

1 **Title: Beyond inappropriate fire regimes: a synthesis of fire-driven declines of threatened mammals**
2 **in Australia**

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20 **Short-running title:** Fire-driven declines of threatened mammals

21 **Type of article:** Review

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28 **ABSTRACT**

29 Fire can promote biodiversity but changing patterns of fire threaten species worldwide. While scientific
30 literature often describes ‘inappropriate fire regimes’ as a significant threat to biodiversity, less attention has
31 been paid to the characteristics that make a fire regime inappropriate. We go beyond this generic description
32 and synthesize how inappropriate fire regimes contribute to declines of animal populations, using threatened
33 mammals as a case study. We developed a demographic framework for classifying mechanisms by which
34 fire regimes cause population decline, and applied the framework in a systematic review to identify fire
35 characteristics and interacting threats associated with population declines in Australian threatened land
36 mammals (n=99). Inappropriate fire regimes threaten 88% of Australian threatened land mammals. Our
37 review indicates that intense, large, and frequent fires are the primary cause of fire-related population
38 declines, particularly through their influence on survival rates. However, several species are threatened by a
39 lack of fire and there is considerable uncertainty in the evidence base for fire-related declines. Climate
40 change and predation are documented or predicted to interact with fire to exacerbate mammalian declines.
41 This demographic framework will help target conservation actions globally and would be enhanced by
42 empirical studies of animal survival, dispersal, and reproduction.

43 **Keywords:** biodiversity, demographic processes, dispersal, extinction, fire frequency, movement,
44 reproduction, survival, wildfire.

45

46 **1 INTRODUCTION**

47 Fire is an important ecological process that can promote biodiversity (Jones & Tingley, 2021). Yet human
48 actions are transforming fire activity and at least 4,400 species worldwide face threats associated with
49 changing patterns of fire (Kelly et al., 2020). This includes 16% of all mammalian species classified as
50 threatened with extinction by the *International Union for Conservation of Nature* (IUCN) (Kelly et al., 2020).
51 While numerous research papers and policy documents describe ‘inappropriate fire regimes’ as a major
52 threat to biodiversity, the specific characteristics that make a fire regime inappropriate receive less attention.
53 Understanding the mechanisms through which inappropriate fire regimes cause population declines is critical
54 for addressing biodiversity loss (McLauchlan et al., 2020) and is likely to create opportunities for more
55 effective conservation actions (Nicol et al., 2019).

56 Four main factors make identifying the characteristics of inappropriate fire regimes difficult. First, fire regimes
57 involve multiple components, including fire frequency, intensity and season (Gill, 1975), and their spatial
58 dimensions. Second, population declines associated with fire regimes can be caused by a range of
59 mechanisms that directly and indirectly influence animal survival, colonization, and reproduction (Whelan et
60 al., 2002). Third, fire regimes and their impacts on populations may be a consequence of interactions
61 between fire and other processes such as climate change (Hale et al., 2016), grazing (Probert et al., 2019),
62 habitat fragmentation (Driscoll et al., 2021) and predation (Hradsky, 2020). Finally, the diverse life-history
63 characteristics and habitat requirements among biotic communities lead to a variety of responses to fire
64 regimes within (Senior et al., 2021) and between (Jones & Tingley, 2021) ecosystems.

65 Demographic approaches offer a way forward. Considering the effects of fire on key processes that shape
66 populations – survival, reproduction and movement (Begon & Townsend, 2020) – provides a way to identify
67 the mechanisms that underlie fire-driven population declines and forecast population changes. For example,
68 Miller et al. (2019) developed a demographic approach to synthesize fire seasonality effects on plant
69 populations and explore traits that make species vulnerable to decline. To date, demographic approaches for
70 application in fire-prone ecosystems have primarily been developed to explore the ecology of plants (Keith,
71 1996; Miller et al., 2019). While important steps have been taken to develop conceptual demographic
72 frameworks for animals (Whelan et al., 2002), they have not been applied systematically to assess threats
73 related to inappropriate fire regimes at a continental scale.

74 Our overarching aim is to go beyond inappropriate fire regimes as a generic descriptor of threatening
75 processes by applying a demographic approach to synthesize *how* fire regimes influence populations of
76 threatened animals. We do this using a case study of Australian land mammals, a distinctive and mostly
77 endemic group of species that continues to suffer high rates of population decline (Geyle et al., 2018;
78 Woinarski et al., 2015). More than 300 terrestrial mammalian species are native to Australia, but their recent
79 and ongoing declines are exceptionally high with over 10% of species extinct since European colonization
80 (Woinarski et al., 2015). A further 99 taxa (species, subspecies, or populations) are listed as threatened with
81 extinction under the Australian Government's key environmental legislation, the *Environment Protection and*
82 *Biodiversity Conservation Act 1999 (EPBC Act)*. Disentangling the causes of Australian mammalian declines
83 has proved difficult, but a consensus is emerging that multiple drivers are in play, including modification of
84 fire regimes, predation by introduced mammals, and habitat loss and fragmentation (Doherty et al., 2015;
85 Fisher et al., 2014; Johnson, 2006; McKenzie et al., 2007).

86 We asked three main questions: 1) What are the underlying mechanisms by which inappropriate fire regimes
87 cause population decline?, 2) Which characteristics of fire regimes, on their own or via interactions with other
88 processes, are associated with population decline of Australia's threatened mammals?, and 3) Are threats
89 posed by inappropriate fire regimes associated with particular mammalian taxonomic groups or ecosystems?

90 We expect this demographic approach will be useful for assessments of other fauna in fire-prone
91 ecosystems across the globe, as well for developing policies and actions to conserve Australia's distinctive
92 mammalian fauna.

