

# Going Through Hell:

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DRIVERS OF INVERTEBRATE DETRITIVORE RECOVERY AFTER FIRE

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Dante Alighieri's *Divina Commedia* provided inspiration for the thesis structure: Chapters 2, 3 and 4 map onto Inferno, Purgatorio and Paradiso, respectively, moving from surviving the fire event through the post-fire environment to recolonisation.

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*Soli Deo Gloria.*

## Statement of Authorship

This thesis includes work by the author that has been published or accepted for publication as described in the text. Except where reference is made in the thesis, this thesis contains no other material published elsewhere or extracted in whole or in part from a thesis submitted for the award of any other degree or diploma. No other person's work has been used without due acknowledgement in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

Primary collaborators in the papers presented within this thesis are Associate Professor Heloise Gibb and Senior Lecturer Nick Murphy.

All authors contributed to the planning of experiments, of which the hypotheses and research questions were devised by JJG. JJG executed experiments and surveys in the field, collated, analysed and organised data for publication, and authored the primary text of all papers. HG and NM edited draft manuscripts and indicated areas which required further development.

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A handwritten signature in black ink, appearing to read 'JJ Grubb', with a stylized, cursive script.

Joshua Grubb, 24 December 2019

### **Note on format of Thesis by Compilation**

This thesis is presented as a series of four research data papers that have been submitted for publication in peer-reviewed scientific journals, or which are in preparation for submission therein. Every paper is a stand-alone work which addresses the broad theme of detritivore recovery after bushfire. Repetition between papers is accordingly inevitable. All papers are in preparation for publication for peer-reviewed scientific journals, or are in the process of submission.

The entire thesis is bounded by a general introduction and synthesis of results.

## List of submissions for publication

Joshua J. Grubb, N. P. Murphy and H. Gibb. In for the long game: Behavioural changes prevent long-term effects of fire on the trait-mediated distributions of flightless detritivores. (submitted for publication)

## Abstract

Fire is a prominent disturbance in Australian forests. Its effects on detritivores are of special concern, as they influence fire regimes through fuel load decomposition. However, fire also kills detritivores and destroys their habitat, so knowing what drives their recovery is necessary to understand the link between decomposition and fire. This project aimed to identify mechanisms that drive detritivore recovery following a severe, landscape-level forest fire in south-eastern Australia. I sampled three microhabitats (litter, logs and soil, representing different refugia), measured post-fire microclimate, and dispersal and physiological/behavioural traits of key detritivore taxa. Protection from fire and the post-fire environment depended on microhabitat, as abundance declined in litter, but increased in soil following prescribed burns, while effects on log detritivores were more complex. Most measured detritivore taxa were physiologically sensitive, which interacted with site characteristics, including temperature, to determine assemblages. Further, burning did not affect site microclimate 7-8 years after severe wildfire or interact with physiology to change assemblages. However, detritivores from severely burnt forest preferred higher temperatures and lower humidities, indicating legacy effects of fire. Finally, some detritivores appear to recolonise from unburnt forest refuges, rapidly if winged, but slowly if wingless, while others survive *in situ*. This project revealed that detritivore recovery from fire depends first on their ability to survive *in-situ*, after which dispersal and physiological traits become important in the post-fire environment. In addition, long-term habitat changes resulting from wildfire may limit recovery. These results suggest that preserving unburnt refuges would promote detritivore recovery after prescribed burns and especially after severe wildfires. These results and others are discussed in the context of land management and future research directions are proposed.

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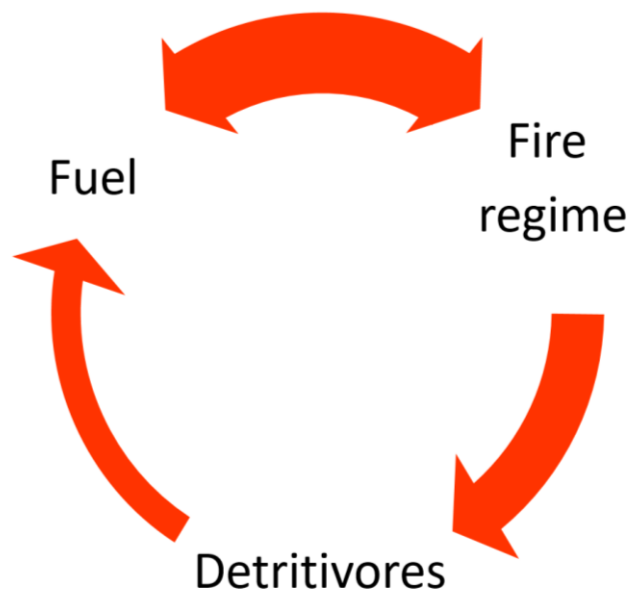
## General introduction

Fire is perhaps the most prominent and integral disturbance in many Australian forests. It exerts considerable impacts on the biological communities and ecological processes of these ecosystems (Bengtsson, 2002; Burrows, 2008; Williams et al., 1994). Of particular interest are its effects on soil fauna, as they are one of the three global drivers of decomposition (detritivores, litter quality and climate; García-Palacios et al., 2013). The decomposer community is composed of microbes, fungi and invertebrates (Gessner et al., 2010). Generally, microbes and fungi chemically break down organic plant matter, often to inorganic constituents (Wolters, 2000; York et al., 2012). Invertebrates physically fragment detritus and also mix with the soil, which accelerates chemical decomposition (Anderson, 1988). In addition, invertebrates may also harbour symbiotic micro-organisms that contribute to chemical breakdown of detritus (Ramanathan and Alagesan, 2012; Ulyshen, 2016).

Invertebrate detritivores thus have great influence on fuel build-up, particularly fine fuels such as leaf litter, and so are important determiners of fire behaviour (Bond and Keeley, 2005; Brennan et al., 2009; Buckingham et al., 2015; Podgaiski et al., 2014; Sullivan et al., 2012). However, fires initially destroy part or all of the litter and humus layers, and reduce detritivore abundance and species richness (Podgaiski et al., 2014; Springett, 1976). This creates the possibility of a negative feedback loop between fire and detritivores: if detritivores do not recover sufficiently from fire impacts, fuel loads may increase to the point of favouring future fires (Fig 1).

In addition, invertebrate detritivores are likely to be the most susceptible of the three drivers of decomposition to local disturbance and change over management timescales (e.g. 20-40 years), meaning they are of special relevance when deciding how to best manage fire regimes, for either conservation or hazard reduction purposes (Farská et al., 2014; Gessner et al., 2010). However,

despite their importance in fire ecology, few studies have sought to understand the drivers and adaptations influencing invertebrate detritivore recovery from fire.



*Figure 1.* Diagram illustrating the potential for a negative feedback loop between fire regime and detritivores by way of fuel loads. If fire suppresses detritivores, fuel loads are ‘released’ potentially leading to further fires.

The response of invertebrates results from aspects of their biology interacting with components of the fire regime. Fire regimes describe how ecosystems experiences fire, and are defined by reference to several components, namely the intensity, frequency, seasonality, severity (especially vegetation layer(s) burnt) and patchiness of fire (Patrik Krebs et al., 2010). Thus, for instance, intensity is likely to predominately affect *in-situ* survival by eliminating individuals, while seasonality may interact with life history, and frequency may interact with speed of post-fire population growth.

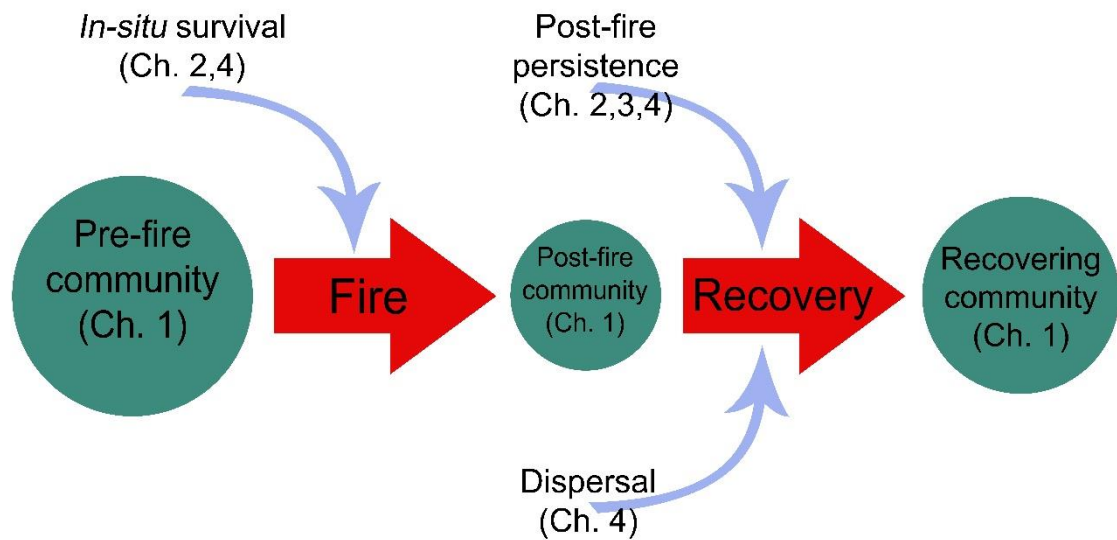
The possibility of a negative feedback loop is more likely if the incidence and extent of severe fires increases, as predictions of hotter and dryer weather in much of south-eastern Australia indicates they will (Clarke et al., 2011; Stephens et al., 2014). In addition, anthropogenic fire regimes have

become globally dominant over the last few hundred years (Bowman et al., 2011; Pausas and Keeley, 2009; Pechony and Shindell, 2010). These changes to fire occurrence, including frequency, extent and severity, can alter ecosystem functioning and community composition (Bowman et al., 2016; Perry et al., 2014). For example, depending on the system, fire suppression may allow fuel loads to increase, raising the chance of a severe fire (Stephens et al., 2014). Similarly, more frequent burning can slow microbial decomposition, making detritivores essential contributors to the post-fire restoration of this process (Brennan et al., 2009). Understanding the recovery of detritivores is thus especially relevant for future fire management.

Although many detritivore species are likely to be well adapted to fire, given its long history in most Australian forests, climatic and anthropogenic changes may introduce new stressors that detritivores are not adapted to deal with (Bradstock et al., 2002; James, 1988; Wikars and Schimmel, 2001). Although large, severe wildfires may be a natural occurrence, ecosystem recovery afterward takes longer, as they have a greater impact relative to low severity fires (Hamman et al., 2007; Hutto, 2008; Robinson et al., 2014; Romme et al., 2011). High fire severity causes greater habitat loss and higher mortality during and after the fire, while greater burn extent means longer dispersal distances for recolonising invertebrates, all of which may combine to significant negative effect for the detritivore community (Arnold et al., 2017; Buckingham et al., 2015; Malmström, 2010). Ground-dwelling arthropods are often among those most adversely affected by changes, such as more frequent or intense burning, at least over the short term, compared to other invertebrate groups, possibly because they are not immediately favoured by post-fire plant growth and many are poor dispersers (Barratt et al., 2009; Bezkorovainaya et al., 2007; York, 1999).

While the impacts of such fires can last several years (e.g. Watson et al., 2012), much research on invertebrates has focused on the first one to three years after fire, so we currently do not have a good understanding of long-term recovery (New, 2014). This is especially true of large, high-severity fires, since they must be studied opportunistically. To better understand how detritivores might respond to severe burning, their recovery from fire can be divided into three stages: *in situ* survival, post-fire survival and recolonisation (Fig 2; Whelan et al., 2002). Although fire initially reduces detritivore abundance quite drastically, *in-situ* survival may be possible through the use of refugia (Brennan et al., 2011; Robinson et al., 2013; Wikars and Schimmel, 2001). Such refugia may include surprising places, such as the crown of grass trees, which may only reach 25°C while other parts of the plant burn at up to 515°C (Brennan et al., 2011). However, a more common refuge is likely to be the soil, which provides excellent insulation from heat, allowing some individuals to survive even under intense fire conditions (Raison et al., 1986). The second stage of recovery depends on habitat changes resulting from burning, especially alterations in the quality and input of litter, habitat structure and microclimate. The loss of litter and canopy cover, especially where crown fires have occurred, may result in xeric conditions and higher temperatures, posing a major challenge to the survival and population growth of detritivores, many of which are desiccation-sensitive (Dias et al., 2013; Ehbrecht et al., 2019; Friend, 1986; Lazo-Wasem, 1984; Pettit and Naiman, 2007; Silveira et al., 2009; Swengel, 2001; Warren et al., 1987). However, even sensitive species could persist by altering their habitat choice and/or phenotype. For instance, some detritivores may move deeper into the soil to avoid harsh conditions or reduce water loss by increasing body size (Buckingham et al., 2015; Vlug and Borden, 1973). Finally, as conditions change over time, particularly as vegetation regrows, opportunities for recolonisation may open for species otherwise unable to survive (Driscoll et al., 2010). Unburnt patches, or those only suffering low intensity burns, will form the source populations for such species (Robinson et al., 2013). The extent and position of such patches, especially how far they are from the fire interior, and the dispersal ability of detritivores will be critical to recolonisation.

If species are unable to survive by these means (i.e. *in situ*, through the post-fire environment, or recolonise) local extinction may result from high severity fires.



*Figure 2.* Schematic outline of the factors contributing to detritivore community recovery after fire, with references to what aspect(s) each thesis chapter focuses on. The circle size indicates species richness/abundance at each stage of community recovery.

## Aims and approach of the thesis

This project aimed to identify mechanisms by which the detritivore community recovers following a severe, landscape-level wildfire, with reference to each stage of recovery. The design of this project follows the recommendation of Driscoll et al. (2010), who pointed out that the ability to determine species responses to fire depends on a mechanistic rather than a descriptive approach. By identifying how species' traits interact with the environment, it is possible to predict responses to disturbance and habitat change, which is valuable information when making management decisions (Driscoll et al., 2010). Studies using a high taxonomic resolution (i.e. beyond the order

level) are uncommon, so it is currently not possible to appreciate how species-level adaptations contribute to recovery after fire (Teasdale et al., 2013). For this project, Amphipoda, Isopoda, Diplopoda and Lepidoptera larvae were selected as representing dominant detritivore taxa in the study system. I identified the first three to morphospecies, and the last to family or order, to detect changes in detritivore assemblages, including which species were sensitive to or favoured by burning, and also to identify traits important for survival. However, because these detritivorous taxa are not well known (Paoletti et al., 2007), particularly at my study sites, I first described their temporal and spatial variability by sampling them during both the day and night, over three seasons and two years, and in two microhabitats (litter and logs), to provide background knowledge of this community (Chapter 1) for the remaining chapters.

Drawing on these data and the general understanding of detritivore biology, I selected several characteristics likely to influence their post-fire recovery. Whilst most studies concentrate on leaf litter invertebrates, detritivores occupy a diverse range of habitats, from soil to logs to bark to fungi. These habitats offer different levels of protection from both fire and the post-fire environment. I therefore selected litter, logs and, for chapter 2, soil, as appropriate microhabitats to sample, as they comprised the majority of habitat available to detritivores in this system. My second chapter addressed the question of how detritivores might survive *in-situ* and post-fire by assessing the detritivore community before and after prescribed burns, with an eye to determining how the three different microhabitats might act as refugia from the immediate impacts of fire. Two general biological characteristics of detritivores stood out as especially relevant to recovery in the post-fire environment and recolonisation. The first was that detritivores are often sensitive to desiccation and high temperatures, likely a reflection of the humid environment they occupy, and second, they are often flightless, since wings can be damaged when moving through plant detritus. Of the taxa used in this study, Amphipoda, Isopoda



and Diplopoda are wingless and have 'leakier' cuticles than insects, and are thus more susceptible to hot and dry conditions (Boer, 1961; David and Handa, 2010; Lazo-Wasem, 1984; Warburg, 1987; Zimmer, 2002). Detritivorous Lepidoptera larvae are a notable exception for both these traits and provided a useful comparison. My third chapter thus measured ambient temperature and humidity at both burnt and unburnt sites to test if post-fire habitat changes altered microclimate. I then determined if microclimate changes interacted with physiological traits (live weight, critical thermal maximum, and behavioural temperature and humidity preferences) to affect detritivore community composition. Finally, I tested if distance from the fire edge predicted detritivore abundance, and determined if the ability to fly influenced recovery of detritovore taxa (Chapter 4).

The mechanistic approach adopted in this study proved worthwhile: by using high taxonomic resolution, and characterising physiological and dispersal traits, while sampling over a large area after a severe, landscape-level fire, this thesis was able to determine how detritivore traits and habitat occupancy drive the recovery process, leading to some management recommendations, and identified specific areas where further study would provide additional clarity.

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# Chapter 1: Spatial and temporal drivers of a forest detritivore community

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## Abstract

We explored the poorly understood topic of how detritivore communities vary across timescales and microhabitats in temperate Australian *Eucalyptus* forest, and what environmental factors might drive this variation. We collected macroinvertebrate detritivores across thirty sites, over three seasons and three years, both day and night, and from two microhabitats: leaf litter and logs. Despite significant taxonomic overlap, litter and log microhabitats supported distinct communities over all time scales, highlighting the importance of sampling more than one microhabitat to properly characterize the detritivore community. In general, detritivores were positively associated with detritus-related variables or those indicating more mature forest (such as canopy cover). Climate was also important for both litter- and log-dwelling detritivores, with one important Amphipod species of twenty-seven detritivore taxa declining with temperature. Further, the detritivore community was more temporally variable in litter than in logs, especially in abundance and richness. Logs provided greater thermal buffering than litter, which may explain this difference in community stability. Despite evidence from previous studies that activity is higher at night, no difference between day and night log and litter communities were detected, suggesting that relative abundance does not change. We conclude that the detritivore community is sensitive to environmental variation, especially in climate and detritus structure, but that logs provide a stable source of colonisers for the fluctuating litter environment under favourable conditions. Future studies should consider multiple microhabitats, and where possible, span several seasons, particularly in the litter. Given the greater stability of communities in logs, post-

harvest retention of logs and conducting prescribed burns in a way that leaves logs intact may be useful management options to conserve detritivore communities.

“From the literature it is known that woodlice are badly equipped for life on land” (Boer, 1961)

Keywords: Microhabitat; Desiccation; Decomposition; Climate variation

## Introduction

The spatial and temporal variation of assemblages within ecosystems strongly influences ecological processes. For instance, the diversity and abundance of soil fauna exerts significant control over decomposition rates, and therefore, the patchiness of spatial distribution of species at different scales will impact decomposition (David, 2014; De Smedt et al., 2018c; Gessner et al., 2010; Hättenschwiler et al., 2005). It can be challenging to characterize such variation within invertebrate assemblages, as most encompass a broad taxonomic and ecological range. One such community about which little is known is detritivores, including many invertebrates which are responsible for an average of ~37% of decomposition globally (David, 2014; García-Palacios et al., 2013a; García-Palacios et al., 2013b; Zhang et al., 2015). Decomposition is essential to ensure the flow of nutrients through an ecosystem, since up to 90% of plant biomass escapes herbivory and is decomposed (Cebrian, 1999; Gessner et al., 2010). Investigating the spatial and temporal drivers of variation in detritivore communities will thus increase understanding of how these factors affect ecological processes.

There are reasons to regard particular temporal and spatial scales/measurements as generally important in ecology, depending on the community in question. Some of the most important

resources driving spatial distribution are the location of food, sufficient space, shelter, brood/nesting sites and mates (Maher and Lott, 2000). Detritivores are patchily dispersed through space, occupying soil, logs, fungi, ground plants and leaf litter, containing detritus of varying origins, quality, and stages of decomposition, and this indicates that microhabitats are an important and appropriate scale for sampling. Similarly, although temporal variation of communities and species can be measured over a range of time periods, the important challenges that individual organisms encounter generally occur at the scales of the day (circadian clock), season and year (photoperiodic calendar; Kostal, 2011). While the underlying genetic regulation of the circadian clock and photoperiodic calendar is complex and not well understood, an organism's rhythms ultimately reflect and are driven by ecological constraints, such as those related to physiology (Muraro et al., 2013; Saunders, 2011). Thus, temporal patterns of animal behaviour, growth, reproduction and activity, are ultimately driven by day length, and seasonal and/or yearly variation in climate (Kostal, 2011).

Identifying the aspects of invertebrate detritivore biology that drive temporal and spatial variation will increase our ability to predict responses to environmental change. In temperate forest systems, many abundant non-insect macroinvertebrates that contribute substantially to decomposition (such as isopods, amphipods and diplopods) are sensitive to desiccation due to their relatively 'leaky' cuticles, low critical thermal maximums and high humidity preferences (Ch. 3; Boer, 1961; David and Handa, 2010; Lazo-Wasem, 1984; Warburg, 1987; Zimmer, 2002). For instance, desiccation tolerance has been found to explain isopod species distributions at the local scale, with relatively tolerant taxa being found in more exposed environments (Brigić et al., 2017; De Smedt et al., 2018a; De Smedt et al., 2018b; Dias et al., 2013). Thus, detritivores could be expected to be distributed in time and space in ways that minimize desiccation (Boer, 1961; Denlinger and Armbruster, 2014).



Amount or kinds of detritus may thus be important predictors of the detritivore community, since these factors may mitigate climatic extremes through insulating effects (Facelli and Pickett, 1991; Pouska et al., 2016; Villegas et al., 2010). Indeed, the amphipod *Arcitalitrus sylvaticus* cannot survive longer than two days at less than 100% humidity and 30°C, and therefore relies on humid microhabitats for survival (Lazo-Wasem, 1984; Villegas et al., 2010). The requirement for climatically buffered microhabitats is also reinforced by the low dispersal capabilities of many detritivore species, which are often wingless, because wings can be damaged by crawling through plant debris (Bonte et al., 2012; Menz et al., 2016). Thus, spatial distributions of detritivores could be expected to be sensitive to the distribution of different microhabitats and their associated microclimates.

Temporal distributions are also likely to be affected by detritivore biology, especially their physiological tolerances. For instance, the climatic similarity of spring and autumn mean these seasons are likely to have relatively similar and higher detritivore species abundances compared to summer, because they are more hospitable to desiccation-sensitive detritivores (Crawford, 1992; Lindeman, 1991; Moeed and Meads, 1985; Paris, 1963). In addition, since climatic conditions across microhabitats will be more similar in wetter than dry seasons, and some, such as logs, may be moister than others (e.g. leaf litter), differences in abundance between microhabitats may be more pronounced in dryer seasons (e.g. García-Roger et al., 2011). Patterns are also likely to appear over shorter timescales as, for example, some terrestrial invertebrates limit their activity during the day according to humidity or temperature (Iacarella and Helmuth, 2012; Ottesen, 1990; Parmenter et al., 1989). Further, many invertebrate detritivores are nocturnal, which could have evolved in response to the cooler and more humid conditions at night. Thus, the scales of both

the season and day are likely to be especially important in determining temporal variation in the detritivore community.

Spatial and temporal distributions interact, as a refuge that provides shelter against dry or hot conditions may not necessarily supply other resources, forcing detritivores to move among microhabitats (Hassall and Tuck, 2007). For instance, detritivores may retreat to logs or soil in the summer, expanding their habitat occupancy to leaf litter in the cooler months of the year, similar to other invertebrates (Lira et al., 2013; Stapp, 1997). In addition, desiccation sensitivity or body size affects how much time isopod and millipede species spend foraging vs sheltering, and can reduce the consumption of high quality food in drier environments (Dias et al., 2012; Semenyuk and Tiunov, 2019). While such movement might be less evident for specialists predominately in one microhabitat, generalists might regularly move across several microhabitats (Brückner et al., 2018; Wardhaugh, 2014). Competition for space may also explain habitat partitioning, even between species that are otherwise habitat generalists (Friend and Richardson, 1977; O'Neill, 1967). Movement between microhabitats (or fluctuations in abundance) could also be driven by seasonality of food or habitat resources (Grimbacher et al., 2018; Lira et al., 2013; Wardhaugh, 2014). For example, detritivores may respond to seasonally dependent litter falls, similar to the very close synchrony between insect life cycles and the growth of their host plants (Forkner et al., 2008; Grimbacher et al., 2018; Scriber and Slansky, 1981).

Dispersal-limited detritivores are likely to rely on *in-situ* survival in disturbance-prone ecosystems, which would be enhanced by being flexible in their habitat occupancy. However, this may not be possible for desiccation sensitive taxa, as the available habitat is quite limited. Temporal flexibility in microhabitat occupancy may thus become important in the context of disturbance for such

species, since species may have to move between microhabitats to survive (Lancaster, 2000). For instance, in a fire-prone ecosystem, where summer is the driest month, sheltering in the soil could provide protection not just from low humidity but also fire (Radea and Arianoutsou, 2012; Sgardelis et al., 1995). Similarly, conditions are typically hotter and dryer after fires, owing to the loss of leaf litter and canopy cover (Balch et al., 2008; Raison et al., 1986a; Savage and Vermeulen, 1983). Since such conditions may persist for several years, until vegetation recovers, so behavioural responses and species loss/gain may result in long-term shifts in the spatial and temporal distribution of detritivores, as is also seen in birds (Brennan et al., 2009; Haslem et al., 2011). For example, isopods in clear-cut forests are less active during the day than those in unfelled forest (Tuf and Jeřábková, 2008). However, it is also possible that detritivores may compensate for such habitat changes by increasing body size, which improves water retention (Buckingham et al., 2015). Thus, spatial variation in detritivore communities is likely to be explained by the extent of different microhabitats, especially those that have lower temperatures and higher humidity, and the temporal variation likely to occur over the scales of day and season, particularly in ecosystems that experience disturbance, such as fire.

In this study, we aimed to quantify key sources of spatial and temporal variation determining the composition of temperate detritivore communities. We asked four questions regarding their temporal and microhabitat distribution:

1. Do macroinvertebrate detritivore assemblages differ in richness, abundance and composition among microhabitats? We predicted that detritivore assemblages would differ between litter and logs, and this difference would persist across seasons.

2. What are the environmental drivers of variation in the detritivore community? We predicted that climate- and detritus-related variables would be the primary organizers of detritivore community composition.

3. Does the activity of the detritivore community differ between night and day? We predicted detritivore abundance and richness would be greater at night in response to increased humidity, and thus assemblages would appear to differ between day and night because of differences in tolerance among species. In addition, we predicted detritivores would be more commonly detected in logs during the day and in the litter at night.

4. How do detritivore communities vary among seasons? We predicted that detritivore assemblages would be most similar in spring and autumn and that richness and abundance would be greater than in summer, due to more favourable conditions, especially higher humidity.

## Methods

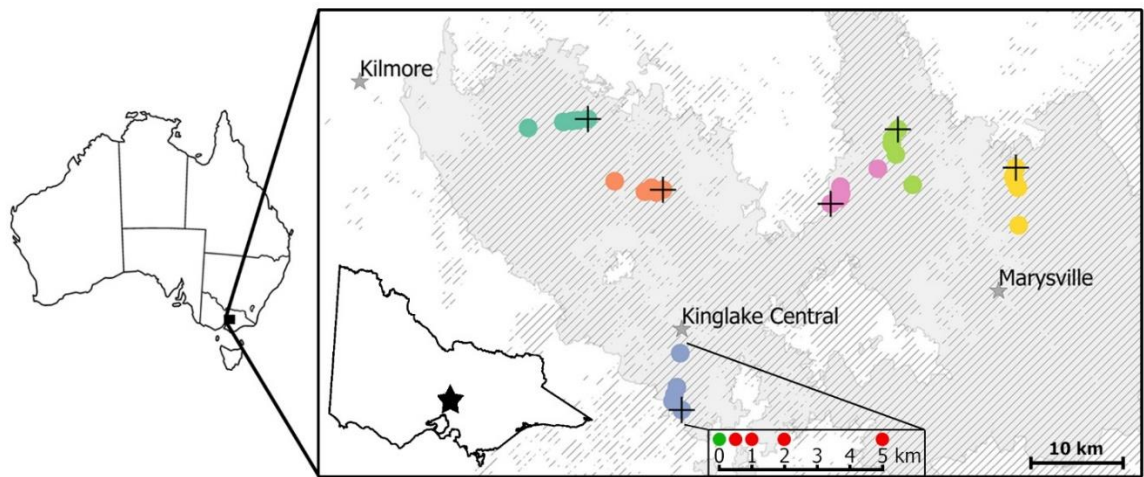
### Study sites

This study was conducted in forests ~50km north-east of Melbourne, in south-eastern Australia (Fig. 1). Sites were in dry sclerophyll forest, dominated by messmate (*Eucalyptus obliqua*) and peppermint gum (*Eucalyptus radiata*), with an understory of Austral bracken (*Pteridium esculentum*), *Acacia spp.* and *Eucalyptus spp.* saplings. Site altitude ranged from 252 m to 816 m. Sites were set along six 5 km transects, with five sampling points (sites) each located within or just outside the boundary of the Kilmore East-Murrindindi fire complex (Fig. 1). The fire began on 9<sup>th</sup> February 2009 and burnt over 228,000 ha, severely burning much (but not all) of the area (Leonard et al., 2014). The first site along each transect did not burn in 2009 had been unburnt for at least 20 years prior to 2009. The remaining four sites on each transect were severely burnt (crown

scorch/fire) in the 2009 fires. All sites except three (clear-felled 12 and 14 years prior to 2009) had not been logged for at least 20 years prior to 2009. Although it is possible that unburnt sites had escaped burning because they were distinct, there are several reasons why this was not considered a major confounding factor. All sites were in dry sclerophyll forest and of the topographic measures (slope, PADIR, altitude), only altitude was marginally higher in burnt than unburnt sites ( $p = 0.01-0.05$ ; Appendix, Table 8) when analysed using a manylm, which is above the threshold of  $\alpha=0.001$  we consider appropriate for this analysis. Other habitat differences (such as canopy cover and number of logs) could be attributed to the impact of burning. Finally, the Black Saturday fires were so severe in places that topography no longer had its usual mitigating effect, meaning that unburnt patches were often dependent on the weather conditions rather than site features (Leonard et al., 2014). To capture temporal variation, litter and log samples were taken in summer, spring and autumn across three years, except logs were not sampled in 2015 (Table 1). Sampling that occurred from December-February was classed as summer, March-May as autumn and September-November as spring. No winter sampling was undertaken due to time constraints and difficulty in accessing some sites in wet conditions. Sites were sampled during daylight (between 08:00 and dusk) for day samples, and between dusk and 01:30 for night samples.

*Table 1.* Year and season of sampling periods, along with microhabitat type sampled and whether night samples were taken. Number of transect points sampled (n) are also given.

Year	Season	Litter	Log	n (day)	n (night)
2015	Summer	✓		30	4
	Autumn	✓		30	7
	Spring	✓	✓	30	12
2016	Autumn	✓	✓	30	12
	Spring	✓	✓	30	NA
2017	Summer	✓	✓	6	NA



*Figure 1.* Map of study sites, located in south-eastern Australia, and their positions relative to three towns (grey stars). Colours indicate different transects and crosses (+) are unburnt sites and the beginning of each transect. Inset at bottom shows distances for transect sampling points (green = unburnt, red = burnt). The grey outline indicates fire extent, and hatching indicates forest.

#### Ambient and microhabitat microclimate measurements

Temperature and relative humidity were measured at all sites using Tinytag Plus<sup>®</sup> loggers in weather stations (similar to Stevenson Screens; used to ensure ambient conditions were measured and were not influenced by rain or sunlight) placed 10 cm above the ground to record near-ground conditions. Readings were collected every half hour for one year (1 February 2016-2017). Temperature and percent relative humidity (% RH) were measured for each season using the following indices: average maximum temperature and % RH; highest maximum temperature, minimum temperature and % RH; average day and night temperature and % RH; the number of days over 95% RH, under 20% RH, over 35°C and under 1°C.

Microhabitat temperatures were measured using thermocron ibuttons<sup>®</sup> (Maxim Integrated Systems, temperature accuracy  $\leq \pm 0.5^\circ\text{C}$ ) at five sites (initially 3 unburnt, 3 burnt) over one year, from 1 June 2016 to 31 May 2017. ibuttons<sup>®</sup> were placed in three microhabitats: 1) the interface of leaf litter and soil, 2) under logs and 3) 5 cm under the soil surface. Although soil samples

containing invertebrates were collected, they were not analysed due to time constraints, however, sub-surface soil temperatures were taken to allow comparison to other microhabitats. To minimise disturbance to soil, we used a soil corer to make a hole and pushed ibuttons® horizontally into the soil, then filled the hole by replacing the core. One to four ibuttons® were used per microhabitat per site, and spaced at 10m intervals to ensure they could be retrieved. If ibuttons® were found outside the microhabitat where they were placed (e.g. dug up by animals), the data were discarded for that period. Due to ibutton® failure, winter and spring comparisons of microhabitats were based on five sites (3 unburnt, 2 burnt) and summer and autumn on four sites (2 unburnt, 2 burnt). For the same reason, data was missing from some dates and filled by substituting the average for that day from the other sites within the same microhabitat. Maximum, minimum and average daily temperatures (days were measured from sunrise to sunrise, using Murrindindi, Victoria as the location; data from Geoscience Australia, 2019) were then averaged for each microhabitat/site where appropriate (ibutton® failure meant some microhabitats only had one ibutton® per microhabitat/site).

Environmental variables were measured in summer, autumn and spring 2015, and autumn and spring 2016, although characteristics that change very slowly were not measured every season (e.g., number of standing trees, for instance, was unlikely to change substantially over 3 years and was measured once; full list of environmental variables measured in Appendix 1, Table 2). PADIR (Potential Annual Direct Incident Radiation) was calculated using equation 2 from McCune and Keon (2002) using latitude, slope and aspect (the latter two were obtained from GIS data provided by Geoscience Australia (2017); Ch. 1 Appendix Equation 1). We counted live and dead standing trees (diameter at breast height  $\geq 10$  cm) and logs (diameter  $\geq 10$  cm) within a 5 m radius at ten points distributed evenly along a 100 m transect at each site in summer 2015. Canopy and understory cover (small trees/shrubs below level of canopy), and, within a 1 m radius, litter, plant

(ground plants <1m tall) and bare ground cover were visually estimated at five 10 m intervals along one 50 m transect per site per season (except for summer 2015, when the 100 m transect was used). At the same time and locations, litter depth (carpenter's square) and soil volumetric water content (Fieldscout TDR 100 soil moisture meter probe, Spectrum Technologies, USA, and DSMM500, General Tools & Instruments, USA) were measured at three haphazardly chosen points within a 25 x 25 cm quadrat, selecting the nearest continuous patch of litter > 625m<sup>2</sup> as the sample point. The few missing values for environmental variables (reflecting equipment being unavailable or data errors), were replaced to ensure a balanced analysis with average values from all samples for that sampling period.

The following measurements were made of logs containing invertebrates in spring 2015 and 2016, and autumn 2016. Decomposition was classified according to Lindenmayer et al. (1999), where freshly fallen logs = 1, solid log without bark = 2, sapwood decomposing = 3, entire log decomposing, but still retaining shape = 4, and completely disintegrated logs with no discernible shape = 5. Burn severity of logs was estimated on a similar scale, where 0 = unburned, 1 = scorched (<15% burnt), 2 = a mixture of severe burning and unburnt (<85% burnt), and 3 = entirely blackened. We used the equation for cylinder volume ( $V = \pi * r^2 * \text{length}$ ) to estimate log volume based on measurements of log radius and length; values were halved for laterally split log fragments (not unusual at our sites).

