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## Limits to post-fire vegetation recovery under climate change

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	<p>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 demographic constraints from 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.</p>

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**Summary Statement**

Although many vegetation communities will remain resilient to changing fire regimes under climate change in the short-term, longer-term changes to vegetation structure, demography and species composition are likely, with subsequent impacts to ecosystem function. Resilience will depend on species-specific adaptations to fire, with resprouting species likely to be most resilient.

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**39 Abstract**

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

**57 Keywords**

58 Wildfire, climate change, resprouting, obligate seeding, herbivory, heat stress, germination,  
59 mortality

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## 67 **1. Introduction**

68 In 2019-20, a series of mega-fires burnt an estimated 21% of the total temperate forest biome in  
69 Australia (Boer et al., 2020). These fires, termed the 'Black Summer' fires, more than doubled  
70 the estimated area burnt in a single fire season in eastern Australia (Nolan et al., 2020b), and  
71 resulted in an unprecedented extent of high severity fire (Collins et al., 2021) in the modern fire  
72 management record. These fires coincided with record low rainfall and high temperatures  
73 (Bureau of Meteorology, 2019). Similar fire seasons have also occurred in many other regions  
74 globally in recent years, including North America (Williams et al., 2019, Kirchmeier-Young et al.,  
75 2019), South America (Bowman et al., 2019b) and the Mediterranean (Turco et al., 2019).  
76 These types of extreme fire seasons raise important questions about the capacity of ecological  
77 communities to respond to climate-driven changes in fire regimes.

78 Many plant species and ecological communities are well-adapted to local historical fire regimes,  
79 broadly defined as the frequency, severity, seasonality and extent of fire (Whelan, 1995, Gill,  
80 1975, Turner, 2010). Shifts in local fire regimes can test the resistance and resilience of species  
81 and communities to fire (Karavani et al., 2018). At the same time as fire regimes are changing,  
82 climate change is affecting other abiotic and biotic disturbances, such as drought, heatwaves  
83 and insect outbreaks. Since wildfires typically coincide with drought and elevated temperatures,  
84 (Nolan et al., 2020a, Pook, 1986, Dowdy and Mills, 2012), climate change driven increases in  
85 these abiotic disturbances (Kirono et al., 2020, Hoegh-Guldberg et al., 2018) are expected to  
86 coincide with increases in wildfire frequency, severity and extent. Climate change effects on  
87 biotic disturbances, such as insect outbreaks, are more difficult to predict, and are likely to be  
88 both positive and negative (Pureswaran et al., 2018). Here, we explore the overlapping and  
89 often antagonistic influence of these disturbances with changing fire regimes.

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

101 In this review, we summarise the suite of mechanisms involved in plant or population level  
102 responses to fire, and then examine how climate-driven shifts in fire regime, combined with  
103 other abiotic and biotic disturbances, can affect post-fire vegetation recovery. We begin by  
104 outlining the different plant responses to fire. We then separately examine two key post-fire  
105 responses that facilitate vegetation recovery, namely resprouting and fire stimulated  
106 recruitment. To distil the complexity of these interacting mechanisms, we present them as  
107 conceptual models (Fig. 1 and 2). With respect to resprouting, we explain how plant persistence  
108 depends on the impacts of fire on plant structure and resources, such as non-structural  
109 carbohydrate reserves and bud banks (Fig. 1a). We then outline how overlapping disturbances  
110 (additional fires, drought, herbivory, etc.) affect resprouting and may lead to resprouting failure  
111 (Fig. 1b). With respect to post-fire recruitment, we first examine the different recruitment  
112 mechanisms (seed release, flowering and germination) in isolation (Fig. 2a), and then examine  
113 the likely impacts of different disturbances in combination with changes in fire regimes (Fig 2b).  
114 While we illustrate our review with literature primarily from Australian temperate and

115 Mediterranean ecosystems, in particular forests, the mechanisms governing plant and  
116 community responses to fire that we discuss here are applicable to many ecosystems globally.

117

## 118 **2. Overview of plant responses to fire**

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

126 Resprouting is a key plant functional trait that enables plants to persist following disturbances  
127 (Bond and Midgley, 2001). Post-fire resprouting occurs when meristematic tissues, specifically  
128 buds, are protected from fire (Clarke et al., 2013). Resprouting can occur: (1) belowground, from  
129 roots and rhizomes; (2) basally, from buds located at or belowground, e.g. from lignotubers; (3)  
130 epicormically, from stems and branches; and (4) apically, from the apical meristem (Clarke et  
131 al., 2013; Fig. 3). Belowground and basal resprouting is more widespread than aerial  
132 resprouting (i.e. epicormic, apical); with the latter predominantly occurring in arborescent life  
133 forms (Clarke et al., 2013, Pausas and Keeley, 2017). Resprouting is considered an expensive  
134 strategy in terms of allocation to belowground roots and/or storage organs and protection of bud  
135 banks. Consequently, resprouting species may predominate at productive sites (Pausas et al.,  
136 2016, Pausas and Bradstock, 2007, Knox and Clarke, 2005), although converse relationships  
137 between resprouting and productivity have also been observed (Hamill et al., 2016).

138 Seed germination following fire is a common post-fire recruitment strategy. For species with fire-  
139 cued seed germination, seeds can either be stored in the soil or on the plant in woody structures  
140 (Fig. 3). Serotiny, the extended storage of plant-stored seeds which are released after fire, is  
141 observed to occur in lower productivity sites compared to soil-storage of seeds, as a strategy to  
142 limit predation on seeds (Keeley et al., 2011). Species that only recover from fire via fire-cued  
143 seed release and/or germination are termed “post-fire obligate seeders” (Prior and Bowman,  
144 2020), whereas species that recover from fire via both seeding and resprouting are termed  
145 ‘facultative resprouters’ (Clarke et al., 2015). Another recruitment strategy is fire-cued flowering  
146 (Lamont and Downes, 2011; Fig. 3).

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

153 Invariably, vegetation communities are often identified by the post-fire response of the dominant  
154 or most easily-identified vegetation – such as an overstorey comprised of resprouting trees –  
155 however, many vegetation communities support species with a mix of post-fire responses. For  
156 example, across eucalypt forests, approximately 50% of species are facultative resprouters,  
157 21% are obligate resprouters and 27% are obligate seeders (Clarke et al., 2015). For simplicity,  
158 in the following sections we will consider each of the post-fire responses individually,  
159 recognising that each of these responses may co-occur within a single vegetation community.

160

### 161 **3 Post-fire resprouting**

### 162 **3.1 Mechanisms impacting post-fire recovery of resprouting plants**

163 We consider resprouting as a continuum ranging from belowground resprouting to aerial  
164 resprouting from the upper branches of trees, with plant resistance / persistence following fire  
165 increasing along this continuum (Fig. 1a). Mechanisms contributing to post-fire mortality include  
166 changes to both plant structure and access to resources. Plant structural changes include  
167 physical damage to stems and roots and consumption of bark during fire. Changes to resources  
168 include hydraulic limitations due to xylem cavitation, depletion of non-structural carbohydrates  
169 and depletion of bud-banks.

#### 170 **3.1.1 Impacts on structures: basal scarring and physical damage to roots**

171 Trees that survive fire may suffer cambium necrosis of part of the stem base, which is referred  
172 to as 'basal scarring' (Fig 4). Cambium necrosis exposes heartwood to decay and fire. Over  
173 time, the excavation of heartwood will compromise the structural integrity of stems, increasing  
174 the likelihood of collapse during subsequent disturbances (Fig. 1, Fig. 4, Whitford and Williams,  
175 2001, Gibbons et al., 2008). The presence of basal scarring can substantially increase the  
176 probability of topkill, i.e. death of above-ground biomass (e.g. +20%; Collins, 2020, Collins et al.,  
177 2012), and the likelihood of mortality by causing tree collapse (Collins, 2020, Bowman and  
178 Kirkpatrick, 1986). The nature and size of basal scarring required to cause tree hollow formation  
179 has not been well studied, nor has the role of bark type in susceptibility to basal scarring. Basal  
180 scarring is, however, more likely to be prevalent in larger trees, which are typically older and  
181 have therefore had increased exposure to fire (Parnaby et al., 2010, Collins et al., 2012, Collins,  
182 2020).

183 Any physical damage to roots may decrease structural stability of the plant or affect access to  
184 water and nutrients. There are very few studies of fire impacts on roots, although studies from  
185 boreal Scots pine forests and semi-arid sagebrush shrubland in western USA indicate that fire

186 can reduce fine root biomass, particularly under prolonged smouldering combustion driven by  
187 large biomass accumulation (Rau et al., 2009, Smirnova et al., 2008, Hood et al., 2018).  
188 However, most surface and canopy wildfires often exert a limited impact on roots as the soil is  
189 an excellent thermal insulator (Resco de Dios, 2020).

### 190 **3.1.2 Impacts on structures: damage to bud banks**

191 A requirement for stem and branch survival is that the buds and cambium are sufficiently  
192 protected from high temperatures during fire (Clarke et al., 2013; Fig. 1). Bark thickness is a key  
193 trait determining stem survival during fire, with thicker bark providing greater insulation  
194 (Wesolowski et al., 2014), reducing the likelihood of stem and branch mortality (Lawes et al.,  
195 2011). Fire regimes were thought to account for much of the variation in bark thickness globally  
196 (Pausas, 2015), but recent studies highlight that supporting metabolism and additional  
197 processes may play an important role (Rosell, 2019, Resco de Dios, 2020).

198 Bark thickness develops with stem size and age, hence the likelihood of topkill decreases with  
199 stem size for many eucalypt species (Fairman et al., 2019, Collins, 2020). The position of buds  
200 relative to the bark surface determines the degree of insulation, with higher resprouting success  
201 being observed for species with buds deeply embedded beneath the bark surface, such as  
202 eucalypts (Charles-Dominique et al., 2015). Canopy height can also protect buds and tissues in  
203 the upper stems and branches, though adequate insulation is still required to facilitate stem  
204 survival (Clarke et al., 2013).

205 During fire, some of the protective bark on plants is consumed (Volkova and Weston, 2013,  
206 Nolan et al., 2020c). This reduction in bark thickness reduces the insulation capacity of bark,  
207 thereby increasing vulnerability of stems to cambium necrosis from subsequent fire (Fig. 1, Fig.  
208 5; Wesolowski et al., 2014, Gill and Ashton, 1968, Catry et al., 2012). However, it is unclear  
209 whether the partial loss of bark is sufficient to increase mortality rates of large eucalypts, owing

210 to their deeply embedded buds (Charles-Dominique et al., 2015). Further, the length of time  
211 required for recovery of that bark is largely unknown, due to limited data on bark growth rates.  
212 Bark consumption is dependent on fire intensity and season of burn, which may be a function of  
213 seasonal variation in bark moisture content affecting bark combustion (Chatto et al., 2003).

214 Another hypothesised cause of resprouting failure following short interval fires is bud-bank  
215 limitation (Fig. 1), which represents a reduction in the number of buds available to resprout  
216 (Enright et al., 2011). In a study on resprouting shrubs in south-west Australia, Bell and Pate  
217 (1996) observed bud bank exhaustion after experimental clipping. However, the frequency of  
218 the clipping in that experiment (six months or less) is unlikely to replicate naturally-occurring fire  
219 frequencies. Resprouting failure has also been attributed to a lack of buds following long fire  
220 intervals (Enright et al., 2011). However, these declines in resprouting may be a function of  
221 plant age, rather than fire interval, with declines in bud-banks observed with plant age or size  
222 (Holland, 1969, Hodgkinson, 1998). Thus, while there is some evidence of bud-bank exhaustion  
223 affecting resprouting, further studies are required that replicate the impact of realistic increases  
224 in fire frequency.

### 225 **3.1.3 Impacts on resources: stored carbohydrates and hydraulic limitations**

226 As fire frequency increases and fires increasingly coincide with other disturbances, such as  
227 severe drought, it has been hypothesised that resprouting species may reach the limits of their  
228 capacity to resprout (Karavani et al., 2018; Fig. 3, Fairman et al., 2016, Resco de Dios, 2020).  
229 This phenomenon has been termed 'resprouting exhaustion syndrome' (Karavani et al., 2018).  
230 Resprouting exhaustion has largely been attributed to depleted carbohydrate reserves. There is  
231 some indirect evidence for carbohydrate limitation driving resprouting exhaustion from  
232 observations of declines in root and stem starch reserves following a resprouting event (Bowen  
233 and Pate, 1993, Smith et al., 2018). While temporary declines in starch are to be expected, a

234 complete consumption of starch reserves has only seldom been documented. That is, while  
235 limited carbohydrate concentrations may impact resprouting capacity, direct evidence for this  
236 phenomenon is still scarce.

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

### 253 **3.2 Impacts of shifts in fire regimes on resprouting**

254 Research to date indicates that resprouting species are typically resilient to frequent, low  
255 intensity fires (Bennett et al., 2013, Watson et al., 2020, Guinto et al., 1999). There is also  
256 mounting evidence that resprouting species can also remain resilient in response to repeated  
257 crown fires (Fairman et al., 2019, Williams et al., 1999, Collins, 2020). Thus, resprouting species



258 are likely to persist under increasing fire intensities. However, there may be demographic shifts  
259 (Fig. 1b). For example, in forest trees, small trees are most vulnerable to high fire severity, and  
260 complete loss of these plants can occur in extreme cases (Bennett et al., 2016). Large trees  
261 generally maintain high rates of resprouting, even after repeat high severity fires (Collins, 2020,  
262 Fairman et al., 2019, Williams et al., 1999). However, large trees may be vulnerable to  
263 increased fire frequency, which increases the prevalence of cambium damage, leading to  
264 eventual tree collapse or mortality (Fairman et al., 2017).