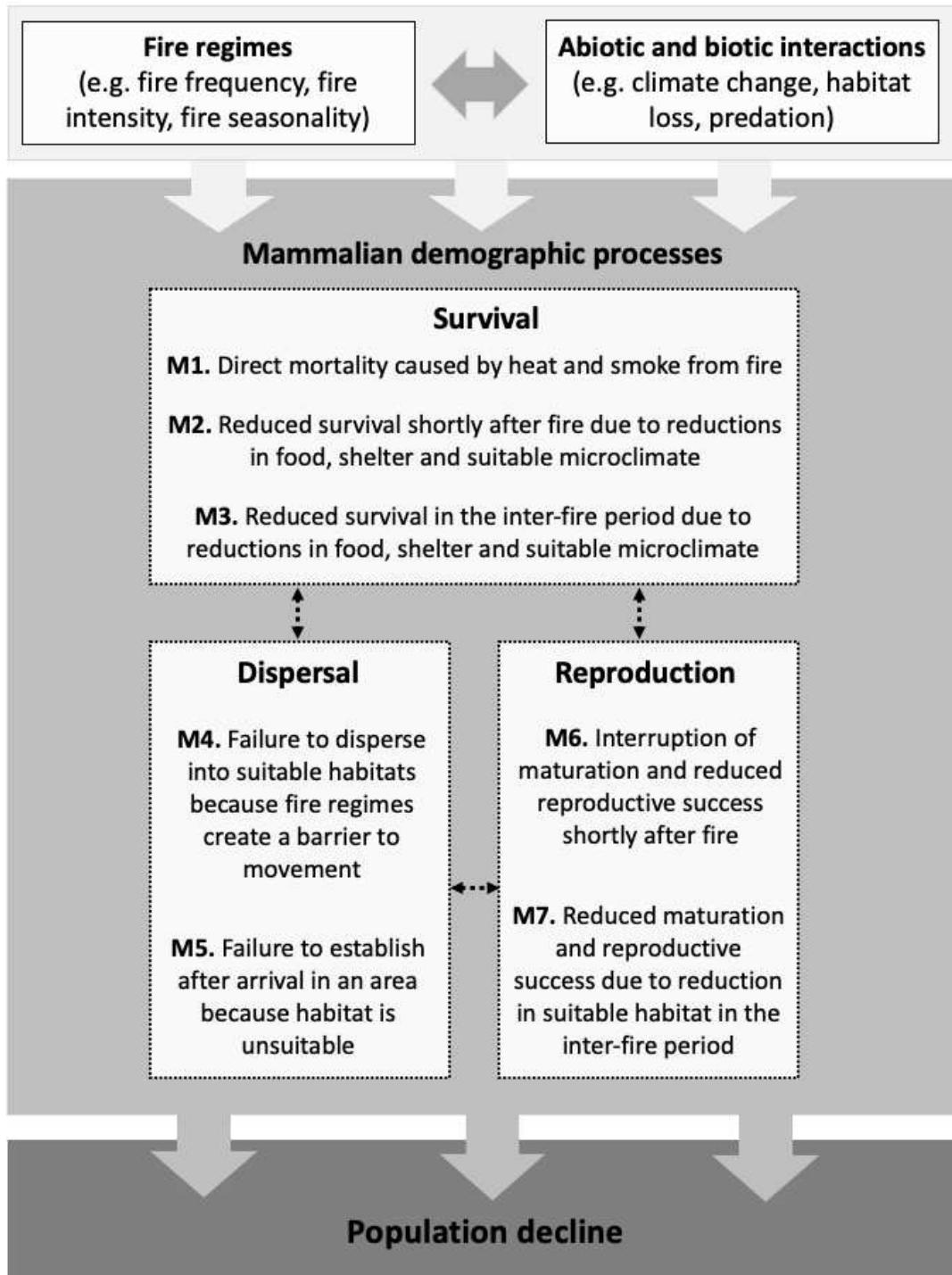
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94 **2 DEMOGRAPHIC APPROACH AND SYSTEMATIC REVIEW**

95 In summary, we identified three groups of demographic processes that are fundamental to changes in
96 population size – survival (deaths), reproduction (births) and movement into and out of a population
97 (immigration and emigration) (Begon & Townsend, 2020) – and seven mechanisms by which fire may impact
98 these processes (Figure 1). We then systematically reviewed conservation assessments (two
99 comprehensive sources) and primary literature on Australian terrestrial mammals listed as threatened under
100 the *EPBC Act*, and applied the demographic framework to identify which characteristics of fire regimes, and
101 interacting abiotic and biotic processes, are associated with the seven fire-driven mechanisms of population
102 decline. The demographic framework is informed by Keith (1996), who identified mechanisms of fire-related

103 population declines of plants, and Whelan et al. (2002), who emphasized critical life-cycle processes that
104 relate to fire-driven population changes.

105 We define inappropriate fire regimes as patterns of fire that may plausibly cause one or more taxa to decline.
106 In many cases, we expect that inappropriate fire regimes result from modified patterns of fire. But it is
107 possible that historical fire regimes applied under new environmental conditions could also cause
108 mammalian populations to decline.



109

110 **FIGURE 1. A demographic framework for assessing fire-driven mechanisms of population decline**
111 **and extinction.** Fire regimes and their interactions with other abiotic and biotic processes can negatively
112 impact three demographic processes – survival, movement, and reproduction – via seven primary

113 mechanisms (M1 – M7), leading to mammalian population decline and extinction. Arrows between the
114 dashed boxes represent relationships between demographic processes and, in turn, these processes
115 influence population change. A population may decline if fire reduces one or more of these demographic
116 processes, and extinction occurs when the number of individuals declines to zero. The timing of each
117 mechanism in relation to fire events or recurrent fire varies among species, and populations may decline
118 because of one mechanism or a combination of mechanisms depending on a species' life-history and habitat
119 preferences.

120 **2.1 Description of fire-driven mechanisms of mammalian decline and extinction**

121 ***Survival: Mechanisms 1, 2 and 3***

122 Fire can cause population decline by reducing the survival of individual mammals in three main ways. First,
123 fire can directly kill animals through exposure to high temperatures or smoke (Mechanism 1) (e.g. Koprowski
124 et al., 2006; Silveira, 1999). Second, animals may survive a fire event but experience reduced rates of
125 survival in the days, weeks and months after fire due to the depletion of food or shelter resources in recently
126 burned areas (Mechanism 2) (Morris et al., 2011). Resource depletion can result from a single fire event or
127 the cumulative impacts of multiple fires (Pardon et al., 2003), and operate at local (e.g. 1-10s ha), landscape
128 (e.g. 1,000s-10,000s ha) and regional (e.g. 100,000s ha) scales. Third, fire-related reductions in survival can
129 occur over years and decades if there is a decline in the quality of habitat and crucial resources following
130 long intervals without fire (M3) (Arthur et al., 2012; Sherman & Runge, 2002). For example, some species
131 benefit from early or mid-successional habitats that may become unsuitable after long periods without fire
132 (Hayward et al., 2005). This could be a result of the senescence of food plants or adverse changes in
133 vegetation structure and shelter availability.

134 The spatial dimensions of fire regimes can mediate Mechanisms 1, 2 and 3, through the effects of internal
135 fire refuges (Shaw et al., 2001; Robinson et al., 2013) and habitat complementation (Kelly et al., 2017).
136 Interactions with other processes, including predation, can also influence mammalian survival after fire
137 (Hradsky, 2020). Here we group mechanisms of decline based primarily on demographic processes, and
138 later link fire-regime characteristics and interacting threats to these mechanisms through systematic review.

139 ***Movement: Mechanisms 4 and 5***

140 Movement within and between habitat patches of differing fire histories is a key determinant of animal
141 distribution and abundance in fire-prone ecosystems (Nimmo et al., 2019). Colonization is a particularly
142 important process involving the movement of animals, and includes dispersal to and establishment in new
143 locations (or in locations where animals were previously present, called recolonization) (Hanski, 1999). We
144 identify two mechanisms of decline relating to colonization and recolonization: failure to disperse into suitable
145 habitats because fire regimes create a barrier to movement (Mechanism 4) and failure to establish after
146 arrival in an area because habitat is unsuitable (Mechanism 5). Failure to disperse into suitable habitats
147 (Mechanism 4) may be mediated by fire regimes that change the connectivity of habitats (Banks et al.,
148 2013). A barrier to movement could be plausibly created by recently burned vegetation (Banks et al., 2015)
149 or long unburned vegetation (Gavin et al., 1999; Pereoglou et al., 2013), depending on the species' life-
150 history and habitat requirements. Failure to disperse can result in population decline due to reductions in
151 population size or gene flow (Sherman & Runge, 2002).

