Does pyrodiversity beget alpha, beta or gamma diversity? A case study using reptiles from semi-arid Australia

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Abstract

Aim: A common assumption in fire ecology and management is that landscapes with a greater diversity of fire-ages will support a greater diversity of animal species (i.e. 'pyrodiversity begets biodiversity'). This assumption is based on the idea that landscapes with a more diverse fire history provide a greater array of post-fire habitats, leading to a greater number of species within the landscape. We assessed the hypothesis that pyrodiversity begets biodiversity by enhancing community differentiation (β diversity), resulting in increased landscape-scale richness (γ-diversity). We used reptiles as a case-study.

Location: The mallee region of south-eastern Australia.

Methods: We used a study design in which 'whole' fire mosaics (12.6 km^2) were the unit of replication. Study landscapes (n=28) were selected to represent a gradient in the diversity and extent of fire age-classes. We surveyed reptiles by using pitfall traps at 10 sites within each landscape (280 sites in total). Reptile data were used to characterise reptile assemblages at the landscape-scale in three ways; alpha (average within-site diversity), beta (between-site diversity) and gamma diversity (total diversity).

Results: The diversity of fire age-classes had little influence on the alpha, beta or gamma diversity of reptile assemblages. The properties of fire mosaics that most influenced assemblages were the extent of structurally important fire age-classes. The extent of long-unburned vegetation increased beta diversity but reduced alpha diversity of the total reptile assemblage, essentially cancelling each other out at the landscape scale.

Main conclusions: This study highlights the importance of considering multiple measures of diversity when exploring the influence of landscape properties on biodiversity, as 'null' results at the landscape scale (gamma diversity) can result from contrasting patterns in alpha and beta diversity. Using fire to create habitat mosaics, at the scale of this study, is unlikely to enhance the status of reptiles in the region.

Keywords: fire ecology, patch-mosaic burning, pyrodiversity, reptiles, fire management, semi-arid, β-diversity

(A) Introduction

Fire influences ecosystems throughout the world by altering the distribution of key resources for plants and animals (Bowman *et al*., 2009). Different species often peak in abundance at different seral stages following fire, due to changes in the availability of resources as time since fire progresses (Hutto *et al*., 2008; Smith *et al*., 2013**).** Consequently, many authors advocate managing for a mosaic of patches of differing fire ages as a means of maximising species diversity (Parr & Andersen, 2006); assuming that diversity of fire-ages is a surrogate for biodiversity, or that “pyrodiversity begets biodiversity” (Martin & Sapsis, 1992). Management based on this logic is known as ‘patch-mosaic burning’ and has been integrated into fire management throughout the world (Parr & Brockett, 1999; Keith *et al*., 2002). However, despite widespread application, there is a growing body of empirical evidence which questions the relevance of the pyrodiversity hypothesis to a range of taxa (e.g. Pastro *et al*., 2011; Davies *et al.*, 2012; Kelly *et al*., 2012; Taylor *et al*., 2012).

One matter frequently overlooked is the level of diversity that pyrodiversity is expected to influence; α, β or γ diversity (or all three) (Pastro *et al.*, 2011). Alpha-diversity is the diversity of species at a particular site, β-diversity represents the difference in species identities between sites, and γ-diversity refers to the diversity of species pooled across sites within a landscape (Whittaker, 1960, 1972; Anderson *et al*., 2011). Conceptually, the pyrodiversity begets biodiversity hypothesis is built on the notion of community differentiation (Pastro *et* *al.,* 2011). Landscapes with a greater diversity of fire-ages are predicted to have greater between-site diversity; that is, higher β-diversity. This is because such landscapes are presumed to be more heterogeneous across space owing to the strong influence of time since fire on vegetation structure (e.g. Haslem *et al.,* 2011). Higher β-diversity, it is assumed, will result in a greater number of species in the landscape as a whole; that is, higher γ-diversity (Fig 1a).

