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Landscape modulators and resource accumulation in a post-fire eucalypt woodland

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ABSTRACT

In resource-limited environments patch development is a critical component of ecosystem function. Resource patches at both fine and broad scales are temporally dynamic, and the resources they provide change in response to broad-scale ecological disturbances such as fire. Here we consider temporal changes in perennial vegetation patches by measuring the fine-scale development of physical patch layers in response to a broad-scale abiotic process, fire. Until recently, such fundamental shifts in patch structure have, for the most part, been widely assumed and quantitatively ignored. Fundamental shifts in post-fire litter composition are important for predicting fire behaviour and may be useful in identifying the range of conditions or thresholds under which the arrangement of fuel components affects future fire behaviour. We describe the post-fire development of physical patch layers associated with two eucalypt mallee tree species (*Eucalyptus dumosa* and *Eucalyptus socialis*). We quantified tree, litter bed and canopy dimensions for sites with fire histories ranging from 4 to 42 years, focussing on the development of the sub-canopy litter bed. There were strong linear relationships between tree size and litter bed size with increasing time since last fire. After we accounted for tree and litter bed size, fire history still had a significant effect on the composition of the litter bed with sticks, seeds and fragments generally increasing and leaves generally decreasing with greater time since fire. There were no significant differences between the two tree species studied for any relationship with time since fire. Our results document the temporal, fine-scale changes in litter accumulation and composition following fire in a mallee woodland, indicating that substantial shifts in composition occur, likely affecting the flammability of the litter bed. More specifically, we have shed light on post-fire trends in litter accumulation, a fundamental component of patch development. This study provides us with a better understanding of fine-scale resource patch development, allowing us to predict shifts in resources at broader scales. By understanding how landscape modulators and their surrounding environment influence the development of patches, we are in a better position to predict how changes in these drivers are likely to affect ecosystem processes.

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1. Introduction

Arid and semi-arid ecosystems function effectively by concentrating limited resources into discrete patches (Noy Meir, 1979; Ludwig et al., 1997). These nutrient- and water-rich resource patches can buffer surface temperatures and provide habitat for organisms (Whitford and Kay, 1999). The stark contrast in resource quality and quantity between the resource patch and the surrounding matrix can also significantly alter local species assemblages. Some resource patches are constructed by organisms that exploit, modify and concentrate resources. Examples include the resource-rich pits created by soil foraging animals (Whitford and Kay, 1999) and the resource patches that form

around perennial vegetation (Shachak et al., 2008). Widespread fine-scale patch creation and development by dominant biota, such as perennial plants, can significantly alter landscape productivity and resource diversity at broad spatial scales (Ludwig et al., 1997), which, in turn, affects the abundance and diversity of patch-dependent biota (Shachak et al., 2008). Organisms that create and maintain resource patches and are dominant at broad scales are known as landscape modulators (*sensu* Shachak et al., 2008).

At broad scales, landscape patchiness and associated biodiversity are also driven by abiotic processes such as fire. Such broad-scale abiotic processes have long been recognised as major drivers of biodiversity (Bradstock et al., 2005). Current literature, however, suggests that fine-scale resource patches created and maintained by biota may be more important for maintaining biodiversity than those created and maintained by broad-scale abiotic processes such as fire (Loreau et al., 2001; Shachak et al., 2008). Fire can modify the spatial and temporal arrangement of broad- and fine-scale

Abbreviations: ANCOVA, Analysis of Covariance; N, nitrogen; PERMANOVA, Permutational Multivariate Analysis of Variance; SEM, Structural Equation Model.

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patches and affect their constituent biota for many decades after the event (Russell-Smith et al., 2010). In highly flammable communities, a regime of regular, natural fires of varying intensity and size can structure landscapes into a mosaic of different patches, each with different stages of recovery (Gill et al., 2003; Bradstock et al., 2005). Fire is, therefore, an important modulator of resources and resource patches, and in resource-limited environments such as semi-arid woodlands, this has dramatic effects on ecosystem structure and productivity (Noble, 1989; Cohn and Bradstock, 2000). At finer spatial scales, fire homogenises resource patches formed around trees, reducing resource diversity at the fine patch and inter-patch scales. However, this fine-scale loss of resource diversity is often short-lived due to the temporal dynamics of patches. Shachak et al. (2008) proposed that patches such as those associated with perennial vegetation are temporally dynamic and cycle through stages of resource contrast with their surrounding matrix. As patches develop, they become increasingly more complex, physically and chemically altering soil properties and providing a greater array of habitats and potential food sources for organisms across both small and large spatial scales. When patches decay through processes such as fire, resource contrast with the surrounding matrix is initially reduced, but develops again over time (Shachak et al., 2008).

The development of post-fire species assemblages is generally related to the extent to which patch types re-establish after fire. A range of patch types co-exist after fire, providing a multi-layered habitat for diverse groups of fauna. However, not all patch types co-exist at the same time. For example, over time a tree can create spatially complex patches, with multiple layers such as litter beds that develop rapidly on the soil surface, hollows that develop slowly in the canopy, and strips of bark on the trunk that develop at an intermediate rate. A classic example of such multi-layered resource patches occurs in Mediterranean woodlands where evergreen, sclerophyllous shrubs and trees are dominant at broad scales, creating and maintaining resource patches (Gabay et al., 2012). In Australia's Mediterranean climatic zones, mallee (*Eucalyptus* spp.) is the dominant vegetation community. Mallee trees have a growth form characterised by multiple stems that develop from a lignotuber root system. They are well adapted to periodic fires, and the stems resprout in as little as 2 weeks after fire (Noble, 1997). A range of fire histories typically occur across an entire landscape, resulting in a mosaic of multi-layered resource patches that vary in size and development. The physical elements of these multi-layered resource patches such as litter beds, canopy, trunks and arboreal bark strips also provide fuel for future fires.

