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Frameworks for identifying priority plants and ecosystems most impacted by major fires

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ABSTRACT

Globally, many species and ecosystems are experiencing landscape-scale wildfires ('megafires') and these events are predicted to increase in frequency and severity as the climate warms. Consequently, the capability to rapidly assess the likely impacts of such large fires and identify potential risks they pose to the persistence of species and ecosystems is vital for effective conservation management. In this review, we propose novel frameworks to identify which plant species and ecosystems are most in need of management actions as a result of megafires. We do this by assessing the impacts of a fire event on plants and ecosystems in the context of the whole fire regime (current fire event combined with recent fire history) and its interactions with other threatening processes, rather than simply considering the amount of habitat burnt. The frameworks are based on a combination of key species' traits related to mechanisms of decline, components of the fire regime that are most likely to have adverse impacts on species or ecosystem recovery, and biotic and environmental factors that may amplify fire impacts or pose barriers to post-fire recovery. We applied these frameworks to guide management priorities and responses following the extensive 2019/2020 fires in southern Australia, and we illustrate their application here via a series of worked examples that highlight the various mechanisms of post-fire decline the frameworks address. The frameworks should be applicable to a broader range of fire-prone biomes worldwide. Our approach will (1) promote the development of foundational national datasets for assessing megafire impacts on biodiversity, (2) identify targeted priority actions for conservation, (3) inform planning for future fires (both prescribed burning and wildfire suppression), and (4) build awareness and understanding of the potential breadth of factors that threaten plants and ecosystems under changing fire regimes.

Keywords: disease, drought, fire frequency, fire history, fire planning, fire regime, fire response, fire severity, fire spatial extent, herbivory, life history traits, recovery actions, threats, weeds.

Fires as a driving force in Australian vegetation

Australian vegetation has been shaped by fire over evolutionary timescales (Kemp 1981; Lamont *et al.* 2019) because fire is a major factor affecting the life histories and ongoing persistence of plants, animals and ecosystems. Increasing fire activity in the landscape since the mid- to late-Tertiary (30–60 million years ago) is supported by evidence of increasing deposits of charcoal in the paleorecord, notwithstanding periodic fluctuations (Lynch *et al.* 2007). Similarly, the rising importance of fire on Australian vegetation through time is evidenced by the co-incident proliferation of traits associated with recovery from fire, such as epicormic resprouting, serotiny, fire-stimulated seed germination and the expansion of fire-prone biomes across the continent (Clarke *et al.* 2015). Fire continues to maintain contemporary vegetation structure across Australia, with vast areas (~70%) of the continent's vegetation being dependant on fire as the major disturbance promoting successional processes (Russell-Smith *et al.* 2007). Further, the non-linear patterns of fire behaviour define and maintain some vegetation boundaries, most notably between rainforest and sclerophyll communities (Bowman 2000).

Fire regimes vary across the landscape because fire-regime components (frequency, intensity/severity, season and type; Box 1) exhibit biogeographic patterns related to climatic factors at regional, continental and subglobal scales (Bradstock *et al.* 2005; Murphy *et al.* 2013; Young *et al.* 2017). However, fire regimes also vary markedly across the landscape owing to environmental factors such as topography (Miller and Murphy 2017), local weather and vegetation feedbacks (Zylstra 2018), along with anthropogenic factors (Bird *et al.* 2016). Ecosystems occurring in different climatic zones thus comprise species that evolved under different fire regimes and vary in their sensitivity to changes in fire-regime components, as well as the magnitude and direction of those changes. Just because a species or ecosystem is burnt in a fire does not mean there has been an adverse impact on that entity. Understanding the likely impacts of fires on plant species and ecosystems requires knowledge of how fire regimes affect species and their life histories in the context of recent and historical fire regimes, and the varying sensitivities of ecosystems across the landscape to different components of the fire regime. Persistence of species depends on interactions between population processes and fire regimes (Keith 1996, 2012). Declines may occur when one or more components of the fire regime moves outside a species' tolerable range. For example, population declines are likely to occur in obligate-seeding or non-resprouting plants (*sensu* Pausas *et al.* 2004) if fires recur before these species can replenish their seed banks.

The survival of populations of plants and animal species is strongly influenced by the fire regime (Box 1; Gill *et al.* 1981; Whelan 1995; Keith 1996; Bradstock *et al.* 2002, 2012; Bowman *et al.* 2019), population vital rates (survival, stage transitions, recruitment) in combination with environmental factors such as climatic fluctuations (e.g. drought), anthropogenic impacts (clearing and fragmentation that affect fire behaviour and spread), and herbivory and competition with other species (native or exotic). The impacts of a fire event therefore depend on the interactive effects of environmental factors, fire regime components and species' life histories. Further, as changing climates reduce plant survival and reproductive rates, the range of fire regimes that facilitate species persistence are predicted to become more restricted (the concept of interval squeeze, Enright *et al.* 2015), potentially leaving many species and ecosystems vulnerable to decline. More extreme fire weather is predicted under a changing climate, likely increasing the frequency and severity of fires (and potentially reducing fire patchiness and fire refugia), along with the extent and severity of droughts and storms (Bradstock 2010; Cary *et al.* 2012; Miller and Murphy 2017; Abram *et al.* 2021), all of which affect ecological responses to fires (Miller and Murphy 2017). The widespread fires that occurred in south-eastern Australia in the summer of 2019/2020 are consistent with predicted outcomes of global warming (Nolan *et al.* 2020*a*), as are recent large wildfires in California (Keeley and Syphard 2021) and Mediterranean Europe (Ruffault *et al.* 2020).

Fire management for biodiversity conservation relies on an ability to accurately identify and implement fire regimes that facilitate species persistence and maintain diverse plant communities and ecosystems. In essence, this means identifying and avoiding those fire regimes that are likely to be detrimental to the persistence of species and ecosystems. Species and associated vegetation evolved under lightning-ignited fires driven by climatic, topographic and edaphic drivers until the arrival of Indigenous Australians (at least 50–60 000 years ago) who used fire and initiated additional human ignitions. In the past 230 years, fires initiated by European settlers include prescribed ignitions for management purposes (e.g. pastoral management and more recently, hazard reduction), accidental ignitions and arson. Ignitions have therefore not only increased in frequency with human intervention, but also in their spatial and temporal distribution across landscapes, seasons and years. Such ignitions have led to fire regimes diverging in different directions from natural patterns through different eras of human activity, as well as because of past and current climate changes. Fire regimes in contemporary Australia are a product of fires that originate from both natural (primarily lightning) and human ignitions (Indigenous burning and planned fires for pastoralism, fuel reduction or conservation, along with arson or accidental fire escapes; Bowman *et al.* 2020). Understanding of how alterations to fire regimes affect plants and other biota has only recently begun to develop (Parson and Gosper 2011; Keith 2012; Kelly *et al.* 2020).

Fires of human origin add to the natural complexity of fire regimes in the landscape; however, conversely, European land management practices may also supress the outcomes of natural ignitions through active fire suppression and landscape fragmentation (Parsons and Gosper 2011). Many current applications of fire by humans aim to reduce fuel loads, either over broad-scale landscapes, or in and around areas that contain dwellings and other assets. Fire is also used to promote regeneration in logged forests. Unplanned fires (wildfires resulting from lightning or unintentional human ignitions) combine with this prescribed fire matrix to create complex patterns of fire regimes in different parts of the landscape (Bradstock *et al.* 2005). The consequences are expressed in the interval, timing and spatial dimensions of fire regimes (Bond and van Wilgen 1996). For example, some patches are frequently burnt or have short intervals between some successive fires, whereas others are rarely burnt or remain entirely unburnt, either because fragmentation has isolated them from fire pathways, or because feedbacks have allowed them to develop low-flammability properties. Event characteristics, including fire severity, seasonality and extent, all vary spatially and temporally

Box 1. The fire regime and related components that cause declines in biodiversity

What is the fire regime?

There are four main elements of the fire regime (Gill 1975; Department of Agriculture, Water and the Environment 2022) and several additional fire components that can affect biodiversity. The impacts they can have on plants and ecosystems can result from individual elements or the interactions among them. Biological impacts are described below at the level of species' populations, but each has implications for ecosystems depending on the structural, functional and compositional roles of the species in their ecosystems (Akçakaya *et al.* 2020). Biological impacts are as follows:

Core elements

Frequency

Definition: The number of fires per unit time at a point in the landscape.
Impacts: Fire frequency can affect two main components of plant life histories:

- Recruitment:
  - Frequent fires that do not allow time for replenishment of the soil or canopy seed bank will lead to population declines, and where the seed bank is exhausted, local extinction can occur in obligate-seeding species (immaturity risk, Nolan *et al.* 2021).
  - Successful recruitment of plants from juvenile to adult in resprouting species requires development of organs that allow resprouting after fire (e.g. lignotubers, bulbs, rhizomes, etc.). Frequent fire can eliminate juvenile plants before their regenerative organs develop sufficiently to be able to survive and resprout (Auld 1990; Keith 1996).
  - Infrequent fire may see standing plants senesce and seed banks decay, resulting in population decline until seed banks are ultimately exhausted over long inter-fire periods (e.g. Auld and Scott 2004). This is most likely to occur in species with both short-lived standing plants and seed banks and in which recruitment is rarely successful in the inter-fire period (Keith 1996).
  - Infrequent fire may lead to competitive exclusion by ecosystem dominants (Keith and Bradstock 1994).
- Survival:
  - Frequent fire can delete bud banks and starch reserves or structural integrity of resprouting species and reduce their capacity to resprout and/or cause structural weakening (Keith 1996; Nolan *et al.* 2021).

Intensity

Definition: Energy output or heat release from fire per unit time at a point in the landscape.
Impacts: see *Fire severity* below.

Season

Definition: The time of year of a specified fire event.
Impacts: There are at least eight ways in which fire season can affect plant life cycles (see Miller *et al.* 2019 and Keith *et al.* 2020*c* for details). Fire season may limit population persistence through reductions in adult survival and growth, post-fire flowering and seed production, the magnitude of seed banks, juvenile growth and maturation, tolerance of seeds to heat, post-fire seed survival and establishment, and dispersal distances.

Type

Definition: Whether a specified fire event at a point in the landscape burns at or above ground level (consuming live/dead biomass), or below ground level (consuming semi-decomposed organic matter, such as peat, coal).
Impacts: Relative to above-ground fires, below-ground fires can cause elevated mortality of seeds and regenerative organs, leading to greatly reduced post-fire recovery (Keith *et al.* 2022*a*).

Additional fire components that can affect biodiversity (after Nolan *et al.* 2021; Department of Agriculture, Water and the Environment 2022)

Severity

Definition: The amount of organic matter consumed in a fire event at a point in the landscape (see Keeley 2009 for review of terms fire severity, fire intensity and burn severity).

Impacts: Effects of both fire intensity and severity depend on the exposure of critical plant tissues to lethal temperatures (both above and below ground). In turn, this depends on aspects of fire behaviour as well as the location of the critical plant tissues. Both fire intensity and fire severity can be useful indicators of exposure to lethal temperatures under particular circumstances, but neither precisely represents temperature exposure. Whereas, fire intensity is challenging to measure in real time (Alexander 1982), a number of real and proxy metrics are available to estimate fire severity, either on-ground or from remote sensors, with before/after fire comparisons or from post-fire observations only (Keeley 2009). Each of these methods involves simplifying assumptions that fail to hold in some circumstances.

Positive and negative effects of high exposure to lethal temperatures (i.e. fire severity) are known.

- *Negative*. Heating may be sufficient to kill plant tissues leading to plant mortality or a reduced capacity to resprout (e.g. Whelan and Ayre 2022) or, in trees, a reduced ability to resprout from the canopy or trunk and an increased risk of charring and stem collapse (Mackenzie *et al.* 2021; Nolan *et al.* 2021).
- *In species with canopy seed banks – positive and negative*. Sufficient heating may be needed to cause rapid opening of fruits to release seeds after a fire (Clarke *et al.* 2010), but too much heating may be lethal to seeds in those species with thin-walled fruits that are exposed to high temperatures, e.g. *Hakea* species (Bradstock *et al.* 1994), *Picea mariana* (Splawinski *et al.* 2019) or fruits that are not clustered (*Eucalyptus, Kunzea, Leptospermum*, Judd and Ashton 1991).
- In species with soil seed banks:
  - *Negative*. Fires that lead to high levels of soil heating (usually severe fires) can kill seeds close to the soil surface and this is of most concern in small-seeded species that cannot germinate from deeper in the soil profile (Bond *et al.* 1999; Auld and Denham 2005).
  - *Positive*. Physically dormant species (and many physiological or morphophysiological dormant species) require a degree of soil heating to promote germination. Although responses vary across species and habitats, some species respond well to high levels of soil heating but will not germinate with low or little soil heating (Auld and O'Connell 1991; Palmer *et al.* 2018).

Extent

Definition: Area within the spatial boundary of a fire event.
Impacts:

- Small fires may lead to high levels of herbivore and predator impacts on post-fire recovering vegetation because of edge effects (Tasker *et al.* 2011; Keith 2012).
- Small fires may increase the risk of high fire frequency as available fuel in surrounding unburnt areas may carry a future fire into and across the small burnt areas.
- Large fires may reduce the availability of fire refugia (*sensu* Meddens *et al.* 2018) that may be needed as a source for post-fire population recovery (depending on fire patchiness; see below), but large fires are not homogeneous (Bradstock 2008).

Patchiness

Definition: The spatial configuration of patches with different fire characteristics (varied levels of severity, including unburnt) within a specified area.
Impacts:

- Patchy fires may increase the risk of high levels of herbivore and predator impacts on post-fire recovering vegetation because of edge effects (Tasker *et al.* 2011; Keith 2012).
- Patchy fires may increase the risk of high fire frequency as available fuel in surrounding unburnt areas may carry a future fire into and across the patchily burnt areas, even when the preceding fire occurred very recently.
- Patchiness in fires promotes the availability of fire refugia that may be needed as a source for post-fire population recovery (e.g. Bird *et al.* 2013), although the nature of what level of patchiness is beneficial remains uncertain (Parr and Andersen 2006).

across different landscape and pyroclimate types, (e.g. see Russell-Smith *et al.* (2007) for variation in fire seasonality across Australia). In summary, landscapes have both complex spatial patterns of fire regimes, as well as complex requirements for the persistence of the full diversity of plant species, vegetation communities and ecosystems under recurring fires.

Significance of the Australian 2019/2020 wildfires

The fires that occurred in south-eastern Australia in the 2019/2020 fire season were among the most extensive of southern Australia's European era (Davey and Sarre 2020; Nolan *et al.* 2020*a*). The fires burnt ~7 Mha across south-eastern

Australia between September 2019 and March 2020 and burnt a greater proportion of Australia's temperate broadleaf and mixed forest biome than any other global forest biome in the past 20 years (Boer *et al.* 2020; Collins *et al.* 2021). Much of the area was estimated to have burnt at high severity (Collins *et al.* 2021) and the fires affected a substantial proportion of the known ranges of large numbers of vertebrate fauna (Ward *et al.* 2020; Legge *et al.* 2022), vascular plant species (Auld *et al.* 2020; Gallagher *et al.* 2021), terrestrial (Lindenmayer and Taylor 2020; Keith *et al.* 2022*b*) and aquatic (Silva *et al.* 2020) ecosystems. This created huge challenges for land managers dealing with the conservation of biodiversity and demonstrated the need for frameworks to guide what species and ecosystems are most likely to have been adversely affected as a result of the 2019/2020 Australian wildfires.

