Understanding the effects of fire on invertebrates in Australian temperate and sub-tropical forests: the value of long-term experiments

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ABSTRACT

Fire is a common feature of Australian forests and prescribed burning is a routine management strategy, often utilised to mitigate the effects of wildfire. However, the impacts of fire on terrestrial invertebrates are poorly understood. Here we provide an overview of continuing long-term fire studies in temperate and sub-tropical forest ecosystems, with a focus on terrestrial invertebrates. Longitudinal fire study sites exist in southern Queensland, New South Wales, Victoria, Western Australia and Tasmania. Most studies have focussed on fire frequency and have identified certain taxa or taxonomic groups that prefer either habitat associated with long unburnt areas, habitat associated with more frequently burnt areas or those that show no response to varied fire frequency. The limited number of studies investigating fire season report similar findings, but there are few studies that have focussed on other components of the fire regime. Long-term experiments are important when studying the effects of various fire regimes on invertebrate assemblages as responses often take time to be expressed, and may follow changes in habitat availability associated with interactions between components of the fire regime. We recommend that ecological studies continue to utilise long-term study sites through monitoring programs to improve our understanding of how invertebrate taxa respond to fire regimes; and to better identify the important role of invertebrate groups in ecosystem functioning (e.g. for nutrient cycling, pollination).

Key words: fire regime, habitat, fire frequency, prescribed burning, animal populations

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Introduction

Fire is part of the environment and has shaped the composition, structure and distribution of plant and animal communities of many Australian ecosystems over millions of years (Bowman *et al.* 2012). Fire can have both direct (short-term) and indirect (longer-term) effects on animals. Individual fires may directly impact upon individuals by causing injury or death, or those individuals may survive by escaping (emigration) or seeking shelter (in refuges or through dormancy in a protected location). Longer-term impacts result from the fire causing changes to some aspects of the environment (such as resources) which, in turn, affect the fauna. Unsuitable conditions after a fire may lead to emigration (or death); with persistence at that location influenced by food availability, competition and/or predation, and the capacity of an organism to reproduce or recolonise from outside the area directly impacted. Over time, responses of animal populations will be influenced not only by features of a particular fire (e.g. intensity, patchiness), but by processes occurring after the fire. A better understanding of these responses will assist land managers who might use fire as a tool and need to balance both asset protection and conservation objectives (Penman *et al.* 2011).

Some faunal groups show distinct patterns in abundance post-fire, with communities exhibiting successional responses to habitat change (the 'habitat accommodation model', see Monamy and Fox 2000, 2010) although time-since-fire alone is often a poor predictor of faunal response (Driscoll and Henderson 2008; Di Stefano *et al.* 2011; Swan *et al.* 2015). The investigation of time- and habitat-related responses post-fire is practically most often undertaken with a chronosequence (space-for-time) approach, however it is most effectively studied using longitudinal studies (following a site over time). Short-term studies (i.e. those that focus on only one or two fire events) often fail to detect patterns that are a response to variation in the characteristics of the organisms studied, the properties of the fire (previous history, intensity and coverage), the landscape and the climate (e.g. pre- and post-fire weather) (Whelan *et al.* 2002). Ecological research carried out at sites over long time periods has provided valuable insights into factors affecting the long-term maintenance of forest productivity (Bormann and Likens 1994) and those driving changes in population dynamics (Brown and Ehrlich 1980). Permanent long-term monitoring plot data have been used to track change over time after repeated prescribed fires (e.g. Waring *et al.* 2016) and habitat fragmentation (McClenahan *et al.* 2016). However, time-related response (inter-fire interval) is only one component of the fire regime (*sensu* Gill 1975) which has shaped life-history traits and therefore long-term responses to repeated fires. Impacts to faunal populations and communities are most likely when the fire regime is outside the evolutionary experiences of organisms, and/or there are interactions with other processes (e.g. competition, predation etc.). Impacts of altered fire regimes are therefore most effectively studied through long-term experiments, where fire season, intensity and frequency can be directly manipulated, with spatial and temporal replication.

