

1 **Interactive effects of climate change and fire on metapopulation viability of a forest-**
2 **dependent frog in south-eastern Australia**

3 Running head: Fire and climate change influence population viability

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19

20 **Abstract**

21 Climate change directly affects the suitability of habitats for species, but also indirectly alters
22 natural disturbances such as fire, which can negatively impact species' persistence.
23 Developing accurate predictions of climate change impacts requires estimates of the
24 interactive effects of climate and disturbance regimes at both population and landscape
25 scales. Here we couple a habitat suitability model with a population viability model to
26 examine the interactive effects of climate change and altered fire regimes on a fire-
27 responsive frog species across its geographic range in south-eastern Australia. By 2100, we
28 predict expected minimum abundances (EMA) to decline by 66% (under GFDL-CM2 A1FI
29 climate projections) or 87% (CSIRO Mk3.5 A1FI) in the absence of fire. Increased frequency
30 of low-intensity fires reduced EMA by less than 5%, whereas increased frequency of high-
31 intensity fires reduced EMA by up to 40% compared with the no-fire scenario. While shifts in
32 fire regimes are predicted to impact metapopulation viability, these indirect effects of fire
33 are far less severe than the direct impact of climate change on habitat suitability. Exploring
34 the interactive impacts of climate change and altered disturbance regimes can help
35 managers prioritize threats across space and time.

36

37 **Keywords**

38 amphibian; fire regime; ecological niche model; matrix population model; niche-population
39 model; Maxent; population viability analysis; RAMAS; habitat suitability model

40

41 **Introduction**

42 Climate change is one of the most significant challenges for the conservation of biodiversity
43 in the 21st century (Heller and Zavaleta 2009). Even small shifts in climate can directly affect
44 survival (Chamaille-Jammes et al. 2006), reproductive output (Forchhammer 1998; Crick and
45 Sparks 1999; Winkler et al. 2002), resource availability (Visser 2005) and habitat use
46 (Telemeco et al. 2009). Climate change may also alter biotic interactions that affect the
47 suitability of habitat for interacting species (Meynecke 2004; Cahill et al. 2013; Moritz and
48 Agudo 2013). A relatively small number of native species are predicted to benefit by
49 extending their distributions into previously unoccupied areas (Thuiller et al. 2005; Hamann
50 and Wang 2006; Van der Putten et al. 2010). However, for most taxa, currently suitable
51 habitat is predicted to decrease in spatial extent, and undergo considerable fragmentation
52 (Meynecke 2004; Thuiller et al. 2005; Penman et al. 2010). Under such circumstances,
53 persistence will depend on an ability to maintain viable populations in remaining pockets of
54 habitat, or an ability to colonise and persist in newly available habitat.

55

56 Climate change is also likely to impact species indirectly through altered disturbance
57 regimes. The severity, frequency and seasonality of drought, flood and wildfire are all
58 predicted to change under future climate scenarios (Palmer et al. 2008; Allen et al. 2010;
59 Bradstock et al. 2012). Species are adapted to specific disturbance regimes, and the
60 alteration of these regimes may affect habitat suitability or key population processes
61 (Whelan 1995; Keith 1996; Wardell-Johnson 2000). However, integrating shifts in
62 disturbance regimes into projections of climate change impacts is difficult due to a poor
63 understanding of the link between climate and most forms of disturbance (Bradstock et al.
64 2014).

65

66 Predicted changes in fire regimes, for example, are extremely uncertain due to the
67 interactive effects of the key drivers of fire in different landscapes. Most studies have
68 predicted that wildfires will increase in frequency and intensity under climate change, but
69 most of these predictions are based solely on predicted increases in the frequency and
70 severity of fire weather (Bergeron and Flannigan 1995; Fried et al. 2004; Hennessy et al.
71 2005; Pitman et al. 2007; Westerling and Bryant 2008; Clarke et al. 2011). Annual area burnt
72 is one spatial expression of fire regimes, and is a function of four switches – weather,
73 biomass, fuel moisture, and ignitions (Archibald et al. 2009; Bradstock 2010). Several
74 opposing forces influence fire regimes under future climates. Firstly, severity of fire weather

75 has been predicted to increase globally (Westerling et al. 2006; Matthews et al. 2012; Clarke
76 et al. 2013), although average wind speed, a key predictor of fire behaviour, is predicted to
77 decrease (McVicar et al. 2008). Secondly, leaf litter, a major component of biomass, is
78 predicted to decrease in many forests and woodlands due to decreased moisture and
79 increased temperature (Penman and York 2010; Matthews et al. 2012; Thomas et al. 2014).
80 Decreases in biomass may in turn result in a decrease in fire intensity and spread. However,
81 these changes may be offset by increases in the concentration of carbon dioxide. Elevated
82 carbon dioxide concentration increases the structural complexity of fuels by thickening
83 woody vegetation and increasing foliage cover (Eamus and Palmer 2007; Donohue et al.
84 2013), thereby increasing fuel loads. Thirdly, fuel moisture is likely to decrease with
85 increasing temperature and seasonal reductions in rainfall (Matthews et al. 2012). Fourthly,
86 ignitions are expected to increase under future climate scenarios (Price and Rind 1994;
87 Syphard et al. 2007; Penman et al. 2013b; Romps et al. 2014), potentially increasing fire
88 frequency and extent. However, the relative importance of each these variables, as well as
89 their feedbacks and the influence of humans on ignition patterns and frequencies, are
90 extremely uncertain, making definitive statements about future fire regimes difficult.

