Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

PROCEEDINGS B

rspb.royalsocietypublishing.org

Research

Cite this article: Smith AL, Landguth EL, Bull CM, Banks SC, Gardner MG, Driscoll DA. 2016 Dispersal responses override density effects on genetic diversity during post-disturbance succession. *Proc. R. Soc. B* **283**: 20152934. http://dx.doi.org/10.1098/rspb.2015.2934

Received: 8 December 2015
Accepted: 26 February 2016

Subject Areas:
ecology

Keywords:
density dependence, fire, habitat fragmentation, landscape genetics, movement ecology, demographic population model

Author for correspondence:
Annabel L. Smith
e-mail: annabel@smithecology.org

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2015.2934 or via http://rspb.royalsocietypublishing.org.

THE ROYAL SOCIETY PUBLISHING

Dispersal responses override density effects on genetic diversity during post-disturbance succession

Annabel L. Smith[1], Erin L. Landguth[2], C. Michael Bull[3], Sam C. Banks[1], Michael G. Gardner[3,4] and Don A. Driscoll[1,5]

[1]Fenner School of Environment and Society, Australian National University, Fenner Building 141, Linnaeus Way, Canberra, Australian Capital Territory 2601, Australia
[2]Division of Biological Sciences, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
[3]School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia
[4]Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia
[5]School of Life and Environmental Sciences, Deakin University Geelong, 221 Burwood Highway, Burwood, Victoria 3125, Australia

ALS, 0000-0002-1201-8713

Dispersal fundamentally influences spatial population dynamics but little is known about dispersal variation in landscapes where spatial heterogeneity is generated predominantly by disturbance and succession. We tested the hypothesis that habitat succession following fire inhibits dispersal, leading to declines over time in genetic diversity in the early successional gecko *Nephrurus stellatus*. We combined a landscape genetics field study with a spatially explicit simulation experiment to determine whether successional patterns in genetic diversity were driven by habitat-mediated dispersal or demographic effects (declines in population density leading to genetic drift). Initial increases in genetic structure following fire were likely driven by direct mortality and rapid population expansion. Subsequent habitat succession increased resistance to gene flow and decreased dispersal and genetic diversity in *N. stellatus*. Simulated changes in population density alone did not reproduce these results. Habitat-mediated reductions in dispersal, combined with changes in population density, were essential to drive the field-observed patterns. Our study provides a framework for combining demographic, movement and genetic data with simulations to discover the relative influence of demography and dispersal on patterns of landscape genetic structure. Our results suggest that succession can inhibit connectivity among individuals, opening new avenues for understanding how disturbance regimes influence spatial population dynamics.

1. Introduction

Dispersal maintains genetic diversity and adaptive potential in natural populations [1] and has a profound influence on spatial population dynamics [2]. The processes by which human-caused and natural habitat fragmentation influence dispersal have been well studied [3]. Less is known about the effects of spatial habitat heterogeneity generated through disturbance and succession, within a single, non-fragmented vegetation type. If dispersal is influenced by structural habitat succession, disturbance regimes at spatial or temporal scales that cause extinction or prevent recolonization could be analogous to habitat fragmentation [4]. Understanding how succession affects dispersal and genetic diversity is therefore critical to predict how natural and management-driven disturbance regimes will influence population connectivity [4–6].

Landscape genetics analyses that relate habitat suitability indices to spatial patterns of genetic diversity can reveal how disturbance influences gene flow [7–9]. Patterns of landscape genetic structure are usually attributed to habitat-mediated dispersal (e.g. [10]). However, spatial genetic structure is shaped by multiple processes. For example, variation in habitat suitability

© 2016 The Author(s) Published by the Royal Society. All rights reserved.

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

can affect both dispersal and population density, and these parameters are often correlated [11]. In such cases, it is difficult to determine what drives landscape genetic patterns because density affects genetic diversity through genetic drift, even without variation in dispersal [12–14]. False inferences might be drawn if complementary ecological or behavioural data are not incorporated into genetic models of dispersal [15].

A secondary problem is that disturbance can have instant and profound effects on population structure resulting from displacement and direct mortality [16]. Untangling the initial genetic impact of a disturbance event from the ongoing effects of habitat succession on dispersal is difficult with genetic data alone [17]. Signals of population genetic structure from past landscapes might also mask contemporary differences in dispersal rates [18]. Simulation experiments combined with empirical genetic and demographic data can allow deeper insights into the mechanisms behind variation in genetic diversity [19] but such multi-faceted studies are rare [5].

We combined a replicated field study of movement and gene flow with an individual-based, spatially explicit simulation experiment to assess the effect of fire-driven habitat succession on dispersal in the Australian knob-tailed gecko, *Nephrurus stellatus*. The species has a strong and regionally consistent response to fire: population density increases for approximately 15 years after fire then declines sharply, such that it is rare (less than 10% of peak density) 30 years or more after fire [20,21]. This early successional response to fire, reflecting variation in density rather than detectability, is driven partly by changes in reproduction and survival [20]. As burrowers, *N. stellatus* can probably survive fire and recently burnt habitat is conducive to their foraging in open, sandy spaces [21]. We tested the hypothesis that increasing habitat complexity during post-fire succession [20] inhibits movement and dispersal, thus decreasing genetic diversity. We tested this explicitly by analysing how gene flow was affected by landscape resistance based on spatial models of fire history. We then used an individual-based genotypic simulation to determine whether the effects of habitat change on genetic diversity were driven by changes in dispersal, population density or both.

To reveal the mechanism for population decline during succession, it is critical to obtain data from sub-optimal habitat, but sample sizes in these areas are always small, even with immense sampling effort [20]. Genetic data have limitations in this context, but our unique combination of genetic data with mark–recapture movement data and simulation provides a powerful approach for detecting population trends over ecological timescales. Furthermore, we focused on analytical methods appropriate for unequal sample sizes (e.g. individual rather than population-based analyses). Where small sample sizes were unavoidably used in our analyses, we challenged our results with sensitivity analysis to ensure that changing sample sizes did not affect our overall conclusions [22]. The link between data and simulation is the strongest aspect of our study. This is the first integration of landscape resistance and population density into a spatially explicit genotypic simulation of which we are aware. Support for our hypothesis would indicate that successional changes in vegetation structure, in otherwise continuous habitat, influence connectivity and spatial population dynamics.

2. Material and methods

(a) Study system

Our study region was the semi-arid (average annual rainfall: 296–361 mm) Eyre Peninsula, South Australia, where conservation reserves remain among land predominantly used for agriculture (figure 1*a*). *Nephrurus stellatus* is largely restricted in its distribution to this region. We sampled four large reserves (6476–130 148 ha): Heggaton Conservation Reserve, Hincks Wilderness Area, Munyaroo Conservation Park and Pinkawillinie Conservation Park (electronic supplementary material, figure S1). The dominant vegetation is 'mallee' woodland, characterized by short (less than 6 m), multi-stemmed *Eucalyptus* trees, with a shrubby midstorey and *Triodia* grass ground-layer [20]. Large, severe wildfires, commonly ignited by summer lightning, occur on a 40–100 year timescale [23]. We characterized fire history within reserves using spatial data on the number of years since the most recent fire (South Australian Department for Environment, Water and Natural Resources). A more complex fire history at Hincks meant our sites also spanned a range of fire frequencies (0–5 fires since 1953; electronic supplementary material, figure S1).