Periodic low-intensity fire (e.g. prescribed burning) is a conspicuous management strategy in virtually all of Australia's dry forest communities. While it is primarily used to reduce fuel levels, little is known about the effects of its repeated use on natural ecosystems over long time-scales (Penman *et al.* 2011). Since the 1950s, conscious of the debate around possible effects of this fire mitigation strategy on Australian temperate and sub-tropical forests, long-term research projects were established by management agencies in southern Queensland, NSW and Victoria. While often initially focussing on the effects of planned burning on timber resources, these projects all diversified to include a strong biodiversity component and became the basis for much of the later developments in fire ecology research and management policy (see York and Friend 2016). In this paper we present an overview of those projects and other long-term fire studies in Western Australia and Tasmania; focussing on their terrestrial invertebrate component and the value of long-term studies in elucidating fire effects. While a number of the projects are of a sufficient scale to study vertebrate responses, small plot sizes for some (designed with tree studies in mind) make them ideal for studying taxa that operate at smaller spatial scales. As a group, invertebrates are numerous, diverse, and play important functional roles in ecosystems (Beattie 1995; Raven and Yeates 2007). Their response to fire is poorly understood (New *et al.* 2010) and they are not often directly incorporated in forest management considerations (but see Robinson and Tunsell 2014). With changing management practices involving the use of fire we require a more sophisticated understanding of the impact of fire on this biodiverse and functionally important group (York *et al.* 2012).

While there have been a relatively large number of long-term fire studies initiated since 1950, few remain functional today. Here we present an overview of existing projects using fire in an experimental context, focusing on forest environments in southern Australia. We have defined long-term as having continued for more than 10 years (Lindenmayer *et al.* 2012), although we include one study of seven years as there is a commitment to ongoing monitoring. Not all projects have a published invertebrate component, but we include them for completeness and future reference. There are a number of similar projects in the tropical savanna landscapes of northern Australia; however, as the fire regimes are vastly different we have not included them here (see Williams *et al.* 2003; Andersen *et al.* 2014).

Study areas and Methods

Figure 1 shows the distribution of study sites across temperate and sub-tropical forests with aspects of projects that incorporate invertebrates summarised in Table 1.

Queensland – Bauple fire experiment

The Queensland Government (Department of Agriculture and Fisheries and Department of National Parks, Sport and Racing) maintain three long-term fire experiments in south-east Queensland. The Bauple fire experiment is located in Bauple State Forest, near Maryborough, in dry sclerophyll forest, dominated by spotted gum (*Corymbia citriodora* subsp. *variegata*). This experiment has three treatments (each a separate compartment) of annual burning, burning every three years on average, and no burning. The annual burn treatment was initiated in 1952 with the three year burn treatment commencing in 1973. The long unburnt area was last burnt in 1946, however after a wildfire burnt part of this area in 2006 additional monitoring plots were established.

Queensland – Peachester fire experiment

This experiment is located in Peachester State Forest south-west of Nambour, in wet sclerophyll forest, dominated by blackbutt (*Eucalyptus pilularis*). It has three continuing blocks each with three treatments (unburnt, two-year burn and four-year burn). Unburnt blocks were last burnt in 1969 with burning treatments commencing in 1971-2.

Queensland – Sub-coastal heathland experiment

The sub-coastal heathland experiment is located in Scientific Area 1 (near Beerwah) and in State Forest 451 (Mt Bilewilam, Cooloola, near Rainbow Beach), which is now part of the Great Sandy National Park. The vegetation is predominantly wallum heath, *Eucalyptus*/*Banksia* open forest and woodland. This experiment has three blocks, each with three treatments: burning every 3 years, burning every 5 years, and no burning. As each block represents a different vegetation type there is no true replication. The experimental treatments began in 1976 (Beerwah sites) and 1978 (Cooloola site).