152 If dispersing animals arrive in a given area, colonization may still fail if they are unable to establish
153 (Mechanism 5). Similar to barriers to dispersal, establishment limitation due to lack of resources could
154 plausibly occur in recently burned areas or long unburned areas, depending on the species' habitat
155 requirements (Woinarski et al., 2005).

156 ***Reproduction: Mechanisms 6 and 7***

157 Successful reproduction by surviving individuals or dispersing colonists is essential for the recovery of
158 populations after fire events and the persistence of populations under recurrent fire (Whelan et al., 2002). In
159 the short-term, fire can directly reduce reproductive success by interrupting the recruitment of mature
160 individuals into the breeding population, delaying breeding by already mature individuals or reducing the
161 availability of food or nesting resources needed for successful reproduction (Mechanism 6) (Griffiths & Brook,
162 2015). This is more likely if fire occurs during the breeding season (Morris et al., 2011) or when individuals
163 are at vulnerable life stages (e.g. juvenile) (Laurenson, 1994).

164 Maturation and reproductive success can also decrease if habitat suitability declines in the inter-fire period,
165 i.e., when there are long intervals without fire (Mechanism 7). Reduced maturation and reproductive success
166 may occur if the extent or carrying capacity of suitable habitat decreases in response to long-term fire
167 exclusion (Sherman & Runge, 2002).

168 **2.2 Threatened species data and assessment of fire-related threats**

169 We conducted a systematic review of the 99 Australian terrestrial mammalian taxa (including species,
170 subspecies, and distinct populations) currently listed as Critically Endangered, Endangered and Vulnerable
171 under the *EBPC Act* and applied our demographic framework.

172 First, we identified whether each taxon was considered at risk of fire-related threats in two comprehensive
173 sources: the Australian Government Species Profile and Threats Database (hereafter 'SPRAT';
174 <https://www.environment.gov.au/cgi-bin/sprat/public/sprat.pl>) and The Action Plan for Australian Mammals
175 2012 (hereafter 'Action Plan'; Woinarski et al., 2014). These sources use several terms to describe fire-
176 related threats including "inappropriate fire regimes", "wildfire", "change in fire regimes", "modified fire
177 regimes" and "habitat change due to altered fire regimes".

178 Second, for each taxon considered at risk from a fire-related threat, we systematically reviewed two
179 comprehensive sources and the primary literature. This included: (i) the SPRAT and related documentation
180 (Conservation Advice, Listing Advice, Recovery Plan); (ii) taxon profiles in the Action Plan; (iii) primary
181 literature cited in the SPRAT and Action Plan that underpinned the inclusion of fire as a threat and
182 interactions with other processes (n = 164 papers); and (iv) additional primary literature (published 2010-
183 2020) identified through systematic search in the Web of Science (n = 39). Recent primary literature was
184 identified after harvesting key references from the SPRAT and Action Plan, and included searching the
185 scientific name and common names of each taxon in Web of Science along with the terms *fire OR *burn*
186 (see Supporting Information for details on all references analyzed in the systematic review).

187 Third, we used the information from all those sources to apply our demographic framework and identify the
188 fire-driven mechanisms of decline, the associated fire-regime characteristics, and the processes that were

189 considered to interact with fire. We considered variations in five fire-regime characteristics that could lead to
190 mammalian population decline via ‘inappropriate’ fire regimes: 1 - *fire frequency* (high or low) – the number
191 of fires in a given period; 2 - *fire intensity and severity* (high or low) – energy released from a fire (intensity)
192 and its impact on plant biomass (severity); 3 - *fire patchiness* (uniform or patchy) – the configuration of post-
193 fire landscapes including burns that are more uniform (i.e. coarse-scale patches of the same type) or patchy
194 (i.e. fine-scale patches that are interspersed); 4 - *fire seasonality* (altered season) – consistently earlier or
195 later peak flammability or longer periods of high flammability; and 5 - *fire size and amount* (large or small) –
196 the size of fire events and the total amount of area burned by one or more fires. We then searched for
197 evidence of links between the fire-regime characteristics and the seven mechanisms of decline described in
198 our demographic framework.

199 We also recorded eight ecological processes that could interact with fire to affect mammals: 1 - climate and
200 extreme weather (including linked changes in weather and climate such as pre- or post-fire drought and
201 extreme fire weather); 2 - disease that directly influences animal populations; 3 - disease that influences
202 habitat (i.e. vegetation dieback); 4 - grazing activity (including associated impacts of trampling and browsing
203 by native or introduced herbivores); 5 - habitat loss and fragmentation; 6 - predation by introduced animals
204 (e.g. cats, domestic dogs, foxes); 7 - predation by native animals (e.g. birds, dingoes, snakes); and 8 - weed
205 invasion.

206 The quality of scientific evidence varies (Pullin & Knight, 2003) and preliminary analyses indicated that levels
207 of evidence of fire-related threats differed among taxa and sources. Therefore, we established a method for
208 classifying levels of evidence supporting reported fire-related threats and mechanisms of decline, and
209 applied it systematically throughout the analysis (Table 1). We considered four types of empirical studies
210 (manipulative experiments, longitudinal study, natural experiment and simulation modelling; following Driscoll
211 et al., 2010a), as well as descriptive work, opinions of experts and anecdotal evidence, when assessing
212 strength of evidence (see Figure S1 of Supporting Information for additional details). We acknowledge that
213 deep knowledge of fire and mammals is held by local and Indigenous peoples across Australia. A limitation
214 of the present review is that it is restricted to scientific literature and policy documents.

215 To enable synthesis across taxa, we followed Van Dyck and Strahan’s (2008) groupings of species with
216 similar taxonomy and ecology. We also recorded the vegetation types that each taxon inhabits, following
217 vegetation classifications described by Keith (2017), according to information available in the primary
218 literature, SPRAT and Action Plan (Tables S1 and S2).

219 **TABLE 1.** Levels of scientific evidence for classifying fire-driven mechanisms of decline, associated fire-
220 regime characteristics and interacting ecological processes.

