Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire

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Summary

1. Managing fire to achieve hazard reduction while providing for biodiversity conservation is complex in fire-prone regions. This challenge is exacerbated by limited understanding of post-fire changes in habitat and fuel attributes over time-scales commensurate with their development, and a paucity of empirical research integrating the effects of fire on these attributes.

2. We used a 110-year post-fire chronosequence to investigate temporal development in habitat resources used by fauna, and fuels for fire in semi-arid Mallee vegetation, south-eastern Australia. Fire-history mapping previously limited investigation to 35 years post-fire. The patterns of temporal change over 110 years for 13 variables, representing key attributes of habitat and fuel, were explored using nonlinear mixed models and data from 549 sites.

3. Most habitat and fuel attributes exhibited changes in abundance and rate of development over extended periods, emphasizing the importance of documenting post-fire dynamics over long time-frames. Further, developmental patterns were mostly nonlinear, indicating that a shorter temporal perspective (e.g. 20–30 years post-fire) may obscure, or provide an inaccurate understanding of, long-term changes.

4. There were striking differences in the post-fire dynamics of some habitat and fuel attributes. Leaf litter and spinifex grass *Triodia scariosa*, which function as both habitat and fuel, increased rapidly after fire followed by a plateau or slow decline after 20–30 years. In contrast, live tree stems were not predicted to develop hollows until 40 years, after which time the density of live hollow-bearing stems, an important habitat feature, increased steadily.

5. *Synthesis and applications*. Fire affects the development and abundance of resources over substantially longer periods than can be examined using fire-mapping based on satellite imagery. Our results demonstrate that post-fire changes in mallee vegetation influence fire hazard and faunal habitat in different ways. Critically, the cover/abundance of most primary fuel sources did not increase substantially beyond around 30 years post-fire; whereas important habitat attributes changed in ways that affect faunal occurrence for over a century. Fire management must explicitly acknowledge the potential for fire to affect fauna and fuel differently, and for these effects to operate over time-frames that may extend well beyond current understanding.

Key-words: Australia, fire chronosequence, generalized additive mixed model, mallee vegetation, prescribed fire, succession, wildfire

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Introduction

Fire is a natural process that shapes the structure and function of ecosystems across the globe (Bowman *et al.* 2009). Wildfire can also threaten human life and assets in fire-prone regions (Bradstock 2008). For both reasons, considerable attention and resources are invested in fire management, with prescribed fire commonly being used to reduce the risk of uncontrollable wildfires (Fernandes & Botelho 2003). Fire management for hazard reduction, however, may not be compatible with conservation objectives (Morrison *et al.* 1996). The potential for prescribed fire to negatively affect biodiversity is increased by inadequate understanding of biotic responses to fire (Clarke 2008; Driscoll *et al.* 2010) and strong public pressure to minimize fire hazard (Stephens & Ruth 2005). Successfully balancing fuel reduction and biodiversity considerations is a challenge faced by managers in fire-prone systems throughout the world (James & M'Closkey 2003; Ucitel, Christian & Graham 2003).

A key issue in addressing the potentially competing demands of fuel reduction and biodiversity conservation is the length of time over which successional processes operate, compared with the short time-period over which changes in fuels or biota have often been documented. Techniques such as dendrochronology and radiocarbon dating have allowed examination of post-fire dynamics across extended time-frames (e.g. 230 years: Pare & Bergeron 1995; 2355 years: Lecomte *et al.* 2006), but more commonly research is constrained to periods of known fire-history (e.g. < 40 years: Sah *et al.* 2006; Driscoll & Henderson 2008). Temporal mismatches between decades or centuries of successional change (Lecomte *et al.* 2006; Mack *et al.* 2008), and the much shorter period over which changes in biota frequently have been studied, hamper effective fire management.

A second issue concerns understanding of post-fire dynamics in fuel sources and habitat attributes used by fauna for foraging, refuge or breeding. Empirical research into fire-fauna relationships has largely been undertaken in isolation from studies investigating the association between fire and fuel (Ucitel, Christian & Graham 2003). Thus, there are few explicit guidelines for managers attempting to address both considerations.

Post-fire responses of fauna are often interpreted using a framework of secondary succession (Friend 1993; Fox, Taylor & Thompson 2003; Torre & Diaz 2004). This approach is based on the understanding that vegetation succession following fire drives faunal occurrence via the differential availability of resources along post-fire temporal gradients (Fox 1982). Other factors may also influence faunal responses to fire, such as altered biotic interactions (Higgs & Fox 1993), abiotic conditions (Letnic *et al.* 2004), and fire frequency/scale (Bradstock *et al.* 2005). However, associations between faunal occurrence and habitat attributes, and the strength of post-fire succession in many vegetation types (Hanes 1971; Vandvik *et al.* 2005), means that understanding fire–fauna relationships will benefit from knowledge of changes in habitat resources over time-frames commensurate with successional processes.

