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The effect of fire-management on invertebrates within a South African savanna

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Abstract

Fire plays a key role in determining the structure and function of savanna ecosystems, without which the characteristic open grassland would be lost, along with the high biodiversity it supports. Over recent decades human development has meant that savanna systems have become heavily utilised, requiring burn management to be undertaken. As savannas are regarded as fire-prone systems, this practise had become an unquestioned tradition. Despite the wide use of burn regimes as a management tool, little is known about the effect of burning on non-focal taxa.

This study looks at both the long and short-term effects of burning, in a South African game reserve, on invertebrates within a patch mosaic structure. Since invertebrates encompass a broad group of organisms, analysis was divided into three levels based upon location within the ecosystem. Changes in the abundance and diversity of invertebrates at ground level, grass level and tree level were studied. The short-term study showed that ground invertebrate abundance increased following a burn event, whereas, grass and tree invertebrates showed declines. Analysis of invertebrate abundance and diversity within six different burn ages enabled the long-term effects of a patch mosaic burn regime to be monitored. Ground invertebrate abundance was high in recently burnt patches compared to undisturbed sites. Grass invertebrates declined immediately following the burn event in the short-term study; however, abundances remained similar across the burn ages in the long-term study. In contrast to grass and ground invertebrates, the abundance of tree invertebrates increased as the level of disturbance decreased; with the highest abundance being found in the unburnt site.

This study provides a general understanding of the effect burning can have on the invertebrate community; while opening new doors into a relatively untouched subject. Future research into this would be beneficial for the maintenance of the complex savanna ecosystem.

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Introduction on the effects of fire management on all taxa in savannas

Chapter 1: Introduction on the effects of fire management on all taxa in Savannas

Savanna ecosystem and fire management

Savanna ecosystems cover 65% of Africa, as well as large portions of Australia and South America (Archibold, 1995). The key drivers of change within a savanna are: variable rainfall, natural disturbances (such as lightning strikes) and herbivore grazing, which makes them naturally heterogeneous environments (Mistry, 1998; Parr and Chown, 2003). The savanna ecosystem is characterised by sparsely populated trees, providing an open canopy over continuous grassland. There are four major determinants of this grassland biome: (1) plant available moisture, (2) plant available nutrients, (3) fire and (4) herbivory (Frost et al., 1986). Fire plays a major role in determining the structure, function and dynamics of the savanna system, enabling the establishment and maintenance of this biome over other vegetation types (Bond and Parr, 2010; Parr and Chown, 2003). Without fire, substantial areas of savanna grassland could develop into closed canopy woodland due to bush encroachment (Bond *et al.,* 2005). The occurrence of frequent fires over the past eight million years has also seen the evolution of fire-adapted and fire-dependent flora and fauna; showing the importance of fire in this ecosystem (Bond *et al.*, 2005).

Studies have shown the frequency of natural fires is dependent on the accumulation of grass biomass, or fuel load (Bond and Van Wilgen, 1996). Govender et *al.* (2006) showed that grass biomass accumulates within 4-5 years after a burn event, causing a decline in grazing quality and loss of grass vigour. The fire return period in South Africa is between 3-6 years; but with the fuel load accumulating faster, leaving burning to natural causes could potentially lead to large areas of savanna burning at high intensities (Bond and Van Wilgen, 1996). High intensity burns can cause damage to other landscapes as well as being more harmful to the savanna itself. Therefore, increasing the fire frequency has become a common management practise to avoid wide spread, high intensity fires (Govender *et al.,* 2006).

Globally savanna regions are modified by human development, including subsistence agriculture, mining and game management (Andersen *et al.,* 1998). Regardless of human interference, fire still plays a role in the maintenance of savannas; however, the ignition and timing of these events is now infrequently due to natural causes. The majority of the fires in savannas are lit by people in the context of land clearing, property protection and livestock management. Prescribed burning is also widely used for conservation management, and is an essential ecological factor in the maintenance of savanna ecosystems (Trollope and Trollope, 2004). As a management tool, fire removes the accumulated dead plant material and stimulates growth of new leaves, with higher nutritional value (Dörgeloh, 1999). Despite regrowth being of superior foraging value, it is limited by the level of soil moisture. Consequently, the timing of these fires is essential for optimum regrowth (Parrini and Owen-Smith, 2010). Frequency and method of burning is a topic of discussion both within South Africa and globally. Within South Africa, a frequency of a 4-5 year burn cycle is often used to reduce the fuel load (Govender *et al.*, 2006). The main three burning systems used within South Africa are:

(1) **Lightning burning system** – Primary ignition source is lightning, with little or no human interference.
(2) **Patch mosaic burning system** – Burning a series of pre-defined patches on rotation, maintaining diversity of the land but also following a clear burning pattern
(3) **Range condition burning system** – Burning pattern and frequency is dependent on vegetation condition and a prediction of how the grassland will respond to the burn (Govender *et al.*, 2006).

Overall, burning controls the balance between grass and woody plants (Govender *et al.,* 2006), as well as alleviating the nutritional stress to mammals which occurs during the dry season when grasses become senescent (Hobbs and Spowart, 1984; Vemeire *et al.,* 2004).

Due to the importance of fire as a management tool, research into the effects of burning on the biotic and abiotic components of the ecosystem, have been conducted in savanna regions since the early twentieth century (Trollope and Trollope, 2004).However, despite the use of burning regimes in land management being well established (and in many cases it is an unquestioned tradition; Gillon, 1983); information on the effect of fire in these biomes is often lacking. Research into the effect of fire has been directed towards vegetation and mammal studies, with limited focus on birds and very few studies looking into the effects on reptiles, amphibians and invertebrates. Therefore, many responses to fire are only understood in more general terms.

The remainder of this introduction reviews work that has been published on vegetation, mammals, birds and invertebrates. It is based upon the identification of 124 primary research papers in peer-review literature as well as reviews and books, identified from bibliographic searches. Following on from this, the current level of primary research undertaken at each taxonomic group has been presented graphically.

Effect of fire management regimes

Vegetation

The overall goal of fire management in conservation is usually to maintain healthy populations of a focal species. However, in practise, it is difficult to monitor all species. The impact of fire on savanna vegetation has dominated fire management strategies in conservation and, hence, has been a key element in the majority of research. While rainfall is regarded as having the primary influence on vegetative productivity (Bredenkamp *et al.*, 2002); fire and grazing are key factors in determining vegetation structure and composition (Scholes and Walker, 1993).

Fynn *et al.* (2004) assessed the effect of burning and mowing on grass and forb diversity in a grassland ecosystem. Both are forms of disturbance that enable new leaf growth from the disturbed grasses. Mowing, however, does not remove the dead plant material that has accumulated, and it remains as litter. This study showed that burning in the summer, before the rainy season, increased grass species richness by 22% relative to triennial burning; whereas, mowing caused a decrease in species richness of 37%. Removing dead material and competition for light are therefore, key factors in maintaining high species richness, and allowing colonisation of grass species to a burnt area. Other studies have supported this theory, showing that burning reduces the intensity of competition for limiting resources, by modifying the abundance and vigour of competitive dominants (Wilson and Tilman, 1993; Collins *et al.*, 1998). Grass species richness also declines in undisturbed areas, in contrast to forb species richness, which appear unaffected by a lack of disturbance (Fynn *et al.,* 2004). Wilson and Tilman (1993), Collins *et al.* (1998) and Fynn *et al.* (2004) all support the supposition that savanna ecosystems depend on frequent fire disturbance to maintain diversity.

Frequent fires increase woody plant mortality; reducing the competition for resources, which benefits grass species. In a reserve, this prevents bush encroachment, ensuring that the density of trees remains sparse, to maintain an open canopy (Van Wilgen *et al.* 2011). Bush encroachment typically results in reduced grass species richness due to increased competition for resources, as well as removing some of the niches that the grassland ecosystem provides.

It is well understood that immediately following a burn event, palatable grasses increase (Gureja and Owen-Smith, 2002), and that the consequent decline in dead tissue results in greater forage efficiency in burnt areas (Hobbs and Spowart, 1984). This effect can last for an extended period following the burn. The regrowth that occurs following a burn has been shown to be of high nutritional quality (Hobbs and Spowart, 1984; Dörgeloh, 1999), although the quantity is often relatively low. The height and biomass of the regrowth increases progressively once adequate rains have fallen (Gureja and Owen-Smith, 2002).

Mammals

In southern African savannas, this new growth of palatable grasses following fire (Dörgeloh, 1999), is valuable in winter and spring when food quality and quantity are limiting for mammals (Tshuma *et al*., 1988). However, it has been shown that the relative use of burnt areas varies between ungulate species. This variation in foraging habits appears to be due to either morphology or competitive displacement (Grobler, 1981; Rowe-Rowe, 1992). Grobler (1981) noted that shorter grass grazers, such as impala (*Aepyceros melampus*) and blue wildebeest (*Connochaetes taurinus*), keep grass lengths short in new burns, thus preventing species that seek taller vegetation (e.g. roan (*Hippotragus equinus*), zebra (*Equus burchelli*) and Lichtenstein hartebeest (*Alcelaphus lichtensteinii*)), feeding on the new burn (Gureja and Owen-Smith, 2002). This study showed a temporal separation of feeding on the burn is generated through the morphological requirements for grazing. Gureja and Owen-Smith (2002) also noted that, both prior to a burn, and following it, the five ungulates studied (roan, tsessebe, Lichtenstien hartebeest, sable (*Hippotragus niger niger*) and zebra) exhibited a degree of ecological separation in terms of the landscape regions that they occupied, related in part to local geology. This suggests that burning does not necessarily result in an immediate influx of ungulates.

Roans have been shown to graze to a greater extent in burnt areas with a regrowth height of at least 60mm (Heitkönig and Owen-Smith**,** 1998). Sable show slightly different foraging requirements, and have been recorded moving into burnt areas only when vegetation exceeds 60-70mm (Grobler, 1981). This supports other work showing that sable seldom used the burn areas (Gureja and Owen-Smith, 2002). The limited use of the burn by sable may be due to competition between ungulates for the high quality vegetation on the burn (Parrini and Owen-Smith, 2010). In addition, impala and wildebeest may indirectly compete with sable for regrowth forage as they preferentially feed on the shorter, initial foliage, and prevent further growth. In contrast, a study at Pilanesberg National Park, South Africa, showed that, following hillside burning, sable moved into these patches, utilising the new burn (Magome *et al.*, 2008). These studies suggest that species specific preferences exist in the use of burnt areas, which is related not only to the length of vegetation but to the burn's geographical location. However, the variation among studies suggests further research is required to fully understand these species requirements, and to better understand both the long and short-term impacts of burning on ungulates and other fauna.

The increase in higher quality vegetation on a burn means that large mammalian herbivores can graze for longer in one patch, and spend less time searching for palatable grass due to the new growth (Parrini and Owen-Smith, 2010). This may alter their energy expenditure and therefore, body condition. Sables have been shown to graze preferentially on a previous year's burn rather than adjacent new burns with insufficient regrowth (Parrini and Owen-Smith, 2010). It is clear that ungulates select forage based on a number of factors. Therefore, for management planning it is important to understand all parameters, which affect graze selection for mammals, to be able to plan sustainable and efficient burn regimes.

As mentioned above, fire regimes in game reserves often have a focus on supporting large mammalian herbivores; with burning aiming to maintain vigour and palatability of the grass sward (Kraaij and Novellie, 2010). The maintenance of other biodiversity is therefore a secondary objective. Van Wilgen *et al.* (2004)

advised that, for most management objectives, fires should be burnt following the first rains that initiate the wet season growth. However, burns at this time are of limited value to mammalian herbivores as the rains facilitate growth of unburnt areas as well. Therefore, to alleviate nutritional stress, burning should be planned before the rains, to provide a small amount of high quality flora before the main flush of natural growth. For the purpose of both ungulate grazing and for optimising biodiversity, it appears that a patch mosaic of burns is the most beneficial landscape scale management strategy, providing newly burnt areas for grazing before the rains, but also maintaining older vegetation patches. This allows herbivores to partition time between high quality low quantity vegetation, and low quality high quantity sites (Brockett *et al.* 2001; Vemeire *et al*., 2004), as well as maintaining a wider range of habitats and niches for other organisms.

A few studies have assessed the effect of fire management on small mammals. Such populations are sensitive to fire and can change drastically in response to burning (Andersen, *et al.,* 2012). Considering their sensitivity, the effects of fire on such species should be closely monitored. However, to date, there has been limited work, particularly in southern Africa (Yarnell *et al*. 2007). Small mammals often survive the initial effects of the fire by sheltering in underground holes or unburnt patches (Yarnell *et al.*, 2007; Yarnell *et al*., 2008). However, over time, populations decline following fire (Fuller and Perrin, 2001), which is thought to be the result of the changes in vegetation structure causing emigration and increased exposure to predators (Clark and Kaufman, 1990). For example, *Saccostomus pratensis* appeared to survive well following the burn event, but a steady decline was noted by Yarnell *et al.* (2007) in the three months following the fire. On the other hand, Yarnell *et al.* (2007) also found that the reduction in small mammal densities following fire were only temporary for other species, for example *Saccostomus campestris* and *Mus indutus*, with populations recovering under favourable conditions. Therefore, in terms of threats to small mammals, burns are only harmful in the short-term. However, burns might be more harmful at night, when many small mammals are active, increasing the risk of direct mortality. Lightning ignited fires, which occur in summer, may also impact populations severely by reducing their breeding resources (Yarnell *et al*. 2007).

Birds

Birds are highly mobile species, and therefore, direct impacts of burning are low (Lawrence, 1966; Bendell, 1974). However, as some bird communities are driven by changes in vegetation (MacArthur and MacArthur, 1961; Bouwman and Hoffman, 2007) fire will have a significant, although indirect, impact on birds. Valentine *et al.* (2007) showed the importance of vegetation structure on bird assemblages, suggesting that bird species abundance increases or decreases according to their preferred habitat structure, which is partly determined by fire (Woinarski and Recher, 1997; Davis *et al.,* 2000; Chalmandrier *et al.,* 2013).

In general, avian species richness and densities increase immediately following the burn, compared to an unburnt control site; with more species being recruited to the burnt areas than displaced by burning (Mills, 2004; O'Reilly *et al.,* 2006; Bouwman and Hoffman, 2007). This may be because birds, being highly mobile species, are able to respond rapidly to changes in habitat or food availability (Mills, 2004; Smucker *et al.* 2005). For example, short-term increases of granivorous species on recently burnt sites have been attributed to the release of seeds following the fire, for example pale-headed rosella (*Platycercus adscitus*) (Hutto, 1995; Valentine *et al.*, 2007). Similarly, the removal of dense understory vegetation may increase exposure of seed resources for granivores, in turn attracting more individuals to the site due to increased food availability (Valentine *et al.,* 2007).

Likewise, fire adapted vegetation in savannas can affect the resource abundance for nectivores. Post-fire flowering events may be attracting nectar-feeding species (Recher *et al.,* 1985); however, Valentine *et al.* (2007) found that although there was an increase in nectivores post-burn (for example the little friarbird (*Philemon citreogularis*)) there was not a conspicuous flowering event post-burn. As many non-obligatory nectivores include invertebrates in their diet, the increase in these species on post-burn sites may be due to a temporary shift in diet from nectar to invertebrates (Higgins *et al.,* 2001). Post-burn there is an immediate increase in insect carcasses that non-obligatory nectivores may be utilising (Daubenmire, 1968).

Overall, the general increase in bird diversity is believed to be due to enhanced heterogeneity created by the fire (Bouwman and Hoffman, 2007). However, the response pattern will vary depending on the feeding guild, size, and habitat requirements of each species. The initial increase in species diversity and abundance post-burn is partly due to opportunists being attracted to the burn. Many take advantage of greater accessibility to food such as insects, small mammals and reptiles disabled by the burn (Bouwman and Hoffman, 2007). These opportunists, such as cattle egrets (*Bubulcus ibis*) and black-headed herons (*Ardea melanocephala*), decline once food sources are depleted, and therefore, their presence is only temporary and periodic. This is because they do not remain on the burn overnight; they travel from their roosts to the burn to feed. Many bird species use the burn in this way, for example helmeted guineafowl (*Numida meleagris*), northern black korhaan (*Afrotis afraoides*) and swainson's spurfowl (*Francolinus swainsonii*) - only being present on the site during the day, and returning to vegetation cover on nearby unburnt plots in the evening (Bouwman and Hoffman, 2007). These post-burn colonisers often reduce visits to the burn site once vegetation begins to recover. Other opportunists come to the burn to take advantage of the newly open landscape for breeding opportunities, e.g. temminck's courser (*Cursorius temminckii*) and crowned lapwings (*Vanellus coronatus*) (Parr and Chown, 2003). Again, many of these colonisers move on following vegetation regrowth and upon completion of breeding.

Immediate post-burn opportunists are adapted to track variable and shifting resource bases, such as these burnt grassland patches (Dean, 1987). In contrast, some bird species (such as the black-chested prinia (*Prinia flavicans*)) are site-tenacious, and - although they are initially displaced by the fire front - they return to their territories quickly (Bouwman and Hoffman, 2007). Competition can therefore arise following a burn between these site-tenacious birds and opportunistic colonisers. One example is the crowned lapwing; this species will fight to attain territories by acting aggressively to other birds (Bouwman and Hoffman, 2007). This competition can cause decline in some species abundances, showing that fire can affect some species negatively.

Long-term responses of birds are poorly understood, with very few longitudinal studies being conducted (Driscoll *et al.,* 2010). However, some studies have noted a decline in avian species richness and abundance, following the short-term increases previously mentioned (Valentine *et al.,* 2007). As the abundance and accessibility of food resources and breeding habitat declines, due to vegetation recovery, those birds initially attracted to the burn area disperse

(Woinarski and Recher, 1997). Bouwman and Hoffman (2007) noted that species richness and densities returned to initial conditions after a few months. What is less well understood is how repeated periodic fires effects the vegetation structure in the long-term, influencing the suitability of the habitat for birds in this dynamic system (Valentine *et al.,* 2007).

Vegetation structure directly and indirectly affects bird diversity and abundance. Direct effects include providing cover from predation, and vegetation requirements for nesting and foraging (Brawn *et al.* 2001; Parr and Chown, 2003). However, vegetation structure also affects invertebrate diversity and abundance, therefore, indirectly affecting the abundance of insectivores on the site. Fire may reduce the amount of vegetation that remains on the land. However, those plants and seeds that do remain are often well adapted to fire events and often produce flushes of new growth in the form of epicormic shoots, vegetative regrowth and resprouting (Gill, 1981; Whelan, 1995, Valentine *et al.*, 2007). This new growth can attract arthropods (Force, 1981; Swengel, 2001), which in turn temporarily increases food resources for insectivorous birds. Other studies have suggested that arthropod abundance is resilient to the effect of fire (Parr *et al.*, 2004; Andersen *et al.*, 2005), which would mean that changes in insectivore abundance may not be affected by invertebrate abundance. This resilience is well documented; however, the short-term changes in arthropod abundance immediately following the burn may promote the initial flush of birds seen on burn sites, for example lilac-breasted rollers (*Coracias caudatus*) and yellow throated miners (*Manorina flavigula*).

The variation in results across the current range of studies shows that the understanding of invertebrate response is limited. The majority of passerines and non-passerines feed on invertebrates at some time in their life-cycle. Most chicks are fed invertebrates by their mother, or have invertebrates as a primary or secondary food source. Hence the changes seen in birds following a burn event are closely linked to changes seen in the invertebrate community. It is therefore clear that, to understand the effect of fire on birds, the effect of fire on invertebrates needs to be investigated.

Invertebrates

Invertebrates include all animals apart from the subphylum Vertebrata, with May (1988) estimating that 97% of animal species are invertebrates. Despite the diverse nature of this group, very few studies have been published on invertebrate responses to fire (Swengel, 2001; Parr *et al.,* 2004). However, with the increased focus on holistic effects, understanding the response of all aspects of the ecosystem is vital to ensure that the correct fire management practices are in place, and to ensure that non-target taxa are not being negatively affected (Driscoll *et al.,* 2010). As previously mentioned, in order to understand avian response to fire, the effect of fire on their invertebrate food source also needs to be studied (Daubenmire, 1986).

The invertebrate community suffers high mortality during the combustion and shock phases of the burn (Warren *et al.,* 1987). The shock phase refers to the period extending from the passage of the fire, to the time when vegetation regrowth begins. The length of this period, and hence the extent of the mortality of invertebrates, is dependent on the burning season, and the post-burn climate conditions (Warren *et al.,* 1987). High mortality of invertebrates due to fire is well documented (Rice, 1932; Seastedt, 1984; Anderson *et al.,* 1989). The immediate death of surface invertebrates and soil dwellers that live in the top 5cm of the soil is common; with those soil invertebrates that can burrow down or live below the top 5cm of soil, escaping mortality via combustion. The deeper soil dwelling species that are able to survive the combustion phase, may still decline overtime due to the dry conditions that develop during the shock phase (Rice, 1932; Seastedt, 1984).

Most studies that assess invertebrate responses to fire analyse the responses at the level of order (Rice, 1932; Cancelado and Yonke, 1970; Nagel, 1973; Warren *et al.,* 1987), rather than family, genus or species. This due to the high level of identification skill required to identify invertebrates below the level of order in the field. There are also difficulties in collecting enough species specific data for analysis, using general invertebrate collection methods such as pitfall trapping and sweep netting.

Many of the invertebrate orders respond to fire in a similar way, showing an immediate decline after the fire, followed by a recovery period that leads to greater abundance of individuals on the burn site, compared to an unburnt control (Warren *et al.,* 1987). This pattern of decline and recovery is seen for Acari (Gleim et al., 2014), Hemiptera (Rice, 1932), Hymenoptera (Bulan and Barrett, 1971), Lepidoptera (Hurst, 1971), and some Orthoptera (Warren *et al.,* 1987). Within some orders, such as Coleoptera, different families show contradictory responses to fire, which may be due to the wide range of niches occupied by species in these orders. Rice (1932) found that burning caused a decline in the abundance of Coleoptera three months following the burn; whereas, Hurst (1971) found an increase in leaf beetles (Chrysomelidae) and weevils (Curculionidae) (two families within Coleoptera) over the same time period. Although these studies were conducted in slightly different habitats, it shows that the response of invertebrates is more complicated than that seen at the level of order. This may be a reason why so few studies have been conducted on invertebrates, as identification to the species level is very difficult, requiring a high level of knowledge of all invertebrate species.

Some invertebrate orders show no change in abundance following burning; for example Diptera abundances did not differ between burnt and unburnt areas in Illinois (Rice, 1932). Van Amburg *et al.* (1981) however, showed that families within the order Diptera show a varied response to fire, as already noted in Coleoptera above. Therefore, Rice's (1932) results showing no change in Diptera abundance between burnt and unburnt sites may be due to the fact that some Diptera families decline while others increased leading to an overall neutral change in abundance. This near neutral response of an order has also been noted in studies that looked at Hemiptera population changes (Van Amburg *et al.,* 1981). These neutral changes observed are uncommon, with the majority of studies showing a general decline and subsequent increase in invertebrate abundance following a burn (Rice, 1932).

Resistance and adaptation to burning events have been seen in a number of invertebrate species. Ants, in particular fire ants (*Solenopsis sp.*), increase following the burn as their habitats allow them to survive the combustion phase, and their tolerance of dry soil makes them well adapted to survive the shock phase (Warren *et al.,* 1987). The increase in abundance is possible due to their social habits being conducive to rapid recolonisation (Ahlgren, 1974). Sub-terrain termites also appear to be resistant to the effects of fire, surviving the combustion phase (as they live in soil habitats), and then showing an increase in the recovery phase (Trapnell *et al,.* 1976). Finally, some Orthoptera have shown resistance to the negative effects of fire, with short-horned grasshoppers (Acrididae) escaping the flames due to their flying ability, followed by quick repopulation of burnt areas (Warren *et al.,* 1987). Some species have adapted to use the burning event to their advantage. The abundant vegetation regrowth that follows burning has been shown to enhance some female Orthoptera maturation, and hence cause an increase in the number of eggs laid, increasing their total population size (Deschamps and Wintrebert, 1966).

Affects of fire on invertebrates are acute or chronic and can vary due to several factors including: fire characteristics, invertebrate species, the timing of burn in relation to development stage, post-burn weather and the mosaic of the burn ages (Warren *et al.,* 1987). Understanding the invertebrate response is a broad and currently under-developed field of research. Further work is therefore required to begin to unravel and understand the patterns observed in publications. Initially, understanding invertebrates is important to ensure a holistic view on how fire affects all aspects of the ecosystem. However, invertebrates are particularly important as they are a building block for a large number of food webs within the African savanna. Mammals, birds, reptiles and amphibians all rely on invertebrates for food. Decomposition and decay in the natural environment is also highly dependent on invertebrates, and therefore understanding how they respond to fire will affect how wood, dead fauna and soil may be processed or decomposed. Invertebrates are also a key unit in both the carbon and nitrogen cycle. This shows that fully understanding how fire and burn management programmes affect invertebrate communities, and the way they interact with the ecosystem, is vital.

Breadth of current publications

It is crucial that fire research be well documented, as these studies inform management and conservation practices on national parks and reserves (Parr and Chown, 2003). Each publication often has a specific focal group or species. Figure 1.1 shows the specific focus of each of the 124 primary research papers previously mentioned (page 3). Each of these publications can be categorised into one of five key focal taxa groups: vegetation, mammals, birds, invertebrates and amphibians and reptiles. Searches and selections were based on the following set of criteria:

- The article had to be a primary study and not a review.
- The study had to take place within an African savanna.
- The article must have been published in a journal; no “grey literature” was used. Grey literature being any “in house” reports produced by a reserve or organisation, personal communication or observations. Articles must be published citations.
- Some articles had focussed on more than one of the five key groups; these were included as one article in the total count but regarded in each group as a separate paper. This would only be the case where there was clear focus on each group (e.g. Andersen et al., 2012).
- Search terms: fire, savanna, mammals, birds, invertebrates, vegetation, burning, Africa, reptiles and amphibians.

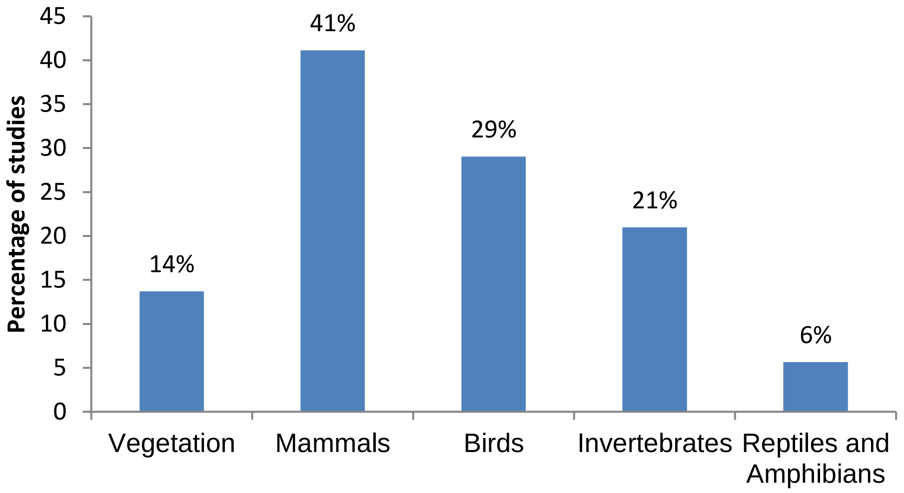

Figure 1.1: Percentage of published studies on the effects of fire on each of the major taxa in African savannas.

As seen in Figure 1.1 the majority of the work has focused on the effect of fire on mammals (41% of the studies). Some of these investigations concentrated on a single mammal and others looked at overall effects of burning on mammals in general. Surprisingly, these results show that only 14% of papers specifically focussed on the effects of burning on vegetation. In reviewing these papers, there appeared to be a greater understanding of the effect of fire on vegetation compared to other taxa, and therefore, the low percentage of studies that specifically focussed on this taxa is unusual. One explanation for this is that, although the number of papers that specifically focus on vegetation is low, the majority of studies that look at the effect of burning have to have a vegetation element to the project. Therefore, although the main focus of the paper may not be vegetation, data is usually collected on vegetation to inform any changes identified in the focal faunal group. This means that greater knowledge on the effect of burning on vegetation is acquired without it being a focal point for many studies.

It is clear from Figure 1.1 that that further research should focus on the invertebrates and reptiles and amphibians. Reviewing these papers and assessing the gaps in knowledge helped informed the direction of my research.

Aims of the project

The aim of this project was to explore the use of burning in a South African savanna as a management tool, to optimise biodiversity across taxa. This was done by assessing the short-term effects of burning on the diversity and distribution of invertebrates; and the long-term effects of burning on invertebrate populations, in order to inform conservation management. Throughout this report reference to invertebrate levels refers to the three levels of invertebrates recorded in this study - ground level, grass level and tree level. The project had two key areas of assessment:

1. Monitoring the long-term effect of fire management on invertebrates. A range of burn ages were used to record the variation in invertebrate diversity and abundance. Invertebrates were assessed on three levels: ground, grass and tree canopy.
2. Monitoring the short-term effects of fire on invertebrates. Changes in diversity and abundance were assessed at different post-burn time periods. Invertebrates were monitored at three levels; as in the long-term study.

Assessing the long-term effect of fire on invertebrates was included since it enabled a greater understanding of the benefits and flaws of a patch mosaic burning system on invertebrate communities across the savanna. This understanding is beneficial to reserve managers in determining burn cycle periods, enabling the best recovery not only in vegetation for mammals, but for all levels of the ecosystem. Invertebrate response within the mosaic is vital for insectivores both mammalian, e.g. aardvark (*Orycteropus afer*), and avian e.g. arrow-marked babbler (*Turdoides jardineii*) and the fork tailed drongo (*Dicrurus adsiilis*). Therefore, understanding the invertebrate response to fire in the long-term can establish the role each burn age can play in a diverse patch mosaic which can sustain a high diversity of not only mammals, but invertebrates and birds as well.

The short-term study enabled the immediate effects of the fire on invertebrates to be identified, and allowed a fine scale analysis of the recovery of invertebrates following the burn event. An understanding of the immediate and short-term responses of invertebrates to burning enabled the rate of recovery to be determined for higher taxa that are dependent on invertebrates. It also helps in understanding the responses of those species have become fire adapted. For example the fork tailed drongo actively seeks savanna burns and the abundance of this species, and many other avian species, increases significantly immediately following a burn event (Bouwman and Hoffman, 2007). Understanding the effect of the burn on invertebrates in this short time period would enable a better understanding of the responses seen in many avian species for future studies.

Chapter Two

The long-term effect of burning mosaics on invertebrate communities

Chapter 2: Long-term effect of burning mosaics on invertebrate communities

Introduction

South African savannas are universally recognised for their importance in the conservation of the diverse flora and fauna that rely on this grassland ecosystem (Reyers et al., 2001). As discussed in chapter 1, fire management has long been used as a tool in nature conservation and game ranching within these savanna areas (Van Wilgen et al., 1990). Over time, the policies and practices of fire management have changed as research and knowledge into the effects of burning have developed.

Unfortunately, poor management strategies and human encroachment on the savanna ecosystem, has lead to loss of habitat and degradation of the ecosystem (Trollope, 1990; Driver et al., 2012). Unsustainable agricultural practices (such as over-cultivation, which reduces soil fertility and over-grazing on open access land) and inappropriate fire regimes cause damage to the savanna and the surrounding sites (Ker, 1995; Maphisa et al., 2009). These are just a few of the threats facing the savanna ecosystem; with the South African savanna being under particular threat, due to South Africa’s limited land protection (Hoekstra et al., 2004).

National parks protect only 7% of South African savannas, with a further 17% protected by small private game reserves (Cousins et al., 2008). It is clear that with these reserves now protecting such a large proportion of the South African savanna, conservationists are looking to them to contribute towards the protection of biodiversity within this ecosystem (Parr and Chown, 2003). As these reserves are privately owned, knowledge regarding the conservation value of these sites can be limited, and little is known about whether the goals of these reserves are conservation based (Driver et al., 2012). Some private reserves are too mammal focussed, aiming to primarily ensure mammal abundances, which can be detrimental when try to maintain high biodiversity (Cousins et al., 2008).

