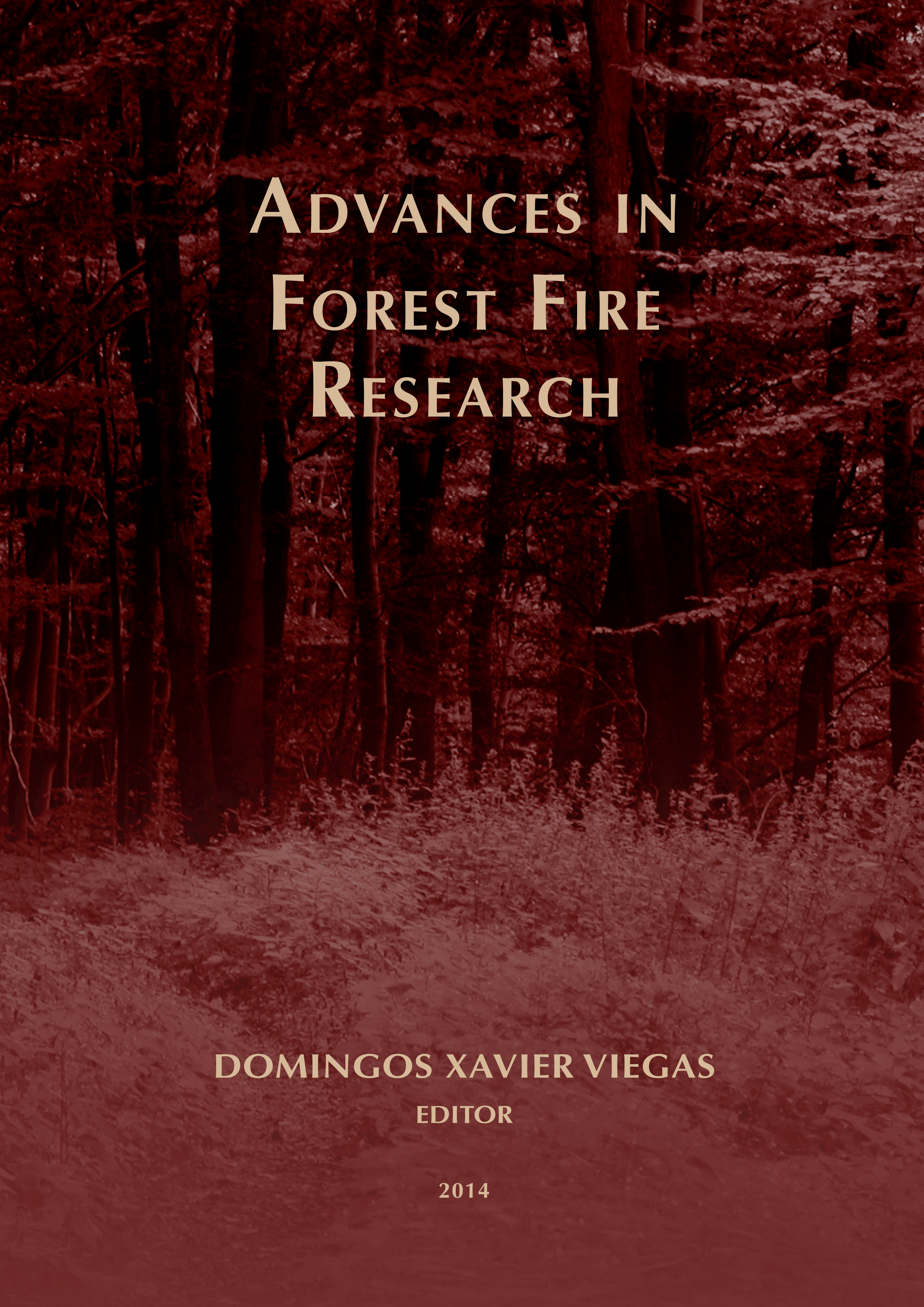

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Changing fire regimes: The response of litter-dwelling invertebrates to altered seasonality and frequency of fire

