

Influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence

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ABSTRACT

Aim Fire affects the structure and dynamics of ecosystems world-wide, over long time periods (decades and centuries) and at large spatial scales (landscapes and regions). A pressing challenge for ecologists is to develop models that explain and predict faunal responses to fire at broad temporal and spatial scales. We used a 105-year post-fire chronosequence to investigate small mammal responses to fire across an extensive area of ‘tree mallee’ (i.e. vegetation characterized by small multi-stemmed eucalypts).

Location The Murray Mallee region (104,000 km²) of semi-arid Australia.

Methods First, we surveyed small mammals at 260 sites and explored the fire responses of four species using nonlinear regression models. Second, we assessed the predictive accuracy of models using cross-validation and by testing with independent data. Third, we examined our results in relation to an influential model of animal succession, the habitat accommodation model.

Results Two of four study species showed a clear response to fire history. The distribution of the Mallee Ningau *Ningau yvonneae*, a carnivorous marsupial, was strongly associated with mature vegetation characterized by its cover of hummock grass. The occurrence of breeding females was predicted to increase up to 40–105 years post-fire, highlighting the extensive time periods over which small mammal populations may be affected by fire. Evaluation of models for *N. yvonneae* demonstrated that accurate predictions of species occurrence can be made from fire history and vegetation data, across large geographical areas. The introduced House Mouse *Mus domesticus* was the only species positively associated with recently burnt vegetation.

Main conclusions Understanding the impact of fire over long time periods will benefit ecological and conservation management. In this example, tracts of long-unburnt mallee vegetation were identified as important habitat for a fire-sensitive native mammal. Small mammal responses to fire can be predicted accurately at broad spatial scales; however, a conceptual model of post-fire change in community structure developed in temperate Australia is not, on its own, sufficient for small mammals in semi-arid systems.

Keywords

Conservation, disturbance, habitat accommodation model, mallee, succession, wildfire.

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INTRODUCTION

Management of fire for biodiversity conservation is a global issue (Parr & Andersen, 2006; Bowman *et al.*, 2009). Fire-

dependent ecosystems cover over 50% of the terrestrial land surface (Shlisky *et al.*, 2007) and contain a large proportion of the world’s biota. Moreover, fire can affect ecosystems over long temporal scales (decades to centuries) and at large spatial

scales (landscapes to regions) (Turner *et al.*, 2003; Bradstock, 2008). There is growing concern over the impact of fire on biodiversity (Noss *et al.*, 2006; Lindenmayer *et al.*, 2008). For example, inappropriate fire regimes have been linked to population declines of mammals, birds and reptiles across Australia (Cogger *et al.*, 1994; Maxwell *et al.*, 1996; Garnett & Crowley, 2000). A major challenge for ecologists is to develop ecological and statistical models that can explain and predict faunal responses to fire.

Conservation management in fire-prone environments is often constrained by inadequate ecological knowledge (Driscoll *et al.*, 2010). A key issue relates to the decades or centuries over which post-fire changes take place, compared with the short time period over which fire responses have been documented (Parr & Chown, 2003). Such temporal mismatches limit ecological understanding (Clarke, 2008; Clarke *et al.*, 2010). A second issue relates to the small spatial extent at which fire responses typically are studied, compared with the large geographical areas over which fire and fire management occur (Parr & Chown, 2003). This disparity means that the consistency and robustness of fire responses are rarely evaluated at spatial scales commensurate with land management (Freckleton, 2004). Thus, ecological managers often have little guidance with which to make decisions regarding long-term and broad-scale fire management.

Developing conceptual models that synthesize and predict species' responses to fire is one option to provide guidance to ecological management (Friend, 1993). Fox (1982) published a seminal paper in which he developed a model of animal succession to describe the post-fire changes in a small mammal community of eastern Australia. The 'habitat accommodation model' proposed that faunal species enter the post-fire succession when vegetation structure becomes suitable for them. As the structure of the vegetation changes and becomes less suitable for a species, it will be excluded from the succession, or become reduced in abundance, by competitors (Fox *et al.*, 2003). This model is supported by studies of small mammals in shrublands of Australia (temperate heathland), North America (chaparral) and South Africa (fynbos) (see Fox *et al.*, 1985; Monamy & Fox, 2010). However, there has been only limited evaluation of predictions from the habitat accommodation model across broad spatial scales and in applying the model to inter-fire periods of decades and centuries. In addition, there has been no assessment of the model for small mammal communities of semi-arid shrublands and woodlands. Addressing such knowledge gaps may provide valuable insight into the utility of this model to conservation management.

Here, we present the results of a broad-scale natural experiment conducted in the Murray Mallee region of semi-arid southern Australia. We surveyed small mammals at 260 sites, arrayed along a chronosequence of 1–105 years post-fire. 'Mallee' vegetation offers a model system for investigating post-fire changes in animal populations: the structure of this eucalypt-dominated vegetation is strongly associated with fire (Bradstock & Cohn, 2002). In addition, the development of

predictive models to age mallee vegetation has enabled examination of post-fire temporal changes extending to over a century (Clarke *et al.*, 2010).