An issue often neglected in the pyrodiversity hypothesis is the role of the properties of fire mosaics *other than* the diversity of fire-ages in influencing diversity. Increasing the total extent of a preferred fire age could increase α-diversity, as species are added to sites of a preferred fire-age only when their spatial requirements are met (Kelly *et al.,* 2012; Taylor *et al.,* 2013). However, this could also favour a particular suite of species that specialise within a given fire-age, which are then repeated throughout the landscape, thereby reducing β-diversity (Fig 1b; also see Pastro *et al.,* 2011). Such contrasting relationships between α and β-diversity, which have been documented in agricultural landscapes (Tylianakis *et al.,* 2005), have the potential to cancel each other in terms of γ-diversity. An improved understanding of how fire mosaics influence biodiversity will be gained by exploring changes in α, β and γ-diversity across whole landscapes that differ in the diversity and extent of fire-ages.

One reason that these questions are not well-addressed is because fire ecology has focussed mainly on local successional trajectories of species following fire, such that most studies are conducted at the site-level. By contrast, questions about patterns of diversity across ‘whole’ landscapes (*sensu* Bennett *et al.* 2006), particularly those concerned with the drivers of community differentiation, require a landscape perspective. That is, both response and predictor variables characterise entire fire mosaics, allowing a direct comparison of fauna in fire mosaics that differ in the extent and diversity of fire-age classes (e.g. Taylor *et al.* 2012).

Here, we explore how the properties of 'whole' fire mosaics influence α, β and γ-diversity of reptile communities across a ~100,000 km^2 study area within the fire-prone 'mallee' ecosystem of south-eastern Australia. This study builds on previous work within the region on individual reptile species (Nimmo et al., 2013), that found no reptile species were associated with the diversity of fire-age classes within a landscape. This is the first study to examine the effects of the properties of fire mosaics on reptile assemblages, and at all three levels of diversity for any taxonomic group. Our experimental design samples both response and predictor variables across entire landscapes, thereby allowing a direct comparison of biodiversity in different fire mosaics. Further, because the sampling design is hierarchical, with sites nested within landscapes, it is well suited for assessing how fire affects species diversity at the α, β and γ levels. This is the first study to explore the effects of fire mosaics on reptile communities, and to test the pyrodiversity hypothesis on any taxonomic group at all three levels of diversity.

The study taxa, reptiles, are a major component of the fauna of semi-arid Australia, with approximately 60 species occurring in the study region. Mallee reptiles often show clear responses to fire because their shelter substrates are strongly affected by fire (Nimmo *et al.*, 2012; Smith *et al.*, 2013). The high diversity of reptiles and the fire-prone nature of mallee ecosystems make this an ideal system for exploring the role of fire mosaics in influencing fauna. Our aims are to: 1) test the hypothesis that pyrodiversity enhances reptile diversity; 2) increase understanding of how pyrodiversity influences α, β and γ-diversity; and 3) examine whether the properties of fire mosaics other than pyrodiversity influence α, β and γ-diversity.

(A)Methods

(B) Study area

The study area encompasses 104,000 km^2 in the Murray Mallee region of south-eastern Australia, including parts of three states: Victoria, New South Wales and South Australia (see Appendix S1). The main vegetation is 'tree mallee' dominated by eucalypts with a 'mallee' growth form (i.e. multiple stems arising from an underground lignotuber). Further descriptions of the study area can be found in Haslem *et al*. (2010; 2011). The fire regime within the study areas is characterised by large (>10,000 ha) fires typically ignited via lightning strikes during the spring and summer months, with inter-fire intervals of predominately >35 years (Avitabile *et al*., 2013).

(B) Study design

We selected 28 study landscapes, each a 4 km diameter circle (12.6 km^2 in size), located > 2 km apart (mean separation = 130 km, range = 6.3 - 217 km). Landscapes were stratified by: 1) the proportional extent of 'old' mallee (i.e. vegetation >35 years since fire) (range 0-100%) and 2) the number of fire age-classes (from 1-7). The properties of fire mosaics were quantified by mapping all fires in the study region between 1972 and 2007 from Landsat imagery, with a pixel resolution of 25 x 25 m (Avitabile *et al*., 2013). Maps were converted to shape files for use in GIS.

Surveys for reptiles were undertaken at 10 sites within each of the 28 study landscape (i.e. *n* = 280 sites). Placement of sites was determined firstly by the extent of each fire age-class (i.e. 0-10% = 1 site, 10-20% = 2 sites, 20-30% = 3 sites etc); and secondly to capture topographic variation (dune, swale) within fire age-classes. Sites were typically >100 m from the boundaries of fire scars, >25 m from access roads, and >200 m apart. Where possible, at least one site was placed in each quadrant of the landscape.

