heat shock to break dormancy.

Successful seedling establishment post-fire will depend on a range of factors, including competition (Stoneman, 1994), the post-fire environment and changes in soil fertility and microbial communities. The post-fire environment is typically nutrient rich and supports rapid seedling growth (Chambers & Attiwill, 1994), unless the topsoil has been eroded (Barry, Janos, Nichols, & Bowman, 2015). Fire impacts on microbial communities are not well studied. Available studies have shown either increases, decreases or little change in both pathogenic fungi and beneficial microbial communities (Chambers & Attiwill, 1994; Lygis, Vasiliauskaite, Stenlid, & Vasaitis, 2010; Motiejūnaitė et al., 2014).

4.1.3 | Fire-stimulated flowering

Fire-stimulated flowering occurs across many fire-prone regions globally, but may only account for a small number of species in some ecosystems, for example, up to 10% of species in heathlands and savannas in Australia and South Africa (Lamont et al., 2019). In Australia, most post-fire flowering species are monocots, in particular orchids (Lamont & Downes, 2011). The exact triggers of fire-stimulated flowering are not well understood (Lamont & Downes, 2011; Pyke, 2017).

Observational studies indicate that heat, smoke and/or defoliation may all trigger post-fire flowering, however, these factors are correlated and it is difficult to disentangle which drivers are important (Pyke, 2017). For example, in the genus *Xanthorrhoea* (Figure 3f), higher rates of post-fire flowering have been observed following spring or summer fires, compared to autumn or winter fires (Gill, 1997; Lamont, Swanborough, & Ward, 2000). These results may indicate that temperature is the cue for post-fire flowering in these species, with season of burn associated with fire intensity (Lamont & Downes, 2011). However, differing responses with season of burn may also be due to seasonal circadian rhythms (Lamont & Downes, 2011). In the same genus, experimental defoliation has been shown to either induce far fewer flowering spikes than following fire (Specht, 1981; Taylor, Monamy, & Fox, 1998), or induce similar rates of flowering to fire (Gill & Ingwersen, 1976; Lamont, Wittkuhn, & Korczynskyj, 2004). Finally, observations of fire-stimulated flowering in *Xanthorrhoea* have also been attributed to smoke, due to observations of post-fire flowering in plants 200 m from fire (Curtis, 1998). In addition to exogenous factors, plant size or age may also influence rates of post-fire flowering. For example, in *Xanthorrhoea preissii*, post-fire flowering frequency was positively correlated with plant height, which in turn is positively correlated with plant age in this genus (Lamont et al., 2000).

4.2 | Impacts of shifts in fire regimes on recruitment

Successful post-fire establishment from soil and canopy seed banks is affected by broader climate-driven fire regime shifts, including season and fire intensity (Figure 2b). Increases in fire intensity can reduce the available seed bank, by killing a higher proportion of seeds during a

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fire. For example, Etchells, O'donnell, Mccaw, and Grierson (2020) found local extinction of a dominant understorey species in sites subject to extreme severity fires. Similarly, Palmer, Denham, and Ooi (2018) found total exhaustion of the soil seed bank for some species after extreme fire meant that the risk of recruitment failure from a subsequent fire was increased.

Other interactions may also lead to state shifts in community composition. For example, variation in fire season can interact with rainfall to determine recruitment success, especially for species with physiologically dormant soil seed banks (Miller et al., 2019; Ooi, 2019), but also for species with canopy seed banks, if drought has triggered pre-fire seed release (Espelta et al., 2011). Another example from soil seed banking species can be found for increasing fire severity and related soil heating. Palmer et al. (2018) concluded that those species with smaller seeds would be selected against under a regime of regular extreme fire events because of the higher chance of lethal temperatures generated in the upper soil profile. This means that surviving seeds would only be found at greater depths, from where it is difficult for small seeds to successfully emerge (Liyanage & Ooi, 2018).