(b) Study design and field data

We sampled DNA from 764 *N. stellatus* individuals (Hincks = 494, Pinkawillinie = 216, Munyaroo = 32, Heggaton = 22; electronic supplementary material, table S1) over six consecutive sampling seasons (the spring/summer period when mallee lizards are most active), from December 2004–February 2005 (season 1) to November 2009–February 2010 (season 6) (electronic supplementary material, table S1). Ninety-three per cent of samples were collected in the final three seasons and, at a given site, samples were collected over a maximum of four seasons and usually only over one or two seasons (electronic supplementary material, table S1). All DNA samples were collected after the most recent fire in each reserve (except samples from three individuals which were excluded from the landscape resistance analyses; electronic supplementary material, table S1).

We sampled 39 permanently marked sites within the four reserves (90% of samples) and sampled 80 individuals opportunistically among sites to achieve a more continuous sampling distribution. This mixed sampling approach is suitable for detecting gene flow barriers [24]. Given the strong population response to fire, sample sizes varied from one to 95 individuals per site (figure 1*b*; electronic supplementary material, table S1). Many of our analyses focused on individuals as sampling units, avoiding the need for consistently large samples from pre-defined population units. Individual-level landscape genetics analyses are especially suited to detecting recently established (1–15 generations) landscape barriers to gene flow [18], such as those potentially created by fire and succession. Samples were collected from habitat spanning 0.7 and 57 years after fire (figure 1*b*; electronic supplementary material, table S1) and were separated by average distances of 3.2 km (range 0–13.8). These distances are on a similar spatial scale to the extent of natural and prescribed fires in mallee [23] and to commonly reported extents of genetic structure in lizards (e.g. [7,25]).

Geckos were captured in pitfall traps [21] or by hand (electronic supplementary material, table S1). For initial captures, a single back-toe tip was clipped as a unique season mark and as a DNA source. Blood and tissue from the toe were stored, respectively, on FTA paper (Whatman) and in liquid nitrogen or 5 ml ethanol/physiological saline (1 : 1). Visible Implant Elastomer (Northwest Marine Technology) was used to mark geckos and reliably identify individuals upon recapture [20]. We recorded the age class (adult or juvenile based on size,

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

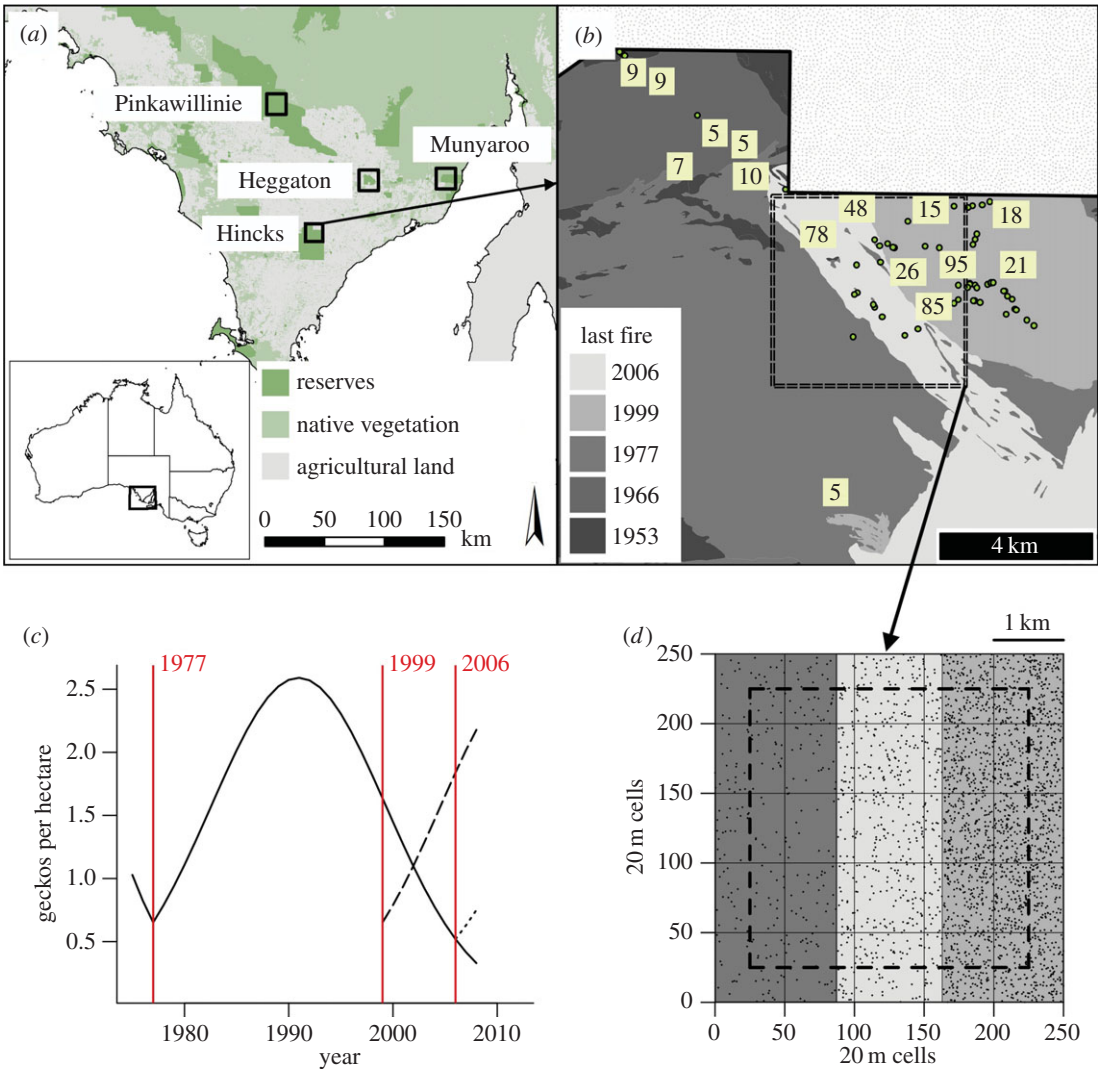


Figure 1. (*a*) *Nephrurus stellatus* DNA was sampled across fire mosaics in four conservation reserves, South Australia (maps of all reserves in the electronic supplementary material, figure S1). (*b*) We achieved the largest sample size (494) at Hincks and based our simulation experiment on a section of this landscape (indicated by the square). Boxed numbers indicate sample sizes at fixed sites, and dots indicate individual samples collected continuously across the landscape. (*c*) The simulation experiment used estimates of population density for habitat burnt in 1977 (solid line), 1999 (dashed line) and 2006 (dotted line). Vertical lines indicate fire years, based on the fire history at Hincks. (*d*) The landscape at the end of the simulation (2008) included three different successional stages (3, 10 and 31 years after fire), with varying population density (black dots = individuals). Individuals outside the buffer (dashed line) were excluded from the analysis. (Online version in colour.)

[20]) and sex of adults (electronic supplementary material, table S1). All geckos were released at their capture location within 24 h of processing.

