

Managing fire mosaics for small mammal conservation: a landscape perspective

Luke T. Kelly^{1*}†, Dale G. Nimmo¹, Lisa M. Spence-Bailey², Rick S. Taylor², Simon J. Watson¹‡, Michael F. Clarke² and Andrew F. Bennett¹

¹Landscape Ecology Research Group, School of Life and Environmental Sciences, Deakin University, Burwood, Vic. 3125, Australia; and ²Department of Zoology, La Trobe University, Bundoora, Vic. 3086, Australia

Summary

1. Fire is a major driver of ecosystem structure and function worldwide. It is also widely used as a management tool to achieve conservation goals. A common objective is the maintenance of 'fire mosaics' comprising spatially heterogeneous patches of differing fire history. However, it is unclear what properties of fire mosaics most enhance conservation efforts. Here we focus on the spatial and temporal properties of fire-prone landscapes that influence the distribution of small mammals.

2. We surveyed small mammals in 28 landscapes (each 12.6 km²) representing a range of fire histories in the Murray Mallee region (104 000 km²) of semi-arid Australia. Generalised linear mixed models were used to examine the influence of five landscape properties on the capture rate of individual species and the species richness of native small mammals. We investigated the influence of the proportional extent of fire age-classes, the diversity of fire age-classes, the extent of the dominant vegetation type, rainfall history and biogeographic context.

3. Three of four study species were associated with the spatial extent of fire age-classes. Older vegetation was found to provide important habitat for native small mammals. Overall, however, rainfall history and biogeographic context were dominant influences: for example, the species richness of native mammals was positively associated with above-average rainfall. There was little evidence that the diversity of fire age-classes influenced either the capture rate of individual species or species richness.

4. *Synthesis and applications.* In fire-prone environments, habitat availability can change markedly over short time-scales. Sufficient habitat at a suitable seral stage within the landscape is a key requirement for species conservation. In mallee ecosystems, the retention of older vegetation is recommended to create more desirable fire mosaics for native small mammals. In addition to such spatial properties of mosaics that are amenable to manipulation, an understanding of how ecological processes affect the biota (such as variation in rainfall-driven productivity) is also essential for informed conservation management.

Key-words: disturbance, habitat, landscape ecology, mallee, semi-arid, wildfire

Introduction

Wildfire is a major driver of ecosystem structure and function worldwide (Bond, Woodward & Midgley 2005; Bowman *et al.* 2009). It is also widely used to manage habitats to achieve

conservation goals: notably in Africa (Parr & Chown 2003), Australia (Andersen *et al.* 2005) and North America (Noss *et al.* 2006). Fire management increasingly is focused on managing landscapes to maintain 'fire mosaics', comprising spatially heterogeneous patches of differing fire history (Brockett, Biggs & van Wilgen 2001; Bradstock *et al.* 2005). However, almost any fire regime will create a 'mosaic': what is lacking is a body of empirical data that distinguishes the characteristics of mosaics that will most enhance the conservation of fauna in particular ecosystems (Clarke 2008; Driscoll *et al.* 2010).

Several mechanisms have been proposed, which directly link the distribution and abundance of fauna with the properties

*Correspondence author. E-mail: ltkelly@unimelb.edu.au

Present addresses:

†School of Botany, University of Melbourne, Parkville, Vic. 3010, Australia.

‡School of Environmental Science, Institute for Land, Water and Society, Charles Sturt University, Thurgoona, NSW 2640, Australia.

of fire mosaics (Bradstock *et al.* 2005; Parr & Andersen 2006). First, animal species may depend on resources that vary temporally in response to time-since-fire (or fire history) (e.g. Fox 1982). Under this hypothesis, changes in the spatial extent of different fire age-classes will modify the total amount of these resources available in the landscape and thereby influence the distribution and abundance of species. Secondly, because different taxa exhibit different responses to fire history, it is argued that heterogeneous mosaics composed of patches of differing fire history will provide a range of resources that will enable the persistence of a species-rich biota in the landscape (e.g. Briani *et al.* 2004). This hypothesis has been encapsulated by the expression 'pyrodiversity begets biodiversity' (Parr & Andersen 2006). Thirdly, individual species may require resources present in multiple components of the landscape: for example, patches of recently burnt vegetation adjacent to older vegetation (e.g. Firth *et al.* 2010). The composition of a fire mosaic may determine whether or not such species can occur. Finally, during a fire event, unburnt patches in the landscape can provide refuges for animals. Following a fire, these patches can provide a source for recolonisation into disturbed areas (Bradstock *et al.* 2005).

Studies of small mammals have been influential in the development of fire ecology. Such studies have, for example, provided insights into post-fire succession in animal communities (Fox, Taylor & Thompson 2003), the influence of fire frequency on fauna (Pardon *et al.* 2003) and the interactions between fire, rainfall and other ecological processes (Letnic & Dickman 2005). However, the relative influence of different spatial properties of fire-prone landscapes on small mammals, and other faunal groups, is poorly known. This is because data are primarily collected at a site level and do not allow direct comparison and understanding of how the combinations of spatial features that make up the whole landscape – the extent, composition and configuration of elements – influence fauna. To date, a whole-of-landscape approach (where the unit of study is the landscape) has largely been restricted to studies of fragmented agricultural systems (Bennett, Radford & Haslem 2006; Mortelliti *et al.* 2011).

We conducted a broad-scale natural experiment in the Murray Mallee region of semi-arid southern Australia. 'Mallee' shrubland and woodland offers a model system for investigating fire mosaics. This eucalypt- and spinifex-dominated vegetation is highly flammable, landscape structure is strongly associated with fire history and large tracts of native vegetation occur in conservation reserves. We surveyed small mammals in 28 landscapes (each 12.56 km²) selected to represent a range of fire histories and therefore different fire mosaics. In particular, we examined five landscape properties: the proportional extent of fire age-classes, the diversity of fire age-classes, the extent of the dominant vegetation type, rainfall history and the biogeographic context of the landscape. We sought to establish the relative influence of each of these properties on the distribution of small mammals in the region.

