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1 ORIGINAL ARTICLE

2

3 **Contrasting patterns of genetic diversity in two lizard species across fire**

4 **mosaics**

5

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19 **Running title:** Fire effects on lizard genetic diversity

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23

24

25 **Abstract**

26

27 ‘Fire mosaics’ are often maintained in landscapes to promote successional diversity in
28 vegetation with little understanding of how this will affect ecological processes in animal
29 populations such as dispersal, social organisation and re-establishment. To investigate these
30 processes, we conducted a replicated, spatio-temporal landscape genetics study of two
31 Australian woodland lizard species (*Amphibolurus norrisi* (Agamidae) and *Ctenotus atlas*
32 (Scincidae)). Agamids have a more complex social and territory structure than skinks, so fire
33 might have a greater impact on their population structure and thus genetic diversity. Genetic
34 diversity increased with time since fire in *C. atlas* and decreased with time since fire in *A.*
35 *norrisi*. For *C. atlas*, this might reflect its increasing population size after fire, but we could not
36 detect increased gene flow that would reduce loss of genetic diversity through genetic drift.
37 Using landscape resistance analyses, we found no evidence that post-fire habitat succession or
38 topography affected gene flow in either species and we were unable to distinguish between
39 survival and immigration as modes of post-fire re-establishment. In *A. norrisi*, we detected
40 female-biased dispersal, likely reflecting its territorial social structure and polygynous mating
41 system. The increased genetic diversity in *A. norrisi* in recently burnt habitat might reflect a
42 temporary disruption of its territoriality and increased male dispersal, a hypothesis that was
43 supported with a simulation experiment. Our results suggest that the effects of disturbance on
44 genetic diversity will be stronger for species with territorial social organisation.

45

46 **Keywords**

47

48 Biodiversity conservation; dispersal; disturbance; fire regime; habitat fragmentation; landscape
49 genetics; mallee; reptile

50

51

52 **Introduction**

53

54 Fire is a natural driver of ecological dynamics, but modern changes in land use have altered fire
55 regimes in ecosystems around the world (Butz 2009; Regan *et al.* 2010). Some animal species
56 are threatened by recent increases in the extent and frequency of fire (Lyet *et al.* 2009; Sanz-
57 Aguilar *et al.* 2011), while others decline with less frequent fires (Templeton *et al.* 2011). Fire
58 management often combines prescribed burning and fire suppression to maintain ‘fire mosaics’,
59 assuming that successional diversity in vegetation will benefit biodiversity overall (Parr &
60 Andersen 2006). However, there is little understanding of the spatial and temporal scales at
61 which fire mosaics allow animal species to persist in a landscape (Kelly *et al.* 2012; Nimmo *et*
62 *al.* 2013).

63

64 Fire, or lack of fire, can fragment suitable habitat for some animal species (Neuwald &
65 Templeton 2013) by imposing barriers to dispersal (Levy *et al.* 2010; Prevedello *et al.* 2010).
66 Extinction risk may be elevated in populations fragmented by fire mosaics through declines in
67 genetic diversity and population fitness (Frankham 1997). This risk may be determined by
68 quantifying gene flow and genetic diversity in animal species across fire mosaics. Other factors
69 that may influence gene flow such as population density (Konvicka *et al.* 2012), topography
70 (Cushman *et al.* 2006) and geographic distance (Wright 1943) can be incorporated into
71 landscape genetics analyses, with fire mosaics, to understand the factors influencing genetic
72 structure (Cushman & Landguth 2010). This approach has shown how fire influences genetic
73 diversity and spatial genetic structure of some animal species (Brown *et al.* 2013; Schrey *et al.*
74 2011a; Spear & Storfer 2010). For example, in early successional species, limited genetic
75 structure at large spatial scales suggests that high dispersal rates allow rapid colonisation of
76 recently burnt habitats (Pereoglou *et al.* 2013; Pierson *et al.* 2013). Investigations in a wider

77 range of taxa and landscapes are needed to help develop generalised models to explain how fire
78 affects genetic diversity in natural populations (Banks *et al.* 2013).

79

80 If fire causes local extinction, dispersal from surrounding unburnt habitat is essential for re-
81 establishment (Holland & Bennett 2011). Dispersal may be less important if re-establishment is
82 initiated by survivors of the fire (Banks *et al.* 2011; Peakall & Lindenmayer 2006). The mode by
83 which animal populations re-establish after fire is largely unknown (Clarke 2008). Genetic
84 studies could fill this knowledge gap and provide guidance for the spatial scales of fire
85 management that allow species persistence in a landscape (Driscoll *et al.* 2010).

86

87 Displacement following habitat disturbance, such as fire, can alter social and mating systems
88 and thus the genetic structure of animal populations (DiBattista *et al.* 2011; Schrey *et al.* 2011b).
89 Areas surrounding burnt habitat could experience increased immigration of displaced animals
90 (Banks *et al.* 2012). Untangling effects of long term habitat succession from effects of an initial
91 displacement after fire may be difficult with ‘snap-shot’ space-for-time studies (Driscoll &
92 Hardy 2005; Porter 1999). Although rarely done, monitoring change in population structure over
93 time more powerfully assesses the impact of fire on animal populations (Driscoll *et al.* 2010).
94 Combining spatial and temporal sampling approaches may provide an efficient compromise for
95 examining population structure under complex fire regimes.

96

97 We used spatio-temporal sampling and landscape genetics analyses to investigate initial and
98 long-term impacts of fire regimes on the population genetic structure of two Australian lizard
99 species (*Amphibolurus norrisi* (Agamidae) and *Ctenotus atlas* (Scincidae)). Both are generally
100 more abundant in late successional vegetation and decline in abundance after fire (Driscoll &
101 Henderson 2008; Driscoll *et al.* 2012; Smith *et al.* 2013). However, their post-fire recovery
102 varies regionally, involving factors other than simply time since fire (Driscoll & Henderson

103 2008; Driscoll *et al.* 2012; Smith *et al.* 2013). To incorporate this regional variation, we
104 replicated our study in four independent landscapes; a necessary but often overlooked approach
105 in landscape genetics (Short Bull *et al.* 2011). We characterised fire regimes by fire frequency
106 and time since fire, and also investigated effects of population density and topography on gene
107 flow. By comparing the genetic structure of two different lizard species, we sought to provide
108 insights into how different life histories might influence population responses to fire. Fire may
109 have a greater effect on social structure and thus genetic diversity in agamid lizards that have
110 more complex social and territory structure than skinks (Martins 1994; Stamps 1983). We asked
111 four questions (Table 1):

- 112
- 113 1. Does spatial variation in fire regime, topography and population density influence gene
114 flow and genetic diversity?
 - 115 2. Is there an immediate, temporal effect of fire in the landscape on genetic structure?
 - 116 3. Is post-fire re-establishment facilitated by survivors, or by immigration from unburnt
117 habitat?
 - 118 4. Can effects of fire on genetic diversity be explained by differences in demographic
119 attributes such as age and sex structure, social and mating system or sex biased
120 dispersal?

121

122

123 **Methods**

124

125 *Study region & target species*

126

127 We sampled four conservation reserves on Eyre Peninsula, South Australia (Fig. 1): Hincks

128 Wilderness Area (33°45' S, 136°03' E; 66,658 ha), Pinkawillinie Conservation Park (32°54' S,

129 135°53' E; 130,148 ha), Munyaroo Conservation Park (33° 21' S, 137° 12' E; 20,139 ha) and
130 Heggaton Conservation Reserve (33°22' S, 136°31' E; 6,476 ha). The region has an average
131 annual rainfall between 296 mm and 361 mm. The main topographic features are white sand
132 dunes, occurring in large, parabolic fields or longitudinal ridges interspersed by hard, reddish-
133 brown swales (Twidale & Campbell 1985). The dominant vegetation in all reserves is low (<6
134 m) mallee woodland, characterised by multi-stemmed *Eucalyptus spp.* (*E. costata* and *E.*
135 *socialis*), commonly associated with *Melaleuca uncinata*, *Callitris verrucosa* and *Triodia*
136 *irritans* (Specht 1972). Large, severe wildfires occur on a 10-100 year time scale, commonly
137 ignited by summer lighting (Bradstock & Cohn 2002).

138
139 *Amphibolurus norrisi* and *C. atlas* are both common in mallee of southern Australia (Wilson &
140 Swan 2010). *Amphibolurus norrisi*, absent from Pinkawillinie, was sampled from three reserves
141 only (Fig. 1). With increasing time since fire (TSF), the semi-arboreal *A. norrisi* increases in
142 abundance at Heggaton (Driscoll & Henderson 2008) but is unaffected at Hincks (Smith *et al.*
143 2013). The reason for this regional variation is currently unknown. *Ctenotus atlas* inhabits
144 *Triodia* grasses (Pianka 1969) which peak in density approximately 30 years after fire (Haslem
145 *et al.* 2011). Population recovery after fire in *C. atlas* is likely driven by variation in rainfall and
146 grazing that interact with fire regimes to affect the distribution and abundance of *Triodia spp.*
147 (Driscoll *et al.* 2012; Nimmo *et al.* 2012). Home range sizes in *A. norrisi* range between 0.13
148 and 2.03 ha (South 2010) and *C. atlas* can move on average 6 m per day (Heffernan 2008). Five
149 other *Ctenotus* species have mean recapture distances of 7–27 m (Read 1998). Agamid lizards
150 often defend territories and have polygynous mating systems while such complex social
151 structure is less common in skinks (Griffiths 1999; Martins 1994; Peters & Ord 2003; Stamps
152 1983).