The scale and severity (*sensu* Box 1) of the 2019/2020 fires was clearly unprecedented and influenced by the trend for increased area of forest burning driven by climate change (Canadell *et al.* 2021). Diagnosing the potential impacts of these fires is not straightforward because fire is a recurring event, even if only rarely, in virtually all of the ecosystems affected (Keith and Tozer 2017; Miller and Murphy 2017). To forecast potential declines, a variety of factors need to be evaluated, including the complex patterns of antecedent fire history, regional variability in pre- and post-fire weather, diverse land uses within the fire footprint and an array of threats posed by alien predators, herbivores, competitors and pathogens that pose considerable risks of adverse impacts to plant species and ecosystem recovery. Timely assessments across the full range of biota and their national or global distributions are essential to inform effective management responses.

Frameworks for rapidly predicting impacts of fire events on plant species and ecosystems

Framework aims

Here we present novel predictive frameworks developed to identify, first, plant species and, second, ecosystems that are expected to have been most affected following a major wildfire event, so that those most in need of management actions can be identified. These frameworks go beyond simple reporting of how much habitat was burnt in a fire. The Frameworks assume that risks of decline from fire-related impacts are related to the proportion of the species/ecosystem range affected by a given mechanism of decline, in a comparable way to assessing risk ranking on the basis of geographic distribution in IUCN Red List Criteria (Keith *et al.* 2018). They build on the understanding that fire regime impacts (Box 1) are important in the response of biodiversity to individual fire events (Bradstock *et al.* 2012; Keith 2012; Miller and Murphy 2017) as are both biotic and abiotic factors, including threats from, in particular, weeds, pests and pathogens and human impacts. We integrated these components into a scheme that permits comparisons of relative exposure to impacts across either species or ecosystems. The frameworks are decision support tools to guide identification of species and ecosystems that are likely to need active management during post-fire recovery, including what factors may need to be addressed in such recovery. We provide worked examples of applications of these frameworks from the emergency response to the 2019/2020 Australian bushfire season, noting that they are equally applicable to other major wildfire events within Australia and globally. The frameworks

1. provide transparent, logical pathways for decision-making that supports well reasoned strategic policy, management and resourcing responses in an emotionally charged post-fire social environment when fires occur;
2. identify the key issues that need to be addressed to ameliorate impacts of megafires on plants and ecosystems. This includes consideration of the fire regime and its components (Box 1), species' life histories, ecosystem processes, environmental conditions and other biotic and abiotic threats;
3. use available data to prioritise species and ecosystems for post-fire conservation management, including field-impact assessments and any necessary recovery actions (both immediate and medium- to long-term); and
4. allow for ongoing re-evaluation of which species and ecosystems are most likely to be at risk from future fires and landscape-scale threats.

Summary of framework elements

Here we describe related individual frameworks that were designed for species and ecosystems respectively. The frameworks predicted the likelihood of poor post-fire recovery via three components (mechanisms, sensitivity and exposure):

1. Mechanisms of decline and their interactions, e.g. combinations of life-history traits and threats that make species prone to population declines or local extinctions if they are affected within the spatial extent of a fire;
2. Sensitivity of species and ecosystems to the identified mechanisms of decline (e.g. sensitivity to high fire frequency or to fire-promoted pathogens (such as *Phytophthora* or myrtle rust)); and
3. Exposure in the landscape where these mechanisms are most likely to be expressed (e.g. the overlap/intersection of species' or ecosystem distributions with the spatial extent of the fire event being investigated (excluding unburnt patches and refugia that do not burn) AND the particular threat of concern).

Each framework includes 11 criteria or mechanisms of decline (across four main themes, see below) related to the fire regime, environmental conditions, life history of species and concurrent threats (Fig. 1, Tables 1, 2). These mechanisms are as follows:

- Components of the fire regime (see Box 1 for explanation terms and potential impacts on biodiversity) that are most likely to have adverse impacts on species or ecosystem recovery through disruption of life-history processes (I, fire sensitivity; II, short fire intervals; III, high fire severity; IV, recruitment failure)
- Fire-environment abiotic interactions, including prevailing environmental conditions (for species: V, drought; VI, erosion; VII, elevated temperatures; or for ecosystems: V, drought; VI, erosion, disturbance or pollution; and VII, altered hydrology)
- Fire-biotic interactions, including sensitivity of species or ecosystems to a fire and biotic threats to post-fire recovery (VIII, herbivore impacts; IX, disease; X, weed invasions)

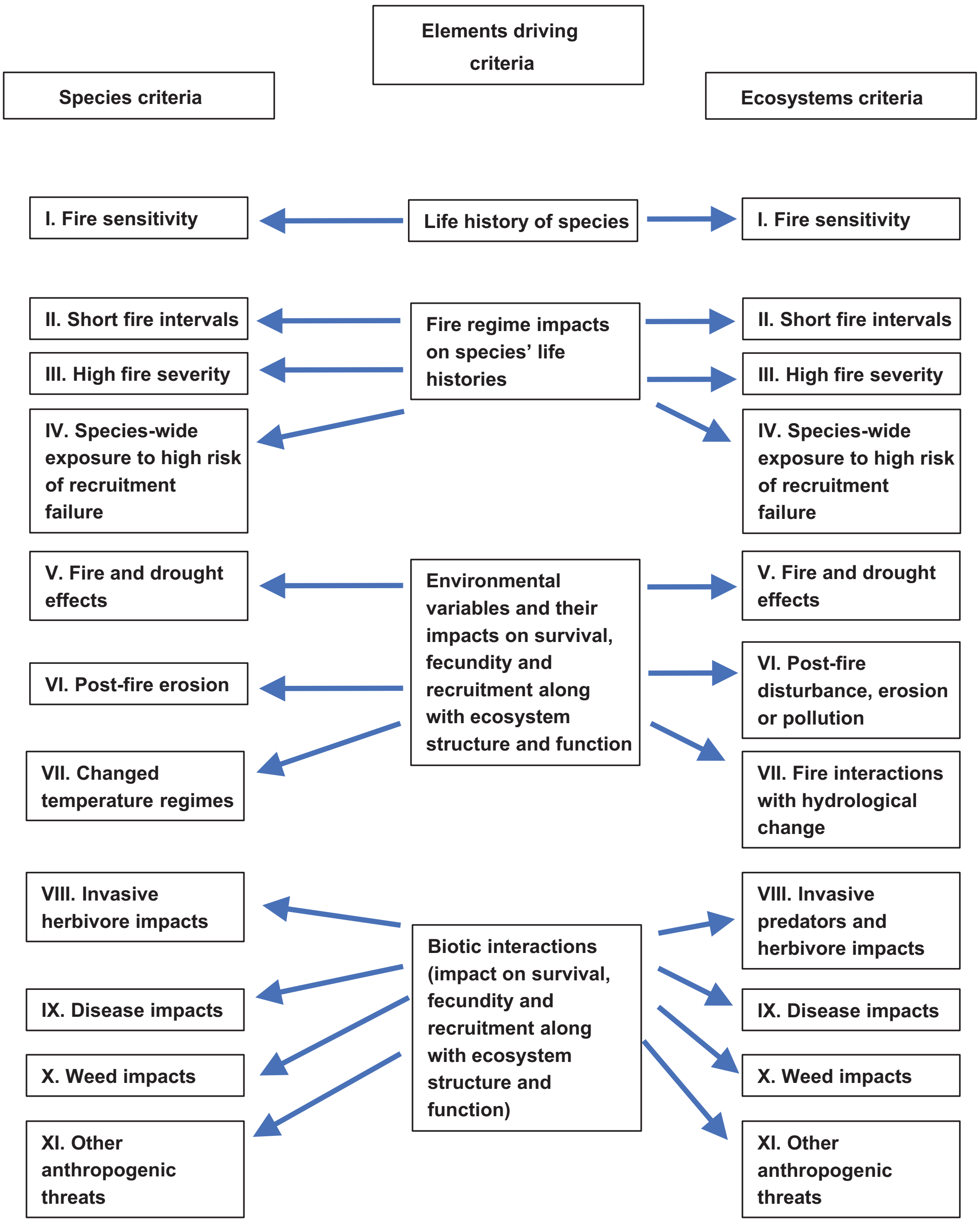


Fig. 1. Summary of major elements for post-fire assessment criteria in frameworks for identifying priority plant species and ecosystems most affected by major fires.

Table 1. Prioritisation framework for assessment of plant-species impacts following major fire events such as the Australian 2019/2020 bushfires. Risk is high (red), medium (orange), low (yellow) and no risk (no colour). Framework criteria are in dark grey, while main subcriteria are in light grey.

Criterion I. Fire sensitivity				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND at least one of (b) or (c):				**OR** neither (b) nor (c) apply:
(b) Long-lived tree prone to collapse from basal charring				
(c) Cannot resprout AND has no seed bank				
Criterion II. Short fire intervals				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND these sites or habitat have experienced one or more fires within either (b), (c) or (d):				**OR** neither (b), (c) nor (d) apply:
(b) The preceding 5 years for non-woody species				
(c) The preceding 15 years for woody species (excluding long-lived trees prone to collapse from basal charring)				
(d) The preceding 50 years for long-lived trees prone to collapse from basal charring				
Criterion III. High fire severity				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt at high severity in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Survival of standing plants and/or seed bank is known or suspected to be sensitive to high fire severity				
Criterion IV. Species-wide exposure to high risk of recruitment failure (obligate-seeding species only)				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	>0%	>0%	>0%	0%
AND:				**OR**:
(b) Known sites or habitat presently comprising immature plants*:	≥50%	≥30% and <50%	>0% and <30%	0%
**Based on the sum of known sites or habitat burnt in the major fire event AND known sites or habit that were <u>unburnt</u> in the major fire event but experienced one or more fires within either:* *i) The preceding 5 years for non-woody species* *ii) The preceding 15 years for woody species (excluding long-lived trees prone to collapse from basal charring)* *iii) The preceding 50 years for long-lived trees prone to collapse from basal charring*				
Criterion V. Interactive effects of fire and drought				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND Evidence or likelihood of (b) or (c):				**OR** neither (b) nor (c) apply:
(b) Significant pre-fire drought AND either (i) Resprouter or (ii) Obligate seeder without a persistent soil seed bank				
(c) Incidence of post-fire drought within 18 months of the major fires				
Criterion VI. Post-fire erosion				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of severe post-fire soil erosion leading to mortality of individuals or depletion of soil seed banks				
Criterion VII. Elevated winter temperatures or changed temperature regimes				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50% (obligate seeders)	>0% and <30% (obligate seeders) OR >0% and <50% (resprouters)	0%
AND both ((b) and (c):				**OR** (b) or (c) does not apply:
(b) Cold stratification known or suspected to be needed for successful seedling recruitment post-fire				
(c) Evidence or likelihood of elevated winter temperatures in the first year or two post-fire				
Criterion VIII. Post-fire herbivore impacts				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50% (obligate seeders)	>0% and <30% (obligate seeders) OR >0% and <50% (resprouters)	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant post-fire grazing impacts				
Criterion IX. Fire-disease interactions				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant pathogen or disease susceptibility				
Criterion X. Weed invasion				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant weed impacts post-fire				
Criterion XI. Localised anthropogenic disturbances as plausible threats				
	High	Medium	Low	No risk
(a) Known sites or habitat burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood that species has been significantly impacted by one or more plausible anthropogenic threats not addressed by Criteria I-X above				

Table 2. Prioritisation framework for assessment of ecosystem impacts following major fire events such as the Australian 2019/2020 bushfires. Risk is High (red), medium (orange), low (yellow) and no risk (no colour). Framework criteria are in dark grey, while main subcriteria are in light grey.

Criterion I. Fire sensitivity				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Ecosystem with functionally important components that lack effective post-fire persistence and dispersal mechanisms				

Criterion II. Short fire intervals				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND Ecosystem has experienced one or more fires within either (b), (c) or (d):				**OR** neither (b), (c) nor (d) apply:
(b) The preceding 5 years for grasslands and non-woody ecosystems				
(c) The preceding 15 years for woodland, heath (excluding those on rock outcrops) or dry forest ecosystems				
(d) The preceding 50 years for rainforest, wet eucalypt forest, rock outcrop, alpine or semiarid/arid ecosystems				

Criterion III. High fire severity				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt at high severity in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Ecosystem has components (species groups, habitat features, substrates) known or suspected to be sensitive to fire severity (i.e., high severity fire is likely to cause death or serious damage and recovery is not certain)				

Criterion IV. Ecosystem-wide exposure to high risk of recruitment failure				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	>0%	>0%	>0%	0%
AND:				**OR**:
(b) Evidence or likelihood of significant cumulative or lagged impacts from two or more mechanisms (Criteria I-III, V-XI) within the burnt area				

Criterion V. Interactive effects of fire and drought				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND Evidence or likelihood of either (b) or (c):				**OR** neither (b) nor (c) apply:
(b) Significant pre-fire drought within the 18 months prior to the fire event				
(c) Significant projected post-fire drought within 18 months after the fire event				

Criterion VI. Sensitivity and exposure to post-fire disturbance, erosion or pollution				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of severe post-fire disturbance, erosion or pollution impacts				

Criterion VII. Fire interactions with hydrological change				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant impacts from hydrological change				

Criterion VIII. Post-fire interactions with invasive predators and herbivores				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant post-fire grazing or predation impacts				

Criterion IX. Fire-disease interactions				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant pathogen/disease impacts post-fire				

Criterion X. Weed invasion				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood of significant weed impacts post-fire				

Criterion XI. Localised anthropogenic disturbances as plausible threats				
	High	**Medium**	**Low**	**No risk**
(a) Ecosystem distribution burnt in major fire event:	≥50%	≥30% and <50%	>0% and <30%	0%
AND:				**OR** (b) does not apply:
(b) Evidence or likelihood that ecosystem has been significantly impacted by one or more plausible anthropogenic threats not addressed by Criteria I-X above				

- Fire–human interactions, including XI, localised anthropogenic disturbances such as disturbances from vehicles or foot traffic, rubbish dumping, clearing of habitat and logging (among others).

Framework application

The two frameworks (Fig. 1, Tables 1, 2) were developed and implemented nationally in Australia, for species and ecosystems respectively, following the 2019/2020 fire season. The criteria enable each species or ecosystem assessed to be assigned to an ordinal category ('high', medium', 'low', 'no impact' or 'data deficient') on the basis of spatial thresholds drawn from the IUCN risk-assessment protocols (Bland *et al.* 2017). Categories are indicative of the risk of recovery failure and decline, as follows:

- *HIGH*: high degree of exposure to the risk of decline. An urgent assessment of initial fire impacts and threats to recovery is required and post-fire monitoring of recovery where impacts are significant.
- *MEDIUM*: medium degree of exposure to the risk of decline. Assessment of initial fire impacts and threats to recovery is required and post-fire monitoring is recommended.
- *LOW*: low degree of exposure to the risk of decline. Post-fire monitoring may be conducted opportunistically during site visits.
- *NO IMPACT*: negligible exposure to the risk of decline or not burnt in the fires.
- *DATA DEFICIENT*: insufficient data to enable an assessment.