Materials and methods

STUDY AREA

The Murray Mallee region (104 000 km²) encompasses an extensive system of reserves managed primarily for biodiversity conservation (Fig. 1). The landscape is of low elevation (≤ 100 m above sea level), with moderate topographic variation provided by undulating dune and swale systems. Large tracts of native vegetation are characterised by stands of 'tree mallee' (i.e. vegetation dominated by *Eucalyptus* spp. with a multitemmed growth form). Three types of mallee vegetation have been identified and mapped across the study region: Triodia Mallee, Heathy Mallee and Chenopod Mallee (Haslem *et al.* 2010).

Mallee vegetation is fire-prone: an area equivalent to 40% of tree mallee vegetation in the region was burnt between 1972 and 2007 (S.C. Avitabile, unpublished data). Lightning is the major source of ignition. Mallee eucalypts and the perennial hummock grass, *Triodia scariosa* N.T. Burbidge, are the primary sources of surface fuel (Bradstock & Cohn 2002). Wildfires exceeding 100 000 ha typically occur in the region every 10–20 years, although longer fire intervals are common for any given location (Clarke *et al.* 2010). Smaller fire events occur more frequently.

The climate of the region is semi-arid; mean annual rainfall ranges from 218 mm in the north to 329 mm in the south. Rainfall typically is non-seasonal, and the interannual variability is high. Mean daily maximum temperatures in summer range from 30–33 °C, and temperatures >40 °C are common. Winters are mild, with mean daily maximum temperatures ranging from 15–18 °C.

FIRE HISTORY MAPPING

Landsat imagery was used to map the fire history of the study region from 1972 to 2007. Imagery was acquired from Landsat Multispectral Scanner (MSS) (1972–1988), Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) (1989–2005). Fire events were digitised using composites of 15 satellite images at a resolution of 25 m² (TM and ETM+) to 50 m² (MSS) (ENVI version 4.2). Fire maps were then exported to ArcView 9.2 for data checking and the addition of attribute data. Fires initially were dated to the intervals of available satellite images (e.g. 1977–1980). We obtained the year of each fire by consulting spatial data prepared by land management agencies and by contacting local experts. All data were compiled in a geographic information system (GIS) to form a complete regional fire history map (spanning 35 years), which provided a basis for selecting study landscapes.

LANDSCAPE AND SITE SELECTION

Twenty-eight landscapes were selected for study, each a circular area 4 km in diameter (12.56 km²). Landscapes were selected to represent variation in two key properties: the proportional extent of vegetation aged >35 years post-fire and the diversity of post-fire ages present. Landscape selection was stratified to ensure spatial coverage of the Murray Mallee region, with 14 landscapes located in each of the southern and northern halves of the study area. The size of study landscapes represented a scale large enough to encompass a range of post-fire histories and a scale appropriate to the distribution and ecology of small mammal populations. Neighbouring landscapes were non-overlapping and separated by at least 2 km. In summary, study landscapes ranged from those largely covered by recently burnt vegetation, to those containing several post-fire age-classes, to those mainly composed of older vegetation.

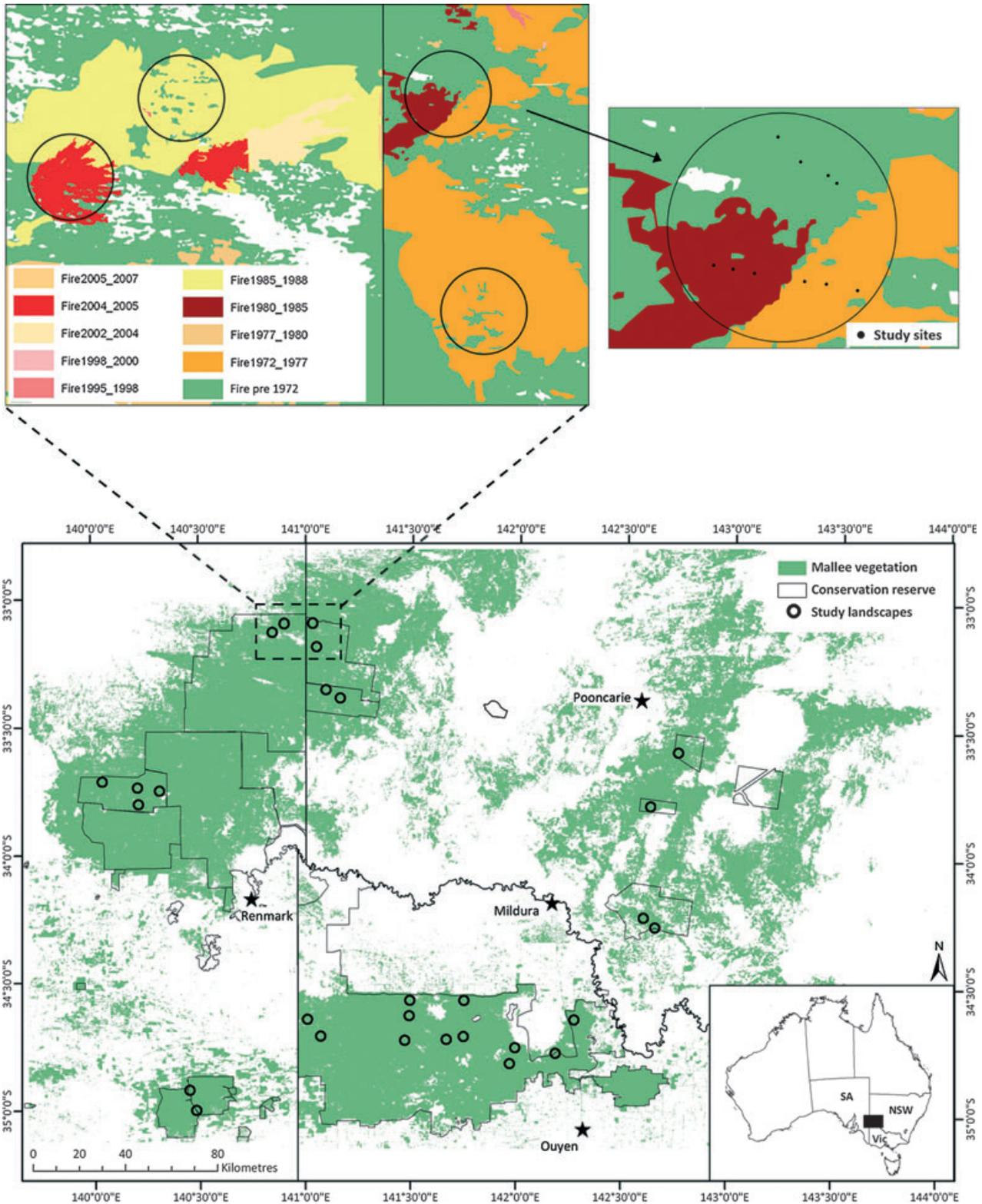


Fig. 1. Location of the Murray Mallee region in southern Australia (green shading indicates mallee vegetation). Study landscapes (4 km diameter: 12.6 km²) are shown as open circles.

