

Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes

Sam C. Banks, Lachlan McBurney, David Blair, Ian D. Davies and David B. Lindenmayer

S. C. Banks (sam.banks@anu.edu.au), L. McBurney, D. Blair, I. D. Davies and D. B. Lindenmayer, *The Fenner School of Environment and Society, The Australian National Univ., Canberra, ACT, Australia.*

Identifying where animals come from during population recovery can help to understand the impacts of disturbance events and regimes on species distributions and genetic diversity. Alternative recovery processes for animal populations affected by fire include external recolonization, nucleated recovery from refuges, or in situ survival and population growth. We used simulations to develop hypotheses about ecological and genetic patterns corresponding to these alternative models. We tested these hypotheses in a study of the recovery of two small mammals, the Australian bush rat and the agile antechinus, after a large (> 50 000 ha), severe wildfire.

The abundance of both species was severely reduced by fire and recovered to near or above pre-fire levels within two generations, yet we rejected a hypothesis of recovery by external recolonization. While the agile antechinus showed genetic evidence for far greater dispersal capacity than the bush rat, neither species showed gradients in abundance or genetic diversity with distance from unburnt forest during population recovery.

Population recovery was driven by local-scale processes. However, the mechanisms differed between species, resulting from the spatial impacts of fire on habitat suitability. Agile antechinus populations recovered through population growth from in situ survivors. The bush rat followed a model of nucleated recovery, involving local recolonization from micro-refuges in topographic drainage lines.

Nucleated recovery by the bush rat was associated with changes in dispersal, and fine-scale patterns of genetic admixture. We identified increased dispersal by females during recovery, contrasting with male-biased dispersal in unburnt forest. Such flexibility in dispersal can potentially increase recovery rates compared to expectations based on dispersal behavior within undisturbed populations.

Our study shows how the initial distribution of survivors, determined by fire effects on resource distribution, determines the subsequent scaling of population recovery patterns, and the sensitivity of population distribution and genetic diversity to changing disturbance regimes.

Ecological disturbances such as wildland fires can have major impacts on the distribution and abundance of species and the genetic diversity of populations (Turner 2010, Banks et al. 2013). While the abundance of some species is largely unaffected by disturbances such as fire (Banks et al. 2015), disturbance events cause severe declines in abundance, or local extinctions, for many others (Lindenmayer et al. 2013). For species negatively impacted by disturbance events, identifying the source of individuals for population recovery is an important research issue. A key distinction relates to whether population recovery is driven primarily by external recolonization from undisturbed areas, by nucleated recovery from refuges inside the disturbed area, or from in situ survivors. This distinction has important ecological and genetic implications because it influences the sensitivity of population distributions (Romme et al. 1998) and genetic diversity (Davies et al. 2016) to variation in the frequency and size of disturbance events, and availability of refuges.

To illustrate the relevance of these three recovery processes for population distribution and genetic diversity of species negatively affected by fire, we describe how they mediate the scale-dependence of species responses to fire (or other disturbance) events. Where the principal process driving recovery is external recolonization, we predict the occurrence of gradients in abundance and genetic diversity during recolonization (Knight and Holt 2005, Roques et al. 2012). Over the longer term, increasing size and frequency of fire can place thresholds on the capacity of populations to recover between fire events, leading to patchy population distributions (Romme et al. 1998), and can affect genetic diversity within, and differentiation among, populations across the landscape (Davies et al. 2016). However, these predictions are dependent on the scaling of disturbance size and dispersal distance, with population distribution and genetic diversity less sensitive to fire size or frequency when dispersal capacity is high relative to the size of fires (Davies et al. 2016).

In contrast to the external recolonization model, recovery patterns are unaffected by fire size if the key process driving recovery is reproduction by in situ survivors (or seed banks, in the case of many plant species). Likewise, gradients in genetic diversity with distance from unburnt habitat are not expected where recovery is driven by in situ residual populations. Population distribution and genetic patterns are largely insensitive to long-term variation in disturbance size and frequency under this model of recovery, unless rates of survival or population recovery are very low (Davies et al. 2016). In the latter scenario, increases in the magnitude or duration of post-fire genetic drift may lead to increased genetic structure within burnt landscapes.

In between these extremes sits a nucleated recovery model (Turner et al. 2003), in which populations recover from survivors in refuges within the boundaries of the disturbed area. The key distinction between this model and the in situ recovery model is that recovery occurs via recolonization from spatial 'nuclei' within the burnt area, as opposed to the simple pattern of population density increase with no distributional shift expected under the in situ model. Landscape features that act as refuges facilitating nucleated recovery may include areas where survival of the fire event was higher (such as areas that remain unburnt or burnt areas that provide structural shelter from fire) or features where resource availability in the post-fire environment enables greater survival (Mackey et al. 2012, Robinson et al. 2013). Under the nucleated recovery model, the spatial distribution or grain of refuges may be the key scale-related parameter influencing scale-dependence of population recovery and genetic diversity in disturbed areas. A general prediction under the nucleated recovery model is that species will show restricted distributions and environmental associations in burnt relative to unburnt habitat, and the recolonization phase during this model may feature genetic admixture from multiple refuges, as has been observed under long-term climate-driven range contraction and expansion dynamics (Petit et al. 2003).

In this study, we investigated the processes and patterns of population recovery of two small mammals that suffered major population reductions as a result of a large fire in the montane forests of Victoria, Australia, in 2009 (the 'Black Saturday' bushfires). As with many severe forest fires, this event had diverse impacts on forest structure and mammalian fauna (Banks et al. 2011a, Lindenmayer et al. 2013, 2014, Smith et al. 2014). While such fire events are typical of the historical disturbance regime in this ecosystem (McCarthy et al. 1999), their frequency and spatial contiguity are expected to increase due to climate change and interactions with other disturbance types such as logging (Lindenmayer et al. 2011, Taylor et al. 2014). Thus, the scaling of recovery and the dependence on external or refuge-driven recolonization are important for understanding the sensitivity of populations to future disturbance scenarios. The design of our sampling and analyses was framed around three key questions.

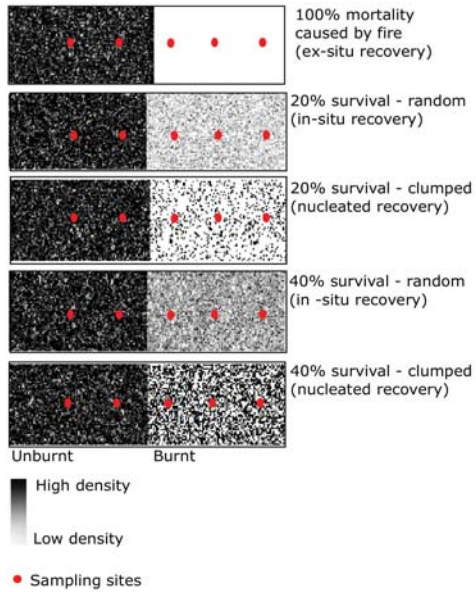
1) Is population recovery driven by external recolonization? We established a replicated study design that enabled testing of recovery processes on the landscape scale, by measuring spatial gradients in abundance and genetic

diversity across sites within landscape blocks spanning the fire boundary, and sampled annually over three years post-fire. The general expectations of ecological and genetic patterns under the external recolonization, in situ recovery and nucleated recovery models are likely to be influenced by the spatial and temporal scales of sampling, as well as the scales of the relevant environmental (fire) and ecological (dispersal, birth rate) processes (Romme et al. 1998, Davies et al. 2016). Hence, our specific expectations of these models were informed by simulations framed around the life history of the two study species, the agile antechinus *Antechinus agilis* and the bush rat *Rattus fuscipes* and our study system and spatiotemporal sampling design (Fig. 1, Supplementary material Appendix 1). We expected the abundance data to have high power to distinguish recolonization from the other scenarios, as the more dispersive of the two species (the agile antechinus; Banks and Lindenmayer 2014) was predicted to be able to colonise only the most proximal site from unburnt habitat over the timescale of our empirical study. Thus, strong gradients in abundance with distance to unburnt habitat were an expected characteristic of this model. In fact, simulations with 'extreme' dispersal capacity (mean of negative exponential dispersal distance distribution = 1000 m for both sexes) relative to that described for the agile antechinus still yielded very strong gradients in abundance. Populations of the bush rat (lower dispersal; Peakall et al. 2006) were not predicted to be able to recover due to recolonization over the timeframe of the study (Fig. 1).

2) Is population recovery facilitated by refuges? Both of our study species are widely distributed in unburnt forest in this region. We tested for post-fire refuge associations by modelling spatiotemporal occurrence data in relation to spatial heterogeneity in key environmental variables, accounting for time-since-fire effects and hypothesizing occurrence under a reduced set of environmental conditions in burnt habitat compared to unburnt habitat under a refuge model. Although we did not use the site-level abundance and genetic data to test for refuge effects, our simulations suggested that the nucleated recovery model facilitates greater population growth and reduced loss of genetic diversity than an in situ survival model under high (80%) fire-induced mortality, but such differences were not apparent when survival rates were high (40% in our models) and populations recovered rapidly with no loss of genetic diversity (Fig. 1).

3) What dispersal processes operate during population recovery? We used spatial analyses of genotypic data to compare dispersal patterns among the two species, and to test for signals of increased or decreased immigration in recovering sites in burnt landscapes relative to unburnt landscapes. We used fine-scale genetic spatial autocorrelation analyses (Banks and Peakall 2012) to test for shifts in sex-specific dispersal strategies associated with population recovery. We predicted a shift away from sex-biased dispersal under a model of population recovery by recolonization, as the driver of dispersal behaviour shifted from inbreeding avoidance (Lawson Handley and Perrin 2007) to colonisation of empty habitat (Simmons and Thomas 2004, Gauffre et al. 2009).

