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RESEARCH ARTICLE

Fire-related threats and transformational change in Australian ecosystems

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Abstract

Aim: Megafire events generate immediate concern for wildlife and human well-being, but their broader ecological impacts likely extend beyond individual species and single fire events. In the first mechanistic study of fire effects focussed on ecosystems, we aimed to assess the sensitivity and exposure of ecosystems to multiple fire-related threats, placing impacts in the context of changing fire regimes and their interactions with other threats.

Location: Southern and eastern Australia.

Time period: 2019–2020.

Major species studied: Australian ecosystems.

Methods: We defined 15 fire-related threats to ecosystems based on mechanisms associated with: (a) direct effects of fire regime components; (b) interactions between fire and physical environmental processes; (c) effects of fire on biological interactions; and (d) interactions between fire and human activity. We estimated the sensitivity and

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exposure of a sample of 92 ecosystem types to each threat type based on published relationships and spatial analysis of the 2019–2020 fires.

Results: Twenty-nine ecosystem types assessed had more than half of their distribution exposed to one or more threat types, and only three of those were listed as nationally threatened. Three fire-related threat types posed the most severe threats to large numbers of ecosystem types: high frequency fire; pre-fire drought; and post-fire invasive predator activity. The ecosystem types most affected ranged from rain forests to peatlands, and included some, such as sclerophyllous eucalypt forests and heathlands, that are traditionally regarded as fire-prone and fire-adapted.

Main conclusions: Most impacts of the 2019–2020 fires on ecosystems became apparent only when they were placed in the context of the whole fire regime and its interactions with other threatening processes, and were not direct consequences of the megafire event itself. Our mechanistic approach enables ecosystem-specific management responses for the most threatened ecosystem types to be targeted at underlying causes of degradation and decline.

KEYWORDS
climate change, ecosystem collapse, ecosystems, fire frequency, fire impacts, fire regimes, Red List of Ecosystems, threatened ecological communities, threatening process

1 | INTRODUCTION

The 2019–2020 'Black Summer' fires across temperate and subtropical Australia were the most prolonged, radiative and extensive on record (Abram et al., 2021) and among the most severe (Collins et al., 2021), burning continually over 5 months across 10 million hectares. They were associated with historically low fuel moisture during prolonged and severe drought, episodically extreme fire weather and serial lightning ignitions (Abram et al., 2021). These conditions are consistent with climate change projections that have played out in similar fire events during the past decade in Australia and temperate regions of most other landmasses (e.g. Halofsky et al., 2020).

While such fires stimulate a range of ecological studies, most focus only on event effects (Bond & Van Wilgen, 2012) at the species level and do not address mechanisms of decline or traits that confer fire resistance, avoidance and ability to recover (e.g. Godfree et al., 2021; Ward et al., 2020), although a few species-level studies consider traits and/or interval effects (Gallagher et al., 2021; Legge et al., 2020). Relatively few studies assess fire effects on biodiversity at higher levels of ecological organization (communities, ecosystems), and most report only the areas of different ecosystems that were burnt, with or without reference to fire severity (e.g. Lentile et al., 2007). We are unaware of any studies that assess the mechanisms of fire-related threats to biodiversity at the ecosystem level, or place ecosystem impacts of single events in the context of the fire regime (Barrett & Yates, 2015).

A number of signatory countries to the United Nations Convention on Biological Diversity are equipped with legislation and policy instruments that address ecosystem levels of biodiversity (Bland et al., 2019). In Australia, the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act) provides for assessment, listing and protection of threatened 'ecological communities', defined as assemblages of [interacting] species within a particular area. State and territory jurisdictions within Australia, with constitutional responsibilities for land management, have complementary instruments for protection of ecological communities or vegetation types, which serve as representations of ecosystem types (Keith, 2009). These policy frameworks have developed asynchronously, and semi-independently across Australian jurisdictions over past decades, resulting in complex relationships among listed entities defined at different levels of thematic resolution in different jurisdictions (Nicholson et al., 2015). Work is now underway to harmonize and co-ordinate listing processes, the listings themselves, and regulatory and conservation actions across jurisdictions, although at present analyses and planning must operate within the legacies of policy development. This need was strongly emphasized in the aftermath of the 2019–2020 fires, which generated much public concern about their ecological impacts and initiated a major mobilization of public and private resources to support the recovery of Australian biodiversity.

This study of bushfire impacts on ecosystems was commissioned by the Australian government to inform allocation of recovery funding for fire-affected ecosystems and to identify needs for updating the current listings of threatened ecological communities under national legislation. We first identified a list of ecosystem types at finer thematic resolution than major vegetation formations (including threatened ecological communities) to be targeted for assessment.

We reviewed available spatial data on the distribution of these ecosystem types and resolved inaccuracies. We then identified a set of fire-related threat types, based on different mechanisms that may result in ecosystem degradation, which we define as sustained transformation of ecosystem structure, function or composition of its biota. We estimated the sensitivity of each ecosystem type to degradation as a result of exposure to each threat type. Finally, we carried out spatial analyses to quantify the exposure of each ecosystem type to each threat type. The analysis revealed the diverse range of ecosystems at risk of degradation as a result of the 2019–2020 fires. It also demonstrated the need to review and update current statutory listings of threatened ecological communities, and the importance of interactions between fire and other processes as threats to biodiversity, especially climate change and invasive species.

2 | METHODS

The study was carried out in southern Australia (Figure 1) within an area bounded by the south-eastern, southern and south-western coasts of mainland Australia (including Kangaroo Island) and an arc extending from Bowen in central Queensland through Broken Hill (New South Wales, NSW), Wyalla (South Australia, SA), Kalgoorlie (Western Australia, WA) and Shark Bay (WA). The study area covered 2.2 million km^2, of which 101,600 km^2 (4.6%) was burnt in 2019–2020 according to the National Indicative Aggregated Fire Extent dataset (NIAFED; DAWE, 2020). We used Australian vegetation formations described by Keith and Tozer (2017) to represent major biomes and developed spatial data for their distribution by reinterpreting map data from the Australian Government (2015).

