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Detecting invertebrate responses to fire depends on sampling method and taxonomic resolution.

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Abstract

New knowledge about the responses of species to fire is needed to plan for biodiversity conservation in the face of changing fire regimes. However, the knowledge that is acquired may be influenced by the sampling method and the taxonomic resolution of a study. To investigate these potential sampling biases, we examined invertebrate responses to time since fire in mallee woodlands of southern Australia. Using a large-scale replicated study system we sampled over 60,000 invertebrates with large pitfall traps, wet pitfall traps, and sweep nets, and undertook analyses at morphospecies and order level. Large pitfalls and sweep nets detected several strong fire effects whereas wet pitfall traps detected few effects. Invertebrate abundance in sweep nets was highest shortly after fire due to grasshopper outbreaks. Several additional morphospecies showed strong preferences for different stages in the post-fire succession. In contrast with morphospecies effects, analyses at order level either failed to detect fire effects or were driven by the most abundant species. For fire research to produce credible results with the potential to guide management, it must use a range of sampling techniques and undertake analyses at (morpho) species level. Homogeneous fire management, such as fire suppression in fragmented landscapes or widespread frequent burning for asset-protection, is likely to cause declines in fire-affected invertebrates.

Key words: fire management, time since fire, succession, trapping method, morphospecies

Introduction

Fire plays an integral role in shaping and maintaining many ecosystems around the world (Bond & Keeley 2005). However, land-clearing, extreme management practices such as complete fire suppression and climate change are altering the way that fire affects ecosystems (Williams *et al*. 2001; Whitlock *et al*. 2003; Brennan *et al*. 2009). There is currently debate about the best way to manage fire to balance built asset protection with conservation of native vegetation and wildlife (Morrison *et al*. 1996; Parr & Andersen 2006; Driscoll *et al*. 2010a). Fire suppression could threaten species reliant on recently burnt habitat (Wikars 2002; Woinarski *et al*. 2004) but burning too frequently can have a negative impact on species which rely on mature vegetation (Andersen *et al*. 2005; Moretti *et al*. 2006). Understanding the response of a wide range of species to fire is therefore a prerequisite for planning effective fire management (Driscoll *et al*. 2010a, b).

As a community recovers after fire the vegetation undergoes succession, changing in species composition and structure. This pattern of recovery means that the suitability of the habitat for animal species may also change over time (Fox 1982; Letnic *et al*. 2004). Such change is the basic premise of the habitat accommodation model of succession (Fox *et al*. 2003). The model predicts that a species abundance will be highest at its optimum successional stage of vegetation recovery. In partial support of this model, preferences for a particular stage of regeneration have been shown in a number of taxa including reptiles (Singh *et al*. 2002; Fenner & Bull 2007; Driscoll & Henderson 2008), mammals (Fox 1982; Letnic *et al*. 2004), birds (Smucker *et al*. 2005) and invertebrates (Moretti *et al*. 2004; Paquin 2008; Rodrigo *et al*. 2008; Driscoll *et al*. 2010c). These preferences mean that managing fire to maintain habitat at different successional stages (i.e. a fire mosaic) could enable the maintenance of biodiversity (Richards *et al*. 1999; Moretti *et al*. 2004). However, a better understanding of wildlife ecology in fire prone ecosystems is needed to define acceptable bounds for the spatial and temporal scales of fire mosaics (Bradstock et al. 2005; Parr & Andersen 2006; Clarke 2008). A first step towards understanding the potential importance of fire mosaics for conservation is to discover if species show a strong successional response and only occur at a particular time since fire (Driscoll & Henderson 2008). This will help determine the extent to which a fire mosaic may be important.

Invertebrates are the largest component of global biodiversity, play a major role in herbivory, nutrient cycling and maintaining soil structure (Lavelle *et al*. 1997) and are an important food source for many vertebrate species (Losey & Vaughan 2006). Incorporating information about invertebrates into fire management plans should therefore be a priority, but invertebrates are often ignored in fire ecology research (New *et al*. 2010). Most previous studies of invertebrate fire ecology have focused on coarse taxonomic groups or functional groups (Bailey & Whitham 2002; Moretti *et al*. 2006; Engle *et al*. 2008; Fattorini 2010; Radford & Andersen 2012). While functional groups provide a way to simplify responses to fire in an ecologically meaningful way (Langlands *et al.* 2011) understanding species level responses is essential in order to quantify extinction risk under changing fire regimes (Driscoll *et al.* 2010b). Many of the studies that do look at species level responses also only examine a small number of taxa (e.g. Formicidae, Andersen 1991; Coleoptera, Gandhi *et al*. 2001, Driscoll & Weir 2005; Araneae, Langlands *et al*. 2006) limiting the scope of inference. It is also typical for such studies to use only one sampling method, usually pit-fall traps of one size. Different methods sample biased subsets of the fauna, so results based on a single approach will not represent the response of invertebrates across the community (Abensperg-Traun & Steven 1995). Management recommendations should be based on knowledge of fire responses for many species within a community rather than on a narrow subset (Clarke 2008; Driscoll *et al*. 2010b; Pyrke & Samways 2012). Using a range of methods and morphospecies classifications is an efficient way to achieve this (Oliver & Beattie 1996; Derraik *et al*. 2002; Pyrke & Samways 2012).