91

92 Accurate predictions of climate change impacts on species require estimates of the
93 interactive effects of climate and disturbance regimes at population and landscape scales.
94 Correlative habitat suitability models (HSMs) (Elith and Leathwick 2009) are commonly used
95 to infer the impact of climate change (Meynecke 2004; Araújo and New 2007). However,
96 these models typically use coarse estimates of dispersal to estimate realised distributions
97 (e.g., no dispersal vs. unlimited dispersal) , and do not explicitly incorporate demographic
98 parameters that influence extinction risk (Pearson and Dawson 2003; Fordham et al. 2012).
99 Recently, these limitations have been addressed by coupling HSMs with population viability
100 analyses (PVAs) (Keith et al. 2008; Brook et al. 2009; Dullinger et al. 2012; Fordham et al.
101 2012). PVAs use key demographic variables to estimate a populations' risk of decline, often
102 simulating various alternative management scenarios. Coupling HSMs with PVAs allows for
103 spatially explicit predictions of metapopulation extinction risk while accounting for dispersal
104 between the temporally dynamic locations of suitable habitat patches (Keith et al. 2008;
105 Conlisk et al. 2012; Fordham et al. 2012; Swab et al. 2012; Bonebrake et al. 2014). Few
106 studies, however, have examined the interactive effects of climate change and disturbance
107 regimes on metapopulation viability (but see Keith et al. 2008; Swab et al. 2012).

108

109 Frogs are considered extinction-prone globally (Houlahan et al. 2000; Stuart et al. 2004) and
110 are likely to be extremely susceptible to future climatic changes (Pounds et al. 2006;
111 Lemckert and Penman 2012). Species that occur predominantly in fire-prone vegetation will
112 be further impacted by climate-driven shifts in fire regimes. The impacts of different fire
113 regimes on frog species are poorly understood (Penman et al. 2006b) but are likely to vary
114 with fire intensity, species' life history traits, and the exposed life stages (Bamford 1992;
115 Driscoll and Roberts 1997; Pilliod et al. 2003; Woinarski et al. 2004; Penman et al. 2006b;
116 Penman and Towerton 2007).

117

118 Given the uncertainties about the impacts of climate change on fire regimes, it is important
119 to examine the response of extinction-prone biota across the potential spectrum of fire
120 frequency and intensity combinations that may occur in the future. Results of such studies
121 will help identify fire regimes associated with high extinction risk and clarify whether these
122 vary depending on future climate (Keith et al. 2008; Swab et al. 2012). Once high-risk fire
123 regimes are identified, we may be able to develop management strategies that reduce the
124 probability of such regimes arising under future climates. In this study, we couple a HSM and
125 a PVA to examine the interactive effects of climate change and fire regime on a fire-
126 responsive frog species. Many studies have examined shifts in predicted suitable habitat
127 under climate change without explicitly considering dispersal or impacts of other threats
128 such as fire. Here we overcome these limitations by explicitly considering dispersal and shifts
129 in habitat suitability under changing climates and a range of fire regimes. This coupled
130 modelling approach brings several advantages. First, it allows us to explicitly test effects of
131 fire regimes on the species under changing climates, and the interaction between these
132 threats on the viability of the species over a 100-year period. Second, this approach
133 estimates the viability of the species directly by integrating demographic data, rather than
134 inferring viability based on habitat suitability alone. As a result, we are able to estimate the
135 relative threat to persistence due to fire and to climate change, which we would not have
136 been able to do if we did not have a coupled model. Finally, the landscape-level impacts of
137 fire on metapopulation viability would not be captured in either a standalone HSM approach
138 or a static PVA. In undertaking this analysis, we specifically aimed to assess whether the fire
139 regimes that are most detrimental to this species under current climates are also
140 detrimental under future climates, and explore whether we can develop management
141 strategies to mitigate the risk of extinction under such regimes.

142

143 **Materials and methods**

144

145 *Study species*

146 The study focused on the Giant Burrowing Frog, *Heleioporus australiacus*, as this species is
147 restricted to fire-prone native vegetation throughout its range, primarily dry forest and
148 heathland (Penman et al. 2004). *Heleioporus australiacus* is a large myobatrachid species
149 found in native vegetation along the coast and adjacent ranges of south-eastern Australia
150 (Figure 1). Climate strongly influences the species' current distribution (Penman et al. 2005b,
151 2007b) and behaviour (Penman et al. 2006a). Longer-term climatic variation has also shaped
152 the species' distributional extent. There are currently six species within the *Heleioporus*
153 genus, with all other species occurring in south-western Australia (Cogger 2000). Molecular
154 evidence indicates that *H. australiacus* evolved from a west to east migration five million
155 years ago and has subsequently been isolated due to changing climates that caused loss of
156 forest cover in southern Australia (Maxson and Roberts 1984; Roberts and Watson 1993).

157

158 The species spends most of its time at depths of 1-30 cm below the soil surface (Lemckert
159 and Brassil 2003; Penman et al. 2008c). It is most active after rainfall, when it forages above
160 ground (Penman et al. 2006a). After summer or autumn rains, the species moves to
161 breeding sites such as hanging swamps, small creeks and wet heath (Littlejohn and Martin
162 1967; Daly 1996; Penman et al. 2006c). *Heleioporus australiacus* is currently listed as
163 *vulnerable* on the IUCN Red List, and under Australian Commonwealth and State legislation.

