

# Optimal fire histories for biodiversity conservation

## Submitted version

**Authors:** Luke T. Kelly<sup>1,\*</sup>, Andrew F. Bennett<sup>2</sup>, Michael F. Clarke<sup>3</sup>, Michael A. McCarthy<sup>1</sup>

**Affiliations:**

<sup>1</sup>School of Botany, ARC Centre of Excellence for Environmental Decisions, University of Melbourne, Parkville, Victoria 3010, Australia.

<sup>2</sup>Landscape Ecology Research Group and Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Victoria 3125, Australia.

<sup>3</sup>Department of Zoology, La Trobe University, Bundoora, Victoria 3086, Australia.

\*email [ltkelly@unimelb.edu.au](mailto:ltkelly@unimelb.edu.au)

The final version is available from the corresponding author ([ltkelly@unimelb.edu.au](mailto:ltkelly@unimelb.edu.au)) or via <https://onlinelibrary.wiley.com/journal/15231739> and should be cited as:

Kelly, L.T., Bennett, A.F., Clarke, M.F. & McCarthy, M.A (2015) Optimal fire histories for biodiversity conservation. *Conservation Biology*, 29, 473-481.

**Title: Optimal fire histories for biodiversity conservation**

**Authors:** Luke T. Kelly<sup>1,\*</sup>, Andrew F. Bennett<sup>2</sup>, Michael F. Clarke<sup>3</sup>, Michael A. McCarthy<sup>1</sup>

<sup>1</sup>School of Botany, ARC Centre of Excellence for Environmental Decisions, University of Melbourne, Parkville, Victoria 3010, Australia.

<sup>2</sup>Landscape Ecology Research Group and Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Victoria 3125, Australia.

<sup>3</sup>Department of Zoology, La Trobe University, Bundoora, Victoria 3086, Australia.

\*email [ltkelly@unimelb.edu.au](mailto:ltkelly@unimelb.edu.au)

**Running head:** Fire and biodiversity conservation

**Key words:** birds, biodiversity index, fire mosaic, geometric mean, patch-mosaic burning, pyrodiversity, reptiles, small mammals

**Word count:** 5699

## **Abstract**

Fire is used as a management tool for biodiversity conservation worldwide. A common objective is to avoid population extinctions due to inappropriate fire regimes. However, in many ecosystems, it is unclear what mix of fire histories will achieve this goal. We determined the optimal fire history of a given area for biological conservation with a method that links tools from 3 fields of research: species distribution modeling, composite indices of biodiversity, and decision science. We based our case study on extensive field surveys of birds, reptiles, and mammals in fire-prone semi-arid Australia. First, we developed statistical models of species' responses to fire history. Second, we determined the optimal allocation of successional states in a given area, based on the geometric mean of species relative abundance. Finally, we showed how conservation targets based on this index can be incorporated into a decision-making framework for fire management. Pyrodiversity per se did not necessarily promote vertebrate biodiversity. Maximizing pyrodiversity by having an even allocation of successional states did not maximize the geometric mean abundance of bird species. Older vegetation was disproportionately important for the conservation of birds, reptiles, and small mammals. Because our method defines fire management objectives based on the habitat requirements of multiple species in the community, it could be used widely to maximize biodiversity in fire-prone ecosystems.

## **Introduction**

Fire is a global driver of ecosystem structure, function, and change (Bowman et al. 2009). It is also widely used as a management tool in Africa, Australia, the Mediterranean Basin, and North America (Keeley et al. 2011). A common management objective is to avoid population extinctions due to inappropriate fire regimes (Driscoll et al. 2010a). However, in many ecosystems, it is unclear what mix

of fire histories will achieve this goal (Parr & Andersen 2006). Major challenges for scientists are to better understand biodiversity responses to fire and to help managers define conservation targets that can be incorporated into a decision-making framework.

Fire management increasingly is focused on managing landscapes to maintain heterogeneous patches of differing fire history (Bradstock et al. 2005). Because animal species may depend on resources that vary temporally in response to fire history, it is argued that heterogeneous fire mosaics provide a range of resources that enable the persistence of a species-rich community (reviewed by Parr & Andersen 2006). This concept is encapsulated by the expression “pyrodiversity promotes biodiversity” (Martin & Sapsis 1992) and is implemented by patch mosaic burning (Brockett et al. 2001). Recent work has challenged the blanket application of this approach because some fire age classes provide disproportionately important habitat (Kelly et al. 2012; Taylor et al. 2012) and because not all fire patterns are ecologically meaningful (Parr & Andersen 2006; Davies et al. 2012). A new approach to fire management is required that clearly defines conservation objectives based on the habitat requirements of multiple species in the community.

There is growing interest in the use of biological indices to understand environmental change and to set conservation objectives (Butchart et al. 2010). Recent work demonstrates that the geometric mean of species’ relative abundance is a useful measure of biodiversity (Buckland et al. 2011; Di Stefano et al. 2013). This index has several advantageous properties: it is a measure of the relative abundance of multiple species; it is sensitive to changes in the relative abundance of rare species; it reflects community evenness; and it can be used to generate a composite index from surveys of multiple taxa (Buckland et al. 2011). The geometric mean abundance of species underpins indices currently used for monitoring biodiversity, including the Living Planet Index which is being used for reporting as part of the Convention for Biological Diversity (Butchart et al. 2010). The use of the geometric mean as a biodiversity index also has a theoretical grounding. McCarthy et al. (2014) developed an index based on

the geometric mean of species abundance that is related to the extinction risk of plant and animal populations. In the presence of deterministic declines, the mean time to extinction of species in the community is expected to be linearly related to the logarithm of the geometric mean abundance (McCarthy et al. 2014). In summary, the geometric mean is a useful measure of the responses of multiple species to environmental change, such as temporal changes following fire, because of its useful mathematical properties and strong theoretical grounding.

