

Does fire affect the ground-dwelling arthropod community through changes to fine-scale resource patches?

Alan B. C. Kwok^{A,C} and David J. Eldridge^{A,B}

^AEvolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

^BOffice of Environment and Heritage, c/o Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia.

^CCorresponding author: Email: a.kwok@unsw.edu.au

Abstract. In semiarid ecosystems, perennial trees create resource patches beneath their canopies by providing shade and accumulating litter. These patches are often distinctly different from inter-tree areas, which support scattered hummock grasses. Although patchiness is regarded as an important driver of faunal diversity, it is not known how it is affected by disturbances such as fire. In this study, we tested how resource patches and fire affect the ground-dwelling arthropod community. We sampled ground-dwelling arthropods under the canopy of mallee (*Eucalyptus* trees), and in adjacent open areas in: (1) an area burnt over 30 years ago ('long unburnt'), and (2) an area burnt 4 years ago (recently burnt). Five taxa (cockroaches, isopods, spiders, jumping spiders and wasps) were more abundant under the canopy than in the open across both burn treatments, whereas ants showed the opposite pattern. Irrespective of patch type, silverfish, wasps and isopods were more abundant in the long-unburnt stand than the recently burnt stand. Ants showed the opposite pattern. Both long unburnt and recently burnt stands supported a similar abundance of beetles, cockroaches and spiders. Our results demonstrate that many arthropod taxa are affected by the resources provided by trees (litter, shade), even in areas recently burnt by fire. This is likely to change over time and in relation to further disturbance.

Additional keywords: fertile island, fire, landscape modulator, mallee, patch.

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Introduction

In all terrestrial ecosystems, perennial vegetation affects the distribution of biophysical and biotic ecosystem components. In resource-limited ecosystems (e.g. arid and semiarid systems), the patch beneath and around perennial vegetation is characterised by different physical and soil properties (water movement, Kropfl *et al.* 2002; Eldridge and Freudenberger 2005; nutrients, Smith *et al.* 2012), compared with areas away from plants. The vegetation directly provides resources (e.g. food) and habitat for a range of animals, supporting unique biotic communities in the landscape (Dean *et al.* 1999; Oliver *et al.* 2006; Agra and Ne'eman 2009; Bennett *et al.* 2009). Organisms vary in the way that they exploit the differences in resources across this patch–interpatch boundary and can be classified as patch-dependent, patch-independent or neutral, depending on this usage.

Ecological processes that affect the development of resource patches can have significant consequences for both patch-dependent and patch-independent species. Fire directly affects patch formation and development, often being catastrophic and destroying the patch and its associated resources such as shade, litter and fruit (Shachak *et al.* 2008; Travers and Eldridge 2012).

By directly affecting plants, fire also therefore controls future patch development. The loss of resource patches, and the habitat they may provide, may result in declines or complete extirpation of patch-dependent species, but an increase in patch-independent species. How faunal communities are structured in relation to fine-scale resource patches has been increasingly well documented, particularly in the last decade (Mazia *et al.* 2006; Barton *et al.* 2009; Nakamura *et al.* 2009; Barton *et al.* 2010). However, the influence of ecological disturbance on faunal communities within and between resource patches has been relatively poorly studied, despite seemingly strong theoretical and logical links (though see Agra and Ne'eman 2009; Bennett *et al.* 2009).

Leaf litter is a ubiquitous component of all terrestrial ecosystems, forming an important part of the aboveground resource patch in most ecosystems. Litter is a critical resource for a range of fauna in terrestrial ecosystems, being used as a food substrate by detritivores (e.g. isopods, beetles, mites) and as habitat by a range of taxa such as arthropods (Silveira *et al.* 2010), lizards (Driscoll *et al.* 2012) and birds (Benshemesh 1989). The quantity, quality and type of litter can affect individual species (Bultman and Uetz 1984) and faunal

communities (Donoso *et al.* 2010). Patches of leaf litter can also provide refugia for invertebrates (Loeser *et al.* 2006). There have been, however, few studies showing how multiple taxa are affected by the distribution of leaf litter at relatively fine spatial scales (e.g. within a single vegetation community type).

In this study, we investigate whether mallee (*Eucalyptus* spp.) trees create habitat islands for ground-dwelling arthropods in south-eastern Australia, and whether this is affected by fire. In mallee communities, the ground surface beneath mallee trees is characterised by a dense layer of leaf litter, the development of which is directly controlled by wildfires (Haslem *et al.* 2011; Travers and Eldridge 2012). To investigate the importance of this subcanopy patch, we sampled the ground-active arthropod community in the leaf litter beneath the tree canopy and in open areas away from the tree. To examine the influence of fire, we conducted this sampling at two contrasting stages of community development (Haslem *et al.* 2011; Travers and Eldridge 2012): (1) at patch 'maturity' (30 years post fire, hereafter 'long-unburnt'), and (2) early in patch development, 4 years post fire (hereafter 'recently burnt').

