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Promoting Optimal Habitat Availability by Maintaining Fine-Grained Burn Mosaics: A Modelling Study in an Australian Semi-Arid Temperate Woodland

Ben J. French [1,*], Brett P. Murphy [2] and David M. J. S. Bowman [1,*]

[1] Fire Centre, School of Natural Sciences, University of Tasmania, Hobart, TAS 7005, Australia
[2] Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT 0810, Australia; brett.p.murphy@cdu.edu.au
* Correspondence: ben.french@utas.edu.au (B.J.F.); david.bowman@utas.edu.au (D.M.J.S.B.)

Abstract: The pyrodiversity–biodiversity (P–B) hypothesis posits that spatiotemporally variable fire regimes increase wildlife habitat diversity, and that the fine-grained mosaics resulting from small patchy fires enhance biodiversity. This logic underpins the patch mosaic burning (PMB) paradigm and reinforces the benefits of Indigenous fire management, which tends to promote pyrodiversity. However, tests of the P–B hypothesis and PMB paradigm are few. One of the most comprehensive field evaluations—a snapshot study of pre-existing fire mosaics in south-east Australian semi-arid mallee eucalypt woodlands—found little support. To explore the longer-term effects of fire mosaic grain size on habitat availability and biodiversity, we combined published data from the mallee study with a simple fire simulation. We simulated 500 years of landscape burning under different fire sizes. In the resulting mosaics, we assessed the proportional mixture and patch configuration of successional habitat states, then summarised habitat availability through time using a composite index based on the published fire history responses of 22 vertebrate taxa from the mallee study. Small fires formed fine-grained mosaics with a stable habitat mixture and with habitat diversity occurring at fine scales. Large fires formed coarse-grained mosaics with the opposite properties. The fine-grained mosaics maintained optimal habitat availability for vertebrate diversity over 500 years, while the fluctuating habitat mixture in the coarse-grained mosaics was unlikely to maintain maximum vertebrate diversity. Broadly, our results support the P–B hypothesis and justify further field-testing and evaluation of PMB programs to manage both pyrodiversity and biodiversity in the mallee and other flammable landscapes.

Keywords: biodiversity conservation; fire mosaics; fire simulation; fire size; Indigenous fire management; mallee; mosaic grain size; patch mosaic burning; pyrodiversity

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1. Introduction

Fire is a key ecological disturbance which is highly variable in time and space [1]. The primary conceptual framework used to understand how fires affect biota is the 'fire regime', a summary of temporal and spatial patterns in the occurrence and characteristics of repeat fires. Many components have been used to describe fire regimes including fire frequency, intensity, severity, type (including crown, surface, and ground fires), seasonal timing, and the extent and pattern of area burnt [2,3]. Typically, the fire regime concept is applied with a relatively narrow focus on temporal aspects of fire occurrence at a single point in space [4], as these are simple to measure and readily linked to classic ecological models, such as life history cycles of species and secondary succession of communities. In contrast, spatiotemporal patterns are more difficult to describe because of the inherent complexity that comes from considering additional dimensions (in both time and space) [5]. Hence, mapping spatial patterns of fire extent and severity, and their variation through time, remains a major research frontier. Nonetheless, it has been posited that spatiotemporal fire

patterns strongly influence biota, including the contentious hypothesis proposed by Martin and Sapsis [6] that "pyrodiversity begets biodiversity".

This pyrodiversity–biodiversity hypothesis (P–B hypothesis) posits that spatiotemporal heterogeneity in fire regimes (i.e., pyrodiversity) promotes biodiversity by creating and maintaining a diverse mosaic of fire-mediated habitat states. For instance, more fine-grained mosaics may promote biodiversity because they contain more habitat niches and resources at small scales [6]. Following this logic, proponents of the P–B hypothesis argue that wildland fire managers should use small, patchy fires to create fine-grained habitat variability [6], an approach known as "patch mosaic burning" (PMB) [7,8]. However, the ecological merit of the PMB management paradigm has been questioned, largely because empirical evidence of the effects of fine-grained mosaics is both sparse and conflicting, leading to a lack of consensus on which mosaic patterns are desirable [9]. Nonetheless, there is increasing recognition that Indigenous fire management (prior to disruption by European colonists) sustained biodiversity and involved the use of fine-scale burning, and thus is an example of PMB [10,11]. Advancing understanding of the P–B hypothesis and the PMB paradigm is clearly important for both fundamental and applied reasons, but this is hampered by the practical difficulties in studying the effects of fire mosaics on biota at appropriate spatial and temporal scales.