The majority of savanna fires occur between August and November, in the dry season (Brockett et al. 2001). Burn regimes are designed to enhance the grazing opportunity for mammals, ensuring removal of poor vegetation and reducing bush encroachment, in addition to encouraging the growth of palatable grasses (Parrini and Owen-Smith, 2010). As scientific research has shifted over the years, management practices have changed from a mammal focus, to a more holistic approach. This ensures that management practices allow conservation of a high biodiversity within the savanna ecosystem, in addition to the specific aims of the reserve (Driscoll et al., 2010).

The development of new burn regimes, based on current research, now focus on improving heterogeneity (Brockett et al. 2001; Parr and Anderson, 2006). Fire and level of herbivory are the two elements that can be managed within a fenced reserve in attempts to maintain this heterogeneity within the landscape, and hence high biodiversity (Brockett et al. 2001; Van Wilgen et al., 2003).

Most fenced reserves now have specifically designed fire treatments which take into consideration: the size of an area burnt, fire intensity, spatial variation and temporal variation. Many reserves use a patch-mosaic system, burning specific patches on a rotational cycle lasting between 3-6 years, aiming to keep burn patterns as natural as possible (Brockett et al., 2001). Since savanna systems are adapted to natural frequent fires, supporters of patch-mosaic burning argue that the burn practice should simulate this process, whilst maintaining enough temporal variation to ensure a large number of habitat niches are accessible within the same fenced area (Brockett et al. 2001; Fuhlendorf and Engle, 2001).

Although there are many observational benefits of patch-mosaic and high frequency burn regimes, there has been little quantitative data to support a link between these fire regimes and high biodiversity (Driscoll et al. 2010; Parr and Andersen, 2006; Van Wilgen et al. 2011). As stated previously (Chapter 1), much of the work has focussed on mammals and vegetation. In particular, there is very little research focussing on the effect of these burn regimes on non-focal taxa, such as birds and invertebrates (Brockett et al., 2001). As shown in Chapter 1, current research is often limited to specific species or the immediate effect of the burn event.

The aim of this study was to address some of these gaps in research, with a focus on the long-term effects of a patch-mosaic burn regime on the invertebrate community. Many studies have shown that there is an immediate decline in invertebrate abundance directly after the burn event; however, few studies have looked at the recovery period for invertebrates over longer time periods (Parr and Chown, 2003). Understanding the diversity of invertebrates within each burn age is important to ensure that the burn cycle period within managed reserves is optimal for mammals without being detrimental to invertebrates (Rice, 1932; Cancelado and Yonke, 1970; Nagel, 1973; Warren et al., 1987). This study focused on the changes in abundance and diversity of invertebrate orders, at ground, grass and tree level. Invertebrate communities vary enormously between different habitats; therefore, it is important to assess invertebrate communities at the three levels as each represents a unique micro-habitat. Resource availability is very different between the three levels, for examples dung beetles are usually ground invertebrates as they need access to dung for reproduction (Hanski and Cambefort, 2014). The burn event itself affects the micro-habitat at each level very differently, due to different burning rates and proximity to the flames.

Predictions

Based on previous studies, and background knowledge, it would be expected that ground invertebrates would show a decline in abundance and diversity on the recently burnt sites due to loss of individuals in the shock and combustion phases (Warren *et al.,* 1987). Furthermore, the least disturbed sites (i.e. unburnt sites, or sites that are more than 6 years post-burn) are also likely to show a decline in ground invertebrates, due to high volume of vegetation biomass, and often an increase in bush encroachment (Valentine *et al.* 2007).

Grass invertebrates are likely to show an increase in abundance and diversity in sites that are within the burn regime. This is not true for the most recently burnt sites, for which a decline in invertebrates would be expected due to loss of habitat (Warren *et al.,* 1987). Previous studies suggest that in the older sites (over 6 years post-burn) a decline in grass invertebrate would be expected, as grass diversity is likely to be diminished, and competition increased (Brockett et al., 2001).

Finally, in contrast to the above, it would be expected that tree level invertebrate abundance and diversity would be higher in the older the burn sites compared to those in a rotation burning pattern (0-3 years post-burn). This is based on the fact that reduced disturbances can lead to bush encroachment and hence an increase in tree density and diversity (Parr and Chown, 2003).

Materials and methods

Study Site

The study was based at Mankwe Wildlife Reserve (MWR), which is situated in the North-west province of South Africa (25°15′S, 27°17′E), approximately 4km east of Pilanesberg National Park (Yarnell et al., 2007). The reserve is 4750ha and is primarily made up of mixed bushveld (Yarnell et al., 2007). The climate is sub-arid, with a mean annual rainfall of 573mm, most of which falls between October and March (Willis et al., 2013). The mean daily temperature ranges from 11^{o}C in July to 24^{o}C in December, with extremes of -6^{o}C -40^{o}C (Yarnell et al., 2007, Willis et al., 2013).

The reserve was fenced in 1982 when AEL mining developed a commercial explosive factory just outside Mogwase; this factory went out of commission in 1994 (Willis et al., 2013). MWR developed in the buffer zone of this factory and covers 4105ha of the site, with a fenced area inside the factory region (655ha) (Willis et al., 2013). The fire regime in the main reserve area is rotational and has been managed and documented since 1993, making the site perfect for analysing the long-term effects of burning on invertebrates (Yarnell et al., 2007, Willis et al., 2013). The whole site is divided into 22 distinct areas, separated by roads or firebreaks, and burnt on a 4-5 year cycle (Figure 2.1). Most managed fires are done between June and September and are cold burns. This means that they are done at the coolest part of the day and run with the wind to encourage a fast burn, reducing damage to soil and trees (Willis et al., 2013). The reserve also contains an unburnt site located in the fenced area, which was last burnt over 20 years ago.

Data Points

Data collection throughout the reserve was undertaken using points randomly assigned to each burn patch using Geographic Information Systems (GIS). Within each burn area 10 points were randomly assigned under the criteria that each point was 250m apart from another and at least 50m from a road (Figure 2.1). These criteria ensured that each data point could be considered independent for analysis, as well as ensure data collection was not biased. Once at the field site some points had to be relocated for safety reasons and some changes were made based on recent burn activity.

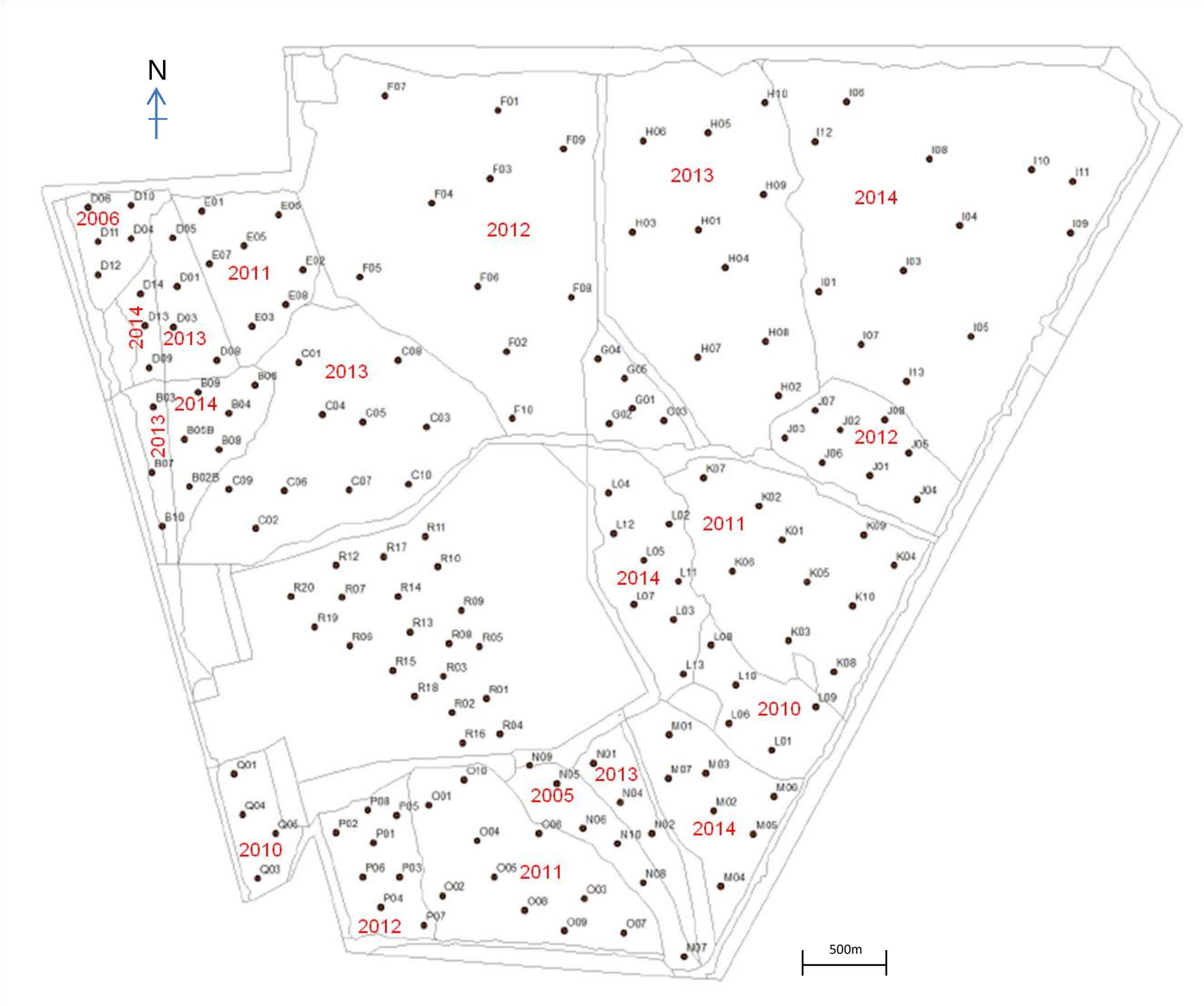

Figure 2.1: Map of Mankwe Wildlife Reserve, showing distinct patches and data collection points

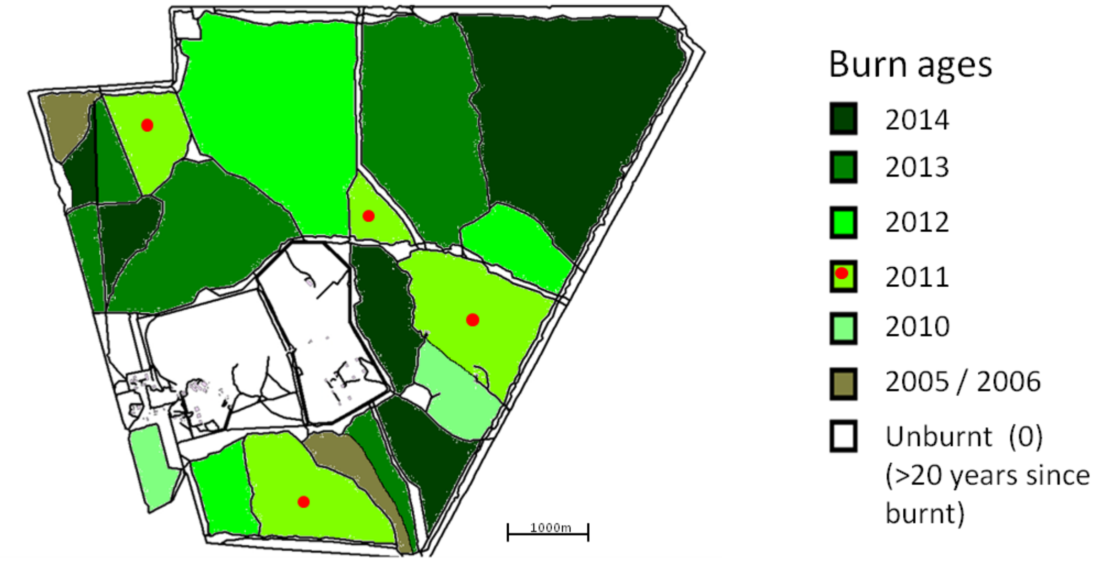

Figure 2.2: Map showing the burn mosaic at Mankwe Wildlife Reserve in 2014. The age in the key denotes when the patch was last burnt

As seen in Figure 2.2, there are seven distinct burn ages. For this study three different patches were needed for each burn age, with each patch containing at least five points which were randomly selected from the 10 points allocated to the areas by GIS. This ensured that any patterns seen between burn ages could be attributed to burn age and not location on the reserve. The 2010 burn age did not have enough data points or patches to meet the study criteria, and was therefore excluded, leaving six burn ages. The burn ages included in this study can be seen in Table 2.1. Only 11 data points were used in the 2005/2006 burns, across two areas (Table 2.1). This was due to the limited availability of this burn age on the reserve, with only two areas burnt around this time. It was decided that this age group would still be considered even with four fewer points, as this 2005/2006 burn could bridge the gap between the unburnt site and the other burn ages. The aim was that this burn age would enable a broader long-term assessment of changes in the invertebrate community.

Finally, the data points within the unburnt group were all collected from within the factory fence and therefore, came from one area on the reserve. The points within this area were evenly distributed, ensuring any difference seen between this age group and another would be due to burn age and not location.

Unfortunately, unlike the other groups the points had to be within this one area as this is the only unburnt site on the reserve.

Date of last burn	Number of years undisturbed by fire	Number of areas used	Number of points
2014	0	3	15
2013	1	3	15
2012	2	3	15
2011	3	3	15
2005/2006	9/10	2	11
Unburnt	>20	1	15
TOTAL	-	**15**	**86**

Table 2.1: Burn ages used in the study and the spread of the data points for each group.

Data Collection

To holistically assess the effect of fire on invertebrates, data collection was split into three levels: ground level, grass level and tree level, each with a unique micro-habitat. Splitting data in this way allowed us to determine specific changes in each distinct invertebrate community, as well as make an overall assessment of changes in invertebrate abundance.

The collection method of invertebrates at each level was variable due to their unique nature. Ground invertebrates were collected in pitfall traps, grass invertebrates in sweep nets and tree invertebrates were collected by beating trees. All invertebrates collected where identified by eye, or using a 40x eye lens.

Pitfall trapping

Ground invertebrates were sampled at each point using two pitfall traps placed 20m apart; each being placed either 10m north or 10m south of the central point. The pitfall traps consisted of plastic cups 6cm in diameter and approximately 10cm deep. Traps were placed in the ground, ensuring the cup edge was at ground level, and the cups were half filled with soapy water (Sutherland, 2006). The soapy water consisted of a small amount of washing up liquid and water. This ensured invertebrates that fell into the trap drowned and could not fly or crawl out of the trap; soapy water was used over plain water as it evaporated more slowly. Some studies have used anti-freeze in pitfall traps to prevent decay of the invertebrates caught; however due to the presence of mammals, and other species within the vicinity of the traps, there was the potential they may try to drink the liquid. As anti-freeze can be harmful if ingested it was decided that soapy water would be safer.

The traps were left at each point for three nights, and each pot was covered with a quarter of a paper plate held up using toothpicks (Parr and Chown, 2001). The plate was used to try and reduce evaporation of liquid from the pitfall trap. The presence of the plate caused the traps to be more visible; in order to prevent animals interfering with the trap, the plate was covered in sticks and vegetation from the surrounding area for camouflage (Sutherland, 2006). On sites with limited vegetation, due to a recent burn, the plates were rubbed in the soot left behind from the burn event, ensuring that the top of the plate was black, like its surroundings. The time period of three nights was chosen to ensure coverage of invertebrate activity, without risking complete loss of liquid from within the trap, as well as reducing the chance of the traps being swamped by ants or being flooded by rainwater.

All traps were placed and collected between 9th October 2014 and 12th November 2014, ensuring that all samples were collected within the shortest time period possible to reduce the effect of climate on the invertebrate samples. Each point was sampled once, with two pitfalls being placed during the trapping event.

On collection, each trap was emptied into a specimen pot with a sealable lid, each with a unique number. A small amount of anti-freeze was added to each sample pot to preserve the samples until the invertebrates could be identified and counted. Invertebrates were identified to the level of order using keys and information in Tilling (1987) and Picker et al. (2004). For each trap, the total count for each order was recorded.

Sweep netting

Grass level invertebrates were sampled at each point by running two 50m sweep net transects, heading east and west, from the centre of each point. Each transect consisted of 50 sweeps, keeping the net within the vegetation layer when present (Sutherland, 2006). On recently burnt sites the sweep net was kept close to the ground, with the aim of covering any vegetation present. At the end of each transect the contents of the net was transferred to a zip lock bag, each with a unique number. The contents of each bag were then identified to the level of order using keys and information in Tilling (1987) and Picker et al. (2004). Once all invertebrates in the bag had been identified they were released into surrounding grassland. As with the pitfall traps all sweep net samples were collected within one month between 9th October 2014 and 2nd November 2014.

Tree beating

Flying invertebrates and tree level invertebrates were sampled using the tree beating method. At each point two trees were selected to be sampled; the closest tree north of the point, and the closest tree south of the point. Tree density remained similar across all points, within each burn age. Tree density varied between burn ages, as this is an effect of the burn; older burn ages would have a higher tree density which may suggest more invertebrates. Therefore in selecting a sample tree, to ensure data collected would be independent, certain criteria had to be met. The specimen had to be over 3m in height, and the branches selected had to be a minimum of 1m above the ground. Trees had to be selected north and south of the point, ensuring the two trees were not in direct contact. Each tree was beaten twice using a wooden pole, with a 1m x 1m white sheet being held beneath (Sutherland, 2006). Two branches were hit on each tree, with each branch being beaten 10 times, ensuring each tree was beaten a total of 20 times. After 10 beats on a branch, the invertebrates that had collected on the white sheet were identified to the level of order (in the same way the sweep net samples and pitfall samples were identified) and counted before being released back to the grassland. The invertebrate counts from the two branches were combined to give the total invertebrate sample for the tree.

Data analysis

All three invertebrate response variables (ground, grass and tree) were considered separately; the reason being the data from the three levels cannot be merged as the collection methods for each level are not comparable. Once all data were entered into excel (Microsoft Excel, 2007) it was checked against raw data again before manipulating it for use in other packages such as R (R Core Team, 2014). Each pitfall trap collected was a unique data point, as was each tree used in tree beating. However, the data from the two sweep net transects at each point were combined, as the distance between them was too small to be confident they were separate samples since they started from the same central point.

Abundance

Average abundance of total invertebrates was calculated for each collection method across the burn ages; this was done using R (R Core Team, 2014). Averages were calculated by adding all pitfall traps, sweep net points, or tree data together and dividing by the number of samples collected. This gave an average count of invertebrates per collection method (i.e. per pitfall trap, per combined point sweep net transects and per tree) for each burn age. By using averages in this way it alleviated errors created by a reduced number of points in the 2005/2006 burn sites. Similarly, R was used to calculate, and graphically depict, the average abundance of each invertebrate order, in order to assess how this varied across the different burn ages. Differences between average abundance of invertebrates at different burn ages, for each invertebrate level, were quantified using Kruskal-Wallis tests, using a PMCMR package in R (Pohlert, 2014). Kruskal- Wallis non-parametric test was used instead of an ANOVA as the data was not normally distributed. For Kruskal-Wallis, a 95% confidence limit was used to compare the strength of the differences between the six burn ages. To determine the pairwise comparison for each burn age a Tukey test and Kramer (Nemenyi) test, with Tukey-Dist approximation for independent samples, was undertaken in R. 95% confidence limits were used to determine the strength of the comparison.

Order Accumulation Curve

Species accumulation curves are used to estimate the number of species within a particular area, and can also be used to indicate the accuracy of a fauna survey in representing the fauna that is present within a particular area (Thompson and Withers, 2003). This study looked at the level of order rather than species so the curve would represent order accumulation rather than species. As part of this study looks at the effect of burning on the invertebrate community it is important to see how representative the data collected is, to determine the relevancy of conclusions drawn in this study. For each invertebrate level an order accumulation curve was created in R (R Core Team, 2014), using the vegan package (Oksanen et al., 2016). For each burn age a separate curve was produced as each burn age would be expected to have different invertebrate communities.

Diversity

The overall diversity of invertebrates within each burn age, at each invertebrate level, was calculated using the Shannon and Simpson indices. Shannon index is an information statistic and Simpson Index is a dominance index, which gives more weight to common or dominant species.

The output of the indices both produced similar results and therefore, the average diversity value was calculated using the Shannon index only. The average diversity of invertebrates at each level was assessed by calculating the diversity of invertebrates at each point, within each burn age the diversity values were grouped based on invertebrate level and the average diversity value was calculated. Each burn age consisted of 15 data points, excluding 2005/2006 burn, which only contained 11 data points (Table 2.1). For ground invertebrates, each pitfall trap was used as a data point. For grass invertebrates two sweep net transects, collected at each point, were combined and used as one data point. Finally, for the tree level invertebrates, each tree was identified as a data point. As with the abundance data, statistical analysis was undertaken using Kruskal-Wallis non-parametric test; a non-parametric test was selected over a parametric one way ANOVA, as the data was not normally distributed. The 95% confidence limit was used to compare the strength of the differences between the six burns

Dominant order selection

The effect of fire regimes on unique orders is an important part of this project and allows fine scale analysis of invertebrate responses to fire. South Africa has such a wide variety of invertebrate orders, that only the dominant invertebrates were studied in this project. For each invertebrate level the total count of invertebrates, across all burn ages, were combined and divided by the number of unique orders recorded. This number gave the average presence count for each order; those orders showing total counts lower than the average were excluded. Abundance values for each order were then entered into R, and the mean abundance of each order was calculated for each burn age. Ants were collected as a separate group, rather than in the order of Hymenoptera, as they were easy to separate and their count would have significantly skewed the Hymenoptera count.

Non-parametric multi-dimensional scaling

To assess the differences in the order composition between the burn ages, non-parametric multidimensional scaling (NMDS) was performed using Bray distances. NMDS was used to visualise the composition differences between each burn age, enabling identification of any unique compositions created by the burn regime (Holland, 2008). This was performed in R using the vegan package (Oksanen et al., 2016), and each invertebrate level was analysed separately. Abundance data for each invertebrate level was separated into orders and presented in a matrix, this enabled a symmetrical matrix of pairwise distances to be calculated (Holland, 2008). Plots were generated within this package and ellipses were added to the plot to group each burn age, enabling visual differences to be identified between burn ages.

Results

In total over the six burn ages, 86 points were sampled (Table 2.1) enabling the collection of 172 pitfall traps, 172 sweep net transects and 172 tree-beating samples. Within the 172 pitfall traps 11449 individual invertebrates were collected over 20 orders. The 172 sweep net transects captured 2818 individual invertebrates across 19 orders, and finally the tree beating collected 3151 individuals over 14 orders.

Abundance

Effective analysis on the abundance of invertebrates at each level required two unique approaches. Initially, all invertebrates within each collection were combined to analyse the overall response of invertebrates to the burn regime. However, it became apparent that ants were dominant, especially within the ground invertebrates (Figure 2.12, Table 2.2). This made meaningful analysis on the invertebrate data difficult; therefore ants were removed from the overall analysis not only for ground invertebrates but for all levels. The data was not normally distributed and therefore, non-parametric tests were used.

Years since burn	**Ground Invertebrate abundance**		**Grass Invertebrate abundance**		**Tree Invertebrate abundance**	
	Ant	Total (excl ants)	Ant	Total (excl ants)	Ant	Total (excl ants)
0	1291	495	3	54	70	230
1	1614	1128	16	424	153	367
2	1735	711	32	633	309	482
3	847	392	15	700	60	512
9	1782	263	12	544	50	400
Unburnt	965	226	4	381	54	464

Table 2.2: Total sum of ants and invertebrates excluding ants collected at each burn age, across each invertebrate level. Shows the extent to which ants dominate the pitfall sampling

The abundance of ground invertebrates varies significantly between each burn (Kruskal-Wallis, H_5=30.92, p<0.001; Figure 2.3). It is clear from Figure 2.3 that the unburnt site, which has remained unburnt for the last 20 years, has a significantly lower mean abundance of ground invertebrates than sites burnt within the last two years (Table 2.3). The data therefore suggests that the burn event increases ground invertebrate abundance; furthermore, Figure 2.3 shows that the ground invertebrate abundance for one year post-burn is not only significantly greater than the unburnt sites (Table 2.3), but appears to show some increase in invertebrate abundance compared to recently burnt sites (0 years since burn). However, there is no significant difference between invertebrate abundance in recently burnt sites compared to one year post-burn sites (Table 2.3). It is clear from Figure 2.3 that the interquartile distance (IQD) of one year post-burn sites (IQD = 37.75) is much larger than recent burn sites (IQD = 8.75). This disparity within the one year post-burn sites may be unique to this data, or the high IQD may suggest other factors could be affecting the increase in invertebrates, such as site location and soil condition.

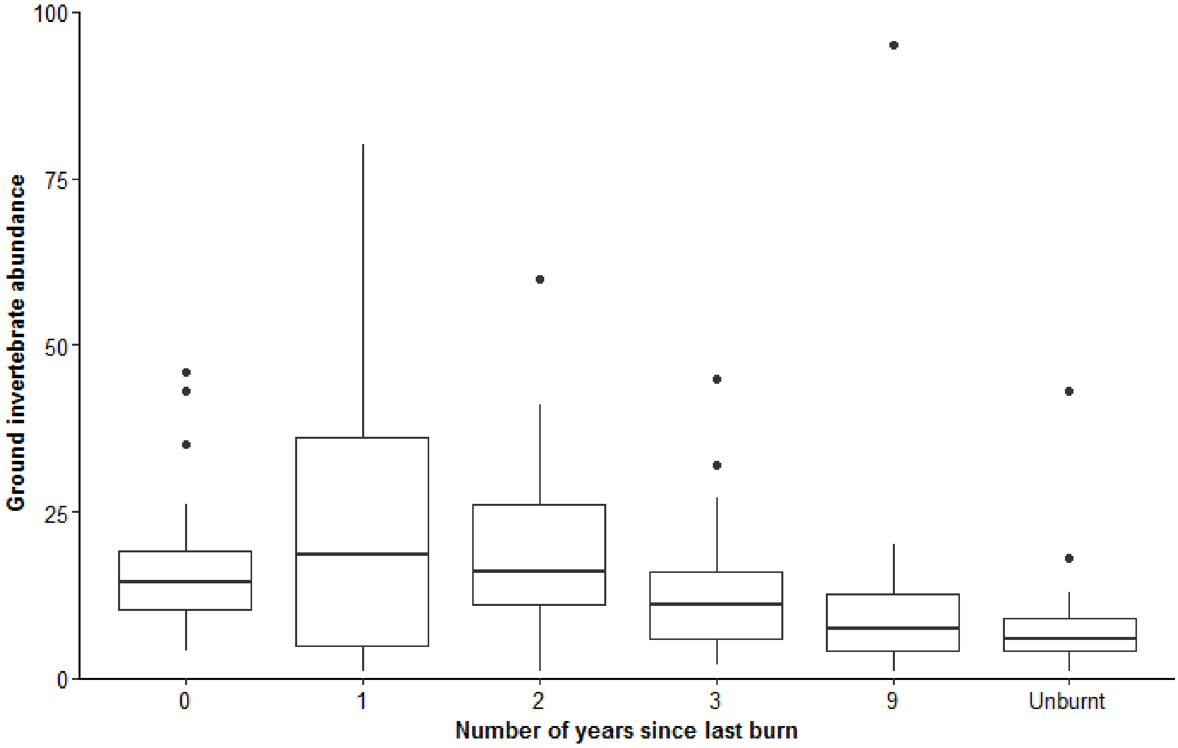

Figure 2.3: The abundance of ground invertebrates collected in pitfall traps over six different burn ages represented in box and whisker plots. (0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22, Unburnt: N=30). Bars show the minimum and maximum values up to 1.5 x IQD, with black dots showing outliers that are ±1.5 x IQD.

Kruskal-Wallis	Nemenyi post-hoc test		
	Comparing burn ages	Stat value (2DP)	p-value
H_5=30.92 p<0.001	0 vs. Unburnt	5.50	0.001
	1 vs. Unburnt	5.50	0.002
	2 vs. Unburnt	6.11	<0.001
	3 vs. Unburnt	3.20	0.209
	0 vs. 1	0.02	1.000

Table 2.3: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on ground invertebrate abundances across six different burn ages. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

The burn regime also has a significant effect on the abundance of grass invertebrates (Kruskal-Wallis; H_5=43.44, p<0.001), but unlike the ground invertebrates, the grass invertebrate abundance is only significantly different in the recently burnt sites (Table 2.4). Data collection from recent burn sites occurred within three months of the burn event; therefore, as a burn event removes the grass layer, there was very little vegetation during sweep net sampling on recent burn sites. The significant decline in grass invertebrates in the recent burn may therefore be due to the loss of the grass layer (Figure 2.4). The invertebrate population in this grass layer appears to increase to abundance levels seen in the unburnt site within one year of the burn (Figure 2.4). This is supported by the Nemenyi test, which shows that there is no significant difference in grass invertebrate abundance between the one year post-burn and the unburnt site (Table 2.4). One year post-burn grass invertebrate abundance is also similar to the abundances seen for the other burn ages, excluding the recent burn (Table 2.4). This suggests that the significant decline caused by the burning event is only temporary. As the grass layer recovers, the invertebrate population also appear to recover, returning to pre-burn abundance levels.

Analysis of ground and grass invertebrate abundances both immediately showed distinct burn ages that were significantly affected by the burn regime (Figures 2.3 and 2.4). Figure 2.5 suggests that the tree level invertebrates are largely unaffected by the burn regime, showing similar means and medians (Table 2.5). However, there is a significant difference in tree invertebrate abundance across the different burn ages (Kruskal-Wallis; H_5=19.90, p=0.001). Further statistical analysis showed that the recently burnt sites have a significantly lower tree invertebrate abundance than the unburnt or 9 years since burn sites (Table 2.6).

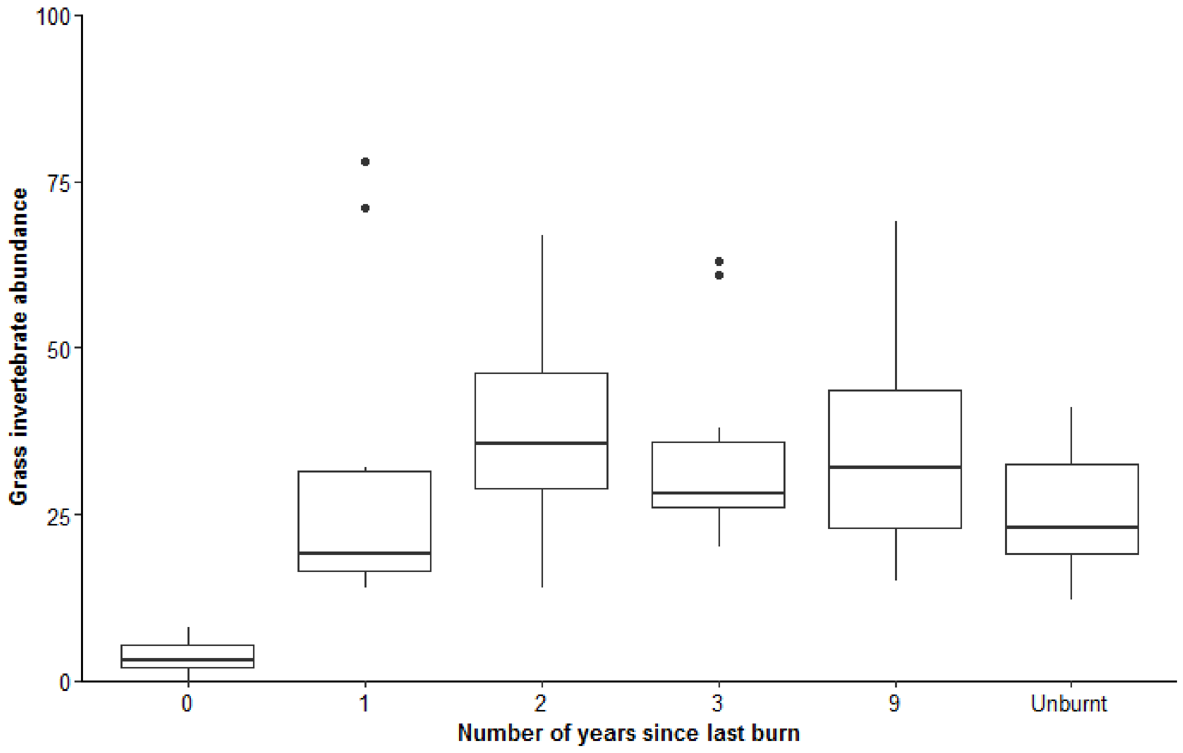

Figure 2.4: The abundance of grass invertebrates collected in sweep net transects over six different burn ages represented in box and whisker plots. (0: N=15, 1: N=15, 2: N=15, 3: N=15, 9: N=11, Unburnt: N=15). Bars show the minimum and maximum values up to 1.5 x IQD, with black dots showing outliers that are ±1.5 x IQD.