2.1 | Selection and mapping of ecosystem types for assessment

We assumed that ecological communities or vegetation types defined by government agencies served as suitable proxies for terrestrial ecosystem types (Keith, 2009). These were selected for assessment if their distribution intersected the 2019–2020 fire footprint and either: (a) they were listed as threatened under the EPBC Act; (b) they were listed as threatened under state or territory legislation; or (c) they were recognized in state agency vegetation classifications and were identified in the Australian Government's rapid assessment (Keith et al., 2021) as warranting more detailed evaluation. Distribution maps were obtained from Commonwealth and State government agencies (sources for each map in Supporting Information Appendix S1). We critically evaluated the maps against the available descriptions of the ecological communities and vegetation types, and corrected minor errors in the spatial data where they were found. In a few cases, ecological communities were included within broader map units and we clipped the distributions of the broader units using environmental or biogeographical variables identified from the descriptions. A total of

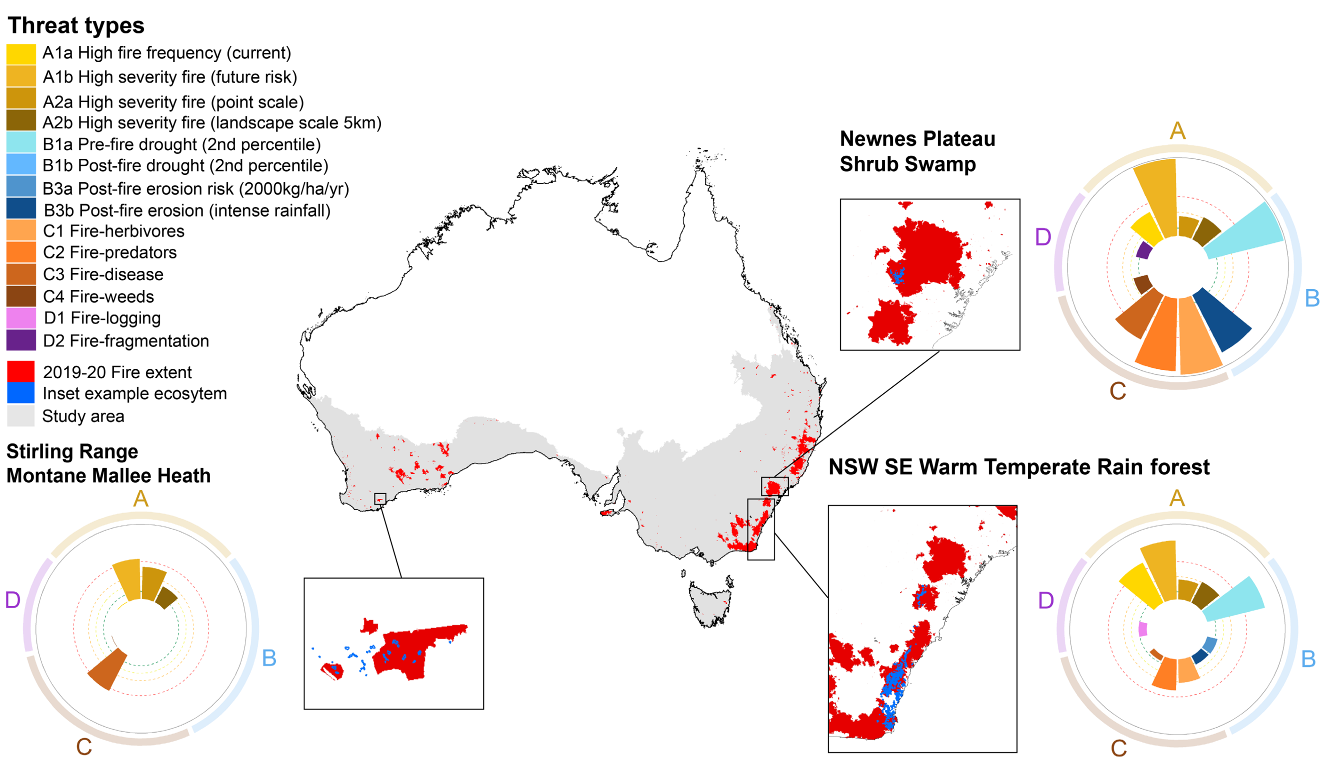

FIGURE 1 Study area with extent of fires in 2019–2020 season showing exposure to fire-related threat types (Table 1) for three example ecosystem types that represent different kinds of shrublands, rain forests and wetlands. Radial bars indicate proportion of distribution (0–100%) exposed to each threat type (see legend) for each ecosystem type. Details in Supporting Information Appendix S3

92 ecosystem types were identified for assessment and were distributed across a total of 204,300 km^2 of the study area, of which 8.7% was burnt in 2019–2020.

2.2 | Identification of fire-related threats

We identified 15 plausible threat types with the potential to affect ecosystems from published literature on the ecological effects of fire regimes (Table 1). Fire is one of several types of disturbance regime that act as assembly filters and evolutionary pressures shaping ecosystem properties (Keith et al., 2022). While certain fire regimes sustain the properties of particular ecosystems, other fire regimes or interactions with other assembly filters (biotic and abiotic) may promote degradation of properties, disassembly and ultimately ecosystem collapse in a diverse range of ecosystem types (e.g. Gibson et al., 2018; Halofsky et al., 2020; Sales et al., 2020; Tepley et al., 2018). The 15 threat types fall within four major groups (Table 1): direct effects of fire regimes; interactions between fires and physical environmental processes; interactions between fires and biotic processes; and interactions between fires and human activities.

2.3 | Spatial indicators of threat types

We used the NIAFED to estimate the extent of fires in the study area during the 2019–2020 fire season. To select spatial indicators of threat types described in Table 1, we critically evaluated available spatial datasets. We sought spatial variables that: (a) faithfully represented the process(es) underlying each threat; (b) were temporally appropriate to the ecosystem pressure and response; (c) were spatially comprehensive across the study area; and (d) were preferably published in peer-reviewed literature and/or freely available through public data portals.

We compiled suitable spatial data for continuous, ordinal or binary indicators representing 10 of the 15 threat types (Supporting Information Appendix S2). For six types (A1, A2, B1, B3, D1, D2), we identified a single spatial variable as a suitable indicator with a high degree of certainty. We derived two metrics to examine different temporal expressions of exposure to high fire frequency in the past (A1a) and future risk (A1b), based on a fire history spatial layer for 1968–2020 merged from three sources (Supporting Information Appendix S2, A1). Similarly, we derived two different spatial expressions, for exposure to fire severity at point (A2a) and landscape scales (A2b). To estimate exposure to canopy fire at each of these scales, we used the maximum area from the intersection of ecosystem distributions with two alternative fire severity mapping algorithms, one based on a supervised random forest image classification and the other based on normalized burn ratio (Supporting Information Appendix S2, A2).

We estimated exposure to pre-fire (B1a) and post-fire (B1b) drought, respectively, for a 6-month period immediately prior to the peak fire season and for the first post-fire year, from spatial data layers interpolated from weather station data (Supporting Information Appendix S2, B1). To estimate exposure to post-fire erosion and sedimentation, we used Yang's (2010) hillslope erosion model (B3a, available only for NSW) and a spatial layer of rainfall intensity (B3b, for the entire study area) for the early post-fire period 15 January–15 March 2020 interpolated from weather station data (Supporting Information Appendix S2, B3).