153

154 *Study design & sampling strategy*

155

156 We collected DNA samples from 177 *A. norrisi* and 377 *C. atlas* individuals from 38 sites
157 within the four reserves (*A. norrisi* = 26 sites, *C. atlas* = 31 sites) (Fig. 1). We sampled over six
158 consecutive sampling seasons (the spring/summer period when mallee lizards are most active),
159 from Dec 2004 – Feb 2005 (season 1) to Nov 2009 – Feb 2010 (season 6) (Table S1 in
160 Supporting information). At each site, samples were collected over one to four sampling seasons
161 (Table S1). Sample sizes varied from one to 34 individuals per site (Fig. 1, Table S1), so many
162 of our analyses focussed on individuals as the sampling units (e.g. Pritchard *et al.* 2000; Rousset
163 2000), avoiding the need for large sample sizes and for pre-defined population boundaries.
164 Analyses focussing on the population level were restricted to subsets of the data (Table 1).

165

166 Sites were sampled from four days to 49 years after fire (Fig. 1, Table S1) and were separated
167 by average distances (range) of 4.7 (0.3-15.2) km at Hincks, 4.7 (0.6-11.6) km at Pinkawillinie,
168 1.4 (0.5-1.8) km at Munyaroo and 3.5 (0.5-6.6) km at Heggaton (Fig. 1). These distances are at a
169 similar spatial scale to natural and prescribed fires in mallee (Bradstock & Cohn 2002) and to
170 commonly reported extents of genetic structure in lizards (e.g. Berry *et al.* 2005; Schrey *et al.*
171 2011b; Smith *et al.* 2009). At Hincks, with the most complex fire history, our sample sites also
172 spanned a range of fire frequencies (0-5 fires since 1953, Fig. S1). At five of six sample sites
173 burned during our study, we sampled both before and after the fires (Fig. 1, Table S1). Two sites
174 at Pinkawillinie (P3 and P4, Dec 2005) and one site at Hincks (I4, Dec 2006) were burnt by
175 unplanned summer wildfires. One site at Hincks (I3, April 2006) and two sites at Heggaton (N4
176 and S4, April 2006) were burnt during prescribed fires conducted for a related study (Driscoll *et*
177 *al.* 2012). The unplanned and prescribed fires were all of high severity, consuming all above
178 ground vegetation.

179

180 Lizards were captured in pitfall traps as previously described (Smith *et al.* 2013) or hand-
181 captured at three sites (Table S1). We used toe-clips to identify individuals upon recapture
182 (Smith *et al.* 2013) and recorded the age (adult or juvenile) and sex of lizards collected at ‘grid’
183 sites at Hincks and Pinkawillinie (Table S1). Genetic analyses included all sampled individuals
184 except where indicated. Blood and tissue from clipped toes were stored, respectively, on FTA
185 paper (Whatman) and in liquid nitrogen or 5 ml ethanol/physiological saline (1:1). Lizards were
186 processed at a field base and released the following day at the capture location.

187

188 *Microsatellite DNA data*

189

190 We extracted DNA from FTA paper (Smith & Burgoyne 2004) or from tissue samples using a
191 modified Gentra kit (Qiagen). We amplified DNA at the polymorphic microsatellite DNA loci
192 described by Smith *et al.* (2011), and used a subset of those loci that showed spatially consistent
193 patterns of Hardy-Weinberg equilibrium and inconsequential levels of linkage disequilibrium
194 (13 loci for *A. norrisi*: AmNo04, AmNo05, AmNo11, AmNo12, AmNo18, AmNo20, AmNo25,
195 AmNo26, AmNo29, AmNo30, AmNo36, AmNo37, AmNo39; nine loci for *C. atlas*: CtAt02,
196 CtAt03, CtAt08, CtAt09, CtAt12, CtAt15, CtAt18, CtAt24, CtAt30). Samples were genotyped
197 on an ABI 3730 instrument (Applied Biosystems) with the size standard GS500 (-250) LIZ and
198 alleles were scored with GeneMapper 4.0 (Applied Biosystems).

199

200 *Question 1. Spatial drivers of gene flow and genetic diversity*

201

202 The spatial effects of fire on gene flow and genetic diversity were investigated using all of the
203 samples and analyses of genetic diversity, genetic structure and landscape resistance (Table 1).

204

205 *Genetic diversity.* To determine if post-fire succession affected genetic diversity, we analysed
206 variation in two different diversity measures: site-level allelic richness standardised for sample
207 size (N) and individual heterozygosity. Sample sizes varied across sites so we standardised
208 allelic richness to N = 5 to encompass the full site variation in TSF. We conducted sensitivity
209 analyses to test whether sample size influenced effects of TSF on allelic richness. To do this, we
210 calculated allelic richness for N = 6 to 10. As N increased, the number of sites included in the
211 analysis decreased, so we lost power to test effects of TSF but were able to examine if the
212 general pattern was consistent.

213
214 We used standArich (Alberto 2006) in R 3.0 (R Core Team 2013) to calculate allelic richness
215 for each N. First, we performed multiple random reduction (Leberg 2002) for all sample sites
216 with ≥ 5 individuals. This produced a table of randomly subsampled individuals ranging from
217 one to the number of individuals at the sample site (Alberto 2006). We conducted 100 random
218 subsamples for each sample size at each site (Leberg 2002). Second, we calculated allelic
219 richness standardised for each sample size of interest (N = 5 to N = 10). We used linear mixed-
220 effects models in the lme4 library (Bates *et al.* 2013) for R to examine the effect of TSF on
221 allelic richness for each N. Because we sampled multiple sites within a single fire boundary, we
222 fitted fire (a factor naming individual fire events) as a random effect and TSF and reserve as
223 fixed effects. We examined interactions between TSF and reserve for *C. atlas*, but not *A. norrisi*
224 which had a smaller range of TSF values within reserves. To estimate the effect of TSF on
225 individual genetic diversity we first calculated the proportion of typed loci that were
226 heterozygous in each individual. We modelled heterozygosity with the same formulation as for
227 allelic richness (including interactive effects of TSF and reserve for both species), but also
228 included site as an additional random term to account for potential dependence among
229 individuals at the same site.

230

231 For both the allelic richness and heterozygosity analyses, we calculated P -values using Wald
232 tests (Welsh 1996). We removed interactive terms and subsequently the reserve term if they
233 were not significant ($P > 0.05$). Parameter estimates and standard errors were obtained using the
234 AICcmodavg package (Mazerolle 2012).

235

236 *Genetic structure.* Spatial patterns of genetic structure corresponding to fire mosaics could
237 indicate that gene flow was influenced by fire history. We examined population genetic
238 structure in each species within each reserve separately and over the entire study region to infer
239 broader patterns of gene flow. For each data set we used two different Bayesian clustering
240 models. One was a non-spatial model implemented in STRUCTURE 2.3.2, which uses a
241 Markov-chain Monte Carlo (MCMC) method to first identify the number of clusters (K) in a
242 sample at Hardy-Weinberg equilibrium and then assign each individual probabilistically to a
243 cluster (Pritchard *et al.* 2000). The second was a spatial MCMC model implemented in
244 GENELAND 3.3.0, similar to STRUCTURE but including geographic coordinates for each
245 individual (Guillot *et al.* 2005). GENELAND is more sensitive to weak genetic structure
246 because spatially adjacent individuals are more likely to be in the same cluster (Guillot *et al.*
247 2005).

248

249 We ran STRUCTURE using the admixture and correlated allele frequency models for 500,000
250 MCMC repetitions after a burn-in of 200,000, with five independent runs of each K from 1 to 8.
251 We inferred the number of clusters in each data set by selecting the K with the highest mean
252 estimated model log-likelihood across the independent runs (Pritchard *et al.* 2000). We ran
253 GENELAND for 500,000 MCMC repetitions, allowing K to vary between 1 and 10. We used
254 the Dirichlet allele frequency model because the correlated allele frequency model can
255 overestimate K (Guillot *et al.* 2005) and we found it was unstable in preliminary analyses. We
256 set spatial uncertainty of geographic coordinates to a conservatively high estimate of 1000 m to

257 allow for large home-range movements (Read 1998; South 2010). We discarded the first
258 125,000 repetitions and then inferred K from the mode of the posterior distribution. Five
259 independent runs were conducted to check for consistency of results.

260

261 *Landscape resistance.* We developed five independent landscape resistance models based on
262 features that might influence gene flow in the two lizard species: isolation by distance, sand
263 dune topography, population density, time since fire and fire frequency (Table 2). The landscape
264 features we examined related to previously derived measures of habitat suitability (see Table 2)
265 which could affect gene flow through effects on either dispersal or population density. Our
266 overall analysis approach was to (1) calculate genetic distance between all pairs of conspecific
267 individuals within reserves as a measure of gene flow, (2) generate values of landscape
268 resistance between pairs for each resistance model and (3) use simple (Mantel 1967) and partial
269 (Smouse *et al.* 1986) Mantel tests in a causal modelling framework (Cushman & Landguth
270 2010; Cushman *et al.* 2006; Legendre 1993) to determine the effects of each resistance model on
271 gene flow separately.

