Resilience of open forests and shrublands to contrasting fire interval sequences in a Mediterranean environment of south-west Western Australia [1]

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Abstract

There is limited information about how biota respond to different fire regimes, especially at a whole-of-community level. We studied the response of vascular plants, ants, beetles, vertebrates and macrofungi to different fire interval sequences resulting from planned and unplanned fires in ecosystems of southwestern Australia. Using data spanning 1972–2004, we investigated community-level responses to consecutive short (SS: ≤ 5 years), consecutive long (LL: ≥ 10 years), one very long (VL: 30 years), or mixed/moderate (M: 6–9 years) fire interval(s) in forest and shrubland ecosystems. All sites were sampled at a common time-since-fire of ~ 4 years. The influence of fire interval sequences on taxonomic groups was minimal and difficult to detect, suggesting a biota that is highly resilient to fire. There was weak evidence of compositional differences between SS and LL/VL regimes for plants, ants, beetles and macrofungi but no difference between either of these regimes and the M-regime. Occasional short (3–5 years) intervals between fires are unlikely to have a persistent effect on community composition, though a sustained regime of short or long intervals may alter species composition and/or abundance. We suggest that variability in fire intervals is important for long-term conservation of the biota.

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Introduction

The interaction between fire regimes and biodiversity conservation is an important management issue in the megadiverse and fire-prone ecosystems of south-west Western Australia (SWA). Prescribed burning for wildfire mitigation in SWA forest ecosystems became part of State Government policy in 1954, but was not fully implemented until the 1960s (McCaw and Burrows, 1989). Examination of historical fire regimes in SWA and their impacts at a 'whole-of-community' level therefore makes an important contribution to a critical appraisal of the resilience of biota to prescribed burning for the dual purposes of fuel reduction and biodiversity conservation.

Fire interval (time between fires) is recognized as one of the factors that can influence the persistence of many groups of organisms, including flora (Bradstock et al. 1997) and invertebrates (York 2000; Andersen et al. 2003). The influence of fire intervals on fauna and fungi is less well known. One of the objectives of prescribed burning by the DEC is to maximize species diversity by maintaining a range of post-fire ages, and incorporating a range of fire interval patterns in the landscape (Burrows 2008). The results presented in this paper critically investigate the second aspect of this management objectives – what is the effect on biota of contrasting fire interval patterns through time?

In the fire ecology literature, there has been an emphasis on studying the effects of short fire intervals on the resilience of biodiversity, usually in comparison to long-unburnt (so-called 'control') sites. While these studies have demonstrated significant differences in species composition between treatments, they are of little value to managers in fire-prone biomes who rarely implement fire regimes at either extreme of the spectrum. In this study, we controlled for time-since-fire and investigated a range of fire interval regimes that included the occurrence of consecutive short fire intervals and a regime of longer intervals.

In this study, we retrospectively constructed fire interval sequences from the fire history records using the methods of Wittkuhn and Hamilton (2010). We investigated species richness and composition of plants, ants, beetles, vertebrates and macrofungi of shrublands and forests in SWA in response to the following fire interval sequences: moderate or mixed interval regime, consecutive short (≤ 5 years) intervals, consecutive long (≥ 10 years) intervals or very long (30 years) intervals. Our intention was to test for differences in species richness and/or community composition between sites burnt with contrasting fire interval sequences, and to determine whether differences persist through time.

Methods

Study area and fire history

The 50 000 ha study area was situated in the Warren bioregion in SWA (Fig. 1). The landscape is gently undulating and consists of open sclerophyll eucalypt forest and woodland on lateritic uplands interspersed with low-lying seasonally-inundated shrublands. Climate of the area is Mediterranean, with warm, dry summers (December to February) and mild, wet winters (June to August). Average annual rainfall ranges from 900–1100 mm across the study area.