The primary objective of this study was to examine the influence of fire history on the distribution and ecology of small mammals. First, we developed statistical models of species' occurrence over a century-long post-fire chronosequence. We considered the responses of males, females and breeding females separately, to investigate long-term temporal processes. Second, we assessed the predictive accuracy of models using cross-validation and by testing on an independent data set (collected from different sites at different times). This enabled an evaluation of the consistency and robustness of broad-scale fire responses. Third, we examined these results in relation to the habitat accommodation model of animal succession. Based on this conceptual model, we expected a predictable sequence of mammalian succession, closely linked to vegetation regeneration following fire.

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 (Land Conservation Council, 1987). Large tracts of native vegetation are characterized by stands of 'mallee' shrubland and woodland (i.e. vegetation dominated by *Eucalyptus* spp. typically < 5 m height with a multi-stemmed growth form). 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 interannual rainfall variability is high. Mean daily maximum temperatures in summer range from 30 to 33 °C, and temperatures > 40 °C are common. Winters are mild, with mean daily maximum temperatures ranging from 15 to 18 °C (Australian Bureau of Meteorology, <http://www.bom.gov.au/>).

The structure and composition of mallee vegetation is strongly influenced by fire (Bradstock & Cohn, 2002). For example, we have previously documented post-fire temporal changes in key habitat attributes used by mallee fauna, such as spinifex cover and hollow tree stems (Fig. 2; Haslem *et al.*, 2011). Wildfires exceeding 100,000 ha typically occur in the region every 10–20 years. Smaller fire events occur more frequently (Land Conservation Council, 1987). Mallee eucalypts are the primary source of surface fuel, and flammable *Triodia* hummocks play a major role in fire spread (Bradstock & Cohn, 2002). Lightning strikes are the main source of ignition (S. Avitabile, unpublished data). An important feature of mallee vegetation is the ability of mallee eucalypts to regenerate from underground lignotubers following fire, by coppicing multiple new stems (Specht, 1981). Fire in mallee

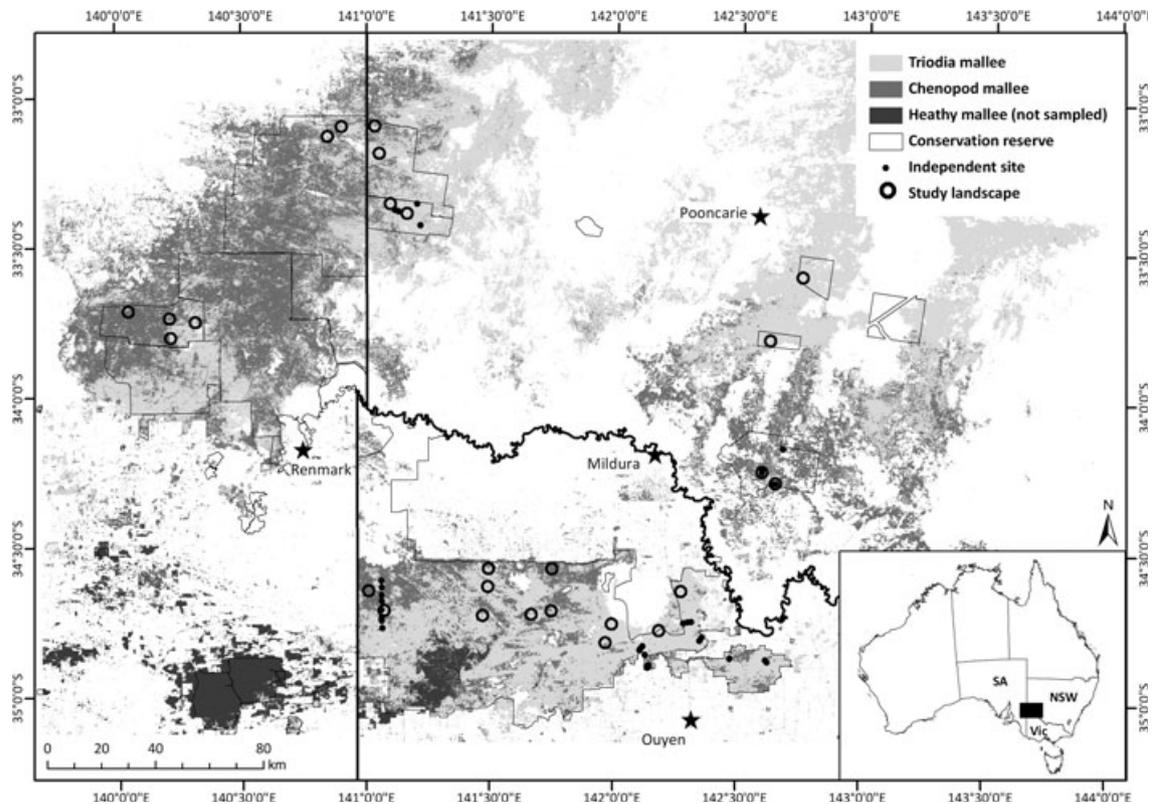


Figure 1 Location of 26 study landscapes (open circles) in the Murray Mallee region of southern Australia. All study sites ($n = 260$) were situated within these landscapes. Independent validation sites ($n = 34$) are shown as black circles. The distribution of mallee vegetation [light grey, *Triodia* Mallee; mid grey, *Chenopod* Mallee; dark grey, *Heathy* Mallee (not sampled)] and the location of conservation reserves (polygons) are shown. White areas have been cleared of native vegetation, mainly for cropping and sheep grazing.

