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1 An experimental test of whether pyrodiversity promotes mammal diversity in a
2 northern Australian savanna

3

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26 **Abstract:**

- 27 1. The increasing awareness that a fire regime that promotes biodiversity in one system can
28 threaten biodiversity in another has resulted in a shift away from fire management based on
29 vague notions of maximising pyrodiversity, towards determining the optimal fire regime
30 based on the demonstrated requirements of target species.
- 31 2. Here, we utilised a long-running, replicated fire experiment on Melville Island, the largest
32 island off the northern Australian coast, to test the importance of pyrodiversity for native
33 mammals in a northern Australian savanna landscape. We first developed statistical models to
34 determine how native mammal abundance has responded to nine years of experimentally-
35 manipulated fire frequency. Next, given each species' modelled response to fire frequency,
36 we identified the level of pyrodiversity and optimal mix of fire frequencies that would be
37 expected to maximise mammal diversity and abundance, and minimise extinction risk. This
38 was done for both the entire mammal assemblage and for the mammal species currently
39 declining on Melville Island.
- 40 3. Fire frequency was a significant predictor of abundance of the northern brown bandicoot
41 (*Isodon macrourus*), black-footed tree-rat (*Mesembriomys gouldii*), brush-tailed rabbit-rat
42 (*Conilurus penicillatus*), grassland melomys (*Melomys burtoni*), pale field-rat (*Rattus*
43 *tunneyi*), and mice/dunnarts but not of the common brushtail possum (*Trichosurus vulpecula*).
- 44 4. The geometric mean abundance (GMA) of the entire mammal assemblage was positively
45 associated with pyrodiversity, but peaked at an intermediate value. Hence, maximising
46 pyrodiversity would reduce native mammal assemblage GMA below its potential maximum.
47 The fire history for an area that maximised the entire native mammal assemblage GMA
48 consisted of 57% long-unburnt, 43% triennially burnt and <1% annually burnt. Pyrodiversity
49 did not reduce the extinction risk, nor increase the GMA of declining mammals above that
50 predicted in areas entirely annually or triennially burnt.
- 51 5. *Synthesis and applications:* We demonstrate a useful approach with which to develop fire
52 management strategies based on the demonstrated requirements of target species. By

53 comparing the optimal fire regime identified for the conservation of threatened species and
54 that identified for the entire mammal assemblage, we demonstrate the flexibility of this
55 approach to tailor fire management to address specific management priorities in other fire-
56 prone environments.

57 Keywords: extinction risk, fire experiment, Melville Island, northern Australia, pyrodiversity, tropical
58 savanna, native mammal diversity.

59

60 **Introduction:**

61 Fire is a global ecosystem driver (Bond et al., 2005, Bowman et al., 2009, Kelly and Brotons, 2017),
62 with profound effects on the evolution of biological communities and ecological processes (Gill et al.,
63 1981, Whelan, 1995, Bond and Van Wilgen, 1996). As a result, fire plays an integral part in the
64 functioning of some biomes (Bowman et al., 2011). The clearing of vegetation, livestock grazing,
65 introduction of exotic plants and animals, alteration of ignition sources and patterns, and the active
66 suppression of fires associated with the expansion of human society has disrupted fire regimes on a
67 global scale, causing substantial ecosystem change and biodiversity loss (Bowman et al., 2011).
68 Worryingly, the disruption of fire regimes is likely to become exacerbated by global climate change
69 (Bowman et al., 2009). Fire also represents one of the few tools for conservation management at the
70 landscape scale. In many fire-prone environments, fire management follows the ‘patch mosaic
71 burning’ paradigm, which attempts to establish and maintain a fine-scale, heterogeneous mosaic of
72 varying fire histories (Parr and Andersen, 2006), under the assumption that “pyrodiversity begets
73 biodiversity” (Martin and Sapsis, 1992). However, this approach lacks a solid empirical or theoretical
74 basis, and has also been criticised for lacking clear operational guidelines that specify which aspects
75 of pyrodiversity should be maximised (Parr and Andersen, 2006, Taylor et al., 2012). This uncertainty
76 has recently stimulated critical analyses of the relationship between pyrodiversity and biodiversity
77 (Parr and Andersen, 2006, Taylor et al., 2012, Kelly et al., 2016). For example, while Tingley et al.
78 (2016) demonstrated that pyrodiversity promotes bird diversity in Californian conifer forests, Taylor

79 et al. (2012) found no such pattern in a semi-arid region of south-eastern Australia, and suggested that
80 burning for fire-mediated heterogeneity could actually threaten the avian fauna in this system. The
81 validity of patch-mosaic burning has also been questioned for reptiles (Nimmo et al., 2013) and
82 mammals (Kelly et al., 2012) in semi-arid Australia. These inconsistent results highlight the context-
83 specificity of pyrodiversity requirements, and the risks associated with the blanket application of a
84 management paradigm focused on maximising pyrodiversity. Hence, fire management for
85 biodiversity conservation must be directly underpinned by the demonstrated fire requirements of the
86 target species (Andersen et al., 2014, Swan et al., 2015, Kelly et al., 2016).

87 Fire has shaped Australian landscapes for millions of years (Kershaw et al., 2002, Crisp et al., 2011),
88 and has been managed by humans for up to 50,000 years of Aboriginal history. The breakdown of
89 traditional burning practices has been implicated in the decline of a range of taxa across northern
90 Australia, including the native cypress pine (*Callitris intratropica*) (Bowman and Panton, 1993),
91 granivorous birds (Franklin, 1999), and more recently the catastrophic collapse of native mammal
92 populations (Firth et al., 2010, Woinarski et al., 2011, Ziembicki et al., 2014). In an attempt to
93 mitigate these declines, prescribed management fires are widely applied across northern Australian
94 savannas (Andersen et al., 2005). Creating a fine-scale fire mosaic and increasing the amount of long-
95 unburnt vegetation are often key objectives of fire management for biodiversity conservation in
96 northern Australia (Woinarski and Winderlich, 2014). However, with limited and sometimes
97 conflicting empirical data relating Australian biota to specific fire patterns, this approach may be
98 ineffective, and even potentially threaten important biodiversity values.

