





CONTRIBUTED PAPERS

How to prioritize species recovery after a megafire

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Abstract

Due to climate change, megafires are increasingly common and have sudden, extensive impacts on many species over vast areas, leaving decision makers uncertain about how best to prioritize recovery. We devised a decision-support framework to prioritize conservation actions to improve species outcomes immediately after a megafire. Complementary locations are selected to extend recovery actions across all fire-affected species' habitats. We applied our method to areas burned in the 2019–2020 Australian megafires and assessed its conservation advantages by comparing our results with outcomes of a site-richness approach (i.e., identifying areas that cost-effectively recover the most species in any one location). We found that 290 threatened species were likely severely affected and will require immediate conservation action to prevent population declines and possible extirpation. We identified 179 subregions, mostly in southeastern Australia, that are key locations to extend actions that benefit multiple species. Cost savings were over AU\$300 million to reduce 95% of threats across all species. Our complementarity-based prioritization also spread postfire management actions across a wider proportion of the study area compared with the site-richness method (43% vs. 37% of the landscape managed, respectively) and put more of each species' range under management (average 90% vs. 79% of every species' habitat managed). In addition to wildfire response, our framework can be used to prioritize conservation actions that will best mitigate threats affecting species following other extreme environmental events (e.g., floods and drought).

KEYWORDS

actions, Australia, bushfire impacts, climate change, conservation, fire

Resumen

Debido al cambio climático, los mega incendios son cada vez más comunes y tienen un impacto repentino y extenso sobre muchas especies en inmensas superficies, lo que deja a los tomadores de decisiones con incertidumbre sobre cuál es la mejor manera de priorizar la recuperación. Diseñamos un marco de apoyo a las decisiones para priorizar las acciones de conservación para mejorar los resultados para las especies inmediatamente después de un mega incendio. Para esto, se seleccionan localidades complementarias para extender las acciones de recuperación por todos los hábitats de las especies afectadas por el incendio. Aplicamos nuestro método a las áreas afectadas por los mega incendios de 2019–2020 en Australia y analizamos las ventajas de conservación del método mediante la

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comparación entre nuestros resultados y aquellos de un enfoque en la riqueza de especies (es decir, la identificación de las áreas que recuperan de manera rentable la mayor cantidad de especies en cualquier localidad única). Encontramos que 290 especies amenazadas estuvieron probablemente afectadas de manera severa y requerirán acciones inmediatas de conservación para prevenir la declinación poblacional y la posible eliminación. Identificamos 179 subregiones, la mayoría en el sureste de Australia, que son localidades clave para extender las acciones que benefician a muchas especies. El ahorro en los gastos fue de más de AU\$300 millones para reducir el 95% de las amenazas para todas las especies. Nuestra priorización basada en la complementariedad también extendió las acciones de manejo posterior al incendio a una mayor proporción del área de estudio en comparación con el método de riqueza de especies (43% versus 37% del paisaje gestionado, respectivamente) y colocó más de la distribución de cada especie bajo manejo (en promedio 90% versus 79% del hábitat manejado de cada especie). Además de la respuesta a los incendios, nuestro marco puede usarse para priorizar las acciones de conservación que mitiguen de mejor manera las amenazas que afectan a las especies después de otros eventos ambientales extremos (p. ej., inundaciones y sequía).

PALABRAS CLAVE

acciones, Australia, cambio climático, conservación, impacto de los incendios, incendios

【摘要】

由于气候变化, 特大火灾变得越来越常见, 且对广大地区的许多物种产生突然的、广泛的影响, 这导致决策者难以确定最佳的优先恢复次序。本研究设计了一个决策支持框架来对保护行动进行优先排序, 以改善大火发生后对物种的影响。我们提出, 选择互补的地点可以将恢复行动扩展到所有受火灾影响物种的栖息地之中。我们将该方法应用于2019-2020年澳大利亚发生大火的地区, 并通过比较我们的结果与位点丰富度方法(即在一个地点确定高成本效益地恢复最多物种的地区)的结果, 评估了其保护优势。我们发现, 有290个受威胁物种可能受到严重影响, 需要立即采取保护行动, 以防止种群减少或灭绝。我们还确定了179个主要在澳大利亚东南部的亚区域, 作为扩大行动以帮助多个物种恢复的关键地点。我们的结果可以在减少所有物种中95%的威胁的情况下, 节约超过3亿澳元的成本。与位点丰富度方法相比, 我们基于互补性优先排序的方法还在研究区域的更大范围推广了火后管理行动(分别为受管理景观的43%和37%), 管理范围更多地覆盖了每个物种的分布范围(每个物种受管理的栖息地分别为平均90%和79%)。除了应对野火之外, 我们的框架还可以用于在其他极端环境事件(如洪水和干旱)中确定保护行动的优先次序, 以最好地减缓对物种的威胁。【翻译:胡怡思, 审校:聂永刚】

关键词: 火灾, 澳大利亚, 丛林火灾影响, 行动, 保护, 气候变化

INTRODUCTION

Earth's climate is changing; thus, many regions are experiencing larger, more frequent (Lindenmayer & Taylor, 2020), higher intensity “megafires” (Mantgem et al., 2013; Stephens et al., 2020) that are often occurring in lengthened fire seasons (Jolly et al., 2015). Megafires burn >400 km² (Lindley et al., 2019) and can be disastrous for biodiversity (Ward et al., 2020a), people, and infrastructure (Jolly et al., 2015). For example, in 2019–2020, megafires occurred across eastern, southern, and western Australia, affecting more than 96,000 km² of faunal habitat (Ward et al., 2020a)—an area bigger than Hungary and over 100 times larger than California's largest megafire (United States Census Bureau, 2018).

Anthropogenic drivers, including climate change, altered land management practices, and invasive species, cause changes in contemporary fire regimes (Berry et al., 2011; Lindenmayer et al., 2020; Zylstra, 2018). Native species vary in their ability to cope with changed fire regimes, predominately due to differences in life histories and functional traits (Caturra et al., 2000; Clarke et al., 2015; Whelan, 1995). For example, many woody plant species, such as obligate-seeding trees and shrubs, need hot fires to disperse and germinate seeds, making fire an essential element for maintaining populations (Bowman et al., 2016; Regan et al., 2010). However, if two fires occur in quick succession, with a shorter gap than age to maturation, obligate seeders can be extirpated. Similarly, some animal species tolerate a single fire better than others due to traits, such as mobility,

burrowing, high reproductive capacity, and opportunistic diets (Tulloch & Dickman, 2007). Because each species is adapted to a specific fire regime, some can suffer declines and possible extinctions if fire events occur more frequently and with greater intensity to which the species and its habitat are adapted (Lindenmayer & Possingham, 1995; Tulloch et al., 2016).