Ten survey sites were established in each landscape. Site selection was stratified according to the proportional extent of post-fire age-classes of vegetation in the landscape (proportional extent of 0.02–0.10 = one site, 0.10–0.20 = two sites, 0.20–0.30 = three sites,

etc.). Within each post-fire age-class, sites were located to represent the range of vegetation types and topographic positions (dune, swale, flat) present. Potential sites were first chosen using fire history and vegetation maps, and later checked for suitability in the field.

Wherever logistically possible, sites were located in all four quadrants of the landscape (to ensure appropriate spatial coverage) and were typically >200 m apart (range 175–685 m).

SMALL MAMMAL SURVEYS

At each survey site, we established a line of pitfall traps comprising ten 20-L plastic buckets, spaced 5 m apart, connected by a continuous 300-mm-high flywire drift fence. Small mammal surveys were conducted at each of these 280 sites (i.e. 28 landscapes \times 10 sites) four times starting in October–November 2006 (Spring), January–February 2007 (Summer), October–November 2007 (Spring) and January–February 2008 (Summer). Each survey period consisted of five consecutive nights of trapping and traps were checked daily. Elliott aluminium box traps (33 \times 10 \times 10 cm) were used to complement pitfall trapping in Spring, but not in Summer (to ensure the welfare of animals during high summer temperatures). In Spring surveys, five Elliott traps were placed adjacent to the pitfall line at each site. The species, mass, sex, age-class and reproductive status of each animal were recorded, and hair clipping was used to mark individuals to identify recaptures during each survey period. Nomenclature for mammals follows van Dyck & Strahan (2008).

A large wildfire modified three landscapes during Spring 2006. Because of changes to mosaic structure, the spring 2006 data from these three landscapes were excluded. The fire history of these landscapes was remapped, and small mammals were subsequently surveyed twice in Spring 2007. In total, we completed 56 000 pitfall trap nights and 14 000 Elliott trap nights. Prior to statistical analysis, data from the 10 sites established in each landscape were pooled. We also grouped data from small mammal surveys to represent two distinct time periods: Spring/Summer 2006/2007 and Spring/Summer 2007/2008. This grouping, based on the warm-season breeding period of several species, enabled an examination of the effects of rainfall on animal populations during the study.

EXPLANATORY VARIABLES

Study landscapes were characterised by variables representing five mosaic properties. The extent of post-fire age-classes was represented by three subgroups: (i) the extent of vegetation < 10 years post-fire, (ii) the extent of vegetation 10–35 years post-fire and (iii) the extent of vegetation > 35 years post-fire. The diversity of post-fire age-classes was represented by the Shannon–Wiener diversity index of the proportion of each individual fire year in the landscape. The proportional extent of *Triodia Mallee* was used to describe the vegetation types occurring in the landscapes: those mosaics with less *Triodia Mallee* typically contained increasing proportions of *Chenopod Mallee*. Variables relating to fire history and vegetation type were calculated in FRAGSTATS version 3.3 (McGarigal *et al.* 2002).

The recent rainfall history of each landscape was represented by the amount of rainfall (mm) summed over a 12-month period. Monthly rainfall data were obtained from the closest weather station (Australian Bureau of Meteorology, <http://www.bom.gov.au/>) to each landscape [$n = 9$, mean distance to closest station = 25 km (range 4–50 km)]. Summed rainfall totals were calculated for 12-month periods prior to small mammal surveys at four time-lags: 3, 6, 9 and 12 months. Each time-lag was calculated as of November 2006 and November 2007 (the midpoint of the first survey during each grouped Spring/Summer trapping period).

Study landscapes were arrayed along a 200-km north-south axis (Fig. 1). Temperature increases and precipitation decreases from south to north (Pausas & Bradstock 2007). Northing of each land-

scape was included as an explanatory variable because it captured much of the biogeographic variation present in the study region. Summary data for each explanatory variable are shown in Table S1 in Supporting information.

STATISTICAL ANALYSES

We used generalised linear mixed models (GLMMs) to investigate small mammal responses to explanatory variables. GLMMs are a useful extension of generalised linear models and allow sources of correlation structure in the data to be modelled as random effects (Zuur *et al.* 2009). For models of individual species, the response variable was the capture rate of a species at a landscape, for each grouped survey period: Capture rate = total captures of individual animals/total trap nights. Recaptured animals were excluded from this calculation. For marsupials, which were not commonly recorded in Elliott box traps, capture rate was calculated from pitfall trap effort only. For rodents, which were captured in both pitfall traps and Elliott traps, capture rate was calculated using the combined trap effort of both survey techniques. For statistical analyses, capture rates were expressed as captures per 1000 trap nights and rounded to the nearest whole number. For the model of species richness, the response variable was the total number of native small mammal species captured in a landscape, for each grouped survey period.

Prior to fitting the regression models, we carried out graphical exploration of relationships between response and explanatory variables using scatter plots. This served two purposes: first, to identify the presence of nonlinear relationships and secondly, in the case of landscape variables with several correlated subgroups, to select (for each response variable) one subgroup from each set to include in regression models. Thus, for landscape variables relating to the extent of post-fire age-classes and rainfall history, only the subgroup with the strongest relationship with the response variable was included in further analyses. Selection of subgroups was also guided by our knowledge of the ecology of each study species. Landscape variables included in final models were not highly correlated (Pearson correlation coefficients < 0.5).