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Abstract

Mediterranean climate regions are experiencing changes that are projected to have significant impacts on patterns of temperature and rainfall, thereby affecting key ecosystem drivers such as fire regimes. In the sclerophyll-dominated vegetation communities of southern Australia, land managers are responding to increased wildfire probabilities through the use of more frequent low intensity (prescribed) fire. With burning occurring more often throughout the year, plant and animal communities are experiencing altered fire regimes; with changes to both frequency and season of burn. Here I report on the results of a long-term, replicated study, investigating the effects of fire frequency (high vs low) and seasonality (autumn vs spring) on a biodiverse and functionally important component of the fauna (litter-dwelling invertebrates). At the ordinal level, three broad patterns of response were detected: (i) no effect of fire treatment on abundance, (ii) a burning treatment effect, suggesting that fire in any season and at any frequency lowers abundance, and (iii) a significant negative effect of fire frequency on abundance. No season of fire effects were apparent for any group. The mechanisms underpinning these responses warrant further investigation, particularly in light of proposed increases in the amount of prescribed fire to be applied to these forest systems in coming years.

Keywords: climate change, fire regime, invertebrates, prescribed fire

1. Introduction

The application of prescribed fire in many regions is becoming more common amid forecasted increases in the frequency and severity of wildfire under climate change (Stephens *et al.* 2012; Cary *et al.* 2012; Flannigan *et al.* 2013). For example, in the state of Victoria in south-eastern Australia, a long term program of prescribed burning on an annual rolling target of 5% of public land (equating to a minimum of 385,000 ha per year) was introduced following severe wildfires in 2009 (Attiwill and Adams 2013). Historically, primarily for safety reasons, prescribed burning in these temperate ecosystems has been undertaken during autumn (Luke and McArthur 1978), however to meet new burn targets managers are now applying fire whenever weather conditions allow. As a consequence prescribed fires are occurring across a broader range of seasons and, potentially, with increased frequency (i.e. reduced intervals between successive burns). Understanding the implications of such changes in the fire regime for biodiversity is therefore critical (Bradstock *et al.* 2010; Penman *et al.* 2011).

As a group, invertebrates are numerous, diverse, and play important functional roles in ecosystems (Beattie 1995; Raven and Yeates 2007). Through their role in the breakdown and decomposition of organic matter and the release of materials to the soil environment, invertebrates have a positive influence on the availability of nutrients for plant growth and on soil physical properties. In Australia there have been a number of studies on the effects of low-intensity prescribed fire on invertebrates, particularly in regard to the interval between such fires (fire frequency); with fewer examining the season of burn. Following two short rotation (three-year interval) low-intensity fires in spring in Victoria, Collett *et al.* (2003) found that arthropod diversity had increased following the second fire, caused by greater evenness of individuals among taxa rather than any change in taxon richness. Three fires over an eight-year period had no cumulative impact on springtails and earthworms (Collett 1999) or on richness or composition of beetle communities (Collett and Neumann 1995), but the effects of individual fires were quite variable. In contrast, two autumn fires over a five-year period produced a significant decrease in springtails, mites and earwigs and an increase in ant activity (Collett 1998). From studies based in Western Australian, Majer (1980, 1985) concluded that spring burning may be more detrimental to the soil-surface fauna than autumn burning. Some impacts however may be cumulative and take many years to manifest themselves. Examining the effects of seven fires over a 20 year period in sclerophyll forest in New South Wales, York (1999a) showed significantly lower ordinal diversity of surface-active and litter-inhabiting invertebrates in frequently burnt sites compared to unburnt sites.

With changing management practices involving the use of fire, concern has been recently expressed about the potential impacts of altered fire regimes on invertebrate diversity in both Mediterranean woodlands (Quartau 2009) and Australian temperate forests (New *et al.* 2010; York 2012). This paper utilises a long-term fire experiment to build on existing research; evaluating both the independent and combined effects of changed frequency and season of planned fire on litter-dwelling terrestrial invertebrates.