Despite considerable debate on the importance of fire for mallee-dependent fauna (e.g. Driscoll and Henderson, 2008), many studies have demonstrated strong relationships between the post-fire recovery of mallee communities and a range of taxa (Clarke et al., 2010) such as reptiles (Caughley, 1985), birds (Woinarski, 1999), arthropods (Noble et al., 1990) and mammals (Kelly et al., 2010). Although there has been a significant focus on post-fire shifts in plant and animal assemblage in mallee communities, there are few data, to our knowledge, on the post-fire changes to these multi-layered resource patches that typify mallee communities (but see Haslem et al., 2011).

Our study examines the spatial and temporal changes in multi-layered resource patches after fire in mallee communities. We investigate resources at the scale of individual trees (*sensu* Shachak et al., 2008) using white mallee (*Eucalyptus dumosa* A. Cunn. ex J. Oxley) and red mallee (*Eucalyptus socialis* F. Muell. ex Miq.) as models of landscape modulators. We measure the spatial shift in resource patch size in response to fire history along a continuum of fire histories across the landscape. Given the identical structure of these two species, we did not expect to record differences in relationships between patch layers. However, given that litter fall

can be species-specific (Miller and Urban, 1999) we compared them to test whether there was any species-dependent variation in the composition of the litter bed across the different fire histories. We expected that changes within the canopy and trunk of our mallee models would correspond with shifts in the environment of the sub-canopy patch. We quantified the dimensions of the physical patch elements, i.e. the tree and litter layer associated with our mallee trees across a range of fire histories, focussing on the spatial and compositional development of the litter patch (litter bed layer), quantifying and comparing litter bed dimensions and composition as a function of time since fire.

2. Methods

2.1. Field site

Our study was undertaken inside two large conservation areas, Tarawi Nature Reserve and Australian Wildlife Conservancy's Scotia Sanctuary in south western, New South Wales, Australia (33°43'S, 143°02'E). This area is semi-arid, receiving about 280 mm annual rainfall, however there are very few years in which this amount is actually received. Rainfall is highly irregular throughout the year and spatially variable across a scale of tens of kilometres. Winters are mild, with daily mean maximum temperature of 17 °C and a daily mean minimum temperature of 6 °C in July. Summer is typically hot with a January mean daily maximum temperature of 33 °C and a mean daily minimum of 19 °C (BOM, 2011).

Our study was conducted in a dune mallee community; a low open woodland located on long, low (relief to 7 m) east-west trending sand dunes. Dune mallee is generally dominated by an open overstorey of mallee (multi-stemmed) trees (*Eucalyptus gracilis* F. Muell., *E. dumosa*, *E. socialis*) and an understorey of scattered perennial hummock grasses (*Triodia scariosa* N. T. Burb. subsp. *scariosa*). However as mallee trees resprout from lignotuberous roots after fire, in recently burn sections mallee appear as hummock to shrub-sized plants for approximately 10 years after fire. Individual trees grow as a cluster of stems, which may be isolated or clumped with other individuals, forming large connected litter layers. The perennial hummock grasses that dominate the inter-tree matrix are highly flammable and their role in fuel connectivity is well established (Noble, 1989, 1997). Shrub cover to 2 m is sparse on the dunes, with widely-spaced individuals of predominantly *Senna artemisioides* subsp. *filifolia* (Benth.) Randall and *petiolaris* Randell, and *Acacia burkittii* F. Muell. ex Benth (Keith, 2004). At our study site, the soils are mainly calcareous, brownish and siliceous sands sparsely capped with biological soil crusts.

2.2. Experimental design

In January 2011, we sampled nine areas with known fire histories ranging from 4 to 42 years since fire. All sampled areas were located within 20 km of each other, and were assumed to have burned under equivalent, relatively high intensity fires based on vegetation characteristics. More specifically the mallee vegetation at all sites had re-sprouted from lignotubers, rather than continuing growth from stems which existed before the fire which can happen after low intensity fires.

At each of our nine burn areas, we randomly selected 20 sites. At each site we measured two trees, one of each species (total $n = 360$). To minimise edge effects we did not sample within 30 m of the edge of a given burn area. Sampling was limited to *E. socialis* and *E. dumosa*. We identified these species based on leaf and bark traits, and fruits where possible. Due to size limitations of some burn areas we could not always find an equal number of

each species (i.e. 20 of each species) at each burn area. At worst a minimum of 16 individuals representative of a species were selected for sampling. However, in this case 24 individuals of the other species were sampled to maintain orthogonality at the burn area level. This restricted our use of 'species' as to a covariate, rather than a factor in our parametric analyses (see Section 2.4.1 below).