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

### 270 **3.3 Impacts of overlapping disturbances on post-fire resprouting**

#### 271 **3.3.1 Drought**

272 An increase in drought and associated heatwaves with climate change is already resulting in an  
273 increase in forest mortality and canopy die-off events globally (Allen et al., 2015, Ciais et al.,  
274 2005, Breshears et al., 2021). For example, prior to and during the Black Summer fires in  
275 eastern Australia in 2019-20, there were widespread observations of canopy die-off (Fig. 7; De  
276 Kauwe et al., 2020, Nolan et al., 2021). If a drought is severe enough to trigger plant mortality in  
277 resprouting species, and there is additional mortality following fire, then there will be higher  
278 rates of overall plant mortality when severe drought precedes fire. Similarly, when severe  
279 drought follows fire, there is likely to be higher rates of overall plant mortality (Pratt et al., 2014).

#### 280 **3.3.2 Heatwaves and heat stress**

281 Heatwaves are rapidly increasing in intensity, duration and frequency, including a longer  
282 heatwave season (Hoegh-Guldberg et al., 2018). Heat stress, when coupled with drought  
283 stress, increases plant mortality before fire (Allen et al., 2010, Teskey et al., 2015) and may also  
284 potentially increase the damage sustained to living plants during a fire. Drought stress causes  
285 stomata to close, increasing leaf temperatures and therefore leaf level tissue damage and  
286 mortality (Teskey et al., 2015), but heat stress itself can cause leaf damage (French et al.,  
287 2019). Damaged and dead leaves may increase fire intensity, thereby increasing the risk of  
288 post-fire mortality.

289 Irrespective of drought, plant physiological responses to heat stress require a range of  
290 mechanisms to protect against protein denaturation, rebuild damaged proteins and maintain the  
291 integrity of cell membranes (Wahid et al., 2007). Upregulation of heat shock proteins and  
292 isoprenes, which are commonly synthesised in response to heat stress in many species,  
293 including eucalypts, represent the diversion of stored photosynthates and other compounds  
294 from growth (including re-sprouting) and reproduction (Teskey et al., 2015, Bitá and Gerats,  
295 2013). For example, many crop studies have demonstrated reduced flowering, and  
296 subsequently reduced yields, following heat stress (Bitá and Gerats, 2013). Increasing  
297 frequency of heat stress events potentially compounds the problem. The time between heat  
298 stress events required for photosynthetic tissue recovery varies from hours to days (Curtis et al.,  
299 2014, Karim et al., 1999), likely complicated by the presence of accompanying stressors and the  
300 health of the plant to begin with. However, recovery of non-structural carbohydrate reserves and  
301 plant biomass may take much longer. More research on between-stress intervals under  
302 combined heat and drought stress is crucial to understanding vegetation resilience and ability to  
303 re-sprout, and recruit, after fire.

### 304 **3.3.3 Insect outbreaks**

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

#### 315 **4 Post-fire recruitment**

##### 316 **4.1 Mechanisms underpinning post-fire recruitment**

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

##### 322 **4.1.1 Post-fire seed release**

323 Seed release from serotinous cones is usually triggered when heat from fire causes death of the  
324 supporting stem and/or degradation of the binding resin (Lamont et al., 2019). Serotiny occurs in  
325 temperate and Mediterranean ecosystems, including Australia, North America, the  
326 Mediterranean Basin, and South Africa (Lamont et al., 2020). Since seed release is dependent  
327 on heat for some species (pyriscent species, sensu Lamont et al., 1991), but can happen upon

328 death of the supporting stem in others, it can therefore also occur in the absence of fire giving  
329 rise to questions regarding risk spreading strategies among different species (Lamont et al.,  
330 2019). For example, opening of *Allocasuarina* and *Hakea* cones may occur when individuals are  
331 subject to drought, whereas many *Banksia* species require fire-related high temperatures for  
332 follicles to open (Espelta et al., 2011). However, the rate of seed release varies with the  
333 temperature the cones are exposed to, with lower temperatures producing slower seed release.  
334 Furthermore, the length of time seeds are held in the canopy seed bank, can influence the rate  
335 at which seeds are released from open follicles, with species with long seed retention times  
336 producing slower rates of seed release following fire (Clarke et al., 2010). Very recent work has  
337 also questioned the size of the available seed bank that is actually retained by serotinous  
338 species in long unburnt sites. Whelan and Ayre (2020) found in a long-term longitudinal study  
339 that seed banks of the serotinous shrub *Banksia spinulosa* maintained a relatively small seed  
340 bank, even after more than 20 years. Regeneration was dependent on seeds produced in just a  
341 few years prior to the fire event, with predation from birds (cockatoos) and insects causing most  
342 of the seed bank decline.

#### 343 **4.1.2 Post-fire germination and seedling establishment**

344 The generation of dormancy-breaking and germination cues, primarily heat shock, smoke and  
345 their interaction, is essential for the recruitment of many species, with some maintaining a  
346 greater level of dependence on fire cues than others (i.e. obligated to fire cues) (Ooi et al.,  
347 2014, Collette and Ooi, 2017). Temperature thresholds required to break seed dormancy varies  
348 across species. For example, in Australian fire-prone ecosystems, temperatures required to  
349 break seed dormancy can vary from 40–100 °C (Ooi et al., 2014). The mechanisms underlying  
350 this variation in temperature thresholds are not well studied. However, there is growing evidence  
351 that seed size is negatively correlated with temperature thresholds (Ooi et al., 2014). Higher  
352 temperature thresholds in smaller seeded species are hypothesised to be a function of these

353 seeds being buried at shallow soil depths, and therefore being exposed to higher temperatures  
354 during fire than larger seeds, buried deeper within soil (Ooi et al., 2014). In addition to heat  
355 cues, smoke-cued seed germination has also been observed in a large number of species from  
356 across Australia and many fire-prone regions around the world (Keeley and Pausas, 2018).

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

368 Successful seedling establishment post-fire will depend on a range of factors, including  
369 competition (Stoneman, 1994), the post-fire environment and changes in soil fertility and  
370 microbial communities. The post-fire environment is typically nutrient rich and supports rapid  
371 seedling growth (Chambers and Attiwill, 1994), unless the topsoil has been eroded (Barry et al.,  
372 2015). Fire impacts on microbial communities are not well studied. Available studies have  
373 shown either increases, decreases or little change in both pathogenic fungi and beneficial  
374 microbial communities (Chambers and Attiwill, 1994, Motiejūnaitė et al., 2014, Lygis et al.,  
375 2010).

#### 376 **4.1.3 Fire-stimulated flowering**

377 Fire-stimulated flowering occurs across many fire-prone regions globally, but may only account  
378 for a small number of species in some ecosystems, e.g. up to 10% of species in heathlands and  
379 savannas in Australia and South Africa (Lamont et al., 2019). In Australia, most post-fire  
380 flowering species are monocots, in particular orchids (Lamont and Downes, 2011). The exact  
381 triggers of fire-stimulated flowering are not well understood (Pyke, 2017, Lamont and Downes,  
382 2011).

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

#### 399 **4.2 Impacts of shifts in fire regimes on recruitment**

400 Successful post-fire establishment from soil and canopy seed banks is affected by broader  
401 climate-driven fire regime shifts, including season and fire intensity (Fig. 2b). Increases in fire  
402 intensity can reduce the available seed bank, by killing a higher proportion of seeds during a  
403 fire. For example, Etchells et al. (2020) found local extinction of a dominant understorey species  
404 in sites subject to extreme severity fires. Similarly, Palmer et al. (2018) found total exhaustion of  
405 the soil seed bank for some species after extreme fire meant that the risk of recruitment failure  
406 from a subsequent fire was increased.

407 Other interactions may also lead to state shifts in community composition. For example,  
408 variation in fire season can interact with rainfall to determine recruitment success, especially for  
409 species with physiologically dormant soil seed banks (Miller et al., 2019, Ooi, 2019), but also for  
410 species with canopy seed banks, if drought has triggered pre-fire seed release (Espelta et al.,  
411 2011). Another example from soil seed banking species can be found for increasing fire severity  
412 and related soil heating. Palmer et al. (2018) concluded that those species with smaller seeds  
413 would be selected against under a regime of regular extreme fire events because of the higher  
414 chance of lethal temperatures generated in the upper soil profile. This means that surviving  
415 seeds would only be found at greater depths, from where it is difficult for small seeds to  
416 successfully emerge (Liyanage and Ooi, 2018).

### 417 **4.3 Impacts of overlapping disturbances on post-fire recruitment**

#### 418 **4.3.1 Drought**

419 Pre-fire seed production is likely to be affected by increased drought events under climate  
420 change, which may consequently reduce post-fire seed germination rates. For example, in the  
421 Mediterranean obligate seeding shrub in Western Australia, *Banksia hookeriana*, seed  
422 production is reduced in years following below average rainfall (Henzler et al., 2018). Drought  
423 may also reduce the availability of seeds in serotinous species, where it triggers seed release

424 prior to fire (Martín-Sanz et al., 2017). Drought may also impact on post-fire flowering, although  
425 we are not aware of any studies that explicitly examine this.

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

#### 433 **4.3.2 Heatwaves and heat stress**

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

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



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

#### 454 **4.3.3 Insect outbreaks**

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

464

### 465 **5. What might the future hold for vegetation communities in the face of intensifying fire** 466 **regimes and overlapping disturbance events?**

467 Changes in climate, and subsequent changes in disturbance regimes, may create a  
468 misalignment between fire regimes and community traits, which may not become apparent until  
469 after one or more fires (Johnstone et al., 2016). Here, we build on our review of post-fire

470 resprouting and recruitment by examining three different case study communities with differing  
471 post-fire responses, to provide a viewpoint of how climate change may affect post-fire recovery  
472 of vegetation communities.

### 473 **5.1 Case study 1. Resprouting eucalypt forests of southern Australia**

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

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

488 Perhaps the greatest source of uncertainty for post-fire recovery of resprouting eucalypt forests  
489 under climate change is the impacts of overlapping disturbance and stress events on  
490 resprouting, and the impacts of increasing fire frequency on obligate seeding shrubs. There is  
491 evidence that resprouting eucalypt trees recovering from defoliation are more vulnerable to  
492 insect infestation. These trees may enter a “die-back spiral” whereby new nutrient-rich foliage is  
493 attacked by insects and the capacity to keep producing new leaves declines (Landsberg, 1983).

494 This phenomenon has been widely observed where the defoliating event was drought, rather  
495 than fire (Crombie and Milburn, 1988). However, this phenomenon has largely been restricted to  
496 fragmented forests and woodlands present within agricultural landscapes. The combined  
497 impacts of severe drought and heatwaves, followed by severe fires, on resprouting eucalypts  
498 remains highly uncertain.

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

## 504 **5.2 Case study 2. Australian rainforest communities**

505 Australian rainforests have a restricted distribution, with contraction of once widespread  
506 Gondwanan relict rainforest linked to increased fire over millennial time-scales (Cadd et al.,  
507 2019, Bowman, 2000). Fire regimes in Australian rainforests are typified by infrequent surface  
508 fires (Murphy et al., 2013). Following fire, up to 91% of species, primarily angiosperms, have the  
509 capacity to resprout basally (Clarke et al., 2015). In contrast, rainforest communities dominated  
510 by gymnosperms exhibit far less capacity for resprouting. For example, in cool temperate  
511 Tasmanian rainforest communities dominated by the conifer *Athrotaxis cupressoides*, post-fire  
512 mortality rates of up to 68% have been reported (Bowman et al., 2019a). Fire-cued recruitment  
513 is relatively uncommon, with only 20% of species exhibiting a fire-resistant seed bank (Clarke et  
514 al., 2015). Seed recruitment is therefore likely to be heavily dependent on recruitment from fire  
515 refugia. For example, in Tasmanian rainforest, post-fire recruitment of rainforest species was  
516 observed in areas subject to low severity, patchy burns, which did not cause mortality of  
517 overstorey species (Hill and Read, 1984).

518 It is clear that many Australian rainforest communities can successfully recover after infrequent,  
519 low severity surface fires (Adam, 1992, Russell-Smith and Stanton, 2002, Knox and Clarke,  
520 2012). But what is the fate of rainforest ecosystems in the face of intensifying fire regimes and  
521 overlapping disturbances?

522 With increased fire frequency, severity, and/or drought, rainforest communities are likely to be  
523 invaded by pyrophytic species (Russell-Smith and Stanton, 2002, Adam, 1992, Berry et al.,  
524 2011). Pyrophytic species are those whose reproduction is enhanced, or even dependent, on  
525 fire (Fletcher et al., 2020). High severity fire combined with the establishment of pyrophytic  
526 species can cause cascading effects on rainforests. These effects include abrupt declines in  
527 canopy cover and aboveground live biomass, promoting higher surface fuel loads and drier  
528 microclimates, rendering the rainforests more susceptible to subsequent fires, and transitions to  
529 alternate vegetation types (Fletcher et al., 2020).

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

538

### 539 **5.3 Case study 3. Obligate seeding eucalypt forests of south-eastern Australia**

540 There are 84 known species of obligate seeding eucalypts in Australia (accounting for <10% of

541 the eucalypt complex of species), i.e. species that lack post-fire resprouting but exhibit fire-  
542 stimulated seed germination. These obligate seeding eucalypts including low statured species  
543 from low-medium rainfall areas (Nicolle, 2006), and species from high rainfall areas  
544 representing some of the tallest (90+ m) trees on Earth (Nicolle, 2006, Sillett et al., 2015). Two  
545 of these tall species (*Eucalyptus regnans* and *E. delegatensis*; hereafter, 'ash' eucalypts) have  
546 been widely studied due to their importance for biodiversity and timber production (Ashton,  
547 2000, Flint and Fagg, 2007), and are a useful case study for exploring the responses of obligate  
548 seeders to changing fire regimes. The most common model for the relationship of ash eucalypts  
549 with fire is stand replacement (Ashton, 2000). Severe fires kill mature adult trees, which are  
550 afforded little protection by thin bark, and do not possess a strong resprouting capacity (Waters  
551 et al., 2010). However, with low severity fire, i.e. surface fires, survival can be upwards of 90%  
552 (Benyon and Lane, 2013).

553 Given the approximately 20-year window where regenerating ash forests are incapable of  
554 regenerating (Flint and Fagg, 2007, von Takach Dukai et al., 2018), these forests face  
555 'immaturity risk' (Keeley et al., 1999) when abrupt shifts in fire frequency occur that result in  
556 return intervals of high severity fire of < 20 years. Potential for broad-scale eucalypt re-  
557 colonisation of twice-burned ash forests via seed from outside the fire area is unlikely, given the  
558 poor seed dispersal capacity (Thomson et al., 2011, Griffin, 1980, Flint and Fagg, 2007).