(B) Reptile surveys

At each site, 10 pitfall traps (20 L plastic buckets) were spaced at 5 m intervals, connected by a 50 m drift fence (~20 cm high). Pitfall trapping was carried out for five nights in spring and summer during 2006/07 and 2007/08 in each landscape, resulting in ~56,000 trap-nights. A large wildfire during spring 2006 modified three landscapes. Because of changes to mosaic structure, the spring 2006 data from these landscapes were excluded, and they were subsequently sampled twice in spring 2007. Trap lines were checked daily. All reptiles were identified, marked with a small dot of paint to identify recaptures during each five night survey period, and released near the point of capture.

(B) Modelling the diversity of reptiles

We used an information theoretic approach to examine relationships between α, β and γ-diversity of reptiles (the response variables), and the properties of fire mosaics (predictor variables). We were interested in variation in community structure as it relates to landscape properties, as opposed to directional turnover (Anderson *et al*., 2011). We used species richness as the measure of diversity: γ-diversity was the total number of reptile species recorded in a landscape, α-diversity was the mean number of species per site within each landscape, and β-diversity was calculated using Whittaker's (1972) measure as β-diversity = (γ-diversity / α-diversity)-1.

All three diversity measures were calculated first for the entire pool of reptile species, and then for subsets of species based on shelter preferences and commonness. Shelter preference subgroups of reptiles were chosen because elements of their shelter are known to be strongly fire-affected (Haslem *et al*., 2011) and such preferences have formed the basis of conceptual work on reptile post-fire succession (Lindenmayer *et al.*, 2008), particularly in mallee ecosystems (Caughley *et al.* 1985; Driscoll and Henderson 2008; Nimmo *et al.*, 2012; Smith *et al.*, 2013). As with previous studies of reptiles (Caughley et al., Driscoll and Henderson 2008), species were classified into one of three shelter-preference categories (burrowing, spinifex hummock, or litter dwellers) by using field guides and expert opinion (refer to Appendix S3 for details). A subgroup of 'common' species was also considered in order to remove the potentially large effect of rarer species on counts of species richness. Species were regarded as 'common' if they were captured in at least seven out of the 28 study landscapes.

We selected five predictor variables to describe properties of study landscapes. Four of these were calculated in FRAGSTATS version 3.3 (McGarigal *et al*., 2002) from spatial data in ArcMap version 9.2 (ESRI, 2006). These were: 1) the proportional extent of mallee vegetation <10 years since last burnt, 2) the proportional extent of mallee vegetation >35 years since last burnt, 3) the extent of mallee vegetation with an understorey of spinifex grass ('triodia mallee', see Haslem *et al*., 2010), and 4) the diversity of fire patches of different age-classes (Table 1; Appendix S2). Variables representing the configuration of fires (a possible surrogate for fire intensity) were also explored, but were found to be highly collinear with the extent of fire-ages, as landscapes with a large proportion of a given fire age typically had a more aggregated configuration. Thus, to avoid unreliable parameter estimates due to collinearity between predictors, we included only extent variables. In addition, the northing co-ordinate of the centre of each landscape was used to represent the position of each landscape along an environmental gradient of increasing aridity, from south – north in the region (Pausas & Bradstock, 2007).

Prior to model selection, univariate models of the relationship between each response and predictor variable were generated, in which linear and logarithmic terms were compared using Akaike's Information Criterion corrected for small samples (AICc), to assess the appropriate form of the relationship.

Generalised linear mixed models (GLMMs) were developed using combinations of the five predictor variables (as fixed effects) (Table 1). The subregion (i.e. north or south of the Murray River) and the reserve system (e.g. Murray Sunset National Park, Scotia Sanctuary) in which each study landscape was located were included as random effects (Table 1) to account for possible non-independent error structure in the data. AICc was used to compare and rank models (Burnham and Anderson, 2002). To calculate the difference between the best model and all others in the candidate set, differences in AICc values (Δ_i) were calculated. Models with $\Delta_i \leq 2$ have substantial support (Burnham & Anderson, 2002). We calculated Akaike weights (w_i), which represent the probability that a model is the best in the set. In the absence of a clear ‘best’ model (i.e. $w_i < 0.9$), model averaging was conducted to determine the influence of each explanatory variable. Model fit was assessed using marginal and conditional coefficients of determination (Nakagawa & Schielzeth, 2012). A predictor variable was considered to have an influence on the response variable (diversity measures) if the coefficient ± 95% confidence intervals did not overlap with zero.