Species or ecosystems should be assessed against as many criteria as possible, depending on available data. Outcomes of each criterion are evaluated concurrently, with the highest category of concern across all criteria being used to allocate a species or ecosystem to an overall category, recognising that factors driving decline may operate independently or interact in complex ways, and hence the criteria are best not combined in an additive or multiplicative manner (Burgman *et al.* 1999; Keith 2009). This emulates the approach used in established frameworks such as the IUCN Red List Criteria for Threatened Species (IUCN 2022) and IUCN Red List Criteria for Ecosystems (Bland *et al.* 2017). Separate reporting on each criterion also allows an informed comparison of the factors driving the highest likelihood of decline for groups of interest, such as groups of species or higher taxa (e.g. families), life-form groups, fire-response groups, or regional floras.

Species or ecosystems for which the highest ranking is 'NO IMPACT' on the basis of assessments of at least three criteria are assigned an overall rank of NO IMPACT, but otherwise must be assigned to the 'DATA DEFICIENT' category until at least three criteria are assessed. This is an important distinction and highlights species or ecosystems with important knowledge gaps that require addressing for their effective conservation management.

Dealing with interactions across criteria

While the frameworks require assessment of each criterion individually, interactions among criteria may also arise. In such cases, it is useful to recognise that individual criterion outcomes may be affected by other factors. For example, a pre-fire drought may exacerbate the impact of high fire severity. This may occur where pre-fire drought reduces the capacity for species to resprout post-fire, although prior depletion of carbohydrate reserves and the impact of this effect vary with fire severity. In many such cases, the measurement of impacts (post-fire recovery) will necessarily include outcomes of the interaction among factors because each factor cannot be clearly separated when assessing (or sampling) post-fire impacts. In other interactions among criteria, there may be temporal differences in the expected timing of impact; for example, the interaction between high fire frequency and post-fire herbivory is a two-step process, with initial impacts of high fire frequency and subsequent impacts of herbivory on recovery. When examining the strength of these effects through one-off sampling of post-fire recovery, often all that can be measured is their combined interaction. Hence, in most cases, major interaction effects are included by recognising the combined effects on species or ecosystems under each driving criterion in the frameworks. When the level of impact of individual factors within interactive effects can be identified, one option is for the rank to be increased by one level when there is a synergistic (or additive) interaction of threats, and decreased by one level where there is a compensatory interaction (in the same fashion as application of the IUCN Red List criteria at regional or national scales; IUCN 2012).

Data issues

Data requirements

Assessing priorities for post-fire conservation action requires data on the spatial distribution and fire-response traits of species and ecosystems, as well as the distribution, extent and severity of threats and other relevant environmental factors. Assessing impacts after a major fire event specifically requires data on fire spatial extent and fire-severity mapping for the fire event being investigated, as well as reliable fire-history mapping. Data availability will vary among assessment areas, taxa and ecosystems, and it is important to aim for standardised national fire-related datasets (Bowman *et al.* 2020). Here, we provide several examples to illustrate the types of data that could be used in the assessments and the need to address standardisation, licensing, transparency and efficient workflows, drawing on the assessments of potential impacts for plants (Auld *et al.* 2020; Gallagher 2020; Gallagher *et al.* 2021, 2022) and ecosystems (Keith *et al.* 2020*a*, 2022*b*) conducted in response to the Australian 2019/2020 fire season.

Assembling species and ecosystem lists

An appropriate target list of species or ecosystems forms the foundation of any assessment of impacts or management needs after a fire event. Ideally, all species co-occurring within the spatial extent of the fire event should be targeted for assessment. This requires species-occurrence information (see below) and validation of current species nomenclature against a taxonomic authority, including identifying taxonomic synonyms. For instance, the Australian Plant Census provides up-to-date information on the status of taxonomic names of Australian plants, and similar resources exist in many countries (e.g. USA: https://www.itis.gov/) and globally (e.g. The Plant list, http://www.theplantlist.org/ and Plants of the World Online http://www.plantsoftheworldonline.org/; Catalogue of Life: https://www.catalogueoflife.org/). Checking of taxonomy can be automated through workflows in R using packages such as taxise (Chamberlain and Szöcs 2013), or via online portals such as the Taxonomic Resolution Naming Service (TNRS; https://tnrs.biendata.org/).

For ecosystems, the analogous data required are a typology that identify all the ecosystem types within a study area at a suitable level of thematic resolution. The units of the typology should represent the critical processes and dependencies that sustain ecosystem components and functions. IUCN's Global Ecosystem Typology (GET, Keith *et al.* 2020*d*) provides a suitable framework for this purpose. The GET facilitates the integration of national or jurisdictional-level typologies based, for example, on the classification of vegetation communities under a hierarchy of types, with similar functional responses to fire regimes in combination with the posited threats.

Spatial data on species and ecosystem occurrence

National and international databases can be used to access georeferenced information on occurrences of species. For instance, international resources such as the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) or national resources such as the Australasian Virtual Herbarium (AVH; https://avh.chah.org.au/) provide open access to vouchered records of species occurrence. Herbarium specimens have several advantages over unvouchered records of species-occurrence information, including verification of taxonomic identity by experts, the ability to trace information back to a vouchered collection and to update analyses following taxonomic revisions (Heberling and Isaac 2017). However, bias in spatial patterns of sampling in herbarium specimens towards roads and access tracks may limit the accuracy of species ranges inferred from them (Haque *et al.* 2017). To address this issue, secondary sources of information on species range may be used in conjunction with herbarium occurrence data, such as records with lower standards of verification (e.g. research-grade observations in iNaturalist, https://www.inaturalist.org/), data from systematic vegetation surveys (e.g. BioNet systematic flora surveys, https://www.environment.nsw.gov.au/atlaspublicapp/UI_Modules/YETI_/FloraSearch.aspx), expert-derived range maps, or the spatial projections from species distribution models. Ideally, multiple lines of evidence about species occurrence should be used in parallel when applying the frameworks and the highest risk (most precautionary) category across the different sources used to rank species.

Steps should be taken to minimise spatial inaccuracies of species-occurrence records. For example, the full, original, as-held data for any unique threatened species records should always be obtained directly from the original custodian to ensure accurate locality descriptions and georeferences (because sensitive information is often denatured prior to incorporation into third-party repositories). Checking georeferences for consistency against the location description allows detection of erroneously georeferenced points that may otherwise bias predictive modelling of species distri butions or population-level assessments of fire impact/escape. This highlights the need for resourcing to maintain and update databases of reliable species occurrence records so that georeferences are an accurate representation of the location information.

For ecosystems, maps of proxy units such as vegetation types can be obtained from government repositories or scientific literature, or generated via a wide range of remote-sensing and modelling approaches (Bredenkamp *et al.* 1998). Similar verification and error-correction procedures should be applied as those recommended above for species.

Fire-response traits for species and ecosystems

The framework criteria use a suite of traits to identify species or ecosystems that are susceptible to different fire-related causes of decline. Traits are the measurable characteristics of organisms that shape their ecological performance (Westoby *et al.* 2002; Gallagher *et al.* 2021) and in the context of post-fire assessment frameworks, specifically include factors such as habit, woodiness, fire-response strategy (capacity to resprout versus only recruit via post-fire seedings, *sensu* Pausas *et al.* 2004; Clarke *et al.* 2015; Prior and Bowman 2020), seed-bank type (canopy- vs soil-stored), seed-dormancy types (physical, physiological and morphophysiological, among others) as well as various germination requirements and drought-avoidance mechanisms. It is now possible to source data on plant species traits directly from large, aggregated databases such as TRY (Kattge *et al.* 2020), LEDA (Kleyer *et al.* 2008), BIEN (Maitner *et al.* 2018) and AusTraits (Falster *et al.* 2021), as well as from more bespoke datasets for particular plant groups (e.g. bryophytes; Bernhardt-Römermann *et al.* 2018; or plant parts; e.g. roots; Iversen *et al.* 2017). Fire-response traits may also be sourced from environmental management agencies that use ecological information in planning for prescribed burning.

For some species, multiple observations of the same trait may lead to conflicts in assigning species to categories (e.g. because of natural variation, variation owing to particular factors such as fire severity, observer error etc.), and strategies are required for choosing the appropriate trait value. For instance, consensus across datasets may be used to assign a species as woody or non-woody. Similarly, continuous or ordinal trait values may need to be partitioned or aggregated to form appropriate categories. This may include grouping information on growth forms (e.g. tree, shrub, grass, herb) and standing plant longevity (e.g. annual, biennial, perennial) to inform woody and non-woody categories. As per species-occurrence records, prior to use, taxonomic names associated with trait observations need to be assessed for consistency and taxonomic synonyms to ensure alignment with the species list of interest.

The requirement for large, comprehensive datasets on plant traits and plant responses to components of the fire regime (including variation in responses), in addition to comprehensive and spatially accurate databases of species-occurrence records, highlights the need for forward planning and investment. These databases need to be established and maintained at the national scale in advance of future megafire events to enable a rapid and effective responses.

Framework criteria and their assessment

The 11 criteria representing key mechanisms of post-fire decline identified in each framework (Tables 1, 2) and the potential methods for assessing each criterion are presented below.

Criteria relating to morphological traits

I. Fire sensitivity

Some plant species, including some functionally important species within ecosystems, have no means of *in situ* persistence through fire events, because they lack regenerative organs, and on-site propagule storage (e.g. R-P- of Pausas *et al.* 2004) or long-distance dispersal traits to facilitate recolonisation. Some species or ecosystems may currently persist in disequilibrium states and may be incapable of re-establishment under present-day conditions. Examples include certain rainforest species (Boxes 2, 3) and peatlands, forests or heaths dominated by paleo-endemic species (e.g. Kirkpatrick *et al.* 2010; Bliss *et al.* 2021). A single fire event may eliminate these entities or substantially diminish their role in the community, an effect that persists until they slowly disperse and re-establish from unburnt patches.

Assessing fire sensitivity. There is no globally comprehensive database on fire sensitivity of plant species, although geographically scoped fire-response databases and classification schemes (e.g. Gill and Bradstock 1992) can inform fire sensitivity, as may data held in global or regional databases such as TRY (Kattge *et al.* 2020) and AusTraits (Falster *et al.* 2021). Pausas *et al.* (2004) compiled data on a small number of species that lacked regenerative organs and seed banks to support post-fire recovery by sprouting or seeding respectively (R-P-), and this was also flagged by Prior and Bowman (2020). Information on the susceptibility of species to single fire events can also be based on available scientific literature (e.g. *Athrotaxis*, Bliss *et al.* 2021) and expert opinion.

Species: long-lived trees that are prone to collapse from prolonged basal charring during fires are candidates for Criterion I (Table 1, Boxes 2, 3). For example, Gallagher (2020) used trait and spatial information to identify 463 rainforest-tree taxa greater than 30 m in maximum height (taking height as a proxy for longevity) using the AusTraits database. Long-lived tree species sensitive to fire may also occur in low-productivity environments and require substantial time (>30–50 years) to regenerate and set seed post-fire.

Ecosystems: Keith *et al.* (2020*a*) identified ecosystems that rarely experience fire and were sensitive to a single fire event, because species with key structural or functional roles lack regenerative organs and seed banks that enable autogenic recovery. The main ecosystem types that include such species are rainforests and samphire shrublands and herbfields, sphagnum bogs, as well as peatland ecosystems, because peat is combustible should substrate fires occur, and may take many decades or centuries to re-accumulate to similar depths. Most rainforest trees have thin bark (Lawes *et al.* 2013) and, even though a surprising number has basal regenerative buds, top-kill resulting from fires with scorch heights as low as 2 m may result in structural transformation of large stands that may take many decades to re-establish their mesic micro-climate, arboreal substrates for tree-dependent flora and fauna and structural complexity.

Exposure of fire-sensitive species and ecosystems to any fire event can be estimated by intersection of their distributions with the fire extent (e.g. for the Australian 2019/2020 fires – the National Indicative Aggregated Fire Extent Dataset; Department of Agriculture, Water and the Environment 2020).

Criteria relating fire-regime impacts on species' life-history processes

II. Short fire intervals (high fire frequency)

The effects of high-frequency fire regimes on species persistence, community composition and structure through disruption of life histories and resource availability are well established (e.g. Keeley and Brennan 2012; Enright *et al.* 2015; Kelly *et al.* 2020). Both species and ecosystems may vary in their capacity to persist under repeated, short fire intervals. Exposure to short temporal intervals between successive fires can disrupt

(i) the replenishment of seed banks which are essential to post-fire recruitment and population persistence;

Box 2. Species criteria: fire sensitivity (Criterion I) and fire-disease interactions (Criterion IX)

Case study: *Eidothea hardeniana* (nightcap oak, Proteaceae).

Eidothea hardeniana (photo: Simone Cottrell, Royal Botanic Gardens and Domain Trust).

Background: *Eidothea hardeniana* is a rainforest species the life-history of which is poorly known. It is restricted to the Nightcap Range in north-eastern New South Wales, Australia. The total population is very small.

Conservation status: Critically Endangered (IUCN Red List, Forster *et al.* (2020); *EPBC Act*).

Relevant life-history traits

- **Habit:** thin-barked, long-lived, rainforest tree up to 15–40 m (Weston and Kooyman 2002) with lichen-encrusted bark.
- **Fire response:** a weak resprouting capacity (basal coppicing) in response to low-severity fire. Prone to collapse from basal charring. Mortality is expected to increase with increasing fire severity.
- **Seed bank:** It produces large seeds protected by a hard nut, which may facilitate zooballochory, although the seed may contain cyanogenic compounds and has been observed to be consumed entirely, possibly by rodents. No persistent seed bank. May maintain a juvenile bank of plants, but these are often killed by fire.

Biotic/abiotic/fire regime threats: some impact of weeds (*Cinnamomum camphorum* Camphor Laurel, NSW Saving our Species 2021). May be adversely affected by the introduced pathogen *Phytophthora cinnamomi*.

Estimate of known sites/habitat burnt in the 2019/2020 fires: over 90%.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria I and IX (Table 1).

Management response: post-fire survey suggests that approximately a quarter of individuals were burnt in the 2019/2020 fires with approximately two-thirds of these plants being killed and most of the rest reduced to resprouting from the base of the trunk (NSW Saving our Species 2021). A very long fire-free period (at least 50–100 years) is considered necessary to allow any recovery; so active protection of the known sites from fire is essential.

(ii) the development of organs and physiological states that allow resistance to fire in juvenile plants of resprouting species; and

(iii) the re-establishment of ecosystem structure altered by fire effects on foundational elements (e.g top-kill of long-lived trees, consumption of peat and other organic substrates).

Box 3. Species criteria: fire sensitivity (Criterion I); short fire intervals (Criterion II); fire and drought (Criterion V) and fire-disease interactions (Criterion IX)

Case study: *Wollemia nobilis*, the Wollemi Pine (Araucariaceae), a long-lived tree prone to scarring and collapse from prolonged basal charring.

Wollemia nobilis with scorched foliage after fire (photo: John Spencer, NPWS).

Wollemia nobilis with severe basal charring of trunk after fire (photo: Steve Clarke, DPE).

Background: *Wollemia nobilis* is a recently discovered rainforest species. It is a monotypic genus, with *Wollemia* pollen being abundant 65–34 million years ago, then steadily declining in response to cooling and drying during the northward movement of Australia (NSW Department of Environment and Conservation 2006). It is now known from one population (four small stands) in warm temperate rainforest in Wollemi National Park New South Wales (NSW; Benson and Allen 2007). Endemic to NSW, Australia. Restricted to gorges in Wollemi National Park, west of Sydney, Australia.

Conservation status: Critically Endangered (IUCN Red List, Mackenzie and Auld, in press; *EPBC Act*).

