

Effects of long-term fire exclusion and frequent fire on plant community composition: A case study from semi-arid shrublands

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Abstract Time since last fire and fire frequency are strong determinants of plant community composition in fire-prone landscapes. Our study aimed to establish the influence of time since last fire and fire frequency on plant community composition and diversity of a south-west Australian semi-arid shrubland. We employed a space-for-time approach using four fire age classes: ‘young’, 8–15 years since last fire; ‘medium’, 16–34; ‘old’, 35–50; and ‘very old’, 51–100; and three fire frequency classes: burnt once, twice and three times within the last 50 years. Species diversity was compared using one-way ANOVA and species composition using PERMANOVA. Soil and climatic variables were included as covariables to partition underlying environmental drivers. We found that time since last fire influenced species richness, diversity and composition. Specifically, we recorded a late successional transition from woody seeders to long-lived, arid-zone, resprouting shrub species. Fire frequency did not influence species richness and diversity but did influence species composition via a reduction in cover of longer-lived resprouter species – presumably because of a reduced ability to replenish epicormic buds and/or sufficient starch stores. The distinct floristic composition of old and very old habitat, and the vulnerability of these areas to wildfires, indicate that these areas are ecologically important and management should seek to preserve them.

Key words: disturbance, floristics, prescribed burning, species diversity, succession.

INTRODUCTION

Fire is one of the most widespread ecosystem disturbances across the globe. Because of its strong influence on ecosystem function and composition (Bond & Keeley 2005), a thorough understanding of the effects on local biota is necessary to inform fire management for biodiversity conservation (Driscoll *et al.* 2010). Knowledge of how different fire regimes (the combined influence of fire frequency, interval, intensity, behaviour and spatial configuration) affect species composition is particularly important (Gill & Allan 2008). In many fire-prone ecosystems, species possess biotic traits which allow them to survive and persist following fire and, in some circumstances, their persistence is reliant on a particular fire regime (Keeley *et al.* 2011a, 2011b). Persistence of such species may be compromised if the regime becomes altered by human interventions or climatic changes (Noble & Slatyer 1980; Keeley *et al.* 2011a).

Most Mediterranean fire-prone systems show an early post-fire peak in plant species richness followed by a

gradual decline as species reach their limits of longevity and are not replaced (Bond & van Wilgen 1996; Keeley *et al.* 2011a). Over longer periods of fire exclusion, changes in plant species richness and composition are less predictable (e.g. Gosper *et al.* 2013a). Senescence of dominant overstorey species may have differing effects on understorey plant species, some increasing, and others decreasing in abundance, in response to changing microclimate and competition (Capitaniao & Carcaillet 2008; Gosper *et al.* 2012b, 2013a). Aside from true obligate seeders, which tend to be confined to the seed bank with time and may disappear if seed longevity is limited, long-term vegetation dynamics are determined by the incidence and patterns of inter-fire seedling recruitment (Baeza *et al.* 2006). Furthermore, progressive structural or soil changes, such as accumulation of soil nutrients, litter and organic matter, can benefit some species over others, resulting in long unburnt vegetation having distinctive plant species composition (Gilliam & Platt 1999; Cohn *et al.* 2011). Resprouting species are generally longer lived and therefore more persistent than seeders in long unburnt vegetation; however, some studies have demonstrated high levels of resprouter mortality after long periods of fire exclusion (Enright *et al.* 2011).

In ecosystems where fire is a regular occurrence, vegetation may never, or rarely, reach a stage which could be

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[Correction added on 23 August 2016, after first online publication: References to Doherty (unpublished data) and Davis *et al.* (2016) have been updated in the main text.]

described as 'long unburnt' (e.g. where senescence is commonplace). However, in arid and semi-arid shrublands and woodlands, fire intervals are generally longer, and plant growth and vegetation recovery proceed at relatively slow rates (Pausas & Ribeiro 2013). Fire dynamics within these ecosystems need to be studied over decades and centuries to properly understand such patterns (Gosper *et al.* 2013a, 2013b; Moffet *et al.* 2015).

Although the effects of increased fire frequency on biota are less well studied than the effects of time since last fire, a severe reduction of obligate seeder species richness and cover is often recorded (Whelan *et al.* 2002). Shortened fire intervals may prevent individuals reaching reproductive maturity and extended fire intervals may cause soil- or canopy-stored seed to become unviable (Whelan *et al.* 2002; Miller & Dixon 2014). Although frequent fire generally promotes resprouting species over seeders, very short fire intervals may negatively impact on some resprouting species when there is insufficient time between fires to replenish carbon reserves and/or vegetative buds needed for regeneration (Wright & Clarke 2007; Enright *et al.* 2011).

These issues are particularly relevant in the dense, fire-prone shrubland vegetation occurring in semi-arid transitional zones occurring between Mediterranean-type and arid climates, such as in California, South Africa and southern Australia (Clarke *et al.* 2008; O'Donnell *et al.* 2010; Masubelele *et al.* 2014). Well-aerated fine fuels, exposure to wind/solar radiation, low and variable rainfall, persistent dead foliage, large fuel loads and dense vegetation are typical characteristics of these ecosystems which contribute to their predisposition to fire (Clarke *et al.* 2008; Keeley *et al.* 2011a; Dalglish *et al.* 2015). Western Australia's southern semi-arid region is a transitional zone at the northern and eastern limits of the Southwest Botanical Province. The region contains many ecosystems and species representative of both the Southwest and neighbouring Eremaean (arid) Provinces and thereby has high plant diversity (Payne *et al.* 1998; Beard *et al.* 2000). The area holds intact representations of vegetation once found extensively throughout the heavily cleared wheatbelt further south, including about 18 000 km² of dense *Acacia-Allocasuarina-Melaleuca* shrublands on yellow sandplain, which is the focus of this study (Payne *et al.* 1998; Beard *et al.* 2013).