We estimated the exposure to post-fire herbivore activity from the maximum extent across five major invasive pests in the study area (horses, pigs, goats, deer and rabbits) based on distribution maps derived from consensus of generalized occurrence maps and atlas records (Supporting Information Appendix S2, C1). We applied a similar approach to estimate exposure to post-fire disease based on distribution maps for root rot, myrtle rust and Bell-miner associated dieback (Supporting Information Appendix S2, C3). We estimated exposure to post-fire predators from the product of modelled population density and relative frequency of native : introduced mammals, using the maximum value of foxes and cats (Supporting Information Appendix S2, C2). We estimated exposure to post-fire weed competition based on spatially aggregated occurrence records of 732 designated invasive plants species from the Australian Virtual Herbarium, Atlas of Living Australia and BioNet Atlas (Supporting Information Appendix S2, C4).

We estimated exposure to fire-logging interactions from logging history maps for a portion of the study area in NSW and Victoria (Supporting Information Appendix S2, D1). No spatial data on logging could be obtained for the relatively small burnt forested areas in other parts of the study area. We estimated exposure to fire–fragmentation interactions from a binary raster of native vegetation cover by calculating the proportion of native vegetation within a 500-m neighbourhood of a 100-m focal cell.

In the absence of spatial data, we assessed two threat types qualitatively. We assessed exposure to peat fires by identifying ecosystem types that had combustible substrates; primarily forested wetlands and peat bogs (Supporting Information Appendix S2, A4) and exposure to interactions between fire and human access by identifying ecosystem types around and within areas of high human activity. We did not assess effects of out-of-season fires (A4) because the 2019–2020 occurred primarily within the austral fire season (late spring–summer). Finally, given the influence of climate change on ecosystem exposure to high fire frequency (A1), high fire severity (A2), fire–drought interactions (B1), and interactions between fire and invasive species (e.g. C4), we did not carry out additional analyses to estimate exposure to fire–climate change interactions. Full details of the derivation of spatial indicators of threat types, their data sources and their limitations are given in Supporting Information Appendix S2.

2.4 | Sensitivity to threats

We defined sensitivity as the severity of ecosystem degradation (simplification of structure, loss of function or diversity) likely to result from exposure to a given threat type. We estimated the sensitivity of each ecosystem type, given exposure to each threat, type. First we assigned the ecosystem types to Ecosystem Functional Groups by matching their structural and functional features and distributions to published descriptions (Keith et al., 2020). With reference to published literature on fire effects (e.g. Table 1) and by consensus, we ranked each functional group as high, medium or low sensitivity to each threat type, and then adjusted ranks for individual ecosystem types within each functional group (Auld et al., in review). A few ecosystem types were ranked 'not affected' by particular threats where no mechanism existed (e.g. subterranean ecosystems were not affected by fire–herbivore interactions, C1 in Table 1). Structuring the assessment of threat sensitivity using the Global Ecosystem Typology (Keith, Ferrer-Paris, et al., 2020) ensured consistency of ranks among functionally similar ecosystems.

2.5 | Analysis

For continuous and ordinal spatial indicators of each threat type, we defined threshold values denoting the level of threat severity at which appreciable effects on ecosystems are likely to occur. To estimate exposure to high fire frequency (threat type A1, Table 1), we scaled these thresholds to three broad levels based on time frames inferred from expected development rates of seed banks, regenerative organs and growth forms as proxies for recovery of habitat features and population persistence (Keith, 1996). To estimate the effects of high fire frequency we used fire frequency thresholds of ≤ 50 years for rain forest, pyric humid eucalypt forest, alpine ecosystems and semi-desert and desert ecosystems; ≤ 15 years for dry sclerophyll pyric forests, woodlands, heathlands and mires; and ≤ 5 years for tussock grasslands, based on the life histories of constituent biota (Keith, 2004). Although fire intervals even longer than 50 years may cause appreciable degradation of rain forest, humid eucalypt forest, alpine and some desert ecosystems, we set an indicative minimum bound of 50 years because fire history data prior to 1970 become less reliable and less complete. The available fire history data also limited this application to the most recent fire interval. Although considerable variation in responses occurs within and between ecosystem types, these scaled generic thresholds should provide an informative overview for continent-wide exposure to high frequency fire (see Auld et al., in review for rationale).

We used the threshold values to convert continuous and ordinal values of indicators to binary format, consistent with the spatial data for binary indicators. We then intersected these binary layers with the mapped distribution of each ecological community and the mapped extent of 2019–2020 fires (DAWE, 2020) to estimate exposure of each community to each fire-related threat type. We reported results based on the thresholds that produced the greatest discrimination of exposure across different ecosystem types. We expressed estimates of exposure as a proportion of total community distribution and compared exposure and sensitivity graphically among all ecosystem types examined.

3 | RESULTS

A diverse range of ecosystems, from fire-prone shrublands to rain forests that rarely burn, were affected by contrasting fire-related threats across southern Australia (Figure 1). Five of the 92 ecosystem types assessed had more than 90% of their extent burnt in the 2019–2020 fires (three additional types in the Stirling range, Western Australia, had > 90% burnt during 2018–2020), 29 had more than half of their extent burnt, and 61 had more than 10% of their extent burnt (Figure 2, Supporting Information Appendix S3). We ranked the exposure of ecosystem types to each threat type as extreme, high, moderate or appreciable based on whether > 80, > 50, 30–50 or 10–30% of their distribution was affected, respectively (Figure 2). Almost one-third (29) of the ecosystem types assessed had more than half of their distribution exposed to one or more of the 10 quantified threat types; 16 types had high exposure (≥ 50% of distribution) to four or more threat types; and one (Newnes plateau shrub swamp) had high exposure to six threat types (Supporting Information Appendix S3). Only three of the 29 ecosystems with more than half their distribution exposed to a threat type were listed as nationally threatened ecological communities at the time of the 2019–2020 fires; three more are currently under assessment for listing; and a total of 12 are currently listed in state jurisdictions.

Nine ecosystem types were highly exposed (≥ 50% of distribution) to high frequency fires, based on the three threshold classes we applied (threat type A1), as a result of the 2019–2020 fires (indicator A1a; Figure 2, Supporting Information Appendix S3). Seven of these were ranked as highly sensitive, none of which were listed as nationally threatened (Figure 3). These were primarily wet eucalypt forests (Ecosystem Functional Group T2.5), with one dry eucalypt forest (T2.6) and one subalpine woodland (T4.4). The 2019–2020 fires also caused 26 ecosystem types (29 types when 2018 Stirling range fires are included) to become highly exposed to future risks of frequent fires (indicator A1b; Supporting Information Appendix S3), should fire recur within their respective fire interval thresholds. This was the most pervasive of all threat types (Figure 2), affecting multiple rain forest ecosystems (T2.3, T2.4), peatlands (FT1.6), heathlands (T3.2) and wet eucalypt forests, including the nine types already exposed to high frequency fires.