The long-term consequences of megafires could be dire for many species (Pickrell & Pennisi, 2020). Preventative actions, such as managing ecosystems to reduce megafires and identifying key refugia to protect, have become critical (Wintle et al., 2020). However, when megafires do occur, postfire actions are also required. In most ecosystems, the first months after a megafire are the time when fire-sensitive species are at their most vulnerable (Alexandra & Finlayson, 2020; Lindenmayer et al., 2019; McGregor et al., 2014). Failing to act during this critical window could exacerbate threats to populations of plants and animals already in poor condition through reduced resources, drought, invasive species, or increased fire competition as a result of burned habitat (Hradsky et al., 2017; McGregor et al., 2014; Souza et al., 2015). For example, fires provide an opportunity for invasive plants (Brooks et al., 2004; Vitousek, 1990), creating barriers to ecosystem recovery, including altering flammability of the site (Berry et al., 2011; Buckley et al., 2007) and increasing frequency of megafires. Invasive predators can hunt more successfully after fire due to the removal of complex understory that provides protection for native species (McGregor et al., 2014). Invasive herbivores can degrade remaining unburned areas through increased pressure and overexploit recovering growth in burned areas (Duncan, 2020).

To mitigate postfire impacts and assist biodiversity recovery immediately after a megafire, conservation scientists, decision makers, and practitioners require a way to rapidly assess where and how to reduce threats to species (Wintle et al., 2020). Improved prioritization approaches to prevent severe species declines immediately after an extreme environmental event need to address damage cause by the event and cumulative threats that may affect already threatened populations. Identification of types and locations of affected species, their threats, and actions that will most benefit affected species are needed to guide this emerging resource-allocation problem.

We devised a decision-support framework, the complementarity-based approach, to specifically assist prioritization of 22 broad-level conservation actions that prevent severe species declines immediately after a large stochastic event. The framework combines species and threat distribution data with fire extent and intensity to produce a list of species distinguished by their level of risk of severe, irreversible decline after a fire. In our approach, the spatial prioritization decision tool Zonation (Lehtomäki & Moilanen, 2013) is used to find the set of locations where actions deliver the greatest return on investment across all affected species. Sets of areas are complementary (i.e., protect as many species as possible without unnecessary overlap [Chadés et al., 2015]), connected (i.e., actions close to other actions are more efficient than widely dispersed actions [Wenger et al., 2018]), and cost-effective (i.e., meet objectives at minimal cost). We applied our approach

to areas burned in the Australian 2019–2020 bushfires and used a site-richness approach (i.e., identifying areas that cost-effectively recover the most species per location) to assess its advantages (Figure 1).

METHODS

Study region and species

We considered 43 temperate, Mediterranean, and subtropical bioregions across 2.2 million km², as defined in the Interim Biogeographic Regionalization for Australia (IBRA) data set (Commonwealth of Australia, 2018).

We used 100-m² gridded resolution species distribution models (SDMs) of all terrestrial invertebrates, mammals, birds, reptiles, plants, and amphibians listed as threatened under the Environment Protection and Biodiversity Conservation (EPBC) Act 1999 (Commonwealth of Australia, 1999). The SDMs were developed in Maxent with information from a database of species observation records and national-scale environmental data and expert elicitation (Commonwealth of Australia, 2020a). Data are categorized as known to occur (areas identified as habitat), likely to occur (areas identified as habitat within ecologically sensible distances from known locations but excluding known-to-occur areas), and may occur. We used only known to occur' and likely to occur areas.

We excluded freshwater and marine species due to spatial complexities of these ecosystems and uncertainties in how fire affects them. We focused on Australian threatened species because they are at risk of extinction in the near future (species list in Appendix S1). Some populations of unlisted species may also be so heavily affected by a megafire as to be threatened with extinction; our method can be adapted easily to incorporate any list of species regardless of threat level.

Fire severity and species impacts

To calculate the area and intensity of the fire's impacts on each species' habitat, we overlaid the Australian Google Earth Engine Burnt Area Map (Aus GEEBAM, downloaded July 9, 2020) (Commonwealth of Australia, 2020b) with habitat for each species. We recategorized each species' habitat in terms of total area of habitat burned with very high (vegetation is clearly consumed), high (vegetation is mostly scorched), moderate, and low severity (some or moderate change detected when compared with unburned areas) and total area of unburned habitat remaining and calculated the percent habitat in each category. The GEEBAM data set includes satellite imagery from July 1, 2019 to February 13, 2020 and contains Sentinel 2 images. The GEEBAM represents the difference between the normalized burned ratio (NBR) before and after fire:

$$\text{NBR} = \frac{\text{NIR} - \text{SWIR}}{\text{NIR} + \text{SWIR}}, \quad (1)$$

where NIR is near infrared and SWIR is shortwave infrared wavelengths. The GEEBAM classes were derived using the change in NBR for each IBRA subregion and each broad national vegetation information system vegetation type at 40-m² resolution. The classes were designed for rapid response and were not trained with ground data and, therefore, do not have confidence interval or accuracy reports.

To identify threatened species highly affected by the megafire, we used two decision rules for all EPBC Act listed species: >10% of habitat affected by fire + <2000 km² area of occupancy remaining or >10% of habitat affected by fire + <20,000 km² extent of occurrence remaining. These thresholds were chosen based on International Union for the Conservation of Nature (IUCN) and federal government guidelines for assessing conservation status of native species under the EPBC Act (Commonwealth of Australia, 2000; IUCN, 2012) (species and their extent and intensity of burned habitat in Appendix S2).

We did not limit our study to species that have been historically threatened by changed fire regimes because many species will likely become threatened by fire as fires increase in extent and frequency and occur at different times of the year (Jolly et al., 2015; Lindenmayer & Taylor, 2020; Stephens et al., 2020; van Mantgem et al., 2013). For example, over 50% of the Gondwana Rainforests were affected by the 2019–2020 bushfires, thus, many species sensitive to fire may now be at risk (Kooyman et al., 2020). Also, vegetation clearing in Australia has extirpated many species from their previous ranges (Ward et al., 2022); some remain in only a few locations (Szabo et al., 2011). This makes them particularly vulnerable to future large fires.

Threats and actions

A published taxa–threat–impact data set (Ward et al., 2021) was used to identify and extract the threats affecting study species. This data set is a complete, validated, consistent, and taxon-specific threat and impact data set for all EPBC Act listed taxa in Australia and was collated using published and unpublished data and expert elicitation. The data set applies the IUCN Threat Classification Scheme and Threat Impact Scoring System and to eight broad-level threats and 51 subcategory threats for 1795 threatened taxa. We used the data set to identify and extract all threatening processes of low, medium, or high intensity for each species in the study area.

We identified a corresponding presence-absence spatial representation of all threatening processes based on existing spatial data sets (Table 1), which we used to provide indicative areas of presence and absence, rather than definitive locations.

We overlaid threat maps with species affected by each threat to create individual broad-level action maps for postfire species recovery. Where threat maps did not exist, we assumed that the broad-level action could be carried out over the species' entire range (i.e., habitat retention; management of fire, problematic native herbivores, invasive plants, problematic native plants, or

fungal pathogens; prevention of recreational activities; and provision of supplementary resources), resulting in 22 broad-level action maps. Each broad-level action was split into subactions based on land tenure (Geoscience Australia, 2004) and fire severity (Commonwealth of Australia, 2020b). For example, fire suppression action maps for species were allocated to areas that did not burn or experienced low- and moderate-severity burns under the assumption that very-high-severity and high-severity burn areas would not burn again for at least 12 months (Table 2 & Appendix S3).

