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Multi-century changes in vegetation structure and fuel availability in fire-sensitive eucalypt woodlands

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ABSTRACT

Understanding how communities change with time since fire is critical for identifying appropriate fire return intervals for biodiversity conservation. In infrequently-burnt communities, vegetation structure, habitat features and fuel availability can change over time-scales much longer than can be measured using contemporary remote-sensing approaches, creating challenges for conservation and fire management. To characterize longer-term patterns of vegetation structural change, we measured vegetation cover, ground cover, tree density and stand basal area across a multi-century time-since-fire sequence derived from growth ring-size relationships in fire-sensitive *Eucalyptus salubris* woodlands of south-western Australia. We hypothesized that: (i) vegetation structural components reflecting fuel availability increase with time since fire; (ii) recovery of vegetation structural components with time since fire requires long time-frames; and (iii) vegetation components indicating senescence are more evident in mature than intermediate fire-age classes. All vegetation structural components showed significant differences between time-since-fire classes (termed 'young', 'intermediate' and 'mature'), and to a lesser extent between years of sampling. The two vegetation structural components with the highest covers overall, and hence likely greatest contributors to fuel availability, were vegetation 4–10 m high and ground fuel. These two layers showed non-monotonic changes indicating a peak at intermediate times since fire (~35–150 or 35–250 years; depending on the model used to estimate stand age), conflicting with the common assumption that fuel availability increases with time since fire. Total stand basal area increased rapidly after fire then appeared to stabilize beyond about 100 years, with competition likely mediating density-dependent thinning such that declining plant density offset increasing trunk size. There was little evidence for an increase in standing dead vegetation in mature woodlands such as would suggest significant senescence when long-unburnt. Replacement of mature woodlands with intermediate time-since-fire woodlands with greater cover and connectivity of key fuel layers potentially instigates a self-reinforcing fire regime shift favouring larger and/or more uniform fires. If such changes eventuate, substantial losses in conservation values in *E. salubris* woodlands are likely. Elucidating these changes in vegetation structure and implications for conservation management only became feasible due to the development of methods to estimate the time since fire of vegetation not burnt for hundreds of years.

1. Introduction

Fire is one of the greatest forms of disturbance to terrestrial communities, and plays an important role in shaping vegetation patterns and plant community composition and structure in most seasonally dry landscapes (Bond and van Wilgen, 1996; Bond et al., 2005). As ecosystems recover from fire, changes occur in the composition and structure of vegetation affecting the mass, spatial arrangement and condition of fuels, and availability of habitat for fauna. Understanding how ecosystem structure changes with time since fire is therefore critical for identifying appropriate fire return intervals for biodiversity conservation and in predicting the behaviour of fires (Álvarez et al., 2009; Gosper et al., 2012).

Changes in the characteristics of fuels influences the flammability of ecosystems, with a variety of response forms of flammability to time since fire recorded, including relatively constant flammability with time since fire, a rapid increase to an asymptote, or an initial increase followed by a decline (McCarthy et al., 2001). Despite this, fire management has often assumed monotonic increases in flammability with time since fire premised on quantitative increases in fuel and changes in fuel arrangement and connectivity (Kitzberger et al., 2012). In many fire-prone

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communities, fire management for biodiversity conservation is based on the assumptions that long-unburnt vegetation declines in vigour (senescence; Bond, 1980) and above-ground plant species richness (Egler, 1954), both of which can be alleviated by fire. These assumptions on changes in fuel availability and community diversity coalesce in fire management approaches based on models postulating 'idealised' time since fire age class distributions and maximum and minimum acceptable fire intervals for specific vegetation communities (Fire Ecology Working Group, 2002, 2004).

In ecosystems dominated by slow growing, long-lived plants, changes in vegetation structure, composition and habitat features after fire may occur over decadal to century time-scales (Clarke et al., 2010; Haslem et al., 2011; Gosper et al., 2013, in press). Understanding community response to fire requires time series or space for time studies spanning these temporal scales (Watson et al., 2012; Gosper et al., in press). Yet, there are a variety of technical and logistical challenges in determining the time since fire of vegetation not burnt more recently than the period covered by contemporary sources documenting fire events, such as satellite images, aerial photos or historical records, which often only cover the last 30–60 years. Many chronosequence studies (e.g. Parsons and Gosper, 2011), therefore, have necessarily artificially truncated times since fire for long-unburnt vegetation, with poorly-understood consequences (Clarke et al., 2010; Gosper et al., in press). Generally, there is a poor understanding of patterns and time scales of temporal changes in vegetation structure after fire in many communities largely stemming from this inability to determine the time since fire of long-unburnt vegetation. This may have substantial biodiversity conservation implications, as this lack of knowledge may constrain fire management decisions where there are concerns over recent shifts in fire regimes (Parsons and Gosper, 2011), projected changes in fire regimes in the future (Prober et al., 2012), or potentially incompatible fire management objectives (Haslem et al., 2011).

The Great Western Woodlands (GWW) form the world's largest extant Mediterranean-climate woodland, with *Eucalyptus* woodlands occurring in mosaic with mallee, shrublands and salt lakes over ~160,000 km^2 (Watson et al., 2008; Prober et al., 2012). Like most other Mediterranean-climate regions, recurrent fire is a feature of the landscape (Cowling et al., 1996; O'Donnell et al., 2011a). The GWW are unique among Mediterranean-climate regions in the extent of woodland (10–25 m in height) occurring at relatively low rainfall (200–400 mm per annum; Prober et al., 2012). Mature woodlands, because of their open tree canopy structure and patchy distribution of shrubs and litter, have a low probability of burning relative to other vegetation types occurring across the same landscape (O'Donnell et al., 2011a). However, major fires in the region do occur during severe weather, especially when drought conditions follow wet and cool conditions in spring and summer of the preceding year, sustaining large fires which may burn for weeks or months (>100,000 ha; McCaw and Hanstrum, 2003; O'Donnell et al., 2011b). Recent decades have seen a number of large wildfires in the GWW, with fire intervals over this period being much shorter than in the analogous (other than in the degree of landscape fragmentation) adjoining Western Australian wheatbelt (Parsons and Gosper, 2011).