In comparison to other semi-arid shrublands, such as that of Spain and California (e.g. Baeza *et al.* 2006; Clarke *et al.* 2008), the fire response of the Western Australian shrublands is largely unknown at the species and ecosystem levels, with most studies focusing on the south-eastern portion which is dominated by mallee (multi-stemmed *Eucalyptus* spp.) rather than *Acacia* (e.g. O'Donnell *et al.* 2010; Gosper *et al.* 2012a, 2012b) Further uncertainty arises because of lack of

information on fire adaptations and responses of plant species of the region; for instance it is not known if the species have strongly developed fire traits similar to southwest heathland species, such as resprouting, serotiny and fire-cued germination (Miller & Dixon 2014; Clark *et al.* 2015) or if they are more closely associated with arid *Acacia*-dominated ecosystems which generally have limited fire adaptations (Hodgkinson 2002).

The region has recently received a surge in conservation initiatives from both government and non-government organizations, with many pastoral leases now managed for conservation (van Etten 2013). These land managers are concerned about the increasing prevalence of fire, in particular large wildfires that homogenize landscapes. Our study area has been subject to several large wildfires in recent decades, with only about 33% of the sandplain shrublands older than 50 years (T. Doherty, unpublished data). The diversity, species associations and ecological importance of these long unburnt areas are largely unknown, and these areas potentially provide refuge for fire sensitive flora and fauna, such as the malleefowl (*Leipoa ocellata*) (Parsons & Gosper 2011) and conifers *Callitris* sp. (Prior *et al.* 2011). Parsons and Gosper (2011) noted that some long unburnt areas of the sandplain shrublands may be undergoing senescence and potentially provide a unique structure and species composition. Over the last 40 years, approximately 20% of the sandplain shrublands have experienced more than one fire (E. van Etten, unpublished data, 2013); hence, the frequency of large wildfires is also a concern for land managers. Increases in fire frequency not only mean a reduction in long unburnt/mature habitat in the landscape, but may also threaten fire sensitive species which require a particular length of time between fires to grow and reproduce (Miller & Dixon 2014).

Detailing plant diversity and composition across a number of fire ages, including the very long unburnt areas, will assist in determining fire requirements of the region and informing land managers of appropriate fire age class distributions that best conserve plant diversity across the landscape. Our study aimed to establish the effects of time since last fire and fire frequency on plant species diversity and composition of south-west Australian semi-arid sandplain shrublands. Specifically we predicted that:

- 1) species diversity will decline with time since last fire;
- 2) longer unburnt shrublands will have distinct species composition to that of younger shrublands;
- 3) the ratio of resprouting to seeding species will increase with time since last fire;
- 4) species diversity will decrease as fire frequency increases;
- 5) increasing frequency of fire will result in altered species composition; and

- 6) the ratio of resprouter to seeder species will increase with fire frequency.

METHODS

Study area

The study area covers approximately 350 000 ha across the Avon Wheatbelt and Yalgoo bioregions, approximately 300 km north-east of Perth, Western Australia and 200 km inland from the coast (Fig. 1). We conducted this study within the Joseph land system, characterized by dense shrub vegetation on gently undulating yellow sandplains derived from weathering of underlying granite (Payne *et al.* 1998). The Joseph land system is widespread throughout the Yalgoo bioregion and comprises about 42% of the study area. All fire scars studied here originated from wildfires as no prescribed burning is currently carried out in the study area, nor has it been in the recent-past.

Sampling strategy

A space-for-time approach was used to study the effect of time since last fire and fire frequency on plant community composition and diversity. Fifty three (53) sites were selected for the time since last fire study, with each grouped into one of four fire age classes that we defined based on previous studies (Parsons & Gosper 2011; Dalglish *et al.* 2015): ‘young’ (8–15 years), ‘medium’ (16–34 years), ‘old’ (35–50 years) and ‘very old’ (51–100 years) (Appendix S1). Each site in the first three classes was burnt only once in the period 1965–2010 to avoid

confounding effects of fire frequency. Thirty seven (37) sites were selected for the fire frequency study, each last burnt 8–15 years prior to reduce confounding effect of time since last fire. These sites were burnt either once, twice or three times in the period 1965–2010 (Appendix S1).

To reduce the potential influence of other factors on the response variables (species diversity or composition) we: (i) selected sites from the same broad vegetation-landform type (Joseph land system); (ii) avoided ecotones by placing sites at least 500 m from other land systems; (iii) employed true replication of sites by positioning each site in a spatially distinct fire scar, or spatially disjunct patches of Joseph land system for the large fire scars; and (iv) measured a range of environmental variables at each site and used them as covariables in the analyses where they were found to be correlated with the response variable.

At each site, we established a 20 × 20-m plot and visually estimated the cover of each plant species occurring in the plot, with the lead author present during all surveys to standardize estimates. The size of the plot was chosen after constructing species–area curves at 10 sites (Knuckey 2012). We categorized the regeneration mode of each species by inspecting shrub stems to determine if the species had regenerated by resprouting or seeding following last fire and combined this with published information (Appendix S2) to establish regeneration mode.

Penetrable soil depth, surface cryptogam cover, leaf litter cover, water infiltration rate and Munsell soil colour and hue were recorded at each site (Appendix S3). Topsoil (0–5 cm depth) was also collected at each site and analysed in the lab for pH, conductivity, total N, total P, reactive iron (Fe) and particle size composition (Appendix S3).