Fire history data for the study area, spanning 1972/73 to 2004/05, consisted of shapefiles digitised from fire maps into a geographic information system (GIS) (Hamilton et al., 2009). Readers are referred to Boer *et al.*, (2009), Hamilton *et al*. (2009) and Wittkuhn and Hamilton (2010) for fire statistics for the region. In this study, all sites had the same time-since-fire to control for its influence on species assemblages (~ 4 years at the commencement of biological surveys; Table 1). The entire study area was burnt by wildfire or prescribed burning in the fire season of 2002/03.

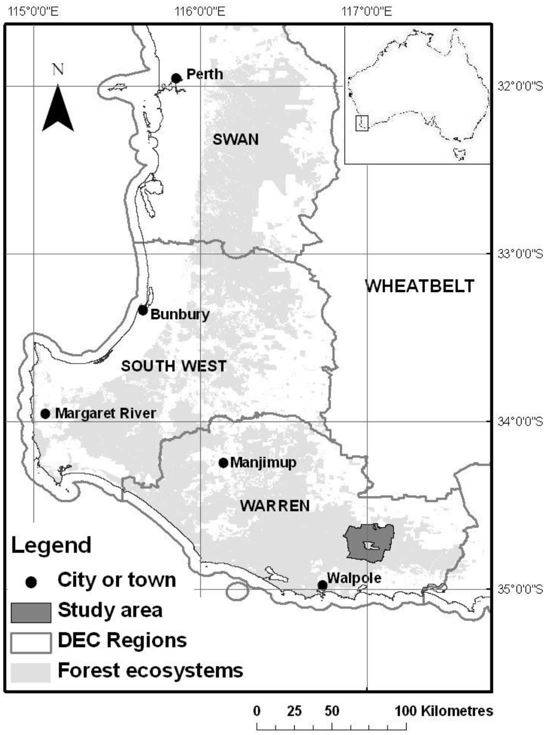

Figure 1—**Study area (source: Wittkuhn & Hamilton 2010).**

Table 1— *Attributes of the study sites. 'VC' = vegetation complex (CA = Caldyanup which represents the seasonally inundated shrubland/sedgeland in drainage basins; COy1 = jarrah forest on lateritic uplands; COp1 = jarrah forest on shallow gritty sands). 'Fire interval sequence' and its 'Abbreviation' are classifications based on the 'Actual fire intervals' which are presented in reverse time series.*

Site no.	Vegetation type	VC	Fire interval sequence	Abbreviation used in text	Actual fire intervals (y)	Years in which fires occurred a
1	Shrubland	CA	Short-short	SS	12-4-5-9	2002-1990-1986-1981-1972
2	Shrubland	CA	Short-short	SS	12-4-5-9	2002-1990-1986-1981-1972
13b	Shrubland	CA	Short-short	SS	8-3-3-14	2002-1994-1991-1988-1974
19b	Shrubland	CA	Short-short	SS	8-3-3-14	2002-1994-1991-1988-1974
5	Shrubland	CA	Mixed	M	12-9-9	2002-1990-1981-1972
10	Shrubland	CA	Mixed	M	11-7-9	2002-1991-1984-1975
12	Shrubland	CA	Mixed	M	11-7-9	2002-1991-1984-1975
14	Shrubland	CA	Mixed	M	11-7-9	2002-1991-1984-1975
15	Shrubland	CA	Mixed	M	8-10-8	2002-1994-1984-1976
18	Shrubland	CA	Mixed	M	8-10-8	2002-1994-1984-1976
22	Shrubland	CA	Mixed	M	12-9-9	2002-1990-1981-1972
21	Shrubland	CA	Long-long	LL	11-19	2002-1991-1972
23	Shrubland	CA	Long-long	LL	11-19	2002-1991-1972
29	Shrubland	CA	Long-long	LL	11-19	2002-1991-1972
3c	Forest	COy1	Short-short	SS	12-4-5-9	2002-1990-1986-1981-1972
20b,c	Forest	COy1	Short-short	SS	8-3-3-14	2002-1994-1991-1988-1974
17c	Forest	COy1	Short-short	SS	8-10-4-4	2002-1994-1984-1980-1976
7	Forest	COy1	Short-short	SS	8-10-4-4	2002-1994-1984-1980-1976
4	Forest	COy1	Mixed	M	12-9-9	2002-1990-1981-1972
6c	Forest	COy1	Mixed	M	12-9-9	2002-1990-1981-1972
8	Forest	COy1	Mixed	M	8-10-8	2002-1994-1984-1976
16c	Forest	COy1	Mixed	M	8-10-8	2002-1994-1984-1976
9c	Forest	COp1	Mixed	M	11-7-9	2002-1991-1984-1975
11c	Forest	COp1	Mixed	M	11-7-9	2002-1991-1984-1975
24	Forest	COp1	Mixed	M	12-9-9	2002-1990-1981-1972
25	Forest	COp1	Long-long	LL	11-19	2002-1991-1972
26c	Forest	COp1	Long-long	LL	11-19	2002-1991-1972
30	Forest	COp1	Long-long	LL	11-19	2002-1991-1972
28c	Forest	COp1	Very long	VL	30	2002-1972