Resolving how spatial patterns of burning affect biodiversity is challenging because the influence of fire mosaics on biota may be subtle and interactive with other controls, such as climate variation and soil fertility [12]. Hence, proving a causal link between pyrodiversity and biodiversity demands manipulative experiments, but controlling the detailed configuration of fire occurrence at landscape scales for long enough to affect wildlife assemblages is impractical and prohibitively expensive. Indeed, the few landscape-scale experiments examining how biodiversity responds to fire have focussed on the effects of fire frequency and severity rather than spatial pattern [13–15] and hence cannot easily illuminate the effects of pyrodiversity. A more realistic approach is to use 'space-for-time' substitutions to assess how biodiversity varies with pre-existing pyrodiversity patterns, whilst controlling for environmental variability. In such studies, pyrodiversity has been operationally defined as a variation in severity or fire recurrence around a point [16,17] or in terms of the arrangement of vegetation age classes, the so-called 'invisible' and 'visible' fire mosaics, respectively [9]. One of the most comprehensive space-for-time studies of the P–B hypothesis undertaken globally is the Mallee Fire and Biodiversity Project [18]. That study explored correlations between landscape pyrodiversity—defined as evenness in the proportional extent of three vegetation age classes emergent from previous landscape burning—and the abundance and diversity of reptiles, birds, and small mammals [19–21]. The study was explicitly designed to guide managers in using fire to optimise biodiversity outcomes [22–24].

Space-for-time studies allow the pyrodiversity–biodiversity nexus to be explored at spatial and temporal scales which would not be achievable with manipulative approaches; however, they have often overlooked detailed spatial patterns of the fire mosaic. For instance, in the Mallee Fire and Biodiversity Project, pyrodiversity was defined based solely on the proportional mixture of habitat types defined by time since fire. This approach does not differentiate coarse-grained mosaics, in which habitat types occur in large continuous blocks, from fine-grained mosaics, in which habitat type varies at small spatial scales. Further, the range of mosaic grain sizes that can be studied using space-for-time approaches is limited to what already exists in a landscape. In the case of the Mallee studies, there was a deficit of fine-grained mosaics in the study region, which had been dominated by large lighting-ignited fires in recent times [25,26]. Such differences in fire mosaic grain size sit at the core of the P–B hypothesis and underpin the PMB management paradigm [6,8], so this lack of configurational detail is problematic.

An alternative to empirical approaches is to use computer simulations, in which the effects of pyrodiversity on biodiversity can be investigated by creating and maintaining a spectrum of mosaic grain sizes over long time scales. Previous studies have shown that

basing computer simulations on real-world data provides a powerful means to investigate the pyrodiversity–biodiversity coupling. For example, Trauernicht et al. [27] combined field surveys and a simple simulation model to show that long-unburnt patches, essential for recruitment of the fire-sensitive savanna conifer *Callitris intratropica*, are rare in coarse-grained fire mosaics. Simulations have also been used to explore how fire mosaics affect faunal assemblages. To date, such studies have focused on proportional coverage of fire age classes [15], have considered grain size only at coarse spatial scales [28,29], or have focused on the responses of a small subset of species [5,30], limiting their capacity to resolve the long-term effects of fine-grained mosaics on biodiversity more broadly.

To advance the question of whether the long-term maintenance of fine-grained mosaics can promote biodiversity, we manipulated fire size independently of the average annual area burnt in a simulated mallee landscape over 500 years, and assessed the availability of habitat for vertebrates in the resulting mosaics, using published data from the Mallee Fire and Biodiversity Project [24]. We (a) used simple metrics to describe how the configuration of habitat mosaics varied with fire size; (b) determined how habitat availability for vertebrates varied through time in relation to fire size; and (c) tested the hypothesis that fine-grained fire mosaics promote the optimal mix of post-fire habitat required to maximise vertebrate diversity.

To be clear, the aim of this study is to test the basis of the P–B hypothesis and the PMB paradigm, rather than to specify real-world management recommendations using simple models, as has been done previously for this biome (e.g., [24,31,32]). Resolving the basis of the P–B hypothesis (and hence the PBM paradigm) is both theoretically and practically important. If our simple simulation based on real-world data demonstrates an enduring effect of fire mosaic grain size on habitat availability for biodiversity, this would provide an impetus for further research and investment in PMB as a conservation management tool. Determining the specific patterns of PMB which should be applied to a fire-prone system would require building more realistic and complex models, as well as undertaking large-scale field trials [30].