Six ecosystem types were locally exposed to high severity fire (A2a; Figures 2 and S3, Supporting Information Appendix S3) across ≥ 30% of their range, but none were highly exposed (≥ 50%). At landscape scales (5-km radius), however, five types were highly exposed and a further eight were ≥ 30% exposed (A2b, Supporting Information Appendix S3). All but three of those types were ranked as highly sensitive to landscape-scale high severity fire, and the majority were temperate wet eucalypt forests (T2.5) and rain forests (T2.3, T2.4). None of these were listed as nationally threatened but one is currently under assessment.

Of the 17 ecosystem types ranked as highly sensitive to peat fires (A4, not quantified), only one (state-listed Newnes plateau shrub swamp) was exposed to peat fires over a large portion of its range

TABLE 1 Fire-related threat types and the ecological mechanisms by which they may affect ecosystem structure, function and composition

Threat type	Mechanism
A. Fire regime components	
A1. High fire frequency	High fire frequency may disrupt life cycle processes in some organisms, such as seed bank accumulation, development of habitat structures and resources (Andersen, 2021; Keith, 1996; NSW Scientific Committee, 2000). Extensive fires may predispose ecosystems to risks of high fire frequency, depending on timing of subsequent fires
A2. High fire severity	High fire severity may cause long-term disruption to ecosystem structure and function, alteration to habitat suitability by limiting resources, or cause long-term population declines in species that cannot compensate high mortality with reproduction or immigration (Lindenmayer et al., 2013; Whelan, 1995). Recurrence of severe fires prior to recovery exacerbates effects (Coop et al., 2016)
A3. Out-of-season fires	Out-of-season fires may disrupt phenological processes, limit population turnover or expose organisms to risks of mortality (Miller et al., 2019). Effects are likely to be exacerbated by recurring out-of-season fires
A4. Substrate fires	Fires that consume organic substrates may cause long-term alteration to ecosystem structure and function, destroy regenerative organs and propagules, and alter habitat suitability, given long time frames required for peat accumulation (Fryirs et al., 2021)
B. Fire–environmental interactions	
B1. Fire–drought interactions	Droughts immediately before or after fires impose additional stress on plants and animals, either by depleting their resources or health, or by limiting resources to support post-fire recovery, reproduction, or recruitment (Choat et al., 2018; Crowther et al., 2018)
B2. Fire interactions with hydrological change	Fires may increase impacts of hydrological change (via surface or ground water) by accelerating ecosystem adjustments to new stable states under altered water availability, with consequent changes to ecosystem structure and function (Keith, Benson, et al., 2020)
B3. Post-fire erosion, sedimentation or pollution	By temporarily increasing exposure of soil surfaces, fires may increase risks of erosion and sedimentation by intense rainfall or wind events in the early post-fire period, causing long-term changes to ecosystem structure and function (Shakesby & Doerr, 2006)
B4. Fire–climate change interactions	Climate change may threaten ecosystems through multiple combinations of the mechanisms outlined above (Kelly et al., 2020). For example, climate change is driving changes in fire regimes, including increased frequency, severity, extent and seasonal shift. It is also increasing the severity and duration of droughts and intense rainfall events and altering bioclimatic habitat suitability for invasive species
C. Fire–biotic interactions	
C1. Post-fire interactions with invasive herbivores	Herbivores may concentrate in post-fire regrowth to exploit foraging resources, limiting survival and growth of post-fire seedlings and resprouts (Giljohann et al., 2017; Leigh & Holgate, 1979). They may also degrade ecosystem function by reducing plant biomass and litter and disrupting soil structure (Eldridge et al., 2019), and these effects are likely exacerbated by fire
C2. Post-fire interactions with invasive predators	Predators may concentrate and hunt more efficiently in burnt areas where shelter of prey is reduced, causing selective declines in vertebrate and macro-invertebrate components of ecosystems (Hradsky, 2020; Murphy et al., 2019). The major invasive predators in southern Australia are foxes and cats
C3. Fire–disease interactions	Fires accelerate or amplify impacts of diseases, either by increasing the invasiveness and infectiousness of the disease or by increasing the susceptibility of affected organisms. The most important diseases for Australian terrestrial ecosystems (e.g. root rot, myrtle rust and Bell-miner associated dieback) affect foundational plant species that contribute to ecosystem structure and function, including energy sequestration, nutrient cycling and habitat provision. Other diseases that affect specific groups of component organisms (e.g. chytridiomycosis, psitticine circoviral disease) were not considered in this analysis Fires accelerate rates of mortality in vegetation infected with root rot disease (primarily *Phytophthora cinnamomi*), causing long-term alterations to ecosystem structure and function (Moore et al., 2015) https://www.environment.gov.au/biodiversity/threatened/publications/threat-abatement-plan-disease-natural-ecosystems-caused-phytophthora-cinnamomi-2018 Fires expose young post-fire regrowth to increased risks of infection by myrtle rust disease (*Austropuccinia psidii*), causing increased tree and shrub mortality and long-term alterations to ecosystem structure and function (Carnegie & Pegg, 2018; Pegg et al., 2020) Fires in forests infected by Bell-miner associated dieback (tree death associated with psyllid outbreaks, suppression of insectivorous birds by Bell miners *Manorina melanophrys*, and understorey invasion by *Lantana camara*) are likely to increase rates of tree mortality due to the limited ability of trees in poor health to sustain post-fire recovery, accelerating long-term decline of ecosystem structure and function (Silver & Carnegie, 2017; Stone, 1996).

(Continues)

TABLE 1 (Continued)

Threat type	Mechanism
C4. Fire–invasive plant interactions	Fires may promote invasion of introduced plants by temporarily increasing the availability of nutrients, light and soil water (Milberg & Lamont, 1995). These weed invasions may competitively exclude some native plant species and reduce habitat suitability for some native animal species. The risks are greatest where existing infestations act as propagule sources and where processes such as fragmentation and eutrophication enhance habitat suitability for weeds relative to native plants
D. Fire–human disturbance interactions	
D1. Fire–logging interactions	Legacies of past timber extraction and post-fire disturbance associated with roading and salvage logging operations may disrupt post-fire regenerative processes, with associated declines in ecosystem structure and function (e.g. Lindenmayer et al., 2012)
D2. Fire–fragmentation interactions	Habitat fragmentation reduces movement of organisms and fire spread across landscapes, and also reduces effective population sizes. These effects decrease rescue effects and recolonization of biota among remnant ecosystem fragments, reducing their biological diversity and functioning (Driscoll et al., 2021)
D3. Fire–human access interactions	Legacies and post-fire disturbance associated with human use, intensification of vehicular and pedestrian access, recreational activities and refuse disposal, may disrupt post-fire regenerative processes when ecosystems are in a sensitive state, with associated declines in ecosystem structure and function (Sun & Walsh, 1998)

