



Animal population decline and recovery after severe fire: Relating ecological and life history traits with expert estimates of population impacts from the Australian 2019-20 megafires

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ABSTRACT

Catastrophic megafires can increase extinction risks; identifying species priorities for management and policy support is critical for preparing and responding to future fires. However, empirical data on population loss and recovery post-fire, especially megafire, are limited and taxonomically biased. These gaps could be bridged if species' morphological, behavioural, ecological and life history traits indicated their fire responses. Using expert elicitation that estimated population changes following the 2019–20 Australian megafires for 142 terrestrial and aquatic animal species (from every vertebrate class, one invertebrate group), we examined whether expert estimates of fire-related mortality, mortality in the year post-fire, and recovery trajectories over 10 years/three generations post-fire, were related to species traits. Expert estimates for fire-related mortality were lower for species that could potentially flee or shelter from fire, and that associated with fire-prone habitats. Post-fire mortality estimates were linked to diet, diet specialisation, home range size, and susceptibility to introduced herbivores that damage or compete for resources. Longer-term population recovery estimates were linked to diet/habitat specialisation, susceptibility to introduced species; species with slower life histories and shorter subadult dispersal distances also had lower recovery estimates. Across animal groups, experts estimated that recovery was poorest for species with pre-fire population decline and more threatened conservation status. Sustained management is likely needed to recover species with habitat and diet specialisations, slower life histories, pre-existing declines and threatened conservation statuses. This study shows that traits could help inform management priorities before and after future megafires, but further empirical data on animal fire response is essential.

1. Introduction

Fire activity is changing across the world, driven by changes in climate, land use and vegetation (Wu et al., 2021). Although fire is a disturbance process integral to many ecosystems (He et al., 2019), shifts in fire patterns and regimes are increasing the extinction risks of many species (Kelly et al., 2020), underscored by recent extreme fire seasons in the Amazon, Siberia, California, Europe and Australia (Duane et al., 2021). Extreme fire events can cause sudden and marked changes to populations and extinction risk that require swift policy and management responses to mitigate population declines and hasten recovery (Legge et al., 2022b). The 2019–20 Australian megafires attracted global attention and triggered urgent management responses for hundreds of vertebrate, invertebrate, and plant species (Dickman et al., 2022; Gallagher et al., 2021a; Legge et al., 2022a; Marsh et al., 2021).

Understanding how fires affect populations is critical for shaping rapid conservation responses, as well as fire management actions more broadly. For instance, knowing the bounds of appropriate intervals

between fires to support population persistence can help to calibrate management actions such as prescribed burning (Tulloch et al., 2016). Yet empirical data on how populations respond to fires, especially fires of increasing size and severity, are limited and biased towards particular taxonomic groups (Jolly et al., 2022; Pausas and Parr, 2018; Rowley et al., 2020). In plants, these data gaps have been bridged by using species' ecological and life history traits to help understand and predict the impacts of fire on populations (Gallagher et al., 2021a; Gallagher et al., 2022; Keith, 2012; Keith et al., 2022). This approach has been used less in animals, partly because of patchy data on both animal traits and population responses to fire (Blaum et al., 2011; Driscoll et al., 2010; Driscoll et al., 2020; Westgate et al., 2012). In addition, animal mobility complicates the understanding of fire responses (Nimmo et al., 2019), and many contextual factors can moderate how traits affect survival, with the result that populations of a given species respond differently across sites and fire events, and data from multiple studies are needed to discern patterns (Keith, 2002; Nimmo et al., 2014; Pausas and Parr, 2018; Whelan et al., 2002). Despite this variability, using

information on traits to help prioritise species and management actions could be valuable when large numbers of species need to be assessed rapidly, and knowledge about the population response to threats (in this case, fire) is scant and disparate (Driscoll et al., 2010; Gallagher et al., 2021b).

Morphological, behavioural, ecological, and life history traits of animal species are likely to underpin differing responses to fire, through their associations with survival, reproduction, and movement (Engstrom, 2010; Santos et al., 2022a; Santos et al., 2022b; Whelan et al., 2002). Animals can be affected directly by fire if they die during a fire event from the flames, heat and/or smoke (Jolly et al., 2022; Peters et al., 2021), or flee the area (Nimmo et al., 2019; Nimmo et al., 2021). Fire can also affect animals indirectly, by altering habitat, reducing or increasing the availability of food, shelter, and other resources, and by modifying ecological processes, such as competition and predation (Engstrom, 2010; Whelan et al., 2002). Species' traits could mediate both direct and indirect sources of mortality. For example, individuals of species that shelter in rock crevices or deep burrows may be more protected from fire than individuals of species sheltering in flammable vegetation. Small-bodied animals may be better able to survive fire by using small spaces (e.g., soil cracks) to shelter. Alternatively, large-bodied or flying animals may be able to escape the fire front by moving away. Individuals of species living in fire-prone habitats that have co-evolved with fire may recognise when fires are approaching and respond more appropriately than individuals of species occurring in habitats that rarely burn (Álvarez-Ruiz et al., 2021; Law et al., 2022a; Lee et al., 2022; Nimmo et al., 2021). In the post-fire environment, changed resource availability may mean that animals that are habitat or dietary specialists may struggle to meet their needs and experience greater mortality, while generalists could be less affected or even benefit (Culhane et al., 2022; Dickman and Happpold, 2022; Lee et al., 2021). Some populations may face elevated predation after fire because shelter (i.e., vegetation, leaf litter, logs) is removed, and predators may be attracted to the burnt area (Doherty et al., 2022; Hradsky, 2020). Species that are not usually susceptible to certain predators may become so after fire (Doherty et al., 2022; Loy, 1997). Similarly, competition for scarce resources, including from introduced species, may increase after fire (Fuhlendorf et al., 2009; Legge et al., 2023; Tuft et al., 2012).

When fires reduce population sizes, the ability to recover is likely to be related to a species' life history traits, as well as some ecological traits (Keith, 2002; Whelan et al., 2002). For example, species with low fecundity may struggle to repopulate via in situ reproduction, while species with limited dispersal abilities may be slow to repopulate from surrounding unburnt areas (Banks et al., 2017; Liedloff et al., 2018; Nimmo et al., 2019; Shaw et al., 2021). Furthermore, population recovery may also depend on population parameters associated with pre-fire extinction risk broadly, including the pre-fire population size and trend, and the range size (e.g. Webb et al., 2021), which are themselves influenced by environmental conditions, such as drought, the antecedent fire regime, and other threatening processes.

The 2019–20 Australian megafires affected 104,000 km² of eastern and southern Australia (DAWE, 2020). Several assessments were rapidly undertaken to prioritise fire-affected fauna species for policy attention, conservation status review, and management action (Geary et al., 2022; Legge et al., 2022a; Legge et al., 2022b). The assessments relied on structured expert elicitations to estimate population responses and identify the management actions required, because of the paucity of existing empirical data, and the logistical and safety constraints in surveying populations immediately after the fire event. In this paper, we examine whether species traits, as well as pre-existing indicators of extinction risk, are related to expert-elicited estimates of animal population loss (from both direct and post-fire mortality) and population recovery following the 2019–20 Australian megafires. Our work spans five vertebrate groups, and one invertebrate group (142 terrestrial and aquatic species in total), collectively occurring across most of the spatial extent of the megafires. Our aim is to improve our understanding of

which traits experts may be using as proxies for the response of animals to fire, and to encourage further collation of trait information (Gallagher et al., 2020) so that conservation interventions after future fires can be prioritised quickly.

2. Methods

2.1. Species selection

The 2019–20 megafires burned >104,000 km² of the temperate and subtropical bioregions of southern and eastern Australia (DAWE, 2020) (Fig. 1). We focussed on terrestrial and aquatic animal species with distributions intersecting with the 2019–20 fire footprint. The species set covered all five vertebrate classes and one genus of invertebrates (freshwater spiny crayfish, *Euastacus* spp.) and totalled 142 taxa (140 species and two additional subspecies, hereafter referred to as species; Supplementary Material Table A1). Given the mix of taxonomic levels included, we refer to the bird, reptile, frog, fish, mammal and spiny crayfish species sets as 'animal groups'. The set comprised 16–34 species from each animal group and was selected from species whose distributions overlapped with the fire extent (mostly by >10 %), weighted to include threatened species (i.e. 102 (72 %) of the 142 taxa were listed as threatened under Australian federal environmental law (the Environment Protection and Biodiversity Conservation Act 1999), by the IUCN Red List of Threatened Species, or in vertebrate group action plans. The species set included all species except one from an earlier prioritisation of fire-affected fauna that informed recovery investment by the Australian Government (Legge et al., 2022a; Legge et al., 2022b); the peppered tree frog (*Litoria piperata*) was excluded because its traits are unknown, and it was either extinct prior to the megafires or is not a valid taxon (Gillespie et al., 2020).