We made three predictions regarding how invertebrate taxa would be distributed in relation to resource patches and fire history. First, in the long-unburnt community, canopy patches will support a community of ground-active arthropods different to that found in open, unmodulated patches. This will be driven by higher relative abundances of taxa that prefer litter and shade (i.e. isopods, wasps, beetles, silverfish and spiders; Uetz 1979; Nakamura *et al.* 2009). Second, owing to destruction of the tree and subcanopy patch due to fire several years earlier, we predicted that there would be no differences in arthropod community composition between the canopy and open patches in the recently burnt communities, owing to minimal physical differences between the two patch types. Third, there will be differences in arthropod assemblage composition between recently burnt and long-unburnt communities, with a lower abundance of modulator-associated taxa and a greater abundance of taxa associated with open patches in the recently burnt community.

Methods

Study area

This study was conducted in January 2011 at the Australian Wildlife Conservancy's Scotia Sanctuary, which is located 150 km south of Broken Hill, NSW, Australia (33°43'S, 143°02'E). The climate is characterised by low and variable rainfall (mean annual rainfall: 250 mm), high evapotranspiration (~1500 mm year⁻¹), hot summers (daily mean temperature: 30°C, daily maximum: 47.8°C, daily minimum: >15°C) and cool winters (daily mean: ≤17°C, daily maximum: 32.2°C, daily minimum: ≤6°C) (Australian Wildlife Conservancy 2011).

Vegetation community

The study was conducted in dune-mallee woodland. Dune-mallee communities within the study area are located on long, low (relief to 7 m) east-trending sandy dunes dominated by an overstorey of mallee trees (*Eucalyptus dumosa* A. Cunn. ex J. Oxley and *E. socialis* F. Muell. ex Miq.) scattered between 5 and 50 m apart. Within inter-tree areas, scattered perennial

hummock grasses (*Triodia scariosa* N.T. Burb.) dominate the ground to low strata. The projected foliage cover of mallee trees and leaf litter in dune-mallee communities varies depending on when the community was last burnt. Canopy cover generally increases rapidly to between 20 and 30% until ~30 years post fire, after which time it stabilises (Haslem *et al.* 2011). Similarly, leaf litter and woody debris cover stabilises at approximately 30% ~25 years after fire. At our study site, the soils are mainly calcareous, brownish and siliceous sands.

We conducted this study in two areas with different fire histories. The recently burnt community was located in an area of mallee that was burnt by wildfire approximately 4 years before sampling. The long-unburnt community was located in an area of mallee that had not been burnt by fire in ~30 years. These two areas were separated by a distance of 10 km, although they are both part of a large, contiguous patch of mallee vegetation. In both communities, shrub cover to 2 m is sparse, with widely spaced individuals of predominantly *Senna artemisioides* subsp. *filifolia* Randell and *petiolaris* Randell, and *Acacia burkittii* F. Muell. ex Benth.

The size and extent of the resource patch differed between the long-unburnt and the recently burnt community. In our study area, a typical mallee canopy is seven times larger 30 years post fire compared with 4 years post fire (~145 v. 23 m², Travers and Eldridge 2012; Fig. 1). Furthermore, the litter bed is deeper in the long-unburnt community (~55 mm at 30 years cf. 15 mm at 4 years), with a greater mass (1.4 ± 0.1 kg m⁻² at 30 years cf. 0.9 ± 0.1 kg m⁻² at 4 years). The litter bed also extends further from the base of the tree (2.6 m at 30 years cf. 0.7 m at 4 years; Travers and Eldridge 2012).

Sampling design

The study was conducted at 16 sites within mallee-dominated dunes: eight long-unburnt, and eight recently burnt communities. All sites were separated by at least 500 m. At each site, two subsites ~250 m² were established ~100 m apart. Within each subsite, arthropods were sampled from within two naturally occurring patch types: canopy and open (Fig. 1). Canopy patches were located in the area of litter and woody debris on the ground surface, around the base but within the drip-line of mallee trees. Open patches were located in inter-tree areas dominated by *T. scariosa*, at least 10 m away from any tree canopy. Although open areas are not strictly patches in the typical sense of an area concentrating resources (as in Ludwig *et al.* 2004), we refer to these spots of the landscape as patches for brevity. Open patches are naturally devoid of litter and woody debris. We consider canopy patches to be 'modulated' as they are created and maintained by the landscape modulator (mallee trees) as in Shachak *et al.* (2008). Open patches, in contrast, are relatively 'unmodulated'. We acknowledge that *T. scariosa* modulates its surroundings, though this is at a much finer spatial scale compared with mallee trees. In total, we sampled 64 patches (2 fire histories × 8 sites × 2 subsites × 2 patch types).