559 Climate change has recently sharpened the focus on understanding the risk of short-interval fire  
560 for ash forests, and a number of frameworks have recently been developed to conceptualise  
561 these risks. Two recent developments have been the 'landscape trap' (Lindenmayer et al.,  
562 2011) and the 'interval squeeze' models (Enright et al., 2015) – the former postulates that  
563 'intrinsic' stand-level factors like fuel load and disturbance influence the risk of decline of ash  
564 forests; while the latter emphasises 'extrinsic' factors like fire weather and climate (also  
565 supported by Ferguson and Cheney, 2011). Bowman et al. (2016) attempted to reconcile these

566 two theories, concluding that recent patterns of fire in the Victorian alps lend support to the  
567 'interval squeeze' model, though they did note a minor role of stand-level factors such as stand  
568 age.

569 The 2019-20 Australian fire season resulted in major impacts to ash type forests in Victoria,  
570 elevated by the recent history of large landscape fires in that state (Fairman et al., 2016,  
571 DELWP, 2020b). Approximately 83,000 ha of ash forest were estimated to be impacted during  
572 the 2019-20 fire season, 30% of which was immature. Approximately 18,000 ha of this forest  
573 were severely burned and, without management intervention, will cease to be dominated by ash  
574 eucalypts. Of these burnt ash forests, 12,000 ha have been resown by forest managers, the  
575 largest single forest reseeded program conducted by forest managers within the state (DELWP,  
576 2020 pers. com.).

## 577 **6. Conclusions – where to from here?**

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

### 589 **6.1 Key knowledge gaps**

590 Key knowledge gaps surrounding post-fire recovery in the face of other interacting stress events  
591 include (i) fire frequency-related impacts, including the potential for resprouting exhaustion, and  
592 subsequent mortality of resprouting plants; (ii) the effects of drought and heatwaves interacting  
593 with fire regime shifts on seed quality and availability, and subsequent impacts to post-fire  
594 recruitment; (iii) the effects of climate change on vegetation growth rates and, therefore, rates of  
595 post-fire recovery; and (iv) the capacity of species to adapt to changing fire regimes and  
596 changing climate.

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

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

613 Vegetation growth rates may be enhanced by increased atmospheric CO<sub>2</sub> and associated  
614 changes in climate (Donohue et al., 2009), which could potentially decrease post-fire recovery  
615 times. However, in Australian ecosystems, the evidence for enhanced vegetation productivity  
616 under elevated CO<sub>2</sub> is mixed, due in part to soil nutrient limitations (Ellsworth et al., 2017, Yang  
617 et al., 2020). Precipitation patterns are likely to be much more influential on vegetation  
618 productivity than elevated CO<sub>2</sub> (Duursma et al., 2016, Green et al., 2019). The effects of  
619 increased temperatures on vegetation growth rates under climate change are also mixed. While  
620 increased temperatures can increase productivity in temperature-limited ecosystems (Zhu et al.,  
621 2016), the majority of Australia's forests are not temperature limited, and increased  
622 temperatures are instead likely to reduce productivity (Bowman et al., 2014). Clarification of  
623 what drives these variations in response is essential in order to accurately model post-fire  
624 recovery under climate change.

625 The capacity of ecosystems to adapt to climate change is dependent on species dispersal  
626 capabilities as well as their capacity to adjust to changing conditions (Booth et al., 2015). Many  
627 species exhibit phenotypic plasticity, or genetic variability, which manifests in differing  
628 responses to disturbance across a species' range. For example, increasing resistance to xylem  
629 cavitation has been observed with increasing aridity, in populations of the same species  
630 (Anderegg, 2015). Intra-specific variation in post-fire responses, in particular resprouting  
631 capacity, has also been observed in some species. For example, *Eucalyptus obliqua* is a  
632 resprouting species, except for in wetter sites where it behaves as a fire-intolerant species,  
633 possibly due to hybridisation with the thinner barked *Eucalyptus regnans* (Ashton and Chappill,  
634 1989, Moore, 2015). Conversely, *Eucalyptus delegatensis* is predominately an obligate seeding  
635 species, but a resprouting sub-species is found in drier areas (Rodriguez-Cubillo et al., 2020).  
636 Other types of stress may also influence resprouting capacity. For example, *Banksia ericifolia* is  
637 an obligate seeding shrub species, but resprouting populations have been found in areas



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

643

## 644 **6.2 Future research directions**

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

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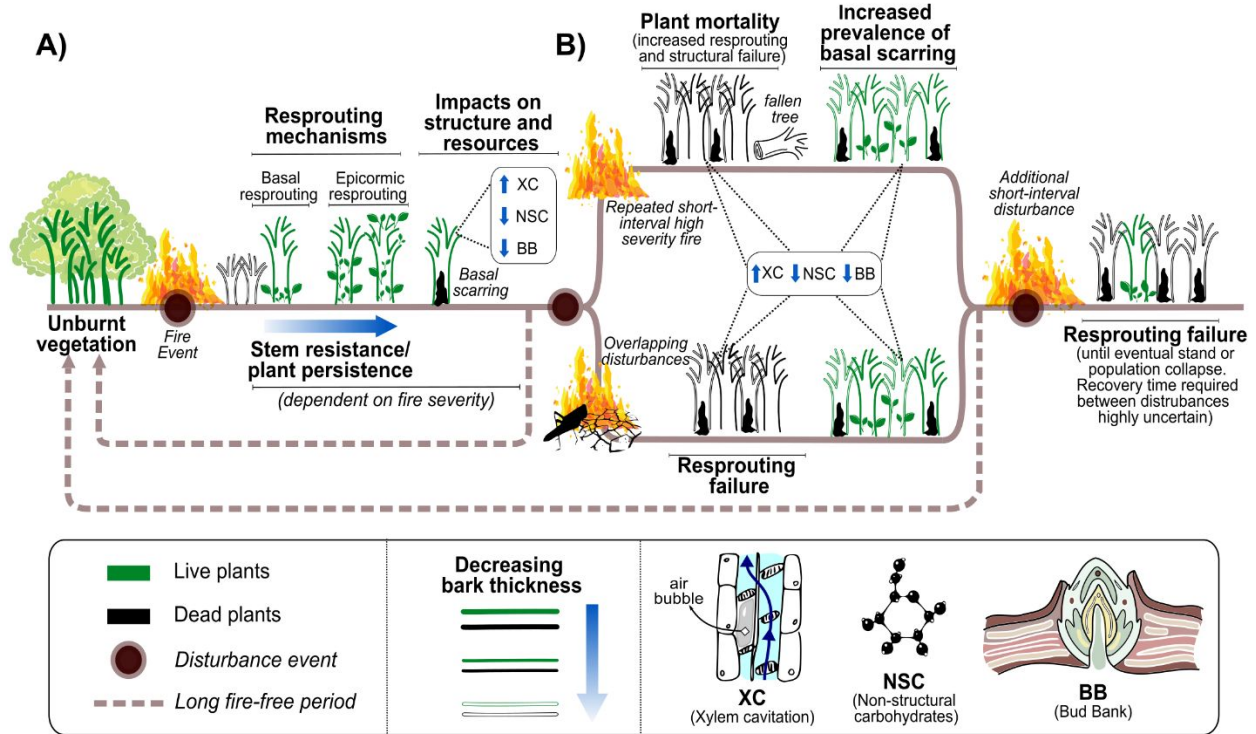


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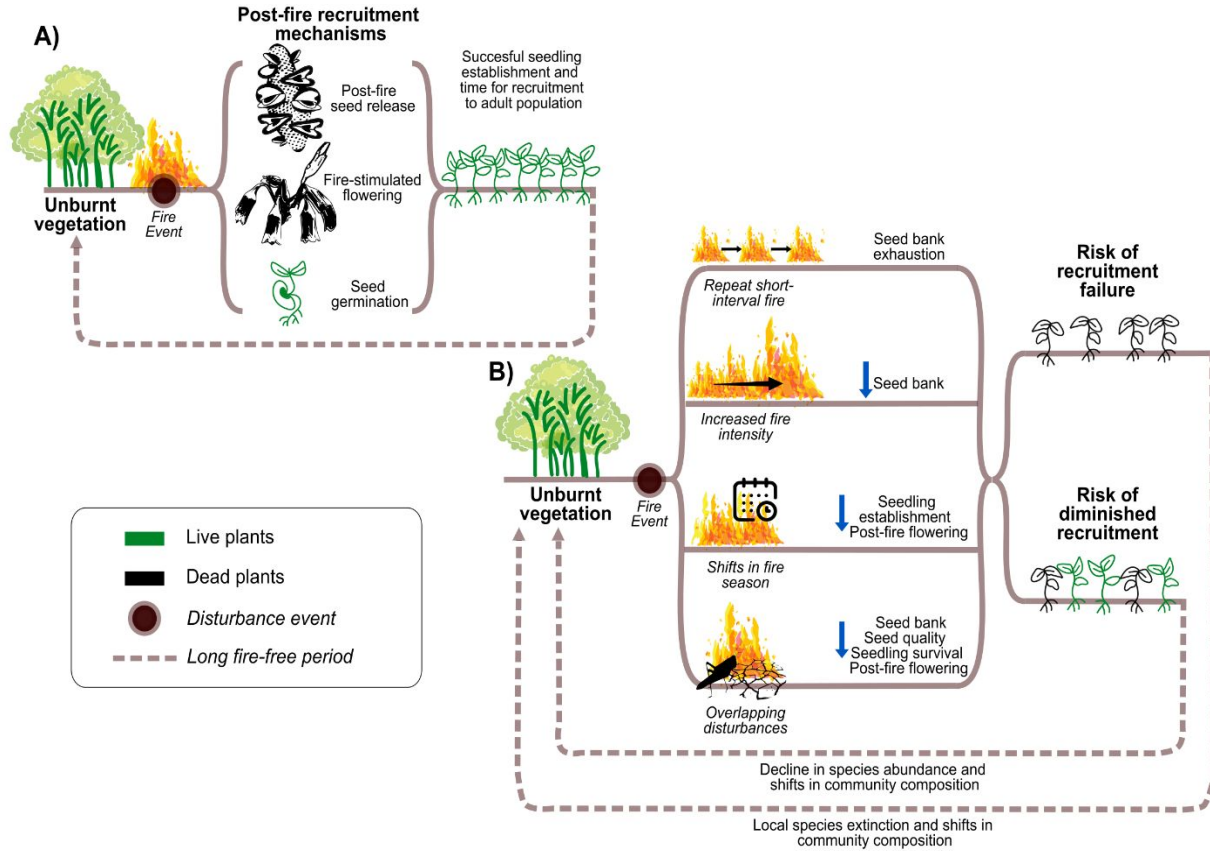
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1195 **Figures**

1196

1197 **Fig. 1** (a) Overview of mechanisms involved in post-fire recovery via resprouting under (a)  
 1198 historical fire regimes; and (b) changing fire regimes and overlapping disturbances due to  
 1199 climate change. Also illustrated are population transitions (brown lines). Moving from left to right  
 1200 (solid lines), the figure illustrates (i) the range of resprouting responses and structural and  
 1201 physiological changes to trees following a single fire event; (ii) responses following either a  
 1202 repeated short-interval fire event or overlapping disturbance events (i.e. when other abiotic or  
 1203 biotic disturbances, such as insect outbreak or drought, coincide with fire); and (iii) eventual  
 1204 stand collapse following repeated short-interval disturbance events. The dashed lines indicate  
 1205 population recovery trajectories in the absence of repeated disturbances.



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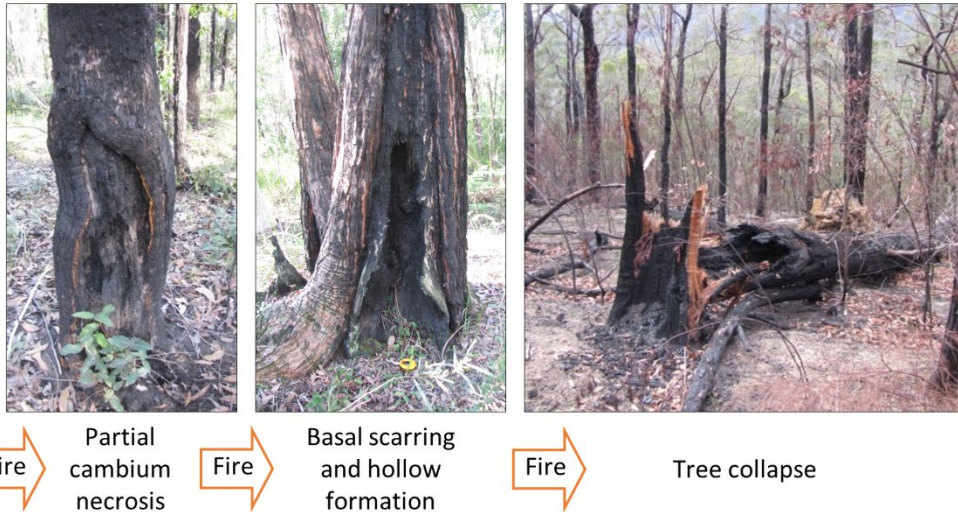
1207 **Fig. 2.** Overview of mechanisms involved in post-fire recovery via seed recruitment under (a)  
 1208 usual fire regimes; and (b) changing fire regimes due to climate change. The figure also gives  
 1209 an overview of population transitions (brown lines). The dashed lines indicate population  
 1210 recovery trajectories in the absence of disturbance.