We devised a method for determining the optimal fire history of a given area for biodiversity conservation and used it in a case study. Our case study is based on extensive field surveys of birds, reptiles, and small mammals in semi-arid Australia (Kelly et al. 2011; Nimmo et al. 2012, Taylor et al. 2012, Watson et al. 2012). Our framework links tools from three fields of research: species distribution modeling, composite indices of biodiversity, and decision science (Fig. 1). First, we developed statistical models of species' responses to fire history. Second, we determined the optimal allocation of successional states in a given area based on the geometric mean of species relative abundance. Finally, we showed how conservation targets based on this index can be incorporated into a decision-making framework for fire management.

## **Methods**

### ***Case study data***

The Murray Mallee region of southeastern Australia (~104 000 km<sup>2</sup>) contains extensive tracts of fire-prone vegetation characterized by mallee eucalypts with a shrubby 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. Between 1972 and 2007, an area equivalent to 40% of the mallee vegetation in the region burned (Avitabile et al. 2013; Appendix S1). Eighty-nine percent of the burned area was due to 16 large (>10,000 ha) wildfires (Avitabile et al. 2013). Lightning is the major source of ignition. An important feature

of mallee vegetation is the ability of mallee eucalypts to regenerate from underground lignotubers following fire (Noble 2001). Fire in mallee vegetation typically is stand replacing; therefore, time since fire is a useful measure of structural and floristic differences in the vegetation (Haslem et al. 2011). Land managers in the region currently use the distribution of successional states to guide fire management operations (Sandell et al. 2006).

Our case study data were collected as part of a large-scale natural experiment. We employed a space-for-time approach to investigate the responses of three vertebrate groups (reptiles, small mammals, and birds) to time since fire. Animals were surveyed in 28 study landscapes (each 12.6 km<sup>2</sup>) at sites arrayed along a chronosequence of 1-110 years post-fire. Reptiles and small mammals were systematically surveyed with pitfall traps and aluminium box traps at each site over 2 years (see Kelly et al. [2011] and Nimmo et al. [2012] for details), and birds were surveyed with timed point counts over the same period (Watson et al. 2012, Taylor et al. 2012).

We used data from sites in Triodia Mallee vegetation typical of sandy flats and dunes and characterized by an understory of hummock grass *Triodia scariosa*. Triodia Mallee vegetation is the dominant and most fire prone of the two main vegetation types in the region. It comprises 58% of the native vegetation in the region, a total of 18,755 km<sup>2</sup>. The other major vegetation type, Chenopod Mallee, is less flammable. Most species of birds, reptiles, and small mammals do not respond strongly to fire in Chenopod Mallee (Kelly et al. 2011; Nimmo et al. 2012; Watson et al. 2012). Thus, the data set consisted of 4001 records of 70 bird species from surveys at 326 sites, 5238 captures of 54 reptile species from surveys at 186 sites, and 826 captures of six small mammal species from 186 sites.

The fire history of study sites was determined using two methods. For sites burned since 1972, Landsat satellite imagery from 15 individual years (1972–2007) and existing fire history maps were used to identify the exact year of the most recent fire. We mapped fires at a resolution of 25 m<sup>2</sup> (1972-1988) to

50 m<sup>2</sup> (1989-2005) (Avitabile et al. 2013; Supporting Information). For sites burned 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 to 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).

### ***Steps in determining optimal fire management for biodiversity conservation***

Our framework and the sequence of analyses for determining optimal fire management for biodiversity conservation had 3 steps: determining animal responses to fire history with species distribution models; calculating biodiversity indices and optimal distribution of successional states; and identifying the optimal management strategy with decision science (Fig. 1).

In step 1, we used generalized additive mixed models (GAMMs) to determine animal responses to time since fire. The GAMMs provided a flexible way to build species distribution models because they fit non-linear relationships and account for correlation structure in spatially clustered data (Wood 2006). We modeled the response variable as the presence or absence of a species at a site. When species are at low prevalence, as was the case in our data set, probability of occurrence is highly correlated with relative abundance. Hereafter, our focus is on probability of occurrence, due to the nature of the data set. Time since fire was entered as a non-linear smoothed term. The degree of smoothing was calculated as part of the model fitting procedure (Wood 2006). . Landscape was entered as a random effect to account for spatial correlation in the data between clusters of sites. The model of  $Y_{i,j,k}$ , the occurrence of species  $j$  at site  $i$  in landscape  $k$ , was

$$Y_{i,j,k} \sim \text{binomial}(1, p_{i,j,k}) \text{ and}$$

$$\text{logit}(p_{i,j,k}) = s(t_i) + b_{j,k} \quad , \quad (1)$$

where  $p_{i,j,k}$  is the probability of species  $j$  being present at site  $i$  in landscape  $k$  and  $s$  is a smoothing function of  $t_i$ , which is time since fire at site  $i$ . The term  $b_{j,k}$  is independent and an identically distributed normal random variate with mean zero and standard deviation  $\sigma_j$  that was estimated from the data.