2.2. Expert elicitation

Full details of the structured elicitation method used to derive the estimated population response to fire are provided in Legge et al. (2022a). That study used the 'IDEA' protocol (Investigate, Discuss, Estimate, Aggregate), which is a modified 4-step Delphi process that aims to manage many of the biases of experts, such as overconfidence, anchoring and group think (Hemming et al., 2018). A group of 51 experts with diversity in experience, gender and age was selected, noting that all had expertise in fire ecology and/or particular species groups. The 51 experts were divided into panels of 7–10 experts for each animal group, based on their relevant expertise. After providing initial judgements, experienced facilitators asked experts to question and discuss knowledge and judgements (via online workshops for each group), then experts had the opportunity to revise their judgements. At all stages, judgements were anonymous, so that experts did not feel pressured to alter their estimates in the face of highly regarded/experienced researchers. The round two (revised) judgements were then aggregated for analysis. Aggregating judgements from a diverse group of experts has been demonstrated to provide more accurate judgements than relying on the most well-regarded expert (Burgman et al., 2011).

We focus here on elements of the elicitation pertinent to the trait analysis. For each animal group, experts estimated the proportional population change at three time points at a hypothetical site that was completely affected by severe fire: at one week after fire, one year after fire, and 10 years or three generations after fire (whichever was longer for the taxon in question). For each species, we calculated the group average estimate at each time point, then calculated the change in those group averages between time-points. The hypothetical site contained habitat typical for the species and was of unconstrained size. Severe fire was defined as all ground material burned by fires, and upper canopy heavily scorched to completely consumed; we restricted our attention to severe fire as it is expected to cause the greatest population declines. For aquatic fauna, severe fire-related impacts were defined as having some

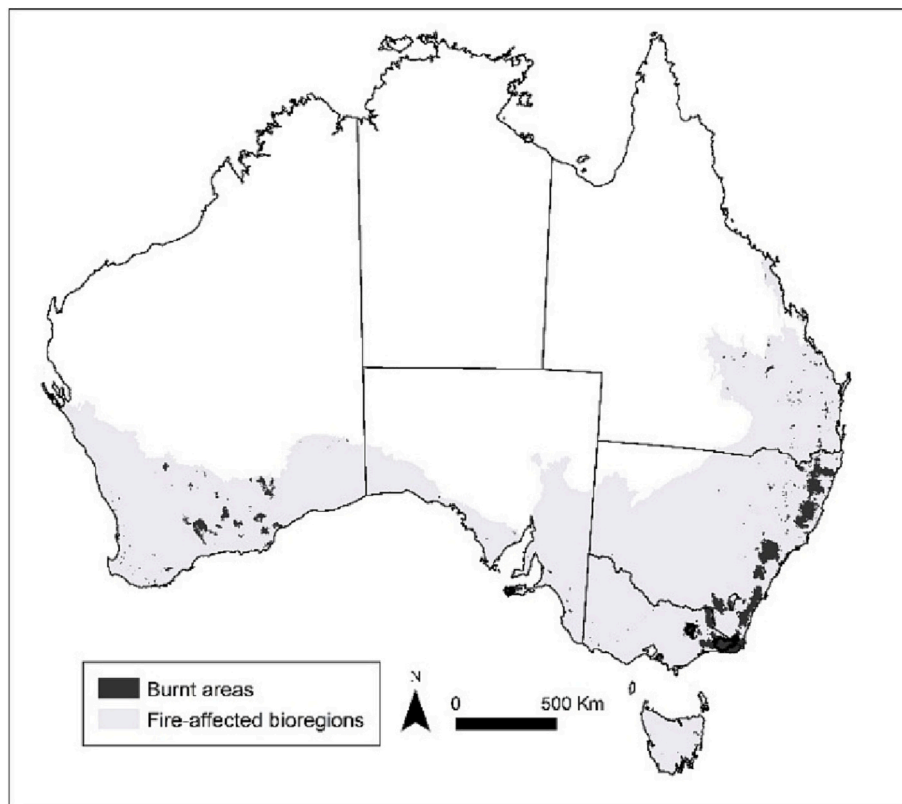


Fig. 1. Map of Australia showing fire-affected bioregions of southern and eastern Australia and the areas burnt in the 2019–20 fire season.

(or all) of these features: substantial ash and sediment in the water body, substantial burned debris in the water body, evidence of bank or tributary erosion, and heavy impacts on water quality. These features lead to increased water temperature, stream pH, nutrients, ash, and sediment loads, which can cause mortality in aquatic fauna (Gomez Isaza et al., 2022).

In animal groups containing more mobile species (mammals and birds in this study)—where individuals could potentially escape the burned area—experts estimated the proportions of the population that were killed by the fire, and that survived the fire but fled the area, so that we could separate emigration from mortality. In our analysis, we focus on fire-related mortality. Our estimates assumed no post-fire management and no subsequent comparable fire over the next 10 years/three generations, because we were interested in population response to fire without any moderating effect of interventions or large-scale disturbances.

All experts were provided with information on past empirical studies of fire response, behavioural, ecological and life history traits and parameters of general extinction risk for each species (see below), and told they were able to draw on whatever information they wished. We note the issue of circularity associated with anchoring by providing information prior to the elicitation, and facilitating group discussions (Burgman, 2015). However, experts were provided with information on a large array of traits, and the purpose of the analysis was to understand whether experts' population estimates were more consistently related to some species traits than others. Experts varied substantially in their responses (Legge et al., 2022a), highlighting that they had different conceptual models underpinning how species respond to fire and management and justifying our exploration of trends in a suite of traits and across taxa.

2.3. Population response, species traits, and parameters of general extinction risk

We aimed to explore the relationship between species' traits and expert estimates of the direct and post-fire mortality, and the capacity of species to recover. We used three response variables relating to population change over different time periods. Direct mortality was the population loss (%) from just before fire to one week after severe fire (temporary emigrants are counted as alive). Post-fire mortality was the population change (%) from one week after severe fire, to one year later. Finally, the capacity to recover was the population change from one year after fire to 10 years/three generations later. Estimates of population changes for each species are available in Table A1.

For each species in the analysis, we assembled information on morphological, behavioural, ecological and life history traits from global and national conservation assessments (IUCN Red List, EPBC Act threatened fauna) and species group compilations (Chapple et al., 2019; Garnett and Baker, 2021; Gillespie et al., 2020; Greer, 2020; Hossain et al., 2018; McCormack, 2012; Woinarski et al., 2014), augmented in a few cases by expert knowledge from the author group for some species-trait combinations, based on their own field experience or on the known traits for closely related species. The traits used in the models of direct mortality, post-fire mortality, and capacity to recover after fire, are shown, with justification, in Table 1. Given the constrained number of species within each animal group, traits with multiple categories were condensed into two or three levels; for example, shelter sites were categorised as offering high (deep burrows, under rocks, in water), medium (hollows in trees or large logs), or low (in or under vegetation, under bark, on surface) protection from fire (Table 1). Trait values and population parameters for each species are available in Table A1.

We also examined the relationships between pre-existing indicators of extinction risk, represented by range size (Extent of Occurrence), population trend (Declining/Not declining), and conservation status (Least Concern; Near threatened + Vulnerable + Data Deficient;

Table 1

The traits examined for their relationship to expert estimates of population changes caused by direct mortality from severe fire, post-fire mortality in the year after severe fire, and the longer-term capacity to recover after severe fire. In the matrix of traits versus the three population responses, grey cells indicate that the trait was not used as it was not relevant (e.g., the ability to flee is relevant for direct mortality, but not post-fire mortality nor capacity to recover). The rationale for trait inclusion is shown in each cell. For categorical traits, the levels into which traits were classed is shown (details of the trait values for each species are in Table A1).