272

273 Using SPAGEDI 1.2 (Hardy & Vekemans 2002) we calculated genetic distance between each
274 pair of conspecific individuals as a_r , an individual analogue to $F_{ST} / (1 - F_{ST})$ (Rousset 2000). We
275 generated values of landscape resistance between each pair using a method based on circuit
276 theory which takes into account all possible pathways between pairs (rather than the single,
277 least-cost pathway used in many studies) (McRae & Beier 2007). We compiled each resistance
278 model on a separate raster grid with a 20 m resolution in ArcMap 10 (ESRI) and then calculated
279 resistance between each pair for each model using CIRCUITSCAPE 3.5.4 (McRae & Beier
280 2007). We defined the extent of our study landscapes with a 500 m buffer around the samples to
281 encompass movement distances for both species (South 2010). We repeated the analysis using a
282 5 km buffer to encompass potential longer dispersals (Hoehn *et al.* 2007; Templeton *et al.* 2011)

283 but found no meaningful effects of changing the buffer distance so only report results from the
284 500 m buffer analysis. The fire frequency resistance model was analysed only for Hincks with
285 its more complex fire history (Fig. S1). At Heggaton, we conducted separate resistance analyses
286 for samples collected before and after the 2006 prescribed fires (see Question 2). For the other
287 three reserves, we included only samples collected after the most recent fire.

288
289 Analyses were conducted using the mantel function in the ecodist library (Goslee & Urban
290 2007) for R 3.0 (R Core Team 2013). *P*-values were obtained with 5000 joint randomisations of
291 rows and columns of one matrix (Goslee & Urban 2007). For isolation by distance models, we
292 used simple Mantel tests and one-tailed *P* values to determine significant ($\alpha = 0.05$)
293 relationships between genetic and geographic distance within reserves (Goslee & Urban 2007).
294 For other resistance models we used partial Mantel tests and two-tailed *P* values to determine
295 significant relationships between genetic distance and landscape resistance, given the spatial
296 distance between samples (Goslee & Urban 2007). When there was a significant correlation in
297 the first partial Mantel test, we calculated the effect of the isolation by distance model on
298 genetic distance while controlling for the landscape resistance model. Where the first partial
299 Mantel test was significant and the second test was non-significant we inferred significant
300 effects of that landscape resistance model on genetic distance (Cushman *et al.* 2006; Legendre
301 1993).

302
303 The sand dune topography model was based on elevation data sourced from the Shuttle Radar
304 Topographic Mission one-second bare earth version of Australia (CSIRO 2011). Elevations
305 were projected as points and interpolated with ANUDEM (Hutchinson 2011) to create digital
306 elevation models that distinguished dunes from swales (Fig. S2). The three fire-related
307 resistance models (TSF, fire frequency and population density) were derived from two different
308 spatial data sets, one containing the year of the most recent fire, the other containing the number

309 of fires since 1953 (South Australian Department for Environment, Water and Natural
310 Resources). For the population density model we used the mean number of captures predicted
311 from TSF (Smith *et al.* 2013) enabling us to parameterise areas we had not sampled. Estimates
312 were available for Hincks and Pinkawillinie only, so we generated predictions for Munyaroo
313 and Heggaton using published data (Table S2, Fig. S3). We examined the population density
314 model of gene flow only for locations where there was a significant response to TSF (*A. norrisi*
315 at Heggaton, *C. atlas* at Hincks and Pinkawillinie). The TSF and population density landscape
316 models were both based on the same spatial data set derived from the most recent fire in each
317 reserve. The difference between the models was that the TSF model examined linear effects of
318 the number of years since fire, while the population density model allowed non-linear responses,
319 reflecting population responses in each species (Smith *et al.* 2013).

320

321 *Question 2. Immediate, temporal drivers of post-fire genetic structure*

322

323 The immediate impacts of fire were investigated by comparing genetic structure before and after
324 fire across the whole landscape at Heggaton, where we had similar numbers of pre- and post-fire
325 samples (Fig. 1). For each species, we applied the landscape resistance analysis method
326 described for Question 1 to the pre- and post-fire samples separately.

327

328 *Question 3. Modes of post-fire re-establishment*

329

330 Sources of re-establishment were investigated using samples from five of the six sites that
331 burned during the study (Fig. 1, Table S1). We examined results from the STRUCTURE and
332 GENELAND analyses of the whole sample within reserves, described for Question 1. If genetic
333 structure was detectable, genetic differentiation between pre- and post-fire samples may indicate
334 a stronger role of immigration than re-establishment from local survivors of the fire. We also

335 applied STRUCTURE analyses separately to *C. atlas* samples from each site that burned during
336 the study (sample sizes for *A. norrisi* were too small (≤ 7 , Table S1)) to compare the sensitivity
337 to detect genetic structure between pre- and post-fire samples.

338

339 *Question 4. Demographic drivers of genetic diversity*

340

341 At ‘grid’ sites at Hincks and Pinkawillinie (Table S1) where age and sex were recorded, we
342 summarised proportions of adults and juveniles and proportions of adult males and adult
343 females for each species. We used binomial generalised linear mixed models in lme4 to analyse
344 whether the age and sex ratios were affected by TSF, reserve (for *C. atlas* only) and sampling
345 season for each species separately. Site was fitted as a random effect. To investigate sex-biased
346 dispersal in each species, we used simple Mantel tests of isolation by distance on data from
347 adult males and adult females separately.

348

349 To determine if fire-related genetic patterns could be explained by demographic changes in *A.*
350 *norrisi*, we simulated genetic data for two demographic scenarios using EASYPOP 2.0.1
351 (Balloux 2001). *Ctenotus atlas* did not have any detectable genetic structure within reserves so
352 we did not simulate its population structure. For each scenario, we used a two-dimensional
353 spatial model of 10 x 10 cells and generated data for 10 populations, each with 30 males and 30
354 females. We simulated data for 13 independent loci, each with 18 possible allelic states (Smith
355 *et al.* 2011). We used a two-phase mutation model, weighted with 5% infinite alleles model and
356 95% step-wise mutation model (Di Rienzo *et al.* 1994) and a mutation rate of 0.0001. Alleles
357 were randomly assigned in the initial population.

358

359 First, we simulated populations with isolation by distance in males but not females to mimic the
360 observed patterns in our empirical data. These were used to represent populations in unburnt

361 habitat with stable social structures and mating systems. We specified a polygynous mating
362 system (typical for agamids (Stamps 1983)) with 50% matings by subordinate males. We set the
363 proportion of migration to 0.5 for males and 1 for females, and the mean dispersal distance to 4
364 for males and 12 for females. We ran the stable scenario for 20 generations, based on a
365 generation time of 2 yr (South 2010) and 40 years since fire – relatively long unburnt habitat in
366 our study system.

367
368 Second, we simulated populations with disrupted mating systems and increased male dispersal –
369 a scenario which may occur immediately after fire (Banks *et al.* 2012). We specified a random
370 mating system and set the proportion of migration to 1 and the mean dispersal distance to 12 for
371 both sexes. We ran the disturbed scenario for two generations to represent populations in the
372 first four years after fire.

373
374 We simulated 20 replicates of each scenario to determine consistency in results, calculated mean
375 allelic richness, and used simple Mantel tests to test for isolation by distance among simulated
376 populations.

377

378

379 **Results**

380

381 *Question 1. Spatial drivers of gene flow and genetic diversity*

382

383 *Genetic diversity.* Each species showed significant main effects of TSF on allelic richness,
384 standardised to a sample size of five individuals. Allelic richness increased with TSF in *C. atlas*
385 ($P = 0.037$, Fig. 2a) and decreased with TSF in *A. norrisi* ($P = 0.003$, Fig. 2b). In *A. norrisi*, but
386 not *C. atlas*, there were also main effects of reserve, with Munyaroo having significantly lower

387 allelic richness than Hincks and Pinkawillinie ($P < 0.001$, Fig. 2c). Sensitivity analyses showed
388 consistent significant effects of TSF on allelic richness across all sample size standardisations
389 except $N = 7$ ($P = 0.09$) and 10 ($P = 0.07$) for *C. atlas* (Table S3, Fig. S4, Fig. S5). The reserve
390 effect on allelic richness in *A. norrisi* disappeared when $N > 6$ because it was driven by the site
391 at Munyaroo which had only six individuals. There were no effects of TSF or reserve on
392 individual heterozygosity in either species.

393

394 *Genetic structure.* Both within each reserve and across the whole study region, STRUCTURE
395 indicated that all conspecific individuals belonged to a single genetic cluster (Fig. S6). However,
396 GENELAND suggested that *C. atlas* individuals at Hincks were genetically different from those
397 at the other reserves (Fig. 3a, Fig. S7), although assignment probabilities were always $< 71\%$
398 suggesting only weak differentiation (Fig. 3a). One ‘ghost’ cluster (Guillot *et al.* 2005) to which
399 no individuals were assigned was also identified (the dark band at the bottom of Fig. 3a). For *A.*
400 *norrisi*, GENELAND results indicated that individuals at N3 and N4 (last burnt in 1960) were
401 genetically differentiated from the other six sites at Heggaton (Fig. 3b, Fig. S7) but there was no
402 differentiation across the fire mosaic at the southern Heggaton sites (Fig. 3b). There was no
403 convincing evidence of genetic structure in any other data set from individual reserves or across
404 the study region (Fig. S6, Fig. S7, Fig. S8). Thus, there was no evidence that patterns of genetic
405 structure were related to fire regimes.

406

407 *Landscape resistance.* There were no significant effects of landscape resistance on genetic
408 distance in *C. atlas* (Table S4). For *A. norrisi*, we found significant isolation by distance at
409 Hincks ($r_M = 0.128$, $P < 0.001$) and at Heggaton, both before ($r_M = 0.153$, $P = 0.034$) and after
410 ($r_M = 0.162$, $P = 0.045$) the 2006 fires, while at Munyaroo, there was a significant effect of the
411 TSF model on genetic distance ($r_M = 0.555$, $P = 0.045$). There, individuals in long-unburnt

412 habitats were more genetically different from each other than individuals in recently burnt
413 habitat.