2. Materials and Methods

2.1. Study Area

The Murray Mallee region in southeastern Australia contains large areas of highly flammable open woodlands dominated by low-stature, multi-stemmed *Eucalyptus* trees (known as mallees) [33]. We focus our study on the dominant vegetation type in the region, Triodia mallee, in which hummock grasses (*Triodia* spp.) form much of the surface fuel. The climate is semi-arid, with a north–south rainfall gradient across the region ranging from 218 to 329 mm in mean annual rainfall. The terrain consists of undulating dune and swale systems, with few topographic barriers to fire spread. Indeed, large (>10,000 ha) fires have prevailed in the region in recent decades, predominantly ignited by lighting [26]. Fires generally fully consume the hummock grasses and topkill the mallees, which then resprout from lignotubers below ground level [34]. Given that fires are typically stand-replacing, time since fire is a useful index of habitat type [35]. The region's extensive tracts of uncleared vegetation and the fact that fire severity and topography are relatively uniform make this an ideal study system to explore the effects of the spatiotemporal patterns of fire occurrence on the biota.

2.2. Fire Simulation

We assessed the long-term influence of fire size on mosaic grain size and habitat availability in a simulated mallee landscape. To do this, we implemented a simple fire simulation in the computer program R v.3.6.1 [36] using a hypothetical 10,000 km^2 square reserve (i.e., 100 × 100 km), with a spatial resolution of 1 km^2. We ran fire simulations over a 500-year period. Across this period, the average annual probability of fire at a point in the landscape was set to 0.01 for all simulations (i.e., on average, 1% of the landscape burns per annum regardless of fire size), a reasonable value considering documented fire

regimes in the mallee [37]. Each year, we generated a spatially autocorrelated surface of the probability of fire, using a spherical variogram model (command '*vgm*' in the package '*gstat*' in R [38,39]). Each year, we simulated whether each 1 km^2 cell in the reserve burned, based on the probability of fire for that cell (for simplicity, fire probability was independent of time since fire). The range of fire sizes was varied by changing the range of spatial autocorrelation in the variogram model, so that increasing the 'range' term increased the maximum fire size. The simulation was repeated 300 times, each with a different range of spatial autocorrelation (fire size) stipulated. The minimum range of spatial autocorrelation in all simulations was 0 (i.e., each grid cell behaves independently) but maximum values varied between simulations from 2 to 10,000, so that while very small fires were always possible, typical fire size varied between simulations. For presentation, we converted the range of spatial autocorrelation to a more intuitive measure of fire size by calculating the area-weighted mean fire size across each of the 300 simulations.

Having created long-term fire histories, for each year we classified individual grid cells as one of three habitat types based on the time since they were last burnt; these were early (0–10 years), middle (11–35 years), and late (>35 years) successional habitat. These classifications are those utilised by Kelly et al. [24], who regarded them as representing distinct habitat types in terms of structure and floristics.

2.3. Exploring Mosaic Configuration

To explore how the configuration of the habitat mosaic varied with fire size, for each simulation run we calculated average values across the time series for five metrics. These were (a) the area-weighted mean size of habitat patches of each type; (b) the number of discrete patches of each habitat type; (c) the distance from each habitat patch to the nearest neighbouring patch of the same type; (d) the length of each type of habitat boundary (i.e., early–middle, early–late, middle–late); and (e) the minimum radius to encounter two and three habitat types from each landscape pixel.

2.4. Characterising Availability of the Optimal Habitat Mix for Vertebrate Diversity

We assessed how habitat availability varied through time under a spectrum of fire size scenarios using published field data on the post-fire habitat associations of vertebrate species in the mallee. In the Mallee Fire and Biodiversity Project, vertebrate field surveys were conducted over 2 years across 28 mallee landscapes with various fire histories [19–21]. Kelly et al. [24] used these data to develop models of probability of occurrence for individual species in early, mid, and late successional habitat classes, and to calculate the optimal mixture of these habitat states to maximise vertebrate diversity in the landscape. We assessed how the availability of this optimal habitat mix varied between fire size scenarios over 500 years of burning.

In their study, Kelly et al. [24] only considered species found at 15 or more study sites to be common enough to analyse, a criterion met by 51 of the 130 vertebrate species recorded. Of this subset, 22 species showed strong differential usage of post-fire successional states. Kelly et al. [24] modelled the probability of occurrence (which was strongly correlated with relative abundance) of each of these fire-responsive species in relation to time since fire using generalised additive mixed models (GAMMs). They then averaged the model predictions across the time since fire window for early, mid, and late successional habitat classes, to calculate the probability of occurrence for each species in each class. Using these values, Kelly et al. [24] could estimate the probability of a species occurring in a landscape based on the proportional mixture of early, mid, and late successional habitat.

To assess how different habitat mixtures influenced overall vertebrate diversity and abundance, Kelly et al. [24] combined the individual species data into a composite biodiversity index—the geometric mean of probability of occurrence (G). There are several advantages to G as a biodiversity index, including that it is unaffected by differences in detectability between species, it is sensitive to changes in the occurrence of less common species, and that it correlates with extinction rates [40,41]. Using a simple numerical op-

timisation procedure, Kelly et al. [24] then determined the proportional mixture of early, mid, and late successional states which maximised G, and was hence optimal for vertebrate diversity. They defined this optimal state as $G \geq 0.29$.