| | Trait | Direct mortality from radiant heat and smoke | Mortality caused by post-fire conditions | Capacity to recover long-term |
|-----------------------------------|--|--|---|---|
| Behavioural and ecological traits | <i>Category levels</i> | | | |
| | Ability to flee (Birds, Mammals, Reptiles) • <i>Poor</i> = slow-moving or sedentary species • <i>Medium</i> = medium-large, fast-moving species • <i>Better</i> = volant mammals, or fast-flying aerial birds | Highly mobile species may be more able to escape a fire front | | |
| | Shelter site protection (Birds, Mammals, Reptiles, Frogs) • <i>High</i> = in rocks, water, deep burrows, fossorial • <i>Medium</i> = hollows in tree or logs • <i>Low</i> = under bark, in/under veg, shallow burrow, on surface | Some shelter sites used routinely by a species offer more protection from a fire front | | |
| | Size (Birds, Mammals, Reptiles, Crayfish) Measured by weight or length, depending on group; relative size categories used when mammals, birds and reptiles combined • <i>Birds</i> : Small=<20g; Medium=20–100g; Large=>100g • <i>Mammals</i> : Small=<35g; Medium=35–5500g; Large=>5500g • <i>Reptiles</i> : Small=<15cm; Medium=15–50cm; Large=>50cm or log wt3 • <i>Frogs and fish</i> : n/a (all small) • <i>Crayfish</i> : Small=<50mm; Large=>50mm | Small animals may be able to shelter more effectively from fire; alternatively larger species may be better able to flee | Small animals may find it easier to find sufficient resources in a post-fire environment | Recovery may be faster for small animals if resources are easier for them to find |
| | Habitat type (Birds, Mammals, Reptiles, Fish, Crayfish) Fire frequency of dominant habitat: • <i>Low</i> = rainforest, riparian, wetland, wet eucalypt forest, alpine heath/grassland; thick riparian vegetation (fish); streamside burrows (crayfish) • <i>Medium</i> = heathland, heathy woodlands • <i>High</i> = eucalypt forest/woodland, grassland; thin riparian vegetation (fish); terrestrial burrows (crayfish) | Species in habitats that burn frequently may be more resilient to fire due to selection pressure. For fish, species reliant on riparian vegetation may be less resilient. Spiny crayfish with burrows that connect to streams may be less resilient than species with terrestrial burrows. | Species in habitats that burn frequently may be more resilient. Fish species reliant on riparian vegetation (for food, shade, or as a sediment filter) may be more affected by fire. Spiny crayfish with burrows that connect to streams may be less resilient than species with terrestrial burrows. | Species in habitats that burn frequently may recover more quickly. In the case of aquatic species, species heavily reliant on riparian vegetation may recover more slowly. Spiny crayfish with burrows that connect to streams may be less resilient than species with terrestrial burrows. |
| | Habitat type (Frogs) Permanency of breeding habitat • <i>Ephemeral ponds</i> (burns frequently) • <i>Permanent streams</i> (does not burn) • <i>Soaks</i> (very rarely burns) | Species breeding in permanent water habitats protected from fire; species breeding in ephemeral habitats may be pre-adapted to shelter from fire; species of soaks may be most vulnerable. | Permanent water habitats least changed by fire; species breeding in ephemeral ponds pre-adapted to cope with change; soaks most changed and these species may be most vulnerable | Permanent water habitats least changed by fire; species breeding in ephemeral ponds pre-adapted to cope with change; soaks most changed and these species may be most vulnerable |
| | Habitat specialisation (Birds, Mammals, Reptiles, Crayfish) • <i>Specialist</i> (and intermediate) • <i>Generalist</i> | | Habitat specialists may not be able to locate suitable habitat in a post-fire environment | Habitat specialists may recover more slowly as they await the return of key resources |
| | Diet (Birds, Mammals, Reptiles) • <i>Plant</i> = herbivore, granivore, frugivore, nectarivore, fungivore • <i>Animal</i> = predator, scavenger, omnivore, insectivore | | Species with plant-based diets may have a higher risk of starvation in the post-fire environment awaiting the return of leaf or seed resources, compared species with animal-based diets, including scavengers | Species with plant-based diets may recover more slowly if these resources take more time to recover |
| | Diet specialisation (Birds, Mammals, Reptiles, Fish) • <i>Specialised</i> (and intermediate) • <i>Generalist</i> | | Diet specialists may have a higher risk of starvation in the post-fire environment if their specialist food resources are scarce | Diet specialists may recover more slowly if their specialist food resources take longer to recover |
| | Home range size (Birds, Mammals) • <i>Small</i> = <10 ha • <i>Large</i> = >10 ha | | Species with large home ranges may find it harder to locate enough resources across their range in the post-fire environment; alternatively, they may be more accustomed to foraging over large areas | Capacity to recover may be harder for species with large area requirements, if they need to maintain very high movement activity for prolonged periods |
| | Susceptibility to introduced predators (Birds, Mammals, Reptiles, Frogs, Crayfish) • <i>Low</i> (and not) • <i>High</i> (and medium) | | Species may become more susceptible to introduced predators in a post-fire environment due to the loss of vegetation cover | Recovery may be slower in species exposed to high predation pressure from introduced species |
| | Susceptibility to introduced herbivores (Mammals, Reptiles, Frogs, Fish) • <i>Low</i> (and not) • <i>High</i> (and medium) | | Species may become more susceptible to introduced herbivores (via resource competition or habitat degradation, including to stream banks) in a post-fire environment. | Recovery may be slower in species exposed to high competition pressure, or to habitat degradation, caused by introduced species |
| Life history traits | Sociality (Birds, Mammals, Reptiles) • <i>Group</i> = living in social groups • <i>Not-group</i> = everything else | | Individuals of social species may face greater mortality in a post-fire environment risk if part of their group has been killed | Sociality may constrain reproductive rates and dispersal rates, thus slowing recovery |
| | Sub-adult dispersal distances (Birds, Mammals, Reptiles, Frogs, Fish) • <i>Short</i> = <10 km • <i>Long</i> = >10 km | | | Species with longer sub-adult dispersal distance may recolonise more easily, and thus populations may recover more quickly |
| | Generation time (Birds, Mammals, Reptiles, Fish, Crayfish); or Age of first reproduction (Frogs) • <i>Years</i> | | | Species with short generation times, or those that begin breeding at an earlier age, may recover more quickly |
| | Reproductive output (young per year: Mammals, Reptiles, Frogs (annual egg complement), Fish, Crayfish respectively; Birds excluded because only 1 species was 'Many') • <i>Few</i> = 1–2; 1–5; <50; <300; <100 • <i>Many</i> = >2; >5; >50; >300; >100 | | | Species with higher reproductive output may recover more quickly |

Endangered + Critically Endangered) of each species, with their capacity to recover between one year and 10 years/three generations post-fire.

2.4. Statistical analysis

We examined the relationships of traits to each of the three variables representing population responses after fire (i.e., direct mortality, post-

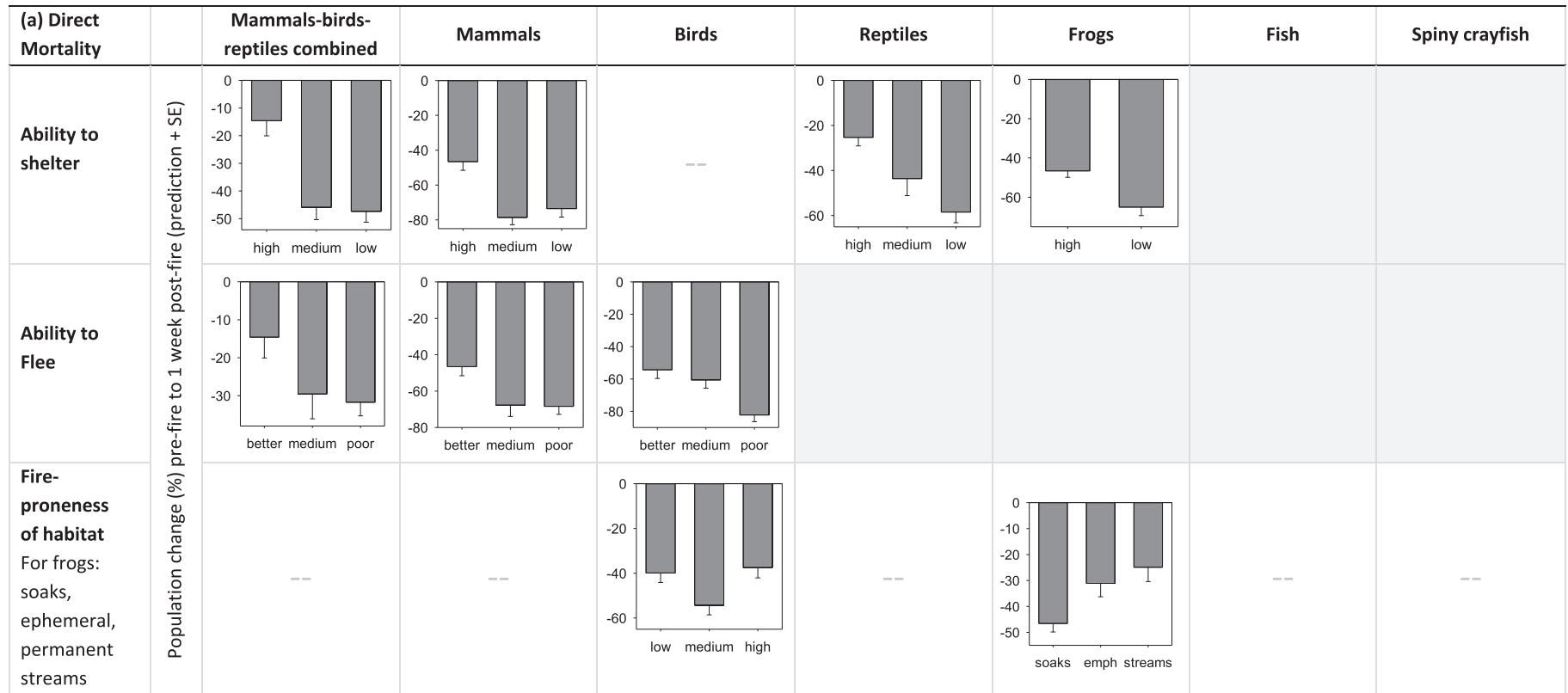


Fig. 2. Traits that influenced estimates of (a) direct mortality from severe fire, (b) mortality in the year after fire, and (c) population recovery between one year and 10 years/three generations after fire, for different animal groups. Graphs show predictions with standard errors for traits included in the best models for each animal group. Traits not included in the best models are denoted as ‘-’; traits not tested in the models have greyed-out cells. Traits not retained in any models for direct mortality: body size. Traits not retained in any models for post-fire mortality: diet specialisation, habitat specialisation, and susceptibility to introduced predators. Traits not retained in any models for population recovery: fire-proneness of habitat.