We explored the sensitivity of outcomes to fire impact assumptions by rerunning the cost-effective analysis assuming no fire had taken place (Appendices S4 & S6), which allowed us to examine the actions needed for most species, the priority subregions, and the cost of actions in the absence of fire.

Cost estimates of actions

Twenty-two broad-level actions and 16 subactions were identified to mitigate the key threatening processes. For 14 of the 16 subactions, we estimated costs with actual cost expenditures recorded for similar activities implemented through New South Wales' Saving our Species (SoS) program (NSW Office of Environment and Heritage 2018). The SoS data set contains 102 “method level 3” (ML3) actions and finer level details on the “action plan costs” underlying each of the ML3 actions. We used the median costs per hectare per year of 15 ML3 actions to represent the costs of 15 of our postfire recovery actions. For the remaining seven postfire recovery actions, the relevant information was available in the finer level details from the action plan cost field. New South Wales had the largest area of habitat burned; hence, we assumed that on average, costs per hectare would be similar across the fire-affected areas. However, average cost data are imprecise, and costs will vary spatially and temporarily. Further, although data quality controls, error checking, and vetting were completed prior to our analyses, additional inaccuracies may exist given that multiple users input their individual expenditures. We may have missed some components of actions and their costs (e.g., costs of 1080 baiting and vehicle hire to deploy baits were not included).

The costs of protected area management and lost opportunity were not identified by SoS. For these, we collated reported costs in the peer-reviewed and gray literature to calculate per hectare costs. Protected area management was specified as actions required to maintain a protected area (e.g., staff overheads), except invasive species management, disease management, and signs, and was estimated at AU\$14.12/ha/year (Maggini et al., 2013; Taylor et al., 2011). Opportunity costs were used only on private land when species were affected by grazing. Opportunity costs were calculated using an agricultural profitability layer (Marinoni & Garcia, 2018) to identify landowner opportunity costs (i.e., lost income due to repurposing agricultural land for conservation) for the areas that would be restored for biodiversity.

TABLE 1 Overview of threats and conservation actions needed for fire-affected species

Threat	Threat map	Map resolution and reference	Action
Habitat loss, degradation, fragmentation	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Protected area covenants
Inappropriate fire regimes	Unburned, low, and moderate fire severity throughout the habitat of the affected species	1) Fire maps: 35 m ² Commonwealth of Australia 2020b 2) Species maps: 100 m ² Commonwealth of Australia 2020a	Fire suppression
Invasive plants	No threat map available; therefore, target area is within the low, moderate, high, and extreme fire severity within the habitat of the affected species	1) Fire maps: 35 m ² Commonwealth of Australia 2020b 2) Species maps: 100 m ² Commonwealth of Australia 2020a	Invasive plant management
Livestock grazing	Catchment scale land use of Australia Agricultural productivity	1) Land use: 50 m ² ABARES 2021 2) Agricultural productivity: 1 km ² Marinoni and Garcia, 2018	Grazing management
Recreational activities	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Recreational management
Phytophthora	<i>Phytophthora</i> species distribution models (SDM)	1) 1 km ² Pintor and Kennard, 2018	<i>Phytophthora</i> management
Invasive pig	Invasive pig SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive pig management
Invasive cats	Invasive cat SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive cat management
Invasive foxes	Invasive fox SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive fox management
Problematic native herbivores	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Native herbivore management
Invasive goats	Invasive goat SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive goat management
Loss of resources	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Provision of supplementary resources
Logging	Catchment-scale land use of Australia	1) 50 m ² ABARES 2021	Forestry management
Chytrid fungus	Chytrid fungus threat map	1) 1 km ² Pintor and Kennard, 2018	Chytrid management
Invasive rabbits	Invasive rabbit SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive rabbit management
Invasive horses	Invasive horse SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive horse management
Feral cattle	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Feral cattle management
Aerial canker and myrtle rust	Aerial canker and myrtle rust SDM	1) 1 km ² Pintor and Kennard, 2018	Aerial canker and myrtle rust management
Problematic native plants	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Habitat management for problematic native plants
Other fungal pathogens	No threat map available; therefore, target area is throughout the habitat of the affected species	1) 100 m ² Commonwealth of Australia 2020a	Other fungal pathogens management
Invasive rodents	Invasive rodent SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive rodent management
Invasive deer	Invasive deer SDM	1) 1 km ² Pintor and Kennard, 2018	Invasive deer management

Spatial prioritization framework

We developed our complementarity-based approach to assist decision makers in prioritizing conservation actions to implement up to 12 months after a large conservation disaster.

The approach selects complementary locations to extend actions across all species distributions. We used a site-richness approach (which focuses on recovering the most species in any one location) to assess the conservation advantages of the complementarity-based approach. Although complementarity

TABLE 2 Overview of broad-level actions identified to mitigate threats to fire-affected species

Broad-level action	Tenure	Subactions	Burn severity	Location of action
Habitat retention	private	covenant	unburned, low, moderate, high, and very high fire severity	across entire species distribution
	public	protected area	unburned, low, moderate, high, and very high fire severity	across entire species distribution
Fire management	public and private	fire suppression	unburned, low, and moderate fire severity	across unburned and low and moderately burned areas of species distribution
Invasive plant management	public and private	weeding	low, moderate, high, and very high fire severity	target threat and species overlap
	public	prevent access into habitats	low, moderate, high, and very high fire severity	target threat and species overlap
Grazing management	private	fencing, monitoring, lost opportunity cost	unburned, low, moderate, high, and very high fire severity	target threat and species overlap
Recreation management	public	signs, monitoring (cameras)	unburned, low, moderate, high, and very high fire severity	target threat and species overlap
<i>Phytophthora</i> management	private	covenant, signs, monitor	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
	public	signs, monitor, protected area	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
Invasive pig management	private and public	baits	unburned	target threat and species overlap
	public	baits, traps, aerial shooting, ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	private	baits, traps, ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
Invasive cat management	private and public	baits, traps	low, moderate, high, and very high fire severity	target threat and species overlap
	private and public	baits	unburned	target threat and species overlap
Invasive fox management	private and public	baits, traps	low, moderate, high, and very high fire severity	target threat and species overlap
	private and public	baits	unburned	target threat and species overlap
Native herbivore management	private and public	small fence around affected species, supplementary feeding of problematic native herbivores	low, moderate, high, and very high fire severity	target threat and species overlap
Invasive goat management	public	ground shooting, aerial shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	private	ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	private and public	ground shooting	unburned	target threat and species overlap
Provision of supplementary resources	public and private	supplementary resources	low, moderate, high, and very high fire severity	target burned sites and species overlap

(Continues)

TABLE 2 (Continued)

