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1 **Seed size mediated dormancy thresholds: a case for the selective pressure of fire on**
2 **physically dormant species**

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4 **Running title: Seed size and dormancy-breaking thresholds**

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19 **Abstract**

20 In physically dormant species, fire-generated heat breaks seed dormancy, with dormancy-
21 breaking temperature thresholds varying among species. Fire-related heating decreases with
22 depth, due to the insulating effects of soil. Concurrently, smaller seeded species are restricted
23 to germinating near the surface because of limited reserves within such seeds. We
24 hypothesised that dormancy-breaking temperature thresholds of physically dormant species
25 would be higher in smaller seeded species, to ensure emergence is restricted to shallower soil
26 depths, and that seed survivorship would follow the same pattern. This was tested
27 experimentally for 14 species from south-eastern Australia, and by using a larger data set of
28 species compiled from the literature to assess if any patterns hold across a broader group.
29 Seed size was negatively related to dormancy-breaking temperature thresholds. Mortality at
30 100°C showed a positive relationship with seed size. Our findings suggest that small-seeded
31 species are subject to fire-related selection pressure that results in higher dormancy-breaking
32 temperature thresholds and resistant to hotter temperatures, which may act as a depth
33 detection mechanism. By using a broader range of species, we highlight that this relationship
34 is strong, and representative of species across a number of phylogenetic groups.

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37 **Additional key words: dormancy thresholds - fire-adapted traits - fire-prone ecosystem**
38 **- germination - physical dormancy - seed size - seed trait - seedling emergence depth -**
39 **seedling recruitment**

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INTRODUCTION

Fire is one of the key stimulants for seed germination and seedling establishment in many fire-prone ecosystems (Whelan, 1995; Fenner & Thompson, 2005). Soil temperatures generated during fire act as a seed dormancy-breaking cue (Auld & O’Connell, 1991; Thanos *et al.* 1992; Jeffery, Holmes & Rebelo, 1988; Moreira & Pausas, 2012; Liyanage & Ooi, 2015). This is one of the most widely studied phenomena for physically dormant fire-following species (Baskin & Baskin, 2014; Hudson, Ayre & Ooi, 2015). The impermeable seed coats of physically dormant seeds prevent germination until they are ruptured by such increased soil temperatures, allowing the gas and water exchange required to initiate germination (Thanos & Georghiou, 1988; Baskin & Baskin, 2014).

The fire-related soil temperatures that are needed to break physical dormancy (dormancy-breaking temperature thresholds) have been found to vary among and within species, and are likely to play an important ecological role, by distributing seed germination over space and time (e.g. Auld & O’Connell, 1991; Pérez-García, 1997; Liyanage & Ooi, 2015). As an example, variation in dormancy-breaking temperature thresholds among species can range from as low as 40°C to approximately 100°C, with heat-induced mortality becoming prevalent from 120°C for species from Australian fire-prone ecosystems (Auld & O’Connell, 1991; Hanley, Unna & Darvill, 2003; Ooi *et al.*, 2014). This distribution of thresholds has generated the hypothesis that species coexistence is supported by variation in germination response across the landscape due to the inherent patchiness of soil heating in fire-prone ecosystem (Auld & O’Connell, 1991; Herranz, Ferrandis & Martínez-Sánchez, 1998; Hanley *et al.*, 2003). Similar variation within species may provide the same support for the persistence of species (Tavşanoğlu & Çatav, 2012; Liyanage & Ooi, 2015).

66 Few studies have investigated the mechanisms that may allow for the maintenance of
67 variation in dormancy-breaking temperature thresholds. One example, by Liyanage, Ayre &
68 Ooi (2016), found that seedling performance covaried with different dormancy-breaking
69 thresholds. Seeds with low dormancy-breaking thresholds produced better performing
70 seedlings, which the authors concluded would benefit them because environments resulting
71 from low severity fires are more competitive than those left after high severity fires. This
72 offset would subsequently lead to the maintenance of variation in this dormancy trait. Hanley
73 *et al.* (2003) and Tavşanoğlu & Çatav (2012) also found that germination proportions after
74 heat shock treatments varied with seed size, at the inter- and intra-specific level for physically
75 dormant species from fire-prone Mediterranean systems. They suggested that this
76 relationship, which indicated that species with small seeds had higher dormancy-breaking
77 temperatures, also supported coexistence, particularly after hot fires which produce high soil
78 temperatures. This was attributed to the allometric relationship between seed size and ability
79 to successfully emerge from depth of burial within the soil seed bank, identified by Bond,
80 Honig & Maze (1999) for a number of fire-following species.