2. Methods

The study incorporates five areas (known locally as the ‘Fire Effects Study Areas’, FESA) within a 25 km radius in the Wombat State Forest, about 100 km north-west of Melbourne, Victoria, south-eastern Australia. The areas have an underlying geology of Ordovician sedimentary rock, and are at elevations ranging from 590 to 760 m above sea level. Topography varies from mostly flat (slopes 0-4°) to hills of low to moderate relief (slopes up to 21°). The climate is temperate, with annual rainfall in the range 814-901 mm, with the majority falling in winter and spring (Tolhurst and Flinn 1992). Native vegetation of the study areas is open to tall-open forest (tree heights 10 to >30 m, projective foliage cover 30-70%; Specht 1981). Dominant trees are Messmate Stringybark *Eucalyptus obliqua,* Narrow-leaf Peppermint *E. radiata* and Candlebark *E. rubida*. The understorey is characterised by a sparse shrub layer up to four metres in height (e.g. *Acacia* spp.), and ground layer of Austral Bracken (*Pteridium esculentum*) and native perennial grasses, forbs and rushes. Open to tall-open forests such as these are likely to be burnt more frequently under ongoing commitments to extensive use of prescribed fire on Victoria’s public land (DSE 2012).

The study was established in 1985, and used a randomised block design involving a long-unburnt control (reference state) and four prescribed fire treatments randomly allocated within each of the five study areas (total of 25 treatment areas). The four fire treatments involved a factorial combination of two fire seasons (autumn or spring), and two fire frequencies (nominally every 3 or 10 years); that is, Autumn High-frequency (AH), Autumn Low-frequency (AL), Spring High-frequency (SH), and Spring Low-frequency (SL). Nominal prescribed fire intervals of three and ten years were chosen to represent, respectively, the shortest interval for sufficient recovery of surface fuels to carry a fire in these forests, and the likely return interval of prescribed fire based on local fire management practice. Prescribed fires in all treatments in this study were considered to be of low intensity (Tolhurst & Flinn 1992). Mean inter-fire intervals ranged from 2.7–5.7 years in the High-frequency treatments, and 8.5-16 years in Low-frequency treatments (see Bennett *et al.* 2013 for further detail).

To sample topographic variability, three plots (ridge, slope and gully) were established in each of the five burn treatments in each of the five areas; giving 75 plots overall. In 2012, twenty 2000 cm^3 samples of surface litter were systematically collected along 2 x 18 m orthogonal transects at each plot. Samples were bulked and sieved on site using a litter sifter (Upton & Mantle 2010); with a single sample for each plot returned to the laboratory. Invertebrates were extracted over four days using Tullgren funnels at the University of Melbourne. Samples were stored in 70% alcohol and identified to Order or equivalent using a binocular dissecting microscope and appropriate taxonomic keys.

Effects of prescribed fire treatments on invertebrate abundance were tested using Analysis of Variance (ANOVA) in Genstat 16th Edition. A factorial plus added control model with area as a random factor, treatment as a fixed factor, and plot nested within treatment by area, was used to examine the overall effects of prescribed fire (Control versus Fire treatments), as well as the effects of prescribed fire season (Autumn versus Spring) and frequency (High versus Low), and their interactions.

3. Results

In total 276,314 individuals from 23 broad taxonomic groups were collected. A number of groups were poorly represented and/or unlikely to be effectively sampled using litter extraction, with data for 15 groups sufficient to undertake analyses (Table 1). Overall, there was a significant effect of fire frequency on total invertebrate abundance (P = 0.009) with both Autumn High-frequency (AH) and Spring High-frequency (SH) treatments resulting in a substantial decline in mean invertebrate abundance (Table 1).

Table 1. Summary statistics of invertebrate abundance and ANOVA results for comparisons of five burning treatments (AL: Autumn Low-, AH: Autumn High-frequency; C: Unburnt; SL: Spring Low-, SH: Spring High-frequency). B: significant burn treatment effect, F: significant burn frequency effect (P<0.05), ns: not significant. – indicates groups poorly represented and/or unlikely to be effectively sampled using litter extraction (not tested).