164

165 FIGURE 1 APPROXIMATELY HERE

166

167 The impact of fire is likely to be greatest on adult *H. australiacus* (Penman et al. 2008b).
168 During the adult phase, individuals spend >99% of their time in the forest away from
169 breeding areas (Penman et al. 2008c) and it is these areas that are more likely to burn during
170 a low or high intensity fire (Penman et al. 2007a; Collins et al. 2013). Low-intensity fires are
171 likely to result in low mortality of adult frogs, due to the fossorial nature of the species, and
172 the patchiness (Penman et al. 2007a) and low soil heating associated with low-intensity fires
173 (Penman et al. 2006b; Penman and Towerton 2008). Conversely, high-intensity fires tend to
174 result in greater adult mortality (Penman et al. 2004), as such fires are more homogenous
175 (Bradstock et al. 2010) and result in higher soil heating (Humphreys and Craig 1981;
176 Bradstock et al. 1992). To a lesser extent, fire may affect tadpole mortality. Breeding occurs

177 immediately after the fire season for this species, and increased sedimentation of the
178 streams following a fire has been postulated to increase tadpole mortality (Penman et al.
179 2004). This effect is likely to be greater after high-intensity fires, which are expected to burn
180 more of the riparian zone (Penman et al. 2007a; Collins et al. 2013).

181

182 *Predictive modelling*

183 Estimating the extinction risk of *H. australiacus* under future climate and fire regime
184 scenarios involved four main steps. First, we built a predictive HSM that related the current
185 distribution of the species to environmental covariates. Second, we used this HSM and
186 projections of future climatic conditions to predict future habitat suitability. Third, we used
187 published and unpublished data and expert knowledge on *H. australiacus* vital rates and
188 dispersal to build a stage-structured, stochastic matrix population model. Finally, this matrix
189 model was coupled with the HSM in order to perform a spatially-explicit PVA under future
190 climate and fire scenarios. Fire scenarios were not spatially explicit, but incorporated a range
191 of probabilistic fire return intervals and intensities as catastrophes in the PVA. We describe
192 each of these steps in detail below.

193

194 *Habitat suitability model*

195 Locality data for the HSM were compiled from survey and museum records held by the New
196 South Wales Office of Environment and Heritage, the Victorian Department of Environment
197 and Primary Industries, and the Australian Museum. Records were carefully checked by
198 experts on the species by viewing the records overlaid on Google Earth satellite images and
199 with other GIS data, and zooming in to consider locational accuracy. Erroneous and
200 unreliable records were removed. Records were thinned so that locations were separated by
201 a minimum distance of 1 km to reduce pseudo-replication and survey bias, with preference
202 given to the most recent records. This resulted in a set of 250 presence records across the
203 species' range. The experts judged the resulting dataset to be a reasonable and unbiased
204 sample of the species distribution. A set of 9120 background points (a sample representing
205 conditions throughout the region of interest; Elith et al. 2011) was sampled from within a
206 region defined by the four bioregions in which the species occurs (Sydney Basin, South
207 Eastern Highlands, South East Corner, South East Coastal Plain) (Environment Australia
208 2000).

209

210 Spatial environmental data layers (resolution of 9 arc-seconds, approximately 281 m) were
211 selected as potential predictors of suitable habitat based on previous studies of the species
212 (Penman et al. 2004; Penman et al. 2007b) (Table 1). HSMs containing different subsets of
213 predictors were then fitted using the Maximum Entropy algorithm of Phillips *et al.* (2006) ,
214 an appropriate method for modelling presence-background data that also performs well for
215 prediction (Elith et al. 2006). Models used hinge features with a regularization multiplier of
216 1.5 to create models with smoothed responses that would extrapolate in a biologically
217 realistic manner (Elith et al. 2010). An iterative model fitting approach was taken. Each
218 model was initially evaluated by experts to ensure realism of response curves and
219 predictions. In models accepted by experts, variables providing small contributions (<1%)
220 were removed and the models refitted and rechecked by the experts. We primarily relied on
221 expert opinion for model evaluation, but also checked that model fit was reasonable using
222 the area under the receiver-operating characteristic curve (AUC) on training data.

223

224 TABLE 1 APPROXIMATELY HERE

225

226 Future habitat suitability was estimated by projecting HSMs to future environmental
227 conditions predicted by two global climate models (GCMs). All climatic variables were
228 predicted to change in the future; we assumed temporally static vegetation extent and
229 topographic characteristics of the landscape. We used GCMs appropriate to the study region
230 – CSIRO Mk 3.5 and GFDL-CM2 (Perkins et al. 2007; Suppiah et al. 2007) – and we assumed
231 the A1FI (fossil fuel intensive) emissions scenario, which predicts a large temperature
232 increase and most closely resembles the realized trajectory (Working group 3 2000; Peters et
233 al. 2013). Individual projections of spatial climate data were made for the years 2030, 2050,
234 2070 and 2100 using the algorithms supplied in ANUCLIM v6.1

235 (<http://fennerschool.anu.edu.au/files/anuclim61.pdf>) and the CSIRO OZCLIM

236 (www.csiro.au/ozclim/) climate change grids, and these were linearly interpolated to
237 create projections for each year for the 100 year period from 2000 to 2099 (Keith et al.
238 2008).