414

415 *Question 2. Immediate, temporal drivers of post-fire genetic structure*

416

417 There were no changes between the pre- and post-fire samples from Heggaton that would
418 indicate an immediate, temporal effect of fire on landscape genetic structure (Table S4).

419

420 *Question 3. Modes of post-fire re-establishment*

421

422 At the sites that burned during the study, samples collected before or after fire were genetically
423 indistinguishable, whether analysed alone or with other samples from the same reserve.

424 Although we observed genetic differentiation at Heggaton using GENELAND (Fig. 3b), this
425 was related to the spatial location of samples, rather than whether they were collected before or
426 after fires.

427

428 *Question 4. Demographic drivers of genetic diversity*

429

430 We observed a female biased sex ratio in both species at Hincks (Table S5) but could not
431 differentiate between a demographic effect or an effect of sex differences in capture rates. There
432 were no significant effects of TSF, location or sampling season on age structure or sex ratio in
433 either species.

434

435 For *A. norrisi* at Hincks we found significant isolation by distance in adult males ($r_M = 0.180$, P
436 $= 0.022$) but not adult females (Table S4), indicating female-biased dispersal. The significant
437 isolation by distance in the overall sample for *A. norrisi* (adults and juveniles) was unlikely to

438 have been driven solely by relatedness among pre-dispersed juveniles because the same effect
439 was observed in adult males. There was no evidence for sex-biased dispersal in *C. atlas* (Table
440 S4).

441
442 Our first simulation consistently produced significant isolation by distance in males but not
443 females (Table S6), reflecting the pattern in our empirical data. The second simulation, with a
444 disruption of the polygynous mating system and increased male dispersal, resulted in no
445 isolation by distance for either sex (Table S6) and an increase in mean allelic richness (first
446 simulation = 11.8, second simulation = 17.3; $t = -80.13$, $P < 0.001$).

447

448

449 **Discussion**

450

451 We discovered contrasting effects of fire on genetic diversity in two lizard species. Allelic
452 richness decreased with TSF in *A. norrisi* and increased in *C. atlas* (Question 1). We found
453 isolation by distance in *A. norrisi* but no consistent effects of fire-related habitat features or
454 topography on gene flow in either species (Question 1). We found no evidence of an immediate,
455 temporal effect of fire on gene flow in either species (Question 2) and we were unable to
456 distinguish between survival and immigration as modes of post-fire re-establishment (Question
457 3). Post-fire habitat succession did not appear to affect movement or dispersal in our study
458 species, contrasting studies of other animal species (Murphy *et al.* 2010; Templeton *et al.* 2011).
459 In the absence of habitat resistance to gene flow, the observed effects of TSF on genetic
460 diversity might be related to changes in the social structure and mating system (Pilot *et al.* 2010;
461 Ross 2001) or population size (Frankham 1996) following fire (Question 4). Alternatively, we
462 might have had insufficient resolution in our genetic markers to detect effects of fire on gene
463 flow. We discuss these biological hypotheses and statistical caveats below.

464
465 Female-biased dispersal in *A. norrisi* likely reflects the territorial social structure and
466 polygynous mating system common in agamids (Griffiths 1999; Martins 1994; Stamps 1983)
467 and documented in the closely related *A. muricatus* (Peters & Ord 2003). Our simulations
468 showed that short-term disruptions of this social structure can increase genetic diversity,
469 explaining the higher allelic richness in *A. norrisi* from recently burned habitat. Disrupted social
470 structure has caused elevated genetic diversity through increased outbreeding in lemon sharks
471 (*Negaprion brevirostris*) following habitat loss (DiBattista *et al.* 2011) and in mountain
472 brushtail possums (*Trichosurus cunninghami*) following fire (Banks *et al.* 2012). In *A. norrisi*,
473 the decline in allelic richness with TSF might reflect a stabilisation of the social structure,
474 through establishment of territories and increased relatedness among proximate individuals (e.g.
475 Gardner *et al.* 2001). At Munyaroo, genetic distance between individuals was lower in more
476 recently burnt habitat, supporting a hypothesis of strong social structure in long-unburnt habitat.
477 However, we did not observe this at the other reserves so continued research of lizard behaviour
478 across fire mosaics is needed to provide further support to our hypothesis.

479
480 For *C. atlas*, increased genetic diversity with TSF might result from changing population
481 density. Genetic diversity is positively related to population size (Frankham 1996) and fire
482 decreases population density in *C. atlas* (Smith *et al.* 2013). However, we did not find variation
483 in gene flow that has accompanied habitat-related changes in genetic diversity in other lizards
484 (Berry *et al.* 2005; Hoehn *et al.* 2007; Levy *et al.* 2010). In another late-successional skink
485 species, *Plestiodon reynoldsi*, Schrey *et al.* (2011b) reported that genetic diversity increased
486 with TSF, reflecting changes in population density and gene flow. Increases in population size
487 without immigration would lead to decreases in genetic diversity through genetic drift over
488 successive generations (Lacy 1987). *Ctenotus atlas* must therefore maintain gene flow as

489 population size increases but we could not detect increased gene flow that would reduce loss of
490 genetic diversity through genetic drift.

491
492 Maintenance of gene flow through dispersal in fire-prone ecosystems may be an adaptation to
493 temporally dynamic habitats (Brown *et al.* 2013; Pereoglou *et al.* 2013; Pierson *et al.* 2010).
494 Fire mosaics did not appear to form dispersal barriers in either of our study species, supporting
495 this suggestion. This assumes we collected enough samples from across the landscape to detect
496 barriers (Berry *et al.* 2004) and that the time between disturbance and sample collection was
497 long enough for barriers to form (Landguth *et al.* 2010). Our study landscapes were
498 characterised by complex fire mosaics. A more pronounced effect of fire on genetic structure
499 might occur in more heterogeneous habitats, where entire habitat patches are burned and
500 population bottlenecks occur (Banks *et al.* 2013).

501
502 Despite disagreement over the reliability of the causal modelling approach that we followed
503 (Cushman *et al.* 2013; Graves *et al.* 2013; Guillot & Rousset 2013; Legendre & Fortin 2010),
504 there are few available alternatives that circumvent the problems identified. Cushman &
505 Landguth (2010) suggested that causal modelling can reliably identify a correct model of
506 landscape resistance among competing hypotheses. Others have claimed poor performance of
507 this approach because it assumes linearity between distance matrices (Legendre & Fortin 2010)
508 and disregards information about a range of factors (mating, dispersal, inheritance) influencing
509 gene flow (Graves *et al.* 2013). These issues may have limited our ability to detect effects of
510 landscape resistance on gene flow. However, the weak genetic structure revealed by non-
511 distance-based analyses (STRUCTURE) suggest that landscape resistance patterns would be
512 difficult to detect in our study system. Cushman *et al.* (2013) found partial Mantel tests had
513 inflated Type I error rates but low Type II error rates. This bias would have limited impact on
514 our conclusions because most of our partial Mantel tests were insignificant. Guillot & Rousset

515 (2013) showed that simple Mantel tests are appropriate for analysing isolation by distance so our
516 conclusions regarding isolation by distance in *A. norrisi* are unlikely to be biased.

517

518 Detecting temporal genetic changes to infer that fire disrupted gene flow or that re-
519 establishment occurred through immigration might require stronger genetic structure than we
520 found in our target species (Berry *et al.* 2004). We recommend long-term DNA sample
521 collection in fire-prone ecosystems to develop better understanding of the effect of fire on
522 genetic structure of natural populations. Further studies should focus on those species with
523 limited dispersal relative to the spatial scale of fire mosaics which are likely to most be affected
524 by fire management decisions.

525

526 By comparing two ecologically different lizard species we discovered species-specific genetic
527 responses to post-fire habitat succession. We propose that differences in the relationship
528 between genetic diversity and TSF resulted from differences in the influence of population
529 density and social structure. We predict stronger effects of disturbance on genetic diversity for
530 species with stable social organisation. Our study has shown how genetic investigations can help
531 uncover part of the mechanism that causes species to vary in their distribution and abundance
532 under different fire regimes (Banks *et al.* 2013; Keith 2012). Such studies are necessary to
533 ensure that fire management is conducted at spatial and temporal scales appropriate for
534 biodiversity conservation.

535

536

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553

554

555 **References**

556

557 Alberto F (2006) standArich: an R package to estimate population allelic richness using
558 standardized sample size. CCMAR, University of the Algarve, Portugal.
559 <http://www.ccmар.ualg.pt/maree/software.php?soft=sarich>

560 Balloux F (2001) EASYPOP (Version 1.7): a computer program for population genetics
561 simulations. *Journal of Heredity*, **92**, 301-302.

562 Banks SC, Blyton MDJ, Blair D, McBurney L, Lindenmayer DB (2012) Adaptive responses and
563 disruptive effects: how major wildfire influences kinship-based social interactions in a forest
564 marsupial. *Molecular Ecology*, **21**, 673-684.

565 Banks SC, Cary GJ, Smith AL, Davies I, Driscoll DA, Gill AM, Lindenmayer DB, Peakall R
566 (2013) How does ecological disturbance influence genetic diversity? *Trends in Ecology and*
567 *Evolution*, **28**, 670-679.

568 Banks SC, Dujardin M, McBurney L, Blair D, Barker M, Lindenmayer DB (2011) Starting
569 points for small mammal population recovery after wildfire: recolonisation or residual
570 populations? *Oikos*, **120**, 26-37.

571 Bates D, Maechler M, Bolker B (2013) lme4: linear mixed-effects models using S4 classes. R
572 package, version 0.999999-2. <http://lme4.r-forge.r-project.org/> (accessed October 2013).