Management of fuel–fire relationships has been informed by the positive associations between fuel availability, wildfire severity, and time-since-fire (Hanes 1971; Sah *et al.* 2006). Thus, the use of prescribed fire is often guided by fuel characteristics, and understanding temporal patterns in fuel accumulation (Fernandes & Botelho 2003). For example, estimates of fuel loads are widely used to measure fire hazard in parts of southern Australia (McCarthy, Tolhurst & Chatto 1999). Such estimates can identify maximum tolerable fuel loads (Burrows 2008) and, when combined with predictions of fuel accumulation, suggest optimum inter-fire intervals for hazard reduction (Department of Sustainability and Environment 2008). Documenting temporal patterns in fuel development is critical if such management approaches are to effectively reduce wildfire hazard (Sah *et al.* 2006).

Our study system, the Murray Mallee region in south-eastern Australia, is strongly influenced by fire. Large wildfires (*c.* 100 000 ha) typically occur somewhere in the region on a bi-decadal basis (Noble & Vines 1993), and prescribed fire is used to minimize the risk of wildfires burning extensive areas (Sandell *et al.* 2006). Fire also affects the status of native fauna (Brown, Clarke & Clarke 2009; Kelly *et al.* 2010). Current fire-history mapping based on satellite imagery restricts investigation of post-fire responses in habitat and fuel to a 35-year period. We use empirical data and age predictions for sites of previously unknown fire-age (Clarke *et al.* 2010) to investigate post-fire dynamics over a chronosequence extending to 110 years. We address two objectives: (i) to document post-fire resource dynamics across a 110-year chronosequence, and establish whether extending the time-scale under examination alters the resultant understanding of post-fire change; and (ii) to explicitly compare post-fire trajectories of habitat attributes and fuel sources.

Materials and methods

STUDY AREA

The study area encompasses ∼100 000 km^2 of the Murray Mallee, a low-lying region covering parts of Victoria, South Australia and New South Wales, Australia (see Fig. S1, Supporting Information). The climate is semi-arid (220–330 mm rainfall/year) with high summer temperatures (mean daily maxima ≥32 °C) and mild winters (mean daily maxima 16 °C) (data supplied by the Australian Bureau of Meteorology). The region is characterized by extensive dune/swale systems that reflect underlying variation in soil characteristics and moisture availability (Land Conservation Council 1987).

The current distribution of native vegetation has been strongly influenced by agriculture, primarily cereal cropping and stock grazing: remnant native vegetation occurs predominantly on less fertile soils of the dunefields (Land Conservation Council 1987). The most common vegetation, tree mallee, comprises short (typically < 5 m), multi-stemmed ('mallee') *Eucalyptus* trees above an understorey of shrubs and perennial and ephemeral grasses. An important feature of this vegetation is the ability of mallee eucalypts to regenerate from underground lignotubers after fire by coppicing multiple new stems (Gill 1981).

Fire is a dominant process in the study area. Tree mallee vegetation is highly flammable and the reproductive strategies of many plant

species are strongly tied to fire events (Bradstock & Cohn 2002). Key components of perennial fuels include the hummock-forming grass *Triodia scariosa* N.T. Burbidge, leaf litter accumulated beneath trees, and decorticating ribbons of bark (Bradstock & Cohn 2002). After large rainfall events, ephemeral grasses also provide a critical fuel source that connects the otherwise patchily-distributed perennial fuels (Noble & Vines 1993). Wildfires are actively suppressed in much of the region and prescribed fire is used predominantly to reduce fire hazard (Sandell *et al.* 2006).

STUDY DESIGN

This study is part of a project examining landscape-level responses of multiple taxa to the properties of fire mosaics. Consequently, the 549 sites included here were grouped in 26 clusters, each representing an individual landscape unit of 12·6 km^2 (Fig. S1). The mean distance between study landscapes was 130 km (range: 6–218 km) and all were located within conservation reserves.

Previous work identified and mapped three broad types of tree mallee vegetation across the region (Haslem *et al.* 2010). Here, we focus on the two most extensive types: Triodia Mallee (TM) and Chenopod/Shrubby Mallee (hereafter Chenopod Mallee, CM). These communities differ on the basis of canopy dominants, understorey composition, soil and topography. Triodia Mallee is characterized by an increased abundance of *T. scariosa*, an important habitat component for fauna (Bennett, Lumsden & Menkhorst 2006) and a key source of fuel (Noble, Smith & Leslie 1980). The understorey of Chenopod Mallee comprises a diversity of low chenopod shrubs, many of which have low flammability (Pausas & Bradstock 2007).