#### Litter and log invertebrate sampling

To determine the importance of microhabitat, detritivore communities were examined from both leaf litter and logs. Litter invertebrates were extracted using Tullgren funnels from litter samples



removed down to the mineral soil from the 625 cm<sup>2</sup> quadrat (litter volume range 450-2316 cm<sup>3</sup>) where litter depth was measured (n=5 per site per sampling period). The litter was left for a minimum of four days in the funnels and removed when completely dry. Invertebrates were collected into vials of 100% ethanol under the funnels.

Log invertebrates were sampled using log searches, conducted in spring 2015, spring and autumn 2016, and summer 2017, at all 30 sites. Logs >9 cm diameter were visually located by walking haphazardly through the plots within <200m of the transect and then searched by rolling and/or dissecting a section (usually 30-60 cm), by hand and the assistance of a hammer and small crowbar. Some logs were unable to be searched, as they were too large to be rolled or the wood too solid to be pulled apart, though it was often possible to search under bark. This method was considered appropriate for the target taxa, since they were not borers capable of occupying solid wood requiring a rearing/extraction approach, but instead occupied decayed wood and existing holes/cracks. When thorough searching of visible surfaces on the log and the ground where the log touched the ground did not yield any more specimens, the next log was searched, until 30 minutes had elapsed (time included searching for logs and collecting invertebrates from logs; time spent labelling was excluded). Specimens from logs were collected directly into 100% ethanol. Since logs were reasonably visible at our sites, our ability to locate logs reflected log density, meaning sampling reflected relative abundance at our sites.

Four groups of abundant macro-arthropod detritivores were selected for study; other taxa were not selected to allow a larger number of samples to be processed. These included 3 distinct flightless taxa (Diplopoda, Amphipoda and Isopoda) and one taxon winged as adults (Lepidoptera larvae; only collected from litter, as they could not be located reliably by sight on logs). The

Lepidoptera were identified to family if possible and were otherwise assigned to order; the flightless taxa were identified to species/morphospecies where possible, and unidentifiable specimens (such as some immatures) attributed to the closest taxonomic group (family or order). Taxonomic experts were consulted for Diplopoda (Robert Mesibov) and keys used for Amphipoda and Isopoda included (Friend, 1987; Green, 1961; Green, 1974).

### Analysis

Because our design was not fully crossed in every sampling period, different datasets were used for each analysis depending on the variables available (Table 1; Ch. 1 Appendix, Table 1). We used linear mixed models (negative binomial distribution) to compare richness and abundance of invertebrate communities between time of day, season and microhabitat (logs vs litter), with transect as a random effect (R package lme4; Bates et al., 2014). Sampling period was also included as a random effect, nested within site, to account for temporal variation where datasets spanned more than one season and/or year. Estimated marginal means were then used to conduct post-hoc tests where applicable (R package emmeans; Lenth, 2017). To compare detritivore community composition between time of day, season and microhabitat, we used multiple general linear regression (manyglm, R package mvabund; Wang et al., 2014; Wang et al., 2012). These linear mixed models and manyglm tests were run with and without logged sites to determine if logging affected results; where a difference in main effects was detected, logged sites were excluded. To determine how the environment influenced the detritivore community, we used manyglm, and analysed the litter and log communities separately. For manyglm temporal analysis, year and season were included as separate fixed factors to clarify individual species' response, while sampling period (each year/season combination) was included as a fixed factor in abundance and richness GLMMs, as there were only 5 periods.

To reduce the large number of environmental variables (Appendix 1, Table 2), all were plotted using principal components analysis (PCA; princomp, R base 'stats' package), allowing us to identify groups of correlated variables. Prior to PCA, all environmental variables were standardised using two standard deviations (Gelman, 2008). Since it was difficult to see differences clearly when all points were plotted, values were first averaged across seasons and years for each site when plotting the PC axes. To eliminate temporal variation in the PCA axes, the first three litter principal component scores were regressed against season. For logs, season + year was regressed against PCA1, year for PCA2 and season for PCA3, as these factors were significantly associated with variation in the PCA axes. The residuals from the linear models were then used as main effects in manyglm models to control for habitat variation. Manyglm models were run with three PCA residual variables, season, year and transect as main effects. In addition, general linear mixed models were run to test the association between abundance and richness, and the three PCA residual variables, with the random effects of season, nested within year, then within site. Burn status was not included in these models, as the purpose was to identify other spatio-temporal patterns and habitat drivers of the detritivore community.

We used linear mixed models to determine if maximum, minimum and average temperature differed between microhabitats and from the ambient temperature for each season, with date nested within site as a random effect. Residual plots were checked for normality, and the response variable log transformed or a Gaussian distribution with a log link used where necessary. Estimated marginal means were then used for post-hoc pairwise comparisons, and model means were plotted with standard error for pairwise comparisons. We also compared the absolute

highest maximum and minimum temperatures recorded per season between microhabitats with a linear model (since there was only one value/season, no random effects were included).

All manyglms were run with the following parameters: 999 permutations and negative binomial distribution (with resampling method "pit.trap"), and transect was included as a main effect in all analyses to account for spatial variation. Where datasets included more than one year or season, year and/or season was included as a main effect to account for temporal variation. All manyglm models were visually checked for normality with Dunn-Smith residual plots. When a main effect with more than two levels was significant, pairwise comparisons were used to identify which levels were significant. To determine if individual taxa were responsible for main effects, we used the univariate post-hoc results from the manyglm analysis. To aid visualisation of categorical main effects for these taxa, average fitted values were plotted with standard error, which was obtained by first averaging across seasons/years, then calculating SE across transects. For continuous main effects, all fitted values were plotted, with a general linear regression line  $\pm$ SE for visualisation purposes (quasi-Poisson distribution). P-values were unadjusted for multiple comparisons, as this was considered overly conservative (e.g. García, 2004), and instead  $\alpha < 0.001$  was used to assess significance for all post-hoc univariate manyglm results. MDS plots using Bray-Curtis similarities on transformed data were used to visualise significant main effects from manyglm results. Since it was difficult to see differences clearly when all points were plotted, count data was averaged across seasons/years where applicable (rounded to the nearest whole number), then summed across sites within each transect before plotting an MDS.

## Results

A total of 8448 detritivores were collected (2448 from logs and 6000 from litter), and twenty-seven detritivore species and morphospecies were identified (24 from logs and 24 from the litter; full list Appendix 1, Table 3). Specimens that could not be identified to morphospecies were taken to the order or family level ( $n = 3801$  specimens), which were predominately from the orders Lepidoptera and Diplopoda (2410 and 809 individuals respectively) and pooled under class (immature Diplopods), order or family for analysis of a total of 37 taxa.

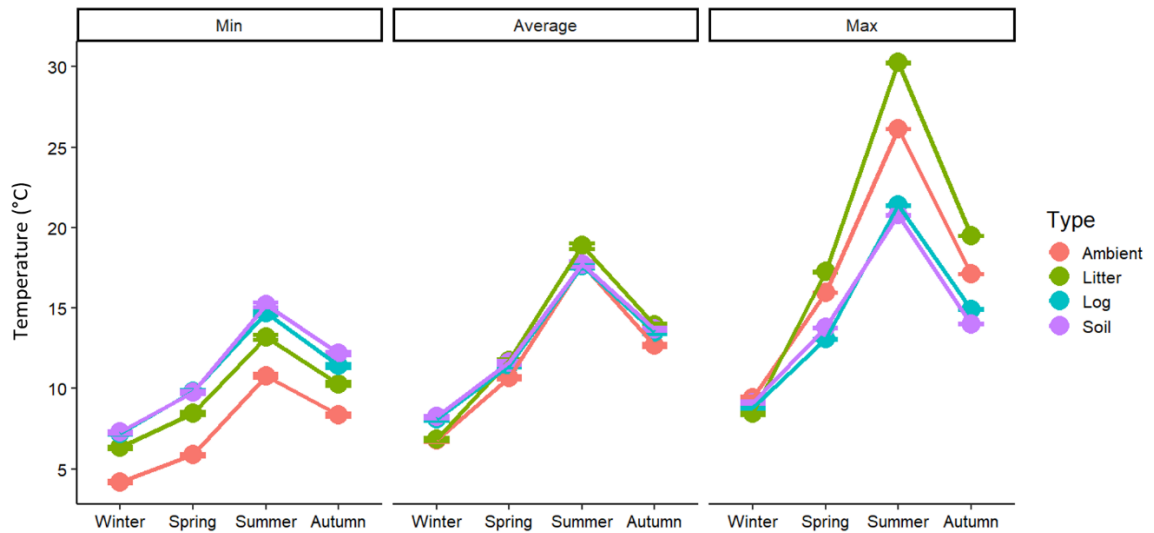
### *Habitat and climate/environmental variables*

The litter PCA axes 1, 2 and 3 explained 38%, 11% and 9% respectively (total 58% variation) of the variance among 26 environmental variables, while the log PCAs explained 27%, 11% and 9% respectively of the variance among 33 environmental variables (total 47% variation; Ch. 1 Appendix, Table 2, Figure 1). Variables with a contribution  $\geq 0.3$  to each axis were considered important (summary Table 2; full table Ch. 1 Appendix, Table 2). Logged sites slightly altered results and were excluded from analysis, as they resulted in dead trees contributing to PC3 rather than alive trees, as well as log length touching ground. Temperature was associated with PC1 in both litter and log ordinations, while humidity also contributed negatively to the log PC1 (Table 2). Forest structure variables and site slope were associated with PC2 in the litter ordination, and with PCA3 in the log ordination (Table 2). Canopy, understory, litter and ground plant cover contributed to PC3 in the litter ordination, while litter and ground plant cover, log decomposition and site altitude contributed to PC2 in the log ordination (Table 2). These principle components were used to control for environmental variation in further analysis of temporal and spatial variation.

All three microhabitats (litter, logs, soil) were more thermally buffered than the ambient temperature, except that higher temperatures were recorded from litter than from the ambient loggers. Differences in maximum temperatures among microhabitats were most pronounced in summer, while the difference in minimum temperatures did not change as much with season (Figure 2). This may have been caused by the ambient Tinytag temperature loggers being housed within weather stations and thus protected from the direct effects of sunlight, while the ibuttons in the litter were more exposed to sunlight. Temperatures under logs were more buffered than litter, and were similar to the soil. While the absolute highest maximum temperatures did not clearly differ between microhabitats and ambient, the absolute minimum was always higher in log and soil relative to the ambient, and never dropped below zero in any microhabitat, despite some ambient sub-zero temperatures (Ch. 1 Appendix Figure 2).

*Table 2.* Summary table of environmental variables with contributions of  $\geq 0.3$  to PCAs. Red and blue indicates positive or negative contributions to each axis, respectively. A complete table is included in Ch. 1 Appendix, Table 2.

Principal component:	1	2	3
<b>Litter PCA</b>			
Average day temp °C	0.30		
Average night temp °C	0.31		
% Canopy cover			0.34
% Understory cover			-0.30
Alive trees		0.34	
Dead trees		-0.33	
% litter cover			-0.32
% ground plant cover			0.36
Slope		-0.44	
<b>Log PCA</b>			
Average day temp °C	-0.31		
Average night temp °C	-0.32		
Average night % RH	0.30		
% Understory cover			-0.35
Alive trees			0.36
% litter cover		0.41	
% ground plant cover		-0.34	
Slope			-0.39
Altitude		0.31	
Log decomposition		0.32	



*Figure 2.* Maximum, minimum and average temperatures (model estimated values) recorded for three microhabitats and ambient in all four seasons. Error ( $\pm$ SE) is very small and barely visible. Error bars that do not overlap are significantly different (Ch. 1 Appendix, Fig 3).

*1. Do detritivore assemblages differ in richness, abundance and composition among microhabitats, and are these differences temporally mediated?*

Multivariate analysis showed that assemblages differed between litter and logs across all sampling periods (Table 3). There was no interaction between microhabitat and time of day, indicating little directional movement of detritivores between the two microhabitats over a day, except possibly in spring (Table 3). However, post-hoc pairwise analysis attributed the day/night\*microhabitat interaction in spring to differences between microhabitats, meaning there was no evidence of movement between habitats between day and night (Figure 3). Assemblages were significantly different in spring and autumn in both microhabitats, while summer assemblages were unable to be distinguished clearly from spring and autumn, likely because of the lower sample size. Similarly, there was an interaction between season and microhabitat (Table 3; Figure 1), which could not be attributed to any species ( $\alpha \leq 0.001$ ). A post-hoc test including all sampling periods showed that ten taxa (from Diplopoda and Isopoda) were more abundant in one microhabitat than another, four in litter and six in logs (Figure 4); additionally, 70% of taxa were found in both microhabitats



(Ch. 1 Appendix Table 3). Five of these taxa also showed a response in spring, always preferring the same microhabitat as in the overall test (Figure 4; Appendix 1, Figure 8).

*Table 3.* Manyglm testing for differences between litter and log detritivore communities, as well as the interaction between microhabitat type and time (day or night), and season. Transect, year and season were included as fixed effects in place of random effects. Significant p-values are in bold, while daggers indicate where a post-hoc could attribute results to specific taxa.

Model	Terms	All		Spring		Autumn		Summer	
		Dev.	p	Dev.	p	Dev.	p	Dev.	p
Microhabitat and season	Microhabitat	375.7	<b>0.001</b> <sup>†</sup>	302.8	<b>0.001</b> <sup>†</sup>	97.3	<b>0.001</b>	37.3	<b>0.021</b>
	Transect	625.8	<b>0.001</b>	482.4	<b>0.001</b>	268.1	<b>0.001</b>	64.8	<b>0.013</b>
	Year	99.7	<b>0.001</b>	96.2	<b>0.001</b>				
	Season	173.3	<b>0.001</b>						
	Microhabitat*Season	68.2	<b>0.002</b>						
Microhabitat and day/night	Microhabitat	245.4	<b>0.001</b>	181.6	<b>0.001</b>	100.6	<b>0.001</b>		
	Day/night	32.0	0.579	35.9	0.304	26.0	0.741		
	Transect	553.5	<b>0.001</b>	366.2	<b>0.001</b>	380.7	<b>0.001</b>		
	Season	168.0	<b>0.001</b>						
	Microhabitat*Day/night	27.0	0.290	37.4	<b>0.025</b>	15.0	0.559		

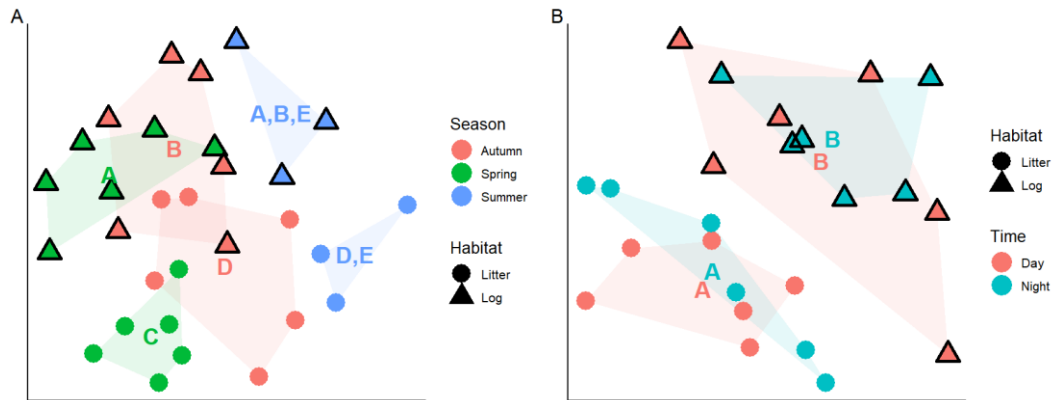


Figure 3. MDS plots comparing litter and log detritivore communities A) between seasons and B) between day and night in spring. Letters indicate the results of a post-hoc manyglm pairwise comparison. The kernel outlines each season or time of day, for each microhabitat, and letters are positioned at the group centroids.

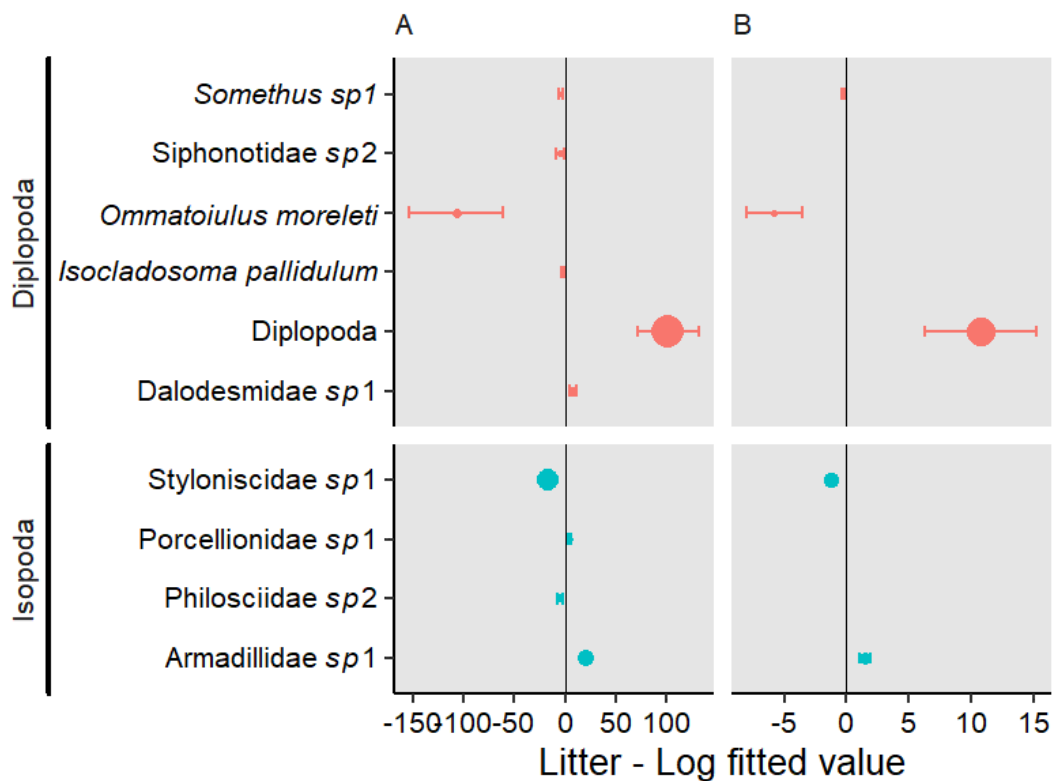


Figure 4. Average fitted values  $\pm$  SE for ten taxa that were more abundant in one microhabitat than another for A) all seasons and B) spring. Points above zero indicate taxa more abundant in litter, those below zero more abundant in logs. Point size indicates the relative contribution of each species to the main effect. Colour indicates taxon.

## 2. What are the environmental drivers of the detritivore community?

Abundance and richness of detritivores in the litter increased with canopy and ground plant cover and declined with understory and litter cover (PC3), while log abundance and richness was not correlated with environmental PCs (Table 4; Figure 5A, B). All three PCA axes interacted significantly with the litter detritivore community, while PCA axes 1 and 3 were important for the log community (Table 4). Post-hoc tests identified three taxa responsible for these trends. Firstly, litter-dwelling *Styloniscidae* sp. 3 increased with canopy and ground plant cover, and declined with understory and litter cover (litter PCA 3; Table 4; Figure 5C). Secondly, *Keratroides* sp. 1 declined with increasing temperature (PC1) in the litter (Table 4; Figure 5D). And finally, log-dwelling *Brachyiulus pusillus*, an introduced millipede, declined with number of live trees, but increased with understory cover and slope (log PC3; Figure 5E). Due the impact of logged sites on the principal components, they were excluded from these analyses.

*Table 4.* Manyglm and generalised linear mixed model (GLMM) results testing the effect of environmental PCA residuals on the litter and log detritivore community, abundance and richness. Year, season and transect were included as fixed effects in the manyglm in place of random effects. GLMMs were run with sampling period nested within transect as a random effect. Significant p-values are in bold, while daggers indicate where a post-hoc test could attribute results to specific taxa.

Community (manyglm)	Litter		Log	
	Dev.	p	Dev.	p
Year	89.4	<b>0.005</b>	54.8	<b>0.022</b>
Season	253.3	<b>0.001</b>	83.8	<b>0.024</b>
Transect	436.6	<b>0.004</b>	383.4	<b>0.001</b>
PC1 residuals	75.4	<b>0.005†</b>	39.8	<b>0.040</b>
PC2 residuals	55.0	<b>0.046</b>	30.0	0.305
PC3 residuals	88.9	<b>0.003†</b>	87.4	<b>0.001†</b>
Abundance (GLMM)	z	p	z	p
PC1 residuals	-1.4	0.153	1.0	0.340
PC2 residuals	0.5	0.628	0.6	0.522
PC3 residuals	2.2	<b>0.025</b>	-0.1	0.955
Richness (GLMM)				
PC1 residuals	-1.9	0.053	1.6	0.113
PC2 residuals	0.8	0.426	0.1	0.889
PC3 residuals	3.0	<b>0.003</b>	1.6	0.119

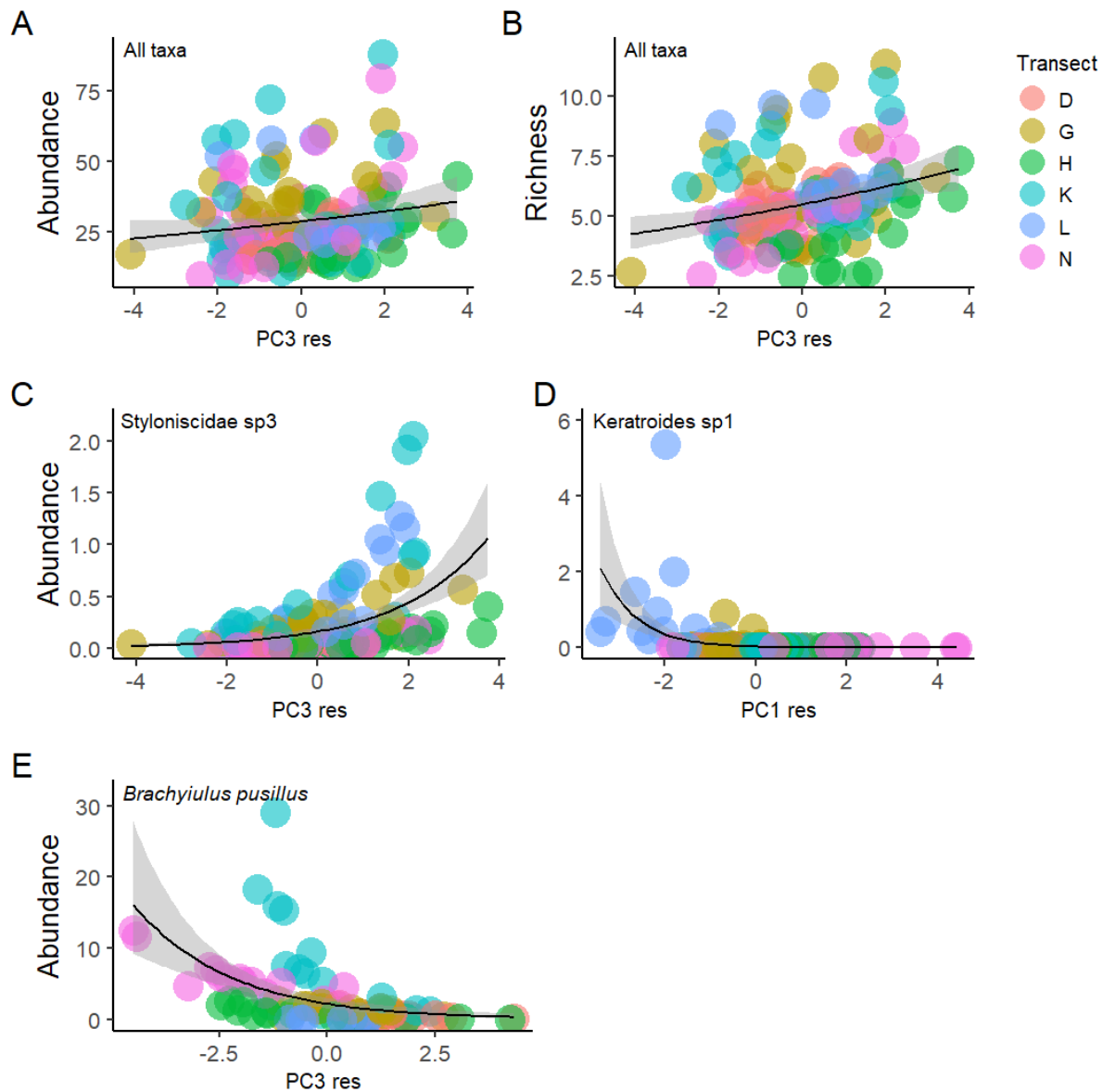


Figure 5. Fitted values from GLMM models for litter A) richness and B) abundance plotted against PCA residuals. Fitted values from manyglm models, plotted against PCA residuals for C) Styloniscidae sp. 3 and D) Keratroides sp. 1 from the litter detritivore community, and E) *Brachyiulus pusillus* from the log detritivore community. Regression lines  $\pm$  SE are included to aid visualisation.

### 3. Does the activity of the detritivore community differ between night and day?

We found no difference in richness or abundance between day and night, for either litter or logs, and this held true for each season (Ch. 1 Appendix Fig 4, Table 4). In addition, manyglm results showed no difference in community composition according to time of day, and so no post-hoc tests were run (Ch. 1 Appendix Table 4). Inclusion of previously logged sites in the analyses did not affect these results.

### 4. How do detritivore communities vary among seasons?

Both the abundance and richness of litter detritivores differed across seasons, which was largely due to samples from one period (spring 2015) showing higher richness and abundance than all others (Ch. 1 Appendix Figure 5, Table 5). The results for summer 2015 were lower in litter detritivore richness than spring and autumn 2015 (Ch. 1 Appendix Figure 5, Table 5). However, in logs, neither abundance, nor richness varied across sampling periods (Ch. 1 Appendix Table 5). Inclusion of previously logged sites did not change the results for abundance or richness, or the litter community analysis. However, they were excluded from the log community analysis to avoid any possibility that our results were influenced by logging, as they changed marginally significant effects for year to marginally non-significant when excluded (Ch. 1 Appendix Tables 5, 6).

Multivariate analysis showed differences across seasons in both the litter and log communities (Ch. 1 Appendix Table 5). The litter community also differed across years, while the log community did not (although only one season (spring) was sampled across years for log invertebrates; Ch. 1 Appendix Table 5). Post-hoc analysis for litter seasons showed *Arcitalitrus sylvaticus*, *Brachyiulus pusillus* and unidentified/immature diplopods increased in abundance in spring relative to autumn and summer (Ch. 1 Appendix Figure 6), but could not attribute the yearly effect to any taxon. Post-hoc analysis of the log community could not attribute the effect of season to any taxon.

## Discussion

We found that some aspects of detritivore communities vary predictably in time or space, or in both. Firstly, the communities in litter and logs were substantially different (48% taxa significantly less abundant or absent in one microhabitat), despite overall high species overlap (70%), and this distinction was retained across time of day, season and year. Secondly, several environmental variables, including those related to climate, topography and microhabitat, influenced the detritivore community, but interestingly, their effects depended on microhabitat. Thirdly, we found no difference in the detritivore community between day and night; however, the litter detritivore community was more temporally variable (across season and year) than the log community (season only), which may be related to the greater temperature buffering in logs relative to litter. Together, these results indicate that temperature and detritus inputs are important environmental determinants of the detritivore community, but also highlight the importance of sampling across time scales and habitats to develop a clear understanding of the community.

### ***Litter and logs maintain distinct detritivore assemblages***

Microhabitats are critical determinants of invertebrate communities, and on land play a significant role in mitigating the extremes of climate allowing otherwise sensitive species to persist (Baudier et al., 2015; Cowling et al., 2004; González del Pliego et al., 2016; Scheffers et al., 2014). Despite much research showing the importance of microhabitats in freshwater invertebrate communities (e.g. Brooks et al., 2005), a corresponding interest in terrestrial systems is less common. We found that litter and logs supported distinct assemblages, and this result persisted across seasons, consistent with other studies (Lindsay and Cunningham, 2009; Ziesche and Roth, 2008). This difference may have been driven in part by dietary or morphological specialisation, since many

detritivores show preferences for particular forms of detritus and/or the microorganisms growing thereon, as currently documented most clearly in beetles and mites (Brückner et al., 2018; Garrick et al., 2019; Lassau et al., 2005; Wardle et al., 2004). However, physiology is also a deciding factor in microhabitat use. For example, Armadillidae sp. 1 and Porcellionidae sp. 1, which are considered desiccation tolerant, were most common in the litter, while the more moisture-sensitive Styloniscidae sp. 1 and Philosciidae sp. 1 were most abundant in the more stable temperatures (and likely humidity) of logs (Ch. 3; Cloudsley-Thompson, 1962; Dias et al., 2012; Edney, 1951; Edney, 1968; Green, 1974; Schmidt and Wägele, 2001). Although isopods are commonly thought to inhabit leaf litter, many species select other microhabitats, such as logs (Judd, 2004; Warburg, 1993). Our results suggest the greater thermal buffering provided by logs could partly explain such preferences.

The distribution of detritivores that we observed may reflect factors in addition to thermal buffering of detritivore habitats. Different microhabitats can provide different food sources, such as particular types of fungus, and competition for food or space can also explain microhabitat partitioning among species (Crawford, 1992; Enghoff, 1993; Maraun et al., 2003; O'Neill, 1967; Wolters and Ekschmitt, 1997). This may be the case for the four millipede morphospecies that were more abundant in logs (*Isocladosoma pallidulum*, Somethus sp. 1, Siphonotidae sp. 2, *Ommatoiulus moreletii*), and one that was more common in litter (Dalodesmidae sp. 1). This is because, although millipedes are usually more sensitive to desiccation than insects, humidity tolerance does not appear to play as strong a role as it does in isopods (Crawford, 1992; Sterzyńska et al., 2015). In addition, unidentified diplopods, which were predominately juveniles (pers. obs.), favoured the litter and were ~3 times more abundant in spring, suggesting the litter is a nursery environment, as the soil is for many millipede species (Golovatch and Kime, 2009). In the case of *O. moreletii*, an introduced species, its preference for logs may reflect the general lack of deep



litter (a habitat it occupies in its home range; Bailey, 1990), at our sites. Little specific information is available on Australian Diplopoda that might explain the habitat occupancy we observed, although the sucking mouthparts of Siphonotidae sp. 1 suggest specialised diet may drive habitat occupancy patterns in this species (Black, 1997). Overall, these results show that to adequately capture the detritivore community, surveying more than one microhabitat is necessary, and could be further improved by incorporating other habitats, such as moss and soil.

***Detritivore communities are driven by topography, and climate and microenvironmental gradients***

Ultimately, spatial distribution is driven by environmental factors that influence resource availability (Wardhaugh, 2014). Microclimate and forest structure were important for both litter and log detritivores. However, the litter community was more responsive to environmental variation than the log community, which may reflect higher decomposition rates of leaf litter relative to logs (Mackensen et al., 2003; Raison et al., 1986b). Specifically, litter detritivore abundance and richness increased with canopy cover and ground plant cover, but decreased with litter and understory cover. Other studies have found bulk density of litter to be positively correlated with detritivore biomass, but canopy loss with lower diversity (Blair et al., 1994; Richardson et al., 2018). We were able to attribute this response at the community level to one morphospecies, Styloniscidae sp. 3 (Isopoda), a small, relatively soft-bodied species. Styloniscidae are characteristic of wet forests and found in very humid conditions, due to their branchial respiration and inability to conglobate (roll into a ball; Green, 1974). They are thus likely to depend heavily on microhabitat for shelter, which raises the question as to why they declined with increasing litter cover. An explanation is that greater canopy cover is associated with more mature forest, in this case, a longer time since burning, and so they may be responding to litter

decomposition stage rather than litter cover (Birk and Bridges, 1989). Temperature also affected the litter community, with *Keratroides* sp. 1 (Amphipoda) declining with increasing average temperature, consistent with evidence that amphipod activity and spatial distribution is limited by temperature, in part because it affects water-loss (Cowling et al., 2003; Lazo-Wasem, 1984; Morritt, 1987; Walsh et al., 1994).

Somewhat surprisingly, abundance and richness of log detritivores did not change with any environmental variables. This may be due to logs being so well buffered from climatic changes that other factors are not especially important. Also, no log characteristics affected the log community, although it did respond to forest structure variables, which could affect log characteristics indirectly. In particular, the introduced millipede *Brachyiulus pusillus* declined with the number of trees when collected from logs, but increased with understory cover (associated with severe burning) and slope (steeper slopes denuded of ground plants by fire showed clear evidence of erosion and litter movement, even eight years after burning relative to flatter sites, per. obs.), which appears to be consistent with its preference for more disturbed sites (Mesibov, 2000), since leaf litter tended to be washed down steeper sites and not retained (pers. obs.). This may indicate that some macroinvertebrate detritivores use logs opportunistically for shelter (Boer, 1961; Dangerfield and Hassall, 1994), and thus respond to variables that are more likely to directly affect litter than logs. Taken together, our results show that temperature, litter quality, and aspects of forest structure that likely affect the amount and quality of detritus, are important predictors of the detritivore community.

### ***Detritivore assemblages did not differ between day and night***

Detritivorous taxa, including Collembola, Diplopoda, Amphipoda, Isopoda, are often nocturnal and move more at night (Frampton et al., 2001; Friend, 1981; Friend, 1986; Griffin and Bull, 1995; Smith and Larimer, 1979; Tuf et al., 2006). The level of nocturnal activity has been related to desiccation tolerance in isopods (Boer, 1961; Cloudsley-Thompson, 1956) and might be similar for amphipods (Friend and Richardson, 1977). Similarly, millipedes can be harder to find at night, because they are more easily located in shelters during the day, while being dispersed over the ground at night (Mesibov, 1998). Despite this evidence and contrary to our predictions, time of day did not affect the number of invertebrates detected in either litter or log habitats. Instead, our results indicate that detritivores display high microhabitat fidelity over a 24-hour period, meaning day sampling is sufficient to capture detritivore diversity. Generally speaking, these detritivores did not appear to be occupying other microhabitats, such as the soil or logs, during the day and emerging to the litter/soil surface at night, as has been recorded for other detritivorous taxa (Friend and Richardson, 1977; Friend, 1986; Paris, 1963; Walker et al., 2009). This result may be partly due to some litter taxa being found on the outside of logs during log sampling, which may explain the high species overlap between the two habitats. However, 48% of flightless taxa (diplopods, amphipods and isopods) were clearly associated with one habitat regardless of time of day. The lack of movement suggests that either there is no need for detritivores to move beyond the habitat that they currently occupy, or that taxa with no clear preference, the microhabitats are at equilibrium, where immigrants are matched by emigrants.