99 Here, we utilise a long-running (9-year) fire experiment on Melville Island (Richards et al., 2012) to
100 evaluate the relationship between pyrodiversity and native mammal diversity in a northern Australian
101 savanna. We first examine the relationship between experimental fire treatments and mammal
102 diversity and abundance. We then use specific estimates of species abundances in each fire treatment
103 to investigate the relationship between simulated pyrodiversity and mammal diversity and extinction
104 risk. In doing so, we identify the specific proportions of different fire treatments within a simulated
105 landscape that maximises native mammal diversity and minimises extinction risk.

106

107 **Materials and methods:**

108 Study site:

109 Melville Island is Australia's second largest island (5788 km²), and the larger of the two main Tiwi
110 Islands, located 20 km off the coast of Australia's Northern Territory (Fig. 1). The islands experience
111 a tropical monsoonal climate, with a wet season (November–April) in which over 90% of the annual
112 rainfall occurs (Australian Bureau of Meteorology, 2015). There is a substantial annual rainfall
113 gradient on Melville Island, from 1400 mm in the east, to 2000 mm in the northwest. The major
114 vegetation types are savanna woodlands and open forests dominated by *Eucalyptus miniata*, *E.*
115 *tetradonta* and *Corymbia nesophila*, with a predominantly grassy understorey. Shrub density is highly
116 variable, and studies on the mainland have shown that it is negatively affected by frequent, high-
117 intensity fires (Russell-Smith et al., 2003, Woinarski et al., 2004).

118 Fire mapping of the Tiwi Islands from 2000–2013 has shown that an average of 54% of the savannas
119 were burnt each year, with 65% of this area burning in the late dry season when fire intensity tends to
120 be highest (Richards et al., 2015).

121 Despite no evidence of recent changes in fire intensity or frequency, feral animal densities or invasive
122 weeds on the Tiwi Islands, native mammal populations appear to have declined significantly over the
123 past 15 years, especially the brush-tailed rabbit-rat (*Conilurus penicillatus*), black-footed tree-rat
124 (*Mesembriomys gouldii*) and northern brown bandicoot (*Isoodon macrourus*) (Davies et al., 2016, H.
125 Davies, *unpublished data*).

126

127 Data collection:

128 In 2008, 18 experimental fire plots (each 50–100 ha) were established at four locations across the
129 western half of Melville Island as part of the Tiwi Carbon Study (see Richards et al. 2012 for details)
130 (Fig. 1). The experiment tests three contrasting fire regimes: (1) annual burning in the early dry

131 season; (2) triennial burning in the early dry season; and (3) no burning (henceforth referred to as
132 long-unburnt). Each treatment is replicated six times, with one replicate of each treatment at Imalu,
133 Taracumbi, and Pickertaramoor, and three replicates of each treatment at Shark Bay (Fig. 1). Prior to
134 the experiment, all plots were burnt at intervals of 1–3 years (Richards et al., 2012). The mean Byram
135 fire-line intensities of the annual and triennial experimental burns were 650 and 1850 kW m⁻¹
136 respectively (A. Richards, *unpublished data*).

137 In December 2013, four vertically downward-facing motion-sensor camera traps were established in
138 each of the 18 fire plots (72 cameras in total) to monitor native mammals. These cameras were left
139 operating continuously for two years, being removed during this period only when plots were burnt,
140 with cameras re-deployed as soon as possible after burning. All cameras were ReconyxTM PC800
141 Hyperfire Professional cameras, with infra-red flash (Reconyx Inc., Holmen, USA). Cameras were
142 deactivated between 8:00 and 18:00 daily, and were programmed to take ten image bursts per trigger.
143 The sensitivity of each camera was set to high, with cameras re-arming five minutes after being
144 triggered.

145

146 Data analysis:

147 To investigate changes in native mammal populations in response to the experimental manipulation of
148 fire frequency, we first derived response variables from camera images to characterise native mammal
149 diversity and abundance in each of the 18 fire plots. Diversity was expressed as the mean number of
150 species recorded per 100 trap nights, and abundance of each native mammal species was calculated as
151 the proportion of total camera trap-nights the species was recorded. There is a positive relationship
152 between the number of individuals of a species recorded at a site in live-traps and the proportion of
153 nights the species was recorded on cameras traps on Melville Island (See Fig. S1 in supplementary
154 material). We calculated this abundance metric for: the northern brown bandicoot, black-footed tree-
155 rat, common brushtail possum (*Trichosurus vulpecula*), brush-tailed rabbit-rat, grassland melomys
156 (*Melomys burtoni*) and pale field-rat (*Rattus tunneyi*). Species smaller than 50 g (native mice

157 [*Pseudomys* spp.] and dunnarts [*Sminthopsis* spp.]) could not be reliably identified, and were
158 combined as a single group referred to as ‘mice/dunnarts’. We note that this group could comprise of
159 up to four individual species: delicate mouse (*Pseudomys delicatulus*), western-chestnut mouse
160 (*Pseudomys nanus*), red-cheeked dunnart (*Sminthopsis virginiae*), Butler’s dunnart (*Sminthopsis*
161 *butleri*). The northern brush-tailed phascogale (*Phascogale pirata*) and northern sugar glider
162 (*Petaurus breviceps*) were also recorded, but too infrequently for meaningful analysis of abundance.

163 We used generalised linear models (GLMs) to investigate how native mammal diversity and
164 abundance, as well as the abundance of each species, was related to fire frequency. To do this we
165 compared four models: a null model, two separate models containing the single main effects of ‘fire
166 treatment’ and ‘site’, and a model containing both ‘fire treatment’ and ‘site’. While time since fire
167 inevitably fluctuated over the period of data collection, we consider our focus on fire frequency as
168 warranted as it characterises a fire regime, not a single fire event. We included the ‘site’ variable to
169 account for spatial autocorrelation. Given the small sample size (n=18), site-specific variation in fire
170 response could not be assessed. Model selection was based on a robust form of Akaike’s Information
171 Criterion, AIC_c , an index that favours both model fit and model simplicity (Burnham and Anderson,
172 2002). Models with lower values of AIC_c are considered to have greater support relative to other
173 models in the candidate set.