We amplified DNA for 14 polymorphic microsatellite loci that showed spatially consistent patterns of Hardy–Weinberg equilibrium and linkage equilibrium (loci: 06, 09, 11, 16, 18, 23, 28, 31, 33, 35, 38, 43, 46, 47) [26]. Apart from site-level genetic diversity and F_{ST}, all analyses focused on the individual-level.

(c) Population genetic structure

We characterized population genetic structure with Bayesian clustering [27,28] over the entire study region to infer broad patterns of genetic differentiation and separately within each reserve to examine local patterns across fire mosaics (details in the electronic supplementary material). We also examined F_{ST} between all pairs of reserves and sites within reserves where sample sizes were more than 10 (thus long-unburnt sites with low gecko densities could not be examined using F_{ST}). These analyses did not explicitly incorporate spatial fire history but allowed us to examine *post-hoc* if genetic differentiation related to fire mosaics.

(d) Genetic diversity

To determine whether post-fire habitat succession affected genetic diversity, we analysed variation in site-level allelic richness, site-level observed (H_O) and expected heterozygosity (H_E) (details in the electronic supplementary material) and individual heterozygosity (the proportion of typed loci that were heterozygous in each individual). Sample size (N) varied across sites so we standardized allelic richness, H_O and H_E to $N = 5$ to encompass the full site variation in time since fire (TSF). We conducted a sensitivity analysis to test whether sample size ($N = 6$–10) influenced effects of TSF on site-level genetic diversity [22]. As N increased, the number of sites included in the analysis decreased, so we lost power to test effects of TSF, but were able to determine whether the general patterns were consistent.

We used linear mixed-effects models in the R [29] package 'lme4' [30] to examine if TSF affected allelic richness, H_O and H_E for each N [22]. Multiple sites were sampled within a single fire boundary, so we fitted fire (a factor naming individual fire events) as a random effect. TSF and reserve were fitted as fixed effects and our starting model included their main and interaction terms. We removed the interaction term, and

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

Table 1. Five spatial models of landscape resistance based on features that could affect gene flow in *Nephrurus stellatus*. These features could affect gene flow by positively or negatively influencing rates of dispersal through suitable habitat or by influencing population density. Electronic supplementary material contains detail about how landscape resistance values were derived.

spatial model	grid cell values	potential ecological importance	predicted relationship
IBD	1	genetic distance can increase with geographical distance [33].	+
sand dune topography	metres above sea level	sand dunes are the dominant topographic features in our study system. *Nephrurus stellatus* is more common on dunes than swales as it is a burrower and forages in open, sandy spaces [21].	±
TSF-linear	number of years since most recent fire (1–57)	marked changes in vegetation structure with TSF occur at our study sites [20] and habitat structure can affect dispersal in lizards [4].	±
TSF-nonlinear	mean no. captures predicted from TSF [21]	population density in *N. stellatus* changes nonlinearly with TSF [20,21] and population density can affect gene flow [34].	±
fire frequency	number of fires since 1953 (0–5)	fire can have cumulative effects on animal populations through demographic impacts of repeated burning [35] or changes in habitat structure [36]	±

subsequently reserve, if p was more than 0.05. We modelled individual heterozygosity with the same formulation as for the site-level variables, but included site as an additional random term to account for potential dependence among individuals at the same site.

(e) Movement

In our previous, formal mark–recapture study of *N. stellatus*, we found variation in survival and reproductive rates with TSF, but not variation in detectability [20]. Trapping surveys were standardized so that all TSF categories received equal trapping effort (full details in [20]). For this study, we used the same mark–recapture data to determine whether habitat succession affected movement in *N. stellatus*.

The dataset was 307 observations of distances between capture locations within sites (Hincks = 237, Pinkawillinie = 70) from 173 individual geckos in seasons 4–6 (electronic supplementary material, table S1). We only included recaptures within a single trapping period (less than or equal to 15 days), because there were very few recaptures between periods at long-unburnt sites to allow full analysis. A single movement record probably underestimated the actual distance moved between captures and observations were restricted to 1 ha trapping grids [20]; 120 m was the longest movement recorded. These data therefore represent short-range and short-term movements, an informative comparison to our genetic analyses which infer longer distance dispersal [31].

We calculated the movement rate (metres moved/number of days between captures) for all geckos captured more than once. For geckos captured more than twice, each movement was included as a separate observation (e.g. geckos captured four times had three observations). With a high proportion (30%) of zero distances in our data, we first investigated whether TSF affected movement propensity (electronic supplementary material). We then considered, just for geckos that moved, how movement rate was affected by TSF (using a three-level factor: 3, 10 or 30 years). We developed 14 candidate models to examine effects of TSF, minimum temperature (a strong predictor of *N. stellatus* capture rates, [20]) and three covariates: sex, age and reserve. We included TSF and minimum temperature in all models. The candidate set included the global model (all covariates) and all additive formulations nested within it. We included first-order interactions of each covariate with TSF and, for comparison, a null model (no predictor variation) and a model with only minimum temperature. We initially fitted individual (18% of geckos were measured more than once) and fire as random effects. However, the variance on both random terms was approximately zero so we fitted normal linear models and ranked them by AICc weight. We made inference from the top-ranked model, appropriate for model sets including interactions [32].

(f) Landscape resistance

To examine spatial variation in gene flow within reserves, we developed five independent, univariate landscape resistance models based on knowledge of habitat suitability in *N. stellatus*: isolation-by-distance (IBD), TSF-linear, TSF-nonlinear, fire frequency (Hincks only) and sand dune topography (table 1 shows how grid cells were parametrized and details of their derivation are in the electronic supplementary material). These landscape features could affect gene flow by influencing rates of dispersal through suitable habitat (negatively [10] or positively [37]) or by influencing population density [38]. The TSF-linear and TSF-nonlinear models were based on the spatial configuration of TSF but with different values. TSF-linear used the number of years since fire, while TSF-nonlinear used an index of abundance (electronic supplementary material), reflecting nonlinear population responses in *N. stellatus* [21]. We compiled each resistance model separately on a 20 m resolution raster grid in ArcMap 10 (ESRI).

For every pair of geckos within reserves, we calculated Rousset's genetic distance [13] in SPAGEDI v. 1.2 [39] and landscape resistance in CIRCUITSCAPE v. 3.5.4 [40]. We conducted causal modelling [41] in the R package 'ecodist' [42] using simple and partial Mantel tests to examine the effects of each resistance model separately on genetic distance (electronic supplementary material). At Hincks and Pinkawillinie where age and sex were recorded ('grid sites', electronic supplementary material, table S1), we analysed all geckos, all adults, adult females and adult males separately. We also conducted multiple regression of distance matrices (electronic supplementary material) and simple Mantel tests on each landscape resistance model as a comparison to the partial Mantel approach [43].

(g) Simulation experiment

We designed a simulation experiment to separate the effects of post-fire habitat succession and population density on genetic diversity and gene flow. Our simulation was designed to test a specific biological question, rather than explore effects of the full

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

range of parameter variation. Thus, we focused on realistically parametrizing the model using the sampled landscape and demographic data on the study species. The experiment was based on the landscape at Hincks (figure 1*b*,*d*) where we had the largest sample size and greatest knowledge about spatial genetic structure. The simulated landscape covered 5 × 5 km with a 20 m spatial resolution to match our landscape resistance models. The simulation spanned 31 years (1977–2008) to encompass the fire history at Hincks. We fitted *N. stellatus* density estimates [20] to a TSF model [21] (electronic supplementary material) to obtain continuous density values for the simulation (figure 1*c*).