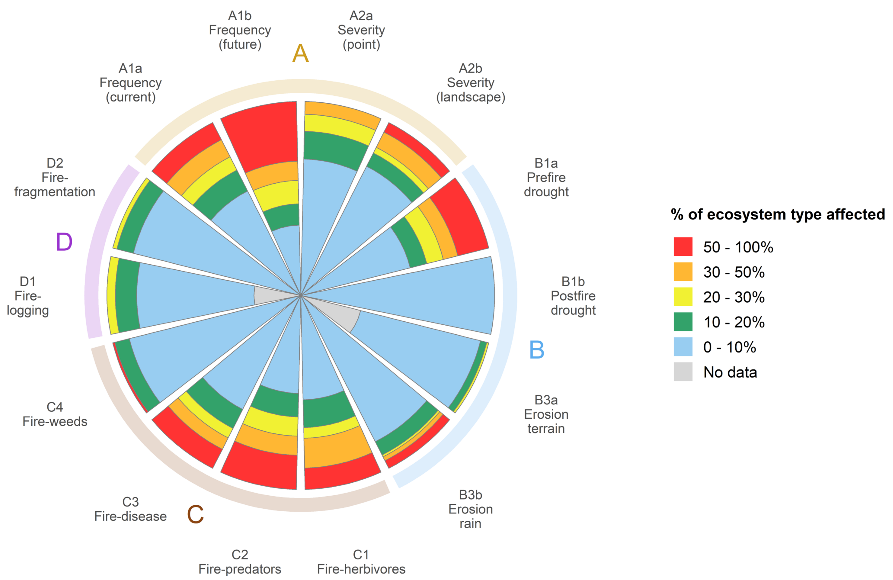

FIGURE 2 Number of ecosystem types ($n = 92$) with different levels of exposure (based on % of distribution affected) to nine of the 15 fire-related threat types spatially quantified for analysis. Threat types are grouped by A (direct effects of fire regimes), B (interactive effects of fire and physical environmental factors), C (fire effects via biotic interactions) and D (fire effects amplified by human activity). Note that four threat types have two spatial metrics (A1 – high fire frequency in current and future time frames; A2 – fire severity at point and landscape scales; B1 – pre-fire and post-fire drought; B3 – fire erosion risk and intense post-fire rainfall). Statistics for A1b include 2018 fire in the Stirling Range (see text). See Table 1 and Supporting Information Appendix S3 for definition and measurement of threat types

during 2019–2020, while peat consumption was observed at multiple sites for one other type (nationally-listed Alpine sphagnum bogs), and localized peat fires were reported in three other types of peatlands and forested wetlands (Supporting Information Appendix S3).

Interaction between fire and pre-fire drought was among the most pervasive threat types (B1a; Figures 2 and 3, Supporting Information Appendix S3), with 15 ecosystem types highly exposed, including nine experiencing extreme levels of exposure (> 80% of distribution burnt after severe drought), and a further eight ecosystem types moderately exposed (30–50% of distribution). The highly exposed ecosystem types include rain forests, wet eucalypt forests, peatlands, a subalpine woodland and a dry eucalypt forest, primarily in an arc from the Border Ranges (southeast Qld) to East Gippsland (Vic). None of these are listed as nationally threatened, but three are currently under assessment and eight are listed in state jurisdictions. In contrast, none of the ecosystem types were exposed to severe post-fire drought (B1b, Figure 3, Supporting Information Appendix S3) across more than 2% of their distribution based on the second percentile of rainfall. A few localized ecosystem types had exposure to the lowest 10th percentile of post-fire rainfall, but there were no reports of drought symptoms observed in the field.

Although exposure could not be quantified, 13 of the 17 wetland ecosystem types examined underwent hydrological changes prior to the 2019–2020 fires (B2). In most cases, this was due to changes in