573 Berry O, Tocher MD, Gleeson DM, Sarre SD (2005) Effect of vegetation matrix on animal
574 dispersal: genetic evidence from a study of endangered skinks. *Conservation Biology*, **19**, 855-
575 864.

576 Berry O, Tocher MD, Sarre SD (2004) Can assignment tests measure dispersal? *Molecular*
577 *Ecology*, **13**, 551-561.

578 Bradstock RA, Cohn JS (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. In
579 *Flammable Australia: the fire regimes and biodiversity of a continent*. eds Bradstock RA,
580 Williams JE, Gill AM. Cambridge University Press, Cambridge.

581 Brown SM, Harrison KA, Clarke RH, Bennett AF, Sunnucks P (2013) Limited population
582 structure, genetic drift and bottlenecks characterise an endangered bird species in a dynamic,
583 fire-prone ecosystem. *PLOS One*, **8**, e59732.

584 Butz RJ (2009) Traditional fire management: historical fire regimes and land use change in
585 pastoral East Africa. *International Journal of Wildland Fire*, **18**, 442-450.

586 Clarke MF (2008) Catering for the needs of fauna in fire management: science or just wishful
587 thinking? *Wildlife Research*, **35**, 385-394.

588 CSIRO (2011) One-second SRTM digital elevation model. Commonwealth Scientific and
589 Industrial Research Organisation. [http://www.csiro.au/science/One-second-SRTM-Digital-](http://www.csiro.au/science/One-second-SRTM-Digital-Elevation-Model.html)
590 [Elevation-Model.html](http://www.csiro.au/science/One-second-SRTM-Digital-Elevation-Model.html)

591 Cushman S, Wasserman T, Landguth E, Shirk A (2013) Re-evaluating causal modeling with
592 Mantel tests in landscape genetics. *Diversity*, **5**, 51-72.

593 Cushman SA, Landguth EL (2010) Spurious correlations and inference in landscape genetics.
594 *Molecular Ecology*, **19**, 3592-3602.

595 Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex
596 landscapes: testing multiple hypotheses with causal modeling. *The American Naturalist*, **168**,
597 486-499.

598 Di Rienzo A, Peterson AC, Garza JC, Valdes AM, Slatkin M, Freimer NB (1994) Mutational
599 processes of simple-sequence repeat loci in human populations. *Proceedings of the National*
600 *Academy of Sciences USA*, **91**, 3166-3170.

601 DiBattista JD, Feldheim KA, Garant D, Gruber SH, Hendry AP (2011) Anthropogenic
602 disturbance and evolutionary parameters: a lemon shark population experiencing habitat loss.
603 *Evolutionary Applications*, **4**, 1-17.

604 Driscoll DA, Hardy CM (2005) Dispersal and phylogeography of the agamid lizard
605 *Amphibolurus nobbi* in fragmented and continuous habitat. *Molecular Ecology*, **14**, 1613-1629.

606 Driscoll DA, Henderson MK (2008) How many common reptile species are fire specialists? A
607 replicated natural experiment highlights the predictive weakness of a fire succession model.
608 *Biological Conservation*, **141**, 460-471.

609 Driscoll DA, Lindenmayer DB, Bennett AF, Bode M, Bradstock RA, Cary GJ, Clarke MF,
610 Dexter N, Fensham R, Friend G, Gill AM, James S, Kay G, Keith DA, MacGregor C, Russell-
611 Smith J, Salt D, Watson JEM, Williams RJ, York A (2010) Fire management for biodiversity
612 conservation: key research questions and our capacity to answer them. *Biological Conservation*,
613 **143**, 1928-1939.

614 Driscoll DA, Smith AL, Blight SR, Maindonald J (2012) Reptile responses to fire and the risk of
615 post-disturbance sampling bias. *Biodiversity and Conservation*, **21**, 1607–1625.

616 Frankham R (1996) Relationship of genetic variation to population size in wildlife.
617 *Conservation Biology*, **10**, 1500-1508.

618 Frankham R (1997) Do island populations have less genetic variation than mainland
619 populations? *Heredity*, **78**, 311-327.

620 Gardner MG, Bull CM, Cooper SJB, Duffield GA (2001) Genetic evidence for a family
621 structure in stable social aggregations of the Australian lizard *Egernia stokesii*. *Molecular*
622 *Ecology*, **10**, 175-183.

623 Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological
624 data. *Journal of Statistical Software*, **22**, 1-19.

625 Graves TA, Beier P, Royle JA (2013) Current approaches using genetic distances produce poor
626 estimates of landscape resistance to interindividual dispersal. *Molecular Ecology*, **22**, 3888-
627 3903.

628 Griffiths AD (1999) Demography and home range of the frillneck lizard, *Chlamydosaurus kingii*
629 (Agamidae), in northern Australia. *Copeia*, **1999**, 1089-1096.

630 Guillot G, Estoup A, Mortier F, Cosson J-F (2005) A spatial statistical model for landscape
631 genetics. *Genetics*, **170**, 1261-1280.

632 Guillot G, Rousset F (2013) Dismantling the Mantel tests. *Methods in Ecology and Evolution*, **4**,
633 336-344.

634 Hardy OJ, Vekemans X (2002) SPAGEDI: a versatile computer program to analyse spatial
635 genetic structure at the individual or population levels. *Molecular Ecology Notes*, **2**, 618-620.

636 Haslem A, Kelly LT, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Avitabile SC, Callister
637 KE, Spence-Bailey LM, Clarke MF, Bennett AF (2011) Habitat or fuel? Implications of long-
638 term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of*
639 *Applied Ecology*, **48**, 247-256.

640 Heffernan LD (2008) *Microhabitat selection by lizards in southern Australia's semi-arid*
641 *Murray-Mallee region*. Unpublished Honours Thesis, La Trobe University, Bundoora.

642 Hoehn M, Sarre S, Henle K (2007) The tales of two geckos: does dispersal prevent extinction in
643 recently fragmented populations? *Molecular Ecology*, **16**, 3299-3312.

644 Holland GJ, Bennett AF (2011) Recolonization of forest fragments by a native rodent following
645 experimental 'extinctions'. *Austral Ecology*, **36**, 521-529.

646 Hutchinson MF (2011) *ANUDEM version 5.3, user guide*. Fenner School of Environment and
647 Society, Australian National University, Canberra.

648 Keith DA (2012) Functional traits: their roles in understanding and predicting biotic responses
649 to fire regimes from individuals to landscapes. In *Flammable Australia: fire regimes*,

650 *biodiversity and ecosystems in a changing world*. eds Bradstock RA, Gill AM, Williams RJ, pp.
651 97-125. CSIRO Publishing, Collingwood, Victoria.

652 Kelly LT, Nimmo DG, Spence-Bailey LM, Taylor RS, Watson SJ, Clarke MF, Bennett AF
653 (2012) Managing fire mosaics for small mammal conservation: a landscape perspective. *Journal*
654 *of Applied Ecology*, **49**, 412-421.

655 Konvicka M, Zimmermann K, Klimova M, Hula V, Fric Z (2012) Inverse link between density
656 and dispersal distance in butterflies: field evidence from six co-occurring species. *Population*
657 *Ecology*, **54**, 91-101.

658 Lacy RC (1987) Loss of genetic diversity from managed populations: interacting effects of drift,
659 mutation, immigration, selection, and population subdivision. *Conservation Biology*, **1**, 143-158.

660 Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G (2010)
661 Quantifying the lag time to detect barriers in landscape genetics. *Molecular Ecology*, **19**, 4179-
662 4191.

663 Leberg PL (2002) Estimating allelic richness: effects of sample size and bottlenecks. *Molecular*
664 *Ecology*, **11**, 2445-2449.

665 Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**, 1659-1673.

666 Legendre P, Fortin M-J (2010) Comparison of the Mantel test and alternative approaches for
667 detecting complex multivariate relationships in the spatial analysis of genetic data. *Molecular*
668 *Ecology Resources*, **10**, 831-844.

669 Levy E, Kennington WJ, Tomkins JL, LeBas NR (2010) Land clearing reduces gene flow in the
670 granite outcrop-dwelling lizard, *Ctenophorus ornatus*. *Molecular Ecology*, **19**, 4192-4203.

671 Lindenmayer DB, Wood JT, MacGregor C, Michael DR, Cunningham RB, Crane M,
672 Montague-Drake R, Brown D, Muntz R, Driscoll DA (2008) How predictable are reptile
673 responses to wildfire? *Oikos*, **117**, 1086-1097.

674 Lyet A, Cheylan M, Prodon R, Besnard A (2009) Prescribed fire and conservation of a
675 threatened mountain grassland specialist: a capture-recapture study on the Orsini's viper in the
676 French alps. *Animal Conservation*, **12**, 238-248.

677 Mantel N (1967) The detection of disease clustering and a generalized regression approach.
678 *Cancer Research*, **27**, 209-220.

679 Martins EP (1994) Phylogenetic perspectives on the evolution of lizard territoriality. In *Lizard*
680 *Ecology: Historical and Experimental Perspectives*. eds Vitt LJ, Pianka ER, pp. 117-144.
681 Princeton University Press, Princeton, N.J.

682 Mazerolle MJ (2012) AICcmodavg. R package, version 1.26. [http://cran.r-](http://cran.r-project.org/web/packages/AICcmodavg/index.html)
683 [project.org/web/packages/AICcmodavg/index.html](http://cran.r-project.org/web/packages/AICcmodavg/index.html) (accessed January 2013).

684 McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations.
685 *Proceedings of the National Academy of Sciences USA*, **104**, 19885-19890.