Models of spatial population recovery



Legend for simulation predictions of abundance and genetic diversity under alternative recovery models

- 0% survival
- ▲- 20% survival-random
- △- 20% survival-nucleated
- 40% survival-random
- 40% survival-nucleated

Simulated expectations under alternative recovery models

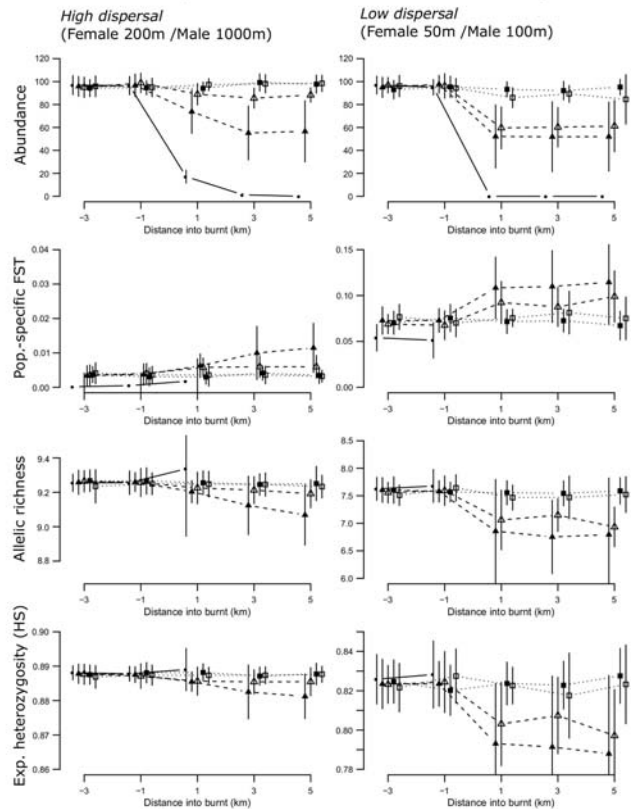


Figure 1. Simulated outcomes of alternative spatial recovery scenarios after fire for hypothetical species approximating the life history of the bush rat (low dispersal = 100 m mean of negative exponential dispersal distance distribution for males and 50 m for females; Peakall et al. 2003, Peakall and Lindenmayer 2006) and the agile antechinus (high dispersal = 1000 m for males and 200 m for females; Banks and Lindenmayer 2014). We used the model of Davies et al. (2016) to simulate the effects of a single fire event (after a 999 yr burn-in) on the abundance and genetic diversity (at 10 microsatellite loci with 10 alleles at generation 0, and $10^{-4}k$ -alleles mutation rate) of two species on a 200×50 cell rectangular landscape, with cells representing 100×100 m (1 ha) and maximum densities of 6 individuals ha^{-1} . Both sexes are polygamous and females select males randomly from those within a 4-cell radius. The sampling scheme for data analysis approximated that of the empirical study, with samples collected at five sites (of 400×400 m) spaced at 2 km intervals across the burnt/unburnt boundary at the end of the second generation after the fire event (equivalent to the final year of our data collection). Results are shown for the 'high birth rate' scenario (8 offspring per female per year).

Methods

Study region and study species

We conducted our study in the tall montane forests of the Central Highlands region of Victoria, south-eastern Australia. Our sites were situated at elevations between 500 and 950 m in forest dominated by an overstorey of mountain ash *Eucalyptus regnans* with a component of shining gum *E. nitens* and the patchy, aspect-dependent presence of *E. obliqua* and *E. cypellocarpa* in the lower-altitude sites. This landscape was burnt in February 2009 by the 'Black Saturday' fires that affected over 50 000 ha of mountain ash forest in this region (Burns et al. 2015). A large proportion of the affected area was burnt at high severity, killing the 50–80 m tall overstorey *E. regnans* (an obligate seeder) through crown burn or scorch. High-density regeneration of seedlings occurred on all sites, with regrowth reaching over 200 cm in height by 2011 (Smith et al. 2014).

The agile antechinus and the bush rat are the two most abundant small terrestrial mammals in the region (Cunningham et al. 2005). The agile antechinus is a

carnivorous marsupial weighing between 20 and 40 g. Individuals den communally in tree hollows and generally forage at ground level (Lazenby Cohen and Cockburn 1991). The species has a semelparous life history in which all males die immediately after the breeding season in late winter (August–September). In this region, females produce 6 to 8 offspring in August–September each year, and a small proportion of females may survive to breed in a second year. Post-weaning dispersal is strongly male-biased (Cockburn et al. 1985, Banks et al. 2005a), with males in fragmented habitat dispersing an average of 1400 m (Banks and Lindenmayer 2014).

The bush rat is a native Australian rodent (approx. 100–200 g) with a broad diet of fungi, arthropods, seeds, fruit, and other plant tissue (Warneke 1971). Females produce up to eight offspring per litter, most commonly during a peak breeding season from November to January. Females may produce multiple litters per year, although one litter per season is common in unburnt habitat in our study region (Robinson 1987, White et al. 1996). The lifespan of most animals is less than 15 months (Robinson 1987). Previous field and genetic studies suggest male-biased

dispersal (Robinson 1987, Peakall et al. 2003), although the genetic data are consistent with dispersal being restricted to far shorter distances (< 200 m) than the agile antechinus (Peakall et al. 2003, Peakall and Lindenmayer 2006).

Experimental design and trapping protocols

We established three linear blocks spanning the burnt-unburnt forest boundary, with sites spaced at 2 km intervals, such that within each block there were two sites in unburnt forest (1 and 3 km from the fire boundary) and three sites in burnt forest (1, 3 and 5 km from the fire boundary; Fig. 2). We established our blocks in areas burnt at high severity, where there was typically an abrupt edge between burnt and unburnt forest (Banks et al. 2011a). Variation in fire severity and forest age were not factors in our study design, and we selected our block locations to be representative of the moderate to high severity fire impacts observed across the majority of the burnt area. Initial surveys identified no impacts of minor variation in fire severity on the occurrence of survivors of these two species (Banks et al. 2011a). Each site comprised 75 folding aluminium Elliott traps set up as two perpendicular lines of 37 traps spaced at 15 m intervals and originating at a common trap point (Fig. 2). The aim of this design was to maximise coverage of local topographic diversity within each site. We mapped the location of each trap point initially with a hand-held averaging GPS, and used detailed field validation to ensure the accuracy of mapping of trap positions relative to neighbouring traps and our digital elevation model (DEM) GIS layers of local topography. We trapped at each site for three nights in July 2009, 2010 and 2011 using standard protocols (Banks et al. 2011a). Captured animals were handled in cloth bags, identified to species and sex (the latter verified with genetic markers), weighed and marked with a white paint pen to identify recaptured individuals within a session. A 2 mm ear biopsy was taken from the right ear of each animal and stored in 95% ethanol for DNA extraction. Animals were released at the point of capture within five minutes of being removed from the trap.

DNA extraction and genotyping

We extracted DNA from all samples using Qiagen 96-well plate DNeasy extraction kits. We genotyped all bush rat samples with the 11 autosomal microsatellite loci D14Rat75, D15Rat123, D17Rat70, D18Rat96, D2Rat118, D3Rat80, D5Rat33, D7Rat128, D8Rat123 and E5, and the X chromosome microsatellite DXRat2 and the SRY sex determination marker as described in Peakall et al. (2006). We genotyped all agile antechinus samples with the microsatellite loci Aa1A, Aa2G, Aa2H, Aa4D, Aa7F, Aa7H, Aa2B, Aa2E, Aa4A, Aa4K, Aa7D and Aa7M (Kraaijeveld-Smit et al. 2002) and a Y chromosome SRY locus (Watson et al. 1998) as described in Banks et al. (2005b). PCR products were run on an ABI3100 sequencer and scored with GeneMapper software at AGRF laboratories. The microsatellite panels used for the bush rat and agile antechinus samples were the best-performing subset of loci from those previously used for studies of these species in this region (Banks et al. 2005b, Peakall et al. 2006, Kraaijeveld-Smit et al. 2007).

Analysis of spatial and temporal patterns of abundance among sites within blocks

To test landscape-scale patterns of small mammal abundance among sites and years, we used generalised linear mixed models to test for effects of fire ($Burnt = 1/0$) and time since fire ($Year$ factor with levels = 2009, 2010, 2011 or as a linear ' $Years\ since\ 2009$ ' effect). We fitted the $Burnt$, $Year\ Burnt + Year$ and $Burnt \times Year$ models (with both representations of year effects). We then compared these models against the same models that also included an interaction between $Burnt$ and $Distance$, a variable representing the distance of the site from the burnt/unburnt forest boundary (and the three-way interaction with $Burnt$, $Distance$ and $Year$) to test for spatial gradients in abundance expected under an ex-situ recovery by recolonization model (Fig. 1). We fitted all models in the glmmADMB R package (Fournier et al. 2012, Skaug et al. 2015) with a random effect of site, and used negative binomial models instead of Poisson models due to overdispersion