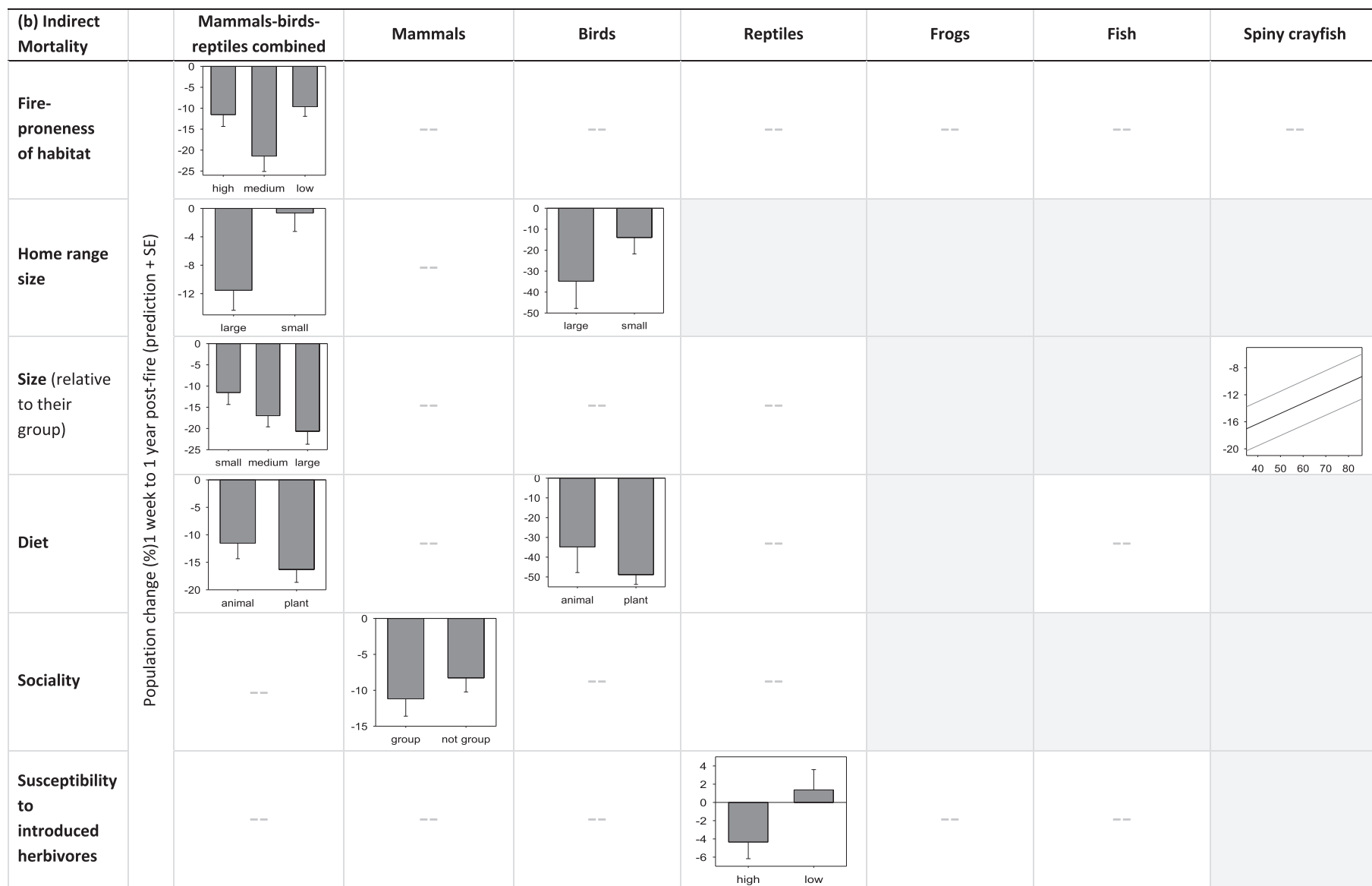


Fig. 2. (continued).

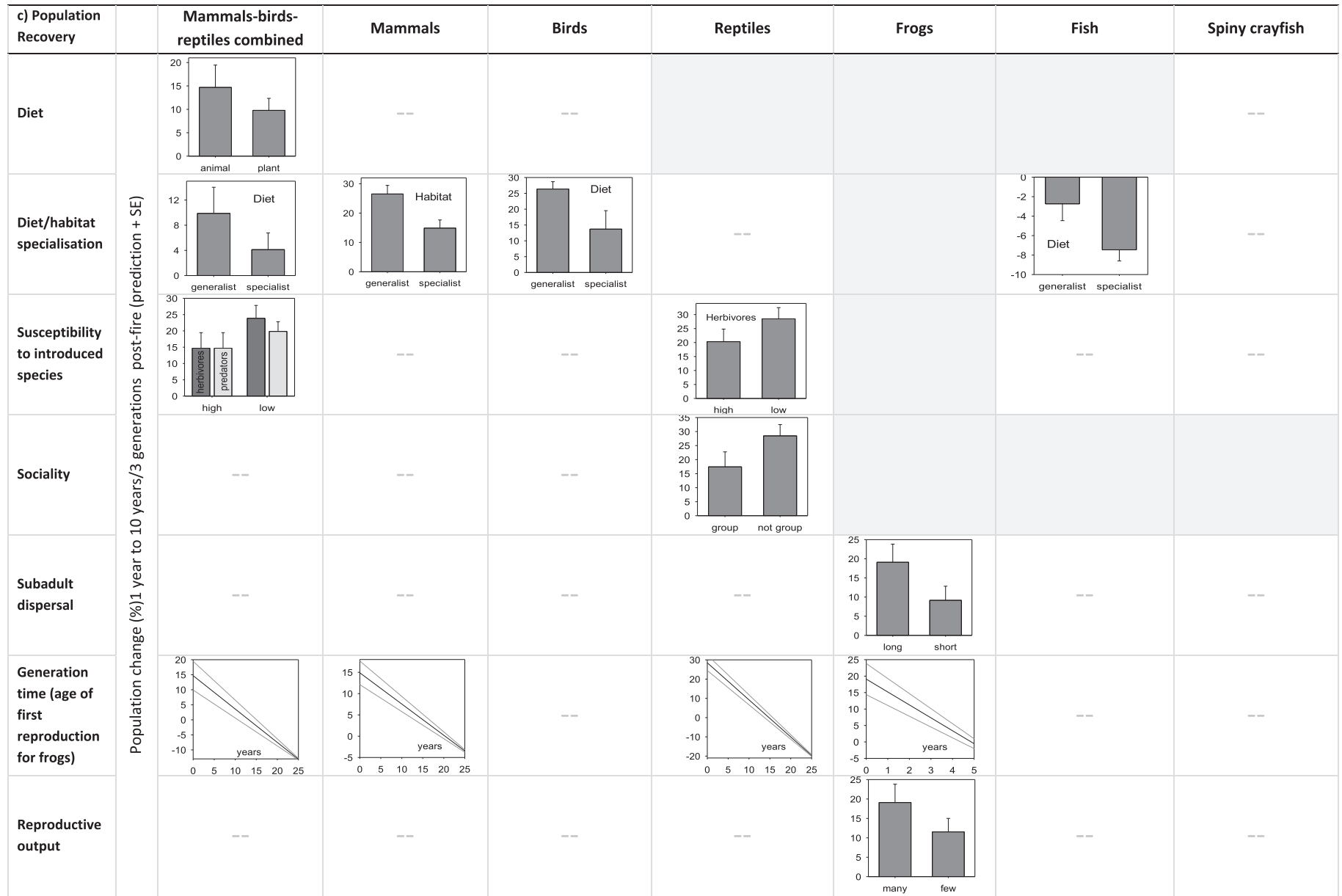


Fig. 2. (continued).

fire mortality, capacity to recover) using linear models in the statistical program R (R Core Team, 2022). Models that assume a Gaussian error structure are robust to many underlying distributions (in terms of type 1 error, power, precision and bias) if low sample size is not combined with extreme outliers, overdispersion or dependency of datapoints (Knief and Forstmeier, 2021). We assessed dispersion and outliers of a normal approximation for the error structure using qq plots, and found balanced dispersion with minimal outliers. We checked for dependence of data among related species by testing the random effect of Family in a mixed model using the lme4 package (Bates et al., 2022). There was no evidence of such dependence (random effects explained 0.1 % of the variance). Consequently, we used the base R:lm function to estimate parameters according to the formula:

$$y_i = \beta_0 + \beta_1 x_{i1} + \dots + \beta_T x_{iT} + \epsilon_i, \text{ with } \epsilon_i \sim N(\mu, \sigma)$$

where y_i is the % population decline parameter for species i , β_0 is the intercept (starting point) and $\beta_1 \dots \beta_T$ are the predicted effects (β) of Traits 1 to T , ϵ_i is the error approximating a normal distribution N with mean μ and variance σ .

