

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 km²) 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 characterize 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, fire management, patch-mosaic burning, pyrodiversity, reptiles, semi-arid, β -diversity.

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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, 2008; Smith *et al.*, 2013). Consequently, many authors advocate managing for a mosaic of patches of differing fire-ages as a means of maximizing 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 (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 hypothesis that pyrodiversity begets biodiversity 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 species 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.*, 2012). However, this could also favour a particular suite of species that specialize within a given fire-age, which are then repeated throughout the landscape, thereby reducing β -diversity (Fig. 1b; also see Pastro *et al.*, 2011).

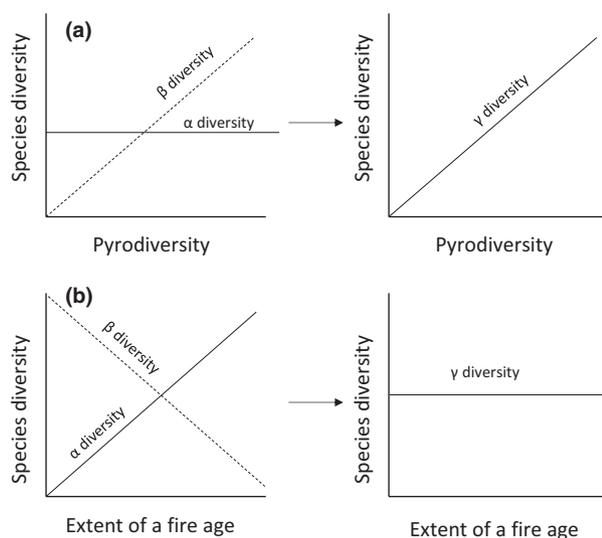


Figure 1 Theoretical relationships between the properties of fire mosaics and α and β diversity, and the hypothetical outcome of those relationships on patterns in γ diversity.

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 out 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 characterize 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 *c.* 100,000 km² 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 whole 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.

The study taxa, reptiles, are a major component of the fauna of semi-arid Australia, with *c.* 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.

METHODS

Study area

The study area encompasses 104,000 km² 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' dom-

inated 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 characterized by large (> 10,000 ha) fires typically ignited via lightning strikes during the spring and summer months, with interfire intervals of predominately > 35 years (Avitabile *et al.*, 2013).

Study design

We selected 28 study landscapes, each a 4 km diameter circle (12.6 km² 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 to 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 m × 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 topographical 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.

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 (c. 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 c. 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.

Modelling the diversity of reptiles

We used an information theoretical 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 land-

scape, 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 = $(\gamma$ -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, 1985; Driscoll & Hendersen, 2008; Nimmo *et al.*, 2012; Smith *et al.*, 2013). As with previous studies of reptiles (Caughley 1985; Driscoll & Hendersen, 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 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 ArcMap 9.2., 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 coordinate of the centre of each landscape was used to represent the position of each landscape along an environmental gradient of increasing aridity, from south to 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 logarithmical terms were compared using Akaike's information criterion corrected for small samples (AICc), to assess the appropriate form of the relationship.

Generalized 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 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 coordinate 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) |
| Subregion | Either north or south of the Murray River |
| Reserve system | Geographical clusters of reserves within the Murray Mallee region |

(Table 1) to account for possible non-independent error structure in the data. AICc was used to compare and rank models (Burnham & 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, 2013). A predictor variable was considered to have an influence on the response variable (diversity measures) if the coefficient \pm 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).

RESULTS

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 to 35 (mean = 26), α -diversity for study landscapes ranged from 7.6 to 13.7 (mean = 10.2), and β -diversity ranged from 0.9 to 2.6 (mean = 1.7).

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).

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).

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).

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

Table 2 Results from Generalized 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 | AICc | 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 |
| β diversity | SPINIFEX + NORTHING + LONG UNBURNED + RECENTLY BURNED | 8 | -37.79 | 99.17 | 1.41 | 0.13 |
| | SPINIFEX + NORTHING + LONG UNBURNED + RECENTLY BURNED | 8 | 3.42 | 16.73 | 0.00 | 0.33 |
| γ -diversity | SPINIFEX + LONG UNBURNED + RECENTLY BURNED | 7 | 0.53 | 18.55 | 1.82 | 0.13 |
| | NORTHING | 5 | -59.80 | 132.33 | 0.00 | 0.25 |
| γ -diversity | 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 |
| β diversity | LONG UNBURNED | 5 | -30.44 | 73.61 | 1.51 | 0.10 |
| | 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 |

AICc, Akaike's information criterion corrected.