Many of the *Eucalyptus* species that dominate GWW woodland communities are sensitive to fire, being killed by complete canopy scorch. Even in those GWW woodland *Eucalyptus* species in which a proportion of the population resprouts after fire (Yates et al., 1994), growth is slow and hence changes in vegetation structure after fire may occur over protracted periods. Dense seedling recruitment of the dominant trees typically follows fires and significantly alters vegetation structure (Yates et al., 1994). Currently, there is substantial uncertainty regarding temporal changes in woodland structure and the time periods over which these changes occur (Hopkins and Robinson, 1981). Further, once mature woodlands are disturbed by fire, positive feedback between fire and post-fire vegetation structure may render regenerating vegetation more susceptible to further fire than mature woodlands (O'Donnell et al., 2011a); yet for fire management, the typical monotonic increase in fire behaviour rating with time since fire is assumed to apply (DEC, 2010). Recurrent fire in short succession could lead to unfavourable management outcomes including the loss of habitat features of long-unburnt vegetation important for a range of fauna (Watson et al., 2012), decline in carbon stocks (Berry et al., 2010) and decline in the extent of mature woodland vegetation communities which are distinct in floristic composition (Gosper et al., in press).

To inform fire management we aimed to characterize changes in vegetation structure and fuel availability over periods of more than 300 years after fire in *Eucalyptus salubris* (Gimlet) woodlands. We used a chronosequence approach (i.e. substituting space for time), with times since fire determined through a combination of satellite imagery, growth ring counts and growth ring-plant size relationships (Gosper et al., 2013). Based on common assumptions employed in fire management, we hypothesized that (1) vegetation structural components reflecting fuel availability increase with time since fire; (2) recovery of vegetation structural components with time since fire requires long time-frames; and (3) vegetation senescence is more evident in mature than intermediate fire-age classes.

2. Material and methods

2.1. Survey plots

We established 76 plots in *E. salubris* woodlands distributed along the western edge of the Great Western Woodlands, south-western Australia; mostly near Karroun Hill (30°14′S, 118°30′E); Yellowdine (31°17′S, 119°39′E) and Parker Range (31°47′S, 119°37′E). This area has a semi-arid Mediterranean climate (see Gosper et al., 2013 for more climatic details). The region supports a mosaic of mallee, scrub-heath and woodland, with vegetation type determined locally by edaphic factors, and influenced by historic disturbances. All plots had a dominant crown layer of *E. salubris*, sometimes in association with other eucalypts. *E. salubris* is a non-lignotuberous tree widespread across the GWW (Brooker et al., 2002) that is killed by complete canopy scorch.

Regions chosen for sampling each contained extensive areas last burnt in recent (<10 years) and older (>38, but likely to be less than 60 years; Gosper et al., 2013) fires, and large areas with no evidence of contemporary fire. Plots were distributed in these times since fire across the geographic spread of sampling, with additional plots last burnt between 10 and 38 years ago sampled in the limited localities where such fires had occurred.

Stand age was determined through a combination of Landsat image interpretation, growth ring counts and growth ring-size relationships (see Gosper et al., 2013 for full details). We assume that stand age is equivalent to time since the last fire. There is little doubt over the validity of this assumption in young stands, however, it remains possible that some older stands may have experienced milder (ground) fires that did not result in widespread death of canopy trees. Post-fire observations indicate very high (close to 100%?) mortality when fires pass through *E. salubris* woodlands. Further, *E. salubris* has a very thin protective bark layer (~3 mm in width) compared with co-occurring eucalypts in which some individuals are able to resprout following fire (e.g. bark thickness of ~10 mm in *E. salmonophloia*) (Prober and Macfarlane, 2013), which lends support to our contention that fires that pass through *E. salubris* woodlands lead to extensive mortality of canopy trees.

Information on aspects of the fire regime other than time since fire (such as intensity and previous fire intervals), was not available.

Gosper et al. (2013) test models with a variety of terms and transformations of growth rings to estimate time since fire. Here we use the two best-performing plausible models: (i) estimates based on untransformed growth rings predicted by *E. salubris* diameter at the base (D_{10}) plus plot location (Model 2; Gosper et al., 2013), and (ii) square-root transformed growth rings predicted by *E. salubris* diameter at the base (D_{10}) plus plot location (Model 5), acknowledging that the former likely underestimates times since fire of the oldest plots and that the later likely overestimates them. Whichever model is used, the certainty of plot time since fire declines with increasing time, particularly beyond 200 years (Gosper et al., 2013). The sample age range produced from Model 2 was 2–370 years post-fire and for Model 5 was 2–1460 years post-fire. Analyses were conducted using the lower range of times since fire generated by Model 2, although for interpretation purposes the equally valid alternative time since fire scale from Model 5 has been added to figures as a second *x*-axis (approximate) and to the text in parentheses. Gosper et al. (2013, in press) contain a listing of the location and time since fire of all plots except for a small set of additional plots sampled specifically for this study (Supplementary Material, Table S1).

Each plot consisted of 50 × 50 m of relatively uniform vegetation located within 1 km of vehicular tracks and sited within either Nature Reserves or Unallocated Crown Land. Plots were spaced at least 250 m apart, and at least 500 m apart for plots of the same time since fire. As fires across this landscape can be very large (McCaw and Hanstrum, 2003), it was usually necessary to place multiple plots within the one fire scar in each district. This potentially creates problems in disentangling location and fire event effects (Hurlbert, 1994). Further, the 'space-for-time' (or chronosequence) approach involves the comparison of stands of different times since fire over the one study period (2010–2012), contrasting the more desirable longitudinal approach of documenting changes in a stand as they occur with the passage of time. The 'space-for-time' approach assumes that the plots are truly comparable (other than in time since fire), or at least that differences between them are randomly distributed across times since fire (Hurlbert, 1994) and that fire event effects (Bond and van Wilgen, 1996) do not confound time since fire effects. Although there is subsequently a degree of uncertainty in attributing differences to time since fire alone, we have taken a number of steps to minimise the difficulties for interpretation. First, we sampled across a wide geographic area which had different fires, in a variety of years. Second, our analyses concentrate on the detection of trends over time, rather than solely determining differences between individual times since fire, which would be confounded by sampling a limited number of fire events. Third, the spread of plots in various times since fire across the study area suggests that systematic location bias confounding time since fire effects are unlikely (Gosper et al., in press).