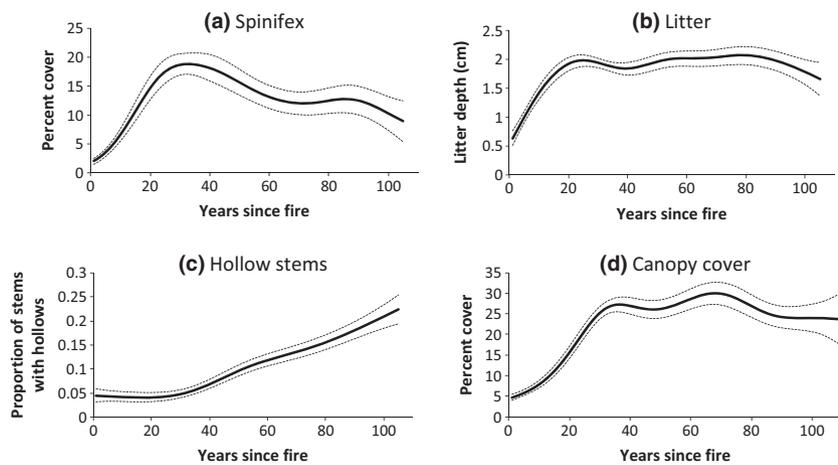


Figure 2 Predicted post-fire changes in several key structural attributes of mallee vegetation across a 105-year time period (modified from Haslem *et al.*, 2011). Solid lines represent predictions from regression models; dashed lines represent ± 1 SE. Results are shown only for *Triodia* Mallee vegetation type.

vegetation is typically stand replacing, and therefore fires effectively reset vegetation succession to ‘year zero’.

Previous work has identified and mapped mallee vegetation associations across the study region (Haslem *et al.*, 2010). Here, we focus on the two most widespread vegetation types. *Triodia* Mallee, typical of sandy flats and low dunes, is dominated by an overstorey of *Eucalyptus dumosa* and *E. socialis* and an understorey of the perennial hummock grass *Triodia scariosa*. *Chenopod* Mallee is common on heavier soils

and swales, where *E. oleosa* and *E. gracilis* frequently occur with an understorey of low perennial shrubs such as *Maireana* spp. and *Atriplex* spp.

Study design

We employed a space-for-time approach to investigate small mammal responses to fire. We surveyed small mammals at 260 sites, arrayed along a chronosequence of 1–105 years post-fire

Table 1 Distribution of 254 study sites across the 105-year post-fire chronosequence and two vegetation types, included in statistical analyses.

| Post-fire age | Vegetation type | | Total sites |
|---------------|-----------------|-----------------|-------------|
| | Triodia Mallee | Chenopod Mallee | |
| 1–5 | 33 | 5 | 38 |
| 6–10 | 20 | 1 | 21 |
| 11–20 | 1 | 0 | 1 |
| 21–30 | 32 | 3 | 35 |
| 31–40 | 54 | 25 | 79 |
| 41–50 | 7 | 6 | 13 |
| 51–60 | 15 | 9 | 24 |
| 61–70 | 8 | 5 | 13 |
| 71–80 | 4 | 5 | 9 |
| 81–90 | 7 | 6 | 13 |
| 91–105 | 4 | 4 | 8 |
| TOTAL | 185 | 69 | 254 |

For clarity, years since fire have been tabulated at intervals of 5–15 years. NB: six sites were excluded as outliers (see text).

(Table 1). This study is one component of a broad investigation examining the responses of multiple taxa to the properties of fire mosaics. As a result, the sites included in the current investigation are grouped into clusters representing 26 study landscapes, each a circular area 4 km in diameter (12.56 km²; Fig. 1). (NB: sites in two additional landscapes were not included because these landscapes represented a different vegetation type.)

Study landscapes were selected to represent the range of post-fire histories in the region and to ensure maximum spatial coverage of the study area. Ten survey sites were established in each landscape. Site selection was stratified according to the proportional extent of post-fire ages of vegetation in the landscape. Within each age class, sites were located to represent the range of local vegetation types 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 spatial coverage) and were typically > 200 m apart (mean minimum distance between neighbouring sites = 245 m, range 175–685 m). Sites were treated as spatially independent: a pilot study undertaken in October–November 2006 recorded no movement of animals between neighbouring sites during a combined 9000 pitfall and Elliott trap-nights, at a total of 120 sites.

The fire age of study sites was determined using one of two methods. For sites burnt since 1972, Landsat satellite imagery from 15 individual years (1972–2007), combined with existing fire history maps, was used to identify the exact year of the most recent fire. For sites burnt prior to 1972, the lack of historical records and satellite imagery necessitated an alternative approach. We used regression models to quantify the relationship between stem diameter and tree age (indicated by

fire-year) for each eucalypt species at sites of known fire-year (Clarke *et al.*, 2010). These models were then used to estimate tree age, and thus infer fire-year, for sites for which fire-year was unknown (i.e. prior to 1972) but stem diameter data were available. Validation of these models with independent data revealed a strong correlation between actual and predicted tree ages (Clarke *et al.*, 2010), confirming the reliability of this approach.

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 260 sites four times: starting dates were October–November (spring) 2006, 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 × 10 × 10 cm) were used to complement pitfall trapping in spring surveys, 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. Reproductively active females were defined by the presence of pouch young or evidence of lactation (enlarged nipples). In total, we completed 56,000 pitfall trap-nights and 14,000 Elliott trap-nights.