To avoid the limitations of many previous invertebrate-fire studies we examined the fire response of a mallee woodland invertebrate community at the morphospecies level using multiple sampling methods. The aims of this study were to 1) determine which morphospecies had significant changes in abundance with time since fire, 2) determine the influence of sampling method and classification level on the ability to detect ecological effects of fire and 3) compare the time investment and outcome of different sampling methods. Addressing these issues is essential to manage fire in a way that conserves biodiversity.

Methods

Study sites

We sampled invertebrates at Hincks Wilderness Area (66,658 ha; 33° 46' 10" S, 136° 03' 24" E) and Pinkawillinie Conservation Park (130,148 ha; 32° 54' 30" S, 135° 53' 23" E) on the Eyre Peninsula, South Australia (Fig. 1) during summer 2010. Both reserves contain large areas of mallee vegetation (multi-stemmed *Eucalyptus* spp. up to 6m tall in our study region) surrounded by land cleared for agriculture. The landscape consists of parabolic and longitudinal siliceous sand dunes over solid limestone, calcrete bedrock (Twidale *et al*. 1985). The annual average rainfall is approximately 300 mm. Mallee typically experiences fire on a decadal (10-100 yr) time scale (Bradstock & Cohn 2002) but can remain unburnt for over 100 years (Clarke *et al.* 2010). Both of our study reserves have a documented history of planned and unplanned fires dating back to the 1950s.

Survey Design

We used a chronosequence survey design to examine the effect of time since fire on invertebrate abundance (Driscoll *et al.* 2010b). At each reserve, two 1 ha sites were sampled in each of three fire categories: burnt 4-5, 9-11, and over 40 years ago (Fig. 1). Replicate sites in each category were separated by approximately 1 km. To minimise edge effects, we placed all sites at least 200 m from the fire edge and/or the park boundary (Driscoll & Henderson 2008).

All sampling sites straddled sand dunes and incorporated dune ridges, slopes, and dune bases which, at some sites descended to the hard, clayish swale. All sites were selected for their sandy soil, presence of *Triodia irritans* (an important habitat for many animal species) and for their similar topography and vegetation (dominated by *Eucalyptus spp*. and *Melaleuca uncinata)*. The 4-5 yr sites were characterised by a low (< 1 m), sparse canopy with very little leaf litter and large areas of bare sand. The 9-11 yr sites had a 1-2 m canopy with moderate leaf litter and bare ground and the >40 yr sites had a high canopy (> 2 m), many shrubs, dense leaf litter and little bare ground (Smith *et al*. 2012). At each location we sampled two sites within each fire category meaning that conditions were similar for replicate sites within fire categories. This form of pseudoreplication is often unavoidable in fire ecology because of limited fire histories within landscapes (Whelan *et al*. 2002) but we accommodated this in our analysis using mixed-effects models (see *Analysis*). At each site we used three sampling methods to collect invertebrates: large pitfall traps, sweep netting and wet pitfall traps.

Large pitfall traps

The large pitfall traps were used concurrently for a related reptile study (Smith *et al.* 2012) and consisted of 20 L plastic buckets (28.5cm diameter) buried flush with the ground and placed midway along a 10 m plastic drift fence (black plastic, 30cm high). Traps were arranged in 5 x 5 grids with 25 m between each bucket and the direction of the fences alternating at right angles. Samples were collected over a six day period in summer, January 2010 (Hincks 7th-12th, Pinkawillinie 21st-26th). During this time daily minimum and maximum temperatures averaged 20°C and 38°C at Hincks and 17°C and 33°C at Pinkawillinie. A total of 300 large pitfall traps (100 in each treatment) were sampled during the survey. Invertebrates smaller than 3mm in length and ants were not collected from the large pitfall traps because of time constraints. This trapping method therefore had a collection filter in addition to the bucket size limiting the invertebrates sampled.

Sweep netting

At each site invertebrates were sampled along four 100 m transects (within the large pitfall trap grids) using butterfly nets approximately 40 cm in diameter and 1 m in length. To incorporate potential time of day effects associated with diel activity patterns in invertebrates we sampled each site twice, once before 10am or between 3pm and 7pm and once between 10am and 3pm. Each transect was sampled by two people walking approximately 15 m apart at a steady pace for 10 min. All vegetation including tree canopies, shrubs, understory and bare ground was swept with the nets. All invertebrates were collected from the nets at the end of each transect and preserved.

Wet pitfall traps

Wet pitfall traps consisted of plastic jars 10 cm deep and 4 cm in diameter containing approximately 60 mL of 9 % salt water and a drop of detergent to reduce surface tension. Twenty traps were set at each of the twelve sites giving a total of 240 traps with 80 in each treatment. Wet pitfalls were placed approximately five meters away from, and perpendicular to the fence of the large traps. The traps were open for seven days during January 2010 (Hincks 6th – 13th, Pinkawillinie 20th – 27th), corresponding closely with the large pitfall trap collection dates.