Taxon	Treatment (Abundance MEAN±S.E.)					ANOVA
	AL	AH	C	SL	SH	
Mites	2542.7±424.5	1901.9±264.4	2220.7±279.8	2770.7±373.3	1797.5±259.1	F
Amphipods	28.7±11.7	4.1±0.9	27.7± 5.8	26.3±7.6	9.1±3.5	F
Spiders	66.9±11.4	49.0±12.1	77.7±7.2	58.8±9.5	48.1±8.0	B,F
Cockroaches	9.1±1.5	7.5±1.1	7.0±1.1	0.7±0.7	6.8±0.8	ns
Centipedes	8.1±2.7	8.7±1.9	7.0±1.6	9.8±1.8	7.2±2.4	ns
Beetles	131.7±19.0	97.5±11.7	119.9±15.1	133.7±13.9	89.2±10.8	F
Springtails	701.5±149.2	340.2±50.1	1507.3±358.6	917.5±272.2	566.3±122.4	B
Earwigs	1.4±0.6	1.9±0.5	0.3±0.2	1.5±0.5	1.1±0.4	-
Diplopods	25.4 15.4	5.5±2.1	21.7±9.1	10.6±2.9	5.0±2.0	ns
Bristletails	0.0 0.0	0.1±0.1	0.1±0.1	0.0±0.0	0.0±0.0	-
Flies	0.4±0.2	0.6±0.2	1.2±0.3	1.1±0.3	0.3±0.1	-
Webspinners	0.0±0.0	0.0±0.0	0.4±0.3	0.0±0.0	0.0±0.0	-
Bugs	18.1±2.3	10.4±1.6	17.8±2.9	12.5±2.6	12.7±1.9	ns
Ants	43.9±7.2	41.7±7.9	46.3±14.7	48.3±6.2	59.2±12.4	ns
Wasps	7.3±1.1	8.4±1.1	10.6±3.5	8.9±1.5	5.6±0.9	ns
Woodlice	13.9±3.1	9.7±2.7	23.7±4.0	15.3±2.9	7.9±3.4	B
Larvae	251.9±33.9	182.0±23.9	243.4±35.4	267.3±31.9	206.0±22.8	F
Velvet worms	0.1±0.1	0.0±0.0	0.0±0.0	0.1±0.1	0.0±0.0	-
Grasshoppers	0.1±0.1	0.1±0.1	0.1±0.1	0.1±0.1	0.1±0.1	-
Pseudoscorpions	2.7±0.7	3.2±0.9	5.7±1.7	6.0±2.1	1.2±0.4	ns
Barklice	1.9±0.6	0.1±0.3	1.1±0.4	1.9±0.5	1.2±0.3	-
Scorpions	0.2±0.1	0.3±0.2	0.1±0.1	0.2±0.1	0.0±0.0	-
Thrips	73.9±19.4	66.9±11.5	100.6±26.2	94.1±17.9	98.5±19.9	ns
Total	3931.0±555.1	2741.3±282.2	4442.2±576.0	4393.7±566.5	2924.1±317.1	F

When individual groups were considered, there were 3 basic patterns of response (Figure 1). Firstly, for seven groups (cockroaches, centipedes, diplopods, bugs, ants, wasps and barklice) there was no effect of fire treatments on their abundance at plots, suggesting that numbers of these groups were not impacted by fire in any season or at any frequency. Secondly, for three groups (spiders, springtails and woodlice) there was an effect of the burning treatment, suggesting fire (in any season and at any frequency) lowers their abundance. Thirdly, for five groups (mites, amphipods, spiders, beetles and larvae), there was a significant effect of fire frequency on their abundance. No season of fire effects were apparent for any group.