We employed a space-for-time approach to investigate post-fire temporal dynamics, with sites of differing fire-ages representing a post-fire chronosequence. Fire in tree mallee vegetation removes both the canopy and understorey (Caughley 1985), resetting the system to 'year zero'. Importantly, for this reason both wildfires and prescribed fires in this system are commonly 'stand-replacing' and have similar effects on post-fire succession. To ensure results were not influenced by fire intensity, sites considered to have been burnt only partially/patchily in the most recent fire, based on the occurrence of multiple cohorts of eucalypt stems, were excluded from analyses.

DATA COLLECTION

A range of vegetation characteristics was assessed at each site. The percentage cover of different types of ground cover (bare ground, cryptogamic crust, leaf litter, plant matter, logs), and the depth of leaf litter, were recorded at 1-m intervals along a 50-m transect (*n* = 50 sample points). Vegetation structure was assessed at each sample point by recording the number of vegetation contacts with a vertical ranging pole in four height strata (<0·5 m, 0·5–1 m, 1–2 m, >2 m). Quadrats were established to record: (i) the characteristics of *Eucalyptus* trees and stems (50 × 4-m quadrat) including canopy height, number of trees, number stems/tree, stems with hollows, amount of decorticating bark/tree; and (ii) the number of logs (50 × 10-m quadrat). Vegetation data were collected between June and August 2007.

We selected 13 variables to represent habitat attributes for fauna, and fuel sources for fire (Table 1). These variables include measures of the availability of specific habitat or fuel resources (e.g. *T. scariosa*, leaf litter, tree hollows), and characteristics of habitat structure and fuel distribution (e.g. vegetation cover in different height strata). They are referred to as 'habitat' when viewed from the perspective of fauna, and 'fuel' when considered in relation to fire; many constitute both. For example, *Triodia* hummocks and leaf litter are used for foraging

and refuge by many of the 55 reptile species occurring in the region; but also are a primary source of surface fuels that sustain fires. Ephemeral grasses, associated with large fires (Noble, Smith & Leslie 1980), were not investigated as their occurrence is more strongly influenced by rainfall than time-since-fire.

The fire-age of study sites was determined using two methods. Landsat satellite imagery from 15 individual years (1972–2007), combined with local knowledge, was used to identify the exact year of the most recent fire for sites burnt since 1972. For sites burnt before 1972, the lack of historical records and satellite imagery necessitated an alternative approach. We used linear regression models to quantify the relationship between tree age (indicated by fire-year) and mean stem diameter for each eucalypt species at sites of known fire-year (Clarke *et al.* 2010). These models were then used to predict tree age (thus infer fire-year) for sites where fire-year was unknown but stem diameter data were available. Validation of these models with independent data from new sites revealed a highly significant correlation between known and predicted tree ages (*r* = 0·71, *P* < 0·001, *n* = 88) (Clarke *et al.* 2010) confirming the reliability of this approach. The fire-age of sites was calculated as the difference between actual/predicted fire-year and 2007 (when vegetation data were collected). Sites with a predicted fire-age >110 years were excluded from analyses due to low sample sizes.

Table 2 shows the distribution of sites across the 110-year fire chronosequence, and two vegetation types, investigated. The lack of sites aged between 11 and 20 years reflects reduced fire activity between 1987 and 1996.

STATISTICAL ANALYSES

We used generalized additive mixed models (GAMMs: Wood 2006; Zuur *et al.* 2009) to investigate patterns in the development of each habitat/fuel attribute across the post-fire chronosequence. Three factors contributed to the selection of this approach. First, inspection of raw data showed that nonlinear models were appropriate. Generalized additive models (GAMs) are nonparametric regression models that use smoothing functions to fit nonlinear response curves (Wood 2006). Secondly, the clustered distribution of sites (grouped in landscape units) suggested a mixed model approach. Mixed models are recommended when data are structured by some factor (here, landscape unit) that introduces systematic variation of potential influence over the relationship between predictor and response variables (Zuur *et al.* 2009). Lastly, differences in the structure, floristic composition and abiotic associations of Triodia Mallee and Chenopod Mallee indicated that time-since-fire responses might differ between vegetation types. To account for this, we used 'variable coefficient' GAMMs which produce different smoothed terms for each level of a categorical variable (Wood 2006; Zuur *et al.* 2009).

Models were fitted with 'landscape' as a random effect and a separate smoothed term for time-since-fire in each vegetation type. The amount of smoothing used to model time-since-fire was selected internally during the model-fitting process (Wood 2004). Outliers, as identified by residual plots, were removed from final models (see Table 3). Models were evaluated using a measure of model fit (deviance explained) and cross-validation.