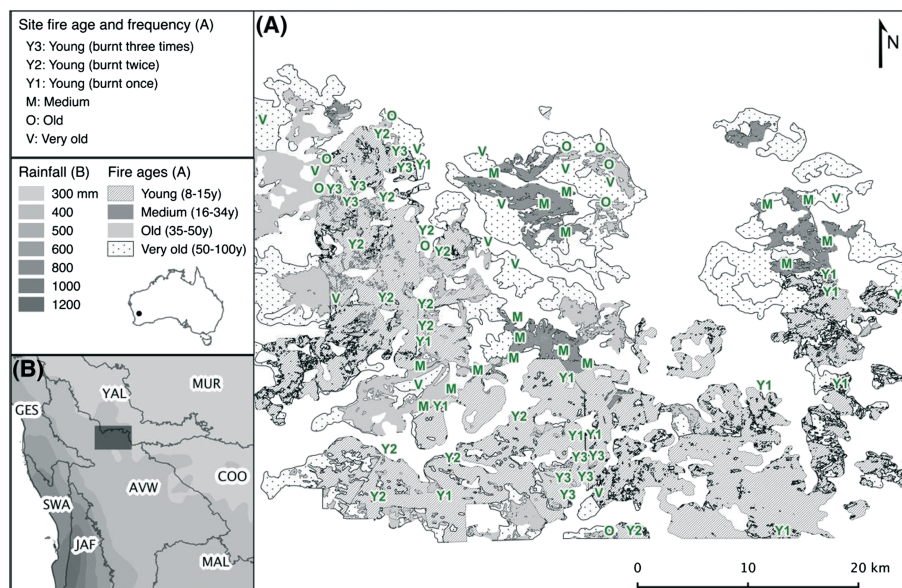


Fig. 1. Location of survey sites (A) and study area in south-western Australia in relation to biogeographic regions and annual average rainfall isohyets (B). Part A: fire scars are only shown for the Joseph land system and all solid white areas represent other vegetation types. Part B: GES, Geraldton Sandplains; YAL, Yalgoo; MUR, Murchison; SWA, Swan Coastal Plain; AVW, Avon Wheatbelt; COO, Coolgardie; JAF, Jarrah Forest; MAL, Mallee.

Data analysis

We compared mean species richness and Shannon–Weiner diversity index among fire age and frequency classes using one-way ANOVA in SPSS v22. To assess the influence of soil variables on species richness and diversity, we then used soil variables correlated with species richness/diversity as covariables in an Analysis of Covariance (ANCOVA). This effectively tests for differences among fire age/frequency classes once variability because of key soil variables is removed. Species were classified into broad functional types based on their dominant mode of regeneration after fire (seeder/resprouter) and their general habit (woody/herbaceous) (Appendix S2). Comparisons were then made among fire age and frequency classes in terms of mean cover and species richness of these functional types using one-way ANOVA. Because overall plant cover is expected to increase with time since last fire, we performed these comparisons using both relative cover (as a proportion of the total cover at a site) and absolute cover (as measured at each site). Shapiro–Wilk and Levene’s tests were undertaken to confirm normality of residuals and equal variance among fire classes, respectively, justifying the use of one-way ANOVA and ANCOVA.

Because of a known climatic gradient across the study area (Fig. 1), we performed ANOVAs of annual rainfall (mm), temperature (°C) and aridity index (ratio of precipitation to potential evaporation) for each fire class to ensure sampling was randomized according to these factors (Appendix S1). BIOCLIM within the Atlas of Living Australia was used to predict climate variables for each site (ALA, Atlas of Living Australia 2014). ANOVA was also conducted on the geographic distance between sites, within fire classes, to ensure classes were similarly spatially separated (Appendix S1).

Differences in species composition among fire age and fire frequency classes were tested using Permutational Multivariate Analysis of Variance (PERMANOVA) in PRIMER v6 with PERMANOVA+ (Clarke & Gorley 2006; Anderson *et al.* 2008). The Bray–Curtis measure of similarity was used to compare species composition among sites and fire classes based on square-root transformed species cover data. We first performed PERMANOVA using the compositional similarity among sites only, and then repeated the analysis including various soil and climatic covariables. The selection of covariables was based on those: (i) with significant correlations with species composition; and (ii) likely to be independent of fire (e.g. cryptogam and litter surface cover were not selected as they were likely to be influenced by fire age). For time since last fire, covariables used were soil depth, reactive Fe, mean annual rainfall and mean annual temperature. For fire frequency, covariables used were soil depth, reactive Fe, 250 to 1000- μm soil fraction, mean annual rainfall, mean annual temperature and time since last fire (the latter being included because time since last fire, although broadly similar, varied from 8.7 to 13.3 years). Restricting the number of covariables was important to reduce the possibility of model overfitting. Similarity percentages analysis (SIMPER) in PRIMER v6 was performed

to determine species and regeneration modes which contributed to the top 80% Bray–Curtis dissimilarity among young and very old age classes.

RESULTS

Environmental and spatial factors

The majority of soil variables were not significantly different among fire age classes (Appendix S3). Levels of total N in surface soil were below detectable levels for all medium-aged sites (16–34 years), but were very similar among the other age classes. Surface phosphorus levels followed a similar pattern (Appendix S3), suggesting a dip in soil fertility after several decades without fire but an eventual return to levels of younger stands after a long absence of fire. Surface cryptogam and leaf litter cover both increased with time since last fire, whilst water infiltration rates declined (Appendix S3). There was only one soil variable that differed among fire frequency classes: the proportion of the 250 to 1000- μm fraction, which was significantly greater in sites burnt three times compared to sites burnt once or twice only (Appendix S3).

Species richness and diversity

Species richness differed significantly among fire age classes and generally declined with time since last fire (Table 1; Fig. 2). Young and medium fire age classes were not significantly different from each other, having means of 15 and 15.4 species per site respectively, but were significantly higher than old (13.7 species) and very old sites (12 species; Fig. 2). The proportion of 250 to 1000- μm soil fraction was the only fire-independent variable significantly correlated with species richness, increasing with species richness (Pearson’s $r = 0.285$; $P = 0.038$). Using the 250 to 1000 μm fraction as a covariable for ANCOVA did not alter findings for species richness, although F values ($F_{4,52} = 3.87$; $P = 0.015$) were slightly lower than with no covariables.