Broad-level action	Tenure	Subactions	Burn severity	Location of action
Forestry management	private	covenant	unburned, low, moderate, high, and very high fire severity	target threat and species overlap
	public	protected area	unburned, low, moderate, high, and very high fire severity	target threat and species overlap
Chytrid management	private	covenant, signs, monitor	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
	public	signs, monitor, protected area	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
Invasive rabbit management	private	fences, baits, ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	public	fences, baits, ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	private and public	fences	unburned	target threat and species overlap
Invasive horses management	private	ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	public	aerial shooting, ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	private and public	ground shooting	unburned	target threat and species overlap
Feral cattle management	private	ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	public	aerial shooting, ground shooting	low, moderate, high, and very high fire severity	target threat and species overlap
	private and public	ground shooting	unburned	target threat and species overlap
Aerial canker and myrtle rust management	private	covenant, signs, monitor	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
	public	signs, monitor, protected area	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
Habitat management for problematic native plants	private and public	weeding	low, moderate, high, and very high fire severity	target threat and species overlap
	public	prevent access into habitats	low, moderate, high, and very high fire severity	target threat and species overlap
Other fungal pathogens management	private	covenant, signs, monitor	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
	public	signs, monitor, protected area	unburned, low, moderate, high, and very high fire severity	avoid threat and species overlap
Invasive rodent management	private and public	baits	unburned, low, moderate, high, and very high fire severity	target threat and species overlap
Invasive deer management	public	ground shooting, aerial shooting	low, moderate, high, and very high fire severity	target threat and species overlap

has been widely acknowledged as a keystone concept for spatial conservation planning for at least two decades (Moilanen, 2008; Sarkar & Margules, 2002), richness-focused approaches are still routinely used to identify priority locations for climate refugia (e.g., Keppel et al., 2015), evaluate biodiversity cobenefits of carbon-maximizing conservation plans (e.g., Ferreira et al., 2018), and find hotspots of conservation conflict in agricultural landscapes (Shackelford et al., 2015).

Maximizing regional species recovery with the complementarity approach

We used a spatial prioritization decision tool, Zonation (version 4.0) (Moilanen et al., 2011, 2012), to identify a species-balanced set of cells for conservation action by considering important conservation considerations, such as complementarity (Chadés et al., 2015; Tulloch et al., 2013) and connectivity (Bektas, 2006; Wenger et al., 2018). We prioritized species habitat for broad-level actions at a resolution of 1 km² based on a core-area Zonation cell removal rule (Moilanen & Wintle, 2007). Zonation's core-area rule uses a maximum-coverage approach to identify areas that maximize the representation of habitat for multiple species by iteratively removing cells with the smallest occurrence for the most valuable feature over all biodiversity features in that cell (Moilanen et al., 2012). The benefit of the complementarity-based approach is that it is calculated as an overall value for an entire set of selected cells (rather than a cell-based value) because cells that complement each other (by having different species) will have a higher combined benefit than cells with redundancies. Species are also weighted by their extinction risk and proportion of habitat affected by fire. A cell in the complementarity-based approach can receive a high value if even one species has a relatively important occurrence there (e.g., if the species only occurs in the one cell). The output is an importance ranking of each cell across the region in meeting the spatial prioritization goals. The prioritization approach was used to find a complementary set of cells that can be managed to maximize reduction of threats to all species after fire. Recognizing that some species are more highly affected by fire and are closer to extinction than other species, we weighted each species with a value calculated as the proportion of habitat burned multiplied by extinction risk with the conservation feature weightings system in Zonation (Moilanen et al., 2012). We did not include the likelihood of response to the management prescribed for either of the two approaches because for most highly affected species, these data do not exist.

Maximizing local species richness with a site-richness approach

The site-richness approach ranks cells by their cost-efficiency value (i.e., expected benefit divided by the cost of management). The benefit of acting in a location accounts for the number of species being managed there, proportion of fire-affected habitat for each species, and risk of species extinction. The highest

cost-efficiency rank indicates the highest benefit to cost ratio, whereas the lowest cost-efficiency indicates the lowest benefit to cost ratio.

The site-richness approach identifies areas requiring management by setting an approach of maximizing the richness of high-risk species being managed in any location. We prioritized cost-effective (CE_{*i*}) cells with the following formula:

$$CE_i = \frac{B_i}{C_i}, \quad (2)$$

where B_i is the benefit of managing all threats to all species in area i and C_i is the total cost of subactions required to mitigate all threats to species present in area i (Auerbach et al., 2015).

The benefit of managing a species at a cell was estimated as the likely magnitude of threat reduction that would be achieved by the actions. Benefits were then summed across all species at a cell, weighted by each species the extent of fire-affected habitat and extinction risk. We calculate benefit (B_i) as:

$$B_i = \sum F_j E_j \frac{A_{ij}}{M_{ij}}, \quad (3)$$

where F_j is the proportion of the habitat of species j that was affected by fire (a weighting factor to assign higher weight to species with greater proportions of their total habitat burned), E_j is the risk of extinction of species j (a second weighting factor to assign higher weight to species with higher likelihood of extinction), A_{ij} is the number of subactions in cell i for species j , and M_{ij} is the maximum number of subactions required for species j . Dividing A_{ij} by M_{ij} ensures that we selected cells where the most threat reduction can occur, assuming all threats are equal. We assumed threats are equal due to the complexities of threats affecting species at various scales, interactions among threats, and feasibility of managing threats. The risk of species extinction E_i was determined from the EPBC Act Guidelines (which is the same for the IUCN Red List Guidelines), whereby a species is designated as critically endangered if the predicted probability of extinction is >0.5 in 10 years, endangered for >0.2 in 20 years, and vulnerable for >0.1 in 100 years (Commonwealth of Australia, 2000; Redding & Mooers, 2006). If the approach were to be reapplied in cells of different sizes, the benefits would also need to be weighted by the area over which the benefit is likely to be achieved.

Our complementarity-based approach goes beyond a site-richness approach, which typically identifies the locations where actions are most cost-effective (i.e., have high benefits and low costs [Auerbach, 2015]), but ignores complementarity between which species are benefitting from management (Mair et al., 2021). Our approach identifies cells and actions that complement each other (by having different species) and hence have a higher combined benefit than cells selected independently—it considers the idea that the whole is different from the sum of the parts.

For each of the two approaches, we identified the top 30% of the most highly ranked cells from each output. The 30%

threshold was chosen because this is a standard target in conservation prioritizations (Di Minin et al., 2013; Leathwick et al., 2008; Mikkonen & Moilanen, 2013; Santangeli et al., 2016) and aligns with international conservation goals (e.g., Post-2020 Global Biodiversity Framework [Secretariat of the Convention on Biological Diversity, 2021]). To produce the cost-effectiveness curve for the site-richness approach, we divided the spatial benefit layer by the cost layer (using ArcGIS version 10.8) and reordered cells from highest to lowest based on cost-efficiency. We determined the cumulative sum of both cost and benefit in R 1.2.5033. Finally, we measured the results for the entire study region and made comparisons for each subregion. For the complementarity-based approach (Figure 4), we used the cost needed for the top fraction (used as the cost) and the average proportion of every species habitat managed (used as a surrogate for benefit), both of which are Zonation outputs (Appendix S5). We examined the sensitivity of outcomes from the complementarity-based approach to the assumption that all the selected species were negatively affected by the fire. Because there is typically a proportion of species that have no detectable change in abundance caused by one fire event, we reran the main prioritization to include only the 166 species listed as threatened by fire under Australia's Environment Protection and Biodiversity Conservation Act 1999 (Appendix S4).