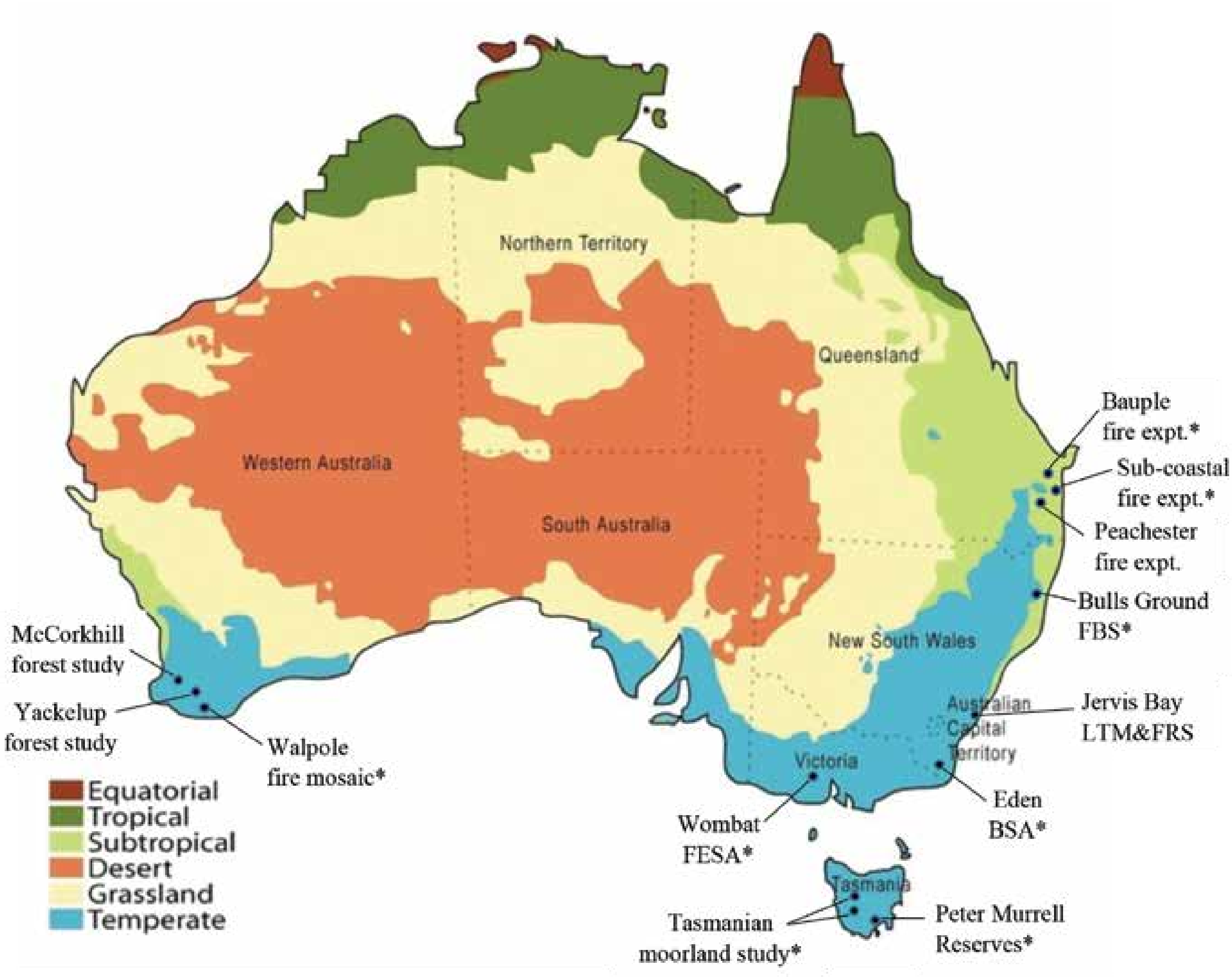

Figure 1. Location of long-term fire study sites within temperate and sub-tropical forests. * indicates sites with an invertebrate component.

While many aspects of these experiments have been published (e.g. Guinto *et al.* 2001; Lewis and Debuse 2012; Lewis *et al.* 2012) much of the work is ongoing. The effect of fire on ant communities has been assessed in Bauple State Forest where Vanderwoude *et al.* (1997a, b) investigated the effect of fire frequency on species richness and functional group composition. Eliott (2015) explored the use of Cerambycid beetles as bioindicators in Bauple State Forest. In heathland at Cooloola, Manwaring *et al.* (2015) compared the abundance of invertebrates (with a focus on ants) between a long unburnt site and sites that had been burnt at three and five year intervals.

New South Wales - Bulls Ground Frequent Burning Study

The F8/2.9 (Bulls Ground) Frequent Burning Study, currently managed by the Forestry Corporation of NSW, is located in Lorne State Forest in even-aged coastal blackbutt (*E. pilularis*) regeneration on the mid-north coast of New South Wales. The study was initiated in March 1970 when fourteen permanent research plots (each 0.1 ha. within a buffer zone of ~1 ha.) were established in areas of young regrowth (11 years old). Seven were randomly allocated as burning treatments (burnt), the remaining seven as control (unburnt) plots from which fire was excluded (7 × 2 randomised block design). Fuel reduction burning was implemented in autumn whenever fuel build-up permitted, generally every 3 years from 1970 – 1992 inclusive, then in 2000 and 2004. The burning regime is currently on hold while the project is reviewed.

In February 1991, two years after fire, surface active invertebrate communities were assessed by a single summer pitfall trapping program (York 1999a). The sites were again sampled two years after fire in February 1994, concentrating on invertebrates specifically utilizing the leaf litter layer (York 1999b). Results were initially reported at the taxonomic level of Order, with beetles, spiders, bugs, flies and ants subsequently analysed at species level (York 1999a, 2000). While these studies do not enable a description of changes over time, they do provide a unique opportunity to assess the long-term impact (20+ years) of this management practice. Later studies investigated the role of CWD in conserving fire-prone ant communities (Andrew *et al.* 2000), and the effects of fire on invertebrate-mediated decomposition (Brennan *et al.* 2009) and insect

Table 1. Summary of terrestrial invertebrate research undertaken at long-term fire research sites in temperate and sub-tropical Australian forest ecosystems.