We acknowledge that this design uses space-for-time substitution to investigate whether modulation was affected by fire as we were only able to sample one recently burnt and one long-unburnt area, potentially meaning that fire history is pseudoreplicated (Hurlbert 1984). Consequently, it is possible that any differences we observed in the arthropod community between the

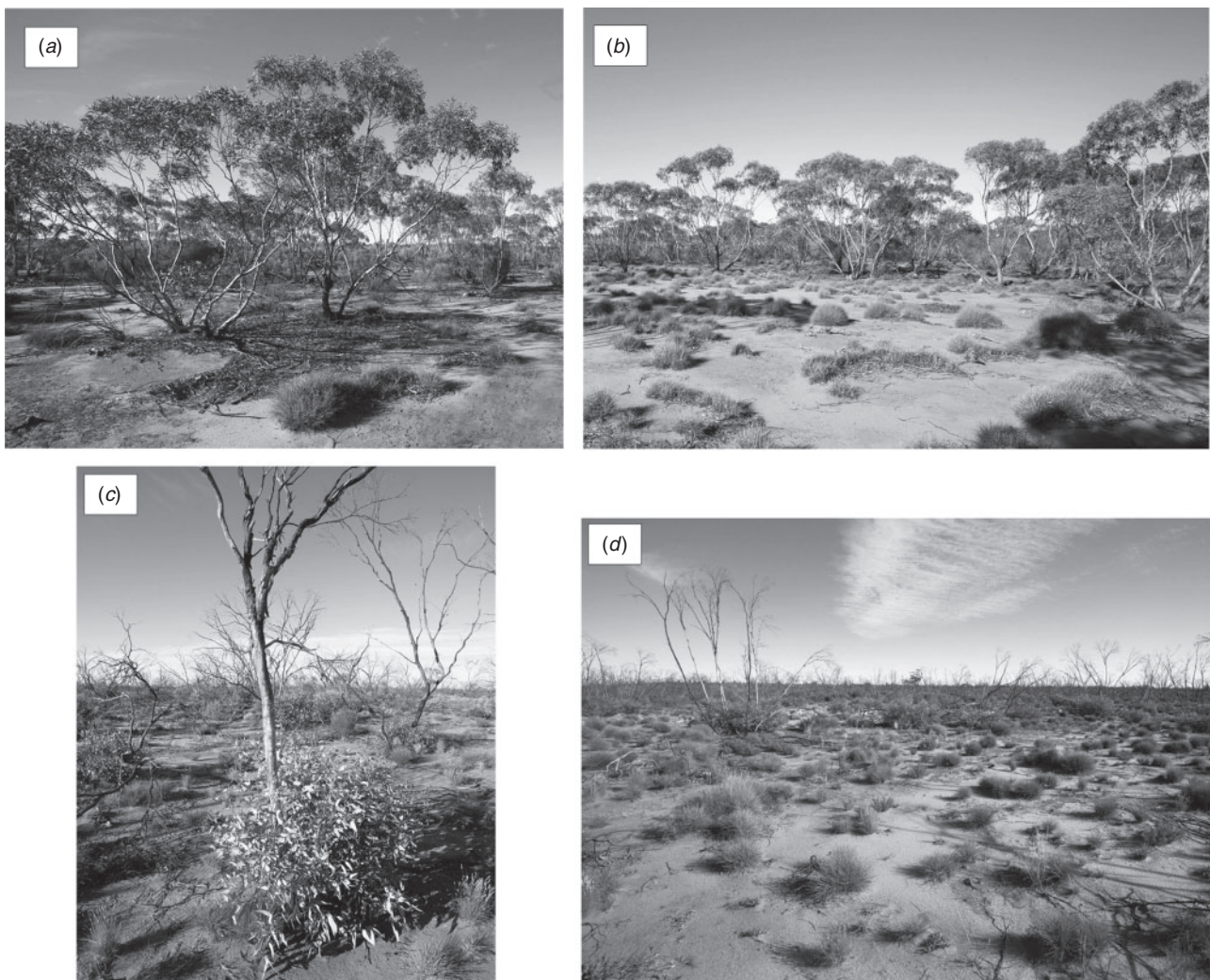


Fig. 1. Photographs of a typical mallee community, showing (a) long-unburnt resource patch under canopy; (b) long-unburnt open patch; (c) recently burnt patch under canopy; and (d) recently burnt open patch.

two communities were due to intrinsic differences between the areas that existed before the fire, rather than the fire itself. As fire destroys fine-scale patchiness (Haslem *et al.* 2011) in many communities including mallee (Travers and Eldridge 2012), as well as the fact that these patterns are likely generated by fine-scale variation in ecological conditions, we believe that any observed differences are the result of fire. Furthermore, the recently burnt and long-unburnt communities were only 10 km apart, and were part of a large, contiguous area of mallee vegetation, likely supporting similar arthropod communities and subject to the same patch creation, destruction and colonisation processes irrespective of fire. However, we acknowledge the limitations of our sampling design, and this should be taken into consideration when interpreting our results and explanations.

Arthropod sampling

We sampled ground arthropods in each plot using pitfall traps: plastic cups (70-mm diameter by 70 mm deep) filled with a small amount of propylene glycol and buried under the litter and

woody debris layer flush with the ground surface. Five cups were placed in each patch. In both the recently burnt and long-unburnt communities, traps were placed within the leaf litter layer and spaced evenly apart, always within the drip-line of the canopy. Traps were thus constrained by the visible spatial extent of the litter and woody debris patch. In open patches, traps were spaced in a ring, ~1.5 m apart from each other. Traps were left open for 7 consecutive nights. We acknowledge that pitfall sampling favours mobile and active fauna but we used this method to ensure standardised methods were used across all treatments.

We also acknowledge that the methods used do encompass some potential variability in sampling intensity between patches. Thus, although the total area of the canopy patch sampled is the same in both communities, the proportion of the patch sampled is actually greater in the recently burnt stand. We acknowledge this is a limitation of the methods though this was somewhat unavoidable owing to the decision to keep the total area sampled consistent.