239

240 *Demographic model*

241 A spatially-explicit, stochastic matrix population model based on annual time steps was
242 constructed in RAMAS GIS v5 (Akçakaya and Root 2005). We considered three distinct life
243 history stages (tadpoles, juveniles and adults) and only modelled females as males were

244 considered non-limiting. Tadpoles metamorphosed after either one or two seasons (Daly
245 1996; Penman et al. 2004). Based on field observations of growth rates across the species'
246 range, we assumed individuals were juveniles for three years before joining the breeding
247 population. Demographic rates were estimated from published information (Daly 1996;
248 Anstis 2002; Lemckert and Brassil 2003; Penman 2005; Penman et al. 2006a; Penman and
249 Lemckert 2007; Penman et al. 2008b; Penman et al. 2008c), unpublished data, and expert
250 knowledge.

251

252 Vital rates varied between life stages, and annually due to environmental and demographic
253 stochasticity. Environmental stochasticity was assumed to follow a lognormal distribution
254 and demographic stochasticity was modelled by sampling the number of survivors from a
255 binomial distribution and the number of offspring (fecundity) from a Poisson distribution.
256 Survival rates were lowest and most variable in tadpole stages, and were greatest and least
257 variable in the large adult stage (Table 2). Fecundity varied between years with a CV of 20%.
258 Variation in survival and fecundity were assumed to be correlated within populations.
259 Elasticities for the model are presented in Table 3 and demonstrate that the model is most
260 sensitive to adult survival. Spatial autocorrelation in environmental stochasticity (i.e.
261 temporal fluctuation in vital rates) was based on a correlation-distance function derived
262 from annual rainfall data from meteorological stations in the region (Fordham et al. 2012).
263 Breeding and non-breeding behaviour of the species is strongly linked to rainfall (Penman et
264 al. 2006a; Penman et al. 2008b; Penman and Brassil 2010).

265

266 A contest model (Akçakaya and Root 2005) was adopted to represent density dependence of
267 vital rates, given the species' relatively long generation length and evidence of territorial
268 behaviour in breeding (Penman et al. 2004) and non-breeding habitats (Penman et al.
269 2008c). The carrying capacity of each population was estimated from relative habitat
270 suitability values predicted by the HSM (see Model integration below).

271

272 TABLE 2 APPROXIMATELY HERE

273

274 Annual dispersal rates between populations (defined as grid cells; see below) were
275 estimated from radio-telemetry (Penman et al. 2008c) and capture-recapture data from
276 unpublished pitfall-trapping studies. Most recorded movements of the species involve
277 distances less than 300 m (Penman et al. 2008c). Dispersal was assumed to predominantly

278 occur in the juvenile stage, particularly in the first year, and movement was only possible
279 between four neighbouring cells in the cardinal directions. Juveniles were modelled as being
280 20 times more likely to disperse than other terrestrial stages. Based on grid geometry, the
281 average annual probability of dispersal to a neighbouring grid cell was 0.0044. Dispersal
282 rates varied annually with a CV of 5%.

283

284 Low- and high-intensity fires were included separately in models as stochastic
285 “catastrophes” that reduced abundances of all life stages (Table 2). Fires were not spatially
286 correlated, i.e. fires in one cell did not affect adjacent cells. However, as explained below,
287 the PVA was run on an aggregated grid with cell size approximately 10 km x 10 km. This
288 resolution exceeds the areal extent of all low-intensity fires and many of the wildfires in the
289 region. Due to uncertainty about future fire regimes, we considered probabilistic fire return
290 intervals of 10, 20, 30 and 40 years. The 20-year return interval approximates the current
291 fire regime in the north of the species’ range (Bradstock et al. 2012), while the 30-year
292 interval is more representative of that experienced in the south.

293

294 *Model integration*

295 The HSM and demographic model were coupled following the procedures described by Keith
296 *et al.* (2014). HSM prediction grids were transformed to an equal-area projection (Australian
297 Albers) with a resolution of 281 m. Cells with predicted habitat suitability less than the fifth
298 percentile of suitability at training occurrence points were considered unsuitable and set to
299 a value of 0. The 281 m cells were then aggregated (by summing suitability scores) to 9,835
300 m cells. Subsequently, aggregated grid cells with values less than the first percentile of the
301 values at training occurrence points were excluded, as they represented very small and
302 potentially diffuse areas of suitable habitat. Each cell formed a population unit or patch for
303 modelling purposes. Carrying capacity of each patch was calculated as a linear function of
304 the habitat suitability of that patch multiplied by the number of individuals that would occur
305 in optimal habitat. Field data suggest *H. australiacus* has an approximately 1:1 sex ratio
306 (Penman *unpublished data*). Individuals have non-overlapping home ranges of 0.04 ha, with
307 no difference between the sexes (Penman et al. 2008c). Within a 281 m cell, we assumed
308 one breeding site was present. Outside breeding events, the species shelters at sites that are
309 generally at least 75 m from the nearest stream. Using these data, we estimated that
310 optimal habitat would support approximately 10 females per hectare, which translates to 73
311 females per 281 m grid cell. For each time step, carrying capacity of each patch was

312 estimated as HS^{*73} , where HS is the aggregated habitat suitability value from the HSM at
313 each 9,835 m cell.

314

315 For patches associated with known occurrences, the initial abundance was assumed to be at
316 carrying capacity and at a stable age distribution. All other patches were assumed to be
317 unoccupied. The model was then run for a burn-in period long enough to ensure the
318 metapopulation occupancy reached equilibrium. One thousand iterations were
319 subsequently run for each combination of fire scenario and climate model for the 100-year
320 period from 2000 to 2099. For comparison purposes, we also ran 1,000 iterations under
321 stable climatic conditions. Outputs were compared with respect to estimates of expected
322 minimum abundance (EMA), calculated as the mean, across simulations, of the 100-year
323 population size trajectories' minima (McCarthy and Thompson 2001).