State	Experiment name	Forest type	Experimental treatments	Studies	Taxa & Methods	Focus	Findings
QLD	Bauple Fire Experiment. Exp. 51, Bauple SF.	Dry sclerophyll forest	Annual burning (commenced 1952), 3 year cycle (commenced 1973) and long unburnt. Treatments not spatially replicated. Part of unburnt treatment burnt by wildfire in 2006 – new monitoring plots established.	Vanderwoude *et al.* 1997a,b	Ants with pitfall traps.	Species richness and functional group composition.	Richness higher on burnt treatments. Assemblage composition varied between treatments.
				Eliott 2015	Cerambycid beetles with flight intercept traps.	Species composition.	Beetle richness and composition varied between treatments.
	Sub-coastal Heathland Experiment. Mt. Bilewilam, Cooloola)	Low open eucalypt and Banksia woodland	3 year cycle, 5 year cycle and unburnt. Treatments commenced in 1978 and are not spatially replicated.	Manwaring *et al.* 2015	Terrestrial invertebrates using pitfall traps.	Ant abundance.	Ants considerably more abundant on frequently burnt treatments.
NSW	Expt. F8/2.9 Bulls Ground Frequent Burning Study	Wet sclerophyll forest (low productivity)	Randomised block design: 2 treatments (3 year cycle/unburnt) × 7 replicates. Treatments commenced in 1970, last burnt 2004. Currently under review.	York 1999a York 1999b	Terrestrial invertebrates with (a) pitfall traps and (b) litter extraction.	Abundance of beetles, spiders, bugs, flies and ants.	Assemblage composition of all groups varied substantially between treatments and between pitfall and litter samples.
				York 2000	Reanalysed ant data from York 1999a,b at the species level	Compared pitfall and litter extraction results and incorporating environmental predictors in the analyses.	Richness similar between treatments but composition substantially different. Composition influenced by habitat structure and associated levels of insolation.
				Andrew *et al.* 2000	Ants - litter extraction.	Compared ant fauna in litter adjacent to logs with that in open areas.	Ant fauna near logs on burnt sites similar to that in long unburnt areas.
			In 2000 the design was modified to a split-plot structure with burning withheld from some frequently burnt plots and fire introduced to some long unburnt plots.	Brennan *et al.* 2009	Invertebrates & fungi - litter bags.	Examined fire effects on invertebrate-mediated decomposition.	Fire influenced invertebrate abundance and composition, which in turn influenced decomposition rates.
				Christie & York. 2009	Arboreal invertebrates - canopy leaf sampling.	Compared rates of insect herbivory between treatments.	No effect of fire on leaf herbivory.
	Eden Burning Study Area	Dry sclerophyll forest (Timbillica Dry Shrub Forest)	Six treatments, randomly allocated to six experimental units in each of three blocks: unlogged no burn, logged no burn, unlogged frequent burn, logged frequent burn, unlogged routine burn, and logged routine burn. Study commenced in 1987. Project currently under review.	Andersen *et al.* 2009	Surface-active and arboreal ants - modified pitfall traps.	Reported at species level.	Richness increased with fire frequency and harvesting. Differences were most marked in the arboreal fauna.