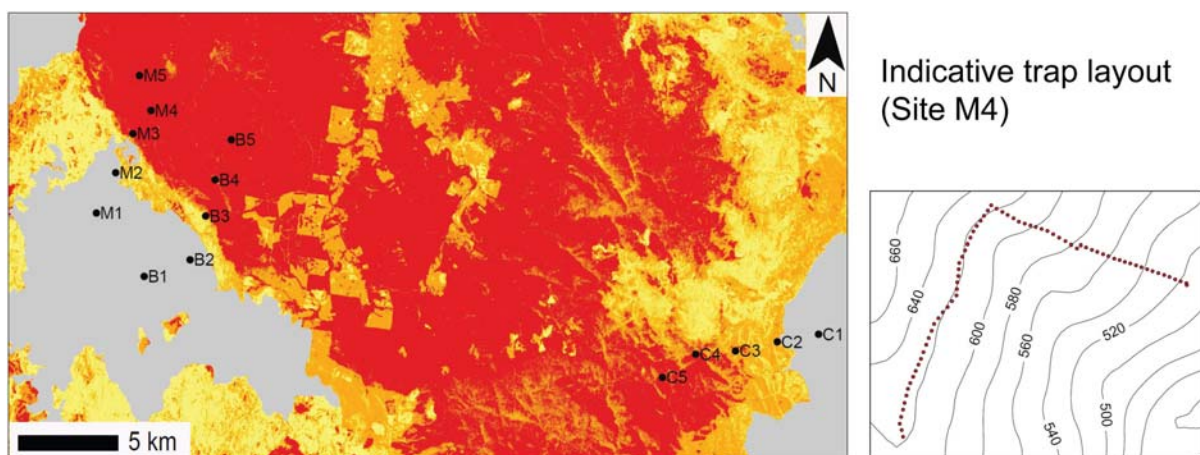


Figure 2. Map showing the spatial arrangement of study sites within blocks (M, B, C) in relation to the fire extent (grey = unburnt in 2009, red/yellow = burnt in 2009 with red being high severity and yellow low-moderate severity fire), and the layout of the 75 traps within sites, using site M4 as an example.

of our data (the ratio of residual deviance to the degrees of freedom was greater than one). We compared our models according to the sample size-corrected Akaike's information criterion (AIC_C).

Analysis of spatial and temporal capture patterns within sites

To investigate fine-scale spatial and temporal patterns of occurrence within sites, we used GLMMs of the probability of capture of a new individual (i.e. excluding recaptures) at each trap point. Trap success was a binary variable coded as the number of captures of a new individual at each trap point in relation to the number of potential capture events at that trap point within an annual survey (maximum = 3). The latter was calculated as the total number of trap nights at each trap point corrected by subtracting the number of recaptures, captured non-target species, or trap interference events (e.g. closed and empty traps). We fitted GLMMs with a logit link function, with random effects coded to represent trap points within sites to account for the repeated-measures nature of the data across the three years.

An exploratory spatial analysis of capture patterns identified spatial autocorrelation of occurrence of both species (although more apparent in the bush rat; Supplementary material Appendix 2). Therefore, we fitted and compared models with and without a spatial autocovariate to account for spatial dependence in trapping success among neighbouring traps. The spatial autocovariate was calculated with the 'autocov_dist' function of the 'spdep' R package (Bivand et al. 2013, Bivand and Piras 2015), based on the average value of the response variable over all traps within a 40 m radius (typically two traps either side of the focal trap). We also tried 80 and 120 m thresholds, but these did not change our inference.

In our model selection, we first compared a series of 'base models', featuring all combinations of the variables *Burnt* and *Year* (using year as a factor or as a linear years-since-fire trend), including interactions between them, and found best AIC_C support for the interaction model (with the linear trend effect best supported for the bush rat). We then sequentially compared this against a series of models featuring local environmental variables that could potentially influence spatial and temporal patterns of post-fire population recovery. The models were structured as $Burnt \times Year \times Env$ and $Burnt \times Year + Env$, where *Env* is the local environmental variable. These variables included topographic wetness index (*TWI*) (Moore and Hutchinson 1991), and two variables representing the eastern and northern components of slope and aspect, termed *p* (cosine(aspect) \times sine(slope)) and *q* (sine(aspect) \times sine(slope)), respectively (Hutchinson 1998). These are continuous functions of slope and aspect, equalling zero on flat slopes and with largest magnitude on steep slopes. These variables were derived from a 20-m resolution digital elevation model (DEM) created in ANUDEM (Hutchinson 2011) and relate to the presence of drainage lines in the landscape and to topographic variation in rates of post-fire seedling regeneration and therefore ground cover (Smith et al. 2014).

Analysis of genetic diversity and structure among blocks and sites

To investigate spatial and temporal patterns of genetic diversity and structure within and among sites in each block, we grouped samples according to site and year, and measured summary statistics, including the number of alleles (N_A), expected heterozygosity (H_E) and observed heterozygosity (H_O), and F_{IS} , in GenALEx 6.501 (Peakall and Smouse 2006, 2012) for all site/year combinations, excluding those with fewer than 5 samples (sample size was included as a covariate in later analyses of variation in genetic diversity). We tested for deviations from Hardy-Weinberg equilibrium using site/year samples with greater than 25 individuals. We used Arlequin 3.1 (Excoffier and Lischer 2010) to quantify hierarchical patterns of genetic structure (total/block/site) for the 2011 data, when genetic sample sizes for both species were greatest, using 1000 permutations for significance testing. We also used the GESTE program (Foll and Gaggiotti 2006) to estimate the effect of block, *Burnt*, *Distance* (to unburnt boundary) on population-specific F_{ST} .

We fitted a series of GLMMs to test for effects of fire, year and sample size on genetic diversity within each site in each year (excluding those with $n < 5$). The response variables were N_A , H_E , H_O and F_{IS} represented at the level of individual autosomal loci. We used random effects of site and locus to account for repeated visits to sites over the three years, and for variation in diversity among loci. We then used AIC_C to compare a series of models including all combinations of effects of *Burnt* and *Year*, the interaction $Burnt \times Year$, log-transformed sample size (LnN) (Bashalkhanov et al. 2009), and *Distance* to unburnt habitat (in interaction with *Burnt* and $Burnt \times Year$). All models included an intercept and block effect, and were fitted as Gaussian GLMMs in the glmmADMB R package.

Analysis of fine-scale genetic patterns within and among sites

To compare fine-scale spatial genetic structure within and among burnt and unburnt sites, we used spatial autocorrelation analyses of multilocus genotypes. First, we used a standard spatial autocorrelation analysis for each species to characterise the magnitude and scale of spatial autocorrelation in genotypes, using distance class boundaries of 200 m (neighbouring individuals within sites), 1, 3, 5 and 7 km to cover the progressive distances from one site to another within a block). Autocorrelation r values were calculated within each block to avoid inflating apparent spatial structure within blocks by year effects or by genetic structure among blocks (Banks and Peakall 2012), and combined over blocks as described in Peakall et al. (2003). We did not split these data by year for this initial analysis as preliminary investigation revealed similar spatial patterns within years and between years. Significance of combined r_c values was assessed with 1000 permutations and 95% confidence intervals around r_c calculated with 1000 bootstrap iterations.

We conducted a second spatial autocorrelation analysis for the bush rat and agile antechinus to test whether fine-scale spatial genetic structure differed between burnt and

unburnt sites, and between males and females. We quantified autocorrelation among genotypes of individuals sampled in the same site, in the same year and in different years. First, we calculated combined r_c values (combining over blocks as in Peakall et al. 2003) for individuals sampled in the same site and year, comparing among burnt and unburnt sites. Second, we calculated correlograms (within each block, combining r values over blocks) and coded our 'geographic' distance matrices to split genetic distances into those among males and females in the same site, in the same year and in different years. For both species, we expected stronger fine-scale autocorrelation among females in unburnt forest, consistent with previous documentation of sex-biased dispersal (Peakall et al. 2003, Banks et al. 2005a). We assessed the significance of r_c values with 1000 permutations and compared the magnitude of r_c values by evaluating overlap among 95% bootstrap confidence intervals, as this test has been found to have low false positive error rate (Banks and Peakall 2012).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.k47b2>> (Banks et al. 2016).

Results

Analysis of spatial and temporal patterns of abundance among sites within blocks

We captured 528 individual bush rats (plus 212 recapture events) and 483 individual agile antechinus (254 recaptures). Boxplots of abundance patterns in burnt and unburnt sites over time are shown in Fig. 3. Analysis of site-level abundance of the bush rat yielded greatest support for a model featuring an effect of *Burnt*, *Year* and an interaction between these variables ($AIC_C = 263.6$), predicting an initial reduced abundance in burnt sites compared to

unburnt sites (with burnt sites having an average of 20% as many bush rats as unburnt sites). There was a temporal increase in abundance over all site types (especially in 2011), but stronger increases in abundance in burnt sites than unburnt sites, such that the abundance of the bush rat was greater in burnt sites than unburnt sites by 2011 (Table 1, Supplementary material Appendix 3, Fig. A1). Note that the second-ranked model (ΔAIC_C 0.009) featured a *Block* effect, with significantly fewer bush rats captured in the Cambarville block, and we present this model in Table 1 due to the extra information it contained. The best model that contained a *Burnt* \times *Distance* effect had a ΔAIC_C score of 4.6 (Supplementary material Appendix 3, Table A1) but neither the main effects nor the interaction had significant effects on the number of bush rats captured ($p = 0.280$ and 0.197 , respectively). This suggested no major landscape-scale 'spillover effects' from unburnt habitat during post-fire recovery.

While the abundance of the agile antechinus was less severely impacted by the 2009 fire than the abundance of the bush rat, the recovery of the agile antechinus was slower. The best-supported negative binomial models of the number of agile antechinus captured at our sites featured main effects of the variables *Burnt*, *Year* and *Block*, predicting an approximate 43% reduced abundance in burnt sites compared to unburnt sites in 2009, increases in abundance across burnt and unburnt sites in 2011, and more agile antechinus in the Murrindindi block than the other blocks (Table 1, Supplementary material Appendix 3, Fig. A1). The second most parsimonious model featured a *Burnt* \times *Year* interaction (ΔAIC_C 1.73), although this effect was non-significant ($p = 0.122$; Supplementary material Appendix 3, Table A2). Models featuring distance gradients in abundance from the burnt/unburnt boundary were not strongly supported, with the best such model having a ΔAIC_C of 6.09 and no significant effects of *Distance* (Supplementary material Appendix 3, Table A2).