To assess habitat availability for vertebrates in our simulated mosaics, we applied the functions of Kelly et al. [24] in order to calculate a time series of G for the 22 vertebrate species whose probability of occurrence was found to vary significantly between post-fire successional states. We examined how varying the size of fires affected G, and the likelihood of the reserve being in an optimal state of habitat availability. We note that Kelly et al. [24] found that the optimal state differs between the vertebrate groups (i.e., birds [10 species], reptiles [11 species], mammals [1 species only]), with birds having a much stronger preference for late successional habitat than reptiles. However, like Kelly et al. [24], we focused on a single value of G to describe the occurrence probability of all species across these three groups.

3. Results

3.1. Mosaic Configuration

Fire size drove clear differences in how habitat was configured. Regimes of smaller fires resulted in more fine-grained mosaics, in which there were a greater number of habitat patches throughout the landscape (Figure 1b) with shorter distances between late patches (Figure 1c), although the patches tended to be smaller (Figure 1a). Regimes of larger fires resulted in more coarse-grained mosaics, in which habitat patches were fewer, larger in size, and more isolated. In fine-grained mosaics, boundaries between habitat types were more extensive (Figure 1d) and multiple habitat types occurred in closer proximity throughout the landscape than in coarse-grained mosaics (Figure 1e).

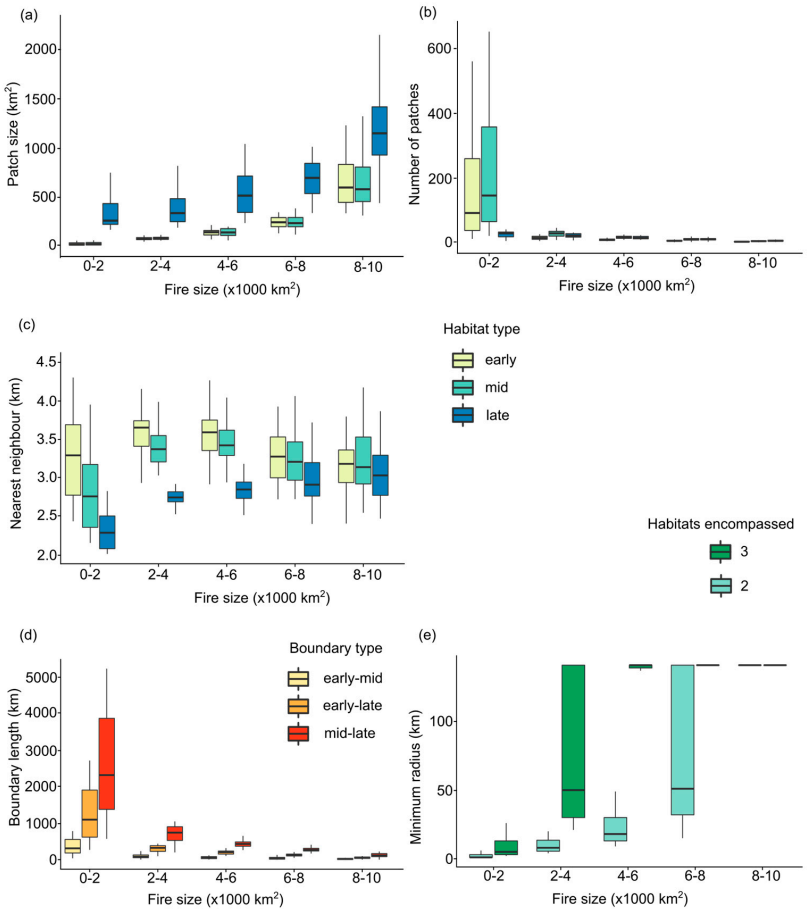


Figure 1. Boxplots showing how habitat mosaic configuration differed between 300 simulated mallee landscapes, which were subjected to burning at different spatial scales for 500 years. The range of fire sizes

was varied between simulations (X-axes correspond to area-weighted mean fire size in km^2) with the average annual area burnt held constant at 1% of the landscape. From the resulting habitat mosaics, average values were calculated for several metrics describing the configuration of early (0–10 years since fire), middle (11–35 years since fire), and late (>35 years since fire) successional habitat patches. These metrics were (**a**) the area-weighted mean size of discrete patches (km^2); (**b**) the mean number of discrete patches; (**c**) the mean distance separating patches from the nearest patch of the same type (km); (**d**) the mean summed length of habitat boundaries (km); and (**e**) the median radius to encompass two and three habitat types from each pixel in the landscape (km). The lower and upper boundaries of the coloured boxes correspond to the 25th and 75th percentiles, respectively. The horizontal bar inside each box indicates the median, and lower and upper error lines denote the range of the data.