2.3. Measuring tree and litter bed patch layers

A range of measurements were made at each tree including tree height, elliptical canopy area, and diameter of the largest stem ~30 cm above the ground surface, consistent with recent studies in mallee (i.e. Clarke et al., 2010). Litter bed size was recorded on six radial transects crossing the entire litter patch. Along these transects we measured the depth of the litter bed and the distance to the edge of the continuous litter patch in order to calculate a litter bed depth profile for each transect. Litter volume was calculated from the sum of six partial volumes derived from the integrated area under the curve of quadratic equations fitted ($R^2 > 0.99$) to each individual length and depth transect measurements. A standardised sample of litter in a 0.2 m diameter quadrat was collected at the midpoint of the first transect at each tree. Litter was dried at 60 °C to a constant weight, sieved to remove soil and particles less than 2 mm², hand-sorted into five components (leaves; sticks; bark; seeds; fragments < 4 mm²) and weighed. Litter load (kg m⁻²) and bulk density (kg m⁻³) were calculated from this sample. Litter bed mass was approximated by adjusting

the litter bed volume with the bulk density of litter (Bradstock and Gill, 1993).

2.4. Statistical methods: tree and litter patch dimensions

Tree height, canopy area and the diameter of the largest stem were $\log_e(x+1)$ transformed and litter area, mass and volume fourth-root ($x^{0.25}$) transformed to ensure homogeneity of residuals prior to analysis.

2.4.1. Spatial and temporal development of the multi-layered patch

Linear regressions were used to quantify all possible combinations of allometric relationships between the litter bed dimensions (litter area, litter mass, litter volume) and tree dimensions (tree height, canopy area, largest stem diameter). The best linear relationship for each litter bed dimension is reported. A Principal Components Analysis (PCA) was then used to reduce all tree and litter bed dimension data to a single unitless Patch Score for each tree. The Patch Scores were compared across treatments with a nested two-factor Analysis of Covariance (ANCOVA) where species was binary-transformed and used as the covariate. Factors included our nine levels of time since fire (burn area, fixed) and site nested within time since fire (random). The ANCOVA was run in the *Minitab* (2007) package.

2.4.2. Compositional shifts in the litter patch

To quantify litter bed properties, we calculated litter load and litter composition (i.e. the proportional mass of each individual

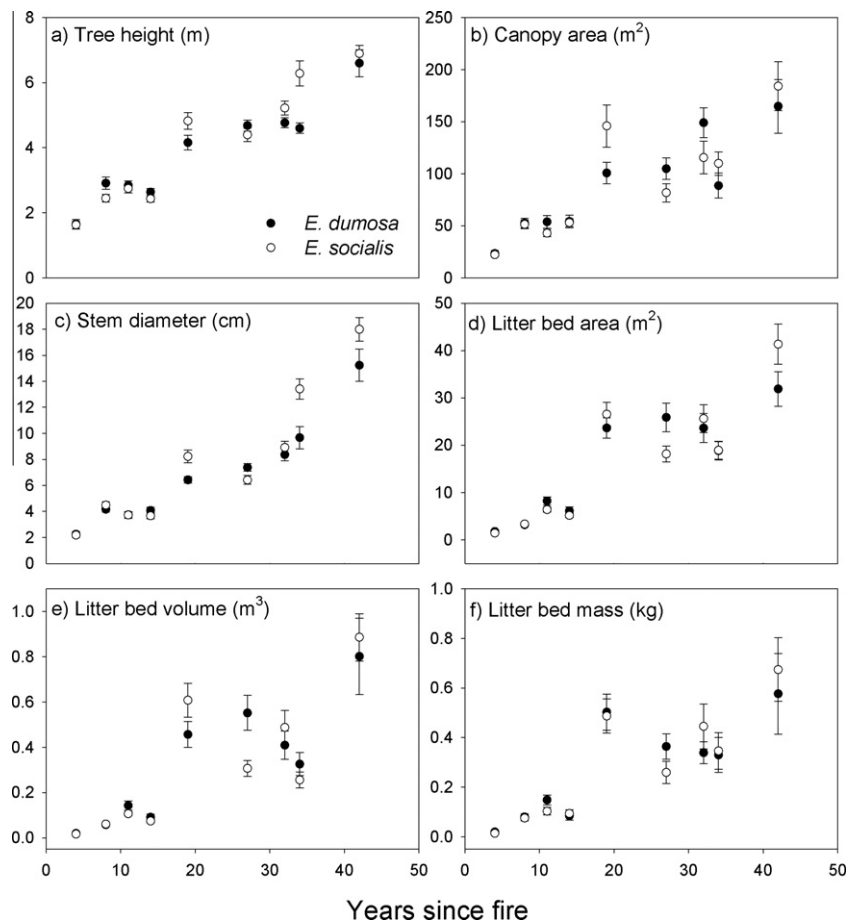


Fig. 1. Mean (±SE) for all tree and litter bed dimensions for both species, for sampled years since fire. The black circles represent *Eucalyptus dumosa* while the white circles represent *Eucalyptus socialis*. The y axis units are given in the sub-title for each individual graph.

component, leaves, sticks, bark, reproductive structures and frass). To quantify shifts in litter load with increasing time since fire, the mean for each species at each burn site was used in a linear regression.