Sevenfold cross-validations were used to assess the stability and predictive accuracy of models (Pearce & Ferrier 2000). This involved randomly dividing study landscapes into seven groups ('folds'), fitting a model to data from six folds, then using it to predict to data from the seventh fold. This process continued until all sites had predictions derived from independent data. The mean correlation (and associated

Table 1. Variables used to represent habitat and fuel attributes in tree mallee vegetation, and their roles in providing these resources

Variable	Description	Role of resource[a]		Abbreviation
		Habitat[b]	Fuel[c]	
Specific resource types				
Triodia scariosa	Percent cover of *Triodia scariosa* (<0·5 m high)	F/R/B	S,f	Triodia
Leaf litter	Mean depth (cm) of leaf litter ≥1 cm deep	F/R/B	S,f	Litter
Overall ground fuel	Combined percent cover of leaf litter (≥1 cm deep), plant matter and logs	F/R	S,v	GroundFuel
Logs	Density of logs >3 cm diameter and >50 cm length (no./ha)	F/R/B	S,c	Logs
Decorticating bark	Mean ordinal measure across trees, where: (i) no hanging bark (>30 cm in length); (ii) hanging bark present <50% stem surface area; (iii) hanging bark present >50% stem surface area	F/R	L,c	Bark
Tree hollows – live stems	Estimated density of live hollow-bearing tree stems (no./ha)	R/B	n/a	Hollows(Live)
Tree hollows – dead stems	Estimated density of dead hollow-bearing tree stems (no./ha)	R/B	n/a	Hollows(Dead)
Tree hollows – proportion stems	Overall proportion of tree stems containing a tree hollow	R/B	n/a	HollowProportion
Habitat structure/fuel distribution				
Tree stems	Estimated density of tree stems (no./ha)	Collectively represent habitat structure rather than specific habitat resources	Represents coarse standing fuel density	StemDensity
Low vegetation cover	Percent cover of plant matter (dead or alive) <0·5 m high		S,v	LowCover
Mid vegetation cover	Percent cover of plant matter (dead or alive) 0·5–2 m high		U,v	MidCover
Canopy vegetation cover	Percent cover of plant matter (dead or alive) >2 m high		C,v	CanopyCover
Canopy height[d]	Canopy height (m) determined using a range finder		Represents canopy fuel height	CanopyHeight

[a] Information collated from cited references.
[b] F = foraging habitat, R = refuge/shelter habitat, B = breeding habitat.
[c] S = surface fuel, U = understorey fuel, L = ladder fuel, C = canopy fuel, f = fine fuel (<3 cm), c = coarse fuel (>3 cm), v = variable fuel size.
[d] Data available for a reduced number of sites (see Table 3).

standard error) between observed and predicted values, averaged across folds, was used to evaluate models. The median of three cross-validation trials is reported.

Regression modelling and cross-validation were undertaken using the mgcv package v.1.4–1 (Wood 2004) and source scripts (also used to calculate model deviance: Elith, Leathwick & Hastie 2008) in R v.2.8.0 (R Development Core Team 2008).

Results

All habitat/fuel attributes except the density of dead hollow-bearing stems, Hollows(Dead), showed a significant relationship with time-since-fire (Table 3). Two attributes, Triodia and MidCover, exhibited significant post-fire responses in only one

Table 2. Distribution of 549 study sites across the 110-year post-fire chronosequence. Years-since-fire has been split into 10-year intervals for Triodia Mallee (TM) and Chenopod Mallee (CM) vegetation

Years-since-fire	Number of sites	
	TM	CM
1–10	89	12
11–20	0	0
21–30	50	6
31–40	124	51
41–50	15	22
51–60	28	30
61–70	22	25
71–80	13	12
81–90	15	10
91–100	8	7
101–110	5	5
Total	369	180

Table 3. Results of models describing the relationship between habitat/fuel attributes and time-since-fire. Details of the smoothed terms for time-since-fire in Triodia Mallee (TM) and Chenopod Mallee (CM) are shown for each attribute, together with the number of sites sampled in each