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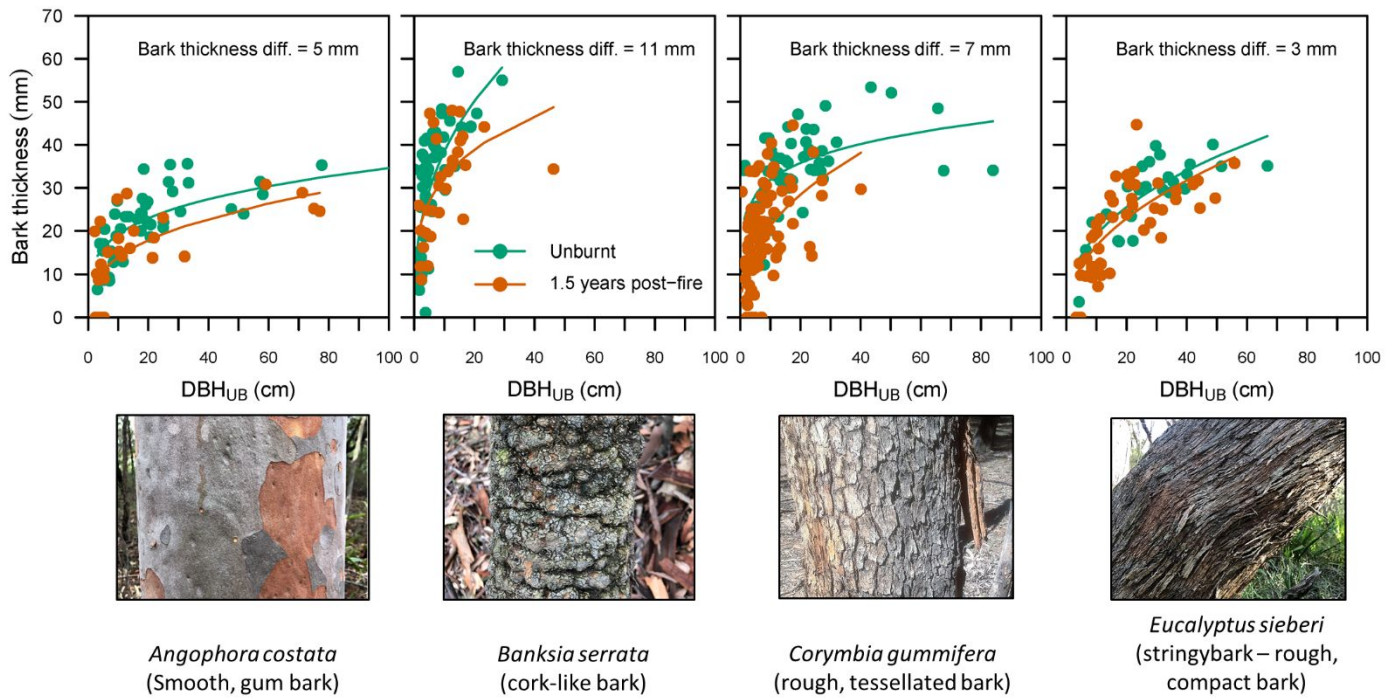
1213 **Fig. 3.** Examples of post-fire resprouting and recruitment, all photos taken in south-eastern  
 1214 Australian ecosystems. (a) basal resprouting in *Eucalyptus* sp. (b) epicormic resprouting in  
 1215 *Angophora* sp. (c) apical re-growth in *Xanthorrhoea* sp. (d) seedling germination in *Eucalyptus*  
 1216 sp. (e) serotinous cone in *Banksia* sp. (f) post-fire flowering in *Xanthorrhoea* sp. Photo credits:  
 1217 R. Nolan.



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1219 **Fig. 4.** Conceptual overview of the process of basal scarring and tree collapse from  
 1220 repeated fires. Photo credits: L. Collins.

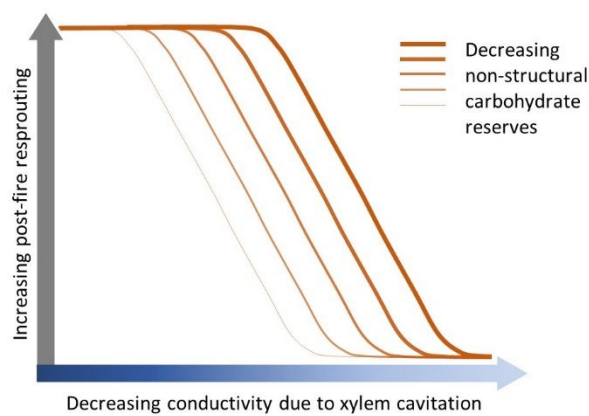
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1223 **Fig. 5.** Power regressions of bark thickness as a function of stem size (diameter at breast height  
 1224 under bark,  $DBH_{UB}$ ) illustrating a trend of thinner bark in recently burnt trees. Recently burnt  
 1225 trees were subject to canopy fire 1.5 years prior to measurement, while unburnt trees had not  
 1226 been burnt for at least 10 years prior to measurement. Also presented are the difference in bark  
 1227 thickness between burnt and unburnt trees when  $DBH_{UB}$  is 20 cm. Data collected from dry  
 1228 sclerophyll forest in eastern Australia (Nolan et al., 2020c).



1229

1230 **Fig. 6** Hypothesised probability of resprouting exhaustion, due to carbohydrate and water  
 1231 limitations. As non-structural carbohydrate reserves are depleted, and xylem cavitation  
 1232 increases, resprouting is expected to decline. Several processes, such as shading or protracted  
 1233 water scarcity, could deplete NSC stores and induce eventual C starvation. This conceptual  
 1234 model is derived from studies on resprouting failure, xylem embolism and carbohydrate  
 1235 depletion in chaparral shrubland (Pratt et al., 2014) and *Quercus* spp. (Resco de Dios et al.,  
 1236 2020).

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1240 **Fig. 7.** Images of eucalypt woodland in south-eastern Australia during severe drought in 2019-

1241 20, illustrating understorey and tree canopy die-off. Photo credits: R. Nolan.

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 
<b>Avoidance of fire impacts</b>				
Occurrence of fire refugia	↓	↓	↓	↕
Persistence of landscapes subject to low severity and low frequency fire regimes	↓	↓	↓	↕
<b>Post-fire resprouting</b>				
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	↓	↓	↓	↓
<b>Post-fire recruitment</b>				
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     
  High confidence     
 "NA": no identified pathway disturbance would impact on mechanism / process  
 Decrease     
  Low or medium confidence  
 No change

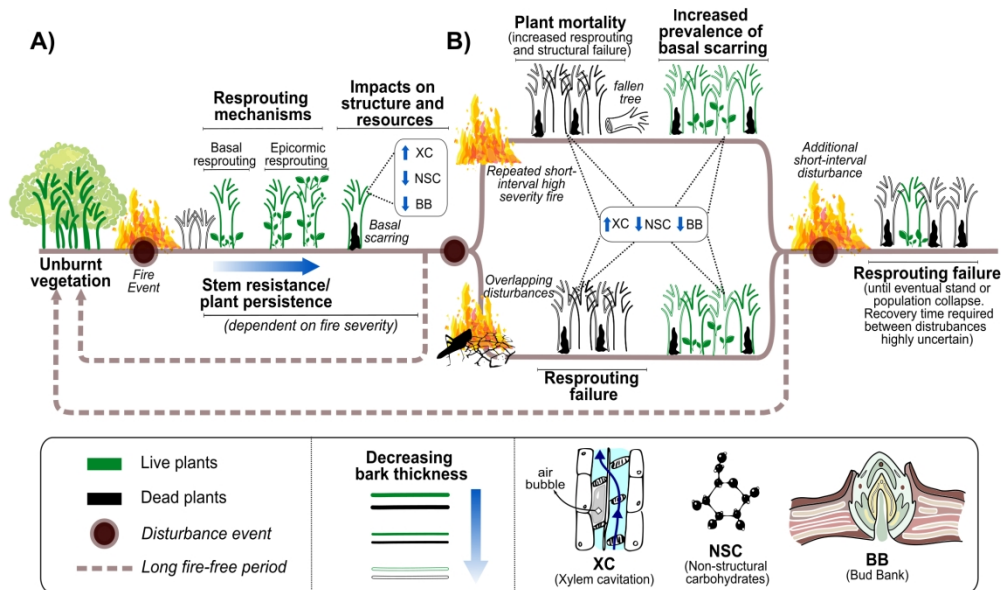
1242

1243 **Fig. 8.** Summary of mechanisms involved in post-fire recovery, and potential changes under  
 1244 climate induced changes in intensification of fire regimes (e.g. increased fire frequency, extent,  
 1245 severity and shifts in seasonality). Also shown are the potential influences of increasing  
 1246 incidence of stress and disturbance events on post-fire recovery. Mechanisms indicated with

1247 high confidence (blue) are those that are well supported in the literature, whereas mechanisms  
1248 with low or medium confidence (orange) are not well studied.

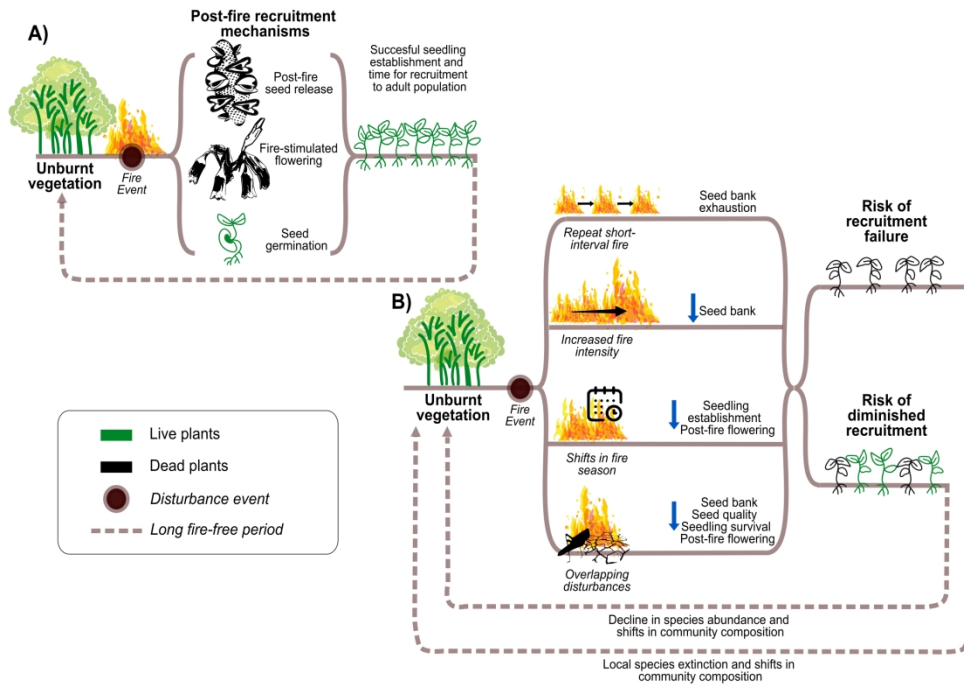
1249

Do not distribute



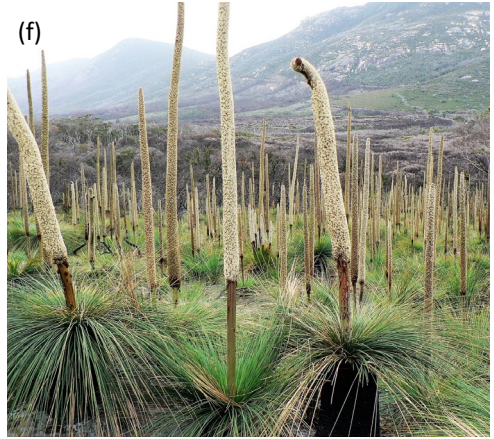
(a) Overview of mechanisms involved in post-fire recovery via resprouting under (a) historical fire regimes; and (b) changing fire regimes and overlapping disturbances due to climate change. Also illustrated are population transitions (brown lines). Moving from left to right (solid lines), the figure 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.

483x293mm (118 x 118 DPI)



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.

526x368mm (118 x 118 DPI)



distributed



Partial  
cambium  
necrosis



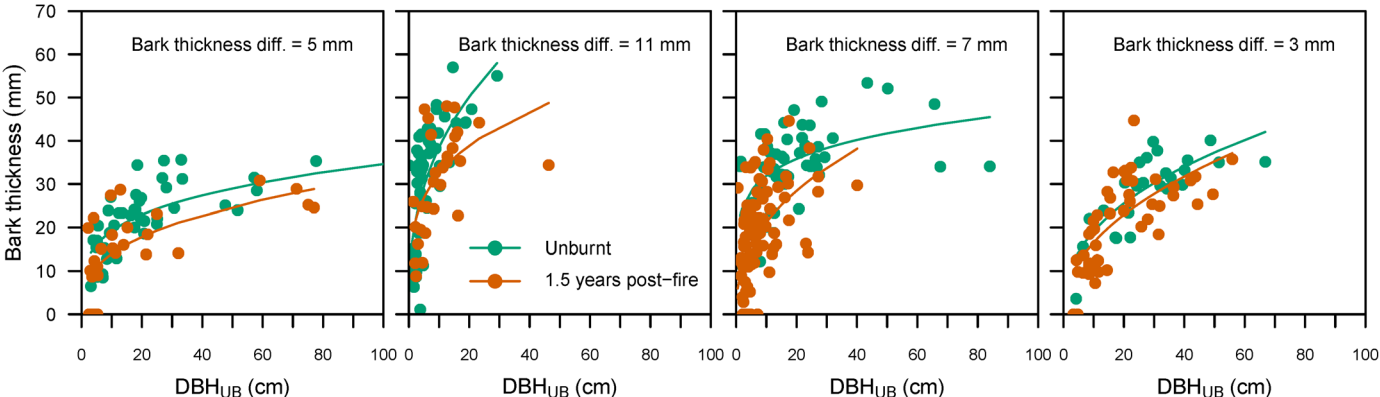
Basal scarring  
and hollow  
formation



Tree collapse

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*Angophora costata*  
(Smooth, gum bark)



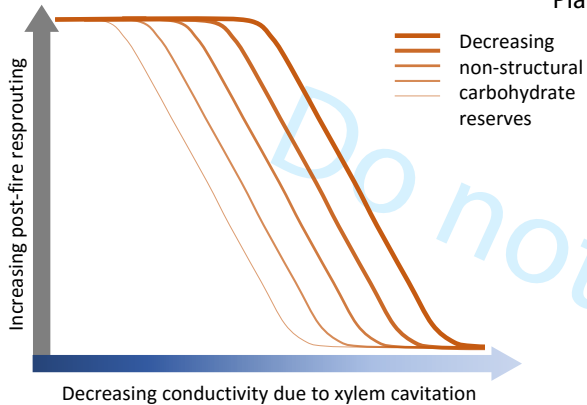
*Banksia serrata*  
(cork-like bark)



*Corymbia gummifera*  
(rough, tessellated bark)



*Eucalyptus sieberi*  
(stringybark – rough, compact bark)







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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
				
<b>Avoidance of fire impacts</b>				
Occurrence of fire refugia	↓	↓	↓	↑↓
Persistence of landscapes subject to low severity and low frequency fire regimes	↓	↓	↓	↑↓
<b>Post-fire resprouting</b>				
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	↓	↓	↓	↓
<b>Post-fire recruitment</b>				
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

↑ ↓ → High confidence

↓ Decrease

↑ ↓ → Low or medium confidence

→ No change

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

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2 **Running head:** Limits to post-fire recovery

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**39 Abstract**

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

**57 Keywords**

58 Wildfire, climate change, resprouting, obligate seeding, herbivory, heat stress, germination,  
59 mortality

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## 68 1. Introduction

69 In 2019-20, a series of mega-fires burnt an estimated 21% of the total temperate forest biome in  
70 Australia (Boer et al., 2020). These fires, termed the 'Black Summer' fires, more than doubled  
71 the estimated area burnt in a single fire season in eastern Australia (Nolan et al., 2020b), and  
72 resulted in an unprecedented extent of high severity fire (Collins et al., 2021) in the modern fire  
73 management record. These fires coincided with record low rainfall and high temperatures  
74 (Bureau of Meteorology, 2019). Similar fire seasons have also occurred in many other regions  
75 globally in recent years, including North America (Williams et al., 2019, Kirchmeier-Young et al.,  
76 2019), South America (Bowman et al., 2019b) and the Mediterranean (Turco et al., 2019).  
77 These types of extreme fire seasons raise important questions about the capacity of ecological  
78 communities to respond to climate-driven changes in fire regimes.

