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Restoring habitat for fire-impacted species' across degraded Australian landscapes

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Abstract

In the summer of 2019–2020, southern Australia experienced the largest fires on record, detrimentally impacting the habitat of native species, many of which were already threatened by past and current anthropogenic land use. A large-scale restoration effort to improve degraded species habitat would provide fire-affected species with the chance to recover and persist in burnt and unburnt habitat. To facilitate this, decision-makers require information on priority species needs for restoration intervention, the suite of potential restoration interventions, and the priority locations for applying these interventions. We prioritize actions in areas where restoration would most likely provide cost-effective benefits to priority species (defined by each species proportion of habitat burned, threat status, and vulnerability to fires), by integrating current and future species habitat suitability maps with spatially modelled costs of restoration interventions such as replanting, removing invasive species, and implementing ecologically appropriate fire management. We show that restoring the top ∼69% (112 million hectares) of the study region (current and future distributions of priority species) accounts for, on average, 95% of current and future habitat for every priority species and costs ∼AUD\$73 billion yr^{-1} (AUD\$650 $\mathrm{hectare}^{-1}\ \mathrm{yr}^{-1}$) annualized over 30 years. This effort would include restoration actions over 6 million hectares of fire-impacted habitat, costing ∼AUD\$8.8 billion/year. Large scale restoration efforts are often costly but can have significant societal co-benefits beyond biodiversity conservation. We also show that up to 291 MtCO2 (∼150 Mt DM) of carbon could be sequestered by restoration efforts, resulting in approximately AUD\$253 million yr^{-1} in carbon market revenue if all carbon was remunerated. Our approach highlights the scale, costs, and benefits of targeted restoration activities both inside and outside of the immediate bushfire footprint over vast areas of different land tenures.

1. Introduction

The degradation and loss of species' habitat due to agriculture, urbanisation, mining, and logging are key drivers of local and global species extinction and ecosystem collapse (Brondizio *et al* 2019, Bergstrom *et al* 2021). The impact of direct human activities on species habitats are exacerbated by additional pervasive and ongoing threatening processes, such as changed fire regimes (Rogers *et al* 2020), climate change (Dowdy *et al* 2019), and invasive species (McBurnie *et al* 2015, Williams *et al* 2015, Driscoll *et al* 2019). Knowledge of collective impacts has helped drive global ambitions for ecosystem restoration, including Sustainable Development Goal 15, which outlines the need to protect, restore, and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, halt and reverse land degradation, and halt biodiversity loss (United Nations Sustainable Development Goals 2015).

Safeguarding Earth's remaining non-degraded, intact ecosystems is an urgent priority (Watson *et al* 2016, Di Marco *et al* 2019). However, protecting and managing intact habitat is not sufficient to secure the future of biodiversity (Strassburg *et al* 2020, Mappin *et al* 2021), particularly given remaining habitats are dwindling in extent and intactness (Williams *et al* 2020). Large-scale restoration efforts are also required if threatened flora and fauna are otherwise unable to recover and persist. Recovery of species and ecosystems at large scales is an underlying ambition of the Convention of Biological Diversity, of which 196 nations are signatories (Secretariat of the Convention on Biological Diversity 2021), as well as the UN Decade on Ecosystem Restoration (United Nations Environment Program 2018).

Restoration is the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed (SER 2004). Ecosystem degradation, damage, and destruction can be caused directly by anthropogenic land use and management practices (Commonwealth of Australia 2001), inappropriate fire regimes (Rogers *et al* 2020), and non-native species (McBurnie *et al* 2015, Williams *et al* 2015, Driscoll *et al* 2019). Restoration success depends upon understanding the drivers of degradation in a location, and addressing these through targeted restoration activities (Ghazoul and Chazdon 2017). Restoration activities can include supplementation of biota as well as managing land use and removing threatening processes.

The intensity of restoration activities varies on a continuum from passive to active approaches: from natural regeneration, to assisted natural regeneration, active restoration, reconstruction, and fabrication (McDonald *et al* 2016). Some ecosystems can only recover when the anthropogenic process leading to degradation ceases (Meli *et al* 2017). For example, assisted natural regeneration might take place where livestock or invasive herbivore grazing on native vegetation is removed, whereas ecosystems that are not affected by other degrading activities may recover passively without further intervention (Wilson 1994, Cramer and Hobbs 2007, Hough-Snee *et al* 2013). However, it can take many decades for passively restored sites to approach reference states (Vesk *et al* 2008, Shoo *et al* 2016, Neilly *et al* 2021). Ecosystems are typically degraded by several simultaneous drivers, for example, vegetation clearing, invasive animals and plants, livestock grazing, and altered fire regimes. Hence successful restoration may require a combination of passive and active approaches such as proactively reinstating flora species, ongoing management of invasive species, and re-establishing ecological regimes (Vesk *et al* 2008, Shoo *et al* 2016, Meli *et al* 2017, Prach *et al* 2020, Neilly *et al* 2021) that account for climate change (Reside *et al* 2018, Prober *et al* 2019).