Arthropod samples were identified to order, but in the case of spiders, jumping spiders (Salticidae) were treated as a separate group from other spiders owing to their different mode of locomotion. Additionally, all spiders (including Salticidae) were sorted to morphospecies for the purposes of further analysis of species richness and individual species responses. We consider only macrofauna that we consider reasonably representatively sampled by pitfall traps. Thus, certain taxa (e.g. Collembola, Hemiptera), though sampled frequently, were not included in analyses.

Statistical analyses

In the following statistical analyses, the abundance of organisms in each faunal taxa was calculated as the mean of the two replicates for each treatment configuration owing to the close physical proximity of the replicates to each other. We used generalised linear models (GLM) to test for differences in the total number of ants, beetles, isopods, spiders, jumping spiders, silverfish, wasps, or the number of spider morphospecies between patch types (canopy, open), fire histories (recently burnt and long-unburnt), and their interaction. As sites were essentially part of one contiguous fire history (i.e. recently burnt or long-unburnt), the term site was omitted from univariate analyses. This allowed more powerful testing of main effects. Each taxon was analysed in a separate model using a negative binomial distribution. The choice of distribution was based on visual analysis of the residual graphs (following Zuur *et al.* 2009). All GLM analyses were conducted in the program *R* (R Development Core Team 2011) using the *MASS* package (Venables and Ripley 2002).

We used a two-way permutational multivariate analysis of variance (PERMANOVA, Anderson and Gorley 2008) to test for differences in the arthropod community composition between the patch types, fire histories, and the interaction of these factors. However, unlike the univariate data, the multivariate analyses included tests for site effects nested within fire history. However, this term was always statistically non-significant ($P > 0.05$) and was subsequently pooled for analyses, where appropriate, and was not considered further. The arthropod community included all broad arthropod orders (described above). Significant main effects were further tested using pairwise *t*-tests. We used canonical analysis of principal coordinates (CAP) to display patterns of community composition within each treatment. To examine the magnitude of the differences in community composition among patch types and fire history, we compared dissimilarity values based on similarity of percentages (SIMPER). These values were based on a Bray–Curtis similarity matrix, with increasing dissimilarity values representing increasing dissimilarity among two treatments. All abundance data were square-root-transformed before all multivariate analyses to account for non-normal distributions. All multivariate analyses were conducted within the *PRIMER* (Clarke and Gorley 2006) *PERMANOVA+* (Anderson and Gorley 2008) statistical package.

Results

A total of 56 934 invertebrates were sampled in this study. Ants were the dominant group (88% of the total number of

invertebrates), followed by Collembola (5%), spiders (including Salticidae, 2%) and beetles (1%). We do not consider Collembola further. All other groups each accounted for <1% of the total number of invertebrates sampled.

Effect of patch type on arthropod abundance

Ants were the only taxa to be consistently more abundant in the open patch than the canopy patch, and this was consistent for both recently burnt and long-unburnt communities (Patch (P): $P < 0.001$; P × Fire History (FH) interaction: $P > 0.05$; Table 1; Fig. 2a). Beetles and silverfish were equally abundant in the canopy and open patches in both recently burnt and long-unburnt communities (P: $P > 0.05$; P × FH interaction: $P > 0.05$; Table 1; Fig. 2b, c). Five taxa were more abundant in the canopy patch than the open patch, in both recently burnt (B) and long-unburnt (UB) communities: cockroaches, isopods, spiders, jumping spiders and wasps (P: $P < 0.05$; P × FH interaction: $P > 0.05$; Table 1, Fig. 2d–h).

Effect of fire on arthropod abundance

Three taxa were more abundant in patches in the long-unburnt community than the recently burnt community: silverfish (UB: 3.13 ± 0.53 cf. B: 0.47 ± 0.12 ; $P < 0.001$), isopods (UB: 0.81 ± 0.37 cf. B: 0.03 ± 0.03 ; $P < 0.001$) and wasps (UB: 4.22 ± 1.03 cf. B: 2.00 ± 0.40 ; $P < 0.001$) (Table 1, Fig. 2c, e, h). In each case, this was independent of patch type (P × FH interaction: $P > 0.05$, Table 1, Fig. 2c, e, h).

Recently burnt and long-unburnt communities supported a similar abundance of beetles (B: 4.16 ± 0.89 cf. UB: 3.53 ± 0.55), cockroaches (B: 0.56 ± 0.12 cf. UB: 0.38 ± 0.13), spiders (B: 10.06 ± 1.14 cf. UB: 11.59 ± 0.83) and jumping spiders (B: 1.28 ± 0.24 cf. UB: 1.59 ± 0.41), irrespective of patch type (P: $P > 0.05$; P × FH interaction: $P > 0.05$) (Table 1, Fig. 2b, d, f, g). Ants were the only taxa more abundant in the recently burnt community than the long-unburnt community (B: 670 ± 189 cf. UB: 245.30 ± 33.33 ; B: $P < 0.001$).