Relevant life-history traits

- **Habit:** tree up to 40 m high, with frequent coppicing (Jones *et al.* 1995).
- **Fire response:** adult plants are capable of resprouting after fire, but trunks are susceptible to basal charring that causes trunk damage and may lead to trunk death/fall (Mackenzie *et al.* 2021). Juvenile plants are largely killed by fire. It is likely to require century-scale fire-free periods for recovery and persistence and was, therefore, identified as potentially sensitive to fire intervals of less than 50 years.
- **Seed bank:** annual seed release from canopy-held cones, but no persistent seed bank. Maintains a long-lived juvenile bank of plants (Zimmer *et al.* 2014); however, these can be eliminated by fire and need decades to be replaced.

Biotic/abiotic/fire regime threats: affected by of exotic pathogens (*Phytophthora* spp.; Bullock *et al.* 2000; Puno *et al.* 2015). Major threats of increased fire frequency in combination with climatic drying (Mackenzie *et al.* 2021).

Estimate of known sites/habitat burnt in the 2019–2020 fires: 100%.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria I, II, V and IX (Table 1).

Management response: post-fire survey confirmed that all sites were burnt in the 2019/2020 fires, albeit at low severity, whereas some plants experienced basal charring of trunks and trunk loss (Mackenzie *et al.* 2021). Most of the juvenile bank of plants was killed, although a few juvenile plants escaped being burnt. A fire-free period of at least 50–100 years is recommended for recovery (Mackenzie *et al.* 2021).

Species most susceptible to (i) and (ii) include obligate seeders (i.e. species that lack regenerative organs and rely entirely on seed germination for post-fire recovery (e.g. R-P+ species of Pausas *et al.* 2004, Boxes 4, 5) and resprouters (i.e. species with the capacity to generate new shoots from dormant buds post-fire; e.g. R+P+ or R+P- species of Pausas *et al.* 2004)) that may suffer high mortality rates. The time required to replenish seed banks after fire varies among species, among populations within species and with environmental conditions (Clarke *et al.* 2009; Palmer *et al.* 2018; Keeley and Pausas 2019). For many species, at least 2–15 years between successive fires is needed to ensure that a seed bank is sufficiently replenished to enable post-fire recovery after future fires. In addition, some trees may require long fire-free periods to be able to regrow new vascular tissue required for recovery. Some ecosystems need long fire-free intervals for habitat restoration (e.g. to rebuild peat deposits, arboreal substrates and structures for tree-dependents, re-establishment of decomposers and detritivores in woody debris). On a precautionary basis, and in the absence of complete species-specific data on primary juvenile periods, time for replenishment of seed banks or time for development of resprouting mechanisms in juvenile plants (see below), thresholds of 5 years for non-woody species (e.g. grasses, herbs, forbs), 15 years for woody species (e.g. shrubs, trees, lianas) and 50 years for long-lived trees prone to collapse from basal charring (see below) can be considered a reasonable minimum time-frame for post-fire recovery (Criterion II, Table 1), on the basis of available species information. However, environmental conditions such as primary productivity, precipitation and soil nutrient status, and other factors that limit seed-bank accumulation, such as granivory, will underpin recovery times and spatial variation in these factors may be considered in assessments against these criteria.

Short intervals between fires may also kill juveniles of resprouting plants before they develop sufficient fire resistance to survive subsequent fires. The most susceptible species are resprouters that are slow to develop regenerative/resistance structures (i.e. lignotubers, thick bark, rhizomes) or slow to replace mortality because of low fecundity, and these processes become more limiting on population persistence when resprouting and survival rates through fires are relatively low. There is little available data on the time needed for the development of fire resistance in juvenile plants (e.g. Auld 1990; Denham and Auld 2012) but such data suggest that at

Box 4. Species criteria: short fire intervals (Criterion II); species-wide exposure to high risk of recruitment failure (Criterion IV), fire and drought (Criterion V)

Case study: *Hakea pachyphylla* (family Proteaceae), obligate seeder with a canopy seed bank.

Background: shrub, endemic to NSW, Australia. Restricted to high elevations in the Blue Mountains, west of Sydney, Australia, and in Budawang Ranges to south-west of Sydney.

Conservation status: Vulnerable (IUCN Red List, Barker and Keith 2020). Not currently listed as threatened nationally in Australia under *EPBC Act*.

Relevant life-history traits

- **Habit:** shrub up to 2 m high, that 'Grows in heath or mallee-heath, usually on exposed sites, sometimes in swampy areas or along creeks' (PlantNet (The NSW Plant Information Network System, Royal Botanic Gardens and Domain Trust, Sydney) 2022*a*).
- **Fire response:** probably killed by fire (obligate seeder; Benson and McDougall 2000). A close relative (*H. propinqua*) is also known to be an obligate seeder (Benson and McDougall 2000). May require multi-decadal or century-scale fire-free periods for recovery and persistence, and was therefore identified as potentially sensitive to fire intervals of up to 50 years. Primary juvenile period unknown, but 2–5 years for related *H. propinqua*, so it likely to be >5 years in higher-elevation sites.
- **Seed bank:** maintains a persistent canopy seed bank held in woody fruits on branches.

Biotic/abiotic/fire regime threats: major threats are peri-urban clearing; increased fire frequency, in combination with climatic drying; and increased likelihood of post-fire drought.

Estimate of known sites/habitat burnt in the 2019/2020 fires: 69–87%.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria II, IV and V (Table 1).

Management response: a large proportion of the species distribution was burnt in the 2019/2020 fires. Some 50% of known sites had previously been burnt in the past 15 years and the 2019/2020 fires, therefore, burnt over significant areas still recovering from previous fires. This and pre-fire drought conditions may have limited seed-bank accumulation in the canopy prior to the 2019/2020 fires. The 2019/2020 fires resulted in most of the distribution of this species, now being present as seedlings recovering from fire (few sites now have any adult plants) and the risk of another fire occurring before a sufficiently large canopy seed bank is re-established is a major threat to population persistence.

Box 5. Species criteria: short fire intervals (Criterion II); high fire severity (Criterion III), species-wide exposure to high risk of recruitment failure (Criterion IV), fire and drought (Criterion V), post-fire erosion (Criterion VI)

Case study: Banksia *paludosa* subsp. *astrolux* (family Proteaceae), obligate seeder with a canopy seed bank.

Banksia paludosa subsp. *astrolux* with individual killed by 100% leaf scorch in fire on RHS and live individual on LHS (photo: Tony Auld)

Background: shrub, endemic to NSW, Australia. Restricted to a very small distribution south-west of Sydney, Australia.

Conservation status: not threatened, but currently under assessment for listing because of the impacts of the 2019/2020 fires.

Relevant life-history traits

- **Habit:** shrub up to 5 m high, lacking a lignotuber (George 1996).
- **Fire response:** killed by fire (obligate seeder) (Baird and Benson 2021). May require multi-decadal fire-free periods for recovery and persistence.
- **Seed bank:** maintains a persistent canopy seed bank held in woody fruits on branches, but fruits may not hold seeds for very long before opening and the species relies on ongoing new fruit production to maintain its seed bank.

Biotic/abiotic/fire regime threats: the distribution of the species experienced significant pre-fire drought. Over 50% of known sites had previously been burnt in the past 15 years and, hence, the 2019/2020 fires burnt over significant areas that were still recovering from previous fires. Some 20–70% of sites were predicted to have been burnt at high severity and high soil erosion was a possibility. The 2019/2020 fires were predicted to result in virtually all mature plants being killed and any recovery is at risk of a subsequent fire occurring before a sufficiently large canopy seed bank is re-established.

Estimate of known sites/habitat burnt in the 2019/2020 fires: approximately 100% of range burnt.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria II–VI (Table 1). Approximately 100% of the known distribution of the species was estimated to have been burnt in the 2019/2020 fires.

Management response: almost the entire distribution of the species was burnt. All plants that received 100% leaf scorch were killed. A few plants escaped fire or received <100% leaf scorch and survived because they occurred on sandstone rock shelves with little fuel. These surviving plans may act as local refugia in some (but not all) sites. Pre-fire seed-bank accumulation on burnt plants was generally low, resulting in no seedling recruitment under a large number of plants that were killed in the fire. One large site had virtually no post-fire seedling recruitment. This may have been due to pre-fire drought causing premature seed release, with the seeds then being killed in the fire, or a lack of serotiny in the species. All sites were burnt at low severity, although high-severity fire occurred adjacent to sites. No erosion impacts were evident. Ongoing persistence at sites is dependent on high survival of seedling recruits, and at least one large site has had significant population decline.

The Framework predicted impacts of the 2019/2020 fire that would reduce effective post-fire seedling recruitment and this was borne out in post-fire field surveys, although there was variation among sites. On-going management of sites is needed to ensure that fires are excluded for at least the next 10–15 years, until a sufficiently large canopy seed bank is re-established.

least 7–15 years between successive fires is needed to ensure the juveniles of woody plant species can develop their fire-regenerative organs to a point where at least some individuals are capable of surviving fire, although some species such as mallee eucalypts may require at least 25 years. Furthermore, since fire tolerance generally increases with age, (at least initially), longer intervals are required to avoid population declines in cases where rates of recruitment are low, relative to adult mortality (Bradstock and Myerscough 1988). Investment trade-offs between development of regenerative organs and fecundity typically result in lower rates of recruitment in resprouters than non-resprouters (Bond and van Wilgen 1996), limiting capacity for population recovery after successive fires that cause non-trivial levels of mortality among established plants (e.g. in Australian heathlands, Keith *et al.* 2007 or Californian chaparral, Airey Lauvaux *et al.* 2016). There is scope to modify the thresholds set in the criteria for species (5 years non-woody and 15 years woody species; Criterion II, Table 1) to accommodate variation among species, should data be available.

Finally, some long-lived trees may suffer basal scarring where fires (or other factors related to fires such as falling trees or limbs) damage and/or kill bark tissue. This enables subsequent fires to smoulder into heartwood and weaken the structural integrity of the tree, causing mortality, collapse and structural change to the ecosystem (Box 3). Trees with thin bark are most prone to this impact and replacement depends on fecundity and growth rates. In Australia, many rainforest trees and some eucalypts are susceptible and are likely to require at least 50 years between successive fires to enable partial recovery and replacement. We suggest 50 years as a minimum working threshold for analysis at the present time, given that completeness of fire-history records diminishes with age (see below), although the biological recovery processes will often be substantially longer.

Ecosystems that lack woody species, such as some wetlands and grasslands, may be resilient to frequent fires where recurrence time is as short as 5 years. For fire-prone woody sclerophyll ecosystems, such as, for example, heathlands, dry sclerophyll forests and shrubby wetlands, up to 15 years may be needed between successive fires to ensure recovery of function and persistence of biota. Considerably longer periods are required to permit recovery of wet sclerophyll forests, rainforests, and obligate seeder-dominated eucalypt woodlands (Gosper *et al.* 2018). This is particularly the case for those dominated by fire-sensitive ash eucalypt species (Box 6) that are susceptible to 'landscape traps' (Lindenmayer *et al.* 2011), characterised by positive feedbacks that 'trap' the system in states with simplified and more flammable structure, with regimes of frequent fire preventing the re-establishment of low-flammability moist micro-climates beneath an established canopy. Although the eucalypt dominants of these systems may take up to 20 years before seed-bank accumulation commences, re-establishment of the structural complexity and habitat features such as large crowns and tree hollows are likely to require more than a century. Even in tall wet sclerophyll forests dominated by epicormically resprouting trees, recovery of structural complexity and re-establishment of breeding populations of resident biota may take 50 years. As well, despite regenerative organs of trees, individual trees that make disproportionate contributions to structure and function of wet sclerophyll forests and rainforests may suffer cumulative structural damage from successive fire scars (Benson 1985). Their loss can result in long-term structural transformation unless replacement levels are maintained by ongoing recruitment into large-tree size classes.

Assessing short fire intervals (high fire frequency). Estimates of exposure to high fire frequency can be based on spatial data capturing the annual time series of fires in concert with post-fire field reconnaissance and local knowledge where available. Fire-history data can be sourced from time series of remote-sensing imagery and open access-derived products already exist estimating the extent, duration, speed and direction of fire at a global scale (Andela *et al.* 2019). Fire-history mapping is also maintained by environmental and fire management agencies at either regional, state or national levels (e.g. https://datasets.seed.nsw.gov.au/dataset/fire-history-wildfires-and-prescribed-burns-1e8b6). Remotely sensed satellite imagery is not available prior to the late 1970s, and imagery requires

Box 6. Ecosystem criteria: short fire intervals (Criterion II)

Case study: Kosciuszko-Namadgi Alpine Ash Moist Grassy Forest ecosystems affected by high-frequency fire.

Alpine ash forest showing successive cohorts of trees killed in fires. Large trees >50 cm diameter at breast height (centre middle ground in left image, left middle ground in right image) were killed by a fire in 2003). Other large trees have since fallen and are less visible. Saplings <30 cm dbh (throughout both images) were recruited from seed dispersed from the canopy seed banks of the large trees and were subsequently killed during the 2020 fire. All trees are alpine ash (*Eucalyptus delegatensis* subsp. *delegatensis*). Only a few of the post- 2003 cohort had begun to bear fruit prior to the 2020 fires and recruitment of eucalypts in the current post-fire vegetation is sparse and spatially variable (left: Alpine Ash Moist Grassy Forest, Sawyers Hill, Kosciuszko National Park. Photo Genevieve Wright, DPIE. right: near Tumut Pond reservoir, Kosciuszko NP. Photo David Keith, Feb. 2021).

Background: a tall to very tall wet sclerophyll forest dominated by *E. delegatensis* and *E. dalrympleana* with a diverse shrubby understorey and dense herbaceous ground cover (NSW DPE; G. Wright and G. Robertson, unpubl. data). Endemic to steep, sheltered flanks of the Australian Alps mostly at 1000–1600 m elevation from northern Kosciuszko National Park to the Victorian alps.

Conservation status: not threatened, but currently under assessment for listing due to the impacts of the 2019/2020 fires.

Relevant life-history traits

- **Habit:** dominant trees up to 50 m high, lacking a lignotuber.
- **Fire ecology:** driven by the population dynamics of the fire-sensitive dominant tree species. Low-intensity fires consume shrub and ground strata, promoting regeneration of short-lived perennial flora, whereas trees generally have high survival rates from basal scorch. Very high fuel loads promote intense conflagrations at multi-decadal intervals when ignition coincides with infrequent severe fire-weather events. Severe fires are stand-replacing and may cause local extinctions of fire-sensitive animal species.
- **Seed bank:** dominant trees maintain a persistent canopy seed bank held in woody fruits on branches.

Biotic/abiotic/fire regime threats: approximately 40% of the total distribution has been burnt at least twice in the past 50 years (burnt in both the 2003 and 2019/2020 fires, Keith *et al.* 2022*b*). In such situations, there was little established canopy seed bank when the 2019/2020 fires occurred.

Estimate of known sites/habitat burnt in the 2019/2020 fires: up to 60%.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criterion II (Table 2).