81

82 The relationship between dormancy-breaking temperature threshold and the depth that
83 seedlings can successfully emerge from is still not well documented in fire-prone ecosystems.
84 Generally, successful seedling emergence from the seed bank depends on an interaction
85 between the dormancy-breaking cues received in order to initiate seed germination, and the
86 available seed reserves that enable the seedling to reach the soil surface to complete their
87 establishment (Leishman *et al.*, 1992; Bond *et al.*, 1999; Fenner & Thompson, 2005;
88 Thompson & Ooi, 2013). The ability of seedlings to emerge from depth increases with an
89 increase in seed size, and emergence of smaller seeded species is restricted near to the soil
90 surface (Gulmon, 1992; Jurado & Westoby, 1992; Jurik, Wang & Vanderwalk, 1994; Bond *et*

91 *al.*, 1999; Leishman *et al.*, 2000). Higher soil temperatures are found near the soil surface
92 during fire, and the insulating effect of soil reduces fire-induced heating with soil depth
93 (Auld, 1986). Subsequently, there are two mechanisms by which smaller seeded species can
94 ensure emergence occurs at shallower depths, by maintaining (i) higher dormancy-breaking
95 temperature thresholds, and (ii) seeds that are able to endure hotter temperatures. Small-
96 seeded species with low dormancy-breaking temperature thresholds are more likely to
97 produce a “suicidal” germination response from seeds held too deeply in the soil profile. It is
98 likely that large seeded species would therefore have less selective pressure for maintaining
99 such traits.

100

101 Understanding the interactions between seed size, dormancy-breaking temperatures and
102 seedling emergence depths is important for developing predictions of post-fire plant
103 regeneration in response to differing fire severities (Hanley *et al.*, 2003) and how fire may
104 have shaped variability in seed traits. However, there are few accounts in the literature that
105 have tested the relationship between seed size and germination response over a range of
106 temperatures, along with the associated patterns of mortality and seedling emergence ability
107 (Bond *et al.*, 1999; Hanley *et al.*, 2003). This is an important inclusion for fully
108 understanding the mechanisms driving threshold variation.

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110 Key studies which have investigated the correlation between these seed traits in heat-
111 responsive physically dormant species include Tavşanoğlu & Çatav (2012), who investigated
112 a single fire-following species (*Cistus salviifolius*) using a single temperature treatment
113 (120°C) to assess germination response and within species seed size variation, and Hanley *et*
114 *al.* (2003), who studied germination response under a range of temperature treatments of
115 eight species. Both found a positive correlation between seed size and germination after heat

116 treatments, suggesting that the lower response in small seeds was due to a higher threshold.
117 In contrast, studies that have found no (or even the opposite) relationship between seed size
118 and heat tolerance have come from studies using species from a range of dormancy types
119 and/or from non-fire-prone or mixed habitats (Ribeiro *et al.*, 2015 – in the fire-prone *Cerrado*
120 and non-fire-prone forest in Brazil; Ruprecht *et al.*, 2015 – in non-fire-prone European
121 grasslands).

122

123 In our study, we explored the relationship between seed size and germination and mortality of
124 species from three dominant plant families with physical dormancy in Australian fire-prone
125 ecosystems. Specifically, we experimentally tested the relative ability of 14 species to
126 germinate and survive after heat-shock and emerge from different soil depths and related
127 these responses to seed size. We then used a larger data set compiled from the literature,
128 combined with our smaller experimental dataset, to further assess if the patterns found hold
129 across a broader representation of species from fire-prone regions. We hypothesised that
130 dormancy-breaking temperature thresholds of physically dormant species would be higher in
131 smaller seeded species, to ensure emergence is restricted to shallower soil depths, and that
132 seed survivorship would follow the same pattern. The following specific questions were
133 addressed,

134

135 (1) Is there a relationship between seed size and maximum soil depth that seedlings can
136 emerge from?

137 (2) Is there a relationship between seed size and the temperature required for maximum
138 germination and mortality among species?