### ***Litter assemblages were more seasonably variable than log assemblages***

Invertebrate communities are almost always highly seasonal, in large part because they follow changing temporal patterns of resource availability (Wardhaugh, 2014). In our study, abundance

and richness of litter detritivores was similar across most seasons, except when they were both significantly higher in spring 2015, and richness slightly lower in summer 2015, while log-dwelling detritivores showed no such difference. This suggests that capturing temporal variation is more important when studying the litter community than the log community. We considered the possibility that higher temporal variation in the litter community relative to the log community was influenced by the inclusion of Lepidoptera in the litter community, which contains many species with a strong seasonal life cycle, but post-hoc analysis did not support this explanation. Rather, the higher litter detritivore variation mirrors the greater thermal variation in litter relative to logs, and it is likely that humidity also displays the same pattern (Geiger et al., 1995). Because the litter community appears more variable across time, it may benefit from supplements from the more temporally stable log community. A similar study has suggested preserving litter adjacent to logs in areas that experience frequent burning may conserve ant biodiversity (Andrew et al., 2000). Our study has implications for overall detritivore community robustness: since logs harbour many species found in the litter (though not all), they may act as a source population for the litter, meaning they may become particularly important following disturbances.

The relatively high abundance and richness of litter detritivores in spring 2015 is challenging to explain. Rainfall was below average in winter and spring 2015, while temperatures were colder in winter and higher in spring (Bureau of Meteorology, 2015a; Bureau of Meteorology, 2015b), so the increase in richness and abundance does not match the general preference associations with humid environments and low thermal tolerance exhibited by the detritivores studied here (Ch. 3). Our initial prediction that autumn and spring, being the most climatically similar seasons of the year in this temperate system, were the least likely to show differences in community was therefore unsupported. However, the slightly lower richness in summer does support our hypothesis, suggesting that climatic factors are more important in dryer months, which is

expected given general detritivore physiology. Part of the variation across seasons was due to the higher abundance of unidentified/immature Diplopoda in spring, which is consistent with evidence that much millipede egg hatching is seasonally dependant (David et al., 1999; Huynh and Veenstra, 2016). *Arcitalitrus sylvaticus* and *Brachyiulus pusillus* were also more abundant in litter in spring than autumn and summer, which could reflect life history features, such as seasonally dependent mortality or reproduction, or behaviour, such as retreat to refuges during summer. While these results suggest conditions favouring a population boom in 2015, subsequent analysis of environmental variables did not reveal anything markedly different from the other sampling periods (Ch. 1 Appendix, Table 7, Fig 7). Other, unmeasured environmental factors or population stochasticity may thus be responsible for the higher abundance in spring 2015.

## **Conclusion**

Overall, the detritivore community varied substantially at the spatial scale of microhabitat and the temporal scale of season, variation that appeared to be partly driven by microclimate and amount of detritus. Litter communities were more seasonally variable and more susceptible to environmental factors than the log community, which appears to be driven in part by greater thermal variation in the litter. The relative stability of the log community and despite significant overlap with the litter community suggests that log-associated detritivores are well positioned to take respond to favourable conditions in the litter. Movements between these habitats could stabilize the overall detritivore community despite to variation in climate and disturbance. In addition, our results clearly show that sampling only litter or logs, or only one season of the litter, is inadequate to describe the detritivore community and would miss important sources of variation. Further, Andrew et al. (2000) has shown retained log-associated litter microhabitats are likely to make significant contributions to ant biodiversity following prescribed burns. Our results suggest a similar possibility, that retaining logs could act as potential source populations for the litter, especially in the context of disturbance, since logs and associated habitats could be expected

to provide protection from the greater thermal variation relative to unburnt or uncut forest. Thus, we consider it would be worth investigating if logs do act as source populations for detritivores following logging and prescribed burns.

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## Chapter 1: Appendix

**Table 1.** Datasets used in analyses. Unless otherwise stated, the number of sample points (n) for each dataset is 30.

Analysis		Datasets
microhabitat*season		Spring 2015
		Autumn 2016
		Spring 2016
		Summer 2017 (n=6)
microhabitat*time of day		Spring 2015
		Autumn 2016
Litter		Logs
PC analysis	All sampling periods	Spring 2015
		Autumn 2016
		Spring 2016
		Summer 2017 (n=6)
Day/night	Summer 2015 (n=4)	Spring 2015 (n=12) Autumn 2016 (n=12)
	Autumn 2015 (n=7)	
	Spring 2015 (n=12)	
	Autumn 2016 (n=12)	
Season	All sampling periods	Spring 2015
		Autumn 2016
		Spring 2016
		Summer 2017 (n=6)

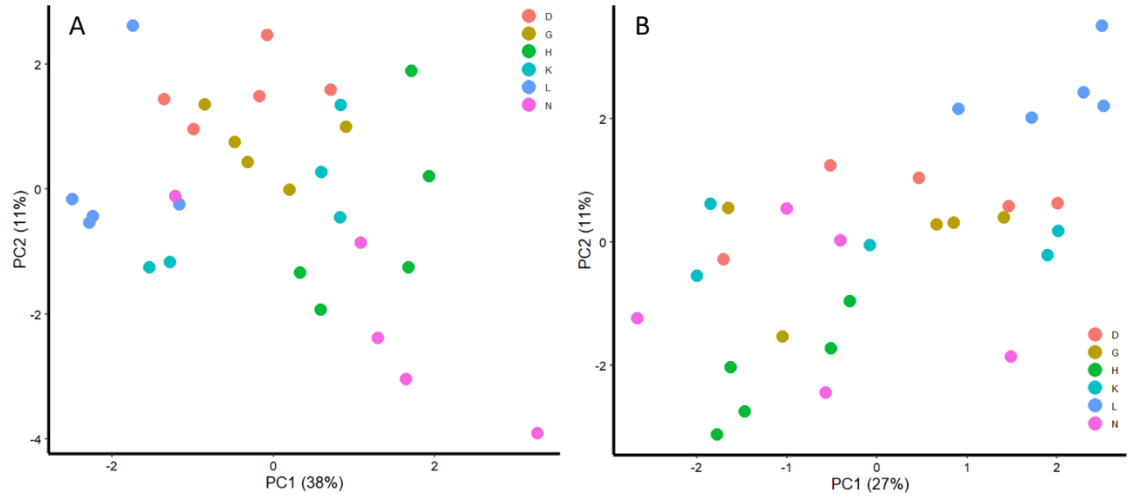
**Equation 1.** Equation used to calculate predicted potential annual direct radiation (PADIR) from McCune and Keon (2002), using latitude, slope and folded site aspect.

$$-1.236 + 1.350 * \cos(\text{Latitude}) * \cos(\text{slope}) - 1.376 * \cos(\text{folded aspect}) * \sin(\text{slope}) * \sin(\text{Latitude}) - 0.331 * \sin(\text{Latitude}) * \sin(\text{slope}) + 0.375 * \sin(\text{folded aspect}) * \sin(\text{slope})$$

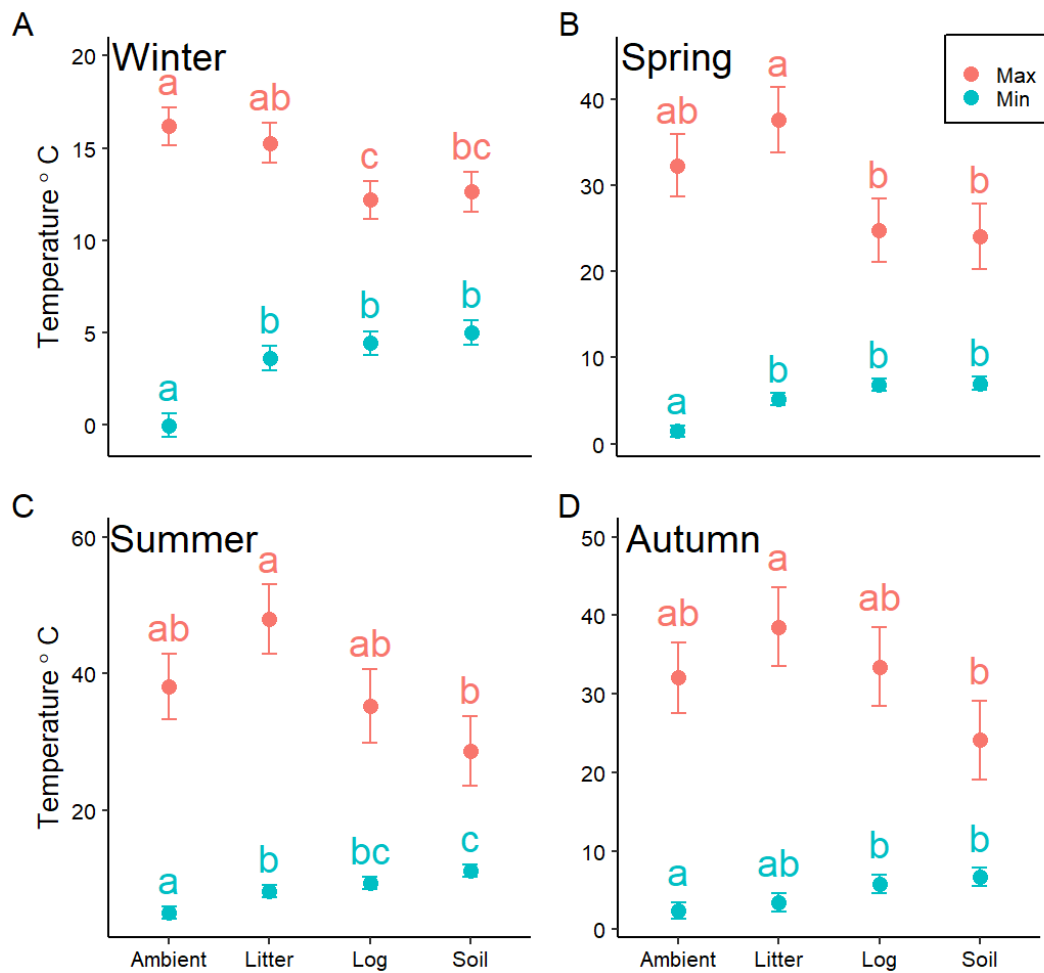
**Table 2.** Environmental variables included in litter and log PCA, with their contributions to each axis.

Variable	Litter			Log		
	PCA 1	PCA 2	PCA 3	PCA 1	PCA 2	PCA 3
Days <1°C	-0.11	0.19	-0.13	0.10	0.20	0.13
Days >35°C	0.25	0.13	-0.23	-0.28	0.09	0.07
Average day °C	<b>0.31</b>	0.08	0.01	<b>-0.32</b>	-0.03	0.09
Average night °C	<b>0.31</b>	0.04	0.07	<b>-0.32</b>	-0.03	0.05
Absolute max °C	0.25	0.12	<b>-0.31</b>	-0.06	-0.14	-0.13
Average max °C	0.25	0.12	<b>-0.31</b>	-0.27	0.05	0.00
Absolute min °C	0.24	-0.08	0.21	-0.19	-0.24	0.00
Days <20%RH	0.26	0.15	-0.13	-0.28	0.09	0.10
Days >95%RH	-0.26	0.10	-0.27	0.28	0.01	0.03
Average day %RH	<b>-0.30</b>	-0.04	-0.10	<b>0.30</b>	0.10	-0.13
Average night %RH	-0.28	0.08	-0.22	<b>0.30</b>	0.06	0.00
Average max %RH	-0.25	0.15	-0.24	0.28	0.01	0.06
Absolute min %RH	-0.25	-0.19	0.12	0.26	-0.17	-0.09
Alive trees	-0.07	<b>0.32</b>	0.29	0.07	0.21	0.26
Dead trees	0.00	<b>-0.34</b>	-0.04	0.01	0.14	<b>-0.34</b>
Log number	0.00	-0.12	<b>0.34</b>	-0.01	-0.02	-0.05
% Canopy cover	0.01	<b>0.34</b>	0.28	-0.05	-0.07	<b>0.36</b>
% Understory cover	-0.14	-0.24	-0.18	0.04	0.15	<b>-0.40</b>
% bare ground cover	0.17	-0.25	0.05	0.00	-0.25	-0.13
% ground plant cover	-0.02	-0.13	0.04	0.08	<b>-0.32</b>	0.00
% litter cover	-0.12	0.29	-0.07	-0.07	<b>0.41</b>	0.08
Litter depth	-0.07	0.08	0.09	-0.04	0.12	-0.04
Soil VWC	-0.22	-0.04	0.07	0.21	0.04	0.14
Altitude	-0.08	-0.02	0.27	0.08	<b>0.32</b>	-0.07
PADIR	0.03	-0.20	-0.22	-0.01	-0.03	-0.18
Slope	0.08	<b>-0.44</b>	-0.12	-0.08	-0.20	<b>-0.34</b>
Log burn severity				0.08	0.08	0.13
Log decomposition				-0.04	<b>0.31</b>	-0.17
Log length				0.12	-0.14	0.28
Log width				-0.08	0.29	0.03
Log volume				-0.04	0.09	0.06
Log length touching ground				0.11	-0.12	<b>0.31</b>
Log volume touching ground				-0.05	0.13	0.09

The litter PCAs 1, 2 and 3 explained 38%, 11% and 9% of the total variance respectively, while the log PCAs explained 27%, 11% and 9% respectively. Variables with a contribution >0.3 were considered important and are bolded.

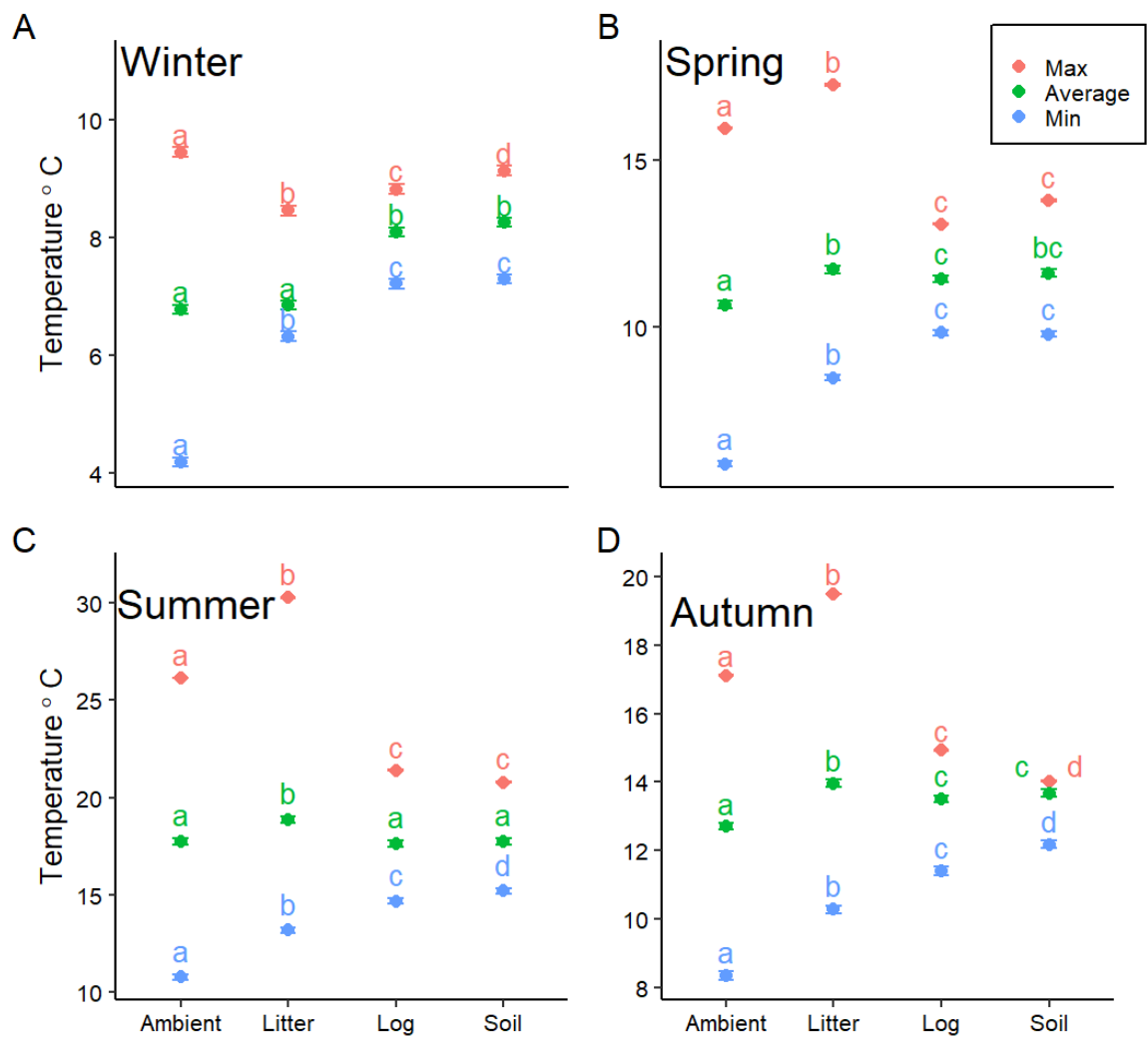


**Figure 1.** Plots of the first two principal components for A) litter and B) log environmental variables. Colour indicates transects.



**Figure 2.** Absolute maximum and minimum temperatures recorded for three microhabitats and ambient. Letters indicate results of pairwise comparisons within either maximum or minimum temperatures.





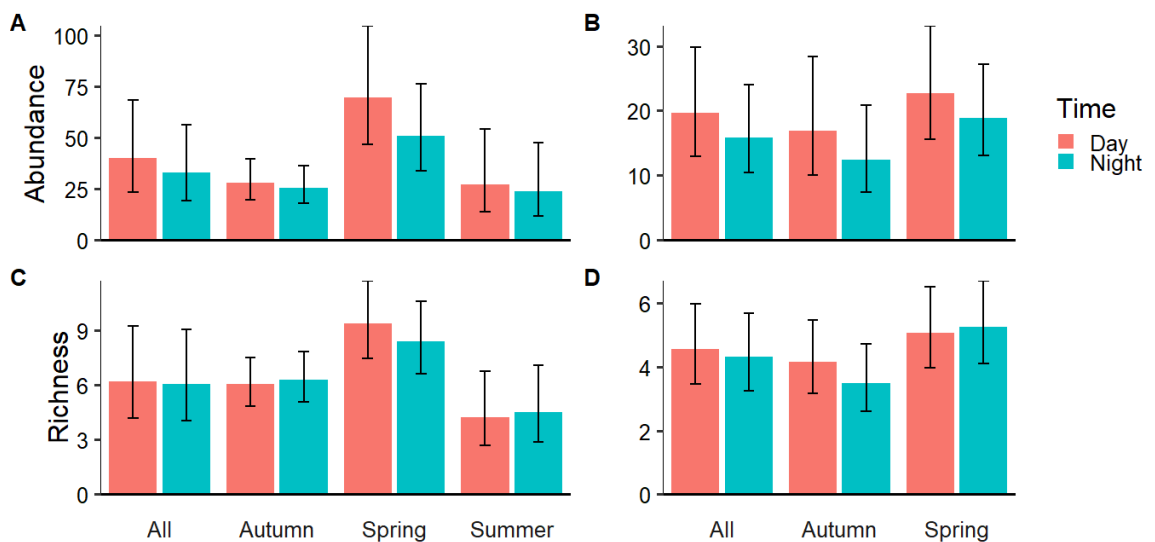
**Figure 3.** Maximum, minimum and average temperatures (model estimated values) recorded for three microhabitats and ambient in all four seasons. Error ( $\pm$ SE) is very small and barely visible. Letters and SE indicate results of pairwise comparisons within either maximum, minimum or average temperatures.

**Table 3.** Comparison of detritivore taxa found in litter and log habitats. P = present (grey cells), A = absent. Of the 33 total taxa, 70% (23) were found in both habitats.

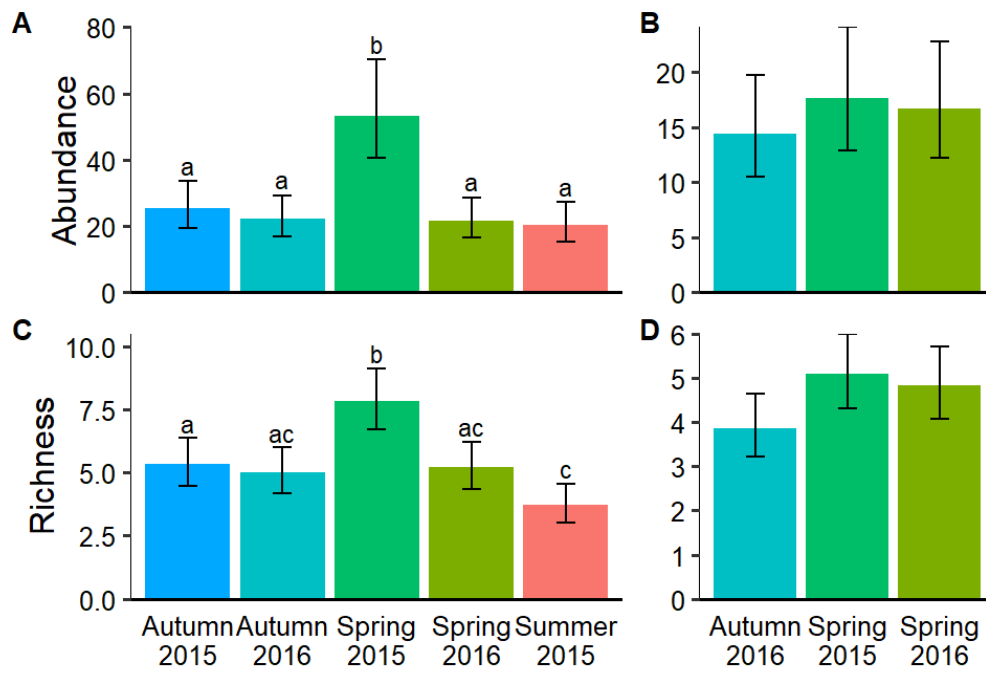
Taxa	Logs	Litter
<b>Amphipoda</b>		
Amphipoda unknown	P	P
Amphipoda sp. 1	P	P
<i>Arcitalitrus</i> sp. 1	P	P
<i>Arcitalitrus sylvaticus</i>	P	P
<i>Keratroides</i> sp. 1	P	P
<b>Diplopoda</b>		
Diplopoda unknown	A	P
Chordeumatida sp. 1	A	P
Polyxenida sp. 1	A	P
Polydesmida unknown	P	P
<i>Hoplatessara pugiona</i>	P	P
<i>Isocladosoma pallidulum</i>	P	P
<i>Paredrodesmus</i> sp. 1	P	P
<i>Somethus</i> sp. 1	P	P
<i>Pogonosternum laetificum</i>	P	P
Dalodesmidae sp. 1	A	P
Dalodesmidae	P	P
<i>Gephyrodesmus regilacus</i>	P	P
<i>Victoriocambala buffalensis</i>	P	P
Siphonotidae sp. 1	P	P
Siphonotidae sp. 2	P	A
<i>Ommatoiulus moreleti</i>	P	P
<i>Brachyiulus pusillus</i>	P	P
<b>Isopoda</b>		
Armadillidae unknown	A	P
Armadillidae sp. 1	P	P
Armadillidae sp. 2	P	P
Porcellionidae sp. 1	P	P
Philosciidae sp. 1	P	P
Philosciidae sp. 2	P	A
Styloniscidae unknown	A	P
Styloniscidae sp. 1	P	P
Styloniscidae sp. 2	P	A
Styloniscidae sp. 3	P	P
Styloniscidae sp. 4	P	A
Total unique taxa	4	6
% unique taxa	12	18

**Table 4.** GLMM results comparing detritivore richness and abundance between day and night in two microhabitats, overall and within seasons. Season and site were included as a random effects in GLMM models. Manyglm results comparing detritivore communities between day and night in two microhabitats, overall and within seasons. Site, year and season were included to account for spatial-temporal variation in manyglm. Significant p-values are in bold.

Micro-habitat	Analysis	Response	Predictor	All		Spring		Autumn		Summer	
				D/z	p	D/z	p	D/z	p	D/z	p
Litter	GLMM	Abundance	Day/Night	-1.5	0.144	-1.6	0.117	-0.5	0.636	-0.5	0.593
	GLMM	Richness	Day/Night	-0.3	0.785	-0.8	0.416	0.3	0.746	0.2	0.862
	manyglm	Composition	Day/Night	33.6	0.505	38.5	0.233	16.67	0.933	20.6	0.267
		Fixed factors	Site	417.7	<b>0.001</b>	283.1	<b>0.003</b>	307.4	<b>0.001</b>	42.8	<b>0.014</b>
		Fixed factors	Year	205.3	<b>0.001</b>			47.2	0.063		
		Fixed factors	Season	42.5	0.142						
Log	GLMM	Abundance	Day/Night	-1.3	0.202	-0.8	0.422	-1.4	0.170	NA	
	GLMM	Richness	Day/Night	-0.4	0.682	0.2	0.957	-0.8	0.396	NA	
	manyglm	Composition	Day/Night	25.8	0.526	34.1	0.142	18.6	0.623	NA	
		Fixed factors	Site	325.6	<b>0.001</b>	98.0	<b>0.003</b>	209.3	<b>0.001</b>		
		Fixed factors	Year	88.0	<b>0.001</b>						



**Figure 4.** Estimated marginal means  $\pm$  95% confidence intervals obtained from general linear mixed models, for detritivore abundance in A) litter and B) logs, and for richness in C) litter and D) logs, overall and for each season. Red bars indicate day, teal indicates night.



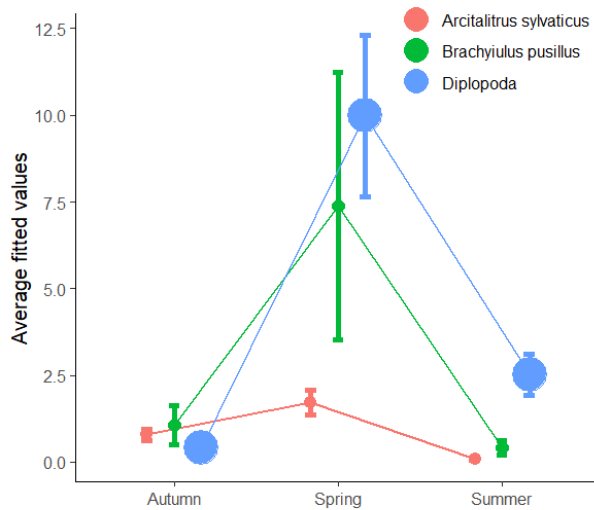
**Figure 5.** Abundance  $\pm$ SE for A) litter and B) log detritivores, and richness  $\pm$ SE for C) litter and D) log detritivores, across sampling periods

**Table 5.** Generalised linear mixed model results comparing abundance and richness of detritivores from two microhabitats between different sampling periods, with site as a random effect. Manyglm community results compare differences in seasons and years for both litter and log detritivore communities, with site as a fixed effect to control for spatial variation. Significant p-values are in bold, while daggers indicate where community results could be attributed to specific taxa. Sampling period refers to unique season/year periods.

Microhabitat	Response	Predictor	D/z	p
<b>Litter</b>	Abundance	Sampling period	39.7 <sub>4</sub>	<b>&lt;0.001</b>
	Richness	Sampling period	49.6 <sub>4</sub>	<b>&lt;0.001</b>
	Composition	Season	216.8	<b>0.001†</b>
		Year	84.4	<b>0.001</b>
		Site	491.8	<b>0.001</b>
<b>Log</b>	Abundance	Sampling period	2.9 <sub>2</sub>	0.238
	Richness	Sampling period	5.5 <sub>2</sub>	0.063
	Composition	Season	60.7	<b>0.003</b>
		Year	41.7	0.059
		Site	383.9	<b>0.001</b>

**Table 6.** Manyglm community results comparing differences in seasons for log detritivore communities including logged sites. Site was included as a fixed effect to control for spatial variation.

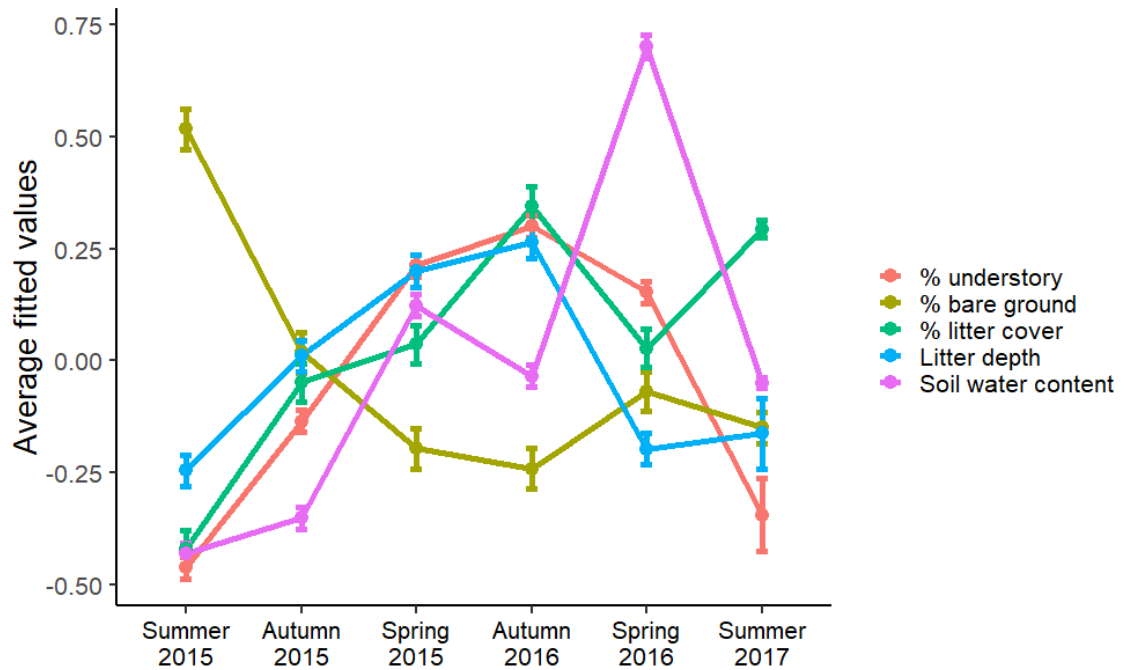
Response	Predictor	D/z	p
Composition	Season	64.7	<b>0.001</b>
	Year	46.5	<b>0.027</b>
Fixed effect	Site	419.8	<b>0.001</b>



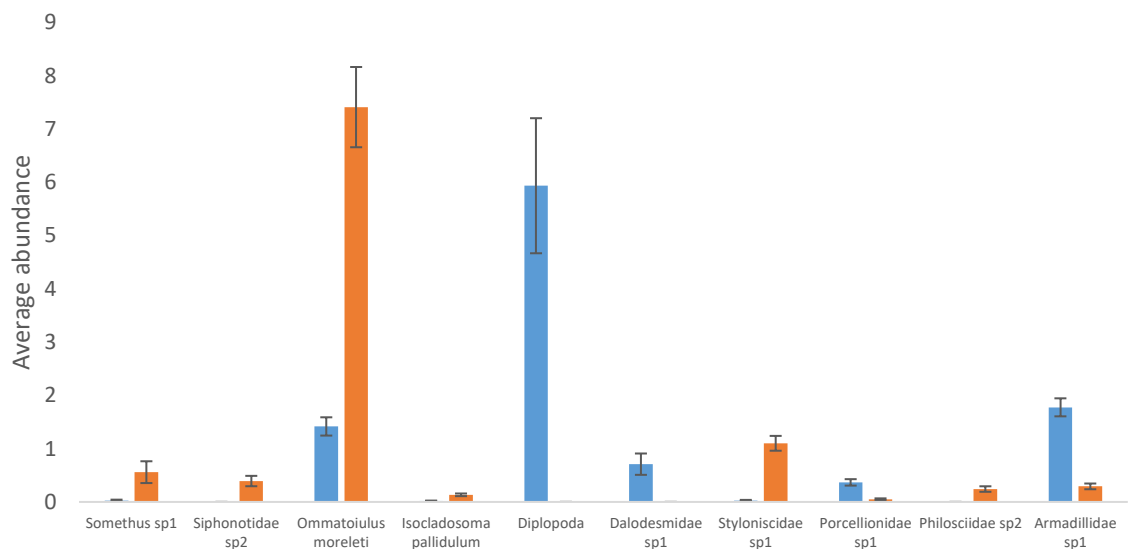
**Figure 6.** Litter detritivore taxa showing significant variation with season in manyglm post-hoc tests adjusted for multiple comparisons (i.e.,  $p \leq 0.001$ ). Mean predicted values  $\pm$ SE were obtained from manyglm models by averaging across years then sites.

**Table 7.** Manylm results testing if environmental variables differed according to sampling period. Daggers indicate effects could be attributed to particular variables. Logged sites had no effect on these results.

Terms	F	p
Sampling period	98.1	<0.001†
Site (covariate)	220.1	<0.001



**Figure 7.** Environmental variables that differed significantly by sampling periods, according to post-hoc results from manylm. Logged sites had no effect on these results. Values are model average fitted values  $\pm$  standard error.



**Figure 8.** Average abundance  $\pm$  SE of detritivore taxa that were significantly higher in abundance in one microhabitat (blue = litter, orange = logs) than another across all seasons. Diplopoda refers to immature/unidentified Diplopods.

**Table 8.** Results of manylm analysis testing the difference in abiotic variables between burnt and unburnt sites, for variables measured for two microhabitats. ANOVA tests of the manylm models were run with 9999 permutations, and season, year and sampling point as fixed factors. Post-hoc results indicate whether variables were higher or lower in burnt sites relative to unburnt sites. Significant p-values are in bold.

Variable	Litter			Log		
	Df	F	p	Df	F	p
<b>Burning</b>	(1, 139)	282.4	<b>&lt;0.001</b>	(1, 85)	20.5	<b>0.029</b>
<b>Season</b>	(2, 137)	2905.7	<b>&lt;0.001</b>	(2, 83)	35.2	<b>0.001</b>
<b>Year</b>	(2, 135)	56.9	<b>0.008</b>	(2, 81)	116.8	<b>&lt;0.001</b>
<b>Site</b>	(5, 130)	655.9	<b>&lt;0.001</b>	(5, 77)	12.9	<b>0.014</b>
<b>Post hoc results</b>						
	F	Lower	Higher	Summary	Lower	Higher
<b>Burning</b>	282.4	Canopy *** Live trees * Log number *	Understory *** Dead trees *** Altitude *	20.5		Log burn severity ** Log decomposition *

p =\* <0.05 \*\*<0.01 \*\*\* <0.001



## Chapter 2: Does microhabitat determine the impact of prescribed burning on invertebrate detritivores?

Authors: J. Grubb, H. Gibb and N. Murphy

### Abstract

Prescribed burns are widely used in landscape management to protect assets, enhance primary production and promote conservation around the globe. However, invertebrate detritivores, which influence decomposition and thus affect fuel loads and fire regimes, are vulnerable to anthropogenic fire regimes. The diverse range of microhabitats occupied by these animals offer differing levels of protection from fire, and thus effects of prescribed burns on this community should be microhabitat dependent. We tested this hypothesis by comparing the detritivore community across three microhabitats (leaf litter, soil and logs) before and after five prescribed hazard reduction burns in *Eucalyptus* forest in south-eastern Australia. The effects of prescribed burning were microhabitat-dependent, with the greatest losses of detritivores in the leaf litter, consistent with the reduction of litter habitat after burning. Following burning, abundance increased in the soil, independent of depth, relative to unburnt control sites, possibly because soil provided the most thermally buffered microhabitat. Within burnt sites, increasing burn area and severity reduced the abundance of detritivores across all microhabitats studied and also reduced richness in both the litter and soil. For logs, detritivore abundance depended on an interaction between ground and log burn severity, and indicated that invertebrates move into logs under severe burns, but not other conditions. We suggest that reducing burn severity and increasing the likelihood of logs surviving prescribed burns will conserve the detritivore community in this ecosystem.