Kruskal- Wallis	Nemenyi post-hoc test		
	Comparing burn ages	**Stat value (2DP)**	**p-value**
H_5=43.44 p<0.001	0 vs. 1	5.09	0.004
	0 vs. 2	8.02	<0.001
	0 vs. 3	7.36	<0.001
	0 vs. 9	6.97	<0.001
	0 vs. Unburnt	5.54	0.001
	1 vs. 2	2.93	0.301
	1 vs. 3	2.26	0.598
	1 vs. 9	2.29	0.587
	1 vs. Unburnt	0.44	1.000

Table 2.4: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on grass invertebrate abundances across six different burn ages. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

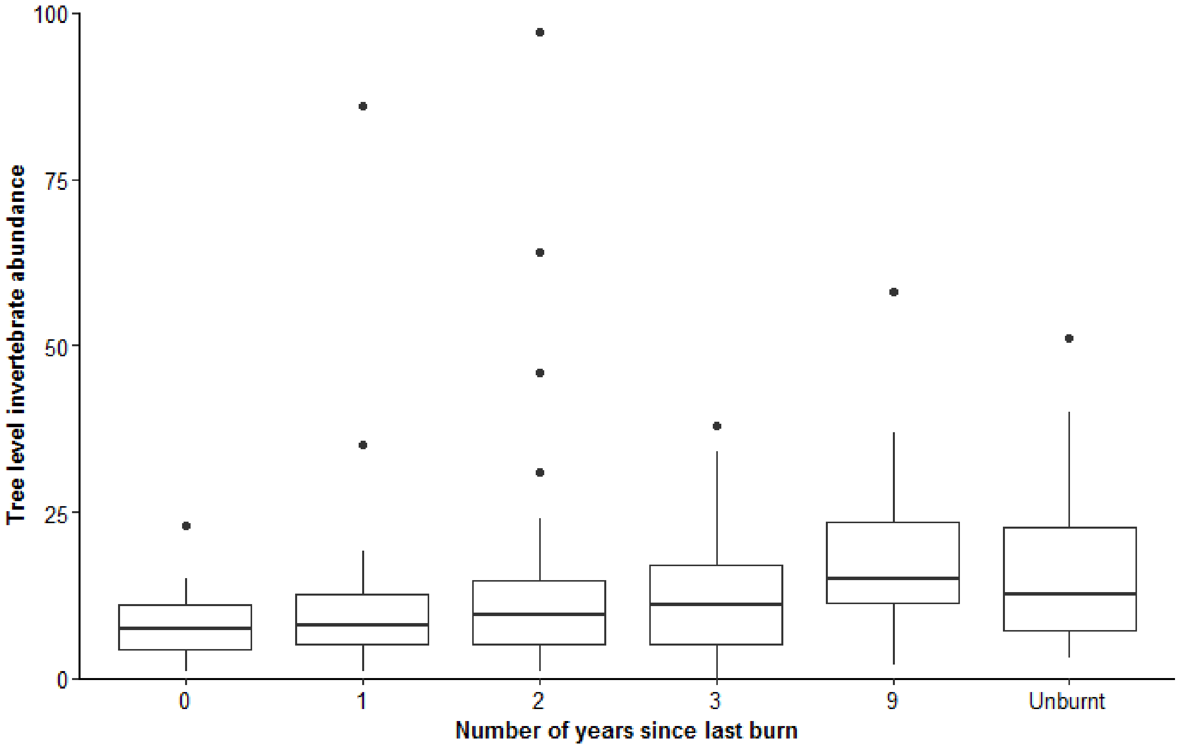

Figure 2.5: The abundance of tree level invertebrates collected by tree beating over six different burn ages represented in box and whisker plots. (0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22, Unburnt: N=30). Bars show the minimum and maximum values up to 1.5 x IQD, with black dots showing outliers that are ±1.5 x IQD.

Burn age (Years since burn)	Median (2DP)	Mean (2DP)
0	7.50	7.67
1	8.00	12.23
2	9.50	16.07
3	11.50	17.07
9	15.00	18.18
Unburnt	12.50	15.47

Table 2.5: Mean and median values for tree level invertebrate abundance within six different burn ages.

Kruskal-Wallis	Nemenyi post-hoc test		
	Comparing burn ages	Stat value (2DP)	p-value
$H_5 = 19.90$ p = 0.001	9 vs. 0	4.56	0.016
	9 vs. 1	3.88	0.067
	9 vs. 2	2.99	0.280
	9 vs. 3	2.33	0.565
	9 vs. Unburnt	1.36	0.930
	Unburnt vs. 0	5.56	0.001
	Unburnt vs. 1	2.74	0.380
	Unburnt vs. 2	1.88	0.811
	Unburnt vs. 3	1.06	0.976

Table 2.6: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on tree level invertebrate abundances across six different burn ages. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

The two sites which show the minimum level of fire disturbance (unburnt and nine year post-burn) show the only significant variation in tree level invertebrates across the study when compared with the recent burn only (Table 2.6). This suggests that if some patches remain undisturbed by fire for longer periods than the burn regimes usually allow, the tree invertebrate population increases, above that noted for sites regularly burnt. The increase in tree invertebrates in these less disturbed sites may be due to increased bush encroachment in the older burn ages. However, these older sites are not significantly different to 1, 2 or 3 years post-burn sites therefore, increases seen in these older sites have only be seen when compared to a heavily disturbed site (Table 2.6).

In terms of invertebrate abundance, the burn seems to immediately affect all levels of the invertebrate community; causing significant declines in tree and grass invertebrates within the first few months of the burn event. In contrast, significant increases in ground invertebrates were noted within these months following the burn. All changes in invertebrate abundance appear to be short lived, with the invertebrate population at all three levels quickly returning to levels similar to those identified in the unburnt sites. Recovery to unburnt levels appears to occur within one year for grass and tree invertebrates, but takes three years for ground invertebrates. This increase for ground invertebrates may be due to the removal of a dispersal barrier (grass swards) which means movement on the ground is less restricted. As the grasses recover (which can take years depending on the weather) movement of ground invertebrates may be reduced as they move to the grass layer. Secondly, the increase in grass density may decrease movement; this along with the transfer of invertebrates to the grass layer may be the cause of ground invertebrate decline back to unburnt levels (Table 2.4).

Order Accumulation Curves

In this study order was used to assess communities rather than species and therefore curves refer to order richness not species. For all three invertebrate levels, order accumulation curves were produced, one for each burn age, and the point at which the curve asymptotes equals the number of orders that would be discovered if infinite search effort is expended. In order accumulation curves the asymptote is considered to occur at a gradient of less than 0.3 (Llorente, 1993).

Figure 2.6 shows the order accumulation curve for ground invertebrates across the six different burn ages. All curves, excluding three years post burn, reached the asymptote within the sampling undertaken, showing that the amount of pitfall traps collected is representative of the orders present within all areas. The three years' post burn site curve did not asymptote, suggesting that more samples need to be collected within this burn age. However, the slope between the last two points is 0.44, so although the asymptote was not reached within the study; which can also be seen in the graph as the slope is still on a shallow incline, it is quite a good representation of the site. The higher order richness within this burn age suggests that it may be an optimum burn age for a wider range of invertebrates, therefore when considering burn regimes, three year burn sites need to be considered more favourably. All curves show very similar order richness (Figure 2.6), with the unburnt showing the lowest order richness.

The order accumulation curves were also done for the grass invertebrates and the tree invertebrates (Figure 2.7, 2.8). All accumulation curves within both levels reached their asymptote within the sample sizes collected; showing that tree beating and sweep netting methods used in this study can be considered representative of the invertebrate communities the study is assessing.

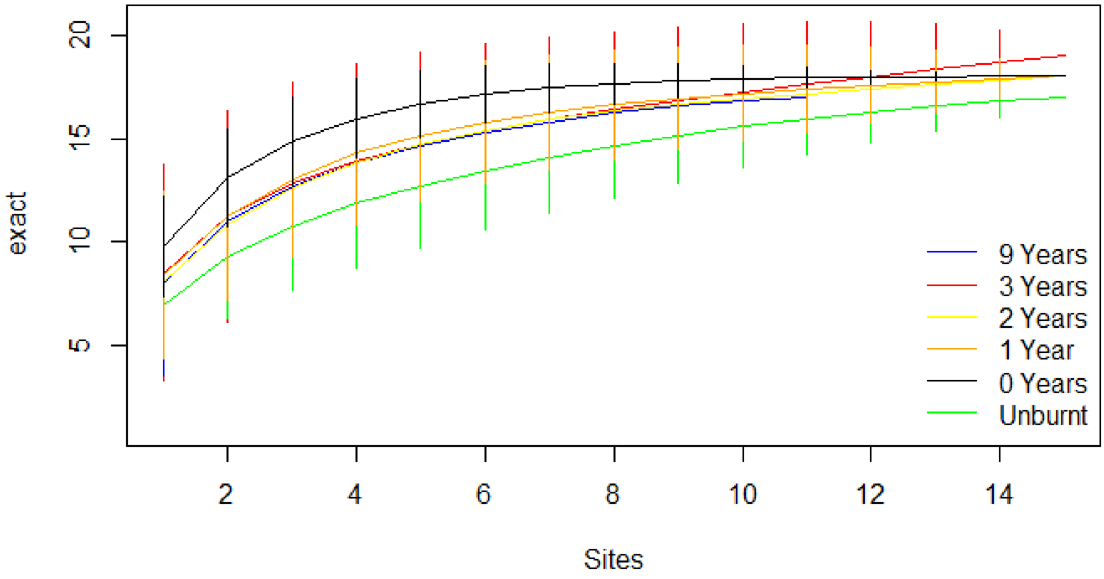

Figure 2.6: Order accumulation curve for ground invertebrate orders caught within pitfall traps across six different grassland burn areas (0 years : N=15, 1 year: N=15, 2 years: N=15, 3 years : N=15, 9 years: N=11, Unburnt: N=15).

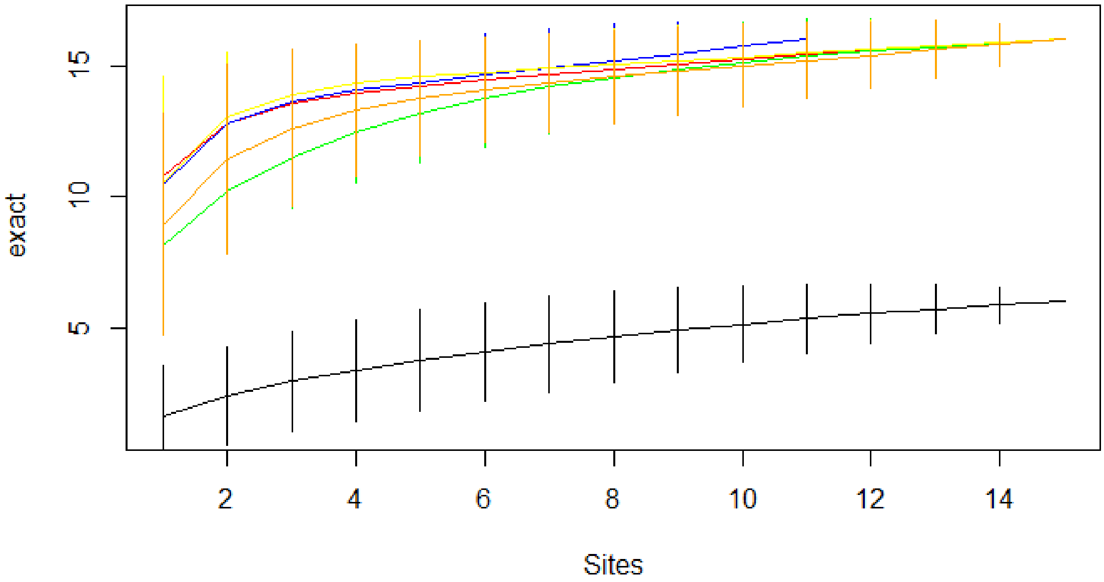

Figure 2.7: Order accumulation curve for grass invertebrate orders caught within sweep nets across six different grassland burn areas (0 years : N=15, 1 year: N=15, 2 years: N=15, 3 years : N=15, 9 years: N=11, Unburnt: N=15).

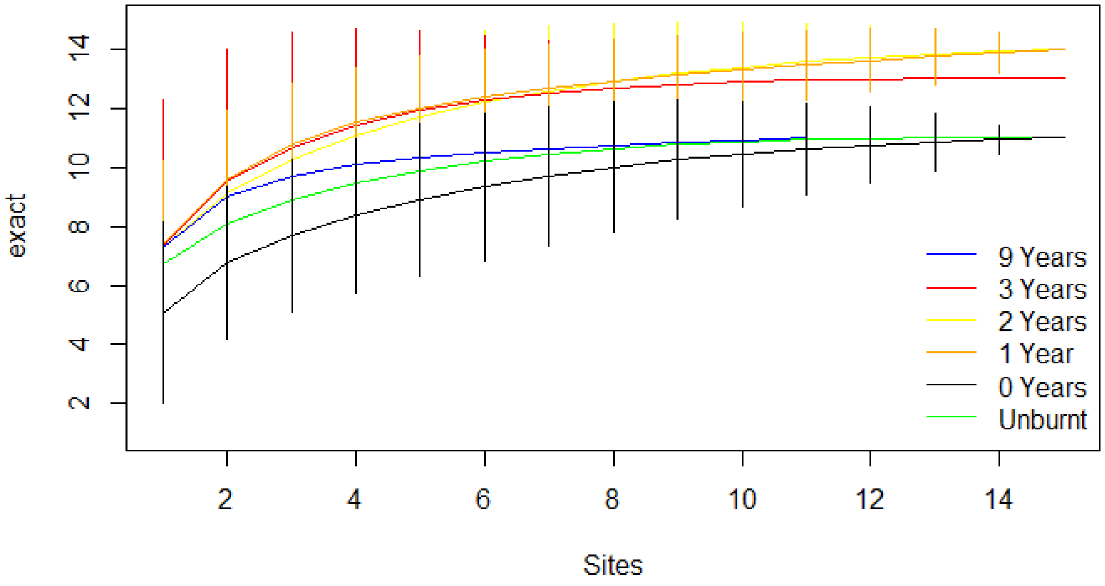

Figure 2.8: Order accumulation curve for tree invertebrate orders caught by tree beating across six different grassland burn areas (0 years : N=15, 1 year: N=15, 2 years: N=15, 3 years : N=15, 9 years: N=11, Unburnt: N=15).

The order richness within the grass level invertebrates shows a clear divide between those sites within the burn cycle (0, 1, 2, 3 and 9 year old sites) and the unburnt control site (Figure 2.7). The order richness is much lower within the unburnt site, whereas those sites within the burn cycle appear to have very similar, with higher order richness.

There is a divide in order richness between sites when looking at tree invertebrates (Figure 2.8). The two older sites (nine years post burn and unburnt) and the recently burnt site all show very similar order richness, much lower than those sites that have been more recently burnt. This suggests that generally tree invertebrate communities are more diverse where disturbance is relatively frequent. Although, the burn event itself does appear to cause a decline in richness, which may be due to the fact that only specialist species survive the burn. What is clear from Figure 2.8 is that although order richness is lower in the recently burnt sites recovery to higher order richness can occur within one year of the burn event, showing the effect may be beneficial rather than harmful, as a complete lack of disturbance also causes the low level of order richness (Figure 2.8)

Diversity

In order to assess the diversity of invertebrates at each level, the Shannon index and Simpson index were used. Initially, all data points within each data collection method were combined, and the Shannon and Simpson values compared. This analysis showed that both methods presented similar data and therefore, it was concluded that only the Shannon index was required to assess diversity.

Diversity of ground invertebrates does not appear to vary much between the different burn ages (Figure 2.9). The only burn age that shows a significant change in ground invertebrate diversity is the nine years post-burn sites (Table 2.7). The nine year post-burn site shows a significantly lower diversity than the recently burnt sites; however, neither site is significantly different to another burn age (Table 2.7). The increase in diversity in the recent burn, compared to the nine year post-burn, may be linked to the increase in ground invertebrate abundance that is seen in recent burns. However, one issue with this data is that only 22 data point were collected for the nine year post-burn sites, compared to 30 for all other burn ages. The lower sample size may have affected the diversity values in the nine year post-burn sites.

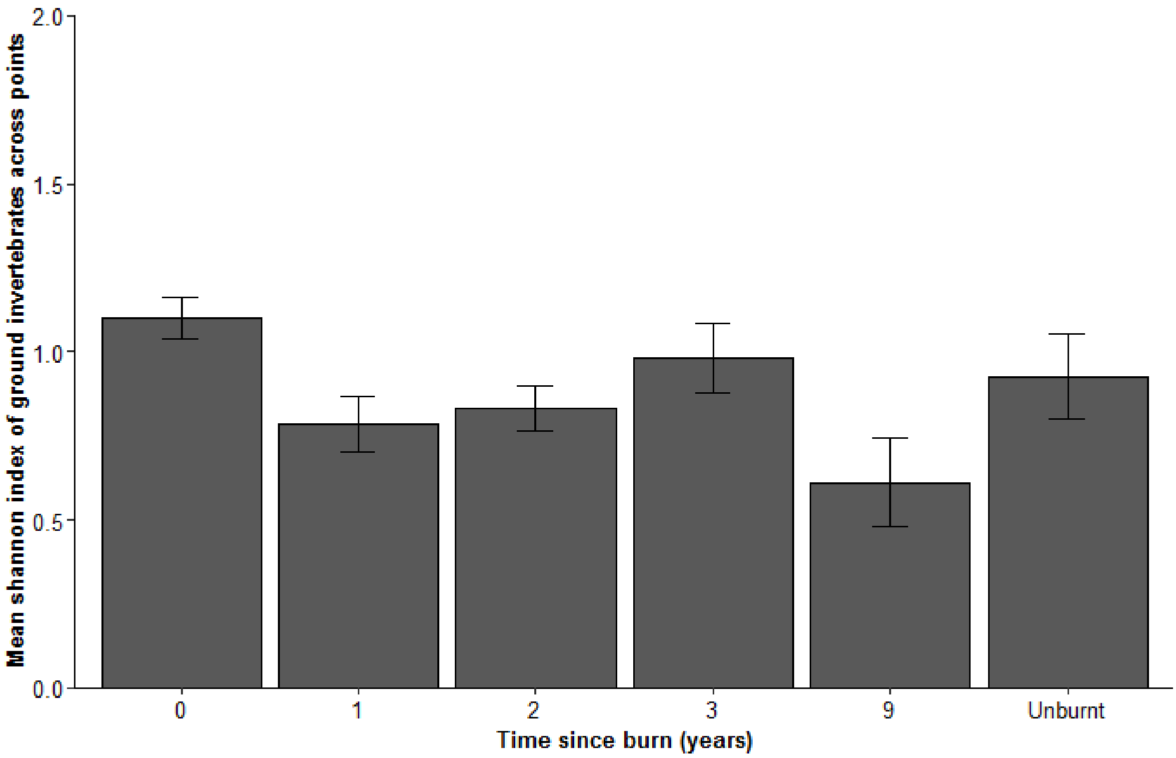

Figure 2.9: Average Shannon index values for ground invertebrates collected pitfall traps, over different burn ages. (Unburnt: N=30, 0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22). Error bars show ±1SE.

Invertebrate Level	**Kruskal-Wallis**	**Nemenyi post-hoc test**		
		Comparing burn ages	**Stat value (2DP)**	**p-value**
Ground invertebrates	$H_5 = 15.43$ $p = 0.009$	0 vs. 9	5.06	0.005
		0 vs. 1	3.36	0.165
		0 vs. Unburnt	2.29	0.588
		9 vs. Unburnt	2.96	0.291
Grass invertebrates	$H_5 = 41.00$ $p < 0.001$	0 vs. 1	5.39	0.002
		0 vs. 2	7.21	<0.001
		0 vs. 3	8.01	<0.001
		0 vs. 9	6.37	<0.001
		0 vs. Unburnt	5.23	0.003
		1 vs. 3	2.63	0.429
		1 vs. Unburnt	0.16	1.000
Tree level invertebrates	$H_5 = 7.21$ $p = 0.206$	N/A		

Table 2.7: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on diversity values calculated for each point using Shannon index. Six different burn ages were compared. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

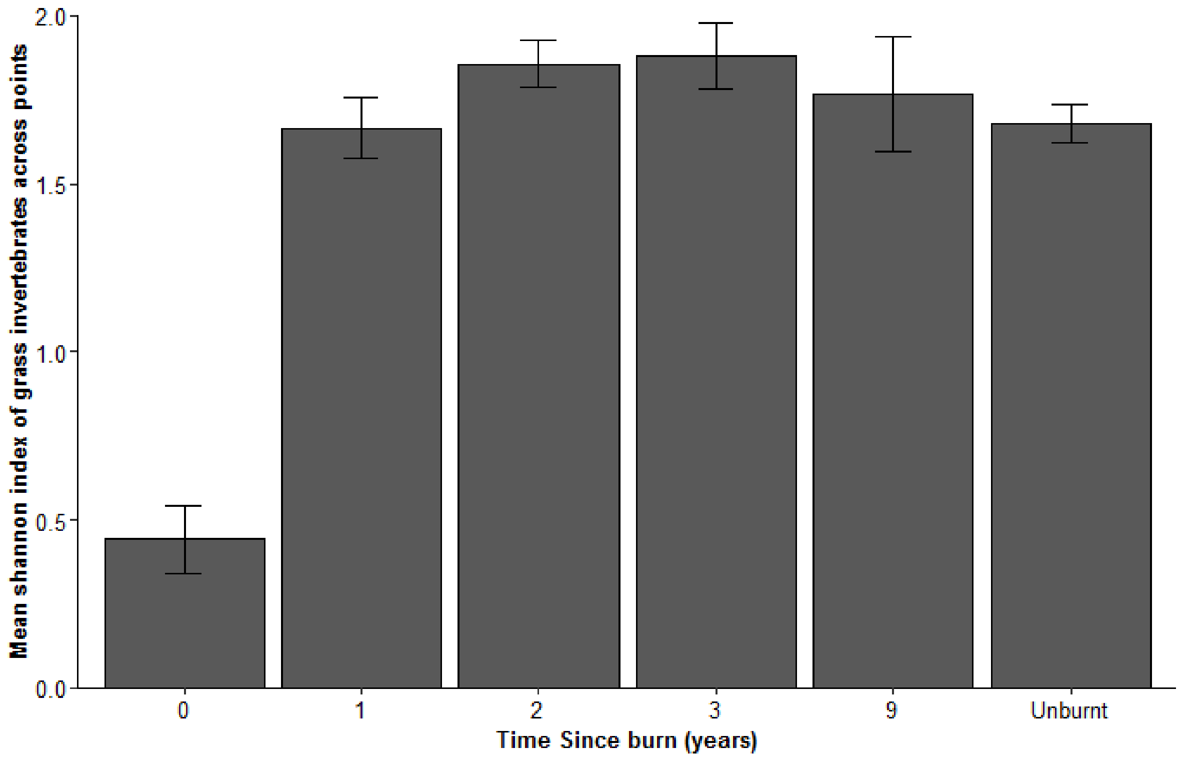

Figure 2.10: Average Shannon index values for grass invertebrates collected using sweep net transects, over different burn ages. (Unburnt: N=15, 0: N=15, 1: N=15, 2: N=15, 3: N=15, 9: N=11). Error bars show ±1SE.

As with the ground invertebrates, the average Shannon values for grass invertebrates show very little change in diversity between the burn ages, excluding the recent burn (Figure 2.10). The diversity of invertebrates in the recent burn sites is significantly lower than the other burn ages (Table 2.7). As with the abundance data the loss of vegetation in the grass layer removes habitat and therefore causes a decline in invertebrate orders. Finally, for tree invertebrates the average Shannon values show no significant difference in diversity between each burn age (Figure 2.11; Table 2.7).

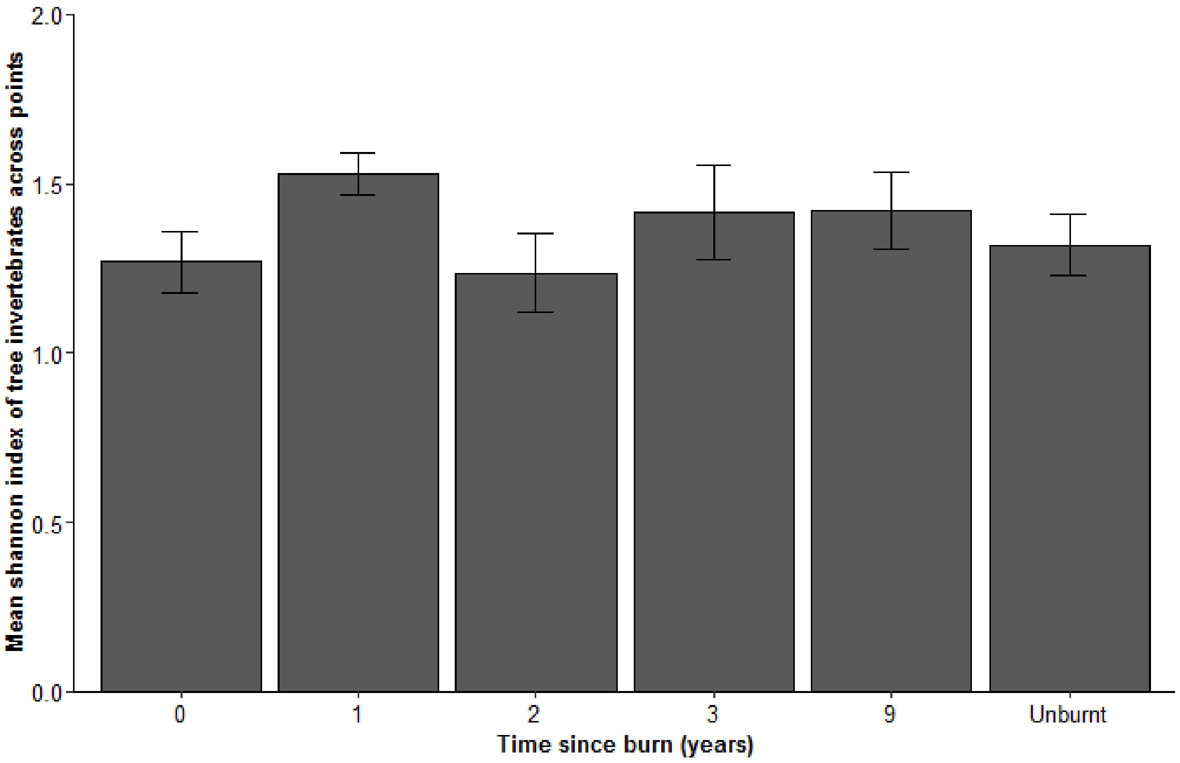

Figure 2.11: Average Shannon index value for tree level invertebrates over different burn ages collected via tree beating (Unburnt: N=30, 0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22). Error bars show ±1SE.

Order Abundance

As the diversity and abundance for total invertebrates showed some variation between burn ages, orders that were present at or above the average presence level for a collection method were studied to see if any particular orders were affected by the burn regime. For ground invertebrates, orders had to be present in over 64 sample pots; for grass invertebrates, orders had to be present in over 28 sweep nets, and finally for tree level invertebrates the order had to be present in at least 46 tree beating samples.

The total invertebrate abundance analysis showed that the unburnt site had significantly lower invertebrate abundances than those sites within the burn regime (Table 2.3). Some orders also follow this trend, with Collembola and ants showing significantly greater invertebrate abundances in the sites that are more frequently burnt (0, 1 and 2 year post-burn sites) than in the unburnt site (Table 2.8). However, many of the orders show no significant change in the ground invertebrate abundance across the six burn ages (Figure 2.12, Table 2.8). Although, Figure 2.12 suggests that Orthoptera, Coleoptera and Araneae show greater invertebrate abundance in the recent burn compared to the unburnt site, analysis shows that this is not statistically accurate. What is clear from this data is that the low invertebrate counts for each order (excluding Collembola and ants) mean that the standards of error are large. Therefore, it is not possible to reach statistically valid conclusions on the effects of a burn regime on these orders. Figure 2.12 does suggest a number of orders that may need investigating further, with more data, but overall shows that with the data gathered here the burn regime does not appear to be having a radical effect on any particular ground level invertebrate order.

Assessing the effect of the burn regime on grass invertebrates revealed that the abundance of grass invertebrates is significantly lower in the recent burn compared to all other burn ages (Table 2.4, Figure 2.4). This conclusion was drawn from the overall data collected. Figure 2.13 separates the grass invertebrate orders, and in many cases, this pattern remains. Orthoptera, Hymenoptera, Lepidoptera, Thysanoptera and Phasmatodea all show a complete absence in the recent burn sites. However, Table 2.9 shows that all of these orders show no significant change in the abundance of grass level invertebrates over the six burns. Phasmatodea does show some variation but not in the recent burn sites (Table 2.9). Although a complete loss of some orders is not significant, Hemiptera is significantly lower in the recent burn site compared to the unburnt (Table 2.9) - suggesting that the loss of vegetation is having a more dramatic effect on this large and diverse order.

The 2012 burn (two years post-burn site) appears to show the greatest abundance of grass level invertebrates (Figure 2.13, Table 2.9). The overall abundance analysis (Table 2.4) does not show that the two year post-burn sites have a higher abundance of grass invertebrates. However, when looking at Figure 2.4 the box and whisker plot does appear to be slightly higher than the other burn ages. Diptera, Hemiptera and Araneae all show significantly greater abundances in the two year post-burn sites compared to other burn ages (Table 2.9). Figure 2.13 also shows that ants, Coleoptera, Hemiptera and Thysanoptera have greater mean abundances in the two year post-burn site than other burn ages. Although these orders do not show a significant increase in the 2012 burn site, due to a small sample size and hence large standard of error, it does suggest that grass invertebrates may be benefitting from this medium age burn.

Although some orders show lower abundances in the recent burn, and some in the one year post-burn sites, these appear to recover to pre-burn levels and in some cases exceed them (Figure 2.13). Hemiptera show a significant increase in abundance between the unburnt and the two year post-burn sites, showing a relatively rapid recovery (Table 2.9). Similarly, Araneae show a significant increase in abundance between the one year post-burn site and the two year post-burn site. Therefore, although there may be decline in invertebrates immediately following the burn (Figure 2.4, Table 2.4), Figure 2.13 does not suggest that any order is being eradicated by repeated burning and orders recover relatively quickly.

Tree level invertebrates showed no significant change in diversity in response to the burn regime; however, Table 2.6 showed that the unburnt and nine year post-burn sites had significantly larger abundances than the recent burn site. Separating the orders has shown that Hemiptera is the only order that significantly supports this decline in tree level invertebrates (Table 2.10). As this is one of the largest and most diverse invertebrate orders, lower abundances in this order alone could have driven the lower abundances recorded when looking at abundances overall (Figure 2.5, Table 2.6). In contrast, Acari appear to have a significantly larger abundance in the two year post-burn site compared to the nine year post-burn site (Table 2.10). This suggests that Acari benefit from the increased fire disturbance. However, looking at Figure 2.14, the standard error on this order is so large that further data will need to be collected to support this. As Acari usually require hosts to feed, their reduced presence in the nine year post-burn site may not be due to the burn regime but may be in regard to lower mammals within older burn sites - as they are often over grazed and have less nutritionally valuable grasses (Parr and Chown, 2003). All other orders show no significant response to the burn regime, indicating similar abundance levels across all burn ages.