4.3 | Impacts of overlapping disturbances on post-fire recruitment

4.3.1 | Drought

Pre-fire seed production is likely to be affected by increased drought events under climate change, which may consequently reduce post-fire seed germination rates. For example, in the mediterranean *Banksia hookeriana*, seed production is reduced in years following below average rainfall (Henzler, Weise, Enright, Zander, & Tietjen, 2018). Drought may also reduce the availability of seeds in serotinous species, where it triggers seed release prior to fire (Martín-Sanz, Callejas-Díaz, Tonnabel, & Climent, 2017). Drought may also impact on post-fire flowering, although we are not aware of any studies that explicitly examine this.

In addition to impacts on post-fire reproduction, drought can decrease seedling survival (Richards & Lamont, 1996). For example, in mediterranean shrublands in western Australia, declines in rainfall with climate change are predicted to reduce recruitment success for many species, placing these species at increased risk of local extinction if fire frequency increases (Enright et al., 2014). Seedlings are generally considered more vulnerable than mature plants to stress events due to less access to deep soil moisture reserves and smaller non-structural carbohydrate reserves (Niinemets, 2010).

4.3.2 | Heatwaves and heat stress

Seed bank persistence during the inter-fire period, and through the fire event itself, is required to ensure sufficient seeds are available for recruitment post-fire. The long-term persistence of physically dormant species is dependent on maintenance of their dormancy, which is largely determined by dormancy-breaking temperature thresholds.

Soil temperatures will increase during heatwaves and will also increase during drought, as vegetation cover declines and solar radiation at the soil surface increases. These increased soil temperatures can be high enough to break some temperature thresholds for dormant seeds (Ooi et al., 2014; Ooi, Auld, & Denham, 2012). Thus, species with relatively low dormancy-breaking temperature thresholds are at risk of germinating prior to fire, thereby diminishing soil seedbanks. Conversely, for some species, seed production may initially increase under climate change, for example, species where seed production is currently temperature limited (Petrie et al., 2017). However, any potential benefits of increased temperature on seed production are dependent on changes in water availability (Boucher et al., 2020).

Heat stress may further impact on recruitment, by affecting seed production either before or following fire, with heat stress known to affect hormones related to pollination, fruit set and seed development (Ozga, Kaur, Savada, & Reinecke, 2017). To date, research on heat stress and flowering and seed production has largely been restricted to agricultural species, thus potential impacts on species with fire-cued flowering are highly uncertain. If seed production is successful, heat stress can decrease seed viability (Ooi, 2012). Finally, heat stress (as with drought) can also impact on post-fire recruitment by reducing survival rates of vulnerable seedlings.

4.3.3 | Insect outbreaks

There is evidence that seedlings can be highly resilient to herbivory in the absence of other stressors but, during drought, this resilience is likely to be reduced (Collins et al., 2018; Giljohann et al., 2017). The effects of herbivory on seedling survival may also be dependent on soil fertility and species diversity. For example, in experimental fire in Brazilian savanna and Amazonian forest, both density and diversity of seedling recruits were increased when nitrogen was experimentally added (Massad et al., 2013). In the same study, rates of herbivory were higher in plots with low species diversity. Thus, insect outbreaks are most likely to affect recruitment by decreasing seedling survival, particularly if plants are already stressed, with impacts potentially more pronounced if species diversity is low.

5 | WHAT MIGHT THE FUTURE HOLD FOR VEGETATION COMMUNITIES IN THE FACE OF INTENSIFYING FIRE REGIMES AND OVERLAPPING DISTURBANCE EVENTS?

Changes in climate, and subsequent changes in disturbance regimes, may create a misalignment between fire regimes and community traits, which may not become apparent until after one or more fires (Johnstone et al., 2016). Here, we build on our review of post-fire resprouting and recruitment by examining three different case study communities with differing post-fire responses, to provide a viewpoint of how climate change may affect post-fire recovery of vegetation communities.

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5.1 | Case study 1. Resprouting eucalypt forests of southern Australia

Eucalypts are the dominant canopy trees across Australian forests (Gill & Catling, 2002). The vast majority of eucalypt species resprout following fire (Nicolle, 2006), with many also exhibiting post-fire recruitment (Clarke et al., 2015). Eucalypt forests typically support an understory community comprised of a mix of resprouting and obligate seeding shrubs (Clarke et al., 2015).