The habitat of many species of Australian native flora and fauna has been degraded by multiple processes, including changed land use, altered fire regimes, and introduced species (Kearney *et al* 2019, Ward *et al* 2021). In addition to centuries of ongoing degradation, in the 2019–2020 summer, Australia experienced the largest fire season on record (Boer *et al* 2020). These fires burned ∼104 000 km^2 of vegetation across southern Australia, with 545 flora (Gallagher *et al* 2021) and 114 fauna identified as immediate priorities for conservation action due to a substantial proportion of their habitat being impacted, their threat status, and their high sensitivity to fire (Legge *et al* 2022). Of the 114 priority fauna species, 90 (68 vertebrates and 22 invertebrates) were listed as threatened by IUCN, and/or national legislation (Legge 2022), driven mostly by habitat loss, fragmentation, and degradation (Ward *et al* 2021). A multi-threat analysis is required to assess opportunities to address the many processes that degrade species habitat—which then helps to recover these priority species. This involves bringing together information on the most cost-effective locations for restoring burnt and unburnt habitat for each species, and the types of interventions for effective and efficient habitat restoration that address multiple causes of degradation (Geary *et al* 2022).

Here we prioritize cost-effective restoration areas that deliver the greatest recovery benefits for priority species. We combine maps of native vegetation loss and drivers of degradation within the distributions of all priority fauna species after the 2019–2020 Australian megafires with the cost of various restoration actions. We account for multiple drivers of degradation by using maps of invasive rabbit distributions, agricultural land use, fire history, logging, invasive weed distributions, and large invasive herbivore distributions. For each driver we prescribe a set of restoration interventions and costed these spatially, including management (Yong *et al* 2022) and opportunity costs.

Restoration outcomes can take many years to manifest (Vesk *et al* 2008), over periods in which many species distributions are expected to shift due to climate change (Thuiller 2004, IPCC 2021). We include both current fauna distributions and potential future (year 2085) fauna distributions in our prioritization (Jones and Davidson 2016) to ensure pre-emptive restoration priorities, while acknowledging the uncertainty involved in long-term future species distributions. Restoration efforts over large areas can have significant socio-economic costs and benefits. We showcase an example by estimating the potential carbon sequestration outcomes of our restoration prioritisation, which could help fund species habitat restoration efforts. While our research focuses on vertebrates most heavily affected by the 2019–2020 Australian fires, our approach is relevant to any set of species, in other geographic regions.

2. Methods

2.1. Study area

The study region is spread across the current and future species distributions of 114 native Australian animal species. This area extends across 162 million ha (21%) of terrestrial Australia.

2.2. Restoration for priority species after 2019–2020 bushfires

Our primary prioritization objective was to maximize cost-effectiveness of restoration efforts for priority species, which include managing the key drivers of degradation, from invasive herbivores to native forest logging. We chose 114 target terrestrial and freshwater fauna species and subspecies (from here on referred to as ‘species’) identified as ‘priority’ or ‘provisional priority’ for urgent conservation following the 2019–2020 bushfires (Legge 2022). These species were identified based on the extent to which their range has potentially been burnt, threat status before the fires, and the physical, behavioural, and ecological traits which influence their vulnerability to fire. This included 17 birds, 16 fish, 16 frogs, 20 mammals, 23 reptiles, and 22 crayfish (see supplementary material 1). Current presence-absence range maps were sourced from various datasets (Graham *et al* 2019, Southwell *et al* 2020, 2022), while modelled future species distributions were obtained from Graham *et al* (2019) (median proportional range contraction = 52%, range = −639%–99%). The future projections of species distributions were modelled using scenarios for the year 2085 for Representative Concentration Pathway 8.5 (the ‘business as usual’ scenario and reflects the current global emissions (Schwalm *et al* 2020)) and 18 General Circulation Models. We took the 50th percentile of modelled future suitability across each of the General Circulation Models to locate potential future suitable habitat under a severe climate change future (Graham *et al* 2019). To examine the sensitivity of optimal restoration options to Representative Concentration Pathways, we also analysed future projections of species distributions using scenarios for the year 2085 for Representative Concentration Pathway 4.5 (the intermediate stabilization scenario) and 18 General Circulation Models (see supplementary material 2 and figure S1).

2.3. Threats, actions, and costs

Habitat restoration was prioritised to mitigate seven types of threats through a suite of actions and sub-actions (table 1). The costed sub-actions are assumed to be completed all at once, repeated at various times over 30 years, and applied at the same intensity within both burnt and unburnt landscapes (Yong *et al* 2022). We assumed that restoring species habitat in areas used for irrigated agriculture, dryland agriculture, or plantations (as of 2010 (Commonwealth of Australia 2020a)) would involve replanting vegetation (i.e. tube stock, tree guards, and watering), but replanting would not be required in any other areas. We explored the sensitivity of this assumption by rerunning the prioritization including all areas currently used for agriculture as of 2020 (supplementary material 2 and figure S2). This sensitivity analysis allowed us to explore the maximum replanting cost needed within cleared landscapes. Although there is potential for recolonisation of plant species at sites via dispersal in agricultural landscapes, our approach did not account for this passive restoration potential due to the alteration of the soil conditions and microclimates in agricultural landscapes which are necessary for recruitment of native taxa, and dispersal limitations in fragmented landscapes (Fensham *et al* 2016, Price *et al* 2021).