State	Experiment name	Forest type	Experimental treatments	Studies	Taxa & Methods	Focus	Findings
VIC	Wombat Fire Effects Study Area	Dry sclerophyll forest (open to tall-open forest).	Randomised block design involving a long-unburnt control and four prescribed fire treatments randomly allocated within each of the five study Areas. Treatments involved a factorial combination of two fire seasons (autumn or spring), and two fire frequencies (nominally every 3 or 10 years). Study commenced in 1985. Note: Research reported in the various papers by Neumann, Tolhurst and Collett only used the Blakeville site (i.e. no spatial replication of treatment). York (2014) utilised the full experimental design (5 Areas).	Neumann & Tolhurst 1991	Pitfall traps and soil extraction - surface-active arthropods and earthworms.	Effects of single spring and autumn fires on abundance.	Short-term negative effects on abundance.
				Collett *et al.* 1993	Pitfall traps and soil extraction - surface-active arthropods and earthworms.	Two short rotation fires in spring.	Short-term negative effects on abundance for some groups.
				Collett and Neumann 1995. Companion paper to Collett *et al.* 1993	Pitfall traps – beetles to species level.	Two short rotation fires in spring.	No discernible negative effects for most groups; a reduction in numbers of Staphylinidae.
				Neumann *et al.* 1995. Companion paper to Neumann and Tolhurst 1991	Pitfall traps - beetles to species level	Single spring and autumn fire.	Some short-term changes detected, but no clear effects of fire treatment.
				Collett 1998	Pitfall traps – surface-active arthropods	Two short-rotation autumn fires.	Some short-term changes detected, but no clear effects of fire treatment.
				Collett 1999	Pitfall traps – surface-active arthropods	Three short-rotation spring fires.	Some suggestion that short interval spring fires might have a negative impact on some groups.
				Collett 2003. Collates and compares information from Collett *et al.* 1993 and Collett 1999	Pitfall traps – surface-active arthropods	Two short rotation spring and autumn fires.	Some short-term changes detected, but no clear effects of fire treatment.
				Collett and Neumann 2003	Pitfall traps – surface-active arthropods	Summary report.	See above.
				York 2014	Invertebrates - litter extraction.	Twenty-seven years of short and long rotation spring and autumn fires.	At the Ordinal level there were no effects of fire season, but some groups showed a negative effect of fire frequency.
WA	Walpole Fire Mosaic Project	Open sclerophyll forest and woodland interspersed with low-lying seasonally inundated shrublands and grasslands.	Long term monitoring project; commenced in 2004. Sites established to represent the range of vegetation types and fire histories.	Invertebrate monitoring data is currently being analysed and prepared for publication.	Mosaics project used a composite strategy of light trapping, foliage beating, area searching and pitfall trapping.	Using a BACI design to investigate effects of a fine-grained fire mosaic.	Invertebrate data currently undergoing analysis.
			From 2006-8 an associated study used the mosaic sites and adjoining forest areas.	Wittkuhn *et al.* 2011	Pitfall traps – ants and beetles to species level.	Used a retrospective approach to examine a range of inter-fire intervals from short (≤5 yrs.) to very long (30 yrs.).	Some evidence of compositional change between fire interval categories.

State	Experiment name	Forest type	Experimental treatments	Studies	Taxa & Methods	Focus	Findings
TAS	Peter Murrell Reserves study	Black peppermint, heathy woodland, heath and buttongrass moorland.	Annual monitoring at sites in the fire mosaic since 2010.	Invertebrate monitoring data is currently being analysed and prepared for publication.	Pitfall traps.	Pre- and post-burn assessments of burnt and adjacent unburnt blocks.	Invertebrate data currently undergoing analysis.
	Tasmanian Mooreland Study	Lowland and montane moorelands dominated by sedges and shrubs surrounded by woodland and forest.	Long-term monitoring post-fire: lowland sites (7 years), montane sites (14 years). BACI design: Burning treatment randomly allocated to 3 (of 6) blocks at each site.	Driessen 2016	Annual summer sampling with pitfall traps and sweep nets. All taxa to Ordinal level.	Longitudinal study to monitor post-fire changes over time.	Taxa declined in abundance immediately after fire, with most recovering by 6 years. Composition of foliage-active invertebrates at the lowland site differed between burned and unburned plots 14 years after fire.

herbivory (Christie and York 2009).

New South Wales – Eden Burning Study Area

The Eden Burning Study Area (EBSA) was established in dry sclerophyll forest at Yambulla State Forest in southeast NSW in 1987-8 to examine the effects of timber harvesting and prescribed burning on vegetation structure and floristics, fuel characteristics and some faunal groups. The EBSA was designed to study effects at an operational scale, taking into account spatial variation and physical environmental factors; it is also currently managed by the Forestry Corporation of NSW. The experiment was initially established as a two-factor randomised block design, however this was subsequently modified so that the combinations of logging and burning were implemented as six treatments, randomly allocated to six experimental units in each of three blocks. The treatments were: unlogged no burn, logged no burn, unlogged frequent burn, logged frequent burn, unlogged routine burn, and logged routine burn. Experimental units ranged in size from 8-56 ha (mean = 32 ha), with 'frequent burn' comprising a two-year inter-fire interval and 'routine burn' a 3-5 year interval in regrowth stands and 4-7 years in unlogged stands. For full details of the experimental design see Binns and Bridges (2003).

A number of studies have been conducted on vascular plants (e.g. Penman *et al.* 2008; Penman and Towerton 2008) and a number of vertebrate studies are ongoing. Andersen *et al.* (2009) investigated the long-term impact of logging and burning, and their interaction, on ant communities; sampling both ground-dwelling and arboreal fauna.

New South Wales – Jervis Bay long-term monitoring and fire response study

In 2003 a long-term monitoring project was initiated within Booderee National Park near Jervis Bay. Sites cover a wide range of vegetation types including forest, woodland, heathland and sedgeland. A wildfire in late 2003 burnt most (134) of these sites, initiating a long-tern post-fire monitoring program. A range of vertebrate taxa are being monitored (see http://fennerschool.anu.edu.au/research/projects/jervis-bay-long-term-monitoring-and-fire-response-study).