324

325 Sensitivity of the model was tested by independently increasing or decreasing each of the
326 transition probabilities and the effect of fire on survival by 20%. Values were altered for the
327 20-year fire return interval scenario with climatic changes predicted by the CSIRO Mk 3.5
328 model. These sensitivity analyses were conducted for both low- and high-intensity fire
329 scenarios. Model sensitivity was measured using the change in the Expected Minimum
330 Abundance (EMA), with models considered sensitive to a parameter if the EMA changed by
331 more than 20%.

332

333 **Results**

334

335 The final HSM included six variables, five of which represent aspects of climate (Table 4).
336 Summer rainfall, extant vegetation, rainfall seasonality and annual mean temperature were
337 the primary drivers in the model (see supplementary material for the full Maxent output).
338 The model was judged as sensible by the experts, and had high discrimination capacity, with
339 an AUC of 0.897 on training data. Under current climatic conditions, the model predicted
340 higher suitability in northern areas where there were substantially more species
341 observations. Under the projections of both GCMs, the HSM predicted considerable
342 contraction of suitable habitat to the south of the species' range and into higher elevation
343 sites (Figure 2; Figure 3). The CSIRO Mk3.5 model predicted a marginally smaller future
344 distribution than the GFDL-CM2 model.

345

346 TABLE 4 APPROXIMATELY HERE

347

348 Regardless of GCM, temporal changes in habitat suitability due to climate change were more
349 influential than fire regimes in determining EMA. When using CSIRO Mk3.5 projections of
350 future climate, EMA decreased by approximately 87% relative to the no climate change
351 scenario for a given fire scenario (Figure 4). Similarly, GFDL-CM2 projections led to a
352 reduction in EMA of approximately 66% (Figure 4). The influence of fire regime on
353 abundance was consistent across future climate scenarios. Low-intensity fire regimes
354 resulted in very small reductions (<5%) in EMA relative to an equivalent scenario without fire
355 and the result was consistent regardless of the inter-fire interval. In contrast, high-intensity
356 fire regimes resulted in large reductions in EMA that increased as fire interval decreased. At
357 a 40-year interval, EMA was reduced by approximately 10% compared to a no-fire scenario,
358 whereas at a 10-year interval it was reduced by approximately 40% (Figure 4). The worst-
359 case scenario was a regime of frequent high-intensity fires (10-year intervals) which reduced
360 the EMA to 7.8% (CSIRO Mk3.5) or 21.1% (GFDL-CM2) of the scenario lacking fire and
361 climate change.

362

363 The model was not considered sensitive to any of the vital rates in the model (Table 5).

364 FIGURES 2, 3, 4 APPROXIMATELY HERE

365 TABLE 5 APPROXIMATELY HERE

366 **Discussion**

367 Habitat suitability models estimate direct effects of climate change on habitat suitability, but
368 often ignore synergies between spatial threats. We have shown that interactions between
369 climate change and disturbance regimes can be important when considering the impacts of
370 climate change. Species are adapted to specific fire regimes, which are likely to shift as a
371 result of climatic change. Our results suggest that for *H. australiacus*, the direct impact of
372 climate change on habitat suitability will far outweigh any potential shifts in fire regimes
373 throughout the species' range. However, avoiding frequent, high-intensity fires could still
374 produce benefits to the viability of the metapopulation. These results can assist
375 conservation managers in developing plans to mitigate the direct impacts of climate change
376 on habitat suitability.

377

378 *Impacts of fire on metapopulation viability*

379 Changes in fire regimes were predicted to impact the viability of the *H. australiacus*
380 metapopulation under both current and future climates, but the magnitude of this impact
381 varied according to the combination of fire interval and fire intensity. Specifically, our results
382 indicate that fire frequency affects metapopulation viability only when fires are of high
383 intensity. Interestingly, the effect of fire was consistent under a stable and changing climate.
384 Modelled low-intensity fires were based on observations of prescribed fire that were patchy
385 and resulted in low adult mortality (Penman et al. 2007a). Soil temperatures experienced in
386 such fires are not sufficient to result in mortality for the majority of individuals in the fire
387 area (Penman et al. 2006b; Penman and Towerton 2008). In contrast, high-intensity fires
388 result in greater heating of the soil (Humphreys and Craig 1981; Bradstock et al. 1992),
389 causing higher mortality in the adult population. The effects of high-intensity fires are
390 exacerbated by the timing of fires, which occur immediately prior to the breeding season
391 and are thus expected to reduce reproduction capacity within the population. The overall
392 reduction in metapopulation abundance associated with frequent, high-intensity fires
393 therefore reflects the inability of populations to recover from larval mortality, but
394 particularly from high adult mortality between successive fires (Table 3).