Actions including invasive weed management, large invasive herbivore management, invasive rabbit management, ecologically appropriate fire management, logging management, and agricultural management were required across the entire landscape where both the threat and priority species occur. Management at this scale ensures that threats are managed throughout the entire distributions of priority species, to minimize further degradation (e.g. weed removal or ensuring burnt areas do not burn again until an ecologically appropriate time, (Enright and Thomas 2008)). European colonisation of Australia has resulted in some ecosystems experiencing inappropriate fire regimes which can degrade the landscape (Barger *et al* 2018, Ward *et al* 2021). We are not prescriptive on details of fire management actions required for each ecosystem as local scale knowledge is best placed to guide the fire regime that meets the ecological needs of a particular location for persistence and restoration of biodiversity,

Table 1. Overview of all actions and sub-actions required for restoration (adapted from (Yong *et al* 2022)).

Threat	Action	Costed Sub-actions
Applies to all threats	Applies to all actions	Post-fire/pre-action office planning, post-fire/pre-action field planning, post-action monitoring, post-action evaluation
Irrigated/dryland agriculture and plantations	Replanting	Replanting, weed control
Invasive weeds	Invasive weed management	Intensive weed control
Large invasive herbivores	Large invasive herbivore management	Shooting, mustering
Invasive rabbits	Invasive rabbit management	Shooting, fumigation, warren ripping, viral biocontrol
Inappropriate fire regimes	Ecologically appropriate fire management	Fire break establishment, aerial burning (including ground support for suppression), ground burning
Logging	Logging management	Mapping, policy change/compliance/awareness, liaison officers
General agricultural land use	Agricultural management	Payments to landholders for lost opportunity, education and communication, sustainable co-management of land, fencing

as well as to balance the social and cultural benefits and risks. We also assume that ecologically appropriate fire regimes are implemented from now according to the modelled pre-1750 vegetation groups (Commonwealth of Australia 2020b); however, climate change and other related dynamics will continue to shift appropriate fire regimes and management. We acknowledge that a limitation of these modelled pre-1750 vegetation groups is that they are heterogeneous and do not support a dynamic framework for fire management. We costed ecologically appropriate fire management that aim to reduce the size and intensity of large burns where necessary, and excluded all fire suppression, ignition surveillance and detection, readiness, and training costs and the costs associated with damage resulting from catastrophic fire, due to context specificity, the stochasticity involved in large fire events, and complexity. We included the costs of post-action monitoring and evaluation of sub-actions) because it is an important part of best-practice management. We expect management effectiveness to be better understood across all threats over time, assuming interventions are implemented using an effective adaptive management approach.

Spatially variable cost layers were used to estimate costs for replanting, invasive weed management, invasive rabbit management, general agricultural management, large invasive herbivore management, fire management, and logging management (Yong *et al* 2022). These spatially variable cost layers consisted of four cost components: labour, travel, consumables, and equipment. The cost layers were at 1 × 1 km resolution and represent an annualized Present Value cost of actions over a 30 year period with a 4% discount rate. Several multipliers were used consistently within each spatially variable cost layer, including 30% for on-costs and 10% for on-site contingencies (Yong *et al* 2022). For all areas that are used for agriculture in the study region, we used an agricultural profitability layer (Marinoni and Garcia 2018) to identify land owner opportunity costs (i.e. lost income due to native vegetation being restored on agricultural land) for the areas that would be restored for biodiversity under the replanting and agricultural management strategies. We removed ‘unrestorable’ areas such as cities, infrastructure, intensive horticulture and animal production, utilities, active mines, and communication and transportation infrastructure using a land use dataset (Commonwealth of Australia 2020a), under the assumption that these land use types are unlikely to be restored to deliver biodiversity benefits.

2.4. Spatial prioritization

We used the tool Zonation (Moilanen *et al* 2006) for the spatial prioritization because of its ability to produce a hierarchical prioritization of the landscape based on the occurrence of biodiversity in sites by iteratively removing the least valuable remaining sites (taking into account biodiversity benefits and costs) while accounting for connectivity and complementarity. We used current and future species distribution maps for each species, and an aggregated cost of the seven actions for restoration, within Core Area Zonation (which ensures equal representation of species in top ranked cells). Our inputs included 114 maps of current suitable habitat for species, 53 models of future suitable habitat for species, and one aggregated cost layer, all of which have a 1 km^2 resolution. This produced a priority rank map for the entire landscape and a set of performance curves that described the quality of the solution (Moilanen *et al* 2011). We set Zonation to remove one cell at a time, with no penalty for long boundaries, meaning that while connectivity is important, it did not primarily drive the ranking of important cells. We explore the sensitivity of this analysis by running a second Zonation analysis that focuses on ensuring connectivity by penalising long boundaries to enable future species dispersals (supplementary material 2).

Species were weighted (0–1) based on the estimated overall population (OP) decline due to the 2019–2020 bushfires (Legge *et al* 2022). This weighting multiplies the proportion burnt with sensitivity to fire which was provided through expert elicitation (Legge *et al* 2022). Legge *et al* (2022) used the below formula:

$$\mathrm{OP}_{\mathrm{immed}} = (U \times P_{\mathrm{none\_immed}}) + (M \times P_{\mathrm{mild\_immed}}) + (S \times P_{\mathrm{severe\_immed}}), \tag{1}$$