For shifts in composition, we used a Permutational Multivariate Analysis of Variance (PERMANOVA) with Patch Score as a covariate to account for pre-existing differences in tree and litter bed size. Factors included time since fire (fixed) and species (fixed) and their two- and three-way interactions with the covariate. The analyses were performed on a Euclidean distance-based resemblance matrix of the proportional mass data of the 5 litter components with 9999 permutations (type III sums of squares). Except for ANCOVA (Minitab, 2007), all analyses were performed in the PRIMER v6 program with the additional PERMANOVA+ statistical package (Anderson et al., 2008).

2.4.3. Tree, litter and fire as a system

We used Structural Equation Modelling (SEM) to test the relationships among time since fire, canopy area, litter bed area and litter composition. SEM accounts for the direct and indirect effects of each variable on the response variable and estimates the strength of these effects (Grace, 2006). The SEM consists of a diagram of complex multivariate cause-effect relationships. An *a priori* causal framework is constructed to logically represent the expected multivariate relationships, against which field data are tested. This is done by comparing the covariance structure of the data that are implied in the *a priori* model with the covariance structure of the observed data (Grace, 2006). We used a maximum likelihood based goodness-of-fit test to assess the degree of fit between observed and predicted covariance structures. Our model posits that time since fire has both a direct effect on litter bed composition but also indirect effects, which are moderated by canopy area or litter bed area. With five separate models, we examined the direct and indirect effects on the proportional mass of leaves, sticks, bark, seeds and fragments. The proportional mass of each component was $\log_e(x + 1)$ transformed prior to analysis. Each of our models was saturated, i.e. all possible pathways between all variables were accounted for. The significance of our models could therefore not be tested, but their relative strengths are based on the amount of variance explained in our five response variables (Grace, 2006). All SEM models were performed in AMOS 20.0 (SPSS Inc. 2009) software.

3. Results

3.1. Spatial and temporal development of the multi-layered patch

There was a general increase in the size of the trees and their associated litter patches for both tree species with increasing time since fire (Fig. 1), but considerable spatial variability among trees within the same fire history. The strongest linear relationships among tree and litter bed dimensions occurred between canopy area and litter bed area ($R^2 = 0.70$, $P < 0.001$; Fig. 2a), canopy area and litter bed mass ($R^2 = 0.57$, $P < 0.001$; Fig. 2a), and tree height and litter bed volume ($R^2 = 0.66$, $P < 0.001$; Fig. 2b), where each litter bed dimension increased with greater time since fire.

Our Patch Score, which integrated all canopy and litter patch dimensions and was derived from the Principal Components Analysis (Table 1), explained 86% of the variation in the multi-layered patch data. We found significant shifts in the Patch Score with increasing time since fire, indicating that overall patch size is increasing ($F_{8,171} = 107.30$, $P < 0.001$). There was also significant spatial variability in Patch Score among our sites within a fire history ($F_{171,179} = 1.45$, $P = 0.007$). However there was no significant

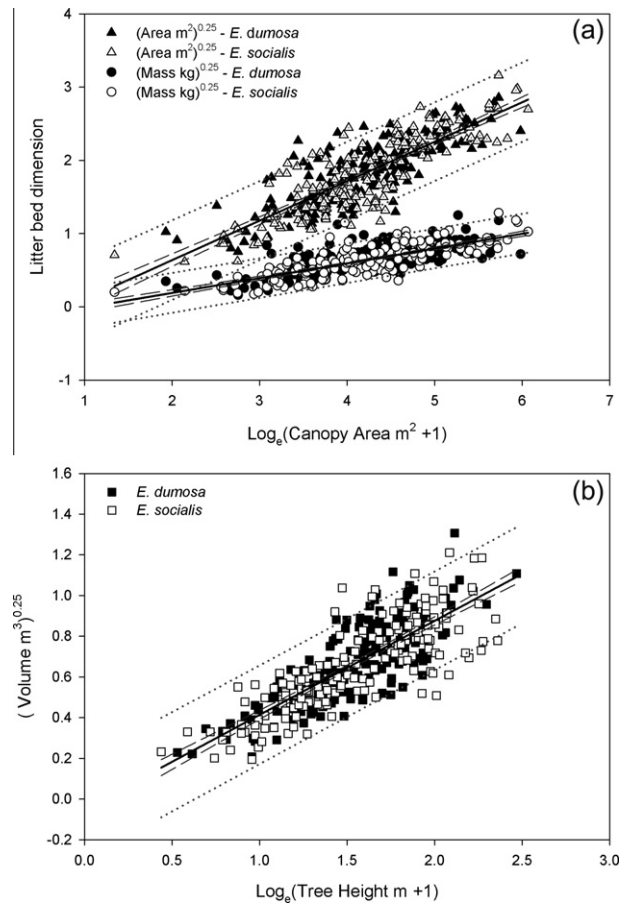


Fig. 2. Linear regression of (a) litter bed area (triangles) and litter bed mass (circles) on tree canopy area and (b) litter bed volume on tree height (squares). Black symbols represent *Eucalyptus dumosa* and white symbols represent *Eucalyptus socialis*. Linear regression models: Fourth-root of litter bed area (m^2) = $0.539 \times \log_e(\text{canopy area (m}^2) + 1) - 0.441$ ($R^2 = 0.70$; $P < 0.001$); Fourth-root of litter bed mass (kg) = $0.202 \times \log_e(\text{canopy area (m}^2) + 1) - 0.215$ ($R^2 = 0.57$; $P < 0.001$); Fourth-root of litter bed volume (m^3) = $0.462 \times \log_e(\text{tree height (m)} + 1) - 0.048$ ($R^2 = 0.66$; $P < 0.001$). Blue long dash lines represent 95% confidence band and red dotted lines represent 95% prediction band.