27c	Forest	COp1	Very long	VL	30	2002-1972

a Fire years in SWA occur from ~ spring to autumn (~September until April in the following year). Fire years are typically denoted as, for example, 2002/03. In this table, we have simplified to 2002 (for the example given).
b Sites 13, 19 and 20 were last burnt by prescribed fires during November 2002, while all other sites were last burnt by wildfire during March 2003.
c Indicates the subset of sites used for fungi surveys.

Using GIS, we investigated sequences of actual fire intervals by simplifying each fire interval from the recorded fire history into one of three groups: short (≤ 5 years), moderate (6–9 years) or long (≥ 10 years), and joining them together to form a fire interval sequence (Wittkuhn and Hamilton, 2010). We identified polygons with successive short fire intervals (SS-regime), and polygons with successive long fire intervals (LL-regime) during the period from 1972/73 to 2004/05. All other polygons were considered a 'mixed' or 'moderate' (M) regime, except for one polygon with a single fire interval of 30 years (burnt in 1972 and 2002). This interval is one of the longest for the study area (Wittkuhn and Hamilton, 2010), and is referred to as a 'very long' (VL) regime (Table 1).

We investigated two common vegetation types that occur in a landscape mosaic: (1) Shrubland, which occurred in seasonally-inundated lowlands and were dominated by monocotyledons (especially Cyperaceae spp.) and small shrubs (< 1 m tall) predominantly from the families Myrtaceae, Fabaceae and Proteaceae; (2) Forest, dominated by jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) to 20 m tall with a shrubby mid-storey and species-rich understorey. Forest sites included examples of two Collis (CO) complexes which differ slightly in soil type and vegetation structure: COy1, described as being on lateritic and yellow duplex soils, and COp1 on shallow gritty yellow duplex soils, usually without laterite (Havel and Mattiske, 2000).

Biological surveys

At each site, a 2 ha sampling grid was established to examine the extent to which different sequences of past fire intervals influence richness, abundance and composition of a wide range of taxonomic groups (vascular plants, macrofungi, ground-dwelling invertebrates and vertebrates). Survey methods are described in Wittkuhn et al. (2010).

Data analysis

One-way anova was used to test for differences in mean species richness between fire regimes within each vegetation type and taxonomic group. To compare the richness of plants, ants and beetles between forest and shrubland sites, we used a two-way anova with vegetation type as the first factor, and fire interval sequence as the second factor.

Variation in community composition was investigated for each taxonomic group using non-metric multidimensional scaling (nMDS) on a Bray-Curtis dissimilarity matrix of log(x+1) transformed data (except vertebrate fauna which was square root transformed).