We modeled all native bird, reptile, and small mammal species that occurred at  $\geq 15$  sites. We assessed the strength of such relationships by plotting model predictions and confidence intervals and by calculating the proportion of deviance explained for each model. The GAMMs were run in R statistical software version 2.15.0 (<http://www.r-project.org/>) with the package `gamm4` version 0.1-5 (Wood 2006).

In step 2, we classified mallee vegetation of sandy flats and dunes into three successional states: early (0-10 years), middle (11-35 years), and late (36-110 years). Exploratory analysis indicated that these age classes represent distinct structural and floristic elements: early successional vegetation is characterized by bare ground and small, coppicing eucalypts; middle vegetation is characterized by high cover of *T. scariosa*; and late vegetation is characterized by larger trees (Haslem et al. 2011). Our aim was to determine the optimal combination of these three successional states for biodiversity conservation.

Based on the GAMM results, we identified the vertebrate species that were clearly associated with time since fire (Supporting Information). For these species only, we calculated the probability of occurrence in each age class by averaging the GAMM model predictions over the period defined by each age class (Supporting Information). The average probability of occurrence of species  $j$  in a given area depended on the proportion of that area that was early ( $a_E$ ), middle ( $a_M$ ), or late successional ( $a_L$ ). Thus, the probability of occurrence of species  $j$  in a given area was

$$P_j = q_{E,j}a_E + q_{M,j}a_M + q_{L,j}a_L \quad , \quad (2)$$



where  $q_{c,j}$  is the probability of occurrence of species  $j$  in age class  $c$  and  $c$  takes values of  $E$ ,  $M$ , or  $L$ .

The geometric mean, averaging over  $n$  species in the area, was  $G = \exp\left(\frac{1}{n} \sum_{j=1}^n \log P_j\right)$ . The age structure that maximizes the geometric mean will vary depending on the number of species that occur in particular successional states and the probability of occurrence of those species in the different successional states. An advantage of using the geometric mean is that it is sensitive to changes in the relative abundance of sets of species (Buckland et al. 2011). Small differences in the probability of occurrence of less common species between age classes represented large percentage differences, so the habitat requirements of these species were influential. By contrast, if an arithmetic mean were used (and calculations done on an additive scale), common species would be given more weight because their range in probability of occurrence is often larger.

We used numerical optimization to determine the values of  $a_E$ ,  $a_M$ , and  $a_L$  that would maximize the geometric mean ( $G$ ), averaging across the species in the community, subject to the constraint  $a_E + a_M + a_L = 1$ . We calculated the optimal allocation of successional states that maximized the geometric mean for birds and reptiles as separate groups and for all vertebrate groups combined. Optimizations can be done in a variety of software packages; we used the GRG (Generalized Reduced Gradient) Nonlinear method in Microsoft Excel. To illustrate this method, we compared the results of this numerical optimization to current fire history maps and to a fire management scenario representative of the pyrodiversity hypothesis.

In step 3, we identified the optimal management strategy with decision science. Decision theory provides tools for setting conservation objectives and helps managers achieve these objectives (Possingham et al. 2001). One such tool is stochastic dynamic programming (SDP), a mathematical optimization method used to identify strategies that will best achieve a given objective, given the state of the system. Richards et al. (1999) used SDP to determine the optimal fire management strategy for a

nature reserve in semi-arid heath mallee. They developed a mathematical model (a Markov chain model) of succession and fire and predicted the chance of a reserve moving from one combination of successional states to another, given the fire management strategies implemented. Richards et al. (1999) defined a desirable state as one where the reserve contained high successional diversity. We used the model of Richards et al. (1999) to show how managers could achieve a conservation target based on strong empirical data.

Following Richards et al. (1999), we assumed the state of the system was the proportion of the vegetation in each of three successional states (early, middle, and late); the state of the system can change over time probabilistically due to succession and to fires that can be planned or unplanned; and the management strategies available include fighting all wildfires, letting all wildfires burn, intentionally burning 10% or 20% of the middle successional vegetation; and intentionally burning 10% or 20% of the late successional vegetation. Our objective was to maximize the expected number of years the reserve is in a desirable state over the next 30 years. We defined the desirable state (the conservation target) based on the optimal distribution of successional states identified in step 2. We assumed all sites had an equal probability of wildfire because previous work (Richards et al. 1999) shows that the optimal management strategy is similar even if different successional states have different probabilities of fire. The model parameter values can be changed so that the probability of wildfire depends on the successional state.

## **Results**

Regression modelling indicated that 10 of 23 bird species, 11 of 25 reptile species, and one of three small mammal species were strongly associated with time since fire (Supporting Information). Six of 10 bird species associated with fire reached their highest probability of occurrence in late successional vegetation, three bird species were most likely to occur in middle successional vegetation, and one bird

species was most likely to occur in early successional vegetation (Supporting Information). For reptiles associated with time since fire, four of 11 species reached their highest probability of occurrence in middle successional vegetation, four species in early successional vegetation, and three species in late successional vegetation. The only small mammal with a strong fire response, *N. yvonneae*, reached highest probability of occurrence in middle and late successional vegetation (Supporting Information).