2.2. Vegetation sampling

To sample vegetation structure we measured tree density and size, ground cover and the vertical distribution of vegetation. At each plot, two 50 m transects were established along the north and west sides and a 70 m transect was placed diagonally through the centre starting in the north-west corner. Along these transects, 50 vertical point placements were made with a 12.5 mm diameter pole, extendable to 3 m in height, marked in 10 cm increments. Intercepts were sampled at 3 m intervals; 16 along each side and 18 on the diagonal. At each pole placement we recorded the presence or absence of an intercept between the pole and any vegetation in the following height classes: 0–12, 12–25 and 50–100 cm, and 1–2, 2–4, 4–10 and >10 m. The presence/absence of intercepts with vegetation greater than 4 m in height was visually estimated, with the height of any intercepted vegetation checked using a hypsometer (Nikon Forestry 550). Intercepts with live and dead vegetation (entirely dead plants or dead limbs, but not individual dead leaves on otherwise live limbs) were recorded separately, as were point placements which did not intercept any vegetation (termed 'foliar gaps'). Additionally, at each of the 50 point placements, ground cover was recorded by placing the pole 1 m perpendicularly to each side of the transect. At each point ($n = 100$) ground cover was recorded as being either 'ground fuel', 'bare' (including rock) or 'cryptogam' based on the dominant cover type (if multiple types were present) under the pole intercept. All dead vegetation on the ground surface was classed as ground fuel, so includes shed leaves, twigs, buds, fruits, bark, branches and logs, without any attempt to divide these into flammability classes, calculate mass or volume. As such, ground fuel cover should be interpreted as an assessment of the spatial coverage of potentially flammable material, but not necessarily a reflection of the quantity of material available for combustion. Cryptogam cover was based on a visual field assessment of the presence or absence of soil crust organisms, including moss, lichens and cyanobacteria. In cases where ground cover placements intercepted live vegetation, the ground surface under foliage was recorded. These methods provided an objective measure of abundance reflecting but not equivalent to projective cover (due to the effect of pole width on intercepts), and are hereafter referred to as 'cover'. Intercept counts were converted to a single proportion cover value per layer/ground cover class per plot.

Tree size data was collected by sampling 16 trees by use of a modified version of the point-centred quarter method (Cottam and Curtis, 1956). We measured the diameter at the base (D_{10}) of trunks, tree height and distance from the corner of the nearest tree in each of the four compass quadrants radiating from the four corners of each plot. Diameter at the base was used rather than the more standard breast height owing to the low, multiple-branching habit of *E. salubris.* From these measurements, we calculated tree density per plot and total cross-sectional area per tree. Total basal area per plot was calculated by multiplying mean cross-sectional area per tree by tree density.

Plots were sampled in either spring 2010, spring 2011 or spring 2012, with all time since fire classes sampled in more than one year. Annual rainfall varied markedly between sample years, with rainfall in 2010 at a nearby weather station with a long period of records (Merredin) being the 4th lowest in over 100 years, while rainfall in 2011 was above average and in 2012 marginally below average (Bureau of Meteorology, 2013). Variation between sample years resulted in limited floristic differences (Gosper et al., in press) and plausibly affects other aspects of vegetation structure, such as ground fuel cover. Where we have incorporated a factor for year of sampling in our analyses, we have classified it as a fixed factor with two classes – 2010 ($n = 52$) and a combined 2011–12 ($n = 24$). Consequently, results should be interpreted as being for differences between this combination of an exceptionally dry year versus two not atypically dry years.

2.3. Statistical analysis

To test the degree of correlation and redundancy among vegetation structural variables, a correlation matrix was constructed using PRIMER (Version 6.1.11, PRIMER-E, Plymouth, UK). Strong negative correlation ($r > 0.7$) was found between tree height and density ($\log_{10}$ transformed) (Supplementary Material, Table S2). As intra-specific competition among canopy trees appears to exert a strong influence on post-fire successional processes (Gosper et al., in press), tree density was retained in univariate analyses while tree height was omitted. Strong positive correlations occurred between cover in 12–25, 25–50 and 50–100 cm height classes; as the midpoint of this range, cover 25–50 cm was retained. Finally, high negative correlation existed between cover of ground fuel and bare ground. Given the potentially important role of ground fuel in fuel availability, this was the variable retained.

For the purpose of some analyses where categorical age classes were appropriate, we divided our samples into 'young', <20 years post-fire ($n = 23$); 'intermediate', 35–120 (35–200) years post-fire ($n = 26$); and 'mature', >140 (>260) years post-fire ($n = 27$). Using categorical age classes places artificial divisions along a continuous scale, but does reflect gaps in the range of times since fire sampled and was associated with substantial changes in vegetation composition (Gosper et al., in press).

PRIMER was used in Principal Components Analysis to examine the relationship between plots in vegetation structure, using normalised (Clarke and Gorley, 2006) values for all variables except basal area. Basal area was excluded because: (i) it was calculated from tree density; and (ii) some plot times-since-fire were derived from relationships between the number of growth rings and tree diameter plus location (Gosper et al., 2013) suggesting a lack of independence between times since fire and stand basal area. PERMANOVA and PERMDISP, using the Euclidian distance resemblance measure, were used to test for differences in overall vegetation structure and dispersion respectively between time since fire classes, sampling year and their interaction.

ANOVA, using Statistica (Version 7.1, Statsoft, Tulsa, OK, USA), was used to test for differences in individual vegetation structural variables (excluding those with high correlations as described above) and time since fire classes, sampling year and their interaction. From these results key contributors to fuel availability were identified and relationships between these and time since fire were tested with simple regression models using the polynomial standard curves regression module of Sigmaplot (Version 10.0, Systat Software Inc., Chicago, IL, USA), and model selection based upon minimising Akaike Information Criterion (AIC). Models tested represented a range of biologically plausible scenarios of temporal trends in vegetation change: a consistent rate of increase/decrease over time (linear), an accelerating rate of change over time (exponential), a rapid increase or decrease to an asymptote (power, inverse or logistic), or a change in the trajectory of the relationship at an intermediate time since fire (such as due to competition; quadratic). Alternative model forms and summary statistics are included in Supplementary Material (Table S3). To reduce the leverage of the few longest-unburnt plots, we applied square-root transformation to plot time since fire. For basal area, we explore relationships with time since fire only using those plot times since fire derived from Landsat imagery or complete growth ring counts that are completely independent of tree size. This truncated relationships at 100 years post-fire.

3. Results

PERMANOVA and PCA indicated there were clear changes in overall vegetation structure between time-since-fire classes (Pseudo-F = 25.5, $df_{2,70}$, $P = 0.001$) and survey year (Pseudo-F = 2.04, $df_{1,70}$, $P < 0.05$) in *E. salubris* woodlands, but no significant interaction (Pseudo-F = 1.04, $df_{2,70}$, not significant) or differences in dispersion (Supplementary Material, Table S4) between these experimental factors that might otherwise complicate interpretation. Vegetation structure of all time since fire classes (young (Y), <20 years post-fire; intermediate (I), 35–120 (35–200) years post-fire; and mature (M), >140 (>260) years post-fire) were significantly distinct based on pair-wise comparisons (Y vs. I $t = 4.63$, $P = 0.001$; Y vs. M $t = 6.06$, $P = 0.001$; I vs. M $t = 4.00$, $P = 0.001$), illustrating that vegetation structural changes occur across the breadth of the chronosequence.