Differences in species composition between vegetation complexes and fire interval sequences were tested using the PERMANOVA procedure on similarity matrices for each taxonomic group. PERMANOVA partitions the variation in multivariate data between one or more a priori groups. The procedure is non-parametric incorporating permutations to test for significance, thereby not relying on normality assumptions (Anderson, 2001). For plants, ants and beetles, we ran a two-factor PERMANOVA with vegetation complex (shrubland vs COy1 vs COp1) and fire interval sequence (SS vs M vs LL, and VL in forests) as the factors (Table 2). We included three contrasts, which are *a priori* comparisons that further partition the sums of squares attributable to a factor. The contrasts were: (1) shrubland vs forest, where the shrubland complex was compared with the combined COy1 and COp1 sites; (2) COy1 vs COp1, which is a comparison between the two forest complexes; and (3) SS vs LL+VL sites, to test for differences between the extremes of fire interval sequences. The two-factor PERMANOVA permits an assessment of the interaction between vegetation complex and fire regime. For vertebrates and macrofungi, a two-factor PERMANOVA was used to test the main effects of vegetation complex (comparing the two forest complexes COy1 vs COp1) and fire interval sequence.

Results

There were 403 vascular plant species, 112 ant species, 378 beetle morphospecies, 37 vertebrate fauna species and 395 macrofungi species recorded in this study. Species richness for all groups did not differ between sites with contrasting fire interval sequences, and this was the case for both forest and shrubland (Table 2).

The nMDS ordinations and PERMANOVA results demonstrated a clear distinction between forest and shrubland sites in terms of the species composition of vascular plants, ants and beetles (Fig. 2; Table 3).

Sites were not clustered according to their corresponding fire regime groups for either forest or shrubland when data for all taxonomic groups were analysed by nMDS (Fig. 2). However, PERMANOVA results for macrofungi suggested a different species composition due to fire regimes (P = 0.039), and results for plants (P = 0.039), ants (P = 0.085) and beetles (P = 0.089) suggested a different species composition between SS sites and LL/VL sites (Contrast 3 in Table 3).

Table 2 *— Mean species richness (± sem) for taxonomic groups at sites with short-short (SS), mixed/moderate (M), long-long (LL) and very long (VL) fire interval sequences in forest and shrubland. P-values are given from one-way anova between fire interval sequences down each column.*

Fire regime	Forest Plants	Ants	Beetles	Vertebrates	Fungi	Shrubland Plants	Ants	Beetles
SS (n=4)	82±4	24±2	35±4	11±1	142±15	76±11	16±2	27±6
M (n=7)	91±7	25±1	34±4	13±1	135±17	68±9	16±2	30±3
LL (n=3)	91±7	26±2	32±6	12±1	150±9[b]	81±6	18±2	28±5
VL (n=2)	101±6	25±1	33±1	12±3		-	-	-
All sites[a]	90±4	25±1	34±2	12±1	141±8	73±5	16±1	29±2
P-value	0.561	0.751	0.979	0.290	0.783	0.635	0.790	0.923

[a] n = 16 for forest; n = 14 for shrubland

[b] Derived from a combination of two VL sites (sites 27 and 28) and one LL site (site 26).

Table 3— *P-values from 2-factor PERMANOVAS testing the variation in species composition for the taxonomic groups on sites with contrasting fire interval sequences in forest and shrubland. The two factors were vegetation complex (shrubland vs COy1 vs COp1) and fire interval sequence (SS vs M vs LL, and VL for forest sites). The design incorporated contrasts to compare shrubland vs forest (C1), the two forest vegetation complexes (C2), and the subset of SS vs LL+VL sites (C3). Where data allowed, interaction effects were also tested. Results for vertebrates and fungi were restricted to forest sites; hence the P-value testing the main effect of vegetation complex has been placed alongside C2 to more accurately reflect the test.*