RESULTS

The 2019–2020 Australian bushfires affected 76,000–96,000 km² of vegetation. High- and very-high-intensity fires encompassed >36,000 km² (46% of all burned areas in study region), and moderate- and low-intensity fires encompassed >42,000 km² (54% of all burned areas in study region) (Figure 2). Using our framework, we identified 290 threatened species that met our criteria for needing immediate conservation attention based on their risk rating (Appendix S2). Most species were affected by all three categories of fire intensity; 268 threatened species were affected by very-high-intensity fires, 273 were affected by high-intensity fires, and 273 were affected by moderate- and low-intensity fires.

Of the 22 broad-level actions, each species required, on average, three broad-level actions to mitigate threats (median = 3; range 1–9) (Figure 3). The top three actions required by most species were habitat protection (100% of all species; $n = 290$), fire suppression (57% of all species, $n = 166$), and invasive plant management (36% of all species, $n = 103$).

Different taxonomic groups required different sets of broad-level actions. For example, while habitat protection and provision of supplementary resources were the key actions for mammals (100% and 92% of mammals, respectively), habitat protection and fire suppression were the most prevalent actions for most birds, plants, reptiles, and insects (with 71%, 53%, 88%, and 100% of species in these taxonomic groups requiring both actions, respectively). Frogs, however, mostly required habitat protection (100% of species) and chytrid fungus management (92% of species).

When we prioritized cost-effective postfire actions with the site-richness approach, 37% of the 423 subregions ($n = 158$) contained the top 30% of the landscape (i.e., priority locations) that provided the highest cost-efficiency. Many priority locations were found in the southwest, such as Fitzgerald subregion, and in the southeast, including South East Coastal Ranges and Snowy Mountains subregions (Figure 4a). Actions in these 158 subregions delivered the greatest return on investment for the highest concentrations of affected species (i.e., those that have high extinction risk and high proportions of burned habitat) but ignore complementarity among these subregions. In contrast, using the complementarity-based approach, we found that to equitably manage as many species as possible, postfire recovery action locations were dispersed across 43% of subregions ($n = 179$). The top 30% of the landscapes occurred mostly in subregions in the southeast (e.g., South East Coastal Ranges, Monaro, and Snowy Mountains) (Figure 4b). A key area of interest that emerged in both approaches is Gippsland in the Australian state of Victoria, due to the extensive impact of fire in that subregion in combination with habitat for many threatened species.

Based on the assumptions and median cost data in our analyses, approximately AU\$2.7 billion (~AU\$5751/km²) would be needed to mitigate all threats related to postfire recovery across all the habitat for all 290 threatened species that were severely affected by the bushfires (Figure 5). Our results showed that—depending on the approach taken—between AU\$440 million (site-richness approach) and AU\$609 million (complementarity-based approach) would be needed to manage the priority locations (~142,000 km²). The priority locations in the site-richness approach encompassed some proportion of 287 of the 290 species' habitats. There were three species not included in any area identified with this approach because they did not occur in the most species-rich areas. The proportional average of each species' prioritized habitat was 79% (max = 100%, min = 0%), with an average area of 3264 km² (range 0–82,855 km²) (Appendix S5). In comparison, the top priority areas of the complementarity-based approach prioritized on average 90% (max = 100%, min = 13%) of every species' habitat (mean = 3500 km², range 1–155,000 km²). This means that the complementarity-based approach prioritized more of each species' habitat when the top 30% of priority locations were selected, compared with the site-richness approach that missed some species completely. Under the site-richness approach, AU\$1.3 billion was needed to reduce 95% of threats across all species managed, whereas AU\$903 million was needed to manage an average area of 95% of every species' habitat under the complementarity-based approach.

DISCUSSION

Ready-to-use prioritization frameworks that help decision makers allocate funds to actions, post megafire, are critical for guiding action for recovering species as quickly as possible. They also allow for transparent and robust decision-making processes, ensuring that the limited resources allocated to conservation are spent efficiently and cost-effectively