Our full factorial experiment encompassed stable and changing population densities, and uniform compared with dynamic (increasing resistance with TSF) landscapes: Scenario 1 (Sc1) = stable density, uniform landscape (null model); Scenario 2 (Sc2) = stable density, dynamic landscape; Scenario 3 (Sc3) = changing density, uniform landscape; Scenario 4 (Sc4) = changing density, dynamic landscape. We ran three versions of the stable density scenarios (Sc1 and Sc2) to encompass the range of observed densities at the end of the simulation (0.75, 2.18 and 0.33 geckos/hectare at 3, 10 and 31 years since fire, respectively; figure 1*c*). We simulated genotypes in CDPOP 1.2.21 [44], which incorporates landscape-resistance surfaces from CIRCUITSCAPE and allows resistance to change during the simulation.

Sc1 and Sc2 are unrealistic given their stable population density (*N. stellatus* density changes with succession) but were necessary to understand the influence of the dynamic landscape without changes in density. The primary aim of this modelling component was to determine the importance of dispersal to genetic diversity given the known fluctuations in population density. Thus, to explore mechanisms of successional change in gene flow and genetic diversity, we focused on comparisons between Sc3 and Sc4 in which density changes mirrored those of natural populations of *N. stellatus*. This allowed us to determine whether habitat succession, represented by landscape resistance (present in Sc4 but not Sc3), was necessary to drive change in gene flow and genetic diversity.

In all simulations, individuals became adults after their first year [20] and did not live beyond their fifth year [45]. We calculated the population age distribution (g) as

$$g = \frac{A_{i,1}}{\Sigma A_{i,1}}, \tag{2.1}$$

where $A_{i,1}$ is a Leslie matrix eigen vector [46] with an annual survival rate of 0.343 and a fecundity of 2 [20]. Males and females mated with replacement. There was multiple paternity, no philopatry and an equal sex ratio (common in gecko mating systems). We used the *k*-allele mutation model with a mutation rate of 0.0005 and 14 loci each with 16 alleles (mean number of alleles in our microsatellite data). We used the scaled negative exponential function for dispersal and mating movement (found in other reptiles, e.g. [47]):

$$p = \frac{(a10^{(-b.r)}) - a10^{(-b.\text{thresh})})}{(a10^{(-b.\min(r))}) - a10^{(-b.\text{thresh})}}, \tag{2.2}$$

where $a = 1$, $b = 2$, r is the resistance surface and 'thresh' is a threshold value which we set to 30% for movement (0.3 max(r)) and 40% for dispersal. We conducted preliminary analyses of Sc1 to optimize b and 'thresh' and to determine the burn-in period (15 generations, electronic supplementary material). Simulations were initialized with random genotypes and each was repeated 10 times.

In the uniform landscape (Sc1 and Sc3), all spatial grid cells were equal to 1 during the entire simulation. To simulate the dynamic landscape in Sc2, resistance surfaces representing TSF (table 1) were updated every two generations using the CDCLIMATE module in CDPOP. For Sc3 and Sc4, we manually altered population density during the simulation (no modules were available in which population density and landscape resistance could simultaneously change). To do this, we ran the simulation for two generations at a time (following the burn-in), changed population density using the simulation output and continued using the updated files to initialize the next two-generation stage. This preserved the population genetic structure developing during the simulation (electronic supplementary material, figure S2). For Sc4, the resistance surface was also updated every two generations to simulate the dynamic landscape. When population density increased (e.g. 1978–1990, figure 1*c*), new individuals were randomly added to the grid and genotypes at each locus were generated by randomly sampling one allele each from the most likely mother and father. The parents were sampled using negative exponential mating probabilities (thresh = 0.3; r = current resistance surface). When population density decreased (e.g. 1992–1999, figure 1*c*), individuals were randomly removed. After 1999, density trajectories increased in one section of the landscape and decreased in another (figure 1*c*). This spatial variation was incorporated into the updated files.

Using data from the final year of the simulation (2008) and excluding individuals from a 500 m edge buffer (figure 1*d*), we examined the effect of IBD and TSF on genetic distance (table 1). We compared mean Mantel r-values across the 10 independent simulations to values in the field data. We calculated allelic richness for different sample size standardizations (5, 10, 25, 50 and 75) to examine how genetic diversity was affected by habitat succession at the end of the simulation (3, 10 and 31 years since fire).

3. Results

(a) Population genetic structure

Across the entire study region, Bayesian clustering indicated that individuals from Munyaroo and Pinkawillinie formed distinct genetic clusters, while those from Hincks and Heggaton were similar (electronic supplementary material, figures S3 and S4). There were low but significant values of F_{ST} among all pairs of reserves (0.008–0.031; electronic supplementary material, table S2). Within reserves, Bayesian clustering assigned all individuals to the same genetic cluster (electronic supplementary material, figure S3), indicating generally weak genetic structure across fire mosaics. One pair of sites at Hincks, separated by only 1 km in an area burnt approximately 4 years before sampling, was genetically differentiated ($F_{ST} = 0.008$, adjusted $p = 0.004$). Similarly, at Pinkawillinie, two early successional sites, 1 km apart, were genetically differentiated from each other, and from nearby mid-successional sites ($F_{ST} = 0.015$–0.019; electronic supplementary material, table S2). Mid-successional sites in both reserves separated by the same distance were not genetically different (electronic supplementary material, table S2). These results indicate an initial establishment of genetic structure in the first 4 years after disturbance which disappeared after 7–10 years of habitat succession.

(b) Genetic diversity

Allelic richness decreased with increasing TSF ($p = 0.013$) and did not differ among reserves for $N = 5$ (figure 2). Sensitivity analysis showed an effect of sample size on this relationship (electronic supplementary material, figure S5). For example, when $N = 10$, allelic richness increased with TSF at Pinkawillinie and Munyaroo but decreased at Hincks (TSF × reserve interaction $p = 0.016$; electronic supplementary material, figure S5). Increasing sample size limited our power to detect effects of

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

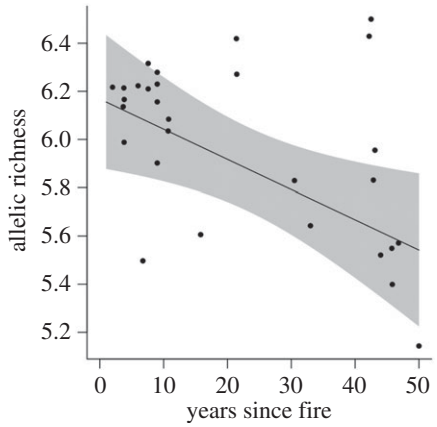


Figure 2. The effect of TSF on allelic richness in *Nephrurus stellatus*, standardized to a sample size of 5. Model estimates and 95% CIs are shown over the data.