Regression modelling and model averaging were performed using the lme4 (Bates *et al.*, 2012) and MuMin (Barton, 2012) packages in R version 2.15.1 (R Development Core Team, 2012).

(A) Results

(B) General trapping results

After 56 000 trap-nights across the 28 study landscapes, we captured >7200 individuals from seven families, representing 55 species of reptiles. The numbers of landscapes in which each species was recorded are given in Appendix S3. Species richness of reptiles in the study landscapes (γ-diversity) ranged from 20 - 35 (mean = 26), α-diversity for study landscapes ranged from 7.6 -13.7 (mean = 10.2), and β-diversity ranged from 0.9 - 2.6 (mean = 1.7).

(B) Model selection

The results of GLMMs using combinations of the five explanatory variables are presented in Table 2. Model averaging was performed to calculate the size and direction of parameter estimates because no single model was identified as clearly the best fitting for any response variable (Akaike weights (w_i) for each of the models with $\Delta_i \leq 2$ were below 0.9: Table 2).

(C) *Alpha diversity*

The α-diversity of spinifex-dwelling reptiles increased in landscapes with a greater diversity of fire-age-classes. However, no other α-diversity measures were influenced by the diversity of fire ages (Fig. 2). The average number of common species per site within a landscape (i.e. common α-diversity) was greater with increasing extent of triodia mallee vegetation in the landscape. Alpha diversity of total species, common species and litter-dwelling species was lower in landscapes with increasing extent of recently burnt vegetation. Additionally, α-diversity of total, common, burrowing and spinifex-dwelling species was lower in landscapes with increasing extent of long-unburnt vegetation (Figs. 2 & 3). Alpha diversity increased as the position along a south-north gradient (Northing) increased, for all species groups except litter-dwelling species (Figs. 2 & 4).

(C) *Beta diversity*

The only influential relationship between β-diversity of reptiles and pyrodiversity was for spinifex-dwelling species, for which β-diversity was lower (i.e. assemblages more similar) in landscapes with more diverse fire age-classes. For the overall reptile community, the β-diversity for total species increased with increasing extent of long-unburned and recently burnt vegetation (Figs. 2 & 3); and the β-diversity of litter-dwelling species also increased with increasing extent of recently burnt vegetation (Figs. 2 & 4). Total assemblages and the assemblages of common species and spinifex-dwelling species had lower β-diversity in landscapes with increasing extent of triodia mallee vegetation (Fig. 2). In relation to the south-north environmental gradient of increasing aridity, β-diversity increased for the total assemblage and for common species and litter-dwelling species in landscapes further north (Figs. 2 & 4).

(C) *Gamma diversity*

The diversity of fire age-classes in a landscape had little influence on the γ-diversity of reptiles (i.e. the total number of species within each landscape) (Fig. 2). Similarly, the extent of triodia mallee vegetation had no influence on the γ-diversity response variables analysed. The proportional extent of either recently burnt vegetation (<10 years since fire) or long-unburnt vegetation within a landscape also had relatively little influence upon reptile diversity (Fig. 1), except for γ-diversity of spinifex-dwelling species, which decreased with increasing extent of long-unburnt vegetation (Fig. 1). The environmental gradient (Northing) was the strongest predictor of increased γ-diversity (Fig. 4).

(A) Discussion

The patch-mosaic burning paradigm underpins fire management policies in regions around the world (Parr & Andersen, 2006; Driscoll *et al*., 2010), and yet has been rarely tested using empirical data (Taylor *et al*., 2012; Kelly *et al*., 2012). Contrary to the prediction that ‘pyrodiversity begets biodiversity’, we did not observe a clear relationship between the diversity of fire age-classes (‘pyrodiversity’) and the diversity of reptile communities. Indeed, with the exception of the α diversity of spinifex-dwelling species, the diversity of fire ages had no positive influence on any diversity measure – α, β or γ. Instead, the properties of fire mosaics that most influenced reptile diversity were the spatial extent of particular fire age-classes. These effects were seen only at the level of α and β-diversity, and were generally secondary to that of the environmental gradient across the study region.

