other species are more abundant in later successional stages (Keith 1996; Keeley et al. 2005). Similar patterns have been observed in faunal communities (Fox 1982; Smucker et al. 2005). Understanding the temporal effects of fire on biota can be used in fire management by identifying important seral stages for species.

The spatial properties of fires are also important in management of fire for biodiversity (Bradstock et al. 2005; Parr & Andersen 2006). Fires generate heterogeneous landscapes consisting of patches with different fire histories (Turner et al. 1994; Bradstock et al. 2005). Such landscapes are often referred to as ‘fire mosaics’ (Bradstock et al. 2005). Landscape heterogeneity is generated by fire in two ways. First, individual fires generate heterogeneity through variation in the rate of fire spread and fuel consumption, creating patches of burnt and unburnt
vegetation and patches of differing fire severity within the fire boundary (Turner et al. 1994). Second, multiple fires through time generate heterogeneity of vegetation age-classes. Both processes contribute to a ‘visible mosaic’ and, where fires overlay each other, an ‘invisible’ mosaic of different fire histories is created (Bradstock et al. 2005).

A common assumption in fire management is that fire mosaics that contain a greater diversity of post-fire successional stages will support a higher diversity of biota; that is, “pyrodiversity begets biodiversity” (reviewed by Parr and Andersen 2006). However, this hypothesis has rarely been tested at the landscape scale. Further, almost any fire or sequence of fires will generate a mosaic of fire ages. What is needed is knowledge of the spatial and temporal properties of mosaics that best provide for the habitat requirements of indigenous species that occur within the ecosystem.

THE MALLEE FIRE AND BIODIVERSITY PROJECT

The Mallee Fire and Biodiversity Project is a collaborative project led by La Trobe and Deakin Universities, working with 12 government and non-government agencies. Its aim is to investigate the effects of fire on selected plants (vascular plants) and animals (birds, mammals, reptiles and some invertebrates – termites, scorpions, centipedes and psyllids) in tree mallee ecosystems of the Murray Mallee region of south-eastern Australia (N.S.W., Victoria and S.A.). The term ‘tree mallee’ is used to define those mallee ecosystems with a dominant Eucalyptus spp overstorey, as distinct from the ‘mallee heathlands’ encountered farther south in the Mallee region. Here, we present an overview of the project, along with some key results.

The project employed a whole-of-landscape
SPATIALLY AND TEMPORALLY CONSISTENT MAPPING OF FIRE HISTORY

We used satellite imagery to develop maps of fire history in the Murray Mallee region from 1972 – 2007 (Fig. 1) (Avitabile et al. in review). These fire history maps are the most consistent and comprehensive available for the region and provide insights into fire regimes and the distribution of vegetation of different post-fire ages. Between 1972 and 2007, more than 1000 fires burnt ~ 40% of tree mallee vegetation within the region. However, 89% of the burnt area can be attributed to 6 large fires (>0.000 ha). Despite this extensive fire activity, recurrent fire at a particular location was rare, with <3% of the area being burnt more than once during this 35-year period (Avitabile et al. in review). The region-wide map (Fig. 1) highlights the importance of data sets that cross jurisdictional boundaries for conservation decision making. Because no individual state’s fire history is representative of that of the entire region, decisions based on state-wide data may be detrimental to biodiversity conservation at regional levels.

TEMPORAL CHANGES IN MALLEE COMMUNITIES AFTER FIRE: EXTENDING THE CHRONOSEQUENCE

Satellite-derived fire maps only provide the age of vegetation burnt since 1972, yet approximately 60% of mallee vegetation is older than this (Avitabile et al. in review). The lack of a known post-fire age of a site presents a challenge because fire management for biodiversity conservation requires knowledge of successional patterns over time-frames commensurate with those at which ecosystems can function. We developed models to predict the post-fire age of sites based on the diameter of mallee eucalypt stems (Clarke et al. 2010). Using satellite imagery and environmental data, maps of the distribution of these vegetation associations were developed at 25 x 25 m resolution (Haslem et al. 2010). Although vegetation maps for mallee vegetation exist for individual states and reserves (White 2006), this map advances region-wide conservation planning, because for the first time a consistent method was applied across the entire region. For example, this map can be used to identify areas of potential habitat for species that rely on particular vegetation associations, such as Mallee Ningaui Ningaui yvonneae Kitchener, Stoddart and Henry, Striated Grasswren Amytornis striatus Gould, and the Mallee Dragon Ctenophorus fordi Storr which are more common in Triodia Mallee (Kelly et al. 2011; Nimmo et al. 2012; Watson et al. 2012a).
classes of vegetation allows managers to determine whether particular age classes are over-represented or under-represented in the landscape, and therefore the likely suitability of the landscape for biota. Using the predictive models described above, the post-fire age of 346 sites burnt prior to 1972 was estimated. If we assume that these sites are a representative sample of the pre-1972 post-fire age-class distribution, then we can gain an understanding of the likely age-class distribution of vegetation in the region.