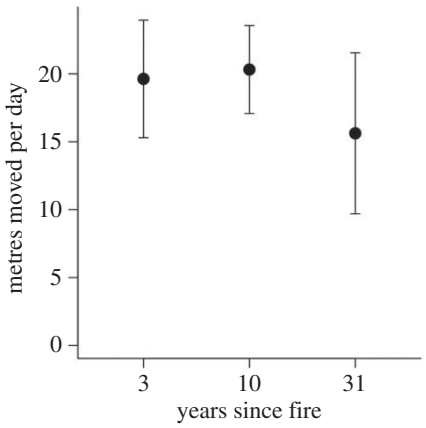


Figure 3. The effect of TSF on *Nephrurus stellatus* movement rate (model estimates and 95% CIs). The model also included minimum temperature and reserve (electronic supplementary material, figure S8).

TSF given the few long-unburnt sites with large sample sizes. However, a decrease in allelic richness over the 50 year succession was observed generally (electronic supplementary material, figure S5). Similarly, H_O and H_E generally decreased with increasing TSF, although not always significantly (electronic supplementary material, table S3 and figure S7). Individual heterozygosity decreased with increasing TSF ($p = 0.042$) and varied among reserves ($p = 0.032$) (electronic supplementary material, figure S6).

(c) Movement

Neither TSF nor any of the covariates affected movement propensity (electronic supplementary material, table S4). The top model for movement rate (AICc weight = 0.19) indicated that the distance moved per day decreased with TSF ($p = 0.031$; figure 3), increased with minimum temperature ($p < 0.001$) and varied among reserves ($p = 0.103$) (electronic supplementary material, figure S8). The temperature only model held a similar AICc weight (0.18; electronic supplementary material, table S4) indicating that effects of TSF and reserve on movement rates were not strong.

(d) Landscape resistance

The TSF-linear and fire frequency resistance models explained spatial patterns of gene flow in *N. stellatus* at Hincks, where our sample sizes were largest. The TSF-linear model indicated increasing genetic distance with increasing habitat resistance (i.e. lower gene flow in long-unburnt habitat) among all geckos (partial Mantel $r = 0.059$, adjusted $p = 0.039$) and all adult geckos (partial Mantel $r = 0.081$, adjusted $p = 0.030$; electronic supplementary material, table S5). The fire frequency model indicated decreasing genetic distance with increasing fire frequency (i.e. lower gene flow in less frequently burnt habitat) among all geckos (partial Mantel $r = -0.063$, adjusted $p = 0.039$; electronic supplementary material, table S5). Regression of distance matrices also indicated significant effects of the TSF-linear and fire frequency models (electronic supplementary material, table S5). Fire frequency and TSF are correlated in this landscape [22] so it is not clear which variable is the key driver of gene flow patterns. However, both of these results indicate that fire increases gene flow in *N. stellatus* and that gene flow declines in unburnt habitat.

The TSF-nonlinear model did not explain genetic distance in *N. stellatus*, suggesting gene flow was more strongly related to linear habitat changes than to changes related to population density trajectories. However, given the strong relationship between density and habitat succession in this system, our simulation experiment was necessary to definitively separate their effects on genetic diversity.

IBD (Mantel $r = 0.112$, adjusted $p = 0.045$; electronic supplementary material, table S5) and significant regression coefficients for all landscape resistance models (electronic supplementary material, table S5) in adult males but not females indicated female-biased dispersal at Pinkawillinie.

(e) Simulation experiment

(i) Stable density scenarios

In the uniform landscape (Sc1), there was a strong effect of stable density level on genetic distance, an effect that was moderated by the dynamic landscape (Sc2) (electronic supplementary material, figure S9a). Effects of TSF on genetic distance were similar to, or stronger than effects in the field data when habitat succession was simulated by landscape resistance under stable density (Sc2) (electronic supplementary material, figure S9*a*). In Sc1 and Sc2, allelic richness was lower in the dynamic landscape (Sc2) than the uniform landscape (Sc1) at all density levels (electronic supplementary material, figure S9*b*). When density was stable, there was a trend for allelic richness to decrease with TSF in the dynamic landscape (Sc2) but not the uniform landscape (Sc1) (electronic supplementary material, figure S9*b*). Thus, the dynamic landscape, which simulated habitat succession, produced stronger patterns of genetic structure than the uniform landscape. It also drove a response in genetic diversity to TSF that, although weak, corresponded more closely to the field data.

(ii) Changing density scenarios

Effects of IBD on genetic distance in Sc3 and Sc4 were similar to effects in the field data (figure 4*a*). There was no effect of TSF on genetic distance when population density changed without successional changes in landscape resistance (Sc3 Mantel $r = 0.002$, figure 4*a*). When population density and landscape resistance changed concurrently, the effect of TSF on gene flow was indistinguishable from the field data (field Mantel $r = 0.059$; Sc4 Mantel $r = 0.045$, figure 4*a*). The effect of TSF on allelic richness was positive in Sc3 and negative in Sc4, the latter showing the same relationship to the

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

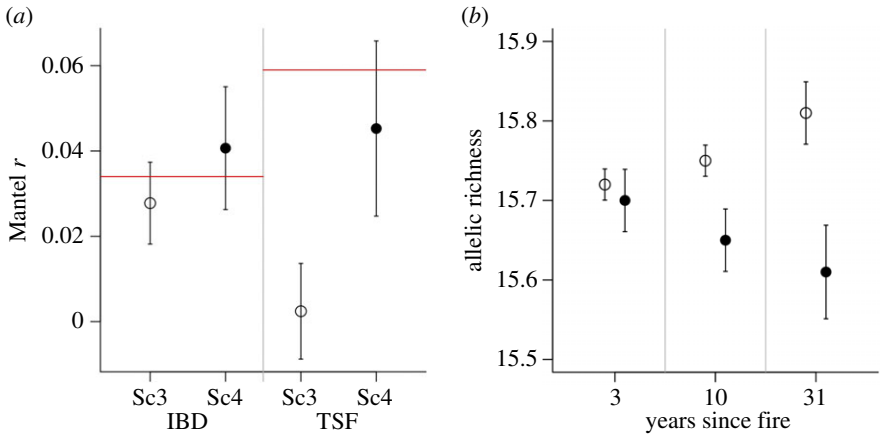


Figure 4. Effects of landscape resistance and population density on genetic structure in simulated genotypic data (mean values and 95% CIs across 10 independent simulations). Population density changed in Sc3 and Sc4, while landscape resistance changed only in Sc4 (electronic supplementary material, figure S9 shows results from Sc1 and Sc2 without variation in population density). (*a*) Simple Mantel test of IBD and partial Mantel test of resistance based on TSF, given geographical distance (IBD). The horizontal line indicates the Mantel *r* for the corresponding test in the microsatellite field data (all geckos at Hincks). (*b*) The relationship between TSF and allelic richness standardized to a sample size of 50 in Sc3 (open circles) and Sc4 (filled circles). (Online version in colour.)

field data (figure 4*b*). Similar effects on allelic richness were observed for different sample size standardizations (electronic supplementary material, figure S10). This comparison between Sc3 and Sc4 suggests that habitat succession altering landscape resistance, along with changes in population density, were necessary to impose the changes in gene flow and genetic diversity that we observed in *N. stellatus*.