174 Using the respective best model based on AIC_c , we predicted the abundance of each species in each of
175 the three fire treatments. Obtaining species-specific estimates of abundance in each fire treatment
176 allowed us to explore the relationship between mammal diversity and simulated pyrodiversity. To do
177 this, we generated 5000 hypothetical, spatially-dimensionless sites with varying levels of
178 pyrodiversity. We randomly varied the proportion of each fire treatment (annually burnt, triennially
179 burnt and long-unburnt) at each of these sites, such that the sum of the proportions of the three fire
180 treatments was equal to 1. Following studies of birds, mammals and reptiles in semi-arid southern
181 Australia (Taylor et al., 2012, Kelly et al., 2012, Nimmo et al., 2013, Farnsworth et al., 2014), we
182 calculated pyrodiversity using the Shannon’s diversity index, scaled such that the maximum (i.e. a site
183 with equal proportions of annually burnt, triennially burnt and long-unburnt vegetation) was equal to

184 1. As used here, Shannon's diversity (pyrodiversity) is maximised when fire treatments are equally
185 represented at the simulated site, and this would hypothetically lead to a maximisation of overall
186 biodiversity values only if each treatment had equal biodiversity value and we acknowledge here that
187 this is a much simplified way in which to quantify pyrodiversity. We used the species-specific
188 estimates of abundance (derived from GLMs) in each fire treatment to obtain an abundance estimate
189 for each species at each simulated site and then calculated the geometric mean abundance (GMA) for
190 each site as equation 1:

$$191 \text{ GMA} = \sqrt[n]{P_{j1} \times P_{j2} \times P_{j3} \times \dots P_{jn}}, \quad \text{eqn 1}$$

192 where n is the number of species, and P_j is the predicted abundance for each species given the
193 simulated fire history. GMA is an appropriate biodiversity index, having heuristic properties that
194 capture a range of desirable criteria with which to assess biodiversity (Buckland et al., 2011, Van
195 Strien et al., 2012, McCarthy et al., 2014). We scaled predicted GMA so the maximum value was
196 equal to 1, and related it to each site's pyrodiversity index.

197 A useful property of GMA is that it tends to be correlated with the proportion of species within an
198 area that are likely to become extinct (McCarthy et al., 2014). Following Giljohann et al. (2015), we
199 utilised this relationship and quantified the change in extinction risk (ER) resulting from different
200 levels of pyrodiversity at each site as equation 2:

$$201 \text{ ER} = 1 - \frac{\left(\frac{1}{\ln(\text{GMA})}\right)}{\left(\frac{1}{\ln(\text{GMA}_{max})}\right)} \quad \text{eqn 2}$$

202 We then plotted the values of both GMA and ER against each site's pyrodiversity index. This was
203 done separately for both the entire assemblage of mammals (seven species) and then for only the three
204 species in significant decline on Melville Island (northern brown bandicoot, black-footed tree-rat,
205 brush-tailed rabbit-rat) (H. Davies, *unpublished data*). By doing so, we identified the specific
206 proportions of the different fire treatments that maximised native mammal diversity and minimised
207 the extinction risk.

208 We conducted a sensitivity analysis to investigate how the identified optimal fire regime was
209 influenced by the variability surrounding each species' abundance estimate. This was done by
210 randomly selecting values from the distribution surrounding each species' predicted abundance and
211 identifying the level of pyrodiversity that maximised the GMA of the entire native mammal
212 assemblage. This was replicated 10,000 times.

213

214 **Results:**

215 The best model of diversity contained the term 'fire treatment', but this model was not significantly
216 better (<2 AIC_c units) than the similar model without this term (Table 1). Therefore, fire treatment had
217 no clear effect on native mammal diversity. However, species composition clearly varied between fire
218 treatments. For all seven species, the best model included the term 'fire treatment', and for all except
219 the brushtail possum, this model was significantly better (≥ 2 AIC_c units) than a similar model without
220 the term 'fire treatment' (Table 1)(for a comparison between the effect size of fire treatment and site
221 on the predicted abundance of each species, see Fig. S2 in supplementary material).

222 Species varied in their preferred fire treatment: the abundances of the black-footed tree-rat, brush-
223 tailed rabbit-rat and 'mice/dunnarts' were highest in annually burnt plots; the abundance of the
224 northern brown bandicoot and pale field-rat was highest in triennially burnt plots; and the abundance
225 of the grassland melomys was highest in long-unburnt plots (Fig. 2). Importantly, due to the logistical
226 constraints of conducting a highly-replicated fire experiment, some of these estimates were uncertain.

227 The geometric mean abundance (GMA) of the entire mammal assemblage was positively associated
228 with pyrodiversity, but peaked at intermediate pyrodiversity (63% of maximum possible
229 pyrodiversity) (Fig. 3a). The fire history of an area that maximised native mammal GMA (i.e. GMA
230 of 100%) consisted of 57% long-unburnt, 43% triennially burnt and $<1\%$ annually burnt vegetation.
231 GMA was 94% for sites composed of entirely long-unburnt vegetation, 83% for entirely triennially
232 burnt sites and 67% for entirely annually burnt sites (Fig. 3a). Mammal GMA at the highest possible
233 simulated pyrodiversity (i.e. equal proportions annually, triennially and long-unburnt) was 95%.

234 Having sites consisting of entirely long-unburnt, triennially burnt or annually burnt vegetation (i.e.
235 those with the lowest possible level of pyrodiversity) increased the average extinction risk by 1.5, 4.0
236 and 8.0%, respectively (Fig. 3a). Maximum pyrodiversity was associated with a 1.0% increase in
237 extinction risk. Given species-specific fire preferences (Fig. 2), each simulated fire management
238 scenario represented a trade-off between the abundance of species. The predicted abundance of each
239 species resulting from different approaches to fire management are summarised in Table 2.