(B) Pyrodiversity and reptile diversity

The pyrodiversity hypothesis received essentially no support from this study at any level of diversity, with one exception (α-diversity of spinifex-dwelling species). That is, landscapes with a more diverse fire history had a similar or lower level of α, β and γ-diversity as those dominated by a single age-class. The premise of the hypothesis is that different fire-age classes provide different kinds of resources, which in turn support different sets of species (Pastro *et al*., 2011): hence, a landscape which comprises a diversity of fire-ages is predicted to support a greater richness of species. However, while reptile species do vary in frequency of occurrence and abundance in relation to post-fire succession in mallee ecosystems, with some favouring early, mid and later fire age-classes (e.g. Smith *et al*. 2012), relatively few species occur *exclusively* in a particular fire age-class (Nimmo *et al*., 2012). Rather, many species occur across a broad range of fire age-classes, albeit in lower abundances in some than others (Driscoll and Henderson 2008; Smith *et al.* 2013). Thus, the presence of additional fire age-classes in a landscape may not necessarily result in greater richness of species. The relevance of pyrodiversity is likely to be even less in systems where faunal species do not show a strong response to time since fire (e.g. Lindenmayer *et al*. 2008).

Our results also highlight the potential variation in communities that can occur in a single fire age-class. Far from being a homogenous set of species repeated in communities throughout the spatial extent of an age class, individual fire age-classes can contain a diverse set of communities due to natural environmental gradients and differing histories.

(B) Properties of fire mosaics

Our study highlights the importance of considering multiple levels of diversity when studying landscape-scale patterns in biodiversity. Although the properties of fire mosaics did not strongly influence γ-diversity of any response variable, patterns of α and β-diversity showed that the properties of fire mosaics do influence reptile communities. Had we studied only γ-diversity, such insights would have been overlooked.

The interplay between α-diversity and β-diversity is of central importance to the findings of this study. For several response variables, a null response to landscape properties in γ-diversity could be explained by contrasting relationships between landscape properties and α and β-diversity. For example, the extent of long-unburned vegetation, which has been shown to be an important driver of the γ-diversity of birds (Taylor *et al*., 2012), did not influence the γ-diversity of reptile communities. However, long-unburned vegetation positively influenced β-diversity, such that landscapes with more long-unburned vegetation had greater variation between communities. This increase in community differentiation may be due to older sites having greater variability in habitat structure as a result of historical effects (e.g. grazing, rainfall events), and different successional pathways that might emerge as time since fire increases (Taylor & Chen, 2010).

The increase in community differentiation in landscapes dominated by long-unburned vegetation was accompanied by a reduction in the average number of species per site. This decline is likely a consequence of a decline in spinifex cover at sites older than 40 years post-fire (Haslem *et al*., 2011). This keystone structure for reptiles in arid and semi-arid Australia is critical to several reptile species which are unlikely to occur in its absence (Pianka 1969). The contrasting relationships of α and β-diversity effectively cancel each other out at the landscape scale, leading to the lack of relationship between long-unburned vegetation and reptile γ-diversity. These findings contrast with those of Pastro *et al.* (2011), who found more congruent patterns of α and β-diversity in lizard communities in response to wildfire and prescribed burning in Australia's arid zone.

Subgroups of species based on shelter preferences also showed patterns in α and β-diversity. The α-diversity of litter dwellers decreased as the amount of recently burned vegetation in the landscape increased, while the α-diversity of spinifex and burrowing species declined as the amount of long-unburned vegetation increased. Such responses relate to the landscape-scale distribution of the shelter resources on which these species depend (see above). These results highlight that the landscape-scale properties of fire mosaics have flow-on effects for the number of species that occur at a given site of a given fire-age. That is, holding the suitability of a site constant (in terms of fire-age), larger numbers of species occur at a site if the spatial extent of a preferred fire-age within a landscape is high. This could be due to some species occurring within a landscape only once a minimal spatial requirement (in terms of a fire-age) is met (Nimmo *et al.,* 2013; Taylor *et al.,* 2013).