The explanatory power of the GAMMs ranged from 0 to 26% (deviance explained).. The Yellow-plumed Honeyeater (*Lichenostomus ornatus*) was positively associated with late successional vegetation, the southern legless lizard (*Delma australis*) reached its highest probability of occurrence in the middle successional vegetation, and the mallee ningau ( *Ningau yvonneae*) was positively associated with middle and late successional vegetation (Fig. 2).

The fire history for an area that maximized the geometric mean probability of occurrence of bird species consisted entirely of late successional vegetation ( $G = 0.29$ : Fig. 2g). Most bird species in mallee vegetation that are associated with fire history prefer older vegetation (Supporting Information). The fire history that maximized the mean probability of occurrence of reptile species was weighted toward the middle successional stage ( $a_M = 0.77$ ), with some older vegetation included ( $a_L = 0.23$ ) ( $G = 0.31$ : Fig. 2h). We do not present the fire history that maximized the probability of occurrence of small mammals because only one species was associated with time since fire. Finally, the optimal fire history for birds, reptiles, and mammals combined was a state comprised of middle ( $a_M = 0.45$ ) and late successional vegetation ( $a_L = 0.55$ ), with a geometric mean of 0.29 (Fig. 2i).

We compared the mix of fire age classes that maximized the geometric mean probability of occurrence with current fire maps of the study region (Supporting Information). We found that the largest nature reserve in the region (Murray Sunset National Park, 6,330 km<sup>2</sup>) was composed of proportions of early

(0.05), middle (0.52), and late (0.42) successional vegetation. This was very similar to the solution that maximized geometric mean relative abundance for birds, reptiles, and mammals combined (Fig 3i).

We also compared values of  $G$  under alternative fire management scenarios. For example, under a scenario of equal proportions of vegetation in each successional age class (representative of the pyrodiversity hypothesis), the value of  $G$  for birds was 0.23. This represented a 21% decline in  $G$  from the optimal solution for that taxonomic group. In this case, the decline in  $G$  was driven by several species with a lower probability of occurrence when there are equal proportions of vegetation in each age class. This includes the Rufous Whistler (*Pachycephala rufiventris*) (61% decline in probability of occurrence), the Striated Pardalote (*Pardalotus striatus*) (46% decline), *L. ornatus* (40% decline), and the Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*) (33% decline).

As an example of how stochastic dynamic programming can be used to inform fire management decisions, we set a broad objective of having at least 35% middle successional and 35% late successional vegetation in the landscape. This target is consistent with the mix of fire age-classes that maximized geometric mean probability of occurrence of all taxonomic groups combined (Fig. 2i). We chose to use this broad target as an example because the exact solution from the geometric mean optimization would be a narrow state for managers to achieve. Applying the model of Richards et al. (1999) showed that the optimal strategy over much of the state space was to fight wildfires. For comparison, we also applied stochastic dynamic programming to the management objective set by Richards et al. (1999) of having at least 20% early successional, 20% middle successional, and 20% late successional vegetation (Fig. 3b). The optimal management strategy clearly was sensitive to the management objectives, particularly whether mid-successional vegetation should be burned (compare Figs. 3a and 3b).

## **Discussion**

An important step in our approach was to clearly define the desirable mix of fire histories for biodiversity conservation based on the responses of multiple species in the community. Thus, we have defined the form of pyrodiversity required to maximize the prevalence of a suite of species that respond to time since fire. Importantly, pyrodiversity, per se, does not increase biodiversity. In our case, maximizing pyrodiversity by having an equal mix of age classes would actually reduce the geometric mean relative abundance of vertebrates below that which could be achieved.

The optimal fire history for the combined bird, reptile, and small mammal species was a successional state comprised of middle and late successional vegetation. In our study area, the middle age class is characterized by a high cover of hummock grass, a keystone structure that provides habitat for a number of reptile and small mammal species (Kelly et al. 2011; Nimmo et al. 2012). Late successional vegetation contains larger eucalypts that provide food and shelter for many bird species (Taylor et al. 2012; Watson et al. 2012). Although some species displayed a preference for recently burned vegetation (e.g. Chestnut-rumped Thornbill [*Acanthiza uropygialis*]), typically they also were able to maintain populations in middle or late successional vegetation. The reverse was generally not true; those species most abundant in older vegetation were rare in recently burned areas (e.g. [*P. rufiventris*]) (Supporting Information).

The geometric mean relative abundance of fire-response species can be used to specify management objectives. It is a measure of the relative abundance (or probability of occurrence) of multiple species and is likely to be correlated with the extinction risk of animal populations (McCarthy 2012). This index better reflects the overall response of the community to fire than the 51 individual species models (see Supporting Information). By defining fire management objectives based on the habitat requirements of multiple species in the community, our approach differs from previous frameworks that assume pyrodiversity is a surrogate for biodiversity (Brockett et al. 2001).