where OP is the overall population; U, M and S are the proportions of the distribution that are unburnt, mildly burnt and severely burnt, respectively, with these summing to 100; and P is the elicited local population proportional change for each severity level and time point (shown in subscript (Legge *et al* 2022)). For example, Greater Glider (*Petauroides volans*) was provided a high weighting of 0.91 as there was an estimated overall severe population decline because of a high proportion of overlap with the 2019–2020 bushfires, plus the species was already listed as Vulnerable to extinction prior to the fires, plus the species is highly sensitive to fire. This weighting ensured that species with high proportions of habitat burnt, high sensitivity to fire, and high threat status consequently had stronger influence over the prioritization process. In Zonation, the overall score of a cell is a function of cost and benefit, where benefit is calculated as an overall value for an entire set of 'selected' cells that complement each other (i.e. by having different species). Cells with a higher number of different, highly weighted species will have a higher combined benefit than cells with redundancies. To identify top priority areas for restoration that align with global biodiversity targets (Secretariat of the Convention on Biological Diversity 2021), we extracted the top 30%, 20%, and 10% of cells as a separate spatial layer using ArcGIS (version 10.4). Using these four different spatial layers (i.e. total area of management, top 30%, top 20%, and top 10% of cells), we overlaid each separate cost layer to estimate the main drivers of cost as well as land tenure (Commonwealth of Australia 2016) to analyse the spatial representation in which the restoration area is owned, leased, reserved or unallocated.

2.5. Co-benefits of carbon sequestration

We used the outputs of the Zonation analysis to quantify the possible carbon sequestration co-benefits that could be delivered from all restoration activities in cleared and vegetated areas to recover priority fauna species after the 2019–2020 bushfires. To calculate the co-benefit of potential carbon sequestration, we used a map of the maximum above ground biomass (reported using t DM) (Roxburgh *et al* 2017) and overlaid major vegetation groups (Commonwealth of Australia 2020b) within the total areas identified for restoration. We then calculated the median dry matter per major vegetation group and multiplied the total hectares by the mean dry matter per major vegetation group with the total potential restoration areas. Taking this final maximum above-ground dry matter value, we multiplied by 25% to incorporate estimates of below-ground carbon that could also be sequestered from such restoration actions (Cairns *et al* 1997). To calculate possible carbon sequestered, we halved dry matter under the assumption that 50% is elemental carbon (Commonwealth of Australia 2015). Elemental carbon was then multiplied by 3.67 to convert from tonnes Carbon (tC) to tonnes of Carbon Dioxide Equivalent (tCO2e). We divided this by 30 to calculate the per year abatement under our 30 year timeframe. To account for the inevitable impact of disturbance (e.g. fire, cyclones, floods) over the 30 year timeframe, we applied a 15% penalty. To calculate possible costs that could be financed through carbon markets, we used AUD$26, which is the spot price for Australian Carbon Credit Units on the secondary market (Yin 2021).

We assume that after these areas have been restored (i.e. all seven threats managed) habitats will be retained in perpetuity, therefore reaching maximum above ground biomass. We note that some areas are already semi-intact (e.g. native vegetation is present but rabbits cause some degradation), so the additional carbon sequestered (i.e. carbon sequestration that occurs without management input) in these areas will be overestimated, yet possibly still accessible through carbon markets (i.e. avoided deforestation/clearing if not threatened species habitat).

3. Results

Our analysis shows that of the 162 million hectares prioritized as important areas for the conservation of priority species (figure 1(A)), 6 million hectares were within the 2019–20 megafire extent (figure 1(B)). The subregions with the greatest number of high priority cells (top 10%) were South East Coastal Ranges (New South Wales), Tasmanian West, and Highlands-Southern Fall (Victoria) driven by cost-effective benefits to species (see supplementary material 1 for details on all subregions). The top ten priority subregions for restoration vary in extent (the subregion

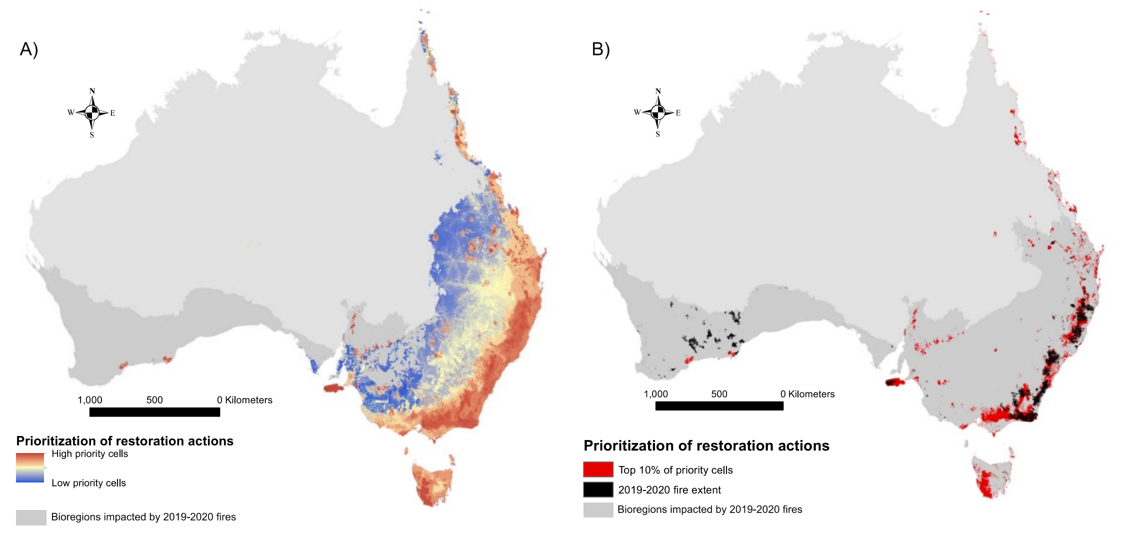

Figure 1. (A) Broad areas for restoration action that maximize threat reduction for all 114 priority species, ranging from high-ranking priority areas (represented in dark orange) to low-ranking priority areas (represented in blue). (B) Top 10% of priority cells for restoration action (represented in red), and the 2019–2020 fire footprint (represented in black). For both maps, light grey represents the Australian mainland border, while dark grey represents the bioregions impacted by the 2019–2020 fires.