139 (3) Are such patterns retained across a broad range of physically dormant species?

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METHODS

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STUDY SPECIES AND SITE

144 All 54 study species (14 used in experiments and 40 additional species in the dataset
145 compiled from the literature) represent members of the Fabaceae, Rhamnaceae and
146 Sapindaceae, are physically dormant and occur in the shrub layer in fire-prone sclerophyll
147 vegetation in temperate climate heaths, woodland and forests (Auld & O'Connell, 1991;
148 Hanley *et al.*, 2003). The population dynamics of all species are fire-driven, and occur in
149 areas which experience naturally occurring episodes of fire every 7 – 30 years (Bradstock &
150 Gill, 2001; Lucas *et al.*, 2007). Soil-stored seed banks of these physically dormant species
151 (and many other species in temperate Australia) are therefore very long-lived, with
152 persistence likely over the scale of multiple decades (Auld, **Keith & Bradstock** , 2000; Ooi
153 *et al.*, 2007). Thirty-seven of the species occur on nutrient-poor soils in the Sydney sandstone
154 basin in south-eastern Australia, where fires occur primarily from October to January (late
155 spring to summer), and rainfall is aseasonal (33°53'S, 151°13'E Auld & O'Connell, 1991).
156 Ten species occur in the transition zone between the temperate east coast and semi-arid
157 interior of south-eastern Australia (31°17'S, 149°0'E – Palmer, 2016), approximately 450km
158 northwest of Sydney, in an area with a similar fire season and rainfall tending to be
159 concentrated more in the summer months (Harden, 1990). The remaining species are found in
160 the Darling Range, approximately 20 km east of Perth, Western Australia (31°57'S, 115°
161 51'E – Hanley *et al.*, 2003), and on nutrient-poor soils where the fire season occurs from
162 December to February (summer) and rainfall occurs during the winter months (Australian
163 Bureau of Metrology, 2016).

164

165 The 14 species used for the experiments conducted in our study are from the Sydney
166 sandstone basin in south-eastern Australia, and include nine obligate seeders (i.e. adult plants
167 are killed by fire and regeneration is dependent on seed germination) and five resprouters (i.e.
168 some proportion of adult plants survive fire by resprouting but still rely on some seed
169 germination for population replenishment) (Table 1). Seeds were randomly collected from
170 15-20 individual plants within a single population of each species. We used seed mass as a
171 measure of seed size. The mean seed mass for each species was determined by weighing 75-
172 100 seeds individually.

173

174 SEED SIZE AND DORMANCY-BREAKING TEMPERATURE THRESHOLD – EXPERIMENTAL DATA

175 The temperatures needed to break physical dormancy and achieve maximum germination
176 (T_{max}) were determined for each species by quantifying germination response to a range of
177 dry heat temperature treatments representative of fire-related soil heating. Three replicates of
178 15 to 25 seeds were independently heated at 40°C, 60°C, 80°C, 100°C and 120°C
179 temperatures in an oven for ten minutes. Due to a lack of seed availability, only 40°C, 60°C,
180 80°C and 100°C temperatures were used for *Aotus ericoides*, *Bossiaea heterophylla*, *Daviesia*
181 *corymbosa*, *Pomaderris notata* and *P. walshii*. Seeds were left to cool after the heat
182 treatments and placed on moistened filter papers in 9 cm Petri dishes for incubation at
183 25/18°C and light/dark conditions on a 12/12 hour cycle. These alternating temperatures were
184 used to mimic summer mean maximum and minimum temperatures of the study region,
185 which is the time that most natural fires occur (McLoughlin, 1998). Germination was
186 recorded at two day intervals for six weeks, and scored on radicle emergence. Three
187 replicates of untreated seeds were also placed on Petri dishes and incubated at the same
188 conditions as a control. These seeds were subsequently scarified and used to calculate the

189 initial viability of the seed lot (see below for details of scarification). Germination was later
190 calculated based on the number of seeds initially viable.

191

192 The mean mortality was determined at end of the incubation period for each temperature
193 treatment separately. At end of the 6th week, ungerminated seeds were tested for viability by
194 pressing them gently using forceps, and any remaining hard ungerminated seeds were
195 manually scarified using a scalpel. Germination of the scarified seeds was followed for 3-4
196 weeks under same incubation conditions. This final number of seeds germinated (during
197 germination trials and after scarification) was used to calculate the total viability of each
198 treatment. Mortality due to heat treatments was determined by subtracting the background
199 number of inviable seeds (i.e. initial inviable seeds from the Control) from the total number
200 of seeds dead after heat treatments.