Fire management goals are more achievable when they are linked to decision-making tools and operational guidelines. Stochastic dynamic programming can help fire managers decide how to achieve conservation targets, given the state of the system (defined here as the amount of early, middle, and late vegetation) and the occurrence of unplanned fires. In this example, applying SDP showed that the optimal fire management strategy over much of the state space was to fight wildfires. Only when the later successional state was dominant was the optimal strategy to burn late successional vegetation to ensure the availability of middle successional vegetation (Fig. 3a). An advantage of using decision theoretic tools to solve conservation problems is that they encourage managers to explicitly state objectives, list management options, and develop a conceptual model of the system (Possingham et al. 2001; Driscoll et al. 2010b). Our results are illustrative only and should not be interpreted as being prescriptive. Application of the model of Richards et al. (1999) could be enhanced by incorporating the spatial dynamics of fire behavior specific to the management area of interest. Alternatively, existing spatially explicit fire behavior models (e.g. Phoenix Rapidfire [Tolhurst et al. 2008]) could be incorporated into a decision theory framework (sensu Possingham et al. 2001).

There are several caveats to our approach. First, while the geometric mean is useful for defining fire management objectives, other indices could also be considered (Buckland et al. 2011). Second, we focused here on time since fire. This is an appropriate measure in this system, where fires are stand replacing (Avitabile et al. 2013) and land managers use the distribution of successional age classes to plan fire management operations (Sandell et al. 2006). Previous work shows that time since fire is a useful predictor of vertebrate distribution in the study region (Kelly et al. 2011; Nimmo et al. 2012; Watson et al. 2012). Nevertheless, other aspects of the fire regime may also be important, including inter-fire interval (Haslem et al. 2012), fire severity (Noss et al. 2006), season of burn (Van Wilgen et al. 1998), and spatial configuration of age classes (Bradstock et al. 2005). Such features could be included by adding further explanatory variables to the model represented by Eq. 1. For example, both time since

fire and fire severity could be included as explanatory variables in a species distribution model and then incorporated in the calculation of the biodiversity index and the optimization.

A third caveat is that the optimal allocation of successional states is sensitive to how they are defined. The definitions we used are based on our knowledge of vegetation change in the system (Haslem et al. 2011), age classes that are correlated with faunal distributions (Kelly et al. 2012; Nimmo et al. 2012; Watson et al. 2012), and age classes that we could map across the region (Avitabile et al. 2012). Lastly, the optimal allocation is sensitive to the species included in the model. We included the major vertebrate species in the region to illustrate the problem; these are relatively well studied. The solution that maximized the geometric mean abundance for birds, reptiles, and small mammals is consistent with the habitat requirements of several threatened mallee bird species (e.g. Mallee Emu-wren [*Stipiturus mallee*] [Brown et al. 2009]). Further research is required to document the fire responses of lesser known taxa, particularly invertebrates.

We focused on a single vegetation type, the most widespread and fire-prone vegetation in the study area, which alone encompasses >18,000 km<sup>2</sup>. With our framework, fire management objectives could also be developed based on multiple vegetation types. This could be done most simply by conducting separate analyses for each local vegetation type, particularly if the faunal community and fire ecology of each vegetation type differ markedly. Alternatively, interactions between vegetation type and fire responses could be modeled in each stage of the analysis. For example, Kelly et al. (2011) modeled the distribution of small mammals by including an interaction between vegetation type and time since fire.

A productive area for future research would be to integrate this approach, with its focus on vertebrate animals, with management guided by the life-history traits of plants for which the aim is to ensure temporal variation within acceptable domains of inter-fire intervals (Gill & McCarthy 1998). A useful starting point would be to simulate landscape-scale fire regimes based on acceptable inter-fire intervals

for plants and to compare those simulated fire histories with combinations that maximize the geometric mean abundance of vertebrates. It is advantageous to use a variety of methods to determine appropriate fire regimes, and we recommend comparing methods based on the requirements of plants and animals with historical records of characteristic fire regimes.

Patch mosaic burning is frequently advocated by management agencies to avoid population declines of birds, mammals, and reptiles (Parr & Andersen 2006). However, the relationship between pyrodiversity and biodiversity differs between ecosystems and regions. We have proposed a broad method that could be adopted by managers in fire-prone ecosystems to determine an appropriate form of pyrodiversity. This includes modeling species' responses to fire history, using a biodiversity index to determine the optimal fire history of a given area, and linking conservation objectives with decision tools. By clearly defining fire management objectives based on the habitat requirements of fire-sensitive species in a community, this approach could be used to maximize biodiversity in fire-prone regions and nature reserves and may help avoid population extinctions due to inappropriate fire regimes.

### **Acknowledgments**

We thank all members of The Mallee Fire and Biodiversity Project, A. Haslem, D. Nimmo, and S. Watson for contributing to the development of the species distribution modeling approach, and S. Richards for providing the SDP model and code. This research was supported by funding from the Australian Research Council Centre of Excellence for Environmental Decisions and the Victorian Department of Sustainability and Environment. Comments from several reviewers improved the manuscript, for which we are grateful.

### **Supporting Information**



Fire history map of the Murray Mallee region of southeastern Australia (Appendix S1); results of generalized additive mixed models describing the relationship between birds, mammals, and reptiles (R) and time since fire in *Triodia* Mallee vegetation of southern Australia (Appendix S2); and average probability of occurrence of fire-responsive species in each successional state (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than the absence of material) should be directed to the corresponding author.