Management response: post-fire assessments have confirmed that recruitment of *E. delegatensis* following the 2019/2020 fires is at least an order of magnitude lower in stands burnt in both 2003 and 2019/2020 than in those that escaped the 2003 fire (M. Doherty, pers. comm.), fundamentally altering the future structure and dynamics of the ecosystem. In such cases, future restoration management may be needed (e.g. direct seeding of canopy dominant *E. delegatensis*; Bassett *et al.* 2015).

classification to accurately capture fire extent over a time interval (Gibson *et al.* 2020). Fire-history mapping from agencies may require licensing agreements and may fail to capture all burnt areas, or have low spatial accuracy, and may itself be derived from, or supplemented by, remotely sensed imagery. Spatial accuracy and completeness of agency fire records diminishes with age. Both fire-history mapping and remote-sensing imagery can be combined to produce a composite resource for analysis; however, it is important that the temporal period assigned to 'annual fire-history layers' from any source reflects the regional conditions and is aligned between datasets prior to them being combined.

Assessment of the short fire-interval criterion (Criterion II, Table 1) also requires data on life-history traits (i.e. woodiness) that can be sourced from databases, published literature and local databases or expert knowledge (see *Fire response traits for species and ecosystems* above).

To assess the impact of short fire intervals, assembled spatial data on fire history should be combined for the temporal period of interest (e.g. all fires in the past 5, 15 or 50 years combined into a single layer) and intersected with species-occurrence data (point occurrences or range polygons) to calculate the proportion of range burnt in the relevant time-step. For example, for woody Australian species burnt in the 2019/2020 fires, evidence of antecedent fires within the past 15 years that resulted in 50% or more of the range burnt at least twice was used to assign species a HIGH risk of limited recovery after the fires (Gallagher 2020). Separate layers were generated for woody and non-woody fire-return intervals. Species range data were then intersected with the spatial layers of fire intervals to assess the proportion of the range exposed to short fire intervals that would be expected to result in population declines (Box 7).

Assessments of exposure to high fire frequency (Keith *et al.* 2020*a*, 2022*b*) on ecosystems were based on a combination of the Global Fire Atlas (Andela *et al.* 2019) and Australian State government agency fire-history spatial data. The proportion of ecosystem distributions burnt in the 2019/2020 fires that were also burnt 5, 15 and 50 years previously was estimated from these data. On the basis of the reasoning presented above, rainforest and wet sclerophyll forest ecosystems were assumed to be sensitive to successive fires within a 50-year period; heathlands, peatlands, dry sclerophyll forests and woodlands were assumed to be sensitive to fires recurring within 15 years; and grasslands were assumed to be resilient to fires recurring more frequently than every 5 years. The 50-year threshold is likely to underestimate the recovery threshold for rainforests and many wet sclerophyll eucalypt forests, but was imposed by limitations on the time series of available fire-history data.

III. High fire severity

High fire severity (*sensu* Box 1) is associated with low survival rates in functionally important groups of plants and animals in many ecosystem types (Lindenmayer *et al.* 2013; Airey Lauvaux *et al.* 2016; Yates *et al.* 2017; Etchells *et al.* 2020). In some plant species, survival of established individuals and/or seed banks may be sensitive to fire severity because of the limitations in the insulating capacity of protective tissues (thickness of bark or walls of serotinous fruits). Species that rely on persistence of long-lived standing plants because of low fecundity (or high fertility with low rates of recruitment) or post-fire regeneration from small serotinous fruits are most susceptible to this mechanism of decline (Box 8). For long-lived trees, these effects may be cumulative through successive fires that undermine their structural integrity. In such cases, fire-severity impacts may

Box 7. Species criteria: fire sensitivity (Criterion I); short fire intervals (Criterion II)

Data usage: intersecting species-range data with the spatial layers of fire intervals (from Gallagher 2020).

Data on traits and fire history were combined with information on the productivity of Australian vegetation to produce an estimate of appropriate fire-return times (e.g. time to enable post-fire regeneration and replenishment of seed banks) across the analysis area. Specifically, a spatial layer of the estimated gross primary productivity (GPP, g C m^{-2} $year^{-1}$) of vegetation calculated using a Vegetation Photosynthesis Model (VPM) at spatial resolution (0.05 degree) was accessed from Zhang *et al.* (2017). Raw values of GPP were classified into four categories on the basis of quartiles (extremely low, low, medium, high) and fire-return times were estimated for each category. Return times required for successful regeneration of some woody taxa in high GPP areas may be longer than 15 years, particularly for fire-sensitive eucalypts and slow-growing taxa.

All areas classified as the Major Vegetation Grouping 'Rainforest' in the National Vegetation Inventory System were excluded from this analysis and assumed to have inappropriate fire regimes if burnt at any time since 1969 because the time required for post-fire recovery is in the order of 50 years or longer.

Fire-return times based on GPP were combined with fire-history data to create a spatial layer of all locations where the interval between the 2019/2020 fires and the previous recorded fire was too short to accommodate plant regeneration. Separate layers were generated for woody and non-woody return times. Species-range data were then intersected with the spatial layers of fire intervals to assess the proportion of the range that is exposed to inappropriately short fire-return times.

Box 8. Species criteria: low degree of exposure to the risk of decline

Case study: *Callitris endlicheri* (black cypress pine), Cupressaceae, a tree with sensitivity to high fire severity.

Background: endemic to eastern Australia on stony hills and ridges in semi-arid to coastal ranges.

Conservation status: not currently considered threatened nationally in Australia; however, a highly disjunct population in Dharawal State Conservation Area on the eastern coast is listed as an Endangered population under the *NSW Biodiversity Conservation Act 2016*.

Relevant life-history traits

- **Habit:** long-lived tree. Primary juvenile period is at least 7 years (Lunt *et al.* 2011).
- **Fire ecology:** killed by fire (obligate seeder) if whole of foliage of tree is scorched or consumed (i.e. complete topkill); otherwise, some capacity to resprout in response to partial top-kill (Denham *et al.* 2016).
- **Seed bank:** maintains a persistent canopy seed bank held in woody fruits on branches.

Biotic/abiotic/fire regime threats: severe localised impacts from past high-severity wildfires have been recorded, particularly as a consequence of fire–herbivore interactions (Criterion VIII; Mackenzie and Keith 2009; Denham *et al.* 2016).

Estimate of known sites/habitat burnt in the 2019/2020 fires: 9–13%.

Assessment against framework criteria for species: predicted to be at LOW risk.

Management response: only a small proportion of the species distribution was burnt in the 2019/2020 fires and no significant likely impacts from other factors were identified.

be more influenced by prolonged basal charring, internal smouldering and subsequent trunk collapse/tree fall, rather than by canopy consumption (only the latter is commonly reflected in fire-severity maps). This highlights an interaction between Criteria II and III (Table 1); high fire severity is likely to have greater impacts on persistence if fires recur at high frequencies relative to recovery rates of the species or ecosystem. Effects may also be exacerbated by drought that reduces water content within insulating tissues prior to fires (Box 9). In contrast, high fire severity may be required to promote germination and recruitment in a number of plant species (Box 1).

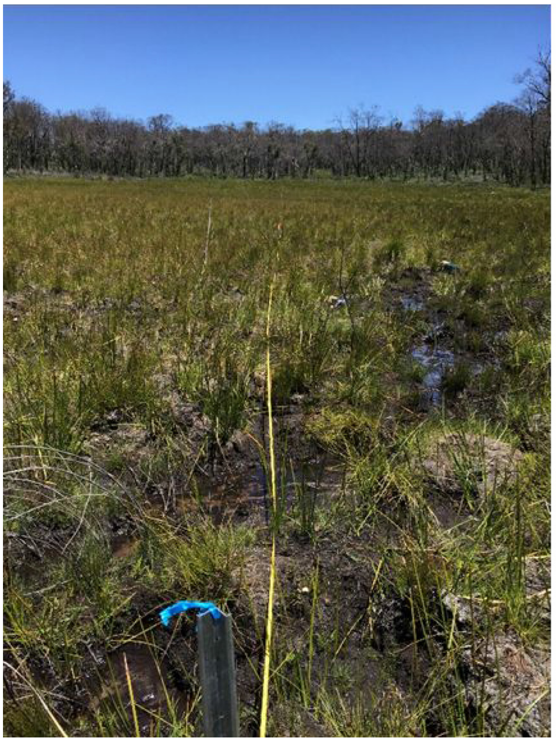
Assessing high fire severity. Spatial metrics that represent fire severity (as a surrogate for the biological impacts of heating in fires, see Box 1) can be derived from satellite imagery and are increasingly available at very high resolutions (e.g. submetre precision). Severity can be gauged through changes in vegetation indices between pre- and post-fire periods, with or without ground-based training data (with implications for map accuracy) or through temperature measurements during fire events. For example, the Australian Google Earth Engine Burnt Area Map (AUS GEEBAM) used the Relativised Normalised Burnt Ratio (RNBR) calculated for burnt areas and adjacent unburnt areas, before and after the fire season to assess fire severity without training data (http://www.environment.gov.au/fed/catalog/search/resource/details.page?uuid=%7B8CE7D6BE-4A82-40D7-80BC-647CB1FE5C08%7D). In contrast, the fire extent and severity mapping (FESM) used artificial-intelligence algorithms applied to training data from prior fires, using multiple indices based on Sentinel 2 imagery to assign pixels to ordinal classes of fire severity (Gibson *et al.* 2020; Collins *et al.* 2021). How applicable such remotely sensed measures of fire severity are to the actual biological impact from the degree of heat produced in fires remains uncertain and requires field verification. *In situ* biological measures of heating can more directly inform inferences about ecological responses at individual sites. These include sedge scorch depth (as an indication of soil heating; Tozer and Auld 2006) and diameters of largest branch tips consumed (as an indication of heating at 0–2 m above ground; Moreno and Oechel 1989; Whight and Bradstock 1999) and char height as an index of flame height (Prior *et al.* 2022).

For species, sensitivity (of standing plants and/or their seed banks) to high-severity fires can be inferred from fire-response databases, relevant literature and expert opinion.

For ecosystems, Keith *et al.* (2020*a*, 2022*b*) examined exposure to high fire severity on the basis of spatial analyses of both FESM (NSW Fire Extent and Severity Mapping; Gibson *et al.* 2020) and related methods applied to Victoria (Collins *et al.* 2021) and GEEBAM (Department of Agriculture, Water and the Environment 2020), which provided national coverage. The highest severity category across all methods was applied to the assessment. Ecosystem sensitivity to high-severity fires was inferred on the basis of their key features. Rainforests and peatlands were assumed to be sensitive on the basis of high proportions of fire-killed plants and combustible peat (Box 9) respectively, whereas wet sclerophyll forests were assumed to be sensitive to canopy fires that may significantly deplete their rich tree-dependent vertebrate and invertebrate fauna.

Box 9. Ecosystem criteria: short fire intervals (Criterion II); high fire severity (Criterion III), species-wide exposure to high risk of recruitment failure (Criterion IV), fire and drought (Criterion V), sensitivity and exposure to post-fire disturbance, erosion or pollution (Criterion VI); fire interactions with hyrdrological change (Criterion VII)

Case study: Temperate Highland Peat Swamp ecosystem: impacts of severe fire, drought and hydrological change.



Post-fire surveys of Temperate highland peat swamps on sandstone, listed as an Endangered Ecological Community under national legislation, in November 2020, 11 months after fire. Left, resilient, hydrologically functional swamp with regenerating hydrophytes. Right, collapsed swamp with very little regenerating vegetation when burnt after the groundwater was drained by underground mining activities. (photos: Newnes plateau, D. Keith, 17 November 2020).

Background: swamps occurring on sandstone from 600–1100 m above sea level. Endemic to NSW, Australia. Restricted to high elevation in the Blue Mountains, and southern highlands.

Conservation status: Endangered (*EPBC Act*).

Relevant life-history traits

- **Habitat:** peat swamps on sandstone.
- **Fire ecology:** many component taxa can rapidly resprout after fire, but are eliminated by peat fires that kill regenerative organs and seeds.
- **Seed bank:** several component taxa have a persistent soil seed bank.

Biotic/abiotic/fire regime threats: a large proportion of the ecosystem distribution was burnt in the 2019/2020 fires, with many occurrences subject to extensive pre-fire drought. Other major threat is changes to hydrology associated with underground longwall mining, primarily on the Newnes plateau (Keith *et al.* 2022*a*).

Estimate of known sites/habitat burnt in the 2019/2020 fires: 50%.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria II–VII (Table 2).

Management response: although a large portion of the area burnt was mapped as high fire severity, subsequent field observations suggest a degree of resilience exhibited by a rapid growth response to post-fire rains (Keith *et al.* 2020*b*). However, the recovery of several swamps was severely impeded by changes to their hydrology caused by underground mining (Keith *et al.* 2020*b*, 2022*a*; Mason *et al.* 2021), with localised recovery failure and high exposure to intense rainfall events suggesting erosion risks. The combined effects of hydrological change, fire and erosion caused collapse of several swamps on the Newnes plateau, which are undergoing transition to eucalypt forest and sparsely vegetated valley bottoms. Therefore, the HIGH ranking status is supported primarily by fire-drought and fire-hydrology interactions.

Vertebrate and invertebrate pollinators (heathlands and some dry sclerophyll forests) and vertebrate dispersal vectors (some rainforests) play important roles in ecosystem recovery. Whereas abundances of at least some of these taxa are reduced in the immediate post-fire years, many are highly mobile and much is still to be learnt about their post-fire recovery response, its dependence on flowering responses, and the subsequent implications for fruit set. Because of these uncertainties, none of the assessment outcomes relies entirely on assumptions about pollinator or disperser responses.

IV. Species-wide exposure to high risk of recruitment failure

High mortality of mature plants increases reliance on compensatory recruitment for population persistence. The implications of recruitment failure are therefore greatest in species in which adults are killed and recovery relies entirely on successful recruitment from seed banks (e.g. R-P+, *sensu* Pausas *et al.* 2004). Significant or total recruitment failure can result from stochastic events and threats such as grazing, weeds, pathogens, drought impacts and/or disruption of seed bank accumulation by subsequent fires (short fire-return intervals). When only a few of many populations are burnt, the unburnt populations provide insurance effects against recruitment failure in burnt populations. Conversely, when a high proportion of the species range is burnt, insurance effects are more limited and the species is at a greater risk of extinction from recruitment failure. Criterion IV addresses this mechanism of threat, which (particularly for obligate-seeding species) arises when one or more recent fire events have occurred across a large portion of the species range with little or no fire-free refugia (*sensu* Meddens *et al.* 2018). Thus, a large proportion of the total population of the species is at risk from recruitment failure, depending on stochastic processes that influence conditions for seedling establishment and maturation, and the occurrence of subsequent fires (Box 10). Obligate seeders with canopy seed banks are most at risk because such seed banks can be completely exhausted after a single fire event. Species with soil seed banks may have more resilience because of seed carryover between fires (e.g. Ayre *et al.* 2009); however, not all species with soil seed banks have this capacity in all situations (e.g. Auld and Denham 2006).

Criterion IV differs from Criterion II, in addressing the risk of future recruitment failure arising from short fire intervals. Criterion IV incorporates a consideration of the recent fire history across the entire species range (in combination with the most recent wildfire) to estimate the extent of the distribution at risk from future fires.

Assessing cumulative exposure to risks from future high fire frequency. Assessing cumulative exposure to high risk requires the intersection of spatial layers for fire extent (including all recent past fires; cf. Criterion II above) with occurrence records or modelled distributions of obligate-seeding species. Obligate-seeding species can be identified from compiled trait datasets, expert knowledge, and field surveys.