79 Many plant species and ecological communities are well-adapted to local historical fire regimes,  
80 broadly defined as the frequency, severity, seasonality and extent of fire (Whelan, 1995, Gill,  
81 1975, Turner, 2010). Shifts in local fire regimes can test the resistance and resilience of species  
82 and communities to fire (Karavani et al., 2018). At the same time as fire regimes are changing,  
83 climate change is affecting other abiotic and biotic disturbances, such as drought, heatwaves  
84 and insect outbreaks. ~~Since W~~wildfires typically coincide with ~~severe~~ drought ~~events~~ and  
85 elevated temperatures, (Nolan et al., 2020a, Pook, 1986, Dowdy and Mills, 2012), climate  
86 change driven increases in these abiotic disturbances but these drought events are expected to  
87 become more severe with climate change (Kirono et al., 2020, Hoegh-Guldberg et al., 2018).  
88 ~~While heatwaves are one of the aspects of climate predicted to increase with highest certainty~~  
89 ~~(Hoegh-Guldberg et al., 2018)are expected to coincide with increases in wildfire frequency,~~  
90 severity and extent. Climate change effects on biotic disturbances, such as insect outbreaks,  
91 are more difficult to predict, and are likely to be both positive and negative (Pureswaran et al.,

92 2018). Here, we explore the overlapping and often antagonistic influence of these disturbances  
93 with changing fire regimes.

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

105 In this review, we summarise the suite of mechanisms involved in plant or population level  
106 responses to fire, and then examine how climate-driven shifts in fire regime, combined with  
107 other abiotic and biotic disturbances, can affect post-fire vegetation recovery. We begin by  
108 outlining the different plant responses to fire. We then separately examine two key post-fire  
109 responses that facilitate vegetation recovery, namely resprouting and fire stimulated  
110 recruitment. To distil the complexity of these interacting mechanisms, we present them as  
111 conceptual models (Fig. 1 and 2). With respect to resprouting, we explain how plant persistence  
112 depends on the impacts of fire on plant structure and resources, such as non-structural  
113 carbohydrate reserves and bud banks (Fig. 1a). We then outline how overlapping disturbances  
114 (additional fires, drought, herbivory, etc.) affect resprouting and may lead to resprouting failure  
115 (Fig. 1b). With respect to post-fire recruitment, we first examine the different recruitment  
116 mechanisms (seed release, flowering and germination) in isolation (Fig. 2a), and then examine

117 the likely impacts of different disturbances in combination with changes in fire regimes (Fig 2b).  
118 While we illustrate our review with literature primarily from Australian temperate and  
119 Mediterranean ecosystems, in particular forests, the mechanisms governing plant and  
120 community responses to fire that we discuss here are applicable to many ecosystems globally.

121

## 122 **2. Overview of plant responses to fire**

123 There are a range of plant responses that ensure persistence or recruitment, which are tightly  
124 linked to fire regime attributes. Fire-resistant species are those that can survive fire without  
125 resprouting new foliage, i.e. the fire causes little damage to them (Midgley et al., 2011).

126 Consequently, fire-resistant traits provide an advantage in low intensity surface fire regimes,  
127 where fire induces limited canopy defoliation, and where fire survival may be achieved through a  
128 combination of plant height and protection of meristematic tissues and the cambium (Midgley et  
129 al., 2011).

130 Resprouting is a key plant functional trait that enables plants to persist following disturbances  
131 (Bond and Midgley, 2001). Post-fire resprouting occurs when meristematic tissues, specifically

132 buds, are protected from fire (Clarke et al., 2013). Resprouting can occur: ~~from:~~ (1)

133 belowground, from roots and rhizomes; (2) basally, from buds located at or belowground, e.g.

134 from lignotubers; (3) epicormically, from stems and branches; and (4) apically, from the apical

135 meristem (Clarke et al., 2013; Fig. 3). Belowground and basal resprouting is more widespread

136 than aerial resprouting (i.e. epicormic, apical); with the latter predominantly occurring in

137 arborescent life forms (Clarke et al., 2013, Pausas and Keeley, 2017). Resprouting is

138 considered an expensive strategy in terms of allocation to belowground roots and/or storage

139 organs and protection of bud banks. Consequently, resprouting species may predominate at

140 productive sites (Pausas et al., 2016, Pausas and Bradstock, 2007, Knox and Clarke, 2005),

141 although converse relationships between resprouting and productivity have also been observed  
142 (Hammill et al., 2016).

143 Seed germination following fire is a common post-fire recruitment strategy. For species with fire-  
144 cued seed germination, seeds can either be stored in the soil or on the plant in woody structures  
145 (Fig. 3). Serotiny, the extended storage of plant-stored seeds which are released after fire, is  
146 observed to occur in lower productivity sites compared to soil-storage of seeds, as a strategy to  
147 limit predation on seeds (Keeley et al., 2011). Species that only recover from fire via fire-cued  
148 seed release and/or germination are termed “post-fire obligate seeders” (Prior and Bowman,  
149 2020), whereas species that recover from fire via both seeding and resprouting are termed  
150 ‘facultative resprouters’ (Clarke et al., 2015). Another recruitment strategy is fire-cued flowering  
151 (Lamont and Downes, 2011; Fig. 3).

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

158 Invariably, vegetation communities are often identified by the post-fire response of the dominant  
159 or most easily-identified vegetation – such as an overstorey comprised of resprouting trees –  
160 however, many vegetation communities support species with a mix of post-fire responses. For  
161 example, across eucalypt forests, approximately 50% of species are facultative resprouters,  
162 21% are obligate resprouters and 27% are obligate seeders (Clarke et al., 2015). For simplicity,  
163 in the following sections we will consider each of the post-fire responses individually,  
164 recognising that each of these responses may co-occur within a single vegetation community.

165

### 166 **3 Post-fire resprouting**

#### 167 **3.1 Mechanisms impacting post-fire recovery of resprouting plants**

168 We consider resprouting as a continuum ranging from belowground resprouting to aerial  
169 resprouting from the upper branches of trees, with plant resistance / persistence following fire  
170 increasing along this continuum (Fig. 1a). Mechanisms contributing to post-fire mortality include  
171 changes to both plant structure and access to resources. Plant structural changes include  
172 physical damage to stems and roots and consumption of bark during fire. Changes to resources  
173 include hydraulic limitations due to xylem cavitation, depletion of non-structural carbohydrates  
174 and depletion of bud-banks.

##### 175 **3.1.1 Impacts on structures: basal scarring and physical damage to roots**

176 Trees that survive fire may suffer cambium necrosis of part of the stem base, which is referred  
177 to as 'basal scarring' (Fig 4). Cambium necrosis exposes heartwood to decay and fire. Over  
178 time, the excavation of heartwood will compromise the structural integrity of stems, increasing  
179 the likelihood of collapse during subsequent disturbances (Fig. 1, Fig. 4, Whitford and Williams,  
180 2001, Gibbons et al., 2008). The presence of basal scarring can substantially increase the  
181 probability of topkill, i.e. death of above-ground biomass (e.g. +20%; Collins, 2020, Collins et al.,  
182 2012), and the likelihood of mortality by causing tree collapse (Collins, 2020, Bowman and  
183 Kirkpatrick, 1986). The nature and size of basal scarring required to cause tree hollow formation  
184 has not been well studied, nor has the role of bark type in susceptibility to basal scarring. Basal  
185 scarring is, however, more likely to be prevalent in larger trees, which are typically older and  
186 have therefore had increased exposure to fire (Parnaby et al., 2010, Collins et al., 2012, Collins,  
187 2020).

188 Any physical damage to roots may decrease structural stability of the plant or affect access to  
189 water and nutrients. There are very few studies of fire impacts on roots, although studies from  
190 boreal Scots pine forests and semi-arid sagebrush shrubland in western USA indicate that fire  
191 can reduce fine root biomass, particularly under prolonged smouldering combustion driven by  
192 large biomass accumulation (Rau et al., 2009, Smirnova et al., 2008, Hood et al., 2018).  
193 However, most surface and canopy wildfires often exert a limited impact on roots as the soil is  
194 an excellent thermal insulator (Resco de Dios, 2020).

### 195 **3.1.2 Impacts on structures: damage to bud banks**

196 A requirement for stem and branch survival is that the buds and cambium are sufficiently  
197 protected from high temperatures during fire (Clarke et al., 2013; Fig. 1). Bark thickness is a key  
198 trait determining stem survival during fire, with thicker bark providing greater insulation  
199 (Wesolowski et al., 2014), reducing the likelihood of stem and branch mortality (Lawes et al.,  
200 2011). Fire regimes were thought to account for much of the variation in bark thickness globally  
201 (Pausas, 2015), but recent studies highlight that supporting metabolism and additional  
202 processes may play an important role (Rosell, 2019, Resco de Dios, 2020).

203 Bark thickness develops with stem size and age, hence the likelihood of topkill decreases with  
204 stem size for many eucalypt species (Fairman et al., 2019, Collins, 2020). The position of buds  
205 relative to the bark surface determines the degree of insulation, with higher resprouting success  
206 being observed for species with buds deeply embedded beneath the bark surface, such as  
207 eucalypts (Charles-Dominique et al., 2015). Canopy height can also protect buds and tissues in  
208 the upper stems and branches, though adequate insulation is still required to facilitate stem  
209 survival (Clarke et al., 2013).

210 During fire, some of the protective bark on plants is consumed (Volkova and Weston, 2013,  
211 Nolan et al., 2020c). This reduction in bark thickness reduces the insulation capacity of bark,

212 thereby increasing vulnerability of stems to cambium necrosis from subsequent fire (Fig. 1, Fig.  
213 5; Wesolowski et al., 2014, Gill and Ashton, 1968, Catry et al., 2012). However, it is unclear  
214 whether the partial loss of bark is sufficient to increase mortality rates of large eucalypts, owing  
215 to their deeply embedded buds (Charles-Dominique et al., 2015). Further, the length of time  
216 required for recovery of that bark is largely unknown, due to limited data on bark growth rates.  
217 Bark consumption is dependent on fire intensity and season of burn, which may be a function of  
218 seasonal variation in bark moisture content affecting bark combustion (Chatto et al., 2003).

219 Another hypothesised cause of resprouting failure following short interval fires is bud-bank  
220 limitation (Fig. 1), which represents a reduction in the number of buds available to resprout  
221 (Enright et al., 2011). In a study on resprouting shrubs in south-west Australia, Bell and Pate  
222 (1996) observed bud bank exhaustion after experimental clipping. However, the frequency of  
223 the clipping in that experiment (six months or less) is unlikely to replicate naturally-occurring fire  
224 frequencies. Resprouting failure has also been attributed to a lack of buds following long fire  
225 intervals (Enright et al., 2011). However, these declines in resprouting may be a function of  
226 plant age, rather than fire interval, with declines in bud-banks observed with plant age or size  
227 (Holland, 1969, Hodgkinson, 1998). Thus, while there is some evidence of bud-bank exhaustion  
228 affecting resprouting, further studies are required that replicate the impact of realistic increases  
229 in fire frequency.

### 230 **3.1.3 Impacts on resources: stored carbohydrates and hydraulic limitations**

231 As fire frequency increases and fires increasingly coincide with other disturbances, such as  
232 severe drought, it has been hypothesised that resprouting species may reach the limits of their  
233 capacity to resprout (Karavani et al., 2018; Fig. 3, Fairman et al., 2016, Resco de Dios, 2020).  
234 This phenomenon has been termed 'resprouting exhaustion syndrome' (Karavani et al., 2018).  
235 Resprouting exhaustion has largely been attributed to depleted carbohydrate reserves. There is

236 some indirect evidence for carbohydrate limitation driving resprouting exhaustion from  
237 observations of declines in root and stem starch reserves following a resprouting event (Bowen  
238 and Pate, 1993, Smith et al., 2018). While temporary declines in starch are to be expected, a  
239 complete consumption of starch reserves has only seldom been documented. That is, while  
240 limited carbohydrate concentrations may impact resprouting capacity, direct evidence for this  
241 phenomenon is still scarce.