PCA indicated a progression in structure from young, to intermediate, to mature time-since-fire classes. Interestingly, mature plots appeared to be returning to close proximity in ordination space to the young class, instead of being the most distant as might be expected if vegetation structure variables showed monotonic changes with time since fire (Fig. 1). Young vegetation was particularly characterised by more bare ground and cover in all height classes to 50 cm, lower cover 4–10 m and shorter trees (Figs. 1 and 2). Vegetation at intermediate time since fire was typified by higher cover of ground fuel and 4–10 m vegetation, with less bare ground and cryptogam cover. More vegetation >10 m in height and more foliar gaps characterised mature vegetation, along with low tree density and less cover of dead vegetation and vegetation in the 50–200 cm classes. Greater cover from 50 to 400 cm high, standing dead vegetation and tree density characterised both young and intermediate plots, while high cryptogam cover typified both mature and young plots.

All individual vegetation structural variables tested with ANOVA were significantly affected by time-since-fire class, but only two (cover of standing dead vegetation and vegetation >10 m in height) were influenced by sampling year and none by the interaction of time since fire and year (Table 1). A number of individual vegetation structural variables showed non-monotonic changes with time since fire, either exhibiting a 'hump-shaped' pattern with greatest values at intermediate times since fire and relatively lower values when young and mature, or the inverse 'U'-shaped pattern. Hump-shaped responses to time since fire were found in cover of ground fuel and vegetation 4–10 m high (Fig. 3b and c). 'U'-shaped responses were recorded in cover of cryptogams and vegetation 0–12 cm high. Tree density and cover of standing dead vegetation and vegetation 25–50, 100–200 and 200–400 cm high showed a monotonic decrease with time since fire, although pair-wise comparisons between time since fire classes exhibited different patterns of decrease (essentially either linear or exponential) across these variables (Table 1). Only proportion cover of vertical gaps between foliage (Fig. 3a) and vegetation >10 m in height showed a monotonic increase with time since fire. From these findings it is apparent that the bulk of standing dead vegetation was contributed by fire-killed plants, and attrition of standing dead material outpaced new mortality of whole plants and/or sections of plants. The vegetation structural components with the greatest

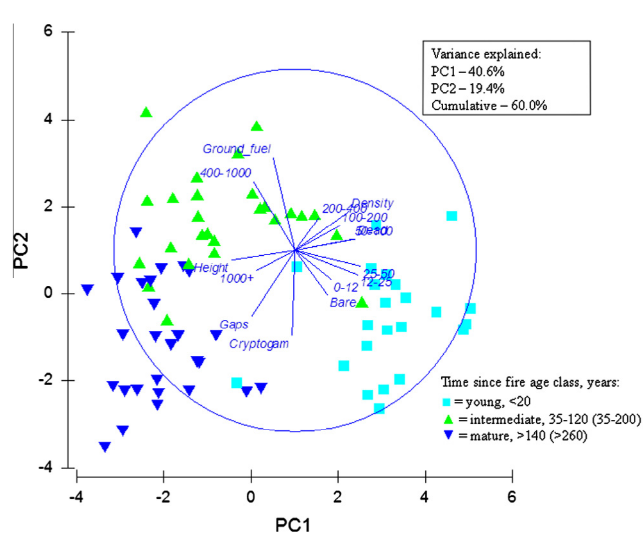

Fig. 1. Principal components analysis of plots by all vegetation structure variables, which are shown as vectors. Note '*dead*' and '50–100' vectors are overlain.

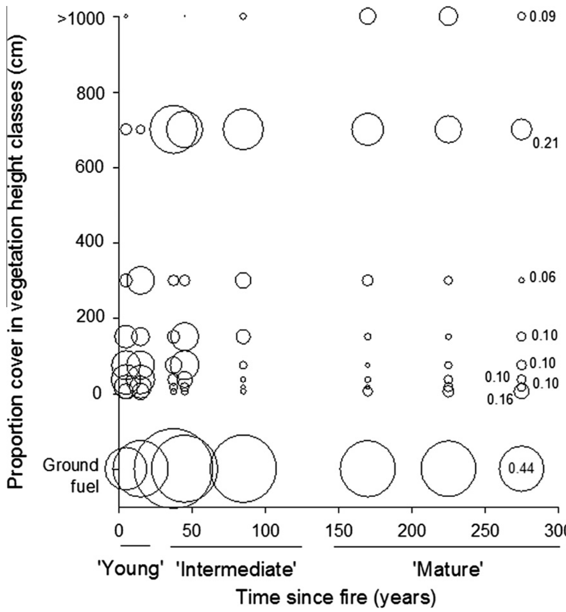

Fig. 2. Bubble plot showing the vertical distribution of flammable fuel in *Eucalyptus salubris* woodlands. Plots were grouped into years since fire classes: 0–10, 11–20, 35–40, 41–50, 51–120, 140–199, 200–249, 250–400 years (alternative classes [see methods]: 0–10, 11–20, 35–40, 41–50, 51–200, 260–449, 450–699, 700–1500 years) and shown at the midpoint of these classes (with the exception of 250–400, which is shown at 275 years since fire reflecting the time since fire of the majority of plots in this class; Gosper et al., 2013). Vegetation height classes are shown at the midpoint of the sample range (0–12, 12–25, 50–100, 100–200, 200–400, 400–1000 cm), with the exceptions that vegetation > 1000 cm is shown at 1000 cm as no upper bound was defined and ground fuel is displayed at −200 for ease of interpretation. The bubble scale (proportion cover) is shown for the last column.

cover overall were ground fuel and vegetation 4–10 m in height (Table 1; Fig. 2).

The overall vegetation profile shows relatively dense, low (<4 m) regeneration through to 20 years post-fire; a very dense and dominant low tree stratum (4–10 m) over the period 35–120 (35–200) years, suppressing cover in subdominant layers; followed by a progression of some cover into the tallest vegetation stratum (>10 m) and some recovery in cover of lower vegetation layers in mature vegetation (>140 (260) years) (Fig. 2).

Total live tree basal area (measured at D_{10}) showed an initial strong increase until about 100 years post-fire, but there was little evidence that basal area responded to time since fire beyond this (Fig. 3d). There was substantial variability in basal area between plots of similar time since fire across the chronosequence.

4. Discussion

4.1. Woodland structure and fuel availability with time since fire

Overall differences in vegetation structure between time-since-fire classes suggest that patterns of fuel availability in *E. salubris* woodlands are likely to vary substantially across the chronosequence. The spatial distribution of vegetation and ground fuel layers play an important role in fuel availability (Bond and van Wilgen, 1996; Gould et al., 2007). While all vegetation structural components reflecting the quantity and spatial arrangement of plant biomass are likely to influence fuel availability, we argue that three layers are particularly significant in *E. salubris* woodlands: vegetation cover 4–10 m high, ground fuel cover and proportion of foliar gaps. Ground fuel and vegetation 4–10 m in height were the flammable fuel layers with greatest covers overall (Fig. 2), hence are presumably critical in driving fire propagation. Cover 4–10 m in height and ground fuel peaked in vegetation of an 'intermediate' time since fire of ~35–120 (35–200) years. Further, greater consistency of canopy height and greater connectivity between understorey and canopy fuels at intermediate times since fire compared to mature woodlands (Fig. 2) presumably also facilitates fire spread by requiring lower flame lengths, and hence lower wind speeds, to bridge vertical and lateral gaps between flammable fuels (Bradstock and Gill, 1993).