240 In marked contrast, when considering only those mammals which are currently declining on Melville
241 Island, there was little evidence of a positive association between pyrodiversity and GMA (Fig. 3b).
242 GMA again peaked at 63% of the maximum possible value of pyrodiversity. However, the optimal
243 balance of fire histories was markedly different compared with that for all mammals. The optimal
244 regime consisted of no unburnt vegetation, and near equal parts annually burnt (51%) and triennially
245 burnt (49%) (Fig. 3b). Native mammal GMA was 99% for sites composed of entirely triennially burnt
246 vegetation, 98% for entirely annually burnt sites and 77% for entirely long-unburnt sites (Fig. 3b).
247 Having a site consisting of entirely triennially burnt or annually burnt vegetation would increase the
248 average extinction risk of the three declining species by less than 1%, while a site consisting of
249 entirely long-unburnt would increase their average extinction risk by 7% (Fig. 3b). Maximum
250 pyrodiversity was associated with a 2.0% increase in the extinction risk for those species currently
251 declining on Melville Island.

252 Multiple combinations of the three fire treatments resulted in the same level of pyrodiversity, but
253 varied in their predicted GMA and extinction risk i.e. those sites along the dotted black lines (Fig. 3).
254 For example, for the entire mammal assemblage, sites with a pyrodiversity value of 63% varied in
255 their predicted GMA by 19% (representing a 4% range in extinction risk). This variability
256 stemmed from the relative dominance of the three fire treatments at each simulated site, with
257 an increasing proportion of annually burnt resulting in lower GMA and higher extinction risk.
258 For those species currently declining on Melville Island, an increasing proportion of long-
259 unburnt resulted in lower GMA and higher extinction risk.

260 From 10,000 replications of our sensitivity analysis, the level of pyrodiversity that
261 corresponded to maximum native mammal GMA averaged 60%, with a 95% confidence
262 interval of 13–98%.

263

264 **Discussion:**

265 Globally, there is a pressing need to identify fire regimes that maximise biodiversity. However, a fire
266 regime that maximises biodiversity in one system may not necessarily do so in another (Farnsworth et
267 al., 2014). As a result, fire management applied without context-specific empirical evidence may not
268 only be a waste of resources but potentially threaten biodiversity (Taylor et al., 2012). In northern
269 Australian savannas, determining the fire regime that most strongly promotes native mammal
270 diversity is a focus of much research, as fire management is widely advocated as a key tool to prevent
271 further population declines (Woinarski and Winderlich, 2014, Davies et al., 2017). By first
272 demonstrating the varied response of individual mammal species to experimentally-manipulated fire
273 frequency, we have provided the first empirical evidence for the relationship between pyrodiversity
274 and both native mammal gamma diversity, and extinction risk, in a northern Australian savanna.

275 We found that predicted mammal diversity (based on geometric mean abundance; GMA) peaked at an
276 intermediate level of pyrodiversity. Hence, maximising pyrodiversity would actually reduce native
277 mammal GMA (albeit slightly) below its potential maximum. This is a similar result to that found for
278 a range of bird and mammal species in the semi-arid Mallee region of south-eastern Australia (Kelly
279 et al., 2012, Taylor et al., 2012, Farnsworth et al., 2014), which have particular requirements for long-
280 unburnt vegetation, rather than heterogeneous fire. Our results suggest that the optimal fire regime for
281 the entire mammal assemblage would be dominated (>50%) by long-unburnt habitat, highlighting the
282 importance of long-unburnt vegetation to maintain mammal diversity in northern Australian savannas.
283 We demonstrate that the predicted mammal diversity and extinction risk at a particular pyrodiversity
284 value depends on the relative dominance of each of the three fire treatments, suggesting that the initial
285 fire state of an area dictates the potential benefits of applying fire management. Importantly,

286 maximum pyrodiversity was associated with a higher predicted diversity of mammals (and lower
287 extinction risk) than the lowest pyrodiversity (i.e. those sites entirely annually, triennially or unburnt).
288 Hence, while pyrodiversity is clearly an important element of a fire regime that can help maintain
289 high diversity, other components of the fire regime may be particularly important e.g. the proportion
290 of the landscape in a particular desired (or undesired) state.

291 Despite the majority of species exhibiting the highest abundance in the annually burnt fire plots, we
292 identified the optimal fire regime for total native mammal diversity as an area composed of mostly
293 long-unburnt and triennially burnt vegetation. While seemingly counter-intuitive, this reflects the
294 mathematical properties of the index we used to quantify native mammal diversity: the geometric
295 mean abundance (GMA). GMA is a useful measure of biodiversity and reflects both evenness and
296 abundance; however, as it works on the multiplicative scale, GMA is most sensitive to changes in the
297 rarest species (Buckland et al., 2011). As the pale field-rat and grassland melomys were infrequently
298 detected compared to the other species, their habitat preferences for triennially burnt and long-unburnt
299 vegetation were particularly influential, thus explaining the importance of these fire regimes for
300 maintaining overall mammal assemblage diversity. Investigating the relationship between
301 pyrodiversity and the diversity and extinction risk of the entire mammal assemblage allowed us to test
302 the relevance of the pyrodiversity hypothesis for northern Australian mammals. However,
303 conservation efforts are often focused on a small subset of species, which are either threatened or
304 locally declining (Drummond et al., 2010).