Table 1

Eigenvectors are the coefficients in the linear combinations of PCA components making up the first principal component for Patch Score and composition score. These scores represent the weightings given to each component in the overall final summary score. The total variance explained by this first axis is also indicated.

PCA component	Patch score eigenvectors
$\log_e(\text{tree height} + 1)$	-0.310
$\log_e(\text{canopy area} + 1)$	-0.673
$\log_e(\text{stem diameter} + 1)$	-0.460
$(\text{Litter bed area})^{0.25}$	-0.427
$(\text{Litter bed volume})^{0.25}$	-0.177
$(\text{Litter bed mass})^{0.25}$	-0.158
Total variance explained	86.0%

variation explained when the two species were considered as covariates of Patch Score ($P = 0.45$).

3.2. Compositional shifts in the litter patch

Litter load (kg m^{-2}) was highly spatially variable, did not differ between tree species, and showed no obvious trend with time

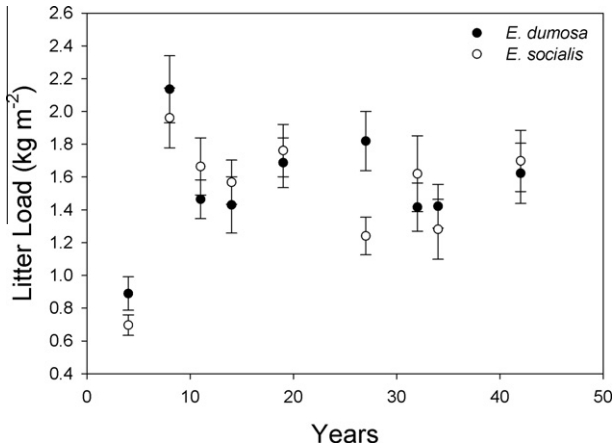


Fig. 3. Mean (\pm SE) litter loads (kg m^{-2}) with increasing time since fire. Black symbols and solid line represent *Eucalyptus dumosa* and white symbols and dashed line represent *Eucalyptus socialis*. The regression for each species shows an insignificant change difference between the two species and represents a non-significant amount of variation in the data, suggesting no change in litter. Regression equations: (*E. dumosa* $\text{kg m}^{-2} = 0.003 \times \text{time since fire (yr)} + 1.465$, $R^2 = 0.02$, $P = 0.72$; *E. socialis* $\text{kg m}^{-2} = 0.004 \times \text{time since fire (yr)} + 1.405$, $R^2 = 0.02$, $P = 0.69$).

since fire (Fig. 3). Linear regression analyses did not reveal any significant variation within the data for either species (*E. dumosa* $P = 0.72$; *E. socialis*, $P = 0.69$; Fig. 3). Despite no shifts in litter load, there were, however, significant shifts in litter composition.

Some litter bed components followed clear trends across fire histories, although there were no distinct trends between the two species. Each component shifted independently with increasing time since fire resulting in dramatic changes in overall litter bed composition. The proportion of leaves declined with increasing time since fire, with a suggestion of a plateau around 20 years since fire (Fig. 4a). This pattern mirrored that for sticks, which gradually increased, peaking at around 30 years post-fire (Fig. 4b). Trends for the proportion of bark were inconsistent, commencing at relatively high proportions, but showing substantial variation across the time since fire gradient (Fig. 4c). The proportion of seeds and fragments followed a similar upward trend with increasing time since fire (Fig. 4d and e).

Patch Score, our measure of patch size, explained a significant amount of variation in the PERMANOVA model of litter composition (Pseudo- $F_{1,324} = 77.06$, $P < 0.001$). Once allowing for the effect of patch size, there was still a significant effect of time since fire on litter composition (Pseudo- $F_{8,324} = 10.35$, $P < 0.001$), suggesting that changes in litter bed composition occur irrespective of changes in tree and litter bed size. However, there was no significant effect of species on litter bed composition ($P = 0.35$). Furthermore, there were significant interactions between our measure of patch size score and time since fire (Pseudo- $F_{8,324} = 1.59$, $P = 0.025$) and between patch size score and species (Pseudo- $F_{8,324} = 1.89$, $P = 0.004$) suggesting different rates of change in litter bed composition among burn sites and between species. Our principal component analysis-derived score for litter composition (% mass) explained 55.9% of the variation in litter composition (Table 1).