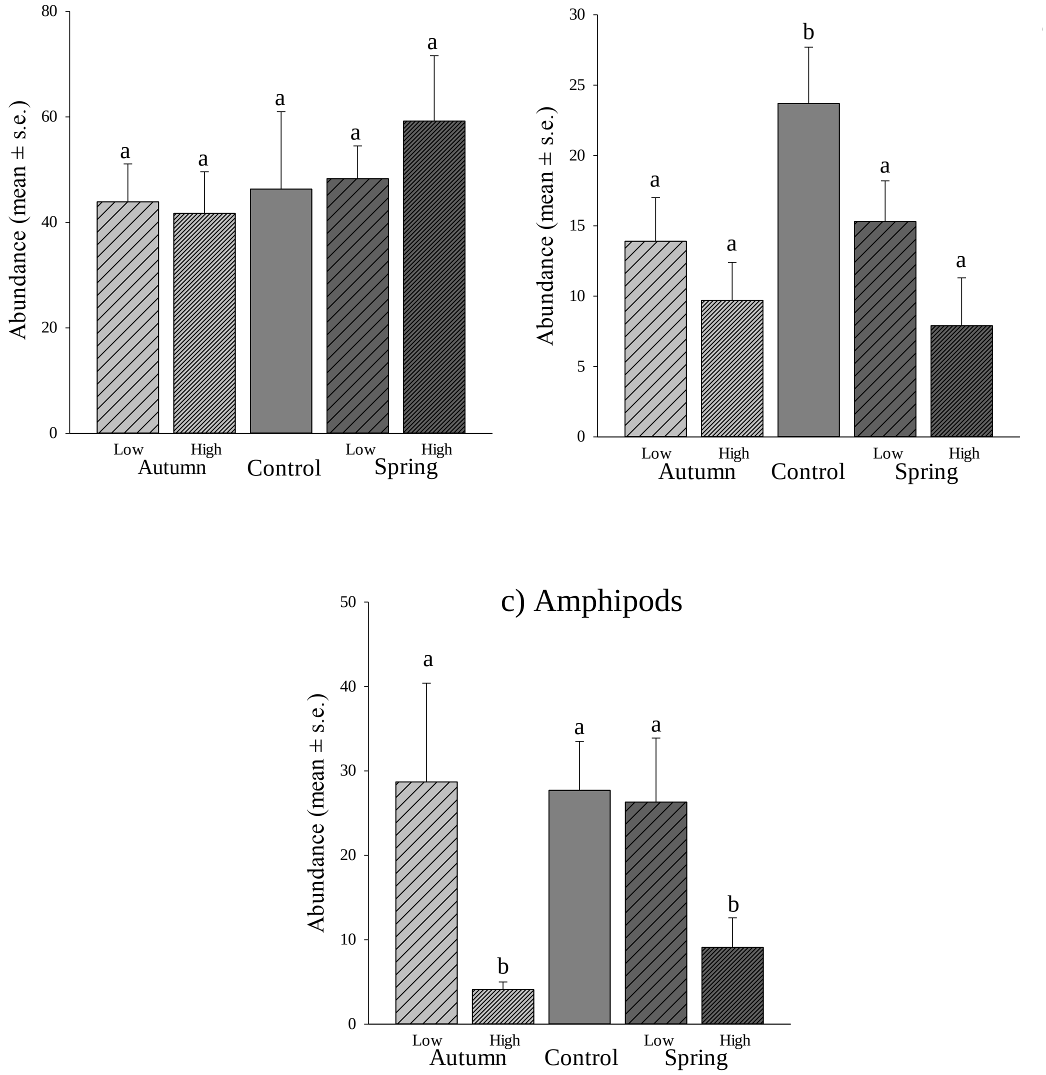

Figure 1. Examples of the three basic patterns of response. a) No effect of fire treatments on abundance e.g. ants. b) Significant effect of the burning treatment, irrespective of season and frequency e.g. woodlice. c) Significant effect of fire frequency e.g. amphipods. Columns with the same letters do not differ significantly, while those with different letters are significantly different in mean abundance (SNK post-hoc test). No season of fire effects were apparent for any group.

4. Discussion

Recent catastrophic wildfire events in Mediterranean-type ecosystems, including in Australia (Cameron *et al.* 2009), California (Keeley *et al.* 2009) and Greece (Pyne 2008), have led to increasing pressure on governments to mitigate fire risk (Teeter 2008; Teague *et al.* 2010). Fire prescriptions often target surface fuel loads in an attempt to reduce the intensity and spread of future wildfires (e.g.