201

202 The best fitting response curve for the germination data across all temperature treatments was
203 used to determine the T_{max} . The equation of best fit was solved using the Newton-Raphson
204 iterative method for each species separately (Hanley *et al.*, 2003), using the R.3.3.0 statistical
205 platform (R Development Core Team, 2016). The T_{max} values of all study species were then
206 plotted against seed size to determine the relationship with dormancy-breaking temperature
207 threshold. The mean percentage mortality was calculated after the 100°C treatment for all
208 species, and after treatment at 120°C for a subset of species (due to the full range of
209 temperatures not able to be tested for some species), and were also plotted against seed size.

210

211 SEED SIZE AND SEEDLING EMERGENCE DEPTH

212 Seeds for all study species except *P. adnata*, *P. walshii* and *P. notata* (due to a lack of
213 available seeds) were tested under experimental conditions to assess their abilities to emerge

214 from different soil depths. Physical dormancy was first broken by scarification, after which
215 seeds were placed on Petri dishes to incubate under the same conditions described above.
216 Three replicates of 10 freshly germinated seeds were then planted at 1, 2, 3 and 5 cm depths
217 in plastic pots (20 cm diameter and 20 cm height) filled with 5:1 sand: vermiculite mixture.
218 The depths were measured from the surface of the sand. Pots were placed in natural light
219 under ambient laboratory conditions and watered regularly to prevent desiccation. Seeds in
220 each pot were separated by 4 cm to control for any neighbor effects. The number of seedlings
221 emerged from each replicate at each depth was recorded over a one month period, and the
222 mean proportion of the final number emerged calculated for each depth. The maximum depth
223 that species could emerge from was plotted against seed weight and the relationship assessed
224 using linear regression.

225

226 SEED SIZE AND DORMANCY-BREAKING TEMPERATURE THRESHOLD – ALL DATA

227 Suitable seed size data, where a relationship with germination and/or mortality response to
228 fire-related temperatures could be calculated, were found for an additional 40 species from
229 similar fire-prone ecosystems (Table S1: Auld & O’Connell, 1991; Hanley *et al.*, 2003;
230 Palmer, 2016), meaning that a maximum of 54 species (literature plus experimental data)
231 could be analysed. For one of these data sets, from Hanley *et al.* (2003), heating of five
232 minutes duration were used, compared to the 10 minute duration in treatments for all other
233 data. We included these data based on the assumption that little differences have been found
234 between five or 10 minute duration heat treatments for numerous species (Auld & O’Connell,
235 1991). T_{max} was calculated for all additional species as outlined above. The full dataset was
236 also used to plot T_{max} and mortality against seed size.

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238

STATISTICAL ANALYSIS

239 All statistical analyses were conducted using R.3.3.0 platform (R Development Core Team,
240 2016). The relationship between T_{\max} , the maximum depth from which each species could
241 successfully emerge from, and mortality was assessed against seed size using Generalised
242 Linear Mixed effects Models (GLMM) (using the lme4 package) with seed size as the fixed
243 factor and genus as the random factor. A Gaussian error structure with log link function was
244 used for T_{\max} and maximum emergence depth data, and a binomial error structure with logit
245 link function was used for the mortality data. The same analyses were repeated for the
246 complete data set (experimental + literature) to assess whether a pattern was detectable across
247 a broader representation of species. Seed size data were first transformed using Log+1.
248 Conditional pseudo R-square values were calculated for each model using the package
249 piecewiseSEM.