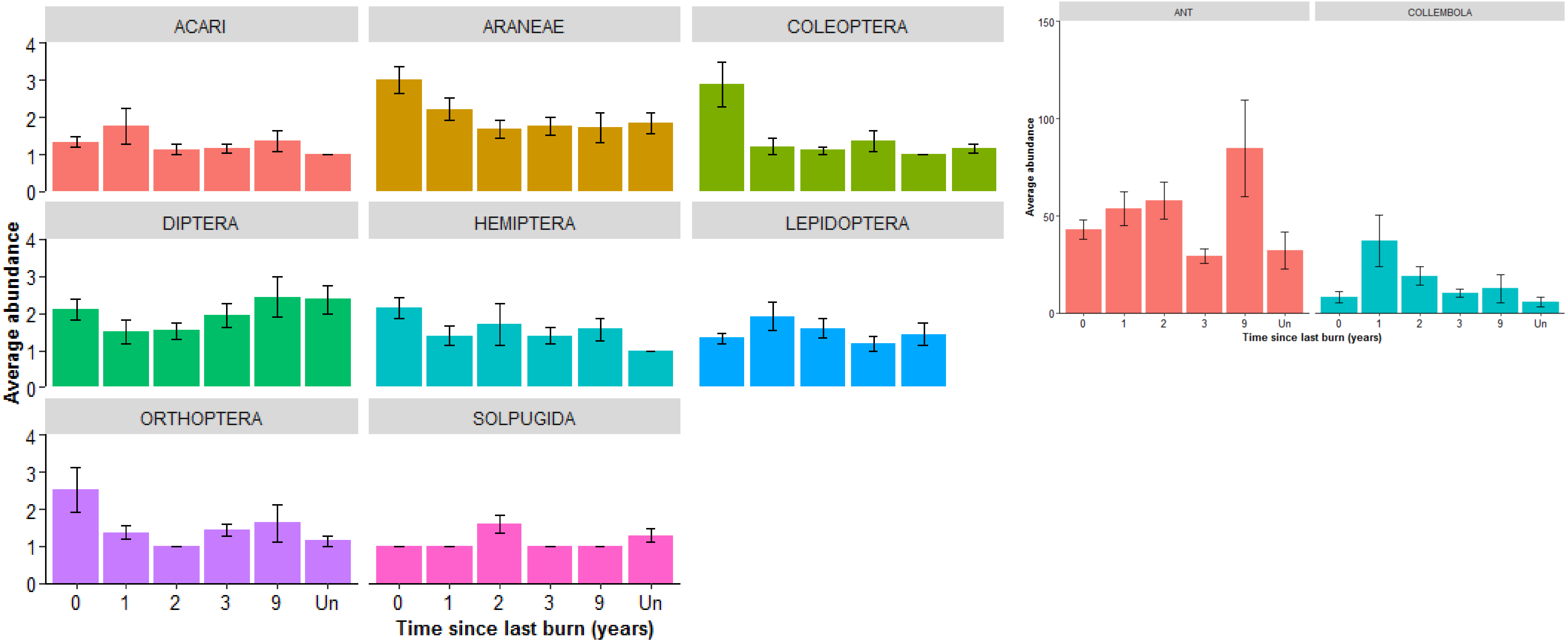

Figure 2.12: Mean abundance of 11 ground invertebrate orders from six different burn ages. Data for these means was collected by using pitfall traps (Unburnt: N=30, 0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22). Ant and Collumbola are separate from the other orders as the abundance for these groups was much grater than the other invertebrates and therefore a greater y-axis range was required. Error bars represents ±1SE.

Order	Kruskal-Wallis		Nemenyi Test		
	H_5	p-value	Comparing burn ages	Stat value (2DP)	p-value
Acari	3.63	0.604	N/A		
Ant	22.83	<0.001	Unburnt vs. 0	4.54	0.017
			Unburnt vs. 1	4.78	0.010
			Unburnt vs. 2	5.10	0.004
			Unburnt vs. 3	1.72	0.830
			Unburnt vs. 9	4.81	0.009
			3 vs. 0	2.78	0.361
			3 vs. 2	3.34	0.169
Araneae	12.360	0.030	0 vs. 1	1.72	0.831
			0 vs. 2	3.90	0.065
Coleoptera	12.62	0.027	0 vs. 1	2.41	0.53
			0 vs. 2	2.53	0.47
Collembola	20.21	0.001	0 vs. 1	3.83	0.074
			Unburnt vs. 0	1.05	0.977
			Unburnt vs. 1	5.19	0.003
			Unburnt vs. 2	4.65	0.013
Diptera	5.62	0.345	N/A		
Hemiptera	6.29	0.279	N/A		
Lepidoptera	2.38	0.666	N/A		
Orthoptera	8.28	0.142	N/A		
Solpugida	13.15	0.022	1 vs. 2	2.39	0.54

Table 2.8: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on the abundance values for the dominant ground invertebrate orders. Abundances were collected across six burn ages using pitfall traps (Unburnt: N=30, 0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22). Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

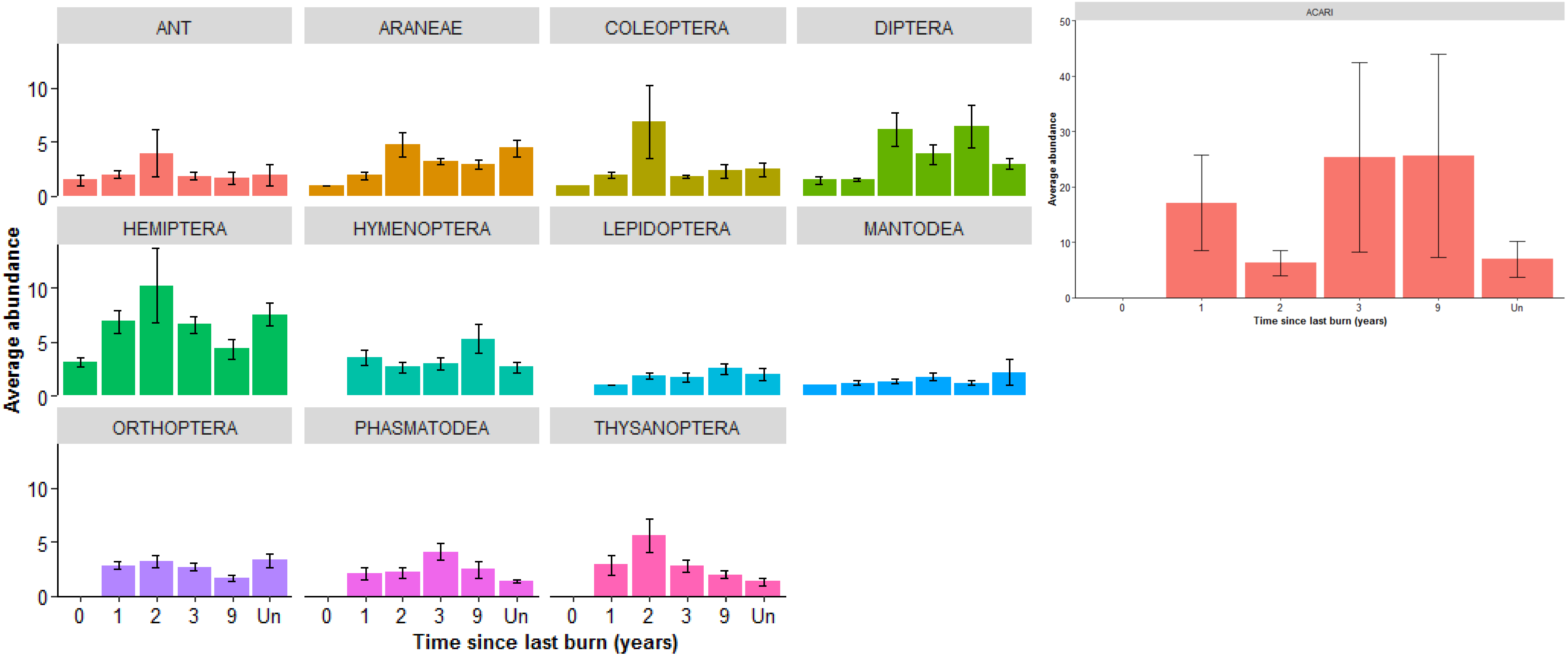

Figure 2.13: Mean abundance of 12 grass level invertebrate orders from six different burn ages. Data for these means was collected by using sweepnet transects (Unburnt: N=15, 0: N=15, 1: N=15, 2: N=15, 3: N=15, 9: N=11). Acari is separate from the other orders as the abundance counts were much high for this order and therefore, a greater y axis range was required. Error bars represents ±1SE.

Order	Kruskal-Wallis		Nemenyi Test		
	H_5	p-value	Comparing burn ages	Stat value (2DP)	p-value
Acari	1.36	0.852	N/A		
Ant	1.73	0.885	N/A		
Araneae	15.92	0.007	2 vs. 0	3.27	0.190
			2 vs. 1	4.06	0.047
			Unburnt vs. 0	3.26	0.193
			Unburnt vs. 1	4.08	0.045
Coleoptera	4.65	0.461	N/A		
Diptera	20.01	0.001	2 vs. 0	4.44	0.021
			2 vs., 1	5.01	0.005
			9 vs. 1	4.02	0.051
			Unburnt vs. 0	2.55	0.464
			Unburnt vs. 2	2.57	0.453
Hemiptera	16.33	0.006	0 vs. 1	3.87	0.68
			0 vs. 2	4.18	0.037
			0 vs. Unburnt	4.54	0.017
Hymenoptera	3.25	0.517	N/A		
Lepidoptera	8.56	0.073	N/A		
Mantodea	1.87	0.867	N/A		
Orthoptera	3.66	0.454	N/A		
Phasmatodea	10.47	0.033	3 vs. Unburnt	4.001	0.037
Thysanoptera	5.24	0.263	N/A		

Table 2.9: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on the abundance values for the dominant grass level invertebrate orders. Abundances were collected across six burn ages using sweep net transects (Unburnt: N=15, 0: N=15, 1: N=15, 2: N=15, 3: N=15, 9: N=11). Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

Order	Kruskal-Wallis		Nemenyi Test		
	H_5	p-value	Comparing burn ages	Stat value (2DP)	p-value
Acari	11.68	0.039	0 vs. 1	1.25	0.950
			0 vs. Unburnt	1.92	0.750
			9 vs. 2	4.17	0.038
			9 vs. Unburnt	2.60	0.440
Ant	5.88	0.319	N/A		
Araneae	7.98	0.158	N/A		
Coleoptera	3.38	0.642	N/A		
Hemiptera	36.00	<0.001	1 vs. 2	1.59	0.871
			9 vs. 0	5.00	0.005
			9 vs. 1	5.48	0.001
			Unburnt vs. 0	5.81	<0.001
			Unburnt vs. 1	6.39	<0.001
			Unburnt vs. 2	4.50	0.019
			Unburnt vs. 3	2.99	0.281
Isoptera	1.65	0.895	N/A		
Lepidoptera	14.16	0.015	0 vs. Unburnt	0.00	1.000

Table 2.10: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on the abundance values for the dominant tree level invertebrate orders. Abundances were collected across six burn ages by tree beating (Unburnt: N=15, 0: N=15, 1: N=15, 2: N=15, 3: N=15, 9: N=11). Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

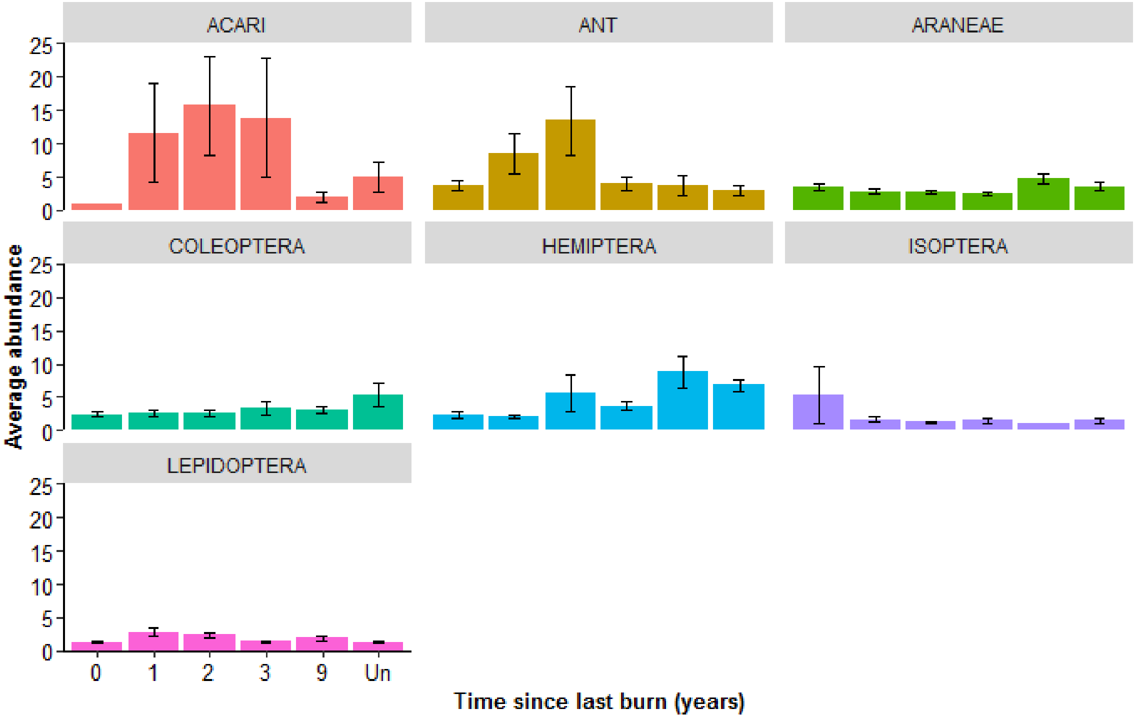

Figure 2.14: Mean abundance of seven tree level invertebrate orders collected from six different burn ages. Data collected for these means was collected by beating trees (Unburnt: N=30, 0: N=30, 1: N=30, 2: N=30, 3: N=30, 9: N=22). Error bars represents ±1SE.

<u>Non-parametric Multi-Dimensional Scaling</u>

Multi-dimensional scaling enables the analysis of the relationship between each point to be determined visually. Each data point can be compared and plotted based on how closely related they are to the rest of the data. Once each data point has been plotted, they are grouped into burn ages using coloured ellipses. The composition of ground invertebrates appears to be very similar across all burn ages at the level of order, with Figure 2.15 showing heavy overlap of all ellipses in the centre of the plot. The unburnt site shows the most variation in contrast to the other burn ages, with a large proportion of points being separated from the central group of burn ages. As well as this, the ellipsis is based to the left of the group with less overlap with the other burn ages.

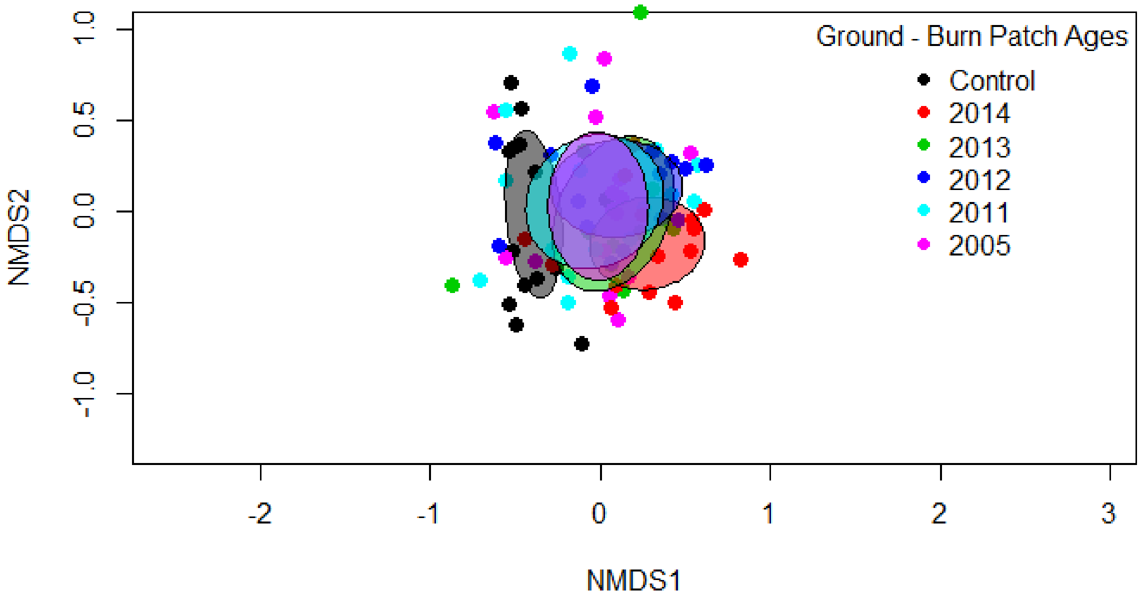

Figure 2.15: Non-parametric multidimensional scaling plot using Bray distance for ground invertebrates collected over six different burn ages. Ellipses group the main points by burn age. Elliptical overlap indicates similarities between two burn ages.

The recent burn also shows variation in composition in comparison to the other burns, with a large proportion of the points separated from the central grouping. The recent burn shows less compositional overlap to the other burn ages, being based on the right of the main group (Figure 2.15). In particular, there is no overlap in ground invertebrate composition between the recent burn and the unburnt site. This suggests that these two sites are very different, although they both overlap with the other burn ages. This suggests the composition of invertebrates remains constant (except at the extremes of the scale) with the unburnt site (>20 years since burn) and the recent burn (0 years since burn) showing a spread of variation from the core. In general, all burn ages are intermediately similar when it comes to ground invertebrates with slight variation at the extremes.

The composition of grass invertebrates appears to have a greater spread of variation than the ground invertebrates (Figure 2.16). Although there is still much overlap with the ellipses, they are less concentrated than for the ground invertebrates. This suggests more variation in the composition of grass invertebrates between the different burn ages. Figure 2.16 shows that 2005, 2011 and 2013 burns show more variation in composition compared to the unburnt and 2012, with the 2013, in particular, splitting more from the centre point of the graph. The two year post-burn site (2012) shows the most composition similarity to all burn ages. This is very similar to the unburnt sites composition; in contrast, the one year post-burn site (2013) shows the greatest diversion from the 2012 (two year post-burn) composition. The intermediate burn ages (2011 and 2005) are very similar to each other with heavy overlap; both have some overlap with 2013 and the baseline 2012. The most distinctive variation in composition is clearly the recent burn, with no overlap of the 2014 ellipsis with the other burn ages, and all data points being separated to the left of the plot (Figure 2.16). This suggests that the immediate effects of burning significantly affect the composition of invertebrates but within one year, the composition has mostly recovered to pre-burn conditions. This plot has shown that the composition of grass invertebrates is more complicated than for ground invertebrates, with burn ages of a similar age grouping together, and those with more extreme disturbances branching off.

The composition of invertebrates at the tree level shows very little variation between any of the burn ages. All ellipses in Figure 2.17 overlap, however there is a large spread of points around the central ellipsis. This shows that although composition is on average very similar between each burn age, there may be variation within each burn age.

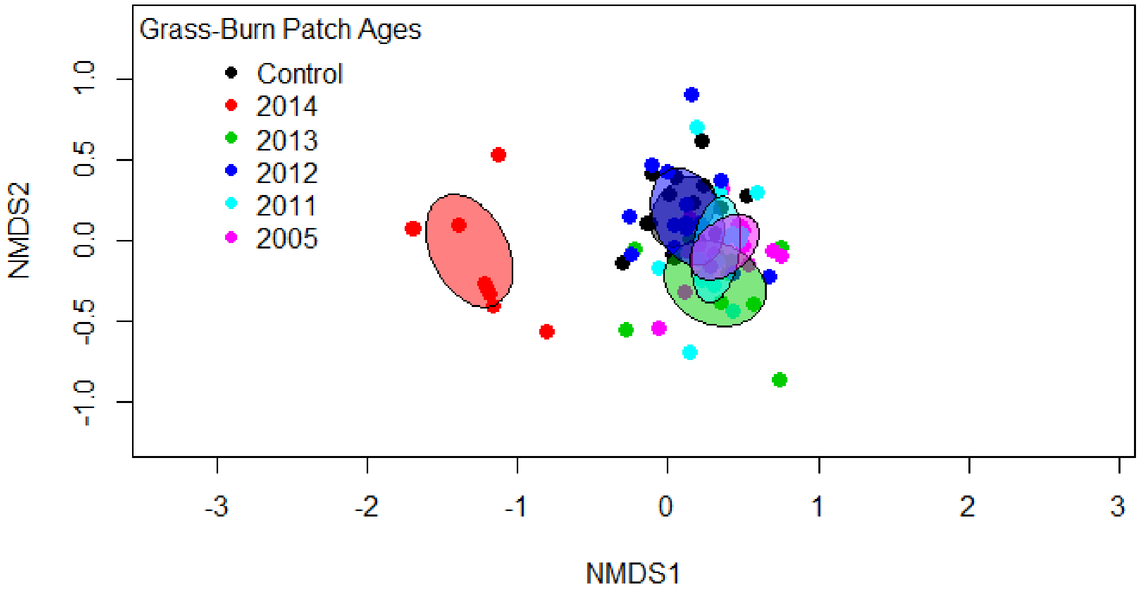

Figure 2.16: Non-parametric multidimensional scaling plot using Bray distance for grass level invertebrate collected over six different burn ages. Ellipses group the main points by burn age. Elliptical overlap indicates similarities between two burn ages.

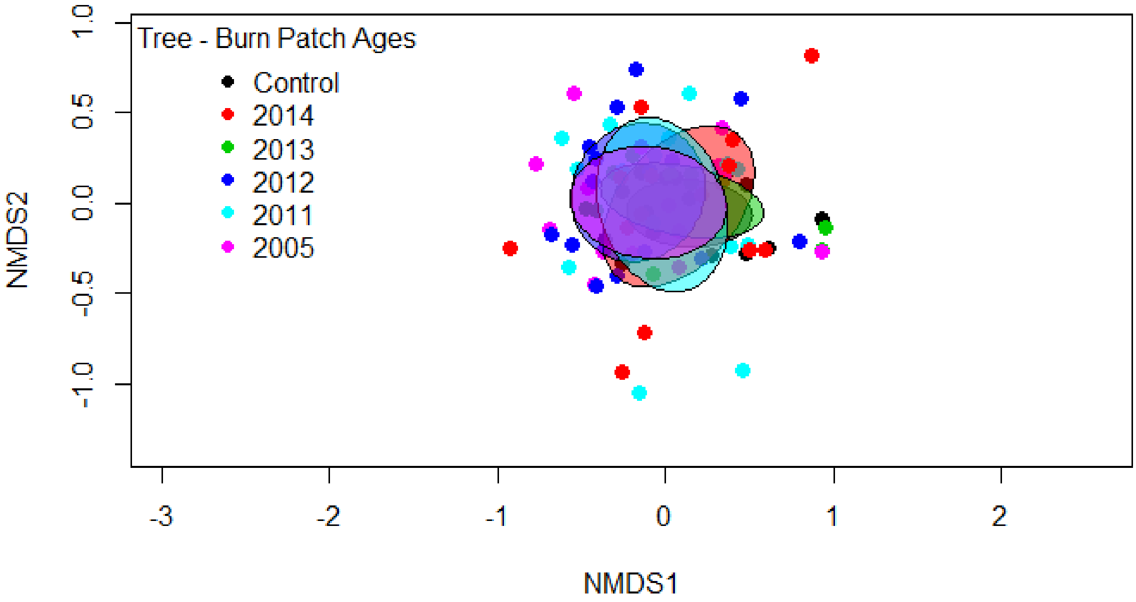

Figure 2.17: Non-parametric multidimensional scaling plot using Bray distance for tree level invertebrate collected over six different burn ages. Ellipses group the main points by burn age. Elliptical overlap indicates similarities between two burn ages.

Discussion

At the beginning of the study it was predicted that ground invertebrates would show a decline in abundance and diversity on the recently burnt sites, due to loss in the shock and combustion phases (Warren *et al.,* 1987). However, this study has shown that ground invertebrates significantly increased following the burn event compared to the unburnt site, suggesting that loss of ground invertebrates in the shock and combustion phases is being counteracted by movement of invertebrates either sub-terrain or from other levels. The increase in ground invertebrates was noted in burn patches up to two years old and appeared to return to unburnt abundance levels in patches three years post-burn and older. Contrary to the predictions, the study has shown that the diversity of ground invertebrates remained unchanged across all burn ages, potentially due to the movement of other orders from grass and tree down to ground level. These unexpected findings suggest that burning is not as harmful to ground invertebrates as expected.

Grass invertebrates showed a decline in abundance and diversity in the recently burnt sites, as predicted. The study also showed that by one year post-burn, invertebrate abundance returned to the level seen in the unburnt site. However, there was no significant decline in grass invertebrates seen in the unburnt site, which is contrary to the prediction. This may be due to the fact that, although the grass diversity has declined, it may not be enough to disrupt the grass invertebrate niches significantly. The diversity of grass invertebrates showed a significant decline in the recent burn, due to loss of vegetation as predicted. The recovery seen in the abundance was also noted in diversity, which return to pre-burn levels within one year post-burn.

The tree level invertebrates showed an increase in abundance in the older burn sites, compared to the recent burn, as predicted. However, there was no significant difference in tree invertebrate abundance between the burn patches within the burn regime (0 years, one year and three years' post-burn). Therefore, the increase seen in the older burn sites was likely to be due to an increase in tree density caused by bush encroachment. In contrast to the prediction, tree invertebrate diversity remained the same across all burn ages, suggesting complete loss of orders within burning was not occurring.

This study collected data on the abundance and diversity of invertebrates at the three levels mentioned, across a range of burn ages which make up the patch mosaic at MWR. Therefore, this discussion will focus on the general affect of the patch mosaic burn on the three invertebrate communities, ground, grass and tree.

Effect of patch mosaic on ground invertebrates

Data collected on ground invertebrates shows that the five year burn regime present on this reserve initially caused an increase in ground invertebrates, in comparison to the unburnt site. This increase in ground invertebrates is significant up to two year post-burn, after which the invertebrate abundance begins to decline, returning to similar levels seen in the unburnt site (Figure 2.3). The increase in ground invertebrates over a relatively short period suggests that the 4-5 year burn regime may be beneficial to maintain a large invertebrate community throughout the patch mosaic. Although intermediate effects can be variable, with some studies showing lower abundances than in unburnt sites, many have shown that invertebrates become more abundant within the interim period between burns (Rice, 1932; Bulan and Barrett, 1971; Lamotte, 1975; Van Amburg et al., 1981; Warren et al., 1987; Reed, 1997).

The nine year post-burn site and the unburnt site (>20 years post-burn) both show lower invertebrate abundances compared to other burn patches, which supports these previous studies. The lower abundances could be due to the increase in the density of grass within these patches, as well as increased bush encroachment (Johnson, 1997; Brawn et al., 2001). Van Wilgen *et al.* (2011) found that bush encroachment could result in a decline in grass species richness, in addition to causing an increase in competition for resources such as light and water. These effects caused by the lack of burning, can lead to a decline, or the removal of some niches that diverse grass ecosystems provide (Swengel, 2001). This study supports this idea, as the invertebrate community is significantly lower in abundance and diversity in the unburnt and nine year post-burn sites (Figure 2.3).

In some studies, the recovery period begins relatively quickly, once the combustion and shock phases of the burn event have ended (Rice, 1932; Bulan and Barrett, 1971; Hurst, 1971; Warren et al., 1987; Anderson et al., 1989). In many of these invertebrate studies, the decline in invertebrates is noted within the first few weeks of the burn event, which this study was unable to monitor as it assessed the long-term effects. However, as already stated increases in the intermediate-term are well documented, and may occur because frequent fires increase shrub and woody plant mortality, which reduces the competition for grasses and other taxa (Wilson and Tilman, 1993; Van Wilgen *et al.*, 2011). By increasing tree mortality, the burn event maintains a more open canopy within the savanna, enabling a wider range of niches to develop and therefore, more ground invertebrates can occupy the grassland (Govender et al., 2006). Another theory on the increase of ground invertebrates could be that warmth demanding insects and pollinators have been shown to associate with recent fires (Moretti and Legg, 2009). The burn event could attract these species and cause the increase seen up to two years post-burn.

The patch mosaic created by the five year burn regime is designed to increase heterogeneity, enabling different ages of grassland to occur within relatively close proximity (Brockett et al., 2001). This heterogeneity should ensure a wider range of niches; which will enable not only the abundances of species to increase, but also the diversity of all taxa to increase. The multi dimensional scaling analysis showed that for ground invertebrates the extreme burn ages provide unique habitats for a more diverse community of invertebrates (Figure 2.15). Therefore, although the short burn regime of five years appears to be beneficial for the abundance of invertebrates, old grassland is also very important to ensure a high diversity of niches is maintained. Driscoll et al. (2010), pooled papers and showed that major changes in grassland ecosystems can occur due to inappropriate fire regimes and that poorly designed regimes can also increase the risk of extinction for many species. Removing the old grassland sites, such as the unburnt and nine year post-burn sites, could cause major changes in the community structure and overall cause a decline in diversity and abundance. A few other studies have shown that having a range of patches of different ages does create an overall increase in biodiversity for mammals and birds (Brockett et al. 2001; Trollope and Trollope 2004). It is clear this study needs to be extended, ensuring the same can be said for invertebrates.

The diversity analysis has shown that the burn does not negatively affect the diversity of ground invertebrates, with the only change in diversity being noted between the recent burn and nine years post-burn sites. The decline seen in the nine year post-burn patches could be because both patches are riparian areas, with very high tree densities, therefore reduced understory growth. The latter could occur due to competition for resources, leading to a loss of grassland habitat for many ground invertebrates (Vetaas, 1992). Secondly, increased activity of ground invertebrates following the burn event could be caused by more soil dwelling invertebrates, and previously less active invertebrates, moving on the surface, which would potentially cause an increase in diversity (York, 1999).

As the diversity appears relatively unaffected by the burn regime it is important to assess if there are any order specific changes that have not been considered. Analysis showed that ants in the unburnt site were found in significantly lower abundances than in the other burn ages. This may be due to reduced activity, caused by increased grass density (York, 1999). However, the significant drop in ant abundance three years post-burn, suggests that ant population vary dramatically from site to site and this may be unrelated to the burn event. Parr et al. (2004) studied the effect of long-term fire regimes on African savanna ants, and found no significant effect of burning on the mean ant species richness and abundance. This suggests that fire is not a determining factor for ants and therefore, this significant variation in the unburnt may be due to another factor such as vegetation type or soil composition.

The only other order that showed significant variation between the burn ages was Collembola. The one and two year post-burn sites appear to have significantly higher abundances of Collembola than the unburnt site (Table 2.8). The increase noted in the newer burns supports overall invertebrate changes in previous studies, which show significant increases in invertebrate abundances at the intermediate level (Lamotte, 1975; Anderson et al., 1989). The increase in Collembola may be due to increased activity on the ground, caused by a reduction in vegetation, resulting from removal of grassland in the previous year. This removal may create an increase in invertebrates passing over the pitfall trap, hence an increase in ground invertebrates (York, 1999). Similarly, the decline in Collembola in the unburnt site may be due to reduced activity. Finally, Collembola prefer moist conditions, and therefore other factors such as soil moisture level will affect the abundance of Collembola (Picker et al., 2002). Therefore, to fully understand the changes in abundance seen here further data needs to be collected referring to soil composition and vegetation.