We did not model the effects of mid-successional vegetation (i.e. 11-34 years since fire) on reptile diversity due to its negative correlation with the extent of long-unburned vegetation. However, the relationships described above suggest that increasing the amount of mid-successional vegetation would positively influence α-diversity, but negatively influence β-diversity of the overall reptile assemblage. Again, important changes in mallee vegetation occur in this fire age: notably, the percentage cover of spinifex reaches a maximum at ~30 years post-fire (Haslem *et al*., 2011). Our results suggest that while spinifex enhances α-diversity, it may reduce β-diversity. Thus, increasing the extent of mid-successional vegetation across the landscape will not necessarily enhance landscape-scale richness, but may be important for individual species (Nimmo *et al.* 2013).

One important caveat of our findings relates to spatial scale. We measured the response of reptile diversity to pyrodiversity at a single spatial scale, whereas patterns in the occurrence of species and the structure of communities can be scale-dependent (Wiens *et al.*, 1989). We cannot discount that heterogeneity induced by fire may influence reptiles at a finer or broader spatial scale than the current study. However, we chose a spatial grain that reflects the scale at which management usually takes place (i.e. kms^2), and one large enough to encapsulate population-level processes for the predominantly small-bodied reptile species studied. Assessing whether the effects of landscape heterogeneity on faunal diversity are scale-dependent is a challenge not only for fire ecology, but also for ecology more generally (Fahrig *et al.*, 2010).

Another factor beyond the scope of the current study is the importance of the ‘invisible mosaic’ (*sensu* Bradstock *et al.*, 2005); that is, the spatial distribution of vegetation with differing ‘fire regimes’ (i.e. the season, interval and intensity of fires, in addition to time since the last fire; Gill 1975). Future research on faunal response to fire mosaics should seek to fill this important knowledge gap.

(B) Biogeographic gradient

The strongest influence on the diversity of reptile communities was the geographic location of the study landscape, with those to the north of the study region (more arid) having a greater diversity of reptiles at all levels. Again, modelling α, β and γ-diversity together highlighted interesting patterns of change in community attributes across this gradient. For γ-diversity, the strong relationship with northing is due to increases in both α and β-diversity: that is, moving from south to north, sites have more species on average *and* there are more diverse assemblages within landscapes. This north-south gradient correlates strongly with aridity, such that landscapes in the north receive less rainfall and higher temperatures than those in the south (Pausas & Bradstock, 2007). Environmental temperatures constrain the ability of reptile species to acquire resources, as temperatures below a species' thermal tolerance zone will prevent activity (Heatwole & Taylor, 1987). Thus, in warmer environments, more reptile species are likely to reach their thermal tolerance zone and remain active, and hence persist (Buckley & Jetz, 2009). Our data suggest that this allows both for more species to persist per unit area *and* for more diverse communities to develop across space.

(B) Implications and conclusions

Many authors have recommended that mosaic burning will benefit biodiversity conservation as it provides a variety of resources for species that depend on different fire age-classes. However, at the scale at which we sampled (landscapes of 12.6 km^2, 4 km diameter), the 'pyrodiversity' or 'patch mosaic burning' paradigm (Parr & Andersen, 2006) was not supported. Similarly, in contemporaneous studies, the species richness of birds (Taylor *et al.*,

2012) and small mammals (Kelly *et al*., 2012) were not associated with fire-mediated heterogeneity in mallee ecosystems. Instead, the species richness of birds was positively associated with the increasing extent of older (>35 years since fire) vegetation in the landscape (Taylor *et al*., 2012).

These results suggest that management of tree mallee vegetation to create a fine-scaled mosaic of different post-fire ages is unlikely to enhance the status of reptiles in this region. Instead, we advocate fire management actions that aim to create and maintain high proportions of mid-successional vegetation (11-34 years since fire) and retain long-unburnt (>50 years since fire) vegetation in order to enhance reptile diversity in the region. This contrasts with other ecosystems, such as tropical savannah woodlands in northern Australia, where fine-scaled application of fire is considered beneficial; for example, at the scale of individual home ranges (Firth *et al*., 2010). Such differences highlight the importance of understanding the ecological role and impacts of fire in different ecosystems, and its relationship with different taxa. Fire remains an important tool for ecological management in fire-prone environments, but management strategies identified in one system are not necessarily transferable, without modification, to others. A valuable area for future research in this region would be to determine the extent to which fire needs to be introduced (*cf.* natural occurrence) to ensure the provision of mid-successional vegetation through time, and the possibility of using strategic burning to protect long-unburned areas from wildfires.