Criteria relating to the impacts of interactions between fire and environmental variability

V. Interactive effects of fire and drought

This criterion addresses the impact that drought may have on plant survival and fecundity, both before a fire and during the post-fire recovery phase. Pre-fire drought can (i) reduce internally stored resources and xylem integrity of resprouting plants that are critical in sustaining post-fire regeneration, and (ii) reduce pre-fire reproductive output, affecting the size of the seed bank available for post-fire recruitment.

Post-fire drought can negatively affect recruitment success by reducing (i) seed germination (because of insufficient soil moisture possibly causing significant seed mortality in some dormancy types, i.e. physically dormant or non-dormant seeds), (ii) seedling survival (through desiccation), and (iii) survival of resprouts (through xylem embolism in susceptible new shoots, cf. Allen *et al.* 2015). Risks from post-fire mortality may be large if drought occurs in the first autumn–winter after fire or the following spring–summer.

Independent of fire, drought can have significant impacts on plant health, leading for example to dieback in eucalypt trees (Choat *et al.* 2018; de Kauwe *et al.* 2020). Pre-fire and post-fire droughts affect the ability of ecosystems and their component flora and fauna to recover after fire, both directly (e.g. Fensham *et al.* 2005) and indirectly, through effects on fire behaviour, severity and extent (Nolan *et al.* 2020*b*).

Assessing interactive effects of fire and drought. Resprouting and obligate-seeding species are both considered at risk from interactive effects of fire and drought, because of

Box 10. Species criteria: species-wide exposure to high risk of recruitment failure (Criterion IV)

Case study: *Acacia bulgaensis*, Fabaceae, an obligate seeder with species-wide exposure to high risk of recruitment failure owing to most plants now being seedlings at risk from a future fire.

Background: endemic to NSW, Australia, in dry to wet sclerophyll forests. Restricted to a very small distribution north-west of Sydney.

Conservation status: currently not listed as threatened.

Relevant life-history traits

- **Habit:** shrub or tree up to 6 m high (PlantNet (The NSW Plant Information Network System, Royal Botanic Gardens and Domain Trust, Sydney) 2022*b*).
- **Fire ecology:** killed by fire (OEH 2014).
- **Seed bank:** maintains a persistent soil seed bank. Seeds with physical dormancy.

Biotic/abiotic/fire regime threats: high fire frequency.

Estimate of known sites/habitat burnt in the 2019/2020 fires: approximately 44% of range burnt.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criterion IV (Table 1).

Management response: just under half of the known distribution of the species was estimated to have been burnt in the 2019/2020 fires, leading to death of standing plants, with recovery dependent on post-fire germination and establishment of seedlings. In addition, another 20–30% of known sites had previously been recently burnt, leaving some 70–75% of known sites with plants present only as seedlings. The 2019/2020 fires were predicted to result in a large proportion of the known population being seedlings recovering from fire and at risk of a subsequent fire occurring before a sufficient seed bank is re-established.

increased mortality, reduced carbohydrate reserves, and a reduced capacity for recovery from seeds. For species, this criterion combines spatial layers of fire extent (see above) and pre- or post-fire drought conditions (see below) and intersects them with species occurrence.

Rainforests, wet sclerophyll forests and peatlands were assumed to be more sensitive to long-lasting changes caused by coincidence of fire and drought than are other ecosystem types because they are most dependent on moisture surplus (Keith *et al.* 2020*a*, 2022*b*), although all ecosystems are potentially susceptible to this process, depending on drought severity in the context of their hydrological niche (Box 9).

Exposure to drought can be estimated from several metrics. For example, Gallagher *et al.* (2021) estimated pre-fire drought by intersecting species-range data with mapping of the accumulated severity of drought conditions in the 12 months prior to December 2019 (i.e. 6–12 months preceding the mega fires). Keith *et al.* (2020*a*, 2022*b*) used the larger of two alternative spatial drought metrics, namely, (i) the percentage of an ecosystem burnt and within the lowest decile of the Australian Bureau of Meteorology's accumulated rainfall deficit for the 18 months prior to December 2019 (Australian Government Bureau of Meteorology 2022); and (ii) the percentage of an ecosystem burnt and within the upper quartile of the accumulated drought-severity index (ADSI) for January 2019–December 2019, a standardised precipitation index defined as the number of standard deviations that observed cumulative precipitation deviates from the long-term average (McKee *et al.* 1993; see also Gallagher *et al.* 2021). Remote-sensing data that relate to the impacts of drought could also be utilised (Nolan *et al.* 2016).

VI. Post-fire erosion (species) or sensitivity and exposure to post-fire disturbance, erosion or pollution (ecosystems)

Intense rainfall events after fires may lead to extensive localised erosion and sedimentation that covers recovering plants in soil and ash and/or depletes, transports or deeply buries soil seed banks. In steep terrain, post-fire erosion may dislodge rocks and trees or cause larger-scale landslides with associated plant mortality. Effects are likely to be localised and evident in the first few months after a fire. Steep habitats, riparian habitats, peaty habitats and unconsolidated floodplains or sandplains below toeslopes are among the most vulnerable to erosion, whereas heavy sedimentation is confined to depositional landforms.

Assessing post-fire erosion (species) or sensitivity and exposure to post-fire disturbance, erosion or pollution (ecosystems). To assess the effects of post-fire erosion, approaches that model the sensitivity (topographic influence) and exposure (occurrence of heavy rainfall within the fireground) of the landscape to loss of topsoil are required (Box 11). Erosion is influenced by extreme rainfall events, erodibility of soils (especially after vegetation cover has been removed, although plant root systems remain intact after fires and provide stability), and the steepness/ruggedness of terrain. Keith *et al.* (2020*a*, 2022*b*) applied a model developed by Yang *et al.* (2018) assuming a scenario

Box 11. Species criteria: post-fire erosion (Criterion VI)

Data usage: erosion impacts on fire-affected species (from Gallagher 2020).

To assess the spatial scale of possible erosion impacts on plant species in relation to the Australian 2019/2020 fires, a spatial layer of extreme rainfall between 15 January and 15 March 2020 was created using daily rainfall data from the Australian Water Availability Project (AWAP) via http://www.bom.gov.au/jsp/awap/. Methods used to derive the AWAP are described in Jones *et al.* (2009). Grid-cell size was aggregated from 0.05 × 0.05 to 0.1 × 0.1 degrees of latitude by using the raster package in R. Daily rainfall data were summed for the 2-month period from 15 January to 15 March for the years 2000–2020. The mean and standard deviation of rainfall for this period were calculated across 2000–2019 (20 years) and compared with rainfall for the same period in 2020 (following the 2019/2020 bushfires) by calculating how many standard deviations this latter period was from the 20-year average. Locations that were two or more standard deviations above from the average rainfall over the previous 20-year period were classified as areas of extreme rainfall.

This spatial layer of extreme rainfall was intersected with the spatial extent of the 2019/2020 fire grounds and a topographic ruggedness index (TRI) derived from a digital elevation model (DEM) at 250 m resolution accessed from https://www2.jpl.nasa.gov/srtm/. TRI was calculated using the spatialEco package in R, which conducts a moving-window analysis of the slope in adjacent cells in a DEM. The window for analysis was 3 × 3 pixels, equating to 0.0075 × 0.0075 degrees, which is approximately 750 m × 750 m. Values of TRI range from 0 to 1700, and were classified into multiple categories as recommended by the spatialEco package authors, as follows: 0–80 = level terrain, 81–116 = nearly level, 117–161 = slightly rugged, 162–239 = intermediately rugged, 240–497 = moderately rugged, 498–958 = highly rugged, 959–above = extremely rugged. All values classified as moderately rugged and above were combined into a single layer of rugged terrain across the study area.

of bare earth (no vegetation) to simulate post-fire conditions and defining high erosion risk on the basis of an estimated mean annual soil loss greater than 5 Mg ha^{-1} $year^{-1}$. Mapped areas exceeding this threshold were intersected with the burnt area for each ecosystem and expressed as a percentage of total ecosystem extent.

Where modelled products are not readily available owing to time constraints, or a lack of expertise, estimates can also be made by combining proxies of erosion risk. For instance, spatial data on extreme precipitation across the fire-grounds combined with terrain characteristics can be used to approximate erosion potential. Suitable spatial proxies include gridded data on topographic ruggedness and the incidence of extreme rainfall events post-fire relative to a reference time period. Several approaches are available for the calculation of topographic ruggedness from digital elevation models (e.g. spatialEco package in R, ArcGIS). Typically, these approaches use moving-window analysis to assess the difference in elevation in target cells relative to adjacent cells.

VII. Fire interactions with changed temperature regimes (species) or hydrological change (ecosystems)

Species. Seed germination of some plants in alpine, subalpine and other cold environments, such as frost-hollows, is reliant on cold-stratification during winter (Cavieres and Sierra-Almeida 2018). If the post-fire winter is unseasonally warm, seedling regeneration may be reduced with flow-on effects on post-fire population size and seed-bank replenishment prior to subsequent fires. Species with short-lived standing plants and/or short-lived seed banks are likely to be most susceptible to such effects on soil seed banks. Ecosystems that comprise large numbers of species or dominant species with temperature-sensitive traits described above are expected to be sensitive to interactions between fire and rising temperatures. In alpine ecosystems, for example, most plants show physiological seed dormancy and a strong need for cold stratification (Fernández-Pascual *et al.* 2021). Enhanced insolation of fire-blackened soils may exacerbate climatic warming effects. For other species, diurnal and seasonal temperature cycles regulate dormancy and germination and changes to these cycles may adversely affect post-fire recruitment because of delayed or reduced germination.

Rising temperatures may also influence post-fire responses of plants through heatwaves, which may reduce survival rates of standing plants before or after fire or deplete seed banks of species with physically dormant seeds. Ooi *et al.* (2009) found evidence that soil surfaces and shallow depths, at which many seeds are stored, may reach high temperatures capable of breaking dormancy, effectively depleting seed banks and reducing the number of seed available for recruitment in the event of a fire.

Ecosystems. Changes in hydrology before or after fire may influence the trajectory of post-fire recovery in some ecosystems (Mason *et al.* 2021; Keith *et al.* 2022*a*). Hydrological changes may be driven by climate change, groundwater extraction and reinjection, floodplain regulation or engineering activities that influence surface or groundwater flow. Climatic drying, for example, can make peatland ecosystems more prone to peat combustion (Prior *et al.* 2020). In some cases, fire may be the trigger for ecosystem adjustment to a new hydrological regime, with coincident loss of biota or functions that were characteristic of the pre-fire system (Keith *et al.* 2020*a*).

There may also be feedbacks to flammability that maintain a new steady state.

Assessing changed temperature regimes (species) or fire interactions with hydrological change (ecosystems). For species, seed-dormancy classification (*sensu* Baskin and Baskin 2014) can be applied to identify species at risk of altered temperature-regime effects on dormancy and germination (i.e. species with physiological (PD) and morphophysiological dormancy (MPD)). Dormancy classes can usually be inferred from generic, and sometimes family, traits (Merritt *et al.* 2007; Ooi 2007; Collette and Ooi 2021), although dormancy type can vary widely within some plant families; for example, the Proteaceae contains of mixture of non-dormant species (such as *Telopea* and *Lomatia*) and PD species with complex dormancy and germination requirements, including *Persoonia* (Emery and Offord 2018). To identify species most at risk, seed-dormancy data can be combined with fire-response data (species killed by fire are entirely dependent on successful post-fire seedling recruitment for persistence) available in traits databases (see above). Additionally, fire-seasonality components (Miller *et al.* 2019, Box 1) or environmental factors across certain habitats may be factors affecting the ability of species to successfully recover after some fires.

For ecosystems, fire interactions with hydrological change can be inferred from expert knowledge of hydrological changes resulting from regional trends in precipitation or from changes in resource exploitation (underground mining, groundwater extraction) that are known to reduce availability of groundwater and/or surface water. Sensitivity of ecosystems may vary. For example, Keith *et al.* (2020*a*) assumed greatest sensitivity in wetlands and rainforests dependent on groundwater and/or a positive climatic water balance.

Criteria relating to biotic post-fire threats

VIII. Post-fire herbivore impacts

Plants are often at their most susceptible (palatable, least resilient and most available) to herbivore activity (e.g. loss of seeds, seedlings, leaf and shoot removal, trampling and substrate degradation) in the post-fire environment where herbivores have enhanced foraging efficiency and converge on regenerating burnt areas to exploit fresh growth (Andersen 1988; Murphy and Bowman 2007; Westlake *et al.* 2020). Concentrations of herbivores may, therefore, increase mortality of both seedlings and resprouters of palatable plants (Mills 1983), and this may vary with fire spatial patterning (Knight and Holt 2005) and severity (Moreno and Oechel 1991). In some cases, such elevated mortality has the potential to eliminate post-fire recovery (Read *et al.* 2021). Effects may be exacerbated when burnt patches are small or have a high perimeter-to-area ratios that promote herbivore incursions in high densities (Tasker *et al.* 2011; Giljohann *et al.* 2017).

While there is very limited information on relative susceptibility of different ecosystems to this threat, those likely to be most sensitive have high diversity or abundance of palatable plants with either limited herbivore defences or limited capacity for regenerative regrowth after biomass reduction. Ecosystems most likely to be affected are those with a high sensitivity and occurring in areas with abundant herbivores (Box 12). These include low-productivity ecosystems, such as alpine ecosystems, heathlands and sclerophyll forests, and semi-arid ecosystems, which may have high exposure to post-fire herbivory because of an abundance of invasive species, domestic livestock or overabundant native herbivores within the surrounding landscapes. Interfaces between low-productivity ecosystems and more productive areas, such as natural grassy ecosystems, pastures and peri-urban lands, may sustain dense herbivore populations in close proximity to susceptible ecosystems. Ecosystems with erodible soils are likely to be susceptible to trampling effects that intensify with herbivore density and body size (e.g. impacts of rabbits and horses on soil structure and stability, and vegetation structure in alpine ecosystems; Leigh *et al.* 1987; Eldridge *et al.* 2019).

Assessing post-fire herbivore impacts. Prior to accessing spatial data on this threat, a short list of both native and non-native herbivores most likely to affect post-fire recovery should be assembled. Each fire ground will differ in its exposure to herbivore impacts relative to the abundance of grazing and browsing animals in the landscape. Gallagher (2020) and Gallagher *et al.* (2022) assessed herbivore impacts using spatial data on the likely distribution of the following five non-native mammal species that are known to cause significant impacts on plant species across their Australian range: horse (*Equus caballus*), pig (*Sus scrofa*), goat (*Capra hircus*), deer (various species) and rabbit (*Oryctolagus cuniculus*). The distributional ranges of these herbivores were inferred from coarse-grained distribution models developed for national pest management planning. Maps of suitable habitat for feral animals can also be constructed from species distribution models, although these are not designed to approximate the density of populations. Auld *et al.* (2020) utilised the available literature and databases noting the identified susceptibility of species to the various herbivores. Keith *et al.* (2020*a*, 2022*b*) estimated exposure of ecosystems on the basis of distribution maps of feral pigs, horses, deer, hares and rabbits derived from consensus of generalised occurrence maps and atlas records. In addition, post-fire browsing by high densities of native herbivores was identified as a threat to montane heathland (Keith *et al.* 2020*a*) and may prove to be a localised threat to some woodland ecosystems subject to on-ground assessment.

IX. Fire–disease interactions

Plant species from particular genera and families are susceptible to diseases such as *Phytophthora* spp., *Armillaria*

Box 12. Ecosystem criteria: short fire intervals (Criterion II); post-fire interactions with invasive predators and herbivores (Criterion VIII); fire-disease interactions (Criterion IX)

Case study: Eastern Stirling Range Montane Heath and Thicket affected by disease.