395

396 TABLE 3 APPROXIMATELY HERE

397

398 Our models simulated impacts of fire on survival, but did not include indirect effects of a
399 changed fire regime. The two most likely indirect impacts are changes in the structural
400 suitability of habitat and alterations to food resources. Altering fire frequency can result in
401 significant shifts in floristic diversity and vegetation structure (Cary and Morrison 1995; Lunt
402 and Morgan 1999; Gent and Morgan 2007; Keith et al. 2007; Penman et al. 2011a).
403 Increased fire frequency generally increases the diversity and extent of ground cover species
404 (Keith 1996; Andersen et al. 2005; Penman et al. 2008a), which decreases habitat suitability
405 for this and other burrowing frog species (Jansen et al. 2001; Penman et al. 2005a).
406 Furthermore, invertebrate diversity is closely linked with floristic diversity and vegetation
407 structure (Andersen et al. 2009; Wittkuhn et al. 2011). Fire frequency also directly impacts
408 invertebrates by altering composition and abundance (York 2000; Andersen et al. 2005).
409 Invertebrates dominate the diet of *H. australiacus* and changes in invertebrate communities
410 may reduce nutritional intake for the species (Penman et al. 2006b), potentially reducing
411 survival and reproductive output. The species may therefore be more susceptible to high
412 frequency, low-intensity fire regimes than suggested by our results. Hence the indirect

413 effects of changes in fire regimes on *H. australiacus* under future climates warrants further
414 examination.

415

416 *Implications for fire management*

417 Our results suggest that fire management actions that reduce the risk of frequent high-
418 intensity fires would be beneficial to *H. australiacus* both now and under possible future
419 climates. Prescribed fire (i.e., controlled, low-intensity fire), is often proposed as a tool to
420 reduce the extent of future fires (Fernandes and Botelho 2003; Penman et al. 2011b).
421 However, there does not appear to be a direct trade-off between high- and low-intensity
422 fires. Several studies have found that to reduce the extent of wildfire in Eucalypt forests by
423 one hectare, three to four hectares of land must be treated with prescribed fire (Boer et al.
424 2009; Price and Bradstock 2011). That is, for every 1% decrease in the average annual area
425 burned by wildfire, managers must increase the annual prescribed burning effort by 3-4%
426 (Bradstock et al. 2012). The net effect is a 2-3% increase in the total area affected by fire in
427 the landscape each year. The combined impact of increased prescribed fire and wildfires
428 would exceed critical thresholds for a number of flora species (Kenny et al. 2004), resulting
429 in significant shifts in community composition and structure, potentially impacting *H.*
430 *australiacus* through processes described above. Additionally, although empirical analysis of
431 fire severity patterns in Eucalypt forests have shown that the probability of high-intensity
432 fires is lower in young fuels (< 5 years old), this is dependent on fire weather (Bradstock et
433 al. 2010; Price and Bradstock 2012; Collins et al. 2013), with the effect of prescribed fire
434 either reduced or lost under extreme fire weather. The majority of area burned by wildfire in
435 the study area occurs under extreme fire weather (Bradstock et al. 2009), suggesting
436 prescribed fire is unlikely to reduce the occurrence, extent or severity of high-intensity fires.

437

438 Clearly, alternate fire management strategies that mitigate the risk of more frequent high-
439 intensity fires are required. One potential solution is the management of ignitions, which has
440 been shown to significantly reduce the extent and impact of wildfires (Cary et al. 2009;
441 Wintle et al. 2011). In the study area, the majority of ignitions are anthropogenic (Penman et
442 al. 2013a). However, to date there are no known successful management approaches that
443 effectively reduce the occurrence of anthropogenic ignitions (Bryant 2008). If successful
444 ignition abatement strategies can be developed and implemented, they offer a means of
445 ameliorating the cumulative impacts of two semi-independent threats. Slower rates of
446 decline that result from such strategies may allow more time for climate mitigation policies

447 to take effect. Regan et al. (2011) similarly showed that appropriate fire management
448 strategies were crucial to limiting the combined impacts of fire and disease on a fire-prone
449 plant species.

450

451 *Climate change impacts on metapopulation viability*

452 While changes in the frequency of high-intensity fires under climate change will impact the
453 viability of *H. australiacus*, the effect is predicted to be small relative to the direct impact of
454 changes in habitat suitability due to climate change (Figure 4). Our models predict climate
455 change will reduce metapopulation viability through an extensive reduction in climatically
456 suitable habitat by 2100 (Figure 2; Figure 3). By that time, suitable habitat is predicted to be
457 confined to a small area in the southern portion of the species' range, where there are few
458 recent records of the species.

459

460 The loss of the northern populations would represent a significant conservation issue for this
461 species. *Heleioporus australiacus* is thought to be composed of two genetically distinct taxa
462 (Penman et al. 2008b), with a geographic division between the two taxa at the current
463 disjunction in the distributional records (Penman et al. 2005b) (Figure 1). Our study suggests
464 that under future climates we might expect the complete extinction of the northern
465 populations, with only the southern populations persisting. Even if the two groups of
466 populations are found to represent a single species, there will be significant losses in its
467 genetic diversity, as well as that of other species that occupy similar ranges. Collection and
468 storage of genetic samples from these populations should be undertaken in an attempt to
469 conserve their genetic diversity.

470

471 *Conservation management*

472 Managing biodiversity through rapid climatic change poses great challenges to conservation
473 managers globally (Heller and Zavaleta 2009). Models such as ours can help scientists and
474 conservation managers identify key management strategies that could be implemented to
475 protect the species. In the case of *H. australiacus*, the key actions we propose based on the
476 results of the study are:

477

- 478 1. Identification of new populations at the southern end of the species' range
479 (potentially guided by predictions of our HSM) and the protection of habitats
480 predicted as suitable by 2100. Our models suggest these areas may be climatic

481 refuges for the species. It is therefore vital to locate and conserve these populations
482 to promote the long term survival of the species. If necessary, assisted migration
483 may also be a viable strategy (McDonald-Madden et al. 2011).