Shannon–Wiener diversity differed significantly among fire age classes and decreased from a mean of 2.39 in young sites to 2.09 in very old sites (Table 1; Fig. 2). Post-hoc tests showed that diversity at very old sites was significantly lower than both young and medium-aged sites (Fig. 2). Soil pH, conductivity and 250 to 1000- μm fraction were positively and significantly (or close to significantly) correlated with Shannon–Weiner diversity ($P = 0.054$, 0.046 and 0.010, respectively). ANCOVA using these three variables as covariables did not alter Shannon–Weiner diversity differences ($F_{6,52} = 5.2$; $P = 0.002$).

Sites burnt three times had significantly higher Shannon–Weiner diversity compared to sites burnt twice, and a similar but non-significant difference to sites burnt once (Table 1; Fig. 3). Sites burnt three

Table 1. Analysis of variance results for comparison of species diversity and cover per plot for all species and for selected functional groups among time since last fire (TSLF) and fire frequency classes. Diversity is the Shannon–Weiner index; R, resprouting species; S, seeder species; W, woody species (therefore WR refers to woody resprouters). Pairwise post-hoc results are shown in Figs 2 and 3

Response variable	TSLF		Fire frequency	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Species richness	4.39	0.008	2.82	0.074
Species diversity	5.69	0.002	3.50	0.041
R richness	4.18	0.010	0.19	0.828
S richness	8.89	<0.001	1.65	0.208
R:S richness	7.89	<0.001	0.80	0.459
Total cover (%)	40.0	<0.001	3.34	0.052
R absolute cover (%)	26.49	<0.001	4.17	0.024
R relative cover (%)	5.03	0.004	1.32	0.281
WR absolute cover (%)	15.73	<0.001	5.27	0.010
WR relative cover (%)	2.91	0.044	3.52	0.041
WR:WS richness	4.08	0.012	1.05	0.360
WR:WS cover	4.76	0.005	1.04	0.366

times had approximately three (20%) more species on average compared to sites burnt less frequently (Table 1; Fig. 3). Both diversity measures were not

significantly correlated to any of the listed environmental variables and ANCOVA was therefore not used.

Functional group diversity and cover

Although total species richness generally declined with time since last fire, the richness of resprouting species increased and was significantly higher in very old sites compared to young sites (Table 1; Fig. 2). Consequently, the ratio of resprouter to seeder species increased with each age class (Table 1; Fig. 2). Both absolute and relative cover of all resprouting species, as well as woody resprouters increased with time since last fire and the absolute cover of woody resprouters was three times greater in very old compared to young sites (Table 1; Fig. 2). The relative cover of woody resprouters in very old sites was also significantly higher than in young sites (Table 1; Fig. 2). Species richness of woody seeders was higher than that of woody resprouters at almost all sites, but declined with time since last fire, whilst woody resprouter species slightly increased in number, meaning species richness of these two functional groups were much more even in very old sites (Table 1; Fig. 2). Nevertheless, woody resprouter cover was higher than that of woody seeders and this

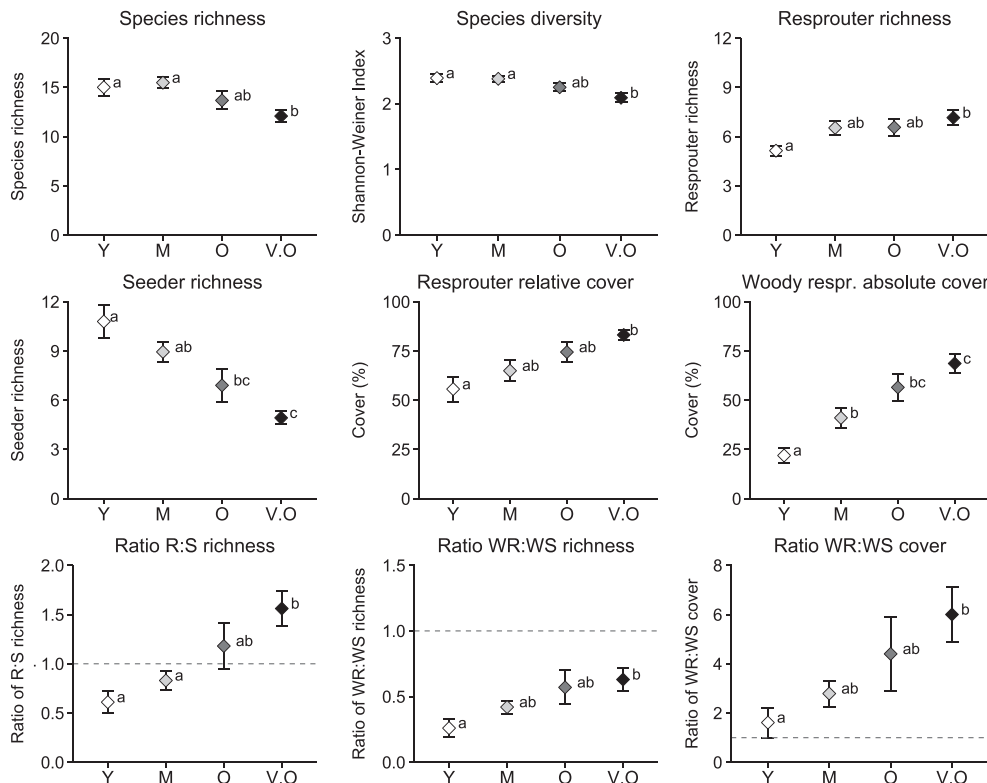


Fig. 2. Means and standard errors for plant species richness, diversity, cover and ratios of resprouter (R) / seeder (S) cover and richness in each time since fire class (Y, young; M, medium age; O, old; V.O, very old). WR and WS refer to woody resprouter and woody seeder respectively. Pairwise differences are indicated using superscripts, with significantly different pairs not sharing the same letter. The horizontal dashed line represents a 1:1 ratio with values above and below the line indicating dominance in either direction.