Eucalypt forests are typically considered highly resilient to shifts in fire regimes (Collins, 2020), although increased fire frequency may trigger changes in eucalypt demography and stand structure, with small trees most vulnerable to fire (Bennett et al., 2016). Indeed, evidence for vegetation transitions in resprouting dominated communities following fire and other disturbances is limited. An exception is Ashton and Chappill (1989), who reported conversion of resprouting eucalypt forest to shrubland following repeated short-interval fires. However, this study was conducted multiple decades after the short-interval fires with little information about the stand condition prior to the fires and antecedent conditions prior to each subsequent fire. The authors speculated that overlapping disturbances contributed to this response.

Perhaps the greatest source of uncertainty for post-fire recovery of resprouting eucalypt forests under climate change is the impacts of overlapping disturbance and stress events on resprouting, and the impacts of increasing fire frequency on obligate seeding shrubs. There is evidence that resprouting eucalypt trees recovering from defoliation are more vulnerable to insect infestation. These trees may enter a ‘die-back spiral’ whereby new nutrient-rich foliage is attacked by insects and the capacity to keep producing new leaves declines (Landsberg, 1983). This phenomenon has been widely observed where the defoliating event was drought, rather than fire (Crombie & Milburn, 1988). However, this phenomenon has largely been restricted to fragmented forests and woodlands present within agricultural landscapes. The combined impacts of severe drought and heatwaves, followed by severe fires, on resprouting eucalypts remains highly uncertain.

The 2019–20 Australian fire season primarily impacted resprouting eucalypt forests (Gallagher et al., 2021). Some of these areas exhibited almost total canopy dieback preceding the fires due to severe drought and heatwaves (Figure 7; Nolan et al., 2021). The combined impact of these fires, drought and heatwaves may take years to become apparent, as it can take years to determine the success of post-fire resprouting and recruitment (Collins, 2020).

5.2 | Case study 2. Australian rainforest communities

Australian rainforests have a restricted distribution, with contraction of once widespread Gondwanan relict rainforest linked to increased fire over millennial time-scales (Bowman, 2000; Cadd, Fletcher, Mariani, Heijnis, & Gadd, 2019). Fire regimes in Australian rainforests are typified by infrequent surface fires (Murphy et al., 2013). Following fire, up to 91% of species, primarily angiosperms, have the capacity to resprout basally (Clarke et al., 2015). In contrast, rainforest communities dominated by gymnosperms exhibit far less capacity for resprouting. For example, in cool temperate Tasmanian rainforest communities dominated by the conifer *Athrotaxis cupressoides*, post-fire mortality rates of up to 68% have been reported (Bowman, Bliss, Bowman, & Prior, 2019). Fire-cued recruitment is relatively uncommon, with only 20% of species exhibiting a fire-resistant seed bank (Clarke et al., 2015). Seed recruitment is therefore likely to be heavily dependent on recruitment from fire refugia. For example, in Tasmanian rainforest, post-fire recruitment of rainforest species was observed in areas subject to low severity, patchy burns, which did not cause mortality of overstorey species (Hill & Read, 1984).

It is clear that many Australian rainforest communities can successfully recover after infrequent, low severity surface fires (Adam, 1992; Knox & Clarke, 2012; Russell-Smith & Stanton, 2002). But what is the fate of rainforest ecosystems in the face of intensifying fire regimes and overlapping disturbances?

With increased fire frequency, severity and/or drought, rainforest communities are likely to be invaded by pyrophytic species (Adam, 1992; Berry, Wevill, & Curran, 2011; Russell-Smith & Stanton, 2002). Pyrophytic species are those whose reproduction is enhanced, or even dependent, on fire (Fletcher, Cadd, Mariani, Hall, & Wood, 2020). High severity fire combined with the establishment of pyrophytic species can cause cascading effects on rainforests. These effects include abrupt declines in canopy cover and aboveground live biomass, promoting higher surface fuel loads and drier microclimates, rendering the rainforests more susceptible to subsequent fires, and transitions to alternate vegetation types (Fletcher et al., 2020).