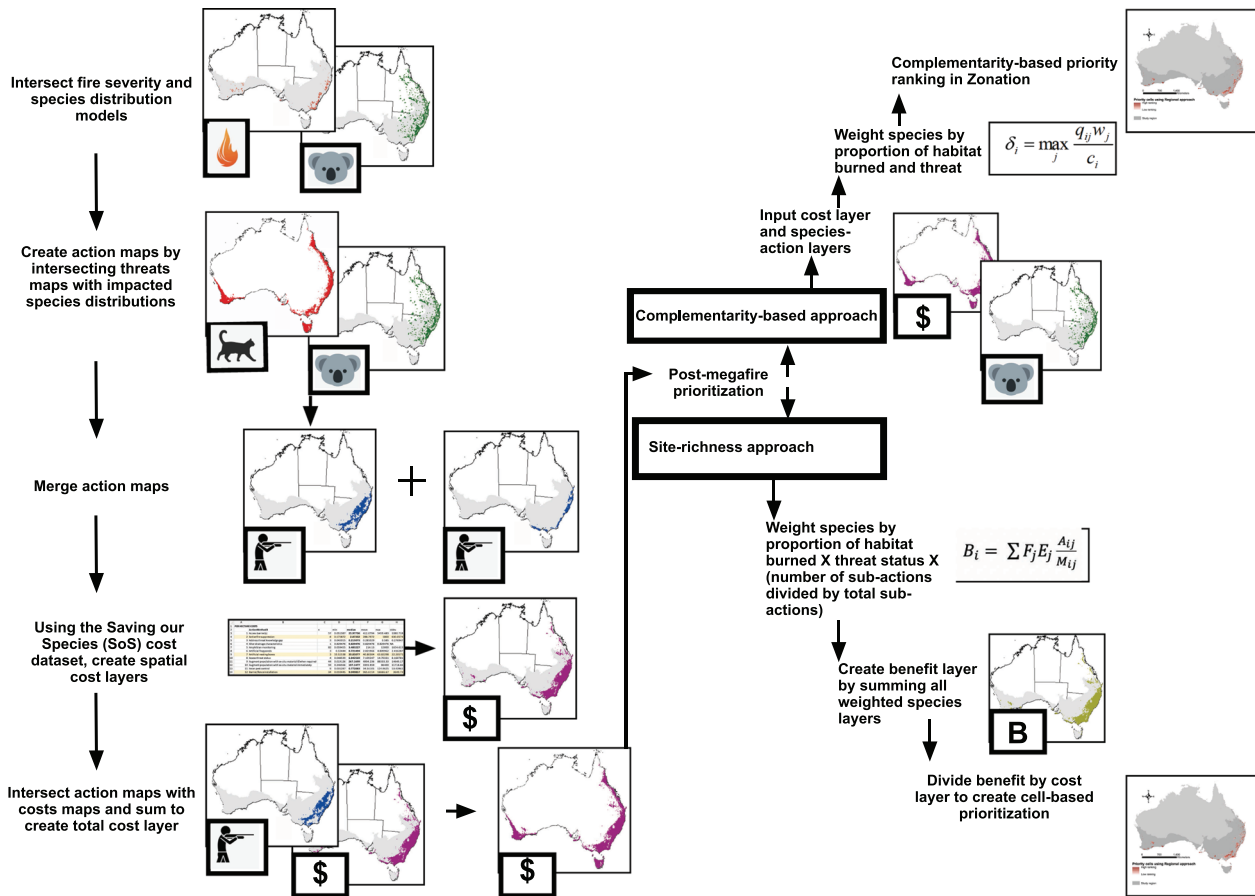


FIGURE 1 Application to Australia of a decision-support framework to prioritize conservation actions to improve species outcomes after a megafire

(Joseph et al., 2009; Waldron et al., 2017). Our decision-support framework explores the considerations needed to prioritize conservation actions needed immediately after a megafire. Our approach builds on conventional prioritization approaches to

fill this critical knowledge gap of prioritizing resources for preventing species decline that come not just from the fire itself, but from the cumulative or exacerbated threats that will likely affect fire-affected species populations.

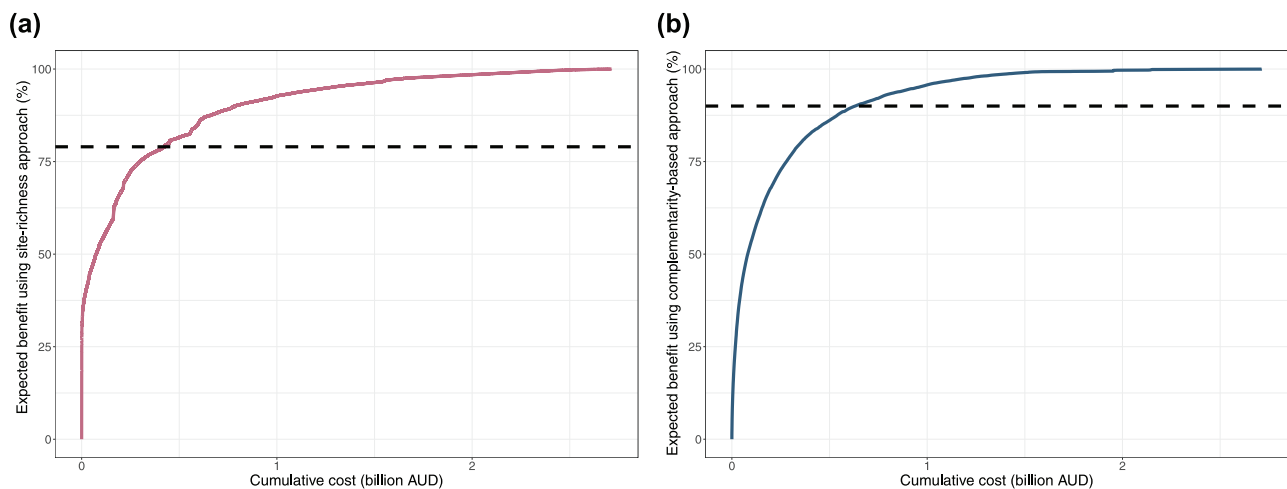


FIGURE 5 Cost-effectiveness curves for (a) site-richness approach and (b) complementarity-based approach to assist decision makers in prioritizing conservation actions after a large conservation disaster (horizontal line, top 30% of ranked cells)