## Introduction

Without fire, the global map of ecosystems would be extensively redrawn as burns are integral to the functioning of many ecosystems (Bond et al., 2005). In fact, fire-adapted plants and animals usually dominate ecosystems that regularly experience fire. Such adaptations include re-sprouting and both above- and below-ground seed banks in plants (Bond and Keeley, 2005), and specialisations for food or habitat that develops post-fire in both vertebrate and invertebrate animals (Hutto et al., 2008; Saint-Germain et al., 2007; Santos et al., 2014). Significant risk for human assets in fire-prone ecosystems, including grasslands and forests, have led to fire suppression in some parts of the world, and more recently, to prescribed burning to reduce the risk of fire (Fernandes and Botelho, 2003; Huntzinger, 2003). Prescribed burning is also undertaken for conservation outcomes, often inspired by the pyrodiversity-biodiversity hypothesis, which suggests that a mosaic of different fire histories will increase species diversity (Parr and Andersen, 2006). Similarly, since some plants rely on fire to release seeds or to remove dead plant biomass, fire can be used to rejuvenate an ecosystem and ensure its persistence (Brockway et al., 2002; Pausas et al., 2017). Thus, prescribed burning has become an important aspect of landscape management across the globe, for asset protection, agriculture, silviculture, conservation and meeting cultural objectives.

A significant concern about prescribed burning is that ecosystems and their species may not be adapted to anthropogenic fire regimes (Driscoll et al., 2010). For instance, natural fires usually occur during the hotter and dryer times of the year, while prescribed burns are often conducted during the cooler months of the year to reduce the chance of releasing unintentional wildfire (Brockway et al., 2002; Glitzenstein et al., 1995). Thus, species that have evolved strategies to survive dry-season fires may be more vulnerable to burns in other seasons (Glitzenstein et al.,

1995; New, 2014). One mechanism potentially driving such a result is that prescribed burns may promote greater penetration of heat into the soil because of their slower movement than do extreme wildfires, thus increasing soil-dwelling invertebrate mortality (Cane and Neff, 2011; Neary et al., 1999).

Invertebrate detritivores are a critically important in relation to fire since they explain up to 37% of decomposition rates and thus influence fuel loads in forests, in particular fine fuels (García-Palacios et al., 2013a; García-Palacios et al., 2013b; Gessner et al., 2010). Prescribed burns are primarily intended to reduce fine fuels, which is an important habitat and food source for invertebrate detritivores (Brennan et al., 2006; C. Brennan et al., 2009; Fernandes and Botelho, 2003; Morrison et al., 1996). If post-fire recovery of this community is negatively affected, consequences could include declines in decomposition and a subsequent increase in fuel loads (Brennan et al., 2009). This could create a negative feedback loop, increasing the chance and severity of fire (Balch et al., 2008; Brennan et al., 2009). Initially, prescribed burning reduces richness and abundance of ground-dwelling invertebrates and can slow decomposition rates in *Eucalyptus* forests, although numbers of many invertebrates may recover within three years (Abbott, 1984; Springett, 1976; Springett, 1979; York et al., 2012). Although some pyrophilic species may be favoured by fire and see increased population numbers (Whelan, 1995), many detritivores are desiccation-sensitive and flightless (David and Handa, 2010; Swengel, 2001), and these traits increase the vulnerability of invertebrate detritivores to fire (Moretti et al., 2006). Invertebrate detritivores tend to be active during the cooler months, while occupying refuges during the hotter months (Ch. 1), which would also increase their protection from fire in the dry season (David and Handa, 2010; Vasconcelos et al., 2009). Thus, burning out of season may lead to higher direct mortality by killing life stages not adapted to fire (Blanche et al., 2001).

Detritivores occupy a diverse range of microhabitats (such as logs, leaf litter and soil, as distinct from 'habitat' which is a more general description of an ecosystem), and some may offer more protection from fire than others. In addition, occupying more than one microhabitat may also increase the possibility of detritivores surviving *in situ* (Robinson et al., 2013). Refugia may be found in unexpected places; for example, Brennan et al. (2011) found some invertebrates survived fire temperatures exceeding 500°C by sheltering inside experimentally burnt grass trees (*Xanthorrhoea preissii*). Similarly, soil provides very good insulation from heat, likely making it an important refuge. For example, temperatures 5 cm below the surface may not exceed 45°C, while those on the soil surface exceed 700°C during a prescribed burn (Raison et al., 1986). Invertebrates buried deeper in the soil can survive impacts of fire due to this insulating effect (Wikars and Schimmel, 2001). However, as above, slower moving burns can reduce the effectiveness of soil as a refuge, since they can transfer more heat to the soil if there is a moderate to heavy fuel load (Certini, 2005; Neary et al., 1999). Nonetheless, soil-dwelling taxa are not always resilient to fires, e.g., burrow-dwelling mygalomorphs can be eliminated by low-intensity prescribed fire and its aftermath (Mason et al., 2018). Fire severity and intensity, as well as burn patchiness, therefore play a key role in determining the distribution of refuges for various faunal elements (Robinson et al., 2014). In the case of flightless invertebrates, such small-scale variation in burn severity is likely to be critical for *in situ* survival. Thus, a key consideration for determining the impact of fire on detritivores is their microhabitat occupancy and potential to occupy refuges (Robinson et al., 2013).

In this study, we tested the immediate impacts of prescribed burning on the detritivore community, with a particular emphasis on their pre- and post-fire distribution across three microhabitats. We hypothesised that, compared with control sites, those experiencing prescribed burns would experience: 1) greater loss of litter habitat; 2) reduced detritivore richness and

abundance associated with altered community composition; and 3) that effects would be mediated by microhabitat, with detritivore losses decreasing along a gradient of litter to logs to soil. We further predicted that: 4) logs and soil would gain taxa after prescribed burns, while the litter would lose taxa; and 5) increasing burn area and severity would increase the negative effects on detritivore richness and abundance, and drive greater community change across all microhabitats.

## Methods

### Sites

This study was conducted in south-eastern Australia, ~60 km north-east of Melbourne (Ch. 2 Appendix Figure 1), at sites ranging from 311 m to 590 m (Ch. 2 Appendix Table 1). Sites were in dry sclerophyll open forest, dominated by *Eucalyptus spp*, with an understory of Austral bracken (*Pteridium esculentum*) and *Acacia spp*.

Prescribed burns were conducted at five sites between the 29<sup>th</sup> of March and 13<sup>th</sup> of April 2016, and the 3<sup>rd</sup> of April and 22<sup>nd</sup> of April 2018. To determine how detritivorous invertebrates responded to prescribed burning, we used a before-after control-impact study design. Prior to burning at each site, we selected two similar plots, an unburned control and a treatment plot upon which the prescribed burn was conducted. Control plots were located in similar vegetation within 500 m of the burn treatment plots. Burns were ignited by the Department of Environment, Land, Water and Planning by perimeter lighting with a drip torch from the windward side of the plot. Burns were lit in the morning and allowed to proceed within the prescribed area until they burnt out. Transects were located near ignition points to ensure they would be at least partially burnt.

### Invertebrate sampling

Detritivorous invertebrates were collected from three microhabitats: leaf litter, soil and logs. Sampling of litter and logs used methods previously established in Chapter 1 as reliable indicators of the detritivore community. Samples were taken 1-7 days before burn ignition and 7-37 days afterward (maximum time between pre and post samples was 38 days), depending on when site access was deemed safe. A 100 m transect of ten equally spaced sample points was marked at each control and treatment site prior to the burn and revisited after the burn. Leaf litter and soil core samples were taken every ten metres along this transect. Litter was collected using a 625 cm<sup>2</sup> quadrat, selecting the nearest unbroken patch of litter to the transect sample point and collected down to the mineral soil. Soil cores (AMS soil corer, width 8.3 cm) were collected to a depth of 12 cm, and split into two samples, one containing the top and the other the bottom 6 cm of soil. Samples were transported in plastic bags and stored in a cool room (~4°C) prior to invertebrate extraction. Due to the limited number of funnels, sample extraction was staggered over several weeks. Invertebrates were extracted from the litter and soil core samples with Tullgren funnels. Litter was left in the Tullgren funnels for at least four days, and soil for at least two days. If samples were damp at the end of this time, they were left in until dry.

Due to the small number of samples (n=10/site) and sites (n=5), a blocking approach was used to ensure sampling reflected the extent of burning at a site rather than random placement of the quadrat. The ground sampled pre-burn was not resampled post-burn. After burning, if the area within 1 m of a transect point was <10% or >90% burnt (visual estimate), a single litter or soil sample was taken and scored as either burnt or unburnt. If the area within 1m at a transect sample point was between 10-90% burnt, two samples were taken, one from burnt and one from unburnt litter or soil. Burn area was calculated for the entire transect by averaging visual estimates of the proportion of burnt ground for all transect sample points. The number of burnt and unburnt

samples included in analysis was then set to reflect average burn area of the transect. The ten samples were filled first from transect points with one sample, then by randomly choosing one sample from the transect points with two samples. For example, if 51% area was burnt, five burnt and five unburnt samples were required; if 3 transect points were singletons all classed as 'burnt', the remaining seven transect points all had two samples each (one burnt, one unburnt) and from these, two burnt samples and five unburnt samples were randomly selected, one from each transect point (sample breakdown provided in Ch. 2 Appendix, Table 2).

Log searches were used to determine the distribution of fourteen detritivore morphospecies from 3 distinct flightless taxa (Diplopoda, Amphipoda and Isopoda) at all sites. These taxa were selected as they are abundant macro-arthropod detritivores at our sites (Ch. 1). Taxonomic experts were consulted for Diplopoda (Robert Mesibov) and keys used for Amphipoda and Isopoda included (Friend, 1987; Green, 1961; Green, 1974). Logs >9 cm diameter were selected by walking haphazardly through the plots within 200m of the transect and then searched by rolling and/or dissecting a section apart (usually 30-60 cm), by hand and the assistance of a hammer and small crowbar. Some logs were unable to be searched, as they were too large to be rolled or the wood too solid to be pulled apart, though it was often possible to search under bark. This method was considered appropriate for the target taxa, since they were not borers capable of occupying solid wood requiring a rearing/extraction approach, but instead occupied decayed wood and existing holes/cracks. When thorough searching of visible surfaces failed to yield additional specimens, the next log was searched, until 30 minutes had elapsed (time included searching for logs and collecting invertebrates from logs; time spent labelling was excluded). Specimens from logs were collected directly into 100% ethanol. It is likely that some logs were resampled postburn since it was not possible to reliably relocate logs after burning, however, since our sampling method did not exhaustively sample or destroy logs, this was not considered a major confounding factor. Since

logs were highly visible at our sites, our ability to locate logs was treated as a function of log density, and thus abundance could be standardised as individuals per unit time per site.

#### Environmental variables

We measured ground cover and burn severity, and assessed decomposition state, burn severity and size of logs at each site. Within a 1 m radius, litter, plant and bare ground cover were visually estimated at each transect sample point. Litter depth (carpenter's square) and soil volumetric water content (Fieldscout TDR 100 soil moisture meter probe, Spectrum Technologies, USA; ThetaProbe, ML2x, Delta-T Devices, England) was also measured at three haphazard points within the litter sample quadrat.

Burn severity of ground cover was estimated within 1 m around each transect sampling point on a scale of one to three: 1) where organic matter (especially leaves) was scorched but still retained its shape and was not completely black; 2) where organic matter was completely blackened and lacked a discernible shape; and 3) where it was completely combusted, as indicated by white ash and/or visible mineral earth. The percent of ground in each severity category was then visually estimated, and summed to determine the overall percent area burnt.

The following measurements were taken during log surveys, although some logs that did not contain invertebrates were not measured pre-burn, due to time restrictions. Decomposition was estimated according to Lindenmayer et al. (1999), where freshly fallen logs = 1, solid log without bark = 2, sapwood decomposing = 3, entire log decomposing, but still retaining shape = 4, and completely disintegrated logs with no discernible shape = 5. Burn severity of logs was estimated on a similar scale, where 0 = unburned, 1 = patchy burning, where severe burning and unburnt portions were evident on the same log, and 2 = entirely blackened. We used log radius and length



with the equation for cylinder volume ( $V=\pi*r^2*length$ ) to calculate log volume; values were halved for laterally split log fragments.

### Analysis

Generalised linear mixed models, with site as a random factor and assuming a Gaussian distribution (where residuals plots were not a random cloud, a beta distribution was assumed for proportional data, or Gamma with a log link for continuous data), were used to determine if any of the environmental variables measured were affected by burning. These were followed by pairwise comparisons of estimated marginal means, to determine if habitat characteristics of control and treatment sites differed before and after fire. To visualise the difference between treatments, a principal components analysis (PCA) plot of abiotic variables was created, after first scaling all variables by two standard deviations (princomp, R base 'stats' package). The area burnt, along with the proportion of each burn severity was also plotted for each prescribed burn. Manylm was used to determine if burn area, ground severity or log burn severity affected abiotic variables at sites that were burnt (ANOVA parameters: 99999 permutations, resampling method "perm.resid", unadjusted p-values and cor.type="R"; all variables scaled by two standard deviations; Gelman, 2008; Wang et al., 2012). Because there was no overall difference in log measurements depending on whether they contained invertebrates (Ch. 2 Appendix, Table 3), all logs were included in further analysis.

To test if abundance and richness changed after fire, we applied generalised linear models based on the negative binomial distribution with site as a random factor, to both the overall community and to each microhabitat. Estimated marginal means were used to conduct pairwise post-hoc comparisons between treatments. We tested if litter volume (estimated as litter depth\*quadrat area) was correlated with abundance and richness using linear mixed models (negative binomial distribution) with treatment\*time nested within site as the random effect. To determine if the

communities were altered by burning, we used manyglm analysis (blocked by site; ANOVA parameters: 999 permutations, resampling method "pit.trap" and unadjusted p-values), followed by post-hoc pairwise comparisons (for taxa and for fixed effects) in cases where the main effects were significant (Wang et al., 2014; Wang et al., 2012). Generalised linear mixed models, with site as a random factor, and estimated marginal means, were used to determine if abundance and richness were affected by the interaction of depth of sample and burning treatment. To determine if the soil community was affected by an interaction of depth and burning, we used manyglm (blocked by site; ANOVA parameters: 999 permutations, resampling method "pit.trap" and unadjusted p-values). Due to sample size limitations, a full three-way interaction of depth\*time\*treatment could not be tested, so analyses of richness, abundance and community were split into two models, one for pre-burn, the other for post-burn samples. For all manyglm analyses in this study, p-values were unadjusted for multiple comparisons, as this was considered overly conservative (e.g. García, 2004), and instead  $\alpha \leq 0.001$  was used to establish significance for all post-hoc univariate manyglm results.

To determine if prescribed burns affected the proportion of species that were lost or gained, or that persisted (while being lost from control plots) or that were unaffected by fire, 95% confidence intervals were calculated using the modified Jeffreys method for proportional data (Dean and Pagano, 2015). Proportions were considered significant if the confidence intervals did not include zero. Taxa were classified by their presence or absence at sites, before and after burning, as per Table 1.

*Table 1.* Method for classifying a taxon's response to burning. Ticks indicate presence, crosses indicate absence at control and treatment sites, before and after burning.

Response	Pre-burn		Post-burn	
	Control	Treatment	Control	Treatment
Loss	✓	✓	✓	✗
Gain	✗	✗	✗	✓
Persisted	✓	✓	✗	✓
Unaffected	✓	✓	✓	✓
Seasonal	✓	✓	✗	✗
	✗	✗	✓	✓
Other	All other combinations			

Using only post-burn samples, we tested if burn severity variables affected the detritivore community in each microhabitat. First, we checked for correlations between the three measures of burn severity: burn area, ground burn severity and log burn severity. If there was a significant correlation with a correlation coefficient of  $>0.8$ , we used the residuals of one variable, obtained from a general linear model in analysis. For the log analysis, ground severity residuals were obtained from a model using a gamma distribution with log link, and zero values were replaced with 0.004 (the next-lowest value) using burn area as the predictor. To determine the effect on abundance and richness, general linear models based on a negative binomial distribution were employed, with sample nested within site as a random effect. In addition, we used `manyglm` to determine the effect of the burn severity variables on the detritivore community for each microhabitat (permutations blocked by site; ANOVA parameters: 999 permutations, resampling method "pit.trap" and unadjusted p-values).

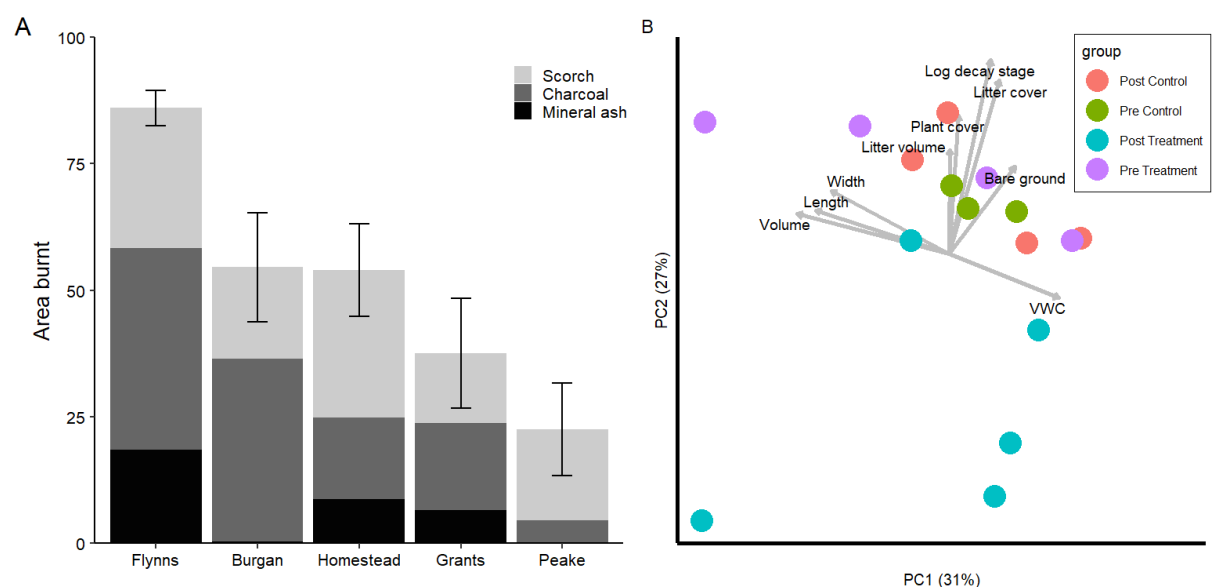
Both the glm and manyglm models included a three-way interaction term (burn area\*ground severity\*log severity) to calculate all possible model combinations of terms. A three-way interaction was not needed to determine if burn severity affected detritivores, but only to investigate if the three measurements of severity interacted. However, no models with a three way-interaction were retained due to limited degrees of freedom, meaning this potential hypothesis could not be tested. The models were then ranked by AIC values, using the dredge function in R for glm models (MuMin package; Barton, 2016) and manually for manyglm models. For glm models, we averaged across models to obtain model-averaged coefficients. Terms with confidence intervals (85% as per Arnold, 2010) including zero were dropped one at a time, first dropping interactions, then any fixed effects. GLM models were further elaborated by dropping non-significant terms. For manyglm models, and where the choice between glm models was still unclear, we chose the model within 4 AICs of the base model that eliminated uninformative parameters (Leroux, 2019), had a lower AIC or was simpler than the remaining models.

Overall abundance, richness and community composition was analysed at the site level, while microhabitats were analysed at the sample level. This meant that average log burn severity values for each site were used in litter and soil analysis, while average burn area and ground burn severity for each site were used for the log analysis. Where significant results were obtained, response variables were plotted against burn severity variables, except where random effects were included, and fitted values were plotted.

## Results

### How does prescribed burning alter habitat variables?

The area burnt by prescribed burns ranged from 23% to 86% (Fig. 2A), and a PCA plot of abiotic variables indicated that post-burn samples were distinct from all others (Fig. 2B). At burnt sites, increasing burn area was associated with increasing bare ground, and the loss of litter cover and volume (Table 2). In addition, ground plant cover, and litter cover and volume were reduced by burning (Ch. 2 Appendix Fig. 2 A, I & Tables 4, 5).



**Figure 2.** A) Percent of area burnt along each burn transect  $\pm$ SE, along with the area attributed to each burn severity (scorch, charcoal and mineral ash); B) principal components analysis of abiotic variables before and after burns (some points missing, due to access restrictions preventing data collection; VWC = soil Volumetric Water Content).

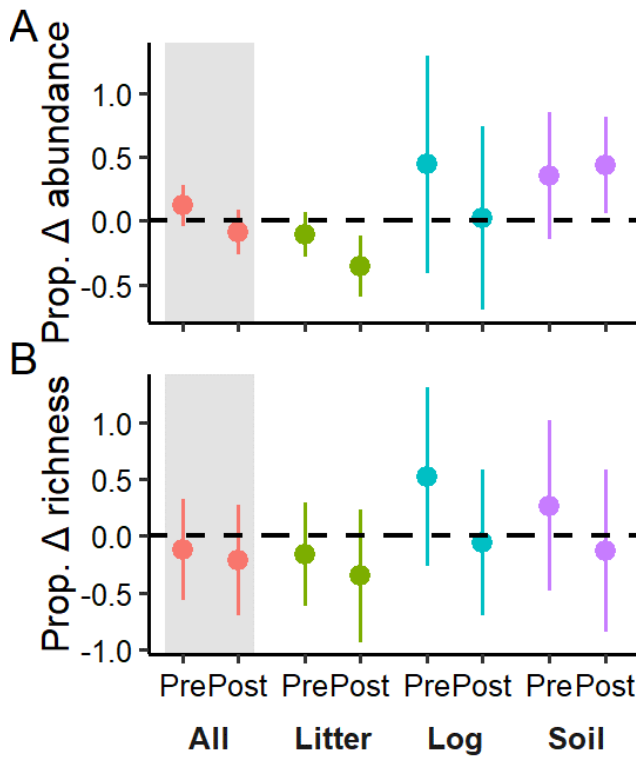
*Table 2.* Main effect and post-hoc pairwise comparison results of a manylm model, testing the effects of burn severity variables on environmental variables for burnt sites (residuals were used for ground and log severity). Significant p-values are in bold.

	Burn area		Ground severity		Log severity	
	F	p	F	p	F	p
Main effects	296.7	<b>0.033</b>	20.6	0.428	253.2	0.269
Pairwise comparison	Coef	p	Coef	p	Coef	p
Litter volume	-2.3	<b>0.016</b>	0.3	1.000	-0.1	0.951
Volumetric water content	-13.9	0.374	20.8	0.557	-4.2	0.050
Bare ground	3.0	<b>0.008</b>	-8.4	0.682	1.6	0.134
Ground plant cover	-8.9	0.111	16.5	0.268	-1.7	0.466
Litter cover	-1.2	<b>0.032</b>	-3.0	0.133	0.1	0.967
Log length	8.4	0.066	-10.5	0.625	2.2	0.416
Log width	2.3	0.631	3.2	0.092	1.4	0.292
Log volume	6.1	0.198	-4.3	0.109	2.0	0.142
Decomposition	1.0	0.177	-1.5	0.366	1.2	0.750

1) Do prescribed burns alter richness, abundance or community composition of detritivores, and are these effects mediated by microhabitat?

Based on comparison of estimated marginal means and splitting comparisons by time, the abundance of litter detritivores declined (average  $-35 \pm 12\%$ ) and soil detritivores increased (average  $44 \pm 37\%$ ) following burning (Fig. 3A; Ch. 2 Appendix Table 6). Aside from this, no change in abundance or richness was attributed to burning (Fig. 3A, B; Table 3). Litter volume was not correlated with abundance ( $\chi^2 = 0.6$ ,  $p = 0.46$ ) or richness ( $\chi^2 = 0.4$ ,  $p = 0.52$ ). Interaction between time and treatment was significant for the comparison over all microhabitats and for litter communities, but pairwise comparisons indicated a distinct post-burn community only in the litter (Table 3; Ch. 2 Appendix Table 7). We could not attribute these interactions to any particular

species based on post-hoc comparisons. In contrast, composition of the soil community was unaffected by burning (Table 4). There was no distinct difference in abundance or richness in the top or bottom of soil cores, relative to control samples, that could be attributed to burning (Table 4; Fig 4 A, B; Ch. 2 Appendix Table 8).



*Figure 3.* Estimated marginal means results showing the difference in A) detritivore abundance and B) richness between control and treatment sites, both before and after fire, for the entire community (grey band), and for three microhabitats. Points below zero indicate lower values at treatment sites, those above zero indicate values are higher at treatment sites. Error bars (95% confidence intervals) that cross zero indicate a significant difference between control and treatment sites.

*Table 3.* Generalised linear mixed models (abundance and richness) using site as a random factor and manyglm (community composition) analysis with site as a permutation blocking factor testing if unburnt sites differed from burnt sites before and after fire, for the overall detritivore community and three microhabitats. Significant p-values are in bold.

	All		Litter		Soil		Logs	
<b>Richness</b>	$\chi^2$	<b>p</b>	$\chi^2$	<b>p</b>	$\chi^2$	<b>p</b>	$\chi^2$	<b>p</b>
Treatment	1.0	0.329	1.7	0.197	<0.1	0.831	0.5	0.491
Time	3.1	0.078	9.9	<b>0.002</b>	0.1	0.787	0.1	0.737
Time*Treatment	0.1	0.776	0.2	0.626	0.6	0.452	1.2	0.269
<b>Abundance</b>								
Treatment	0.2	0.661	7.0	<b>0.008</b>	7.0	<b>0.008</b>	0.5	0.466
Time	16.4	<b>&lt;0.001</b>	72.4	<b>&lt;0.001</b>	9.4	<b>0.002</b>	4.5	<b>0.034</b>
Time*Treatment	3.0	0.084	2.6	0.105	0.1	0.797	0.5	0.465
<b>Community</b>	<b>Dev</b>	<b>p</b>	<b>Dev</b>	<b>p</b>	<b>Dev</b>	<b>p</b>	<b>Dev</b>	<b>p</b>
Treatment	61.5	<b>0.005</b>	44.5	<b>0.016</b>	11.6	0.775	48.1	<b>0.003</b>
Time	53.6	<b>0.014</b>	73.8	<b>0.001</b>	24.3	<b>0.049</b>	32.9	0.074
Time*Treatment	45.7	<b>0.008</b>	31.4	<b>0.034</b>	11.7	0.051	13.0	0.102

*Table 4.* Generalised linear mixed model and manyglm results testing the effect of treatment, depth and their interaction on soil detritivore abundance, richness and community composition for pre- and post-burn collections.

Time	Terms	Abundance		Richness		Community	
		$\chi^2$	<b>p</b>	$\chi^2$	<b>p</b>	Dev	<b>p</b>
Pre-burn	Treatment	0.1	0.755	0.4	0.539	12.7	0.256
	Depth	7.9	<b>0.005</b>	6.5	<b>0.011</b>	30.4	<b>0.009</b>
	Treatment*Depth	0.1	0.819	0.1	0.793	<0.1	0.700
Post-burn	Treatment	3.6	0.057	0.1	0.790	9.5	0.510
	Depth	8.6	<b>0.003</b>	1.9	0.165	20.2	<b>0.039</b>
	Treatment*Depth	6.8	<b>0.009</b>	1.8	0.185	3.0	0.323



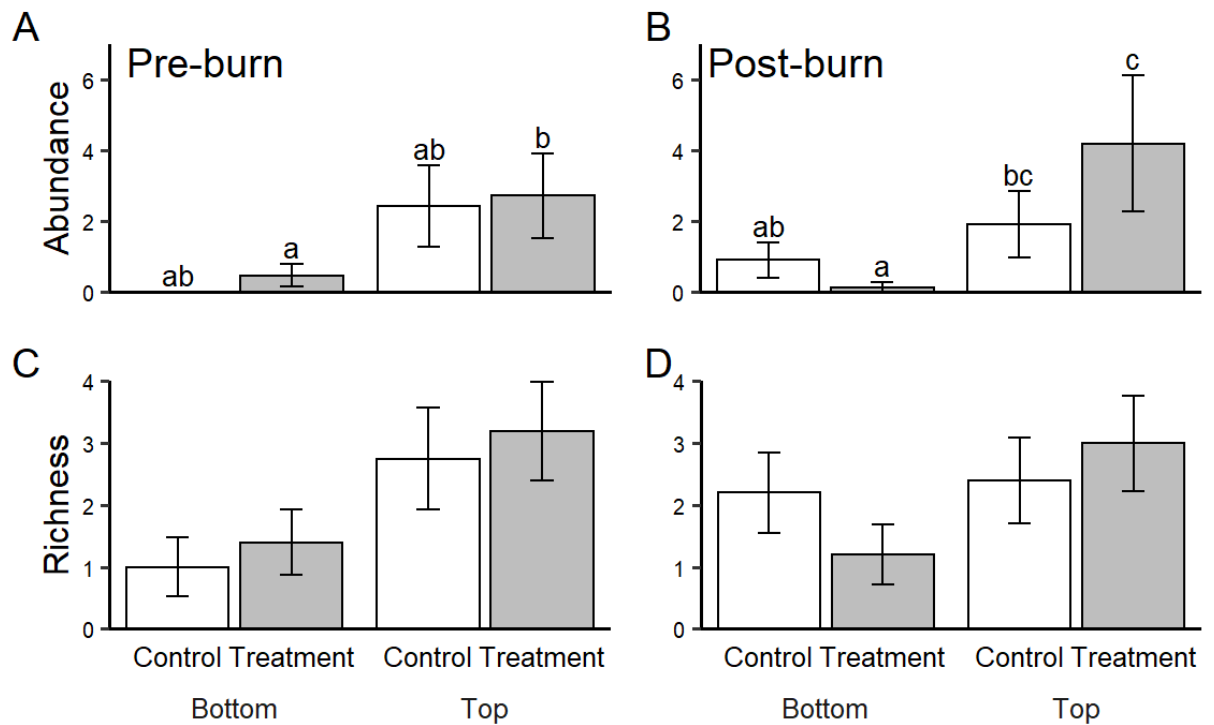
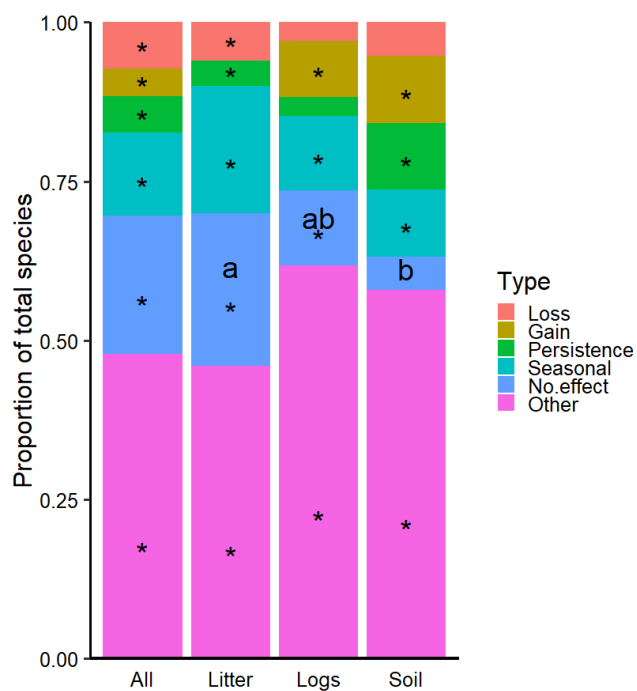


Figure 4. Plots of average pre- and post-burn abundance (A, B) and richness (C, D) in the top and bottom half of soil samples after burning in control and treatment samples. Letters indicate the result of pairwise comparisons.

### 3) Is the loss, gain and persistence of taxa after a prescribed burn influenced by microhabitat?

Overall, ~7% of all detritivore taxa were lost following burning (Fig. 5). This was largely due to the loss of litter taxa, as losses in the soil and logs were non-significant (Fig. 5). Across all sites, ~4% of taxa sampled after the burn were new (not detected in the pre-burn or post-burn control samples), which was due to gains in the log and soil communities (Fig. 5). ~22% of taxa were unaffected by burning, as they were present before and after burning at both control and treatment sites (Fig. 5). The average proportion of species lost, gained, persisting or unaffected across sites did not generally differ significantly among microhabitats (Fig 5; Ch. 2 Appendix Table 9). The only exception was that a greater proportion of taxa was unaffected by burning in litter relative to soil, which may be partly due to the lack of gains in the litter and the higher number of unassigned taxa in soil (Fig 5; Ch. 2 Appendix Table 9). Several taxa could not be assigned to any

group (Fig. 5), often because they were singletons. The presence of taxa that responded consistently to burning in at least some sites (not all taxa were detected at all sites) included Lepidoptera and *Ommatoiulus moreletii* in the litter, which were unaffected by burning (Ch. 2 Appendix Table 10). In addition, Armadillidae sp. 5 was lost from the litter, Armadillidae sp. 4 and Dalodesmidae were gained in the soil, and *O. moreletii* persisted in the soil at burnt sites while being absent from post-burn control sites (Ch. 2 Appendix Table 10). Taxa that were lost in the litter were not among those gained by the soil or logs (Ch. 2 Appendix Table 10).



**Figure 5.** Average proportion across sites of taxa that were lost, gained, persisted, showed seasonal changes, or were unaffected by burning. Detritivores assigned to the 'other' category could not be classed with any other response (see Table 1). Asterisks indicate significant differences with burning, where the confidence intervals (95%, modified Jeffreys method) do not include zero. Letters indicate the differences between microhabitats for unaffected invertebrates, as indicated by pairwise comparisons (there was no difference between microhabitats for the other categories).