Level	Strength of evidence	Criteria
1	Strong evidence based on at least one empirical study of the taxon; with appropriate replication and sample size within the study.	<ul style="list-style-type: none">- At least one manipulative experiment has a control, OR- At least one longitudinal study has ≥ 10 samples (e.g. individual animals recorded, genetic samples collected from unique individuals), OR- At least one natural experiment has ≥ 10 sites, OR- At least one simulation study that incorporates data from an appropriate manipulative experiment, longitudinal data set or natural experiment- No evidence of additional problems relating to replication, sample size or statistical power identified by the authors of the present study.
2	Moderate evidence based on at least one empirical study of the taxon; with low within-study replication, low sample size or other limitations of experimental design.	<ul style="list-style-type: none">- At least one manipulative experiment but with no controls, OR- At least one longitudinal study has < 10 samples (e.g. individual animals recorded, genetic samples collected from unique individuals), OR- At least one natural experiment has < 10 sites, OR- At least one simulation modelling study.
3	Opinions of experts based on ecological reasoning or anecdotal evidence.	<ul style="list-style-type: none">- Opinions based on qualitative field evidence, descriptive work, empirical evidence from congeners, or reports of expert committees.

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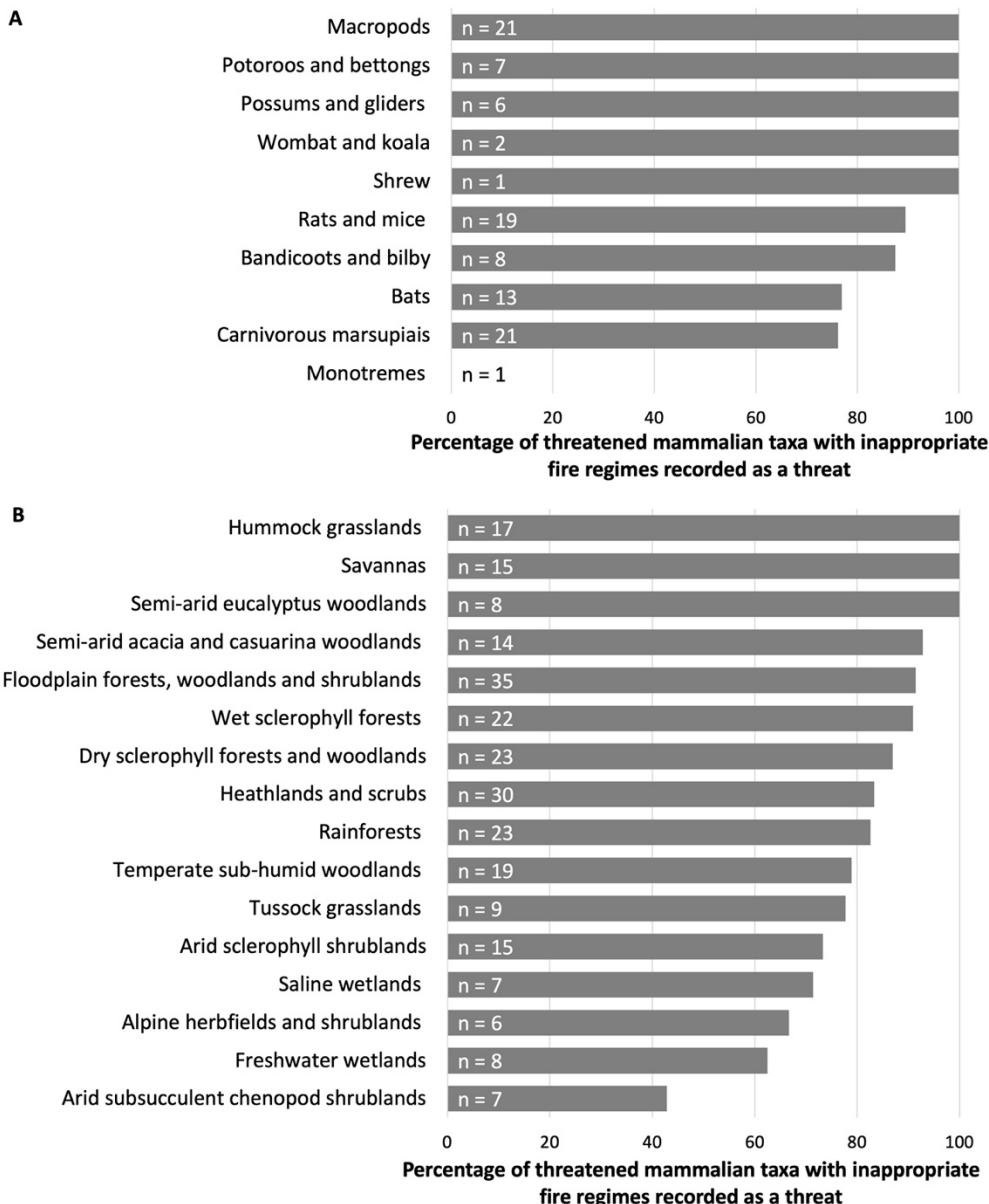
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223 **3 RESULTS**

224 **3.1 Overview**

225 Inappropriate fire regimes are listed as a threat to 88% ($n = 87$) of Australia's terrestrial mammalian taxa
226 listed as Critically Endangered, Endangered and Vulnerable under the *EPBC Act*. For 40% of those taxa ($n =$
227 35) the descriptions of fire-related threats were supported by empirical data (level of evidence 1 = 15%; $n =$
228 13; level of evidence 2 = 25%; $n = 22$) (Table S3). For 60% ($n = 52$) of the threatened terrestrial mammals
229 considered to be at risk due to inappropriate fire regimes, the identification of fire-related threats was
230 underpinned by opinions of experts based on ecological reasoning or anecdotal evidence (level of evidence
231 3).

232 A wide range of taxa have fire listed as a threat (Figure 2A). Moreover, there was evidence that fire threatens
233 mammals inhabiting diverse vegetation types across Australia. For example, fire is a recorded threat for all
234 threatened mammals that occur in hummock grasslands, savannas, and semi-arid eucalyptus woodlands
235 (Figure 2B).



236

237 **FIGURE 2.** Percentage of Australian terrestrial mammalian taxa listed as Vulnerable, Endangered or
238 Critically Endangered with inappropriate fire regimes recorded as a threat according to (A) taxonomic group
239 and (B) vegetation type. n is the total number of threatened mammalian taxa listed as threatened in each
240 taxonomic group (A) and vegetation type (B). Taxa may occur in more than one vegetation type.

241 **3.2 Mechanisms of decline and fire-regime characteristics**

242 The most frequently reported mechanism of fire-related decline was reduced survival shortly after fire due to
243 reductions in food and shelter (M2; Figure 3A), which was identified for 94% (n = 82) of taxa threatened by
244 inappropriate fire regimes. M2 was supported by a higher strength of evidence compared to other
245 mechanisms: level of evidence 1 = 4% of cases identified as M2 (n = 3 taxa); level 2 = 28% (n = 23 taxa);
246 and level 3 = 68% (n = 56 taxa). M2 was closely related to fire regimes with high fire frequency, high fire
247 intensity and severity, and large fire size and amount (Figure 4).