Habitat/fuel attribute	Vegetation type	Sites (no.)	Smoothed term for time-since-fire		
			edf[a]	F	P
Triodia	TM	369	5·33	15·55	< 0·001
	CM	180	1·00	0·12	0·824
Litter	TM[b]	367	5·26	17·11	< 0·001
	CM[b]	178	3·27	4·85	0·001
GroundFuel	TM	369	6·06	26·07	< 0·001
	CM	180	3·63	6·00	< 0·001
Logs	TM[b]	368	6·71	3·72	0·001
	CM	180	1·00	4·94	0·014
Bark	TM	368	1·83	54·04	< 0·001
	CM	180	1·00	29·06	< 0·001
Hollows(Live)	TM	369	3·78	12·53	< 0·001
	CM	180	2·70	11·22	< 0·001
Hollows(Dead)	TM	369	1·00	0·27	0·696
	CM	180	1·00	2·22	0·124
HollowProportion	TM	369	3·03	16·85	< 0·001
	CM	180	1·00	24·62	< 0·001
StemDensity	TM	369	4·39	21·26	< 0·001
	CM[b]	179	4·74	19·37	< 0·001
LowCover	TM	369	5·66	4·54	< 0·001
	CM	180	1·00	4·18	0·026
MidCover	TM	369	6·68	7·07	< 0·001
	CM	180	1·00	0·10	0·853
CanopyCover	TM	369	5·59	32·19	< 0·001
	CM	180	3·08	5·87	< 0·001
CanopyHeight	TM	241	4·48	98·91	< 0·001
	CM	130	3·84	33·61	< 0·001

[a]Estimated degrees of freedom.
[b]One outlier removed (large residual value).

vegetation type: Triodia Mallee. Post-fire dynamics did not differ markedly between vegetation types for most attributes, as shown by overlapping confidence intervals of predictions (Fig. 1).

Most attributes exhibited nonlinear patterns of change following fire (Fig. 1); the trend and rate of their development were not consistent across the 110-year post-fire chronosequence. For example, tree stem density increased relatively rapidly for the first 20 years following fire and then declined; rapidly at first and then at a slower rate after around 50 years post-fire (Fig. 1). Linear responses to time-since-fire were observed only in Chenopod Mallee: the variables HollowProportion and Bark increased, while Logs and LowCover decreased, as time-since-fire increased (Fig. 1).

No attribute had reached a stable state by 35 years-since-fire, the current extent of fire-history records (Fig. 1). The rate of development in some attributes did decrease after 35 years (e.g. GroundFuel [CM], CanopyCover [TM]) but few showed no further change after this time. In contrast, many attributes still exhibited change at 110-years post-fire (e.g. HollowProportion, Bark, Triodia [TM], Litter [TM]).

All attributes, except Bark, showed a marked change in the rate of development at around 20–30 years post-fire (Fig. 1). Developmental shifts took one of three forms: (i) rapid increase followed by slower increase or plateau (Litter, GroundFuel, LowCover, CanopyCover, CanopyHeight); (ii) rapid increase followed by decline (Triodia, Logs, StemDensity, MidCover), or (iii) minimal change followed by increase (Hollows(Live), HollowProportion).

Both methods used to evaluate models, cross-validation and model fit, returned similar results (Fig. 2). CanopyHeight, Triodia and CanopyCover showed the strongest relationship with time-since-fire, and these models had relatively high predictive accuracy and stability. Time-since-fire explained comparatively less variation (< 15%) in MidCover and Logs, and the mean cross-validation correlation for these attributes was low (< 0·3). Between 24% and 37% of variation in the remaining eight attributes was related to time-since-fire, with cross-validation indicating a moderate performance of models explaining these relationships (Fig. 2).

To further examine temporal development in tree hollows, the mean proportion of hollow-bearing stems that were alive and dead was compared for each 10-year post-fire interval (Fig. 3). On average, over 80% of all hollow-bearing stems were dead in fire-age periods ≤40 years-since-fire. Parity in the proportion of live and dead stems containing hollows was not reached until 60 years since last burn.