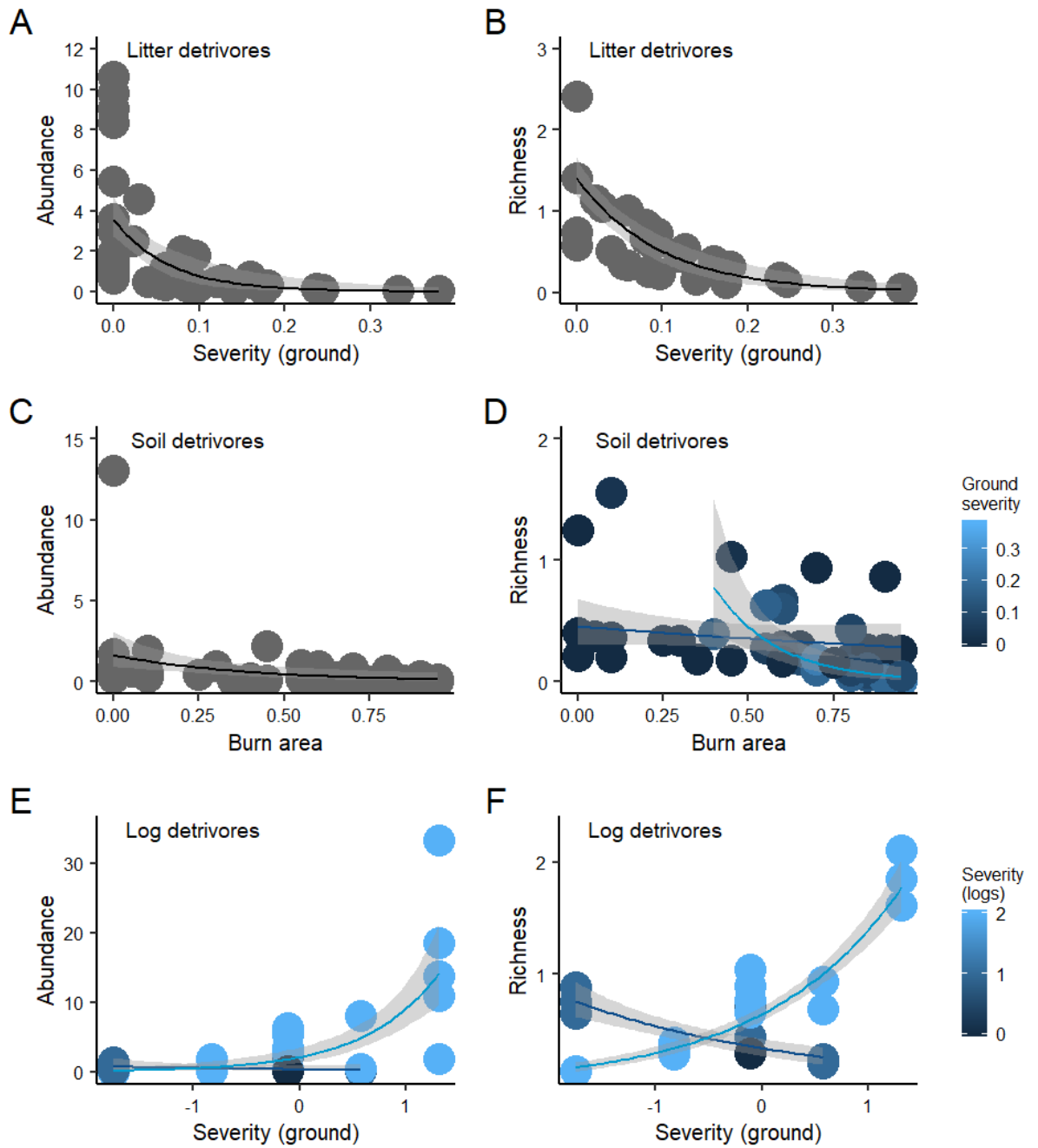
4) Do burn area and severity predict the loss, gain or persistence of taxa and community change across all microhabitats?

Increasing ground burn severity was associated with declines in abundance and richness in the litter (Table 5, Fig 6A, B). Burn area was associated with a reduction in soil abundance, and reduced soil richness, but only when burn severity was high (Table 5, Fig 6D, E). An interaction between ground burn severity and log burn severity indicated that an increase in abundance and richness was associated with severely burnt logs, but only when ground burn severity also increased (Table 5, Fig 6 G, H).

The litter community was affected by several burn severity measures. In particular, increasing log burn severity was associated with increases in *Arcitalitrus sylvaticus* in the litter and ground burn severity with declines in Lepidoptera (Table 5; Fig 7A, B). Comparison of models using AIC values allowed removal of interactions, but was inconclusive for evaluating main effects in the soil community. Therefore, three models were run, one for each burn severity variable. The soil community was not affected by any burn severity variables (Table 5). The log community was affected by burn area and ground burn severity, which could be attributed to increases in the number of *O. moreletii* with increasing ground burn severity, while Armadillidae sp. 1 increased with burn area (Table 5; Fig 7C, D).

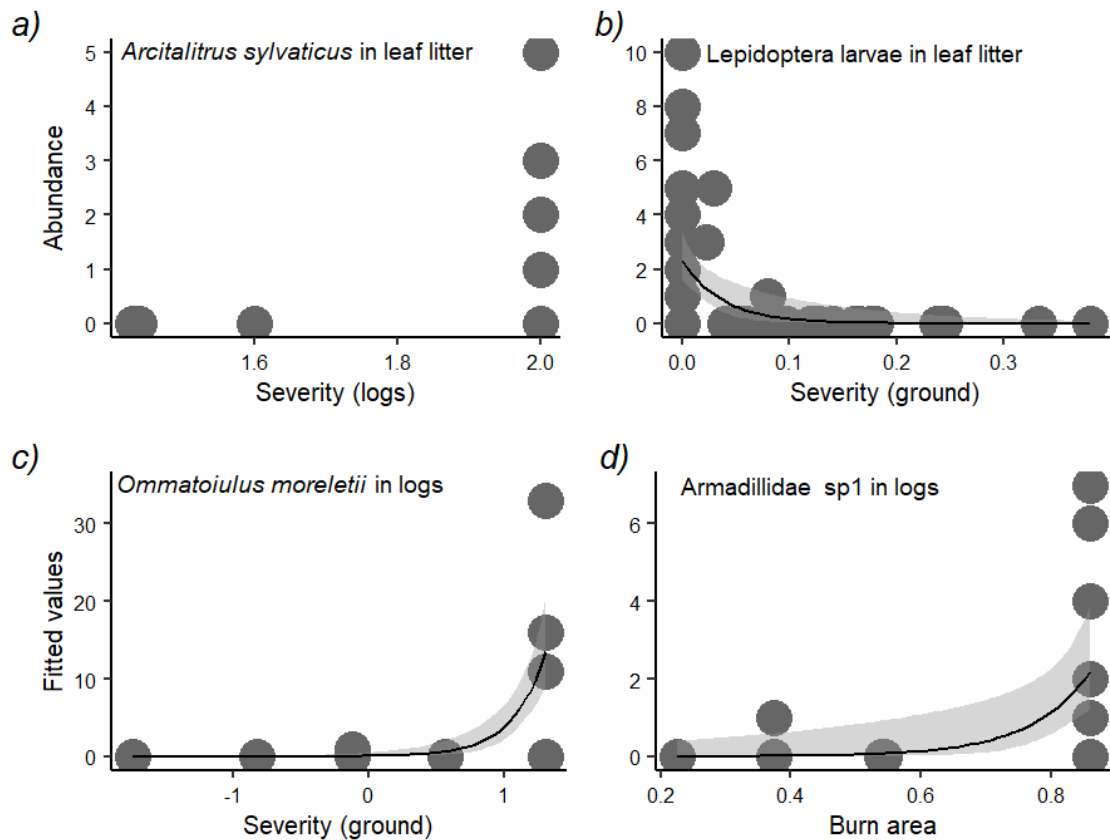
*Table 5.* Generalised linear mixed models (GLMM) results testing the effect of burn area and severity on detritivore richness and abundance, and manyglm results testing the effect of burn severity variables on detritivore community composition in three microhabitats. GLMMs were run with samples nested within site as a random effect, and manyglm models were run with site as a permutation blocking factor to control for spatial variation. These models were considered the best, as they were within 4 AIC of the base model, eliminated uninformative parameters and/or were simpler than other models (see methods). Significant p-values are in bold. Ground severity residuals were used in log analyses.

	Litter		Soil		Logs	
<b>Abundance (GLMM)</b>	<b>t</b>	<b>P</b>	<b>t</b>	<b>P</b>	<b>t</b>	<b>P</b>
Burn area			-2.8	<b>0.005</b>		
Ground severity	-3.0	<b>0.003</b>			-1.926	0.054
Log severity					2.233	<b>0.026</b>
Ground*Log severity					2.657	<b>0.008</b>
<b>Richness (GLMM)</b>						
Burn area			-0.5	0.605		
Ground severity	-3.4	<b>0.001</b>	3.8	<b>&lt;0.001</b>	-2.0	<b>0.043</b>
Log severity					1.3	0.190
Ground*Log severity					2.5	<b>0.011</b>
Burn area*Ground severity			-7.8	<b>&lt;0.001</b>		
<b>Community (manyglm)</b>	<b>Dev</b>	<b>P</b>	<b>Dev</b>	<b>P</b>	<b>Dev</b>	<b>P</b>
Burn area			8.6	0.438	30.1	<b>0.004</b>
Ground severity	39.8	<b>0.001</b>	10.6	0.210	64.6	<b>0.001</b>
Log severity	48.9	<b>0.001</b>	10.7	0.300		



*Figure 6.* Relationships between A) litter detritivore abundance B) litter richness C) soil abundance D) soil richness and E) log abundance and F) log richness and burn severity variables (or their residuals), derived from generalised linear models. Linear mixed models were used and their fitted values were used for all plots. Regression lines  $\pm$ SE are included to aid visualisation. Plot D has two regression lines, representing interacting effects of burn area (x-axis) and ground burn severity (blue colour scale); the dark blue lines are for proportion of severely burnt ground  $<0.1$ , the light blue lines are for severities  $\geq 0.1$ . Similarly, the two lines on plots E and F represent the interacting

effects of ground burn severity (x-axis) and log burn severity (blue colour scale); the dark blue lines are for log severities  $\leq 1$ , the light blue lines are for log severities = 2.



**Figure 7.** Relationships between detritivore taxa in leaf litter (a, b) and logs (c, d) in relation to burn severity variables using fitted values obtained from manyglm models. Ground severity residuals were used in plot C. Regression lines ( $\pm$ SE) are included to aid visualisation.

## Discussion

Prescribed burning is an important part of land management, especially for asset protection, and how it impacts invertebrate detritivores is of special concern because these animals are important decomposers of fine fuel loads. Our study revealed several key responses to a single prescribed burn. First, prescribed burns reduced litter cover and increased the amount of exposed ground, reducing the available habitat for detritivores. Second, although we could not detect a response for most taxa, these changes did alter some assemblages, with different taxa responding in distinct ways. Third, responses depended on microhabitat: while litter detritivores declined in abundance in response to fire, numbers of some soil and log detritivores increased, which suggests movement away from litter habitats post-fire. Fourth, increasing burn area and severity reduced the abundance of soil and litter detritivores, while increasing that of detritivores associated with logs. We discuss these findings and their implications for management.

The impact of prescribed burning on detritivores will be mediated by habitat loss (Ch. 1), which is associated with both direct mortality and post-fire mortality (Keeley, 2009; Saint-Germain et al., 2005). The area burnt at our sites was highly variable, ranging from 22-86%, which translated to variable loss of litter cover and volume and increases in bare ground. If correctly managed, many prescribed burns are patchy, as in this study (Gill et al., 1999), and small-scale patchiness is likely to be especially important in assisting recolonization of flightless invertebrates (Whelan et al., 2002). The obvious immediate impacts of increasing burn area, however, were reductions in the abundance and richness of litter-dwelling taxa. Burn severity also varied in space, ranging from almost no severe burning to about ~20% of total area experiencing severe burning. Amount of severe burning appeared to have the most profound effects on soil detritivore mortality. Given that our measurements were made only a short time after burning, the declines in detritivore diversity associated with habitat loss and fire severity likely reflect mainly *in situ* mortality.

These impacts of prescribed burning on detritivores depended strongly on microhabitat. In particular, soil and logs appeared to provide post-fire refugia for detritivores and are integral to their recovery after fire. Loss of taxa without compensatory gains was greatest in leaf litter, probably because it is the microhabitat most easily and extensively burnt (Coleman and Rieske, 2006; Dress and Boerner, 2004; Wikars and Schimmel, 2001; York, 1999). In contrast, soil and logs gained taxa, and detritivore abundance increased in the soil. Thus, while invertebrates may be subject to higher direct mortality in litter during fires, their movement to other microhabitats during the fire may explain the increases in logs and soil, although these increases are relatively small and could reflect sampling error. Reduced abundance following fire has been observed for some desiccation-sensitive invertebrates, and attributed to lower litter cover and humidity (Ray and Bergey, 2014; Vasconcelos et al., 2009). Thus, the loss of substantial amounts of litter likely created a more exposed post-fire environment that led to additional mortality and further movement (Bowman et al., 2016).

The contrasting effects on invertebrates of burning probably reflects the relative protection that microhabitats afford from heat. Logs that survived burning likely did not experience extreme heat due to low burn intensity and so may have promoted *in situ* survival, and soil is a good insulator from heat, especially as depth increases, while litter provides no such protection (Ch.1; Raison et al., 1986; Wikars and Schimmel, 2001). Although the species that was lost from the litter (Armadillidae sp. 5) was not the same as those gained in the logs and soil, several did appear in the soil (Armadillidae sp. 4, Dalodesmidae) which were not recorded in pre-burn samples. Detected primarily in the litter, Armadillidae sp. 5 is exposed to fire and thus elimination. It is also a small, rather delicate species, potentially more sensitive to desiccation than other Armadillidae (generally more tolerant isopods, Ch. 3). Armadillidae sp. 4 appeared to be a more robust species



likely to have a higher physiological tolerance, so its appearance in the soil may be driven by other requirements, such as food or lack of habitat (Bowman et al., 2016; Friend, 1993). The gain of Dalodesmidae in the soil may reflect the tendency of this family to be found in moister environments (Black, 1997; Mesibov, 2004; Mesibov, 2010). The increase in soil detritivore abundance after fire may thus reflect species-specific responses to microhabitat and post-fire survival strategies, as detritivores respond to dryer/warmer surface conditions following fire by moving (Buffington, 1967). In addition, although logs were lost in the fire (pers. obs.), those that remained gained detritivore taxa. This suggests movement into logs was partly opportunistic and driven by a need to find shelter post-fire.

Increasing burn severity and area appears to have affected *in situ* survival, and was associated with changes in the detritivore community in the litter and soil, likely reflecting mortality and the loss of habitat (Buckingham et al., 2015; Neary et al., 1999; Raison et al., 1986). While overall detritivores increased in abundance in the soil across all sites due to burning, increasing burn area within burnt sites was associated with declines in abundance. More specifically, our results indicate that while increasing burn area in general reduces abundance, it requires severe burning, with deeper heat penetration, to eliminate individuals of most taxa from the soil. Nonetheless, impacts varied. For example, *Arcitalitrus sylvaticus* abundance increased with increasing log burn severity in leaf litter, while Lepidoptera larvae decreased with ground burn severity. The latter result is probably due to direct mortality during the fire, as detritivorous Lepidoptera are relatively desiccation tolerant, surface dwelling taxa and thus exposed to fire (Bauce and Han, 2007; Cowling et al., 2003; New, 2014). Amphipods, such as *Arcitalitrus sylvaticus*, are found under logs as well as in leaf litter (Ch. 1) and are more sensitive to desiccation (Ch. 3; Lazo-Wasem, 1984), so the loss or alteration of log microhabitats by severe burning may have driven individuals of this species from logs and into any remaining litter. In general, high burn severity was associated with

significant detritivore declines in the soil and litter, and in consequent modification of their post-fire microhabitat occupancy.

At low ground burn severities, however, burn severity of logs had no effect on the abundance and richness of detritivores, suggesting that detritivores did not move into logs under more benign conditions. Somewhat unexpectedly, however, as burns became more severe, more severely burnt logs gained detritivores while less severely burnt logs did not. One explanation is that resident log detritivores were lost during the fire and so severely burnt logs were more accessible to surviving detritivores that had lost litter habitat; for instance, there is some evidence that Amphipod niche partitioning is due to space competition (Friend and Richardson, 1977; Richardson and Devitt, 1984). In addition, severe burning may have promoted fungal growth in logs, thereby creating an attractive food and shelter resources after fire (McMullan-Fisher et al., 2011; Wikars, 2002). The introduced *Ommatoiulus moreletii* increased in abundance with ground burn severity in logs, while Armadillidae sp. 1 increased with burn area, which appears to be a response to the loss of litter habitat since they occupy both litter and logs. Although *O. moreletii* prefers logs (Ch. 1) it is highly mobile and capable of colonising a wide range of microhabitats (Baker, 1978). Such flexibility has been observed in some termite species, which can resist fire by the breadth of microhabitats they nest in (Abensperg-Traun and Milewski, 1995). Our results indicate that some detritivores may use a similar strategy to persist after fire. Fire severity thus has complex impacts on the detritivore community, and its effects depend strongly on the microhabitat in question.

## Conclusion & management implications

Our study sheds light on the responses of invertebrate detritivores to prescribed burning, highlighting the immediate impacts, and some potential post-burn effects. We suggest that the detritivore community was generally resilient to prescribed burning. However, this resilience was tempered by both microhabitat and burn severity, with detritivores in litter being most vulnerable to burning. Soil and logs provided refuges for individuals of many taxa, probably because they are more buffered environments (both from the effects of fire and desiccation) that promote recovery of detritivores after fire. Increased burn severity reduced the effectiveness of refuges in soil but not in logs. Although the goal of prescribed burns is to reduce fine fuel loads, these results suggest that there may be benefits for land managers in attempting to reduce burn severity or increase burn patchiness, with an eye towards preventing the loss of burn refugia. Little is known about rates of accumulation and decomposition post-fire, but there is evidence to suggest it takes several years for decomposition to slow litter accumulation in *Eucalyptus* forest, and is likely dependent on litter moisture (Birk and Bridges, 1989; Penman and York, 2010). However, burn strategies that favour refuges from which detritivores can recolonise after fire could foster the recovery of their capacity to decompose fuel loads. Protecting long-unburnt forest patches from burning, and favouring prescribed burns in topographically heterogeneous forest may help to ensure adequate refuges are retained.

## References

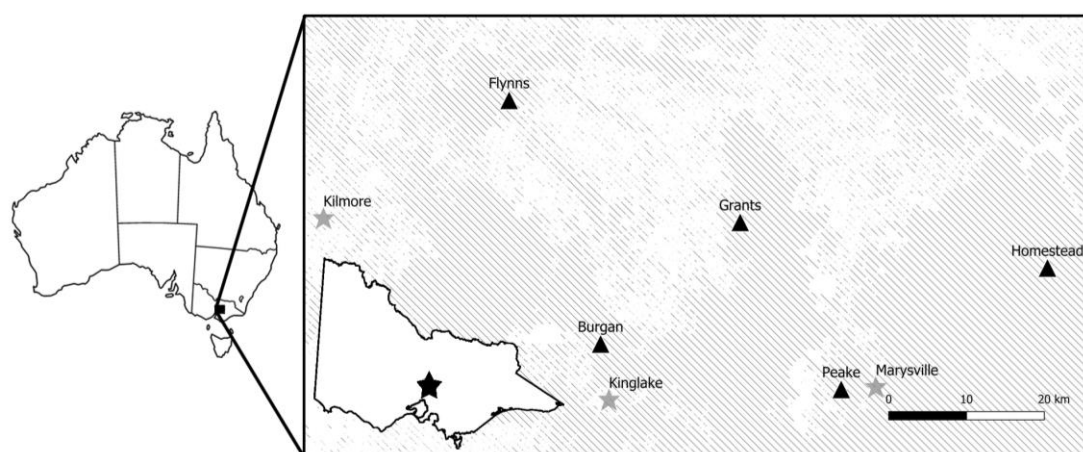
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## Chapter 2: Appendix



**Figure 1.** Map of sites in Victoria, Australia. Triangles indicates sites, hatching indicates the extent of forest.

**Table 1.** Site locations and altitude for treatment and control sites. Pre-burn and post-burn dates are provided for all sites, and burn ignition dates included for treatment sites.

Burn	Treatment			Control			All		
	Latitude	Longitude	Altitude	Latitude	Longitude	Altitude	Pre-burn	Burn date	Post-burn
Grants	-37.315255	145.554349	613	-37.319316	145.552558	614	30/03/2016	13/04/2016	20/04/2016
Flynns	-37.169251	145.22205	570	-37.172158	145.224276	549	23/03/2016	29/03/2016	25/04/2016
Burgan	-37.45276	145.348994	505	-37.454656	145.34795	527	29/03/2016	29/03/2016	5/05/2016
Peake	-37.5103	145.6971	526	-37.5096	145.6979	526	21/04/2018	22/04/2018	17/05/2018
Homestead	-37.3726	145.9989	576	-37.3837	145.9937	523	3/04/2018	3/04/2018	17/05/2018

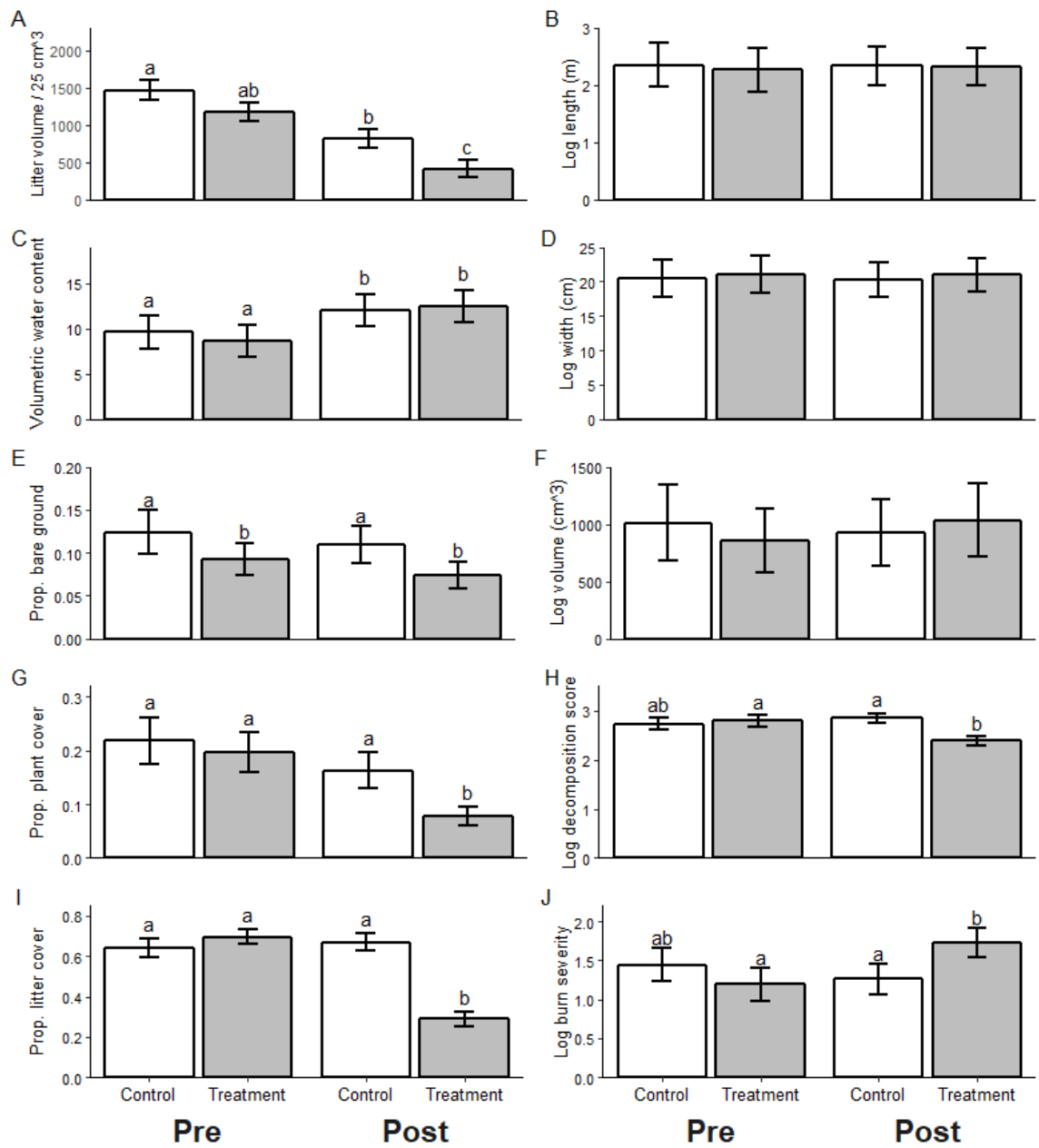


**Table 2.** The number of burnt and unburnt samples collected and those used for analysis. All initial single burnt and unburnt samples were used in analysis, and the remainder were randomly drawn from sample points where two samples were taken (one burnt, one unburnt), so that samples reflected the proportion of burnt area.

Site	% burnt	Initial samples			Final samples	
		# 2 samples	# burnt	# unburnt	# burnt	# unburnt
Grants	38	6	0	4	4	6
Flynns	86	6	4	0	9	1
Burgan	55	7	2	1	5	5
Peake	23	4	0	6	2	8
Homestead	54	9	0	1	5	5

**Table 3.** Results of generalised linear models testing for differences in log characteristics between logs with and without invertebrates, with site/treatment/time as a random effect.

Variable	$\chi^2$	p
Length	0.01	0.916
Log burn severity	1.79	0.182
Decomposition	0.46	0.496
Volume	0.11	0.736
Width	0.15	0.696
Length contact ground	<0.01	0.988
Volume contact ground	0.10	0.756



**Figure 2.** Plots for A) litter volume, B) log length, C) volumetric water content, D) log width, E) proportion bare ground, F) log volume, G) proportion ground plant cover, H) log decomposition score, I) proportion litter cover and J) log burn severity score before and after burning for control and treatment samples. Letters indicate estimated marginal means pairwise comparison results where a significant main effect was detected (see Ch. 2 Appendix Tables 2-3 for analysis).

**Table 4.** Results from generalised linear mixed models (site as a random factor) for ground cover variables. Estimated marginal means results for pairwise post-hoc test. 'T' and 'C' in the emmeans section refer to 'Treatment' and 'Control'.

Terms	Litter volume		Soil water content		Bare ground		Plant cover		Litter cover	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
<b>Treatment</b>	11.8	<b>0.001</b>	0.1	0.743	10.6	<b>0.001</b>	14.0	<b>&lt;0.001</b>	44.5	<b>&lt;0.001</b>
<b>Time</b>	47.6	<b>&lt;0.001</b>	26.3	<b>&lt;0.001</b>	2.9	0.087	38.6	<b>&lt;0.001</b>	81.0	<b>&lt;0.001</b>
<b>Treatment*Time</b>	0.3	0.594	1.2	0.266	0.2	0.669	8.3	<b>0.004</b>	64.5	<b>&lt;0.001</b>
Pairwise comparison	t	p	z	p	t	p	t	p	t	p
Post-C Post-T	2.9	<b>0.024</b>	-0.5	0.955	2.7	<b>0.042</b>	4.7	<b>&lt;0.001</b>	10.4	<b>&lt;0.001</b>
Post-C Pre-C	-4.3	<b>&lt;0.001</b>	2.7	<b>0.041</b>	-0.8	0.843	-2.0	0.193	0.7	0.887
Post-C Pre-T	-2.5	0.057	4.0	<b>&lt;0.001</b>	1.2	0.632	-1.5	0.465	-0.8	0.856
Post-T Pre-C	-6.9	<b>&lt;0.001</b>	3.1	<b>0.010</b>	-3.3	<b>0.007</b>	-6.3	<b>&lt;0.001</b>	-8.8	<b>&lt;0.001</b>
Post-T Pre-T	-5.4	<b>&lt;0.001</b>	4.5	<b>&lt;0.001</b>	-1.6	0.395	-6.6	<b>&lt;0.001</b>	-12.0	<b>&lt;0.001</b>
Pre-C Pre-T	1.9	0.217	1.0	0.727	2.0	0.202	0.8	0.846	-1.5	0.431

**Table 5.** Results from general linear mixed models (site as a random factor) for log measurement variables. Estimated marginal means results for pairwise post-hoc test. ‘T’ and ‘C’ in the emmeans section refer to ‘Treatment’ and ‘Control’.

Terms	Length		Width		Volume		Decomposition		Burn score	
	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p	$\chi^2$	p
<b>Treatment</b>	<0.1	0.873	0.2	0.668	<0.1	0.960	5.1	<b>0.023</b>	3.6	0.058
<b>Time</b>	<0.1	0.959	<0.1	0.932	0.1	0.777	2.0	0.159	2.2	0.131
<b>Treatment*Time</b>	<0.1	0.912	<0.1	0.937	0.6	0.429	5.7	<b>0.017</b>	9.8	<b>0.002</b>
Pairwise comparison	t	p	z	p	t	p	t	p	t	p
Post-C Post-T	0.1	1.0	-0.4	0.981	-0.5	0.966	3.2	<b>0.008</b>	-3.4	<b>0.005</b>
Post-C Pre-C	<-0.1	1.0	-0.1	0.999	-0.3	0.986	0.7	0.883	-1.0	0.730
Post-C Pre-T	0.2	0.999	-0.3	0.987	0.3	0.990	0.3	0.988	0.4	0.982
Post-T Pre-C	-0.1	1.0	0.2	0.996	0.1	1.0	-2.2	0.129	1.7	0.341
Post-T Pre-T	0.1	1.0	<-0.1	1.0	0.7	0.877	-2.6	<b>0.049</b>	3.2	<b>0.011</b>
Pre-C Pre-T	0.2	0.998	-0.2	0.997	0.6	0.925	-0.4	0.981	1.4	0.530

**Table 6.** Estimated marginal means pairwise comparisons of abundance and richness generalised linear mixed models for the difference between control and burnt sites, split by time.

Response	Time	All		Litter		Soil		Logs	
		Z	p	Z	p	Z	p	Z	p
<b>Richness</b>	Pre	0.5	0.595	0.7	0.473	-0.7	0.489	-1.3	0.196
	Post	0.9	0.386	1.2	0.239	0.4	0.715	0.2	0.869
<b>Abundance</b>	Pre	1.0	0.325	1.2	0.241	-1.4	0.165	-1.0	0.305
	Post	-1.5	0.137	2.9	<b>0.004</b>	-2.3	<b>0.024</b>	-0.1	0.957

**Table 7.** Post-hoc pairwise comparison for the significant interaction between time (pre or post) and treatment (control or treatment), for manyglm community analysis.

Pairwise comparison		All		Litter	
		Dev	p	Dev	P
Post-C	Post-T	72.3	<b>0.002</b>	71.1	<b>0.001</b>
Post-C	Pre-T	62.3	<b>0.009</b>	52.2	<b>0.009</b>
Pre-C	Post-T	61.0	<b>0.009</b>	50.1	<b>0.014</b>
Post-C	Pre-C	57.3	<b>0.016</b>	45.5	<b>0.029</b>
Post-T	Pre-T	41.9	0.127	45.4	<b>0.029</b>
Pre-C	Pre-T	30.8	0.339	31.5	0.182
<b>Simplified results</b>					
Pre-Control		b		a	
Post-Control		c		b	
Pre-Treatment		ab		a	
Post-Treatment		a		c	

**Table 8.** Estimated marginal means pairwise comparisons from generalised linear mixed models (site as a random factor) testing for differences in soil abundance according to treatment\*depth interactions.

Pairwise comparison		Pre		Post	
		Z	p	Z	p
Control-Bottom	Treatment-Bottom	-0.2	0.996	1.9	0.218
Control-Bottom	Control-Top	-0.2	0.995	-1.7	0.318
Control-Bottom	Treatment-Top	-0.3	0.995	-3.8	<b>0.001</b>
Treatment-Bottom	Control-Top	-2.5	0.053	-2.7	<b>0.033</b>
Treatment-Bottom	Treatment-Top	-2.8	<b>0.026</b>	-3.6	<b>0.002</b>
Control-Top	Treatment-Top	-0.3	0.990	-2.5	0.053

**Table 9.** Generalised linear model results testing for differences between microhabitats in the response of invertebrates to burning.

Response	$\chi^2$	p
Loss	0.95	0.621
Gain	2.48	0.289
Persistence	0.44	0.802
No effect	5.99	<b>&lt;0.050</b>
Post-hoc for 'no effect' taxa	z	P
Litter vs Log	1.404	0.339
Litter vs Soil	2.439	<b>0.039</b>
Log vs Soil	1.034	0.555

**Table 10.** Taxa that were gained, persisted, showed seasonal changes, or were unaffected by burning, for those showing a consistent response across sites where they were present.

Response	Litter	Logs	Soil
<b>Loss</b>	Armadillidae sp. 5		
<b>Gain</b>			Armadillidae sp. 4 Dalodesmidae
<b>Persisted</b>	Geometridae		<i>Ommatoiulus moreletii</i>
<b>Seasonal</b>	<i>Brachyiulus pusillus</i>	Styloniscidae sp. 2 & 3	<i>Brachyiulus pusillus</i> Immature Diplopoda
<b>No effect</b>	Lepidoptera	<i>Ommatoiulus moreletii</i>	

## Chapter 3: In for the long game: Behavioural changes prevent long-term effects of fire on trait-mediated distributions of flightless detritivores

Short title: **Effects of fire on detritivore distributions**

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### **Authors' Contributions statement**

JG, HG and NM conceived the ideas and designed methodology; JG collected and analysed the data; JG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Abstract

Fire is a crucial disturbance in many ecosystems worldwide. Especially important is the impact of fire on decomposition, as feedbacks between fire and decomposition regulate ground fuel loads, and hence the probability of subsequent fires. Invertebrate detritivores play a major role in decomposition, but most taxa are sensitive to desiccation and high temperatures. To investigate potential post-fire impacts of fire on detritivores, we tested the following three hypotheses eight years after a severe, largescale forest fire in Victoria, Australia: 1) effects of fire on microclimate are still apparent; 2) detritivore taxa from severely burnt forest have greater physiological tolerance for higher temperature and lower humidity than those from unburnt forest; and 3) microclimate interacts with physiological traits to influence detritivore distributions. Microclimate did not differ between burnt and unburnt forest, but several environmental variables did, and importantly, mean humidity preference was higher and mean temperature preference lower for at the assemblage level for unburnt sites. In addition, temperature and habitat variables interacted with temperature-related traits to determine the distribution of detritivores, independent of wildfire. Our results suggest that while detritivore recovery is limited in the short-term by microclimate and habitat, these conditions can select for expression of more tolerant behavioural physiology, allowing detritivores to persist and contribute to decomposition over the long-term following high severity fires.

**Keywords: Behaviour, disturbance regime, fourth-corner analysis, microclimate, physiology**



## Introduction

Fire is among the most common natural disturbances worldwide, drastically altering all aspects of ecosystems, from nutrient cycling to community composition. The impacts are so far-reaching that many species, even whole ecosystems, have evolved to depend on fire (Bowman et al., 2009). However, ecosystem processes also affect fire. For example, fire intensity depends partly on fine fuel load, which is regulated through decomposition and litter accumulation (Penman and York, 2010). Thus, a feedback loop exists whereby decomposition directly affects the severity and frequency of fire, and fire impacts the rate of decomposition. This creates the possibility of detrimental feedback loops: if fire slows decomposition processes by killing decomposers and reducing litter moisture, fire frequency could increase (Brennan et al., 2009; Penman and York, 2010). Thus, if we are to manage these systems effectively, we must understand how fire affects decomposition.