250

251

RESULTS

252 SEED SIZE AND DORMANCY-BREAKING TEMPERATURE THRESHOLD – EXPERIMENTAL DATA

253 Overall germination and mortality for all 14 species showed a similar pattern of increase with
254 increasing temperature treatment (Fig. S2). However, percentage germination in response to
255 temperature treatments differed among species, with T_{\max} ranging from 65.4 to 108.2 °C
256 (Table 1). When T_{\max} was plotted against seed size, there was a significant negative linear
257 correlation (Fig. 1A; $R^2 = 0.37$, $df = 4$, $\chi^2 = 6.192$, $P = 0.012$). Analysis of mortality after the
258 100°C treatment, showed a strong positive relationship between the proportion killed and
259 seed size (Fig. 1B; $R^2 = 0.78$, $df = 3$, $\chi^2 = 127.11$, $P < 0.001$), indicating that smaller seeded
260 species had a greater resilience to higher temperatures. Although all species showed an
261 increase in mortality with increasing temperature treatment, this increase was markedly
262 higher in the case of large-seeded than small-seeded species at high temperatures.

263

264

SEED SIZE AND SEEDLING EMERGENCE DEPTH

265 The emergence of all species showed a decrease with increasing depth that seeds were buried
266 (Table S3). The maximum depth that seedlings could emerge from displayed a positive linear
267 relationship with seed size (Fig. 1C; $R^2 = 0.61$, $df = 4$, $\chi^2 = 9.98$, $P = 0.001$). The proportion
268 emerged from the deepest treatment depth showed noticeable variation among species,
269 ranging from 0 to 0.7, while not surprisingly, the highest proportion of seedling emergence
270 was observed for seeds buried at 1 cm depth (data not shown).

271

272 SEED SIZE AND DORMANCY-BREAKING TEMPERATURE THRESHOLD – ALL DATA

273 When analysing the full dataset of 54 species, there was a strong significant negative
274 relationship between T_{\max} and seed size (Fig. 2A; $R^2 = 0.27$, $df = 4$, $\chi^2 = 5.887$, $P = 0.015$).
275 There was a significant positive relationship between mortality and seed size at both 100°C
276 (Fig. 2B; $R^2 = 0.47$, $df = 3$, $\chi^2 = 318.25$, $P < 0.001$) and 120°C (Fig. 2C; $R^2 = 0.59$, $df = 3$, $\chi^2 =$
277 6.677 , $P = 0.009$).

278

279

DISCUSSION

280 The results of this study showed clear relationships between seed size and dormancy-break,
281 mortality and seedling emergence, which all contribute to understanding the ecological role
282 that variation in dormancy-breaking temperature thresholds play in fire-prone ecosystems.
283 We found a strong negative relationship between seed size and dormancy-breaking
284 temperature thresholds, and a positive relationship between seed size and the ability of
285 seedlings to emerge from depth. These results indicate that smaller seeds, which are restricted
286 to emerging from shallow soil depths, are more likely to have higher dormancy-breaking
287 temperature thresholds, a relationship that aligns with the findings of Hanley *et al.* (2003). By
288 using a broader range of species, our study has shown that the strength of these patterns holds
289 across phylogenetic groups containing physically dormant species.

290

291 During fire, higher temperatures occur in the top 2 cm of the soil profile (Auld & Bradstock,
292 1996; Penman & Towerton, 2008; Santana *et al.*, 2010). The negative linear relationship
293 between seed size and T_{\max} indicates that smaller seeds break their dormancy in response to
294 high soil temperatures, therefore are more likely to germinate when they are closer to the soil
295 surface. For small seeded species in other habitats, light sensitivity has been identified as a
296 mechanism to detect shallow soil depth and therefore improve the likelihood of successful
297 emergence (Woolley & Stoller, 1978; Benvenuti, 1995; Limón & Peco, 2016). High
298 dormancy-breaking temperature thresholds in small-seeded species can therefore also be a
299 depth detection mechanism for fire-following species in plant communities where fire is the
300 main driver of regeneration. Large seeds on the other hand, produce a higher germination
301 response at lower soil temperatures, which would enable them to respond and then germinate
302 from greater soil depths after fire. The patterns observed suggest that there has been strong
303 selective pressure by fire on the development of dormancy-breaking thresholds across the
304 seed size range to allow population persistence.