Effect of patch type and fire on arthropod community composition

We found significant differences in arthropod community composition between canopy and open patches (pseudo- $F = 16.72$, $P < 0.001$, Fig. 3). This was consistent in the recently burnt and long-unburnt communities (P × FH interaction: pseudo- $F = 1.37$, $P = 0.23$, Fig. 3), although the difference was stronger in the long-unburnt treatment (Canopy × Open pairwise $t = 3.24$, $P < 0.001$) compared with the recently burnt treatment (Canopy × Open pairwise $t = 2.38$, $P = 0.01$). Overall, PERMANOVA analyses also indicated differences in the arthropod community composition between the recently burnt and the long-unburnt community (pseudo- $F = 8.99$, $P < 0.001$, Fig. 3). Furthermore, patch type explained 31% of the total variation explained by the model, whereas fire history explained 25% (total variation explained by all factors = 43%).

SIMPER analyses indicated that differences among patch types in arthropod community composition were mainly due to small changes in the abundance of each taxa. The dissimilarity among the four patch types (recently burnt canopy, recently burnt open, long-unburnt canopy, long-unburnt open) ranged in

Table 1. Summary statistics for generalised linear model analyses on abundance of eight arthropod taxa and spider species richness in canopy and open patches in recently burnt and long-unburnt communities

For all models, patch d.f. = 1; fire history d.f. = 1; patch × fire history d.f. = 1; residual d.f. = 28

	Deviance	Residual deviance	<i>P</i>
<i>Ants</i>			
Null		79.967	
Patch	24.981	54.985	<0.001
Fire history	20.788	34.197	<0.001
Patch × Fire history	0.634	33.562	0.426
<i>Beetles</i>			
Null		37.738	
Patch	3.254	34.484	0.071
Fire history	0.397	34.087	0.528
Patch × Fire history	1.327	32.759	0.249
<i>Cockroaches</i>			
Null		24.804	
Patch	6.916	17.888	0.019
Fire history	2.226	15.661	0.465
Patch × Fire history	0.233	15.428	0.628
<i>Isopods</i>			
Null		34.585	
Patch	7.096	27.489	<0.001
Fire history	9.553	17.936	<0.001
Patch × Fire history	0.269	17.667	0.604
<i>Silverfish</i>			
Null		65.392	
Patch	0.055	65.337	0.815
Fire history	31.943	33.394	<0.001
Patch × Fire history	3.045	30.349	0.081
<i>Spiders</i>			
Null		45.905	
Patch	17.823	28.081	<0.001
Fire history	1.774	26.307	0.183
Patch × Fire history	0.337	25.970	0.562
<i>Jumping spiders</i>			
Null		33.142	
Patch	7.587	25.555	<0.001
Fire history	0.668	24.887	0.413
Patch × Fire history	0.069	24.819	0.793
<i>Number of spider species</i>			
Null		40.738	
Patch	13.247	27.491	0.002
Fire history	3.252	24.240	0.431
Patch × Fire history	0.185	24.055	0.667
<i>Wasps</i>			
Null		55.276	
Patch	17.748	37.527	<0.001
Fire history	7.225	30.302	<0.001
Patch × Fire history	0.367	29.934	0.544

value from 20.13 to 37.31. The greatest dissimilarity in community composition was between the recently burnt open and long-unburnt canopy patches, which represent the least structurally complex to the most structurally complex patches. Sixty-one per

cent of the difference between these two patch types was driven by three times as many ants in the recently burnt open patch, whereas 8% of the difference was due to four times as many wasps in the long-unburnt canopy patch. The most similar patch types were the recently burnt canopy and the long-unburnt open. SIMPER analyses indicate that ants accounted for $54.5 \pm 3.8\%$ of the difference between any two patch types; however, this is likely because ants were the most numerically dominant taxa. CAP confirmed that most taxa showed differences in abundance among patch types and in relation to fire (Fig. 3). CAP axis 1 explained 66% of the variation between samples, and represented the difference between long-unburnt canopy patches and all other patch types. CAP axis 2 explained a further 11% of the variation. Cross-validation of CAP results indicated that based on the arthropod community composition, long-unburnt canopy samples could be classified correctly 87.5% of the time. This classification was slightly lower for the other patch types (long-unburnt open = 75%, recently burnt canopy = 62.5%, recently burnt open = 50%).

Spider morphospecies assemblages

In addition to spider abundance, the number of spider species (including Salticidae) was also greater in canopy than in open patches, and this was consistent for the recently burnt and long-unburnt community ($P: P < 0.05$; $FH: P > 0.05$; $P \times FH$ interaction: $P > 0.05$; Table 1, Fig. 4). Overall, the recently burnt and long-unburnt communities had a similar number of spider species (B: 7.44 ± 0.77 cf. UB: 9.13 ± 0.67 ; $P > 0.05$; Table 1).

Most spider species were found in low numbers at only one or two sites, and this prevented formal analyses of species composition. Based on analyses of the most abundant species, however, there was evidence of preference for patch types, and effects of fire. For example, the most abundant taxon was a species of Zodariidae, which was found predominantly in the long-unburnt community (B: $n = 6$ cf. UB: $n = 34$). Furthermore, within the long-unburnt community, this species was found only in the open patch ($n = 34$). A second species of Zodariidae was approximately three times more abundant in the long-unburnt community ($n = 24$ cf. $n = 7$), and in both long-unburnt and recently burnt communities was only found in the canopy patch. A species of Lycosidae was the third most common species, and this species appeared equally abundant in recently burnt and long-unburnt communities (B: $n = 10$ cf. UB: $n = 11$), but in each community, the majority of individuals were found in the canopy patch ($n = 7$ and $n = 9$ for the recently burnt and long-unburnt community respectively).