248 Direct mortality caused by heat and smoke from fire (M1) was the second most frequent mechanism linked
249 with mammal declines, affecting 29% (n = 25) of taxa threatened by fire (Figure 3A). The strength of

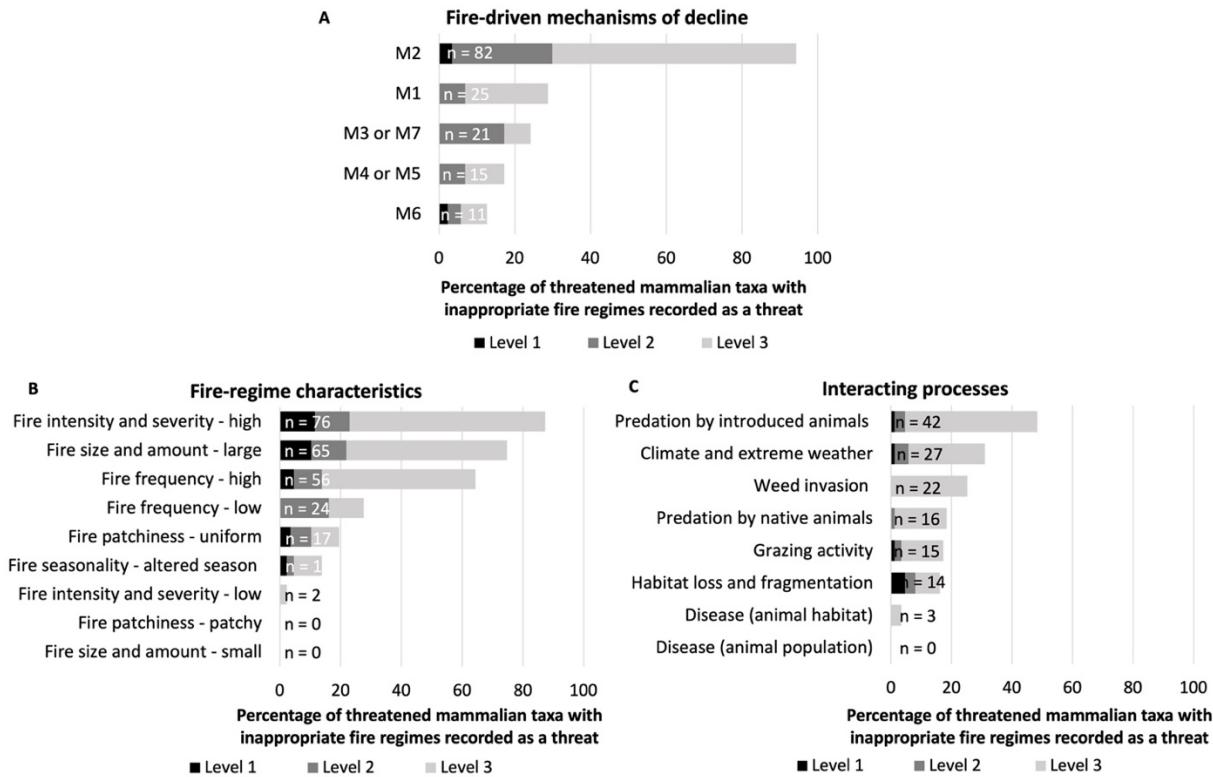
250 evidence for M1 was low, with no cases based on level of evidence 1 (n = 0), 24% of cases (n = 6) based on
251 level of evidence 2 and 76% (n = 19) on level 3. Direct mortality was primarily associated with high fire
252 intensity and severity, and large fire size and amount (Figure 4).

253 For most taxa, reduced survival and reproduction following habitat change in the inter-fire period (M3 and
254 M7, respectively) could not be separated based on available information. When combined, either M3 or M7
255 were inferred for 24% (n = 21) of the taxa threatened by fire (Figure 3A), with no instances of level of
256 evidence 1 (n = 0). However, 71% (n = 15) of M3 and M7 were supported by level 2, and 29% (n = 6) by
257 level 3. M3 and M7 were primarily linked to low fire frequency (Figure 4).

258 Reduced colonization rates in fire-prone ecosystems could not be pinpointed to being caused by either
259 dispersal limitation (M4) or establishment limitation (M5) based on work to date. In total, M4 or M5 were
260 inferred for 17% (n = 15) of taxa threatened by fire (Figure 3A), with no instances of level of evidence 1 (n =
261 0), 40% of the cases (n = 6) supported by level of evidence 2 and 60% (n = 9) by level of evidence 3. M4 and
262 M5 were chiefly associated with large fire size (Figure 4).

263 Finally, interruption of maturation and reduced reproductive success shortly after fire (M6) was reported for
264 only 13% of taxa (n = 11). 18% of the cases were classified as strong evidence (level 1; n = 2), 27% as
265 moderate evidence (level 2; n = 3) and 55% based on expert opinion (level 3; n = 6). This mechanism was
266 not clearly associated with a single fire-regime attribute (Figure 4).