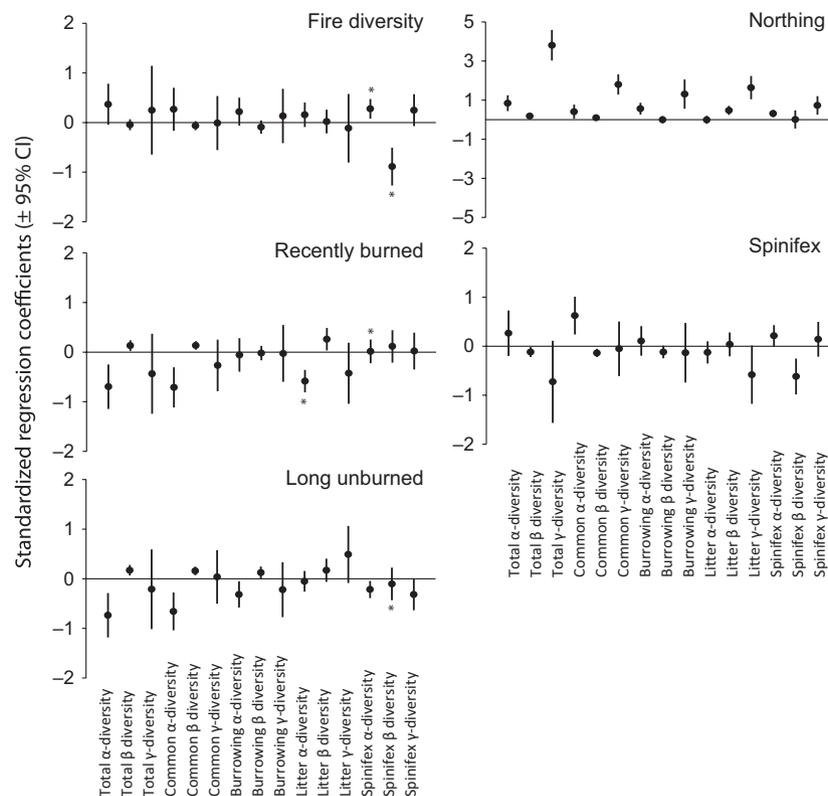


Figure 2 Coefficients (circles) and 95% confidence intervals (lines) of generalized linear mixed models of the response of α , β or γ diversity of reptiles to the properties of land mosaics in semi-arid Australia. *indicates a log-transformed predictor variable.

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. 2), except for γ -diversity of spinifex-dwelling species, which decreased with increasing extent of long-unburnt vegetation (Fig. 2). The environmental gradient (Northing) was the strongest predictor of increased γ -diversity (Fig. 4). A table including parameter estimates and model fit for all models is given in Appendix S4.

DISCUSSION

The patch-mosaic burning paradigm underpins fire management policies in regions around the world (Parr & Andersen, 2006; Driscoll *et al.*, 2010). 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 primarily at the level of α and β -diversity, and were generally secondary to that of the environmental gradient across the study region.

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 & Hendersen, 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