305

306 Perhaps not surprisingly, support for this selection pressure is also found in seed resistance to
307 temperature-induced mortality. A positive linear relationship found between seed size and
308 mortality at high temperatures indicates that smaller seeds are more likely to survive higher
309 soil temperatures. While dormancy-breaking thresholds provide the trigger to detect a near-
310 surface position, resistance to higher fire-related heat shock temperatures enables seeds to
311 persist in this part of the soil profile. Similar patterns of greater tolerance to higher fire-
312 related soil temperatures have also been found to correlate with other seed traits, including
313 dormancy level (Ramos *et al.*, 2016) and seed shape (Ruprecht *et al.*, 2015). Perhaps more
314 importantly, studies using fire-related heat have identified either no or the opposite

315 relationship between seed size and heat tolerance (Rebeiro *et al.*, 2015; Ruprecht *et al.*,
316 2015). In the Brazilian *cerrado* biome (Rebeiro *et al.*, 2015) the species used produced seeds
317 many times larger than those used in our study, and would therefore not be subjected to any
318 selective pressure imposed by emergence depth. Ruprecht *et al.* (2015) used species from
319 non-fire-prone European grasslands where it is unlikely that there would be strong selection
320 for tolerance to heat. This highlights an important point regarding the search for adaptive
321 traits in fire-prone species, namely that the potential for identifying selective pressure is
322 dependent on the mechanistic processes driving the fire/life-history response relationship.

323

324 The positive relationship found between seed size and seedling emergence depth supports
325 that identified by Bond *et al.* (1999) in a study in the South African fynbos. The increase in
326 the ability of seeds to emerge from greater soil depths has been attributed to the amount of
327 seed reserves that are available for utilisation when extending the hypocotyl until it reaches
328 the soil surface (Leishman *et al.*, 2000; Baskin & Baskin, 2014). Larger reserves allow seeds
329 to maximise the tissue column width, to push through from greater soil depths (Bond *et al.*,
330 1999). Although this relationship is often assumed, it has rarely been tested across multiple
331 species, particularly in fire-prone flora.

332

333 Maintaining variation in dormancy-breaking temperatures and tolerance of heat shock may
334 not only determine where species can germinate from within the soil profile, but could also
335 contribute to reducing post-fire seedling competition. The positive relationship between seed
336 size and seedling size means that when large and small seeded species co-occur, small seeded
337 species may be at a competitive disadvantage during the seedling phase (Leishman *et al.*,
338 2000; Lahoreau *et al.*, 2006). However, in general, large seeds are slower to germinate, in
339 fire-prone and other vegetation types (e.g. Moles & Westoby, 2004; Norden *et al.*, 2009). The

340 fact that small seeded species are cued to germinate closer to the soil surface, and that larger
341 seeded species suffer higher mortality at shallow depths, means that smaller seeds are able to
342 establish their seedlings well before the more competitive seedlings from larger seeds emerge
343 from greater soil depths. These mechanisms would contribute to maintaining species
344 coexistence and explaining the role of germination traits in understanding community
345 assembly (Jiménez-Alfaro *et al.*, 2016; Larson & Funk, 2016).

346

347 Within the context of predictions for physically dormant species in our fire-prone habitats,
348 analysis of the larger set of species from the Fabaceae, Rhamnaceae and Sapindaceae shows
349 that it is reasonable to conclude that small-seeded species are subject to a selection pressure
350 to maintain higher dormancy-breaking temperature thresholds. However, many other species
351 which do not have physical dormancy (or hard seed coats) are likely to maintain different
352 mechanisms unrelated to heat. This is supported by several studies in fire-prone regions,
353 where the relationship between seed size and heat was tested for species with a range of
354 dormancy types. For example, Ribeiro *et al.* (2015) found that seed size was negatively
355 related to heat tolerance for tree species from fire- and non fire-prone areas in Brazil, while
356 tolerance to high temperature duration showed a similar correlation with size for non-dormant
357 species in fire-prone Western Australia (Bell & Williams, 1998). Future assessments should
358 consider species with other dormancy characteristics when aiming to understand how
359 variation in regeneration is related to different aspects of the fire regime.