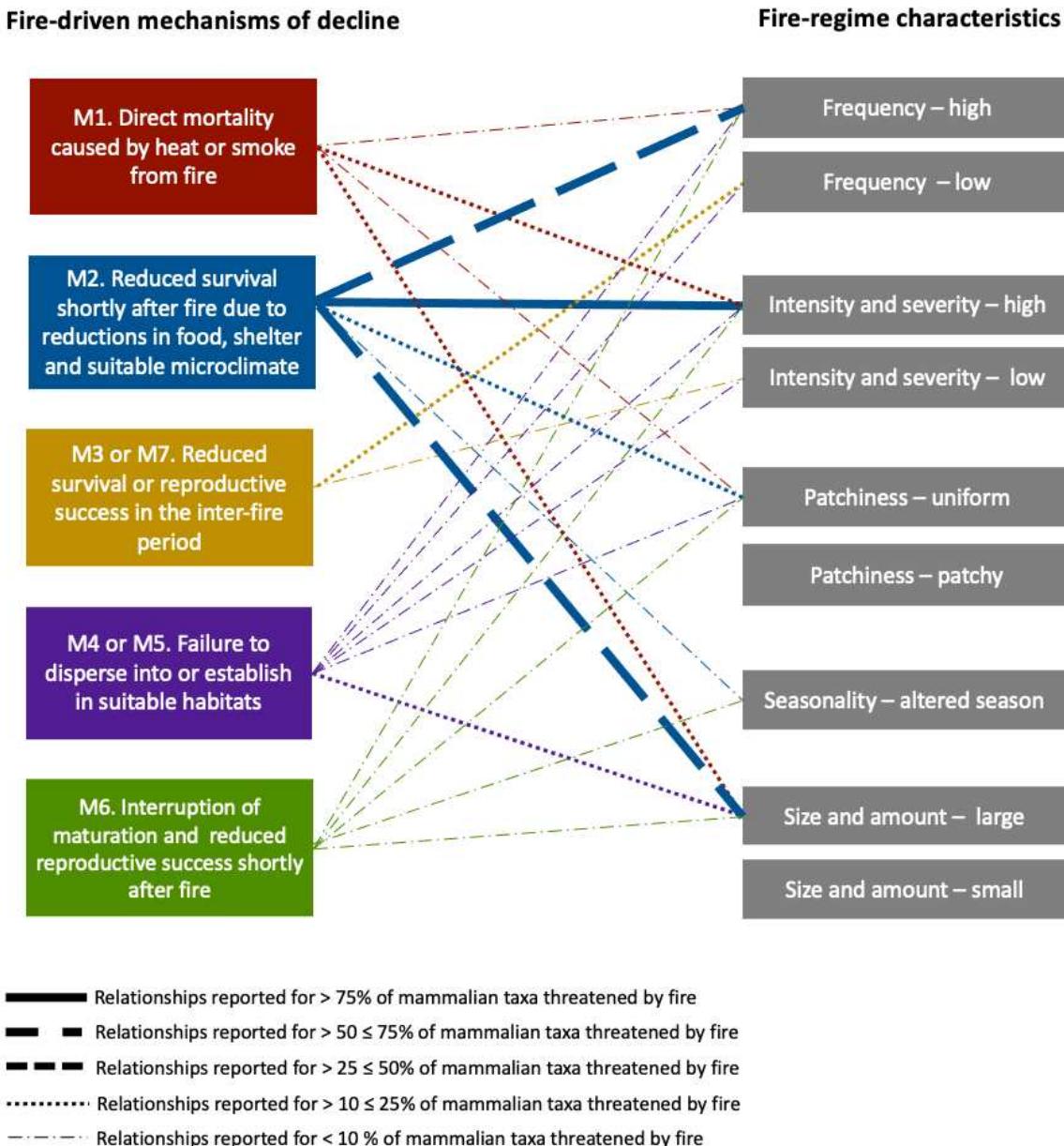
267 Across all seven mechanisms of decline, inappropriate fire regimes were mostly characterized by high fire
268 intensity and severity (87% of mammalian taxa threatened by fire; n = 76) (Figure 3B), large fire size and
269 amount (75%; n = 65) and high fire frequency (64%; n = 56) (Figure 3B). Although measures associated with
270 increased fire activity threaten more species, low fire frequency was a purported cause of inappropriate fire
271 regimes for 28% (n = 24) of threatened mammals (Figure 3B). Patchy fires and small fires and were not
272 reported as a threat to any taxa (Figure 3B) or associated with any of the seven main mechanisms of decline
273 (Figure 4). For some taxa, the role of fire in causing population decline has been tested and, for the fire
274 characteristics explored, considered negligible. That was the case for low fire intensity and severity (n = 6
275 taxa); patchy fires (n = 7), and small fire size and amount (n = 8). The southern brown bandicoot (*Isoodon*
276 *obesulus obesulus*) is an example of species for which the effects of these fire regime characteristics on
277 populations were considered negligible (Supporting Information).



278

279 **FIGURE 3.** Percentage of Australian terrestrial mammalian taxa listed as Vulnerable, Endangered or
280 Critically Endangered with inappropriate fire regimes recorded as a threat summarized by (A) Fire-driven
281 mechanisms of decline; (B) Fire-regime characteristics; and (C) Interacting ecological processes. n is the
282 total number of mammalian taxa threatened by fire for which the mechanisms, fire-regime characteristics or
283 interacting processes were identified through systematic review. A given taxon can be affected by more than
284 one mechanism, fire-regime characteristic or interacting process. Levels of evidence are shown by shading:
285 Level 1 = Strong empirical evidence, Level 2 = Moderate empirical evidence, Level 3 = expert opinion and
286 ecological reasoning (see Table 1 for descriptions of levels).

287



288

289 **FIGURE 4.** Relationships between fire-driven mechanisms of population decline (left) and fire-regime
290 characteristics (right) identified for Australian terrestrial mammalian taxa listed as Vulnerable, Endangered or
291 Critically Endangered with inappropriate fire regimes recorded as a threat. The percentage of taxa for which
292 relationships between the mechanisms of decline and fire regime characteristics have been reported are
293 indicated by different line types. Data are pooled across all levels of evidence.

294 **3.3 Processes that interact with fire regimes**

295 Seven of eight ecological processes were documented or predicted to interact with fire to exacerbate rates of
296 mammalian decline. An association between fire and predation by introduced animals was the most
297 frequently specified interaction, attributed to 48% (n = 42) of threatened mammalian taxa, followed by
298 interactions with climate and extreme weather (25%; n = 27) and weed invasion (25%; n = 27) together.
299 Levels of evidence were low for all interactions (Figure 3C).

300 **4 DISCUSSION**

301 Development and application of a demographic framework at a continental scale showed that inappropriate
302 fire regimes for Australian mammals primarily comprise high-intensity and severe fire, large fire size and
303 amount, and high-frequency fire. Each of these fire characteristics contribute to mammal declines primarily
304 through reduced rates of survival. However, we also identified taxa for which inappropriate fire regimes
305 include a frequency of fire that is too low. That is, some threatened mammalian populations are not getting
306 enough of the 'right' kind of fire. Furthermore, systematic assessment of the levels of evidence underpinning
307 fire-related declines indicated a lack of strong empirical evidence on relationships between demographic
308 processes and fire-regime characteristics. The identification of these important knowledge gaps will help
309 guide new work on animal survival, movement and dispersal in ecosystems that experience fire.

310 **4.1 Defining inappropriate fire regimes**

311 Our review of conservation assessments and primary literature showed that for most threatened Australian
312 mammals, inappropriate fire regimes include high intensity and severity fires, large fire sizes and amount
313 burned, and high-frequency fires. Intense and severe fires generate high levels of heat and smoke and
314 increase the chances of animal mortality (Jolly et al., 2022). For example, declines of koala (*Phascolarctos*
315 *cinereus*) populations have been documented following severe wildfires in forests of south-eastern Australia
316 (Matthews et al., 2016; Phillips et al., 2021), and are probably linked to direct mortality caused by fires and
317 reduced survival shortly after fires. Direct mortality caused by fire has been inferred for a range of mammals,
318 including the western ringtail possum (*Pseudocheirus occidentalis*), red-tailed phascogale (*Phascogale*
319 *calura*) and numbat (*Myrmecobius fasciatus*); however robust studies that directly measure mortality of
320 threatened mammals during high intensity wildfires are rare (see Figure 3A and Supporting Information).
321 Studies of experimental planned burns show that mortality of mammals can be low when fires are patchy
322 and low intensity (e.g. Flanagan-Moodie et al., 2018; Vernes, 2000).