Comparison of the age-class distribution generated by the predictive models with that generated from satellite imagery (1972–2007) (Fig. 2) demonstrates significant truncation in the distribution derived from satellite imagery. The latter indicates an overabundance of vegetation >35 years since fire. However, from the modelled data, this 35+ age class actually represents a range of different post-fire ages extending up to 160 years-since-fire, some of which are at very low frequencies. These rare, older age classes may provide important resources for fauna (e.g. large hollows) (Haslem et al. in press).

**STRUCTURAL CHANGES IN MALLEE VEGETATION AFTER FIRE**

Vegetation structure influences the suitability of a site as habitat for faunal species, but also affects fuel loads; both of which are important considerations for fire managers (Haslem et al. 2011). We used the extended chronosequence (from ageing sites by stem diameters) to model changes in vegetation structure up to 100 years post-fire (Haslem et al. 2011). These models provided important insights into vegetation change. For example, the cover of Triodia increased to reach a peak at 35 years since fire, after which it began to decline. The proportion of eucalypt stems bearing hollows was negligible in the first 40 years post-fire, but continued to increase up to 100 years since fire. The data used to generate these models were collected during a decade long period of below average rainfall. How well they predict the development of habitat and fuel characteristics under different climatic conditions is currently under examination.

The extended chronosequence provides different perceptions of how vegetation attributes change, compared with those gained from a time sequence of only 35 years since fire (i.e. from satellite imagery). For instance, litter depth in Chenopod Mallee vegetation increases approximately linearly up to 35 years since fire. If a longer time-series was not available, it might be perceived that litter depth would continue to increase linearly and accumulate large fuel loads. However, mean litter depth reaches a plateau, such that sites 35 to 100 years since fire do not vary greatly in this attribute (Haslem et al. 2011).
ornatus Gould, Fig 3, Watson et al. 2012a). The Mallee Ningaui (Fig 3), a small dasyurid marsupial, was strongly associated with the cover of *Triodia scariosa*, and consequently it was largely absent in recently burnt vegetation until the age where *Triodia* regenerates to sufficient densities to support the species (Kelly et al. 2010, 2011). Some reptiles that showed a significant response to time since fire, including the Painted Dragon *Ctenophorus pictus* Peters (Fig 3), Coral Snake *Brachyurophis australis* Kreft, and Desert Skink *Egernia inornata* Rosen, had their highest probability of occurrence in early post-fire stages of *Triodia* Mallee (0–5 years), whereas Boulenger’s Skink *Morethia boulengeri* Ogilby was most likely to be occur in very old *Triodia* Mallee (>90 years). Interestingly, many species did not exhibit responses to time since fire, including key invertebrates (Table 1), which indicates that a range of factors other than fire are important for determining their distribution in mallee environments. Through

**POST-FIRE CHANGES IN THE OCCURRENCE OF FAUNAL SPECIES**

Post-fire patterns of faunal succession, whereby species are more or less common in different fire-ages, are documented in many fire-prone ecosystems (Fox 1982). Changes in species’ occurrences were investigated over a century-long time-span by comparing fauna at sites of different post-fire age and thus inferring changes in communities through time (i.e. space-for-time substitution, or chronosequence approach) (Table 1). Some species were more likely to occur in particular post-fire seral stages (see Fig 3 for examples). Sixteen species of birds (out of 30 species investigated) displayed a significant response to time since fire (Watson et al. 2012a). One species was most common in vegetation <5 years since fire, five species in vegetation 20–50 years since fire and 0 species in vegetation >50 years since fire (e.g. Yellow-plumed Honeyeater *Lichenostomus ornatus* Gould, Fig 3, Watson et al. 2012a). The Mallee Ningaui (Fig 3), a small dasyurid marsupial, was strongly associated with the cover of *Triodia scariosa*, and consequently it was largely absent in recently burnt vegetation until the age where *Triodia* regenerates to sufficient densities to support the species (Kelly et al. 2010, 2011). Some reptiles that showed a significant response to time since fire, including the Painted Dragon *Ctenophorus pictus* Peters (Fig 3), Coral Snake *Brachyurophis australis* Kreft, and Desert Skink *Egernia inornata* Rosen, had their highest probability of occurrence in early post-fire stages of *Triodia* Mallee (0–10 years), whereas Boulenger’s Skink *Morethia boulengeri* Ogilby was most likely to be occur in very old *Triodia* Mallee (>90 years). Interestingly, many species did not exhibit responses to time since fire, including key invertebrates (Table 1), which indicates that a range of factors other than fire are important for determining their distribution in mallee environments. Through

**Table 1.** Summary of analyses of responses to time since fire at the site scale for fauna in all taxonomic groups surveyed in the Mallee Fire and Biodiversity Project. Y = significant influence of time since fire upon the probability of occurrence of the species (P<0.05) and the relationship explained > 5% of the variation in the occurrence of the species, N = no significant influence of time since fire on the probability of occurrence of the species, ID = insufficient data for analysis.