305 For any given area, there will be an optimal fire regime that maximises diversity and minimises
306 overall biodiversity loss (Richards et al., 1999). However, even if the optimal fire regime is known, it
307 will often not be feasible to implement due to resource constraints. As such, managers must balance
308 alternative management strategies, each associated with different costs and benefits. As a result,
309 management objectives targeted towards the conservation of threatened species are often prioritised
310 over more common species. For example, the optimal fire regime identified here for the entire
311 mammal assemblage suggested the optimal fire regime would be dominated (>50%) by long-unburnt
312 habitat. Not only was this relationship primarily driven by the habitat requirements of two relatively

313 stable mammal species (grassland melomys and pale field-rat) (IUCN, 1996, Woinarski et al., 2014),
314 but it represents an impracticable target to achieve in the highly fire-prone mesic savannas of northern
315 Australia, where on average over 50% of the landscape burns each year. As such, from a manager's
316 perspective, this approach would be undesirable as it would involve a significant investment of
317 resources for minimal benefit to species of conservation concern. The optimal fire regime identified
318 for declining mammal species was markedly different, and more feasible, to that which would
319 maximise the diversity of the entire mammal assemblage. Increasing pyrodiversity did not drastically
320 reduce the extinction risk, nor increase the GMA of declining mammals above that predicted in areas
321 entirely annually or triennially burnt. However, increasing pyrodiversity in suboptimal areas for these
322 declining mammals (i.e. areas dominated by unburnt habitat) could result in a 7% reduction in
323 extinction risk. Targeting certain areas in the landscape with an empirically based objective highlights
324 how this method might be utilised by managers in the spatial prioritisation of prescribed fire. We
325 acknowledge the limitation that our fire experiment lacked a spatial component. As such, these results
326 may only be relevant for prescribed fire applied at a similar spatial scale i.e. patches 50–100 ha.
327 Importantly, these results demonstrate that once the species-specific fire requirements in any
328 particular area are established, this approach can be utilised to optimise fire management to achieve
329 explicit management priorities, such as the conservation of threatened species.

330 Compared with invertebrates, there has been limited research relating savanna mammal diversity to
331 pyrodiversity (Briani et al., 2004, Griffiths et al., 2015). While our results concur with those of
332 Maravalhas and Vasconcelos (2014), who demonstrated the importance of pyrodiversity for ant
333 diversity in Brazilian cerrado (savanna), they contrast with research of Australian and African
334 savanna invertebrates, which exhibited a high-level of resilience to fire (Parr et al., 2004, Andersen et
335 al., 2014). Again, while our results concur with some studies linking pyrodiversity to the diversity of
336 faunal groups in biomes other than savanna (Tingley et al., 2016, Ponisio et al., 2016), they contrast
337 with others (Taylor et al., 2012, Farnsworth et al., 2014). The inconsistent support for the
338 pyrodiversity hypothesis between biomes and faunal groups emphasises the proposition of Kelly and
339 Brotons (2017) of the need for fire management to be tailored to local conditions.

340 While much of the biota in fire-prone environments has evolved to be remarkably resilient to fire,
341 fire-sensitive elements often persist within the same landscapes (Kelly and Brotons, 2017). The native
342 mammal fauna of northern Australia is a group widely reported to be highly responsive to fire; several
343 studies have demonstrated strong, but marked variation in the response of different mammal species
344 to both experimentally manipulated and naturally varying fire regimes (Corbett et al., 2003,
345 Woinarski et al., 2004, Andersen et al., 2005). For example, Woinarski et al. (2004) demonstrated
346 significant differences in the abundance of native mammal species between an annually burnt area
347 and an area where fire had been excluded for 23 years. They showed that the black-footed tree-rat and
348 common brushtail possum were more abundant in the long-unburnt area, while the northern quoll
349 (*Dasyurus hallucatus*), northern brown bandicoot and pale field-rat were more abundant in the
350 annually burnt area. However, the large-scale, replicated Kapalga fire experiment demonstrated a
351 preference for unburnt areas for five out of seven mammal species, including the northern quoll, fawn
352 antechinus (*Antechinus bellus*), northern brown bandicoot, common brushtail possum and grassland
353 melomys (Andersen et al., 2005). Given the variable requirements of northern Australian native
354 mammal species in relation to fire, any area subject to a spatially homogeneous fire history will
355 inevitably disadvantage some species, thus explaining the positive association between pyrodiversity
356 and native mammal diversity demonstrated here. This is consistent with the predictions of the original
357 pyrodiversity model proposed by Martin and Sapsis (1992). That is, when species have different
358 preferences in relation to fire history, pyrodiversity is required to maximise the persistence of all
359 species. However, in order to develop clear and effective fire management, and avoid the often vague
360 operational guidelines based on pyrodiversity rhetoric, it is vital to determine the optimal level of
361 pyrodiversity to achieve specific management objectives (Parr and Andersen, 2006).

362 While we have suggested fire regimes that may support biodiversity on Melville Island, for a number
363 of reasons this may not necessarily be the case for other areas of northern Australia's savannas. Fire is
364 a stochastic, spatially complex form of disturbance and the fire experiment reported here manipulated
365 only one aspect of the fire regime: fire frequency. As a result we were unable to account for many
366 aspects of the fire regime including the intensity and spatial patterning of fires. As such, our results

367 are based on a much simplified application of fire, and future research should focus on incorporating
368 other aspects of the fire regime into a similar analysis. It is also important to note that our burning
369 treatments did not include high-intensity fires that typically occur late in the dry-season. For example,
370 the intensity of experimental annual fires on Melville Island averaged just 650 kW m⁻¹. By
371 comparison, at Kapalga in Kakadu National Park, the Byram fire-line intensity of experimental annual
372 early dry season fires averaged 2100 kW m⁻¹ (Williams et al., 1998). High-intensity fires have been
373 shown to have both direct (Firth et al., 2010) and indirect negative impacts (Legge et al., 2008, Leahy
374 et al., 2016) on the survival of multiple species in northern Australian savannas. While Andersen et al.
375 (2005) suggested that fires of very low-intensity (occurring in April/early May) could benefit ground-
376 active native mammals, they pointed out that early dry season management fires are typically of
377 higher intensity. As our results are based on small, low-intensity experimental fires, the suggested
378 optimal fire regime may only be applicable in areas where such low-intensity fire regimes are
379 achievable.