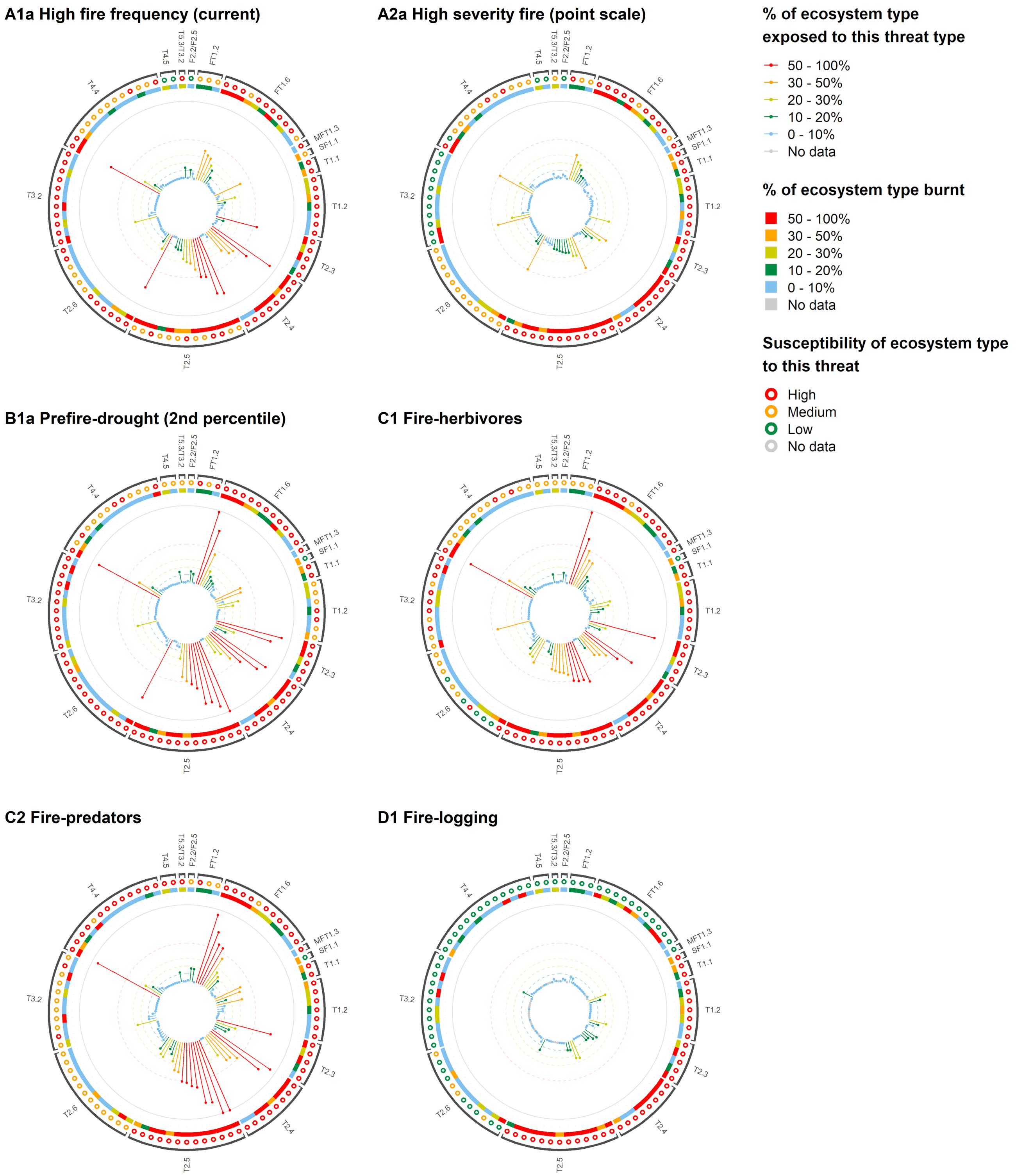

FIGURE 3 Exposure and sensitivity of 92 ecosystem types to six contrasting fire-related threat types as exemplars of the full assessment (see Supporting Information Appendix S3 for data on the full set of 15 indicators and threat types assessed). Ecosystem types are arranged by Ecosystem Functional Groups (Keith, Benson, et al., 2020), labelled on periphery. Length and colour of radial lines show exposure of each ecosystem type to the threat type represented in each circle based on % of mapped distribution intersecting with the spatial indicator for the threat and the mapped spatial footprint of the 2019–2020 fires. Colour of annular bars around periphery represents % of distribution within the fire footprint and colour of small circles around periphery represents ranked sensitivity of respective ecosystem types

surface flows in wetland catchments, but two types (Aquatic root mats in caves, Newnes plateau shrub swamp) experienced substantial loss of groundwater, with the latter also exposed to peat fires (Supporting Information Appendix S3).

Only one ecosystem type (Southern wattle forests in NSW) was exposed to high modelled erosion risk (B3a; Supporting Information Appendix S3) across more than 20% of its distribution, while four had high exposure to intense post-fire rainfall (B3b; Figure 2) within 3 months of the fires. These were peatlands and wet eucalypt forests in the Blue Mountains. None are listed as nationally threatened.

Eleven ecosystem types were highly exposed to post-fire feral herbivore activity (C1; Figures 2 and 3, Supporting Information Appendix S3), including rain forests, wet eucalypt forests, peatlands and a subalpine woodland. While none were listed as nationally threatened, three are currently under assessment and six are listed in state jurisdictions. The most pervasive introduced herbivores were rabbits and deer, although horses and pigs were locally important.

Sixteen ecosystem types were highly exposed to post-fire predator activity (C2; Figures 2 and 3, Supporting Information Appendix S3), which was among the most pervasive of the threat types. These were primarily wet eucalypt forests, as well as some temperate rain forest types, peatlands and woodlands. None were listed as nationally threatened, but two are under assessment and 10 are listed in state jurisdictions. Foxes and cats were similarly pervasive, but foxes had higher predation indices.

Ten ecosystem types were highly exposed to interactions between fire and disease (C3; Figure 2, Supporting Information Appendix S3), with most being rain forests and wet eucalypt forests in warm temperate eastern Australia, and some heath ecosystems in south-western Australia. Two of these are currently under assessment for national listing and nine are listed as threatened in state jurisdictions.

One ecosystem type was highly exposed to post-fire weed invasion while a further nine ecosystem types had appreciable exposure (10–30% of distribution) to post-fire weed invasion (C4; Figure 2, Supporting Information Appendix S3). The highly exposed ecosystem type was a wet eucalypt forest with disturbance legacies, while the other exposed types spanned a range of rain forest, wet and dry eucalypt forest, woodland, shrubland and peatland ecosystems. One of the 10 ecosystem types exposed to post-fire weed invasion is nationally listed as threatened, three are currently under assessment, and a further two are listed as threatened at state level and are part of broader national listings.

Four ecosystem types that are highly sensitive to fire–logging interactions were exposed across more than 20% of their distributions (D1; Figures 2 and 3, Supporting Information Appendix S3). These included two montane rain forests and two montane wet eucalypt forests. In each case, the majority of forestry activity occurred more than 25 years before the 2019–2020 fires. Although the fires burnt appreciable areas of logged forest and some salvage logging operations were undertaken, this occurred mainly in ecosystem types that were not currently listed as threatened in any jurisdiction and not included in our study.

Two ecosystem types had appreciable exposure to fire-fragmentation due to land clearing (D2; Figure 2, Supporting Information Appendix S3), including one dry rain forest type in a rural landscape and one wet eucalypt forest in a peri-urban landscape. Both were listed as threatened at state level and were part of broader national listings. These and several other ecosystem types are likely to have some exposure to disturbance related to post-fire human access (D3, not quantified; Supporting Information Appendix S3).

4 | DISCUSSION

While the magnitude, severity and extent of the 2019–2020 Australian bushfires attracted global concern about their impacts on wildlife, our study demonstrates that far-reaching ecological effects are best identified and understood by placing such events in the context of fire regimes and interacting threats. Our approach illuminated the fire-driven causes and mechanisms of ecosystem degradation and collapse, as well as the mechanisms of associated biodiversity loss. This information is highly valuable for risk assessments (e.g. via Red List of Ecosystems; Keith et al., 2013), management and strategic risk reduction for biodiversity, and for informing immediate and sustained actions. A mechanistic understanding of fire-related risks to ecosystems can also be built into planning and capacity building for future contingencies. In contrast, a disaster approach to conservation that has a more singular focus on fire impacts and recovery from the fire event itself, runs the risk of focusing management responses on the treatment of those symptoms without addressing the full suite of their underlying causes.

Very few of the ecosystem types that we identified as having high sensitivity and exposure to fire-related threats are currently listed as threatened at national level. This partly reflects changes in status resulting from the 2019–2020 fires, and partly reflects ecosystems already at risk that had not yet been assessed for statutory listing as threatened at national level, despite the listing of some at a state level. New statutory listing assessments are currently underway for several ecosystem types identified in our study.

We found that three fire-related threat types posed the most severe threats to large numbers of ecosystem types in southern Australia as a result of fires in 2019–2020: high frequency fire (A1); pre-fire drought (B1); and post-fire predator activity (D2). For these and the other threat types, we discuss the mechanisms that drive risks to ecosystems and options for risk reduction.

Our analysis identified a number of ecosystem types that are highly sensitive and already highly exposed to high frequency fire, and that many more could become affected if fires recur within the next two decades or within the next century, respectively, for sclerophyllous ecosystem types and for high-sensitivity rain forest, wet eucalypt forest, alpine and semi-arid ecosystems. Avoidance of such outcomes will become increasingly difficult as anthropogenic climate change further unfolds, and the frequency of drought conditions (low fuel moisture) and extreme fire weather (high temperatures, low humidity, strong winds) increases in line with projections (Abram et al., 2021).