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

### 258 **3.2 Impacts of shifts in fire regimes on resprouting**



259 Research to date indicates that resprouting species are typically resilient to frequent, low  
260 intensity fires (Bennett et al., 2013, Watson et al., 2020, Guinto et al., 1999). There is also  
261 mounting evidence that resprouting species can also remain resilient in response to repeated  
262 crown fires (Fairman et al., 2019, Williams et al., 1999, Collins, 2020). Thus, resprouting species  
263 are likely to persist under increasing fire intensities. However, there may be demographic shifts  
264 (Fig. 1b). For example, in forest trees, small trees are most vulnerable to high fire severity, and  
265 complete loss of these plants can occur in extreme cases (Bennett et al., 2016). Large trees  
266 generally maintain high rates of resprouting, even after repeat high severity fires (Collins, 2020,  
267 Fairman et al., 2019, Williams et al., 1999). However, large trees may be vulnerable to  
268 increased fire frequency, which increases the prevalence of cambium damage, leading to  
269 eventual tree collapse or mortality (Fairman et al., 2017).

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

### 275 **3.3 Impacts of overlapping disturbances on post-fire resprouting**

#### 276 **3.3.1 Drought**

277 An increase in drought and associated heatwaves with climate change is already resulting in an  
278 increase in forest mortality and canopy die-off events globally (Allen et al., 2015, Ciais et al.,  
279 2005, Breshears et al., 2021). For example, prior to and during the Black Summer fires in  
280 eastern Australia in 2019-20, there were widespread observations of canopy die-off (Fig. 7; De  
281 Kauwe et al., 2020, Nolan et al., 2021). If a drought is severe enough to trigger plant mortality in  
282 resprouting species, and there is additional mortality following fire, then there will be higher

283 rates of overall plant mortality when severe drought precedes fire. Similarly, when severe  
284 drought follows fire, there is likely to be higher rates of overall plant mortality (Pratt et al., 2014).

### 285 **3.3.2 Heatwaves and heat stress**

286 Heatwaves are rapidly increasing in intensity, duration and frequency, including a longer  
287 heatwave season (Hoegh-Guldberg et al., 2018). Heat stress, when coupled with drought  
288 stress, increases plant mortality before fire (Allen et al., 2010, Teskey et al., 2015) and may also  
289 potentially increase the damage sustained to living plants during a fire. Drought stress causes  
290 stomata to close, increasing leaf temperatures and therefore leaf level tissue damage and  
291 mortality (Teskey et al., 2015), but heat stress itself can cause leaf damage (French et al.,  
292 2019). Damaged and dead leaves may increase fire intensity, thereby increasing the risk of  
293 post-fire mortality.

294 Irrespective of drought, plants' physiological responses to heat stress require a range of  
295 mechanisms to protect against protein denaturation, rebuild damaged proteins and maintain the  
296 integrity of cell membranes (Wahid et al., 2007). Upregulation of heat shock proteins and  
297 isoprenes, which are commonly synthesised in response to heat stress in many species,  
298 including eucalypts, represent the diversion of stored photosynthates and other compounds  
299 from growth (including re-sprouting) and reproduction (Teskey et al., 2015, Bitá and Gerats,  
300 2013). For example, many crop studies have demonstrated reduced flowering, and  
301 subsequently reduced yields, following heat stress (Bitá and Gerats, 2013). Increasing  
302 frequency of heat stress events potentially compounds the problem. The time between heat  
303 stress events required for photosynthetic tissue recovery varies from hours to days (Curtis et al.,  
304 2014, Karim et al., 1999), likely complicated by the presence of accompanying stressors and the  
305 health of the plant to begin with. However, recovery of non-structural carbohydrate reserves and  
306 plant biomass may take much longer. More research on between-stress intervals under

307 combined heat and drought stress is crucial to understanding vegetation resilience and ability to  
308 re-sprout, and recruit, after fire.

### 309 **3.3.3 Insect outbreaks**

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

## 320 **4 Post-fire recruitment**

### 321 **4.1 Mechanisms underpinning post-fire recruitment**

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

#### 327 **4.1.1 Post-fire seed release**

328 Seed release from serotinous cones is usually triggered when heat from fire causes death of the  
329 supporting stem and/or degradation of the binding resin (Lamont et al., 2019). Serotiny occurs in  
330 temperate and Mediterranean ecosystems, including Australia, North America, the  
331 Mediterranean Basin, and South Africa (Lamont et al., 2020). Since seed release is dependent  
332 on heat for some species (pyriscent species, sensu Lamont et al., 1991), but can happen upon  
333 death of the supporting stem in others, it can therefore also occur in the absence of fire giving  
334 rise to questions regarding risk spreading strategies among different species (Lamont et al.,  
335 2019). For example, opening of *Allocasuarina* and *Hakea* cones may occur when individuals are  
336 subject to drought, whereas many *Banksia* species require fire-related high temperatures for  
337 follicles to open (Espelta et al., 2011). However, the rate of seed release varies with the  
338 temperature the cones are exposed to, with lower temperatures producing slower seed release.  
339 Furthermore, the length of time seeds are held in the canopy seed bank, can influence the rate  
340 at which seeds are released from open follicles, with species with long seed retention times  
341 producing slower rates of seed release following fire (Clarke et al., 2010). Very recent work has  
342 also questioned the size of the available seed bank that is actually retained by serotinous  
343 species in long unburnt sites. Whelan and Ayre (2020) found in a long-term longitudinal study  
344 that seed banks of the serotinous shrub *Banksia spinulosa* maintained a relatively small seed  
345 bank, even after more than 20 years. Regeneration was dependent on seeds produced in just a  
346 few years prior to the fire event, with predation from birds (cockatoos) and insects causing most  
347 of the seed bank decline.

#### 348 **4.1.2 Post-fire germination and seedling establishment**

349 The generation of dormancy-breaking and germination cues, primarily heat shock, smoke and  
350 their interaction, is essential for the recruitment of many species, with some maintaining a  
351 greater level of dependence on fire cues than others (i.e. obligated to fire cues) (Ooi et al.,  
352 2014, Collette and Ooi, 2017). Temperature thresholds required to break seed dormancy varies

353 across species. For example, in Australian fire-prone ecosystems, temperatures required to  
354 break seed dormancy can vary from 40–100 °C (Ooi et al., 2014). The mechanisms underlying  
355 this variation in temperature thresholds are not well studied. However, there is growing evidence  
356 that seed size is negatively correlated with temperature thresholds (Ooi et al., 2014). Higher  
357 temperature thresholds in smaller seeded species are hypothesised to be a function of these  
358 seeds being buried at shallow soil depths, and therefore being exposed to higher temperatures  
359 during fire than larger seeds, buried deeper within soil (Ooi et al., 2014). In addition to heat  
360 cues, smoke-cued seed germination has also been observed in a large number of species, from  
361 across Australia and many fire-prone regions around the world (Keeley and Pausas, 2018).

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

373 Successful seedling establishment post-fire will depend on a range of factors, including  
374 competition (Stoneman, 1994), the post-fire environment and changes in soil fertility and  
375 microbial communities. The post-fire environment is typically nutrient rich and supports rapid  
376 seedling growth (Chambers and Attiwill, 1994), unless the topsoil has been eroded (Barry et al.,  
377 2015). Fire impacts on microbial communities are not well studied. Available studies have

378 shown either increases, decreases or little change in both pathogenic fungi and beneficial  
379 microbial communities (Chambers and Attiwill, 1994, Motiejūnaitė et al., 2014, Lygis et al.,  
380 2010).

#### 381 **4.1.3 Fire-stimulated flowering**

382 Fire-stimulated flowering occurs across many fire-prone regions globally, but may only account  
383 for a small number of species in some ecosystems, e.g. up to 10% of species in heathlands and  
384 savannas in Australia and South Africa (Lamont et al., 2019). In Australia, most post-fire  
385 flowering species are monocots, in particular orchids (Lamont and Downes, 2011). ~~Of the fire-~~  
386 ~~stimulated dicots, a large majority are herbaceous, in particular orchids (Lamont and Downes,~~  
387 ~~2011).~~ The exact triggers of fire-stimulated flowering are not well understood (Pyke, 2017,  
388 Lamont and Downes, 2011).

389 Observational studies indicate that heat, smoke and/or defoliation may all trigger post-fire  
390 flowering, however, these factors are correlated and it is difficult to disentangle which drivers are  
391 important (Pyke, 2017). For example, in the genus *Xanthorrhoea* (Fig. 3f), higher rates of post-  
392 fire flowering have been observed following spring or summer fires, compared to autumn or  
393 winter fires (Lamont et al., 2000, Gill, 1997). These results may indicate that temperature is the  
394 cue for post-fire flowering in these species, with season of burn associated with fire intensity  
395 (Lamont and Downes, 2011). However, differing responses with season of burn may also be  
396 due to seasonal circadian rhythms (Lamont and Downes, 2011). In the same genus,  
397 experimental defoliation has been shown to either induce far fewer flowering spikes than  
398 following fire (Taylor et al., 1998, Specht, 1981), or induce similar rates of flowering to fire (Gill  
399 and Ingwersen, 1976, Lamont et al., 2004). Finally, observations of fire-stimulated flowering in  
400 *Xanthorrhoea* have also been attributed to smoke, due to observations of post-fire flowering in  
401 plants 200 m from fire (Curtis, 1998). In addition to exogenous factors, plant size or age may

402 also influence rates of post-fire flowering. For example, in *Xanthorrhoea preissii*, post-fire  
403 flowering frequency was positively correlated with plant height, which in turn is positively  
404 correlated with plant age in this genus (Lamont et al., 2000).

## 405 **4.2 Impacts of shifts in fire regimes on recruitment**

406 Successful post-fire establishment from soil and canopy seed banks is affected by broader  
407 climate-driven fire regime shifts, including season and fire intensity (Fig. 2b). Increases in fire  
408 intensity can reduce the available seed bank, by killing a higher proportion of seeds during a  
409 fire. For example, Etchells et al. (2020) found local extinction of a dominant understorey species  
410 in sites subject to extreme severity fires. Similarly, Palmer et al. (2018) found total exhaustion of  
411 the soil seed bank for some species after extreme fire meant that the risk of recruitment failure  
412 from a subsequent fire was increased.

413 Other interactions may also lead to state shifts in community composition. For example,  
414 variation in fire season can interact with rainfall to determine recruitment success, especially for  
415 species with physiologically dormant soil seed banks (Miller et al., 2019, Ooi, 2019), but also for  
416 species with canopy seed banks, if drought has triggered pre-fire seed release (Espelta et al.,  
417 2011). Another example from soil seed banking species can be found for increasing fire severity  
418 and related soil heating. Palmer et al. (2018) concluded that those species with smaller seeds  
419 would be selected against under a regime of regular extreme fire events because of the higher  
420 chance of lethal temperatures generated in the upper soil profile. This means that surviving  
421 seeds would only be found at greater depths, from where it is difficult for small seeds to  
422 successfully emerge (Liyanage and Ooi, 2018).

## 423 **4.3 Impacts of overlapping disturbances on post-fire recruitment**

### 424 **4.3.1 Drought**

425 Pre-fire seed production is likely to be affected by increased drought events under climate  
426 change, which may consequently reduce post-fire seed germination rates. For example, in the  
427 Mediterranean obligate seeding shrub in Western Australia, *Banksia hookeriana*, seed  
428 production is reduced in years following below average rainfall (Henzler et al., 2018). Drought  
429 may also reduce the availability of seeds in serotinous species, where it triggers seed release  
430 prior to fire (Martín-Sanz et al., 2017). Drought may also impact on post-fire flowering, although  
431 we are not aware of any studies that explicitly examine this.

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

#### 439 **4.3.2 Heatwaves and heat stress**

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

444 Soil temperatures will increase during heatwaves and will also increase during drought, as  
445 vegetation cover declines and solar radiation at the soil surface increases. These increased soil  
446 temperatures can be high enough to break some temperature thresholds for dormant seeds  
447 (Ooi et al., 2012, Ooi et al., 2014). Thus, species with relatively low dormancy-breaking  
448 temperature thresholds are at risk of germinating prior to fire, thereby diminishing soil



449 seedbanks. Conversely, for some species, seed production may initially increase under climate  
450 change, for example, species where seed production is currently temperature limited (Petrie et  
451 al., 2017). However, any potential benefits of increased temperature on seed production are  
452 dependent on changes in water availability (Boucher et al., 2020).

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

#### 460 **4.3.3 Insect outbreaks**

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

470

471 **5. What might the future hold for vegetation communities in the face of intensifying fire**  
472 **regimes and overlapping disturbance events?**

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

479 **5.1 Case study 1. Resprouting eucalypt forests of southern Australia**

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

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

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

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

## 511 **5.2 Case study 2. Australian rainforest communities**

512 Australian rainforests have a restricted distribution, with contraction of once widespread  
513 Gondwanan relict rainforest linked to increased fire over millennial time-scales (Cadd et al.,  
514 2019, Bowman, 2000). Fire regimes in Australian rainforests are typified by infrequent surface  
515 fires (Murphy et al., 2013). Following fire, up to 91% of species, primarily angiosperms, have the  
516 capacity to resprout basally (Clarke et al., 2015). In contrast, rainforest communities dominated  
517 by gymnosperms exhibit far less capacity for resprouting. For example, in cool temperate  
518 Tasmanian rainforest communities dominated by the conifer *Athrotaxis cupressoides*, post-fire

519 mortality rates of up to 68% have been reported (Bowman et al., 2019a). Fire-cued recruitment  
520 is relatively uncommon, with only 20% of species exhibiting a fire-resistant seed bank (Clarke et  
521 al., 2015). Seed recruitment is therefore likely to be heavily dependent on recruitment from fire  
522 refugia. For example, in Tasmanian rainforest, post-fire recruitment of rainforest species was  
523 observed in areas subject to low severity, patchy burns, which did not cause mortality of  
524 overstorey species (Hill and Read, 1984).

525 It is clear that many Australian rainforest communities can successfully recover after infrequent,  
526 low severity surface fires (Adam, 1992, Russell-Smith and Stanton, 2002, Knox and Clarke,  
527 2012). But what is the fate of rainforest ecosystems in the face of intensifying fire regimes and  
528 overlapping disturbances?