Discontinuity in ground fuel cover has been suggested as playing a significant role in limiting fire spread under less severe weather conditions in *Eucalyptus* woodlands and other semi-arid vegetation (Bradstock and Gill, 1993; O'Donnell et al., 2011a), contributing to lower probability of burning (Prober et al., 2012). Temporal patterns of change in ground fuel cover were similar to some studies in adjoining communities (*Acacia* shrubland, Parsons and

Table 1
Differences in vegetation structural variables between time-since-fire age classes (Young, <20 years post-fire; Intermediate, 35–120 (35–200) years; Mature, >140 (>260) years) and sampling year as tested with ANOVA. Different lettered superscripts indicate differences between time-since-fire age classes according to post hoc Newman–Keuls tests.

Proportion cover	Young	Intermediate Mean ± SE	Mature	Time since fire (T) $F_{2,70}$	Sample year (S) $F_{1,70}$	T × S $F_{2,70}$
Foliar gaps	0.32 ± 0.02[b]	0.32 ± 0.02[b]	0.45 ± 0.02[a]	17.2***	2.26	2.40
Standing dead veg	0.32 ± 0.02[a]	0.21 ± 0.02[b]	0.14 ± 0.01[c]	34.0***	7.19**,f	0.08
Ground surface						
Ground fuel	0.45 ± 0.03[c]	0.69 ± 0.02[a]	0.52 ± 0.02[b]	19.0***	0.37	1.39
Cryptogam	0.22 ± 0.02[a]	0.14 ± 0.01[b]	0.26 ± 0.02[a]	10.3***	0.74	0.75
Vegetation layers						
0–12 cm[d]	0.16 ± 0.01[a]	0.07 ± 0.01[c]	0.12 ± 0.02[b]	7.74***	2.75	0.50
25–50 cm[d]	0.29 ± 0.02[a]	0.11 ± 0.02[b]	0.09 ± 0.01[b]	41.8***	0.51	0.28
100–200 cm[d]	0.22 ± 0.02[a]	0.18 ± 0.02[a]	0.08 ± 0.01[b]	13.5***	0.91	0.29
200–400 cm[d]	0.17 ± 0.02[a]	0.13 ± 0.01[a,b]	0.10 ± 0.01[b]	6.13**	0.20	3.00
400–1000 cm[d]	0.12 ± 0.01[c]	0.41 ± 0.02[a]	0.28 ± 0.02[b]	57.5***	2.73	1.71
>1000 cm[d]	0.03 ± 0.01[b]	0.03 ± 0.01[b]	0.16 ± 0.02[a]	25.9***	8.87**,f	0.39
Tree density (trees ha^{-1})[e]	9012 ± 3079[a]	1515 ± 259[b]	110 ± 70[c]	104***	0.93	0.01

[d] = square-root (x + 0.1) transformation was applied in response to non-homogenous variances. Means show untransformed values.
[e] = $\text{Log}_{10}(x + 1)$ transformation was applied in response to non-homogenous variances. Means show untransformed values.
[f] In both cases of year of sampling differences, 2010 was greater than 2011–2.
* $P < 0.05$.
** $P \leqslant 0.01$.
*** $P \leqslant 0.001$.