### **Literature cited**

- Avitabile, S.C., et al. 2013. Systematic fire mapping is critical for fire ecology, planning and management: a case study from the semi-arid Murray Mallee, south-eastern Australia. *Landscape and Urban Planning* **117**: 81-91.
- Bowman, D. M. J. S., J. K. Balch, P. Artaxo, et al. 2009. Fire in the Earth system. *Science* **324**:481-4.
- Bradstock R. A., M. Bedward, A. M. Gill, and J. S. Cohn. 2005. Which mosaic? A landscape ecological approach for evaluating interactions between fire regimes, habitat and animals. *Wildlife Research* **32**:409-23.
- Brockett B. H., H. C. Biggs, and B. W. van Wilgen. 2001. A patch mosaic burning system for conservation areas in southern African savannas. *International Journal of Wildland Fire* **10**:169-83.
- Brown, S., M.F. Clarke, and R. Clarke (2009) Fire is a key element in the landscape-scale habitat requirements and global population status of a threatened bird: The Mallee Emu-wren (*Stipiturus mallee*). *Biological Conservation* **142**: 432-445.
- Buckland S .T., A. C. Studeny, A. Magurran, J. B. Illian, and S. E. Newson. 2011. The geometric mean of relative abundance indices: a biodiversity measure with a difference. *Ecosphere* **2**:1-26.

- Butchart, S. H. M., M. Walpole, B. Collen, et al. 2010. Global biodiversity: indicators of recent declines. *Science* **328**:1164-8.
- Clarke, M. F., S. C. Avitabile, L. Brown, et al. 2010. Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. *Australian Journal of Botany* **58**: 363-372.
- Davies, A. B., P. Eggleton, B. J. van Rensburg, and C. L. Parr. 2012. The pyrodiversity-biodiversity hypothesis: a test with savanna termite assemblages. *Journal of Applied Ecology* **49**:422-30.
- Di Stefano, J et al. 2013. Defining vegetation age class distributions for multispecies conservation in fire-prone landscapes. *Biological Conservation* **166**: 111-117.
- Driscoll, D. A., D. B. Lindenmayer, A. F. Bennett, et al. 2010a. Fire management for biodiversity conservation: Key research questions and our capacity to answer them. *Biological Conservation* **143**:1928-39.
- Driscoll, D. A., D. B. Lindenmayer, A. F. Bennett, et al. 2010b. Resolving conflicts in fire management using decision theory: asset-protection versus biodiversity conservation. *Conservation Letters* **3**:215-223.
- Gill, A. M. and M. A. McCarthy. 1998. Intervals between prescribed fires in Australia: what intrinsic variation should apply? *Biological Conservation* **85**:161-169.
- Haslem, A., et al. 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.
- Haslem, A., et al. 2012. Time-since-fire and inter-fire interval influence hollow availability for fauna in a fire-prone system. *Biological Conservation* **152**:212-221.

Keeley, J. E., W. J. Bond, R. A. Bradstock, J. P. Pausas, and P. W. Rundel. 2011. Fire in Mediterranean ecosystems: ecology, evolution and management. Cambridge University Press, New York.

Kelly, L. T., D. G. Nimmo, L. M. Spence-Bailey, A. Haslem, S. J. Watson, M. F. Clarke, and A. F. Bennett. 2011. The influence of fire history on small mammal distributions: insights from a 100-year post-fire chronosequence. *Diversity and Distributions* **17**:462-73.

Kelly, L. T., D. G. Nimmo, L. M. S. Spence-Bailey, R. S. Taylor, S. J. Watson, M. F. Clarke, and A. F. Bennett. 2012. Managing fire mosaics for small mammal conservation: a landscape perspective. *Journal of Applied Ecology* **49**:412-21.

Noble, J. C. 2001. Lignotubers and meristem dependence in mallee (*Eucalyptus* spp.) coppicing after fire. *Australian Journal of Botany* **49**:31-41.

Martin, R. E. and D. B. Sapsis. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. Proceedings of the Symposium on Biodiversity in Northwestern California. Wildland Resources Centre, University of California, Berkeley.