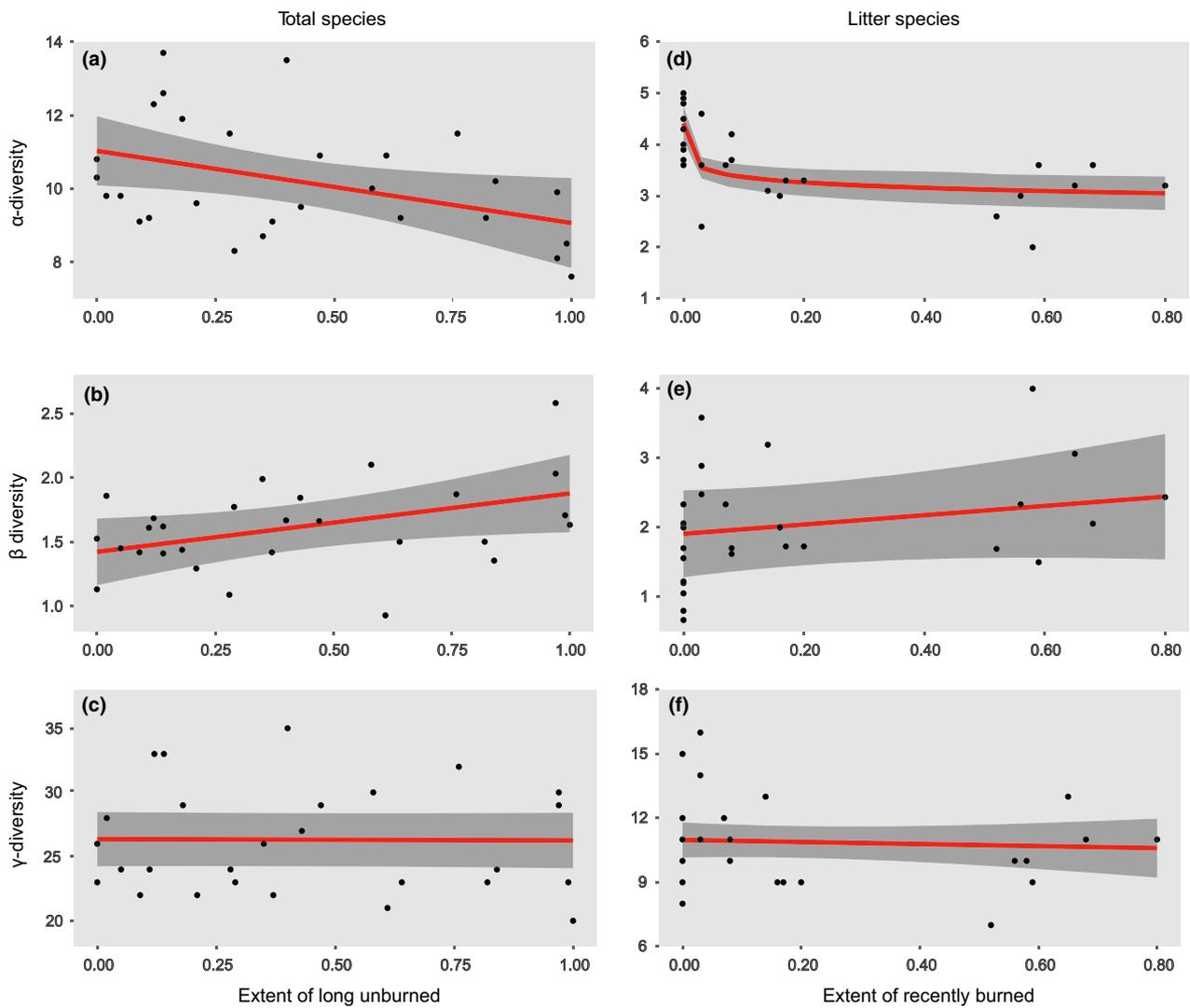


Figure 3 The fitted relationship (solid line) and 95% confidence intervals (dark shaded area) between α , β and γ diversity of reptiles and the properties of fire mosaics, derived from generalized linear mixed models. Models are shown for the total reptile assemblage (a,b, c) and for litter dwelling species (d,e,f).

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.

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, 2011).