Models were compared using the Akaike Information Criterion corrected for small samples (AICc) (Akaike, 1973). The package MuMIN (Barton, 2020) was used for model selection and averaging to estimate parameters that had “substantial support” ($\Delta\text{AICc} \leq 2$) (Burnham and Anderson, 2003). Only traits relevant to the response variable and animal group, and with sufficient data across species, were included in candidate models (e.g., home range size was examined only for mammals and birds, as it is either irrelevant or we lack consistent data for reptiles, frogs, fish, and spiny crayfish; Table 1). Mammals ($n = 34$), birds ($n = 19$) and reptiles ($n = 27$) tended to share trait types (see also Cox et al., 2022), whilst frogs ($n = 21$), fish ($n = 16$) and spiny crayfish ($n = 25$) tended to have group-specific trait types. We therefore ran models for mammals, birds and reptiles combined to achieve a larger sample (i.e., 80 species), as well as running models for each animal group separately. Given the large number of traits relative to the number of species we constrained candidate models for mammals, birds and reptiles combined to include only up to five traits, and models for single animal groups contained only up to three traits.

In a separate model including the entire species set, we explored the relationship of the parameters that relate to general extinction risk (population trend, conservation status, range size) with estimates of the capacity to recover post-fire. Using descriptive graphs and tables, we checked for relationships between traits and population parameters that

could affect interpretation. In the results, we report the R^2 of the best model, the AICc difference from the best to the next best model, and the significance (p -value) of the estimates for each trait that are displayed in graphs (Fig. 2).

3. Results

3.1. Direct mortality from fire

When birds, mammals, and reptiles were considered together, the most parsimonious model of direct mortality from fire included shelter site and ability to flee ($R^2 = 0.535$, next best model $\Delta\text{AICc} = 3.11$) (Fig. 2a). Species that use shelters that are more protected from severe fires (under rocks, in deep holes, or in water) had lower estimates for direct mortality from fire than species typically sheltering under vegetation or bark, or in tree hollows ($\text{Pr} > |T| < 0.0001$). Species that are more able to flee fire (such as highly mobile birds and bats) also had lower estimates for direct mortality than slower moving or less mobile species, such as non-volant small mammals ($\text{Pr} > |T| = 0.0005$).

When each animal group was modelled independently (Fig. 2a), shelter site was a significant predictor of estimated direct mortality in mammals ($R^2 = 0.697$, $\Delta\text{AICc} = 3.11$, $\text{Pr} > |T| < 0.0001$), reptiles ($R^2 = 0.703$, $\Delta\text{AICc} = 1.77$, $\text{Pr} > |T| < 0.0001$), and frogs ($R^2 = 0.530$, $\Delta\text{AICc} = 7.08$, $\text{Pr} > |T| = 0.0005$). The ability to flee was also a significant predictor of estimated direct mortality in mammals ($\text{Pr} > |T| < 0.0001$) and birds ($R^2 = 0.865$, $\Delta\text{AICc} = 5.78$; $\text{Pr} > |T| < 0.0001$). The fire-proneness of habitat was related to estimated direct mortality in birds and frogs. In birds, heathland species (categorised as medium for fire-proneness) had higher mortality estimates than both fire-prone eucalypt forests/woodland and low fire-prone wet forests ($\text{Pr} > |T| = 0.002$). In frogs, species breeding in rainforest soaks (which rarely burn) had the highest estimates for direct mortality, species breeding in permanent streams (which offer most protection from direct fire impacts) had the lowest mortality, and species breeding in ephemeral ponds had intermediate estimates of mortality ($\text{Pr} > |T| < 0.0001$). None of the traits tested in fish or crayfish were related to estimates of direct mortality during fire.

3.2. Post-fire mortality

When data from birds, mammals and reptiles were combined, mortality in the year after severe fire was related to home range, habitat, body size and whether the species' diet is plant- or animal-based ($R^2 =$

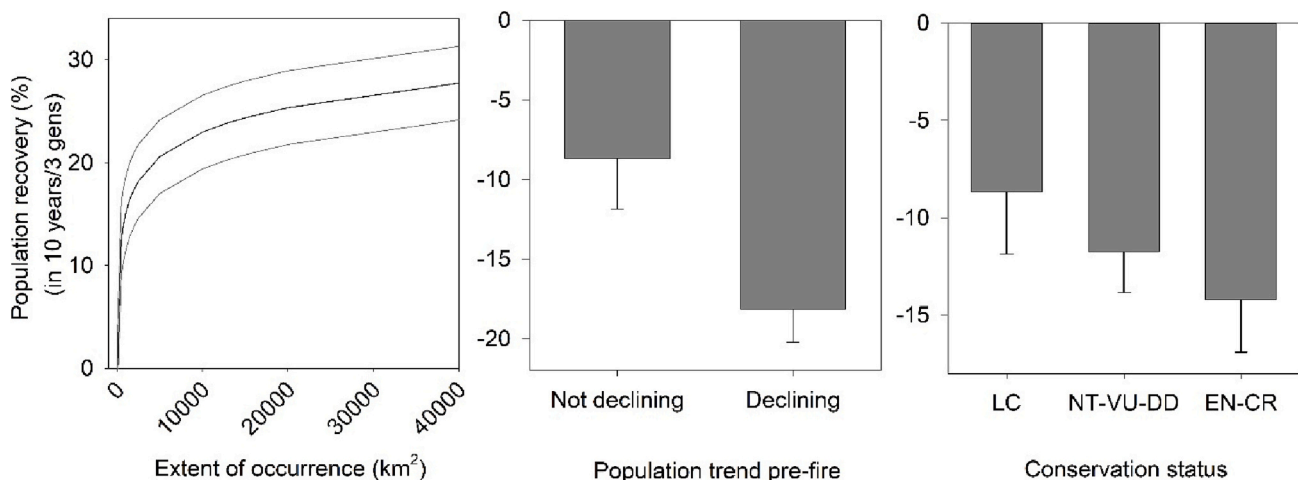


Fig. 3. Parameters relating to general extinction risk that were significant predictors of experts' population recovery estimates after severe fire across all animal groups combined. The population (%) change from one year post-fire to 10 years/three generations after fire was influenced by a species' (a) extent of occupancy (logged); (b) pre-fire population trend; and (c) conservation status (where LC is Least Concern; NT is Near Threatened; VU is Vulnerable; DD is Data Deficient; EN is Endangered; CR is Critically Endangered). Graphs show predictions with standard errors.