Discussion

Most habitat and fuel attributes investigated here showed a significant response to time-since-fire, emphasizing the influence of fire on the temporal availability of resources used by fauna, and fuel accumulation patterns. Time-since-fire had a stronger effect on some attributes than others: over half the variation in the cover of the hummock grass *Triodia scariosa* was attributed to the influence of time-since-fire; whereas it explained only 10% of variation in log density. Many factors other than time-since-fire affect the abundance and development of these resources. For example, other potential influences on log
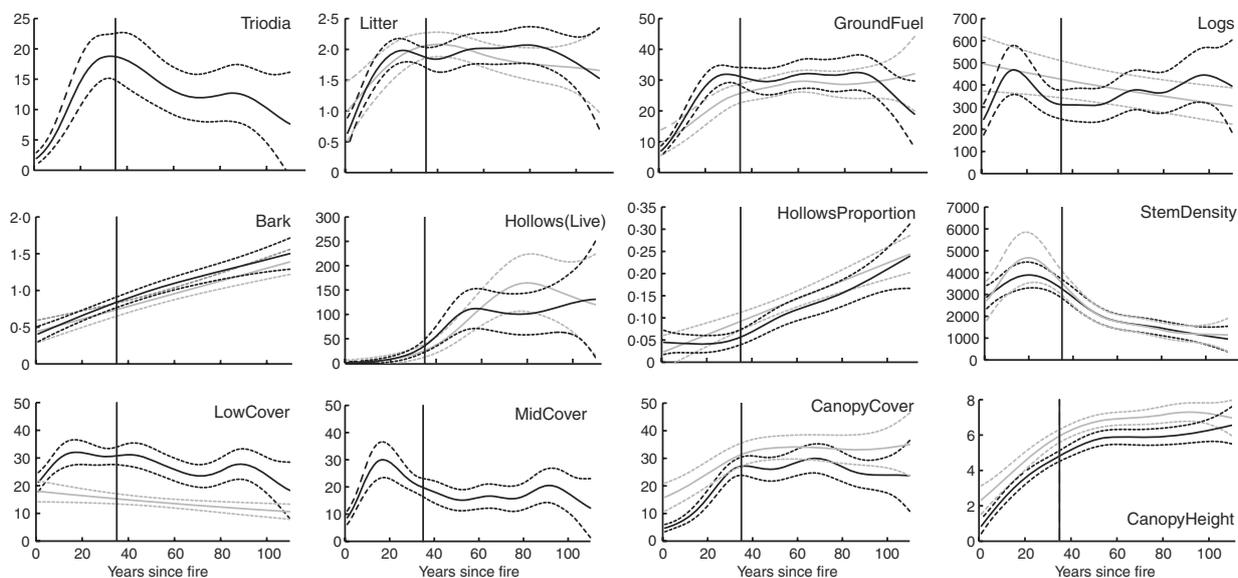
Fig. 1. Predicted post-fire dynamics in habitat/fuel attributes across a 110-year time-frame. Predicted trends and their 95% confidence intervals are shown for Triodia Mallee (black) and Chenopod Mallee (grey). Vertical lines indicate the extent of temporal understanding based on fire-history records. See Table 1 for Y-axis measurement unit.
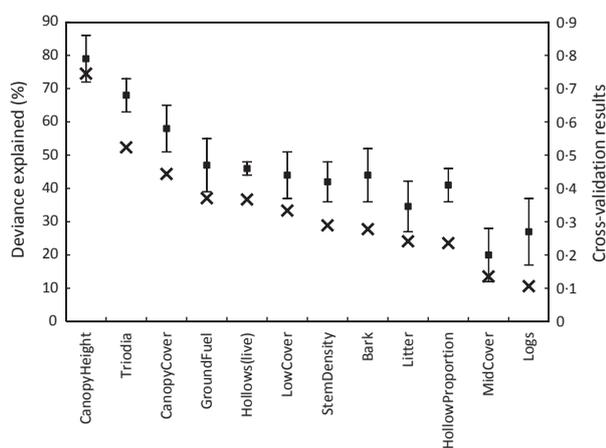

Fig. 2. Measures used in model evaluation: (a) percentage deviance explained (crosses); (b) mean cross-validation correlation (squares, including standard error bars).

density include inter-fire interval and termite activity (Whitford, Ludwig & Noble 1992).

LONG-TERM RESOURCE DYNAMICS FOLLOWING FIRE

Fire-age predictions for sites of previously unknown age (Clarke *et al.* 2010) allowed us to investigate post-fire resource dynamics over a chronosequence three times that provided by fire-history mapping. Extending the chronosequence provided a greater understanding of post-fire changes. First, it highlighted that different resources develop and change in abundance over different time-scales. For example, leaf litter depth and the cover of *Triodia* hummocks increased rapidly post-fire, reaching a maximum within 20–30 years (Fig. 1). Other

attributes displayed a much longer process of development: canopy height reached an asymptote at around 60 years, while the proportion of tree stems with hollows, and the abundance of decorticating bark, continued to increase for over a century (Fig. 1). Such variation in the temporal scale of resource development makes identifying inter-fire intervals that are appropriate for all management objectives difficult.

Secondly, it revealed how attributes change in abundance over long time-frames. The density of fallen timber, for example, varies through time. In Triodia Mallee vegetation, it peaks in the first 20 years post-fire as dead stems collapse, declines over the subsequent 20 years as these stems decay, and gradually increases from 50 to 100 years post-fire as the next cohort of maturing trees shed limbs. The nonlinearity of long-term trends identified here, and in other systems (e.g. Pare & Bergeron 1995; Hall, Burke & Hobbs 2006), has important implications. It suggests that reduced temporal understanding may lead to an inaccurate interpretation of post-fire dynamics. Trends observed over the first 35 years of the chronosequence (the limit of known fire-history) were not indicative of patterns observed in following decades for most attributes. This may have repercussions if feedback mechanisms govern the relationship between vegetation characteristics and fire (e.g. Bradstock 1989a), as management based on shorter-term understanding may favour some species and communities at the expense of others.