Generalised linear mixed models were implemented with a log-link function and Poisson distribution (Venables & Ripley 2002). Landscape variables were standardized by dividing by 2 standard deviations. This allowed effect sizes of variable coefficients to be compared (Gelman & Hill 2007). Explanatory variables were entered as linear fixed effects, as exploratory analyses identified no clear nonlinear relationships. Landscape was entered as a random effect (specifically, a random intercept) to account for possible temporal correlation of sites measured repeatedly (i.e. two grouped survey periods for each landscape, and therefore $n = 56$ for all regression analyses). GLMMs were fitted as full models to allow for the comparison of standardised variable coefficients. We interpreted landscape variables as having a significant influence on response variables where the standard errors of variable coefficients multiplied by two did not overlap zero. Model fit was assessed by Pearson's correlation of the observed vs. predicted values, providing an indication of how closely the two sets of values agree. Pearson residuals were tested for spatial autocorrelation using spline correlograms (Zuur *et al.* 2009). All statistical analysis was undertaken in the R statistical package version 2.13.1 (R Development Core Team 2010). GLMMs were fitted using the package MASS version 7.3-14 (Venables & Ripley 2002). We used this package because it can correct for overdispersion (commonly detected in count data) in Poisson GLMMs. Spline correlograms were produced in the extension package ncf version 1.1-3 (Bjornstad 2009).

Results

Faunal surveys resulted in 1265 captures of seven mammal species. The small mammal assemblage was composed of two species of dasyurid marsupial, the mallee ningau *Ningau yvonneae* (554 captures) and common dunnart *Sminthopsis murina* (290 captures); two marsupial burramyids, the western pygmy possum *Cercartetus concinnus* (183 captures) and the little pygmy possum (18 captures); and three rodents, Bolam's mouse *Pseudomys bolami* (30 captures), Mitchell's hopping mouse *Notomys mitchelli* (11 captures) and the introduced house mouse *Mus musculus* (179 captures). The average species richness of native small mammals in a landscape, per grouped survey period, was 2.8 ± 1.0 SD (range 1–5).

Further details of small mammal captures are provided in Table S2 in Supporting information. We present statistical analyses of the four most commonly encountered species and

the species richness of native small mammals. Spline correlograms provided no evidence of spatial autocorrelation in the residuals of the models presented (Fig. S1 in Supporting information).

CERCARTETUS CONCINNUS

The capture rate of *C. concinnus* was associated with the fire and rainfall histories of the study landscapes. Rainfall had the strongest influence: captures of *C. concinnus* were positively associated with 12-month rainfall totals at a time-lag of 6-months (Table 1). For example, the highest capture rate of *C. concinnus* (54 captures per 1000 trap nights) occurred at a landscape that had experienced above-average rainfall 6 months prior to trapping (Fig. 2a). *Cercartetus concinnus* was also positively associated with the proportional extent of vegetation aged >35 years post-fire (Fig. 2b) and with

Table 1. Results of generalised linear mixed models for individual species of small mammal and species richness of native small mammals

Landscape variable	<i>Cercartetus concinnus</i>	<i>Ningau yvonneae</i>	<i>Sminthopsis murina</i>	<i>Mus musculus</i>	Species richness of native mammals
Extent of post-fire age*	1.08 ± 0.43^b	-0.66 ± 0.31^a	-0.90 ± 0.27 ^b	0.61 ± 0.25^a	-0.18 ± 0.10 ^a
Extent of vegetation type	-0.84 ± 0.52	0.22 ± 0.34	0.09 ± 0.31	0.61 ± 0.35	0.06 ± 0.11
Diversity of post-fire ages	0.40 ± 0.50	0.21 ± 0.33	-0.05 ± 0.31	-0.10 ± 0.33	0.18 ± 0.10
Biogeographic context	1.70 ± 0.46	1.26 ± 0.29	-0.15 ± 0.28	0.85 ± 0.28	0.25 ± 0.09
Rainfall**	2.88 ± 0.34^c	0.42 ± 0.13^d	0.14 ± 0.23 ^d	1.84 ± 0.30^c	0.33 ± 0.09^c
Pearson correlation (<i>r</i>)	0.93 (0.89–0.96)	0.57 (0.36–0.72)	0.11 (-0.15–0.37)	0.78 (0.64–0.86)	0.58 (0.38–0.73)

Species richness calculations excluded the introduced *M. musculus*. Values are standardised variable coefficients ± one standard error. Bold values indicate where coefficient standard errors multiplied by two do not overlap zero. Model fit was assessed using a Pearson correlation (*r*) of observed vs. model-predicted values (95% confidence intervals of correlations are shown in parentheses).

*Extent of post-fire age-class represented by subgroup: < 10 years^a, 10–35 years and > 35 years^b.

**Rainfall represented by subgroup: 3-month time-lag, 6-month time-lag^c, 9-month time-lag^d, 12-month time-lag.

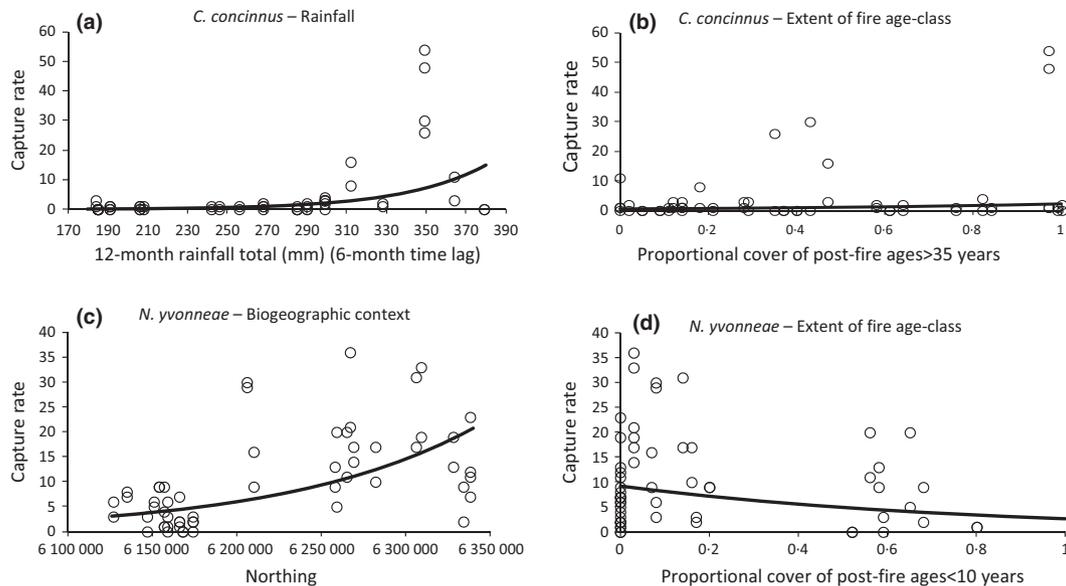


Fig. 2. Predicted capture rates of native small mammals based on generalised linear mixed models. Solid lines represent predictions from selected variables in the full model (with other explanatory variables held at mean values). Circles represent raw data. Capture rate = captures per 1000 trap nights.