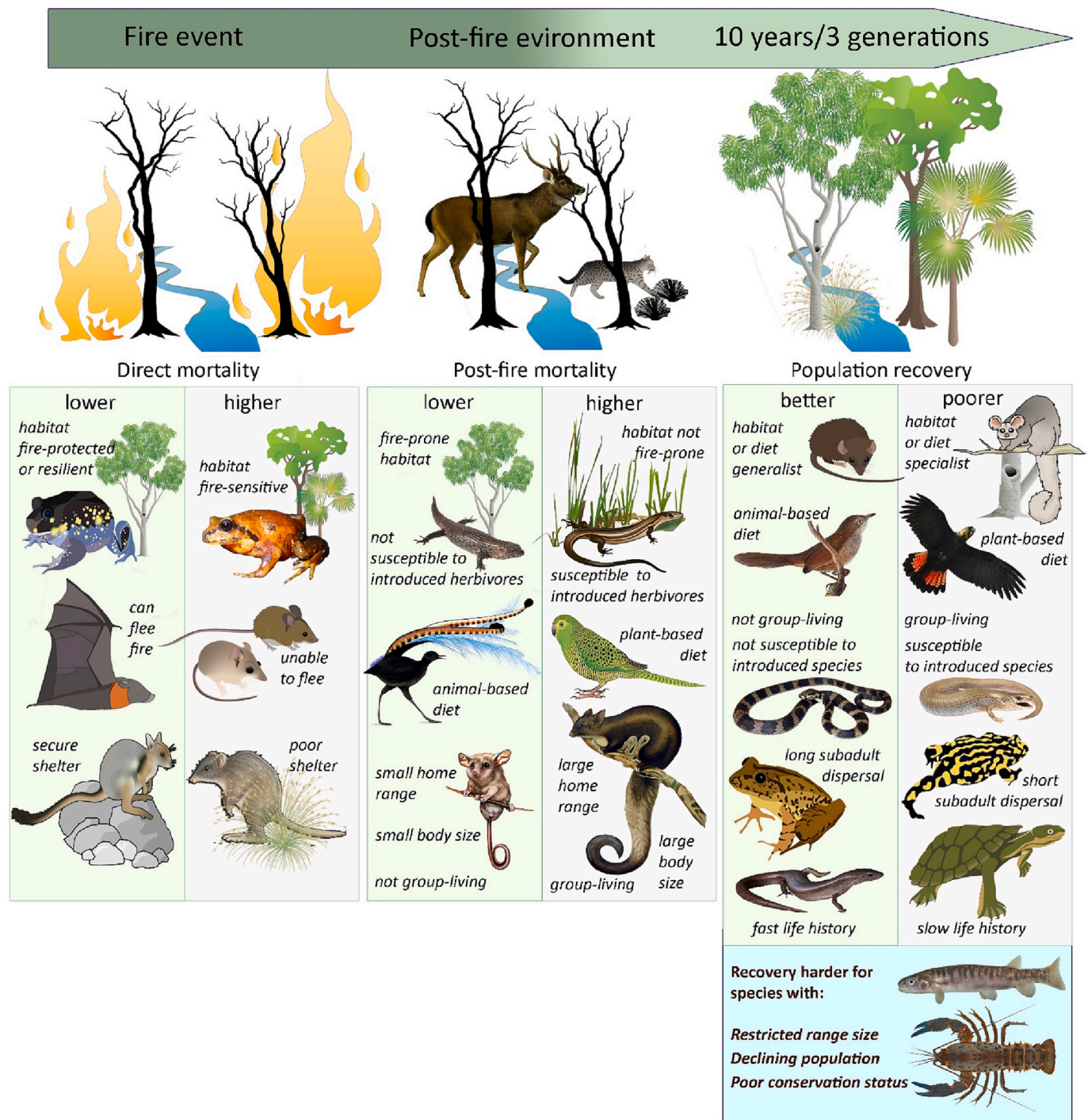


Fig. 4. Summary of the ecological and life history traits, and parameters relating to general extinction risk, that predict expert estimates of direct mortality from fire, mortality in the year after fire (e.g. from lack of resources, impacts from introduced herbivores and predators), and population recovery over 10 years/three generations. For each timeframe and trait, examples of species with contrasting levels of that trait are shown. From top left, species are giant burrowing frog, red and yellow mountain frog; grey-headed flying-fox, Hastings River mouse, Kangaroo Island dunnart; brush-tailed rock-wallaby, long-nosed potoroo; Cunningham skink, glossy swamp skink; superb lyrebird, western ground parrot; eastern pygmy possum, yellow-bellied glider; brown antechinus, greater glider; eastern bristlebird, glossy black-cockatoo; Stephen's banded snake, alpine she-oak skink; giant barred frog, corroboree frog; rainforest cool-skink, Manning River turtle; short-tailed galaxias; spiny crayfish species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.429, $\Delta\text{AICc} = 1.96$; Fig. 2b). Mortality in the year after severe fire was greater for species with large home ranges than species with small home ranges ($\text{Pr} > |\text{T}| < 0.0001$); this may have been influenced by reptiles, which tended to have lower mortality estimates and small home ranges. Heathland species (habitat of medium fire-proneness) also had greater estimated post-fire mortality than species of fire-prone eucalypt forests/

woodland habitats or wet habitats that burn infrequently ($\text{Pr} > |\text{T}| = 0.009$ heath to fire-prone habitats, $\text{Pr} > |\text{T}| = 0.002$ heath to wet-habitats). Populations of large-bodied species (relative to their group) had larger estimated declines than populations of smaller species in the year after fire ($\text{Pr} > |\text{T}| = 0.01$ small to medium, $\text{Pr} > |\text{T}| = 0.002$ small to large). Populations of species with a plant based-diet had greater

estimated declines than did populations of species with an animal-based diet ($\text{Pr} > |\text{T}| = 0.014$).

When each animal group was modelled independently (Fig. 2b), large home range size ($\text{Pr} > |\text{T}| = 0.001$) and a plant-based diet ($\text{Pr} > |\text{T}| = 0.007$) were both strongly related to higher estimated post-fire mortality in birds ($R^2 = 0.903$, $\Delta\text{AICc} = 0.87$). In mammals, social species (group-living) had post-fire mortality estimates that were greater than those for non group-living species ($R^2 = 0.111$, $\Delta\text{AICc} = 1.01$, $\text{Pr} > |\text{T}| = 0.0497$), although the model did not fit the data well. The best model for post-fire mortality in reptiles included susceptibility to introduced herbivore impacts (e.g., trampling, food competition), with susceptible species having higher estimates of post-fire mortality ($R^2 = 0.207$, $\Delta\text{AICc} = 2.54$, $\text{Pr} > |\text{T}| = 0.017$). Body size (occipital carapace length) was an important predictor of estimated post-fire mortality for spiny crayfish, with smaller species having higher mortality estimates ($R^2 = 0.206$, $\Delta\text{AICc} = 2.72$, $\text{Pr} > |\text{T}| = 0.023$). However, only a small amount of the data is explained by body size and body size is strongly related to parameters relating to extinction risk in this group, such as extent of occurrence and reproductive output ($\text{Pr} > |\text{T}| = 0.003$ and $\text{Pr} > |\text{T}| < 0.0001$, respectively), so this relationship may be misleading. None of the traits tested in fish or frogs had a significant effect on estimated post-fire mortality from fire in the first year.

3.3. Capacity to recover after fire

When data from birds, mammals and reptiles were combined, species with diet specialisations had slower estimated population recovery ($R^2 = 0.433$, $\Delta\text{AICc} = 6.82$, $\text{Pr} > |\text{T}| < 0.0001$) (Fig. 2c). Information on diet specialisation was not available for many reptile species, so we also modelled the data without this term, finding that susceptibility to introduced herbivore impacts, generation time, susceptibility to introduced predators and diet (animal- or plant-based) were included in the most parsimonious model ($R^2 = 0.420$, $\Delta\text{AICc} = 0.15$). Species that are susceptible to the impacts of introduced herbivores had lower estimated population recovery than species classed as not susceptible ($\text{Pr} > |\text{T}| = 0.021$). Species with short generation times had greater recovery estimates than species with long generation times ($\text{Pr} > |\text{T}| = 0.0001$). Species with animal-based diets had marginally larger estimates for population recovery over 10 years/three generations than animals with plant-based diets ($\text{Pr} > |\text{T}| = 0.059$). Finally, species that are more susceptible to introduced predators had marginally lower estimates for population recovery ($\text{Pr} > |\text{T}| = 0.086$).

When each animal group was modelled independently (Fig. 2c), population recovery estimates were lower in mammal species with habitat specialisations ($R^2 = 0.438$, $\Delta\text{AICc} = 1.14$, $\text{Pr} > |\text{T}| = 0.0001$) and lower in birds and fish species with diet specialisations ($R^2 = 0.156$, $\Delta\text{AICc} = 0.92$, $\text{Pr} > |\text{T}| = 0.044$ for birds; $R^2 = 0.348$, $\Delta\text{AICc} = 2.41$, $\text{Pr} > |\text{T}| = 0.016$ for fish), although the R^2 values for these models were low. Reptile species that are susceptible to introduced herbivore impacts had lower estimates for population recovery ($R^2 = 0.633$, $\Delta\text{AICc} = 0.75$, $\text{Pr} > |\text{T}| = 0.086$), as did group-living reptile species ($\text{Pr} > |\text{T}| = 0.049$). Life history traits emerged as important across most groups: generation time (or age at first reproduction for frogs) was important in mammals ($\text{Pr} > |\text{T}| = 0.020$), reptiles ($\text{Pr} > |\text{T}| < 0.0001$) and frogs ($R^2 = 0.781$, $\Delta\text{AICc} = 1.66$, $\text{Pr} > |\text{T}| < 0.013$). In addition, frogs with longer sub-adult dispersal distances ($\text{Pr} > |\text{T}| = 0.011$), and higher reproductive output ($\text{Pr} > |\text{T}| = 0.043$) had larger estimated population recovery. No traits were related to population recovery estimates in spiny crayfish.

3.4. Pre-existing extinction risk parameters and population recovery

When all animal groups were combined and pre-existing parameters related to extinction risk were examined, species had poorer population recovery estimates between one year and 10 years/three generations after fire, if they had a small range size ($\text{Pr} > |\text{T}| < 0.001$; Fig. 3a) or were declining before the fire ($\text{Pr} > |\text{T}| < 0.001$; Fig. 3b). There was also

a link with conservation status, with slower recovery in endangered and critically endangered species ($\text{Pr} > |\text{T}| < 0.044$; Fig. 3c) ($R^2 = 0.653$, $\Delta\text{AICc} = 0.12$, next best model $\Delta\text{AICc} = 5.91$).