Globally, while climate and litter quality are significant predictors of decomposition rates, likely through their impact on microbial metabolism and community composition, invertebrate detritivores are responsible for an average of 37% of litter decomposition, which means they play a critical role in determining fuel loads and therefore fire regimes (Brennan et al., 2009; García-Palacios et al., 2013). Many detritivores are ground-dwelling and wingless, and are thus likely to be vulnerable to fire (Robinson et al., 2013). However, most knowledge of invertebrate responses to fire is from studies conducted at the taxonomic level of order, and such work is inadequate to capture community responses (Teasdale et al., 2013). For example, the order Coleoptera (beetles) includes herbivores, detritivores, carnivores and parasites, and their body mass spans at least three orders of magnitude (Naumann, 2000). Despite their functional importance, few studies have examined the recovery of invertebrate detritivore species following fire, or the mechanisms that drive such recovery.

Invertebrate recovery after fire involves three key processes: *in situ* survival, survival in the post-fire environment and recolonisation (e.g. Arnold et al., 2017). For species with limited dispersal ability, surviving the post-fire environment is critical for long-term persistence. Initially, fire greatly simplifies habitat structure, primarily through the loss of canopy, leaf litter and standing trees (Gosper et al., 2013). This is especially true of high severity fires, which can kill mature trees and much of the canopy is lost, even though some species are able to resprout from epicormic buds (Bennett et al., 2016; Pausas and Keeley, 2017; Stephens and Moghaddas, 2005). In addition, abiotic factors such as soil water content, air temperature and wind speed are strongly influenced by vegetation structure and thus microclimates change after fire (Ma et al., 2010; Old, 1969). Such changes will only be ameliorated by vegetation regrowth. Although this can be rapid after fire (Bassett et al., 2017), regrowth does not quickly replace mature trees. Consequently, decade-long biotic and abiotic changes can occur after high severity fires, even in fire-adapted systems (Lecomte et al., 2007), and such changes may perpetuate negative ecosystem consequences.

Temperature and humidity play a critical role in determining invertebrate distributions at global, regional and local scales, depending on species (Addo-Bediako et al., 2000; Cloudsley-Thompson, 1962; Lessard et al., 2011). As above, we know that fire affects microclimate (Ma et al., 2010; Old, 1969), but even when such microclimate changes eventually disappear, their effects on populations may persist, since infrequent, extreme events can have important impacts on physiological evolution (Kingsolver and Buckley, 2017). For example, microclimate or habitat changes after fire may eliminate some species, or act as a selection filter, changing the distribution of traits in a population (Fernández Fernández and Costas, 2004; Podgaiski et al., 2013). These effects are likely to be most pronounced in flightless invertebrates (including many detritivores, such as amphipods; Menz et al., 2016), as they cannot move rapidly from stressful environments.

An excellent method of assessing species response to environmental change is through analysis of traits (McGill et al., 2006). Morphological, physiological, behavioural and life history traits have successfully predicted arthropod distributions and responses to a range of disturbances (Andrew et al., 2013; Gibb et al., 2015a; Parr et al., 2017), including fire (Buckingham et al., 2015; Malmström, 2012; Podgaiski et al., 2013). Traits that interact most directly with microclimate are likely to be related to temperature and humidity tolerance (Chown and Terblanche, 2006). These physiological traits can significantly affect the microhabitats and range available to a species (Baudier et al., 2015; Dias et al., 2013). In addition, body size has many important effects that contribute to survival (Buckingham et al., 2015; Chown and Terblanche, 2006; Hassall et al., 2005), especially following disturbance, as larger animals are more likely to be negatively affected (Dirzo et al., 2014). Behavioural preferences, which also influence how species respond to changes in microclimate, may affect small-scale distributions, and can have fitness consequences (Davis et al., 1998; Guarneri et al., 2002). Detritivore recovery after fire will therefore depend on how traits, particularly physiological traits and behavioural preferences, interact with short- or long-term microclimate changes after fire.

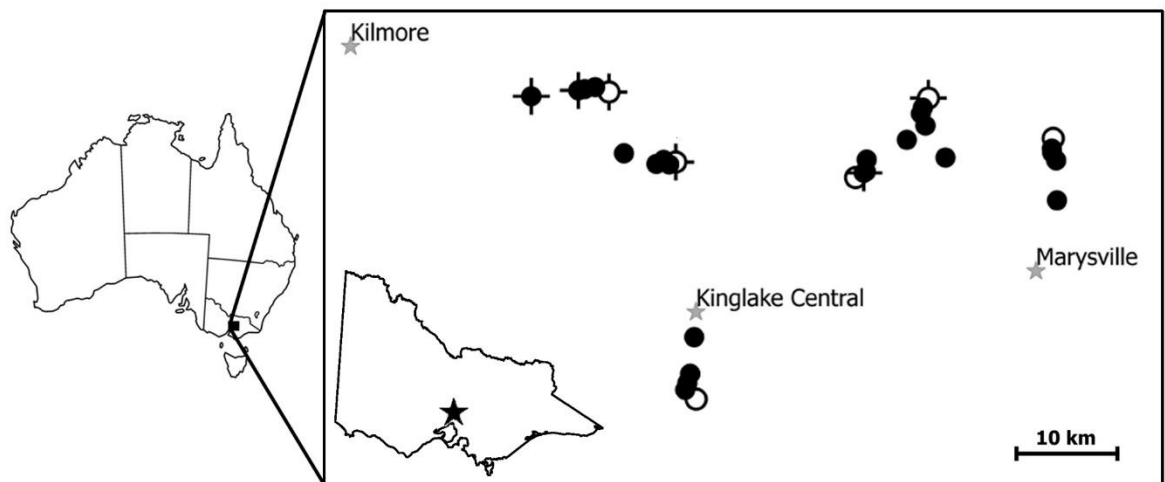
In this study, we investigated the importance of physiological traits for detritivore recovery after fire. We measured habitat variables, microclimate and detritivore distributions in burnt and unburnt forest. We then experimentally determined the critical thermal maximum (CT max), and humidity and temperature preferences of fourteen detritivore species from three taxa (Diplopoda, Isopoda and Amphipoda). We hypothesised that: 1) microclimate would differ between burnt and unburnt sites, with burnt sites warmer and drier than unburnt sites; 2) that invertebrates from burnt sites would be more tolerant of higher temperature and lower humidity than those from

unburnt sites; and 3) that microclimate would interact with physiological traits to determine detritivore species' distributions.

## Materials and Methods

### Sites

This study was conducted in forests north-east of Melbourne, in south-eastern Australia (Fig. 1). Sites were in dry sclerophyll forest, dominated by messmate (*Eucalyptus obliqua*) and peppermint gum (*Eucalyptus radiata*), with an understory of Austral bracken (*Pteridium esculentum*), *Acacia* spp. and *Eucalyptus* spp. saplings. Site altitude ranged from 252 m to 816 m. Sites were set along six 5 km transects, with five sample points (sites) each (Fig. 1). The sites were located within the boundary of the Kilmore East-Murrindindi fire complex, the result of two fires, which began on 9<sup>th</sup> February 2009 and burnt over 228,000 ha, with much of the area experiencing low fire heterogeneity and high fire severity (Leonard et al., 2014). The first site of each transect was unburnt in 2009 and for at least 20 years prior, while the remaining four sites on each transect were severely burnt (crown scorch/burn) in the 2009 fires (Leonard et al., 2014). All sites except three (clear-felled 12 and 14 years prior to 2009) had been unlogged for at least 20 years prior to 2009.



*Figure 1.* Map of study sites, located in south-eastern Australia, and their positions relative to three towns (grey stars). Filled circles (●) are burnt sites, unfilled circles (○) are unburnt sites and the beginning of each transect. Specimens used for experiments were collected from sites marked with a +.

### **Microclimate and habitat**

Temperature and relative humidity were measured at all sites, using Tinytag Plus<sup>®</sup> loggers in weather stations placed 10 cm above the ground to record near-ground conditions (similar to Stevenson Screens; used to ensure ambient conditions were measured and not influenced by rain or sunlight). Readings were collected every half hour for one year (1<sup>st</sup> February 2016-2017). Environmental variables were measured in summer, autumn and spring 2015, and autumn and spring 2016, although not all were measured every season (Table 1; Ch.3 Appendix 2). PADIR (Potential Annual Direct Incident Radiation) was calculated using equation 2 from McCune and Keon (2002) using latitude, slope and aspect (the latter two were obtained from GIS map layers provided by Geoscience Australia, 2017). The number of alive and dead standing trees (DBH  $\geq 10$

cm) and logs (diameter  $\geq 10$  cm) were counted within a 5 m of ten 10 m intervals along a 100 m transect at each site in summer 2015. Canopy and understory cover, and, within a 1 m radius, litter, plant and bare ground cover were visually estimated at five sample points spaced at 10 m intervals along one 50 m transect per site per season (except for summer 2015, when the 100 m transect was used). At the same time and locations, litter depth (carpenter's square) and soil volumetric water content (Fieldscout TDR 100 soil moisture meter probe, Spectrum Technologies, USA, and DSMM500, General Tools & Instruments, USA) were measured at three haphazard points within a 625 cm<sup>2</sup> quadrat, selected in the unbroken patch of litter nearest to the sample point. Environmental variables measured over multiple years were averaged within seasons, and if significantly correlated across different seasons, they were averaged across seasons (Pearson's  $r > 0.45$ ,  $p < 0.02$ ; Ch.3 Appendix 2, Table 1).

### **Log surveys**

Log searches conducted in spring 2015, and spring and autumn 2016, were used to determine the distribution of fourteen detritivore species from 3 distinct flightless taxa (Diplopoda, Amphipoda and Isopoda) at the thirty sites. Taxonomic experts were consulted to identify Diplopoda (Robert Mesibov) and keys used for Amphipoda and Isopoda included (Friend, 1987; Green, 1961; Green, 1974). These taxa were selected as they are abundant macro-arthropod detritivores at our sites, and the sampling methods was previously established as a reliable sampling method (Ch. 1). Logs  $> 9$  cm diameter were visually selected by walking haphazardly through the plots within 200m of the transect and then searched by rolling and/or dissecting a section (usually 30-60 cm), by hand and the assistance of a hammer and small crowbar. Some logs were unable to be searched, as they were too large to be rolled or the wood too solid to be pulled apart, though it was often possible to search under bark. This method was considered appropriate for the target taxa, since they were not borers capable of occupying solid wood requiring a rearing/extraction approach,

but instead occupied decayed wood and existing holes/cracks. When thorough searching of visible surfaces on the log and the ground where the log touched the ground did not yield any more specimens, the next log was searched, until 30 minutes had elapsed (time included searching for logs and collecting invertebrates from logs; time spent labelling was excluded). This sampling method was chosen as other methods tried (standardized litter and soil sampling) missed some species and did not yield sufficient numbers for analysis. Specimens from logs were collected directly into 100% ethanol. Since logs were highly visible at our sites, our ability to locate logs was treated as a function of log density, and thus abundance could be standardised as individuals per unit time per site.

During log surveys in spring 2016, the following measurements were made of all logs searched. Decomposition was estimated according to Lindenmayer et al. (1999), where freshly fallen logs = 1, up to completely disintegrated logs = 5. Burn severity of logs was estimated on a similar scale, where 0 = unburned, 1 = scorched, 2 = a mixture of severe burning and unburnt, and 3 = entirely blackened. We measured log diameter and length and used the equation for cylinder volume to calculate log volume; values were halved for laterally split log fragments. Indices of log decomposition and burn severity and estimates of log volume were averaged for each site.

### **Physiology experiments**

Three physiological traits were measured for all taxa studied: critical thermal maximum ( $CT_{max}$ ; defined below); thermal preference ( $T_{pref}$ ); and humidity preference ( $H_{pref}$ ). We had two objectives: 1) to test if the detritivore assemblage had higher tolerances in burnt forest than in unburnt sites, and 2) to test if traits differed within species between burnt and unburnt forest. Specimens were collected between 20<sup>th</sup> September and 20<sup>th</sup> October 2016 from a subset of five sites (3 burnt, 2

unburnt, Fig. 1; specimens were not collected from logged sites). Specimens were kept overnight in a controlled temperature room at 16°C before being tested the next day. Different individuals were used for each trial. Individuals were weighed live before each  $CT_{max}$  and after each  $T_{pref}$  and  $H_{pref}$  experiment. Most preference experiments were run with individuals of only one species at a time (except amphipod species, which could not be distinguished when alive), but two species were sometimes tested together if <10 individuals of a single species were available; target species were not considered to affect each other's behaviour, as they commonly occupied the same spaces in the field. Preference experiments were run with a maximum of 21 individuals, most being run with 10.

$CT_{max}$  was tested with a Stuart SBH130D block heater. Individuals were held in glass vials stoppered with damp cotton wool to ensure the air was saturated throughout the experiment. Starting at 30°C, temperature was increased by 0.5°C, then left for 3 minutes before ramping another 0.5°C. As the temperature approached 2°C of the species' estimated  $CT_{max}$  (based on pilot runs), the ramping increment was dropped to 0.2°C. Multiple species were sometimes tested in the same experiment due to time constraints, which affected the overall ramping rate, but the rate was only very weakly correlated with  $CT_{max}$  (linear mixed model, species as random effect, marginal  $R^2 = 0.006$ ,  $P=0.011$ ).  $CT_{max}$  was set as the temperature when a specimen could no longer right itself after being flipped onto its back, which was determined by vials being quickly removed from the heat block and tipped on their sides, flipping the specimen onto its dorsal surface (e.g. Andrew et al., 2013).

Thermal preference (defined as the temperature of the location where a specimen was found at the end of the experiment) was tested on a thermal gradient, ranging from ~11°C to ~29°C (dimensions: 117 x 8.5 x 10 cm). Cardboard strips, which were misted before experiments to



maintain humidity, spanned the length of the experimental arena to provide shelter and the arena was covered by plastic to maintain humidity. Individual invertebrates were distributed evenly on top of the cardboard strips, then left for an average of 37 mins. To test all individuals collected the day following their collection, different experiments had to be run concurrently, making it difficult to ensure all experiments ran for the same length of time (times ranged from 30-46 mins). However,  $T_{pref}$  was not correlated with experiment time. Thermal preference was then measured with a laser thermometer (Fluke 62 Mini IR Thermometer) at the place each specimen was found at the end of the experiment.

Humidity preference (defined as the humidity of the place where a specimen was found at the end of the experiment) was tested on a humidity gradient in a plastic chamber (dimensions: 30 x 21.5 x 10.5 cm). Silica gel in 70 ml vials was used to lower humidity at one end, followed by a row of pure glycerine, then by three rows of glycerine/water mixtures (75%, 50% and 25% glycerine respectively), finishing with two rows of pure water (modified from Johnson, 1940, with advice from Gary Clark). Hygrochron ibuttons<sup>®</sup> measured humidity above the solutions (humidity in the first row varied from 6-39%; averages for all seven rows  $\pm$ SD were: 26 $\pm$ 9, 46 $\pm$ 2, 60 $\pm$ 1, 77 $\pm$ 2, 88 $\pm$ 4, 94 $\pm$ 3, 94 $\pm$ 3). Fine mesh was stretched above the vials, covered with cardboard for shelter and the chamber was sealed with a lid (distance between mesh and lid was  $\sim$ 0.5 cm). Invertebrates were introduced haphazardly on the cardboard, except for very active species (from Amphipoda, Philosciidae and Styloniscidae), which were introduced into the centre of the cardboard to prevent their escape. Because experiments had to be run concurrently, experiment times ranged from 29-56 mins (mean = 36 mins).  $H_{pref}$  was not correlated with experiment time. Specimen positions were marked, then matched with the humidity at that location.

## Analysis

Fourteen species were abundant enough for our physiological experiments: two species of amphipods (*Arcitalitrus* sp. 1 (n=19), *A. sylvaticus* (n=56)), five species of isopods (*Armadillidae* sp. 1 (n=60), *Styloniscidae* sp. 1 (n=73), *Philosciidae* sp. 1 (n=79) & sp. 2 (n=34), *Porcellionidae* sp. 1 (n=28)), and seven species of millipedes (*Siphonotidae* sp. 1 (n=82), *Siphonotidae* sp. 2 (n=58), *Victoriocambala buffalensis* (n=64), *Hoplatessara pugiona* (n=17), *Somethus* sp. 1 (n=36), *Pogonosternum laetificum* (n=41) and the introduced Portuguese millipede, *Ommatoiulus moreleti* (n= 59)). However, comparisons between burnt and unburnt forest were possible for only ten species for weight, nine for  $CT_{max}$  and  $T_{pref}$ , and eight for  $H_{pref}$ , because sufficient specimens for the remaining species were not collected from both burnt and unburnt forest. The full species/trait combinations used for each comparison are given, along with trait values, in Ch. 3 Appendix 1, Table 1.

To test if microclimate and topography differed between burnt and unburnt sites, we used multiple linear regression (manyglm from the mvabund package in the R statistical program, with cor.type="shrink" to correct for co-correlation among variables; R Core Team, 2013; Wang et al., 2012). Proportional data was logit transformed, and all variables standardised as z-scores using two SEs (Gelman, 2008). Nine climate and three topographical variables were used in analysis: Potential Annual Direct Incident Radiation (PADIR), altitude (m), slope (degrees), days <1 °C (Days.1.C), days >35 °C (Days.35.C), average site humidity, days < 20% RH (days.H.20), days > 95% RH (days.H.95), average site temperature, highest recorded temperature (abTMax), lowest recorded temperature (abTMin) and lowest recorded humidity (abHMin). A separate analysis used the same protocol to compare 18 vegetation/environmental variables (so potential differences would not be overlooked) between burnt/unburnt sites (Table 1).

We tested for community-level trait differences (mean and variance) between burnt and unburnt sites, using linear mixed models with species as a random effect. Humidity preference (% relative humidity) was logit transformed and weight was log-transformed (since the distribution was highly skewed) prior to analysis. Residuals were log-transformed for tests of variance and zero values replaced with the next-lowest value in the dataset. We also tested for within-species differences in the mean and variance of weight between burnt and unburnt sites using linear mixed models using a burn status\*species interaction with trial as a random effect (other traits could not be tested due to a limited number of trials), followed by post-hoc estimated marginal means tests where the interaction was significant.

To test if traits interacted with environmental variables to explain abundance and presence/absence (referred to as occurrence from here on), we used fourth-corner analysis in the statistical package mvabund in R (Brown et al., 2014; Wang et al., 2012). Microclimate variables were first reduced by removing correlated variables (Pearson's  $r > 0.5$ ,  $p < 0.01$ ). The microclimate, topographic and environmental variables were then combined into a single dataset and correlated variables eliminated (Pearson's  $r > 0.5$ ,  $p < 0.01$ ), giving preference in this order: climate and topography, measured over multiple seasons, correlated with  $> 1$  variable. This order preferred more accurately measured variables and reduced the variable number. Where the choice was unclear, different analyses were run including the variable(s) in question and the model explaining the most variance was kept. Latitude was included to help control for spatial autocorrelation (Ch. 3 Appendix 2, Table 3). The median of four traits ( $CT_{max}$ ,  $H_{pref}$  and  $T_{pref}$  and weight) for each species was included in the trait dataset. Species with missing values for one or more traits could not be used for fourth-corner analysis, so the number of individuals needed to generate averages for each trait was set at five, with two exceptions (three each of *Arcitalitrus sp. 1* and *Hoplatessara pugiona* for one trait,  $T_{pref}$ ; a separate analysis was run to determine if dropping these species

significantly altered results). Both trait and environment datasets were standardised prior to analysis using z-scores, dividing by two SE instead of one (Gelman, 2008). Two models were tested: one with abundance (family = "negative.binomial"), to measure the effects on population size, and the other with occurrence data (family = "binomial"), to measure the effect on assemblage composition. Analyses were run with 999 permutations using resamp = 'pit.trap', to bootstrap the probability for integral transformed residuals and reduce Type I errors, and graphics were produced using a LASSO penalty ("glm1path"), which eliminates interactions that do not improve the model BIC (Brown et al., 2014).

## Results

### **Microclimate and habitat**

The microclimate and topography (slope, PADIR, altitude) of burnt sites did not differ from unburnt sites (manyglm,  $F_{(17,12)} = 5.0$ ,  $p = 0.71$ ). However, environmental variables at burnt sites differed from those at unburnt sites (manyglm,  $F_{(11,18)} = 77.0$ ,  $p = 0.002$ ). A post-hoc manyglm test for environmental variables showed that unburnt sites had higher canopy cover, lower understory cover, less severely burnt logs, a higher percent of living trees and a lower percentage of dead trees (Table 1).

*Table 1.* Results of post-hoc test for a multiple linear regression, comparing environmental variables at burnt and unburnt sites, along with variable abbreviations and descriptions. Significant p-values are in bold.

Description	Season(s)	Years	F-value	P-value
% trees as logs out of total standing trees and logs	Summer	2015	0.09	0.997
% alive standing trees	Summer	2015	13.71	<b>0.017</b>
% dead standing trees	Summer	2015	21.05	<b>0.005</b>
Litter depth (cm)	Summer	2015	5.57	0.283
	Autumn	2015-16	0.51	0.983
	Spring	2015-16	1.49	0.889
% volumetric water content	Summer	2015	0.00	1.000
	Autumn	2015-16	0.11	0.997
	Spring	2015-16	0.30	0.996
Total volume of searched logs	Spring	2016	2.23	0.782
Average log decomposition	Spring	2016	0.09	0.997
Average log burn severity	Spring	2016	13.42	<b>0.017</b>
% canopy cover	All	2015-16	24.64	<b>0.002</b>
% understory cover	All	2015-16	10.38	<b>0.049</b>
% bare ground	All	2015-16	0.31	0.996
% leaf litter cover	All	2015-16	0.61	0.980
% ground plant cover	Summer	2015	1.56	0.889
% ground plant cover	Autumn+	2015-16	0.43	0.989
	spring			

## Physiology

Linear mixed models (LMMER) revealed that the mean and variance of  $CT_{max}$  across species was not affected by burn status (Table 2). The LMMER results for  $H_{pref}$  indicated a singular model fit due to low variance in the 'Species' random effect, but dropping the random effect and running a linear regression did not change the significance of results. However, residual plots improved when the random effect was included and so the LMMER results were retained. Most interestingly, means for  $H_{pref}$  were lower and  $T_{pref}$  higher across the entire assemblage at burnt sites (Table 2; Fig 2). LMMER tests showed no difference in mean weight within species according to burn status (burn status\*species interaction, Chi-squared = 13.2,  $p = 0.152$ ), while one species, *Victoriocambala buffalensis*, had a higher variance of weight at burnt sites (Table 2).

**Table 2.** Linear mixed model (LMMER) test results comparing differences in the mean and variance of each trait according to burn treatment, with species as a random effect. LMMER main effects and post-hoc estimated marginal means results testing for differences in weight variance within species according to burn status. P-values <0.05 are in bold.

Trait	Mean		Variance	
	Chi-value	P-value	F-value	P-value
CT <sub>max</sub>	0.01	0.9438	1.87	0.1712
H <sub>pref</sub>	4.92	<b>0.0265</b>	0.01	0.9364
T <sub>pref</sub>	14.24	<b>0.0002</b>	0.13	0.7192
Weight	0.18	0.6739	3.33	0.0679

Variance		
Main effects	Chi-value	p-value
Burn status	2.5	0.116
Species	226.1	<0.001
Burn status*Species	17.6	<b>0.040</b>

Post-hoc	t-value	p-value
<i>Arcitalitrus sylvaticus</i>	0.221	0.8262
<i>Armadillidae</i> sp. 1	0.017	0.9863
<i>Philosciidae</i> sp. 1	-0.064	0.9493
<i>Styloniscidae</i> sp. 1	1.931	0.0576
<i>Siphonotidae</i> sp. 1	0.590	0.5583
<i>Siphonotidae</i> sp. 2	-1.246	0.2172
<i>Somethus</i> sp. 1	-1.241	0.2172
<i>Pogonosternum laetificum</i>	-1.883	0.0632
<i>Victoriocambala buffalensis</i>	-2.526	<b>0.0150</b>
<i>Ommatoiulus moreleti</i>	-1.887	0.0648

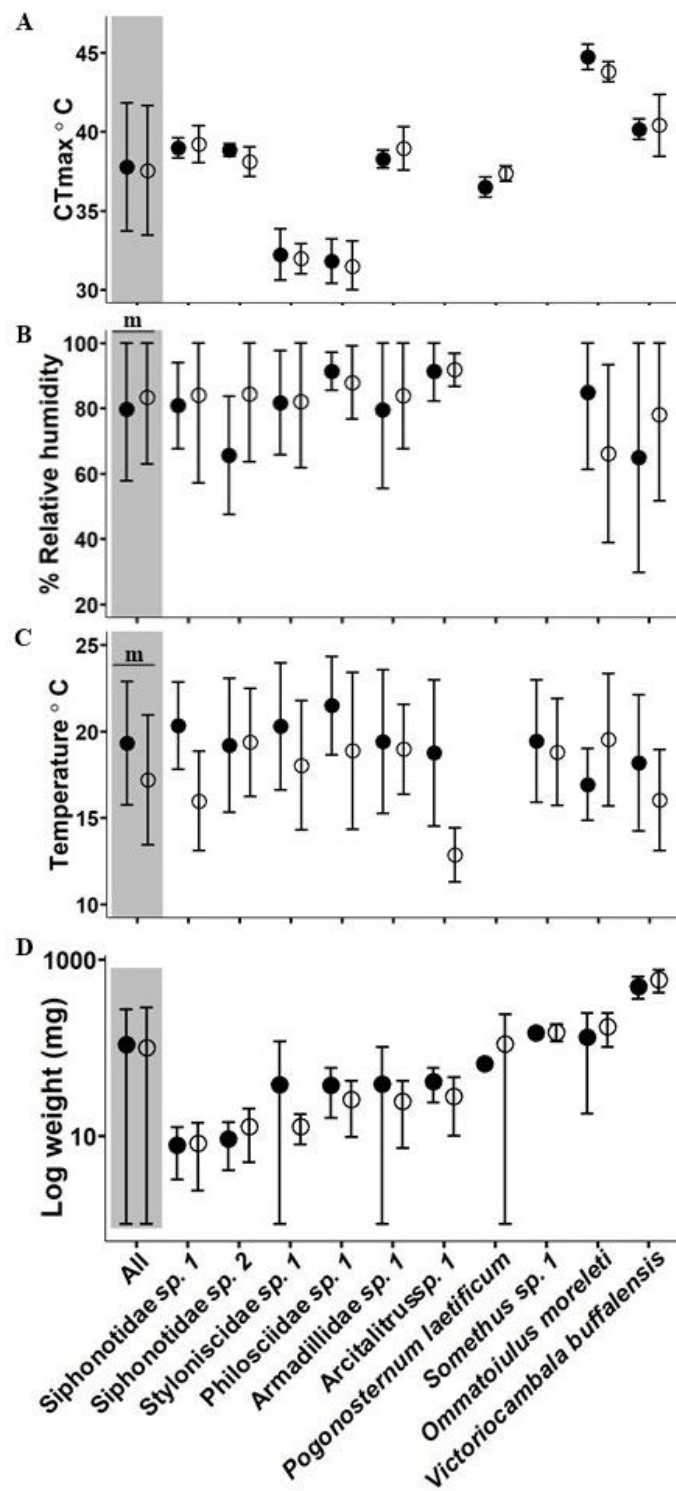
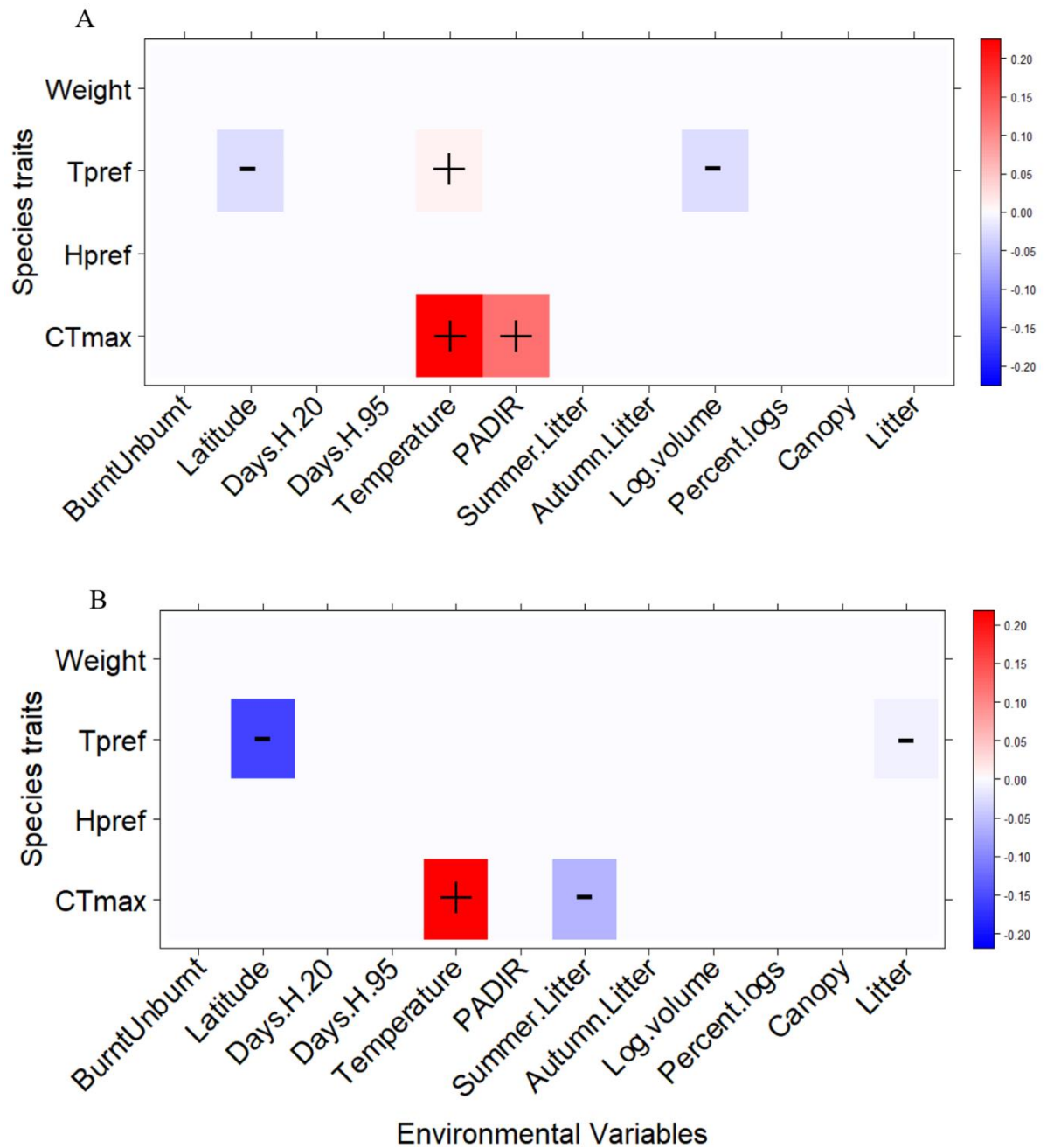


Figure 2. Mean and standard error for: A)  $CT_{max}$ , B) humidity preference, C) temperature preference and B) weight for detritivore species. Species are ordered by increasing weight; filled circles = burnt, unfilled circles = unburnt. Bars indicate significant differences, with m=mean.



### Interaction of environment and traits

The final environmental dataset for fourth corner analysis consisted of 12 variables (Fig. 3; Ch. 3 Appendix 2, Table 3) and all fourteen species were included. Canopy and % logs were correlated with understory and % dead trees. Running the model with either pair of variables did not alter significance; however, canopy and % logs explained more variance and were retained in the final model. The fourth corner model was improved significantly with the addition of traits, compared to the model based only on species abundance ( $D=99.4$ ,  $P=0.007$ ) and occurrence ( $D=91.5$ ,  $P=0.027$ ); excluding the two species with  $T_{pref}$  averages drawn from three individuals (*Arcitalitrus* sp. 1 and *Hoplatessara pugiona*) changed only the weakest interactions ( $T_{pref}$ \*Temperature,  $T_{pref}$ \*Log.volume and  $T_{pref}$ \*Litter were replaced with  $T_{pref}$ \*Days.H.95,  $CT_{max}$ \*Days.H.20,  $H_{pref}$ \*Summer.Litter and  $T_{pref}$ \*Burn status), but did not alter the strongest ( $T_{pref}$ \*Latitude,  $CT_{max}$ \*Temperature,  $CT_{max}$ \*PADIR and  $CT_{max}$ \*Summer.litter; Ch. 3 Appendix 1, Figure 1). The abundance and occurrence models revealed significant interactions between two traits ( $T_{pref}$  and  $CT_{max}$ ) and impact of six environmental variables (latitude, temperature, PADIR, summer litter depth, log volume and litter cover; Fig. 3). Strong positive interactions between  $CT_{max}$  and temperature (both abundance and occurrence) and PADIR (abundance), indicated that species with high  $CT_{max}$  were more abundant at sites with higher temperature and PADIR (Fig. 3). Species with a lower  $CT_{max}$  were found at sites with deeper litter depth in summer (Fig. 3B). A negative interaction between  $T_{pref}$  and latitude (weak for abundance and strong for occurrence), indicated species with higher  $T_{pref}$  were found at more northerly sites (Fig. 3). Finally,  $T_{pref}$  interacted negatively with log volume (abundance) and litter cover (occurrence), and positively with temperature (abundance; Fig. 3). Thus, species with higher  $T_{pref}$  were more likely to be found at sites with smaller logs, less litter cover and higher temperatures (Fig. 3).



*Figure 3.* Standardised interaction coefficient estimates for interaction terms from the fourth corner analysis, testing the relationship between physiological traits and the environment accounting for: A) species abundances; and B) species occurrence. Coefficients shown in red (positive) or blue (negative) were significant in the best model. Cell colour intensity indicates the strength of the interaction (scale shown on side bar).

## Discussion

We investigated whether previous high severity fire continue to affect the distribution of flightless detritivores through its impact on forest structure and microclimate, eight years after fire. We found no lasting impacts on microclimate, but we did detect preference for warmer and dryer conditions at burnt sites, and the recovery of most flightless detritivores eight years on did not appear to be limited by wildfire interacting with physiological traits. Importantly, we determined that common detritivore distributions were determined by microclimate/environment-physiology interactions, independent of burn status. The results thus suggest that short-term environmental changes after fires may initially limit recovery and select for physiological changes within populations that remain long after the occurrence of a severe fire.