landscapes located in northern areas of the study region (Table 1). The diversity of post-fire age-classes and the cover of vegetation types had no clear impact on the capture rate of *C. concinnus* (Table 1). A correlation between observed and model-predicted capture rates indicated good model fit ($r = 0.93$).

NINGAUI YVONNEAE

Although widespread across the study region, biogeographic context had a substantial influence on capture rates of *N. yvonneae* (Table 1). *Ningaui yvonneae* were more common in northern, more arid, locations (Fig. 2c). Fire history was also a significant influence. Landscapes characterised by high proportional cover of recently burnt vegetation (<10 years) contained lower numbers of *N. yvonneae* (Fig. 2d). Finally, capture success of *N. yvonneae* was positively associated with rainfall totals (at a 9-month time-lag) (Table 1). There was a moderate correlation between observed and predicted capture rates ($r = 0.57$) for this species.

SMINTHOPSIS MURINA

We identified no significant relationships between *S. murina* and landscape variables, and model predictions were not correlated with observed capture rates ($r = 0.11$). The species was widespread, occurring in all 28 study landscapes, and the capture rates were relatively high (Table S2). These results

demonstrate that this species occurs in landscapes with a broad range of fire histories under a variety of environmental conditions.

MUS MUSCULUS

Regression modelling showed that capture rates of *M. musculus* were positively associated with the amount of recently burnt vegetation (<10 years) (Fig. 3a). Captures of these species also increased in landscapes with higher recent rainfall totals (at a 6-month time-lag) (Fig. 3b) and in more northern locations (Table 1). We found no clear patterns between capture rates of *M. musculus* and the diversity of post-fire age-classes or the extent of vegetation type (Table 1). A correlation between observed and predicted capture rates indicated good model fit ($r = 0.78$).

SPECIES RICHNESS

Rainfall was a substantial influence on the species richness of native small mammals (Table 1). Species richness was positively associated with 12-month rainfall totals (at a time-lag of 6 months) (Fig. 4a); higher richness occurred in landscapes where rainfall was above the long-term mean. Northing (biogeographic context) was also a positive influence (Fig. 4b). Regression modelling showed no evidence that the extent of older vegetation, the diversity of post-fire age-classes or the cover of *Triodia Mallee* were strong influences on the richness of native small mammals in these landscapes (Table 1). There

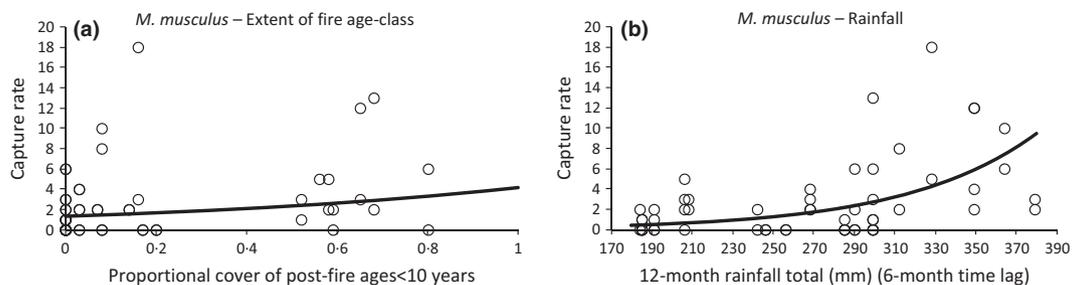


Fig. 3. Predicted capture rates of the introduced *Mus musculus* based on generalised linear mixed models. Solid lines represent predictions from selected variables in the full model (with other explanatory variables held at mean values). Circles represent raw data. Capture rate = captures per 1000 trap nights.

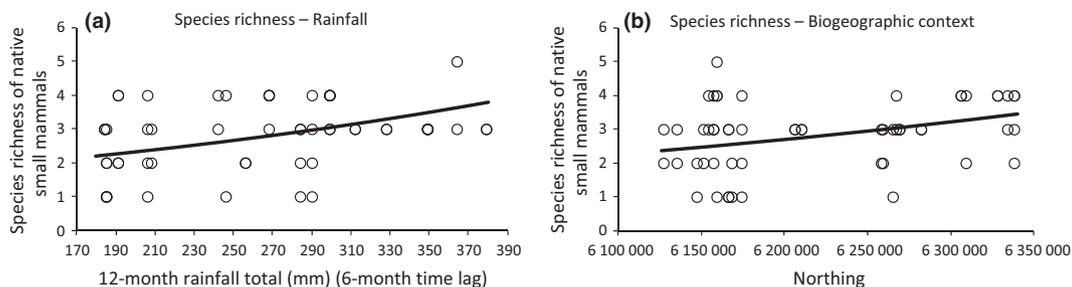


Fig. 4. Predicted species richness of native small mammals based on generalised linear mixed models. Solid lines represent predictions from selected variables in the full model (with other explanatory variables held at mean values). Circles represent raw data.

was a moderate correlation between observed and predicted species richness ($r = 0.58$).

Discussion

We surveyed small mammals in 28 landscapes selected to represent a range of fire histories, and therefore different fire mosaic properties. This approach – whereby the response and predictor variables characterise whole landscapes – allows a direct comparison of the influence of mosaic properties on faunal distributions. To our knowledge, this is the first application of this approach to investigate the responses of mammals to fire mosaic properties. We identified the total extent of habitat, particularly that of a suitable seral stage, as a key spatial property of landscape mosaics in fire-prone environments. Specifically, we found that areas of older post-fire vegetation provide important habitat for native small mammals. However, for most study species, the influence of recent rainfall and the biogeographic context of the landscape were dominant influences on capture rates.