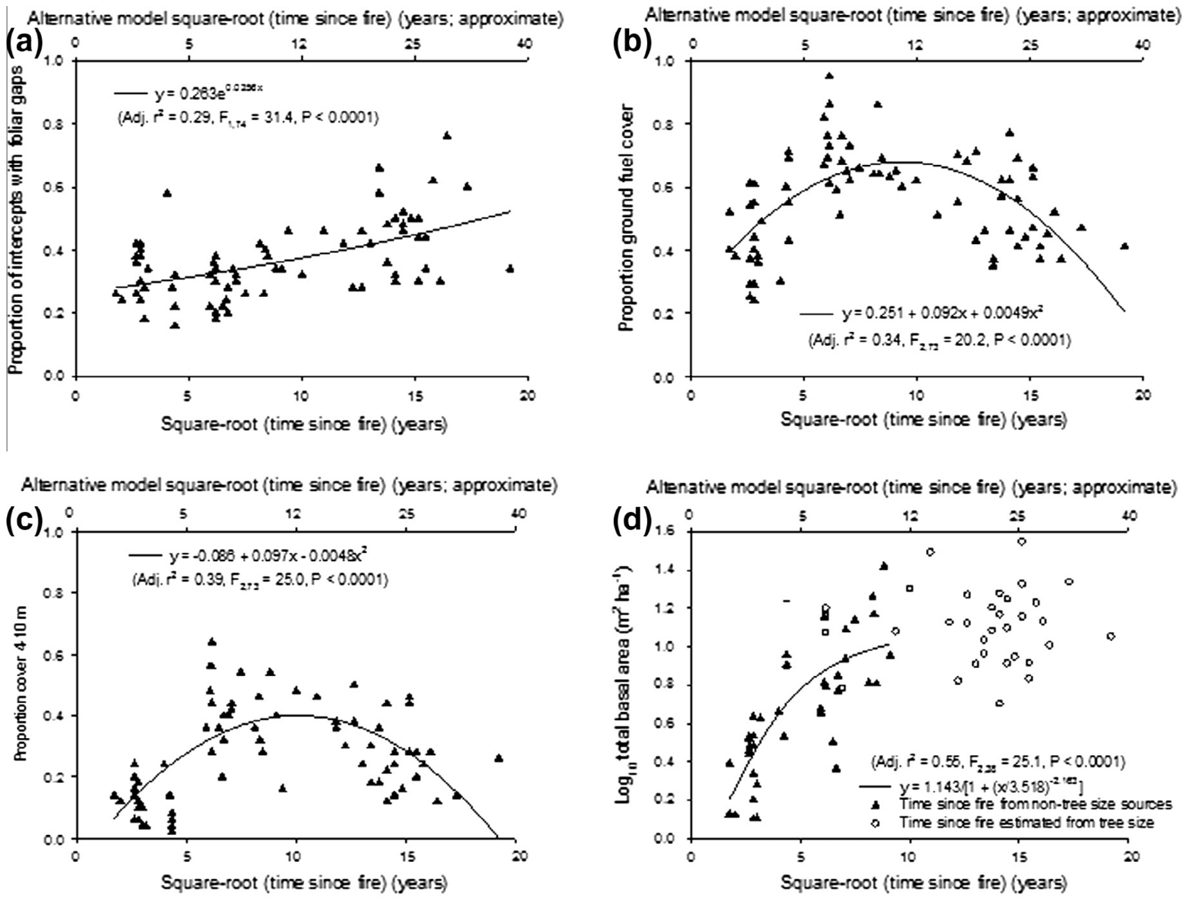

Fig. 3. Changes in structure in *Eucalyptus salubris* woodlands with time since fire: (a) proportion of intercepts with no standing vegetation (foliar gaps); (b) proportion cover of ground fuel; (c) proportion cover of vegetation 4–10 m high; and (d) stand basal area (measured at D_{10}). The basal area regression was conducted using only plots in which time since fire was determined by methods not using growth ring-tree size relationships (closed triangles), although basal areas of the plots with time since fire derived from growth ring-tree size relationships are also shown (open circles) for interpretation purposes. Log_{10} transformation of basal area was required to meet homogenous variance assumptions for regression. All regressions were conducted using the time since fire data from Model 2 of Gosper et al. (2013) (bottom x-axis), but the equally valid alternative time since fire distribution from Model 5 of Gosper et al. (2013) is shown (top *x*-axis; approximate) for comparison. $n = 76$.

Gosper, 2011; mallee, Haslem et al., 2011) but not in others, which showed monotonic increases in cover with time since fire (mallee, Cruz et al., 2010; Parsons and Gosper, 2011; Travers and Eldridge, 2012; mallee-heath, Parsons and Gosper, 2011).

Foliar gaps are likely to have a substantial bearing on fire propagation through reflecting lateral discontinuities in flammable fuel. Foliar gaps increase with time since fire; hence mature vegetation would require greater flame lengths to bridge gaps between foliage. Higher wind speeds (Bradstock and Gill, 1993) and/or greater quantities of fuel are two mechanisms that could plausibly contribute to greater flame lengths. As discussed elsewhere, mature vegetation has lower or equivalent cover (but not necessarily less total mass) than intermediate time-since-fire vegetation in all flammable vegetation layers other than 0–12 cm and >10 m, casting doubt on the possibility that greater fuel quantities may drive the greater flame lengths required to bridge gaps in mature woodlands.

Standing dead vegetation is also an important determinant of flammability in many communities (Baeza et al., 2011), but given the rapid decline of cover to low levels this emergent community trait may be less important in time-since-fire changes in fuel availability in *E. salubris* woodlands.

The combination of greater ground fuel and 4–10 m cover, less lateral gaps in cover and equivalent or greater cover in all other flammable vegetation layers with the exception of cover 0–12 cm and >10 m indicates that intermediate time since fire woodlands support greater fuel availability than other time-since-fire classes, rejecting our first hypothesis. Monotonic increases in overall fuel availability are commonly recorded for Mediterranean ecosystems and *Eucalyptus* woodlands (Rothermel and Philpot, 1973; van Wilgen, 1982; Raison et al., 1983; Gould et al., 2007), but peaked fuel availability at intermediate times since fire have been recorded in Mediterranean shrublands (Baeza et al., 2011) and semi-arid *Eucalyptus* mallee (Haslem et al., 2011). However, it is important to recognise: (i) that these studies vary in how fuel was measured (from quantifying fuel loads in mass per unit area to assessing changes in cover similar to this study) and the length of time post-fire sampled, constraining comparisons; and (ii) that differences in the mass or cover of fuel layers may not directly correspond to differences in fire propagation, due to factors such as fuel bed depth and spatial arrangement (Bond and van Wilgen, 1996). Consequently, it would be desirable to specifically quantify fuel mass, volume, component size distribution and fire behaviour in experimental fires to test the outcomes we have inferred in fuel availability and unequivocally conclude that intermediate time since fire woodlands support more flammable fuel.

There is some evidence to support our interpretation of maximum fuel availability at intermediate times since fire. O'Donnell et al. (2011a) found lower fire interval length and higher dependence of fire interval on fuel age in woodlands at intermediate times since fire (the 'former woodland' vegetation type of O'Donnell et al., 2011a) compared to mature woodlands. Indeed, intermediate-age woodland had similar fire interval length as more fire-prone mallee ecosystems (O'Donnell et al., 2011a).

Two vegetation structural components showed evidence of change based on year of survey. Consistent with exceptionally low rainfall, 2010 samples had higher cover of standing dead vegetation indicating a plant response to water stress of elevated mortality and/or death of a portion of crown volume. In subsequent years this dead material must have been incorporated into the ground fuel layer, although we did not detect this in our data. Higher cover of standing dead vegetation is likely to contribute to higher community flammability (Baeza et al., 2011). The association of low rainfall and higher standing dead vegetation provides a mechanism to explain the findings of O'Donnell et al. (2011b) that climate anomalies contribute to year-to-year variation in fire occurrence and extent across the GWW, specifically that more and larger fires occur in dry conditions that follow on from wetter periods. Vegetation cover >10 m in height was greater in 2010 than subsequent years, although the reason(s) for this difference are unclear.

4.2. Time-since-fire and conservation of woodland biota

E. salubris woodlands appear robust to long periods without fire. Standing dead vegetation decreased with increasing time since fire, suggesting minimal loss of vigour and not providing support for our hypothesis that vegetation senescence is more evident in mature than intermediate fire-age classes. Foliar gaps did increase with time and cover of one of the two tree vegetation layers peaked at an intermediate time since fire, probably reflecting the ongoing density-dependent thinning of the dominant trees and shrubs (Gosper et al., in press). As recruitment events occur in response to a diversity of disturbances in addition to fire (Yates et al., 1994) and plant richness remains high in mature woodlands (Gosper et al., in press), it appears unlikely that fire is essential for perpetuating *Eucalyptus* woodlands in the GWW, contrasting with some species in adjoining communities (mallee-heath; Gosper et al., 2012), other crown-fire *Eucalyptus* communities (Jackson, 1968) and the assumption that fire is required to maintain diversity and vigour in fire-prone communities.

Changes in floristic composition and physical vegetation structure also affect the availability of resources for fauna, as posited in the habitat accommodation model (Fox, 1982). The substantial changes in vegetation structure (as measured in this study) and composition (Gosper et al., in press) observed across the *E. salubris* chronosequence suggest that distinct changes in fauna composition with time since fire are likely across most faunal groups (Fox 1982; Rodrigo and Retana, 2006; Watson et al., 2012).