3.2. The Availability of the Optimal Habitat Mix for Vertebrate Diversity

The overall availability of optimal habitat was clearly enhanced by small fires. At the smallest fire sizes, habitat availability for vertebrates was optimised (i.e., G $\geq$ 0.29) in the landscape for the entire 500-year simulation, while landscapes exposed to very large fire scenarios were optimised for only a very small proportion of the time series, or not at all (Figure 2). We attribute this to increased temporal variability in the habitat mixture under larger fire regimes. Under large fire regimes, the habitat mixture was highly unstable, with the landscape often dominated by just one or two habitat types (Figure 3d). Habitat availability was rarely optimised in these coarse-grained mosaics, and G sometimes dipped very low (Figure 3f). In contrast, the proportional mixture of habitats was remarkably stable through time in the fine-grained mosaics formed under regimes of small fires (Figure 3c), maintaining G at a consistently high level (Figure 3e).

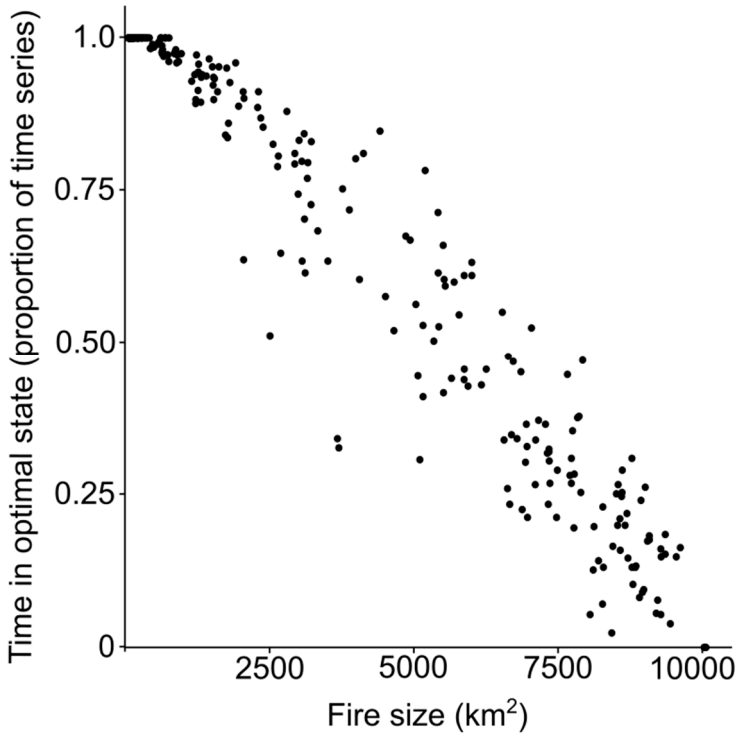


Figure 2. Scatter plot showing how the proportion of the time series in which a 10,000 km^2 simulated mallee landscape is in an 'optimal' state (geometric mean of occupancy $\geq$ 0.29, as defined by Kelly et al. [24]) varies with fire size. Each black dot corresponds to a 500-year fire simulation. The *x*-axis shows area-weighted mean fire size across the time series (km^2).