A large wildfire modified three landscapes during the spring 2006 survey period. Because of changes to mosaic structure, the spring 2006 data from these three landscapes were excluded. These study landscapes were subsequently sampled twice in spring 2007. In addition, we excluded six sites from statistical analyses: three sites estimated to be over 105 years post-fire and three sites located in an uncommon vegetation type (considered outliers). Therefore, $n = 254$ for statistical analyses.

Data analysis

We used generalized additive mixed models (GAMMs; Wood, 2006) to investigate small mammal responses to time since fire and vegetation type. GAMMs provide a flexible framework with which to build species distribution models: first, predictors can be fitted as either nonlinear or linear terms and second, sources of correlation structure in the data can be included in models as random effects (Wood, 2006; Zuur *et al.*, 2009). We modelled the response variable as the detected presence or absence of a species at a site, for data pooled over the entire survey period. In addition, we modelled the presence or absence of males, females and breeding females separately, for a given species. GAMMs were implemented with a logit link function and binomial errors (Wood, 2006). We employed

GAMMs that produce different smoothed terms for each level of a categorical variable (Wood, 2006). This enabled the investigation of the influence of time since fire separately in each of the two vegetation types, Triodia Mallee and Chenopod Mallee. Time since fire was entered as a nonlinear smoothed term. The degree of smoothing of the nonlinear term was calculated as part of the model-fitting procedure using default methods (Wood, 2006). Vegetation type was entered as a dichotomous linear term: a categorical variable that contrasts Triodia Mallee with Chenopod Mallee (i.e. the reference level). Landscape was entered as a random effect to account for expected spatial correlation structure in the data between clusters of sites.

We considered smoothed terms to be statistically significant when *P*-values were < 0.05. However, we treat *P*-values associated with smoothing parameters that are close to a threshold for accepting or rejecting a hypothesis with caution (see Wood, 2006; Zuur *et al.*, 2009) and place greater emphasis on model fit and discrimination ability. Model fit was evaluated using the percentage of null deviance explained (% Dev).

We assessed the predictive ability of each model of species occurrence in two ways: by cross-validation of data from this study and by testing with independent data collected from different sites at different times. For cross-validation, the landscape clusters were randomly divided into seven-folds (groups). A GAMM was built using data from six-folds and then used to predict sites from the seventh-fold. This process was repeated until predictions had been obtained for each of the seven data folds using data separate from the model-building process. The ability of models to accurately discriminate between a species' presence and absence was assessed using the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Pearce & Ferrier, 2000). Models with AUC values of < 0.7, 0.7–0.9 and > 0.9 were interpreted as offering poor, useful and very good discrimination, respectively (Pearce & Ferrier, 2000). The AUC was calculated for predictions for each fold, and we recorded the mean of this value. This procedure was repeated three times for each model, and we report the median AUC value.

Independent test data were obtained from two sources: (1) faunal surveys undertaken in northwestern Victoria in 1985–87 in Murray Sunset National Park, Hattah-Kulkyne National Park and Annuello Reserve (25 sites) (A.F. Bennett, unpublished data) and (2) faunal surveys undertaken in southwestern New South Wales in 2005 (four sites) and 2008 (five sites) in Tarawi Nature Reserve and Mallee Cliffs National Park, respectively [R. Dayman (NPWS), unpublished data]. The faunal survey protocol at independent survey sites was similar to that used in the present study (i.e. pitfall trapping over consecutive days). However, life history data were not always recorded, and we restrict model testing on this data set to species presence or absence. We determined the post-fire age and vegetation type of independent sites using Landsat imagery, vegetation maps (Haslem *et al.*, 2010) and expert local knowledge. All sites were located in Triodia

Mallee or Chenopod Mallee vegetation. Fire age was taken from the mid-point of the data collection period. The post-fire age of the pooled independent sites ranged from 3 to 55 years since fire including: six sites (1–5 years post-fire), 12 sites (10–20 years post-fire), six sites (20–30 years post-fire), three sites (30–40 years post-fire) and seven sites (40–60 years post-fire).

Statistical analyses were undertaken in the R statistical package version 2.9.0 (R Development Core Team, 2010). GAMMs were run in the extension package mgcv version 1.5–5 (Wood, 2006). The percentage of deviance explained and cross-validation were calculated using a modified version of script presented in Elith *et al.* (2008). ROC analysis for the independent data set was undertaken using the package PresenceAbsence version 1.1.3 (Freeman, 2007).

RESULTS

Small mammal occurrence

Faunal surveys resulted in 1213 captures of seven mammal species. The small mammal assemblage was composed of two species of insectivorous/carnivorous marsupials, the Mallee Ningau *Ningau yvonneae* (530 captures at 136 sites) and Common Dunnart *Sminthopsis murina* (280 captures at 147 sites); two insectivore/nectarivores, the Western Pygmy Possum *Cercartetus concinnus* (181 captures at 83 sites) and the Little Pygmy Possum *Cercartetus lepidus* (18 captures at 15 sites); and three omnivorous rodents, the introduced House Mouse *Mus domesticus* (172 captures at 88 sites), Bolam's Mouse *Pseudomys bolami* (30 captures at 18 sites) and Mitchell's Hopping Mouse *Notomys mitchellii* (two captures at two sites). Statistical analyses were undertaken for the four species captured at > 20 sites (those most suitable for regression modelling). Additional summary data for each species, males, females and breeding females are provided in supplementary material (Tables S1 and S2).