After collection, invertebrates from all three survey methods were stored in 70 % ethanol. Samples were identified using the entomology collections at CSIRO, Canberra and the South Australian Museum, Adelaide. Where accurate identification was not possible even after consultation with museum staff, individuals were assigned to a morphospecies.

Data Analysis

To determine whether the mean abundance of each morphospecies varied among fire categories we used Poisson generalised linear mixed models (GLMM) with log link functions. We fitted time since fire, location and their interactions as fixed effects. To account for our pseudoreplicated design we fitted fire (a factor delimited areas burnt in separate fire events) as a random effect. The two sites in each fire category within reserves were thus treated as subsamples rather than true replicates for statistical analysis (Bolker *et al.* 2008). To account for over-dispersion in residual variation we also fitted an observation level random effect that modelled extra-Poisson variation (Maindonald & Braun 2010). GLMMs were fitted using the glmer function in the lme4 package (Bates *et al*. 2011) for R (R Development Core Team, 2009). We obtained predicted values and standard errors using the predictSE.mer function in the AICcmodavg package (Mazerolle 2011).

We obtained *P*-values for multi-level terms (time since fire and its interaction with location) using Wald tests (Harrell 2001). *P*-values for location (a two-level term) were derived from z-scores (fixed effect/SE: Crawley 2002). Given the large number of statistical tests in our analysis we calculated Q-values using the R package qvalue (Storey 2002). Q-values estimate the number of false positive results obtained, thus controlling the false-discovery rate (Storey 2002). Q-values less than 0.05 were taken as significant meaning that 5% of our significant results could be false positives. Only morphospecies found at both locations were analysed to incorporate the replication in our study design and ensure that our focus was on time since fire and not local abundance variation. We analysed data from morphospecies with an equal or greater number of captures than sample sites (12) following Didham *et al.* (1998) (large pitfall traps = 34 morphospecies out of a total of 184; sweep netting = 42/249; wet pitfall traps = 63/144). To determine how taxonomic resolution influenced our results, the analyses were repeated at the order level for each sampling method using all morphospecies within each order. Centipedes in the order Scolopendromorpha could not be assigned confidently to morphospecies as they had desiccated. These were analysed at the order level only.

A Venn diagram was constructed to compare the number of morphospecies sampled with each method and to examine the degree of overlap among methods. A time investment and outcomes table was also compiled to compare the costs and benefits of each method.

Results

A total of 61150 invertebrates was captured during this study: 3343 in the large pitfall traps, 8034 by sweep netting and 49773 in the wet pitfall traps (mostly ants). We identified 461 morphospecies. There was no significant difference in the number of morphospecies detected among the three fire categories by any sampling method. There was no significant difference in total invertebrate abundance among the fire categories using the large pitfall traps (*P* = 0.398) or the wet pitfall traps (*P* = 0.079). The total abundance of invertebrates caught by sweep netting was significantly higher in the 4-5 yr sites than in the 9-11 yr or >40 yr sites (*P* = 0.014).

Large pitfall traps

Of 34 morphospecies analysed from the large pitfall traps the abundance of five was significantly affected by time since fire (Table 1). Lycosidae sp. 1 (Araneae) was most abundant in the 4-5 yr sites while Endacusta sp. 1 (Orthoptera) had lowest abundance in 4-5 yr sites (Fig. 2). Zoridae sp. 1 (Araneae) was more abundant in 9-11 yr sites and Lycosidae sp. 2 (Araneae) and *Platyzosteria* sp. 1 (Blattodea) were more abundant in >40 yr sites (Fig. 2).

A total of 15 invertebrate orders were detected in the large pitfall trap sample. Fourteen of these had no significant response to time since fire. Blattodea was significantly more abundant in long unburnt vegetation (*P* = 0.004, Q = 0.029). This result was not significant when *Platyzosteria* sp. 1 was excluded from the data set (*P* = 0.107, Q = 0.438) indicating the result was driven by the strong response in this species.

Sweep netting

Of the 42 species analysed from the sweep net sample, nine showed a significant response to time since fire (Table 1). *Warramunga* sp. 1 (Orthoptera) was the most commonly captured species and was significantly more abundant in the 4-5 yr sites (Fig. 3). One morphospecies was more abundant in the 9-11 yr sites (Psyllidae sp. 1), one was more abundant in 9-11 and >40 yrs (Lepidoptera sp. 2), and three morphospecies were more abundant in the >40 yr sites (Fig. 3). Two morphospecies were more abundant in the 4-5 yr and 9-11 yr sites than in the >40 yr sites (Fig. 3). Cicadellidae sp. 1 (Hemiptera) showed different peaks in abundance at different locations (Fig 3).

A total of 11 invertebrate orders were detected during the sweep net survey. Orthoptera had a significant response to time since fire with higher abundance in 4-5 yr sites

(P = 0.007, Q = 0.040). Diptera had a significant interaction between fire and location (P = 0.008, Q = 0.040), being more abundant in the >40 yr sites at Pinkawillinie but having no fire response Hincks. These results were not significant when the most abundant species was excluded from the data set (*Warramunga* sp. 1 (Orthoptera) and Culicidae sp. 1 (Diptera)) indicating that the order-level results were driven by the most abundant species.