TEMPORAL DEVELOPMENT OF HABITAT AND FUEL ATTRIBUTES

The relatively rapid increase in the cover of *Triodia* hummocks and the depth of litter layers following fire (Fig. 1) has implications for fauna, as well as fuel accumulation. Mallee vegetation
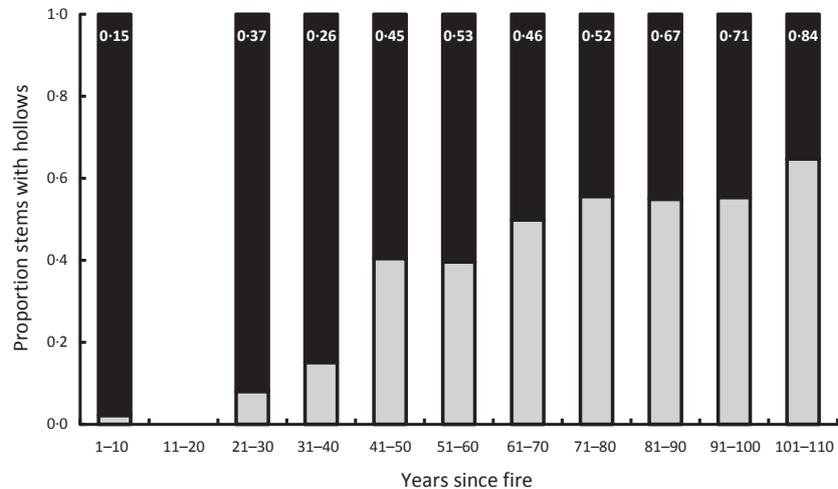
Fig. 3. Proportion of hollow-bearing stems that were dead (black) and alive (grey), averaged across sites in time-since-fire intervals of 10 years. Data for Triodia Mallee and Chenopod Mallee have been pooled; mean numbers of hollow-bearing stems/tree are shown for sites in each interval.

may be suitable for *Triodia*-associated reptiles, such as southern mallee ctenotus *Ctenotus atlas*, within six years post-fire (Caughley 1985), while at least 15 years is required before vegetation is suitable for the *Triodia*-dependent mallee emu-wren *Stipiturus mallee* (Brown, Clarke & Clarke 2009). In terms of its development as a fuel source, it takes around 15 years before *Triodia* hummocks carry fire (Noble & Vines 1993). In contrast, leaf litter often accumulates rapidly to flammable levels, sometimes within five years (Raison, Woods & Khanna 1983). It takes longer for litter layers to provide adequate habitat for the litter-nesting malleefowl *Leipoa ocellata*, which exhibits highest breeding-density 60 years post-fire (Benshemesh 1989); and litter-dependent reptiles, including Boulenger's skink *Morethia boulengeri* Ogilby, which are most likely to occur 100 years post-fire (D. Nimmo unpublished data). However, strong fauna–habitat associations do not always translate into predictable fauna–fire relationships (Driscoll & Henderson 2008). Nonetheless, variation in faunal responses to time-since-fire (see also Briani *et al.* 2004) highlights the complexity of managing fire for biodiversity conservation, even before hazard reduction imperatives are considered.

The slow development of some resources over long periods also has implications for the occurrence of fauna, and the provision of fuel sources. Recently burnt areas are unlikely to provide sufficient decorticating bark for species that use this resource, such as the endangered black-eared miner *Manorina melanotis* which forages amongst bark ribbons (Woinarski 1999). As a fuel resource, hanging bark will likewise have greater influence on fire behaviour in older tree mallee vegetation. Dead trees present similar challenges in the USA, where park management often involves the removal of this fuel type, yet dead trees provide important microhabitats used by many lizard species for shelter, foraging and courting (James & M'Closkey 2003). Species that depend on tree hollows, such as the hollow-nesting striated pardalote *Pardalotus striatus* (Woinarski 1999), are unlikely to find tree mallee suitable for all their requirements until it is at least 40 years old (Fig. 1). It will take many more decades (> 100 years) before live eucalypt stems are of a diameter suitable for large hollow-nesting species

like Major Mitchell's cockatoo *Cacatua leadbeateri* (Clarke 2005). Recurrent fires within 40 years will result in hollows being provided predominately by dead stems (Fig. 3) which are more susceptible to fire. While fire may create hollows or increase their rate of development (Inions, Tanton & Davey 1989), our results suggest it will not markedly increase hollow availability in mallee vegetation, especially in the long-term. The occurrence of hollow-bearing stems was proportionally lowest in early post-fire years, and the density of dead hollow-bearing stems was not related to time-since-fire.

The identification of habitat resources that develop over many decades, and the documentation of associated developmental patterns, can inform fire management by identifying minimum and maximum fire intervals for fauna, as undertaken using plant species attributes (e.g. age at first seed set, longevity: Noble & Slatyer 1980). Management based primarily on fire intervals derived from plant attributes will not be adequate for the provision of all faunal requirements, due to the extended time-frames over which some habitat resources develop (Clarke 2008).