529 With increased fire frequency, severity, and/or drought, rainforest communities are likely to be  
530 invaded by pyrophytic species (Russell-Smith and Stanton, 2002, Adam, 1992, Berry et al.,  
531 2011). Pyrophytic species are those whose reproduction is enhanced, or even dependent, on  
532 fire (Fletcher et al., 2020). High severity fire combined with the establishment of pyrophytic  
533 species can cause cascading effects on rainforests. These effects include abrupt declines in  
534 canopy cover and aboveground live biomass, promoting higher surface fuel loads and drier  
535 microclimates, rendering the rainforests more susceptible to subsequent fires, and transitions to  
536 alternate vegetation types (Fletcher et al., 2020).

537 The 2019-20 Australian fire season burned extensive areas of rainforest, including 70% of warm  
538 temperate rainforest in Victoria (DELWP, 2020a) and 54% of New South Wales Gondwana  
539 World Heritage Area rainforests (DPIE, 2020). In addition to a large extent of rainforest being  
540 subject to fire, the proportion of damaging high severity fire, was much higher than in previous  
541 fire seasons (Collins et al., 2021). Given the array of threats likely to interact with fire to impact  
542 on rainforest stands (e.g. fragmentation and edge effects, disturbances such as drought, and

543 invasive species), management interventions are likely needed to ensure their conservation,  
544 including weed control and perhaps also supplementary planting or seed dispersal.

545

### 546 **5.3 Case study 3. Obligate seeding eucalypt forests of south-eastern Australia**

547 There are 84 known species of obligate seeding eucalypts in Australia (accounting for <10% of  
548 the eucalypt complex of species), i.e. species that lack post-fire resprouting but exhibit fire-  
549 stimulated seed germination. These obligate seeding eucalypts including low statured species  
550 from low-medium rainfall areas (Nicolle, 2006), and species from high rainfall areas  
551 representing some of the tallest (90+ m) trees on Earth (Nicolle, 2006, Sillett et al., 2015). Two  
552 of these tall species (*Eucalyptus regnans* and *E. delegatensis*; hereafter, 'ash' eucalypts) have  
553 been widely studied due to their importance for biodiversity and timber production (Ashton,  
554 2000, Flint and Fagg, 2007), and are a useful case study for exploring the responses of obligate  
555 seeders to changing fire regimes. The most common model for the relationship of ash eucalypts  
556 with fire is stand replacement (Ashton, 2000). Severe fires kill mature adult trees, which are  
557 afforded little protection by thin bark, and do not possess a strong resprouting capacity (Waters  
558 et al., 2010). However, with low severity fire, i.e. surface fires, survival can be upwards of 90%  
559 (Benyon and Lane, 2013).

560 Given the approximately 20-year window where regenerating ash forests are incapable of  
561 regenerating (Flint and Fagg, 2007, von Takach Dukai et al., 2018), these forests face  
562 'immaturity risk' (Keeley et al., 1999) when abrupt shifts in fire frequency occur that result in  
563 return intervals of high severity fire of < 20 years. Potential for broad-scale eucalypt re-  
564 colonisation of twice-burned ash forests via seed from outside the fire area is unlikely, given the  
565 poor seed dispersal capacity (Thomson et al., 2011, Griffin, 1980, Flint and Fagg, 2007).

566 Climate change has recently sharpened the focus on understanding the risk of short-interval fire

567 for ash forests, and a number of frameworks have recently been developed to conceptualise  
568 these risks. Two recent developments have been the 'landscape trap' (Lindenmayer et al.,  
569 2011) and the 'interval squeeze' models (Enright et al., 2015) – the former postulates that  
570 'intrinsic' stand-level factors like fuel load and disturbance influence the risk of decline of ash  
571 forests; while the latter emphasises 'extrinsic' factors like fire weather and climate (also  
572 supported by Ferguson and Cheney, 2011). Bowman et al. (2016) attempted to reconcile these  
573 two theories, concluding that recent patterns of fire in the Victorian alps lend support to the  
574 'interval squeeze' model, though they did note a minor role of stand-level factors such as stand  
575 age.

576 The 2019-20 Australian fire season resulted in major impacts to ash type forests in Victoria,  
577 elevated by the recent history of large landscape fires in that state (Fairman et al., 2016,  
578 DELWP, 2020b). Approximately 83,000 ha of ash forest were estimated to be impacted during  
579 the 2019-20 fire season, 30% of which was immature. Approximately 18,000 ha of this forest  
580 were severely burned and, without management intervention, will cease to be dominated by ash  
581 eucalypts. Of these burnt ash forests, 12,000 ha have been resown by forest managers, the  
582 largest single forest reseeded program conducted by forest managers within the state (DELWP,  
583 2020 pers. com.).

## 584 **6. Conclusions – where to from here?**

585 There are a large number of mechanisms governing plant responses to fire, many of which will  
586 be impacted by climate driven changes in biotic and abiotic disturbances and stress events (Fig.  
587 8). It is well supported in the literature that the frequency of mega-fires is expected to increase  
588 under climate change in temperate Australian ecosystems (Clarke et al., 2016). This was  
589 exemplified in 2019-20, where fires burnt a globally significant 21% of the total temperate forest  
590 biome in Australia (Boer et al., 2020). These increases in fire extent will likely cause a decline in

591 the extent of fire refugia (Collins et al., 2019) as well as push the regimes of fire-prone  
592 ecosystems beyond their historical limits. At present, the ability to predict post-fire responses, or  
593 confidently inform land managers, is limited by a lack of empirical assessment. Here, we  
594 examine some of the key knowledge gaps surrounding interacting stress events related to  
595 climate change that may determine how plant communities will respond to fire.

## 596 **6.1 Key knowledge gaps**

597 Key knowledge gaps surrounding post-fire recovery in the face of other interacting stress events  
598 include (i) fire frequency-related impacts, including the potential for resprouting exhaustion, and  
599 subsequent mortality of resprouting plants; (ii) the effects of drought and heatwaves interacting  
600 with fire regime shifts on seed quality and availability, and subsequent impacts to post-fire  
601 recruitment; (iii) the effects of climate change on vegetation growth rates and, therefore, rates of  
602 post-fire recovery; and (iv) the capacity of species to adapt to changing fire regimes and  
603 changing climate.

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

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

620 Vegetation growth rates may be enhanced by increased atmospheric CO<sub>2</sub> and associated  
621 changes in climate (Donohue et al., 2009), which could potentially decrease post-fire recovery  
622 times. However, in Australian ecosystems, the evidence for enhanced vegetation productivity  
623 under elevated CO<sub>2</sub> is mixed, due in part to soil nutrient limitations (Ellsworth et al., 2017, Yang  
624 et al., 2020). Precipitation patterns are likely to be much more influential on vegetation  
625 productivity than elevated CO<sub>2</sub> (Duursma et al., 2016, Green et al., 2019). The effects of  
626 increased temperatures on vegetation growth rates under climate change are also mixed. While  
627 increased temperatures can increase productivity in temperature-limited ecosystems (Zhu et al.,  
628 2016), the majority of Australia's forests are not temperature limited, and increased  
629 temperatures are instead likely to reduce productivity (Bowman et al., 2014). Clarification of  
630 what drives these variations in response is essential in order to accurately model post-fire  
631 recovery under climate change.

632 The capacity of ecosystems to adapt to climate change is dependent on species dispersal  
633 capabilities as well as their capacity to adjust to changing conditions (Booth et al., 2015). Many  
634 species exhibit phenotypic plasticity, or genetic variability, which manifests in differing  
635 responses to disturbance across a species' range. For example, increasing resistance to xylem  
636 cavitation has been observed with increasing aridity, in populations of the same species  
637 (Anderegg, 2015). Intra-specific variation in post-fire responses, in particular resprouting  
638 capacity, has also been observed in some species. For example, *Eucalyptus obliqua* is a



639 resprouting species, except for in wetter sites where it behaves as a fire-intolerant species,  
640 possibly due to hybridisation with the thinner barked *Eucalyptus regnans* (Ashton and Chappill,  
641 1989, Moore, 2015). Conversely, *Eucalyptus delegatensis* is predominately an obligate seeding  
642 species, but a resprouting sub-species is found in drier areas (Rodriguez-Cubillo et al., 2020).  
643 Other types of stress may also influence resprouting capacity. For example, *Banksia ericifolia* is  
644 an obligate seeding shrub species, but resprouting populations have been found in areas  
645 subject to water-logging or in sites subject to mechanical slashing (Renshaw, 2005). The  
646 capacity of species to adapt to climate change is likely to be greatest in species which have  
647 large geographic ranges and high genetic variability (Alberto et al., 2013). However, the  
648 capacity for populations to adjust through time in the absence of dispersion is a key knowledge  
649 gap in predicting species responses to changing climate and fire regimes.

650

## 651 **6.2 Future research directions**

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

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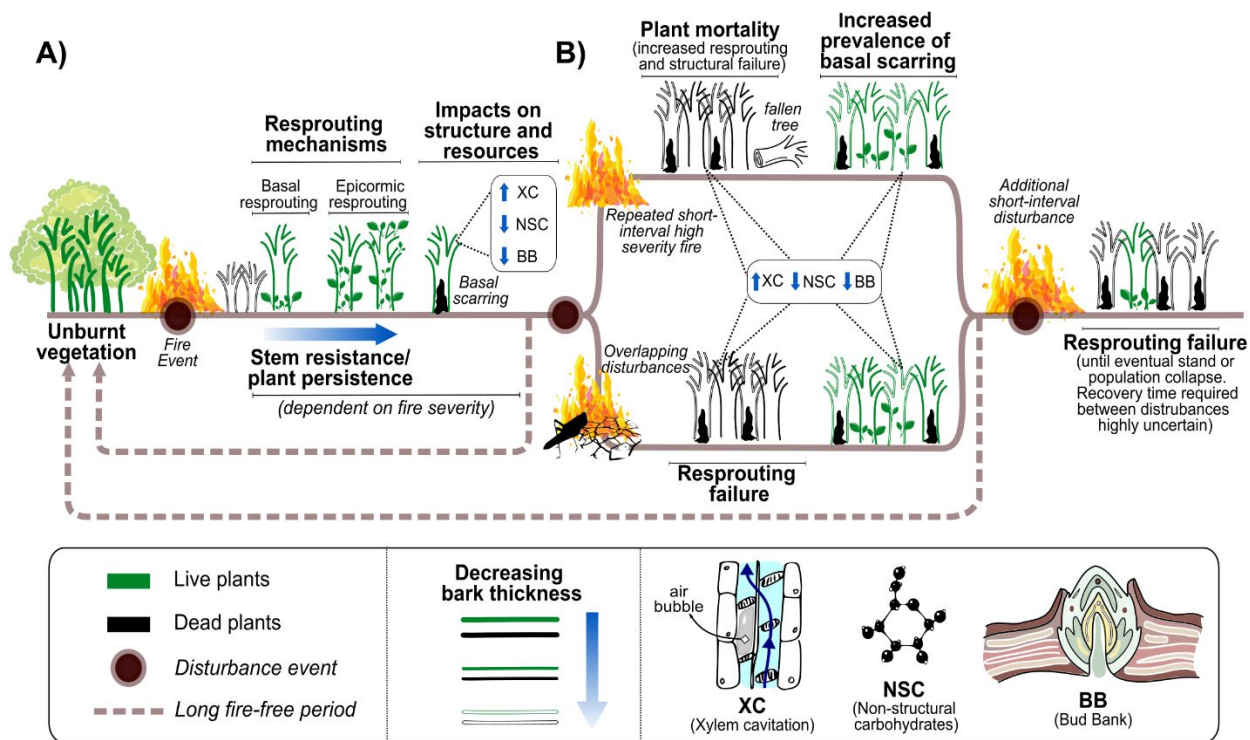


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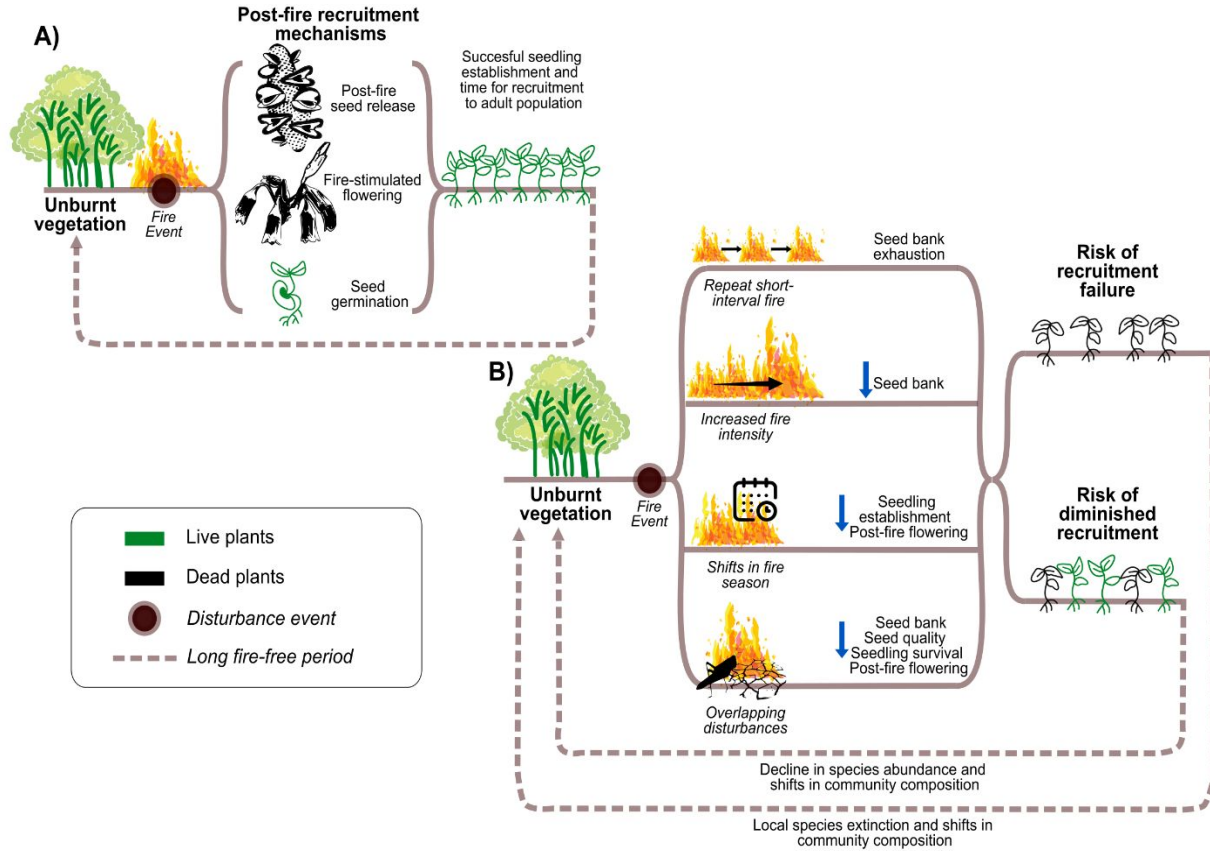
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1202 **Figures**