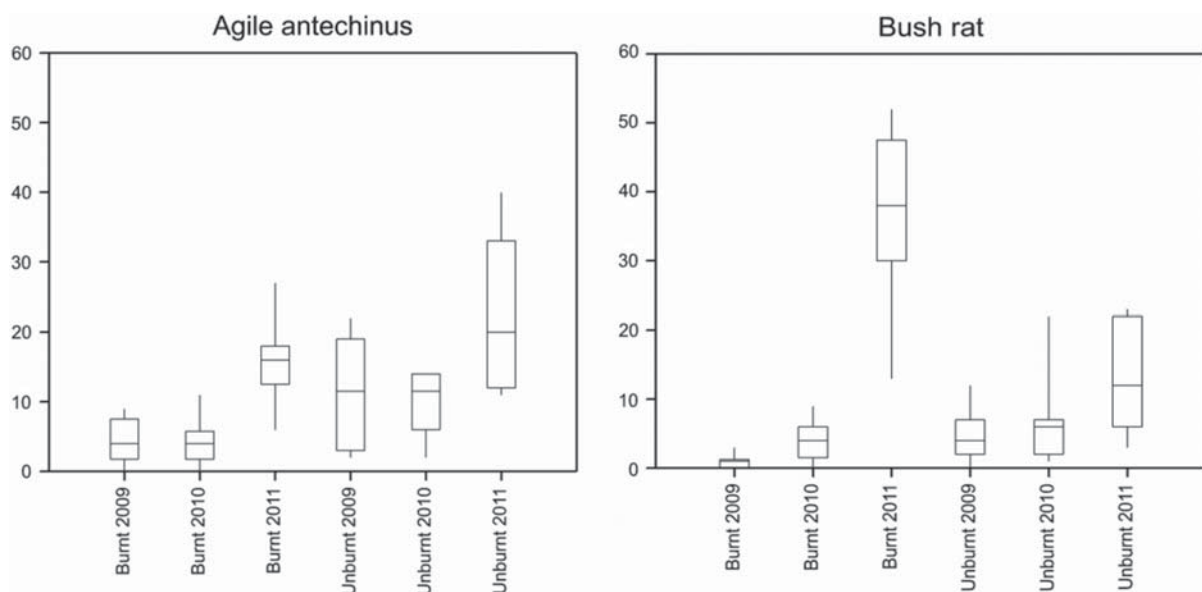


Figure 3. Boxplots showing patterns of abundance of the agile antechinus and bush rat (number of animals per site) in burnt and unburnt sites in 2009, 2010 and 2011.

Table 1. The most parsimonious negative binomial model (GLMM) of the raw number of captures of the bush rat and the agile antechinus at each site in burnt and unburnt habitat from 2009 to 2011.

Bush rat	Variable	Estimate	SE	Z value	p
	Intercept	1.504	0.323	4.65	<0.001
	Burnt	-1.567	0.477	-3.29	0.001
	Year (2010)	0.398	0.297	1.34	0.18
	Year (2011)	1.008	0.278	3.62	<0.001
	Block (C)	-0.604	0.307	-1.96	0.05
	Block (M)	0.211	0.3	0.7	0.481
	Burnt: year (2010)	1.083	0.51	2.12	0.034
	Burnt: year (2011)	2.762	0.473	5.84	<0.001
		Variance	Standard deviation		
	Random term (site)	0.139	0.373		
Agile antechinus	Variable	Estimate	SE	Z value	p
	Intercept	1.814	0.229	7.89	<0.001
	Burnt	-0.582	0.150	-3.88	<0.001
	Year (2010)	-0.047	0.225	-0.21	0.833
	Year (2011)	0.964	0.188	5.12	<0.001
	Block (C)	0.334	0.210	1.59	0.112
	Block (M)	0.822	0.192	4.27	<0.001
		Variance	Standard deviation		
	Random term (site)	5.73e-07	0.0007		

Analysis of spatial and temporal capture patterns within sites

The local environmental associations of captures of the bush rats changed in burnt sites over the duration of the study. The probability of capturing a bush rat was initially lower in traps on burnt sites. Subsequently, bush rat capture rate increased in burnt and unburnt habitat over time but the increase was more rapid in burnt sites. The best model (Fig. 4, Table 2; $AIC_C = 2447.24$) showed that bush rats were likely to be captured on: 1) steeper, south-facing slopes (significant main effect of q) across burnt and unburnt habitat in all years; 2) zones of increasing easterly slope and aspect in unburnt forest, but not in burnt forest ($Burnt \times p$); and 3) drainage lines (areas of high TWI) in burnt habitat after the fire in 2009. However, the probability of capturing a bush rat outside drainage lines (areas of low TWI) increased with time since fire, such that they were more likely to be trapped in areas of low TWI by 2011. In contrast, there was a weak positive effect of TWI on the capture rate of bush rats in unburnt habitat across all years. The closest-ranked model to this model (lacking the main effects of p and q and the $Burnt \times p$ interaction) had little relative support ($\Delta AIC_C = 18.02$). Note that, for both species, we report results for models including the spatial autocovariate, as we considered this to be an important component of the structure of our data and all autocovariate models were ranked higher according to AIC_C than the matching models without the autocovariate. The inclusion of the autocovariate in the models did not change the model rank, significance level of explanatory variables, and direction of their effect, although there were minor changes in the magnitude of estimated effects.

To illustrate the effects of topography, fire and time on bush rat occurrence patterns, we generated spatial predictions from the best model (Table 2) in response to the topographic conditions in one of our trapping sites. These predictions show how bush rats re-occupied the landscape

following initial restriction to drainage-line 'nuclei' with increasing time since fire in burnt but not unburnt sites.

In contrast to the patterns of occurrence of the bush rat, there were no strong topographic associations of occurrence of the agile antechinus in burnt or unburnt habitat. While one model (main effects: $Burnt \times Year \times TWI + Block + Autocovariate$) received greater AIC_C support than the 'base' model ($Burnt \times Year + Block + Autocovariate$; $\Delta AIC_C = 3.9$), none of the additional main effects or interactions were significant ($p > 0.1$ in all cases) and the standard errors of the coefficients were all larger than the estimates themselves. Therefore, we restricted our inference to the base model, which showed initial reduced capture rate in burnt sites, a general increase over years, but a greater increase in burnt sites, such that the rate of capture was similar in burnt and unburnt habitat within three years of the fire (Table 2, Fig. 5).

Analysis of genetic diversity and structure among blocks and sites

Genetic diversity at the autosomal microsatellites was high for the bush rat (mean $N_A = 26.6$; range among loci = 14 to 45; mean $H_T = 0.89$, range among loci = 0.82 to 0.95). For the agile antechinus, the mean number of alleles per locus was 15.5 (10 to 22) and mean H_T was 0.83 (0.66 to 0.92).

A hierarchical AMOVA for the 2011 bush rat and agile antechinus data identified greater genetic structure for the bush rat than the agile antechinus. Meirmans and Hedrick (2011) standardised F'_{RT} (among blocks relative to total) was estimated at 0.044 for the bush rat compared to 0.032 for the agile antechinus ($F'_{RT} = 0.056$ and 0.032, respectively, when the analysis was restricted to unburnt sites only). The major difference in genetic structure between the two species was observed among sites within blocks (F'_{SR}), where genetic differentiation was higher for the bush rat (0.224) than the agile antechinus (0.055). ($F'_{SR} = 0.312$ and 0.056,