INFLUENCE OF LANDSCAPE PROPERTIES

Fire history and vegetation type

A primary mechanism proposed to link the distribution and abundance of fauna with the properties of fire mosaics relates to the amount of suitable habitat in a landscape. Under this hypothesis, animal species depend on resources that vary temporally in response to fire regimes (e.g. Fox 1982; Briani *et al.* 2004). Changes in the spatial extent of different fire histories will modify the total amount of these resources available in the landscape and thereby influence the abundance and distribution of species.

The extent of recently burned vegetation (< 10 years) negatively influenced the capture rate of *N. yvonneae*. This species does not occur at sites immediately after they are burned (Kelly *et al.* 2010). The distribution of *N. yvonneae* is closely associated with cover of the hummock grass, *Triodia* (Bos, Carthew & Lorimer 2002), used for shelter and foraging. *Triodia* hummocks are highly flammable and are consumed by fire, and then recover over subsequent decades (Haslem *et al.* 2011). The proportional extent of older vegetation (> 35 years) positively influenced the capture rate of *C. concinnus*. This preference is consistent with the species' association with large trees and extensive cover of hummock grass (L.T. Kelly, unpublished data). The only species positively associated with recently burnt vegetation was the introduced *M. musculus* – a disturbance specialist.

The total amount of suitable habitat in a landscape may also be determined by the proportional extent of a particular vegetation type, irrespective of fire age. The lack of association of *N. yvonneae* with the proportional extent of *Triodia* Mallee in the study landscapes was surprising, given that the presence of hummock grass is a key determinant of its distribution (Bos, Carthew & Lorimer 2002). However, several landscapes dominated by *Triodia* Mallee were also those with large amounts of

recently burnt vegetation. Although we captured too few *N. mitchelli* to undertake statistical analyses, this species showed a clear preference for landscapes dominated by Heathy Mallee. Six of 11 captures of *N. mitchelli* were from landscapes largely comprised of this relatively uncommon vegetation.

A second mechanism that potentially links the distribution and abundance of fauna with properties of fire mosaics relates to fire-induced habitat heterogeneity. Because different taxa exhibit different responses to fire history, heterogeneous mosaics composed of patches of differing fire history may provide a greater range of resources that facilitate a more species-rich biota than in homogeneous landscapes (Masters 1993; Briani *et al.* 2004). We found little evidence that 'pyrodiversity begets biodiversity' (Parr & Andersen 2006) at the scale of this study, despite deliberately selecting study landscapes with 1–6 post-fire age-classes to represent a broad range in pyrodiversity. This is consistent with our contemporaneous work on birds in these landscapes (Taylor *et al.* 2012). There was a trend for increasing species richness of native mammals with increasing diversity, but it failed to reach statistical significance (Table 1). The lack of such response may be because these species do not have markedly different requirements relating to fire history. Those species that do show a preference for particular seral stages typically favour longer unburnt areas (*N. yvonneae* and *C. concinnus*). Further, most species occur in a wide range of post-fire age-classes, albeit with differing probabilities of occurrence (Kelly *et al.* 2011); and for some, such as *S. murina*, there was little or no relationship between occurrence and post-fire vegetation age at trap sites (Kelly *et al.* 2011).

The diversity hypothesis also relates to individual species. Under this hypothesis, individual species may require complementary resources present in different components of the landscape: for example, patches of recently burnt vegetation adjacent to older vegetation (Firth *et al.* 2010). In the present study, this would be manifest by a significant influence of mosaic diversity (e.g. landscapes containing a mix of recently burnt and older vegetation) on capture rates of individual species. We found no evidence that the diversity of fire age-classes influenced individual species. This may be because the scale of heterogeneity sampled was not at the spatial scale of individual home ranges of these species. Rather, our focus was on larger-scale mosaics typical of the fire-induced heterogeneity that presently occurs in the region. Landscape complementation effects (at the scale of this study) are most likely to be observed for species with larger home ranges, such as the western grey kangaroo *Macropus fuliginosus* (Coulson 1993).

A fourth hypothesis relates to the presence of unburnt patches that provide refuges for animals. Following a fire, these patches can provide a source for recolonisation into disturbed areas (Bradstock *et al.* 2005). While we were unable to specifically test this hypothesis (landscape selection was focussed on other properties of fire mosaics), it seems likely that the presence of unburnt patches will benefit individual species. Immediately following a wildfire that affected three of our landscapes, there was a marked reduction in the occurrence of *N. yvonneae* and in the species richness of small mammals (Kelly *et al.* 2010). The Murray Mallee region experiences very

large fires (> 100 000 ha) within the region on a regular basis (c. 20 year intervals), and in the absence of unburnt refuges, recolonisation of burnt areas at this spatial scale may be slow.

Biogeographic context and rainfall

The geographic scale at which studies must be undertaken when 'whole landscapes' are the unit of study means that environmental gradients across a study region often influence the distribution of species or composition of assemblages (Bennett, Radford & Haslem 2006; Mortelliti *et al.* 2011). Here, the biogeographic context of the landscape was an important influence on three species. For example, *N. yvonneae* was more common in landscapes in the northern, more arid, part of the study area. Differing environmental histories or bioclimatic influences between the northern and southern landscapes may determine specific food and shelter resources. Biogeographic context also was an important influence on several less-common species. For example, *P. bolami* was restricted to the northern half of the region, while *N. mitchelli* was recorded only in the south.

The distribution and abundance of species are influenced not only by the spatial properties of landscapes, but by a range of processes that may be associated with, or independent of, particular spatial patterns. These include processes such as competition, predation and climatic variation (Meserve *et al.* 2003). In this study, spatial and temporal variation in rainfall influenced several species. Recent rainfall history was a particularly strong influence on *C. concinnus* with higher capture rates recorded 6 months after a year of high rainfall. Similarly, *M. musculus*, *N. yvonneae* and the species richness of native mammals were positively associated with rainfall totals. This association of small mammals with rainfall is likely to be driven by changes in primary productivity, and therefore the abundance of food resources (e.g. plants, seeds, invertebrates and pollen). This is consistent with other studies from the Australian arid zone, where rainfall-driven processes have a large influence on small mammal population dynamics (Southgate & Masters 1996; Letnic & Dickman 2010). We propose that higher capture rates of small mammals following high rainfall represent an increase in the abundance of regional populations, as well as a potential increase in the 'trappability' of individuals.