360

361 The selective pressure of soil temperatures on dormancy-breaking temperature thresholds of
362 species with different seed sizes highlights the importance of this key seed trait for predicting
363 regeneration after fires of different severities for the dominant physically dormant group of
364 species. A clear consequence of this relationship is that having high dormancy-breaking

365 temperature thresholds also ensures small seeds remain dormant during low-severity fires.
366 This could be a problem in areas that are adapted to high severity wildfires, but undergo a
367 change in their fire regime, such as being repeatedly burnt by low severity fires implemented
368 for management (Auld & Bradstock, 1996; Penman & Towerton, 2008; Ooi *et al.*, 2014;
369 Liyanage & Ooi, 2015). Under a consistent regime of low severity fire, the recruitment of
370 many smaller seeded physically dormant species may therefore be reduced, or in some cases
371 potentially lost from an area. Recent work has shown that low fire severity can reduce species
372 diversity and abundance (see Ooi *et al.*, 2014), presumably from a reduction of recruitment
373 of physically dormant species, but that the effects of a single low severity event can be
374 reversed by a subsequent high severity fire. Ensuring a combination of both hot and cooler
375 burns in an area over time could therefore reduce the probability of species decline related to
376 fire.

377

378

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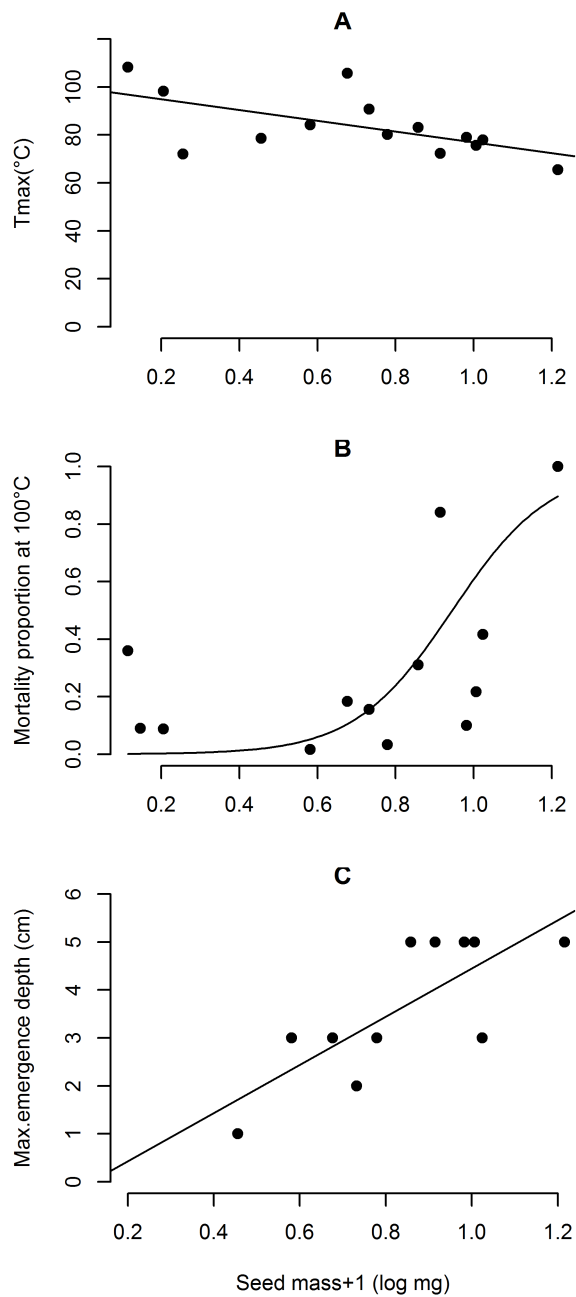
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FIGURES

508 Figure 1. Data for the 14 species tested experimentally in our study, showing the relationships
509 between seed size and (A) the dormancy-breaking temperature required to achieve maximum
510 germination, (B) the proportion of seeds suffering mortality after treatment at 100 °C, and (C)
511 the maximum soil depth from which seeds can emerge.