The 2019–20 Australian fire season burned extensive areas of rainforest, including 70% of warm temperate rainforest in Victoria (DELWP, 2020a) and 54% of New South Wales Gondwana World Heritage Area rainforests (DPIE, 2020). In addition to a large extent of rainforest subject to fire, the proportion of damaging high severity fire was much higher than in previous fire seasons (Collins et al., 2021). Given the array of threats likely to interact with fire to impact on rainforest stands (e.g., fragmentation and edge effects, disturbances such as drought, and invasive species), management interventions are likely needed to ensure their conservation, including weed control and perhaps also supplementary planting or seed dispersal.

5.3 | Case study 3. Obligate seeding eucalypt forests of South-Eastern Australia

There are 84 known species of obligate seeding eucalypts in Australia (accounting for <10% of the eucalypt complex of species), that is, species that lack post-fire resprouting but exhibit fire-stimulated seed germination. These obligate seeding eucalypts including low statured species from low- to medium-rainfall areas (Nicolle, 2006), and species from high-rainfall areas representing some of the tallest (90+ m) trees on Earth (Nicolle, 2006; Sillett, Van Pelt, Kramer, Carroll, &

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Koch, 2015). Two of these tall species (*Eucalyptus regnans* and *Eucalyptus delegatensis*; hereafter, 'ash' eucalypts) have been widely studied due to their importance for biodiversity and timber production (Ashton, 2000; Flint & Fagg, 2007), and are a useful case study for exploring the responses of obligate seeders to changing fire regimes. The most common model for the relationship of ash eucalypts with fire is stand replacement (Ashton, 2000). Severe fires kill mature adult trees, which are afforded little protection by thin bark, and do not possess a strong resprouting capacity (Waters, Burrows, & Harper, 2010). However, with low-severity fire, that is, surface fires, survival can be upwards of 90% (Benyon & Lane, 2013).

Given the approximately 20-year window where regenerating ash forests are incapable of regenerating (Flint & Fagg, 2007; von Takach Dukai, Lindenmayer, & Banks, 2018), these forests face 'immaturity risk' (Keeley, Ne'eman, & Fotheringham, 1999) when abrupt shifts in fire frequency occur that result in return intervals of high severity fire of <20 years. Potential for broad-scale eucalypt re-colonisation of twice-burned ash forests via seed from outside the fire area is unlikely, given the poor seed dispersal capacity (Flint & Fagg, 2007; Griffin, 1980; Thomson et al., 2011). Climate change has recently sharpened the focus on understanding the risk of short-interval fire for ash forests, and a number of frameworks have recently been developed to conceptualise these risks. Two recent developments have been the 'landscape trap' (Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011) and the 'interval squeeze' models (Enright et al., 2015) – the former postulates that 'intrinsic' stand-level factors like fuel load and disturbance influence the risk of decline of ash forests; while the latter emphasises 'extrinsic' factors like fire weather and climate (also supported by Ferguson & Cheney, 2011). Bowman, Williamson, Prior, and Murphy (2016) attempted to reconcile these two theories, concluding that recent patterns of fire in the Victorian alps lend support to the 'interval squeeze' model, though they did note a minor role of stand-level factors such as stand age.

The 2019–20 Australian fire season resulted in major impacts to ash type forests in Victoria, elevated by the recent history of large landscape fires in that state (DELWP, 2020b; Fairman et al., 2016). Approximately 83,000 ha of ash forest were estimated to be impacted during the 2019–20 fire season, 30% of which was immature. Approximately 21,000 ha of this forest were severely burned and, without management intervention, will cease to be dominated by ash eucalypts. Of these burnt ash forests, 12,000 ha have been resown by forest managers, the largest single forest reseeding program conducted by forest managers within the state (DELWP, pers. com.).

6 | CONCLUSIONS – WHERE TO FROM HERE?