SYNTHESIS AND APPLICATIONS

A primary management goal in many fire-prone environments is to protect, maintain and enhance biodiversity. Patch mosaic burning (i.e. introducing heterogeneity in burning patterns) is widely advocated to achieve such goals (Parr & Andersen 2006). This is the case in mallee ecosystems, where fire plays an important role in ecosystem function and is widely used as a management tool (Bradstock & Cohn 2002). This includes using fire to maintain a range of post-fire ages in the landscape to maintain vegetation communities and provide habitat for animals, and to create areas with reduced fuel loads to avoid large, reserve-scale fires (Sandell *et al.* 2006). In combination

with 'natural' fire regimes, management practices will create a range of fire mosaics.

Management of fire mosaics for biodiversity conservation will need to consider both the characteristics of the ecosystem under consideration and the species that are a priority for regional conservation efforts. In this study, we identified the proportional extent of older vegetation as an important spatial property of landscape mosaics for native small mammals in mallee ecosystems. Older vegetation is heterogenous; it includes dense, patchy cover of spinifex, complex ground litter and larger trees, which provide high-quality habitat components for several small mammal species. Given that many important habitat attributes take decades to develop (Haslem *et al.* 2011), the retention of older mallee vegetation (e.g. > 35 years) in the landscape should be encouraged.

Although we found little support for the 'pyrodiversity hypothesis', several important considerations remain. First, we focused here on the direct effects of fire mosaics on small mammals (i.e. how the present mosaic influences species distributions). Fire management will also need to consider the indirect effects of fire, such as the role of fuel reduction in protecting and retaining unburnt vegetation in the landscape. Secondly, at a regional scale, there clearly is a need for a range of fire age-classes to ensure an ongoing supply of successional stages. Thirdly, we modelled the responses of relatively common species. Several other species were relatively uncommon in the region (e.g. *P. bolami* and *N. mitchelli*), and further research is required to identify the influence of landscape-scale properties on these species. Finally, this study was undertaken in an ecosystem that has been modified over the last 150 years. One-third of the historical mammal assemblage is regionally extinct (Bennett, Lumsden & Menkhorst 1989), with declines greatest among small- to medium-sized mammals (e.g. bandicoots, bettongs and stick-nest rats). Any re-introductions of these species will need to consider their possible requirement for fine-scale heterogeneity. The present day mammal assemblage may represent the most resilient species.

Finally, this work highlights the importance of the spatial properties of fire mosaics, which are amenable to manipulation and management, and other ecological processes that also determine habitat quality, in this case, spatial and temporal variation in rainfall-driven productivity. Thus, while the management of fire regimes can be used as a tool to enhance biodiversity, it is critical to recognise that other ecological processes interact with fire-generated spatial patterns to determine the distribution of species and composition of assemblages. Future studies of fire mosaics will benefit from considering the interactions with spatial patterns of other processes, particularly those such as predation and grazing by herbivores that managers can influence.

Acknowledgements

Funding and support were provided by Land and Water Australia, Department for Environment and Heritage (SA), Parks Victoria, Department of Sustainability and Environment (Vic.), Mallee Catchment Management Authority, NSW National Parks and Wildlife Service, Department of Environment and Climate Change (NSW), Lower Murray–Darling Catch-

ment Management Authority, Natural Heritage Trust, Birds Australia, Australian Wildlife Conservancy, and the Murray Mallee Partnership. We are grateful to the Doyle and Barnes families for access to Petro and Lethero Stations, respectively. Thanks to Sarah Avitabile, Lauren Brown, Kate Callister, Angie Haslem and Sally Kenny; and the many volunteers who assisted with fieldwork. Three anonymous referees made useful comments on the manuscript.