Although we found little evidence that pyrodiversity benefits reptile assemblages at the scale studied, there remains a potential need for a range of different fire age-classes at a regional scale to ensure the ongoing provision of optimum habitat for species that favour different age-classes in mallee ecosystems (Nimmo *et al*., 2013). Interestingly, our results pose questions that can be answered only at an even broader scale than the current study; namely, whether creating very coarse-scale mosaics (i.e. at the scale of tens of km^2) of mid and late-successional vegetation would enhance regional diversity by increasing both α-diversity and β-diversity at the landscape scale.

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Supplementary Material

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

Appendix S1 {Study region and study landscapes}

Appendix S2 {Gradient of pyrodiversity across study landscapes}

Appendix S3 {Reptile species list, including number of landscapes occupied}

Appendix S4 {Parameter estimates and model fit of Generalised Linear Mixed Models}

BIOSKETCH

Lisa Farnsworth is an ecologist working with the Australian Wildlife Conservancy; Dale Nimmo is an Alfred Deakin Research Fellow at Deakin University. This work was conducted as part of the Mallee Fire and Biodiversity Project. Author contributions: MFC and AFB initiated the study and all authors contributed to ideas and study design, LMF and DGN jointly led the writing, DGN undertook the statistical analysis, and MFC, AFB and LTK provided editorial comment. All authors contributed to field data collection.

TABLES

Table 1 Explanatory variables used in models to determine the influence of landscape properties on the diversity of reptiles in the Murray Mallee region.

Variable name	**Description**
Northing	The north co-ordinate of each landscape, measured from its mid-point (range =6126593 - 6338134, mean = 6220160)
Recently burned	The proportion of each landscape that is aged 0 – 10 years since fire (range =0 - 0.80, mean = 0.62)
Long unburned	The proportion of each landscape that has not experienced a fire for >35 years (range = 0 -1, mean = 0.42)
Spinifex	The proportion of each landscape with triodia mallee vegetation (range =0 - 1, mean = 0.66)
Fire diversity	Shannon-Wiener diversity index for fire patches in a given landscape (range =0 – 1.28, mean = 0.62)
Sub-region	Either north or south of the Murray River
Reserve system	Geographic clusters of reserves within the Murray Mallee region

Table 2 Results from Generalised Linear Mixed Models for diversity measures of reptile species in study landscapes in the Murray Mallee region. Only models with $\Delta_i \leq 2$ are presented.