Victoria – Wombat Fire Effects Study

The study incorporates five locations (known locally as the 'Fire Effects Study Areas', FESA) within a 25 km radius in the Wombat State Forest; an area of native eucalypt forest about 100 km north-west of Melbourne, Victoria. Vegetation consists of an overstorey dominated by Messmate Stringybark (*E. obliqua*), Narrow-leaved Peppermint (*E. radiata*) and Candlebark (*E. rubida*), and an understorey with sparse shrubs, Austral Bracken (*Pteridium esculentum*) and native perennial grasses, forbs and rushes.

The experiment 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, see Tolhurst and Flinn 1992). 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, autumn low-frequency, spring high-frequency, and spring low-frequency. 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. The study sites are currently managed by the Victorian Department of Environment, Land, Water and Planning.

FESA is a multi-disciplinary study investigating the effects of fire on a range of taxa and processes (see Tolhurst and Flinn 1992; Department of Sustainability and Environment 2003). Invertebrate studies were systematically conducted from 1992-9 at one of the five

Areas (Blakeville); monitoring assemblages over time as successive fire treatments were applied (reviewed by Collett and Neumann 2003). The focus was initially at low taxonomic resolution (Order) with beetles subsequently analysed at species level. All five Areas were sampled in 2012, focussing on the effects of 27 years of fire treatments on litter-dwelling invertebrates (York 2014).

Western Australia – Walpole Fire Mosaic Project

The Walpole Fire Mosaic Project is an operational trial implemented in native forests (London and Surprise forest blocks) 40 km north-east of the town of Walpole in south-west Australia, and is currently managed by the Western Australian Department of Parks and Wildlife. The 50,000 ha. study area is comprised mainly of open sclerophyll forest and woodland interspersed with low-lying seasonally inundated shrublands and sedgelands. The area was stratified according to three dominant landform systems (Caldyanup, Collis and Lindesay) and three fire treatments: no planned fire, routine fire management (5-10 year fire intervals) and fine-grained mosaic burning (small patches burnt every 2-3 years). The project aims to determine whether: a) a fine-grained fire mosaic of post-fire age-classes can be created by the frequent and targeted introduction of fire into the landscape (patch-burning) and, b) this enhances biodiversity conservation through space and time. Monitoring plots were established in 2004 using a Before-After-Control-Impact design, to record the responses to the shifting fire mosaic over time, both at the patch- and landscape-scale. Data from monitoring activities is currently being analysed and prepared for publication. Wittkuhn *et al.* (2011) utilised a selection of monitoring plots from the experiment, coupled with other sites from adjoining forest areas, to investigate the effect of inter-fire interval on a range of taxa, including invertebrates. In 2006-8 they used a retrospective approach with vegetation type (shrubland/forest) and fire interval sequence (short-short/mixed/long-long/very long) as factors to examine effects on abundance and composition, with a focus on ground-active ants and beetles.

Western Australia – McCorkhill and Yackelup forest studies

The McCorkhill forest study is located 22 km west of the town of Nannup in the Blackwood Plateau forest ecosystem. The site is characterised by an overstorey of jarrah (*E. marginata*) and marri (*Corymbia calophylla*) and lies in a high rainfall area (mean annual rainfall 1,050 mm). The site has a history of light selection logging since the mid-1900s and a history of prescribed burning at 5-10 year intervals since the 1950s, with an occasional wildfire. The Yackelup forest study is located 45 km east of the town of Manjimup in the Jarrah Forest South forest system. It also is dominated by jarrah and marri, but is less productive due to its location in a low rainfall area (average annual rainfall 750 mm). The site was lightly logged during the 1960s and 70s and since the 1950s has experienced low intensity prescribed burns in autumn and spring at 7-12 year intervals. Experimental sites were established at both of these study areas in 1986 to investigate the effects of frequent fires in autumn and spring, infrequent spring fires and long-term fire exclusion, on vascular plant communities (Burrows *et al.* 2003, 2010). Long-term monitoring data are currently being analysed and prepared for publication.

Tasmania – Peter Murrell Reserves study

This project is based in two reserves located 12 km south of Hobart. The reserves consist of a variety of vegetation types with substantial areas of black peppermint (*E. amygdalina*), heathy woodland, heath and buttongrass moorland (Driessen *et al.* 2010). Although little is known about previous fire history, after an intense wildfire in 1988 prescribed burning has been carried out on the reserves in autumn and spring to create a mosaic pattern of fire ages. Vegetation, birds, mammals and invertebrates have been monitored annually at a range of sites across the reserves since 2010, with invertebrate data currently being analysed at the Ordinal level (M. Driessen *pers. com.*).