Further research is needed to quantify time since fire effects on fauna in the GWW as there have been few studies to date. Although based on a limited range of times since fire, Recher and Davis (in press) conclude that time since fire affects GWW bird richness, abundance and composition. Open-ground foraging birds (e.g. Australian Magpie *Gymnorhina tibicen*) were particularly prominent in recently-burnt woodlands (Recher and Davis, in press), consistent with low ground fuel cover. Many shrub and canopy-foragers (e.g. whistlers *Pachycephala* spp.) favoured long-unburnt woodlands (Recher and Davis, in press); a plausible response to greater vegetation cover in these layers as the woodlands develop post-fire. Despite high ground fuel cover (Table 1), intermediate-aged woodlands had lower abundance of some litter- and log-associated birds than mature woodlands (Recher and Davis, in press), suggesting that other aspects of ground cover (litter depth, patchiness, coarse woody debris) are also important.

Basal area showed little evidence of change with time since fire beyond about 100 years post-fire, indicating that declines in tree density were largely offset by increasing trunk size. In this semi-arid climate, moisture availability may place an upper limit to basal area, with intra-specific competition mediating the shift from many small trunks to fewer larger trunks with little net change in stand basal area. The large trees characteristic of long-unburnt woodlands, however, presumably play a variety of critical ecological roles, including the development of larger and more hollows that are important for a wide variety of animals (Lindenmayer et al., 2012).

4.3. Research and management implications

Many of the recorded changes in vegetation structure, for example the decline in ground fuel cover in mature woodlands, only became apparent due to the development of methods to estimate the time since fire of long-unburnt vegetation (Gosper et al., 2013). Interpretations of vegetation change solely on the basis of times since fire derived from Landsat imagery in infrequently-burnt communities (i.e. with a mean fire-return interval beyond about 30 years) can thus lead to misleading findings; a conclusion supported by an increasing number of recent studies (Clarke et al., 2010; Haslem et al., 2011; Gosper et al., 2013, in press). Discrepancies in temporal patterns of fuel accumulation from the literature could also reflect the different levels of resolution in determining the time since fire of long-unburnt vegetation between studies (Haslem et al., 2011). Determining the time since fire of long-unburnt stands has led us to conclude that it takes beyond 150 (250) years for characteristics of mature woodlands to develop, by contrast with earlier estimates of 80–100 years (Hopkins and Robinson, 1981), supporting our second hypothesis that recovery of vegetation structural components requires long time frames.

Our study shows that woodlands of an intermediate time since fire may support high fuel availability over long periods. In recent decades there have been several extensive wildfires in the GWW (Watson et al., 2008; Parsons and Gosper, 2011). As a consequence large areas of regenerating woodlands will be passing into a stage of post-fire development with higher cover of some fuels over the period 2025–2150 (2025–2300). Climate change may also play a significant role in future fire propagation, through greater numbers of extreme fire danger days and lightning ignitions increasing fire frequency, although these factors are potentially offset by declining fuel loads under reduced rainfall (Bradstock, 2010; Prober et al., 2012). These processes combined suggest that coming decades could prove highly challenging for fire management in the GWW.

Landscape simulations of communities with similar trends in flammability with time since fire as appear to characterise *E. salubris* woodlands have indicated low resilience to increases in ignition frequency and inter-annual climatic variability (Kitzberger et al., 2012). Replacement and fragmentation of mature woodlands by intermediate time-since-fire woodlands with higher cover and connectivity in key fuels potentially instigates a self-reinforcing fire regime shift favouring larger and/or more uniform (e.g. fewer unburnt patches) fires (Kitzberger et al., 2012). Landscape fire patterns will, however, also depend on the relative quantity and spatial arrangement of woodlands across the landscape with adjoining vegetation communities of varying flammability (O'Donnell et al., 2011a).

If further widespread conversion of mature *E. salubris* woodlands to intermediate time-since-fire woodlands occurs, with intermediate woodlands then caught in a fuel availability-time since fire feedback loop, there are likely to be substantial adverse consequences for many species reliant on mature woodlands (Gosper et al., in press; Recher and Davis, in press).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.08.005.