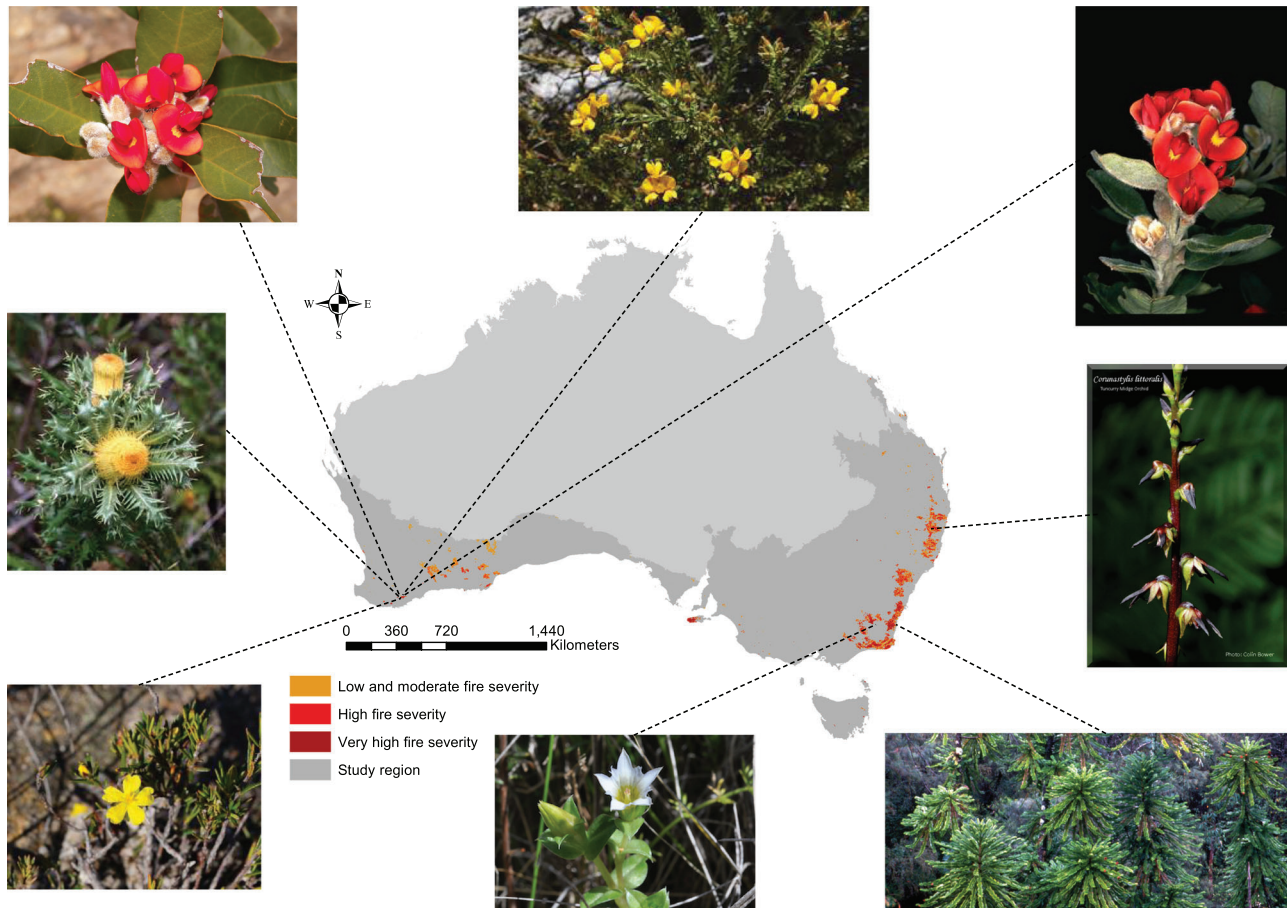


FIGURE 2 Areas affected by the 2019–2020 megafires and eight critically endangered species that experienced very-high- and high-severity fires across more than 30% of their habitat (clockwise from top left): yellow-leaved gastrolobium (*Gastrolobium luteifolium*) (photo by M. Crisp), *Hibbertia barrettiae* (photo by Sarah Barrett), *Gastrolobium vestitum* (photo by M. Crisp), Tuncurry midge orchid (*Genoplesium littorale*) (photo by Colin Bower), Wollemi pine (photo from Royal Botanic Gardens Sydney), Bredbo gentian (*Gentiana bredboensis*) (photo from Australian Network for Plant Conservation), mountain latrobea (*Latrobea colophonae*) (photo by Sarah Barrett), and cactus dryandra (*Banksia ananana*) (photo from Australian Network for Plant Conservation)

The 2019–2020 Australian megafires burned the largest area in a single fire season since European colonization within areas that are normally fire resistant, such as wet gullies, rainforest, riparian strips, and rocky outcrops (Wintle et al., 2020). Given the uniqueness of this event, governments, conservation scientists, and managers had no precedent for designing and implementing a response. The Australian Federal Government has committed AU\$200 million to postfire recovery actions (Wintle et al., 2020; Australian Government, 2021), but this is less than one-third of the AU\$609 million needed under our complementarity-based approach. Currently, 66% of the species in our prioritization are considered low priority in funding schemes (Brazill-Boast et al., 2018), further highlighting the importance of dynamic prioritizations that respond to large-scale disturbances. The recovery and persistence of species requires additional, consistent, and ongoing resources to be effective at the scale needed (Garnett et al., 2018). This is due to the many enduring, complex threatening processes that species faced even before the bushfires, as well as decades after (Bowd et al., 2019).

Although site-richness approaches are still widely used to prioritize conservation actions (Government of Canada, 2021; Keppel et al., 2015; Ravetto Enri et al., 2020; Queensland Government, 2021), we found that focusing on site richness is highly cost-inefficient compared with our complementarity-based approach, with a focus on site richness resulting in an AU\$350 million increase in costs of managing 95% of all threats to species. The site-richness approach maximizes the number of managed species in any one location, yet ignores complementarity, so that disproportionate effort might end up being assigned to species that occur in many sites. The major benefit of this approach is that it is easy to explain and offers insight into areas where quick fixes can be applied; however, risks arise if this approach is used in isolation. That is, important, high-risk species outside hotspot areas may not be targeted for conservation actions and resources may not be spent equitably across species in need. Our action-prioritization results are consistent with recent research focused on global conservation reserve placement, which shows that identifying priority areas for conservation based on species richness produces lower coverage

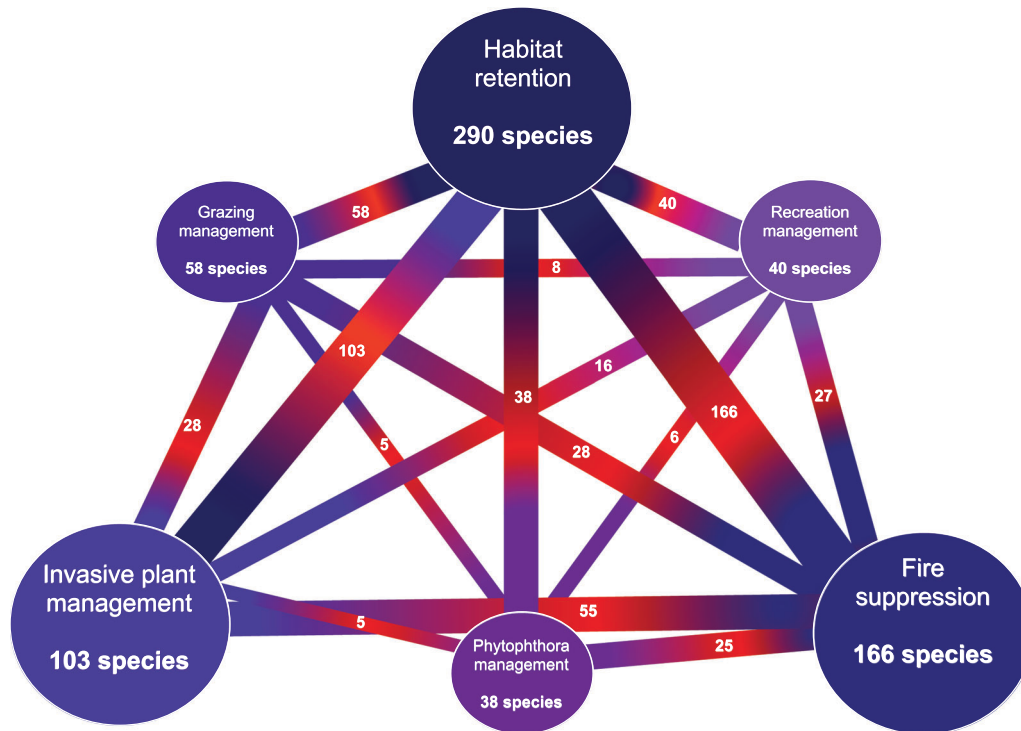


FIGURE 3 The number of Australian threatened taxa that would benefit from each broad-level action (circles) and the number of taxa that would benefit from each pair of broad-level actions (lines connecting circles) (circle size and line thickness proportional to the number of taxa benefited). Only the top six broad-level actions are depicted