sizes range from 442 000 to 1.7 million hectares) and estimated restoration costs (the subregion cost estimates range from AUD$734 million to 2.7 billion yr^{-1}). These areas contain threatened species such as Long-nosed Potoroo (*Potorous tridactylus tridactylus*, proportion habitat burnt = 31%, population decline after ten years or three generations postfire = 22.2%), Regent Honeyeater (*Anthochaera phrygia*, proportion habitat burnt = 19%, population decline after ten years or three generations postfire = 23.5%), and Koala (listed population of *Phascolarctos cinereus* proportion habitat burnt = 10%, population decline after ten years or three generations postfire = 25.4%).

Approximately AUD$16 billion yr^{-1} is needed to manage the top 10% (∼16 million hectares) of all locations. These top 10% of cells cover, on average, 65% of all species habitat included within the analysis. Management of the top 20% of priority locations would cost AUD$41 billion (∼32 million hectares) and manages on average 88% of all species habitat, whereas management of the top 30% of priority locations would cost AUD$68 billion (∼49 million hectares) and manages on average 94% of all species habitat. The cost to restore degraded habitats across all current and future distributions for the 114 priority species is approximately AUD$334 billion yr^{-1} (162 million ha; AUD$2059 ha^{-1}) (figure 2).

Based on the assumptions in our analysis, the most cost-effective restoration target is the top ∼69% of the landscape, which includes on average 95% of every species current and future habitat and costs AUD$73 billion yr^{-1} over 80 years (AUD$650 ha^{-1} yr^{-1}). Restoring the remaining 5% of species habitat costs ∼AUD$261 billion yr^{-1} to restore. Analysis within fire-impacted areas alone revealed that 6 million hectares require restoration actions, costing AUD$8.8 billion yr^{-1} over 30 years. There was very little difference between the cost of restoring all current habitat (AUD$325 billion yr^{-1}) and all current and future habitat (AUD$334 billion yr^{-1}), however, to restore 75% of current habitat there is a reduction in total costs of AUD$303 billion if we ignore future habitat needs (figure 2).

The seven actions targeted for restoration differ in their potential spatial extent and cost. The most expensive action per hectare is replanting, which costs ∼AUD$4225 ha^{-1} (AUD$96 billion yr^{-1} across 23 million ha). Replanting is followed by weed management (figure 3) costing ∼AUD$1415 ha^{-1} (AUD$216 billion yr^{-1} across 153 million ha). The third most expensive action is agricultural management, which costs ∼AUD$30 ha^{-1} (AUD$3 billion yr^{-1} across 118 million ha).

The priority areas for restoration area encompass 18 different land tenures. The tenures with the largest restoration area include freehold land (94 million ha), nature conservation reserves (16 million ha), and pastoral perpetual leases (11 million ha). The cost across these tenures also ranges vastly from AUD$232 billion in freehold land (AUD$2480 ha^{-1}), AUD$18 billion in nature conservation reserves (AUD$1200 ha^{-1}), and AUD$16 billion in pastoral perpetual leases (AUD$1553 ha^{-1}).

Using estimates of Maximum Above Ground Biomass (which defines the maximum upper limit to biomass accumulation for any location within the Australian continent), we found that if vegetation was restored to its maximum carbon potential and remained intact across the entire 162 million hectares, this would equate to 150 Mt of