References

Álvarez, R., Muñoz, A., Pesqueira, X.M., García-Duro, J., Reyes, O., Casal, M., 2009. Spatial and temporal patterns in structure and diversity of Mediterranean forest of *Quercus pyrenaica* in relation to fire. For. Ecol. Manage. 257, 1596–1602.
Baeza, M.J., Santana, V.M., Pausas, J.G., Vallejo, V.R., 2011. Successional trends in standing dead biomass in Mediterranean basin species. J. Veg. Sci. 22, 467–474.
Bureau of Meteorology, 2013. Climate data online. <http://www.bom.gov.au/climate/data/index.shtml?bookmark=200> (8.07.13).
Berry, S., Keith, H., Mackey, B., Brookhouse, M., Jonson, J., 2010. Biomass carbon stocks in the Great Western Woodlands. Research report, ANU Enterprise Pty Ltd, Canberra, Australia.
Bond, W., 1980. Fire and senescent fynbos in the Swartberg, Southern Cape. S. Afr. For. J. 114, 68–71.
Bond, W.J., van Wilgen, B.W., 1996. Fire and Plants. Chapman and Hall, London.
Bond, W.J., Woodward, F.I., Midgley, G.F., 2005. The global distribution of ecosystems in a world without fire. New Phytol. 165, 525–538.
Bradstock, R.A., 2010. A biogeographic model of fire regimes in Australia: current and future implications. Glob. Ecol. Biogeogr. 19, 145–158.
Bradstock, R.A., Gill, A.M., 1993. Fire in semi-arid, mallee shrublands: size of flames from discrete fuel arrays and their role in the spread of fire. Int. J. Wildland Fire 3, 3–12.
Brooker, M.I.H., Slee, A.V., Connors, J.R., Duffy, S.M., 2002. EUCLID: Eucalypts of Southern Australia, second ed. CSIRO Publishing, Collingwood, Australia.
Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth, UK.
Clarke, M.F., Avitabile, S.C., Brown, L., Callister, K.E., Haslem, A., Holland, G.J., Kelly, L.T., Kenny, S.A., Nimmo, D.G., Spence-Bailey, L.M., Taylor, R.S., Watson, S.J., Bennett, A.F., 2010. Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. Aust. J. Bot. 58, 363–372.
Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. Ecology 37, 451–460.
Cowling, R.M., Rundell, P.W., Lamont, B.B., Arroyo, M.K., Arianoutsou, M., 1996. Plant diversity in mediterranean-climate regions. Trends Ecol. Evol. 11, 362–366.
Cruz, M.G., Matthews, S., Gould, J., Ellis, P., Henderson, M., Knight, I., Watters, J., 2010. Fire dynamics in mallee-heath: fuel, weather and fire behaviour prediction in South Australian semi-arid shrublands. Report A.10.01. Bushfire Cooperative Research Centre, Melbourne, Victoria.
Department of Environment and Conservation (DEC), 2010. Bushfire Threat Analysis of the Great Western Woodlands. Prepared by G. Daniel, Department of Environment and Conservation, Perth, Australia, unpublished.
Egler, F.E., 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4, 412–418.
Fire Ecology Working Group, 2002. Analysis of Disturbance by Fire on Public Land in Victoria. Department of Natural Resources and Environment, East Melbourne, Australia.
Fire Ecology Working Group, 2004. Guidelines and procedures for ecological burning on public land in Victoria 2004. Department of Sustainability and Environment, Melbourne, Australia.
Fox, B.J., 1982. Fire and mammalian secondary succession in an Australian coastal heath. Ecology 63, 1332–1341.
Gosper, C.R., Prober, S.M., Yates, C.J., Wiehl, G., 2013. Estimating the time since fire of long-unburnt *Eucalyptus salubris* (Myrtaceae) stands in the Great Western Woodlands. Aust. J. Bot. 61, 11–21.
Gosper, C.R., Yates, C.J., Prober, S.M., in press. Floristic diversity in fire-sensitive eucalypt woodlands shows a 'U'-shaped relationship with time since fire. J. Appl. Ecol. doi: 10.1111/1365-2664.12120.
Gosper, C.R., Yates, C.J., Prober, S.M., Parsons, B.C., 2012. Contrasting changes in vegetation structure and diversity with time since fire in two Australian Mediterranean-climate plant communities. Austral Ecol. 37, 164–174.
Gould, J.S., McCaw, W.L., Cheney, N.P., Ellis, P.F., Knight, I.K., Sullivan, A.L., 2007. Project Vesta – Fire in dry Eucalypt forest: fuel structure, fuel dynamics and fire behaviour. Ensis-CSIRO, Canberra, and Department of Environment and Conservation, Perth.
Haslem, A., Kelly, L.T., Nimmo, D.G., Watson, S.J., Kenny, S.A., Taylor, R.S., Avitabile, S.C., Callister, K.E., Spence-Bailey, L.M., Clarke, M.F., Bennett, A.F., 2011. Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. J. Appl. Ecol. 48, 247–256.
Hopkins, A.J.M., Robinson, C.J., 1981. Fire induced structural change in a Western Australian woodland. Aust. J. Ecol. 6, 177–188.
Hurlbert, S.H., 1994. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.
Jackson, W.D., 1968. Fire, air, water and earth—an elemental ecology of Tasmania. Proc. Ecol. Soc. Australia 3, 9–16.
Kitzberger, T., Aráoz, E., Gowda, J.H., Mermoz, M., Morales, J.M., 2012. Decreases in fire spread probability with forest age promotes alternative community states, reduced resilience to climate variability and large fire regime shifts. Ecosystems 15, 97–112.
Lindenmayer, B.D., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. Science 338, 1305–1306.
McCarthy, M.A., Gill, A.M., Bradstock, R.A., 2001. Theoretical fire-interval distributions. Int. J. Wildland Fire 10, 73–77.
McCaw, L., Hanstrum, B., 2003. Fire environment of Mediterranean south-west Western Australia. In: Abbott, I., Burrows, N.D. (Eds.), Fire in Ecosystems of South-west Western Australia: Impacts and Management. Backhuys Publishers, Leiden, pp. 87–106.
O'Donnell, A.J., Boer, M.M., McCaw, W.L., Grierson, P.F., 2011a. Vegetation and landscape connectivity control wildfire intervals in unmanaged semi-arid shrublands and woodlands in Australia. J. Biogeogr. 38, 112–124.
O'Donnell, A.J., Boer, M.M., McCaw, W.L., Grierson, P.F., 2011b. Climatic anomalies drive wildfire occurrence and extent in semi-arid shrublands and woodlands of southwest Australia. Ecosphere 2 (11), 127. http://dx.doi.org/10.1890/ES11-00189.1.
Parsons, B.C., Gosper, C.R., 2011. Contemporary fire regimes in a fragmented and an unfragmented landscape: implications for vegetation structure and persistence of the fire-sensitive malleefowl. Int. J. Wildland Fire 20, 184–194.
Prober, S.M., Macfarlane, C., 2013. GWW - Sapwood depth, density and water content from eight trees of four eucalypt species at the Great Western Woodlands Flux tower site, collected during April 2013. Terrestrial Ecosystems Research Network Data Discovery Portal. <http://www.tern-supersites.net.au/knb/metacat/lloyd.442.9/html> (26.07.13).
Prober, S.M., Thiele, K.R., Rundel, P.W., Yates, C.J., Berry, S.L., Byrne, M., Christidis, L., Gosper, C.R., Grierson, P.F., Lemson, K., Lyons, T., Macfarlane, C., O'Connor, M.H., Scott, J.K., Standish, R.J., Stock, W.D., van Etten, E.J.B., Wardell-Johnson, G.W., Watson, A., 2012. Facilitating adaptation of biodiversity to climate change: a conceptual framework applied to the world's largest Mediterranean-climate woodland. Clim. Change 110, 227–248.
Raison, R.J., Woods, P.V., Khanna, P.K., 1983. Dynamics of fine fuels in recurrently burnt eucalypt forests. Aust. For. 46, 294–302.
Recher, H.F., Davis, W.E. Jr., in press. Response of birds to a wildfire in the Great Western Woodlands, Western Australia. Pac. Conserv. Biol.
Rodrigo, A., Retana, J., 2006. Post-fire recovery of ant communities in Submediterranean *Pinus nigra* forests. Ecography 29, 231–239.
Rothermel, R.C., Philpot, C.W., 1973. Predicting changes in chaparral flammability. J. For. 71, 640–643.
Travers, S.K., Eldridge, D.J., 2012. Landscape modulators and resource accumulation in a post-fire eucalypt woodland. For. Ecol. Manage. 285, 11–19.
van Wilgen, B.W., 1982. Some effects of post-fire age on the above-ground plant biomass of fynbos (macchia) vegetation in South Africa. J. Ecol. 70, 217–225.
Watson, A., Judd, S., Watson, J., Lam, A., Mackenzie, D., 2008. The Extraordinary Nature of the Great Western Woodlands. The Wilderness Society, Perth, Australia.
Watson, S.J., Taylor, R.S., Nimmo, D.G., Kelly, L.T., Haslem, A., Clarke, M.F., Bennett, A.F., 2012. Effects of time since fire on birds: How informative are generalized fire response curves for conservation management? Ecol. Appl. 22, 685–696.
Yates, C.J., Hobbs, R.J., Bell, R.W., 1994. Landscape-scale disturbances and regeneration in semi-arid woodlands of southwestern Australia. Pac. Conserv. Biol. 1, 214–221.