Source	df	Plants	Ants	Beetles	Vertebrates[a]	Fungi[b]
Vegetation complex (VC)	2	< 0.001	< 0.001	< 0.001	See C2	See C2
C1: Shrub v Forest	1	< 0.001	< 0.001	< 0.001	-	-
C2: COy1 v COp1	1	0.071	0.533	0.576	0.734	0.011
Fire interval sequence (FIS)	3	0.826	0.472	0.813	0.908	0.039
C3: SS v (LL + VL)	1	0.039	0.085	0.089	No test	No test
VC * FIS	2	0.403	0.368	0.429	No test	No test
C1 * FIS	2	0.379	0.348	0.289	-	-
C2 * FIS	0	No test	No test	No test	-	-
VCxC3	0	No test	No test	No test	No test	No test
Residual	22					

[a] Degrees of freedom for vertebrates: VC = 1, FIS = 3, Residual = 11

[b] Degrees of freedom for fungi: VC = 1, FIS = 2, Residual = 6

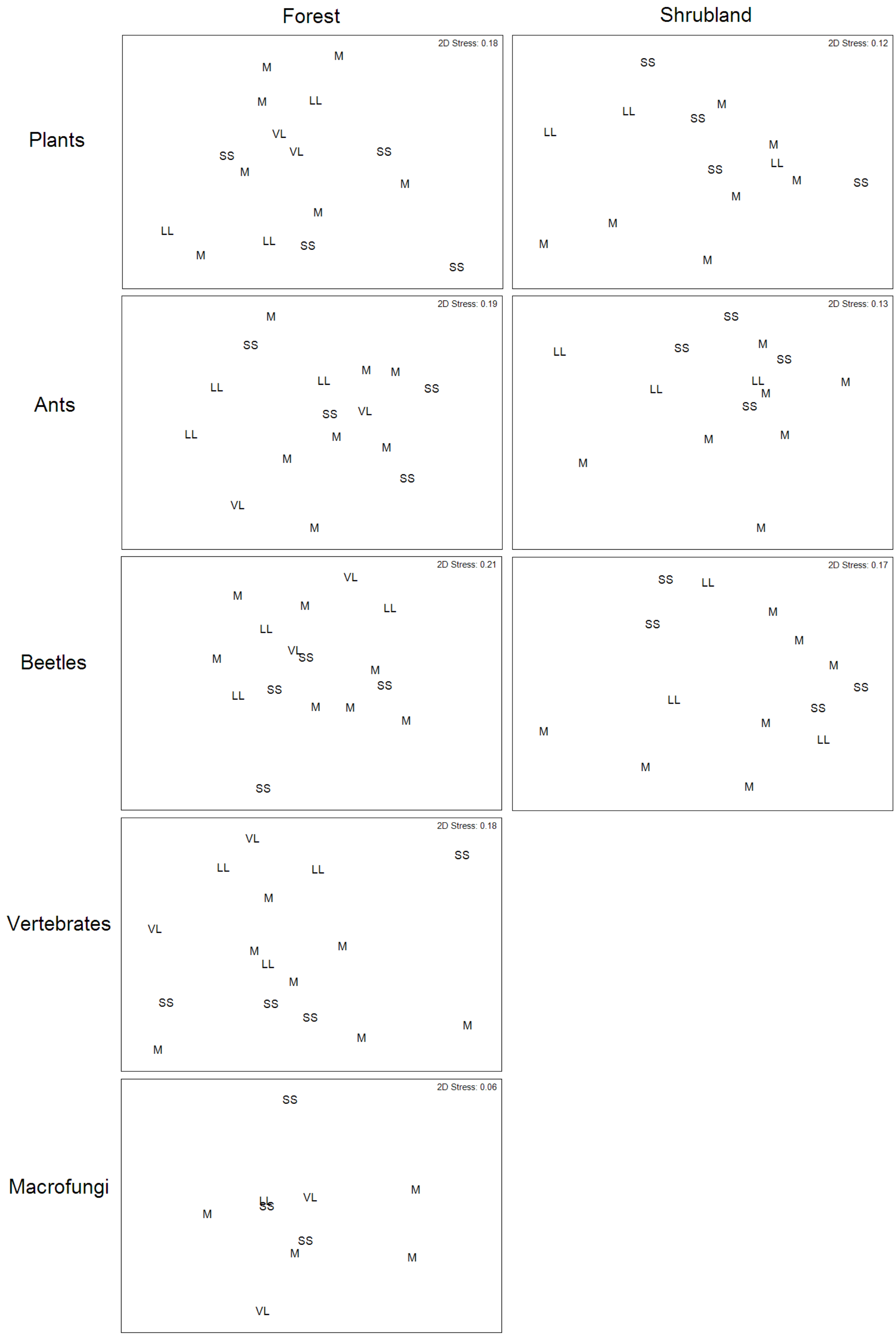

Figure 2— nMDS of sites based on the composition and transformed abundance of each taxonomic group for sites in forest (left) and shrubland (right). Labels represent the fire interval sequence of the site: M = mixed/moderate; SS = short-short; LL = long-long; VL = very long. Fungi and vertebrates were not sampled in the shrubland. (source: Wittkuhn et al. 2010).

Discussion

Our data show that varying fire intervals had minimal effect on the richness and composition of biota associated with forests and shrublands of the Warren bioregion. While there is some evidence that extremes in fire interval sequences influence the composition of plant, ant, beetle and macrofungi communities, occasional short intervals that may result from unplanned fires affecting recently-burnt sites are unlikely to have serious adverse consequences for biodiversity. Fire regimes with sustained intervals at the extreme ends of the spectrum could, however, alter species composition, as has been shown for other ecosystems (Bastias et al., 2006; Cary and Morrison, 1995; Zedler et al., 1983).

Data from the Warren bioregion showed that contrasting fire interval sequences had little effect on species richness which is consistent with a number of other published studies (Bradstock et al., 1997; Hanula and Wade, 2003; Watson and Wardell-Johnson, 2004; Woinarski et al., 2004). This may be due to the variation in fire intervals, particularly at SS sites that have also experienced intermediate (M) and long (L) fire intervals.