There are a large number of mechanisms governing plant responses to fire, many of which will be impacted by climate driven changes in biotic and abiotic disturbances and stress events (Figure 8). It is well supported in the literature that the frequency of mega-fires is expected to increase under climate change in temperate Australian ecosystems (Clarke et al., 2016). This was exemplified in 2019–20, where fires burnt a globally significant 21% of the total temperate forest biome in Australia (Boer et al., 2020). These increases in fire extent will likely cause a decline in the extent of fire refugia (Collins, Bennett, Leonard, & Penman, 2019) as well as push the regimes of fire-prone ecosystems beyond their historical limits. At present, the ability to predict post-fire responses, or confidently inform land managers, is limited by a lack of empirical assessment. Here, we examine some of the key knowledge gaps surrounding interacting stress events related to climate change that may determine how plant communities will respond to fire.

6.1 | Key knowledge gaps

Key knowledge gaps surrounding post-fire recovery in the face of other interacting stress events include: (a) fire frequency-related impacts, including the potential for resprouting exhaustion, and subsequent mortality of resprouting plants; (b) the effects of drought and heatwaves interacting with fire regime shifts on seed quality and availability, and subsequent impacts to post-fire recruitment; (c) the effects of climate change on vegetation growth rates and, therefore, rates of post-fire recovery; and (d) the capacity of species to adapt to changing fire regimes and changing climate.

While high fire frequency is arguably the best understood aspect of the fire regime, impacts of increasing fire frequency on resprouters remain uncertain. The ingredients for resprouting exhaustion, such as an increase in physical damage to plants coupled with increasing severity of drought and heatwaves, have been recorded. However, quantifying how this converts to resprouting exhaustion represents a significant knowledge gap. Furthermore, although the impacts of fire frequency on obligate seeders are better understood, interactions with increased severity of antecedent drought and heatwaves is likely to affect species from across functional groups. For example, heatwaves can decrease seed quality and availability, something that is likely to be important particularly for species with fire-cued seed release and germination, but few studies have investigated this.

Changes to post-fire drought, heatwaves and herbivory, are likely to negatively impact the establishment of seedlings. This highlights the potential importance of shifting fire seasonality, which can influence the timing of seedling emergence and fire-stimulated flowering (Ooi, 2019). Such impacts are likely to differ between climatic regions (Miller et al., 2019). However, many of the mechanisms driving potential impacts have not been well studied, representing another significant knowledge gap.

Vegetation growth rates may be enhanced by increased atmospheric CO_2 and associated changes in climate (Donohue, Mcvicar, & Roderick, 2009), which could potentially decrease post-fire recovery times. However, in Australian ecosystems, the evidence for enhanced vegetation productivity under elevated CO_2 is mixed, due in part to soil nutrient limitations (Ellsworth et al., 2017; Yang et al., 2020). Precipitation patterns are likely to be much more influential on vegetation productivity than elevated CO_2 (Duursma et al., 2016; Green