4. Discussion

Our study highlights that some species traits were consistently related to expert estimates of direct mortality during fire, post-fire mortality, and population recovery following severe fire, for some animal groups (Fig. 4). An animal's ability to flee fire and the type of shelter it uses were related to expert estimates of direct mortality during fire, as was their past exposure to fire, such that species from more fire-prone habitats were generally estimated to have lower direct mortality. Expert estimates of mortality in the months after fire were also related to the fire-proneness of habitat, as well as traits associated with food resources and their acquisition (e.g., diet, home range size and body size), or to threats to these resources (i.e., introduced herbivores). Finally, experts appeared to consider that a population's capacity to recover after fire was related to life history traits (i.e., generation time, age at first reproduction, sub-adult dispersal distance, reproductive output), and traits related to resources (e.g., diet, diet or habitat specialisation, introduced herbivore impacts) were also important predictors of recovery estimates in some animal groups. Population parameters that broadly represent species extinction risk (e.g., population trend, range size, conservation status) were related to expert estimates of population recovery following fire across the animal groups. The experts' estimated population changes tended to relate to traits more often in mammals, birds, reptiles, and frogs than in fish and spiny crayfish. Below, we first consider the interpretational caveats, strengths, and limitations of our analysis, so that the discussion of results that follows is appropriately contextualised.

4.1. Interpretational caveats, strengths, and limitations of the approach

We used estimates for population changes after severe fire that were derived from structured expert elicitation. Empirical data on the association between animal species' traits and vulnerability to fire are limited and taxonomically uneven (Santos et al., 2022b). Structured expert elicitation provides a robust framework to harness expert knowledge to bridge these gaps (Hemming et al., 2018), and is now regularly used to inform policy and management in diverse situations where empirical data are scarce (Camac et al., 2021; Wittmann et al., 2015). In the analysis presented here, using expert elicitation also allowed us to include a larger and broader range of species instead of a small subset with adequate field data. In addition, the approach allows experts to consider the 'average' response of a population at a 'typical' site, thereby sidestepping the site-level variation that can cause populations of the same species to respond in different ways, after different fires, in different places (Keith, 2002; Nimmo et al., 2014; Whelan et al., 2002). Considering the causes of such variation is crucial in site-level management decisions. However, for purposes such as national-scale prioritisations to identify species most vulnerable to fire, or actions most needed after fire, the broader patterns identified in an analysis such as the one presented here (see Section 4.5) are valuable (Gallagher et al., 2021b; Laidlaw et al., 2022).

When estimating population changes for each species, experts relied on their knowledge of species-specific studies reported in the literature and their own field experience to make their judgements. Where empirical data on population responses to fire were lacking, experts generalised based on related species, and likely used species traits to inform their estimations, reinforcing associations between a given trait and fire responses. Our analysis therefore highlights the trait-fire response associations that experts consider are most influential; new empirical data are essential to validate the inferences made here. The existing empirical data mostly come from fires of much smaller scale and lower severity, and are extremely biased towards better-known species

(and taxonomic groups) (Jolly et al., 2022). Post-fire field surveys have increased in taxonomic and geographic scope after the 2019–20 fires, but many of these datasets are still being gathered and analysed (i.e., not yet available), and funding for this work has been short-term (<https://www.dcceew.gov.au/environment/biodiversity/bushfire-recovery/activities-and-outcomes>), meaning information on longer-term recovery will be missing, and comparable data collection after future fire events is not assured.

Our analysis included a large sample of species with diverse behavioural, ecological and life history traits (Table A1). However, there was some sampling bias towards threatened species (72 % of species assessed were threatened) as they are a key focus for conservation action. The range of traits represented in threatened species may differ from the range present in un-threatened species, if these traits also relate to extinction risk more broadly. Although the overall sample was large, the number of species within each taxonomic group was low, especially for some groups (e.g., fish). Thus, relationships between estimated population fire response and some traits may have been missed due to limited statistical power, and conversely, the importance of some traits could be inflated if some taxonomic groups are over-represented. Finally, our study focussed on the relationships between species' traits and the response to severe fire, but the population response will vary with fires of lower severity (Legge et al., 2022a), or with fires of different size and frequency, depending on how the traits specifically influence survival, dispersal, and reproduction (Santos et al., 2022b).

Despite these caveats and limitations, the analysis presented here is valuable because it establishes which traits experts consistently associate with a population response to fire within and across different animal groups; these relationships can and should be tested with empirical data as these become available. Whereas plant ecology has a long history of linking traits to fire responses, the analogous use of traits in animal ecology has progressed much more slowly. Our analysis can help hasten the process of integrating traits into models of animal fire responses. The study also reveals the animal groups where data on fire response and population recovery, and the role of traits in the response and recovery, are especially poor; empirical data from these species (e.g., most fish and invertebrates, many frogs and reptiles) are urgently required. Finally, the analysis highlights that experts associate different types of traits with survival and recovery at different stages after fire, reinforcing that post-emergency management responses need to be flexible to support species during different phases of population decline and recovery.

4.2. Direct mortality from fire

Few studies have measured animal mortality from fire, especially high severity fire, by tracking the fate of individual animals (Jolly et al., 2022). However, fleeing from fire, burrowing into soil and finding non-flammable shelter sites are commonly noted as behavioural responses to fire across terrestrial vertebrates (Álvarez-Ruiz et al., 2021; Geiser et al., 2018; Nimmo et al., 2021; Pausas and Parr, 2018), and studies of the population response to fire often note that the security of the shelter site and the ability to escape the fire front are important determinants of the population loss from fire (Banks et al., 2011; Friend, 1993; Loyn, 1997).

In our analysis, the ability to flee or shelter from fire recurred as important traits that experts associated with their estimates of direct mortality from fires across mammals, birds, reptiles, and frogs. Expert estimates for direct mortality were related to both shelter and ability to flee in mammals; for example, koalas are slow moving and lack secure shelters, making them highly vulnerable to severe fire (Law et al., 2022b). Shelter site was not as important for estimates of direct mortality in birds, probably because they mostly rely on fleeing fire. Conversely, none of the assessed reptile species were deemed able to flee fires. For species relying on in situ fire shelters, such as frogs and small-bodied reptiles, the timing of fire will be important for those species that undertake seasonal habitat shifts. For example, the broad-headed snake (*Hoplocephalus bungaroides*) seeks refuge in rock crevices in winter, but

shelters in tree hollows in summer, making them more vulnerable to summer fires (Webb et al., 2021). Fish and most spiny crayfish species are largely protected from direct fire-related mortality by nature of their aquatic habitat, so the ability to flee or shelter is not relevant in these groups.

Across mammals, birds and reptiles, species associated with habitats that experience fire more frequently were estimated to experience less mortality than species using habitats that burn rarely, possibly because their exposure to fire over evolutionary time has selected for abilities to recognise cues of impending fire and respond appropriately (Nimmo et al., 2021; Pausas and Parr, 2018). In frogs, species that breed in rainforest soak areas that burn extremely rarely (Murphy et al., 2013) had the greatest direct mortality estimates. A recent review of fire impacts on frogs found that species occurring in habitat types that rarely burn tend to shelter under vegetation or in leaf litter, whereas species that occur in habitats that burn often, such as eucalypt woodlands, have more secure shelters such as deep burrows or the stream itself (Mahony et al., 2022). This relationship occurs because frogs depend on moist microclimates for survival: species inhabiting drier, more flammable habitats are adapted to use shelter sites that protect them from hot, dry environments, and until recently these sites were also likely to offer greater protection from fire (Mahony et al., 2022; Mahony et al., 2023). Heathland birds had higher estimates for direct mortality; although heathland was ranked as medium for fire-proneness, when fire does occur the heathland vegetation is more completely consumed than the vegetation of taller forested habitats, possibly amplifying impacts in the judgment of experts (Barton et al., 2014; Burbidge et al., 2018; Keith, 2002; Loyn, 1997).

4.3. Mortality in the post-fire environment

For terrestrial animals that survive a fire event, the post-fire environment presents challenges such as reduced shelter and food resources (and potentially greater competition for those resources), increased predation risk, increased impacts from herbivory and disease (Doherty et al., 2022; Hradsky, 2020; Legge et al., 2023; Pausas and Parr, 2018). In our analysis, traits associated with food resources were most commonly related to variation in estimated population changes in the year after fire. For example, across mammals, birds and reptiles combined, expert estimates of population loss were greater in species with large home ranges. Species with large home ranges may be unable to survive on the resources available from small unburnt refuges within a fire footprint, and unable to expand their range sufficiently to compensate. Similarly, expert estimates of mortality after fire across mammals, birds and reptiles combined were higher in larger-bodied species, which require more food resources to survive than smaller-bodied species. Some smaller-bodied species of mammals, such as some dasyurids, also have adaptations to enter torpor after fire, reducing their energy demands and resource needs; an adaptation that could also reduce predation risk (Geiser et al., 2018). Mammal, bird, and reptile species with a plant-based diet had higher expert estimates for post-fire mortality than those with animal-based diets. After severe fire, digestible plant material may be absent or extremely scarce for a period, but species with an animal-based diet may be able to survive by changing their foraging behaviour, scavenging, switching prey temporarily, or taking advantage of increased visibility of prey (Dickman and Happpold, 2022; Friend, 1993; Geiser et al., 2018; Kelly et al., 2010).