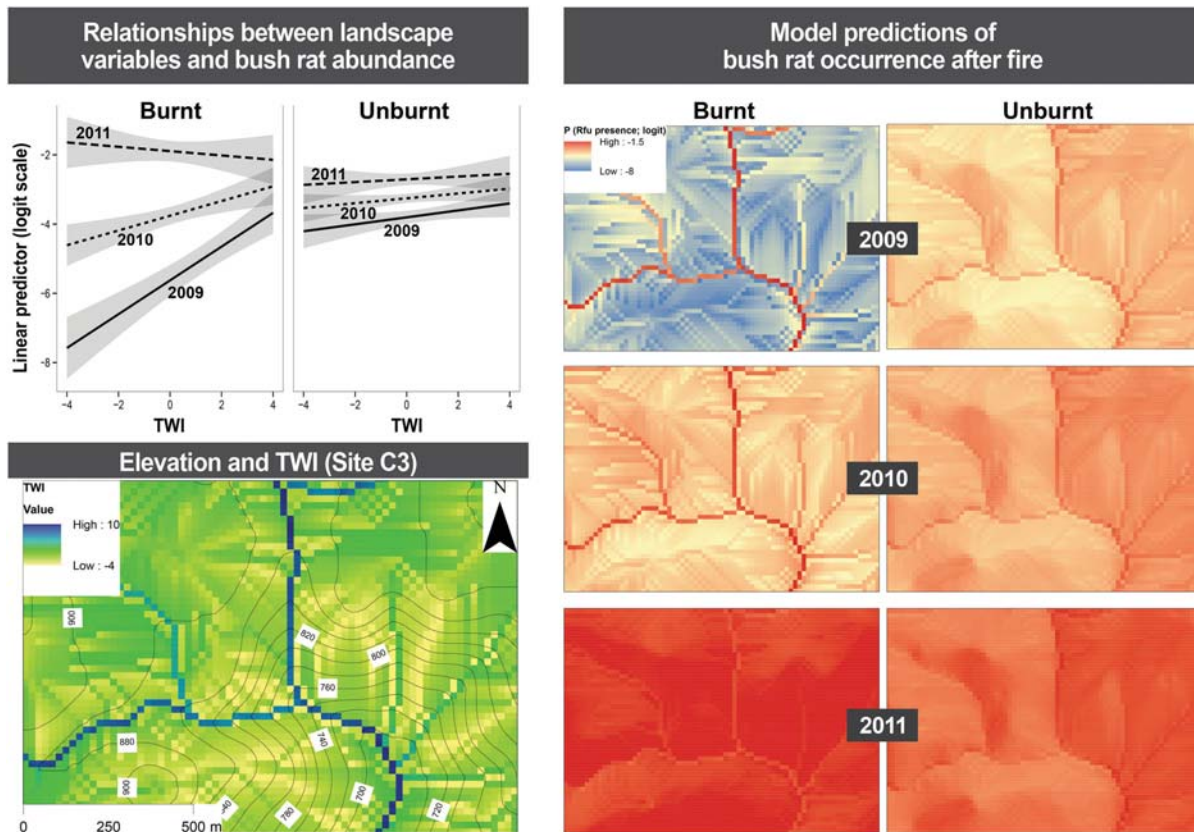


Figure 4. Post-fire recovery and fine-scale recolonization by bush rats: predictions of the probability of capturing a bush rat in a trap were generated from the most parsimonious model as shown in Table 2. The effects of topographic wetness index (TWI) are shown in burnt and unburnt sites over the three years of the study. Predictions were generated for one of the study sites (C3) over each year of the study. Site C3 was burnt, but we present the model predictions applied to the same landscape as if it were unburnt, for contrast. Elevation and topographic wetness index (TWI) data are presented for the site. The model predictions also include effects of the topographic variables p and q , representing a combination of slope and aspect. A larger figure showing the detail of the relationship with these variables is presented in Supplementary material Appendix 3, Fig. A2. For the predictions, the autocovariate was set to the mean of burnt and unburnt sites for each year, and we ignored random effects. The model shows the pattern of ‘nucleated recovery’ of bush rats, with an initial restriction to drainage lines in burnt habitat being followed by expansion to areas of lower TWI as vegetation cover increased. Agile antechinus showed no significant spatial habitat associations within sites.

respectively, when the analysis was restricted to unburnt sites only). Species-specific unstandardised F-statistics among blocks and sites (within blocks) were all significant at the 0.001 level for the bush rat ($F_{ST} = 0.036$, $F_{RT} = 0.005$, $F_{SR} = 0.031$) and the agile antechinus ($F_{ST} = 0.015$, $F_{RT} = 0.005$, $F_{SR} = 0.010$).

Of the population-specific F_{ST} models evaluated in GESTE, the intercept-only models received strong support (posterior probability for the intercept-only model for agile antechinus = 0.792, bush rat = 0.783) and there was little support for any of the environmental or demographic covariates across models (marginal probabilities ranged from 0.052 to 0.072), suggesting no major differences in population-level genetic structure among burnt and unburnt sites.

The impacts of fire and year on genetic diversity metrics among sites differed between the species. For the agile antechinus, there was support only for models with positive effects of log-transformed sample size on N_A , H_E and F_{IS} , and no significant impacts of any of the tested variables on H_O (Supplementary material Appendix 3, Table A4). For the bush rat, H_E , F_{IS} and N_A were positively associated with

sample size, but F_{IS} also was significantly lower in burnt sites compared to unburnt sites. For a given sample size, there was an estimated difference of $-0.081 (\pm 0.019 \text{ SE}, p < 0.0001)$ between F_{IS} in burnt and unburnt sites (Supplementary material Appendix 3, Table A5, Fig. A3). For the bush rat, N_A was also lower in 2010 than in other years (estimate = $-1.187 \pm 0.439 \text{ SE}, p = 0.007$) (Supplementary material Appendix 3, Table A5, Fig. A3).

Analysis of fine-scale genetic patterns within and among sites

Both species showed significant positive autocorrelation of genotypes within blocks (Fig. 6). Consistent with the AMOVA analyses and expectations of greater dispersal and gene flow by the agile antechinus, significantly stronger spatial structure over this scale (based on comparison of bootstrap confidence intervals of first-interval r_c values) was observed for the bush rat than the agile antechinus. Significant spatial autocorrelation was detected within

Table 2. The most parsimonious model of trap-level capture success of the bush rat and the agile antechinus in response to local environmental conditions, fire and year.

Bush rat	Variable	Estimate	SE	Z value	p
	Intercept	-3.656	0.21	-17.4	<0.001
	Burnt	-1.864	0.338	-5.51	<0.001
	Year (TSF)	0.555	0.122	4.54	<0.001
	TWI	0.102	0.107	0.95	0.34
	ρ	-0.39	0.14	-2.78	0.005
	q	-0.282	0.087	-3.24	0.001
	Autocovariate (40 m)	1.382	0.471	2.94	0.003
	Block (C)	-0.638	0.148	-4.32	<0.0001
	Block (M)	-0.125	0.133	-0.94	0.345
	Burnt: year (TSF)	1.36	0.201	6.76	<0.001
	Burnt: TWI	0.395	0.136	2.9	0.004
	Year (TSF): TWI	-0.037	0.07	-0.53	0.593
	Burnt: ρ	0.621	0.173	3.58	<0.001
	Burnt: year (TSF): TWI	-0.25	0.085	-2.92	0.003
		Variance	Standard deviation		
	Random term (trap within site)	0.281	0.53		
Agile antechinus	Variable	Estimate	SE	Z value	p
	Intercept	-3.816	0.192	-19.86	<0.001
	Burnt	-1.019	0.221	-4.6	<0.001
	Year (2010)	-0.138	0.188	-0.73	0.463
	Year (2011)	0.817	0.168	4.85	<0.001
	Autocovariate (40 m)	1.526	0.587	2.6	0.009
	Block (C)	0.303	0.16	1.89	0.059
	Block (M)	0.836	0.156	5.38	<0.001
	Burnt: year (2010)	0.172	0.3	0.57	0.566
	Burnt: year (2011)	0.874	0.25	3.5	<0.001
		Variance	Standard deviation		
	Random term (trap within site)	1.028	1.014		

200 m for both species, suggesting clustering of similar genotypes on a fine scale within sites (maximum distance among traps within sites is ~ 800 m). Only the bush rat showed evidence for significant spatial genetic structuring on a larger scale (1000 m).

The second multilocus spatial autocorrelation analysis revealed significantly stronger spatial autocorrelation among genotypes of bush rats in the same site in unburnt forest ($r_c = 0.089$, 95% CI 0.077–0.101) compared to burnt forest ($r_c = 0.04$, 95% CI 0.037–0.044). This pattern was not observed in the agile antechinus, where multilocus spatial autocorrelation among individuals in unburnt sites ($r_c = 0.013$, 95% CI 0.007–0.019) was very similar to burnt sites ($r_c = 0.017$, 95% CI 0.008–0.026).

Genetic evidence indicated changes in the temporal pattern of sex-biased dispersal by the bush rat in burnt forest. Autocorrelation among genotypes of females in unburnt forest (within and between years) was significantly higher than among males, consistent with male-biased dispersal (Fig. 7). However, r_c values were similar among males and females in burnt forest, suggesting an absence of sex-biased dispersal. The major change in burnt forest relative to unburnt forest was in female r_c values, which were significantly lower than the matching values in unburnt forest. For the agile antechinus, the patterns were consistent with male-biased dispersal in burnt and unburnt forest (Fig. 7), with weak positive spatial genotypic structure among males but strong positive structure among females within sites.

Discussion

Spatial scaling of post-fire recovery patterns and processes

Changes in the frequency, severity and size of fires are likely to have consequences for population distribution and genetic diversity under future climate and land management scenarios (Turner 2010, Banks et al. 2013). Understanding demographic and genetic recovery processes and patterns over multiple scales will be important for predicting these consequences (Griffiths et al. 2015, Davies et al. 2016). However, studies that integrate demographic and genetic

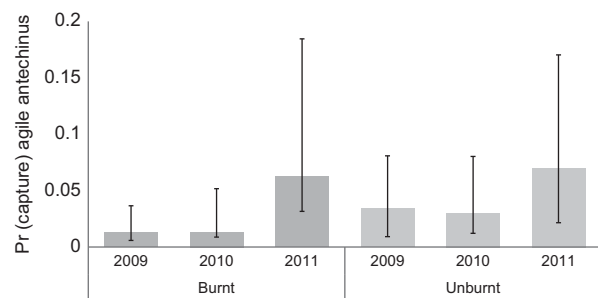


Figure 5. Predictions (and 95% confidence intervals) of trap-level occurrence of the agile antechinus in burnt and unburnt sites with increasing time since fire, generated from the model summarised in Table 2 (for Block M).