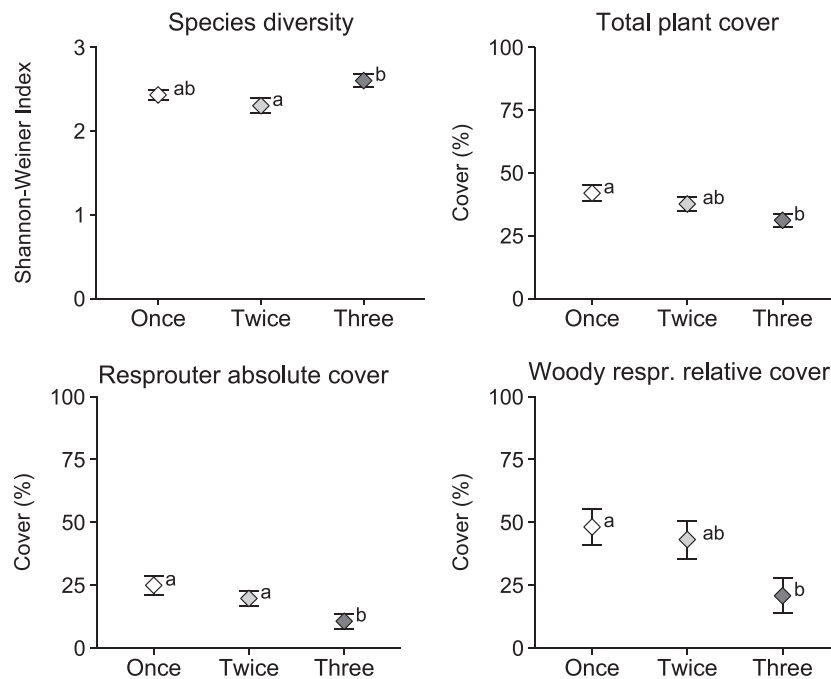


Fig. 3. Means and standard errors for plant species diversity, total plant cover, absolute cover of resprouters (R) and relative cover of woody resprouters (%) in each fire frequency class (burnt once, twice or three times during the period 1965–2010). Pairwise differences are indicated using superscripts, with significantly different pairs not sharing the same letter.

domination by woody resprouters increased significantly with time since last fire (Table 1; Fig. 2).

Sites burnt three times had significantly lower overall plant cover, resprouter absolute cover and both relative and absolute woody resprouter cover than sites burnt once or twice (Table 1; Fig. 3). Absolute cover of woody resprouters in sites burnt three times was almost four times lower than in sites burnt once (Table 1; Fig. 3). No significant differences with increasing fire frequency were found for resprouter/seedler species richness and ratio, or woody resprouter/seedler cover and ratio (Table 1; Fig. 3).

Floristic variation among fire classes

Although plant species composition varied considerably within fire age classes, PERMANOVA demonstrated significant differences among fire age classes (pseudo- $F=2.03$; $P=0.003$). Multivariate dispersion (a distance-based measure of multivariate homogeneity) was not significantly different among fire age classes (pseudo- $F=1.01$; $P=0.500$). PERMANOVA using covariables also revealed significant differences in species composition among time since last fire classes, but with a lower pseudo- F value (Table 2). Post-hoc tests showed very old sites were significantly different to young and medium-aged sites, whereas there was no significant difference among young, medium and old sites (Table 2).

The species contributing to the compositional differences among young and very old vegetation were predominantly large resprouting shrubs (such as *Acacia effusifolia* and *Acacia resinimarginea*) which had greater cover in very old vegetation and together contributed approximately 20% to the overall dissimilarity (Table 3). In comparison, obligate seeder shrubs (such as *Hakea invaginata* and *Acacia stereophylla* var. *stereophylla*) were more common in young sites (Table 3). Notable exceptions include *Acacia acuminata* and *Acacia longispinea* which were more common in young sites (Table 3), but have been observed to resprout following fire (Appendix S2). These two species are believed to be examples of facultative seeders where seedling recruitment is tightly linked to fire (i.e. they need fire to stimulate seed germination, but can also resprout). The regional distributions of these dominant obligate and facultative seeder species tend to be centred to the south of the study area and are generally common throughout the higher rainfall Avon (wheatbelt) bioregion, whereas the dominant resprouting shrubs tend to have distributions spreading more to the north and east of the study area, into more arid areas (ALA, Atlas of Living Australia 2014). Exceptions include *Acacia sibina*, which is nominally listed as a seeder species and is more common in long unburnt vegetation (although its fire response has not been confidently established in this or other studies; Appendix S2), and *Allocasuarina acutivalvis* which is a seeder more commonly found in long unburnt vegetation, but appears to

Table 2. Results of PERMANOVA comparing fire age classes in terms of species composition (in bold) with the inclusion of co-variables soil depth, reactive iron content of topsoil, 250–1000 µm soil fraction, mean annual rainfall and mean annual temperature. Fire age classes: young 8–15 years; medium 16–34 years; old 35–50 years; very old 51–100 years

Variable	Degrees of freedom	SS	Pseudo- <i>F</i>	<i>P</i> (PERMANOVA+)	<i>P</i> (Monte Carlo)
Depth (m)	1	5658	2.39	0.005	0.011
Reactive iron (mg/kg)	1	8851	3.74	0.001	0.002
250–1000 µm fraction	1	3276	1.38	0.168	0.197
Mean rainfall (mm/year)	1	5892	2.49	0.003	0.012
Mean temperature (°C)	1	4102	1.73	0.055	0.073
Time since fire class	3	11988	1.79	0.005	0.015
Residual variance	44	104180			
Total variance	52	143950			
Pair-wise tests:	Den. DOF		<i>t</i> value		
Young, medium	24		1.08	0.309	0.298
Young, old	16		1.14	0.213	0.231
Young, very old	20		1.74	0.005	0.008
Medium, old	19		0.96	0.532	0.488
Medium, very old	23		2.21	0.001	0.001
Old, very old	15		1.35	0.065	0.097

Den.DOF, denominator degrees of freedom; SS, sum of squares.