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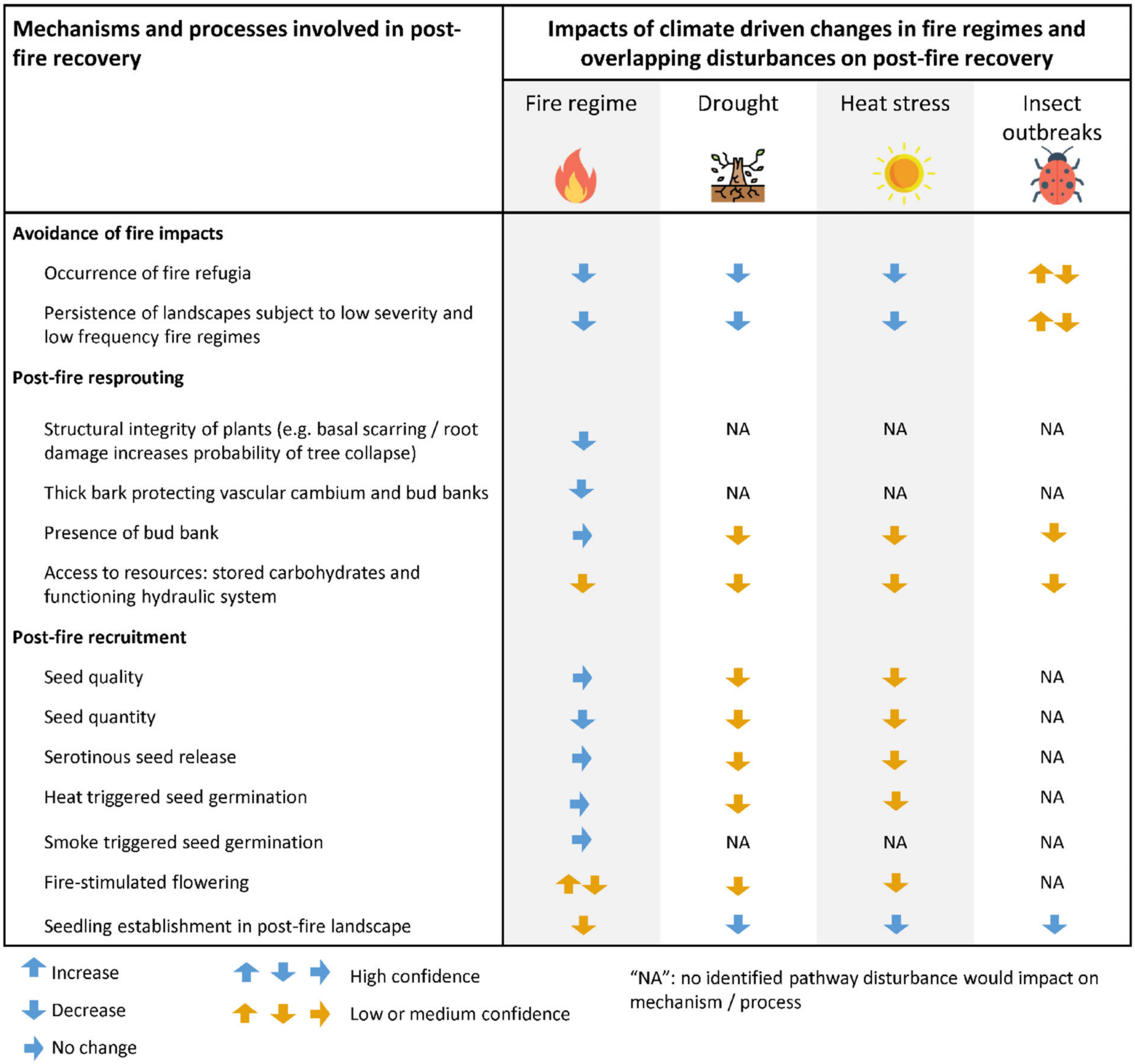

Mechanisms and processes involved in post-fire recovery	Impacts of climate driven changes in fire regimes and overlapping disturbances on post-fire recovery			
	Fire regime	Drought	Heat stress	Insect outbreaks
Avoidance of fire impacts				
Occurrence of fire refugia	⬇	⬇	⬇	⬆⬇
Persistence of landscapes subject to low severity and low frequency fire regimes	⬇	⬇	⬇	⬆⬇
Post-fire resprouting				
Structural integrity of plants (e.g. basal scarring / root damage increases probability of tree collapse)	⬇	NA	NA	NA
Thick bark protecting vascular cambium and bud banks	⬇	NA	NA	NA
Presence of bud bank	➡	⬇	⬇	⬇
Access to resources: stored carbohydrates and functioning hydraulic system	⬇	⬇	⬇	⬇
Post-fire recruitment				
Seed quality	➡	⬇	⬇	NA
Seed quantity	⬇	⬇	⬇	NA
Serotinous seed release	➡	⬇	⬇	NA
Heat triggered seed germination	➡	⬇	⬇	NA
Smoke triggered seed germination	➡	NA	NA	NA
Fire-stimulated flowering	⬆⬇	⬇	⬇	NA
Seedling establishment in post-fire landscape	⬇	⬇	⬇	⬇