<table>
<thead>
<tr>
<th>Taxonomic group</th>
<th>Number of species recorded</th>
<th>Fire response</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Y</td>
</tr>
<tr>
<td>Birds</td>
<td>89</td>
<td>16</td>
</tr>
<tr>
<td>Small mammals</td>
<td>7</td>
<td>2</td>
</tr>
<tr>
<td>Reptiles</td>
<td>56</td>
<td>11</td>
</tr>
<tr>
<td>Termites</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>Scorpions</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Centipedes</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Psyllids (genera)</td>
<td>4</td>
<td>0</td>
</tr>
</tbody>
</table>
this project, the post-fire-age preferences of species of birds, reptiles, mammals and key invertebrates have been investigated, providing important information for conservation management.

INFLUENCE OF POST-FIRE SPATIAL PATTERNS ON FAUNA AT THE SITE SCALE

In comparison with studies of the temporal responses of biota to fire, there have been relatively few studies of the effect of the spatial properties of fire on organisms. The size, shape and patchiness of a fire affect the context of a burned site, and influence the distance that animals must travel to escape fire, or to recolonise sites from external source populations after fire (Brotons et al. 2005; Knight & Holt 2005; Banks et al. 2011). For example, unburnt patches of vegetation within the fire boundary (biological legacies) may act as refuges where organisms can escape the fire, or they may assist animals to recolonise post-fire.

To investigate the spatial properties of fire, we examined the influence of the proximity to unburnt vegetation (i.e. >27 years since-fire) and the presence of small unburnt patches (25–625 m$^2$) on bird communities at 72 sites that were <5 years since fire. Sites distant from unburnt vegetation supported fewer species, whereas sites that contained small unburnt patches supported more species (Watson et al. 2012b). These results suggest that fires of different size and configuration are likely to have different effects on the avifaunal community.

INFLUENCE OF LANDSCAPE PROPERTIES OF FIRE MOSAICS ON FAUNA

Despite a widespread perception that fire mosaics are important, there has been little empirical investigation of the influence of the landscape properties of fire mosaics (e.g. the extent and diversity of post-fire age-classes) on biotic communities (Gill 2008). We compared the faunal communities of landscapes that differed in the diversity of post-fire age-classes and in the extent of long-unburnt vegetation. Contrary to expectations of the ‘pyrodiversity begets biodiversity’ hypothesis, the number of bird species in landscapes was not influenced by the diversity of different seral stages but was positively related to the proportion of older vegetation (>35 years-since-fire) in the landscape (Taylor et al. 2012). Older vegetation was also found to provide important habitat for native small mammals (Kelly et al. 2012).

These findings highlight the complexity of fire management. At the site scale, different species of birds showed different responses to time since fire, suggesting that fire is required to provide habitats representing a range of suitable post-fire age-classes. However, at the landscape scale studied (12.5 km$^2$), the species richness of birds reptiles and small mammals was not related to the local diversity of age classes. Yet, at larger scales, such as the entire Murray-Sunset National Park, a diversity in post-fire age-classes is required to ensure that a progression of seral stages will occur to suit all species in the long term. The challenge is to gain a better understanding of the importance of the diversity of fire age-classes at different spatial scales.

CONCLUSIONS AND IMPLICATIONS

Knowledge of temporal changes in the occurrence and abundance of species after fire is critical to the management of fire to benefit biodiversity (Driscoll et al. 2010). The development of a method to age mallee vegetation (Clarke et al. 2010) beyond that which can be achieved through satellite imagery, or from historical documents, was a key step which has greatly enhanced understanding of species’ long-term responses to fire (Kelly et al. 2011; Watson et al. 2012a; Nimmo et al. 2012).

In terms of the spatial properties of fire mosaics, our study did not find evidence of a significant positive relationship between diversity of fire age-classes and species richness of any taxonomic group. Rather, species responded more clearly to the proportional extent of particular age classes in the landscape; for birds there was a positive relationship with the extent of older vegetation (Taylor et al. 2012).

Following catastrophic loss of life and property during the Black Saturday bushfires in Victoria in February 2009, there has been increasing public pressure to increase the level of prescribed burning to protect assets and human safety. The Victorian Bushfires Royal Commission (Teague et al. 2010) recommended that the state commit to ‘a long-term program of prescribed burning based on an annual rolling target of 5 percent minimum of public land’. If this target is applied to the tree mallee region of Victoria, it will almost treble the total area of tree mallee vegetation burnt per year, on average, by wildfire and prescribed planning combined (1.7% pa) over the last 35 years (Fig. 4). Our results show that key habitat elements develop slowly after fire (Haslem et al. 2011) and that the preference of many
bird species (including threatened species) is for long unburnt mallee (Taylor et al. 2012; Watson et al. 2012a). The application of a 5 percent target is likely to have serious and detrimental implications for conservation of the mallee fauna. In particular, species that are specialists in mid and late seral-stages would be greatly disadvantaged, as the age-class distribution of the region would become biased towards landscapes <20 years since fire.

Although there remains much to learn, the Mallee Fire and Biodiversity Project has made significant advances in understanding the dynamic relationship between biotic communities and fire in mallee ecosystems, and provides a foundation for future research and the management of fire in this region.

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