Fire history and vegetation type

Regression modelling indicated that *N. yvonneae* was positively associated with Triodia Mallee and showed a strong response to time since fire within this vegetation type (Table 2; Table S3). In Triodia Mallee, the model predicts that the probability of occurrence of *N. yvonneae* is low in early post-fire ages (1–5 years), increases rapidly between 5 and 15 years and is high at sites aged between 20 and 105 years post-fire (Fig. 3a). When considered separately, the occurrence of males, females and breeding females was also positively correlated with Triodia Mallee and showed a negative association with recently burnt vegetation (Table 2; Fig. 3b–d). These associations were evident over long time periods. For example, the probability of occurrence of breeding females was predicted to maintain or increase in Triodia Mallee up to 105 years post-fire (Fig. 3d). The model fit for these models was moderate (% Deviance ranged from 19 to 27; Table 2). *Ningau yvonneae*

Table 2 Results of generalized additive mixed models describing the relationship between small mammals and time since fire in mallee vegetation

| Scientific name | Model | Vegetation type (linear term) | Time since fire (smoothed term) | | | % Dev | AUC (cross val) |
|------------------------------|---------|----------------------------------|---------------------------------|----------|----------|-------|--------------------|
| | | | edf | <i>F</i> | <i>P</i> | | |
| <i>Ningauai yvonneae</i> | All | TM*** | 4.49 | 11.31 | < 0.0001 | 27 | 0.79 |
| | | CM | 1.76 | 1.30 | 0.27 | | |
| | Males | TM** | 4.30 | 7.69 | < 0.0001 | 19 | 0.73 |
| | | CM | 1.00 | 2.15 | 0.14 | | |
| | Females | TM*** | 3.46 | 9.53 | < 0.0001 | 22 | 0.73 |
| | | CM | 1.00 | 2.03 | 0.16 | | |
| Breeding females | TM*** | 2.74 | 8.31 | < 0.0001 | 23 | 0.78 | |
| | | CM | 1.00 | 0.61 | 0.44 | | |
| <i>Sminthopsis murina</i> | All | TM | 1.00 | 2.46 | 0.12 | 4 | 0.60 |
| | | CM* | 1.00 | 1.89 | 0.17 | | |
| | Males | TM | 1.00 | 1.74 | 0.19 | 4 | 0.62 |
| | | CM* | 1.00 | 3.47 | 0.06 | | |
| | Females | TM | 1.00 | 0.01 | 0.91 | 1 | 0.50 |
| | | CM | 1.00 | 1.90 | 0.17 | | |
| Breeding females | TM | 1.00 | 3.74 | 0.05 | 4 | 0.62 | |
| | | CM | 1.00 | 1.75 | 0.19 | | |
| <i>Cercartetus concinnus</i> | All | TM | 1.00 | 0.02 | 0.89 | 2 | 0.56 |
| | | CM* | 1.00 | 1.09 | 0.30 | | |
| | Males | TM | 2.09 | 2.02 | 0.13 | 5 | 0.62 |
| | | CM* | 1.54 | 1.36 | 0.26 | | |
| | Females | TM | 1.00 | 2.55 | 0.11 | < 1 | 0.52 |
| | | CM | 1.00 | 0.25 | 0.62 | | |
| Breeding females | TM* | 1.00 | 1.39 | 0.24 | < 1 | 0.54 | |
| | | CM | 1.00 | 7.76 | < 0.01 | | |
| <i>Mus domesticus</i> | All | TM* | 4.28 | 7.78 | < 0.0001 | 16 | 0.67 |
| | | CM | 1.00 | 1.44 | 0.23 | | |
| | Males | TM | 3.57 | 9.93 | < 0.0001 | 6 | 0.55 |
| | | CM | 1.00 | 0.29 | 0.59 | | |
| | Females | TM | 2.96 | 3.32 | 0.02 | 6 | 0.59 |
| | | CM | 1.00 | 2.17 | 0.14 | | |
| Adult females | TM | 3.70 | 6.57 | < 0.0001 | 7 | 0.62 | |
| | | CM | 1.00 | 0.15 | 0.70 | | |

edf, estimated degrees of freedom; % Dev, percentage deviance explained.

Details of the smoothed terms for time since fire in Triodia Mallee (TM) and Chenopod Mallee (CM) are shown for each species. AUC = area under the curve of a receiver operating characteristic analysis, calculated using cross-validation.

Significance of the linear model term (vegetation type).

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

showed no response to time since fire in Chenopod Mallee, where it was generally uncommon.

We identified no clear relationship between time since fire and the distribution of either *S. murina* or *C. concinnus* (Table 2). *Sminthopsis murina* was common in a range of post-fire ages. In both Triodia Mallee and Chenopod Mallee, for example, *S. murina* were captured at > 50% of sites aged 1–5, 31–40 and 61–70 years since fire. *Cercartetus concinnus* was also present in both early and older post-fire ages (Tables S1 and S2). Regression models of *S. murina* and *C. concinnus* males, females and breeding females demonstrated no strong responses to fire history. Although there was a statistically significant relationship between *C. concinnus* breeding females and time

since fire in Chenopod Mallee, the overall fit of the model was poor (Table 2). Similarly, there was some evidence of a negative relationship between *S. murina* and Triodia Mallee (Table 2; Table S3); and *C. concinnus* and Triodia Mallee (Table 2; Table S3); however, the variation in species occurrence explained by these models was low (Table 2).