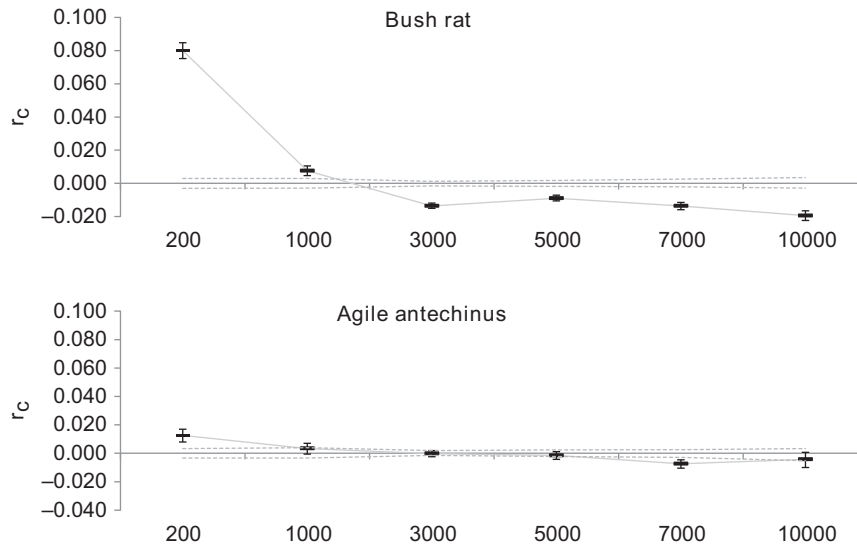


Figure 6. Multilocus correlograms based on genetic and geographic distances among individuals within blocks of sites. Combined r_c estimates (over blocks) are presented with 95% bootstrap confidence intervals (error bars) and 95% confidence intervals of 'null' r_c values based on 1000 permutations.

data to study temporal recovery processes after disturbance are lacking from the scientific literature.

We developed expectations of the distribution, abundance and spatial genetic structure of populations under alternative recovery mechanisms (Fig. 1), and evaluated these against data from two common Australian small mammal species after a large forest wildfire in 2009. The spatial scale of this disturbance was massive, burning over 50 000 ha of mountain ash forest and large areas of adjacent land cover types, yet recovery patterns were either independent of scale, consistent with an in situ recovery model, for the agile antechinus, or scale-dependent on a very fine spatial scale (consistent with a nucleated recovery model) for the bush rat. The spatial ecological and genetic changes exhibited by these species following this large fire were associated with the local spatial dispersion of survivors and subsequent microrefuge-recolonization dynamics. Our demographic and genetic data were inconsistent with the patterns expected under a

process of recovery driven by external recolonization, under which both species were expected to have little capacity for population recovery on the timescale of this study (Fig. 1).

The ecological and genetic patterns documented provide insights into the processes of post-fire recovery, indicating that recovery of these species was driven by local processes including in situ survival (agile antechinus) and nucleated recovery following survival in topographic micro-refuges distributed on scales of hundreds of metres (bush rat; Fig. 4). The apparent lack of any dependence on external immigration for recovery suggests that the spatial scale of fire events is unlikely to influence landscape-scale population distribution and genetic diversity for these species in the long term (Romme et al. 1998). In contrast, the impacts of fire on the spatial pattern of critical resources within the burnt area (such as shelter or food) is likely to influence post-fire ecological and genetic patterns through effects on the spatial dispersion of survivors.

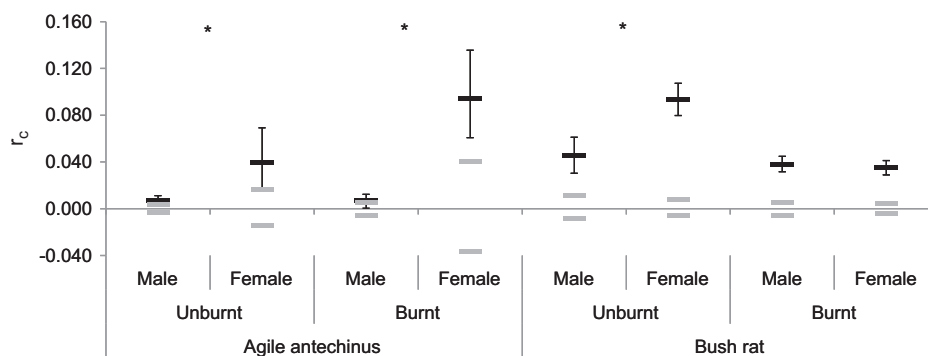


Figure 7. Multilocus spatial autocorrelation analysis of male and female bush rats and agile antechinus in burnt and unburnt habitat, in the same site. Error bars around autocorrelation r values are 95% bootstrap confidence intervals (1000 bootstraps) and grey bars represent the 95% confidence interval of permuted random r values. The autocorrelation r values shown include all individuals sampled over multiple years. Asterisks indicate whether the relevant male and female r_c values differ significantly according to simple comparison of 95% bootstrap confidence intervals. An analysis partitioning genetic distances within and between years is presented in Supplementary material Appendix 3, Fig. A4.

The ecological and genetic data supported the same broad conclusions about post-disturbance recovery, but were complementary in their sensitivity to different biological processes. For instance, small sample sizes precluded meaningful genetic analysis of low-density populations in the first year following the fire, but analyses of spatial patterns of occurrence identified the presence of micro-refuges for one species. Spatial predictions of changes in bush rat distribution over time functioned as ‘recolonization maps’ (Fig. 4) to identify likely patterns of post-fire colonisation from micro-refuges. Genetic analyses supported and refined our understanding of this process by identifying admixture signals consistent with expectations of refuge-recolonization dynamics, as well as associated shifts in dispersal strategy. Below, we discuss the evidence from the ecological and genetic data underlying our conclusions, and the relevance of our findings for the broader understanding of post-disturbance recovery processes in other systems.

Setting the scene for recovery: spatial distribution of resources, refuges and survivors

Both scale-dependent and scale-independent patterns of post-fire recovery have been documented in animals (Brotons et al. 2005, Knight and Holt 2005, Hochkirch and Adorf 2007), with scale-dependent patterns occurring either as gradients in abundance or occurrence with distance from unburnt edges or unburnt patches within the fire boundary (Watson et al. 2012). Scale-dependent recovery patterns occur when recolonization is an important recovery process, and dispersal distances are limited in relation to the scale of the fire, or the spatial dispersion of survivors in refuges. Here, the spatial dispersion of survivors appeared to be the key determinant of subsequent population recovery patterns. Genetic data were consistent with greater dispersal capacity of the agile antechinus than the bush rat (AMOVA and multi-locus spatial autocorrelation patterns among sites within blocks; Fig. 6). However, dispersal and recolonization were not inferred as drivers of recovery in the agile antechinus due to the presence of in situ survivors, and nucleated recovery involving fine-scale recolonization by the bush rat was largely determined by the spatial dispersion of survivors in topographic micro-refugia.

The differences in recovery patterns between the two study species highlight how the impacts of disturbance on resource availability, and hence the spatial dispersion of survivors, is a critical issue determining subsequent recovery processes and patterns for species affected by disturbance events. The spatial dispersion of survivors may range from even or spatially uncorrelated survivors, to fine or coarse-scaled clumped distributions. Two other mammals that occur in these forests serve as ‘bookends’ to illustrate the range of potential recovery patterns and their dependence on resource distribution. The tree hollow-dependent but dietary generalist mountain brushtail possum *Trichosurus cunninghami* had no major limiting changes in abundance or resource distribution after the fire (Lindenmayer et al. 2013, Banks et al. 2015). In contrast, the tree hollow-dependent and folivorous greater glider *Petauroides volans* requires unburnt eucalypt forest canopy for foraging and is restricted

to a coarse-grained patchy distribution after this fire (Berry et al. 2015a), typically in patches of unburnt forest canopy in deep-sheltered gullies (Leonard et al. 2014, Berry et al. 2015b). Thus, its recovery is likely to be dependent on large-scale and long-term habitat recovery and recolonization processes.

The two species in the present study are ecologically more similar in their fire responses than those described above, yet there were key differences in post-fire resource distribution. The key shelter resource for the agile antechinus, live and dead hollow-bearing trees, commonly remain standing after fire and are not strongly influenced by spatial heterogeneity in fire severity (Banks et al. 2011b, Lindenmayer et al. 2013). The bush rat is dependent on ground cover for shelter, and was therefore restricted to the minimal cover provided in fine-scale drainage lines until dense seedling regeneration enabled colonisation of adjacent slopes (Fig. 4) (Banks et al. 2011a, Smith et al. 2014). Within our study sites, these drainage lines were not burnt at lower severity by the fire event, but were associated with greater ground-level structure (e.g. rocks and eroded banks) and vegetation regeneration (Smith et al. 2014). This subtle difference in distribution among the two study species resulted in a difference between in situ recovery and fine-scale recolonization, with associated changes in dispersal and fine-scale genetic structure.

Understanding impacts of fire on the spatial and temporal distribution of critical resources is essential for predicting the processes and patterns of population recovery, and the likely sensitivity of species to fire size and frequency. However, an important extension to the research in this study will be to understand how the specific components of fire regimes influence the availability and spatial distribution of critical resources (Bassett et al. 2015, Burgess et al. 2015). For instance, the time since the most recent fire can be an important determinant of vegetation cover (such as ground-level shelter for the bush rat) and foliage availability, while hollow-bearing tree recruitment can be sensitive to short inter-fire intervals (Banks et al. 2011b, Haslem et al. 2012). Thus, species that are relatively insensitive to single fires may become restricted to refuges in ‘ecosystem greenspots’ (components of the landscape likely to be exposed to regimes of less frequent fire, such as deep gullies) under potential future scenarios of increasing fire frequency (Mackey et al. 2012). As well as reducing the distribution of such species, this process may cause major changes in genetic patterns through disturbance-driven fragmentation and loss of connectivity among populations.