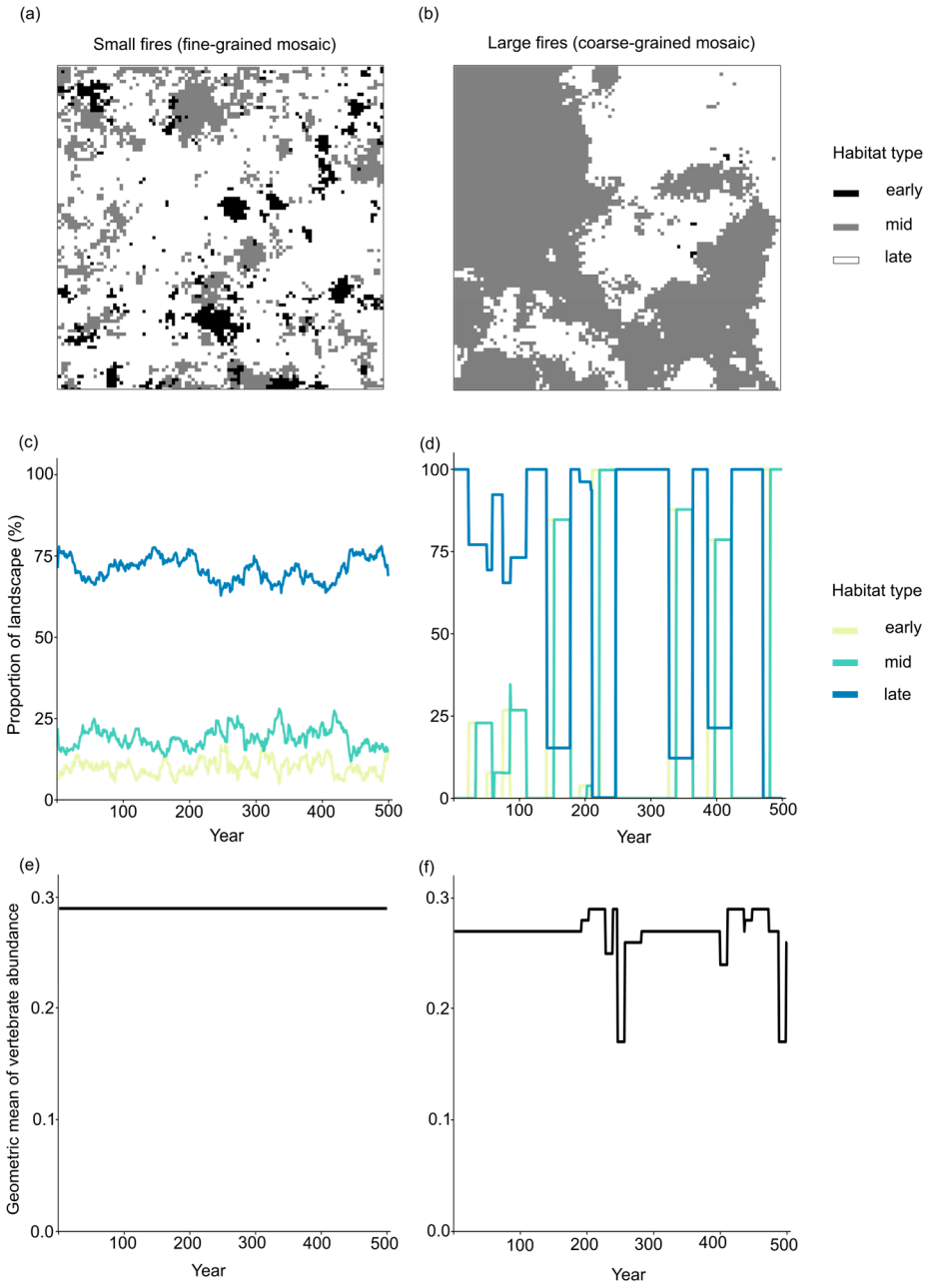


Figure 3. A comparison of simulated mallee landscapes (area = 10,000 km^2) burned under contrasting fire size scenarios for 500 years. The top panels are strongly contrasting examples of habitat mosaics at a single time point under (**a**) small (area-weighted mean fire size = 45 km^2) and (**b**) large (area-weighted mean fire size = 7638 km^2) fire scenarios (two of the 300 fire size scenarios simulated). Middle panels show the areal extent of early (0–10 years since fire), middle (11–35 years since fire), and late (>35 years since fire) successional habitat throughout the time series for the same (**c**) small and (**d**) large fire scenarios. Corresponding time series of vertebrate biodiversity (geometric mean of probability of occurrence of 22 vertebrate species) for (**e**) small and (**f**) large fires are shown in the bottom panels.

4. Discussion

We used a spatially explicit simulation to explore the effects of fire size on the availability of optimal habitat to maximise vertebrate diversity, while controlling for the area burned. We first explored how fire size influenced habitat mosaic configuration, then assessed the availability of optimal habitat through time using a composite biodiversity index, based on field data on vertebrate species occurrence across fire-driven habitat mo-

saics in semi-arid *Eucalyptus* woodlands (mallee) [24]. In our simulated mallee landscapes, fire size clearly affected both the grain size and composition of habitat mosaics. Recurrent, smaller fires created fine-grained mosaics in which habitat patches were less isolated and a diversity of post-fire age classes occurred in close proximity. A regime of larger fires formed coarse-grained mosaics with the opposite properties. Fine-grained mosaics, while spatially dynamic over 500 years, were temporally stable in their habitat mixture, while in coarse-grained mosaics the habitat mixture varied and often changed abruptly. We found that the optimal habitat mixture for vertebrate diversity was rarely present in coarse-grained mosaics, while fine-grained mosaics had a more optimal habitat mixture throughout the time series. As outlined below, these results support our hypothesis that fine-grained fire mosaics created by PMB promote the optimal mix of post-fire habitat to maximise vertebrate diversity, a finding consistent with the pyrodiversity—biodiversity concept [6].