It is important to remember that, although this is an isolated study looking at the effects of burning on invertebrates, any changes recorded in the invertebrate community will affect other important taxa, for example insectivorous birds. Brawn et al. (2001) showed that the bobolink (*Dolichonyx oryzivoru)* feeds on ground invertebrates in burn sites that range from 2-4 years in age. Although this is an American savanna species, the same concept applies. In order to assess the effect the burn cycle has on the ground invertebrate population holistically, it is vital that changes in other taxa are monitored. The increase in invertebrates seen 1-2 years post-burn could be significantly benefiting specific species of birds, and this needs further investigation. What this study has shown is that the burn regime does not cause any detrimental or long-term declines in ground invertebrates and, in general, benefits the invertebrate community. In particular, the maintenance of old burn patches (such as the unburnt and nine year post-burn sites) compliments the regular five year burn regime.

Effect of patch mosaic on grass invertebrates

The burn event caused a significant decline in grass invertebrate abundance and diversity (Figure 2.4, Table 2.4). This decline was to be expected as the burn event removes the vegetation in the grass layer, removing many resources, which invertebrates at this level require to survive (Govender et al., 2006). The decline in invertebrate abundance within a few months (0 years) after the burn is due to a high mortality of grass invertebrates occurring during the combustion and shock phases of the burn event (Warren et al., 1987). This study has shown that some orders (Hymenoptera, Phasmatodea, Thysanoptera, Acari and Orthoptera) are unable to survive the burn event, with no invertebrates of these orders being present in the 0 years post-burn patches (Figure 2.16). This suggests that for these orders, the vegetation itself is essential for survival. However, these orders did not show a significant difference in abundance across the burn events. This may be because the counts were low, making standard errors large. More data needs to be collected at the level of order, using more sweep net transects to identify if the loss of these orders is significant.

Other orders appear to be more resilient, such as ants, Hemiptera, Diptera and Araneae. Ants were unaffected by the fire regime (Table 2.9), which has also been shown by Parr et al. (2004). This may be because they can survive the combustion phase by moving below ground (Trapnell et al., 1976; Warren et al., 1987). Araneae abundance is significantly lower one year post-burn, compared to the unburnt site. This suggests that removal of the grass layer has caused loss of niche habitats and movement corridors that the Araneae require. As spiders can use all three invertebrate levels, movement of Araneae into another level while vegetation is low is not unexpected. Increased Araneae abundance was noted at ground level, which may suggest increased use of the ground due to low vegetation density in the grass level.

Hemiptera significantly declined in the recent burn sites compared to the unburnt, but within two years showed increases in abundance levels over the unburnt counts. This supports previous studies, which have shown that mortality from the burn event causes declines but recovery occurs within one year, often causing abundance of Hemiptera to exceed pre-burn levels (Rice, 1932). One reason for survival of some Hemiptera and a quick recovery following the burn, may be that the majority of Hemiptera species have wings and cannot only escape the initial combustion phase, but can quickly return to the patch (Picker et al., 2004). This increased mobility may be why the Hemiptera are not completely absent from the recent burn sites, although they do show declines in abundance (Rice, 1932; Warren et al., 1987). The same pattern can be seen in Diptera (Figure 2.16).

The ground invertebrate analysis showed that the burn regime might be causing an increase in invertebrate abundance for up to two years following the burn event, which has great support in the literature (Rice, 1932; Cancelado and Yonke, 1970; Nagel, 1973; Warren *et al.,* 1987). The same level of increase did not occur in the grass invertebrates, with the abundance of grass invertebrates returning to the level of an unburnt site, one year after burning. The NMDS supports this similarity, showing that the composition of the unburnt site overlaps the other patches, excluding the recent burn and one year post-burn sites (Figure 2.16). The composition of one year post sites does not fully overlap with the other burn ages. This supports the idea that there is some change in the abundance and diversity of grass invertebrates in the intermediate period, although this study was unable to fully identify this change. The lack of a significant increase in grass level invertebrate abundance, over the unburnt site, during this intermediate-term response (1-3 years post-burn), may be due to other limiting factors. For example, grazing and rainfall play a significant role in determining the structure and composition of vegetation, which in turn affects the abundance and diversity of invertebrates (Scholes and Walker, 1993, Yarnell et al., 2007). Therefore, changes in the grass invertebrates cannot solely be attributed to the burn.

Although the overall data did not suggest a significant increase during the intermediate response period, some orders did. Diptera, Hemiptera and Araneae all show increased abundance two years post-burn in relation to either the recent burn or one year post-burn site. This supports the increase abundance response seen by other studies (Rice, 1932; Lamotte, 1975; Van Amburg et al., 1981; Warren et al., 1987), although it does not exceed the unburnt level.

The patch mosaic created at MWR reduces the risk of extinction of non-focal species in the grass layer. Although the burn initially had a catastrophic effect on invertebrates within the burn patch, this was short lived, as the surrounding patches provide local stability for the invertebrate community as a whole. This allowed recently burnt patches to be re-colonised once the vegetation began to re-grow (Moretti and Legg, 2009). It is this heterogeneity, created by the patch mosaic, which maintains a stable environment for invertebrates and other taxa. The multi-dimensional scaling analysis showed that the recent burn had a very different composition to the other burn ages (Figure 2.16). This change may be due to the removal of vegetation, which caused significant declines in the invertebrate community (Atkinson et al., 2004). The composition of invertebrates within the one year post-burn patch also showed some variation in contrast to the other patches. This provides evidence that the patch mosaic is generating a range of different microhabitats, which increases heterogeneity within the reserve, and in turn should increase biodiversity (Brockett et al., 2001).

Overall, it is clear that the burn event generates a major disturbance to the grass invertebrate community, which without the distinct patch mosaic and burning cycle, could cause long-term declines. If all patches were burnt at once, or natural lightning burns were used without controls, it may cause local extinctions and prevent recovery within the site (Trollope and Trollope, 2004). What this study has shown is that invertebrates are resilient to drastic changes, with the grass invertebrates recovering significantly from the burn event within one year. This quick recovery is not only significant for the survival of the invertebrates themselves, but for other taxa which rely upon them such as insectivorous birds (Sinclair, 1978). Finally, the burn event generates a unique habitat increasing the niche availability across the reserve, which is clear from the NMDS analysis.

Effect of patch mosaic on tree invertebrates

Similarly, to the grass invertebrates, fire causes a decline in tree invertebrates within the first year of the burn event. However, unlike the grass invertebrates, no orders were completely absent immediately following the burn. The reduced mortality may be occurring because the burns done at MWR are cold burns. Many well designed burn regimes in South Africa are undertaken within the colder months between June and August; patches are burnt with the wind and are done while the grass still has some moisture (Yibarbule, 1998). Cold burns require these parameters to make the burn event manageable, ensuring that the fire is a surface burn, only removing the grass layer below the tree canopy (Govender et al., 2006). As the fire is not intended to damage the tree canopy, tree invertebrates are safer from the flames and hence survival of some invertebrates is to be expected (Rice, 1932; Lamotte, 1975; Frost, 1981; Warren et al., 1987).

The only significant variation in tree level invertebrate abundance is seen between the recently burnt site and the two older sites (nine years post-burn and unburnt sites). Figure 2.5 shows that the burn patches representing two years post-burn, have a similar tree invertebrate abundance as the unburnt site. This contradicts previous studies, which have shown that in the intermediate period between burns the invertebrate abundance increases (Lamotte, 1975; Warren et al., 1987; Anderson et al., 1989; Swengel, 2001). However, many of these studies look at sweep netting or pitfall trapping, and therefore do not include the tree level invertebrates in the analysis. As tree level invertebrates are usually exposed to a lower degree of flames the effect of burning on these populations would be expected to vary from ground and grass level (Miller, 1979; Warren et al., 1987). Although the burn has a significant effect on the tree invertebrate abundance, this is only between the recent burn site and old sites; therefore, over the burn regime itself (0-5 year burn cycle, which includes 0-3 year post-burn sites only) the effect is neutral.

The increase in tree level invertebrates in the two older sites may be due to the lack of disturbance in these sites. Limited disturbance in these two sites, allows bush encroachment, creating a diverse tree canopy, providing a wide range of niches for invertebrates to survive (Govender et al., 2006). Increased diversity of flora and increased tree density may explain the increase in invertebrates at this level. This increase in the unburnt and nine year post-burn sites is also noted at the level of order, for example Hemiptera (Table 2.10), which is supported by other studies (Morris, 1975). The diversity of tree species within the unburnt and nine year post-burn sites is likely to be greater than sites within the burn regime (0-5 year's post-burn sites). Therefore, the data shows that the only significant changes are due to a lack of disturbance, whereas sites within the burn regime have similar diversity and abundance values across all ages. Tree invertebrates appeared to be resilient to the burn and showed very few long-term changes in abundance or diversity (Sanaiotti and Magnusson, 1995).

With no significant change in diversity across the burn ages (Table 2.7), and only significant increases seen in the older undisturbed sites, it is not unusual to find that the composition across the burn ages are similar (Figure 2.17). There appeared to be some variation in composition around the central area, which is to be expected as other factors such as tree species will affect the invertebrates present in the samples taken. However, there is a large quantity of overlap, and this suggests that the burn regime is not having a significant effect on the tree invertebrate community.

The lack of a significant long-term change in tree invertebrates is to be expected; however, it must be taken into account that some trees are lost during the burn event (Van Wilgen et al., 2011). Some tree mortality can be beneficial to prevent bush encroachment and maintain an open canopy, which allows grasses to re-grow with limited competition for light and other resources (Trollope, 1974; Govender et al., 2006). The loss of trees may cause a decline in the overall tree invertebrate abundance, due to complete removal of a tree canopy habitat. However, the proportion of trees lost is minimal and as a large number of invertebrate orders have wings, many individuals in these trees would be able to survive by moving into the new grass and shrub vegetation created by the reduced competition for resources (Van Wilgen *et al.,* 2011). Therefore, when looking at all invertebrates in a grassland ecosystem, the loss of some tree invertebrates could be balanced with rapid recovery of grass invertebrates. However, further studies are required to assess the short-term effects of burning on functional invertebrate groups' at all three levels (Chapter 3).

Five year burn regime – Is it beneficial or harmful to the savanna?

Patch mosaics and other burn regimes are widely used across national parks and private game reserves throughout South Africa, to manage mammal populations and the savanna ecosystem (Brockett et al., 2001; Trollope and Trollope, 2004). Research and management practices are now tending towards managing savannas holistically and therefore, understanding the effects of burn regimes on all taxa is essential (Driscoll et al., 2010). Assessing the long-term effects of fire on invertebrates is important to ensure current burn regimes are not negatively affecting non-focal taxa (Gill and Bradstock, 1995; Fisher et al., 2009). This study has started to assess the effect of fire on invertebrates, an area not often covered (Parr and Chown, 2003). Using the five year burn regime in place at MWR the abundance and diversity of invertebrates was assessed at each burn age. This has shown that overall the effect of burning and fire management on invertebrates is minimal. In the long-term the effect is neutral, there are no significant increases or decreases in burn patches compared to an unburnt site. Any declines seen in invertebrates occur within the first year of the burn event and therefore, are likely to be due to mortality of invertebrates in combustion and shock phases of the burn (Warren et al., 1987). The length or extent of these effects is discussed in Chapter 3.

The only invertebrate level that appears to have any significant long-term effect from the burn regime is ground invertebrates (Figure 2.4). Statistical analysis showed that the burn regime benefits the invertebrates, with increases in the abundance up to three years following the burn (Table 2.3). The unburnt and nine-year-old burn, which are left outside the five year burn regime at MWR, have significantly lower mean abundances for ground invertebrates than the recent, one-, two- and three-year-old sites. This suggests that the five year regime, which prevents bush encroachment and removes the grass layer, is beneficial to the ground invertebrates (Gill, 1975; Dörgeloh, 1999). The increase in ground invertebrates within the five year burn cycle shows a positive effect of the burn regime for invertebrates, as well as the mammals the burn regime is intended for (Brockett et al., 2001; Parr and Chown, 2003).

Although further study is required to look in more detail at the functional groups and specific orders effected by the burn regime; this study has shown that fire as a management tool used to maintain spatial heterogeneity across a landscape is not having a negative effect on invertebrates (Brockett et al., 2001). It also appears to be benefiting some invertebrates and this in turn may benefit other taxa, which rely on invertebrates for survival, such as insectivorous birds (Brockett et al., 2001; Parr and Chown, 2003). For conservationists aspiring to maintain the savanna ecosystem, with a wide biological diversity, burning is not a hindrance to this process, and in many ways appears to be beneficial.

Chapter Three

The short-term effects of burning on invertebrate communities

Chapter 3: Short-Term effects of burning on invertebrate communities

Introduction

Fire is a key feature of savanna ecosystems, along with rainfall and herbivory, and is important in maintaining the continuous grass layer under a sparse canopy of trees that define this ecosystem (Andersen et al., 1998). Chapter 1 discusses the anthropogenic burning systems, and stresses the importance of a holistic research aim when assessing the affects of burning on the savanna ecosystem (Andersen et al., 1998); ensuring coverage of not only the effect on mammals but on all other taxa that utilize the savanna. However, despite the known necessity of fire and beneficial effects of fire regimes, information on these effects is fragmented, as explained in Chapter 1 (Bowman, 2000; Parr and Chown, 2003; Bond and Parr, 2010; Driscoll et al., 2010; Andersen et al., 2012).

A large proportion of initial studies conducted were observational, with only a few using experimental fire regimes (Parr and Chown, 2003). The information gathered from these has been useful, and has enabled a general understanding of the effects that fire intensity, season and frequency has on the vegetation (Trollope and Trollope, 2004). In particular, the effect of fire on vegetation is relatively well studied and understood, as explained in Chapter 1. With limited information on the effect of burning on other taxa, well designed burn regimes cannot be prescribed with confidence (Govender et al. 2006). Poorly designed fire regimes can cause substantial changes in the community structure within a savanna, as well as increasing the risk of extinction for many species (Gill and Bradstock, 1995; Fisher et al., 2009; Driscoll et al. 2010). It is therefore vital to ensure that further research is undertaken to assess the response of all levels of the ecosystem to fire. As this knowledge base increases, it will eventually ensure that the correct management practices can be put in place, avoiding non-target taxa (such as birds and invertebrates) becoming endangered or extinct (Driscoll et al., 2010).

There are three main areas of required knowledge in fire management (Driscoll et al., 2010):

1. Direct responses of individual species to the burn event.
2. Understanding how the temporal and spatial spread of a burn regime can affect the biota in the ecosystem.

3. How the burn regimes interact with other biological processes within the ecosystem (e.g. nitrogen cycle, carbon cycle, seed dispersal and species specific interaction such as dung beetles)

In order to maintain a highly diverse savanna grassland, within the remaining protected land in South Africa, accurate knowledge on these three areas is essential (Keith et al., 2002; Clarke, 2008). Assessing the initial or short-term responses to the fire for all taxa is important to understand the movement, declines and recovery of each level of the food web. Research also needs to assess what aspects of the ecosystem are being used by functional groups. For example, for many faunas it is the structural aspects of vegetation (e.g. logs, dense scrub, deep litter and tree hollows (Giaretta et al., 1999; Ding et al., 2008)) that they depend on for breeding and protection. For others, the changes in vegetation affect the use of the grassland, providing areas for foraging, which may previously have been used for shelter (Driscoll et al., 2010). Therefore, a detailed understanding of taxa at multiple levels of the ecosystem (ground, grass and tree) is important to understand how functional groups are utilising the savanna.

There are clearly many gaps in research that need addressing, but one key area that this report focuses on is the short-term effect of fire on invertebrate orders, where few studies have been undertaken despite the diversity of the group (Parr et al., 2004). Research into the short-term effects of fire on invertebrates is essential to ensure that burning is not immediately causing deleterious effects on invertebrate populations (Driscoll et al. 2010). It is well established that invertebrates are a major food source for many bird species, meaning that in order to understand the effect of burning on the avian population, and their continued survival on a site following a burn event, it is vital to understand how fire affects invertebrates (Daubenmire, 1986; Bouwman and Hoffman, 2007).

Measuring the abundance (instead of presence/absence) of each invertebrate order, following the burn event, is essential to assess the detailed effects of the burn. This study therefore aims to address this gap in research. In particular, assessing the changes in invertebrates at three different levels of the savanna ecosystem; ground level, grass level and tree level. Many studies have shown that there is an immediate decline in invertebrates following the burn, but in general these studies have only addressed invertebrates at one level and have inferred that any changes seen occur throughout the ecosystem (Rice, 1932; Warren *et al.,* 1987). This study will add to, and expand, this knowledge, by separating the invertebrates into three levels. This should enable future studies to use these general changes in invertebrate abundance to predict or interpret changes in avian abundances immediately following the fire.

This short-term study enables a more detailed analysis of the effect of burning, allowing the invertebrate population to be monitored following the burn event. This enables a clear understanding of the rate of recovery for different orders, as well as showing survival and movement of specific orders during, and immediately following, the fire. For this study the responses of invertebrates was monitored pre-burn, and within days and weeks post-burn; with the last data being collected only three months following the burn. This narrow time period allowed fine scale changes in invertebrate populations to be monitored. This also helps to explain the presence or absence of other taxa immediately following the burn, for example the fork tailed drongo (*Dicrurus adsimilis*), which appears to be attracted to the fire and recent burn sites (Daubenmire, 1968). This is providing a new level of understanding that the long-term study (Chapter 2) could not access, as it only enabled a snap shot of the invertebrate populations within each burn age. The short-term study enables a continuous monitoring of the burn site, enabling changes in invertebrate orders to be closely monitored over time.

As there is a limited amount of knowledge on the short-term effects of fire on invertebrates; hypotheses for the effects of fire needs to be broad. Immediately following the burn event it is expected that the fire will remove the grass layer and therefore cause an immediate decline in both grass and ground invertebrate abundance and diversity (Rice, 1932; Warren *et al.,* 1987). This may also be true for tree invertebrates as some damage will occur to the surrounding trees, if not directly via burning, then via heat and smoke. Following the initial decline in invertebrates at all three levels, ground invertebrates are expected to make a steady recovery, as are tree invertebrates. However, the recovery of grass invertebrates is expected to be much slower as this is dependent on the rate of regrowth, which in turn is dependent on the rainfall (Brockett *et al.* 2001).

Material and methods

Study Site and Data Points

The study was based at Mankwe Wildlife Reserve (MWR) as it was for the long-term study in Chapter 2. MWR has a five year rotational burn regime, giving the reserve a patch mosaic. The rotational burning means that three patches on the reserve were being burnt in 2014. The aim of this project was to monitor the invertebrate community before and following the burn event. In order to monitor the changes in the invertebrates, two patches were identified as study areas for this project. Each patch being burnt required a control patch which was of a similar burn age before the burning event, and in a similar location to the burnt patch. Figure 3.1 shows the two patches that were burnt in red and the corresponding control patches in blue. Before the burn, patch L (consisting of the control [L_c] and burn area [L_b]) was last burnt in 2010. With only half of this patch being burnt, it provided both the control and burn points for the first pairing. Patch I, in the north east of the reserve (Figure 3.1), was last burnt in 2010. This patch was selected so that the data would not be affected by a variation in burn history. The nearest area of similar burn age was patch K, which was last burnt in 2011. This was selected as the control for patch I (Figure 3.1), due to its proximity and similar burn history. The control and burn patches needed to be in close proximity to reduce the geological variation.

The data points used for this short-term study were the same as those used for the long-term study in Chapter 2 (page 19). Across the two burn patches 20 data points were needed, 10 points in each burn. However, due to the size of patch L only eight points could be used within L_b (Figure 3.1). To counter this, two extra points were added to I, giving patch I a total of 12 data points. The criteria set for control points meant that, due to space and time constraints, for each burn patch only five control points could be used; therefore, a total of 10 control points were followed between two patches (each control patch being in proximity to a corresponding burn). This gives an unbalanced design, which could cause errors in statistically analysis putting more weight on individual samples at each control point. One way of trying to deal with this error in the report was to use averages for all types of analysis. Using random selection for data points also creates some biological and statistical errors due to edge effect. To reduce edge effect, criteria in R ensured that no point would be less than 50m from a road or fence line.

Burn patches could not be selected; patch I and patch L were the two patches being burnt during the field period. Points used in patch K (control for burn patch I) were selected to have similar habitat to patch I, points further in the reserve in this patch were closer to the main dams and had higher tree densities.

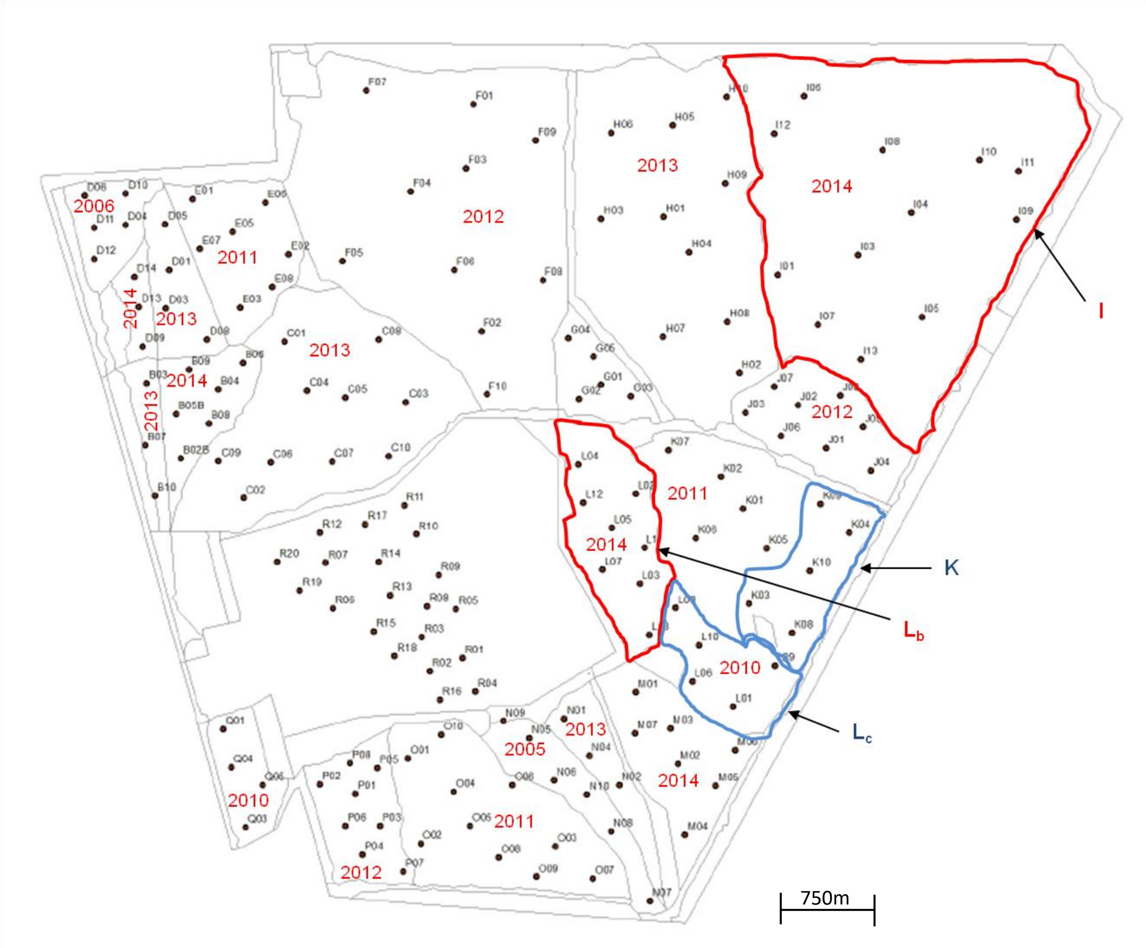

Figure 3.1: Map of Mankwe Wildlife Reserve, showing distinct burn patch areas. The red lines show the two burn patches and the data points within them (patches L_b and I. The blue lines identify the two control patches and the burn lines within them (patches L_c and K).

Data Collection

As with the long-term study in Chapter 2, invertebrates were collected using three methods: pitfall trapping to assess the ground invertebrates, sweep netting to assess the grass invertebrates and tree beating to assess the tree invertebrates. This split enabled a more focused look, not only at the effect of burning on each invertebrate order, but how the fire affects these orders overall, and at the three unique micro-habitats.

Data was collected at both the control and burn sites at set time periods before and after the burn. The control and burn site data points were collected within three days of each other to reduce the effect of climatic variation. Table 3.1 shows the time periods pre-burn and post-burn, at which data was collected within both the control and burn sites. Patch L_b was burnt at the beginning of September and patch I was burnt three weeks later. At each data collection period invertebrate counts were conducted using pitfall traps, sweep nets, and tree beating for each point (a total of 20 points in the burn sites and 10 across the controls).

Data Collection Event	**Time period around burn**
0 (Pre-burn)	3 days before the burn event
1	3 days post-burn
2	2 weeks post-burn
3	1 month post-burn
4	2 months post-burn
5	3 months post-burn

Table 3.1: Data collection points in relation to the burn.

Pitfall Trapping

At each data point two pitfall traps were placed, one 10m north and one 10m south of the central point. Each pitfall trap consisted of a plastic cup, approximately 10cm deep and 6 cm in diameter, dug into the ground ensuring the lip of the cup was at ground level. Each trap contained a small amount of soapy water and was left out for three nights, as in the long-term study (pages 22-23). To reduce evaporation and interference from mammals, a quarter of a paper plate was placed over the top of the cup, held up using toothpicks, and camouflaged with mud, burnt material (in burn areas) and vegetation (Figure 3.2).

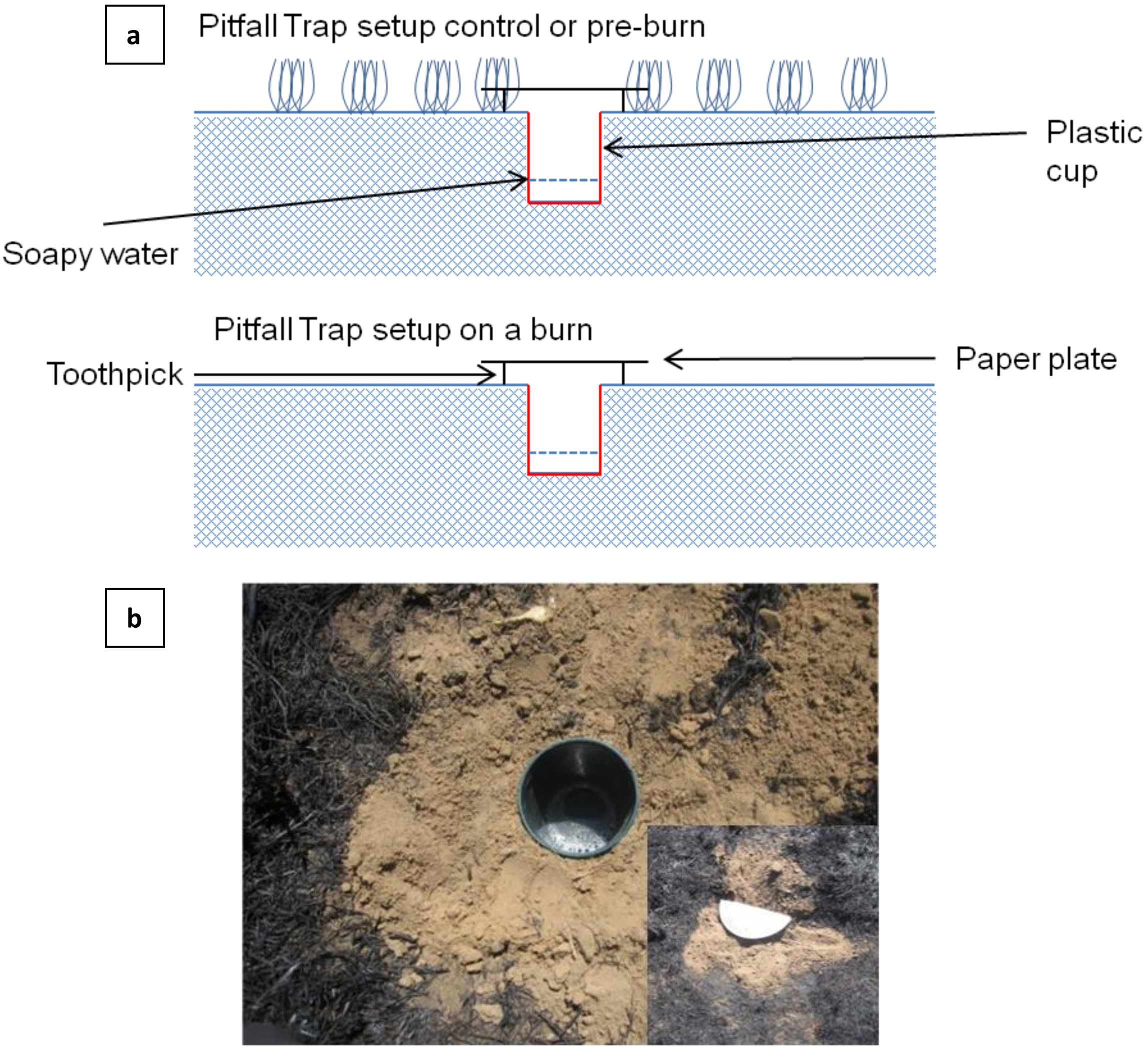

Figure 3.2: **a)** Diagram showing the pitfall trap setup at each data point type.
b) Pitfall trap in the field

After three nights the pitfall traps were collected and the contents of each trap transferred into a specimen pot with a unique code. A small amount of anti-freeze was added to each pot to prevent the samples from degrading before identification could occur. Invertebrates were identified by eye or using a 40x magnification lens to the level of order, using keys and information in Tilling (1987) and Picker et al. (2004). For each trap the total count for each order was recorded.

Sweep netting

Sweep netting was used to collect grass level invertebrates at each point, as in the long-term study (pages 23-24). Two 50m transects were undertaken at each point within each data collection time period (Table 3.1). Each transect consisted of 50 sweeps, ensuring the net remained in the vegetation layer when present. On the burnt sites immediately following the burn there was very little or no vegetation, and in these circumstances the edge of the net was kept close to the ground to gather any invertebrates on the short grass swards that remained. At the end of each transect any invertebrates captured were transferred to a zip lock bag, each with a unique number for identification at a later date. The sample from each transect was identified, by eye or using a 40x magnification lens, to the level of order using keys and information in Tilling (1987) and Picker et al. (2004). Once all invertebrates in the bag had been identified they were released into surrounding grassland.

Tree beating

Tree beating was undertaken to sample invertebrates that live in trees and flying invertebrates. At each data point four trees were selected for tree beating; using the closest tree in each cardinal direction. Sample trees had to be over 3m in height, and branches selected for beating had to be at least 1m above the ground. If two potential sample trees were in close proximity to each other they were no longer independent and in this case the nearest tree in either compartment was used along with one tree from the pair (Figure 3.3).

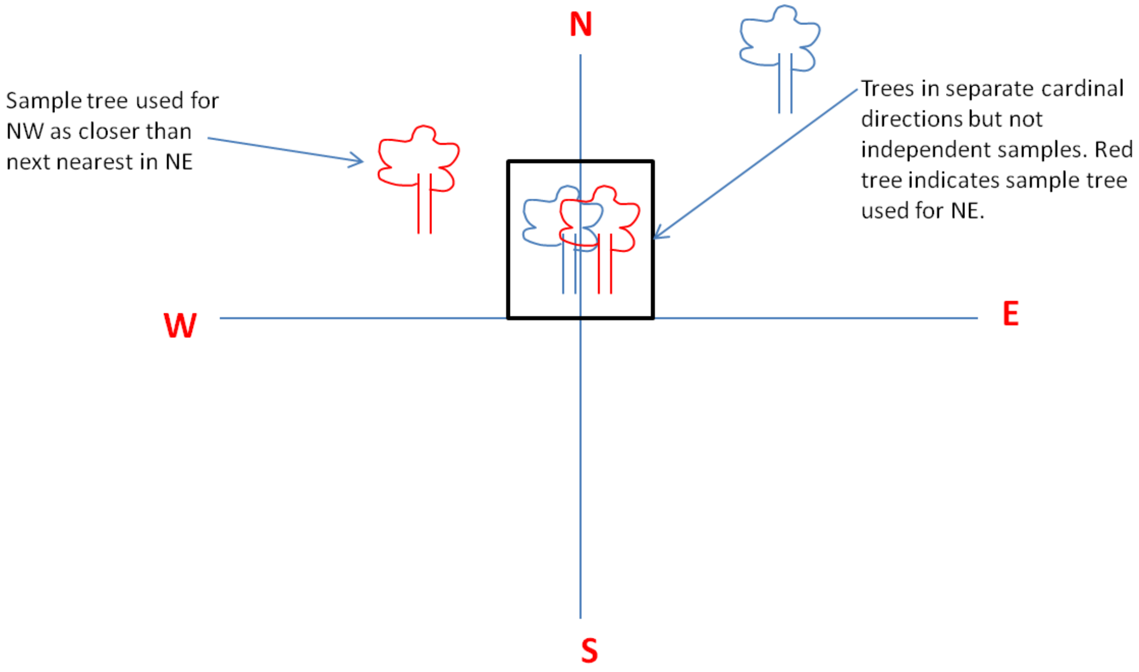

Figure 3.3: Diagram showing tree sample selection when the closest trees are no longer independent.