323 High intensity and severity fires can make habitat unsuitable for a range of threatened mammals by depleting
324 critical food and shelter resources. For example, the abundance of greater gliders (*Petaurus volans*) declined
325 after intense wildfires removed hollow-bearing trees and incinerated foliage, leading to scarcity of food and
326 cover (Chia et al., 2015; Lindenmayer et al., 2013). Larger wildfires typically result in greater area burnt at
327 high intensity and severity (Collins et al., 2021) and can cause widespread reductions in habitat and its
328 connectivity. For instance, a population of swamp antechinus (*Antechinus minimus maritimus*) was
329 considered extinct after a large (>40,000 ha) and severe wildfire in coastal heathlands of south-eastern
330 Australia, with no recolonization detected in the subsequent 15 years (Wilson et al., 2018). Frequent fire can
331 also be harmful: regular high severity fires in savannas of northern Australia have contributed to declines in
332 populations of northern quolls (*Dasyurus hallucatus*) (Andersen, 2021; Griffiths & Brook, 2015), particularly
333 through impacts on reproduction (Griffiths & Brook, 2015). While these and other examples (Supporting
334 Information) are useful in examining characteristics that make a fire regime inappropriate, our results indicate
335 that the impacts of fire regimes on survival, colonization, and reproduction are not documented by empirical
336 evidence for many taxa (Figure 3A; Supporting Information). Further empirical studies will be crucial to
337 reducing this uncertainty.

338 Why does a high frequency of intense and large fires pose a threat to many taxa that have evolved in
339 Australian landscapes subject to recurrent fire? We propose the answer lies in concurrent changes to both
340 mammalian populations and fire regimes. Several threatening processes, on their own and in combination,
341 have reduced the size of mammalian populations, including habitat loss and fragmentation, and predation by
342 introduced species (Doherty et al., 2015; Fisher et al., 2014; Woinarski et al., 2014). Smaller populations of
343 mammals, which are restricted to increasingly narrow geographic areas, are then more likely to be harmed
344 by intense and large fires. Examples of threatened mammals with small population sizes that are threatened
345 by large and intense fires include Leadbeater's possum (*Gymnobelideus leadbeateri*), Gilbert's potoroo
346 (*Potorous gilbertii*) and heath mouse (*Pseudomys shortridgei*). At the same time, there is increasing
347 evidence that fire regimes are changing. For example, mega-fires in 2019-2020 burnt more than seven
348 million ha across eastern Australia (Bowman et al., 2021). These fires were unprecedented in terms of their
349 size and amount of area burned at high severity (Collins et al., 2021) and impacted the habitat of numerous
350 threatened animals (Ward et al., 2020). Even ecosystems that have not historically experienced severe fires
351 are experiencing increased activity of this type of fire e.g. the Gondwanan Rainforests of eastern Australia
352 that are home to threatened mammals such as Hastings River mouse (*Pseudomys oralis*) and brush-tailed
353 rock-wallaby (*Petrogale penicillata*) (Godfree et al., 2021).

354 Interestingly, a low frequency of fire was also an important characteristic of inappropriate fire regimes,
355 documented or predicted to negatively affect 24 threatened mammal taxa. For example, reduced fire
356 frequency leads to an alteration in vegetation structure in part of the northern bettong's (*Bettongia tropica*)
357 geographic range in northern Australia. In the absence of fire for long periods, rainforest-pioneering species
358 dominate the understory, and litter cover accumulates, resulting in a reduction of important food resources
359 for this potoroid (Abell et al., 2006; Bateman & Johnson, 2011). This can lead to population declines due low
360 adult survival (M3) and low recruitment rates (M7). While the scarcity of early-successional habitats or fire-
361 induced resources because of low frequency (or exclusion) of fire has been demonstrated to adversely affect
362 the abundance of several mammals, including some species of macropods (Hayward et al., 2007), rodents
363 (Davies et al., 2018) and arboreal marsupials (Trouvé et al., 2019), there is scant demographic information
364 available to identify mechanisms of decline.

365 **4.2 The biogeography of fire-related declines**

366 Mammals are threatened by fire in a range of Australian ecosystems, from the arid interior of the continent to
367 the coast and oceanic islands. Our systematic review indicates that no single taxonomic group is clearly at
368 higher risk of extinction through inappropriate fire regimes; rather, extant threatened mammals are at risk
369 from inappropriate fire regimes across the board: more than 75% of threatened species in each taxonomic
370 group with more than one species are considered threatened by fire (Figure 2A). This result is consistent
371 with risk assessments presented in the Action Plan for Australian Mammals, one source of data in the
372 present review, which indicate that a wide range of threatened mammals, from different taxonomic groups
373 and ecosystems, are at high risk of extinction from inappropriate fire regimes (Woinarski et al., 2014).

374 The combination of frequent, high severity and large fires have been documented to cause declines of
375 mammalian populations in diverse ecosystems of Australia, including tropical savannas (Lawes et al., 2015),
376 arid grasslands (Letnic & Dickman, 2006) and temperate forests (Lindenmayer et al., 2012). While less
377 common, negative effects of reduced fire activity were also demonstrated for species inhabiting a range of

378 different ecosystems, such as woodlands in north-eastern Australia (Jackson et al., 2020) and hummock
379 grasslands in central Australia (Southgate & Carthew, 2006).

380 Nevertheless, our analyses point to some differences in how fire regimes threaten mammal populations in
381 different regions. For example, the negative influence of altered fire season on mammal populations was
382 more frequently documented in Australian tropical savannas. In these ecosystems, late-dry-season fires tend
383 to be more intense and severe than early-dry-season fires. The timing and intensity of late-dry-season fires
384 can affect reproduction of species such as northern quolls, which have a synchronous annual breeding cycle
385 (Begg et al., 1981; Griffiths & Brook, 2015). There have been few studies on changes in fire seasonality in
386 temperate areas and how they shape mammalian populations, and we encourage further empirical research
387 on this topic. Another way forward would be to combine expert opinion and mathematical modelling to
388 quantify the probability that changes in fire season, and other characteristics of fire regimes on their own or
389 in combination, will drive species to extinction (Hayward, 2009).

390 **4.3 Interactions between fire and other processes**

391 A range of processes were documented to interact with fire and intensify mammal declines. Predation by
392 introduced animals – particularly by red fox (*Vulpes vulpes*) and feral cat (*Felis catus*) – was the most
393 frequent interacting process cited in peer-reviewed papers and policy documents. Introduced predators could
394 exacerbate mammalian declines if hunting activity and/or hunting success increases in recently burned
395 areas, due to the loss of understory vegetation leaving native mammals more exposed (Hradsky, 2020).
396 While there is growing empirical evidence that cats and foxes increase hunting activity in recently burned
397 areas (Hradsky et al., 2017; Leahy et al., 2015; McGregor et al., 2015), our review indicated limited empirical
398 evidence on combined impacts of fire and predation on threatened mammals.

399 Climate and extreme weather were also identified as important processes interacting with fire to contribute to
400 mammalian declines. The combination of extreme drought and severe fire weather contributed to the
401 occurrence of the 2019-2020 mega-fires (Abram et al., 2021), which burnt more than 70% of habitat of the
402 long-footed potoroo (*Potorous longipes*) (Geary et al., 2021). Post-fire drought was another climate-fire
403 interaction identified in our systematic review. For example, native rodents of the genus *Pseudomys* may
404 reach high numbers after periods of high rainfall following fire; however, when fire is followed by drought,
405 vegetation grows slower and resources become scarce, compromising population recovery (Crowther et al.,
406 2018; Hale et al., 2016).