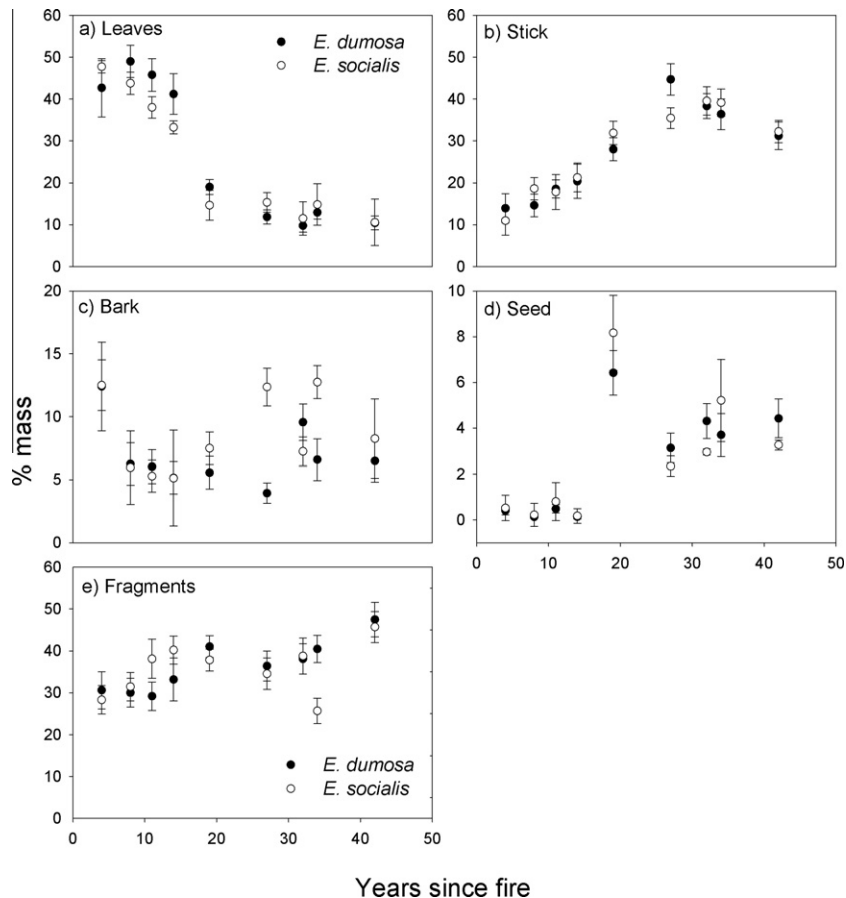


Fig. 4. Mean (\pm SE) percent mass (\pm SE) for every burn site (years since fire) for each species' litter components: (a) leaves (b) bark (c) stick (d) seed and (e) fragments. Black circles represent *Eucalyptus dumosa* and white circles represent *Eucalyptus socialis*.

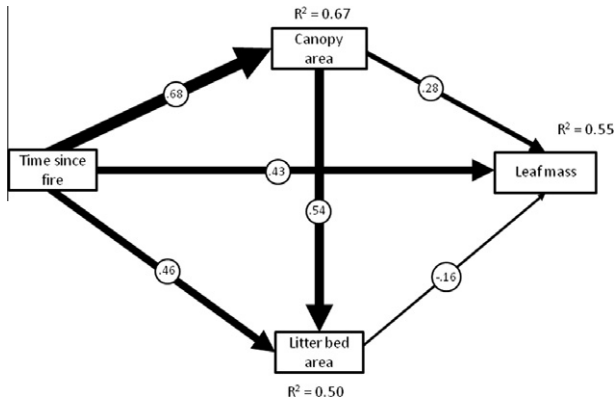


Fig. 5. Structural Equation Model for the proportional leaf mass of the litter bed. The R^2 value above litter composition indicates that the direct and indirect effects canopy size, litter bed area and time since fire account for 55% of the variance in proportional leaf mass in the litter bed. The thickness of the pathways is directly proportional to the strength of the path coefficients. The model is saturated, therefore the chi squared statistic = 0 with 0 df. The pathway coefficients for the remaining litter components can be found in Table 2.

3.3. Tree, litter and fire as a system

For the leaf components of the litter bed, time since fire, canopy and litter bed area explained 55% of the variation in the composition scores (Fig. 5). We found that time since fire alone was the strongest, direct effect on the leaf components. Canopy area had a positive direct effect on the proportion of leaves, while litter bed area had a negative direct effect.

We identified different causal effects for each remaining component (e.g. sticks, bark, etc.) separately (Table 2). For bark, the indirect effect of time since fire mediated by canopy area had a stronger causal effect than the direct effect of time since fire alone. Time since fire, mediated by litter bed area, was the strongest causal effect of sticks, seeds and fragments in our models.

4. Discussion

Our study examined the post-fire development of multi-layered resource patches comprising trees, their canopies and associated litter beds in a *Eucalyptus* mallee community in eastern Australia. In a space-for-time approach we measured the physical patch layers to monitor resource patch development by our landscape modulators. Consistent with our expectations, we found strong positive relationships between tree size and litter bed size, with patch size generally increasing with increasing time since last fire. Overall, there were no differences between the two eucalypt species, nor any trends between litter bed load (expressed as a mass per unit area) and time since fire. We did, however, find substantial shifts

in litter bed composition which appeared to be driven largely by fire history.

4.1. Fire drives litter patch development

For many ecosystems, the processes surrounding post-fire litter dynamics, in particular, litter bed composition, are complex and poorly understood (but see Raison et al., 1983; Miller and Urban, 2000; Haslem et al., 2011). We found strong relationships between fire history and the temporal development of a multi-layered resource patch system, comprising the tree stem and its canopy and litter bed. More importantly, we found significant relationships among each resource patch layer across all fire histories.