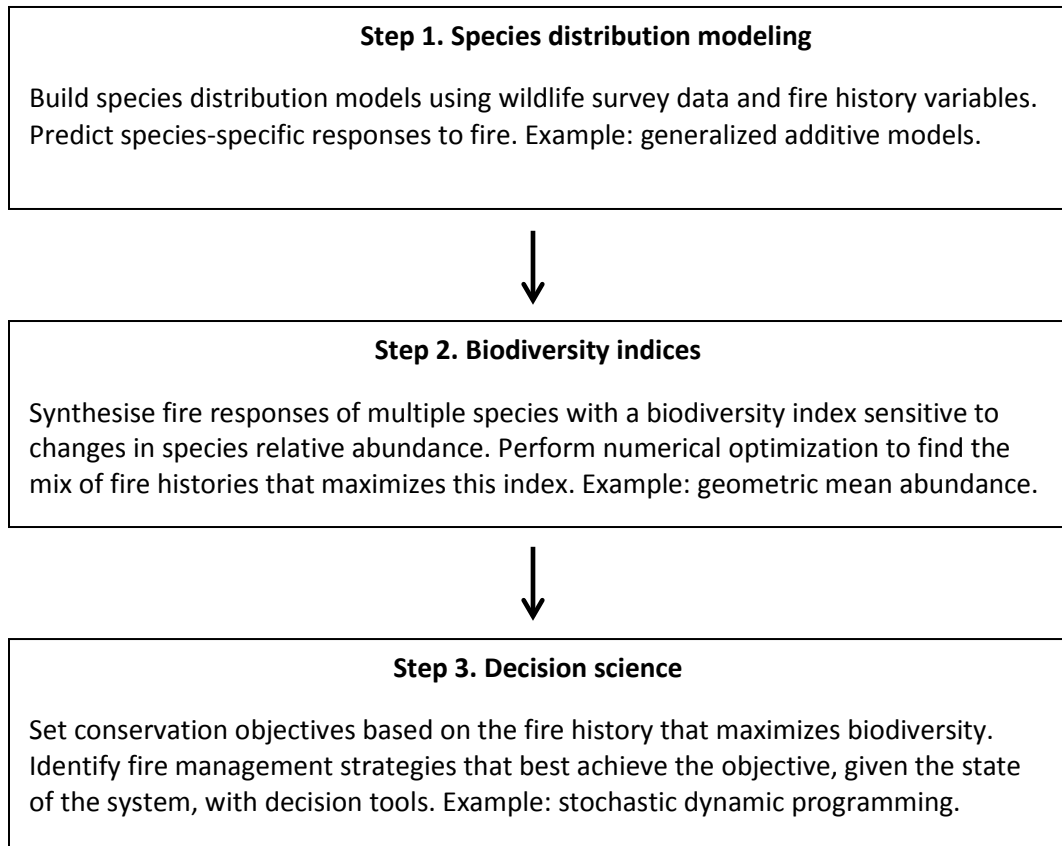
McCarthy, M.A., A.L. Moore, J. Krauss, J.W. Morgan, and C.F. Clements. 2014. Linking indices for biodiversity monitoring to extinction risk theory. *Conservation Biology*. DOI: 10.1111/cobi.12308

Nimmo, D. G., L. T. Kelly, L. M. Spence-Bailey, S. J. Watson, A. Haslem, J. G. White, M. F. Clarke, and A. F. Bennett. 2012. Predicting the century-long post-fire responses of reptiles. *Global Ecology and Biogeography* **21**:1062-73.

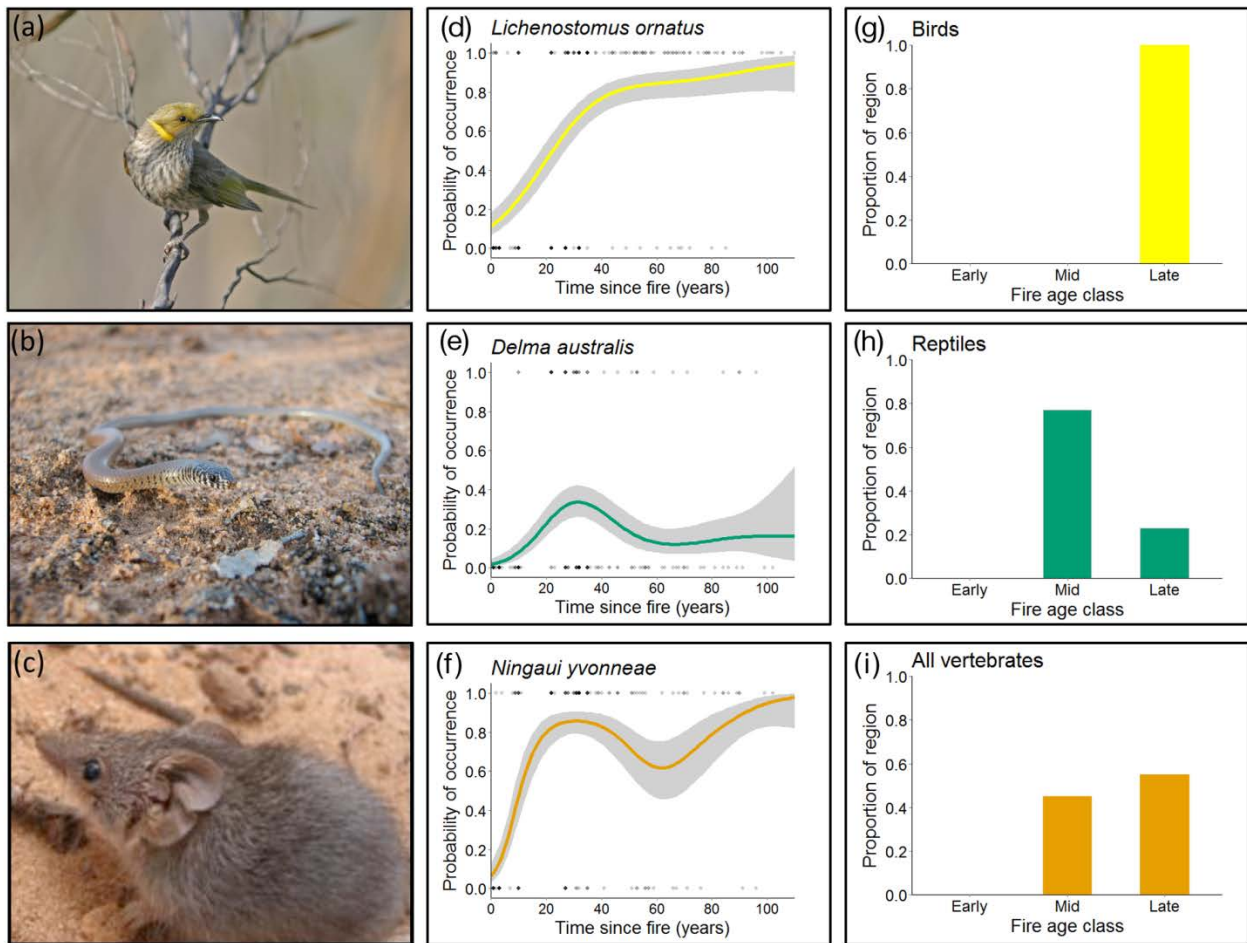
Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* **4**:481-7.