⬆ Increase
⬇ Decrease
➡ No change

⬆ ⬇ ➡ High confidence
⬆ ⬇ ➡ Low or medium confidence

"NA": no identified pathway disturbance would impact on mechanism / process

FIGURE 8 Summary of mechanisms involved in post-fire recovery, and potential changes under climate induced changes in intensification of fire regimes (e.g., increased fire frequency, extent, severity and shifts in seasonality). Also shown are the potential influences of increasing incidence of stress and disturbance events on post-fire recovery. Mechanisms indicated with high confidence (blue) are those that are well supported in the literature, whereas mechanisms with low or medium confidence (orange) are not well studied [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2019). The effects of increased temperatures on vegetation growth rates under climate change are also mixed. While increased temperatures can increase productivity in temperature-limited ecosystems (Zhu et al., 2016), the majority of Australia's forests are not temperature limited, and increased temperatures are instead likely to reduce productivity (Bowman, Williamson, Keenan, & Prior, 2014). Clarification of what drives variations in vegetation growth rates under climate change is essential in order to accurately model post-fire recovery under climate change.

The capacity of ecosystems to adapt to climate change is dependent on species dispersal capabilities as well as their capacity to adjust to changing conditions (Booth et al., 2015). Many species exhibit phenotypic plasticity, or genetic variability, which manifests in differing responses to disturbance across a species' range. For example, increasing resistance to xylem cavitation has been observed with increasing aridity, in populations of the same species (Anderegg, 2015). Intra-specific variation in post-fire responses, in particular resprouting capacity, has also been observed in some species. For example, *Eucalyptus obliqua* is a resprouting species, except for in wetter sites where it behaves as a fire-intolerant species, possibly due to hybridization with the thinner barked *Eucalyptus regnans* (Ashton & Chappill, 1989; Moore, 2015). Conversely, *Eucalyptus delegatensis* is predominately an obligate seeding species, but a resprouting sub-species is found in drier areas (Rodriguez-Cubillo, Prior, & Bowman, 2020). Other types of stress may also influence resprouting capacity. For example, *Banksia ericifolia* is an obligate seeding shrub

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species, but resprouting populations have been found in areas subject to water-logging or in sites subject to mechanical slashing (Renshaw, 2005). The capacity of species to adapt to climate change is likely to be greatest in species which have large geographic ranges and high genetic variability (Alberto et al., 2013). However, the capacity for populations to adjust through time in the absence of dispersion is a key knowledge gap in predicting species responses to changing climate and fire regimes.

6.2 | Future research directions

To address the key knowledge gaps described above, we recommend studies that explicitly examine the impact of overlapping disturbance events on resprouting and recruitment processes. Such studies are a key requirement for developing predictive frameworks for assessing species-level and community-level responses to fire under climate change. For example, the emerging concept of 'resist-accept-direct' defines three different management strategies in response to the trajectory of ecosystem change (Schuurman et al., 2020), namely: (a) resist trajectories of change, by working to maintain or restore ecosystems; (b) accept trajectories of change, without intervention; or (c) direct trajectories of change, by actively intervening to shape ecosystems towards desired new conditions. We suggest that the development of robust predictions, supported by empirical assessment, is crucial for informing ecosystem management in the face of climate change.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

All authors contributed to the conceptualization of the manuscript. Rachael H. Nolan led the writing, with contributions from Luke Collins, Thomas A. Fairman and Victor Resco de Dios on the resprouting sections, Mark K.J. Ooi on the recruitment sections, Andy Leigh on the heat stress sections, Timothy J. Curran on the rainforest case-study and Thomas A. Fairman on the obligate seeding forest case-study. All authors contributed to revising and editing the manuscript.

DATA AVAILABILITY STATEMENT

The data in Figure 5 is available from: https://data.mendeley.com/datasets/njgkxdzx73/2 (Nolan et al., 2020). No other data presented.

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