484 2. Monitoring northern populations to detect an early warning of expected responses
485 to climate change. These populations are predicted to disappear in a relatively short
486 period of time (20-40 years). Identifying declines in these populations will allow
487 managers to decide when to increase their investment in the conservation of the
488 species in these areas. Data from monitoring could be used to validate and revise
489 the model, particularly if a range of fire histories are considered.

490 3. Collection and storage of genetic material to conserve genetic diversity (see above).

491 4. Investigate and develop strategies for reducing human ignitions during extreme fire
492 weather as a means of minimising population declines related to climate change.

493

494

495 *Model limitations*

496 Our modelling approach was selected to provide an assessment of the relative influence of
497 the direct impacts of climate change on habitat suitability and the indirect effects of
498 changing fire regimes. However, there are three major limitations to our modelling
499 approach. Firstly, we did not model spatial autocorrelation in fire (i.e. fire in one grid cell did
500 not affect the probability of fire in adjacent cells). As a result, though there was some
501 probability of fires occurring simultaneously in adjacent or nearby cells, large wildfires (i.e. >
502 10 000 ha) were not explicitly included. In reality, there is spatial and temporal clustering in
503 the probability of a fire occurring (Boer et al. 2008; Bradstock et al. 2009; Penman et al.
504 2013b) that we did not incorporate, and the fire impacts we detected may have been over-
505 estimated unless suitable habitat was similarly autocorrelated. Alternatively, we may have
506 under-estimated the impact of fire as the model did not include extremely large wildfires
507 that have the potential to simultaneously impact a large number of populations or isolated
508 populations in fragmented landscapes. In reality, however, such events are extremely rare.

509

510 Secondly, the model was not capable of incorporating the interactive effects of low and high
511 intensity fires in a meaningful way. Disturbance events in the RAMAS software are treated as
512 independent with a probability of occurrence. In reality, low intensity planned fires will not
513 occur for a given period after a wildfire due to ecological concerns (Kenny et al. 2004).

514 Furthermore, the impact of high intensity wildfire on populations of this species may be

515 altered by previous low intensity fires (Penman et al. 2006b). RAMAS is also incapable of
516 capturing this interaction. Addressing this issue would require a fire regime model coupled
517 with the HSM and PVA.

518 Thirdly, our model assumes that land use and vegetation are static over the study period. As
519 human populations continue to grow, urban areas will continue to encroach on native
520 vegetation (Syphard et al. 2007), thereby decreasing the extent of habitat and shifting
521 vegetation boundaries (Cramer et al. 2001). Climate change is also likely to lead to spatial
522 dynamics in the distribution of vegetation. Our assumption of static land cover is therefore
523 an optimistic scenario and the magnitude of the change may in fact be much greater.
524 Despite these limitations, the aim of our study was to examine the relative contribution of
525 climate change and fire to metapopulation viability. A thorough examination of all the
526 potentially interacting factors would require far more untested assumptions regarding fire
527 regimes and vegetation dynamics, and a more complex modelling framework.

528 **Conclusion**

529 Simulating environmental change and management actions by coupling models of habitat
530 suitability with spatial models of population dynamics provides a means of assessing the
531 relative importance of threats to species, as well as their potential interactions. Our results
532 support the notion that climate change is likely to be the major threat to biodiversity in the
533 coming century. While shifts in fire regimes are predicted to impact the viability of *H.*
534 *australiacus*, the effect is far less severe than direct impacts of climate change. These results
535 are consistent with some studies (Lawson et al. 2010), but contrast with others that found
536 shifts in fire regimes were a greater threat to other species (Swab et al. 2012). Exploring the
537 interactive impacts of climate change and disturbance regimes allows managers to prioritize
538 threats across space and time. In turn, managers can identify conservation actions that
539 increase species' ability to persist in future climates.

540

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 549

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920 **Tables**

921

922 **Table 1: Potential predictors for the habitat suitability modelling process**

Variable	Definition	Source
Annual mean moisture index	Mean of weekly moisture index values 0 to 1	Bioclim v 6.0
Annual mean temperature	Mean of weekly temperatures in degrees Celsius	Bioclim v 6.0
Annual precipitation	Mean annual precipitation in mm/year	Bioclim v 6.0
Extant vegetation	Binary distribution of extant native vegetation (0 = absent, 1 = present)	(Keith 2011)
Highest period radiation	Largest weekly solar radiation estimate	Bioclim v 6.0
Max temp. of the warmest period	The highest maximum temperature in all weeks of the year in degrees Celsius	Bioclim v 6.0
Mean diurnal temperature range	The mean of the weekly diurnal temperature ranges in degrees Celsius.	Bioclim v 6.0
Mean moisture of the lowest quarter	Average moisture index (0 to 1) of the quarter with the lowest moisture index	Bioclim v 6.0
Mean moisture of the highest quarter	Average moisture index (0 to 1) of the quarter with the highest moisture index	Bioclim v 6.0
Min temp. of the coldest period	Average moisture index (0 to 1) of the quarter with the lowest temperature	Bioclim v 6.0
Precipitation of the driest period	Precipitation of the driest month (mm)	Bioclim v 6.0
Rainfall seasonality	SD of the weekly rainfall	Bioclim v 6.0
Slope	Slope of the ground (degrees)	(Keith 2011)
Substrate	A coarse measure of soil type	(Keith 2011)
Summer rainfall	Precipitation falling in summer months	Bioclim v 6.0
Temperature seasonality	SD of the weekly temperature	Bioclim v 6.0
Winter rainfall	Precipitation falling in winter months	Bioclim v 6.0