Our process model indicated that the indirect effect of fire history mediating litter bed area had a stronger effect on more litter bed components than the direct effect of fire history or the indirect effects of canopy area. This reinforces the notion that resource patch development by a landscape modulator is dependent upon its surrounding environment (Shachak et al., 2008). For example, recently burnt sites are characterised by greater wind speed due to surfaces lacking plant cover (Gill and Allan, 2008), potentially enhancing aeolian transport of materials. We also observed smaller trees (<2.3 m), with a higher proportion of leaves in the litter bed (~40%) in recently burnt sites than sites burnt more than 20 years ago (~4.5 m tall, <20% leaves), suggesting that resource heterogeneity, in terms of litter composition, is occurring at broad scales. Resource heterogeneity is driven by processes occurring at multiple spatial scales. At a fine scale, landscape modulators drive resource patch development. Our data show that the temporal stage of litter patch development can define the quantity and composition of the litter. This patch development is intrinsically linked to broader-scale processes such as fire. The mosaic of fire histories at a broader-scale leads to further resource heterogeneity. In terms of litter beds, a mosaic exists where sections of the landscape vary in terms of their litter quantity and composition.

The modelling of individual litter layer components indicated that leaves were the only resource component to have time since fire as the strongest causal factor. Three main leaf attributes may account for the variation in litter bed leaf accumulation. Firstly, the production of leaf litter varies greatly over time, with relatively more leaves senescing in younger growth stages than in mature growth stages (Attiwill, 1979). Also immediately after a fire, there appears to be a large input of leaves from stags that were not completely consumed by the fire. Secondly, the lanceolate shape of *Eucalyptus* spp. leaves allows them to be readily transported by wind. Senescing leaves may land directly in an existing litter patch or in the unvegetated interspaces where they can be subjected to redistribution processes (sensu Schlesinger et al., 1990). In the first few years after fire, mallee trees represent the only areas of resource accumulation until hummock grasses re-establish from

Table 2
Path coefficients and goodness of fit tests for time since fire pathways for each component. Each row represents a model containing the response variable listed in the leftmost column. Otherwise, the model structure is identical to that in Fig. 5, but with different path coefficients. The next five columns list the path coefficients corresponding to the direct and indirect pathways in the models. R^2 is proportion of variance explained in the response variables listed in the leftmost column. All tests reported here indicate a good fit. All models are saturated.

Response variable	Direct paths			Indirect paths		Model R^2
	TSF to individual component	Canopy area to component	Litter bed area to component	Time since fire via canopy area	Time since fire via litter bed area	
Leaves	0.43	0.27	-0.15	0.19	-0.07	0.55
Bark	0.03	0.06	0.06	0.04	0.03	0.11
Sticks	0.15	0.10	0.36	0.07	0.17	0.40
Seeds	0.06	0.10	0.46	0.07	0.21	0.35
Fragments	0.09	0.16	0.33	0.11	0.15	0.36

seed (Cohn and Bradstock, 2000). Thus litter beds receive proportionally less of the wind-transported leaves with increasing time since fire. Thirdly, relatively rapid decomposition rate of leaf material, compared with fine woody materials, results in a faster loss of leaves from mature litter beds, further decreasing the relative mass of leaves in the litter bed with greater time since fire.

The accumulation of more woody resource components in the litter bed is likely due to variations in litter fall rates and the build-up of recalcitrant material with inherently low levels of decomposition (Cornwell et al., 2008). We found that sticks, seeds and fragments increased with greater time since fire. However when modelled, these components were driven by a relatively stronger mediating effect of time since fire on litter bed area, suggesting that post-fire litter bed development plays an important role in their accumulation. Current literature predicts a greater accumulation of poorly decomposing woody components with greater time since fire (Miller and Urban, 2000). Both fine and coarse woody material may take many years to decompose in semi-arid environments (Sinclair, 2004), with <25% mass loss of buried root material after 53 months (Noble et al., 2009). Removal of leaf material would therefore likely lead to an increase in litter fragments, as we found in our model. Seeds were the smallest mass fraction of the litter bed, and did not appear in the litter bed until approximately 20 years after fire, when the canopy and litter bed were already well established. This is likely due to the serotinous nature of *Eucalyptus* spp. (Lamont et al., 1991).

Despite clear post-fire shifts in litter bed composition, we detected highly variable litter bed loads, expressed as a mass per unit area, with no trends with respect to fire history or tree size. Previous research in open woodland ecosystems indicates that litter loads under individual tree canopy crowns vary with tree size and distance from the main stem (Bradstock and Cohn, 2002; McElhinny et al., 2010). For mallee, specifically, we found that litter load was largely independent of the diameter of the litter bed, supporting findings of Bradstock and Gill (1993). We focused on mid-bed litter loads, recording an average litter load of 1.5 kg m⁻² across all fire histories, and within current estimates for mallee of 0.5–1.5 kg m⁻² (Noble et al., 1984; Bradstock and Gill, 1993). In general, larger trees have larger litter resource patches than smaller trees as larger litter loads reflect a greater crown volume per unit area of surface (McElhinny et al., 2010). This may also explain fine-scale patterns of litter arrangement, where litter depth attenuates with increasing distance from the main stem, reflecting the decrease in canopy volume with distance from the main stem (McElhinny et al., 2010).

Litter fall rates are generally species-specific (Miller and Urban, 1999), however we found no significant difference in litter composition between our two species. It seemed possible that patch development in response to fire may differ between species, consistent with the notion of response diversity (*sensu* Elmquist et al., 2003). However our two mallee species are basically structurally and functionally identical. As we found no difference between our two species, it might be possible to extrapolate these trends in litter bed composition across other mallee species that share the same structure and functional roles. This would be beneficial from a management perspective, where a one-size-fits-all approach may be taken more confidently when predicting litter composition.