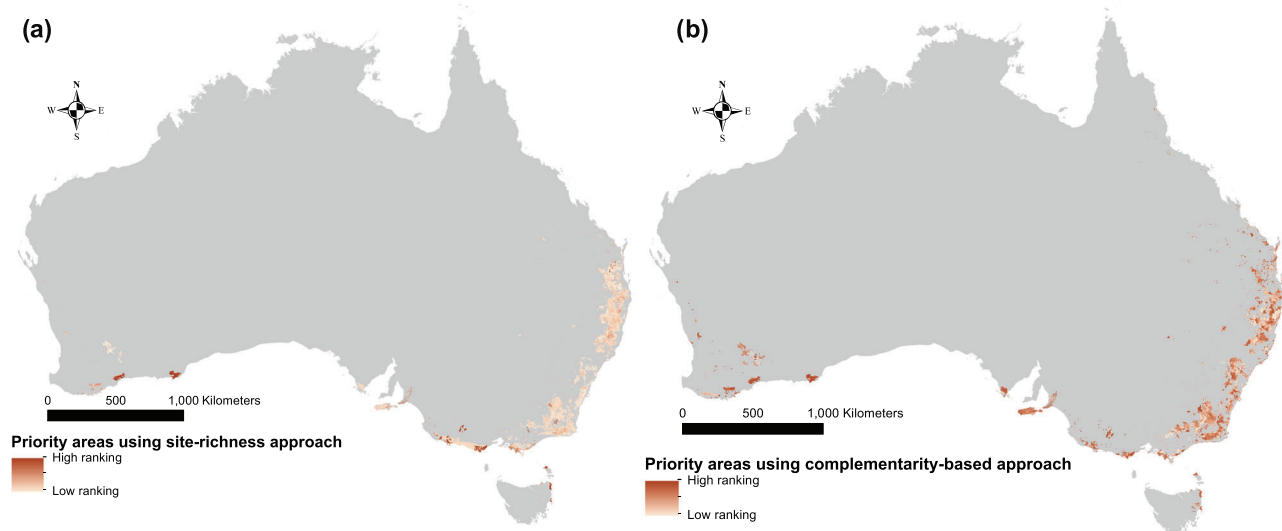


FIGURE 4 Broad areas for conservation action ranging from high-ranking priority areas (red) to low-ranking priority areas (cream) that maximize threat reduction for species highly affected by the megafires: cells containing the top 30% of the landscape that provide the (a) highest cost-efficiency for postfire recovery actions that maximize the number of highly affected species and (b) highest cost-efficient, complementary postfire recovery actions

of species than priority areas based on complementarity (Veitch et al., 2017). Our novel complementarity-based approach highlighted priority areas where many different high-risk species co-occur with many different threats. The areas identified with our approach had relatively low overlap with other national and statewide species conservation prioritizations, which used

different data and did not consider the 2019–2020 megafires (Chadès et al., 2019; Ward et al., 2019a). This suggests that national conservation priorities were affected by this single fire event. The major benefit of our approach is that it offers decision makers a set of important areas for recovering a large number of species affected by bushfires, whereas previous

approaches are designed to prioritize efforts for longer-term threats and response actions.

Our framework builds on previous work that mapped the impact of fire on native species (Fonseca et al., 2017; Godfree et al., 2020) by incorporating many other threats in the context of emergency response. The initial loss of habitat after fire can be detrimental for many species, but they also must survive the impacts of a variety of other threats that occur prefire and may intensify after a fire. Many plants that regenerate in the postfire environment are vulnerable to herbivory by native and invasive species, competition from invasive and other native plants, and desiccation (Wintle et al., 2020). Animals may struggle to find food and shelter and to avoid predation from invasive species (McGregor et al., 2014). Some animals that try to move across the landscape to recolonize new habitats may find their dispersal interrupted by cleared land, fences, and other human disturbances (Ward et al., 2020b). New habitats may be suboptimal in terms of resources or due to competition by other individuals (Wintle et al., 2020). Our research highlights the number of additional threatening processes that can potentially impact species postfire and the importance of multipronged management actions that consider these threats in addition to fire management to reduce impacts and provide the best chance for species survival.

The loss and degradation of habitat from the 2019 to 2020 bushfires occurred on top of decades of land clearing (Ward et al., 2019b). Our results indicated that among the species most affected, the most prevalent additional action needed to recover populations was habitat retention. The retention of habitat postfire in the overall fire footprint and outside the fire footprint (i.e., refuge areas) will be critical to species' persistence and recolonization of burned areas (Berry et al., 2015). In some locations, unburned, unprotected habitat is at risk of being thinned, burned, and cleared for conversion to agricultural land or forestry (Lindenmayer et al., 2019, 2020). Loss and degradation of remnant vegetation risks declines and possible further extinctions of species (Reside et al., 2019) and creates more fire-prone forests (Lindenmayer et al., 2019). The protection of residual vegetation and the species' habitats therein is fundamental.

Although monitoring is a critical component of conservation (Strayer, 1986), we did not include a monitoring cost because we focused on allocating resources toward on-the-ground conservation actions that could be immediately implemented in burned and unburned areas (Possingham et al., 2012). Monitoring for longer than the time frame of our study (12 months) is likely to be required for many species because succession in some of the burned areas can take decades. Immediately after a fire, species may have dispersed or been (at least temporarily) lost from burned habitats and may only return if areas are well managed and provide sufficient food and shelter (Olsen & Weston, 2005; Robley et al., 2016). Effective post-fire monitoring enables managers to track when populations return to burned areas and allows some actions (e.g., supplementary feeding) to be effectively timed. This potentially avoids wasted funding on actions for populations that are not present and perverse outcomes from increasing nonthreatened popula-

tions that could outcompete returning threatened populations (Kubasiewicz et al., 2016).

We relied on numerous existing data sets with inherent uncertainties. For example, we used the most current distribution maps of invasive species (Pintor & Kennard, 2018), but after a fire they may move into areas previously unoccupied, change in density, (McGregor et al., 2014), or be completely removed. Our prioritization method could be adapted to account for such uncertainties by buffering distribution maps or modeling behavioral changes of invasive species to explore whether an increased range size or changed occupancy for invasive species after fire changes the prioritization decision about where to spend limited conservation resources (Jacquemyn et al., 2005). We also used cost information from a New South Wales management program to infer costs in other jurisdictions because this was the most comprehensive data set on management costs available. The costs were, therefore, most certain in New South Wales and less certain in other states, where management costs are not publicly accessible. We also assumed that all species require conservation action. When we relaxed this assumption and prioritized efforts for only species threatened by changed fire (Ward et al., 2021), then the cost of managing threats was reduced from AU\$2.7 to AU\$2.6 billion. Priority locations remained relatively similar, still primarily in the southeast subregions, such as South East Coastal Ranges, Highlands-Northern Fall, and Snowy Mountains, which suggests that the general priority areas were relatively robust to the exact subset of species selected for prioritization (Appendices S4 & S7).

Fires are driven by many synergistic processes, including anthropogenic climate change resulting in intensified drought (Dale et al., 2001) and inappropriate land use and vegetation management (Lindenmayer et al., 2020). With the predicted increases of warming and drying, countries, such as Australia, the United States, and Brazil, can expect more frequent catastrophic fire events in the near future, highlighting the critical need for prioritized emergency response of conservation actions that are holistic in their conservation measures (Dowdy et al., 2019). Although reducing human impacts before fire can enhance system recovery and encourage the natural capacities of species to reproduce and survive within the context of natural disturbance regimes (Frissell et al., 1997), actions after megafires are critical to the survival of many species. Our results illustrated how current knowledge can be combined into a succinct framework to immediately prioritize conservation actions that have the greatest benefits for mitigating postfire impacts and biodiversity recovery. In addition to management allocation after extreme wildfire events, our complementarity-based prioritization framework will be useful for planning recovery from other future environmental disasters like flooding, which are predicted to increase in frequency.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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