### **Microclimate and habitat**

We hypothesised that burnt sites would be warmer and less humid than unburnt sites. However, we found no difference in microclimate eight years after fire. Although few data exist for longer time frames, ecosystems often experience higher soil and air temperatures, and lower humidity for at least one-two years after fire (Ma et al., 2010; Raison et al., 1986); however, our analysis shows that any such effects have largely disappeared eight years after a burn. Changes documented in microclimate have been explained primarily the result of the loss of canopy and litter layers, which increases the amount of light and wind speed within the forest (Chen et al., 1999; Raison et al., 1986). Since the loss of mature trees and canopy cover was still clear at burnt sites, we expected differences in microclimate would persist, at least until forest structure more closely resembled that of unburnt forest. However, shading from understory regrowth (which was vigorous at burnt sites) may have compensated for the loss of mature trees, given its effects in other forests (Gray et al., 2005; Ray et al., 2005). It is also likely that the ambient temperatures we measured are more variable than the microhabitats occupied by detritivores (see Ch. 1), and this

may have obscured differences between burnt and unburnt sites if microhabitats were altered by fire (Villegas et al., 2010). Temporally continuous studies of microclimate changes throughout post-fire succession across a range of forest types/climates are recommended to close this knowledge gap.

## Physiology

Basic microclimatic variables had recovered eight years after fire, but given the extreme severity of the fire, burnt sites will have endured harsh post fire conditions, as there is little doubt that litter microhabitats disappeared post-fire (Leonard et al., 2014; Ma et al., 2010; Old, 1969). We hypothesised that this disappearance would lead to persistent physiological changes in detritivores. Our expectation was supported, as  $T_{pref}$  was higher and  $H_{pref}$  lower across the detritivore assemblage at the burnt sites, with seven of the nine species preferring higher temperatures at burnt sites. This result could indicate plastic phenotypic responses to current differences in microhabitats (and their microclimate) not captured in this study. For example, persistent vegetation differences could increase microhabitat temperature and reduce humidity, meaning that higher  $T_{pref}$ /lower  $H_{pref}$  would be advantageous (Chown and Terblanche, 2006; Gray et al., 2005; Scheffers et al., 2014). However, as we did not detect any lingering microclimatic differences between burnt and unburnt sites, a more likely explanation is the action of selection driven by the immediate post-fire environment. That is, if preference reflects functional implications that affected survival postfire, thus altering the distribution of alleles in the population, it could take some time for allele distributions to return to pre-fire frequencies.

The lack of difference in  $CT_{max}$  and weight among detritivores from burnt and unburnt areas (except for weight variance in *Victoriocambala buffalensis*) may indicate that microhabitats

conditions did not exceed the tolerance in these traits after fire. However, as habitats were clearly affected by fire, we considered four possible explanations for lack of change: 1) these species retreated to refuges during hostile periods and were therefore not exposed to intolerable conditions (Robinson et al., 2013); 2) widespread gene flow from unburnt sites after fire may have obscured any selection or filtering after fire; 3) phenotypic plasticity was invoked in the face of changing conditions (Chown et al., 2007); or 4) physiological stress was primarily compensated for by the changes we detected in behavioural preferences. Given the preference of these detritivores for humid conditions, it is very likely that refuges are essential to post-fire survival. Knowledge of forest detritivore dispersal is limited, but many species are wingless, suggesting that they are dispersal restricted, and this explanation would conflict with our previous suggestion of selection occurring for  $T_{pref}$  and  $H_{pref}$  (Arnold et al., 2017; Menz et al., 2016). Species adept at human-assisted movement, such as the one introduced species in our study, *O. moreleti*, provide a possible exception. Nonetheless, given the remote location of our sites, even this species would require time to recover through anthropogenic dispersal (Baker, 1978). Thus, rapid gene flow among these detritivore populations, appears unlikely to be able to overcome selection by fire, and the dependence on refugia of these taxa may best explain the lack of changes in  $CT_{max}$  and weight.

Fire may have a disproportionate effect on species at either end of the size spectrum, as they are more vulnerable to disturbance (Dirzo et al., 2014; Gibb et al., 2017), and expression of phenotypic plasticity may allow them to overcome such challenging conditions (Chown et al., 2007). Buckingham et al. (2015), for example, showed that, within the same ecosystem, litter-dwelling arthropod species were heavier in severely burnt forest. However, we did not observe this in our data. It is possible that litter species are under greater selective pressure for physiological tolerance following fire than are those commonly associated with logs, which provide a more buffered environment (Ch. 1). Thus log-associated species may not require the physiological

protection offered by a larger body size (Dias et al., 2013). In addition, the two traits that differed between individuals collected from burnt and unburnt areas were behavioural (choice of temperature/humidity), suggesting that behaviour, rather than physiology, responds to selection to meet fire-induced habitat changes in log-associated species. Thus, our results highlight the importance of considering choice of microhabitats in predicting population responses to environmental change. In particular, we suggest that these invertebrate detritivores overcome harsh environments by selecting appropriate refugia.

Fire is a strong selection agent in plant populations (Neeman et al., 2004), but little is known about the evolutionary effects of fire on detritivores. In the absence of observed temperature or humidity differences according to burn status, we consider selection of preference is a more likely explanation of our results than phenotypic plasticity. The demonstrated response of means for higher  $T_{pref}$  and lower  $H_{pref}$  at burnt sites suggests an 'evolutionary lag' where the effects of selection (arising from the post-fire environment) persist for many generations after the selection event (Kawecki, 2008; Lahti et al., 2009). Persistence of such evolutionary legacies will likely depend on population connectivity (Dlugosch and Parker, 2008), since high gene flow following a selection event will swamp any selection signature (Banks et al., 2013). While little is known about the dispersal of many detritivore species, genetic analyses have demonstrated that *Arcitalitrus* species in the study area have highly structured populations, indicating poor gene flow (Menz et al., 2016). This makes *Arcitalitrus* an ideal organism in which to detect evolutionary legacies, but further study of other detritivores is needed to confirm if this is a general trend.

### Trait-environment interactions

Although microclimate did not differ between burnt and unburnt sites, including traits in the fourth-corner analysis increased the model's explanatory power, indicating that microclimate did affect species distributions, in relation to  $CT_{max}$  and  $T_{pref}$ .  $T_{pref}$  interacted negatively with latitude, which could indicate spatial autocorrelation, except that temperature also showed some correlation with latitude (Ch. 3 Appendix 2, Table 3), suggesting that temperature directly drives this result. The abundance and occurrence of species with higher  $CT_{max}$  was positively associated with higher temperature, and for abundance, with higher PADIR. Although  $CT_{max}$  does not change much with latitude, temperature can affect distributions at smaller scales (Kingsolver and Buckley, 2017), as was observed here. The interaction of  $CT_{max}$  and PADIR is slightly more complicated. This is because higher solar radiation (PADIR) could either increase site temperature or instead, by promoting plant growth, lower temperature through shading (Gamon and Pearcy, 1989; Ma et al., 2010; Old, 1969). Although PADIR was not correlated with temperature at our sites (Ch. 3 Appendix 1, Table 3), sites with a higher PADIR might still be warmer and drier overall, as it is a broader measurement than our microclimate measurements (Johansson et al., 2016). Since this explanation is consistent with the  $CT_{max}$ \*temperature interaction, and is biologically coherent, we conclude that both temperature and PADIR limit taxa present in the detritivore community through  $CT_{max}$ .

Habitat structure also plays a strong role in determining invertebrate distributions (Lassau and Hochuli, 2004). The occurrence of species was affected by the negative interaction of  $CT_{max}$  and  $T_{pref}$ , and three habitat variables. It seems sensible that species with a lower  $CT_{max}/T_{pref}$  were found at sites with deeper litter in summer, larger logs and more litter cover, since deeper litter provides greater insulation from heat, which is most extreme in summer, as does more litter and log cover

(Facelli and Pickett, 1991). Together, these interactions suggest that increased ground cover favours species with lower  $CT_{max}$  and/or  $T_{pref}$  because of its insulative effect.

Canopy was the only vegetation variable differing between burnt and unburnt sites in the fourth corner analysis but this variable showed no interaction with traits. Thus, it appears that detritivores were largely unaffected by long-term structural changes in the forest overstory. However, since severely burnt sites have less vegetation and ground cover immediately after fire, both of which would increase site temperature, our results lend some support to the idea that short-term changes could affect detritivore distribution (Knapp, 1984; Rambo and North, 2009). In conjunction with other studies (e.g. Knapp, 1984; Rambo and North, 2009), our results suggest the possibility that the immediate post-fire environment could create a population bottleneck that affects subsequent detritivore distributions through physiological traits.



## **Conclusions**

This study highlights the value of measuring trait-environment interactions to better understand mechanisms driving changes in detritivore assemblages in forest ecosystems. We showed that microclimate and habitat affect the distributions of flightless detritivores through their behavioural and physiological traits, similarly to previous studies using morphological traits (Gibb et al., 2015a; Gibb et al., 2015b). Habitat changes during and immediately following fire might influence regulate the distribution of species in the short-term. Our results suggest that fire leaves a lasting physiological imprint on behavioural traits in detritivores, although evidence is weak for strictly physiological traits. Since these species are likely to be poor dispersers (Arnold et al., 2017; Menz et al., 2016), and given that potential legacy effects were observed eight years after the fire, behavioural changes reflecting either selection or plasticity would enable detritivores to expand the range of potential habitat and refugia following fire. We suggest that this could promote resilience in decomposition processes driven by these species following fire, consistent with other findings from both forest and grassland systems (Buckingham et al., 2015; Podgaiski et al., 2014). We suggest it would be worth investigating if reducing the short-term microclimate impacts of prescribed burns will favour conservation of invertebrate detritivores. That said, this system has experienced severe wildfires for millennia, and the general lack of broad, persistent post-fire changes to detritivores in our results indicates that they are a robust, adaptable and resilient ecological guild.

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**Table 1.** Mean, standard error and median values for physiological traits for each species, for individuals from burnt and unburnt forest.

Species	CT <sub>max</sub> (°C)			
	Burnt		Unburnt	
	Mean±SE (n)	Median	Mean±SE (n)	Median
<i>Arcitalitrus sylvaticus</i>	NA	NA	NA	NA
Armadillidae sp. 1	39±0.4 (9)	39.2	38.3±0.2 (10)	38.3
Philosciidae sp. 1	31.5±0.5 (12)	30.4	31.8±0.4 (10)	31.5
Styloniscidae sp. 1	32±0.3 (10)	31.7	32.2±0.5 (9)	32
Siphonotidae sp. 1	39.2±0.3 (12)	39.5	39±0.2 (10)	39
Siphonotidae sp. 2	38.1±0.3 (10)	38.3	38.8±0.1 (10)	39
<i>Somethus</i> sp. 1	NA	NA	NA	NA
<i>Pogonosternum laetificum</i>	37.6±0.1 (7)	37.7	36.5±0.2 (10)	36.2
<i>Victoriocambala buffalensis</i>	40.4±0.6 (10)	39.8	40.2±0.2 (10)	40
<i>Ommatoiulus moreleti</i>	43.8±0.2 (10)	43.9	44.7±0.2 (10)	44.9
H <sub>pref</sub> (% RH)				
<i>Arcitalitrus sylvaticus</i>	93.2±0.9 (8)	94.8	91.3±3 (8)	96.3
Armadillidae sp. 1	84±6.8 (6)	91	79.5±7.2 (10)	86.8
Philosciidae sp. 1	86.8±3.1 (17)	91.4	91.3±1.8 (9)	94
Styloniscidae sp. 1	87.4±3.5 (16)	94.6	81.7±5 (9)	91.6
Siphonotidae sp. 1	84.1±5.9 (20)	96.9	80.9±3.8 (11)	79.1
Siphonotidae sp. 2	84.4±6 (11)	88.8	65.6±6 (8)	65.8
<i>Somethus</i> sp. 1	NA	NA	NA	NA
<i>Pogonosternum laetificum</i>	NA	NA	NA	NA
<i>Victoriocambala buffalensis</i>	79.7±7.9 (10)	94.3	65±10.1 (11)	87.7
<i>Ommatoiulus moreleti</i>	66.2±8.6 (9)	78.6	84.8±7.1 (10)	94

T <sub>pref</sub> (°C)				
<i>Arcitalitrus sylvaticus</i>	12.9±0.4 (14)	12.1	18.7±1.3 (9)	16.7
Armadillidae sp. 1	18.9±1.4 (10)	17.1	21.5±0.9 (10)	22.6
Philosciidae sp. 1	19±0.8 (10)	19.4	19.4±1.2 (10)	19
Styloniscidae sp. 1	18±1.2 (8)	16.8	20.3±1.1 (10)	20.5
Siphonotidae sp. 1	16±0.6 (20)	15.7	20.3±0.8 (9)	20.8
Siphonotidae sp. 2	19.4±0.9 (10)	19.2	19.2±1.2 (9)	19.4
<i>Somethus</i> sp. 1	18.8±1.1 (6)	18.4	19.4±1.1 (10)	20.4
<i>Pogonosternum laetificum</i>	NA	NA	NA	NA
<i>Victoriocambala buffalensis</i>	16±0.9 (10)	14.9	18.2±1.2 (10)	17.1
<i>Ommatoiulus moreleti</i>	19.5±1.1 (10)	19.2	16.9±0.6 (10)	17.3
Weight (g)				
<i>Arcitalitrus sylvaticus</i>	0.028±0.004 (22)	0.025	0.042±0.003 (29)	0.044
Armadillidae sp. 1	0.023±0.003 (25)	0.021	0.039±0.012 (28)	0.024
Philosciidae sp. 1	0.027±0.003 (39)	0.024	0.036±0.004 (26)	0.036
Styloniscidae sp. 1	0.013±0.001 (34)	0.013	0.038±0.015 (26)	0.013
Siphonotidae sp. 1	0.008±0.001 (52)	0.006	0.008±0.001 (30)	0.007
Siphonotidae sp. 2	0.013±0.001 (31)	0.012	0.009±0.001 (27)	0.008
<i>Somethus</i> sp. 1	0.154±0.011 (8)	0.154	0.147±0.003 (27)	0.15
<i>Pogonosternum laetificum</i>	0.109±0.028 (25)	0.073	0.066±0.002 (10)	0.065
<i>Victoriocambala buffalensis</i>	0.6±0.031 (30)	0.651	0.495±0.024 (31)	0.506
<i>Ommatoiulus moreleti</i>	0.173±0.013 (29)	0.17	0.132±0.021 (30)	0.111



**Table 2.** Overall mean, standard error and median for fourteen detritivore species for four physiological traits, with sample numbers in parenthesis.

Species	Taxa	CT <sub>max</sub> (°C)		H <sub>pref</sub> (% RH)		T <sub>pref</sub> (°C)		Weight (g)	
		Mean±SE (n)	Median	Mean±SE (n)	Median	Mean±SE (n)	Median	Mean±SE (n)	Median
<i>Arcitalitrus</i> sp. 1	Amphipoda	32.8±0.4 (10)	33.1	85±5.8 (6)	91.6	13.6±1.8 (3)	12.4	0.026±0.009 (19)	0.017
<i>Arcitalitrus sylvaticus</i>	Amphipoda	33.8±0.4 (12)	34.2	91.6±1.5 (21)	94.7	15.2±0.8 (23)	14.6	0.035±0.003 (56)	0.033
Armadillidae sp. 1	Isopoda	38.6±0.2 (20)	38.5	81.7±4.5 (20)	86.8	20.2±0.9 (20)	21.2	0.031±0.006 (58)	0.023
Porcellionidae sp. 1	Isopoda	31.3±0.4 (10)	30.9	65.7±12 (8)	76.5	21.2±0.9 (10)	21.5	0.006±0.002 (28)	0.005
Philosciidae sp. 1	Isopoda	31.6±0.3 (22)	31.3	88.8±1.7 (35)	92.6	19.2±0.7 (21)	19.4	0.030±0.002 (74)	0.030
Philosciidae sp. 2	Isopoda	32.5±0.4 (12)	32.1	88.0±1.9 (13)	90.4	18.3±1.4 (9)	16.2	0.025±0.003 (34)	0.025
Styloniscidae sp. 1	Isopoda	32.1±0.3 (19)	31.8	81.9±3.3 (34)	91.5	19.3±0.8 (20)	18.2	0.022±0.006 (71)	0.013
Siphonotidae sp. 1	Diplopoda	39.1±0.2 (22)	39.2	82.9±4.1 (31)	93.5	17.3±0.6 (29)	17.4	0.008±0.001 (82)	0.006
Siphonotidae sp. 2	Diplopoda	38.5±0.2 (20)	38.8	76.5±4.9 (19)	77.4	19.3±0.8 (19)	19.4	0.011±0.001 (58)	0.010
<i>Hoplatessara pugiona</i>	Diplopoda	40.3±0.3 (9)	40.6	91.4±2.4 (5)	93.4	17.2±1.8 (3)	16.6	0.333±0.033 (17)	0.384
<i>Somethus</i> sp. 1	Diplopoda	39.1±0.1 (9)	39.1	83.0±7.2 (11)	94.0	19.2±0.8 (16)	20.3	0.148±0.003 (36)	0.149
<i>Pogonosternum laetificum</i>	Diplopoda	36.9±0.2 (20)	37.0	90.2±3.5 (10)	93.7	18.9±0.7 (11)	19.2	0.099±0.018 (41)	0.073
<i>Victoriocambala buffalensis</i>	Diplopoda	40.3±0.3 (20)	40.0	72.0±6.3 (24)	90.3	17.1±0.8 (20)	15.3	0.544±0.020 (64)	0.533
<i>Ommatoiulus moreleti</i>	Diplopoda	44.3±0.2 (20)	44.2	76.0±6.1 (19)	94.0	18.2±0.7 (20)	18.3	0.152±0.013 (59)	0.125

## Chapter 3: Appendix 2. Environmental variables

**Table 1.** Correlations between environmental variables measured across multiple seasons. Results are reported as Pearson's R (P-value). Numbers next to variables indicate they were averaged across seasons for future analysis. Abbreviations in Table 4.

	Su.Litter.av	Su.Soil.av	Su.Canopy	Su.Understory	Su.Ground	Su.Green	Su.Litter	Spr.Litter.av	Spr.Soil.av	Spr.Canopy	Spr.Understory	Spr.Ground	Spr.Green	Spr.Litter	Aut.Litter.av	Aut.Soil.av	Aut.Canopy	Aut.Understory	Aut.Ground	Aut.Green
Su.Litter.av																				
Su.Soil.av	0.21 (0.27)																			
Su.Canopy1	0.29 (0.12)	0.12 (0.53)																		
Su.Understory2	-0.15 (0.42)	-0.2 (0.28)	-0.2 (0.28)																	
Su.Ground4	-0.09 (0.65)	-0.49 (0.01)	-0.31 (0.09)	0.24 (0.21)																
Su.Green	-0.18 (0.33)	0.15 (0.44)	-0.28 (0.14)	0.15 (0.43)	-0.18 (0.34)															
Su.Litter5	0.19 (0.33)	0.37 (0.04)	0.45 (0.01)	-0.3 (0.1)	-0.83 (0)	-0.4 (0.03)														
Spr.Litter.av	0.2 (0.29)	0.15 (0.42)	0.49 (0.01)	0.11 (0.58)	-0.24 (0.2)	-0.03 (0.87)	0.24 (0.19)													
Spr.Soil.av	-0.03 (0.86)	0.05 (0.81)	0.07 (0.73)	-0.23 (0.22)	-0.34 (0.07)	0.04 (0.85)	0.3 (0.11)	0.2 (0.3)												
Spr.Canopy1	0.38 (0.04)	0.07 (0.71)	0.74 (0)	-0.31 (0.1)	-0.1 (0.61)	-0.32 (0.09)	0.27 (0.15)	0.27 (0.14)	-0.07 (0.73)											
Spr.Understory2	-0.22 (0.25)	0.07 (0.7)	-0.24 (0.2)	0.4 (0.03)	0.06 (0.74)	0.17 (0.36)	-0.16 (0.4)	0.19 (0.31)	0.08 (0.69)	-0.67 (0)										
Spr.Ground4	-0.04 (0.83)	-0.3 (0.1)	-0.17 (0.38)	0.47 (0.01)	0.57 (0)	-0.11 (0.56)	-0.47 (0.01)	0.05 (0.8)	-0.39 (0.03)	-0.12 (0.54)	0.11 (0.56)									
Spr.Green3	0.13 (0.48)	-0.34 (0.07)	-0.02 (0.91)	0.06 (0.76)	0.13 (0.48)	0.22 (0.23)	-0.25 (0.18)	-0.07 (0.71)	-0.05 (0.8)	0.1 (0.6)	-0.33 (0.08)	-0.08 (0.69)								
Spr.Litter5	-0.07 (0.7)	0.48 (0.01)	0.14 (0.47)	-0.37 (0.05)	-0.47 (0.01)	-0.13 (0.49)	0.51 (0)	0.03 (0.89)	0.3 (0.11)	0 (1)	0.2 (0.3)	-0.58 (0)	-0.76 (0)							
Aut.Litter.av	0.22 (0.24)	0.39 (0.03)	0.12 (0.54)	-0.08 (0.69)	-0.48 (0.01)	0.04 (0.81)	0.42 (0.02)	0.25 (0.19)	0.01 (0.98)	0.12 (0.54)	-0.14 (0.45)	-0.25 (0.19)	-0.05 (0.79)	0.2 (0.29)						
Aut.Soil.av	0.11 (0.55)	0.23 (0.23)	0.14 (0.47)	-0.04 (0.82)	-0.45 (0.01)	0.21 (0.27)	0.3 (0.11)	0.46 (0.01)	0.22 (0.25)	-0.15 (0.42)	0.38 (0.04)	-0.31 (0.1)	-0.2 (0.29)	0.36 (0.05)	0.5 (0)					
Aut.Canopy1	0.4 (0.03)	0.05 (0.79)	0.82 (0)	-0.23 (0.22)	-0.19 (0.32)	-0.08 (0.68)	0.22 (0.24)	0.38 (0.04)	-0.06 (0.77)	0.86 (0)	-0.5 (0)	-0.09 (0.63)	0.13 (0.5)	-0.04 (0.84)	0.12 (0.53)	0 (0.99)				
Aut.Understory2	-0.29 (0.12)	-0.24 (0.2)	-0.5 (0)	0.6 (0)	0.34 (0.07)	0.28 (0.13)	-0.48 (0.01)	-0.15 (0.41)	-0.2 (0.29)	-0.59 (0)	0.45 (0.01)	0.47 (0.01)	0.24 (0.2)	-0.51 (0)	-0.22 (0.25)	-0.18 (0.35)	-0.62 (0)			
Aut.Ground4	-0.08 (0.69)	-0.44 (0.02)	-0.38 (0.04)	0.07 (0.7)	0.66 (0)	-0.27 (0.14)	-0.46 (0.01)	-0.41 (0.02)	-0.26 (0.16)	-0.2 (0.28)	0.07 (0.71)	0.5 (0.01)	-0.06 (0.75)	-0.27 (0.15)	-0.36 (0.05)	-0.36 (0.05)	-0.3 (0.1)	0.19 (0.33)		
Aut.Green3	-0.2 (0.3)	-0.18 (0.34)	-0.15 (0.44)	0.24 (0.2)	-0.01 (0.98)	0.32 (0.08)	-0.18 (0.35)	0.11 (0.57)	0.12 (0.54)	-0.25 (0.17)	0.06 (0.77)	-0.05 (0.77)	0.7 (0)	-0.54 (0)	0.05 (0.79)	0.06 (0.76)	-0.22 (0.23)	0.48 (0.01)	-0.17 (0.38)	
Aut.Litter5	0.2 (0.29)	0.5 (0.01)	0.42 (0.02)	-0.23 (0.22)	-0.56 (0)	0.01 (0.95)	0.51 (0)	0.28 (0.14)	0.14 (0.46)	0.35 (0.06)	-0.1 (0.6)	-0.38 (0.04)	-0.43 (0.02)	0.6 (0)	0.27 (0.14)	0.27 (0.15)	0.41 (0.02)	-0.49 (0.01)	-0.73 (0)	-0.55 (0)

**Table 2.** Correlations between topography and microclimate variables. Variables kept for future analysis are in bold. Results are reported as Pearson's R (P-value). Abbreviations in Table 4.

	Days.T.1	Days.T.35	Days.H.20	Days.H.95	Humidity	Temperature	Altitude	Slope.gis	AbTMax	AbTMin
Days.T.1										
Days.T.35	-0.17 (0.37)									
<b>Days.H.20</b>	-0.06 (0.77)	0.8 (0)								
<b>Days.H.95</b>	0.55 (0)	0.17 (0.37)	0.02 (0.91)							
Humidity	0.6 (0)	-0.22 (0.25)	-0.39 (0.03)	0.78 (0)						
<b>Temperature</b>	-0.75 (0)	0.54 (0)	0.44 (0.01)	-0.25 (0.19)	-0.68 (0)					
Altitude	0.51 (0)	-0.53 (0)	-0.34 (0.06)	-0.22 (0.24)	0.27 (0.15)	-0.87 (0)				
Slope.gis	-0.51 (0)	0.31 (0.09)	0.06 (0.75)	-0.47 (0.01)	-0.41 (0.02)	0.42 (0.02)	-0.17 (0.37)			
AbTMax	-0.07 (0.72)	0.91 (0)	0.7 (0)	0.25 (0.18)	-0.16 (0.4)	0.5 (0)	-0.54 (0)	0.25 (0.18)		
AbTMin	-0.9 (0)	0.19 (0.32)	0.06 (0.77)	-0.45 (0.01)	-0.55 (0)	0.75 (0)	-0.58 (0)	0.48 (0.01)	0.11 (0.56)	
AbHMin	-0.42 (0.02)	0.33 (0.07)	0.13 (0.5)	-0.06 (0.77)	-0.15 (0.44)	0.44 (0.01)	-0.41 (0.02)	0.39 (0.03)	0.22 (0.25)	0.4 (0.03)

**Table 3.** Correlations between variables selected from Ch. 3 Appendix 2, Tables 3 and 4, and variables not measured across multiple seasons. Variables kept for fourth corner analysis are in bold. Results are reported as Pearson’s R (P-value). Table continues underneath. Abbreviations in Table 4.

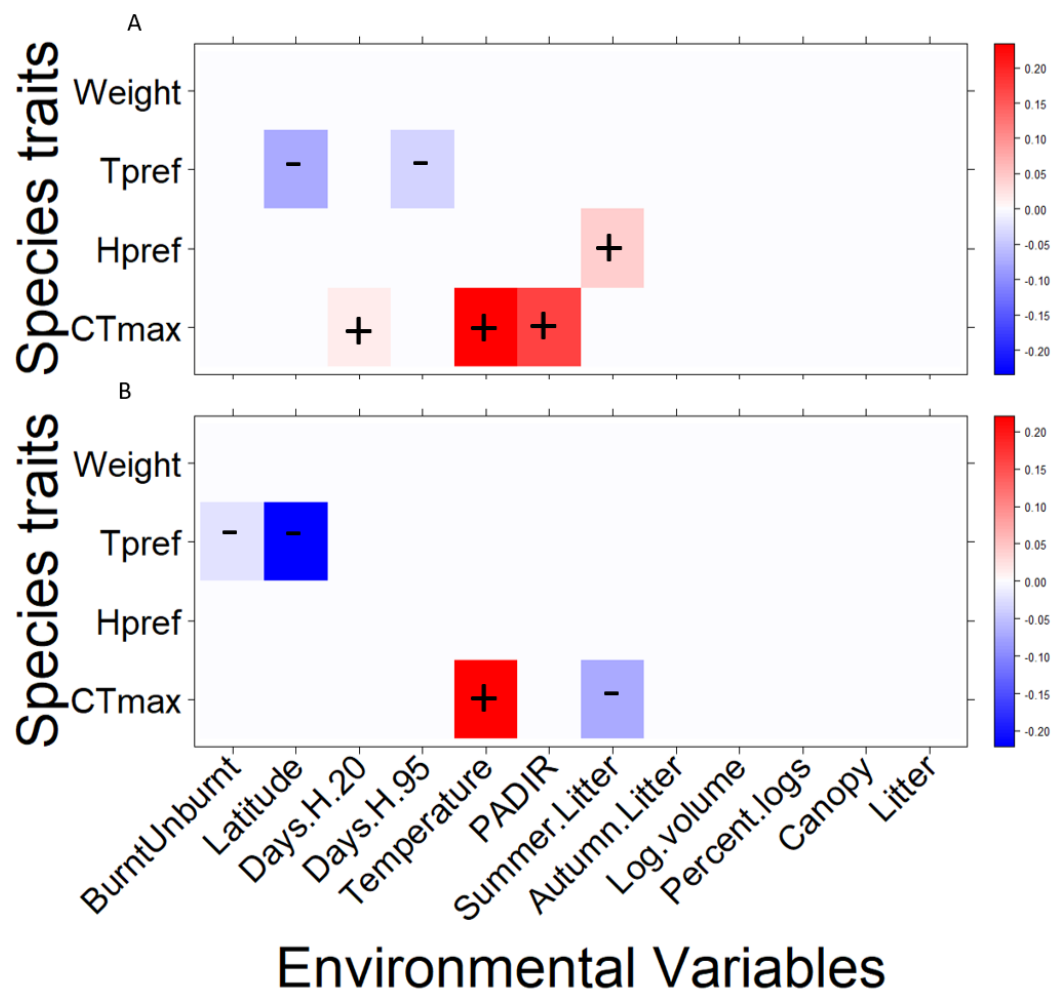
	Latitude	Longitude	Days.H.20	Days.H.95	Temp	PADIR	Su.Lit	Au.Lit	log.vol	tree.log	Canopy	Litter	SAGreen	Ground	Understory	tree.dead	Decomp	Su.Soil	tree.alive	Su.Green	Spr.Lit	Au.Soil	Spr.Soil
<b>Latitude</b>																							
Longitude	0.11 (0.57)																						
<b>Days.H.20</b>	-0.03 (0.86)	-0.3 (0.11)																					
<b>Days.H.95</b>	0.3 (0.11)	-0.48 (0.01)	0.02 (0.91)																				
<b>Temp</b>	-0.71 (0)	-0.12 (0.53)	0.44 (0.01)	-0.25 (0.19)																			
<b>PADIR</b>	0.31 (0.09)	0.39 (0.03)	0.15 (0.43)	-0.07 (0.71)	0.16 (0.4)																		
<b>Su.Lit</b>	0.13 (0.48)	0.12 (0.54)	-0.25 (0.18)	0.01 (0.95)	-0.1 (0.61)	0.13 (0.5)																	
<b>Au.Lit</b>	-0.02 (0.93)	-0.02 (0.91)	-0.39 (0.03)	-0.05 (0.8)	-0.23 (0.23)	-0.05 (0.78)	0.26 (0.17)																
<b>log.vol</b>	0.08 (0.69)	0 (1)	-0.13 (0.49)	-0.01 (0.96)	-0.27 (0.15)	-0.04 (0.83)	-0.05 (0.78)	-0.04 (0.83)															
<b>tree.log</b>	-0.36 (0.05)	0.01 (0.95)	0.01 (0.95)	-0.29 (0.11)	0.34 (0.07)	-0.2 (0.3)	0.04 (0.84)	0.11 (0.57)	-0.05 (0.78)														
<b>Canopy</b>	0.03 (0.86)	-0.13 (0.48)	-0.19 (0.32)	-0.01 (0.95)	0.01 (0.95)	-0.16 (0.4)	0.34 (0.06)	0.12 (0.52)	0.25 (0.17)	0.03 (0.87)													
<b>Litter</b>	0.4 (0.03)	-0.19 (0.33)	-0.11 (0.58)	0.22 (0.25)	-0.39 (0.03)	-0.06 (0.76)	0.12 (0.54)	0.34 (0.07)	0.13 (0.48)	-0.22 (0.24)	0.31 (0.1)												
SAGreen	-0.46 (0.01)	-0.39 (0.03)	-0.03 (0.88)	0.18 (0.34)	0.2 (0.29)	-0.36 (0.05)	0 (0.99)	-0.01 (0.96)	0.14 (0.45)	0.06 (0.76)	-0.06 (0.74)	-0.54 (0)											
Ground	-0.16 (0.41)	0.48 (0.01)	0.18 (0.35)	-0.37 (0.05)	0.39 (0.03)	0.43 (0.02)	-0.05 (0.79)	-0.44 (0.02)	-0.28 (0.13)	0.14 (0.45)	-0.26 (0.16)	-0.8 (0)	-0.01 (0.95)										
Understory	-0.07 (0.7)	0.34 (0.07)	-0.1 (0.61)	-0.05 (0.8)	-0.17 (0.38)	0.02 (0.93)	-0.22 (0.25)	-0.19 (0.31)	-0.19 (0.31)	-0.1 (0.59)	-0.62 (0)	-0.35 (0.06)	0.11 (0.57)	0.27 (0.16)									
tree.dead	-0.15 (0.44)	-0.23 (0.22)	-0.21 (0.26)	-0.1 (0.6)	0.07 (0.7)	-0.41 (0.02)	0.23 (0.22)	0.21 (0.26)	0.12 (0.52)	0.51 (0)	0.67 (0)	0.14 (0.47)	0.09 (0.65)	-0.2 (0.28)	-0.46 (0.01)								
Decomp	0.19 (0.31)	-0.1 (0.6)	-0.25 (0.19)	0.17 (0.36)	-0.38 (0.04)	-0.24 (0.21)	0.35 (0.06)	0.55 (0)	-0.24 (0.19)	-0.17 (0.37)	0.06 (0.76)	0.23 (0.22)	0.04 (0.84)	-0.29 (0.12)	-0.19 (0.32)	0.09 (0.64)							
Su.Soil	0.38 (0.04)	-0.16 (0.39)	0.06 (0.76)	0.06 (0.77)	-0.4 (0.03)	0.06 (0.74)	0.12 (0.52)	0.39 (0.03)	0.09 (0.64)	-0.22 (0.25)	0.1 (0.62)	0.56 (0)	-0.3 (0.11)	-0.52 (0)	-0.08 (0.69)	-0.11 (0.58)	0.24 (0.2)						
tree.alive	0.14 (0.48)	-0.42 (0.02)	-0.25 (0.19)	0.35 (0.06)	-0.28 (0.14)	-0.42 (0.02)	0.18 (0.33)	0.1 (0.6)	0.2 (0.3)	-0.27 (0.15)	0.66 (0)	0.33 (0.07)	0.21 (0.26)	-0.46 (0.01)	-0.37 (0.04)	0.61 (0)	0.34 (0.07)	0.07 (0.7)					
Su.Green	-0.19 (0.32)	-0.11 (0.56)	-0.1 (0.6)	0.05 (0.8)	-0.11 (0.56)	-0.47 (0.01)	-0.26 (0.16)	0.1 (0.59)	0.14 (0.45)	0.23 (0.22)	-0.23 (0.22)	-0.32 (0.09)	0.32 (0.08)	-0.12 (0.53)	0.28 (0.14)	-0.06 (0.76)	-0.04 (0.83)	0.03 (0.88)	-0.17 (0.38)				
Spr.Lit	0 (1)	0.17 (0.36)	-0.55 (0)	-0.15 (0.42)	-0.45 (0.01)	-0.31 (0.1)	0.26 (0.16)	0.25 (0.19)	0.17 (0.37)	-0.01 (0.97)	0.38 (0.04)	0.2 (0.3)	0.01 (0.95)	-0.25 (0.18)	0.07 (0.73)	0.31 (0.1)	0.17 (0.37)	0.15 (0.42)	0.34 (0.07)	0.04 (0.85)			
Au.Soil	0.11 (0.55)	0.21 (0.27)	-0.46 (0.01)	0.02 (0.93)	-0.58 (0)	-0.28 (0.14)	0.15 (0.41)	0.5 (0)	0.24 (0.2)	0.16 (0.38)	-0.02 (0.91)	0.34 (0.07)	-0.09 (0.63)	-0.43 (0.02)	0.11 (0.57)	0.1 (0.6)	0.33 (0.08)	0.23 (0.23)	0.01 (0.95)	0.24 (0.21)	0.46 (0.01)		
Spr.Soil	0.45 (0.01)	-0.2 (0.28)	-0.27 (0.15)	0.39 (0.03)	-0.53 (0)	-0.18 (0.33)	-0.05 (0.8)	0.01 (0.98)	0.2 (0.29)	-0.26 (0.17)	-0.02 (0.9)	0.28 (0.13)	0.02 (0.91)	-0.37 (0.05)	-0.12 (0.53)	0.06 (0.74)	0.4 (0.03)	0.05 (0.81)	0.39 (0.03)	0.02 (0.91)	0.2 (0.3)	0.22 (0.25)	
Log.burn	0.41 (0.03)	0.14 (0.46)	-0.1 (0.58)	0.22 (0.25)	-0.56 (0)	-0.08 (0.66)	-0.16 (0.39)	-0.04 (0.82)	-0.18 (0.33)	-0.17 (0.38)	-0.61 (0)	0.12 (0.52)	-0.21 (0.26)	-0.06 (0.74)	0.62 (0)	-0.37 (0.05)	0.03 (0.86)	0.04 (0.83)	-0.23 (0.23)	0.12 (0.52)	0.12 (0.53)	0.28 (0.13)	0.34 (0.06)

**Table 4.** Description and abbreviations of variables used in analysis.

Abbreviation	Description
PADIR	Potential annual direct incident radiation
Altitude	Site altitude (m)
Slope	Slope (degrees)
Days.1.C	Number of days <1 C
Days.35.C	Number of days > 35 C
Humidity	Average site humidity
Days.H.20	Number of days < 20% RH
Days.H.95	Number of days > 95% RH
Temperature	Average site temperature
AbTMax	Highest recorded temperature at site
AbTMin	Lowest recorded temperature at site
AbHMin	Lowest recorded humidity at site
Burnt	Burn status of site (burnt/unburnt)
Canopy	% Canopy cover
Understory	% understory cover
tree.dead	% of standing trees that were dead
tree.alive	% of standing trees that were alive
tree.log	% of trees as logs
Litter	% ground cover as litter averaged across all seasons
Ground	% ground cover as bare ground averaged across all seasons
log.vol	Average log volume
Decomp	Average log decomposition for site
Log.burn	Average log burn severity for site
Slope.gis	Site slope, from GIS layer
SAGreen	% averaged spring and autumn ground plant cover
Su.Litter.av	Litter depth in summer
Su.Soil.av	% soil volumetric water content in summer
Su.Canopy	% Canopy cover in summer
Su.Understory	% understory cover in summer
Su.Ground	% ground cover as bare ground in summer

(Table 4 continued)

Su.Green	% ground cover as ground plants in summer
Su.Litter	% ground cover as litter in summer
Spr.Litter.av	Litter depth in spring
Spr.Soil.av	% soil volumetric water content in spring
Spr.Canopy	% Canopy cover in spring
Spr.Understory	% understory cover in spring
Spr.Ground	% ground cover as bare ground in spring
Spr.Green	% ground cover as ground plants in spring
Spr.Litter	% ground cover as litter in spring
Aut.Litter.av	Litter depth in autumn
Aut.Soil.av	% soil volumetric water content in autumn
Aut.Canopy	% Canopy cover in autumn
Aut.Understory	% understory cover in autumn
Aut.Ground	% ground cover as bare ground in autumn
Aut.Green	% ground cover as ground plants in autumn
Aut.Litter	% ground cover as litter in autumn



**Figure 1.** Standardised interaction coefficient estimates for interaction terms from the fourth corner analysis, testing the relationship between physiological traits and the environment excluding two species, due to sample size of 3 for one trait: A) species abundances; and B) species occurrence. Coefficients shown in red (positive) or blue (negative) were significant in the best model. Cell colour intensity indicates the strength of the interaction (scale shown on side bar). Abbreviations for environmental variables as for Table 1. Test statistics for A) are  $D=98.22$ ,  $p=0.012$ ; and B)  $D=94.05$ ,  $p=0.021$ .