Fuel continuity plays an important role in influencing wildfire behaviour (Van Wilgen, Lemaitre & Kruger 1985). The continuity of most primary fuels in tree mallee vegetation does not increase substantially beyond around 30 years since fire. After this time, there is a greater distance between surface and canopy fuels, fewer eucalypt stems (coarse standing fuels), and a reduced cover of understorey fuel. The 'opening-up' of vegetation as time-since-fire increases has been observed in this and other systems (Hanes 1971; Clarke, Boulton & Clarke 2005). Nonetheless, there is strong potential for bark to contribute to spotting behaviour in fires (Bradstock & Cohn 2002). Bark continues to accumulate on trees after 30 years post-fire, and may increase fuel continuity and fire-spread in older mallee vegetation.

Post-fire changes in vegetation structure and complexity also have implications for faunal habitats and assemblages (Catling, Coops & Burt 2001; Fox, Taylor & Thompson 2003). For example, the composition of bird communities in tree mallee vegetation aged between 10–30 years differs from

communities occupying older vegetation with a sparser understorey and taller canopy (Woinarski 1999; S. Watson, unpublished data). Patterns of vegetation succession represent a sequence of habitats which benefit different species; hence, descriptions of post-fire change in habitat structure do not provide clear guidance for ecological fire management unless fire plans target particular species (e.g. MacHunter, Menkhorst & Loyn 2009).

FURTHER IMPLICATIONS FOR FIRE MANAGEMENT

Our results demonstrate that the temporal scale of investigation influences the perception of post-fire resource dynamics. Critically, extension of the chronosequence alters understanding of fire–fauna and fuel–fire relationships in different ways, such that management recommendations derived from shorter (< 30 years) and longer (110 years) temporal scales may differ. Results from the longer, 110-year chronosequence indicate greater scope for integrating management for conservation and hazard reduction objectives. Fuel quantity and continuity increased rapidly in early post-fire years, as previously documented in this (Bradstock 1989b; Noble & Vines 1993) and other systems (Raison, Woods & Khanna 1983; Sah *et al.* 2006). However, the longer perspective revealed that most primary sources of fuel did not increase substantially after around 30 years-since-last burn, suggesting a potential plateau in fuel-related fire hazard. In contrast, a short-term perspective precludes appreciation of the importance of the long-term development of some habitat resources (e.g. mature canopy layer, tree hollows) and ongoing changes in vegetation structure and complexity. In combination, these insights suggest a reduced urgency to burn 'long-unburnt' mallee vegetation for the purpose of hazard reduction, and a corresponding opportunity for fire planners to focus greater attention on conservation objectives.

Attributes such as *Triodia* hummocks, leaf litter and decorticating bark provide both important resources for fauna and fuel for fire (Bradstock & Cohn 2002). At local scales, management to reduce these fuels is incompatible with the requirements of animals using these resources for foraging or shelter (e.g. James & M'Closkey 2003; Ucitel, Christian & Graham 2003). Strategic use of prescribed fire to reduce the risk of wildfire involves a trade-off. Maintaining vegetation in early post-fire conditions as a 'fire-break' may prevent extensive wildfire (e.g. > 100 000 ha) and facilitate the persistence of a greater proportion of the landscape at more advanced stages along the post-fire chronosequence (Sandell *et al.* 2006). However, the use of prescribed fire over large areas (e.g. landscape burning) demands careful consideration of the overall amount and spatial distribution of vegetation of all fire-ages (Clarke 2008), and recognition that some habitat components continue to develop for at least a century after fire.

In contrast with tree mallee vegetation, where prescribed fires and wildfires result in similar post-fire changes, in many other ecosystems (such as forests) differing fire severity combined with taller canopy vegetation mean that prescribed fire and wildfire may initiate different post-fire trajectories (e.g. Sah *et al.* 2006). Consequently, the resources available in prescribed fire and wildfire scars of identical fire-ages will also differ. Further research is needed before explicit recommendations can be made about the spatial properties of fire plans, and the effect of differential post-fire trajectories (e.g. prescribed fire cf. wildfire) on resource availability at broad spatial extents. Nevertheless, the impacts of fire on the dynamics of fuel *and* habitat attributes must be considered in fire planning if management is to successfully contribute to both hazard reduction and conservation objectives. Furthermore, the potential for post-fire resource dynamics to operate over temporal scales that exceed current understanding must be factored into management plans.

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Supporting Information

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

Figure S1. Location of 26 study landscapes in Victoria, South Australia and New South Wales, Australia. All study sites ($n = 549$) were situated within these landscapes.