The PERMANOVA provided some evidence ($P < 0.1$) that the composition of plants, ants and beetles differed significantly between SS and LL/VL groups. This indicates the potential for compositional change should particular fire interval sequences be maintained over long periods. For example, maintaining short fire intervals (e.g. ≤ 5 years) may be detrimental to particular taxa, as has been shown in several manipulative and natural field studies for a range of taxonomic groups (Bradstock et al., 1997; Cary and Morrison, 1995; Bastias et al., 2009; Woinarski et al., 2004; Andersen et al., 2006; York 2000). We suggest that substantial ecological change occurred in most of these studies because short fire intervals were maintained over an extended period of time.

The fact that species composition differed between the SS and LL/VL regimes but did not differ from M regimes, suggests that the potential for compositional change is greater at either extreme of the fire regime continuum. This lends support to the intermediate disturbance hypothesis (Grime, 1973) and the importance of a variable fire interval regime for biodiversity conservation. Long association with fire over evolutionary time scales (Hopper, 2003) would be expected to exert strong selective pressure for species with adaptations to withstand or respond to variability in fire interval length. We suggest that the variability in fire intervals that has occurred in our sites makes an important contribution to observed resilience, whereas the maintenance of an invariant short or long interval regime over the longer term would likely lead to substantial ecological change.

The biota of SWA demonstrates a high degree of resilience to a range of fire interval sequences in both shrubland and open eucalypt forest. Application of planned fire has an important contribution to make to the conservation of biodiversity, and is an essential strategy for avoiding the undesirable social, economic and environmental impacts of intense bushfires that may burn out of control during the long dry season in SWA. Further research should focus on understanding how spatial patterns of fire treatments (fine-grained mosaics of burnt/unburnt areas) influence ecosystem processes, biodiversity and the potential for fire spread in the landscape.

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