The introduced *M. domesticus* showed a positive association with Triodia Mallee and, within this vegetation type, time since fire was a significant influence (Table 2). *Mus domesticus* was most common in early post-fire ages: predicted probability of occurrence peaked between 1 and 5 years post-fire, and the species was rare at sites > 20 years post-fire (Fig. 4a). We did not perform regression analyses on the occurrence of breeding

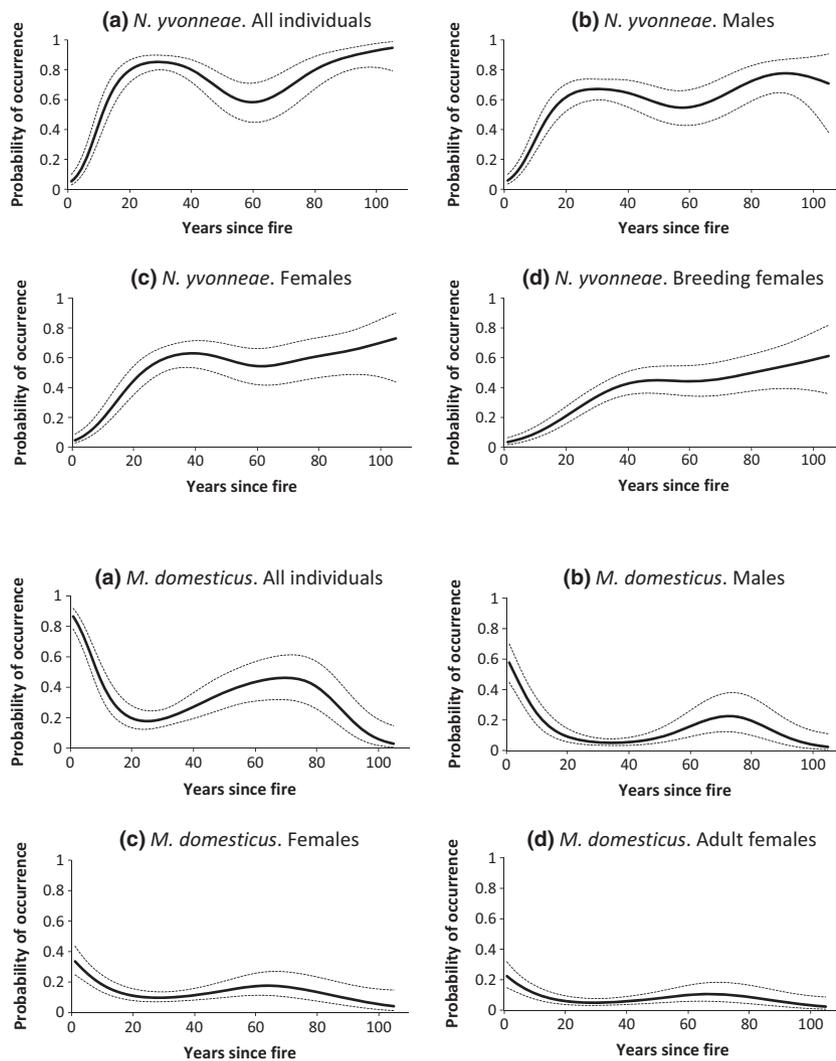


Figure 3 Response of *Ningauai yvonneae* to time since fire across a 105-year period. Solid lines represent predictions of the probability of occurrence from generalized additive mixed models, and dashed lines represent ± 1 SE. Results are shown only for Triodia Mallee vegetation type.

Figure 4 Response of *Mus domesticus* to time since fire across a 105-year period. Solid lines represent predictions from generalized additive mixed models, and dashed lines represent ± 1 SE. Results are shown only for Triodia Mallee vegetation type.

females, recorded at only four sites. Instead, we focused on the distribution of adult females. Models of male, female and adult female *M. domesticus* showed a similar association with recently burnt Triodia Mallee (Table 2; Fig. 4b–d). The fit of each category of *M. domesticus* models was low to moderate (% Dev ranged from 6 to 16; Table 2).

Model discrimination

Internal cross-validation indicated that the model for *N. yvonneae* (all) could accurately discriminate between the presence and absence of the species (median AUC = 0.79). Models of *N. yvonneae* males, females and breeding females produced median AUC values of 0.73, 0.73 and 0.78, respectively. The model for *M. domesticus* (all) showed some evidence of being able to discriminate between the species' presence and absence (one of three cross-validation AUC values was > 0.70); however, the median AUC of 0.67 indicates some uncertainty in model predictions. In addition, AUC values of *M. domesticus* males, females and adult females were low (< 0.70). Cross-validation indicated that models of *S. murina* and

C. concinnus were unable to accurately discriminate between species presence and absence (AUC < 0.70 ; Table 2).

We tested by independent validation only those species models supported by the model-building data set: *N. yvonneae* and *M. domesticus*. The independent data set comprised captures of *N. yvonneae* at 15 of 34 sites. The model for *N. yvonneae* (all) showed excellent predictive ability (AUC = 0.92), indicating a robust model that can accurately discriminate between the presence and absence of the species across a broad geographical area. The independent data set comprised captures of *M. domesticus* at 22 of 34 sites. The model for *M. domesticus* (all) showed a poor level of discrimination (AUC = 0.63).