Heathland with abundant sedges and a remnant *Andersonia axilliflora*, currently in decline on the summit of Stirling Range, south-western Australia (photo: Sarah Barrett).

Background: a heathland and thicket dominated by sclerophyll shrubs, including several narrow-range endemic species, with a prominent ground layer of graminoids and forbs that varies inversely with shrub density. Endemic to Western Australia. Restricted to the highest peaks of the Eastern Stirling Range (total extent less than 400 ha).

Conservation status: Critically Endangered under IUCN Red List of Ecosystems criteria (Barrett and Yates 2015), Endangered *EPBC Act* (but under revision).

Relevant life-history traits

- **Habitat:** heathland with sclerophylly shrubs and abundant sedges.
- **Fire ecology:** a mixture of taxa that resprout after fire and obligate seeders.
- **Seed bank:** a number of component taxa have a persistent soil seed bank, a few with a canopy seed bank.

Biotic/abiotic/fire regime threats: in addition to high fire frequency, extensive exposure and high susceptibility to root rot disease (*Phytophthora cinnamomi*) and post-fire herbivory by dense populations of native herbivores (quokka, *Setonix brachyurus*) has resulted in precipitous declines in disease-sensitive and fire-killed endemic shrubs. This has led to a transition to a Myrtaceae-dominated species-poor mixed shrubland and sedgeland, and apparently extinction of a host-specific hemipteran (Keith *et al.* 2014; Barrett and Yates 2015; Moir 2021). Climate change is also a likely driver of multiple threats.

Estimate of known sites/habitat burnt in the 2019/2020 fires: 28–43% with a further 76% burnt in 2018, so >90% burnt in total across each fire and ~16% burnt in both fires.

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria II, VIII and IX (Table 2).

Management response: Almost entirely burnt within a 2-year period 2018–2020, and exposed to high-frequency fire, with four major fires since 1990. Post-fire field inspections have confirmed major impacts and precarious status of the ecological community. Protection from future fires is critical to avoid further degradation and loss of biodiversity, as is disease mitigation, management of herbivores, *ex situ* conservation of key species and ongoing monitoring (Barrett and Yates 2015).

spp., *Austropuccinia psidii* (myrtle rust), Canker fungi and other pathogens (Box 13). Tissue death caused by these diseases reduces the capacity of plants to acquire resources through their roots and/or leaves. Plants are more sensitive to resource deprivation in the post-fire period and reduced post-fire survival and fecundity rates have been observed in areas infected by disease, such that fire accelerates disease-related population decline (Moore *et al.* 2014; Yates *et al.* 2021). Species that are slow to grow to reproductive age after germination may be particularly susceptible (e.g. to

Box 13. Species criteria: fire–disease interactions (Criterion IX)

Case study: *Rhodamnia rubescens* (Myrtaceae), a species affected by fire and disease.

Rhodamnia rubescens (photo: Jedda Lemmon, NSW DPE).

Background: found from southern coast of NSW to Bundaberg in Queensland, Australia.
Conservation status: Critically Endangered (*EPBC Act*).

Relevant life-history traits

- **Habit:** shrub or small tree up to 25 m (PlantNet (The NSW Plant Information Network System, Royal Botanic Gardens and Domain Trust, Sydney) 2022c).
- **Fire ecology:** some capacity to resprout after fire (Pegg *et al.* 2021), but this may be dependent on fire severity.
- **Seed bank:** no persistent seed bank.

Biotic/abiotic/fire regime threats: major threats of death and dieback from myrtle rust pathogen and impacts of a warming climate.
Estimate of known sites/habitat burnt in the 2019/2020 fires: 34%.
Assessment against framework criteria for species: predicted to be at HIGH risk via criterion IX (Table 1).
Management response: approximately a third of the distribution of the species was burnt in the 2019/2020 fires and the species is known to be markedly affected by myrtle rust. Post-fire field assessments (Pegg *et al.* 2021) have confirmed the predicted fire impacts (including stem dieback and resprouting) and ongoing serious impacts of myrtle rust on resprouting stems.

Phytophthora cinnamomi, Cahill *et al.* 2008), and resprouting individuals in certain families also appear susceptible because young plant tissues are predisposed to infection, such as, for example, myrtle rust affecting trees and shrubs in Myrtaceae (Pegg *et al.* 2021). Disease effects may also be exacerbated by drought.

Diseases may weaken ecosystem resilience to fire, whereas fire may increase susceptibility of key ecosystem components to disease (e.g. Moore *et al.* 2014; Box 12). Ecosystems containing many disease-sensitive species, or structurally or functionally important groups of sensitive species, are most susceptible to this interaction. In Australia, examples include Eastern Stirling Range Montane Heath and Thicket, where many dominant shrub species are affected by *Phytophthora cinnamomi* (Keith *et al.* 2020*a*), and *Melaleuca quinquinervia*-dominated forests of eastern Australia, where epicormic regrowth after fire in the dominant species may be affected by myrtle rust, with significant implications for food availability for nectarivorous birds and mammals (Pegg *et al.* 2021).

Assessing fire–disease interactions. Exposure to key diseases can be estimated by combining existing data on the susceptibility of species to major pathogens (e.g. in Australia, this will include *Phythophthora cinnamomi* and *Austropuccinia psidii*) and inferred from spatially explicit records of disease occurrence supplemented by expert knowledge of the distribution of previous disease activity. Auld *et al.* (2020) and Keith *et al.* (2020*a*, 2022*b*) considered susceptibility to fire–disease interactions on the basis of published data on susceptible taxa to each disease type, expert opinion and, for ecosystems, the importance of the species within each ecosystem.

X. Fire-promoted weed invasion

Some sites are predisposed to invasion by transformer exotic plants. Fire may facilitate expansion of existing infestations or entry of novel exotic species into the native vegetation (especially where weed source populations are within or proximal to burnt areas; Box 14). This can result in subsequent elimination of native species through competition (e.g. Milberg and Lamont 1995; Miller *et al.* 2010). Native species that occur mainly in areas where bushland has been fragmented, disturbed by logging or clearing, or affected by runoff from nutrient sources (e.g. urban infrastructure, improved pasture, wastewater or stormwater disposal etc.), are most susceptible to this mechanism. Invasion of exotic grasses may also initiate fire-feedbacks (Miller *et al.* 2010).

Assessing fire-promoted weed invasion. Lists of invasive plant taxa can be gathered from national and international weed species lists, such as the Weeds of National Significance list in Australia, or the global '100 of the World's Worst Invasive Alien Species list' (http://www.iucngisd.org/gisd/100_worst.php). Occurrence records for each taxon can be accessed from local or global repositories of occurrence records, such as *the Global Biodiversity Information Facility* (GBIF) and combined to create mapping of the exposure of locations to weed invasion using either raw occurrence data or by creating spatial layers of suitable habitat in SDMs. Alternatively, susceptibility to weed impacts can be based on published data to identify susceptible taxa affected by various weeds, expert opinion and for ecosystems, the importance of weed impacts on species within each ecosystem. For example, Keith *et al.* (2020*a*) utilised information from national and state Key Threatening Process documentation, fragmentation by agricultural production or urban/industrial uses (based on visual inspections of maps and imagery in Google Earth), prior and current grazing and logging activity, and weed infestations known to experts. Exposure was then estimated from the intersection of susceptible ecosystems with the 2019/2020 fire extent.

XI. Interactions between fire and localised anthropogenic disturbances

Other plausible threats not addressed by Criteria I–X above may arise as a result of human-linked activities and this criterion is designed to capture their effects on species affected by fires. Often such threats are localised to particular populations, including, for example, disturbance from vehicles or foot traffic, rubbish dumping, illegal collection, removal of woody debris or bushrock and small-scale clearing of habitat (e.g. disturbance from mineral extraction and forestry operations). In all cases, such threats can lead to increased risks to post-fire recovery via the loss of individual plants or whole populations, damage to plants (seedlings or resprouts) recovering after fire, and/or reduced pre- or post-fire fecundity (leading to reduced post-fire recruitment or a reduced rate of seed-bank replenishment).

Assessing localised anthropogenic disturbances. Information on threats to plant species can be found in a range of sources including scientific literature, management plans, national and state databases, unpublished reports and expert opinion, although these are often difficult to access and compile for quantitative analysis. Such threats may be specific to certain taxa (Table 3). Often such threats are restricted to certain sites within the distribution of a species or ecosystem, and overlap of the spatial extent of these sites and the fire footprint is required. Some threats (e.g. illegal collection of orchids) may occur across the distribution of a species.

Application of the assessment frameworks

Spatial scale of application

The framework for species has been applied to plants after the Australian 2019/2020 fires with both a national focus (Gallagher 2020; Gallagher *et al.* 2021, 2022) and a regional

Box 14. Ecosystem criteria: fire sensitivity (Criterion I); post-fire interactions with invasive predators and herbivores (Criterion VIII); weed invasion (Criterion X)

Case study: Milton–Ulladulla Subtropical Rainforest ecosystem affected by fire and weed invasion

Milton– Ulladulla Subtropical Rainforest with a dense infestation of *Solanum mauritianum* (photo: David Bain, DPE).

Background: endemic to coastal lowland areas of the New South Wales southern coast near Milton and Ulladulla, Australia, on alluvium or soils derived from (or enriched by) monzonite.

Conservation status: Critically Endangered (*NSW BC Act* and included within *EPBC Act* Illawarra–Shoalhaven Subtropical Rainforest).

Relevant life-history traits

- **Habitat:** low closed forest with emergent trees and sparse shrub and ground cover dominated by ferns and vines. (NSW Scientific Committee 2011). Complex dry rainforest characterised by gap-phase dynamics and rapid decomposition of organic matter and nutrient cycling facilitated by a moist climate and abundant saprophytes and detritovores.
- **Fire ecology:** low levels of flammability and fuel accumulation, fires are rare, and most tree and vine species have thin bark and are susceptible to top-kill by low- and high-severity fires, with or without basal resprouting.
- **Seed bank:** some species with a soil seed bank, others with a juvenile bank of plants.

Biotic/abiotic/fire regime threats: Milton–Ulladulla Subtropical Rainforest has been extensively cleared and remains as small and fragmented remnants surrounded by agricultural land (NSW Scientific Committee 2011). Ongoing threats include grazing, weed invasion, fire, habitat disturbance and loss (e.g. cutting of trees for firewood, rubbish dumping, road widening and utility easements; NSW Scientific Committee 2011).

Estimate of known sites/habitat burnt in the 2019/2020 fires: 60% of survey sites burnt (Keith *et al.* 2020*a*), 34% of mapped area burnt (Keith *et al.* 2022*b*).

Assessment against framework criteria for species: predicted to be at HIGH risk via Criteria I, VIII and X (Table 2).

Management response: a high proportion of the distribution of the ecosystem was burnt in the 2019/2020 fires. Scorch heights were generally low (<2 m), but stem heating was sufficient to top-kill many trees and trigger mass recruitment of invasive introduced plants such as

Solanum mauritianum. Remnants have been susceptible to weed invasion where canopy disturbance has occurred. Impacts of grazing by domestic stock have been recorded.

Post-fire assessments have confirmed the extensive top-kill of rainforest trees, resulting in increased light penetration which, coupled with the fertile soils and proximal sources of weed propagules, has promoted extensive weed invasion. Canopy regrowth is slow, hampered by poorly developed mechanisms for post-fire recovery, minimal seedling establishment except for *Acacia* spp., and competition from weeds and slow recovery of vine species (D. Bain, unpubl. data; D. Keith, unpubl. data).

Table 3. Examples of localised anthropogenic disturbances as plausible threats identified for NSW plant taxa (Auld *et al.* 2020).

Threat	Example species	Localised anthropogenic disturbances as plausible threats ranking	Overall risk ranking	Impact
Trampling	*Epacris gnidioides*	HIGH	HIGH	Localised visitation can cause plant damage and uprooting of individuals (Department of the Environment, Water, Heritage and the Arts 2008*a*)
Localised site disturbance	*Commersonia prostrata*	LOW	MEDIUM	Damage to plants and habitat from earthworks and vehicle movement (Carter and Walsh 2010)
Vehicle damage	*Micromyrtus minutiflora*	LOW	HIGH	Affected by recreational vehicle damage (NSW Saving our Species 2020)
Mining	*Leucochrysum graminifolium*	HIGH	HIGH	Occurs on rock outcrops and ledges and is susceptible to cliff collapse from underground mining (Benson and McDougall 1994)
Forestry	*Leionema ralstonii*	MEDIUM	MEDIUM	Affected by adjacent clear-felling and forestry operations (Department of the Environment 2014)
Clearing	*Bossiaea oligosperma*	HIGH	HIGH	Disturbance and loss of habitat at one site (Department of the Environment, Water, Heritage and the Arts 2008*b*). Post-fire weed issues affecting recovery after 2019/2020 fires (NSW SOS database, accessed Aug 2021)
Illegal collection	*Diuris disposita*	LOW	LOW	Only known from three populations and subject to illegal collection (NSW Scientific Committee 1998) as well as other threats

one (the state of NSW, Auld *et al.* 2020). These assessments applied the framework to assess fire impacts across a species' national distribution so that priority outcomes were not biased by local/regional impacts. Similarly, Keith *et al.* (2020*a*, 2022*b*) applied the ecosystem framework at the national scale to ecosystems recognised in national and state jurisdictions (the latter particularly for ecosystems largely endemic to a particular state).

The frameworks can be applied to any area of management interest, but it is also important to consider the total distribution of species or ecosystems to provide relevant context. This may help inform management priorities at the scale of reserve networks or bioregions, with species or ecosystems exposed to high impacts throughout their distribution being assigned a higher priority than those exposed to high impacts in the assessment area, but not throughout their range. The benefits of applying the criteria at global or national scales for megafires include a more comprehensive understanding of relative risks to different functional groupings of plants or types of ecosystems, and the factors driving reduced post-fire recovery, along with targeting of subsequent management actions to where they are most needed. Improvements in national datasets on plant species responses to fire and ecological traits will enhance the capacity of such comparisons. Gallagher *et al.* (2021) and Godfree *et al.* (2021) both estimated the percentage of Australian native plant species affected by the 2019/2020 fires, which helped convey the magnitude of potential impacts to a wide audience. However, the additional application of the risk framework for plant species allowed Gallagher *et al.* (2021) to identify key mechanisms driving potential decline, which is the first critical step towards development and implementation of strategies for risk reduction and impact mitigation.

Application to threatened entities

The frameworks can be applied to threatened species and ecosystems to identify those most in need of management action. For example, Gallagher (2020) and Gallagher *et al.* (2021) found that some 67 nationally threatened plants in Australia were likely to decline as a result of the 2019/2020 fires (i.e. medium or high risk) owing to too frequent fire. The framework has also been used to identify priority species for possible statutory listing, and a number of conservation status assessments are currently underway (see https://www.dcceew.gov.au/environment/biodiversity/threatened/seap). This fills an important gap, given that the current statutory listings markedly underestimate the number of plant species (and ecosystems) that are likely to be threatened (Alfonzetti *et al*. 2020). Auld *et al*. (2020) found that over 100 nationally threatened plants that occurred in NSW were likely to decline as a result of the 2019/2020 fires, with an additional 60 NSW endemic species listed as threatened either under the IUCN Red List of Threatened Species or the *NSW Biodiversity Conservation Act* also being likely to decline. These latter 60 species potentially need to be added to the national *Environment Protection and Biodiversity Conservation Act* threatened species list. Finally, some 230 NSW endemics that are not currently listed as threatened under any legislation were identified by Auld *et al*. (2020) as potentially declining because of the megafires. These species are candidates for possible threatened species listings, should the predicted impacts and threats to natural recovery result in population declines in response to the 2019/2020 fires.