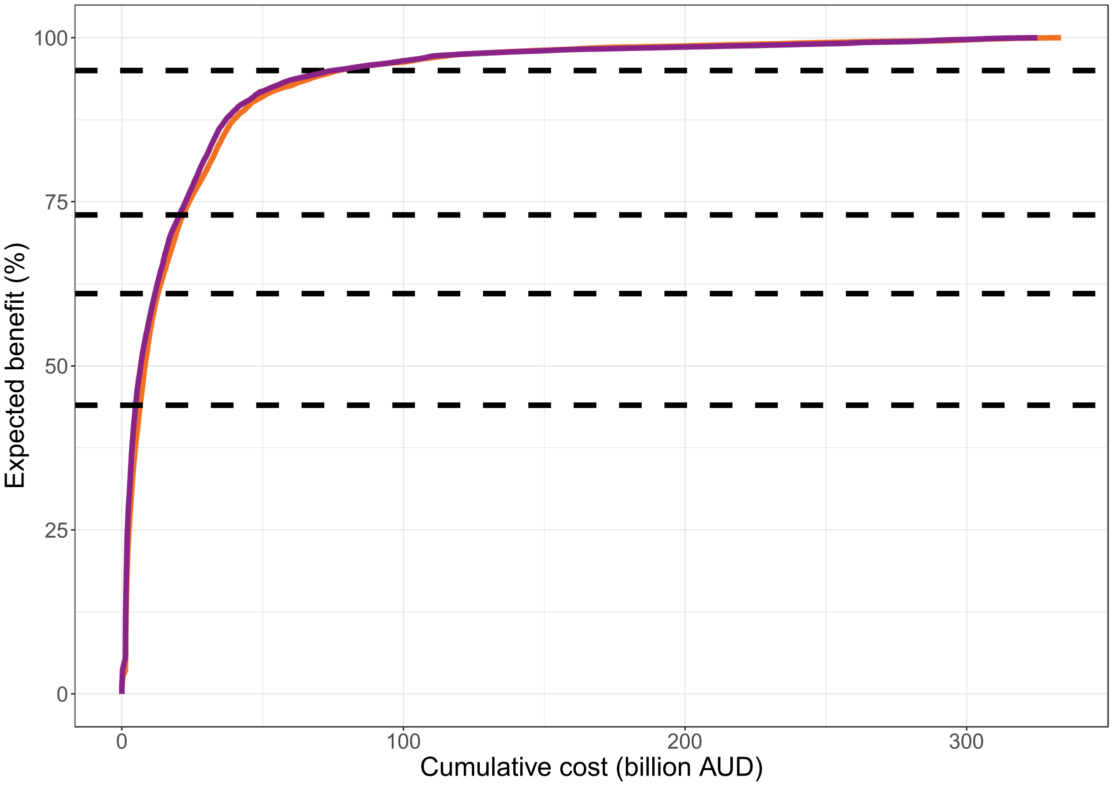

Figure 2. Return on investment curves, highlighting the increase in benefit relative to the increase in spending per year. The benefit for this prioritization is calculated as the average proportional distribution of each species managed for a given set of priority selected cells. Species are also weighted by their extinction risk, fire sensitivity, and proportion of fire-impacted habitat. The horizontal lines indicate the top 51%, 30%, 20%, and 10% of ranked cells. Purple represents managing the current species distributions only, while orange represents the current and future species distributions under predicted climatic change.

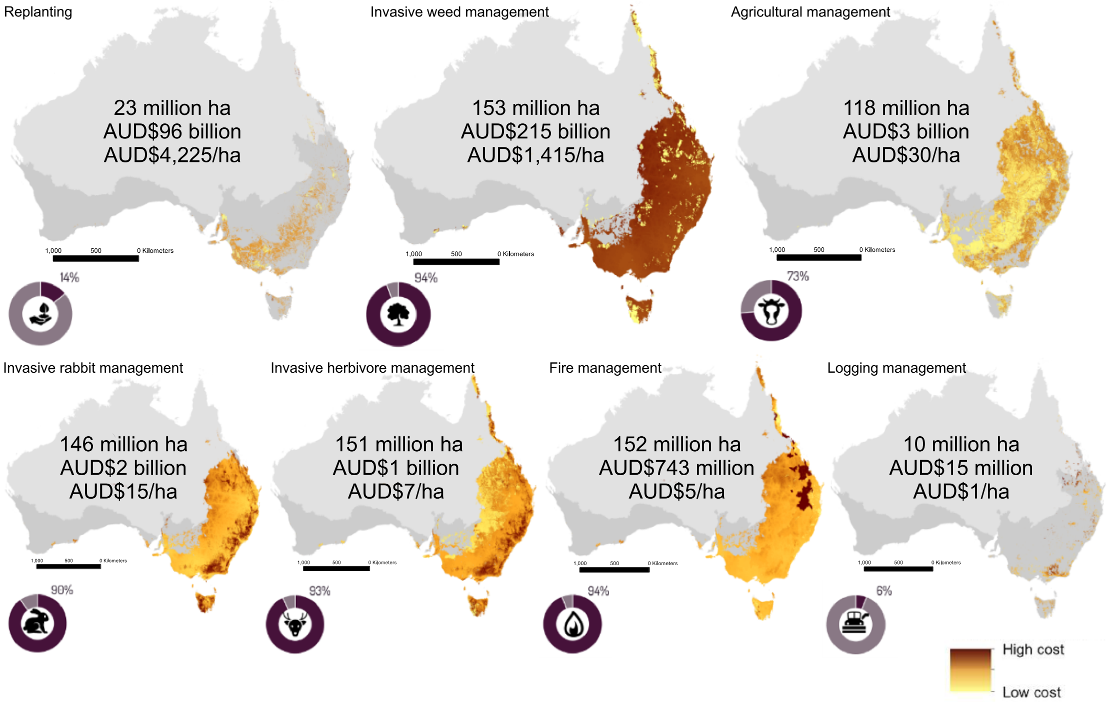

Figure 3. All seven restoration actions required to restore current and future habitats for priority species. Dark brown represents high-cost cells, while yellow represents low-cost cells and light grey represents the Australian mainland border. Each map also contains the total size (ha) of management area per action across priority species distributions, the total cost of management per action across priority species distributions, and the average cost per ha. Pie charts highlight the terrestrial proportion of the study region requiring the various actions. For all maps, light grey represents the Australian mainland border, while dark grey represents the bioregions impacted by the 2019–2020 fires.

dry matter. This translates to ∼292 MtCO2e (using both above and belowground carbon) could potentially be sequestered, which is a Net Present Value of ∼AUD\$253 million yr^{-1} in carbon market revenue if this carbon was remunerated. There were 29 different major vegetation groups identified within the restoration area that ranged in sequestration potential. The most carbon sequestered was in the Eucalypt Woodland group (90 MtCO2e), with the least in Hummock Grasslands (117 000 tCO2e), whereas the most per hectare was in Eucalypt Tall Open Forest (515 t ha^{-1}), with the least in Acacia Shrubland (53 t ha^{-1}).