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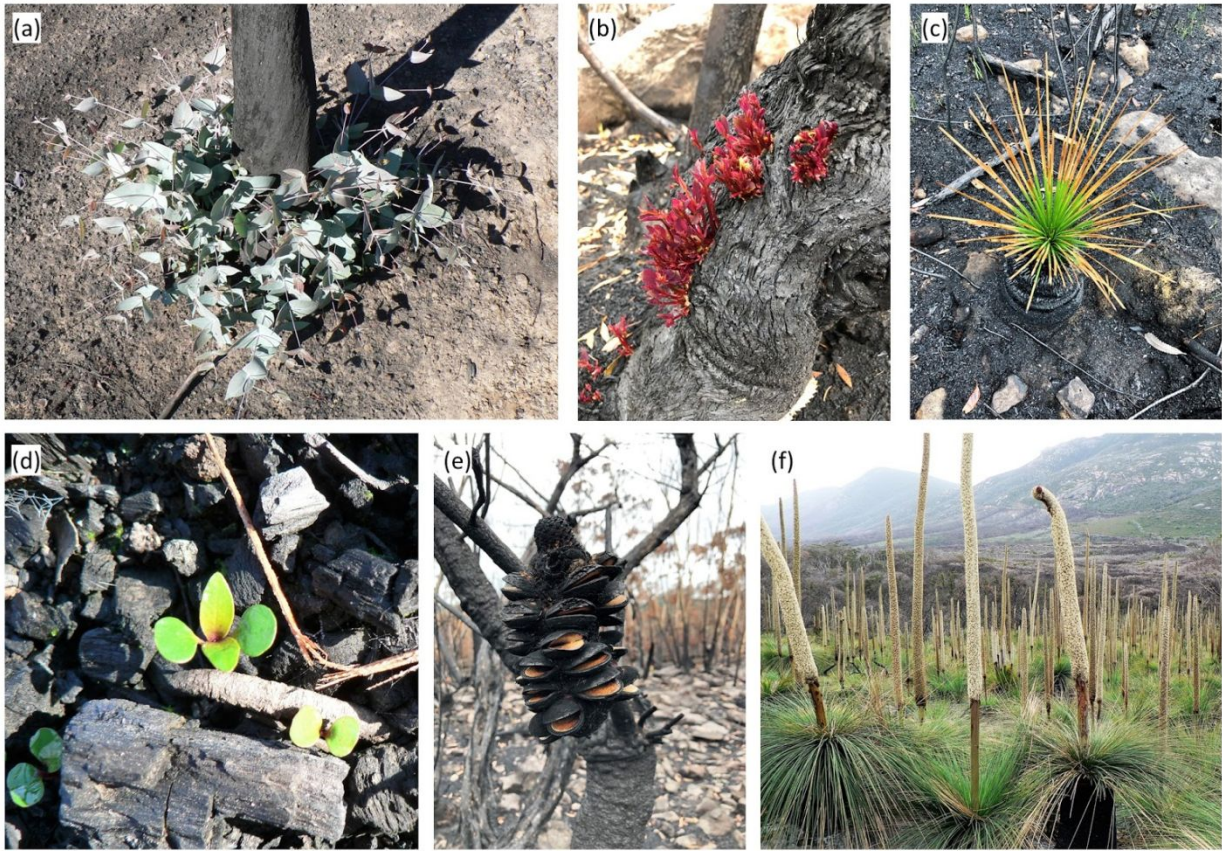
1204 **Fig. 1** (a) Overview of mechanisms involved in post-fire recovery via resprouting under (a)  
 1205 historical fire regimes; and (b) changing fire regimes and overlapping disturbances due to  
 1206 climate change. Also illustrated are population transitions (brown lines). Moving from left to right  
 1207 (solid lines), the figure illustrates (i) the range of resprouting responses and structural and  
 1208 physiological changes to trees following a single fire event; (ii) responses following either a  
 1209 repeated short-interval fire event or overlapping disturbance events (i.e. when other abiotic or  
 1210 biotic disturbances, such as insect outbreak or drought, coincide with fire); and (iii) eventual  
 1211 stand collapse following repeated short-interval disturbance events. The dashed lines indicate  
 1212 population recovery trajectories in the absence of repeated disturbances.



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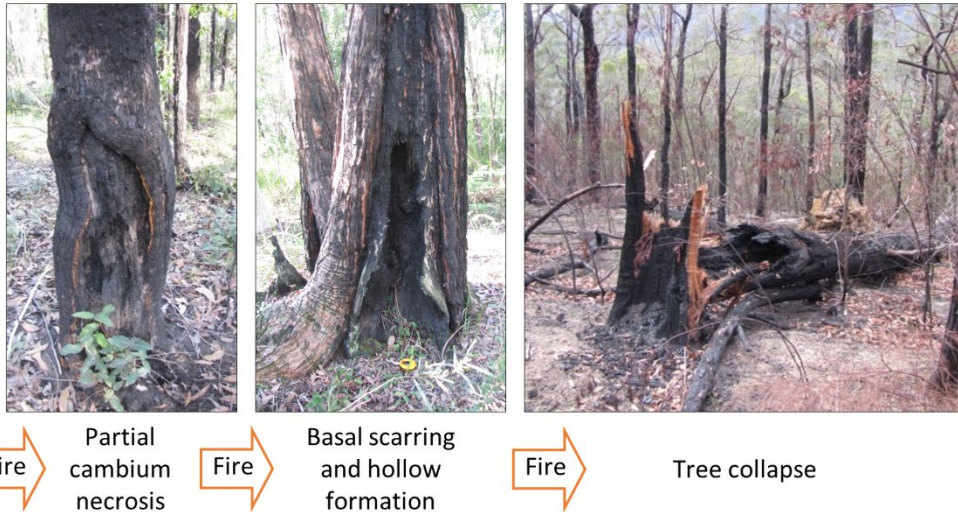
1214 **Fig. 2.** Overview of mechanisms involved in post-fire recovery via seed recruitment under (a)  
 1215 usual fire regimes; and (b) changing fire regimes due to climate change. The figure also gives  
 1216 an overview of population transitions (brown lines). The dashed lines indicate population  
 1217 recovery trajectories in the absence of disturbance.

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1220 **Fig. 3.** Examples of post-fire resprouting and recruitment, all photos taken in south-eastern  
 1221 Australian ecosystems. (a) basal resprouting in *Eucalyptus* sp. (b) epicormic resprouting in  
 1222 *Angophora* sp. (c) apical re-growth in *Xanthorrhoea* sp. (d) seedling germination in *Eucalyptus*  
 1223 sp. (e) serotinous cone in *Banksia* sp. (f) post-fire flowering in *Xanthorrhoea* sp. Photo credits:  
 1224 R. Nolan.



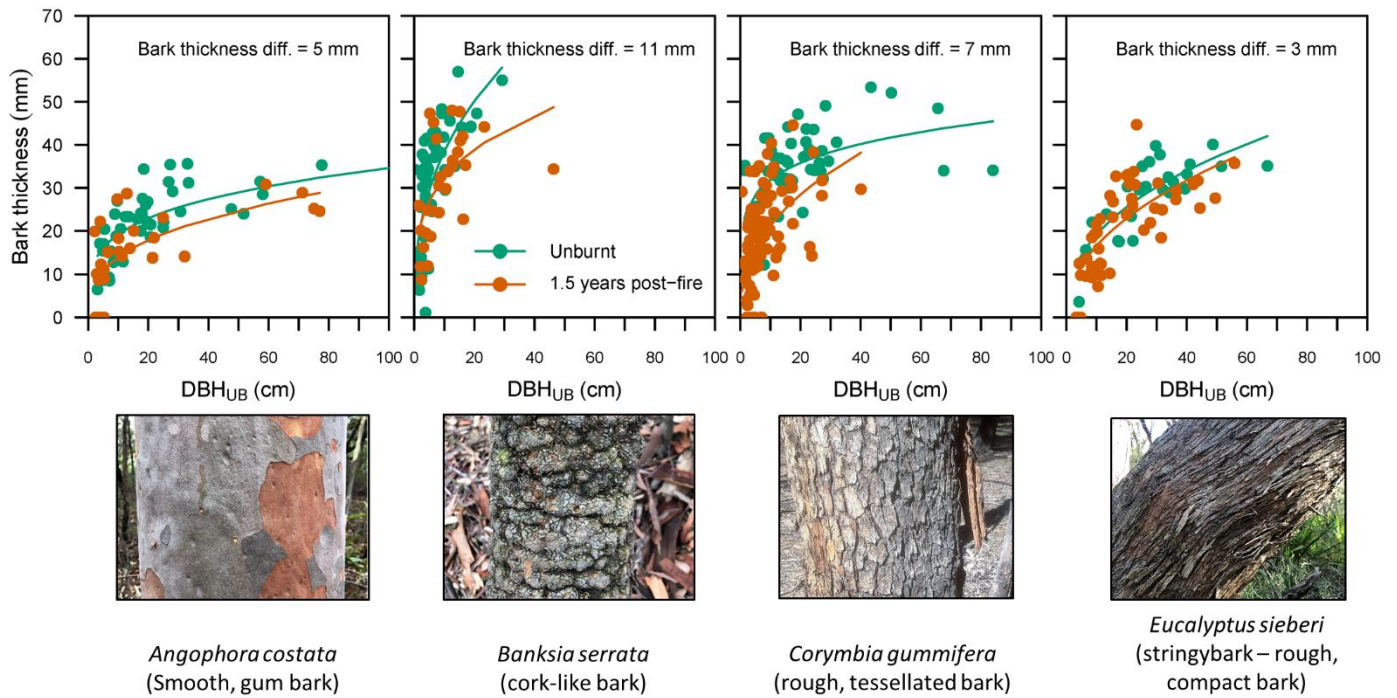
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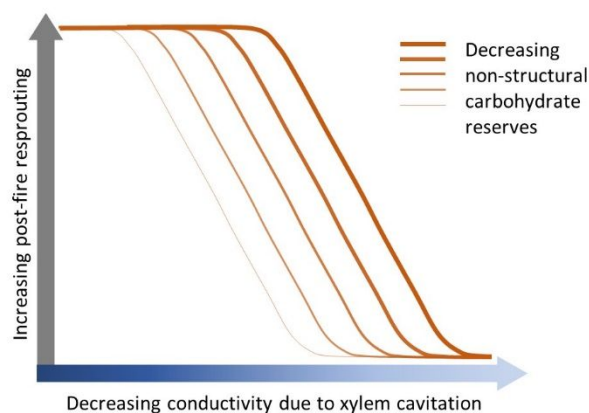
**Fig. 4.** Conceptual overview of the process of basal scarring and tree collapse from repeated fires. Photo credits: L. Collins.



1229



1230 **Fig. 5.** Power regressions of bark thickness as a function of stem size (diameter at breast height  
 1231 under bark,  $DBH_{UB}$ ) illustrating a trend of thinner bark in recently burnt trees. Recently burnt  
 1232 trees were subject to canopy fire 1.5 years prior to measurement, while unburnt trees had not  
 1233 been burnt for at least 10 years prior to measurement. Also presented are the difference in bark  
 1234 thickness between burnt and unburnt trees when  $DBH_{UB}$  is 20 cm. Data collected from dry  
 1235 sclerophyll forest in eastern Australia (Nolan et al., 2020c).



1236

1237 **Fig. 6** Hypothesised probability of resprouting exhaustion, due to carbohydrate and water  
 1238 limitations. As non-structural carbohydrate reserves are depleted, and xylem cavitation  
 1239 increases, resprouting is expected to decline. Several processes, such as shading or protracted  
 1240 water scarcity, could deplete NSC stores and induce eventual C starvation. This conceptual  
 1241 model is derived from studies on resprouting failure, xylem embolism and carbohydrate  
 1242 depletion in chaparral shrubland (Pratt et al., 2014) and *Quercus* spp. (Resco de Dios et al.,  
 1243 2020).

1244





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124

1247 **Fig. 7.** Images of eucalypt woodland in south-eastern Australia during severe drought in 2019-

1248 20, illustrating understorey and tree canopy die-off. Photo credits: R. Nolan.

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 
<b>Avoidance of fire impacts</b>				
Occurrence of fire refugia	↓	↓	↓	↕
Persistence of landscapes subject to low severity and low frequency fire regimes	↓	↓	↓	↕
<b>Post-fire resprouting</b>				
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	↓	↓	↓	↓
<b>Post-fire recruitment</b>				
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     
  High confidence     
 "NA": no identified pathway disturbance would impact on mechanism / process  
 Decrease     
  Low or medium confidence  
 No change

1249

1250 **Fig. 8.** Summary of mechanisms involved in post-fire recovery, and potential changes under  
 1251 climate induced changes in intensification of fire regimes (e.g. increased fire frequency, extent,  
 1252 severity and shifts in seasonality). Also shown are the potential influences of increasing  
 1253 incidence of stress and disturbance events on post-fire recovery. Mechanisms indicated with

1254 high confidence (blue) are those that are well supported in the literature, whereas mechanisms  
1255 with low or medium confidence (orange) are not well studied.

1256

Do not distribute