407 We also identified a range of other processes that interact with fire to exacerbate mammal declines (Figure
408 3C) including habitat loss and fragmentation (e.g. western ringtail possum, *Pseudocheirus occidentalis*;
409 Wayne et al., 2006), grazing activity (e.g. brush-tailed rock-wallaby, *Petrogale penicillata*; Tuft et al., 2012)
410 and weed invasion (e.g. warru, *Petrogale lateralis*; Read and Ward, 2011). However, in policy documents,
411 interactions between threats were often described as ‘potential’, reflecting scarcity of empirical data. New
412 empirical studies focused on interactions between fire and emerging threats should be a priority for future
413 research.

414 **4.4 Implications for fire management and conservation policy**

415 A framework that links changes in populations to fire-regime characteristics will help develop more effective
416 conservation actions and policies (Figure 5) in a variety of global contexts. First, identifying the
417 characteristics that describe inappropriate fire regimes for different species, and understanding the
418 demographic processes underpinning population declines, help orient species-specific actions. Second, a
419 focus on mechanisms helps recognize interactions that cause population declines and hence threats that
420 need to be managed alongside fire. Figure 5 highlights examples of potential conservation actions informed
421 by a demographic approach.

422 A range of emerging actions and strategies will be needed to manage fire for mammal conservation in
423 Australia and globally. These include habitat restoration, Indigenous fire stewardship, planned burning, rapid
424 recovery teams that assist wildlife after fire, reintroductions and targeted fire suppression (Bird et al., 2018;
425 Geary et al., 2021; Martins et al., 2022; Roberts et al., 2022). Models that simulate management alternatives
426 and different fire regimes offer opportunities to explore the effectiveness of potential strategies (Nitschke et
427 al., 2020). Implementation through adaptive management and long-term monitoring is essential for
428 determining which strategies will best promote populations of threatened mammals (Corey et al., 2020;
429 Driscoll et al., 2010b).

Mechanisms of decline		Examples of associated characteristics of fire regimes	Example species and its conservation status under the EBPC Act 1999	Conservation actions informed by a demographic framework
Survival	M1	Very large and intense crown fires cause high mortality during fire events.	 Koala (<i>Phascolarctos cinereus</i>) – Vulnerable.	<ul style="list-style-type: none"> - Trial the strategic creation of areas with low fuels to reduce fire size and intensity, and reduce koala mortality. - Expand and connect remaining habitats to improve dispersal and recolonization in post-fire landscapes.
	M2	Frequent and intense fires deplete food resources.	 Carpentarian Rock-rat (<i>Zyzomys palatalis</i>) – Endangered.	<ul style="list-style-type: none"> - Identify fire intervals suitable for plants that provide food and enhance mammal survival. - Explore the use of low intensity fires to reduce the risk of high intensity fires that cause shortage of food resources.
	M3	Lack of fire results in loss of preferred habitat, food, and den availability, leading to reduced survival.	 Yellow-bellied Glider (Wet Tropics) (<i>Petaurus australis</i>) – Vulnerable.	<ul style="list-style-type: none"> - Ensure fire is frequent enough so that this glider's breeding habitat, eucalypt vegetation, is not encroached by rainforest vegetation - Investigate eucalypts forest and rainforest dynamics under changing fire and climate regimes
Movement	M4	Lack of fire increases vegetation density and creates a barrier to dispersal.	 Bilby (<i>Macrotis lagotis</i>) – Endangered.	<ul style="list-style-type: none"> - Improve understanding of the extent to which vegetation density inhibits bilby movements. - Trial planned fires at an appropriate scale and frequency to promote habitat connectivity.
	M4 and M5	Large and intense fires reduce the availability and connectivity of suitable habitats, decreasing dispersal and establishment in potential habitats.	 Greater glider (<i>Petauroides volans</i>) – Vulnerable.	<ul style="list-style-type: none"> - Enact targeted fire suppression to limit fire occurrence and intensity near glider populations and potential habitat refuges. - Establish protected areas around remaining habitats, and movement corridors, to promote population-wide benefits of dispersal.
Reproduction	M6	Altered fire season, including fires late in the dry season that are large and intense, reduce recruitment and reproductive rates.	 Northern quoll (<i>Dasyurus hallucatus</i>) – Endangered.	<ul style="list-style-type: none"> - Foster relationships between a wide range of stakeholders (the agricultural sector, government agencies, private conservation organizations, Traditional Owners) with means of controlling pest species such as cane toads and cats that limit recruitment in post-fire environments - Protect long unburnt habitats, where nesting resources are abundant, from multiple threats including high severity fire and over-grazing.
	M7	A low frequency of fires limits plant regeneration, and this decline in habitat quality limits reproductive success.	 Northern bettong (<i>Bettongia tropica</i>) – Endangered.	<ul style="list-style-type: none"> - Let bushfires burn under moderate conditions to promote a grassy understorey and enhance reproduction. - Control feral cats that cause high mortality of juveniles and therefore limit recruitment of adults in a range of post-fire environments.

430

431 **FIGURE 5.** A demographic framework informs understanding of fire-driven population declines and
 432 conservation actions that could be taken to address them. The examples of conservation actions include
 433 some that have been implemented and others that have been proposed but not implemented. We
 434 recommend that actions be trialed and implemented through adaptive management that includes regular
 435 monitoring of mammal populations.

436 **5 CONCLUSION**

437 There are exciting opportunities to apply the demographic framework we have developed to other taxa and
438 regions. Recent work indicates that a range of animal taxa face threats related to changes in fire regimes,
439 including amphibians, birds, dragonflies and damselflies, freshwater fishes and reptiles (Kelly et al., 2020).
440 Changes in fire regimes are occurring worldwide, from arid, Mediterranean, temperate ecosystems to the
441 tropics and tundra (Rogers et al., 2020). We anticipate that mechanistic approaches will help understand the
442 causes and consequences of inappropriate fire regimes, and develop conservation policies and actions that
443 address synergistic changes to the global environment.

444 **ACKNOWLEDGEMENTS**

445 J.S was funded by the Holsworth Wildlife Research Endowment, Australian Wildlife Society University
446 Research Grant, and Ecological Society of Australia Student Research Award. L.K was funded by a
447 Centenary Research Fellowship at the University of Melbourne. This project was supported by the Australian
448 Government's National Environmental Science Program through the Threatened Species Recovery Hub.
449 Credit photos: Koala (*Phascolarctos cinereus*) - Gerard Lacz/Shutterstock; Carpenterian Rock-rat (*Zyzomys*
450 *palatalis*) - Damien Stanioch; Yellow-bellied Glider (*Petaurus australis*) - Josh Bowell; Bilby (*Macrotis lagotis*)
451 - Michael Todd; Greater glider (*Petauroides volans*) - Josh Bowell; Northern quoll (*Dasyurus hallucatus*) -
452 John Carnemolla/Shutterstock; Northern bettong (*Bettongia tropica*) - John Cancalosi/agefotostock.

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