Wet pitfall traps

Of the 63 morphospecies analysed from the wet pitfall traps, three significantly varied in abundance among the three fire categories (Table 1). Formicidae sp. 1 (Hymenoptera) and Zoridae sp. 1 (Araneae) were more abundant in the 9-11 yr sites and *Melophorus* sp. 1 (Hymenoptera) was more abundant in the 4-5 yr sites (Fig. 4). A total of 14 orders were detected in the wet pitfall trap survey and none varied significantly in abundance with time since fire. There were also no significant results when the most abundant species in each order was excluded from the analysis.

Comparison of sampling methods

We observed little overlap between the three survey methods in the morphospecies detected (Fig. 5). Of the three methods the wet pitfall traps required the least field effort and captured most invertebrates (Table 2). However, wet pitfall traps required the most time to sort the samples and detected the fewest fire responses (Table 2). Weighted by hours of effort, sweep netting was six times more efficient at detecting invertebrate responses to fire than wet pitfall traps (Table 2).

Discussion

Effect of fire on invertebrate abundance

In our study 23 morphospecies showed a significant response to time since fire. Of these, five species were captured most often in the 4-5 yr or 4-5 yr and 9-11yr sites, four for the 9-11 yr sites only, and seven for the >40 yr or 9-11 yr and >40 yr sites. All of these species had very low numbers in one or two of the fire categories. Our results demonstrate that several invertebrate species specialise on a post-fire successional stage. These species may be at risk of local extinction if fire is not managed at appropriate temporal or spatial scales (Fahrig 1997; York 1999; Driscoll et al. 2012; Pyrke & Samways 2012). This might not have substantial consequences in very large patches of mallee woodland where fires are unlikely to affect the whole patch. In such areas, re-colonisation would be possible from adjacent areas when the optimal time since fire returned (assuming dispersal is not limiting which is currently unknown). The consequences of local extinction may be more severe in fragmented landscapes because entire fragments can be burnt by a single fire and source populations for recolonisation may not be nearby. We do not know if the fire-affected species identified in our study also occur in the surrounding matrix of cleared agricultural land. However, in a previous study, only about a quarter of mallee beetle fauna were found in the agricultural matrix (Driscoll & Weir 2005). The role of the matrix in providing alternative habitat or in limiting dispersal in this system needs to be explored further.

Our results revealed extreme opposite responses to time since fire in species pairs from the same family (Lycosidae, Fig. 2a,b). This finding could be driven by competitive exclusion or niche differentiation where closely related species specialise on different resources (Hardin 1960; Pfennig 2009), facilitating coexistence (Schluter 2000). This pattern is consistent with the habitat accommodation model where one species can competitively exclude another when their key habitat element becomes available (Fox 1982). It also means that predicting the response of animal species to fire based on simple morphological, or family-level traits may not be possible.

Many vertebrates in this ecosystem rely on invertebrates as a source of prey. Insectivorous vertebrates often show abundance differences with time since fire (Fox 1982; Letnic *et al*. 2004; Fenner & Bull 2007; Driscoll & Henderson 2008; Smith *et al*. 2012; Driscoll *et a*l. 2012) and these changes may be driven by variation in the fire response of their prey. Fire regimes have the potential to affect communities at a number of trophic levels, but interactions between fire responses of animal species from different trophic levels have rarely been investigated. Using sweep netting, we found that invertebrates were more abundant in the 4-5 yr sites primarily due to outbreaks of the grasshopper *Warramunga* sp. 1. Insectivorous vertebrates that are able to forage above the ground, such as arboreal reptiles, birds and mammals, may have increased abundance after fire in response to this increase in prey availability (Radford and Andersen 2012). Detailed information about preferred prey across a range of vertebrate species is now needed to examine this possibility.

The mean abundance of most invertebrate morphospecies did not vary significantly with time since fire in this study. There are two potential reasons for this. First, many species may not be affected by time since fire (Herrando *et al.* 2002; Driscoll & Henderson 2008). The resources required for many ground-dwelling invertebrates including spiders, scorpions, centipedes and predatory beetles may be consistently available across post-fire succession stages. If species can survive fire (e.g. by sheltering underground) then the abundance of many species could remain unchanged. Second, many species may have had responses to time since fire that we did not detect. Statistical power of our study was likely to be low, with only two sites in each fire category within each reserve. Large-scale natural experiments have proximate factors such as local rainfall that can increase variation and reduce power (Hargrove & Pickering 1992; Driscoll *et al*. 2010b). Fire severity and frequency also have the potential to affect fauna abundance (Pardon *et al*. 2003; Smucker *et al*. 2005) but were not examined in this study. The invertebrate assemblage can also be highly seasonal and this study was a snapshot of a particular time of year. Sampling throughout the year may give a broader insight into the invertebrate community's response to fire.