686 Murphy MA, Evans JS, Storfer A (2010) Quantifying *Bufo boreas* connectivity in Yellowstone
687 National Park with landscape genetics. *Ecology*, **91**, 252-261.

688 Neuwald JL, Templeton AR (2013) Genetic restoration in the eastern collared lizard under
689 prescribed woodland burning. *Molecular Ecology*, **22**, 3666-3679.

690 Nimmo DG, Kelly LT, Spence-Bailey LM, Watson SJ, Haslem A, White JG, Clarke MF,
691 Bennett AF (2012) Predicting the century-long post-fire responses of reptiles. *Global Ecology*
692 *and Biogeography*, **21**, 1062-1073.

693 Nimmo DG, Kelly LT, Spence-Bailey LM, Watson SJ, Taylor RS, Clarke MF, Bennett AF
694 (2013) Fire mosaics and reptile conservation in a fire-prone region. *Conservation Biology*, **27**,
695 345-353.

696 Parr CL, Andersen AN (2006) Patch mosaic burning for biodiversity conservation: a critique of
697 the pyrodiversity paradigm. *Conservation Biology*, **20**, 1610-1619.

698 Pausas JG, Lloret F (2007) Spatial and temporal patterns of plant functional types under
699 simulated fire regimes. *International Journal of Wildland Fire*, **16**, 484-492.

700 Peakall R, Lindenmayer DB (2006) Genetic insights into population recovery following
701 experimental perturbation in a fragmented landscape. *Biological Conservation*, **132**, 520-532.

702 Pereoglou F, Lindenmayer DB, MacGregor C, Ford F, Wood J, Banks SC (2013) Landscape
703 genetics of an early successional specialist in a disturbance-prone environment. *Molecular*
704 *Ecology*, **22**, 1267-1281.

705 Peters RA, Ord TJ (2003) Display response of the Jacky Dragon, *Amphibolurus muricatus*
706 (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecology*, **28**, 499-506.

707 Pianka ER (1969) Sympatry of desert lizards (*Ctenotus*) in Western Australia. *Ecology*, **50**,
708 1012-1030.

709 Pianka ER (1972) Zoogeography and speciation of Australian desert lizards: an ecological
710 perspective. *Copeia*, **1972**, 127-145.

711 Pierson JC, Allendorf FW, Drapeau P, Schwartz MK (2013) Breed locally, disperse globally:
712 fine-scale genetic structure despite landscape-scale panmixia in a fire-specialist. *PLOS One*, **8**,
713 e67248.

714 Pierson JC, Allendorf FW, Saab V, Drapeau P, Schwartz MK (2010) Do male and female black-
715 backed woodpeckers respond differently to gaps in habitat? *Evolutionary Applications*, **3**, 263-
716 278.

717 Pilot M, Dahlheim ME, Hoelzel AR (2010) Social cohesion among kin, gene flow without
718 dispersal and the evolution of population genetic structure in the killer whale (*Orcinus orca*).
719 *Journal of Evolutionary Biology*, **23**, 20-31.

720 Porter AH (1999) Refugees from lost habitat and reorganization of genetic population structure.
721 *Conservation Biology*, **13**, 850-859.

722 Prevedello JA, Forero-Medina G, Vieira MV (2010) Movement behaviour within and beyond
723 perceptual ranges in three small mammals: effects of matrix type and body mass. *Journal of*
724 *Animal Ecology*, **79**, 1315-1323.

725 Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus
726 genotype data. *Genetics*, **155**, 945-959.

727 R Core Team (2013) R: a language and environment for statistical computing. [http://www.R-](http://www.R-project.org)
728 [project.org](http://www.R-project.org), R Foundation for Statistical Computing, Vienna, Austria.

729 Read JL (1998) The ecology of sympatric scincid lizards (*Ctenotus*) in arid South Australia.
730 *Australian Journal of Zoology*, **46**, 617-629.

731 Regan HM, Crookston JB, Swab R, Franklin J, Lawson DM (2010) Habitat fragmentation and
732 altered fire regime create trade-offs for an obligate seeding shrub. *Ecology*, **91**, 1114-1123.

733 Robinet C, Lance DR, Thorpe KW, Onufrieva KS, Tobin PC, Liebhold AM (2008) Dispersion
734 in time and space affect mating success and Allee effects in invading gypsy moth populations.
735 *Journal of Animal Ecology*, **77**, 966-973.

736 Ross KG (2001) Molecular ecology of social behaviour: analyses of breeding systems and
737 genetic structure. *Molecular Ecology*, **10**, 265-284.

738 Rousset F (2000) Genetic differentiation between individuals. *Journal of Evolutionary Biology*,
739 **13**, 58-62.

740 Sanz-Aguilar A, Anadón JD, Giménez A, Ballestar R, Graciá E, Oro D (2011) Coexisting with
741 fire: the case of the terrestrial tortoise *Testudo graeca* in mediterranean shrublands. *Biological*
742 *Conservation*, **144**, 1040-1049.

743 Schrey AW, Ashton KG, Heath S, McCoy ED, Mushinsky HR (2011a) Fire alters patterns of
744 genetic diversity among 3 lizard species in Florida scrub habitat. *Journal of Heredity*, **102**, 399-
745 408.

746 Schrey AW, Fox AM, Mushinsky HR, McCoy ED (2011b) Fire increases variance in genetic
747 characteristics of Florida Sand Skink (*Plestiodon reynoldsi*) local populations. *Molecular*
748 *Ecology*, **20**, 56-66.

749 Schtickzelle N, Joiris A, Van Dyck H, Baguette M (2007) Quantitative analysis of changes in
750 movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary*
751 *Biology*, **7**, 4.

752 Shanahan DF, Possingham HP, Riginos C (2011) Models based on individual level movement
753 predict spatial patterns of genetic relatedness for two Australian forest birds. *Landscape*
754 *Ecology*, **26**, 137-148.

755 Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK,
756 McKelvey K, Allendorf FW, Luikart G (2011) Why replication is important in landscape
757 genetics: American black bear in the Rocky Mountains. *Molecular Ecology*, **20**, 1092-1107.

758 Smith AL, Bull CM, Driscoll DA (2012) Post-fire succession affects abundance and survival but
759 not detectability in a knob-tailed gecko. *Biological Conservation*, **145**, 139-147.

760 Smith AL, Bull CM, Driscoll DA (2013) Successional specialization in a reptile community
761 cautions against widespread planned burning and complete fire suppression. *Journal of Applied*
762 *Ecology*, **50**, 1178-1186.

763 Smith AL, Gardner MG, Bull CM, Driscoll DA (2011) Primers for novel microsatellite markers
764 in "fire-specialist" lizards (*Amphibolurus norrisi*, *Ctenotus atlas* and *Nephrurus stellatus*) and
765 their performance across multiple populations. *Conservation Genetics Resources*, **3**, 345-350.

766 Smith AL, Gardner MG, Fenner AL, Bull CM (2009) Restricted gene flow in the endangered
767 pygmy bluetongue lizard (*Tiliqua adelaidensis*) in a fragmented agricultural landscape. *Wildlife*
768 *Research*, **36**, 466-478.

769 Smith LM, Burgoyne LA (2004) Collecting, archiving and processing DNA from wildlife
770 samples using FTA(R) databasing paper. *BMC Ecology*, **4**,
771 <http://www.biomedcentral.com/1472-6785/1474/1474>.

772 Smouse PE, Long JC, Sokal RR (1986) Multiple regression and correlation extensions of the
773 Mantel test of matrix correspondence. *Systematic Zoology*, **35**, 627-632.

774 South SL (2010) *Natural history and spatial ecology of Amphibolurus norrisi in southern*
775 *Australia*. Unpublished honours thesis, Flinders University, Adelaide.

776 Spear SF, Storfer A (2010) Anthropogenic and natural disturbance lead to differing patterns of
777 gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biological Conservation*,
778 **143**, 778-786.

- 779 Specht RL (1972) *The Vegetation of South Australia*. AB James, Government Printer, Adelaide,
780 SA.
- 781 Stamps JA (1983) Sexual selection, sexual dimorphism and territoriality. In *Lizard Ecology:
782 Studies of a Model Organism* eds Huey RB, Pianka ER, Schoener TW. Harvard University
783 Press, Cambridge, USA.
- 784 Stephens PA, Sutherland WJ, Freckleton RP (1999) What is the Allee effect? *Oikos*, **87**, 185-
785 190.
- 786 Templeton AR, Brazeal H, Neuwald JL (2011) The transition from isolated patches to a
787 metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology*, **92**, 1736-
788 1747.
- 789 Twidale CR, Campbell EM (1985) The form of the land surface. In *Natural history of Eyre
790 Peninsula*. eds Twidale CR, Tyler MJ, Davies M. Royal Society of South Australia, Adelaide,
791 SA.
- 792 Welsh AH (1996) *Aspects of Statistical Inference*. John Wiley & Sons, Inc., New York.
- 793 Westgate MJ, Driscoll DA, Lindenmayer DB (2012) Can the intermediate disturbance
794 hypothesis and information on species traits predict anuran responses to fire? *Oikos*, **121**, 1516-
795 1524.
- 796 Wilson S, Swan G (2010) *A Complete Guide to Reptiles of Australia*, 3 edn. New Holland,
797 Sydney.
- 798 Wright S (1943) Isolation by distance. *Genetics*, **28**, 114-138.
799

800 **Data accessibility**

801 Appendix S1 includes a spreadsheet containing the genotype and location data for each sampled
802 individual and the spatial distances and landscape resistances for each pair of individuals.

803

804 **Author contributions**

805 ALS, CMB, MGG and DAD designed the research and collected the data; ALS analysed the
806 data and wrote the manuscript with extensive input from CMB, MGG and DAD.