Dispersal responses to disturbance

Two questions underpinning our study related to the role of dispersal and recolonization in population recovery from disturbance events, and whether shifts in dispersal strategy occurred during recolonization processes compared to movement within established populations. Genetic and demographic data suggested no large-scale recolonization, or ‘spillover’ from unburnt habitat outside the fire boundary as a driver of recovery in burnt areas. We suggest three potential reasons for this, acknowledging that this study does

not specifically explore all of these mechanisms. First, dispersal capability of these species is inadequate to facilitate population recovery over the spatial and temporal scale studied (Fig. 1). Indeed, exploratory simulations with male and female mean dispersal distances set at 1000 m (note: agile antechinus dispersal distances are documented as approximately 1000 m for males and 200 m for females; Banks and Lindenmayer 2014) only resulted in 'recovery' of the site most proximal to unburnt habitat (data not shown). Second, priority effects associated with the presence of in situ survivors may prevent large-scale immigration through competitive exclusion by residents (Waters et al. 2013). Third, a likely scenario under which large scale 'spillover' recolonization may occur is increased per capita resource availability (i.e. low population density relative to habitat quality) in burnt areas (Lehtinen and Galatowitsch 2001, Jaquiere et al. 2008), which may occur if fire reduces population abundance by directly killing individuals, instead of by limiting resource availability in the post-fire environment. However, post-fire resource limitation is likely to be common for species other than early successional specialists (Lindenmayer et al. 2013, Nimmo et al. 2014), and recently-burnt habitats are unlikely to be attractive resource-rich dispersal destinations for many species (Banks et al. 2015).

Despite the absence of apparent dispersal responses to fire on a landscape scale, genetic data were consistent with an increase in female dispersal during fine-scale recolonization that was associated with the nucleated recovery pattern of bush rats following fire. This suggests that the capacity for species to recover by recolonization, where required, is greater than might be expected based on observations of dispersal patterns within established populations (Fraser et al. 2015).

We expected that patterns of sex-biased dispersal may change under recolonization scenarios for two potential reasons. First, if male-biased dispersal is an inbreeding avoidance strategy (i.e. to increase male reproductive success (Lehmann and Perrin 2003)), males may reduce their dispersal from occupied refuges when female distribution is limited and patchy (i.e. where the overall availability of mates outside occupied refuges is unpredictable). Second, female dispersal may increase in the presence of adjacent unoccupied habitat when areas outside drainage lines become suitable due to increased ground cover associated with vegetation recovery. Thus, females may switch from philopatry to a colonisation behaviour to capitalise on the presence of increased resource availability in the surrounding landscape (Simmons and Thomas 2004, Gauffre et al. 2009, Hovestadt et al. 2014). While we cannot conclusively identify the specific drivers of this observed pattern, the genetic data were more consistent with an increase in dispersal by females than a reduction in male dispersal. This adaptive shift in dispersal during colonisation behaviour has implications for understanding population distribution under disturbance scenarios, as female philopatry is not a limiting factor in population expansion (Miller et al. 2011). Essentially, predictions of population expansion/recolonization rates based on sex-specific dispersal patterns within established populations may underestimate true recolonization rates if such dispersal responses by females are common.

Implications for genetic diversity

There was no detectable landscape-scale impact of fire on the genetic diversity and structure of the two small mammals studied. Other simulation research has demonstrated that the long-term impacts of disturbance regimes on genetic diversity patterns are strongly mediated by dispersal patterns and by rates of survival of disturbance events (Davies et al. 2016). Indeed, our simulations (Fig. 1) predicted that the high in situ survival inferred for the agile antechinus (from abundance and occurrence data) would result in no losses of genetic diversity following fire. Although the immediate impacts of fire on abundance were greatest for the bush rat (20% of abundance in unburnt sites in 2009), we predicted that the nucleated recovery model inferred from ecological data on this species would be effective at buffering the potential genetic impacts of high mortality caused by fire. Similar to our study species, in situ survival was a likely explanation for maintenance of pre-fire genetic diversity in the Gran Canaria blue chaffinch *Fringilla teydea polatzeki* following a major wildfire (Suarez et al. 2012), while populations of other species affected by disturbance types with a more severe impact on mortality (e.g. volcanic eruption) have led to major declines in genetic diversity in isolated populations (Beheregaray et al. 2003), but not those linked to source populations for recolonization (Spear et al. 2012).

In our study, there were expected effects of sample size on expected heterozygosity and the number of alleles (Nei 1978, Leberg 2002) that were associated with low abundance in post-fire burnt sites, but these populations recovered in abundance to levels similar to unburnt habitat over the three-year duration of the study, and no significant effects of fire were apparent on these metrics over and above the sample size effect. This observation suggests that for species where recovery is slower (on generational timescales), such as late-successional specialists, extended periods of increased genetic drift during population recovery would be expected to increase the genetic impacts of disturbance events (Banks et al. 2013).

We predicted that nucleated recovery from refuges would lead to an admixture phase as individuals recolonise intervening habitat. The bush rat data provided evidence for signals of genetic admixture associated with fine-scale and short-term refuge-recolonization dynamics. Although there were no impacts of fire on genetic diversity metrics relating to allele frequencies in the bush rat, there were effects on genotypic patterns (reduced F_{IS}). This species shows strong spatial clustering of similar genotypes over fine scales (< 200 m; Fig. 7), such that the pattern of fine-scale recolonization from topographic refuges demonstrated in Fig. 4 is likely to lead to heterozygote excess associated with a brief admixture phase. Such patterns have been documented at large scales and over long timeframes following recolonization from glacial refuges (Petit et al. 2003). In the context of ecological disturbance events such as fires, we expect that such spatial patterns of admixture between refuge zones would be apparent over larger spatial scales and longer timeframes when the initial distribution of survivors becomes more coarse-grained in widely-spaced refuges, or the suitability of intervening habitat recovers more slowly. Our simulations indicated that such admixture signals could be enhanced by the female

dispersal response that we observed, where post-fire recolonization is associated with an increase in female-mediated gene flow during recolonization (Supplementary material Appendix 3, Fig. A5).

Concluding comments

We present a novel integration of hypothesis-driven ecological and genetic analyses to understand post-disturbance recovery patterns and processes. We identified differences in the scaling and processes of recovery between species that were associated with resource requirements, and documented shifts in dispersal associated with recolonization as a population recovery mechanism. Two important lines of future research to build on this study are: 1) to understand how the different components of fire regimes (e.g. intensity, frequency, spatial pattern) influence the availability and spatial distribution of critical resources, and therefore the long-term distribution and genetic diversity of species; and 2) the impacts of climatic conditions on population responses to fire. Post-fire climatic conditions may play an important role in mediating population responses (Recher et al. 2009, Pastro et al. 2013). Here, a series of wet years after the fire enabled rapid recovery and population increases in both burnt and unburnt forest. Genetic impacts of disturbances such as fire may be greater if population recovery is delayed by unfavourable conditions such as reduced rainfall.

Acknowledgements – Wade Blanchard and John Stein provided valuable advice and resources for data analyses. Brenton von Takach Dukai and Annabel Smith provided valuable comments on the manuscript and analytical approach. This research was funded by an Australian Research Council Future Fellowship to Sam Banks (FT130100043).

References

- Banks, S. C. and Peakall, R. 2012. Genetic spatial autocorrelation can readily detect sex-biased dispersal. – *Mol. Ecol.* 21: 2092–2105.
- Banks, S. C. and Lindenmayer, D. B. 2014. Inbreeding avoidance, patch isolation and matrix permeability influence dispersal and settlement choices by male agile antechinus in a fragmented landscape. – *J. Anim. Ecol.* 83: 515–524.
- Banks, S. et al. 2005a. The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. – *Mol. Ecol.* 14: 1667–1680.
- Banks, S. C. et al. 2005b. The effects of habitat fragmentation due to forestry plantation establishment on the demography and genetic variation of a marsupial carnivore, *Antechinus agilis*. – *Biol. Conserv.* 122: 581–597.
- Banks, S. C. et al. 2011a. Starting points for small mammal population recovery after wildfire: recolonisation or residual populations? – *Oikos* 120: 26–37.
- Banks, S. C. et al. 2011b. The effects of wildfire on mortality and resources for an arboreal marsupial: resilience to fire events but susceptibility to fire regime change. – *PLoS One* 6: e22952.
- Banks, S. C. et al. 2013. How does ecological disturbance influence genetic diversity? – *Trends Ecol. Evol.* 28: 670–679.
- Banks, S. C. et al. 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.
- Banks, S. C. et al. 2016. Data from: Where do animals come from during post-fire population recovery? Implications for ecological and genetic patterns in post-fire landscapes. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.k47b2>>.
- Bashalkhanov, S. et al. 2009. A simple method for estimating genetic diversity in large populations from finite sample sizes. – *BMC Genet.* 10: 84.
- Bassett, M. et al. 2015. The effects of topographic variation and the fire regime on coarse woody debris: insights from a large wildfire. – *For. Ecol. Manage.* 340: 126–134.
- Beheregaray, L. B. et al. 2003. Genes record a prehistoric volcano eruption in the Galapagos. – *Science* 302: 75–75.
- Berry, L. E. et al. 2015a. The use of topographic fire refuges by the greater glider (*Petauroides volans*) and the mountain brushtail possum (*Trichosurus cunninghami*) following a landscape-scale fire. – *Aust. Mammal.* 37: 39–45.
- Berry, L. E. et al. 2015b. Identifying the location of fire refuges in wet forest ecosystems. – *Ecol. Appl.* 25: 2337–2348.
- Bivand, R. and Piras, G. 2015. Comparing implementations of estimation methods for spatial econometrics. – *J. Stat. Softw.* 63: 1–36.
- Bivand, R. et al. 2013. Computing the Jacobian in Gaussian spatial autoregressive models: an illustrated comparison of available methods. – *Geogr. Analysis* 45: 150–179.
- Brotons, L. et al. 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? – *J. Biogeogr.* 32: 789–798.
- Burgess, E. E. et al. 2015. The influence of a variable fire regime on woodland structure and composition. – *Int. J. Wildland Fire* 24: 59–69.
- Burns, E. L. et al. 2015. Ecosystem assessment of mountain ash forest in the Central Highlands of Victoria, south-eastern Australia. – *Austral Ecol.* 40: 386–399.
- Cockburn, A. et al. 1985. Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp (Marsupialia, Dasyuridae). – *Anim. Behav.* 33: 908–915.
- Cunningham, R. B. et al. 2005. Effects of trap position, trap history, microhabitat and season on capture probabilities of small mammals in a wet eucalypt forest. – *Wildl. Res.* 32: 657–671.
- Davies, I. D. et al. 2016. Implications of recurrent disturbance for genetic diversity. – *Ecol. Evol.* 6: 1186–1191.
- Excoffier, L. and Lischer, H. E. L. 2010. Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. – *Mol. Ecol. Resour.* 10: 564–567.
- Foll, M. and Gaggiotti, O. 2006. Identifying the environmental factors that determine the genetic structure of populations. – *Genetics* 174: 875–891.
- Fournier, D. A. et al. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. – *Optimization Methods Softw.* 27: 233–249.
- Fraser, C. I. et al. 2015. Priority effects can lead to underestimation of dispersal and invasion potential. – *Biol. Invasions* 17: 1–8.
- Gauffre, B. et al. 2009. Sex-biased dispersal patterns depend on the spatial scale in a social rodent. – *Proc. R. Soc. B* 276: 3487–3494.
- Griffiths, A. D. et al. 2015. Fire frequency matters more than fire size: testing the pyrodiversity-biodiversity paradigm for at-risk small mammals in an Australian tropical savanna. – *Biol. Conserv.* 186: 337–346.
- Haslem, A. et al. 2012. Time-since-fire and inter-fire interval influence hollow availability for fauna in a fire-prone system. – *Biol. Conserv.* 152: 212–221.
- Hochkirch, A. and Adorf, F. 2007. Effects of prescribed burning and wildfires on Orthoptera in central European peat bogs. – *Environ. Conserv.* 34: 225–235.