4.2. Litter patch development affects fuel loads and fauna

Despite numerous studies on the succession of post-fire flora and fauna (Haslem et al., 2011; Kelly et al., 2011), there have been relatively few empirical insights into post-fire litter accumulation (Bradstock et al., 2010). Litter is a crucial resource for fauna, providing habitat, foraging substrate and breeding resources (Haslem

et al., 2011). From a functional perspective the accumulation of litter after fire is important, as fire alters landscape-level connectivity of different fuels, potentially affecting future fire regimes (Turner and Romme, 1994; Miller and Urban, 2000; Scarff and Westoby, 2006). Changes to litter composition may shift fine-scale thresholds of fuel composition and connectivity. When optimal conditions for fine-scale connectivity occur in conjunction with optimal landscape and meteorological conditions for fuel connectivity, they could provide conditions required for the peak flammability observed in similar mallee communities (Noble, 1989; Turner and Romme, 1994; Bradstock et al., 2010).

Despite the recognition of fuel load and composition as important indicators of fire intensity, the complex composition of fuel is rarely considered in fuel load models (e.g. Scarff and Westoby, 2006). This study provides new insights into the fine-scale shifts in fuel composition and complexity in response to fire history and patch size. Shifts in post-fire litter composition are important for predicting fire behaviour (Bradstock, 2010) and may be useful in identifying the range of conditions or thresholds under which the arrangement of fuel components affects fire behaviour (Turner and Romme, 1994). Fire return intervals of 15–30 years are typical of dune mallee ecosystems (Bradstock, 1990; Noble and Vines, 1993). In our study, we found a ~20% decrease in the proportion of leaves, and ~20% increase in sticks in the 15–30 years period since fire. At greater times since fire, fragments account for more than 40% of proportional litter bed mass. Changes in composition affect litter bed flammability by altering the combustion rate, silica-free mineral content, low heat value, surface area to volume ratio, particle density, ventilation and depth of the litter bed (Bradstock and Gill, 1993; van Wagendonk et al., 1996; Scarff and Westoby, 2006), which ultimately affect the potential fire intensity. Specifically, leaves are well-ventilated and readily combustible (Scarff and Westoby, 2006). Sticks, however, require greater energy to combust, but will produce a much more intense fire, and likely structure a well-ventilated litter bed. In contrast, fragments are densely packed, and induce a low intensity, smouldering fire because of the poor ventilation (Schwilk and Caprio, 2011). Therefore, shifts in composition will alter fuel properties. In light of our results, time since fire plays a significant role in determining fuel properties of the litter bed, with evidence to suggest that peaks in community flammability coincide with peaks in fuels that burn at relatively high intensities.

At any given time, the resource patches associated with our landscape modulators will be in different developmental stages across the landscape as a result of a mosaic of fire histories. The development stage of resource patches will determine fuel connectivity and thus potential flammability at a local scale (i.e. within an area of common fire history). Also, the connectivity of areas with different potential flammability (as determined by fire history) will affect fuel connectivity at a landscape scale. The connectivity and potential flammability of mosaics is critical to fire management strategies. From a biotic perspective, this mosaic is crucial for landscape-scale diversity in habitat and resources.

In mallee, particularly, the interactions among fire history and litter bed cover and composition have important outcomes for litter-dependent flora and fauna. This interaction can also affect soil stability by limiting the area colonisable by biological soil crusts (Eldridge and Bradstock, 1994). The litter layer is a resource and its availability can affect the sheltering, feeding and breeding habitats of ground-foraging birds, litter dwelling reptiles, and ground dwelling mammals (Kelly et al., 2010, 2011; Haslem et al., 2011). Litter can also directly influence the distribution and abundance of arthropods (Schlesinger et al., 1997). To effectively incorporate our knowledge into management plans, we need to understand the basics of these fundamental interactions. Morton et al. (2009) draw attention to the importance of

recognising the subtle differences, such as shifts in litter composition, in these interactions between different components of ecological communities, particularly in the face of climate change and therefore altered fire regimes.

5. Conclusions

The importance of episodic events, such as fire, and their effects on ecosystem structure and function, are well recognised (Stafford Smith and Morton, 1990; Morton et al., 2009). However, there is a general lack of knowledge surrounding the processes driving the recovery of ecosystems after such episodic events. Fundamental shifts in ecosystem structure and function, such as shifts in landscape modulation and resource patch creation and development have, for the most part, been widely assumed and quantitatively ignored. Here we present a quantitative description of post-fire modulation and resource patch development in a dune mallee ecosystem. Although we focus on the physical components, there is much further scope for quantifying entire resource patch development, such as shifts in soil nutrient concentration.

Understanding the functional response of ecosystems to episodic events such as fire and the successional processes affecting flora and fauna can allow us to improve our predictions about how vegetation will likely change with projected changes in climate (Morton et al., 2011). Here we have demonstrated the complexities involved in post-fire litter accumulation. More specifically, we have shed light on post-fire trends in litter accumulation, a fundamental component of patch development. Patch creation and development are the basis of ecosystem function. By understanding how landscape modulators and their surrounding environment influence the development of patches, we are in a better position to predict how changes in these drivers are likely to affect ecosystem processes.

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