Each sample tree was hit on two different branches using a wooden pole; where possible sample branches were on opposite sides of the tree. A 1m x 1m white sheet was held under the branch as it was hit 10 times. In total each sample tree was hit 20 times. After 10 hits on a branch, invertebrates that had collected on the white sheet were identified to the level of order, by eye or using a 40x magnification lens, and counted before being released back into the grassland. The invertebrate counts from the two branches were combined to give the total invertebrate sample for the tree. For each sample tree the distance from the central point and the direction of the tree was recorded. This data was taken so that the same four trees could be sampled at each collection event (Table 3.1), thus reducing variation that may occur due to tree species or age.

Rainfall

Rainfall is recorded across MWR using five rainfall gauges placed at different locations across the site. Rainfall in South Africa predominates during the summer months. During the time of the study South Africa was going through a drought period. Therefore, the presence of rainfall itself was significant. The start date for the rainfall was recorded, and any data event post that date was recorded as rainfall present. Rainfall was therefore in the model as pre/post the start of the rainy season.

Data analysis

As in the long-term study (Chapter 2), all three invertebrate response variables (ground, grass and tree) were considered separately; due to the fact that data from the three levels could not be merged as the collection methods for each level are not comparable. Once data was entered into excel, it was checked against the raw data before using it for statistical analysis and modelling. Two burn patches were used for this study; the data from the two patches were not separated by patch for initial analysis using each point as a unique data point. This was done as both burn patches had the same burn history, with habitat being similar between the two patches. In modelling analysis patch type was used to determine if any variation occurred between the points within each patch.

Abundance

At each invertebrate level the total abundance was plotted in notched box plots in R (R Core Team, 2014), using ggplot2 (Wickham, 2009). These were simply used as visual representation to identify general patterns, no statistical analysis was done. Therefore the fact that control points had less data values than the burn was not considered an issue at this stage of the study. Each pitfall trap and tree was used as unique data points. However, the two sweep net transects per point (and per event) were combined as the distance between them was too small to be confident that they were separate samples.

Dominant order selection

As with Chapter 2 the abundance change of dominant orders was assessed over the three month period following the burn event. For ground, grass and tree level data the total count of invertebrates recorded at each event were combined and divided by the number of unique orders recorded. This number gave the average presence count for each order; those orders that showed total counts lower than the average were excluded. The average abundance for those orders selected as dominant were then plotted in bar charts in R (R Core Team, 2014) using ggplot2 (Wickham, 2009). As averages were used per pitfall trap, tree and combined sweep net the variation in point number between control and burn was dealt with. Ants were collected as a separate group, rather than in the order of Hymenoptera, as they were easy to identify and their count would have significantly skewed the Hymenoptera count.

Order accumulation curve

Order accumulation curves were produced for each invertebrate level, creating separate curves for each burn event. This was used to get a base line understanding of species richness, but primarily to asses if the samples collected are representative of the fauna present within the area at each event (Thompson and Withers, 2003). As in Chapter 2 (page 25) accumulation curves were created in R (R Core Team, 2014), using the vegan package (Oksanen et al., 2016).

Diversity

For each invertebrate level, diversity was calculated at each data point within the burn and control sites. This was done using the Shannon index; as in the long-term study (page 26) the diversity values showed very little variation between the Shannon and Simpson indexes, and therefore only the Shannon index was used.

A Shannon value was calculated for each data point, within each data collection event. Shannon index was calculated in R using the *Vegan* function (Oksanen et al., 2016). An average diversity value was then calculated for each site type (control and burn), at each time point following the burn. The significant difference between each data collection period was quantified using ANOVA in R (R Core Team, 2014). When the ANOVA test showed an overall significant difference between the data collection events, a post hoc test (Tukey test) was performed in R. For all statistic tests 95% confidence limits were used to assess the strength of the differences.

Modelling

In order to analyse the relationship between the burn event and invertebrate abundance, linear mixed models were required to assess the effect of a number of factors. Using R (R Core Team, 2014) and *lme4* (Bates et al., 2015) a GLMM was run for each invertebrate level using event, site type, patch, rainfall and an interaction term for event and site type as fixed factors. Point was included as a random effect. Sampling period was not required as a factor since all data was collected over the same time period. The variation in time between the patches was covered as a fixed factor in patch. Each model was then dredged in R using *MuMIn* (Barton, 2016); only models with a ΔAIC≤ 6 were considered (Richards et al., 2011). The strongest model was selected based on the ΔAIC, logLik value, and Akaike model weights. Visual inspection of residual plots was also carried out to check for any deviation from normality. Estimates and standard error values from the model outputs were used to understand how each factor affects the invertebrate abundance. The model used for each invertebrate level included the same set up:

Abundance ~ Event + Site_Type + Patch + Rainfall + Event*Site_Type + (1|Point)

Results

Data was collected over six data collection events, as listed in Table 3.1, consisting of 20 burn points and 10 control points for each event over two patches (L and I, Figure 3.1). Therefore, a total of 40 pitfall traps, 40 sweep net transects and 60 tree beats were undertaken in burn areas at each event; with 20 pitfall traps, 20 sweep net transects and 40 tree beats being undertaken in control areas at each event.

Abundance

The data collected on invertebrate abundance at each level was affected by a number of confounding variables. Therefore, analysing the change in abundance had to be modelled using GLMM. Prior to this, notched box plots were generated to visually assess the change in invertebrate abundance over time, for both the control and burn sites.

As with the analysis of the long-term data (Chapter 2, page 28) ants were a dominant group within the data. The high ant abundance throughout all events and sites introduced high heterogeneity into the analysis, and prevented changes in the total abundance of invertebrates to be identified. Therefore, as with the long-term data, ants were removed from the analysis.

Ground Invertebrates

The total abundance of ground invertebrates appears to be unaffected by the burn (Figure 3.4). Within the burn sites, median ground invertebrate abundance does not appear to significantly change over time, with notches of all burn site box’s overlapping. Although this does not completely rule out any significant changes, it suggests that any changes seen in the model may be small. This lack of change is also seen in the control sites; and concurs with the long-term data set which showed that only the unburnt site significantly differed to any other burn age (Chapter 2, pages 29-30). Figure 3.4 appears to suggest that within the first three months following the burn only minimal changes in ground invertebrate abundance are likely to occur, suggesting that ground invertebrates in general are unaffected by the burn event.

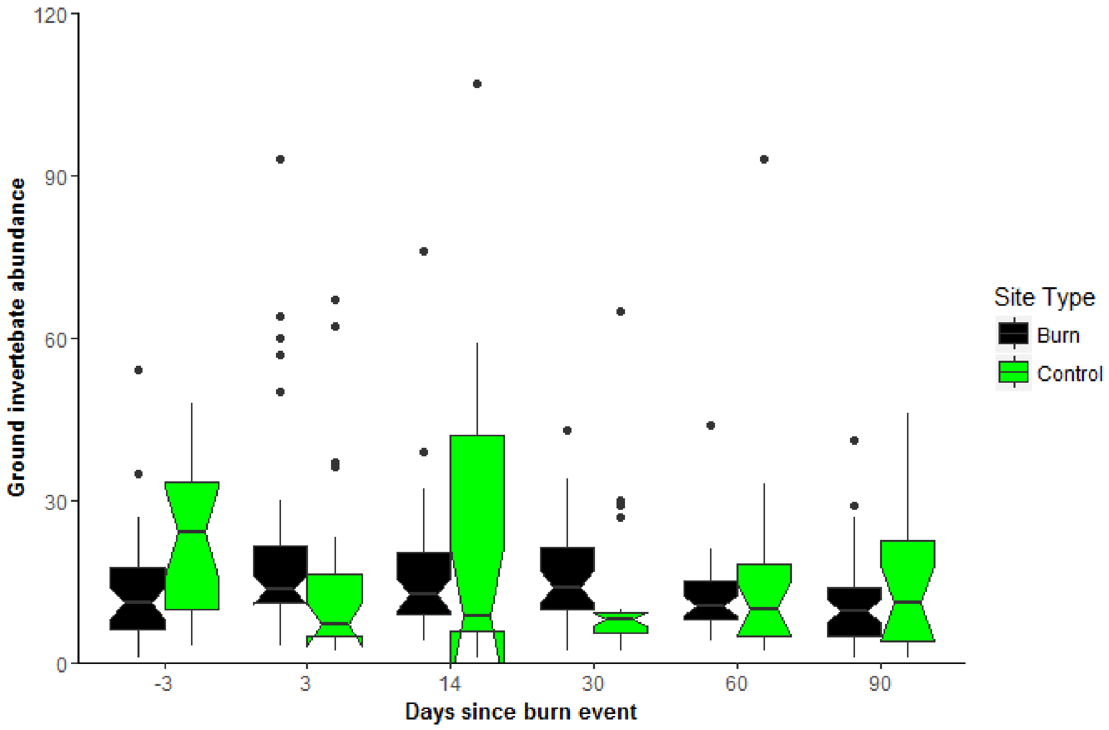

Figure 3.4: A notched box plot depicting the ground invertebrate abundance around a burn event. Notches indicate 95% confidence interval for the median.

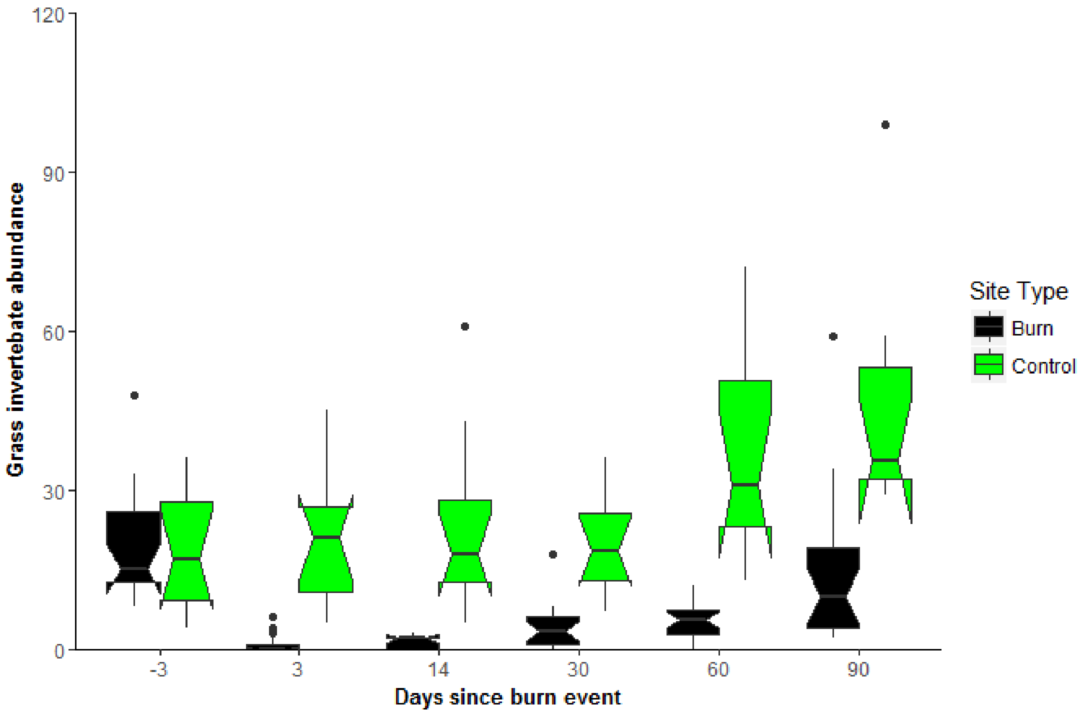

Figure 3.5: A notched box plot depicting the grass invertebrate abundance around a burn event. Notches indicate 95% confidence interval for the median.

Grass Invertebrates

In the burn site the median abundance of grass invertebrates significantly declines following the burn event (Figure 3.5). The notches suggest that immediately following the burn the median significantly declines. From 3 days post-burn the grass invertebrate abundance appears to steadily increase, although this is not significant. Interestingly, Figure 3.5 shows that 90 days post-burn the median abundance is not significantly different to pre-burn levels, suggesting a recovery of grass invertebrates within three months of the burn event. The control site shows no significant change in the grass invertebrate abundance following the burn event (Figure 3.5). Although there appears to be some increase in the grass invertebrate abundance at 60 and 90 days post-burn, the median does not appear to be significantly different to pre-burn or previous post-burn abundances. Although no significant difference is seen in the notch graph, this does not completely prevent some variation occurring; the model will explain significant changes between events more precisely. Therefore, overall the notch graph suggests that the burn event caused a decline in grass invertebrates, with some potential for recovery. As this decline is not seen in the control, it supports the idea that the burn itself is the primary cause of decline (Figure 3.5).

Tree level invertebrates

Tree level invertebrates decline following the burn event, but Figure 3.6 suggests recovery back to pre-burn levels at 60 days post-burn. The decline in the median tree level abundance appears to be significant, but not as large as the decline seen in the grass invertebrates. In the control sites, Figure 3.6 does not suggest a decline in abundance, but does suggest an increase in tree invertebrate abundance above pre-burn levels from 60 days post-burn. The decline in the burn, which is not seen in the control site, suggests that the loss of invertebrates is due to the burn event and not another factor. However, the increase in invertebrates from 60 days post-burn occurs in both the burn and control sites, suggesting other factors are affecting the invertebrate abundance.

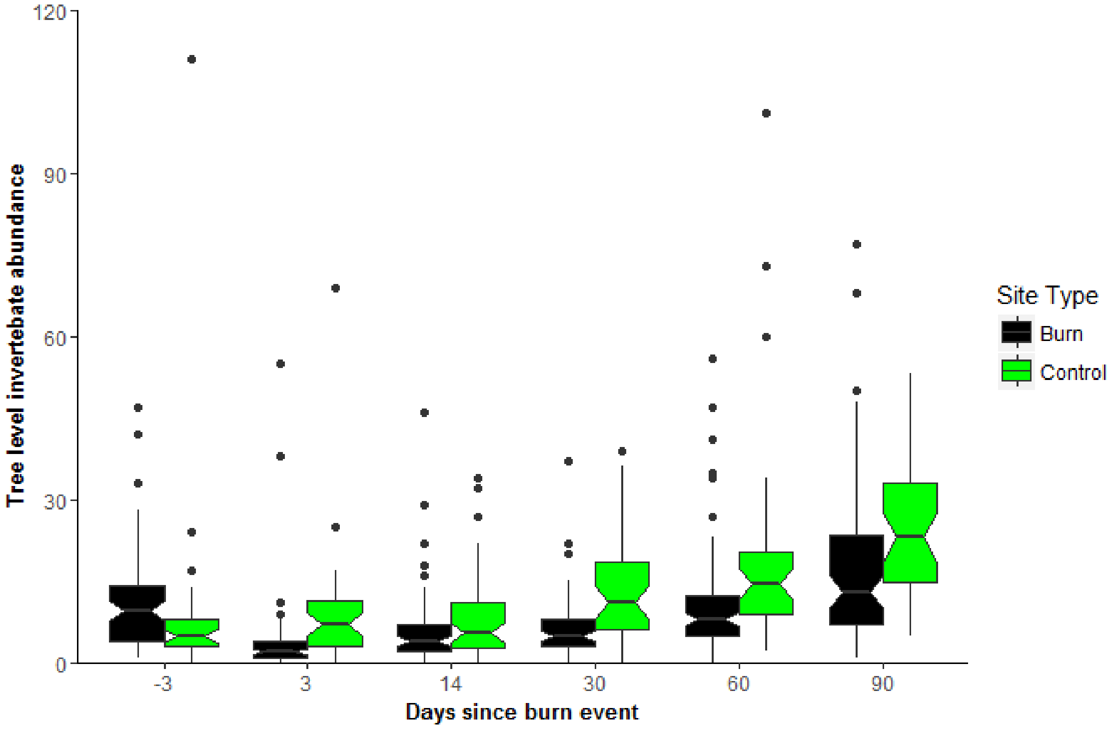

Figure 3.6: A notched box plot depicting the grass invertebrate abundance around a burn event. Notches indicate 95% confidence interval for the median.

Order Accumulation Curves

Order accumulation curves ran for each invertebrate level showed that at each stage both pre and post the burn event; the accumulation curve reached its asymptote. All slopes, excluding tree invertebrates 60 days post burn (Figure 3.96; Red line), reached a slope below 0.3 within the sample size collected. This suggests that the data collected is representative of the total order richness seen throughout the sites during these events. Therefore, it is possible to use this data to suggest changes that may be occurring in the invertebrate community following the burn event.

The order accumulation curves for the ground invertebrates suggests that the order richness for invertebrates steadily increases following the burn event, with 90 days post burn showing the highest order richness (Figure 3.7). What is particularly interesting about this graph is that -3 days (3 days pre burn) the ground invertebrate richness was at its lowest on these sites. This suggests that clearing the fuel load is beneficial for ground invertebrates immediately following the burn; and increasingly so as fresh vegetation begins to come through 14 days post burn and throughout. This links to the richness levels noted in chapter two in that the unburnt site showed the smallest order richness, with one year – three year post burn sites showing progressively more orders (Figure 2.6).

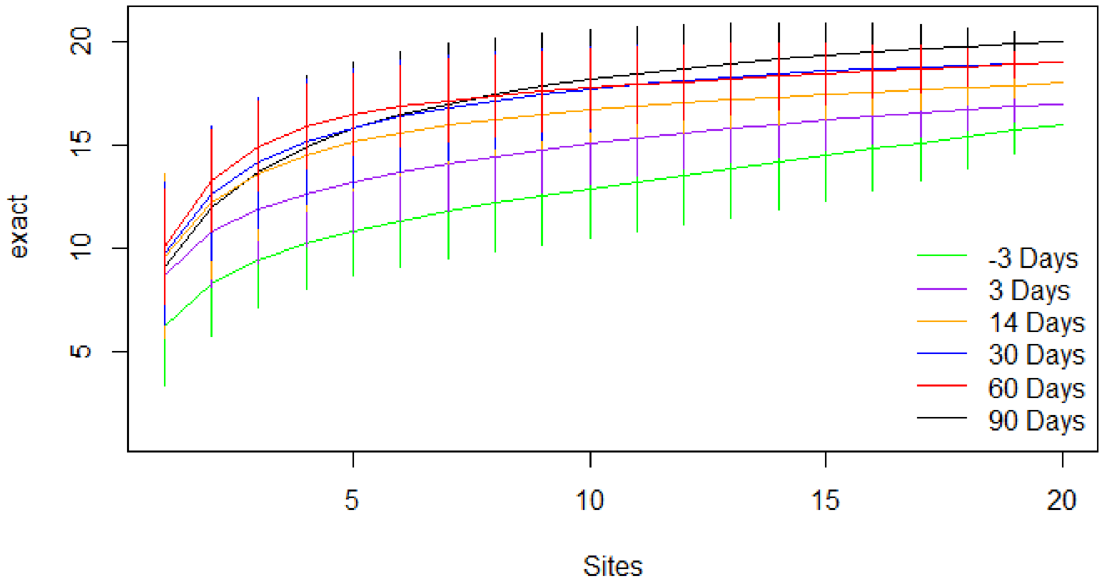

Figure 3.7: Order accumulation curve for ground invertebrate orders caught within pitfall traps across the six burn events surrounding the fire.(-3 days : N=20, 3 days: N=20, 14 days: N=20, 30 days : N=20, 60 days: N=20, 90 days: N=20).

As expected, considering the burn event removes the grass layer vegetation, order richness is greatest pre-burn, and lowest immediately following the burn (Figure 3.8). Figure 3.8 does show that recovery of orders does occur, with the order richness increasing from 30 days post burn. 90 days post burn, although not at the richness of the pre-burn data, shows that the grass level invertebrates are recovering back to pre-burn levels. Therefore, grass level invertebrate response is twofold; immediately following the fire there appears to be a decline in diversity suggesting a complete loss of many orders, followed by a slow but steady return of many orders which within the three months post burn are near recovery to pre burn levels. What this graph does suggest is that less disturbance to the grass, is more beneficial to a wider variety of grass level invertebrates.

The response of tree level invertebrates to fire is also two fold, Figure 3.9 shows that the order richness declines following the burn event, and then recovers above pre-burn levels from 30 days post-burn. 60 days post-burn order accumulation curve showed a continued incline in the slope. Within the survey data collected an asymptote for this event was not reached, and this suggest a higher sample size needs to be taken. However, what is clear from Figure 3.9 is that tree order richness increases from 30 days post burn, attracting more orders than found at pre-burn levels. The slope between the final two points for 60 days post burn for tree invertebrates was 0.45, this suggest that the curve is on a shallow incline and therefore, any orders that are not represented in this study may be minimal.

Overall the order accumulation curves suggest that the invertebrate communities being assess in this short-term study are well represented by the data collected across the 20 points, over two burn patches.

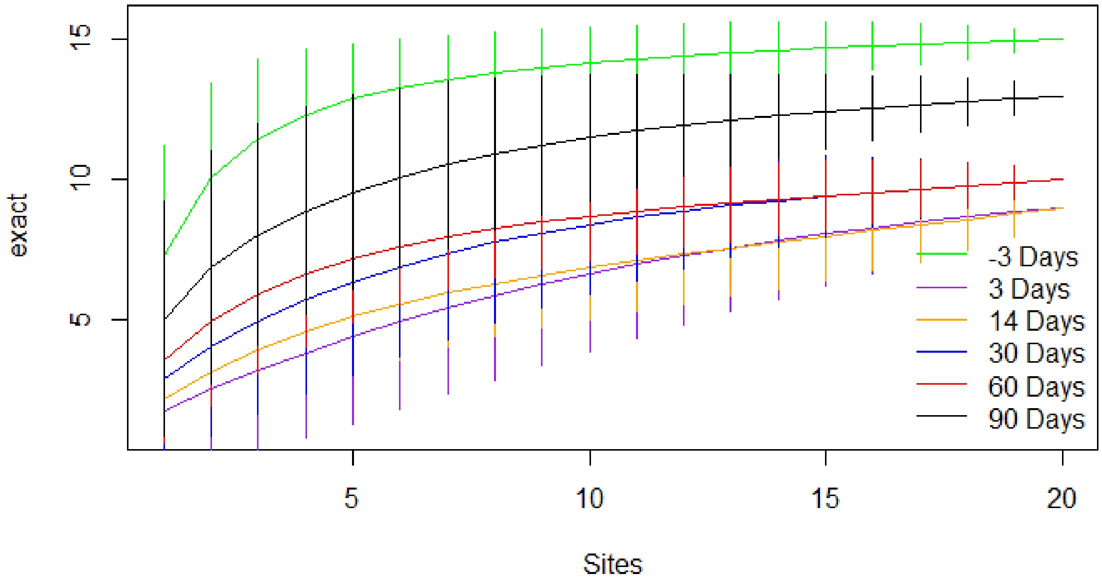

Figure 3.8: Order accumulation curve for grass invertebrate orders caught within sweep nets across the six burn events surrounding the fire.(-3 days : N=20, 3 days: N=20, 14 days: N=20, 30 days : N=20, 60 days: N=20, 90 days: N=20).

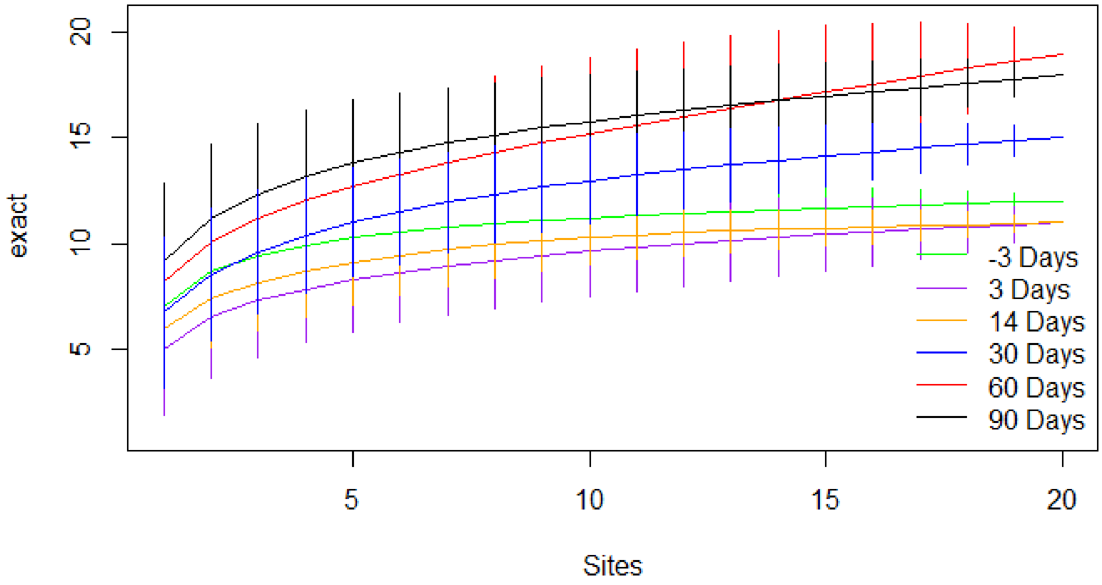

Figure 3.9: Order accumulation curve for grass invertebrate orders caught within sweep nets across the six burn events surrounding the fire.(-3 days : N=20, 3 days: N=20, 14 days: N=20, 30 days : N=20, 60 days: N=20, 90 days: N=20).

Diversity

Ground invertebrates

To assess the diversity of invertebrates at each invertebrate level the Shannon index was used. As with the long-term data, ground invertebrates show no significant change in diversity over time, in either the burn or control (Table 3.2). However, the one way ANOVA (comparing the burn to the control sites), showed that the burn site has a significantly higher diversity than the control site 3 days post-burn and 14 days post-burn (Figure 3.10a,b, Table 3.3). Figure 3.10b shows that the diversity of ground invertebrates 3 and 14 days post-burn has increased compared to pre-burn levels within the control, although not significantly. Hence, the difference in diversity noted at 3 and 14 days post-burn between the burn and control sites could be due to other environmental factors rather than the burn itself.

Invertebrate level	Site Type	ANOVA		Tukey post-hoc test		
		F	p-value	Comparing between events	Difference	p-vale
Ground	Burn	$F_{5,114}$ = 1.34	0.252	N/A		
Ground	Control	$F_{5,54}$ = 1.77	0.135	N/A		
Grass	Burn	$F_{5,114}$ = 33.72	<0.001	-3 vs. 3	1.51	<0.001
				3 vs. 90	0.89	<0.001
				-3 vs. 90	0.62	<0.001
Grass	Control	$F_{5,54}$ = 2.38	0.050	-3 vs. 90	0.34	0.062
Tree	Burn	$F_{5,112}$ = 9.266	<0.001	-3 vs. 3	0.44	<0.001
				-3 vs. 14	0.37	0.003
				-3 vs. 30	0.13	0.708
Tree	Control	$F_{5,54}$ = 2.67	0.032	-3 vs. 90	0.39	0.035

Table 3.2: Statistical output from ANOVA and Tukey post hoc test performed on the diversity values calculated for each point using Shannon index. Six different burn ages were compared. Only key tukey outputs are presented, with significant differences highlighted in red.

Grass invertebrates

It is clear from Figure 3.10c that the burn event significantly reduces the grass invertebrate diversity (Table 3.3). The diversity of grass invertebrates appears to increase after the initial decline, suggesting recovery of orders to the site. Table 3.2 shows that there is a significant recovery in diversity in the post-burn collection events, however, there is still a significant difference between the pre-burn diversity and 90 days post-burn. This shows that although there is some recovery, within the three month period diversity does not return to pre-burn levels (Figure 3.10c, Table 3.2). The long-term analysis in Chapter 2 (page 41) shows no significant change in diversity one year after burning compared to the unburnt site. This suggests that although the diversity of grass invertebrates is still significantly lower than the pre-burn diversity at 90 days post-burn, within one year this may recover. This slower recovery may mean that more grass cover is required to provide a wider range of habitats, thereby supporting a broader range of invertebrates. The invertebrate diversity in the control remains relatively stable throughout the study (Figure 3.10d, Table 3.2).

When comparing the burn to the control at each collection event, a one-way ANOVA showed that the diversity of invertebrates, at all post-burn events, were significantly different, with a lower diversity seen in the burn sites (Table 3.3). As the diversity remains unchanged in the control site throughout the study (Figure 3.10c, Table 3.2), the reduced diversity in the burn sites is likely to be due to the burn event and not another factor. To further qualify this, in the pre-burn collection event there is no significant difference in diversity between the burn and control, therefore the variation in diversity post-burn can be attributed to the burn event (Table 3.3).

Invertebrate level	Event (days since burn)	One Way ANOVA		
		$F_{1,28}$	p-value	R^2
Ground	-3	$2.15e^{-5}$	0.996	-0.036
	3	11.59	0.002	0.268
	14	6.36	0.018	0.156
	30	0.55	0.466	-0.016
	60	1.86	0.184	0.029
	90	2.198	0.149	0.040
Grass	-3	0.5	0.485	-0.018
	3	126.1	<0.001	0.812
	14	122.7	<0.001	0.808
	30	46.33	<0.001	0.610
	60	38.83	<0.001	0.566
	90	32.06	<0.001	0.517
Tree	-3	2.23	0.147	0.041
	3	6.87	0.014	0.168
	14	6.23	0.019	0.153
	30	5.51	0.026	0.135
	60	0.05	0.819	-0.033
	90	3.19	0.085	0.070

Table 3.3: Statistical output from one way ANOVA performed on the diversity values calculated for each point using Shannon index. Diversity values for the control and burn at each event were compared. Significant differences highlighted in red.