Table 3. List of species which account for the top 80% of floristic dissimilarity among young and very old sites as determined by SIMPER analysis. The reproductive mode and life form of species is given. Average abundances are given as (mean) percentage cover. Life form codes: Sh, shrub; HC, hemicryptophyte (rhizome); Geo, geophyte. Fac. (Facultative) Seeders are those which germinate *en masse* after fire but may also regenerate via resprouting

Species	Young average abundance (%)	Very old average abundance (%)	Contribution (%)	Life form and dominant reproductive mode
<i>Acacia effusifolia</i>	2.89	26.42	13.23	Sh, Resprouter
<i>Acacia resinimarginea</i>	1.32	1.77	6.50	Sh, Resprouter
<i>Acacia sibina</i>	0.49	1.37	4.90	Sh, Seeder?
<i>Allocasuarina acutivalvis</i>	0.45	2.69	4.90	Sh, Seeder
<i>Melaleuca uncinata</i>	0.79	1.00	4.14	Sh, Resprouter
<i>Cheilanthes adiantoides</i>	0.00	1.90	3.98	Fern, Resprouter
<i>Acacia acuminata</i>	1.39	0.01	3.63	Sh, Fac. Seeder
<i>Ecdiocollea monostachya</i>	0.18	0.66	3.21	HC, Resprouter
<i>Hakea invaginata</i>	0.96	0.24	3.13	Sh, Seeder
<i>Baeckea</i> sp. 'Wanarra'	0.40	0.32	2.58	Sh, Seeder
<i>Acacia stereophylla</i> var. <i>stereophylla</i>	0.56	0.14	2.38	Sh, Seeder
<i>Borya sphaerocephala</i>	0.07	0.28	2.18	HC, Resprouter
<i>Melaleuca hamata</i>	0.09	0.27	2.15	Sh, Resprouter
<i>Melaleuca leiocarpa</i>	0.00	0.52	1.99	Sh, Unknown
<i>Philotheca deserti</i> ssp. <i>deserti</i>	0.03	0.32	1.89	Sh, Seeder
<i>Hibbertia stenophylla</i>	0.36	0.19	1.88	Sh, Seeder
<i>Acacia longispinea</i>	0.36	0.05	1.81	Sh, Fac. Seeder
<i>Melaleuca cordata</i>	0.30	0.01	1.80	Sh, Seeder
<i>Drosera macrantha</i> ssp. <i>macrantha</i>	0.04	0.30	1.73	Geo, Resprouter
<i>Amphipogon caricinus</i> var. <i>caricinus</i>	0.42	0.14	1.63	HC, Resprouter
<i>Phebalium canaliculatum</i>	0.25	0.01	1.57	Sh, Seeder
<i>Homalocalyx thryptomenoides</i>	0.17	0.03	1.55	Sh, Seeder
<i>Euryomyrtus recurva</i>	0.23	0.01	1.54	Sh, Seeder
<i>Thryptomene australis</i>	0.01	0.14	1.39	Sh, Seeder
<i>Hibbertia arcuata</i>	0.00	0.23	1.37	Sh, Resprouter
<i>Homalocalyx aureus</i>	0.00	0.18	1.36	Sh, Seeder
<i>Thysanotus patersonii</i>	0.08	0.44	1.31	Geo, Resprouter

have weak serotiny with opened fruits and inter-fire recruitment being observed in older stands (Table 3; Appendix S2). Seedlings of many of the resprouting

shrub species were found or observed in long unburnt vegetation (Appendix S2), suggesting inter-fire recruitment occurs commonly in the study area.

The small fern *Cheilanthes adiantoides* was found in the ground layer at 10 of the 13 very old sites, and this species, along with *Cheilanthes sieberi* ssp. *sieberi* and the cormous species *Wurmbea densiflora*, were only recorded at old and very old sites (Appendix S2). Orchids *Pheladenia deformis* and *Ericksonella saccharata* were also both found in far greater numbers in very old sites (Appendix S2). The native conifer *Callitris columellaris* was only found in very old sites and burnt stems of this species were recorded at several medium-aged sites with no evidence of re-establishment at these sites (Appendix S2).

PERMANOVA without covariables (pseudo- $F=2.33$; $P<0.001$) demonstrated significant floristic differences among fire frequency classes. PERMANOVA with selected covariables also showed significant differences among fire frequency classes, although pseudo- F values were lower (Table 4). Covariables used here were time since last fire, mean temperature, soil depth, reactive Fe, 250 to 1000- μm soil fraction and mean rainfall (Appendix S3). Post-hoc tests (following fitting of covariables) showed that sites burnt twice were most likely to be different to sites burnt once or three times; however, sites burnt once and three times were not found to be different to each other (Table 4). Woody resprouters *A. resinimarginea* and *Melaleuca uncinata*, and the putative woody seeder *A. sibina*, were primarily responsible for compositional differences among frequency classes, occurring more commonly in sites burnt twice (Appendix S4).