Four causal factors ('switches') limit the occurrence and spread of fires: ignitions; fire weather; fuel moisture; and fuel mass (Abram et al., 2021). Modelling of these four key drivers of large fires (Clarke et al., 2020) suggests that reducing the rate of ignitions is likely to be the most effective and immediate risk-reduction strategy, principally in areas where ignition rates are high. Although the 2019–2020 fires were initiated largely by lightning strikes (NSW Bushfire Inquiry, 2020), this is unusual in the historical record and many of the fires contributing to high frequency fire regimes stem from human ignitions, including accidental ignitions, infrastructure failure, arson and escape from planned fires (Collins et al., 2015). Measures such as more targeted public announcements, enhanced institutional fire safety protocols, area closures, enhanced enforcement during fire bans and citizen surveillance and reporting could produce a substantial net reduction in fire frequency across the landscape. Although remote dry lightning ignitions may develop into megafires if early suppression efforts fail, reducing the number of fires initiated by human ignitions could alleviate exposure to many of the threat types, including high frequency fire (A1), and interactions between fire, drought (B1), herbivores (C1), predators (C2), diseases (C3), weeds (C4) and fragmentation (D2).

While fuel reduction treatment can effectively meet specific objectives under certain conditions (Penman et al., 2020), it may have a relatively weak and conditional effect that varies with severity of fire weather conditions, the fraction of landscapes treated, the proportion of fuel reduced relative to that which becomes available to burn under extreme conditions and time since treatment (Price et al., 2015). Effects of fuel reduction on the extent and severity of unplanned fires also depend on the location and pattern of treatment, given landscape heterogeneity in topography, fuel moisture dynamics, wind exposure and likely pathways of fire spread (Boer et al., 2009).

The other two causal drivers (increasing frequency of drought and severe fire weather) can only be addressed through rapidly enhanced climate change mitigation actions. Lagged effects of emission reduction on global climate suggest that realization of reduced fire frequency will be slow to unfold (IPCC, 2018). While long-term remedies must address these underlying causes, localized adaptation measures may lessen or forestall impacts in the interim until climate change mitigation begins to influence fire regimes. For example, increased preparedness for immediate pre-fire fuel management and low-impact fire suppression, as was implemented to protect the critically endangered Wollemi pine (*Wollemia nobilis*; de Bie et al., 2021). Similar approaches could be applied to ecosystems with high sensitivity and past or future high exposure to short fire intervals. Complex relationships between prior fuel reduction and unplanned fires suggest that similar outcomes to that achieved for the Wollemi pine are predicated on well-nuanced and highly strategic fuel management focussed on the assets at risk.

Fire–drought interactions erode the resilience of ecosystems by limiting resources to support survival of constituent plants and animals during the fire event and to support population recovery through reproduction in the post-fire months and years. In this study, pre-fire drought was the primary concern because rainfall prior to the 2019–2020 fires was among the lowest on record across large areas of eastern Australia (BOM, 2019). In contrast, severe droughts did not occur during the 12 months after the 2019–2020 fires, except in some areas marginal to the fire footprint (Supporting Information Appendix S2). Rainfall for these areas was in the lowest decline since year 1900 for the 12 months March 2020–February 2021, encompassing the cool season when much of the seedling emergence is expected to occur and the first post-fire summer, which is most critical to mortality of emerged seedlings, animal survivors and xylem embolism in resprouting plants.

Despite limited exposure to drought after the 2019–2020 fires, when severe droughts occur after fire, they could be a similarly influential or even more influential driver of ecosystem degradation than pre-fire droughts. Climate change mitigation is the most direct means of reducing risks to ecosystems from fire–drought interactions. Small-scale actions, such as water supplementation, could be informed by climate modelling, but their effects are largely unexplored and costs and collateral impacts may limit their application.

The impacts of post-fire predation by invasive animals on native faunal components of ecosystems are becoming more widely understood (Hradsky, 2020). Impacts are expected to be greatest for ecosystems in which bird, mammal or invertebrate prey comprise high-diversity communities or have major roles in trophic processes or other functions of the ecosystem. Wet eucalypt forests have these properties and suffered high levels of exposure to this threat type in the 2019–2020 fires. Moreover, south-eastern Australia is the global centre of distribution for this functionally distinctive group of ecosystems (Ecosystem Functional Group T2.5 of Keith, Ferrer-Paris, et al., 2020). Fortunately, there is a plausible means of threat abatement for post-fire predation through increased readiness to implement rapid-response post-fire predator control in and around burnt areas. Moreover, extensive fires potentially offer opportunities for more effective and sustained predator control than at other times in the fire cycle due to increased detectability and foraging activity in recently burnt areas. To be effective in the most challenging circumstances, such management needs to be agile to address immediate influx of predators cued to move into foraging grounds by olfactory detection of smoke (McGregor et al., 2016).

Although the 2019–2020 fires were among the most extensive high-severity fires on record (Collins et al., 2021), only a few ecosystem types were moderately exposed to canopy-scorching fires at point scales and none were highly exposed (A2). Exposure was greater at landscape scales, and several ecosystem types were ranked as more sensitive to high severity fires at landscape scales than point scales. However, these effects likely depend on spatial scale, as our sensitivity analysis showed that exposure varied with the neighbourhood size used to estimate the proportion of the surrounding area burnt at high severity (Supporting Information Appendix S3). Relevant spatial scales for analysis are likely to vary among ecosystem types, as well as the species within them, which have different abilities for early fire detection as well as evasive movement (Nimmo et al., 2021). Although high severity fires are often presumed to generate acute impacts (Fryirs et al., 2021; Godfree et al., 2021; Ward et al., 2020), ecological responses are conditional, and some ecosystem types are relatively insensitive to fire severity. For example, substantial topkill of subtropical rain forest trees occurred in response to scorch heights as low as 2 m, well beneath the canopies that later died (R. M. Kooyman & D. Keith, unpublished data). Some of the wet eucalypt forest ecosystems we examined, such as alpine ash and white ash, are prone to sudden collapse when frequently exposed to high severity fire but are resilient to infrequent high severity fires that initiate a multi-decadal autogenic recovery process (Ashton, 1981). Responses to frequent low severity fires are more gradual and possibly less transformative. Future studies should consider the spatial context and recurrence of high severity fires to improve understanding of their ecological effects and where and how to focus restorative management activities.

Some threat types (e.g. C3, B2, A4, D3) were relatively localized or affected only a narrow range of ecosystem types, yet their impacts may be transformative on ecosystem structure, function, and composition. Several ecosystem types were highly exposed to post-fire acceleration of root rot disease in the Stirling Ranges (WA) where there are many narrow-range endemic plant species highly sensitive to the disease (Barrett & Yates, 2015). Some of these plants have dependent invertebrates with narrow host ranges, one of which appears to have been driven to extinction through the combined effects of fire–disease interaction (C3) and high frequency fire (A1) (Moir, 2021). Similarly, Swamp sclerophyll forests on east coast floodplains were locally exposed to severe myrtle rust infections after fire regrowth, curtailing canopy re-establishment and causing mortality of trophically important canopy trees (Pegg et al., 2020). Management options exist, mainly for preventative hygiene and chemical treatments that enhance disease resistance in plants susceptible to root rot (Barrett & Rathbone, 2018). Prevention and treatment options for other diseases are even more limited, and fundamental research is much needed to explore alternative treatments and increase the efficacy of existing methods.