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

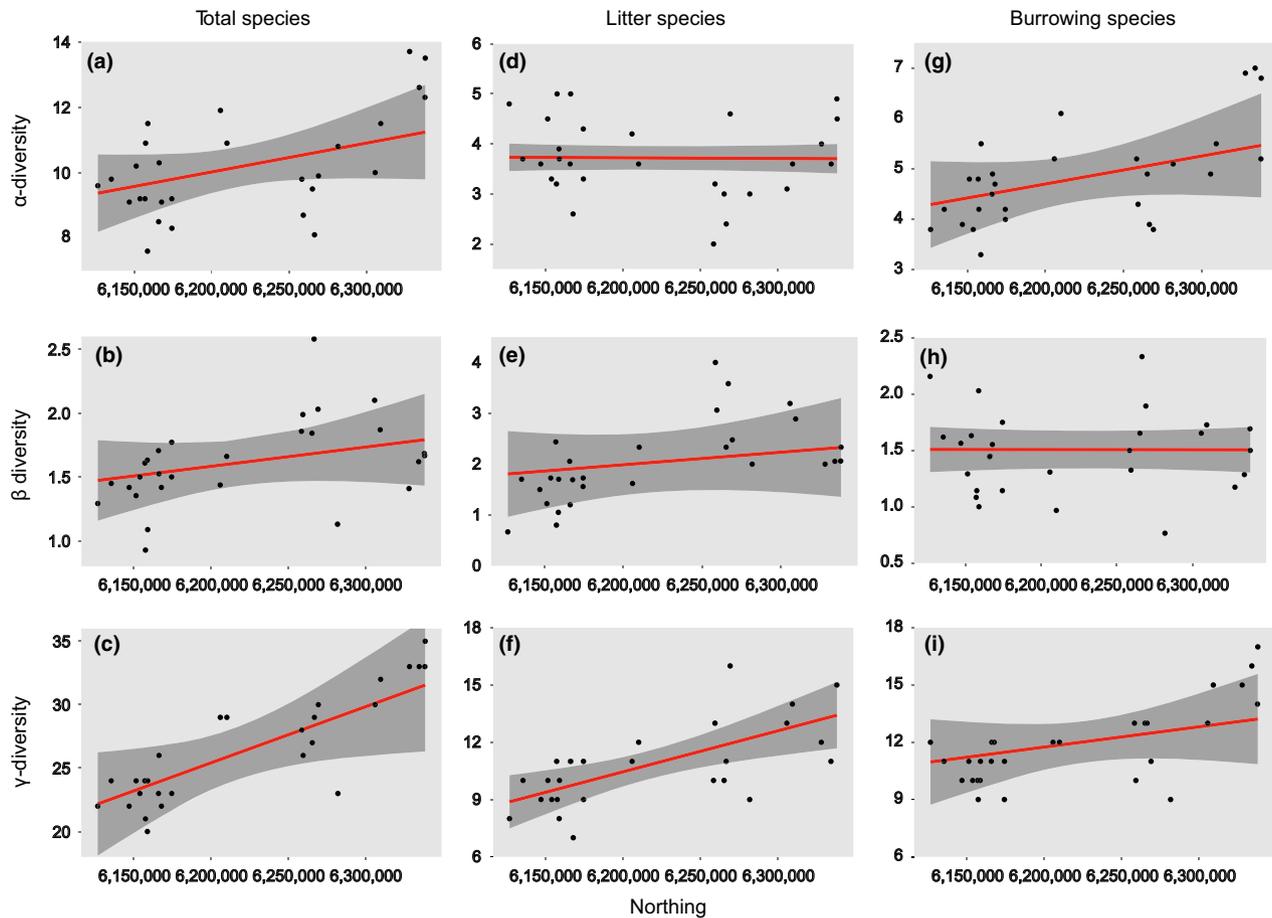


Figure 4 The fitted relationship (solid line) and 95% confidence intervals (dark shaded area) between α , β and γ diversity of reptiles and northing, derived from generalized linear mixed models. Models are shown for the total reptile assemblage (a,b,c), litter dwelling species (d,e,f), and burrowing species (g,h,i).

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 wild-fire and prescribed burning in Australia's arid zone.

Subgroups of species based on shelter preferences also showed patterns in α and β -diversity. For example, 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).

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 vegeta-

tion 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 *c.* 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, 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. kms²), 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.*, 2011).

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.

Biogeographical gradient

The strongest influence on the diversity of reptile communities was the geographical 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.

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 km², 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 to enhance reptile

diversity in the region. This contrasts with other ecosystems, such as tropical savanna 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 km²) 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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SUPPORTING INFORMATION

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 Generalized Linear Mixed Models.

BIOSKETCHES

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.

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