References

- Andersen, A.N., Cook, G.D., Corbett, L.K., Douglas, M.M., Eager, R.W., Russell-Smith, J., Setterfield, S.A., Williams, R.J. & Woinarski, J.C.Z. (2005) Fire frequency and biodiversity conservation in Australian tropical savannas: implications from the Kapalga fire experiment. *Austral Ecology*, **30**, 155–167.
- Bennett, A.F., Lumsden, L.F. & Menkhorst, P.W. (1989) Mammals of the mallee region of south-eastern Australia. *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management* (eds J.C. Noble & R.A. Bradstock), pp. 191–220. CSIRO, Melbourne, Vic.
- Bennett, A.F., Radford, J.Q. & Haslem, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biological Conservation*, **133**, 250–264.
- Bjornstad, O.N. (2009) NCF: spatial nonparametric covariance functions. R package version 1.1-3. Available at: <http://www.CRAN.R-project.org/package=nfc>.
- Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, **165**, 525–537.
- Bos, D.G., Carthew, S.M. & Lorimer, M.F. (2002) Habitat selection by the small dasyurid *Ningaui yvonnae* (Marsupialia: Dasyuridae) in South Australia. *Austral Ecology*, **27**, 103–109.
- Bowman, D., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M.A., Kull, C.A., Marston, J.B., Moritz, M.A., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R. & Pyne, S.J. (2009) Fire in the earth system. *Science*, **324**, 481–484.
- Bradstock, R.A. & Cohn, J.S. (2002) Fire regimes and biodiversity in semi-arid mallee ecosystems. *Flammable Australia: The Fire Regimes and Biodiversity of a Continent* (eds R.A. Bradstock, J.E. Williams & M.A. Gill), pp. 238–258. Cambridge University Press, Cambridge, MA.
- Bradstock, R.A., Bedward, M., Gill, A.M. & Cohn, J.S. (2005) Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research*, **32**, 409–423.
- Briani, D.C., Palma, A.R.T., Vieira, E.M. & Henriques, R.P.B. (2004) Post-fire succession of small mammals in the Cerrado of central Brazil. *Biodiversity and Conservation*, **13**, 1023–1037.
- Brockett, B.H., Biggs, H.C. & van Wilgen, B.W. (2001) A patch mosaic burning system for conservation areas in southern African savannas. *International Journal of Wildland Fire*, **10**, 169–183.
- Clarke, M.F. (2008) Catering for the needs of fauna in fire management: science or just wishful thinking? *Wildlife Research*, **35**, 385–394.
- Clarke, M.F., Avitabile, S.C., Brown, L., Callister, K.E., Haslem, A., Holland, G.J., Kelly, L.T., Kenny, S.A., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J. & Bennett, A.F. (2010) Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Australian Journal of Botany*, **58**, 363–372.
- Coulson, G. (1993) Use of heterogeneous habitat by the Western Grey Kangaroo, *Macropus fuliginosus*. *Wildlife Research*, **20**, 137–149.
- Driscoll, D.A., Lindenmayer, D.B., Bennett, A.F., Bode, M., Bradstock, R.A., Cary, G.J. *et al.* (2010) Fire management for biodiversity conservation: key research questions and our capacity to answer them. *Biological Conservation*, **143**, 1928–1939.
- van Dyck, S. & Strahan, R. (2008) *Mammals of Australia*, 3rd edn. Reed New Holland, Sydney, NSW.
- Firth, R.S.C., Brook, B.W., Woinarski, J.C.Z. & Fordham, D.A. (2010) Decline and likely extinction of a northern Australian native rodent, the Brush-tailed Rabbit-rat *Conilurus penicillatus*. *Biological Conservation*, **143**, 1193–1201.
- Fox, B.J. (1982) Fire and mammalian secondary succession in an Australian coastal heath. *Ecology*, **63**, 1332–1341.
- Fox, B.J., Taylor, J.E. & Thompson, P.T. (2003) Experimental manipulation of habitat structure: a retrogression of the small mammal succession. *Journal of Animal Ecology*, **72**, 927–940.
- Gelman, A. & Hill, J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York, NY.
- Haslem, A., Callister, K.E., Avitabile, S.C., Griffioen, P.A., Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J., Brown, L., Bennett, A.F. & Clarke, M.F. (2010) A framework for mapping vegetation over broad spatial extents: a technique to aid land management across jurisdictional boundaries. *Landscape and Urban Planning*, **97**, 296–305.
- Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S., Taylor, R., Avitabile, S., Callister, K., Spence-Bailey, L., Clarke, M. & Bennett, A.F. (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. *Journal of Applied Ecology*, **48**, 247–256.
- Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Clarke, M.F. & Bennett, A.F. (2010) The short-term responses of small mammals to wildfire in semi-arid mallee shrubland, Australia. *Wildlife Research*, **37**, 293–300.
- Kelly, L.T., Nimmo, D.G., Spence-Bailey, L.M., Haslem, A., Watson, S.J., Clarke, M.F. & Bennett, A.F. (2011) The influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions*, **17**, 462–473.
- Letnic, M. & Dickman, C.R. (2005) The responses of small mammals to patches regenerating after fire and rainfall in the Simpson Desert, central Australia. *Austral Ecology*, **30**, 24–39.
- Letnic, M. & Dickman, C.R. (2010) Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews*, **85**, 501–521.
- Masters, P. (1993) The effects of fire-driven succession and rainfall on small mammals in spinifex grassland at Uluru National Park, Northern-Territory. *Wildlife Research*, **20**, 803–813.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps*. University of Massachusetts, Amherst, MA. Available at: <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Meserve, P.L., Kelt, D.A., Milstead, W.B. & Gutierrez, J.R. (2003) Thirteen years of shifting top-down and bottom-up control. *BioScience*, **53**, 633–646.
- Mortelliti, A., Amori, G., Capizzi, D., Cervone, C., Fagiani, S., Pollini, B. & Boitani, L. (2011) Independent effects of habitat loss, habitat fragmentation and structural connectivity on the distribution of two arboreal rodents. *Journal of Applied Ecology*, **48**, 153–162.
- Noss, R.F., Franklin, J.F., Baker, W.L., Schoennagel, T. & Moyle, P.B. (2006) Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment*, **4**, 481–487.
- Pardon, L.G., Brook, B.W., Griffiths, A.D. & Braithwaite, R.W. (2003) Determinants of survival for the northern brown bandicoot under a landscape-scale fire experiment. *Journal of Animal Ecology*, **72**, 106–115.
- Parr, C.L. & Andersen, A.N. (2006) Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology*, **20**, 1610–1619.
- Parr, C.L. & Chown, S.L. (2003) Burning issues for conservation: a critique of faunal fire research in Southern Africa. *Austral Ecology*, **28**, 384–395.
- Pausas, J.G. & Bradstock, R.A. (2007) Fire persistence traits of plants along a productivity and disturbance gradient in mediterranean shrublands of south-east Australia. *Global Ecology and Biogeography*, **16**, 330–340.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Sandell, P., Tolhurst, K., Dalton, J., Scott, B. & Smith, M. (2006) Fire management prescriptions for the Victorian Mallee parks. *Proceedings of the Royal Society of Victoria*, **118**, 395–412.
- Southgate, R. & Masters, P. (1996) Fluctuations of rodent populations in response to rainfall and fire in a central Australian hummock grassland dominated by *Plectrachne schinzii*. *Wildlife Research*, **23**, 289–303.
- Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity and Distributions*, DOI: 10.1111/J.1472-4642.2011.00842.x
- Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, NY.

Received 27 September 2011; accepted 8 February 2012
Handling Editor: Phil Stephens

Supporting Information

Additional Supporting Information may be found in the online of this article.

Fig. S1. Spline correlograms (of the Pearson residuals) from generalized linear mixed models for individual species of small mammal and the richness of native small mammals. GLMMs were fitted as full models. The maximum lag distance shown is 300 km. Note: the 95% pointwise bootstrap confidence intervals do not overlap zero and there is no evidence of strong spatial autocorrelation.

Table S1. Descriptive statistics of the explanatory variables used to characterise study landscapes.

Table S2. Descriptive statistics of small mammal captures in study landscapes in the Murray Mallee region. *Introduced species.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be reorganized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.