Discussion

In this study, we found that a dominant perennial eucalypt tree affects the structure and composition of the ground-dwelling arthropod community, and that fire plays a key role in this process. This study has three main outcomes. First, at fine scales, mallee trees create distinct patches that support a different ground-dwelling arthropod community to that in open inter-tree patches, effectively becoming habitat islands for some taxa. Second, the canopy patch was important for several taxa in both recently burnt and long-unburnt communities, despite large

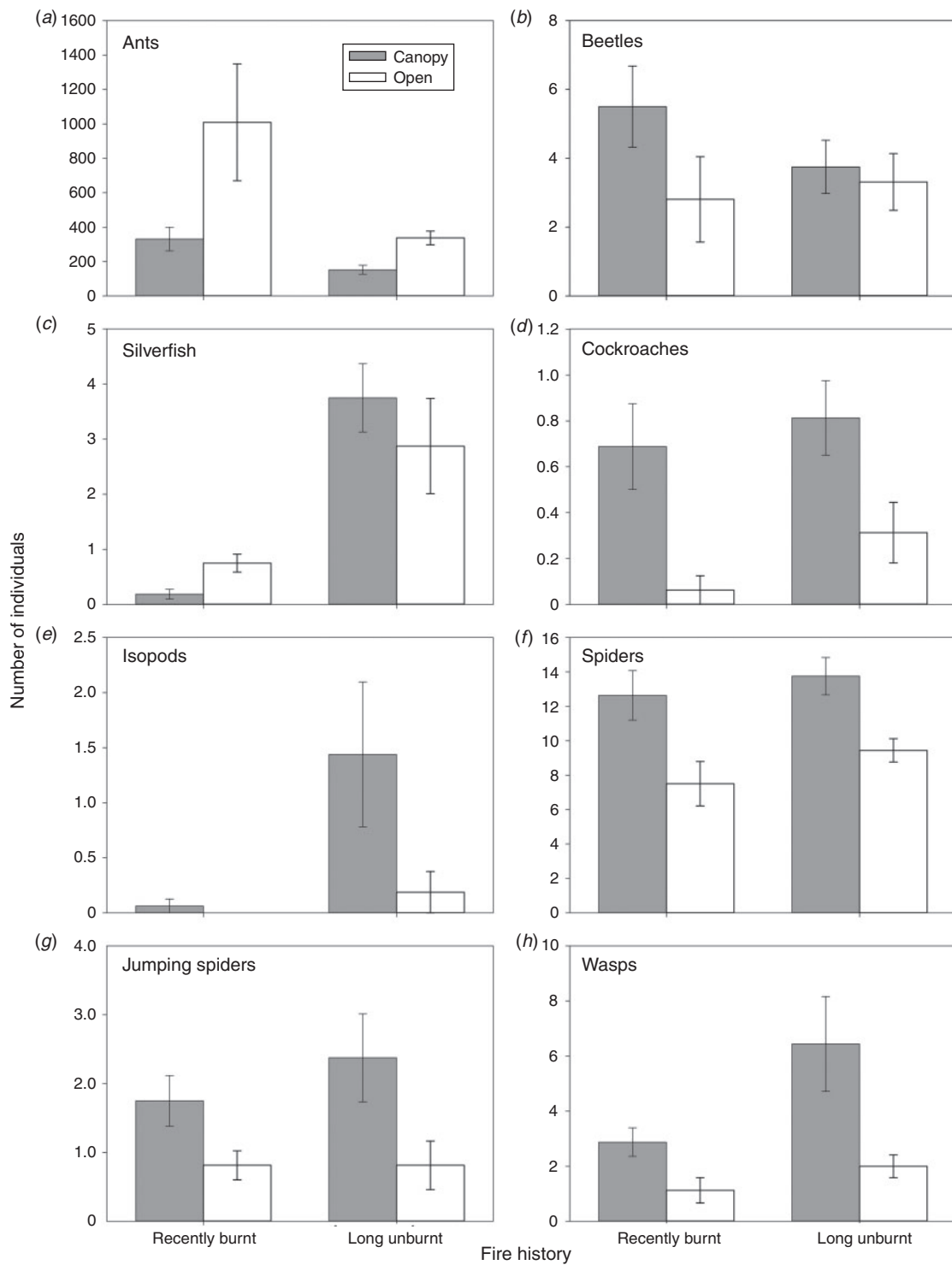


Fig. 2. Mean \pm s.e. abundance of (a) ants, (b) beetles, (c) silverfish, (d) cockroaches, (e) isopods, (f) spiders, (g) jumping spiders, and (h) wasps across two patch types (canopy and open) and in two communities that differ in fire history (recently burnt and long-unburnt). Note different scale of y axis for each graph.

differences in the physical size of the patch. Third, recently burnt and long-unburnt communities supported different arthropod communities, with some taxa virtually absent from the recently burnt community. Our study indicates that in a

mallee woodland, the structure of arthropod communities is influenced by the fine-scale distribution of resource patches, and this is intrinsically tied to a broad-scale ecological disturbance (fire).