Field research has demonstrated that a combination of late and middle successional habitats is necessary to maximise the diversity of bird, mammal, and reptile taxa in mallee landscapes [19,20,42]. Based on these field data, we found that regimes of small fires created mosaics in which the habitat mixture was optimised for vertebrate diversity, which concurs with prior conceptual and simulation modelling of the influence of fire size on habitat mosaics [6,27]. Additionally, our simulations highlight that the habitat mixture is more stable under a regime of recurrent small fires than in landscapes exposed to larger fire events. Our findings seem strongly applicable to Australian landscapes where large, infrequent wildfires have predominated following the disruption of Indigenous fire management [43–45]. For instance, in the Murray Mallee region, contemporary fire mosaics are very coarse-grained, dominated by a handful of large wildfire events which have occurred in recent decades [26]. The specific patterns of Indigenous fire use in the region before the European invasion are unknown [33], but it is likely that fires were more numerous and smaller, as is the case in other semi-arid and arid Australian systems for which information on Indigenous fire use is available [46,47]. Previous work has shown that the fine-grained mosaics which occur under Indigenous burning can allow a greater diversity of habitats to persist, as evidenced by the presence of long-unburnt patches in areas of continuous flammable vegetation where Indigenous PMB continued after the European invasion [27,48–50].

There is evidence that fine-grained burning by Indigenous people can increase the abundance of wildlife, including game species [48,51]. The loss of fine-grained Indigenous burning, for example, has been implicated in the widespread decline of the mala (*Lagorchestes hirsutus*) in central Australia, which was once a major food source for Indigenous hunters [52]. The cessation of Indigenous fire management, and subsequent predominance of coarse-grained fire mosaics, has likely disadvantaged other vertebrates since the European invasion, although this is difficult to quantify given that pre- or early-European baselines are lacking [53]. Furthermore, contemporary studies are likely to be biased against such declining species because rare species are often excluded from analyses. For example, in the mallee, species observed at less than 9% of study sites were excluded from the data set on which we base our study [24].

In topographically subdued landscapes such as the mallee, fire mosaics and fire regimes interact because feedbacks exist between mosaic patterns and fire spread [54]. For example, fire behaviour simulations suggest that in landscapes with continuous uniform fuels, wildfires spread less readily following fine-grained fuel removal than if the same area of fuel was removed in larger blocks [55]. Both recently burnt and long-unburnt vegetation may reduce fire spread and lead to smaller, patchier fires [56–58]. Infrequent large fires, however, can both create coarse-grained mosaics and be a product of them, because more continuous fuels favour fire spread. Additionally, biota that are influenced by fire mosaics can help reinforce them by modifying fuel loads [57,59]. For example, in the mallee, a large ground-dwelling bird (malleefowl, *Leipoa ocellata*) prefers long-unburnt habitat [5] and reduces fire risk by collecting leaf litter to create large nesting mounds [60].

We omitted such feedbacks in our modelling so that fire size was unaffected by underlying mosaic patterns or the biotic assemblage. Further, we simulated homogeneous landscapes comprised only of Triodia mallee (the most common and flammable vegetation type in the Murray Mallee region), whilst real-world mallee systems contain areas of less flammable vegetation, such as Chenopod mallee and *Allocasuarina* woodland [33]. Although mallee systems are renowned for having fewer barriers to fire spread and experiencing larger, more uniform fires than most vegetation types [33], it is likely that our approach exaggerates the capacity of large fire events to completely homogenise the landscape.

Importantly, the index we used to assess the availability of optimal habitat to maximise vertebrate diversity was based only on the areal extent of each habitat type in the landscape. Although this approach has underpinned analyses of species diversity and fire-driven habitat mosaics in northern Australia [15,18], it represents a very simplistic approximation of the actual relationship of vertebrate species to fire mosaics because it is not able to account for the movement of species between habitat patches, nor the role of habitat patch size. For instance, small patches result in more edge relative to interior habitat, which can advantage species which use multiple habitat types or utilise boundaries for hunting [61]. Edge effects may also reduce the utility of small patches; for example, the impact of predation by feral cats and foxes is exacerbated at edges adjacent to recent burns, highlighting the value of a coarse-grained mosaic for some species [62]. It is also well known that some fauna species are sensitive to the spatial configuration of habitat within their home range [63,64]. Prior research has shown that fine-grained diversity benefits species that use multiple habitats for different resources, such as food sources or structural attributes, and hence require habitat diversity within their home range [22]. For instance, the decline of Australian mammal and bird species has been attributed to the prevalence of coarse-grained mosaics, in which their required habitats are rarely juxtaposed. These include the long-nosed potoroo (*Potorous tridactylus*), known to use a number of vegetation types at fine scales [65], and the partridge pigeon (*Geophaps smithii*), a ground-dwelling, granivorous bird, which forages in recently burnt savanna but relies on unburnt cover for nesting [53]. Attaining a sophisticated understanding of how taxa perceive fire-mediated habitat mosaics is challenging, especially for rare species and processes which operate over long time scales, and fire managers lack such detailed information in most cases [30,66]. Thus, to accurately predict the long-term effects of fire patterns on fauna would require a mechanistic understanding of how species utilise habitat mosaics [5,66].