380 The effect of fire regimes on biodiversity can act synergistically with other threatening processes
381 (Driscoll et al., 2010, Andersen et al., 2012). In northern Australian savannas, these include the
382 density of exotic mega-herbivores (Legge et al., 2011), invasive grasses (Rossiter et al., 2003), as well
383 as the density of mammalian predators including the dingo (*Canis dingo*) and feral cat (*Felis catus*)
384 (Leahy et al., 2016). As these other threatening processes vary across the landscape, so too will the
385 optimal fire regime for biodiversity conservation. For example, in areas with high predator densities,
386 it may be that species that would otherwise inhabit more open areas, are forced to shelter in long-
387 unburnt vegetation due to its mitigating effect on predation pressure (McGregor et al., 2015,
388 McGregor et al., 2016, Leahy et al., 2016). The presence and density of the threatened native species
389 for which management is commonly aimed at conserving, also vary across the landscape. Here we
390 have identified the optimal fire regime for the ground-active native mammals of Melville Island.
391 Again, given that a different suite of mammal species occurs in the savannas of mainland northern
392 Australia, the optimal fire management for species conservation will likely differ to some extent.
393 While our study investigated how different fire patterns influence native mammal diversity, future

394 work should also incorporate the fire response of other non-mammal species, especially those thought
395 to be declining and sensitive to fire regimes (e.g. partridge pigeon, *Geophaps smithii*; (Fraser et al.,
396 2003)). Our results were sensitive to the variability in species' specific abundance estimates (due to
397 both the limited replication of our fire experiment and the sensitivity of GMA to rare species). As
398 such, future work utilising this method should include a sensitivity analysis. Furthermore, the
399 approach outlined in this manuscript may be strengthened by the incorporation of diversity metrics
400 other than Shannon's diversity index and GMA.

401 Specific targets that go beyond pyrodiversity rhetoric are necessary for fire management for
402 biodiversity conservation to be operationally effective (Andersen et al., 2005). However, these targets
403 are highly context specific and depend on a range of factors including management priorities, the fire
404 requirements of the species present in a particular area, as well as the presence and severity of other
405 threatening processes. The realisation that a fire regime that promotes biodiversity in one system is
406 often not applicable to another, has resulted in a more concerted effort to develop fire management
407 that is supported by ecological theory, but tailored to local conditions (Farnsworth et al., 2014, Kelly
408 and Brotons, 2017). By utilising a long-running fire experiment we have demonstrated not only the
409 utility of first determining species-specific responses to fire with which to develop fire management,
410 but the flexibility that this approach affords to develop and tailor fire management based on specific
411 and changing management priorities in other fire-prone environments, i.e. conserving threatened
412 species vs. conserving an entire mammal assemblage. While the feasibility of implementing replicated
413 fire experiments is low, conducting correlative pilot studies that are specifically designed to relate
414 biodiversity to fire regimes will greatly improve our ability to develop effective fire management
415 strategies.

416 **Authors' contributions:**

417 HD, MM, AA, BM, W. Rioli, JP, W. Roberts, CK, VK and KBM conceived the ideas and designed
418 the methodology; HD, WR, JP, WR, CK, VK and KBM collected the data; HD and BM analysed the
419 data; HD, MM, AA and BM led the writing of the manuscript. All authors contributed critically to the
420 drafts and gave final approval for publication.

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431

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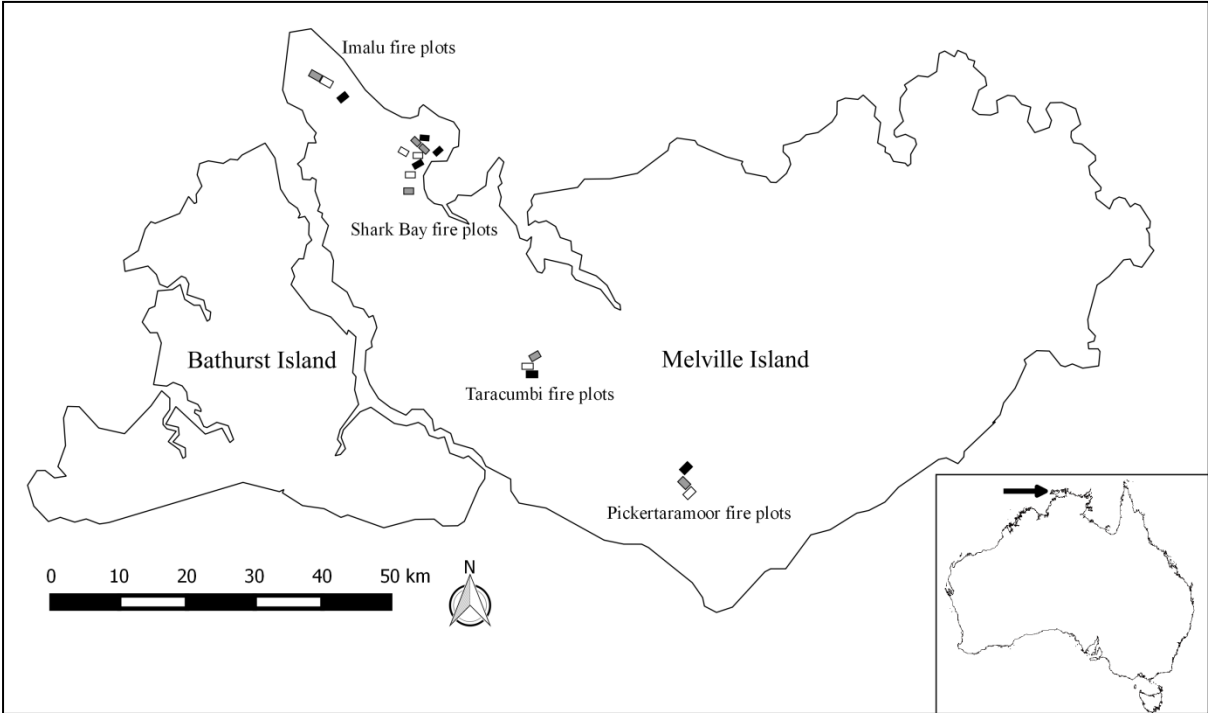
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609 Figure 1: Locations of the 18 experimental fire plots on Melville Island, northern Australia. The
610 black, grey and white rectangles represent the six annually burnt, triennially burnt and long-unburnt
611 plots, respectively. The location of Melville Island relative to mainland Australia is shown in the
612 inset.