Effect of taxonomic level on results

We found few significant responses when we compared changes in invertebrate abundance with time since fire at the order level. Only Blattodea and Orthoptera showed significant responses, but these results were driven by the dominant species in that group. It is not surprising that many studies investigate ecological processes at the invertebrate order level (e.g. Bailey & Whitham 2002; Moretti *et al*. 2006; Engle *et al*. 2008; Radford & Andersen 2012) given the complexity of invertebrate taxonomy. However, our results showed that important ecological responses may not be detected using coarser taxonomic groupings. Erroneous management conclusions are likely to be drawn from studies that undertake analyses using higher taxonomic levels. When used carefully, morphospecies can be a valuable tool in broad scale invertebrate studies (Oliver & Beattie 1996; Derraik *et al*. 2002) and our study has demonstrated the benefit of this approach. However, as discussed previously, statistical power was low so small effects at the order level may not have been detected.

Methods influence interpretation of time since fire impacts

We found little overlap in the morphospecies detected using the three different sampling methods. This is not surprising as the sweep netting samples were collected predominantly from above-ground vegetation whereas the other two methods were sampling mainly ground-dwelling invertebrates. It is well established that different methods will sample different components of the habitat (e.g. dry vs. moist microhabitats: Prasifka *et al*. 2007) but our study demonstrates that different methods reveal different perspectives on the influence of fire within the same vegetation type. If we had only sampled using wet pitfall traps we would not have detected any species that prefer mallee unburnt for > 40 yrs. This could lead to management recommendations that increase the amount of fire in the landscape, with negative consequences for invertebrate species that were more common in long-unburnt mallee (5 out of 17 species with significant responses to fire). Although some studies have shown fire responses in invertebrates using small wet pitfall traps (e.g. Andersen 1991), our study highlights the importance of using a range of methods to gain a broad understanding of invertebrate fire ecology.

Each of our sampling methods included a range of "filters", and these are likely to apply in other studies that use these trapping techniques. For example, our large pitfall traps were dry, so probably captured fewer flying beetles than wet pitfall traps might. There was also some risk that invertebrates in large pitfall traps were predated upon by captured vertebrates, although the risk would have applied in all fire categories. Small (<3mm) invertebrates are very difficult to detect in large pitfall traps because these traps must have some soil in them to help protect captured vertebrates. Each method had different sized filters and sampled different subsets of the invertebrate population (excluding ants meant the large pitfall traps also had a collection filter). Our comparative research approach gave us different perspectives and showed that combining multiple methods can give a more complete representation of fire responses in the invertebrate community.

The results from our study have important implications for fire ecology, field methods and fire management. The contrasting responses of individual species to fire imply that landscapes with a range of seral stages are needed to maintain biodiversity. In fragmented landscapes with small mallee remnants, such a range has not been achieved in the past and local extinctions are expected (Driscoll & Henderson 2008). To reliably determine when there is no response to fire, research must focus on analyses at the species level rather than the order level. Robust management decisions are only possible when based on results arising from a range of trapping methods with data analysed at the species level. Predators that can eat grasshoppers and forage in low shrubs may have a response to fire that is mediated by invertebrate prey. For most generalist predators of arthropods however, prey availability remains unchanged with time since fire.

Current fire management protocols are based on the requirements of a very narrow range of taxa (Clarke 2008). Typically these are based on the fire interval requirements of vascular plants (Keith *et al*. 2002; Menges 2007). Our study has demonstrated that invertebrate species can have strong and contrasting responses to fire. To manage fire in a way that conserves invertebrate biodiversity, a range of successional stages in a landscape are needed, and this may be broader than the range implied by models of plant succession.

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Figure legends

Fig. 1. Invertebrate study locations at A) Hincks Wilderness Area and Pinkawillinie Conservation Park on the Eyre Peninsula South Australia. B & C) at each reserve two sites were sampled in three fire treatments.

Fig. 2. The abundance of five invertebrate morphospecies from large pitfall traps had significant responses to time since fire: a) Lycosidae *sp. 1* (Araneae) b) Lycosidae *sp. 2* (Araneae) c) Zoridae *sp. 1* (Araneae) d) *Platyzosteria sp. 1* (Blattodea) and e) *Endacusta sp. 1* (Orthoptera). Error bars are 95% confidence limits.

Fig. 3. The abundance of nine species caught in sweep nets had significant responses to time since fire: a) *Warramunga sp. 1* (Orthoptera) b) Cicadellidae sp. 1 (Hemiptera) c) *Polyphrades marmoratus* (Coleoptera) d) Cicadellidae sp .2 (Hemiptera) e) Psyllidae sp. 1 (Hemiptera) f) Lepidoptera sp. 1 (Lepidoptera) g) Lepidoptera sp. 2 (Lepidoptera) h) *Dicranolaius sp. 1* (Coleoptera) and i) Mantodea sp. 1 (Mantodea). Error bars are 95% confidence limits. (H = Hincks Wilderness Area, P = Pinkawillinie Conservation Park).

Fig. 4. The abundance of three species caught in wet pitfall trap samples had significant responses to time since fire: a) Formicidae sp. 1 (Hymenoptera) b) *Melophorus* sp. 1 (Hymenoptera) and c) Zoridae sp. 1 (Araneae). Error bars are 95% confidence limits.

Fig. 5. Number of morphospecies detected using large pitfall traps, wet pitfall traps and sweep netting, and the overlap between the three methods. Brackets refer to the number of morphospecies where only one or two individuals were detected.