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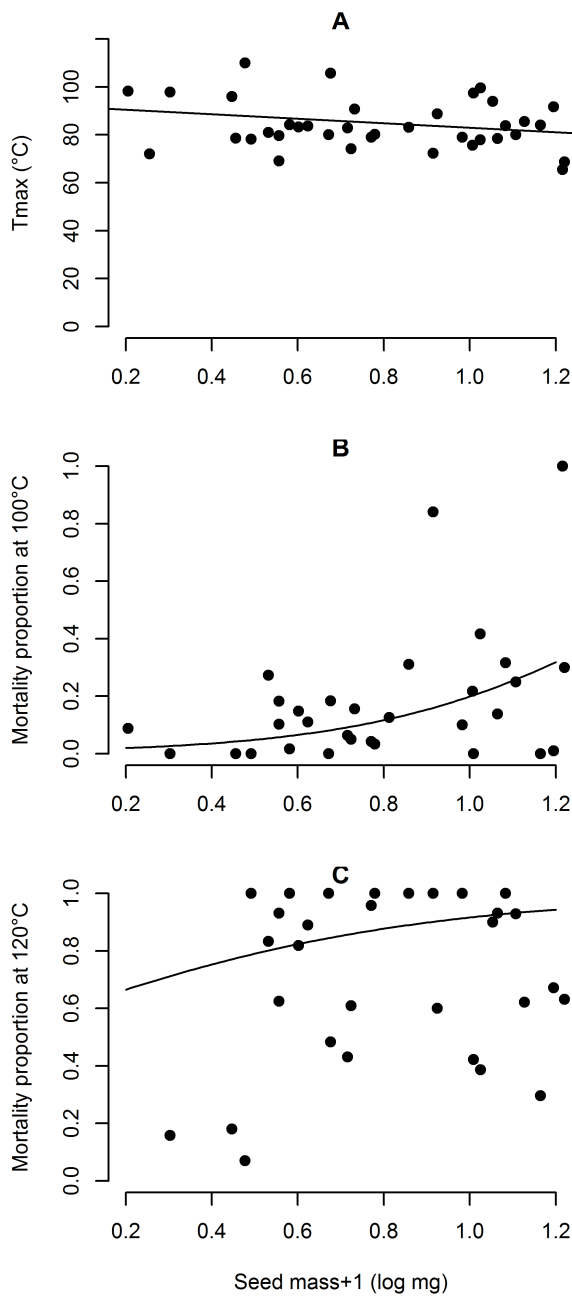
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516 Figure 2. Data for all species, showing the relationships between seed size and (A) the
517 dormancy-breaking temperature required to achieve maximum germination, (B) the
518 proportion of seeds suffering mortality after treatment at 100 °C, and (C) the proportion of
519 seeds suffering mortality after treatment at 120 °C.

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523 Table 1. Mean seed mass, initial viability, dormancy-breaking temperature required to
 524 achieve maximum germination (T_{\max}) and main regeneration mechanism for all study species.
 525 Values are means \pm 1 standard error. OS = obligate seeding and R = resprouting

Species	Family	Seed mass (mg)	Initial viability (%)	T_{\max} (°C)	Main regeneration mechanism
<i>Aotus ericoides</i>	Fabaceae	4.40 \pm 0.84	80.69 \pm 5.97	90.7	R
<i>Bossiaea heterophylla</i>	Fabaceae	15.43 \pm 1.84	95.56 \pm 4.44	65.4	R
<i>Bossiaea stephensonii</i>	Fabaceae	5.01 \pm 0.00	86.67 \pm 6.01	80.2	R
<i>Daviesia corymbosa</i>	Fabaceae	9.15 \pm 1.74	78.33 \pm 5.25	75.6	R
<i>Dillwynia floribunda</i>	Fabaceae	1.86 \pm 0.60	71.67 \pm 10.14	78.6	OS
<i>Dodonaea triquetra</i>	Sapindaceae	3.75 \pm 0.24	72.28 \pm 4.91	105.7	OS
<i>Gompholobium grandiflorum</i>	Fabaceae	8.60 \pm 0.65	100 \pm 0.00	78.9	R
<i>Mirbelia rubiifolia</i>	Fabaceae	2.81 \pm 0.02	93.14 \pm 1.58	84.1	OS
<i>Pomaderris notata</i>	Rhamnaceae	0.40 \pm 0.01	93.00 \pm 0.00	72.02	OS
<i>Pomaderris adnata</i>	Rhamnaceae	0.30 \pm 0.02	92 \pm 0.00	108.2	OS
<i>Pomaderris walshii</i>	Rhamnaceae	0.61 \pm 0.01	100 \pm 0.00	98.21	OS
<i>Pultenaea linophylla</i>	Fabaceae	7.22 \pm 0.09	71.11 \pm 2.22	72.3	OS
<i>Pultenaea stipularis</i>	Fabaceae	9.57 \pm 1.15	65.00 \pm 11.55	77.8	OS
<i>Viminaria juncea</i>	Fabaceae	6.21 \pm 0.13	98.33 \pm 1.67	83.1	R

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