807

808 **Supporting information**

809 Additional supporting information may be found in the online version of this article:

810

811 **Table S1** Sites where DNA samples from *Amphibolurus norrisi* and *Ctenotus atlas* were
812 collected on the Eyre Peninsula, South Australia.

813 **Fig. S1** A spatial mosaic of different fire frequencies at Hincks.

814 **Fig. S2** A digital elevation model used to test the effect of sand dunes on gene flow in
815 *Amphibolurus norrisi* and *Ctenotus atlas*.

816 **Table S2** Results from generalised linear mixed models investigating the effect of time since
817 fire on capture rates in *Amphibolurus norrisi* and *Ctenotus atlas* at Munyaroo and Heggaton.

818 **Fig. S3** The effect of time since fire on capture rates in *Amphibolurus norrisi* and *Ctenotus atlas*
819 at Munyaroo and Heggaton.

820 **Table S3** Results from linear mixed models to examine the effect of time since fire and reserve
821 on allelic richness in *Amphibolurus norrisi* and *Ctenotus atlas*.

822 **Fig. S4** Results from a sensitivity analysis to test how changing the sample size standardisation
823 influenced the effect of time since fire on allelic richness in *Ctenotus atlas*.

824 **Fig. S5** Results from a sensitivity analysis to test how changing the sample size standardisation
825 influenced the effect of time since fire on allelic richness in *Amphibolurus norrisi*.

826 **Fig. S6** Results from STRUCTURE indicating the most likely number of clusters in the samples
827 from *Amphibolurus norrisi* and *Ctenotus atlas*.

828 **Fig. S7** Results from GENELAND indicating the most likely number of clusters in the samples
829 from *Amphibolurus norrisi* and *Ctenotus atlas*.

830 **Fig. S8** Probabilities of assignment to genetic clusters identified by GENELAND.

831 **Table S4** Results from causal modelling of the effect of landscape resistance on genetic distance
832 in *Amphibolurus norrisi* and *Ctenotus atlas*.

833 **Table S5** Age and sex structure of *Amphibolurus norrisi* and *Ctenotus atlas* at Hincks and
834 Pinkawillinie.

835 **Table S6** Mantel tests for isolation by distance and allelic richness from data simulated under a
836 stable demographic scenario and a disturbed scenario.

837 **Appendix S1** A spreadsheet containing the genotype and location data for each sampled
838 individual and the spatial distances and landscape resistances for each pair of individuals.

839

840 **Figure legends**

841

842 **Fig. 1** Samples were collected from 38 sites across fire mosaics in four conservation reserves on
843 the Eyre Peninsula, South Australia. Sample sizes are shown in pink (*Amphibolurus norrisi*) and
844 yellow (*Ctenotus atlas*) boxes. At Heggaton, we used both spatial and temporal sampling
845 strategies as similar sample sizes were collected across the landscape before (*A. norrisi* = 20; *C.*
846 *atlas* = 21) and after (*A. norrisi* = 21; *C. atlas* = 22) prescribed fires in April 2006. At the other
847 three reserves, samples were collected after the most recent fire (Hincks: Dec 2006;
848 Pinkawillinie: Dec 2005; Munyaroo: Oct 1990), except at two sites each at Hincks and
849 Pinkawillinie where samples were collected before and after fires (before/after sample sizes
850 indicated as N/N).

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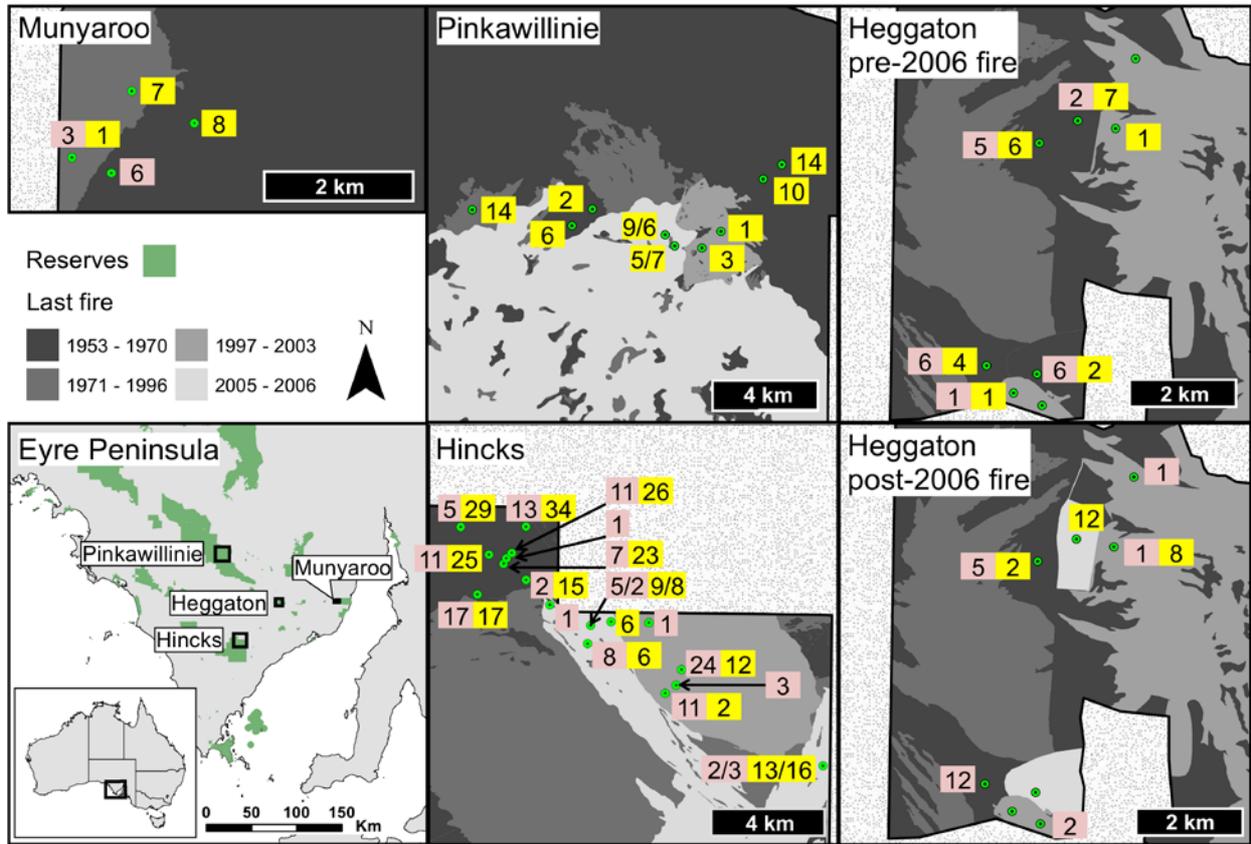
852 **Fig. 2** The effect of time since fire on allelic richness in (A) *Ctenotus atlas* ($P = 0.037$) and (B)
853 *Amphibolurus norrisi* ($P = 0.003$) and (C) the effect of reserve on allelic richness in *A. norrisi*
854 ($P < 0.001$). All results are from a standardised sample size of five individuals. Model estimates
855 are shown over the data in A and B (open circles = Heggaton; closed circles = Hincks; closed
856 triangles = Munyaroo; open triangles = Pinkawillinie). Error bars are 95 % confidence intervals.

857

858 **Fig. 3** Probabilities of assignment to genetic clusters identified by GENELAND (each bar
859 represents an individual lizard). Plots are shown only for data sets in which genetic
860 differentiation was detected. (A) Differentiation between Hincks at the other reserves was
861 evident for *C. atlas* and (B) a distinct cluster was formed by N3 and N4 within Heggaton for *A.*
862 *norrisi*. For Heggaton, the site name and year of last fire is shown below the bars and whether
863 samples were collected (b) before or (a) after the prescribed fires is shown above the bars.