DISCUSSION

We conducted a broad-scale natural experiment to investigate the fire ecology of small mammals in mallee vegetation of semi-arid Australia. We surveyed small mammals at 260 sites, along a 1–105-year post-fire chronosequence, and examined the responses of four species to fire history. An important

aspect of this study was its focus on long-term and broad-scale processes. The occurrence of two species, the native *N. yvonneae* and the introduced *M. domesticus*, was strongly associated with time since fire. Two native mammals, *S. murina* and *C. concinnus*, showed no strong association with fire history.

Effects of fire and vegetation type

Ningauai yvonneae was positively associated with Triodia Mallee. Within this vegetation type, it was largely absent from recently burnt vegetation (< 5 years) and showed a positive association with older vegetation. This relationship was also demonstrated for separate models of *N. yvonneae* males, females and breeding females. *Ningauai yvonneae* shelters in the cover of hummock grass, and individuals regularly forage in the litter layer (Bos *et al.*, 2002; Bos & Carthew, 2003). In Triodia Mallee, a high cover of hummock grass and a deep litter layer are both associated with long-unburnt vegetation (Fig. 2). Thus, the response of *N. yvonneae* to time since fire is likely to be driven by post-fire changes in several attributes of vegetation structure.

Previously, we documented the response of *N. yvonneae* to a wildfire in this region (Kelly *et al.*, 2010). While *N. yvonneae* was common before the wildfire, it was not recorded at burnt sites during surveys undertaken at three, 11, 12 and 14 months post-fire. Here, we greatly extend understanding of the timing of post-fire recovery of *N. yvonneae* by examining longer-term temporal changes. Such changes were particularly apparent for the occurrence of breeding females: the likelihood of encountering individuals carrying pouch young (or lactating) was predicted to increase up to 105 years post-fire. This highlights two important points: first, the extensive time-scale over which fire can affect faunal distribution and second, the value in going beyond measuring the presence or absence of a species, to focus on ecological processes such as reproduction. In this case, the recovery of suitable habitat in the post-fire environment occurred much more rapidly for males than for reproductive females (Fig. 3b vs. d).

Mus domesticus was positively associated with recently burnt Triodia Mallee vegetation, and a high probability of occurrence was apparent at sites aged 1–5 years post-fire. In older vegetation, it typically was rare. This relationship was consistent for males, females and adult females. Recently burnt sites are characterized by large areas of bare ground, reduced canopy cover and the presence of ephemeral herbs and grasses (Bradstock & Cohn, 2002; Haslem *et al.*, 2011). Recently burnt vegetation may provide *M. domesticus* with enhanced foraging opportunities; it has an omnivorous diet and is likely to feed on the green shoots and seeds, which become available following fire (Cohn *et al.*, 2002).

Mus domesticus is well documented as a colonizer of early post-fire environments (Briani *et al.*, 2004; Recher *et al.*, 2009). It can excavate and live in burrows in areas of limited vegetation cover (Menkhorst, 1996), such that sparse vegetation may not impede its persistence at burnt sites. However,

the moderate amount of variation explained by regression models for *M. domesticus* suggests that factors other than time since fire and vegetation type strongly influence its distribution.

We identified no strong relationship between time since fire and the distribution of *S. murina*. This species was common in a wide range of post-fire ages and recorded at more sites than any other mammal species (147 of 254 sites). It also was common in both Triodia Mallee and Chenopod Mallee. Similarly, *C. concinnus* was present across the range of post-fire ages and occurred commonly in both vegetation types. Our results suggest that each of these species is capable of persisting in a range of structural formations within mallee vegetation. Nevertheless, we expect that large areas of recently burnt vegetation with little to no vegetation cover will provide low-quality habitat for *S. murina* and *C. concinnus*. It is likely that the presence of longer unburnt vegetation adjacent to recently burnt vegetation facilitated the use of more open sites and reduced the tendency of animals to be captured exclusively in later post-fire ages. We are currently investigating the landscape-scale influence of fire regimes on each of these species to further explore this issue. We were not able to examine in detail the fire responses of three species captured at few sites: *P. bolami*, *C. lepidus* or *N. mitchellii*.

Predicting species occurrence

Understanding the accuracy of species distribution models aids conservation management over large geographical areas (Guisan & Thuiller, 2005). We assessed the ability of fire history models to discriminate between species' presence and absence using two methods: cross-validation (for all models) and by testing with independent data. For *N. yvonneae*, cross-validation indicated that time-since-fire relationships were consistent across a broad geographical area (i.e. models showed high discrimination ability, AUC \geq 0.70). That is, region-wide, the species was negatively associated with recently burnt vegetation and favoured more mature sites. Testing with independent data further demonstrated that the occurrence of *N. yvonneae* could be predicted accurately at a regional scale based on fire history and vegetation data.

For *M. domesticus*, model evaluation indicated variability in the time-since-fire relationship. While *M. domesticus* was more common in recently burnt Triodia Mallee, cross-validation showed that this preference was not consistent across the region. A similar result was found when *M. domesticus* models were tested on independent data. *Mus domesticus* populations are dynamic, and the abundance of this species changes dramatically in semi-arid Australia owing to rainfall patterns (Singleton *et al.*, 2007). This is particularly evident in agricultural land, which can then influence the status of *M. domesticus* in nearby remnant vegetation (Singleton *et al.*, 2007). It is likely that *M. domesticus* populations in mallee vegetation respond to site rainfall history, as well as time since fire. The discrimination ability of models for *S. murina* and *C. concinnus* was poor, as was expected from low levels of model fit.