Changes in hydrology (B2) associated with declining rainfall and water extraction had already led to drying of aquatic root mat ecosystems in caves (Department of Water, 2016; English et al., 2000; Kretschmer & Kelsey, 2016). Staged and variable changes to cave drip regimes after a high-severity fire above the cave are reported in Bian et al. (2019), with overall shorter term higher mean and peak flows post-fire. They noted limited geochemical evidence of ash-derived solutes in drip waters into the cave post-fire, as ash products were largely volatilized. Hydrological changes (B2) caused by underground mining were also associated with peat fires (A4) that caused major transformation of Newnes plateau shrub swamps, which could be avoided or minimized with changes to mine planning and design (Keith, Benson, et al., 2020). More localized peat fires were also reported in other peatland ecosystems. While some of these may be avoided by catchment or groundwater management (e.g. Sandplain swale swamps in NSW and Qld), others are more directly associated with climatic drying requiring mitigation action as discussed above (e.g. Alpine sphagnum bogs).

The limited evidence of exposure to post-fire weed invasion (C4) may partly reflect resilience to invasions conferred by nutrient limitations in many Australian ecosystems (Gosper et al., 2011), and partly the limited availability of comprehensive data on invasive plant abundance. The 10 ecosystem types identified with appreciable–high exposure to post-fire weed invasion all have legacies of past disturbance or ongoing disturbance, predisposing them to entry of introduced plants. As for introduced herbivores (C1) and predators (C2), the early post-fire period presents important opportunities to control weed abundance during a major (re-)establishment phase, sustaining it at low levels through the next fire cycle.

Several threat types could not yet be quantified due to lack of suitable spatial proxy data, while assessment of others was hampered by limitations on the quality of available data. For example, in contrast to recent developments in severity mapping for surface fires (Gibson et al., 2020), there are currently no systematic data streams that capture incidence or risk of peat fires (threat type A4), in part due to difficulty of detection. Data on pre-fire hydrological changes (B2) and human activity (D3) in burnt areas are available but dispersed across many sources, but these need continual updating to keep pace with rapid change and are difficult to assemble when urgently required for post-fire assessments. The currently available data for herbivore and weed distributions are poor, and results should therefore be treated with caution, particularly where they do not reflect well-documented ecosystem degradation (e.g. Eldridge et al., 2019). Data are also limited for newly emerging threats, such as the effects of fire-retardant chemicals applied during suppression operations in oligotrophic vegetation and freshwater ecosystems (Bell et al., 2005).

Improvements are underway, however, and many of the analyses presented in our study that were enabled by advanced remote sensing and spatial modelling would not have been possible a decade ago. These advances are continuing, for example, with more systematic collection of data on location and levels of fire-retardant application during suppression operations recently commenced. Data on herbivore abundance, diet and physical impacts are currently rudimentary and largely reliant on occurrence records that do not clearly reflect on-ground observations of degradation caused by deer and pigs in rain forests and wetlands or horses in alpine and subalpine ecosystems (e.g. Eldridge et al., 2019). Recent continental-scale modelling of diet and density of vertebrate pest predators indicates potential directions for improvement (Murphy et al., 2019). Similarly, systematic mapping of forest canopy disease is expanding (Silver & Carnegie, 2017).

Map data for individual ecosystem types are similarly variable. Although several public repositories of vegetation map data exist (administered by national government facilities and state agencies), it was necessary to undertake a substantial review process, followed by adjustment and data cleaning to develop maps of sufficient quality faithful to the distribution of the ecosystem types targeted for assessment. A number of ecosystem types of interest (~10%) could not be assessed due to lack of suitable data.

A strength of our approach is its focus on specific mechanisms of threat, separately assessing sensitivity and exposure to each one. This diagnostic approach can help target management to address causes of ecosystem degradation and enables transparency on indicators of threat, which can be substituted or adapted with advances in mechanistic understanding, data quality and availability. Our estimates of sensitivity, given exposure to each threat type, are based largely on our own subjective assessment of evidence in published literature and collective field experience. For some ecosystem types, the knowledge base was scarce and drew from observations on ecologically similar types. Sensitivity estimates were framed around thresholds of threat severity. For high severity fire, for example, this threshold was linked to detectable consumption of canopy foliage, with two alternative algorithms producing broadly comparable results. Assessing each ecosystem type against one of three fire frequency thresholds enabled us to scale estimates of sensitivity to developmental processes, but is likely to oversimplify more complex variation in responses to fire frequency within and between ecosystem types. Moreover, we applied these frequency thresholds as a descriptive tool to gain continental-scale insights into sensitivities and exposure to high fire frequency, and they are not intended for application as fire management thresholds.

5 | CONCLUSION

Ecosystems that have a long evolutionary history of development under recurring fires ought to be equipped to recover their structure, functions and composition autogenically after individual fire events. Whether they do so is predicated on two groups of contextual factors: (a) whether a fire event pushes an ecosystem or its key components beyond its limits of tolerance expressed in each dimension of the fire regime or its spatial expression; and (b) whether the resistance, resilience or regenerative responses to the fire event are compromised by other threatening processes. Our assessment of multiple fire-related threats within these two groups and the associated mechanisms of fire response is the first focussed on ecosystems. It reveals significant fallibilities of particular Australian ecosystems to the combined effects of changing fire regimes and a variety of environmental changes driven directly or indirectly by human activity. While some of these ecosystem types were already protected by statutory listing as threatened, many were not listed, and some of those are now undergoing statutory assessment processes. Most impacts of the 2019–2020 fires on ecosystems were not directly associated with the event, but only became apparent when they were placed in the context of the whole fire regime and its interactions with other threatening processes. Our approach enables the most threatened ecosystem types to be identified and risk reduction strategies to be targeted at underlying causes of ecosystem degradation and decline.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

ETHICS

This desktop study did not require ethics permits.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Australian government agency repositories and published sources listed in Supporting Information Appendices S1 and S2.

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BIOSKETCH

Our research team collaborates on the fire ecology, conservation and spatial analysis of Australian species and ecosystems. We have combined expertise in biogeography, fire ecology, ecosystem ecology, decision science, remote sensing, conservation biology and risk analysis. Several in the team are current or previous members of statutory Threatened Species Scientific Committees, responsible for threatened listing species and ecological communities for legislative protection in Australia and its state jurisdictions.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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