- Parr, C. L. and A. N. Andersen. 2006. Patch mosaic burning for biodiversity conservation: a critique of the pyrodiversity paradigm. *Conservation Biology* **20**:1610-19.
- Possingham, H. P., S. J. Andelman, B. R. Noon, S. Trombulak, and H. R. Pulliam. 2001. Making smart conservation decisions. Pages 225-244 in M. E. Soule and G. H. Orians, editors. *Conservation biology: research priorities for the next decade*. Island Press, Washington.
- Richards, S. A., H. P. Possingham, and J. Tizard. 1999. Optimal fire management for maintaining community diversity. *Ecological Applications* **9**:880-92.
- Sandell, P., K. Tolhurst, J. Dalton, B. Scott, and M. Smith. 2006. Fire management prescriptions for the Victorian mallee parks. *Proceedings of the Royal Society of Victoria*. **118**: 395-412.
- Taylor, R. S., S. J. Watson, D. G. Nimmo, L. T. Kelly, A. F. Bennett, and M. F. Clarke. 2012. Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity and Distributions* **18**:519-29.
- Tolhurst, K., B. Shields, and D. Chong. 2008. Phoenix: development and application of a bushfire risk management tool. *The Australian Journal of Emergency Management* **23**: 47-54.
- Van Wilgen, B. W., H.C Biggs, and A. L. F. Potgieter. 1998. Fire management and research in the Kruger National Park, with suggestions on the detection of thresholds of potential concern. *Koedoe-African Protected Area Conservation and Science* **41**: 69-87.
- Watson, S. J., R. S. Taylor, D. G. Nimmo, L. T. Kelly, A. Haslem, M. F. Clarke, and A. F. Bennett. 2012. Effects of time-since-fire on bird species: how informative are generalized fire-response curves for conservation management? *Ecological Applications* **22**:685-96.

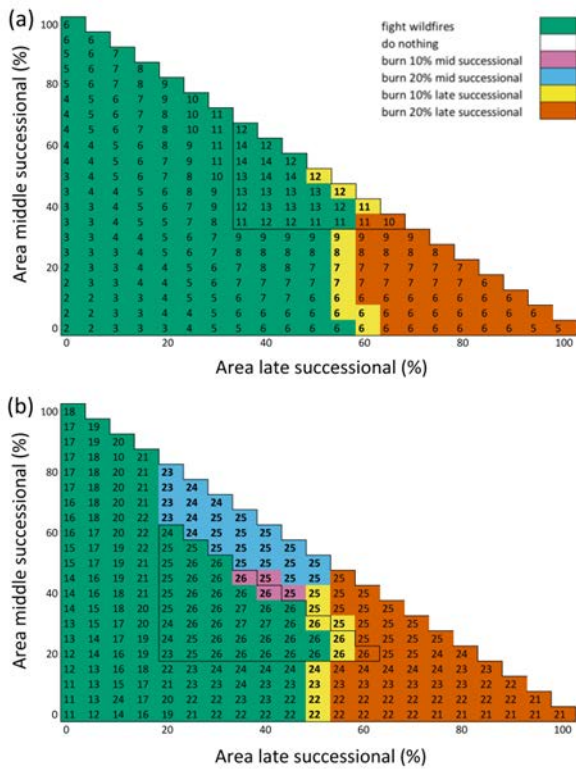
Wood SN. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton, Florida.



**Figure 1.** Steps in the framework for determining optimal fire management for biodiversity conservation.



**Figure 2.** Three species characteristic of mallee vegetation (a) Yellow-plumed Honeyeater (no need to repeat from figure), (b) southern legless lizard, and (c) mallee ningau. (d, e, f) Responses of these species to time since fire over 110 years (solid lines, predictions of probability of occurrence from generalized additive mixed models; shaded areas, aSE 1; diamonds, observed data). Age structure that maximizes the geometric mean probability of occurrence for (g) birds, (h) reptiles, and (i) all vertebrates combined. Photos by (a) Rohan Clarke and (b, c) Lauren Brown.



**Figure 3.** Optimal fire management strategy obtained using stochastic dynamic programming. In both examples, the objective was to maximize the number of years a given area is in a desirable state (represented by the inner triangle). Numbers within the graph are the expected years the reserve is in a desirable state over the next 30 years, for all possible initial states, assuming the optimal strategy is always chosen. Colors are the optimal management strategies, given the state of the system. A desirable state was defined as a landscape comprised of (a) a minimum of 35% middle and 35% late successional vegetation (based on the age structure that maximized geometric mean relative abundance ( $G$ ) for all taxonomic groups combined) and (b) a minimum of 20% early, 20% middle, and 20% late successional vegetation (target set by Richards et al. [1999] for successional diversity).