4. Discussion

Our analysis finds that an investment of approximately AUD\$73 billion yr^{-1} would be needed to restore, on average, the current and future habitat extent of 95% of all 114 priority species (112 million ha). A total of AUD\$334 billion yr^{-1} would be needed to restore all areas. Put in context, the AUD\$334 billion yr^{-1} is approximately equivalent to the combined welfare and health expenditure (AUD\$321.3 billion) for 2020–2021 (Commonwealth of Australia 2020c), while our 2020–2021 COVID-19 response (AUD\$82.5 billion yr^{-1}) is more than what is needed to restore 95% of species habitats. These costs may be partially funded through the Australian carbon market (∼AUD\$253 million yr^{-1} based on a current AUD\$26/tonne, which is estimated to rise AUD\$45/tonne by 2030 if all carbon was renumerated). We found that including restoration of species' likely future habitat distributions costs only an extra 3% above the funding required to restore current habitat, highlighting that climate-ready planning is a cost-effective strategy. This is primarily due to range contractions and/or poleward movement of future distributions. We note that some species may require additional targeted restoration efforts to facilitate movement to refugial areas between current distributions and 2085 distributions, as habitat may only occur intermittently between these periods of change, yet necessary for the survival of the species during these years.

While AUD\$334 billion yr^{-1} is <1% of Australia's 2022 GDP (AUD\$1.331 trillion), it could be considered infeasible, therefore we recommend first focusing on the top 10% of the landscape (costing ∼AUD\$16 billion yr^{-1}). This will still manage ∼16 million hectares and capture on average, 65% of all species habitat included within the analysis. We note that all seven restoration actions outlined in this study have a risk of failure, but there is also potential for enormous co-benefits such as abating the impacts of extreme events (e.g. 2019–2020 megafires), preventing zoonotic disease outbreaks (e.g. Covid-19), reducing salinity, increased agricultural production, and reduced water security (United Nations Environment Programme 2021). Such a widescale restoration effort could also provide economic benefits through creating employment opportunities, particularly in regional areas mirroring the success of other global programs such as *Working for Water* in South Africa (Turpie *et al* 2008) and therefore contribute to the national economy in other ways. Moreover, it has been discovered that protected areas alone provide at least AUD\$134 billion in annual health services (Buckley *et al* 2019) and AUD\$1300 billion to Australia's economy via ecosystems services (Commonwealth of Australia 2020d). An enhanced, functioning network of restored ecosystems across Australia will only build on this.

Our analysis revealed there are substantial opportunities for restoration on government-owned land such as in nature conservation reserves and on pastoral perpetual leases. We identified 94 million ha of freehold land with restoration potential. While currently only a small fraction of the area identified here, state and federal governments already have a range of existing incentive programs that can be leveraged to increase investment on freehold land, such as the Land Restoration Fund (Queensland Government 2022), the Environment Restoration Fund (Commonwealth of Australia 2020e), and the Australian Heritage Grants (Commonwealth of Australia 2019).

Several subregions were hotspots for cost-effective restoration actions to benefit fire impacted priority species, including the Highlands-Southern Fall (AUD\$2 billion), Tasmanian West (AUD\$821 million), and South East Coastal Ranges (AUD\$2.7 billion). These areas contain many fire-impacted threatened species such as Spotted-tailed Quoll, Regent Honeyeater, and Koala and relatively few expansive threats, making them high benefit and low cost. For example, Tasmanian West hosts six priority species, yet with no replanting required and few invasive species, this subregion would be relatively cost-effective to restore compared with regions with many overlapping and interacting threats. The restoration cost difference between these subregions is primarily driven by differences among bioregions in the type and extent of threats that cause degradation, and therefore the restoration actions and costs of these actions. The seven restoration actions differed in spatial extent and cost, with replanting being almost three times more expensive than weeding—the second the most expensive action per hectare. This finding that replanting is more expensive than weeding is in line with previous research on restoration costs (Ponce Reyes *et al* 2016). Despite being extremely costly, we found that a number of regions (e.g. Victorian Riverina, Murray Mallee, and Tintinara) would require intensive replanting efforts to restore biodiversity, due to long term land use of irrigated/dryland agriculture.

While our study focused on the 114 priority species, restoring high priority areas offers many additional co-benefits for biodiversity and carbon. For example, many of the actions we identify in this study's priority areas will be important for other listed (Kearney *et al* 2020, Ward *et al* 2021) and non-listed species, and sustaining other ecological and evolutionary processes that drive many of the ecosystem services humanity relies on (Chazdon 2008, Strassburg *et al* 2020). In addition, if the entire 162 million hectares was restored, 149 000 000 t DM or ∼292 MtCO2e of above and belowground carbon could be sequestered. This translates to approximately 59% of Australian annual carbon emissions (494 million tonnes) and 1% of global annual carbon emissions (34 billion tonnes) (University of New Mexico 2019). These yearly sequestration rates may be overestimated due to disturbances (e.g. disease, fire, or flood) that will occur over our study period which prohibit maximum biomass being achieved. Ambitious climate action not only has benefits to biodiversity, but human health, equitable societies, and economic stability (IPCC 2018, 2021).