- Hovestadt, T. et al. 2014. Gender-specific emigration decisions sensitive to local male and female density. – *Am. Nat.* 184: 38–51.
- Hutchinson, M. F. 1998. Interpolation of rainfall data with thin plate smoothing splines – part ii: analysis of topographic dependence. – *J. Geogr. Inform. Decision Analysis* 2: 152–167.
- Hutchinson, M. F. 2011. ANUDEM version 5.3, user guide. – Fenner School of Environment and Society, Australian National Univ.
- Jaquiere, J. et al. 2008. Habitat quality effects on metapopulation dynamics in greater white-toothed shrews, *Crocidura russula*. – *Ecology* 89: 2777–2785.
- Knight, T. M. and Holt, R. D. 2005. Fire generates spatial gradients in herbivory: an example from a Florida sandhill ecosystem. – *Ecology* 86: 587–593.
- Kraaijeveld-Smit, F. J. L. et al. 2002. Factors influencing paternity success in *Antechinus agilis*: last-male sperm precedence, timing of mating and genetic compatibility. – *J. Evol. Biol.* 15: 100–107.
- Kraaijeveld-Smit, F. J. L. et al. 2007. Comparative genetic structure reflects underlying life histories of three sympatric small mammal species in continuous forest of south-eastern Australia. – *Oikos* 116: 1819–1830.
- Lawson Handley, L. J. and Perrin, N. 2007. Advances in our understanding of mammalian sex-biased dispersal. – *Mol. Ecol.* 16: 1559–1578.
- Lazenby Cohen, K. A. and Cockburn, A. 1991. Social and foraging components of the home range in *Antechinus stuartii* (Dasyuridae, Marsupialia). – *Aust. J. Ecol.* 16: 301–307.
- Leberg, P. L. 2002. Estimating allelic richness: effects of sample size and bottlenecks. – *Mol. Ecol.* 11: 2445–2449.
- Lehmann, L. and Perrin, N. 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. – *Am. Nat.* 162: 638–652.
- Lehtinen, R. M. and Galatowitsch, S. M. 2001. Colonization of restored wetlands by amphibians in Minnesota. – *Am. Midl. Nat.* 145: 388–396.
- Leonard, S. W. J. et al. 2014. Determinants of the occurrence of unburnt forest patches: potential biotic refuges within a large, intense wildfire in south-eastern Australia. – *For. Ecol. Manage.* 314: 85–93.
- Lindenmayer, D. B. et al. 2011. Newly discovered landscape traps produce regime shifts in wet forests. – *Proc. Natl Acad. Sci. USA* 108: 15887–15891.
- Lindenmayer, D. B. et al. 2013. Fire severity and landscape context effects on arboreal marsupials. – *Biol. Conserv.* 167: 137–148.
- Lindenmayer, D. B. et al. 2014. Complex responses of birds to landscape-level fire extent, fire severity and environmental drivers. – *Divers. Distrib.* 20: 467–477.
- Mackey, B. et al. 2012. Ecosystem greenspots: identifying potential drought, fire, and climate-change micro-refuges. – *Ecol. Appl.* 22: 1852–1864.
- McCarthy, M. A. et al. 1999. Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. – *For. Ecol. Manage.* 124: 193–203.
- Meirmans, P. G. and Hedrick, P. W. 2011. Assessing population structure: F_{ST} and related measures. – *Mol. Ecol. Resour.* 11: 5–18.
- Miller, T. E. X. et al. 2011. Sex-biased dispersal and the speed of two-sex invasions. – *Am. Nat.* 177: 549–561.
- Moore, I. D. and Hutchinson, M. F. 1991. Spatial extension of hydrologic process modelling. – *International Hydrology and Water Resources Symposium*, pp. 419–427
- Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. – *Genetics* 89: 583–590.
- Nimmo, D. G. et al. 2014. Why do some species have geographically varying responses to fire history? – *Ecography* 37: 805–813.
- Pastro, L. A. et al. 2013. Effects of wildfire, rainfall and region on desert lizard assemblages: the importance of multi-scale processes. – *Oecologia* 173: 603–614.
- Peakall, R. and Lindenmayer, D. 2006. Genetic insights into population recovery following experimental perturbation in a fragmented landscape. – *Biol. Conserv.* 132: 520–532.
- Peakall, R. and Smouse, P. E. 2006. GenA1Ex 6: genetic analysis in Excel. Population genetic software for teaching and research. – *Mol. Ecol. Notes* 6: 288–295.
- Peakall, R. and Smouse, P. E. 2012. GenA1Ex 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. – *Bioinformatics* 28: 2537–2539.
- Peakall, R. et al. 2003. Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. – *Evolution* 57: 1182–1195.
- Peakall, R. et al. 2006. Mark–recapture by genetic tagging reveals restricted movements by bush rats (*Rattus fuscipes*) in a fragmented landscape. – *J. Zool.* 268: 207–216.
- Petit, R. J. et al. 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. – *Science* 300: 1563–1565.
- Recher, H. F. et al. 2009. Small mammal populations in a eucalypt forest affected by fire and drought. I. Long-term patterns in an era of climate change. – *Wildl. Res.* 36: 143–158.
- Robinson, A. 1987. The ecology of the bush rat, *Rattus fuscipes* (Rodentia: Muridae), in Sherbrooke Forest, Victoria. – *Aust. Mammal.* 11: 35–41.
- Robinson, N. M. et al. 2013. Refuges for fauna in fire-prone landscapes: their ecological function and importance. – *J. Appl. Ecol.* 50: 1321–1329.
- Romme, W. H. et al. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? – *Ecosystems* 1: 524–534.
- Roques, L. et al. 2012. Allee effect promotes diversity in traveling waves of colonization. – *Proc. Natl Acad. Sci. USA* 109: 8828–8833.
- Simmons, A. D. and Thomas, C. D. 2004. Changes in dispersal during species' range expansions. – *Am. Nat.* 164: 378–395.
- Skaug, H. et al. 2015. Generalized linear mixed models using AD model builder. – R package ver. 0.8.2.
- Smith, A. L. et al. 2014. Dominant drivers of seedling establishment in a fire-dependent obligate seeder: climate or fire regimes? – *Ecosystems* 17: 258–270.
- Spear, S. F. et al. 2012. Genetic structure among coastal tailed frog populations at Mount St. Helens is moderated by post-disturbance management. – *Ecol. Appl.* 22: 856–869.
- Suarez, N. M. et al. 2012. Genetic signature of a severe forest fire on the endangered Gran Canaria blue chaffinch (*Fringilla teydea polatzeki*). – *Conserv. Genet.* 13: 499–507.
- Taylor, C. et al. 2014. Nonlinear effects of stand age on fire severity. – *Conserv. Lett.* 7: 355–370.
- Turner, M. et al. 2003. Surprises and lessons from the 1998 Yellowstone fires. – *Front. Ecol. Environ.* 1: 351–358.
- Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. – *Ecology* 91: 2833–2849.
- Warneke, R. 1971. Field study of the bush rat (*Rattus fuscipes*). – *Wildl. Contrib. Victoria* 14: 1–115.
- Waters, J. M. et al. 2013. Founder takes all: density-dependent processes structure biodiversity. – *Trends Ecol. Evol.* 28: 78–85.
- Watson, C. M. et al. 1998. Sex-chromosome elimination in the bandicoot *Isodon macrourus* using Y-linked markers. – *Cytogenet. Cell Genet.* 81: 54–59.
- Watson, S. J. et al. 2012. The influence of unburnt patches and distance from refuges on post-fire bird communities. – *Anim. Conserv.* 15: 499–507.
- White, R. et al. 1996. Reproductive seasonality of the bush rat (*Rattus fuscipes greyi*) in South Australia. – *Wildl. Res.* 23: 317–36.

Supplementary material (Appendix ECOG-02251 at <www.ecography.org/appendix/ecog-02251>. Appendix 1–3.