Table 1. The abundance of 17 invertebrate morphospecies varied significantly with time since fire in mallee vegetation of South Australia.

Sampling method	**Species**	**Order**	**Fire category where most abundant**	***P*-value**	**Q-value**	**Figure reference**
Large pitfall traps	Lycosidae sp. 1	Araneae	4-5yr	<0.001	<0.001	2a
	Lycosidae sp.2	Araneae	>40yr	<0.001	<0.001	2b
	Zoridae sp. 1	Araneae	9-11yr	<0.001	<0.001	2c
	Platyzosteria sp.	Blattodea	>40yr	<0.001	<0.001	2d
	Endacusta sp.1	Orthoptera	9-11yr and >40yr	<0.001	0.012	2e
Sweep netting	*Warramunga* sp.	Orthoptera	4-5yr	<0.001	<0.001	3a
	Cicadellidae sp.	Hemiptera	Interaction	<0.001	<0.001	3b
	Polyphrades marmoratus	Coleoptera	>40yr	<0.001	<0.001	3c
	Cicadellidae sp.	Hemiptera	4-5yr and 9-11yr	<0.001	<0.001	3d
	Psyllidae sp. 1	Hemiptera	9-11yr	<0.001	<0.001	3e
	Lepidoptera sp.	Lepidoptera	>40yr	<0.001	<0.001	3f
	Lepidoptera sp.	Lepidoptera	9-11yr and >40yr	<0.001	<0.001	3g
	Dicranolaius sp.	Coleoptera	>40yr	<0.001	<0.001	3h
	Mantodea sp. 1	Mantodea	4-5yr and 9-11yr	0.002	0.012	3i
Wet pitfall traps	Formicidae sp. 1	Hymenoptera	9-11yr	<0.001	<0.001	4a
	Melophorus sp.	Hymenoptera	4-5yr	0.002	0.041	4b
	Zoridae sp. 1	Araneae	9-11yr	0.001	0.023	4c

Table 2. Time investment and outcomes of three sampling methods used to detect invertebrate responses to time since fire.

Method	**Field effort (hrs)**	**Sorting effort (hrs)**	**No. indiv.s**	**No. species / No. of species analysed**	**No. morphospecies with a fire response**	**No. responses / hr of effort**
Large pitfall traps	60	24	3343	177/34	5	0.059
Sweep netting	32	24	8034	240/42	9	0.161
Wet pitfall traps	28	85	49773	150/63	3	0.027

Figure 1

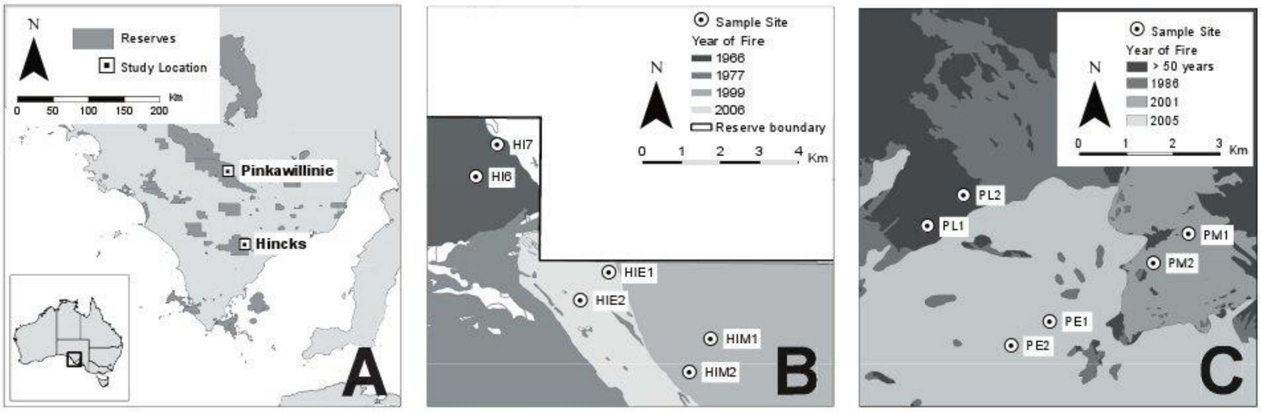

N
Reserves
Study Location
0
50
100
150
200
Km
Pinkawillinie
Hincks
A
Sample Site
Year of Fire
1966
1977
1999
2006
Reserve boundary
N
0
1
2
3
4
Km
HI7
HI6
HIE1
HIE2
HIM1
HIM2
B
Sample Site
Year of Fire
N
> 50 years
1986
2001
2005
0
1
2
3
Km
PL2
PL1
PM1
PM2
PE1
PE2
C