Tasmania – Moorland study

This project is based on two sites: a lowland moorland near Lake Pedder and a montane moorland near Lake St Claire. The vegetation at both sites is dominated by sedges and shrubs, with some grasses and herbs (see Driessen and Kirkpatrick 2017). Although predominantly buttongrass (*Gymnoschoenus sphaerocephalus*), we have included this study as the moorlands are located in a matrix of forest and woodland and are burned, in part, to provide protection to those forests. The project used a longitudinal approach with a BACI design to investigate the long-term (lowland – 7 years and montane – 14 years) response of ground- and foliage-active invertebrates to planned fire (Driessen 2016). The sites have also been utilised to investigate the effects of time since fire (1-65 years) and fire frequency (1-4 fires) (Driessen and Kirkpatrick 2017). Both studies analysed invertebrate data at the Ordinal level and used habitat data as predictors when interpreting responses.

Results and Discussion

Among its many benefits, long-term ecological research allows us to both quantify environmental change and to better understand responses that take time to be expressed (Lindenmayer *et al.* 2012). For example, in the Bulls Ground experiment the observed impacts of frequent burning on living tree carbon stocks were not immediate, with significant differences only being recorded after ~15 years (or five fires) of frequent burning (Collins *et al.* 2014). Similarly, Penman and York (2010) used a 22-year dataset from that experiment to demonstrate the dynamic nature of climate and fire history on rates of litterfall and decomposition, and hence fuel loads, over time. Such findings demonstrate the importance of long-term experiments because major temporal changes in habitat structural complexity and micro-habitat associated with repeated fire regimes are only likely to be apparent over a longer time frame. Potential changes to the population equilibrium of a species as a result of a prescribed fire regime are more difficult to accurately detect in short-term studies that focus on only one or two burns, particularly given the confounding short-term changes to habitats immediately after a prescribed fire.

Although the Wombat Forest FESA sites were sampled systematically over time as the experimental fire regime expressed itself (see Collett 2003), the studies presented in this overview have primarily used the long-term nature of the experiments to look at the cumulative effects of specific elements of the fire regime. While using long-unburnt sites as an experimental control has its limitations (see Wittkuhn *et al.* 2011), the fire frequency treatments described here approximate the upper and lower extremes that may be expected with many temperate and sub-tropical eucalypt forest ecosystems (Gill 2012). As such they provide some guidance as to the range of responses to altered fire regimes that we might expect.

Most of the studies reported here investigated the response of invertebrates to variation in inter-fire interval. Increasing fire frequency usually produces 'winners and losers' (Moretti *et al.* 2004). For example, York (1999a) found that, compared to long unburnt sites, frequently burnt sites had fewer mites (–31%), insect larvae (–35%), flies (–58%) and beetles (–31%) while they had more bugs (+77%), ants (+250%) and spiders (+33%). These changes often express themselves at the community level, with fire producing changes in Ordinal (taxon) richness at sites (York 1999a, b), although these patterns often don't manifest themselves until after several short-interval fires (Wittkuhn *et al.* 2011) and then are often short-lived. For example, at the Wombat FESA, surface-active invertebrates returned to long-unburnt levels within three years (Neumann and Tolhurst 1991; Collett and Neumann 2003) with earthworms, springtails and flies being the most affected groups. This pattern was consistent over time after repeated fires (Collett *et al.* 1993; Collett 1998, 1999, 2003). At the species level, beetles showed no changes in richness after one and two short-rotation spring fires (Neumann *et al.* 1995; Collett and Neuman 1995). In contrast, York (1999a) reported that after seven short-rotation autumn fires beetle species richness was, on average, 27% lower on burnt plots compared to unburnt plots, with accompanying changes in assemblage composition. From short-term studies based in Western Australian, Majer (1980, 1985) concluded that spring burning may be more detrimental to the soil-surface fauna than autumn burning but an understanding of the phenology (seasonality) of invertebrate abundance and activity is needed to fully assess the potential impacts of burning (Koch and Majer 1980; Robbins and Myers 1992; Majer and Heterick 2017 *this volume*).