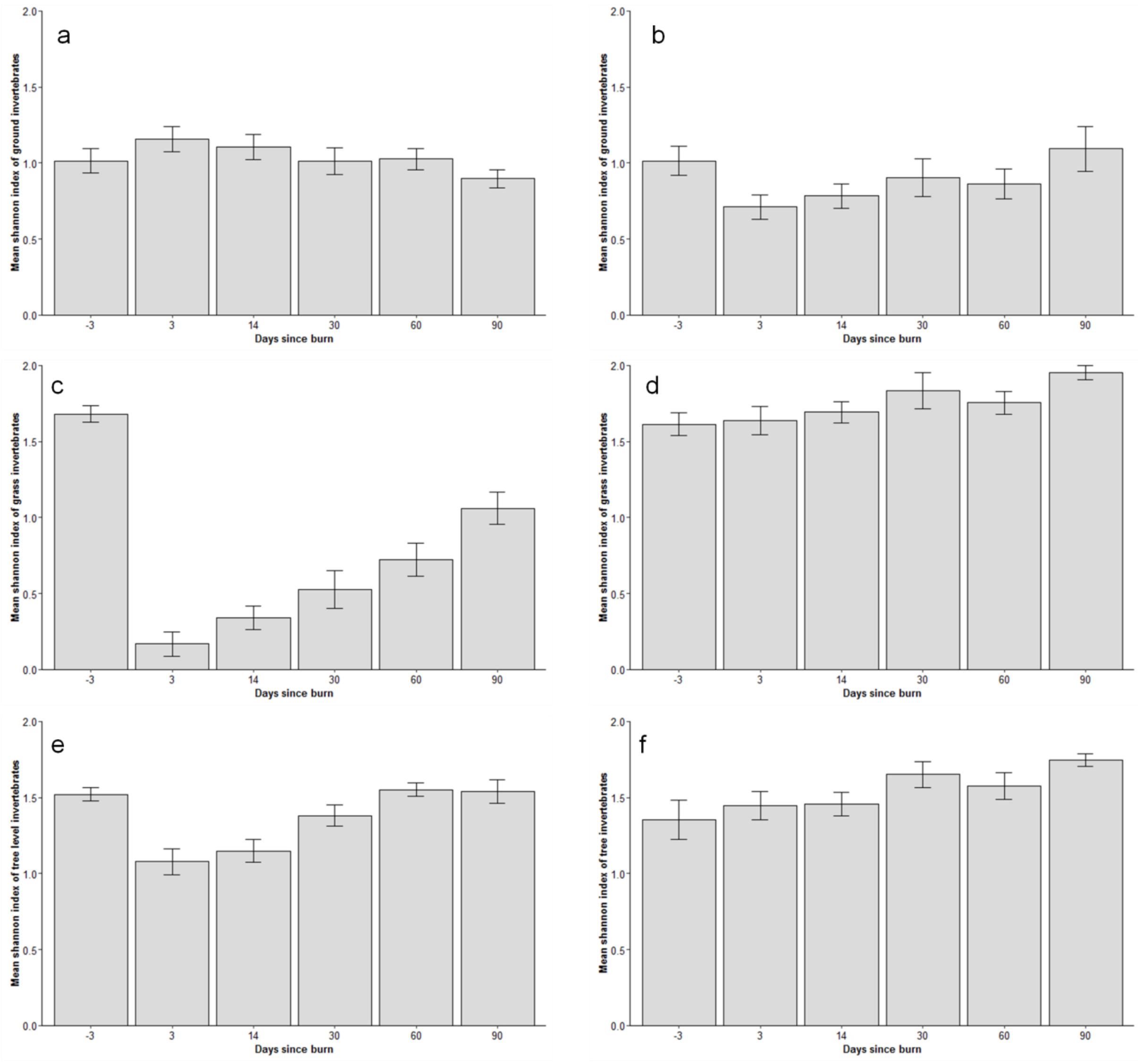

Figure 3.10: Bar charts showing the average Shannon index value for each data collection event. Error bars show ±1SE. (a) Ground invertebrates diversity in the burn, (b) Ground invertebrate diversity in the control, (c) Grass invertebrate diversity in the burn, (d) Grass invertebrate diversity in the control, (e) Tree invertebrate diversity in the burn, (f) Tree invertebrate diversity in the control

Tree Level Invertebrates

Tree invertebrate diversity is significantly affected by the burn event, with a decline in diversity immediately following the burn (Figure 3.10e, Table 3.2). The effect is only short-term and recovery of pre-burn diversity levels occurs 30 days after the burn event, which is shown by a lack of significant difference between the pre-burn and the 30 days post-burn event (Table 3.2). Figure 3.10f shows the change in tree invertebrate diversity in the control; the graph does not appear to show a significant change in diversity over time. However, statistical analysis showed that 90 days post-burn, compared to pre-burn, the diversity significantly increases (Table 3.2) .As with the grass invertebrates this increase is likely to be due to changes in the weather, such as the start of the rainy season.

As with the ground and grass invertebrates, the diversity of tree invertebrates was compared between the control and burn sites at each event. This test simply confirmed that immediately following the burn (3 days to 30 days) the changes in diversity in the burn site were significantly different to the diversity in the control site, showing that the decline seen in the burn is due to the burn event and not other factors (Table 3.3).

Order abundance

As the total invertebrate abundance showed some variation following the burn event, at the grass level and tree level, further analysis was done to see whether these changes were due to specific orders. As explained in the methods the average presence count enabled identification of orders that were present in average or above average number of samples. For ground invertebrates orders had to be present in over 44 sample pots, for grass invertebrates orders had to be present in over 24 sweep nets, and finally for tree level invertebrates the order had to be present in at least 58 tree beating samples.

Ground Invertebrates

Eight unique orders had sample sizes at or above the average presence level. Figure 3.4 suggested that there would be no significant change in ground invertebrate abundance in either the control or burn site. Diptera is the only order in the control site that showed any significant change in abundance following the burn event, and this change is due to an absence of data 3 days post-burn (Figure 3.11b, Table 3.4). Although the notch plot suggested no significant changes in ground invertebrate abundance, Table 3.4 shows that this is not the case for all orders. Acari appear to show declines in abundance following the burn (Figure 3.11a), however this decline is only significant 60 days post-burn (Table 3.4). Araneae, Coleoptera and Orthoptera all appear to have a small increase in abundance 30 days post-burn in comparison to pre-burn levels, although this may be a delayed response to the burn event, other factors may be affecting their abundance.

In contrast to the potential delayed increase in Araneae, Coleoptera and Orthoptera following the burn; Hemiptera immediately presents a significant increase in abundance 3 days post-burn (Figure 3.11a, Table 3.4), but by 14 days post-burn this increase is not longer significant, due to a large standard error. At 30 days post-burn the Hemiptera abundance declines (in comparison to 3 days post-burn) to pre-burn levels (Table 3.4). This suggests that the burn event has an immediate effect on this order, but recovery is rapid. Finally, Collembola also show an increase in abundance following the burn event; however, the statistical analysis showed that pre-burn abundance compared to 3 days post-burn was not significantly different. This is due to the large standard errors around the data, caused by high variability between points (Table 3.4). Interestingly, pre-burn abundances for Collembola are not significantly different to 30 or 60 days post-burn; however, both ages showed significant difference to 3 days post-burn (Table 3.4). This suggests that the increase seen at 3 days post-burn may be an effect of the burn event; however, more data needs to be collected to remove the variability within the data set.

The analysis of these orders suggests that there is some effect of the burn on ground invertebrates. This shows that modelling is vital to fully understand the changes occurring around the burn event, as the notch plot is over simplified, although a good starting point.

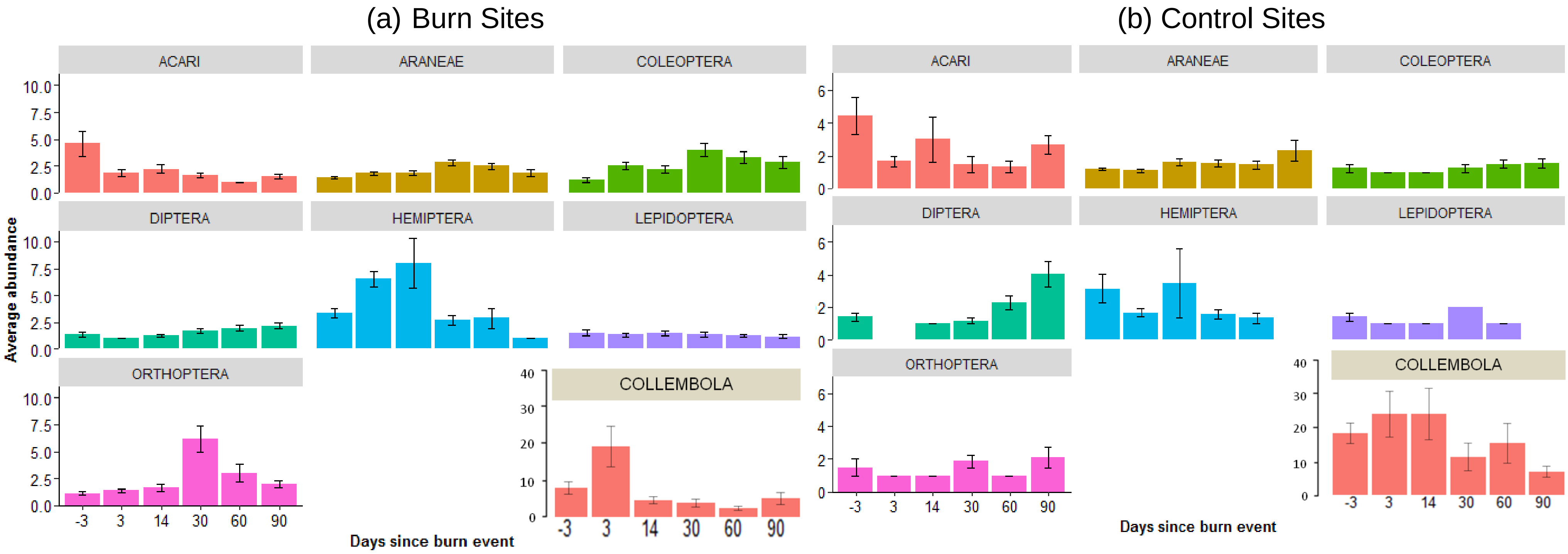

Figure 3.11: Average abundance of ground invertebrates separated into unique orders. (a) Average abundance of ground invertebrates in the burn site, (b) average abundance of ground invertebrates in control sites. Collembola are on a separate scale due to their high abundance. Error bars show ±1SE

Site Type	Order	Kruskal-Wallis		Nemenyi Test		
		H_5	p-value	Comparing burn event (days since burn)	Stat value (2DP)	p-value
Burn	Acari	14.25	0.014	-3 vs. 3	2.12	0.670
				-3 vs. 60	4.45	0.020
				-3 vs. 90	2.62	0.430
	Araneae	18.31	0.003	-3 vs. 30	4.94	0.006
	Coleoptera	14.83	0.011	-3 vs. 3	3.22	0.204
				-3 vs. 30	4.90	0.007
	Collembola	22.67	<0.001	-3 vs. 3	0.87	0.990
				3 vs. 30	4.51	0.018
				3 vs. 60	4.87	0.008
	Diptera	8.05	0.154	N/A		
	Hemiptera	39.20	<0.001	-3 vs. 3	4.09	0.045
				-3 vs. 14	1.47	0.904
				3 vs. 30	5.58	0.001
				14 vs. 90	5.00	0.005
	Lepidoptera	1.98	0.852	N/A		
	Orthoptera	25.38	<0.001	-3 vs. 30	4.67	0.012
				30 vs. 90	3.69	0.095
Control	Acari	7.92	0.161	N/A		
	Araneae	10.45	0.064	N/A		
	Collembola	5.88	0.318	N/A		
	Coleoptera	10.18	0.070	N/A		
	Diptera	12.90	0.012			
	Hemiptera	3.58	0.466	N/A		
	Lepidoptera	9.45	0.051	N/A		
	Orthoptera	8.12	0.150	N/A		

Table 3.4: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on the abundance values for the dominant ground invertebrate orders. Invertebrates were collected at six time points around a burn event using pitfall traps, data was collected from the same points at each event. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

Grass Invertebrates

The notched box plots used for visual assessment of the data, showed a significant decline in the median abundance of grass invertebrates following the burn (Figure 3.5). No corresponding significant change was noted in the control, until 60 and 90 days post-burn, where there appeared to be some increase in the abundance values (Figure 3.5). In separating the data into orders, nine orders met the specified criteria. As the notched plot suggested that total invertebrate abundance declined following the burn, similar responses were expected for each order.

Acari, Hymenoptera and Diptera all appear to show complete removal of the order following the burn event (Figure 3.12a). However, statistical analysis shows that this decline is not significant in any of these orders (Table 3.5). This is due to the fact that the abundance counts for these orders were low with high variability. The only orders within the burn site that showed any significant change was Hemiptera and Orthoptera (Table 3.5). In the case of Hemiptera, the abundance declines at grass level immediately following the burn, showing a similar pattern of change that was seen in Figure 3.5. In contrast, the change in Orthoptera abundance is due to a significant increase at 90 days post-burn; in comparison to 14 days post-burn (Table 3.5). This increase is likely to be due to the arrival or rain.

Orders in the control appear to show more significant changes over time than those in the burn; with Araneae, Coleoptera, Diptera and Hymenoptera showing significant increases in abundance around 60 and 90 days post-burn (Figure 3.12b, Table 3.5). It is clear that these changes are not caused by the burn event, and other factors (such as rainfall), are having a significant impact on the abundance of a number of grass invertebrate orders.

Although the overall visual analysis showed declines in grass invertebrates following the burn event, the low counts of each order in this study have prevented in depth analysis of specific order changes. More data needs to be collected, with large sample sizes in order to begin to understand the order specific changes taking place in the grass layer following the burn.

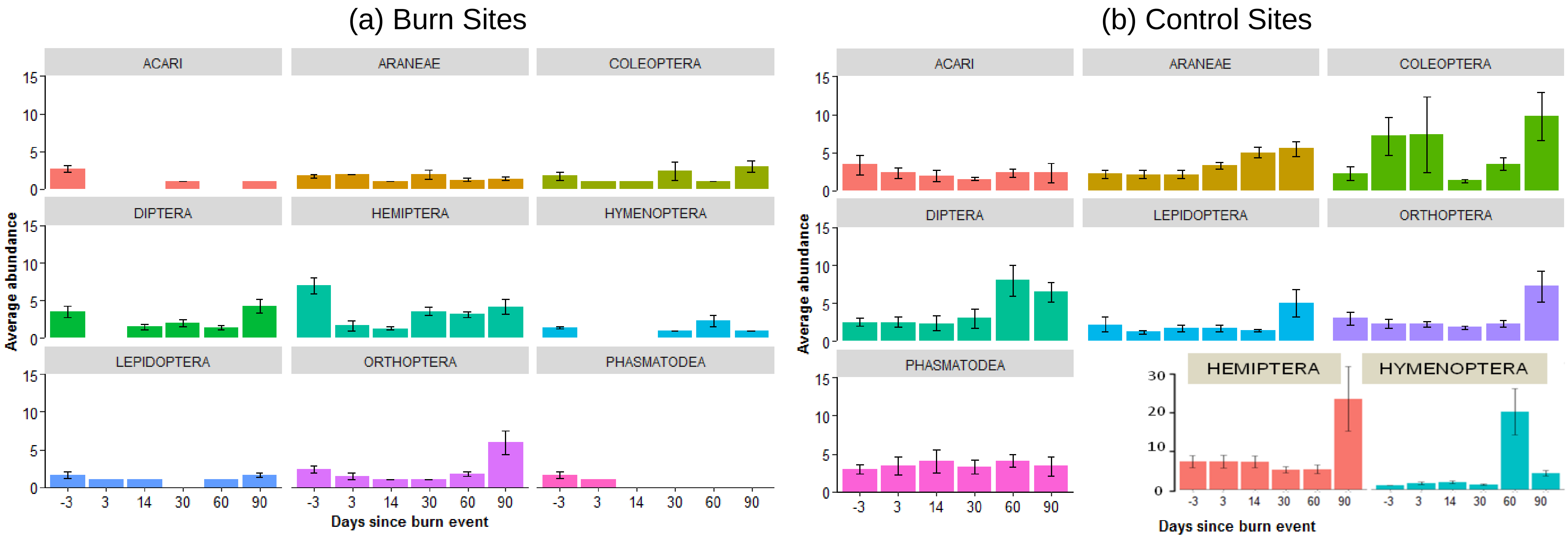

Figure 3.12: Average abundance of grass invertebrates separated into unique orders. (a) Average abundance of grass invertebrates in the burn site, (b) average abundance of grass invertebrates in control sites. Hemiptera and Hymenoptera in the control panel are on larger y-axis scales as both had larger abundances in the control data than other orders. Error bars show ±1SE

Site Type	Order	Kruskal-Wallis		Nemenyi Test		
		H_5	p-value	Comparing burn events (days since burn)	Stat value (2DP)	p-value
Burn	Acari	3.73	0.155	N/A		
	Araneae	5.33	0.377	N/A		
	Coleoptera	8.61	0.126	N/A		
	Diptera	9.29	0.054	N/A		
	Hemiptera	21.72	<0.001	-3 vs. 3	3.79	0.079
				-3 vs. 14	5.63	<0.001
				-3 vs. 30	3.16	0.223
	Hymenoptera	7.33	0.062	N/A		
	Lepidoptera	2.28	0.685	N/A		
	Orthoptera	15.38	0.008	-3 vs. 14	2.76	0.373
				14 vs. 90	4.21	0.034
	Phasmatodea	0.42	0.519	N/A		
Control	Acari	3.97	0.554	N/A		
	Araneae	18.48	0.002	14 vs. 90	4.07	0.046
	Coleoptera	15.34	0.009	-3 vs. 3	2.90	0.312
				30 vs. 60	2.56	0.457
				30 vs. 90	4.29	0.029
	Diptera	16.50	0.006			
	Hemiptera	5.70	0.337	N/A		
	Hymenoptera	25.56	<0.001	30 vs. 60	4.93	0.007
				60 vs. 90	1.64	0.855
	Lepidoptera	4.82	0.438	N/A		
	Orthoptera	6.15	0.292	N/A		
	Phasmatodea	2.22	0.818	N/A		

Table 3.5: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on the abundance values for the dominant grass invertebrate orders. Invertebrates were collected at six time points around a burn event using pitfall traps, data was collected from the same points at each event. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

Tree level Invertebrates

The notched box plot for tree level invertebrates showed some declines in abundance immediately following the burn, with minimal changes in abundance in the control sites (Figure 3.6). In Figure 3.13, all six of the orders analysed show minimal change in abundance over time, in both the control and burn site. Interestingly, the statistical analysis did show some significant differences within orders over time (Table 3.6).

As with the ground invertebrates, the main order showing significant changes is Hemiptera (Table 3.6). Hemiptera abundance declines significantly following the burn event, but within three month shows signs of recovery (Table 3.6). This is seen when comparing 14 days to 90 days post-burn, and further shown by the fact that pre-burn compared to 90 days post-burn showed no significant difference in Hemiptera abundance (Table 3.6). Hemiptera is one of the most diverse orders, and hence any major changes in abundance noted in this order are likely to be well represented in the total analysis.

Interestingly, although Araneae does not show significant declines in abundance immediately following the burn, post-burn data does shows a steady increase (Figure 3.13). This increase leads to a significant difference in Araneae abundance between 3 days and 90 days post-burn (Table 3.6). This suggests that although the burn could initially be having a small negative effect, overall the burn benefits Araneae populations. However, this increase could also be related to other factors such as rainfall, since a similar increase is seen in the control between pre-burn and 90 days post-burn (Table 3.6).

An increase in tree invertebrate abundance between 3 days and 90 days post-burn is also noted in Hemiptera and Coleoptera in the control sites (Table 3.6). This suggests that other factors are affecting the invertebrate population, potentially to a greater extent than the burn event.

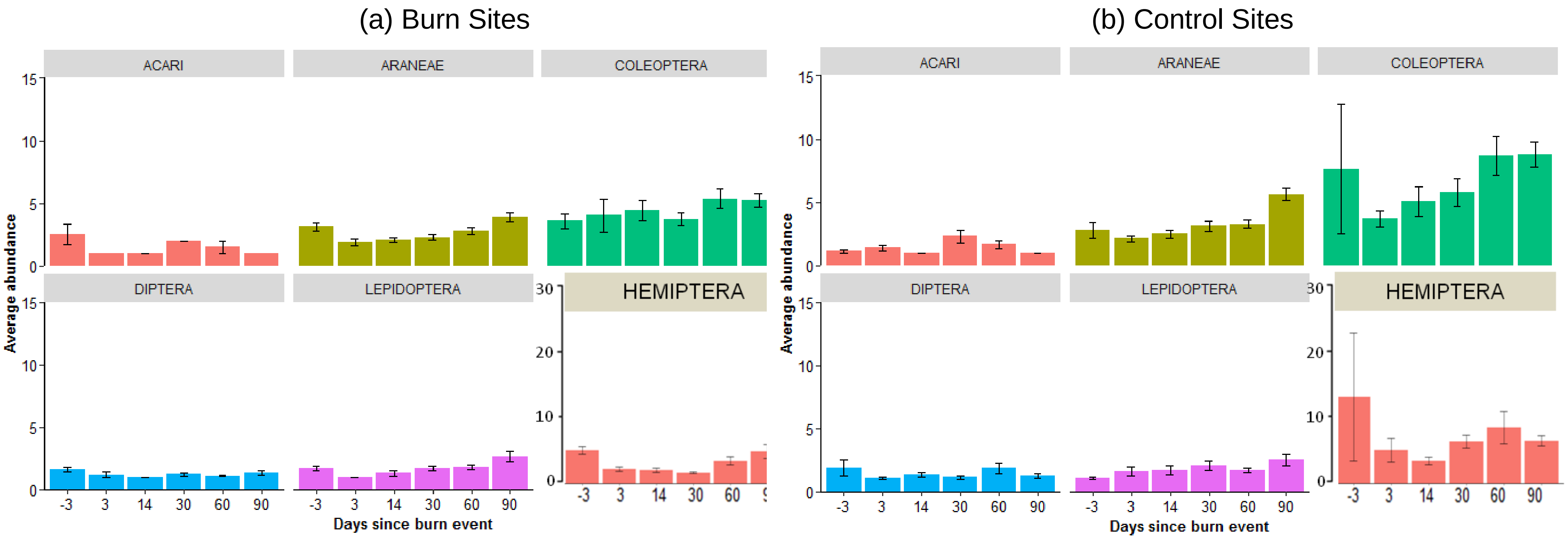

Figure 3.13: Average abundance of tree level invertebrates separated into unique orders. (a) Change in the average abundance of tree level invertebrates in the burn site; (b) change in the average abundance of tree level invertebrates in control sites. Hemiptera are on a separate scale due to their high abundance. Error bars show ±1SE

Site Type	Order	Kruskal-Wallis		Nemenyi Test		
		H_5	p-value	Comparing burn events (days since burn)	Stat value (2DP)	p-value
Burn	Acari	6.87	0.231	N/A		
	Araneae	30.08	<0.001	-3 vs. 3	3.96	0.057
				3 vs. 90	6.14	<0.001
	Coleoptera	16.85	0.005			
	Diptera	7.75	0.171	N/A		
	Hemiptera	35.74	<0.001	-3 vs. 3	4.21	0.035
				-3 vs. 90	1.16	0.964
				3 vs. 14	0.92	0.987
				14 vs. 90	4.92	0.007
	Lepidoptera	14.99	0.010	-3 vs. 3	2.90	0.315
				3 vs. 90	3.96	0.057
Control	Acari	9.69	0.084	N/A		
	Araneae	40.31	<0.001	-3 vs. 90	6.56	<0.001
	Coleoptera	26.21	<0.001	-3 vs. 3	0.44	1.000
				3 vs. 90	5.34	0.002
	Diptera	5.63	0.344	N/A		
	Hemiptera	18.40	0.002	-3 vs. 3	0.89	0.989
				3 vs. 90	4.48	0.019
	Lepidoptera	12.46	0.029			

Table 3.6: Statistical output from Kruskal-Wallis test and Tukey-Kramer (Nemenyi) post hoc test performed on the abundance values for the dominant tree level invertebrate orders. Invertebrates were collected at six time points around a burn event using pitfall traps, data was collected from the same points at each event. Only key outputs from the Nemenyi test are presented, with significant differences highlighted in red.

General Linear Mixed models (GLMM)

Invertebrates at each level are collected using three non-comparable methods. Therefore, a unique GLMM was required for each invertebrate level, in order to assess the effect of the burn event. Visual inspection of the residual plots for all three models did not reveal any deviation from normality. Table 3.7 shows the most parsimonious models for each invertebrate level.

Ground Invertebrates

The GLMM for ground invertebrates was dredged and two models had ΔAIC ≤ 6. Many studies suggest that the cut off with ΔAIC ≤ 2 should be used to identify models with substantial support (Burnham and Anderson, 2001). Model 32 appears to be the most robust model for the data using; patch, rainfall, event, site type and their interaction as fixed effects, along with point as a random factor. It has a ΔAIC < 2, a greater log likelihood value than the other model, and has a weight of 0.759, making it 3.15 times more likely than model 30 to be to be the best explanation for variation within the ground abundance data.

All collection events post-burn show an increase in ground invertebrates in relation to the pre-burn levels, with the most pronounced increase noted 90 days post-burn (0.89 ± 0.05). This suggests that overall the burn event caused an increase in ground invertebrates in the short-term. Furthermore, the model suggests a decline in ground invertebrates 14 days post-burn, in comparison to 3 days post-burn, with the positive effect noted 14 days post-burn (0.09 ± 0.03) being outside the standard error range of the effect noted 3 days post-burn (0.20 ± 0.03). This suggests that the initial spike in abundance is not maintained 14 days post-burn. Comparing the burn site to the control site, the control positively affects the ground abundance, suggesting that the lack of a burn increase ground invertebrates (0.21 ± 0.12), although this increase is less pronounced than other effects, such as event and rainfall. The presence of rainfall appears to decrease the ground invertebrate abundance (-0.72 ± 0.04). Finally, patch 2, or patch I, as an effect appears to cause the ground invertebrate abundance to increase in relation to patch L (0.25 ± 0.11). This suggests that patch L has fewer ground level invertebrates independent of the burn event.

It is clear from the model that each factor has an important role to play in determining the ground invertebrate abundance in response to a burn event.

Weather and location play a vital role in determining abundance and hence structure of the ground invertebrate community.

Invertebrate Level	Model	Event	Patch	Rainfall	Site Type	Event: Site Type	K	logLik	ΔAIC	Weight
Ground	**32**	**+**	**+**	**+**	**+**	**+**	**15**	**-3756.302**	**0.00**	**0.759**
	30	+		+	+	+	14	-3758.537	2.29	0.241
Grass	28	+	+		+	+	14	-587.853	0.00	0.555
	32	**+**	**+**	**+**	**+**	**+**	**15**	**-586.884**	**0.44**	**0.445**
Tree	**32**	**+**	**+**	**+**	**+**	**+**	**15**	**-6715.542**	**0.00**	**0.950**
	30	+		+	+	+	14	-6719.565	5.98	0.048

Table 3.7: Set of the most parsimonious invertebrate abundance models. Top model set containing models with a ΔAIC≤ 6. The most parsimonious model for each invertebrate level is shown in bold, with the number of parameters in each model (K), logLik values, ΔAICs and Akaike model weights being presented.

Grass Invertebrates

As with the GLMM for the ground invertebrates, the grass invertebrate model produced two models with ΔAIC ≤ 6 following dredging (Table 3.7). Model 28 excluded rainfall as an effect within the model, and although this model had the lowest ΔAIC value, it had a lower log likelihood value than the other model. As rainfall was important in the ground and tree invertebrate analysis is was left in the model, and hence the second model was used.

All post-burn events show a decline in grass invertebrate abundances, with no recovery or increase to pre-burn level. However, 90 days post-burn the negative effect of event appears to reduce by -0.52 ± 0.14, which is low in contrast to the decline seen 3 days post-burn (-2.92 ± 0.22). This suggests that grass invertebrates are beginning to recover back to pre-burn levels. 90 days post-burn data occurs following the arrival of rain (60 days post-burn). The presence of rainfall appears to increase the abundance of grass invertebrates by 0.16 ± 0.11, although this increase is small in comparison to effects created by event and patch. Patch I, as noted in the ground invertebrates, has a prominent positive effect on the grass invertebrate abundance (0.89 ± 0.12). This further supports the idea that patch I has a higher invertebrate abundance and diversity than patch L, suggesting other factors (such as vegetation and soil) are affecting the invertebrate abundance.

Tree Level Invertebrates

The GLMM for tree level invertebrates produced two models with a ΔAIC ≤ 6; Model 32 has a higher log likelihood value, a ΔAIC < 2 and is the heavily weighted model (Table 3.7). Analysis of the effect of each fixed factor on the model shows that 3 day post-burn data collection event causes a decline in tree invertebrates (-0.68 ± 0.05), compared to the pre-burn collection. This decline is reduced 14 days post-burn, although the abundance is still negative in relation to pre-burn abundance (-0.09 ± 0.40). This suggests that the tree invertebrates are recovering quickly. This is also shown by an increase in tree invertebrates when comparing the pre-burn level to 30 days post-burn (0.23 ± 0.37). This shows that 30 days post-burn the abundance of tree invertebrates may be exceeding pre-burn levels, depending on the other factors at play.

As with the ground invertebrates, tree invertebrate abundance is greater in control sites compared to burn sites (0.44 ± 0.15), further supporting the effect seen in event, in which the burn event causes an immediate decline in tree invertebrates. However, what is clear from the model is that tree location plays a significant role on invertebrate abundance, with patch I again increasing invertebrate abundance in comparison to patch L (0.40 ± 0.13). In all three models patch I increases invertebrate abundance, showing that all levels of invertebrates appear to respond similarly to other factors not simulated in this model. This is not the case for rainfall, each model has responded differently to the presence of rainfall. Ground invertebrates decline in the presence of rain, whereas grass invertebrate abundance increases. Tree invertebrates increase by a similar estimate to grass invertebrates in response to rainfall (0.20 ± 0.51). This show that the level (ground, grass or tree), at which an invertebrate is found, may also have an effect on its response to fire and other factors.

Discussion

Due to the limited amount of knowledge on this subject, only general prediction could be made at the outset of this study. Previous studies had shown that ground and grass invertebrates would decline immediately following the fire due to the removal of the grass layer, and the initial loss caused by the combustion and shock phases of the burn (Rice, 1932; Warren *et al.,* 1987). This was true for the grass invertebrates within this study, which showed an immediate decline following the burn event followed by a steady recovery. However in contrast to the prediction, the ground invertebrates showed a significant increase immediately following the burn. This may be due to the movement of invertebrates from grass and tree level that survived the combustion and shock phases, therefore causing a temporary increase in ground invertebrates. This increase was shown throughout the three month study, with abundances being greater than pre-burn levels even 90 days post-burn (although the increase was lower than immediately following the burn event).

The diversity of ground invertebrates remained unchanged throughout the three month study on the burn sites, in contrast to the prediction. This was probably due to the increase in abundance of ground invertebrates noted, again due to movement from the other invertebrate levels. In contrast, the grass invertebrates showed a decline in diversity immediately after the burn, followed by a steady recovery (which matches the pattern seen in the abundance), as expected.

It was also predicted that tree invertebrates would decline immediately following the fire, and this study supported this. The decline seen in the tree invertebrates was not a large as the decline seen in the grass invertebrates. Hence, recovery to pre-burn levels was possible during the three month study. This is also true for the diversity, with a decline seen immediately following the burn, but recovery to pre-burn levels seen within the study period.

The immediate response of ground, grass and tree level invertebrates following a burn event was measured in this study by recording pre-burn abundance and diversity, then comparing these values to their equivalent post-burn data. From this study it is possible to draw general conclusions at the three separate invertebrate levels, which will now be discussed in further detail.

Ground invertebrate response to burning

Ground invertebrates appear to benefit from the burn event, increasing in abundance over time. The model showed that even at 90 days post-burn, without any other factors, the ground invertebrate abundance would be 0.88 ± 0.5 greater than at the pre-burn level. This increase in abundance has been noted in other studies (Rice, 1932; Hurst, 1971); however, in most cases this increase occurs at least three months post-burn. The majority of studies show an immediate decline in invertebrates following the burn event (Rice, 1932; Seastedt, 1984; Anderson *et al.,* 1989), which is seen in the grass layer and tree layer of this study.

Warren et al. (1987) found that invertebrates suffer high mortality during the combustion and shock phases. Therefore, immediately following the burn event there should be a significant decline in all invertebrates. The increase in ground invertebrates in this study may be an artefact of the collection method; as the burn reduces the density of grass sward on the ground, increasing the proportion of bare ground. This means that flightless invertebrates have to use to ground to move, and can no longer pass between vegetation, which results in an increase of invertebrates passing over the pitfall trap, hence an increase in ground invertebrates. York (1999) looked at pitfall traps as a collection method in comparing burnt and unburnt plots. The study showed that although some methods demonstrated a decline in all dominant arthropod species, pitfall traps only showed declines for three of these species. The remaining six species, which had previously shown declines, exhibited no change, or an increase, in arthropod abundance. The increase in arthropods in York's (1999) study was attributed to an increased activity level.

The increase in ground invertebrates may not solely be due to an increase in movement and transfer between levels. Some studies have shown that soil invertebrates can burrow down and live below the top 5cm of soil, enabling them to escape mortality via combustion (Rice, 1932; Seastedt, 1984). Therefore, it is possible that these individuals survive the combustion phase; therefore, over time as they resurface, the abundance of ground invertebrates would increase when combined with those invertebrates now moving on the ground due to the removal of grass (Warren et al. 1987).