DISCUSSION

Effect of time since last fire

Time since last fire was a strong determinant of floristics within the study area. As postulated (prediction 1), a

gradual decline in species richness and diversity from 8 to 80+ years post fire was observed. This pattern aligns with the general paradigm for fire-prone ecosystems of Mediterranean-type climates (Bond & van Wilgen 1996) and the 'initial floristic composition' vegetation assembly model (Egler 1954). However, average species numbers per plot declined only marginally (from 15 to 12 species) over this 70+-year period and were reasonably stable in old vegetation. Hence these declines are unlikely to be of critical importance to conservation of plant diversity when placed in the context of the overall compositional changes found.

The greatest differences in community composition occurred among young and very old sites, supporting prediction 2. These changes involved a shift in relative dominance of certain species rather than wholesale replacement by new species over time, again supporting the 'initial floristic composition' paradigm. The changes were characterized by a late-successional floristic transition towards long-lived, arid-zone, resprouting and generally taller shrub species (supporting prediction 3), as has been reported in other fire-prone environments (Kavgacı *et al.* 2010; Gosper *et al.* 2012a). This shift involved genera such as *Acacia* and *Allocasuarina*, supporting studies in similar vegetation of the northern wheatbelt region (Mappin *et al.* 2003; Shackelford *et al.* 2015). These species generally possess classic life history traits of late successional dominants such as slow growth, longevity, competitive persistence and ability to regenerate within mature stands. Rees *et al.* (2001) and our study support the idea that species possessing such traits are major drivers of long-term succession following fire in resource-limited ecosystems (Pausas 2003; Baeza *et al.* 2006; Capitanio & Carcaillet 2008). The type and proportion of resprouters in mature stands (where 60% of species were basal

Table 4. Results of PERMANOVA comparing fire frequency classes in terms of species composition (in bold) with the inclusion of co-variables soil depth, reactive iron content of topsoil, 250–1000 μm soil fraction, mean annual rainfall, mean annual temperature and time since last fire

Variable	Degrees of freedom	SS	Pseudo- F	P (PERMANOVA+)	P (Monte Carlo)
Depth (m)	1	5759	2.24	0.004	0.025
Reactive iron (mg/kg)	1	4092	1.59	0.085	0.128
250–1000 μm fraction	1	3461	1.35	0.198	0.178
Mean rainfall (mm/year)	1	2784	1.08	0.373	0.345
Mean temperature ($^{\circ}\text{C}$)	1	5366	2.09	0.021	0.034
Time since fire (years)	1	3551	1.38	0.156	0.186
Fire frequency class	2	11645	2.27	0.002	0.004
Residual variance	28	71987			
Total variance	36	108650			
Pair-wise tests:	Den. DOF		t value		
Burnt once, burnt twice	19		1.46	0.026	0.039
Burnt once, burnt three times	16		1.12	0.226	0.256
Burnt twice, burnt three times	15		1.41	0.045	0.073

Den.DOF, denominator degrees of freedom; SS, sum of squares.

resprouters) were consistent with that reported from other arid/semi-arid *Acacia* shrublands of Australia (Clarke *et al.* 2015).

Late successional species in our study also included some seeders such as *Allocasuarina* which displayed weak serotiny and inter-fire regeneration. Such species have been described as invasive within sandplain shrubland in the neighbouring wheatbelt because of their increasing dominance in the absence of fire (Gosper *et al.* 2012a; Doherty *et al.* 2015; Shackelford *et al.* 2015). More generally though, we recorded an overall reduction in the diversity and cover of seeders (including facultative seeders such as *A. acuminata*) with time since last fire as reported in other Mediterranean ecosystems (Keeley *et al.* 2005; Gosper *et al.* 2012a). This is despite similar field observations of weak serotiny in several common seeders such as *H. invaginata* and *Grevillea* spp. (Appendix S2). Overall, the fire responses observed here are a mix of typical south-west and arid zone traits, which is not unexpected given the transitional location of the ecosystem.

Long unburnt vegetation is often claimed to hold conservation value, particularly for fauna communities (Watson *et al.* 2012; Doherty *et al.* 2015), and this study represents one of the few examples where such value has been demonstrated for plant communities. Species only found in long and very long unburnt sites include the native conifer *C. columellaris*, which is consistent with its fire sensitive and slow recolonizing attributes (Prior *et al.* 2011). This species is known elsewhere in the study area as occupying margins of eucalypt woodlands on more clayey soils, so it remains unclear whether its niche is defined by soil type, fire exclusion or a combination of both – a consistent ecological puzzle for this genus across Australia (e.g. Cohn *et al.* 2011; Prior *et al.* 2011).

Other notable changes with time since last fire occurred in the understorey of the shrublands. Several ferns, orchids, cormous species and the ‘resurrection plant’ *Borya sphaerocephala*—which is also known from granite outcrops and seasonally wet areas (both fire-sensitive habitats)—showed preferences for long unburnt vegetation. It is not clear what drives such understorey species shifts over time without fire, but one likely contributing factor is the indirect influence of soil characteristics (i.e. fertility, organic matter, leaf litter mats and cryptogams – all of which were found to increase with time since last fire in this study). These characteristics result in favourable soil moisture and nutrient regimes which, in turn, are likely to favour these types of species in very old shrublands. The results of this study are consistent with other work conducted within the study area and more generally within the region, which have recorded several fauna species showing a preference for long unburnt vegetation including the malleefowl (Parsons & Gosper 2011), some small mammals and reptiles

(Doherty *et al.* 2015) and some insectivorous birds (Davis *et al.* 2016).