Application to other priority conservation assets or functional groupings

As well as individual species and ecosystems, the framework criteria could be applied to a range of other priority conservation assets affected by megafires, including keystone species, refugia and key biodiversity areas (*sensu* IUCN 2016). For example, Gallagher *et al*. (2021) examined the spread of impacts for the 2019/2020 Australian megafires across different plant family groupings, highlighting high levels of impacts in three major families (Proteaceae, Fabaceae and Myrtaceae).

Recommended recovery actions

Despite uncertainties in assessments, in many cases the impacts of a number of key threats are sufficiently understood to recommend specific conservation actions for affected species and ecosystems (Table 4). Some actions are needed in the short term (0–2 years after fire), whereas others may require longer-term implementation (>5 years post-fire, Fig. 2). Key recovery actions should be identified for species or ecosystems that are most likely to decline or fail to recover after fire. Prioritisation and implementation of actions should recognise that fire plays a key role in the life history of many plant and animal species, and that the abundance of certain groups such as obligate seeders may fluctuate in response to fire as a consequence of their natural population dynamics (i.e. sustained population declines should be distinguished from population fluctuations, *sensu* IUCN 2022). Other species may recover vegetatively after a fire, but their detectability may be highest during post-fire flowering (e.g. pyrogenic species of terrestrial orchids), with many plants persisting below ground in the intervening period. In these cases, population trends can be difficult to detect and require monitoring designs that are cognisant of life-history dynamics.

Immediate post-fire actions

For species and ecosystems ranked with the potential for medium to high declines (Table 4), the primary recommendation is to undertake post-fire field surveys. These are essential to assess realised impacts and the degree of recovery, verify causes of decline inferred in the assessment, identify any emerging, previously unidentified threats to recovery, and to devise actions to mitigate the threats. This is particularly critical for species that have sites/populations affected by high fire frequency (Criterion II) and species sensitive to fire (Criterion I). For long-lived rainforest trees prone to top-kill and/or collapse from basal charring (Box 5), there is an urgent requirement to conduct field inspections within the first year post-fire so as to assess the scale of tree loss or damage and the rehabilitation actions required.

Development of risk-reduction strategies is essential if an understanding of impacts is to be translated into positive conservation outcomes for both species and ecosystems. Field surveys should inform the relative conservation priorities for recovery actions and the nature and timing of the actions needed for recovery (Fig. 2, Table 4, Box 5) as well as identifying any new or emerging threats. This is essential to modify and update proposed management actions as circumstances change, and to adjust priorities where required, so as to ensure the best possible investment of the limited resources available for post-fire recovery.

Medium- to long-term actions

Depending on the particular threats identified, actions required to assist recovery include the following:

- Development of a fire management plan to reduce the likelihood of future fires burning over recovering sites (Criteria I–III). For example, avoiding additional fires (including hazard reduction burns) in all recently burnt habitat is necessary to allow time for recovery of species and ecosystems.
- Protecting unburnt parts of a species' range, including fire refugia (i.e. no burning or clearing or logging in that habitat) to provide insurance and avoid having the entire species' range at risk from a future fire recurrence at the one time (i.e. avoid risks from Criterion IV for species) and to protect any refugia.

Table 4. Priority actions likely to be needed for species or ecosystems at high risk, or otherwise a priority, following major fires such as Australian 2019/2020 bushfires. All criteria require an immediate priority action of field inspections to assess the impacts of threats to recovery.

Framework criterion	Medium-longer term actions
I. Fire sensitivity	• Monitor resprouting success. • Monitor re-establishment of juvenile banks if species maintain these. • Avoid implemented fires including hazard reduction burns in the vicinity of burnt areas. • Develop a fire-management plan to ensure that any all future fires that threaten to burn over recovering sites are rapidly extinguished. Germplasm collection for species considered a high priority for *ex situ* cultivation and *ex situ* conservation.
II. Short fire intervals	• Avoid implemented fires including hazard reduction burns in all recently burnt habitat (including but not limited to habitat burnt in 2019/2020). • Protect unburnt parts of a species range (i.e. no burning or clearing or logging in that habitat) so as to avoid putting all the entire species' range at risk at once. • Develop a fire management plan to ensure that any future wildfires that threaten to burn over recovering sites are rapidly extinguished. • Monitor species' recovery to determine the time required to replenish seed banks in obligate seeders and the time required for juveniles to become fire resistant in resprouters.
III. High fire severity	• Resprouting plants – assess the proportion of plants resprouting and the survival of resprouts. • If resprouting is markedly reduced or affected, consider translocation.Obligate seeders – assess the magnitude and survival of seedlings. If seed recruitment fails investigate translocation.
IV. Species-wide exposure to high risk of recruitment failure	• Avoid implemented fires including hazard reduction burns in all recently burnt habitat (including but not limited to habitat burnt in 2019/2020). • Protect unburnt parts of a species range (i.e. no burning or clearing or logging in that habitat) so as to avoid putting the entire species' range at risk at once.
V. Interactive effects of fire and drought	• Resprouting plants – assess the proportion of plants resprouting and the survival of resprouts. • If resprouting is markedly reduced or affected by drought, consider translocation options. • Obligate seeders – assess the magnitude of seedling emergence and survival. • If seedling recruitment is limited by drought, consider translocation options.
VI. Post-fire erosion	• Monitor species recovery (resprouting and/or seedling recruitment) in areas subject to erosion. • Consider manual removal of erosive material if it is swamping recovery. • In obligate seeders, consider translocation if the seed bank has been eroded away, resulting in little to no post-fire recruitment.
VII. Elevated winter temperatures or changed temperature regimes	• Assess the timing and magnitude of seedling recruitment and monitor seedling survival. • Consider translocation (population enhancement) in obligate seeders if recruitment fails or is very poor.
VIII. Post-fire interactions with invasive predators and herbivores	• Exclusion or removal of feral grazers, stock and excessive native herbivores by fencing and feral animal control.
IX. Fire-disease interactions	• Treatment of soil or plants to enhance their ability to cope with diseases. • Maintenance of strict phytosanitary measures during site visits to minimise risk of disease transfer and introduction. • Consider translocation (population enhancement) if natural recovery fails.
X. Weed invasion	• Removal and control of weeds that may outcompete natives and impede post-fire recovery.
XI. Localised anthopogenic disturbances as plausible threats	• Exclusion of vehicles, bikes and other human disturbance via signage, fencing and negotiations with local users. • Prevention of further disturbance via fencing, liaison with relevant utility owners and land managers, and education activities. Minimising illegal losses via education, fencing, surveillance and enforcement.

- Avoid works that may affect surface or subsurface drainage or increase erosion risks (Criteria V and VI (species) or V, VI and VII (ecosystems)). In emergency situations, consider options for supplementary watering if post-fire drought conditions are evident (Criterion V).
- Exclusion or control of invasive herbivores or predators (Criterion VIII).
- Maintain suitable disease hygiene and mitigation (Criterion IX).
- Post-fire weed control (Criterion X).
- Minimise any localised site disturbances (Criterion XI).
- Monitoring species' recovery to determine the time required
  – to replenish seed banks (especially in obligate seeders);
  – for juveniles resprouting plants to become fire resistant; and
  – for top-killed trees to recover their stature, structure and reproductive capacity.

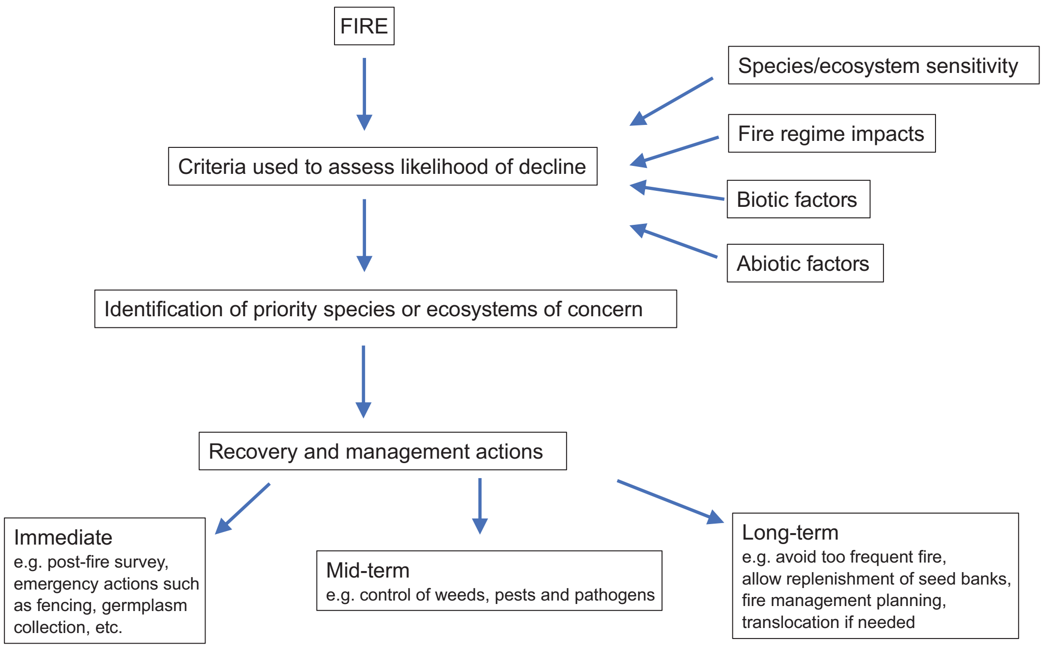


Fig. 2. Context of framework criteria for prioritisation of recovery actions post-fire.

Species or ecosystems that show limited post-fire recovery may require further interventions. These may include collections of seed or vegetative material for various conservation purposes, including restoration and translocation, reintroductions and establishing seed orchards (e.g. Bassett *et al.* 2015; Commander *et al.* 2018; Martyn Yenson *et al.* 2021, Box 15). For some species, emergency germplasm collection may be needed (Martyn Yenson *et al.* 2021), for example because of post-fire impacts of myrtle rust.

Conclusions

Species and ecosystems that have a long evolutionary history of persisting under recurring fires have developed various mechanisms and strategies for recovering their populations or structure, function and composition. Their continued ability to do so is dependent on their tolerance to changing fire regimes, in combination with how other threatening processes compromise resistance, resilience or regenerative responses to the fire event. Here we have highlighted a novel mechanistic approach to rapidly predict the impacts of megafires on plant and ecosystem biodiversity. Key advances on unstructured methods of assessment include the incorporation of (1) fire-regime data (see Box 1; e.g. fire frequency, severity, season, type and fire patchiness), rather than fire extent alone, (2) species life histories, biology and ecosystem properties to define potential mechanisms of decline, and (3) interactions between fire events with biotic and abiotic threats to survival and recovery. The frameworks explicitly recognise that knowledge of the antecedent fire regime in combination with that of coincident biotic and abiotic threats in the landscape are required to predict and understand the impacts of megafire events on species and ecosystems. The frameworks help integrate and contextualise the interpretation of single fire events into fire-regime impacts.

The two assessment frameworks were applied to guide conservation responses to the Australian 2019/2020 mega-fires across southern Australia (Gallagher *et al.* 2021; Keith *et al.* 2020*a*, 2022*b*). They enabled rapid assessment of potential impacts of large fires on plant species and ecosystems, establishing immediate priorities for post-fire surveys, which are now guiding management and monitoring strategies, as well as new statutory listings to protect threatened species and ecosystems.

The post-fire assessment frameworks support rapid decision-making, in part because of their flexibility to utilise a combination of readily available remotely sensed data, detailed species-trait data, available literature and expert opinion. They allow for addition of further criteria should novel threats emerge that affect species and ecosystem recovery. A structured approach that leverages diverse sources of existing knowledge provides a way of informing prioritisation for resourcing of urgent and on-going field inspections and recovery actions.

Although the frameworks were developed as an immediate response to the unprecedented Australian 2019/2020 wildfires, the frameworks can be applied to any fire and any landscape, provided the combination of fire variables, life-history traits, threats to recovery and environmental variables are known or can be estimated or inferred. We

Box 15. Seed collection and translocation as management responses

It is critically important to allow natural systems to recover after fire without intervention. Post-fire recovery can take months or years (and even longer for some species). The focus in the first 12 months after fires should be on eliminating threats to natural recovery rather than on translocation (which itself needs to be well planned and thought out and requires significant lead time, Commander *et al.* 2018).

When to use translocation

If it can be demonstrated that species fail to recover effectively at a site or within an ecosystem after a fire, then consideration of translocation (seed addition or supplementary planting) may be necessary. Note that some fires may kill standing plants, yet not promote seedling recruitment post-fire. A soil seed bank may still be present and this needs to be considered in any assessment of whether translocation is required. Species with certain dormancy types (PD or MPD) may have post-fire germination delayed for over 12 months, depending on timing of fires and favourable conditions for recruitment. Decisions to proceed with translocation should be based on rigorous post-fire site assessments of recovery and should follow appropriate national guidelines on translocation (Commander *et al.* 2018).

Seed collection after fire – risks and benefits

The resilience of many species to fire is dependent on the maintenance of persistent soil or canopy seed banks. Seed banks allow post-fire seedling recruitment and the size of the seed bank (along with fire-related factors such as heat and smoke) and post-fire rainfall, govern the magnitude of post-fire seedling recruitment. Canopy seed banks may be exhausted by a single fire (if all plants are burnt). Soil seed banks are likely to provide some buffer against successive fires because of residual seeds surviving in the soil after a fire (not all seeds will germinate), but soil seed banks too can be locally exhausted in a single fire (Auld and Denham 2006). For population persistence, seed banks need to be sufficiently replenished after a fire before the next fire occurs, otherwise decline will occur. The length of time required to replenish seed banks varies among species and is dependent on life-history attributes. As examples, some taxa have mass-flowering and fruiting soon after fire (e.g. *Actinotus* spp. (Kubiak 2009), *Acacia suaveolens* (Auld 1987)), whereas others may flower early but take 5–10 years to be large enough to produce sufficient seed to replenish their seed banks (e.g. *Grevillea caleyi*, *Darwinia biflora* (Auld and Scott 1997)).

Seed collection (e.g. for *ex situ* conservation or other restoration activities) prior to adequate post-fire replenishment of *in situ* seed banks may limit species' persistence capacity, especially because more frequent fires are predicted under a changing climate, along with a reduction in favourable windows for recruitment (interval squeeze of Enright *et al.* 2015). Consequently, seed collection should be limited for any species until its seed bank has been sufficiently replenished to enable population recovery in the event of a subsequent fire. Cases of urgent *ex situ* conservation may be an exception, and, in such cases, seed collection should be conducted in a way to minimise impacts on *in situ* seed-bank accumulation.

highlight that post-fire surveys of prioritised species and ecosystems are essential to ensure that management priorities are robust and well supported, and to identify the most effective management responses. Finally, the frameworks highlight the need for development and maintenance of national and global plant databases to inform plant and ecosystem responses to fire and other threats.

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Data availability. Data used in this study are available on request from the senior author (tony.auld@environment.nsw.gov.au).

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