Across mammals, birds, and reptiles combined, expert estimates of post-fire mortality were greater for heathland species than species of other habitat types. Severe fires typically remove the majority of heathland vegetation, with structural recovery in some instances slow compared to other habitats (Barton et al., 2014; Loyn, 1997). Many heathland animal species depend on flowers, fruit, or on insect pollinators (that are scarce until flowers re-appear) which may take years to become available again after fire (e.g. Chalmandrier et al., 2013; Denmore and Clingan, 2019). Thus, food resources may be depleted, and

habitat complexity reduced, potentially increasing predation risks, with longer-lasting impacts in this habitat. Our analysis also indicated that experts estimate slightly greater post-fire mortality in social-living mammals; this could occur if the loss of group members compromises the ability of the survivors to access food and shelter resources.

Our results are consistent with recent empirical data on changes in bird, mammal, and frog populations before and after the 2019–20 Australian megafires that found greater population losses in species occupying habitats that normally experience very low fire frequency, in species with plant-based diets and insectivores, and in species with diet specialisations (Heard et al., 2021; Law et al., 2022a; Lee et al., 2021; Lee et al., 2022).

In aquatic species, major post-fire challenges include degradation of water quality by toxins released by burning, eutrophication and anoxia from excessive organic deposition and runoff (Emelko et al., 2016; Harper et al., 2019), and instream habitat degradation and smothering by fire-related sediment influxes following post-fire rainfall (Legge et al., 2022a; Ward et al., 2022). Our analysis did not reveal traits in aquatic species that were consistently related to expert estimates of post-fire mortality. Smaller-bodied spiny crayfish had higher post-fire mortality estimates, but body size is strongly related to other attributes in this group, such as geographic range and reproductive output, which is related to increased vulnerability more broadly (Hossain et al., 2018). In addition, a recent study showed that fish and spiny crayfish species of high-elevation streams, which tend to have small geographic ranges, have lower physiological tolerances to water quality changes than species occurring at lower, or at a range of, elevations (Cramp et al., 2021).

4.4. Long-term recovery

Ecological traits were associated with expert estimates of population recovery variously across the animal groups studied. Experts estimated that recovery was slower in species with diet or habitat specialisations (birds (diet), fish, mammals (habitat)). For example, the bird taxa in our analysis with specialist diets forage on seeds and flowers of plant species that take years to recruit after fire. The two subspecies of glossy black-cockatoo (*Calyptorhynchus lathami lathami* and *C. l. halmaturinus*) feed on seeds of *Allocasuarina* spp. that take ten years to recruit and seed after fire (Berris et al., 2022). Similarly, flower resources for regent honey-eaters *Anthochaera phrygia* also take years to recover after fire (Crates et al., 2022). In mammals, birds and reptiles, experts estimated that recovery would be faster for species with animal-based diets than species with plant-based diets. Although plant biomass is lost in fire, the impact is temporary and post-fire vegetative growth could even offer additional nutritional resources compared to pre-fire conditions due to the increased palatability (Archibald et al., 2019). However, because of our small within-group sample, we combined herbivores with granivores, frugivores, nectarivores and fungivores, which probably blurred interesting differences between those diet categories. Mammal, bird and especially reptile species that are considered susceptible to the impacts of introduced herbivores such as deer and horses were also given slower population recovery estimates by experts, again suggesting that experts consider that habitat condition plays a central role in recovery. In addition, in disturbed habitats other threats such as introduced predators could be worsened.

Life history traits were also significantly related to expert estimates of post-fire population recovery, with species that have slower life histories (i.e., longer-lived or later age of first reproduction, and slower reproductive output) having expert estimates of slower post-fire population recovery across mammals, birds, reptiles, and frogs. This is consistent with the well-documented pattern that long-lived, slow-breeding species face greater extinction risk, as these traits limit the capacity to compensate for increased mortality (Chichorro et al., 2019; Hanna and Cardillo, 2013). Generation time tended to have a stronger effect than fecundity in our analyses, but these two traits tend to be closely related (Chichorro et al., 2019). Other reproductive strategies

not included in our analysis—such as flexibility in breeding behaviour—may also be important. For example, silky mice (*Pseudomys apodemoides*) can rapidly increase in abundance after fire partly due to promiscuous mating systems and female-biased sex allocation (Cockburn, 1981). Experts estimated faster population recovery for frog species with longer sub-adult dispersal distances, suggesting that experts consider the ability to recolonise burned areas by immigration is important.

Threatened and declining species are likely experiencing impacts of several threats, all of which could worsen the impact of fire and make recovery after any disturbance, including fire, more challenging. We found that across all animal groups, experts estimated the poorest recovery trajectories for species with restricted ranges, a declining population and lower conservation status before the fire. These parameters are characteristics associated with risk of decline and extinction under a broad range of scenarios (Cazalis et al., 2022), and the result suggests that small, isolated populations are most susceptible to severe fires.

4.5. Implications for future prioritisation and conservation response

Linking species' traits to fire response for animals remains in its infancy relative to the existence of well-established paradigms for plants (Blaum et al., 2011; Driscoll et al., 2012; Keith, 2012; Westgate et al., 2012). Although there is likely to be much idiosyncrasy among species, our analysis reveals relationships between key animal traits and expert estimates of the direct mortality, post-fire mortality, and longer-term population recovery after fire that could be used to help prioritise species for management intervention after future fires, in the absence of empirical data on these relationships. Given our sample sizes for individual animal groups were modest, we have more confidence in the analyses that combined animal groups, or where traits emerged as important across more than one group. We therefore base our inference about the species that may be most vulnerable to future fire regimes driven by the changing climate, on the collective picture that emerges across the analyses and animal taxon groups.

In our analysis, experts appeared to base their estimates of population response to fire on combinations of traits that came into play at varying times after severe fire. Experts considered that relatively immobile species that use flammable shelter sites suffer the greatest population loss during severe fire, and that species occurring within habitats that are not fire-prone were likely to be worst affected. In the post-fire environment, species with greater or more specialised food requirements—such as species with large home ranges, specialised diets, or diets featuring plant-based resources that take time to recover—were estimated to experience greater mortality. Similarly, species in habitats that rarely burn (such as rainforest), or that burn at high severity (such as heathland), were estimated by experts to suffer ongoing declines after fire, possibly from a combination of food shortage and increased predation. Slower population recovery after fire was predicted for species that rely on habitat and food resources that are slow to re-establish, such as large tree hollows or seeds of slow-maturing plants, or slow to recover, such as stream beds covered in post-fire sediment (Densmore and Clingan, 2019; Haslem et al., 2011; Whiterod et al., 2023). Recovery was estimated to be more challenging for long-lived species with slow life histories, and species with limited sub-adult dispersal. In addition, population recovery was estimated to be especially fragile in species with inherent vulnerabilities such as small range sizes and declining populations. These relationships should be tested with additional empirical data.

Our analysis suggests that experts do not find ecological and life history traits useful for estimating fire impacts in fish and spiny crayfish. This could be because fires affect aquatic systems most profoundly via post-fire sedimentation events, and variation in traits such as diet and fecundity likely have less bearing on the extent of mortality from such events. Instead, parameters like range size may be more critical for determining the longer-term outcome of fire-related sedimentation

events, with restricted range species being highly at risk of extirpation. Alternatively, our knowledge of the relationships between traits and fire response is poorer in these groups. Empirical data are needed to disentangle the contributions of traits and parameters such as range size to species vulnerabilities in aquatic fauna.

The general patterns that emerged from our investigation of how animal traits relate to expert estimates of population loss and recovery after severe fire suggest a range of management strategies to reduce the impacts of future catastrophic fire events. Direct mortality from fire in fire-susceptible species could be lessened by reducing the size, spread rate, and severity of fire, so that less mobile animals have more chance to escape the fire front or persist in small unburnt refuges within the fire footprint, and so that shelter sites that offer moderate levels of protection (such as hollow logs and trees, shallow burrows) are not burnt or overheated. Reducing the size and severity of fires should also mean that more of the critical food and shelter resources are retained in the post-fire environment. In the post-fire environment, reducing pressure from introduced predators and herbivores may be especially important when vegetative cover is slow to re-establish. Protecting unburnt refuges from further fire, or other major disturbances such as salvage logging (Thorn et al., 2018) will support recolonisation of recovering burnt areas. Finally, sustained conservation management for years after fire may be needed for species with slower life histories and with pre-existing vulnerabilities such as restricted ranges and declining populations.

Collectively, this study identifies the critical need to prepare for future megafires with long-term ecological studies and population monitoring across a wide range of species, to inform our understanding of how species' traits will interact with changing environmental conditions and multiplying threats to influence animal survival and population responses.

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CRediT authorship contribution statement

Conceptualisation, Investigation, Writing review and editing: all authors. Methodology: ME, SL, STG, ML, DGN, LR, BCS, NSW, JCZW, HG. Formal analysis, Data curation, Visualisation: ME, SL, HG. Writing – original draft: ME, SL, CJJ, RG, LR. Supervision and funding acquisition: SL, STG, ML, DGN, LR, BCS, NSW, JCZW. Project administration: SL.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. This work was funded by the Australian Government's National Environmental Science Program through the Threatened Species Recovery Hub.

Data availability

Data available as supplementary material

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