4. Discussion

(a) Effects of succession on dispersal and genetic diversity

Empirical landscape resistance analysis indicated that dispersal declined with TSF in *N. stellatus* at Hincks, the reserve with the most complex fire history and where we obtained our largest sample size. These analyses also suggested gene flow was more strongly related to linear habitat changes than changes related to population density trajectories. In the simulated data, gene flow declined with habitat succession, but only when changes in population density were accompanied by habitat changes. Where population density changed without habitat succession (Sc3), gene flow was similar to the null model (Sc1). This suggests that successional change in habitat structure at our sites [20] played a key role in restricting gene flow in *N. stellatus*. Habitat complexity inhibits movement within the perceptual range of ground-dwelling mammals [37], suggesting that succession could impede navigation. For reptiles, recently disturbed habitat is probably more thermally suitable for dispersal [4]. As an insectivore, *N. stellatus* likely benefited from increased invertebrate abundance [48] and may have had increased foraging success in recently burnt habitat [49].

Two pairs of sites within Hincks and Pinkawillinie, burnt approximately 4 years before sampling, showed significant genetic differentiation (measured by F_{ST}) despite being separated by only 1 km. Nearby pairs of sites, 1 km apart and approximately 10 years since fire, were not genetically differentiated. We previously documented, at the same sites, reduced survival and increased reproductive capacity in *N. stellatus* in early compared with mid-successional habitat [20]. The early successional sites were 20–30 years old at the time of the recent fire, so pre-fire population density would have been very low [20]. The immediate demographic impacts of the fire event, including direct mortality, rapid population expansion from a very small number of individuals and subsequent reduced survival rates, probably contributed to early successional genetic differentiation between populations in *N. stellatus* [50]. Our results suggest that demographic processes drove genetic patterns in the short term (up to 4 years), while variation in dispersal had a greater influence on genetic structure during longer term succession (4–30 years).

The simulation component in our study was essential because genetic diversity declines in small populations through genetic drift, even without environmental variation [12]. In *N. stellatus*, population density declines sharply after reaching its peak abundance at approximately 15 years post-fire. When we modelled this change in population density without habitat change (Sc3), genetic diversity increased with TSF, in contrast to the negative relationship observed in our field data. This might reflect population bottlenecks following the 1999 and 2006 fires (i.e. sudden reductions in density decreasing genetic diversity in recently burnt habitat) and suggests that the increase in habitat permeability following fire overrode the immediate demographic effects of fire. This conclusion is supported by the F_{ST} results from our field data showing an immediate increase in genetic structure in recently burnt sites (although these sites did not have reduced heterozygosity; see the electronic supplementary material, figure S7). The time-frame of our simulation, which was relevant to our field data and to the fire regime in our study system, was not long enough to allow genetic drift, even when population density remained constantly low (Sc1; electronic supplementary material, figure S2*a*). This contrasts with evidence from bird populations in which bottlenecks from repeated disturbance drove declines in genetic diversity [35]. Longer term fire suppression in our study system might result in declines in genetic diversity through demographic effects but at the timescales we examined, the genetic diversity changes appeared to be habitat driven.

An important challenge is to determine the magnitude of change in genetic diversity (specifically the adaptive portion,

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

[51]) that would increase extinction risk under changing disturbance regimes. For example, what spatial and temporal scales of fire regimes would cause sufficient declines in genetic diversity to inhibit adaptive potential? Biodiversity indices that relate abundance to species extinction risk could be adapted to genetic diversity metrics for this purpose [52].

(b) Broad genetic structure

Despite the observed effects of disturbance, *N. stellatus* had high gene flow within reserves relative to other lizard species at similar spatial scales (less than 20 km) (e.g. [25]). Theoretically, low dispersal rates will evolve with habitat specialization in temporally stable habitat [53] and high dispersal will evolve in response to regular disturbance [54]. High dispersal in *N. stellatus* might represent an evolutionary adaptation to allow rapid colonization of long-unburnt habitat after fire. High gene flow across fire mosaics in *N. stellatus* could be maintained by long-distance dispersal which, even at low rates, can eliminate genetic structure [55]. This species can disperse several hundred metres through unfavourable habitat [56], so movement through long-unburnt vegetation is likely. In addition, although long-unburnt vegetation provides low-quality habitat, it can sustain some individuals: we re-captured *N. stellatus* in successive years in some long-unburnt (more than 30 years) areas [20].

As a burrower, *N. stellatus* is associated with sandy dune ridges which have short (less than 2 m), dense vegetation [21]. We found no evidence that inter-dune swales with higher clay composition and sparser vegetation imposed a gene flow barrier. Although we used a very high-resolution digital elevation model (1 m), it might not have been a reliable surrogate for finer scale patterns of soil fertility which influence vegetation structure [23]. Acquiring spatial data on this and other disturbances such as grazing intensity [57] would allow us to test the effect of a broader suite of environmental variables on gene flow.

There was little gene flow in *N. stellatus* between reserves now separated by over 100 km of mostly agricultural land. However, F_{ST} values were all less than 0.032, suggesting that, even at this scale, gene flow has not been strongly restricted. This study focused on dispersal within reserves, so we cannot determine if this wider genetic pattern reflects ongoing dispersal through the agricultural matrix, or a residual signal of gene flow across previously connected habitats. The latter seems more likely because analysis of patch occupancy by *N. stellatus* suggests that dispersal is restricted beyond a few hundred metres in agricultural landscapes [56].

5. Conclusion

Landscape genetics provides a valuable tool-set for understanding dispersal across spatially heterogeneous environments. However, expectations about the effects of population density on spatial genetic structure [14] are not routinely considered in landscape genetics studies. We have shown how to untangle the differential effects of dispersal and population density on genetic structure by combining demographic, genetic and spatial environmental data with a simulation experiment. In our target gecko species, we could more confidently attribute variation in genetic structure to dispersal because we observed similar declines in empirical gene flow estimates and movement rates during post-fire succession. Our simulation experiment also suggested that dispersal was the dominant driver of the genetic patterns seen in our field study. We recommend that the relative effects of demography and dispersal are investigated in future landscape genetics studies of other habitat specialist species.

Our results point to succession as a form of habitat fragmentation, which could influence connectivity among individuals and thus spatial population dynamics. This should not be interpreted to mean that disturbance has positive effects on biodiversity generally. *Nephrurus stellatus* is a disturbance specialist and was an exemplar for testing our hypothesis about the effects of habitat succession [58]. Genetic diversity can increase with succession in species which rely on late successional vegetation [7,22] meaning that early successional vegetation might impose a dispersal barrier to late successional species. Future work should quantify disturbance effects on dispersal in a range of taxa with different responses to disturbance. This is critically important as disturbance regimes are changing globally and our study suggests that these changes will influence spatial population dynamics.

Ethics. We followed the 'Australian code for the care and use of animals for scientific purposes' and worked under scientific (S25589 Government of South Australia) and animal ethics (E256 Flinders University) permits.

Data accessibility. Data supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. A.L.S., C.M.B., M.G.G. and D.A.D. designed the field research; A.L.S., E.L.L., S.C.B. and D.A.D. designed the simulation experiment; A.L.S. and D.A.D. collected the field data; A.L.S. analysed the data and wrote the manuscript with extensive input from all authors.

Competing interests. We have no competing interests.