Although the model in this study suggested that the burn event generated an increase in ground invertebrates, it also showed that rainfall had a negative effect on the overall abundance. This can be seen as Figure 3.4 showed that ground invertebrate abundances at 90 days post-burn were similar to pre-burn levels. The model suggests that with event alone, 90 days post-burn would show a significant increase in relation to pre-burn levels, but clearly this is not the case. It appears that although the burn event may be creating an increase in ground abundance over time, rainfall is counteracting this change. The decline in ground invertebrates following the arrival of rain is unusual. One suggestion is that the dry soil in the savanna means that run off is high and therefore, the structure of the soil can be altered, affecting the habitat and movement of invertebrates within this changing environment (Lancaster and Briers, 2008).

The diversity of ground invertebrates remained fairly constant throughout the study, suggesting that all orders responded similarly to the burn event (Table 3.2). This study looked at the effect of the burn on a few key orders to assess whether any specific orders were being affected. Hemiptera abundance within the burn sites declined three days post-burn, but showed rapid recovery, with abundance levels showing no significant difference 14 days post-burn compared to pre-burn levels. Previous studies have shown that Hemiptera is not uniform in its response to burning. Van Amburg et al. (1981) demonstrated a neutral response for Hemiptera following a burn; whereas, Rice (1932) showed that Hemiptera demonstrates the usual decline seen by the majority of orders following a burn event. This variation in response is due to the fact that Hemiptera is a large order containing a wide variety of species within a wide variety of niches. Therefore, to fully understand the steady increase in Hemiptera up to 14 days post-burn, a more detailed look at the responses of species within this order needs to be conducted.

Many studies have shown an immediate decline in abundance followed by an increase for specific orders: Orthoptera (Warren et al., 1987), Hymenoptera (Bulan and Barrett, 1971) and Lepidoptera (Hurst, 1971). These studies therefore support the changes seen in Hemiptera. Oldham (1983) found the same pattern of decline and recovery in Acari. In contrast, in the current study Acari declined following the burn, but there were no signs of a recovery. The logical explanation for this decline is that Acari rely on the grass for transfer from one host to another. Therefore, if this habitat is removed it reduces the success and survival of individuals in that order (Nilsson and Lundqvist, 1978).

Although the majority of studies have shown a general decline and subsequent increase in invertebrate abundance following a burn, neutral changes have been observed in the past (Rice, 1932; Van Amburg *et al.* 1981). Studies that have looked at Hemiptera have shown neutral responses to fire, as explained above (Ochoa and Velasco, 1972; Van Amburg *et al.* 1981). Therefore, the fact that the ground invertebrates did not show a significant decline following the burn event is not unusual (Figure 3.4). Unfortunately, in this study termite abundance was low, and therefore, there was not enough data to show the effect of burning. However, previous work has shown that sub-terrain termites appear to be resistant to the effects of fire (Trapnell et al., 1976); surviving the combustion phase by living deeper than the 5cm level the fire penetrates (Seastedt, 1984). Fire creates an increase in detritus and fallen wood, causing a rise in termite abundance, as they are attracted to the dead material left by the burn (Frost, 1984: Warren et al., 1987; Reed, 1997). The potential for increases from sub-terrain invertebrates would support the general patterns seen in this current study, with ground invertebrates showing an initial increase following the burn. More data needs to be collected to generate large samples sizes for each order.

Collembola appear to respond in the same way as the termites reported by Trapnell et al. (1976); showing an increased in abundance three days post-burn compared to the rest of the post-burn data. This increase may therefore be due to an attraction to fire, smoke or the increased ability to oviposit in freshly burnt wood (Warren et al., 1987; Reed, 1997; Swengel, 2001). Swengel (2001) noted that most species showing high adaptation and attraction to burns typically bore into dead or dying wood. Similarly, Collembola feed on fallen wood and plant detritus, and they have been shown to play an important role in decomposition (Picker et al., 2002). Collembola can retreat into the soil during dry seasons (Detsis, 2000). Therefore, by surviving the combustion phase below the ground, they then may return to the surface post fire (attracted by the wood and detritus). However, to some extent this high abundance immediately following the burn is mirrored in the control (Figure 3.11); which suggests that the increase in Collembola may be caused by other factors.

Overall, this study has shown that following a burn event invertebrate abundances increase, but the diversity of the community in general remains unchanged. This shows that on the whole all invertebrate orders respond in a similar way to the burn event and increases occur across all orders. The order level analysis suggests that some orders were more complicated, with Acari simply declining following the burn. As some orders showed significant increases while others showed declines, this may explain why overall changes were minimal. Despite appropriate data collection in this study, as seen by the order accumulation curves, for some orders the count of individuals per order was too low to make any accurate comparisons. Therefore, in order to accurately analyse all order responses, more data at each event is required.

Grass invertebrate response to burning

In contrast to the ground invertebrates, grass invertebrates significantly declined following the burn event (Figure 3.5). The model showed a significant decline at each post-burn event in comparison to the pre-burn level. Following this immediate decline, the model showed some recovery of grass invertebrates; with the decline in abundance (noted when comparing each post-burn event to pre-burn levels) reducing in value at each subsequent post-burn event. Although a full recovery to pre-burn levels did not occur within the three month period, it showed that recovery of grass invertebrates is possible. This decline and recovery has been shown in many other invertebrate studies (Rice, 1932; Hurst, 1971; Lamotte, 1975; Frost, 1984; Anderson et al., 1989; Samways, 1990; Borth and Barina, 1991; Siemann et al., 1997; Dietrich et al., 1998). The significant decline seen in the burn did not occur in the control site and therefore, it can be concluded that the decline was a response to the burn event and not another factor. The model showed that rainfall does not have a significant effect on the invertebrate abundance, although the presence of rainfall at 60 and 90 days post-burn caused a slight increase in abundance.

Immediate declines in grass invertebrate abundance are caused by a high level of invertebrate mortality during the burn event itself. Daubenmire (1968) and Frost (1984) both noted birds feeding on insect carcasses, such as Orthoptera, immediately following the burn (Swengel, 2001). Warren et al., (1987) and many other studies have called this immediate mortality the combustion phase. Although Daubenmire (1968) and Frost (1984) were able to show direct mortality, many studies, including this current study, show indirect mortality through declines or absences in grass invertebrates post-fire. This is a valid way to prove mortality of invertebrates, as immediately post-burn the majority of dead invertebrates would be either miniscule or unidentifiable ash (Swengel, 2001).

The burn event removed the grass layer, eliminating not only the structural system that the invertebrates live on, but also the food resources provided by the grasses, which are necessary for the survival of many invertebrates. Removal of this habitat takes out a number of niches which many invertebrates rely on. The degree of reduction in grass density and invertebrate abundance relates to the level of exposure to the flames (Buffington, 1967; Lamotte, 1975; Swengel, 2001). In the grass layer the level of exposure is high, causing greater mortality in the initial combustion phase (Warren et al., 1987). Even if the orders in this level survived the combustion phase, there is no or very limited grassland, for them to survive in; this causes greater losses in abundance during what is known as the shock phase (Warren et al., 1987). The shock phase refers the first few weeks after the burn event, in which mortality of invertebrates continues due to exposure and starvation. The decline in grass invertebrates in this study is well supported by other works which show that many invertebrate orders respond in this way to fire (Rice, 1932; Warren et al., 1987).

It is clear that although the burn decimates the grass invertebrate community in the combustion and shock phase, recovery of invertebrates does begin from around 14 days after the burn (Figure 3.5). The arrival of rain 60 days post-burn enhances the recovery of invertebrates, with the model showing that the presence of rainfall increases invertebrate abundance by 0.16 ± 0.11. The arrival of rainfall is beneficial to recovery as it supports the regrowth of vegetation from the seed store in the soil; this can be attractive to re-colonising invertebrates (Swengel, 2001). Data collected three months after the burn does show a significant increase in grass invertebrates compared to three days post-burn, however, it is clear from the model that the invertebrate abundance is still lower than the pre-burn level (Event 5: -0.52 ± 0.14). Recovery back to pre-burn levels, and increased diversity, is slow. However, other studies have shown that significant recovery occurs between three months and twelve months post-burn, although the composition is often different, supported by the long-term study in Chapter 2 (Rice, 1932; Bulan and Barrett, 1971; Nagel, 1973; Van Amburg, et al., 1981; Hansen, 1986; Warren et al., 1987; Reed, 1997). As this study only measured the change in invertebrates up to three months post-burn, it is not possible to determine whether the grass invertebrates will recover to abundance levels similar to, or greater than, pre-burn levels within the three month to twelve month period suggested by these other studies. However, the long-term study in Chapter 2 showed that one year post-burn, the grass invertebrate abundance was not significantly different to the unburnt site, suggesting that full recovery to pre-burn levels is possible (pages 31-32). Further work needs to be done following the burn patches every month within the first year of the burn, to assess if this increase occurs.

Warren et al. (1987) noted that recovery and decline of invertebrates is often varied between orders, causing a change in the composition of the invertebrate community. The diversity within the grass invertebrates significantly declined following the burn event (Figure 3.10c), with no change noticed in the control site (Figure 3.10d). This suggested that the decline in diversity was due to the burn event itself rather than other factors. The order level analysis suggested that some orders are completely removed from the site following the burn event. It showed catastrophic mortality for Acari, Diptera and Hymenoptera, resulting in their absence three days post-burn. Phasmatodea decline immediately following the burn event, although they were not completely absent from the site at three days post-burn. By 14 days post-burn they had been completely eradicated from the site, suggesting that Phasmatodea not only suffer mortality in the combustion stage of the burn, but are completely removed in the shock phase (Warren et al. 1987). The removal of these orders is not mirrored in the control site, signifying that the loss of these orders is likely to be due to the burn event itself, between the combustion and shock phases. In contrast to Phasmatodea; Acari, Diptera and Hymenoptera return to the burn sites within the study period, suggesting that these orders can easily recolonise the burn site (Swengel, 2001). The abundance levels for each order in the burn sites were very low, and therefore no significant changes could be noted, due to large standard errors. Therefore, although the graphs suggest complete removal of orders immediately following the burn, this was not significant due to limited data. For a better understanding of how grass invertebrate orders uniquely respond to the burn, a greater sample size needs to be taken. Therefore, for statistically significant conclusions to be drawn from the data, the study needs to be repeated following more controlled burns along with corresponding control patches.

Hemiptera are one of the most diverse invertebrates orders (Picker, et al., 2001), and in this study there was a significant decline 14 days post-burn compared to pre-burn, followed by an increase 30 days post-burn (Figure 3.12). Although a decline was noted three days post-burn, it was not significantly different (Table 3.5). What is interesting about Hemiptera is that this pattern is the same as that seen for the overall data, and the decline and rapid recovery is also supported by Rice (1932).

The model shows that grass invertebrates increased following the arrival of rainfall (around 60 days post-burn). Order analysis in the control sites showed this increase in abundance for some orders between 60 and 90 days post-burn. Hymenoptera significantly increased at 60 days post-burn, while Coleoptera and Araneae increased at 90 days post-burn (Table 3.5). Many studies have noted that recolonisation of a burn site is most abundant within the year of the burn and significantly increases in the presence of rainfall (Swengel, 2001). Therefore, the increase in invertebrates seen in this study from 60 days post-burn (after the arrival of rain) may be due to regrowth within the in the grass layer. The presence of rain promotes re-establishment of the grass layer habitat, enabling invertebrates to return to these patches, and recover abundances back to pre-burn levels (Zhang et al., 2005). Rainfall also promotes activity and signifies the start of the growing season and for many species the arrival of rain triggers breeding and enhances reproduction, which could also contribute to a spike in the invertebrate abundance (Uvarov, 1931; Wolda, 1988). At 60 and 90 days post-burn, in this current study, there was a significant increase in abundance in response to rainfall; this increase may be representing the initial signs of recovery stimulated by the growth of vegetation, as well as the initiation of reproduction caused by the arrival of rain.

Overall, the short-term response of grass invertebrates to the burn event is a significant decline in abundance, and potentially a complete loss of some order, although these are likely to be temporary. The risk of extinction for localized invertebrate species is of great concern around the world, for example in Africa (Wright and Samways, 1999) and Australia (Greenslade, 1993). However, this study, as with the majority of previous studies, shows that extinctions due to burning are unlikely. This is because of the relatively quick recovery seen within burn sites, which is possible because of the patch mosaic used in many burn regimes (Brockett et al., 2001).

Tree level invertebrate response to burning

The most well documented invertebrate response to fire is that of an immediate decline, due to the combustion and shock phases, followed by a steady recovery, using surviving individuals and natural re-colonizers (Anderson et al., 1989). This response was seen in the tree level invertebrates in this study, although with a reduced decline in abundance and a more rapid recovery compared to grass level. Through personal observation within this study, dead Coleoptera, Araneae and Orthoptera were found while tree beating at three days post-burn. This suggests a high mortality during combustion, not only at grass level as expected, but also at tree level. As the degree of reduction in abundance usually relates to the degree of flame exposure, invertebrates in tree tops usually show a lesser decline in abundance or none at all (Miller, 1979; Force, 1981; Warren et al., 1987; Samways, 1990). This theory is supported by the data in this study, which showed that the decline in grass invertebrates was much greater following the burn event than for tree level invertebrates (Grass: -2.92 ± 0.22; Tree: -0.68 ±0.05).

Recovery in the tree invertebrates appeared to have been quicker than in the grass invertebrates. At both 30 and 90 days post-burn the model suggested that tree level invertebrates significantly increased with respect to the pre-burn levels, suggesting not only recovery back to pre-burn levels but an increase in abundance. Whereas, the grass level invertebrates did not show an increase in abundance in relation to the pre-burn levels. Rapid recovery within the tree invertebrates is to be expected, showing a shallower decline than grass invertebrates; with a large proportion of tree level invertebrates having wings (Swengel, 2001). In fact Panzer (1998) showed that many Lepidoptera and winged Hemiptera were reliant on the trees in the savanna, and showed that frequent burning increased the species richness of these taxa. This suggests that Lepidoptera and Hemiptera may be attracted to trees found in recently burnt sites.

The model suggests that rainfall significantly increased the invertebrate abundance (0.20 ± 0.05), which would also explain the increase seen at 90 days post-burn. As previously stated rainfall increases the growth of vegetation, promotes activity and signifies the start of the growing season (Zhang et al., 2005). Increased vegetation provides more resources for invertebrates, promoting colonisation on the newly burnt sites (Swengel, 2001). The arrival of rainfall also triggers breeding and enhanced reproduction for many species, causing a rapid increase in tree invertebrate abundance (Uvarov, 1931; Wolda, 1988).

Order analysis showed that some orders have unique responses to fire. Hemiptera showed significant declines immediately following the burn event, which was swiftly followed by a steady increase. At 90 days post-burn abundance levels were similar to the pre-burn counts (Table 3.6). Other studies have shown a decline and rapid recovery in Hemiptera following a burn event (Rice, 1932). This pattern has also been shown in other invertebrate orders (Lepidoptera: Hurst, 1971). The low sample sizes presented in the order analysis for trees make it difficult to deduce many patterns from the data. Lepidoptera do show a significant change over time in this current study, although no distinct direction was noted from the analysis (Table 3.6). If a greater sample size could be gathered, similar results to Hurst (1971) showing decline and recovery are likely to be obtained.

Araneae significantly increased throughout the study, following a small decline three days post-burn. This occurred in both the control and burn sites, suggesting that other factors were affecting the abundance of Araneae. This increase was also seen for Coleoptera and Hemiptera in the control site. As the greatest increase appeared to occur after the arrival of rain (rain arrival 60 days post-burn, increase in abundances seen 90 days post-burn), and the fact that the model suggested that rainfall increased invertebrate abundance; it follows that the increase in rain supports colonisation and breeding which may be causing the increased abundances seen in these orders (Zhang et al., 2005, Wolda, 1988).

Overall, the burn event appeared to cause a significant decline in the tree level invertebrate abundance immediately following the burn, even though the degree of exposure to the flames is minimal, as cold burns were used. A rapid recolonisation and recovery of most orders occurred within one month of the burn event, proving that extinction of localized species is unlikely, particularly with the patch mosaic that has been developed on the reserve (Brockett et al., 2001).

Effect of location on the response of invertebrates

Using the GLMM it was possible to analyse the effect of location, within MWR, on the invertebrate abundance. Figure 3.1 shows the location of the two burn areas and the corresponding controls. Considering the distance and variation in soil content, it would not been atypical for the two burn sites to give different abundances. It is clear from all three invertebrate levels that patch I has greater invertebrate abundances that patch L. Site variation is common in conservation research, with many confounding variables that can affect the outcome of the data (Swengel et al., 2001). For this study, two sites where used to try and alleviate the site bias, however the model suggests that another site may be required. Increasing the number of data sites enables more accurate conclusions to be drawn. In order to understand where this variation is coming from more detailed site data needs to be collected, for example vegetation surveys need to be undertaken, as well as soil composition analysis.

Burning: Negative, positive or no effect?

Overall, there appeared to be a significant decline in invertebrate abundance following the burn, which supports previous studies (Rice, 1932; Warren et al., 1987; Anderson et al., 1989). As the collection methods were not comparable it makes broad generalisations on all invertebrates difficult. However, the slight increase seen in the pitfalls may be due to a combination of increased movement and transfer of invertebrates from the grass and tree level. Any flying invertebrates that can escape the fire from the grass or trees may, three days post-burn, have returned to the burn patch and moved into the ground level counts. This is simply speculation, which would require a specific mark and recapture experiment to scientifically assess this relationship between the invertebrate levels. It is clear each invertebrate level has an effect on the others; some changes in invertebrate order abundances occurred across all three levels, due to the fact that many species use all three invertebrate levels. An example of this is dung beetles (Coleoptera).

Dung beetles (Coleoptera) are a well studied example of invertebrates that respond positively to the arrival of rain. This triggers the emergence of dung beetles from dung balls buried under the soil (Hanski and Cambefort, 2014). Dung beetles roll dung balls, once the rainy season has begun, and lay eggs within the balls. These then get buried and the larvae mature; some hatch during the rainy season increasing the dung beetle population immediately (Hanski and Cambefort, 2014). Others are buried and held below ground until the next rain event when they emerge from these dung balls. This emergence causes a spike in Coleoptera, which would not only affect ground invertebrate abundances, but may also cause increases in the grass and tree levels. This shows that even one subset of an order can have a significant effect on the invertebrate abundances in all levels, and that environmental factors such as rain play a vital role in these changes, as well as the burn event itself. Therefore, it is vital that more habitat, site and environmental data are taken to assess the effect these factors are having in the model.

The burn itself can be detrimental to the invertebrate community within a patch; however, the mosaic of the grassland enables the recovery of these communities both in diversity and abundance. The immediate response of invertebrates to a burn event is negative, as the fire causes high mortality. However, in this study, within three months the invertebrate communities were starting to recover. Previous studies have shown that burning eventually increases the invertebrate abundance within an area, and therefore has a positive impact on the biodiversity (Warren et al., 1987). If this study had continued, it may have shown this increase. However, the arrival of rain added an additional effect to the invertebrate abundance, which meant that the significant increases seen in the abundance 90 days post-burn cannot be solely attributed to the burn event.

In terms of fire management and the effect of burn regimes on the ecosystem, this study has shown that burning does not damage the ecosystem at the level of invertebrates in the long-term (Chapter 2). The explanation is not so simple in the short-term; immediately following the burn the high mortality of invertebrates is catastrophic for the invertebrate community within the grass layer, and to some extent in the tree layer. However, this high mortality does create a short-term flush of carcasses, which is beneficial for insectivorous birds (Daubenmire, 1968; Frost, 1984). This flush of carcasses is short-lived, and the decline in invertebrates within the first three months after the burn reduces the food available for insectivorous birds (Daubenmire, 1968). For example, Kopij (2005) showed that magpie shrike (*Urolestes melanoleucus*) and brown-crowned tchagra (*Tchagra australis*) feed mainly on Orthoptera and Coleoptera, therefore the decline in Orthoptera following the burn may have a significant effect on the abundance and survival of these species. It is clear therefore, that more order specific research is required to fully understand how changes in invertebrate abundance affect the food chain following a burn event.

Although it is clear that the declines in invertebrates are short lived, it is essential that a sturdy patch mosaic is in place so that insectivorous birds have a continual food supply. It is clear that by having a patch mosaic, burning can be beneficial not only for invertebrates but for insectivorous birds and many other fauna and flora (Warren et al., 1987). This study has shown that recovery of invertebrates following a burn is rapid. Extinction of invertebrate orders is unlikely and the long-term study in Chapter 2 suggests that burning increases the invertebrate abundance in comparison to an unburnt site.

Chapter Four

General Discussions and Conclusions

Chapter 4: General Discussion and Conclusions

Fire-prone savannah systems in southern Africa are managed using prescribed burning in order to reduce bush encroachment and to alleviate the nutritional stress among herbivores during the dry season (Hobbs and Spowart, 1984; Vemeire et al., 2004; Parrini and Owen-Smith, 2010). Fire has been used as a management tool for centuries for hunting, conservation, farming and the protection of property (Andersen *et al.* 1998). Due to the high level of use throughout history, seasonal burning is often an unquestioned tradition (Gillon, 1983). Despite the wide spread use of burn regimes, there is little information of the effect they have on the savanna ecosystem (Parr and Chown, 2003). This study was undertaken to try and address one aspect of this, by assessing both the long and short-term effects of burning on invertebrate communities. Many previous reviews have noted that more research is required on the effect of burning on non-target taxa such as invertebrates (Parr and Chown, 2003; Driscoll et al., 2010).

The results presented in this study show that overall, in the long-term, burning has a neutral effect on invertebrates in both diversity and abundance between unburnt sites and sites that are included in a burn regime programme. The only invertebrate level that showed any significant response to the burn was the ground invertebrates. The burn event caused an increase in the abundance of ground invertebrates; with the unburnt sites having significantly lower ground invertebrate counts than sites within the burn regime (0 years since burn, 1 year since burn and 3 years since burn). This suggests that the burn event, which removes the grass layer (Govender et al., 2006), enables increased activity and abundance within the ground layer. It is possible that in the nine year post-burn sites the vegetation is too dense to allow movement, which may have caused ground invertebrates to transfer to the grass layer (Warren et al., 1987).

In the grass layer, the only burn age to show a significant change in diversity or abundance was the recent burn. This was further confirmed as the recent burn was seen to have a different invertebrate composition to the other burn ages (Figure 3.14). This variation in composition, along with a significantly lower abundance compared to the other burn ages, is due to a loss of invertebrates in the combustion and shock phase of the burn (Warren et al., 1987). One year post-burn showed similar abundance and diversity to the other burn ages; its variation in composition being due to the fact that recovery is still occurring within some orders. This delay occurs because some orders require specific grass sward densities to re-colonise a site. Once the vegetation has grown then a wide variety of niches develop, which is required to recover the grass level to a similar composition to pre-burn levels (Scholes and Walker, 1993, Yarnell et al., 2007). The only long-term effect of the burn regime on tree level invertebrates is that, when left undisturbed, abundances increase. This is due to the fact that left undisturbed bush encroachment can occur, and there is often an increase in tree density. This usually provides a wider diversity within the tree canopy, enabling more invertebrates to survive within the patch.

Holistically this suggests that at a broad level, burning is not detrimental to invertebrates, and therefore the risk of extinction to these non-focal taxa appears to be minimal. It has been proven that burning benefits herbivores (Mentis, 1978; Parr and Chown, 2003) and this study shows no objection to this management technique. However, it is important to remember that inappropriate fire regimes can lead to major changes in community structure, and declines were seen in grass level invertebrates within the first year of the burn event (Charrette et al., 2006; Fisher et al., 2009; Gill and Bradstock, 1995). In the long-term, the grass invertebrates recovered quickly, but any detrimental changes or removal of a patch mosaic may have more catastrophic effects (Swengel, 2001).

The short-term study showed that the declines previously noted in the long-term study for the grass and tree level invertebrates, occur within three days post burn. However, at both invertebrate levels these declines were only temporary. Tree level invertebrates began to recover back to pre-burn conditions within one month of the burn event. In contrast, the grass level invertebrates did not return to a similar level of abundance to the pre-burn event in this study. Long-term analysis showed that within one year, grass invertebrate abundances had returned to pre-burn levels. This cycle of decline and recovery has been noted in many previous studies that have been mentioned throughout this report (Rice, 1932; Bulan and Barrett, 1971; Lamotte, 1975; Morris, 1975; Frost, 1984; Warren et al., 1987; Anderson et al., 1989). The long-term study confirms that the declines seen are only temporary and the invertebrate communities in both the grass and tree level recovery quickly.

In contrast to the grass and tree level invertebrates, ground invertebrates showed an increase in abundance immediately following the burn and throughout the three month short-term study. This increase may be due to the fact that below ground invertebrates remain relatively unscathed in the combustion phase (Rice, 1932: Warren et al., 1987); combined with the fact that some insect species are attracted to fire, smoke or the increased option to oviposit in freshly burnt wood (Frost, 1984; Warren et al., 1987; Reed, 1997). Many of these species are those which bore into dead and decaying wood and are therefore often found on the ground. The increase in ground invertebrates may be due to the arrival of these orders initially. However, over the three month period the abundance continued to increase. The arrival of rains may have caused dung beetles (Coleoptera) to emerge; further increasing ground invertebrate abundance from 60 days post-burn (Hanski and Cambefort, 2014). Finally, York (1999) showed that the removal of vegetation, revealing a greater proportion of bare ground, increased activity of ground invertebrates. Therefore, the increase in ground invertebrate abundance throughout the study could be a combination of abundance and activity level. This is supported by the increase in ground invertebrate abundance in the long-term data set.

Rainfall and herbivory, along with fire, are the prime driving variables in an African savannah, with frost playing an important role in some areas (Bourliere and Hadley 1970; Walker and Noy-Meir, 1982; Frost et al 1986; Du Toit and Cumming, 1999). As part of the short-term study, the effect of rainfall on the invertebrate abundance was assessed. In the case of both the grass and tree level invertebrates, rainfall has a significant effect on abundance. The model showed that in the presence of rainfall abundances of both invertebrate levels increased. Although this increase, caused by the presence of rainfall, was not significant in the grass invertebrates, it was significant at tree level. Changes in invertebrate abundance caused by rainfall have been noted in previous studies (Uvarov, 1931; Wolda, 1988; Zhang et al., 2005). Rainfall promotes the re-establishment of the grass layer, enabling invertebrates to re-colonise burnt patches, and recover abundances back to pre-burn levels (Zhang et al., 2005). The short-term study only monitored the invertebrate abundance changes in the presence of rain for just over one month (between 60 days post-burn and 90 days post-burn). As invertebrates increase once the grass layer has developed, the increase seen, although not significant, will lag behind the arrival of rain. Therefore, this increase caused by the presence of rain may be the beginning of the re-colonisation of grass invertebrates. If another months worth of data had been collected, it is possible that this value would have been significant, as the vegetation may have grown more and therefore attracted the invertebrates to re-colonise.

In the tree level, as invertebrates had already began to recover by 30 days post-burn, before the arrival of rain, it is possible that the rainfall triggered growth and development not only within the trees themselves, but also for the invertebrates, as for some species rainfall signifies the start of the growing season (Uvarov, 1931; Wolda, 1988). Rainfall has the opposite effect on ground invertebrates; causing a decline in abundance following the arrival of rainfall. As stated in the short-term study, this may be due to the collection method rather than a decline in invertebrates. South African savannas have dry soils before the arrival of rain, therefore runoff is high and this can alter the soil structure (Lancaster and Briers, 2008). Changes in the structure affect the habitat and movement of invertebrates, which could have a negative effect on the ground invertebrate collection. This study and many previously, have demonstrated the significant effect that rainfall and soil condition have on invertebrate communities, either directly or indirectly via vegetation (Lamont et al., 1991; Pugnaire and Lozano, 1997; Bredenkamp *et al.*, 2002; Heelemann et al., 2008).

Future Research

There are still many gaps in research; this study provides a good base point for invertebrate responses to fire at the three invertebrate levels. Further research is required into the effect of fire on specific orders (both in the long-term and short-term), ensuring this is continued at each invertebrate level separately. It is clear that specific invertebrate orders are affected differently by burning, and previous studies have shown that other species (such as magpie shrike (*Urolestes melanoleucus*)) are significantly affected by changes in specific invertebrate orders (Kopij, 2005). Therefore, in order to understand the effect of burning on the savanna ecosystem as a whole, more research needs to undertaken into changes in specific invertebrate orders in response to fire. Additional investigations need to be undertaken to assess the effects of rainfall on invertebrates at each level, not only in general terms, but at the level of order.

This studies primary focus was to understand how the burn regime affects the abundance of invertebrates. Using abundance does show the effect of burning directly on these orders, however to understand the effect of burning on the savanna ecosystem as a whole, the data needs to be relatable to other taxa e.g. birds (Valentine *et al.* 2007). In order to do this, simple abundance does not represent the quantity of food that is available to avian or mammalian species. For example a high count of Collembola in the pitfall traps was seen immediately following the burn, and appeared to be high within burn ages that were one year old. This significant increase shows that Collembola thrive in post burn conditions; however, in terms of providing a viable food source, this may not mean as much as the significant increase in Orthoptera seen 30 days post burn. Collembola can range in length from 0.48 – 1.26mm (Peterson, 1975), whereas Orthoptera range in length from a few millimetres to 11.5cm (Sigfrid Ingrisch, 2009). It is clear just looking at the range of lengths for these two orders that one Orthoptera is likely to provide more energy and be a more valuable food source than Collembola. Biomass and volume therefore need to be considered in future studies in order to ascertain the effect any change in order abundance is having on the ecosystem (Anderson *et al.*, 1989).

Anderson et al. (1989) showed that in sand prairies there was no significant change in abundance of Orthoptera; however, there was a significant increase in Orthoptera biomass in unburnt sites one year after the burn. This suggests that there was more valuable food available to predators in the first year following the burn in the unburnt site. If predator distribution had been assessed, understanding the change in biomass would be vital in understanding the predator abundances. It is clear that due to the diversity of invertebrates, not only in function and structure but in size; biomass or volume needs to be considered. The main limitation to this is that is very difficult to assess in the field. It is feasible to assess the length of invertebrates in the field but they must be caught and measured while alive. This can be very time consuming and may reduce the breadth of the study as measurements must be taken swiftly following capture. Dry weight is another method which would take size of the invertebrate into account; this however cannot be done in the field and would require the transport of samples back to a lab to be analyzed.

The benefit of using abundance to assess invertebrate changes is that it is easy to undertake in the field and you can gather more repeat samples. The ease of the method means that the breadth of the study can be broadened and more burn ages and burn patches can be followed. It also allows you to assess the invertebrates directly and how the orders respond as a whole, without having to identify down to the species level. Abundance also enables changes in diversity to be assessed; a simple biomass average alone is not enough to assess changes. When biomass data is recorded abundance is also taken due to the nature of the data collected, this would allow diversity to be assessed and localised changes between orders can be compared.

This study only begins to understand the effects of fire on invertebrates, but in general terms has shown that burning of this fire-prone system is not detrimental for invertebrates and in some cases can be beneficial. It is clear the effect of burning on invertebrates is a broad topic, which could be taken in many directions: biomass, specific order and invertebrates in relation to decomposition post burn, are just some of the topics that require further research. As invertebrates are essential in the food web of savanna ecosystems, further research needs to be conducted to better understand changes in invertebrate functional groups. More detailed knowledge of this will help ornithologists understand the changes in the avian community in response to fire. This is because insectivores are affected by changes in habitat, as well as changes in the invertebrate abundance, which they directly rely on for food. Climate change is likely to substantially alter fire regimes over the next few decades and therefore, continued study and monitoring of patch mosaic and their effectiveness is essential to ensure that extinction of non-focal taxa is not occurring (Cochrane and Barber, 2009; Flannigan et al., 2009; Williams et al., 2009; Driscoll et al. 2010). A holistic approach to burn regimes has become a focus for private and national game reserve is South Africa (Brockett et al. 2001; Parr and Anderson, 2006). This is only feasible if more research is done into understanding how all flora and fauna within the savanna respond to fire.

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