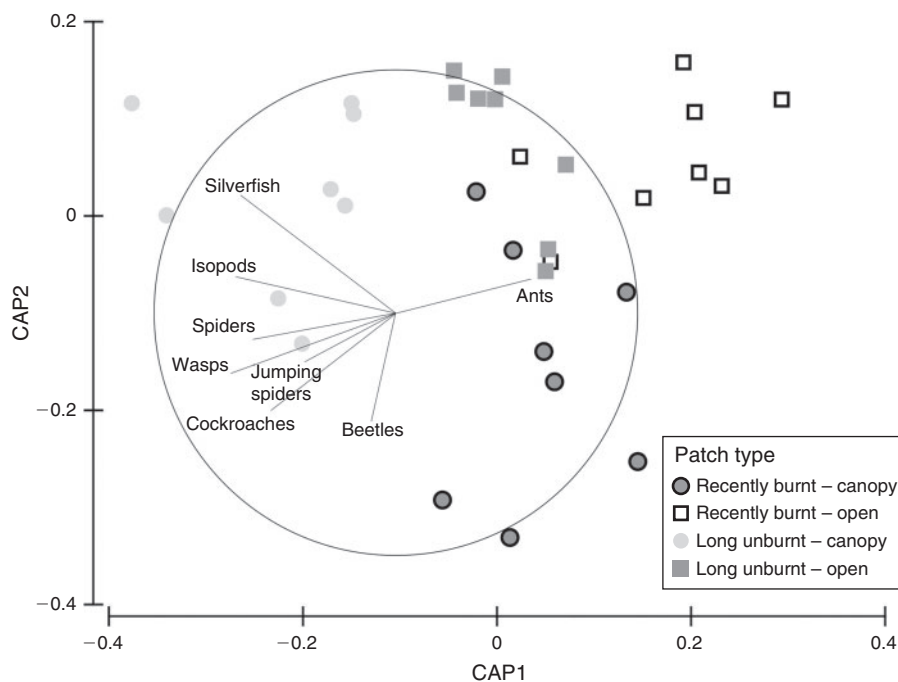


Fig. 3. Canonical analysis of principal coordinates (CAP) of arthropod community composition across two patches (canopy, open) and in two communities that differ in fire history (long-unburnt and recently burnt). Axis CAP1 explained 66% of the variation between samples. Axis CAP2 explained a further 11% of this variation. Vectors indicate Pearson moment correlation for each arthropod taxon, pointing to increases in the abundance of that taxon. The longer the vector, the stronger the correlation.

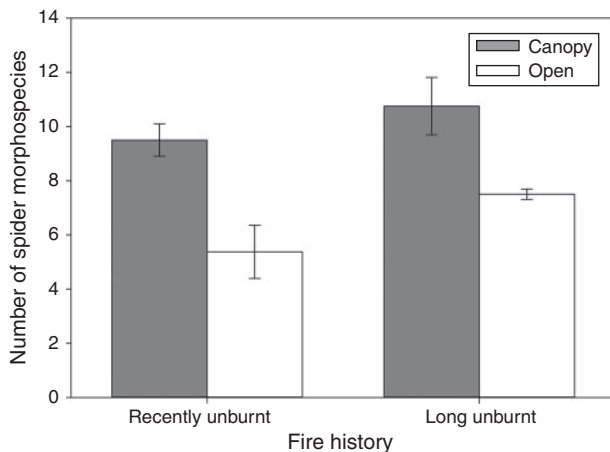


Fig. 4. Mean \pm s.e. number of spider morphospecies across two patch types (canopy and open) and in two communities that differ in fire history (recently burnt and long-unburnt).

Mallee trees structure the distribution of ground-dwelling arthropods

The resource patch beneath mallee trees affected the composition of the arthropod community in both the recently burnt and long-unburnt woodland. Consistent with our first prediction, more arthropods and a greater variety of higher-level arthropod taxa were found beneath the tree canopy than in open areas away from the tree. Indeed, isopods were largely restricted to

well-developed litter patches in the long-unburnt community. We had also predicted that this would only be the case in the long-unburnt community. However, contrary to this, we found that the canopy patch also supported more arthropods in the recently burnt area, including spiders, cockroaches and wasps.

Our results are consistent with studies in arid ecosystems demonstrating the importance of patches around perennial vegetation to biotic communities. For example, these patches support different faunal (Noble *et al.* 1996; Andrew *et al.* 2000; Oliver *et al.* 2006), microbial (Smith *et al.* 1994), fungal (Bennett *et al.* 2009) and floral (e.g. Agra and Ne'eman 2009) communities to the relatively infertile areas between trees (e.g. Noble *et al.* 1996; Andrew *et al.* 2000; Oliver *et al.* 2006). Although our analyses were carried out at a coarse level of taxonomic resolution, it is probable that these patterns manifest into species-specific differences between resource patches (e.g. Liu *et al.* 2012), given well-established relationships between abundance and species richness.