Funding. The research was funded by the Australian Research Council (LP0776604), Native Vegetation Council of South Australia, DEWNR, Wildlife Conservation Fund, Sir Mark Mitchell Research Foundation, Lirabenda Endowment Fund, Ecological Society of Australia and Australian National University.

Acknowledgements. Over 100 volunteers were involved in fieldwork, particularly Samantha Blight, Simone Dalgairns, Juliana Lazzari, Kevin Mayes and Catherine Whitehead. Joe Tilley and the South Australian Department of Environment, Water and Natural Resources (DEWNR) provided field support. We thank Kathy Saint, Terry Bertozzi and Steve Donnellan (South Australian Museum) for laboratory assistance, John Stein for spatial data assistance and Wade Blanchard and Ian Davies for analytical advice. Ross Bradstock, David Keith, Sonia Kleindorfer and Andrew Lowe were involved in project development. Michael Clarke, Sam Cushman and Paul Sunnucks helped improve an early version of the manuscript and valuable comments from four anonymous reviewers improved later versions.

References

1. Bourne EC, Bocedi G, Travis JMJ, Pakeman RJ, Brooker RW, Schiffers K. 2014 Between migration load and evolutionary rescue: dispersal, adaptation and the response of spatially structured populations to environmental change. *Proc. R. Soc. B* **281**, 20132795. (doi:10.1098/rspb.2013.2795)

2. Jackson ND, Fahrig L. 2014 Landscape context affects genetic diversity at a much larger spatial extent than population

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

abundance. *Ecology* **95**, 871–881. (doi:10.1890/13-0388.1)

3. Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. 2013 Conceptual domain of the matrix in fragmented landscapes. *Trends Ecol. Evol.* **28**, 605–613. (doi:10.1016/j.tree.2013.06.010)
4. Templeton AR, Brazeal H, Neuwald JL. 2011 The transition from isolated patches to a metapopulation in the eastern collared lizard in response to prescribed fires. *Ecology* **92**, 1736–1747. (doi:10.1890/10-1994.1)
5. Banks SC, Cary GJ, Smith AL, Davies I, Driscoll DA, Gill AM, Lindenmayer DB, Peakall R. 2013 How does ecological disturbance influence genetic diversity? *Trends Ecol. Evol.* **28**, 670–679. (doi:10.1016/j.tree.2013.08.005)
6. Davies ID, Cary GJ, Landguth EL, Lindenmayer DB, Banks SC. 2016 Implications of recurrent disturbance for genetic diversity. *Ecol. Evol.* **6**, 1181–1196. (doi:10.1002/ece3.1948)
7. Schrey AW, Fox AM, Mushinsky HR, McCoy ED. 2011 Fire increases variance in genetic characteristics of Florida sand skink (*Plestiodon reynoldsi*) local populations. *Mol. Ecol.* **20**, 56–66. (doi:10.1111/j.1365-294X.2010.04925.x)
8. Murphy MA, Evans JS, Storfer A. 2010 Quantifying *Bufo boreas* connectivity in Yellowstone National Park with landscape genetics. *Ecology* **91**, 252–261. (doi:10.1890/08-0879.1)
9. Spear SF, Storfer A. 2010 Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biol. Conserv.* **143**, 778–786. (doi:10.1016/j.biocon.2009.12.021)
10. Peterman WE, Connette GM, Semlitsch RD, Eggert LS. 2014 Ecological resistance surfaces predict fine-scale genetic differentiation in a terrestrial woodland salamander. *Mol. Ecol.* **23**, 2402–2413. (doi:10.1111/mec.12747)
11. Strevens CMJ, Bonsall MB. 2011 Density-dependent population dynamics and dispersal in heterogeneous metapopulations. *J. Anim. Ecol.* **80**, 282–293. (doi:10.1111/j.1365-2656.2010.01768.x)
12. Frankham R. 1996 Relationship of genetic variation to population size in wildlife. *Conserv. Biol.* **10**, 1500–1508. (doi:10.1046/j.1523-1739.1996.10061500.x)
13. Rousset F. 2000 Genetic differentiation between individuals. *J. Evol. Biol.* **13**, 58–62. (doi:10.1046/j.1420-9101.2000.00137.x)
14. Robledo-Arnuncio JJ, Rousset F. 2010 Isolation by distance in a continuous population under stochastic demographic fluctuations. *J. Evol. Biol.* **23**, 53–71. (doi:10.1111/j.1420-9101.2009.01860.x)
15. Leidner AK, Haddad NM. 2011 Combining measures of dispersal to identify conservation strategies in fragmented landscapes. *Conserv. Biol.* **25**, 1022–1031. (doi:10.1111/j.1523-1739.2011.01720.x)
16. Banks SC, Blyton MDJ, Blair D, McBurney L, Lindenmayer DB. 2012 Adaptive responses and disruptive effects: how major wildfire influences kinship-based social interactions in a forest marsupial. *Mol. Ecol.* **21**, 673–684. (doi:10.1111/j.1365-294X.2011.05282.x)
17. Shohami D, Nathan R. 2014 Fire-induced population reduction and landscape opening increases gene flow via pollen dispersal in *Pinus halepensis*. *Mol. Ecol.* **23**, 70–81. (doi:10.1111/mec.12506)
18. Landguth EL, Cushman SA, Schwartz MK, McKelvey KS, Murphy M, Luikart G. 2010 Quantifying the lag time to detect barriers in landscape genetics. *Mol. Ecol.* **19**, 4179–4191. (doi:10.1111/j.1365-294X.2010.04808.x)
19. Landguth EL, Muhlfeld CC, Waples RS, Jones L, Lowe WH, Whited D, Lucotch J, Neville H, Luikart G. 2014 Combining demographic and genetic factors to assess population vulnerability in stream species. *Ecol. Appl.* **24**, 1505–1524. (doi:10.1890/13-0499.1)
20. Smith AL, Bull CM, Driscoll DA. 2012 Post-fire succession affects abundance and survival but not detectability in a knob-tailed gecko. *Biol. Conserv.* **145**, 139–147. (doi:10.1016/j.biocon.2011.10.023)
21. Smith AL, Bull CM, Driscoll DA. 2013 Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression. *J. Appl. Ecol.* **50**, 1178–1186. (doi:10.1111/1365-2664.12119)
22. Smith AL, Bull CM, Gardner MG, Driscoll DA. 2014 Life history influences how fire affects genetic diversity in two lizard species. *Mol. Ecol.* **23**, 2428–2441. (doi:10.1111/mec.12757)
23. Gibson RK, Bradstock RA, Penman T, Keith DA, Driscoll DA. 2015 Climatic, vegetation and edaphic influences on the probability of fire across Mediterranean woodlands of south-eastern Australia. *J. Biogeogr.* **42**, 1750–1760. (doi:10.1111/jbi.12547)
24. Mona S, Ray N, Arenas M, Excoffier L. 2014 Genetic consequences of habitat fragmentation during a range expansion. *Heredity* **112**, 291–299. (doi:10.1038/hdy.2013.105)
25. Levy E, Kennington WJ, Tomkins JL, LeBas NR. 2010 Land clearing reduces gene flow in the granite outcrop-dwelling lizard, *Ctenophorus ornatus*. *Mol. Ecol.* **19**, 4192–4203. (doi:10.1111/j.1365-294X.2010.04810.x)
26. Smith AL, Gardner MG, Bull CM, Driscoll DA. 2011 Primers for novel microsatellite markers in 'fire-specialist' lizards (*Amphibolurus norrisi, Ctenotus atlas* and *Nephrurus stellatus*) and their performance across multiple populations. *Conserv. Genet. Res.* **3**, 345–350. (doi:10.1007/s12686-010-9359-2)
27. Pritchard JK, Stephens M, Donnelly P. 2000 Inference of population structure using multilocus genotype data. *Genetics* **155**, 945–959.
28. Guillot G, Estoup A, Mortier F, Cosson J-F. 2005 A spatial statistical model for landscape genetics. *Genetics* **170**, 1261–1280. (doi:10.1534/genetics.104.033803)
29. R Core Team. 2013 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. (http://www.R-project.org).
30. Bates D, Maechler M, Bolker B. 2013 *lme4: linear mixed-effects models using S4 classes*. R package, version 0.999999-2. See http://lme4.r-forge.r-project.org/.
31. Broquet T, Petit EJ. 2009 Molecular estimation of dispersal for ecology and population genetics. *Annu. Rev. Ecol. Evol. Syst.* **40**, 193–216. (doi:10.1146/annurev.ecolsys.110308.120324)
32. Freckleton R. 2011 Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behav. Ecol. Sociobiol.* **65**, 91–101. (doi:10.1007/s00265-010-1045-6)
33. Wright S. 1943 Isolation by distance. *Genetics* **28**, 114–138.
34. Robinet C, Lance DR, Thorpe KW, Onufrieva KS, Tobin PC, Liebhold AM. 2008 Dispersion in time and space affect mating success and Allee effects in invading gypsy moth populations. *J. Anim. Ecol.* **77**, 966–973. (doi:10.1111/j.1365-2656.2008.01417.x)
35. Barr KR, Kus BE, Preston KL, Howell S, Perkins E, Vandergast AG. 2015 Habitat fragmentation in coastal southern California disrupts genetic connectivity in the cactus wren (*Campylorhynchus brunneicapillus*). *Mol. Ecol.* **24**, 2349–2363. (doi:10.1111/mec.13176)
36. Woinarski JCZ *et al.* 2011 The disappearing mammal fauna of northern Australia: context, cause, and response. *Conserv. Lett.* **4**, 192–201. (doi:10.1111/j.1755-263X.2011.00164.x)
37. Prevedello JA, Forero-Medina G, Vieira MV. 2010 Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. *J. Anim. Ecol.* **79**, 1315–1323. (doi:10.1111/j.1365-2656.2010.01736.x)
38. Wojan CM, Knapp SM, Mabry KE. 2014 Spatial variation in population density affects dispersal behavior in brush mice. *Ecology* **96**, 1661–1669. (doi:10.1890/14-1661.1)
39. Hardy OJ, Vekemans X. 2002 SPAGEDI: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol. Ecol. Notes* **2**, 618–620. (doi:10.1046/j.1471-8286.2002.00305.x)
40. McRae BH, Beier P. 2007 Circuit theory predicts gene flow in plant and animal populations. *Proc. Natl Acad. Sci. USA* **104**, 19 885–19 890. (doi:10.1073/pnas.0706568104)
41. Cushman SA, Landguth EL. 2010 Spurious correlations and inference in landscape genetics. *Mol. Ecol.* **19**, 3592–3602. (doi:10.1111/j.1365-294X.2010.04656.x)
42. Goslee SC, Urban DL. 2007 The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.* **22**, 1–19. (doi:10.18637/jss.v022.i07)
43. Guillot G, Rousset F. 2013 Dismantling the Mantel tests. *Methods Ecol. Evol.* **4**, 336–344. (doi:10.1111/2041-210x.12018)
44. Landguth EL, Cushman SA. 2010 CDPOP: a spatially explicit cost distance population genetics program. *Mol. Ecol. Res.* **10**, 156–161. (doi:10.1111/j.1755-0998.2009.02719.x)
45. Smith AL, Bull CM, Driscoll DA. 2013 Skeletochronological analysis of age in three 'fire-specialist' lizard species. *South Aust. Nat.* **87**, 6–17.