A related caveat is that our simple simulation approach did not consider the interplay between patch dynamics and animal dispersal, instead assuming that all patches were occupied by the animal species associated with that habitat type. In reality, patches can only be colonised if they coincide with a source population in both time and space. Isolated habitat patches may contain a subset of the species to which they are habitable because some species do not reach them. Furthermore, when a habitat type is absent from a landscape, species dependent on that habitat must become locally extinct and then be absent from patches of that habitat which subsequently develop. For these reasons, it is likely that the biodiversity index we used to assess habitat availability overestimates the presence of some species, particularly in coarse-grained mosaics where habitat types disappeared for parts of the time series, and patches tended to be more spatially isolated. These processes are difficult to demonstrate in the field, given the spatiotemporal scales over which they operate. Nonetheless, inappropriate fire regimes have often been implicated in local extinctions [67,68]. Mechanistic simulations, incorporating both fire patterns and species dispersal parameters, are an approach which can be used to study these processes [30,66]. Indeed, one such exercise, which focused on the malleefowl (*Leipoa ocellata*), emphasised the importance of small, patchy fires for its long-term persistence [5,66]. We hypothesise that undertaking such an exercise for a suite of fire-responsive species in the mallee system would reinforce that regimes of large fires decrease biodiversity over long time scales.

Our study contributes to the ongoing debate about the extent to which pyrodiversity maintains biodiversity. The term pyrodiversity was originally coined to include all

landscape variability in fire regimes [6], although it has been recently broadened to encapsulate biotic feedbacks [56]. The field research program on which our simulation was based—the Mallee Fire and Biodiversity Project—operationally defined pyrodiversity as the proportional mixture of separate fire histories [18–21,24,25]. Because the relationship between stand age evenness and vertebrate diversity in the mallee was not monotonic, Kelly et al. [24] concluded that "pyrodiversity does not increase biodiversity per se". However, using the same data, we found that small fire regimes created fine-grained mosaics in which the habitat mixture was optimal for vertebrate diversity, and we interpret this as support for the pyrodiversity–biodiversity hypothesis. It is important to note that the core difference between the empirical field studies [19–21] and our simulation study hinges on long-term patch dynamics. The effects of fire size on habitat mixture disclosed by our simulation are not detectable using field surveys, which focus on patterns in the visible mosaic at a single point in time [16,24].

Martin and Sapsis's [6] pyrodiversity–biodiversity hypothesis asserts that fine-grained mosaics are superior to coarse-grained mosaics for conserving biodiversity. Such fine-grained pyrodiversity is typically delivered using PMB, and our study supports this management approach because a regime of small fires stabilised the mosaic in the optimal habitat mixture for vertebrate diversity in the mallee. Our results also highlight the value of suppressing large unplanned fires in the mallee region, in line with existing recommendations [24]. We acknowledge, however, that there is evidence of the negative effects of small patch sizes on biodiversity [9,69–72]. Furthermore, many species are resilient to a range of fire regimes [13,14]. Therefore, fire management should be appropriate to the context and needs to consider the requirements of any species of special conservation concern. It is more cost-effective and less laborious to burn at larger scales [13,14,73], so managers should create habitat mosaics with demonstrable benefits to biota, rather than uncritically assume fine-grained patchiness is beneficial [9,22]. Furthermore, field data are required to determine the optimal grain size of mosaics for a particular system [66]. To resolve these questions, it would be possible to combine comprehensive field data on species habitat preferences and dispersal parameters with a sophisticated simulation modelling approach [30], although this was not possible using our simpler approach, which was designed only to test a core mechanism underpinning the P–B hypothesis.

5. Conclusions

In the south-east Australian mallee, Kelly et al. [24] concluded that pyrodiversity, defined as evenness in the proportionate mixture of states, does not increase biodiversity. Using the same data, we demonstrate that mosaic grain size—a key element of pyrodiversity, especially in a fire management context—drives major differences in the availability of optimal habitat for vertebrate species. We found that a regime of small fires optimises the proportional mixture of habitat types for vertebrate diversity over long time scales. Our analysis highlights how fine-grained fire-driven mosaics can benefit biodiversity, supporting the Martin and Sapsis [6] pyrodiversity–biodiversity hypothesis and lending support to the patch mosaic burning paradigm. Further research is required to disclose the ecological and ecophysiological basis for associations between fine-grained mosaics and wildlife assemblages highlighted by this study, and to determine the range of environments where the association between pyrodiversity and biodiversity holds. Improving our understanding of the interactions between biodiversity and fire regimes—including pyrodiversity—is a critical step towards improving existing models (e.g., [24,31,32]) intended to guide fire management in this, and other, fire-prone biomes.

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