864

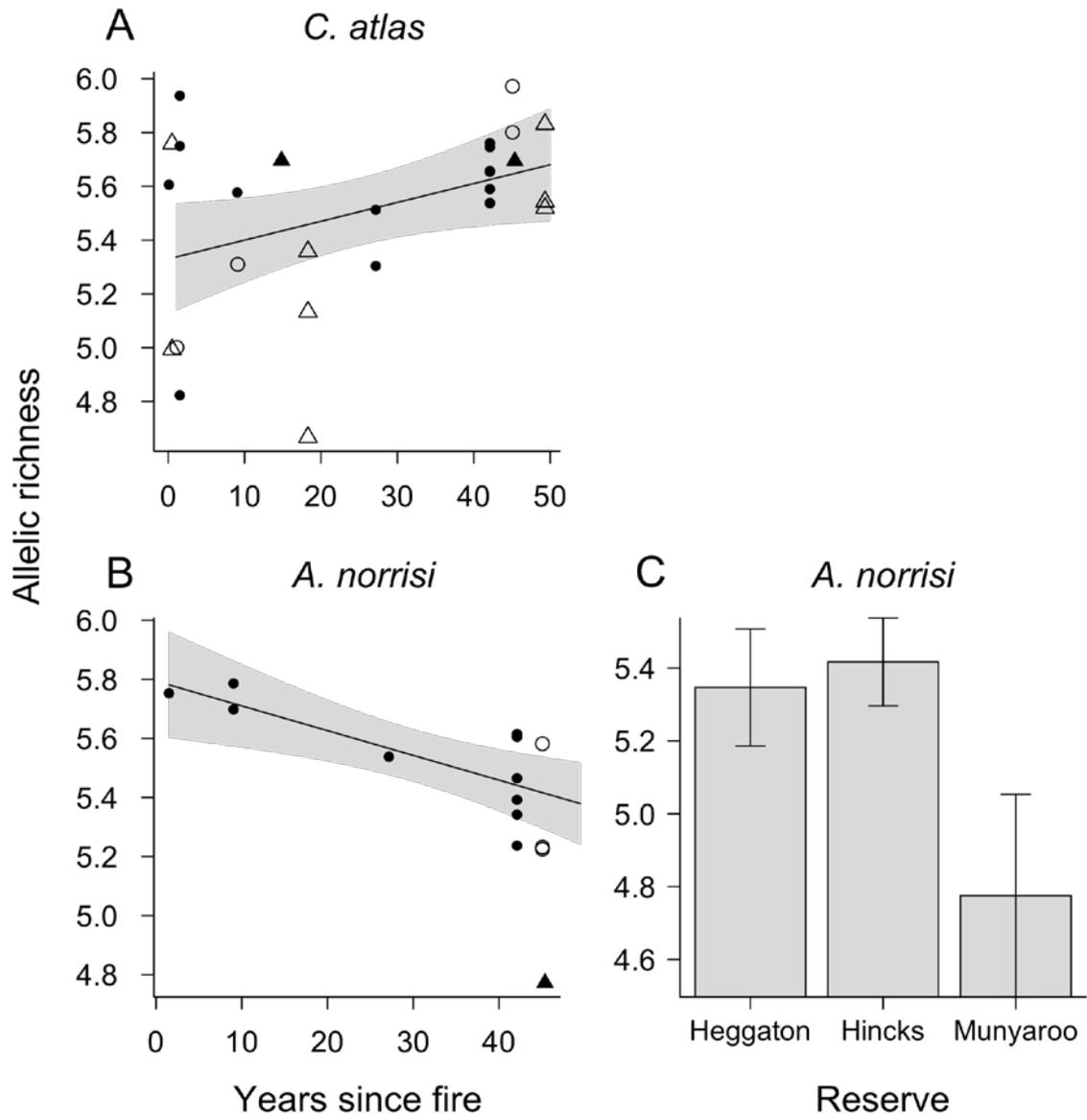
865 **Figure 1**



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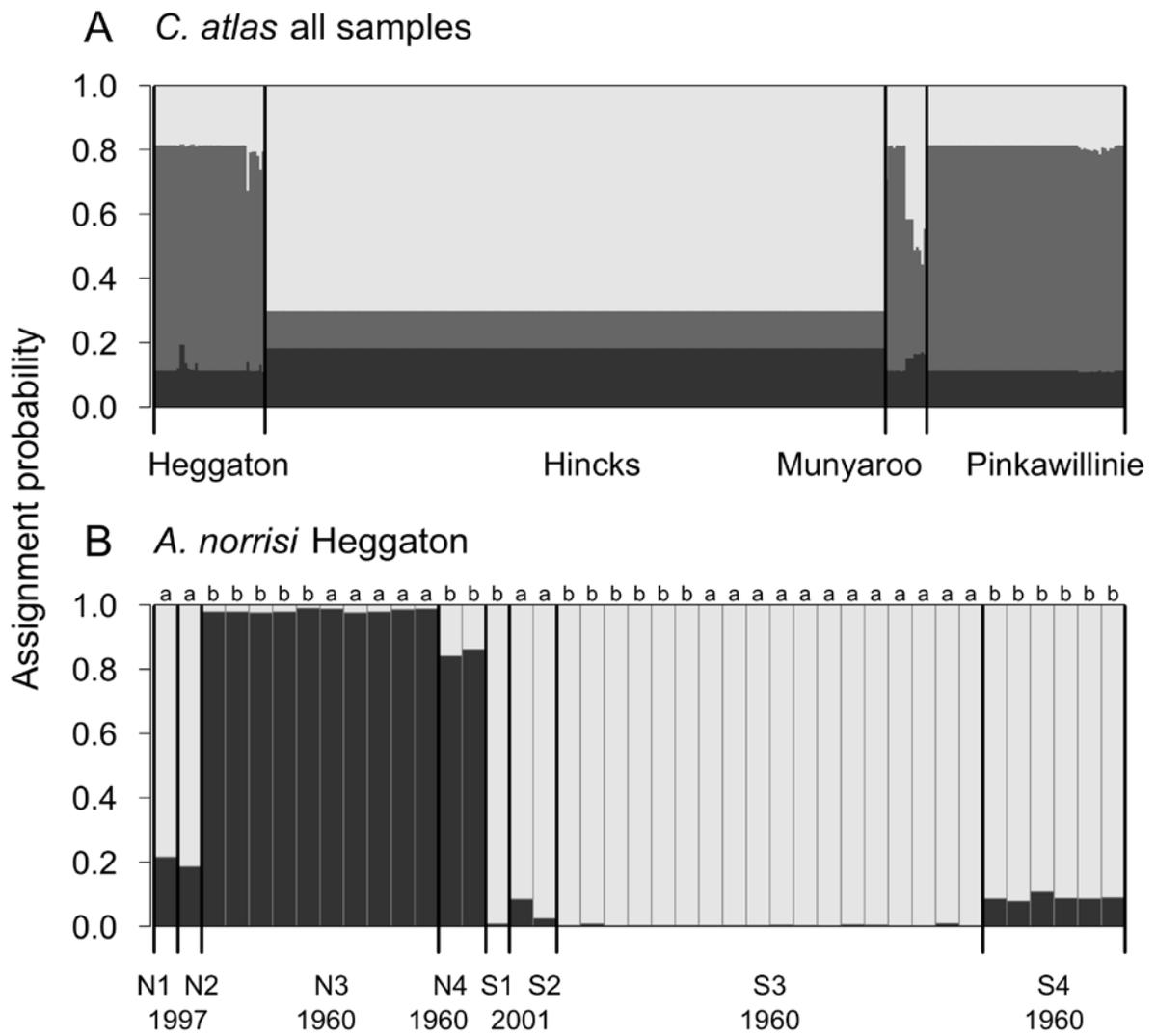


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878 **Table 1** Analytical techniques used to answer our four research questions

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Method	Data set	Level
<i>Question 1. Does spatial variation in fire, topography and population density influence gene flow and genetic diversity?</i>		
Linear-mixed models of time since fire effects on allelic richness	Sample sites with ≥ 5 individuals	Population
Linear-mixed models of time since fire effects on individual heterozygosity	All samples	Individual
STRUCTURE	All samples	Individual
GENELAND	All samples	Individual
Simple and partial Mantel tests of the effects of landscape resistance on genetic distance	All samples except pre-2005/2006 fire samples at Hincks and Pinkawillinie	Individual
<i>Question 2. Is there an immediate, temporal effect of fire in the landscape on genetic structure?</i>		
Simple and partial Mantel tests of the effects of landscape resistance on genetic distance	Heggaton samples pre- and post-fire	Individual
<i>Question 3. Is post-fire re-establishment facilitated by survivors, or by immigration?</i>		
STRUCTURE analysis on samples within the overall sample and on each site separately	Five sites (two at Hincks, two at Pinkawillinie and one at Heggaton) where samples were collected before and after fires that occurred during the study	Individual
<i>Question 4. Can affects of fire on genetic diversity be explained by differences in demographic attributes?</i>		
Generalised linear mixed models of time since fire effects on population age structure and sex ratios	'Grid' sites at Hincks and Pinkawillinie (Table S1) where age and sex were recorded	Population
Simple Mantel tests of isolation by distance in adult males and adult females separately (sex-biased dispersal)	'Grid' sites at Hincks and Pinkawillinie (Table S1) where age and sex were recorded	Individual
EASYPOP simulations of genetic data for stable and disturbed <i>A. norrisi</i> populations	Simulated microsatellite data	Population

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881

882 **Table 2** Five spatial models of landscape resistance based on features that could affect gene flow in *Amphibolurus norrisi* and *Ctenotus atlas*

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Spatial model	Grid cell values	Potential ecological importance
Isolation by distance	1	Genetic distance can increase with geographic distance (Wright 1943).
Sand dune topography	Metres above sea level	<i>Amphibolurus norrisi</i> has been recorded more commonly on dunes than swales (South 2010) and <i>C. atlas</i> depends on <i>Triodia spp.</i> which occur on deep sands (Pianka 1972). Gene flow may be inhibited or promoted by sand dunes if the dunes affect their dispersal ability or population density.
Time since fire (TSF)	Number of years since most recent fire (1-54)	Marked changes in vegetation structure occur with TSF at our study sites (Smith <i>et al.</i> 2012) and habitat structure can affect dispersal and population density in lizards (Berry <i>et al.</i> 2005; Templeton <i>et al.</i> 2011). This model test whether gene flow is affected by TSF in a linear way.
Population density	Mean no. captures predicted from TSF (Smith <i>et al.</i> 2013)	Habitat suitability for lizards does not always change linearly with TSF (Nimmo <i>et al.</i> 2012; Smith <i>et al.</i> 2013). Dispersal through unsuitable habitat may be inhibited (Prevedello <i>et al.</i> 2010; Shanahan <i>et al.</i> 2011) or promoted (Driscoll & Hardy 2005; Schtickzelle <i>et al.</i> 2007) and increased population density can positively or negatively affect gene flow (Robinet <i>et al.</i> 2008; Stephens <i>et al.</i> 1999).
Fire frequency	Number of fires since 1953 (0-5)	Fire can have cumulative effects on animal populations (Lindenmayer <i>et al.</i> 2008) either through demographic impacts of repeated burning (Westgate <i>et al.</i> 2012) or changes in habitat structure (Pausas & Lloret 2007).

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