McArthur 1967; Gould *et al.* 2007). In Australian dry forest systems however, leaf litter can accumulate quickly, often reaching pre-fire levels within 3 years (Penman and York 2010). Maintaining low fuel levels in strategic locations, and/or increasing annual area burnt by prescribed fire, will inevitably lead to increases in the frequency of fire and changed season of burning, as land managers seek to maximise burning opportunities. While sclerophyll forests, woodlands and heaths are dominated by plant species with adaptive responses than enable them to survive periodic burning (Gill 1981; Noble and Slatyer 1981), the impact of fires on terrestrial invertebrates is poorly understood. Because low-intensity fires are often patchy in nature and invertebrates can seek shelter within the soil and in unburnt habitat refuges, it has been suggested (Majer 1980; Campbell and Tanton 1981; Abbott 1984) that periodic fires used for fuel management purposes have few long-term effects on most soil and litter invertebrates. Little is known, however, about the effects of the repeated use of fire over long time scales; particularly as frequent fires can reduce spatial and structural heterogeneity and could have long-term consequences for the survival of invertebrate populations (Collett *et al.* 1993).

This study investigated the impact of 30 years of low-intensity fire on a functionally important component of the forest biodiversity, litter-dwelling invertebrates. Soil- and litter-dwelling invertebrates play an important role in the breakdown of litter and soil organic matter; facilitating the decomposition process and contributing to nutrient availability (York *et al.* 2012). Results from this long-term fire study indicated three broad response patterns. Firstly, for seven groups (cockroaches, centipedes, diplopods, bugs, ants, wasps and barklice) there was no effect of fire treatments on their abundance at plots, suggesting that numbers of these groups were not impacted by fire in any season or at any frequency. York (1999a) found negative effects of frequent fire on cockroaches, centipedes and bugs, although the low numbers caught in that study warrant cautious interpretation. Secondly, for three groups (spiders, springtails and woodlice) there was an effect of the burning treatment, suggesting fire (in any season and at any frequency) lowers their abundance. Collett (1998) found that two autumn fires over a five-year period produced a significant decrease in springtail abundance, while York (1999a) reported reductions in the numbers of spiders, springtails and woodlice with frequent autumn fire. The third broad response identified concerned five groups (mites, amphipods, spiders, beetles and larvae), where there was a significant negative effect of fire frequency on their abundance. High fire frequency has previously been shown to reduce the numbers of these groups (York 1999a).

It is of potential concern that high frequency fire (every ~3 years) significantly reduces the number of mites, amphipods, beetles and insect larvae. Amphipods (landhoppers) and larvae play major roles in litter fragmentation (Schowalter 2000) while many litter-dwelling beetles are associated with decomposer fungi (Lawrence and Slipinski 2013). This suggests a reduction in rates of decomposition and nutrient cycling with more frequent fire; which has implications for both rates of post-fire litter accumulation and forest health (see Brennan *et al.* 2009). The mechanisms underpinning these responses warrant further investigation, particularly in light of proposed increases in the amount of prescribed fire to be applied to these forest systems in coming years. It is most likely that frequent fire influences litter biomass and associated moisture levels (York 1999b; Penman and York 2010), and simplifies habitat structure. Several studies have reported the importance of litter depth and structure as a control of litter invertebrate composition (e.g. Uetz 1979; Michaels and McQuillan 1995). Because of this, litter fauna may take longer to recover after fire than the soil fauna (Majer 1984) and unburnt plants, logs and patches of litter become important refuges for fauna in burnt areas (Majer 1980; Whelan *et al.* 1980; Andrew *et al.* 2000). An interesting finding concerned the lack of a season of fire effect for any group. In earlier studies at this site Collett (1993, 1998, 1999) and Collett and Neumann (1995) observed that effects of individual fires were quite variable, with outcomes for most groups more dependent on the severity of individual fires rather the season of burn. Koch and Majer (1980) have previously emphasised that an understanding of the phenology (seasonality) of invertebrate abundance and activity is needed to fully assess the potential impacts of burning. Future work on this project will target focal groups with an emphasis on understanding responses at the feeding guild or functional group level.

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