Many arthropod taxa are dependent specifically on litter as a resource (Santos *et al.* 1978; Bastow 2011). Their distribution, therefore, is tied to where litter accumulates. Across many ecosystems, litter under large trees has been shown to be moister and cooler than open, unvegetated patches (Weltzin and Coughenour 1990; Shumway 2000), thus creating a less extreme, less variable microclimate. These conditions have direct effects on the distribution of many arthropods, many of which will only utilise the fine-scale patch (e.g. Pearson and Lederhouse 1987; Nakamura *et al.* 2009). In our study, we found the distribution and abundance of several arthropod taxa are

affected in mallee communities. We strongly suspect this is the case in the mallee as litter is almost exclusively found underneath the canopy of perennial trees and shrubs (Smith *et al.* 2012). Furthermore, although we did not quantify litter bed characteristics of our burnt and unburnt communities, detailed research in our study area indicates litter bed development occurs in a fairly predictable manner after large wildfires (Travers and Eldridge 2012). Areas not burnt by wildfire in 30 years have approximately five times more leaf litter, and a three times wider bed than an area burnt only 4 years ago. We suspect that these differences in litter, controlled by fire, are driving observed differences in the arthropod community. It is also possible that biogeographic processes, such as the distance between litter bed patches, or even restricted patches of litter in open areas, may affect fauna communities within the litter itself.

Arthropod community composition differs between burnt and unburnt areas

In our study, only ants were more abundant in the recently burnt community, whereas wasps, isopods and silverfish showed the opposite pattern. The abundance of spiders and beetles did not differ in relation to burning. We had predicted that fire would reduce the abundance of modulator-dependent taxa. Although some taxa appeared to prefer subcanopy patches within the recently burnt community, this did not manifest itself as overall differences between recently burnt and long-unburnt sites (except for isopods and silverfish; see below). Most arthropods are generally regarded as fire-resilient (e.g. Andersen and Muller 2000; Andersen *et al.* 2005; Vasconcelos *et al.* 2008), with declines in abundance immediately following fire often quickly reversed (Abbott *et al.* 2003). These patterns, however, can be quite variable. For example, in spinifex (*Triodia* spp.) grasslands, spider abundance has been reported as being both stable (Langlands *et al.* 2012) and unstable (Langlands *et al.* 2006) in the first 10 years following fire. Furthermore, Harris *et al.* (2003) found few effects of fire on spider communities in eucalypt communities in south-eastern Australia. Ant abundance also shows variable responses to fire (e.g. Andersen and Yen 1985; Andersen and Muller 2000).

Isopods and silverfish were the taxa most affected by fire, effectively being restricted to the island of leaf litter below mallee trees. Higher soil temperatures and reduced food resources (litter) may explain why these taxa had a reduced abundance in burnt areas (Paris 1965; Peters and Campbell 1991; Shachak *et al.* 2008). Our results are consistent with those of other researchers (Abbott 1984; Andersen and Muller 2000; Pitzalis *et al.* 2005), indicating that these taxa may be less resilient to fire than other arthropods and therefore may be dependent on older, more mature areas of vegetation. This may be particularly the case in mallee ecosystems given the slow development of the mallee resource patch following fire (Travers and Eldridge 2012).

We had mixed support for our prediction that there would be no differences in arthropod community composition between the canopy and open patches in the recently burnt community. When the entire arthropod community was considered, there were clear differences between patch types in both communities, despite the recent loss of the resource patch in the recently

burnt community. There are several potential explanations for this. First, the development of the resource patch under trees 4 years after burning may be substantial enough to sustain higher arthropod populations than inter-tree areas. Second, the soil may be an important habitat and refuge for arthropods. As the soil is not as strongly affected by fire as the aboveground ecosystem, predominantly soil-resident arthropods may be relatively unaffected by fire events. Lastly, arthropods may be resilient to fire, as described above. The fact that some taxa appear dependent on the resource patch (cockroaches, isopods) suggests that fire and associated changes to patch development may affect some taxa more than others.

It is well known that pitfall trapping overestimates abundance of ground-active fauna, while underestimating that of less-mobile, more sedentary animals (e.g. Brennan *et al.* 2005; Driscoll 2010), and this should be considered when interpreting the results of the present study. In the context of the present study, additional sampling methods (e.g. leaf litter collection) would have yielded a more comprehensive result. However, our study was not intended to compare differences between the groups of animals (e.g. active *v.* sedentary). Rather, our aim was to compare how the same group differed between patch types and fire histories. In this respect, pitfall traps are appropriate and do clearly illustrate that the abundance of the target taxa differs between treatments.

Fire is a crucial component of biodiversity management worldwide, particularly in forest and woodland ecosystems (Driscoll *et al.* 2010). There is an abundance of research illustrating the effects of fire on individual species and biotic communities. However, there is relatively little information on the mechanisms behind how these changes happen (for example the formation of fine-scale resource patches). In ecosystems where resources are distributed in patches, such as mallee woodlands, fire is often a critical process that determines the development of these patches. It is therefore critical to conservation effort that there is knowledge of species and broader taxon responses to fire and an understanding of how the spatial and temporal arrangement of fires affect the biota (Driscoll *et al.* 2010) at both fine and broad spatial scales.

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