Response variable	**MODEL**	***K***	**Log Likelihood**	**AIC$_c$**	**Δ_i**	**w_i**
Total species						
α-diversity	NORTHING +LONG UNBURNED +RECENTLY BURNED +FIRE DIVERSITY	8	-37.09	97.76	0.00	0.27
	NORTHING +LONG UNBURNED +RECENTLY BURNED	7	-39.18	97.97	0.21	0.24
	SPINIFEX +NORTHING +LONG UNBURNED +RECENTLY BURNED	8	-37.79	99.17	1.41	0.13
β diversity	SPINIFEX +NORTHING +LONG UNBURNED +RECENTLY BURNED	8	3.42	16.73	0.00	0.33
	SPINIFEX +LONG UNBURNED +RECENTLY BURNED	7	0.53	18.55	1.82	0.13
γ-diversity	NORTHING	5	-59.80	132.33	0.00	0.25
	SPINIFEX +NORTHING	6	-58.52	133.04	0.71	0.18
	NORTHING +RECENTLY BURNED	6	-59.08	134.16	1.83	0.10
Common species						
α-diversity	SPINIFEX +NORTHING +LONG UNBURNED +RECENTLY BURNED	8	-34.26	92.10	0.00	0.40
	SPINIFEX +LONG UNBURNED +RECENTLY BURNED	7	-36.65	92.90	0.79	0.27
β diversity	SPINIFEX +NORTHING +LONG UNBURNED +RECENTLY BURNED	8	8.22	7.13	0.00	0.37
	SPINIFEX +LONG UNBURNED +RECENTLY BURNED	7	5.86	7.87	0.74	0.25
γ-diversity	NORTHING	5	-48.44	109.61	0.00	0.43
Burrowing species						
α-diversity	NORTHING +LONG UNBURNED	6	-28.05	72.11	0.00	0.21
	NORTHING +LONG UNBURNED +FIRE DIVERSITY	7	-26.90	73.39	1.29	0.11
	LONG UNBURNED	5	-30.44	73.61	1.51	0.10
β diversity	LONG UNBURNED	5	-8.46	29.65	0.00	0.15
	SPINIFEX +LONG UNBURNED	6	-7.00	30.00	0.35	0.13
	NULL MODEL	4	-10.34	30.42	0.77	0.10
	FIRE DIVERSITY	5	-8.96	30.65	1.00	0.09
	SPINIFEX	5	-9.13	31.00	1.34	0.08
	LONG UNBURNED +FIRE DIVERSITY	6	-7.67	31.35	1.69	0.07
γ-diversity	NORTHING	5	-49.53	111.79	0.00	0.26
	NULL MODEL	4	-51.43	112.60	0.81	0.18
Litter dwelling species						
α-diversity	RECENTLY BURNED	5	-22.33	57.38	0.00	0.38
	RECENTLY BURNED +FIRE DIVERSITY	6	-21.69	59.38	2.00	0.14
β diversity	RECENTLY BURNED	5	-25.27	63.27	0.00	0.17
	LONG UNBURNED +RECENTLY BURNED	6	-23.84	63.67	0.40	0.14
	NORTHING +RECENTLY BURNED	6	-24.04	64.08	0.81	0.11
	NULL MODEL	4	-27.35	64.44	1.17	0.09
	NORTHING +LONG UNBURNED +RECENTLY BURNED	7	-22.63	64.87	1.60	0.08
	NORTHING	5	-26.22	65.17	1.90	0.07
γ-diversity	SPINIFEX +NORTHING	6	-50.90	117.81	0.00	0.17
	SPINIFEX +NORTHING +LONG UNBURNED	7	-49.21	118.02	0.22	0.15
	NORTHING	5	-52.80	118.32	0.52	0.13
	NORTHING +LONG UNBURNED	6	-51.30	118.60	0.80	0.11
	NORTHING +RECENTLY BURNED	6	-51.30	118.61	0.80	0.11
	SPINIFEX +NORTHING +RECENTLY BURNED	7	-50.08	119.77	1.96	0.06
Spinifex dwelling species						
α-diversity	NORTHING +LONG UNBURNED +FIRE DIVERSITY	7	-16.81	53.23	0.00	0.20
	SPINIFEX +NORTHING +LONG UNBURNED +FIRE DIVERSITY	8	-15.16	53.90	0.67	0.15
	NORTHING +FIRE DIVERSITY	6	-19.29	54.58	1.35	0.10
	SPINIFEX +LONG UNBURNED +FIRE DIVERSITY	7	-17.72	55.04	1.82	0.08
β diversity	FIRE DIVERSITY	5	-35.09	82.90	0.00	0.36
	SPINIFEX +FIRE DIVERSITY	6	-34.09	84.17	1.28	0.19
γ-diversity	LONG UNBURNED	5	-36.04	84.81	0.00	0.17
	NULL MODEL	4	-37.78	85.29	0.48	0.13
	FIRE DIVERSITY	5	-36.54	85.81	1.01	0.10
	LONG UNBURNED +FIRE DIVERSITY	6	-35.12	86.24	1.43	0.08
	SPINIFEX +LONG UNBURNED	6	-35.37	86.74	1.93	0.07

FIGURE LEGENDS

Figure 1 Theoretical relationships between the properties of fire mosaics and α and β diversity, and the hypothetical outcome of those relationships on patterns in γ diversity.

Figure 2 Coefficients (circles) and 95% confidence intervals (lines) of generalised linear mixed models of the response of α, β or γ diversity of reptiles to the properties of land mosaics in semi-arid Australia.

* indicates a log-transformed predictor variable.

Figure 3 The fitted relationship (solid line) and 95% confidence intervals (dark shaded area) between α, β and γ diversity of reptiles and the properties of fire mosaics, derived from generalised linear mixed models.

Figure 4 The fitted relationship (solid line) and 95% confidence intervals (dark shaded area) between α, β and γ diversity of reptiles and northing, derived from generalised linear mixed models.