Figure 2

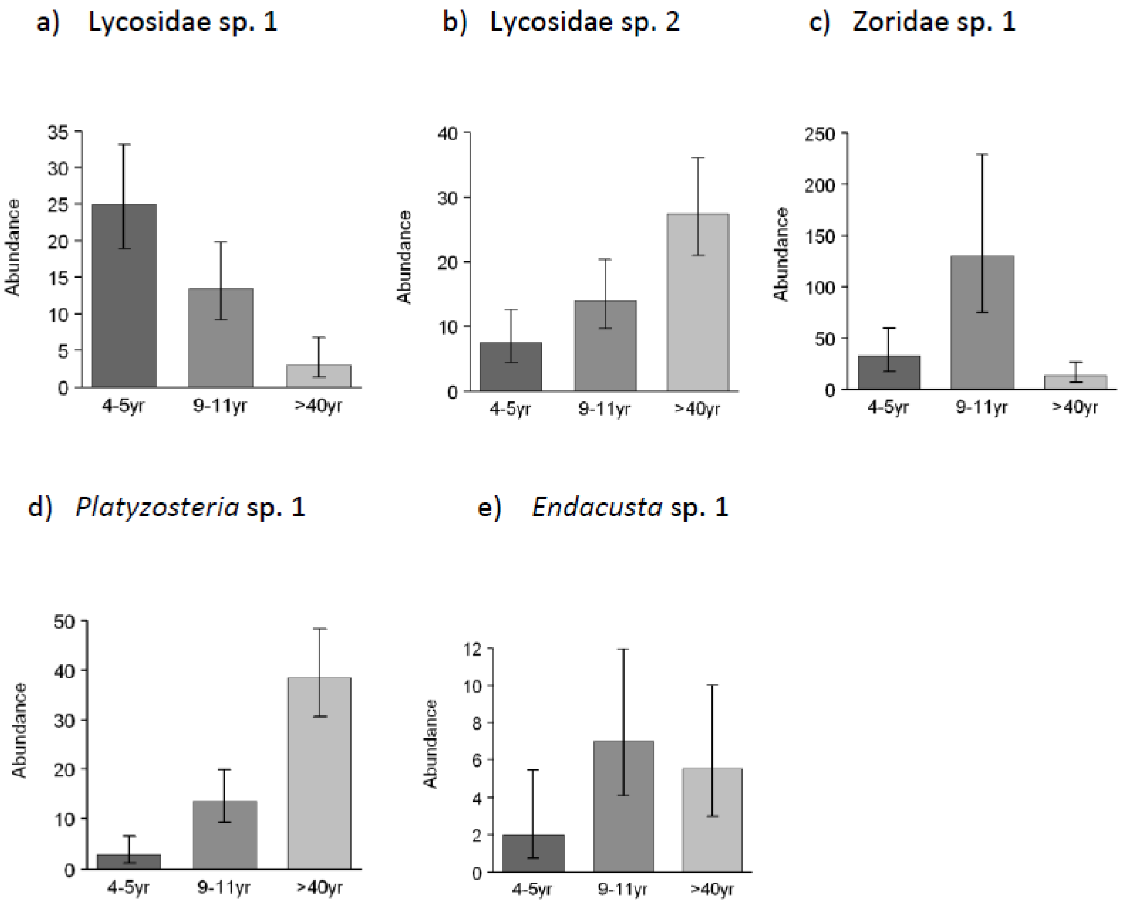
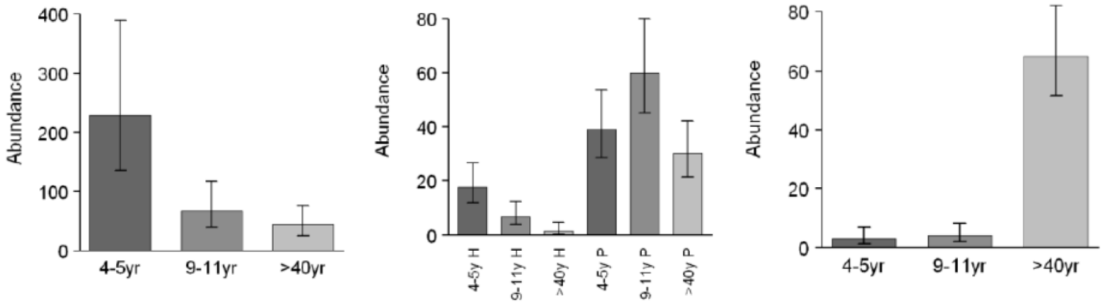

a) Lycosidae sp. 1
b) Lycosidae sp. 2
c) Zoridae sp. 1
Abundance
0
5
10
15
20
25
30
35
4-5yr
9-11yr
>40yr
0
10
20
30
40
0
50
100
150
200
250
d) *Platyzosteria* sp. 1
e) *Endacusta* sp. 1
50
0
2
4
6
8
10
12