Post-fire peaks in plant species richness/diversity are well documented for shrublands of Mediterranean-type climates, and generally occur within the first few years after fire (Keeley *et al.* 2005; Gosper *et al.* 2012a); a limitation of our study is that no such areas (0–5 years old) were available at the time of the sampling. However, a flush of fire ephemerals is known from earlier surveys of the 2000–2 burns, including *Keraudremia integrifolia* and *Glischrocaryon aureum* which persisted in our young sites only, which is consistent with other studies within the broader region (e.g. Gosper *et al.* 2012a). Two ‘poorly known’ sandplain restricted taxa of conservation significance, *Mirbelia* sp. *Cordifolia* (C.A. Gardner 2712) and *Philotheca nutans*, were only recorded at one and two young sites (respectively) in our study, as has been the case in other surveys in the area (see Appendix S2). Such findings suggest that fire may play a role in maintaining some species in these landscapes, although many species we studied are clearly not dependent on fire given their post-fire recruitment and increasing abundance with time since fire. Post-fire monitoring of future fires is recommended to elucidate early successional patterns and to identify species that may be fire dependent.

Effect of fire frequency

Plant species richness and diversity showed no clear trend with fire frequency, therefore not supporting the prediction (4) that species diversity will decrease with increased fire frequency. Despite this, fire frequency was found to be a significant variable affecting species composition across the study area, supporting prediction 5. In particular, long-lived species were affected by a shorter fire interval, having lower vegetative cover in sites burnt three times. Longer-lived species, by definition, take longer to flower and develop re-establishment characteristics in preparation for the next fire event (Bond & van Wilgen 1996; Pausas *et al.* 2004). In contrast, short-lived species remained unchanged, or increased in cover, as they have usually had enough time to prepare for the next disturbance event. Instances where cover of short-lived species increased in frequently burnt shrubland are likely to be a result of lack of competition from long-lived species.

In many cases, but not all, declines in long-lived species with more frequent fire were driven by woody resprouters, explaining the reduction in the resprouter to seeder ratio (contrary to our prediction 6), possibly because of a lack of time between fires to replenish epicormic buds and/or to accumulate sufficient starch store to enable vegetative recovery after fire (Enright *et al.* 2011). The unexpected finding that short fire intervals seem to affect resprouters rather than seeders

suggests that 10–12 years, the minimum observed interval between fires in the study area, is sufficient for most seeder species to re-establish a sufficient soil seed bank. The results from this study support others which detail the impacts of high frequency fire on resprouter species (e.g. Watson & Wardell-Johnson 2004; Enright *et al.* 2011), particularly in semi-arid *Acacia* communities (Anderson *et al.* 2008. Clarke *et al.* 2015).

There were few very frequently burnt areas in the study area (approximately 1% of study area experienced three fires in past 40 years) and results from this study suggest such short intervals between fires are uncommon and are probably confined to the most productive sites, edges of fire scars and/or following times of well above average rainfall, given the general slow post-fire recovery recorded. However if more widespread and frequent burning occurs over the long term (as predicted under a changing climate; Klausmeyer & Shaw 2009), then some species may be eventually eliminated from the system.

Covariables in fire ecology studies

Although well-designed and replicated manipulative experiments allow more precise and confident detection of community changes, costs and time-scales involved can be prohibitive, especially if the aim is to document long-term changes. This study demonstrates the value of covariables in fire ecology studies which use the alternative approach of chronosequences to infer fire effects. Despite recognition that floristics can vary with subtle differences in soil and other site factors, many space-for-time studies erroneously assume that restricting sampling to certain broad soil types, landforms or vegetation communities will negate any influence of environmental variation (Walker *et al.* 2010). Covariables were an important part of our study because of the potential for climatic gradients and soil variables to drive differences among fire classes. As our study has shown, a reasonable amount of floristic variation is associated with the measured environmental variables, even within the same landform. Soil depth alone accounted for about 5% of variation in both the time since last fire and fire frequency analyses. This was relatively important given that fire class accounted for only 12% of the overall variation. Partitioning the variance in vegetation composition associated with measured environmental variables allows for more precise analysis of community changes so that space-for-time studies can be used more rigorously and confidently (Wright & Clarke 2007). Despite the inclusion of covariables in our analyses, we were unable to explain the greater proportion of compositional change and it appears that untested environmental variables and/or stochastic factors are influential and working within our ‘homogeneous’ vegetation/landform unit. This is a common scenario

and, as such, it is always recommended that replicate sites within fire classes of chronosequences are numerous and spread widely and randomly throughout the study area (Gosper *et al.* 2013a, 2013b).

There remains the possibility that differential fire intensity, season and patchiness and post-fire weather may influence floristics following fire (Walker *et al.* 2010; Gosper *et al.* 2013b). As the shrublands are known to experience stand-replacing crown fires, intensity is unlikely to vary dramatically among fire age classes. Similarly, differences in rainfall or post-fire conditions may affect successional rates and trajectories, but again this would be unlikely to vary substantially among fire classes given the spatial spread of sites employed in this study.

Management implications

Recognition of the ecological value of ‘old growth’ sandplain shrubland implies that management of the study area should aim to protect an adequate proportion of such mature vegetation. The broader conservation implication of dynamic floristics linked to time since fire is the need to maintain a range of fire ages in fire-prone ecosystems to maximize the presence of plant species at the landscape scale. Nevertheless, the focus should be on protecting the older stands of shrubland as it is generally easier to maintain a certain amount of young vegetation (e.g. via prescribed burning or planning for inevitable wildfire), whereas old vegetation can be severely reduced in extent from a single uncontrolled wildfire. Once significant areas of old shrubland are lost to fire, it will likely require decades of careful fire management to return to these levels. The spatial extent and configuration of old vegetation which needs to be maintained for conservation are not yet clear. Because of the complex spatial variation and high turnover in plant composition and the successional changes documented here, we recommend the maintenance of many old patches of sandplain shrubland spread throughout the landscape, rather than a smaller number of large patches. Finally, we recommend that sampling be conducted following any future fires in order to gather data on the youngest fire ages (<5 years) for which no data currently exist.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site:

Appendix S1. Study site details.

Appendix S2. Regeneration mode and notes for plant species collected at study sites.

Appendix S3. Measurements and analyses of soil variables.

Appendix S4. List of species accounting for dissimilarity between fire frequency sites.