Downloaded from http://rspb.royalsocietypublishing.org/ on May 4, 2016

46. Clark JS. 2007 *Models for ecological data: an introduction*. Princeton, NJ: Princeton University Press.
47. Díaz JA. 1992 Choice of compass directions around shrub patches by the heliothermic lizard *Psammodromus algirus*. *Herpetologica* **48**, 293–300.
48. Teasdale LC, Smith AL, Thomas M, Whitehead CA, Driscoll DA. 2013 Detecting invertebrate responses to fire depends on sampling method and taxonomic resolution. *Austral Ecol*. **38**, 874–883. (doi:10.1111/aec.12024)
49. Vernes K, Haydon DT. 2001 Effect of fire on northern bettong (*Bettongia tropica*) foraging behaviour. *Austral Ecol*. **26**, 649–659. (doi:10.1046/j.1442-9993.2001.01141.x)
50. Banks SC, Lorin T, Shaw RE, McBurney L, Blair D, Blyton MDJ, Smith AL, Pierson JC, Lindenmayer DB. 2015 Fine-scale refuges can buffer demographic and genetic processes against short-term climatic variation and disturbance: a 22-year case study of an arboreal marsupial. *Mol. Ecol*. **24**, 3831–3845. (doi:10.1111/mec.13279)
51. Mittell EA, Nakagawa S, Hadfield JD. 2015 Are molecular markers useful predictors of adaptive potential? *Ecol.* Lett. **18**, 772–778. (doi:10.1111/ele.12454)
52. McCarthy MA, Moore AL, Krauss J, Morgan JW, Clements CF. 2014 Linking indices for biodiversity monitoring to extinction risk theory. *Conserv. Biol*. **28**, 1575–1583. (doi:10.1111/cobi.12308)
53. Kisdi É. 2002 Dispersal: risk spreading versus local adaptation. *Am. Nat*. **159**, 579–596. (doi:10.1086/339989)
54. Travis JMJ, Dytham C. 1999 Habitat persistence, habitat availability and the evolution of dispersal. *Proc. R. Soc. Lond. B* **266**, 723–728. (doi:10.1098/rspb.1999.0696)
55. Hoehn M, Sarre S, Henle K. 2007 The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? *Mol. Ecol*. **16**, 3299–3312. (doi:10.1111/j.1365-294X.2007.03352.x)
56. Driscoll DA, Whitehead CA, Lazzari J. 2012 Spatial dynamics of the knob-tailed gecko *Nephrurus stellatus* in a fragmented agricultural landscape. *Landsc. Ecol*. **27**, 829–841. (doi:10.1007/s10980-012-9734-3)
57. Driscoll DA, Smith AL, Blight SR, Maindonald J. 2012 Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodivers. Conserv*. **21**, 1607–1625. (doi:10.1007/s10531-012-0267-5)
58. Pereoglou F, Lindenmayer DB, MacGregor C, Ford F, Wood J, Banks SC. 2013 Landscape genetics of an early successional specialist in a disturbance-prone environment. *Mol. Ecol*. **22**, 1267–1281. (doi:10.1111/mec.12172)