These results demonstrate that while accurate predictions can be made at broad scales for individual species, this may be the exception rather than the rule. We were able to make accurate predictions for *N. yvonneae*, but not for three other species. *Ningauï yvonneae* has the most specific habitat requirements (dependent on *Triodia* hummocks), restricted life history (annual breeding, small litters) and probably makes the smallest movements of small mammals in the study region (Bennett *et al.*, 1989). We hypothesize that species that rely on fire-associated vegetation structure will display the most predictable fire responses. The distribution of species with a dynamic and flexible life history will be more difficult to predict based on fire history alone.

Implications for conceptual models

Fox (1982) developed a habitat accommodation model of animal succession to describe post-fire changes in a small mammal community of temperate Australia. Based on this conceptual model, we expected to find a predictable sequence of mammalian succession in semi-arid mallee vegetation, closely linked to vegetation regeneration following fire. Two of four species were associated with post-fire age of vegetation and therefore consistent with a key aspect of this model – that there is a strong link between post-fire vegetation recovery and small mammal distribution. However, two other species showed no relationship with post-fire age of vegetation. Overall, the data do not support the prediction that mammalian communities in mallee vegetation show a consistent sequence of species replacement following fire.

It is unlikely that the absence of a clear mammalian succession is attributable to unpredictable changes in vegetation structure. Although we expect some local variation in vegetation regeneration following fire, key attributes of vegetation structure such as hummock grass cover, leaf litter and hollow tree stems are associated with time since fire across the Murray Mallee region (Fig. 2). Moreover, further analysis of this data set supports the conclusions presented here. While species distribution models based directly on habitat variables perform better, it is likely that the distribution of several species is also influenced by processes other than vegetation succession (L.T. Kelly, unpublished data). For example, there were marked changes in the capture rates of *C. concinnus* between study landscapes and survey periods. In the first year, we captured *C. concinnus* at 78 of 254 sites, while in the second year, it was captured at 12 of 254 sites. First-year surveys were preceded by higher rainfall, while second-year surveys were preceded by lower rainfall.

In arid Australia, small mammal communities display highly variable population dynamics and correlate poorly with structural variables indicative of vegetation succession (Southgate & Masters, 1996; Letnic & Dickman, 2005). Rather, rainfall history and predation pressure appear to be important influences in the arid zone (Dickman *et al.*, 1999; Letnic *et al.*, 2004). Letnic *et al.* (2004) developed a state-and-transition model that highlights multiple states in the composition of

assemblages of arid-zone small mammals, which develop in response to specific environmental conditions. A key element of this model is the strong influence of rainfall-driven changes in food resources on small mammal assemblages (Letnic & Dickman, 2010).

Small mammal communities in semi-arid vegetation appear to be influenced both by predictable factors, such as the trajectory of change in vegetation structure following fire, and by less predictable factors such as rainfall and its effects on food resources. Thus, neither the habitat accommodation model (Fox, 1982), appropriate for more predictable temperate environments, nor a state-and-transition model, developed for the arid zone (Letnic *et al.*, 2004), are adequate on their own for describing changes in small mammal communities following fire in the semi-arid mallee environment.

Conservation management

Mallee ecosystems encompass 250,000 km² of semi-arid southern Australia (Australian Native Vegetation Assessment, 2001). Fire is widely used as a management tool to protect natural and built assets and to maintain and create faunal habitats (Bradstock & Cohn, 2002). *Ningauï yvonneae* is a species of conservation concern in the Murray Mallee region; indeed, it is one of only six vertebrates that has a distribution restricted to mallee vegetation (Menkhorst & Bennett, 1990). Recently burnt vegetation clearly is unsuitable as habitat for *N. yvonneae*. Moreover, the recovery of *N. yvonneae* populations following fire takes place over decades, with changes in the status of reproductive females extending even longer. These relationships are consistent across large geographical areas. Strategic fire management needs to reflect the long-term impact of fire on fauna at extended time-scales. Maintaining long-unburnt areas of mallee vegetation (i.e. 40–100 years post-fire) will be vital to the conservation of *N. yvonneae*.

This study may provide insights for investigations into species' distributions and their conservation in other fire-prone ecosystems. First, by developing statistical models of species' occurrence over a century-long post-fire chronosequence, we were able to understand trajectories of change at a time-scale relevant to successional processes in the ecosystem of study. Second, by surveying small mammals across a broad geographical area, we were able to assess the consistency of post-fire relationships. Collating historical surveys and using them as independent data to test species' distribution models was also advantageous. Finally, interpreting our results in relation to conceptual models has facilitated a comparison with studies from other ecosystems and suggests that small mammal assemblages in semi-arid ecosystems are structured in different ways from those in temperate and arid environments.

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SUPPORTING INFORMATION

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

Table S1 Summary data of small mammal captures in Triodia Mallee in the Murray Mallee region of southern Australia.

Table S2 Summary data of small mammal captures in Chenopod Mallee in the Murray Mallee region of southern Australia.

Table S3 Results of GAMMs describing the relationship between small mammals and time since fire in mallee vegetation. Details of the linear term (vegetation type) are shown for each species.

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BIOSKETCH

Luke Kelly is a post-graduate student at Deakin University, Australia. His interests include fire ecology, landscape ecology, macroecology and vertebrate conservation. This work was undertaken while he was a member of the Mallee Fire and Biodiversity Project.

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