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926 **Table 2: Mean transition rates (and standard deviations) included in the population model**
 927 **(Y = year). Cell values indicate the rate of transition from the stage indicated by the**
 928 **column's header, to the stage indicated by the row's name, with the exception of the first**
 929 **row, which shows the fecundity of each stage. The last two rows show the survival**
 930 **multipliers in years of low and high intensity fires, respectively.**

	Tadpole Y1	Tadpole Y2	Juvenile Y1	Juvenile Y2	Juvenile Y3	Small adult	Large adult
Tadpole Y1	0	0	0	0	0	50 (10)	150 (30)
Tadpole Y2	0.01 (0.002)	0	0	0	0	0	0
Juvenile Y1	0.1 (0.02)	0.1 (0.02)	0	0	0	0	0
Juvenile Y2	0	0	0.25 (0.025)	0	0	0	0
Juvenile Y3	0	0	0	0.25 (0.025)	0	0	0
Small adult	0	0	0	0	0.5 (0.05)	0.25 (0.025)	0
Large adult	0	0	0	0	0	0.5 (0.05)	0.75 (0.025)
Low intensity	0.75	0.75	0.90	0.95	0.95	0.95	0.95
High intensity	0	0.05	0.20	0.40	0.50	0.50	0.50

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935 Table 3: Elasticities in the PVA model based on the stage matrix.

	Tadpole Y1	Tadpole Y2	Juvenile Y1	Juvenile Y2	Juvenile Y3	Small adult	Large adult
Tadpole Y1	0	0	0	0	0	0.0198	0.1012
Tadpole Y2	0.0011	0	0	0	0	0	0
Juvenile Y1	0.1199	0.0012	0	0	0	0	0
Juvenile Y2	0	0	0.121	0	0	0	0
Juvenile Y3	0	0	0	0.1208	0	0	0
Small adult	0	0	0	0	0.1208	0.0377	0
Large adult	0	0	0	0	0	0.1004	0.256

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938 **Table 4: Variable importance as estimated by Maxent.**

Variable	Percent Contribution	Permutation importance
Summer rainfall	68	11.8
Extant vegetation	9.2	4.2
Rainfall seasonality	8.8	44.5
Annual mean temperature	8.5	17.5
Annual mean moisture index	4	20.7
Max temp. of the warmest period	1.5	1.3

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942 Table 5: PVA model sensitivity to input parameters using the 20 year fire interval for the
 943 CSIRO Mk3.5 climate prediction. Each parameter is varied individually while all others are
 944 held constant. Missing values represent cases where the change in parameter results in a
 945 transition rate that exceeds 100%. Values represent the percentage change in the Expected
 946 Minimum Abundance.

947

Parameter	Stage	Decrease 20%	Increase 20%
Survival	All tadpoles	0.89	0.31
	Tadpole year 1	1.73	1.65
	Tadpole year 2	0.73	0.08
	Year 1 juvenile	0.67	2.12
	Year 2 juvenile	1.09	1.25
	Year 3 juvenile	1.08	0.01
	Small adult a	1.23	0.23
	Small adult b	3.01	0.17
	Big adult	1.00	1.21
Fecundity	Small adult	1.43	0.95
	Big adult	1.05	1.70
High intensity fire survival	Tadpole year 1	1.41	
	Tadpole year 2	1.47	0.66
	Year 1 juvenile	0.19	1.16
	Year 2 juvenile	1.09	0.98
	Year 3 juvenile	0.44	1.28
	Small adult	0.24	2.35
	Big adult	3.93	3.43
Low intensity fire survival	Tadpole year 1	0.55	0.72
	Tadpole year 2	0.71	0.32
	Year 1 juvenile	0.15	
	Year 2 juvenile	0.80	
	Year 3 juvenile	1.66	
	Small adult	1.68	
	Big adult	2.46	

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951 **Figure captions**

952

953 **Figure 1: Maxent prediction of habitat suitability for *H. australiacus* under current climatic**
954 **conditions. White circles indicate locations where the species has been observed.**

955

956 **Figure 2: Future predictions of habitat suitability for *H. australiacus*, assuming climate**
957 **changes according to projections of the CSIRO Mk 3.5 model, with emissions following the**
958 **A1FI scenario. Suitability scale is equivalent to that in Figure 1.**

959

960 **Figure 3: Future predictions of habitat suitability for *H. australiacus*, assuming climate**
961 **changes according to projections of the GFDL-CM2 model, with emissions following the**
962 **A1FI scenario. Suitability scale is equivalent to that in Figure 1.**

963

964 **Figure 4: Proportional change in the expected minimum abundance of *H. australiacus* from**
965 **1000 simulations covering the period 2000–2100 under varying fire return intervals for: a)**
966 **stable climate; b) climate change scenario based on the CSIRO Mk3.5 model; and c) climate**
967 **change scenario based on the GFDL-CM2 model. Change is measured relative to a base**
968 **scenario with no fire and constant climate. Note the y-axis scales differ between plots.**
969 **Confidence intervals are not shown as they are not visible at the resolution of the graph**
970 **due to the large sample size (n=1000) in the simulations.**

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