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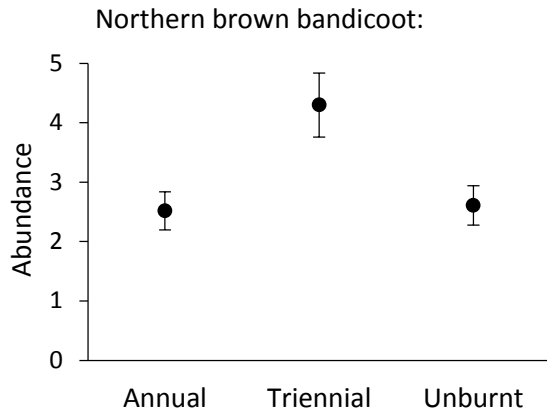
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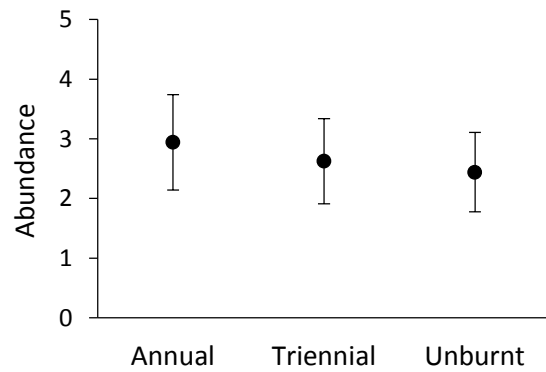
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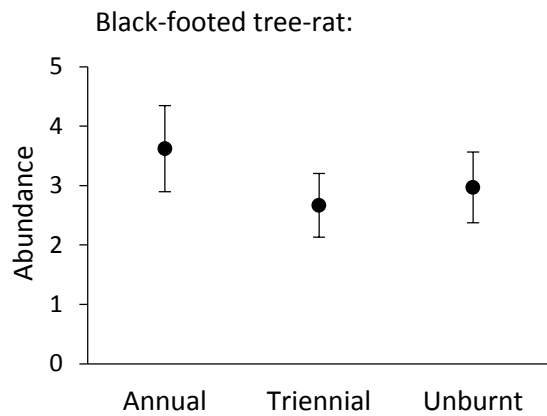
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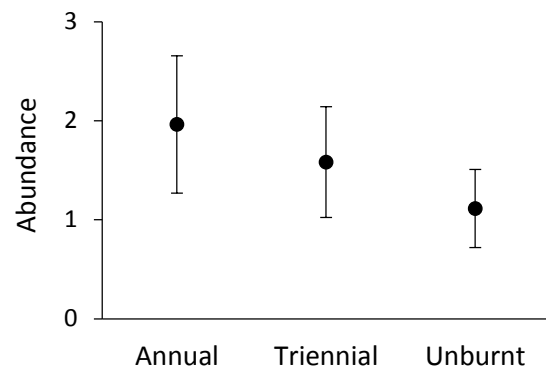
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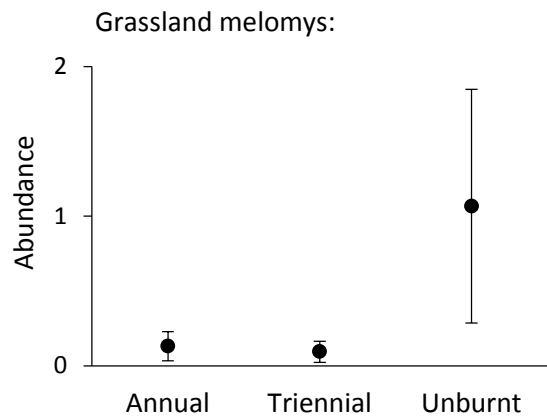
Brush-tailed rabbit-rat:



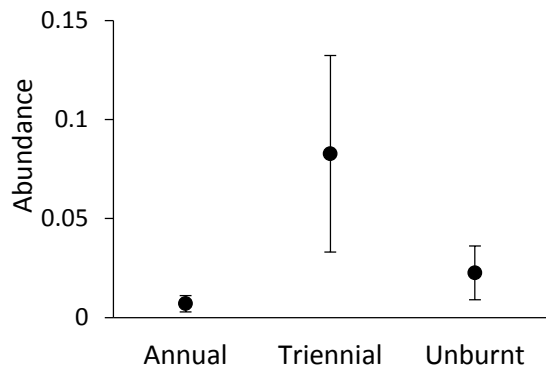
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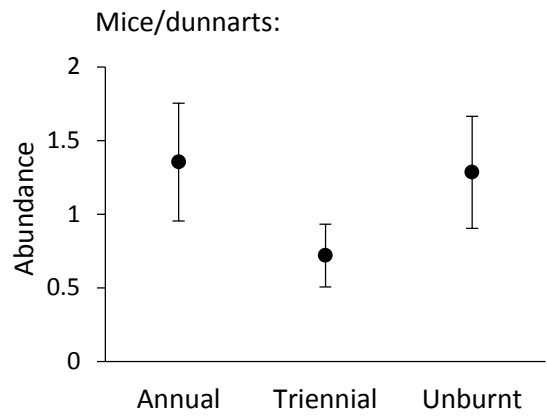
Pale field-rat:



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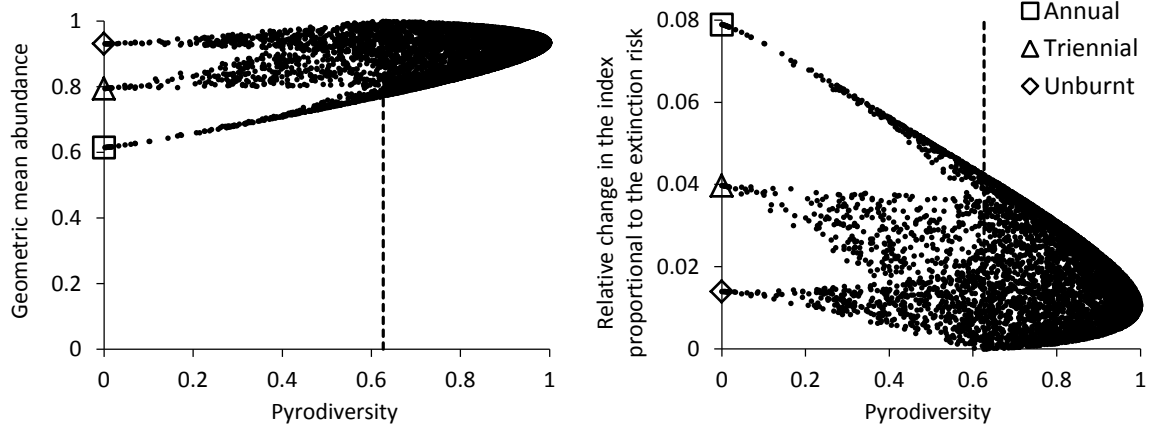
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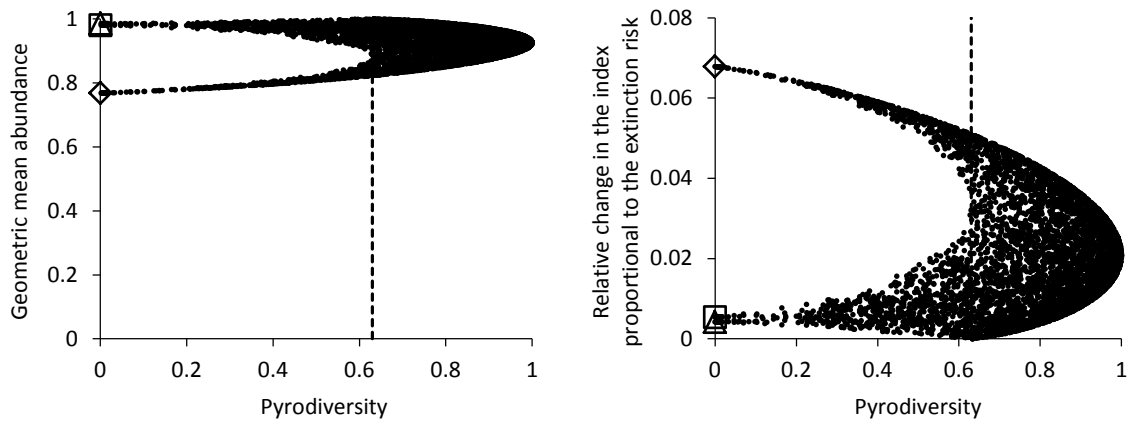
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Figure 2: The predicted index of abundance (\pm SE) of native mammals for each experimental fire treatment.

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638 b)



639 Figure 3: The relationship between pyrodiversity and the geometric mean abundance (GMA) and the
640 relative change in the index proportional to the extinction risk for (a) all ground-active native mammal
641 species; (b) the three declining native mammal species, at 5000 simulated sites. The square, triangle
642 and diamond intercept markers indicate the predicted mammal diversity and extinction risk at sites
643 composed of entirely annually burnt, triennially burnt and long-unburnt vegetation, respectively. The
644 dotted vertical lines indicate the level of pyrodiversity with the maximum predicted mammal GMA
645 and minimum change in extinction risk.
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653 Table 1: Summarises the model selection process for native mammal alpha diversity and species-
654 specific abundance in 18 experimental fire plots across Melville Island, Northern Territory. K
655 indicates the number of parameters; ΔAIC_c is the difference between the model's AIC_c value and the
656 minimum AIC_c value in the candidate set; w_i is the Akaike weight (the likelihood of the model being
657 the best in the candidate set). Bold text indicates significant effect of fire treatment ($\Delta AIC_c \leq 2$,
658 relative to other models in the candidate set). Models with essentially no empirical support ($\Delta AIC_c >$
659 10) are not included in the table.

Response	Model	K	ΔAIC_c	w_i
Native mammal alpha diversity	~ Fire treatment + Site	8	0.0	0.60
	~ Site	6	1.0	0.36
	~ Null model	1	6.0	0.03
	~ Fire treatment	3	8.5	0.01
Native mammal abundance	~ Fire treatment + Site	8	0.0	0.57
	~ Site	6	0.6	0.43
Northern brown bandicoot abundance	~ Fire treatment + Site	8	0.0	1.00
Common brushtail possum abundance	~ Fire treatment + Site	8	0.0	0.67
	~ Site	6	1.5	0.33
Black-footed tree-rat abundance	~ Fire treatment + Site	8	0.0	1.00
Brush-tailed rabbit-rat abundance	~ Fire treatment + Site	8	0.0	1.00
Grassland melomys abundance	~ Fire treatment + Site	8	0.0	1.00
Pale field-rat abundance	~ Fire treatment + Site	8	0.0	0.97
	~ Site	6	7.1	0.03
Mice/dunnart abundance	~ Fire treatment + Site	8	0.0	1.00

660

661 Table 2: Predicted abundance of each native mammal species resulting from different approaches to
662 fire management.

Approach to fire management	Northern brown bandicoot	Common brushtail possum	Black-footed tree-rat	Brush-tailed rabbit-rat	Grassland melomys	Pale field-rat	Mice/dunnarts
Entirely annually burnt	2.52	2.94	3.62	1.96	0.13	0.01	1.35
Entirely triennially burnt	4.30	2.63	2.67	1.58	0.10	0.08	0.72
Entirely unburnt	2.61	2.44	2.97	1.11	1.01	0.02	1.29
Maximum pyrodiversity	3.15	2.67	3.09	1.55	0.43	0.04	1.12
Maximum GMA/ Minimum extinction risk	3.33	2.52	2.84	1.31	0.65	0.05	1.04

663