An increase in ant activity and abundance after single and multiple fires is commonly reported, with this change often driven by particular genera such as *Iridomyrmex* and *Anonychomyrma* (Vanderwoude *et al.* 1997a; Andersen *et al.* 2009; Manwaring *et al.* 2014) or *Rhytidoponera* (York 2000), depending on the forest type. These studies show that ant communities are mediated largely through the degree of ground-level insolation and associated temperature stress as a function of vegetation structure (York 2000; Hoffmann & Andersen 2003), which is dependent on the long-term fire regime. These consistent patterns across experiments have lent support to the use of ants as bioindicators of ecosystem disturbance and recovery (see Hoffmann & Andersen 2003). Ant species richness might increase dramatically (Vanderwoude *et al.* 1997a; York 2000) or stay much the same (Andersen *et al.* 2009), with this response a likely outcome of the spatial patchiness of the fire (for example, fire severity is far more heterogeneous in operational-scale experiments such as the Eden BSA (Penman *et al.* 2007)).

The detection of treatment effects also varied depending on the component of the invertebrate fauna sampled. Andersen *et al.* (2009) reported that ant species richness increased with increasing fire frequency for the arboreal fauna, but not the terrestrial element. This is most likely a consequence of differences in species composition of the two assemblages; as was found by York (1999a, 2000) for ground- and litter-dwelling invertebrates (see also Majer 1997). Leaf litter supports many groups with small populations, such as specialist predator and cryptic ant species, which are susceptible to frequent fire (York 2000). Moisture-dependent groups such as amphipods and insect larvae are also vulnerable to increases in fire frequency (York 2014). Leaf litter associated with logs in frequently burnt areas may however provide a refuge for vulnerable ant species (Andrew *et al.* 2000).

Not all invertebrates are however fire sensitive, and for others there is an interaction between elements of the fire regime. In a study of the effects of fire frequency and season on the abundance of litter-dwelling invertebrates York (2014) identified three general responses. Firstly, some taxa (cockroaches, centipedes, diplopods, bugs, ants, wasps and barklice) show no long-term response to fire. Secondly, some (spiders, springtails and woodlice) show a fire effect, irrespective of fire frequency or season. Lastly, some (mites, amphipods, spiders, beetles and insect larvae) show a negative response to increased fire frequency. None of these groups showed a specific season of fire response, although there was an interactive effect of frequency and season for beetles, with lower mean abundance on sites experiencing high frequency fires in spring.

Conclusions

Mediterranean climate regions around the world 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 (Mouillot *et al.* 2002). A perceived increase in threat of wildfires is likely to see an escalation in the use of prescribed burning (both in extent and frequency) by land managers to improve suppression capability (Driscoll *et al.* 2010; Penman *et al.* 2010). As our biodiversity faces increasing threats from changing climate, pests and weeds, and altered fire regimes, it is essential that we have management strategies underpinned by rigorous science (York and Friend 2014), however an understanding of the responses of a range of plants and animals to fire regimes represents a major knowledge gap in fire management (Driscoll *et al.* 2010). This particularly applies to terrestrial invertebrates which, despite their extraordinary diversity and functional importance, are often overlooked in fire effects studies (New *et al.* 2010).

This overview summarises a limited number of existing long-term research projects which address that issue. These studies across a range of locations and forest types have both illustrated the resilience of many invertebrate groups to disturbance by fire, but also provided insight into the vulnerability of some taxa to an altered regime. Studies of the effects of fire frequency, an important component of the fire regime, have dominated; with only a single project including a consideration of the season of fire (Collett and Neumann 2003; York 2014).

Similarly, the response of only a limited number of taxa, primarily beetles and ants, has been investigated at the species level. Coarse-grained Ordinal level results can often adequately answer broad-scale management questions, however species-level information may be necessary to identify subtle responses to fire (see York 2012). With many specimens retained and curated, it is feasible, with sufficient resources, to broaden existing analyses to include other taxa with likely vulnerabilities to fire-induced habitat changes, with a focus on finer-scale taxonomic responses. Groups associated with decomposition and nutrient cycling would seem an obvious priority (York *et al.* 2012), with taxa involved in other essential ecosystem services such as pollination a focus for future investigations (see Brown *et al.* 2017). Currently, in Western Australia, invertebrates are routinely monitored as part of forest operations in Jarrah forest (FORESTCHECK; see https://www.dpaw.wa.gov.au/about-us/science-and-research/landscape-conservation-research/183-forestcheck Accessed 25/1/17). It would seem pertinent to build on the historical legacy of existing long-term fire experiments to incorporate monitoring of selected invertebrates. From this baseline position the development of explicit questions would then suggest target taxa (see Andersen 1999; York 2012; Eliott 2015) which would form the basis of ongoing long-term fire effects monitoring programs.

Long-term ecological studies of this kind are critical for providing key insights into the dynamic nature of ecosystems (Lindenmayer *et al.* 2012); it is essential that land management agencies continue to support them and integrate their findings into future fire mitigation strategies. 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). 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). Long-term experiments such as those described in this paper are therefore critical to a better understanding of the implications of such changes in the fire regime for biodiversity.

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