Under anthropogenic climate change, fires are expected to increase in severity and intensity across many parts of Australia (Dowdy *et al* 2019). To address this future fire risk, short-term strategies such as ecologically appropriate fire management, alongside long-term restoration efforts aimed at ensuring more resilient ecosystems (Knox and Clarke 2012, Wyse *et al* 2016) will likely deliver more sustainable outcomes for both people and biodiversity. Long-term efforts may include planting or encouraging the growth of less flammable species (Malcolm and Zylstra 2005), including in areas beyond their current biogeographic extent. While we recognise that we need to restore a vast range of habitats for priority species (including those that are fire prone), planting or encouraging the growth of fire-resilient ecosystems in strategic locations may help safeguard these vulnerable habitats. The moisture content of plant biomass contributes to fire risk and can be predicted from factors such as soil water content and plant traits such as specific leaf area and osmotic potential, which affect the probability of ignition (Nolan *et al* 2020). As vegetation is unlikely to burn when it contains high moisture content (Sullivan *et al* 2012), localised efforts might include focussing on restoration of species from rainforest ecosystems (Zimmer *et al* 2015) and wet eucalypt forests ecosystems (Nolan *et al* 2016), even though they may only provide habitat for some priority fauna species. However, to successfully establish mesic or rainforest vegetation, fire will need to be excluded from the system for several decades or more (Cochrane 2003).

The success of strategies which aim to shift vegetation composition to more mesic species via restoration will largely depend on climate conditions (Nolan *et al* 2018). The future balance between major climate phenomena, such as topicalization (Osland *et al* 2021) and cycles related to climate modes (Xie *et al* 2019) which shape drought risk (De Kauwe *et al* 2022) will determine the abiotic conditions available for supporting restoration plantings. The interaction between topicalization and increased drought risk will vary spatially and will largely determine fire extent and dynamics as both contribute to greater fuel accumulation (Osland *et al* 2021). However, before this occurs, there is a need for deeper predictive capacity about topicalization, increased drought risk, and their interaction, as well as increased knowledge on important plant-animal interdependencies. Planning for resilient restoration in these systems can be informed by projections of future climate conditions (Elsen *et al* 2022), and by the sensitivity and safety margin of plant species and human communities to environmental change (Gallagher *et al* 2019). Water can also be actively held in landscapes by 'undraining' swamps and wetlands, implementing ecologically appropriate water management, and restoring riparian zones to slow streamflow. These activities can contribute to the creation of abiotic conditions necessary to sustain mesic vegetation.

While we have included costs to evaluate how well each action was implemented (i.e. post-action monitoring and evaluation), we have not costed outcomes monitoring or adaptive management. We recognise that monitoring and adaptive management are important to ensure land managers focus on learning, with management strategies anticipating the influence of interventions on learning as well as resources (Williams 2011). In practice, this means that the objectives used to guide decision-making explicitly incorporate uncertainty, the potential for learning, and proactive management experiments (Bal *et al* 2018). In this analysis we costed post-action monitoring and post-action evaluation within all seven actions but recognise this is only one step in being able to adjust restoration strategies and costs based on the monitored and evaluated response of the ecosystem and species to different management interventions.

Our analysis provides a high-level estimate of the actions and costs required to restore fire affected species habitat and does not attempt to prescribe specific actions and accurate costs in any particular location. The spatial datasets (e.g. current species range maps, future species distribution models, and maps of fire severity, threats, costs and carbon sequestration)—while the best currently available—contain scale-associated inaccuracies (Pintor and Kennard 2018, Commonwealth of Australia 2020a, Yong *et al* 2022). They have been used here to provide indicative areas of interest, rather than definitive locations of species, threats, fire, or prescriptive costs. Further, we assume that all species are similarly impacted by a particular threat across the intersecting range of the species and the threat. That may not be the case (for example, invasive herbivores may be of higher density in some locations than others, resulting in more heavily degraded sites), therefore the areas and costings in this analysis represent estimations of cost. In addition, actions such as invasive weed management, large invasive herbivore management, and invasive rabbit management were applied only where both the threat and priority species occur, however in some areas, management of the threat may need to occur at much larger scales than the species distributions to be effective. We also assumed that restoration actions would begin immediately and continue into the future, with the added assumption that all species migrations would be feasible.

We recognise that in some cases, species may not be able to track their climatic envelopes due to inherent trait-based dispersal limitations, or due to their habitat being fragmented beyond dispersal capabilities failure to adequately restore habitats, or the presence of other threatening processes such as invasive predators, climate change, or pollution (Ward *et al* 2022). Our assumptions must therefore be seen as optimistic. Future work could unpack the uncertainties around potential configurations of future habitat and the ability of species to disperse between unconnected patches, but this requires detailed information on species' dispersal, survival and reproductive capabilities that is not available for all the species in this analysis.

Harnessing opportunities for restoration across burnt and unburnt areas of Australia involves engaging in bottom-up processes driven by land managers and custodians, that take account of local scale information and preferences. This process should support Indigenous leadership in restoration decision-making on land with Indigenous interests. Future research efforts could further engage with and prioritize the restoration of degraded land inside conservation areas such as protected areas, Indigenous protected areas, other effective area-based conservation measures, private protected areas, or less degraded natural ecosystems outside but near these conservation areas to further minimize cost (Maggini *et al* 2013), and reduce potential conflicts with other priorities (such as agricultural land). For maximum benefit, habitat restoration efforts should be coupled with ambitious retention goals that protect the remaining intact places, manage invasive predators, and limit the spread of disease—actions that were outside the scope of our analysis.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.32942/osf.io/3qx7e. Data will be available from 1 July 2022.

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