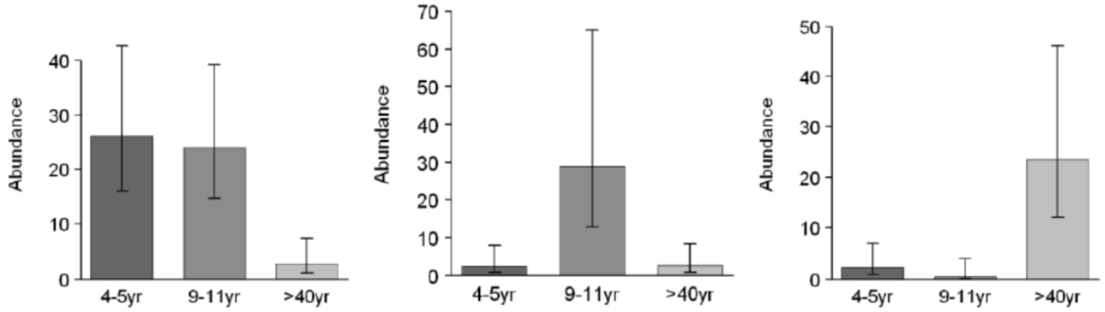
Figure 3



a) *Warramunga* sp. 1

b) Cicadellidae sp. 1

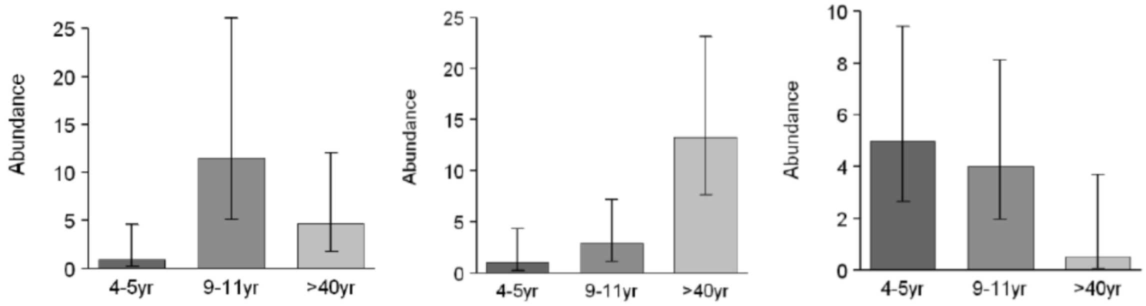
c) *Polyphrades marmoratus*



d) Cicadellidae sp. 2

e) Psyllidae sp. 1

f) Lepidoptera sp. 1



g) Lepidoptera sp. 2

h) *Dicranolaius* sp. 1

i) Mantodea sp. 1

Figure 4

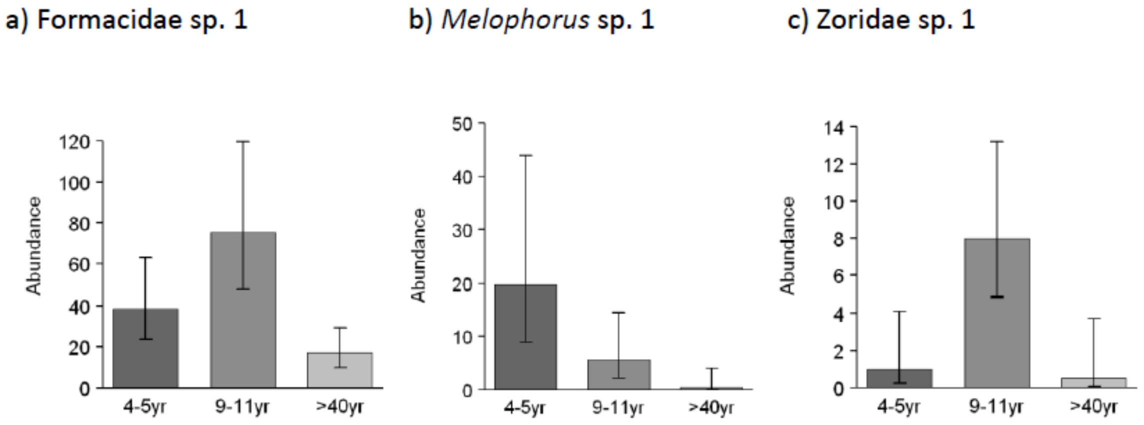
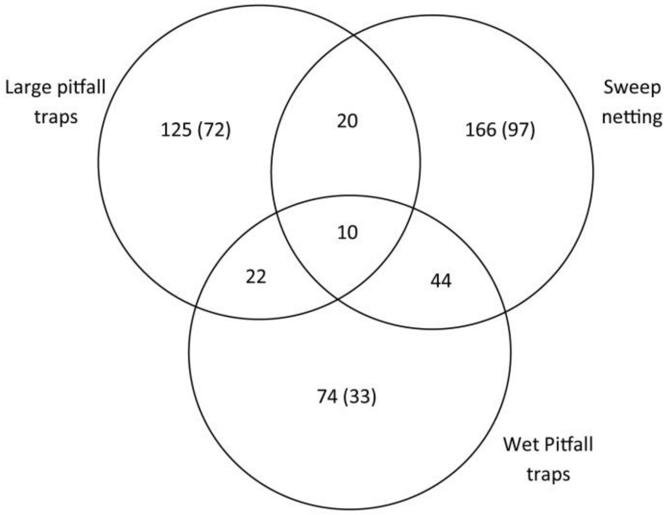

a) Formacidae sp. 1
b) *Melophorus* sp. 1
c) Zoridae sp. 1
Abundance
0
20
40
60
80
100
120
10
30
50
2
4
6
8
12
14
4-5yr
9-11yr
>40yr

Figure 5


Large pitfall traps
125 (72)
20
166 (97)
Sweep netting
10
22
44
74 (33)
Wet Pitfall traps