## Chapter 4: Does isolation by distance following a severe, landscape-level wildfire slow recovery of dispersal-limited detritivores?

Authors: J. Grubb, H. Gibb and N. Murphy

### Abstract

Although fire is a natural disturbance in many ecosystems, predictions suggest the extent of severe fires will increase in some ecosystems. This is concerning for biota that cannot adapt to this change, especially those that are dispersal-limited. In this study, we investigated if the recovery of mostly flightless invertebrate detritivores after a severe wildfire was limited by distance from unburnt forest patches. We compared habitat variables and detritivore abundance/richness in two microhabitats (leaf litter and logs) along ~5 km transects, moving from the edge to the centre of a fire that burned 8 years before this study. We found that burnt and unburnt forest retained distinct assemblages after fire, especially in the litter. We attribute the stronger response of litter taxa to the greater temporal variation in temperature and humidity in the litter as compared to logs. Lepidoptera and Isopoda showed the strongest differences between burnt and unburnt forest, having higher abundances in unburnt forest. This result may reflect changes in litter inputs and quality, as burnt sites still had low canopy cover and high understory cover relative to unburnt sites. We found that overall abundance declined in logs with increasing distance into the burn, but such effects were not observed in the litter. At the taxon-level, only millipede abundance and site occupancy declined with distance from edge of the burn, while some amphipods and isopods actually increased. Our results suggest millipedes may not survive *in situ* as successfully as amphipods or isopods, although their recovery may also reflect slower population growth. Overall, our results indicate that detritivore recovery in this system requires more than eight years and is likely partly contingent on habitat recovery. We suggest that excluding unburnt forest patches



from management burns following large, severe fires is an appropriate management strategy favouring detritivore recovery in light of projections for increases in fire occurrence.

## Introduction

Fire is a major natural disturbance across many ecosystems (Flannigan et al., 2009), and many ecosystems would be substantially altered if fire regime was changed (Bowman et al., 2016; Perry et al., 2014). For example, forests would be replaced by grasslands in many regions if the frequency of burning increased (Bond et al., 2005). Fires are essential for maintaining species diversity and persistence, and the function of many ecosystems across the globe (Burrows, 2008; Pausas and Keeley, 2009). Increasing global dominance of fire regimes by anthropogenic influences over the last few hundred years is thus of particular interest and potential concern (Bowman et al., 2011; Pausas and Keeley, 2009; Pechony and Shindell, 2010). For example, historic fire suppression has altered forest composition and increased tree density in western United States, and resulted in increased attacks from saproxylic beetles (Parker et al., 2006).

Post-fire ecosystem recovery, especially after severe fires is lengthy, and likely prolonged when fire extent increases isolation from potential unburnt refugia. Although factors such as topography and habitat heterogeneity tend to reduce the effects of even the most severe fires, this moderating influence is lost under extreme weather conditions (Bassett et al., 2017; Bigler et al., 2005; Leonard et al., 2014). This influence of weather on fire regime has meant that current climate change models, in which hotter and dryer weather is expected to be more frequent, predict an increase in the severity and extent of fires (Bowman et al., 2009; Brennan et al., 2009; Clarke et al., 2011; Penman and York, 2010). In addition, dryer conditions are predicted to predispose some ecosystems to more frequent burning (Bradstock, 2010; Flannigan et al., 2009). This is of particular interest because large fires can leave large, severely burnt patches with few

refugia (Bradstock, 2008; Leonard et al., 2014; Robinson et al., 2014). In addition, many refugia that remain are floristically distinct from the burnt landscape, reflecting the locally unique character, like topography (e.g. in gullies), that predisposed them to be skipped. Such refugia may not be suitable for maintenance of some species (Clarke, 2002; Gandhi et al., 2001). Thus, the combination of anthropogenic influences and climate change may lead to an increase in the extent of hostile habitat and fewer refugia following fires.

The effects of severe fires on biota are especially important and are at least two-fold. First, taxa may be eliminated and/or their abundance reduced at least initially (Swengel, 2001), effects which become more likely as burn severity increases (Ch. 2). Loss of taxa means that recolonization will be required from refugia for faunal recovery to be complete. Second, some taxa may survive *in situ*, but habitat changes after fire could mean they suffer post-fire mortality due to habitat loss (Banks et al., 2011; Gandhi et al., 2001; Warren et al., 1987) or persist at different abundances relative to unburnt forest. For instance, severe fires can eliminate microhabitats upon which particular taxa depend, and some (e.g. decomposed logs and fine litter) may require a long time for replacement (Banks et al., 2011; Gandhi et al., 2001).

Loss or reduction of such taxa can significantly alter ecosystem function. One group that is especially important for ecological function of forests are the detritivores, as they contribute to natural regulation of surface fuel loads, a critical determinant of fire regime (Brennan et al., 2009; Buckingham et al., 2015). Soil fauna experience increasingly negative effects as fire severity and frequency increase (Malmström, 2010; Moretti et al., 2006), but the effect of increased fire extent is poorly understood. Thus, unburnt refugia are essential to persistence of some invertebrate taxa in the landscape following fire (Gandhi et al., 2001). Detritivores are often flightless, so may be slow to disperse and recolonise from unburned patches following disturbance events, even where habitats are suitable (Arnold et al., 2017; Coleman and Rieske, 2006; Menz et al., 2016). In the

case of severe wildfires, such unburned patches may exist mainly on the fire edge, and be rare within the fire boundary (Leonard et al., 2014). Thus, the distance from fire edge may become important in determining the recovery of species (Arnold et al., 2017). Recovery after fire will thus originate from either *in situ* survivors or recolonising invertebrates from intact habitat.

In an effort to study the significance of such spatial correlates or recolonisation, we examined assemblages of litter detritivores along gradients from the edge to the centre of severely burnt *Eucalyptus* forests. We predicted that 1) habitat would remain different between unburnt and burnt forest, even seven-eight years after severe fire; 2) that detritivore assemblages would differ between burnt and unburnt forest; and 3) that richness and abundance would decline, and community composition change with increasing distance from unburnt areas, reflecting a slow recovery of detritivore species recolonising area that had been severely burnt.

## Methods

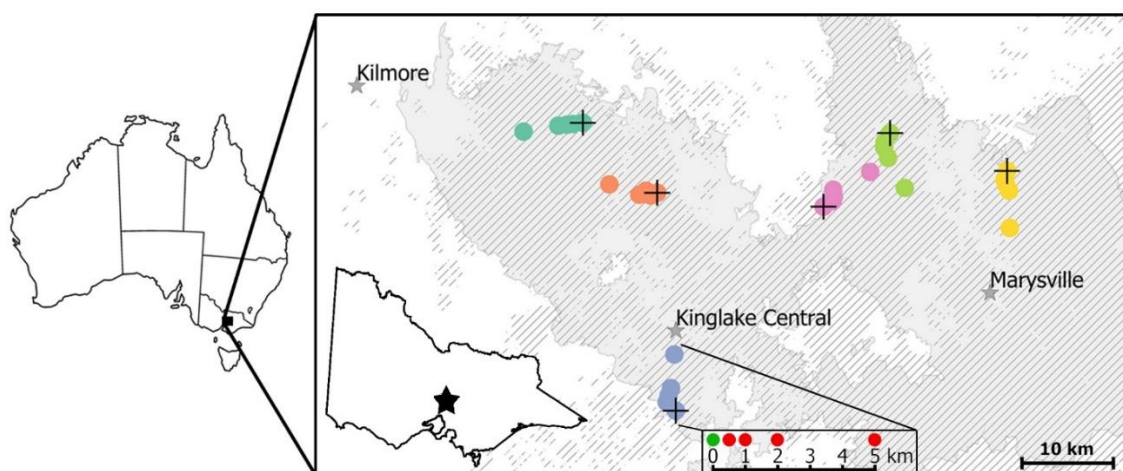
### Study sites

This study was conducted in forests ~50 km north-east of Melbourne, in south-eastern Australia (Fig. 1). Sites were located in dry sclerophyll forest, dominated by messmate (*Eucalyptus obliqua*) and peppermint gum (*Eucalyptus radiata*), with an understory of Austral bracken (*Pteridium esculentum*), *Acacia spp.* and *Eucalyptus spp.* saplings. Site altitude ranged from 252 m to 816 m. Sites were set along six 5 km transects, with five sampling points (sites) each (Fig. 1). The sites were located within (burnt) or just outside (unburnt) the boundary of the Kilmore East-Murrindindi fire complex, the footprint of a massive fire which began on 9<sup>th</sup> February 2009 and burnt over 228,000 ha. The severity of this fire was considered high for much of the area (Leonard et al., 2014). The first site of each transect was located in forest unburnt in 2009 and for at least

20 years prior, while the remaining four sites were placed at increasing distance from unburnt areas along each transect. These latter four sites were in forest that had been severely burnt (crown scorch/fire) in the 2009 fires. All sites except three (clear-felled 12 and 14 years prior to 2009) had been unlogged for at least 20 years prior to 2009. To capture temporal variation, litter and log samples were taken in summer, spring and autumn across three years, although not all were sampled every year (Table 1). No winter sampling was undertaken due to time constraints and difficulty in accessing some sites in wet conditions. Sampling that occurred from December-February was classed as summer, March-May as autumn and September-November as spring.

*Table 1.* Year and season of sampling periods, along with microhabitat type sampled. Number of sites sampled (n) are also given.

<b>Year</b>	<b>Season</b>	<b>Litter</b>	<b>Log</b>	<b>n</b>
2015	Summer	✓		30
	Autumn	✓		30
	Spring	✓	✓	30
2016	Autumn	✓	✓	30
	Spring	✓	✓	30
2017	Summer	✓	✓	6



*Figure 1.* Map of study sites, located in south-eastern Australia, and their positions relative to three towns (grey stars). Colours indicate different transects and crosses (+) are unburnt sites and the beginning of each transect. Inset at bottom shows distances for transect sampling points (green = unburnt, red = burnt). The grey outline indicates fire extent, and hatching indicates forest.

### Microclimate and habitat

Temperature and relative humidity were measured at all sites using Tinytag Plus<sup>®</sup> loggers in weather stations (similar to Stevenson Screens; used to ensure ambient conditions were measured and not influenced by rain or sunlight) placed 10 cm above the ground to record near-ground conditions. Readings were collected every half hour for one year (1 February 2016-2017). Temperature and percent relative humidity (% RH) were measured for each season using the following indices: average maximum temperature and % RH; highest maximum temperature, minimum temperature and % RH; average day and night temperature and % RH; the number of days over 95% RH, under 20% RH, over 35°C and under 1°C.

Environmental variables were measured in summer, autumn and spring 2015, and autumn and spring 2016, although characteristics that change very slowly were not measured every season, (e.g., number of standing trees, for instance, was unlikely to change substantially over 3 years and

was measured once). PADIR (Potential Annual Direct Incident Radiation) was calculated using equation 2 from McCune and Keon (2002) using latitude, slope and aspect (the latter two were obtained from GIS data provided by Geoscience Australia, 2017). We counted live and dead standing trees (diameter at breast height  $\geq 10$  cm) and logs (diameter  $\geq 10$  cm) within a 5 m radius at ten points distributed evenly along a 100 m transect, at each site in summer 2015. Canopy and understory cover, and litter, plant and bare ground cover within a 1 m radius were visually estimated at five 10 m intervals along one 50 m transect per site per season (except for summer 2015, when the 100 m transect was used). At the same time and locations, litter depth (carpenter's square) and soil volumetric water content (Fieldscout TDR 100 soil moisture meter probe, Spectrum Technologies, USA, and DSMM500, General Tools & Instruments, USA) were measured at three haphazard points within a 625 cm<sup>2</sup> quadrat, selecting the nearest unbroken patch of litter to the sample point. The few missing values for environmental variables (due to unavailable equipment or data errors), were replaced with average values from all samples for that sampling period.

During log surveys, the following measurements were made of logs containing invertebrates in spring 2015 and 2016, and autumn 2016. Decomposition was estimated according to Lindenmayer et al. (1999), where freshly fallen logs = 1, solid log without bark = 2, sapwood decomposing = 3, entire log decomposing, but still retaining shape = 4, and completely disintegrated logs with no discernible shape = 5. Burn severity of logs was estimated on a similar scale, where 0 = unburned, 1 = scorched (<15% burnt), 2 = a mixture of severe burning and unburnt (<85% burnt), and 3 = entirely blackened. We used log radius and length with the equation for cylinder volume ( $V = \pi * r^2 * \text{length}$ ) to calculate log volume; values were halved for laterally split log fragments.

### Litter and log invertebrate sampling

Three flightless taxa (Diplopoda, Amphipoda and Isopoda) and one having a winged adult stage (Lepidoptera) were sampled at the thirty sites. These taxa were selected as they are abundant macro-arthropod detritivores at our sites. Sampling of litter and logs used methods previously established as reliable indicators of the detritivore community (Ch. 1). Taxonomic experts were consulted to identify Diplopoda (Robert Mesibov) and keys used for Amphipoda and Isopoda (Friend, 1987; Green, 1961; Green, 1974). To determine the importance of microhabitat, detritivore communities were examined from both leaf litter and logs. Litter invertebrates were extracted from litter removed down to the mineral earth from the 625 cm<sup>2</sup> quadrat where litter depth was measured (n=5 per site per sampling period). The litter was then left for a minimum of four days in Tullgren funnels and only removed once completely dry. Invertebrates were collected into vials of 100% ethanol under the funnels.

Log invertebrates were sampled using visual searches, conducted in spring 2015, spring and autumn 2016, and summer 2017, at all 30 sites. Logs >9 cm diameter were visually selected by walking haphazardly through the plots within <200m of the transect and then searched by rolling and/or dissecting a section (usually 30-60 cm), by hand and the assistance of a hammer and small crowbar. We were unable to search some very large logs, as they were too large to be rolled or the wood too solid to be pulled apart, though it was often possible to search under bark. This method was considered appropriate for the target taxa, since they were not borers capable of occupying solid wood requiring a rearing/extraction approach, but instead occupied decayed wood and existing holes/cracks. When thorough searching of visible surfaces on the log and the ground where the log touched the ground did not yield any more specimens, the next log was searched, until 30 minutes had elapsed (time included searching for logs and collecting invertebrates from logs; time spent labelling was excluded). Specimens from logs were collected

directly into 100% ethanol. Since logs were visible at our sites, our ability to locate logs reflected log density, meaning sampling reflected relative abundance at our sites.

### Analysis

We used principal components analysis (PCA) to summarise environmental variation at burnt sites for use in further analysis. All climate, habitat and topographic variables were included in the PCA. Prior to PCA, all environmental variables were standardised using two standard deviations (Gelman, 2008). Principal components (PC) values were first averaged across years, then seasons for each site when producing PCA biplots, since it was difficult to see differences when all points were plotted. Litter and log datasets were analysed separately, and the first three PC were used in subsequent analysis. Linear mixed models (LMMs) were used to test the effect of distance on each principal component for both microhabitats for burnt sites only. Separate models were run for each PC, with distance, year and season as fixed effects and sampling point nested within site as a random effect. Residuals from these models were included when testing the effects of distance on detritivores. Logged sites were excluded from these and all other analyses.

We used `manyglm` to test for differences between burnt and unburnt sites. ANOVA tests of `manyglm` models were run with 9999 permutations, and season, year and sampling point as fixed factors. When producing plots for visualisation, actual values were first averaged across years, then seasons and transects, where applicable, and standard error was calculated across transects.

We compared the abundance and richness of litter and log detritivores between burnt and unburnt forest using generalised linear mixed models (GLMMs). Season, and sample point nested within transect were included as random effects in both litter and log generalised linear mixed



models. Estimated marginal means and 95% confidence intervals were generated from generalised linear mixed models for visualisation where appropriate. To compare communities between burnt and unburnt forest, we ran two manyglm models, one with a negative binomial distribution and analysed abundance of all taxa, and a second with a binomial distribution and a presence/absence dataset to focus on occupancy, rather than abundance. Both models included year, sampling point (site) and season as fixed factors to account for temporal and spatial variation.

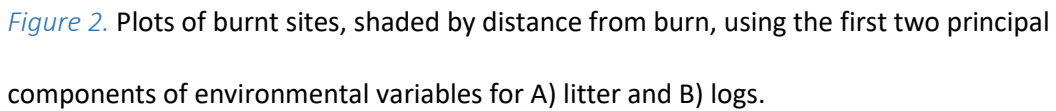
GLMMs were also used to test the effect of distance on richness and abundance for both microhabitats. Sample point nested within transect was included as a random effect for both litter and log models, in addition to season for litter, and season within year for log models. Where appropriate, GLMM fitted values were plotted and a line assuming a quasi-Poisson distribution was fitted to these points  $\pm$ SE to aid visualisation. To determine the effect of distance from edge on communities, we used manyglm, including year, sampling point (site) and season as fixed factors to account for temporal and spatial variation. To test the effect of distance on the detritivore community, manyglm was used. We included the residuals from each PC regression detailed above as fixed factors in both our distance GLMMs and manyglms, to control for environmental variation, while removing the possibility that environmental variables might be correlated with distance. We ran two manyglm models, one with a negative binomial distribution and analysed abundance of all taxa, and a second with a binomial distribution and a presence/absence dataset to focus on occupancy, rather than abundance. Unburnt sites were excluded from analyses of the effects of distance on detritivores, since abundance was generally much higher in unburnt forest, potentially leading to a false positive.

All manyglms were run with 999 bootstraps and resampling using the "pit.trap" method, and Dunn-Smith residual plots were checked for normality. For both manylm and manyglm, post-hoc p-values were unadjusted for multiple comparisons, as this was considered overly conservative (García, 2004), and instead  $\alpha \leq 0.001$  was used for all post-hoc univariate results. The two microhabitats (litter and log) were assessed separately.

## Results

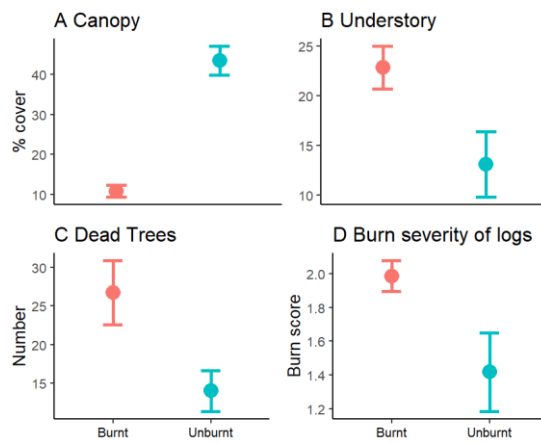
### 1. How does burning and distance from burn edge affect habitat?

For burnt sites, principal components 1, 2 and 3 of litter environmental variables explained 38%, 12% and 10% of the total variance respectively (total 58%), while the log PCAs explained 27%, 12% and 10% respectively (total 48%; Fig 2; Ch. 4 Appendix Table 1). Temperature generally contributed positively and humidity negatively to the first PC axis in the litter dataset, while the opposite effects were seen for PC one in the log dataset (Ch. 4 Appendix Table 1). Number of dead trees and slope were negatively associated with the second litter PC axis (Table 1). Live trees, litter cover and altitude were positively associated with litter PC axis three (Ch. 4 Appendix Table 1). Log PC axis two was negatively associated with bare ground cover, and positively with litter cover, live trees and altitude (Ch. 4 Appendix Table 1). Understory cover and dead trees were negatively, and canopy cover positively associated with log PC three (Ch. 4 Appendix Table 1). Although it is possible that unburnt sites had escaped burning because they were distinct, there are several reasons why this was not considered a major confounding factor. All sites were in dry sclerophyll forest and of the topographic measures (slope, PADIR, altitude), only altitude was marginally higher in burnt than unburnt sites ( $p < 0.05$ ; Appendix, Table 2) when analysed using a manylm, which is above the threshold of  $\alpha = 0.001$  we consider appropriate for this analysis. Other habitat differences (such as canopy cover and number of logs) can be attributed to the impact of burning. Finally, the Black Saturday fires were so severe in places that topography no longer had its usual mitigating effect, meaning that unburnt patches were often dependent on the weather conditions (Leonard et al., 2014).



*Table 2.* Linear mixed model results (ANOVA) testing the relationship between distance from unburnt sites for each of the three principal components. Sample point nested within transect was included as random effects for both litter and log models, in addition to season for litter, and season within year for log models.

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*Figure 3.* Environmental variables significantly different between burnt and unburnt sites (manyln  $p < 0.001$ ). Full results are given in Ch. 4 Appendix Table 2.

Hypothesis 2. Do abundance, species richness and composition of detritivore assemblages differ between burnt and unburnt forest eight years after fire?

Litter detritivores were more abundant and species richness was higher in unburnt sites than burnt sites, but neither abundance nor richness of log detritivores differed according to burn status (Table 3, Figure 4). Similarly, community composition was affected by wildfire in litter but not logs (Table 3). Abundance was lower in burned sites for litter-dwelling Lepidoptera, Psychidae, Porcellionidae sp. 1, Armadillidae sp. 1 & 2 and unidentified Armadillidae (Table 3). In general taxa that showed reduction in occupancy also showed reduced abundance. The only exceptions were *Victoriocambala buffalensis* in the litter and unidentified Dalodesmidae in logs, which only had reduced microhabitat occupancy in burnt forest (Table 3).

**Table 3.** General linear mixed model and manyglm (and post-hoc) results testing the difference between burnt and unburnt sites in abundance and richness of litter and log detritivores. Season, and sample point nested inside transect was included as random effects for both litter and log general linear mixed models. Year, sampling point (site) and season were included as fixed factors in manyglm analysis. Significant p-values are in bold.

Variable	Litter						Log					
	Abundance			Richness			Abundance			Richness		
	z		P	z		P	z		P	z		P
	z	P	D	z	P	D	z	P	D	z	P	D
Burnt/unburnt	7.3	0.007	102.4	0.001	79.2	0.001	0.6	0.423	35.1	0.163	30.0	0.447
Year			70.8	0.001	36.1	0.174			412.6	0.001	54.8	0.005
Site			479.5	0.001	361.7	0.001			99.8	0.002	419.0	0.001
Season			275.5	0.001	161.8	0.001			52.1	0.009	83.4	0.021
Community post-hoc												
Abundance relative to unburnt	Decreasers						Increases					
	Lepidoptera **						Philoscidae sp. 3 *					
	Psychidae **						Brachyiulus pusillus *					
	Immature Amphipoda *											
	Amphipoda sp. 1 (rare) *											
	Styloniscidae sp. 3 *											
	Porcellionidae sp. 1 **											
	Armadillidae sp. 1 ***											
	Armadillidae sp. 2 ***											
	Armadillidae unknown **											
	Porcellionidae sp. 1 ***											
	Armadillidae sp. 2 ***											
	Armadillidae unknown ***											
	Psychidae *											
	Victoriocambala buffalensis *											
Presence/absence relative to unburnt	Unidentified Dalodesmidae *											

p \* <0.05, \*\* <0.01, \*\*\* <0.001

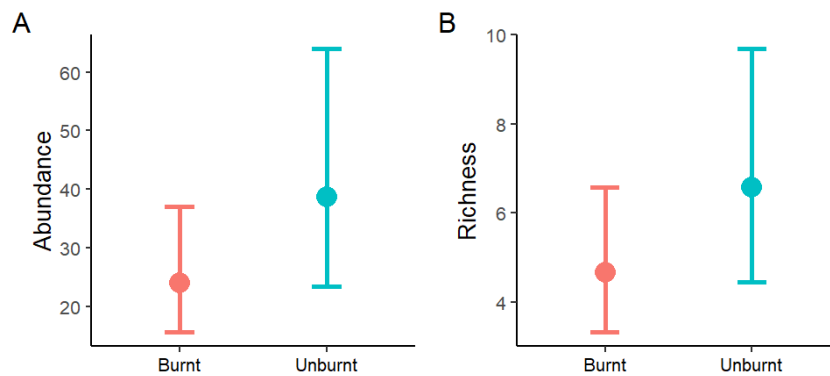


Figure 4. A) Abundance and B) richness of litter detritivores in burnt and unburnt sites, using estimated marginal means and 95% confidence intervals from generalised linear mixed models.

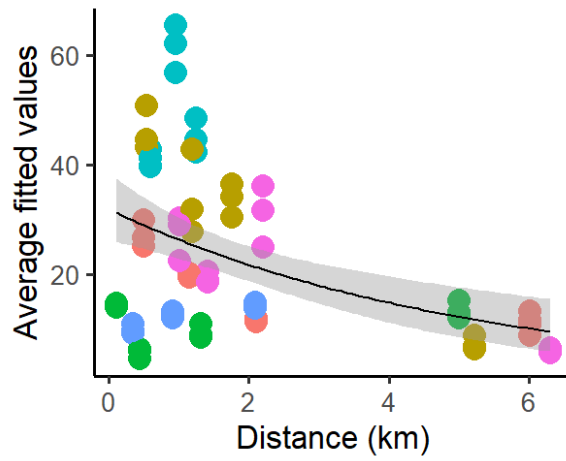
Hypothesis 3. Do species richness and abundance decline, and does composition of assemblages change with increasing distance from fire edge?

Neither abundance nor richness of litter detritivores changed with distance from the unburnt forest, but the abundance of log detritivores declined with distance into the burn, particularly after two kilometres from unburnt patches (Fig 5; Table 4). Both community composition and presence/absence of detritivores changed with distance from the edge in both litter and log communities (Table 4). Post-hoc manyglm comparisons indicated that abundance of *Brachyiulus pusillus*, *Ommatoiulus moreleti* and Siphonotidae sp. 1 declined with distance in both litter and logs (Table 4). In the litter unidentified diplopods and *Victoriocambala buffalensis* decreased but Philosciidae sp. 1 and Chordeumatida (very rare) increased with distance from the burn edge. Interestingly, Amphipoda sp. 1 (rare), *Arcitalitrus sylvaticus* and Stytoniscidae sp. 1 increased with distance in both litter and logs (Table 4). Species that showed an effect of distance on abundance generally followed the same trend when analysed using presence/absence.



**Table 4.** Generalised linear mixed model and manyglm results testing the relationship between distance from unburnt sites and abundance and richness of litter and log detritivores. Sample point nested within transect was included as random effects for both litter and log models, in addition to season for litter, and season within year for log models. Residuals of principal components of habitat properties were used as covariates in all models, while sampling point (site), year and season were included as fixed effects in manyglm models. Significant values are in bold.

Variable	Litter										Log																													
	Community										Community																													
	Abundance					Richness					Abundance					Richness					Abundance					Pres/Abs														
	z	P				z	P				z	P				z	P				z	P				z	P													
Distance	-0.8	0.414	0.5	0.600	72.0	<b>0.005</b>				65.1	<b>0.006</b>				-2.5	<b>0.014</b>	0.2	0.804	48.8	<b>0.026</b>	60.7	<b>0.003</b>																		
PC1 residuals	-1.4	0.157	0.6	0.547	20.9	0.808				18.2	0.939				1.0	0.294	0.9	0.372	15.2	0.935	12.7	0.975																		
PC2 residuals	-0.1	0.925	-0.1	0.954	35.4	0.247				21.1	0.869				1.4	0.168	1.4	0.160	35.4	0.231	45.6	0.081																		
PC3 residuals	-0.8	0.403	0.5	0.614	28.0	0.546				37.3	0.269				0.6	0.519	-0.1	0.908	30.6	0.350	22.1	0.776																		
Site					449.2	<b>0.001</b>				419.7	<b>0.001</b>								425.9	<b>0.001</b>	387.2	<b>0.001</b>																		
Year					47.0	0.065				34.1	0.313								48.1	<b>0.017</b>	52.6	<b>0.021</b>																		
Season					264.4	<b>0.001</b>				211.4	<b>0.001</b>								87.1	<b>0.009</b>	72.0	0.118																		
<b>Community post-hoc</b>					<b>Decreasers</b>										<b>Decreasers</b>										<b>Increases</b>															
Abundance vs distance	<i>Brachyiulus pusillus</i> **										Chordeumatida (rare) **										<i>Brachyiulus pusillus</i> **										Amphipoda sp. 1 (rare) *									
	<i>Ommatoiulus moreleti</i> *										<i>Arcitalitrus sylvaticus</i> *										<i>Ommatoiulus moreleti</i> **																			
	Unidentified Diplopoda *										Philosciidae sp. 1 *										Siphonotidae sp. 1 ***																			
	<i>Victoriocambala buffalensis</i> *										Styloniscidae sp. 1 *																													
Siphonotidae sp. 1 *																																								
Presence/ absence vs distance	Unidentified Diplopoda *										Chordeumatida (rare) **										<i>Brachyiulus pusillus</i> **										Amphipoda sp. 1 (rare) *									
	<i>Victoriocambala buffalensis</i> *										Amphipoda sp. 1 (rare) *										<i>Ommatoiulus moreleti</i> *										<i>Arcitalitrus sylvaticus</i> **									
	Siphonotidae sp. 1 *										<i>Arcitalitrus sylvaticus</i> *										Siphonotidae sp. 1 *										Styloniscidae sp. 1 *									
											Philosciidae sp. 1 *																													
										Styloniscidae sp. 1 *																														



*Figure 5.* Overall abundance of log-dwelling detritivores, using averaged fitted values from a generalised linear mixed model, with a line  $\pm$ SE (quasi-Poisson distribution) provided for visualisation. Colours indicate different transects.

## Discussion

The predicted general increase in extent of wildfires is likely to be especially detrimental for dispersal-limited detritivores as it may become more difficult for them to recolonise central areas of large burns. Thus, we sought to determine if recovery of detritivores after a severe, landscape-level fire was affected by distance from fire edge, and if gradients in habitat could be responsible for any observed effects. We found that both habitats and detritivore assemblages in burnt forest differed substantially from those in unburnt forest eight years after severe wildfire. This was particularly true in leaf litter, where abundance and richness were lower in burnt forest. Habitat did not apparently change with distance from the edge (see also Arnold et al., 2017), but overall abundance of log detritivores nonetheless declined although litter richness and abundance were unaffected. Community analysis indicated that while various taxa increased or decreased with distance from burn edge, particularly in the litter, an overall trend for decline was generally stronger. With the exception of introduced species, taxa influenced by burn status were distinct from those affected by distance from burn edge. The response of detritivores to wildfire thus appeared to fall into two categories: those which persist at low abundances after fire regardless of distance, consistent with *in situ* survival, and those that decrease (or increase) with distance from burn edge.

The effects of fire were still evident after eight years, as the habitat structure of burnt forest remained distinct from unburnt forest, which is likely to be partly responsible for the detritivore responses we observed. While it is possible that such differences are due to unburnt sites escaping burning due to their topographic features, our results indicate that unburnt sites were generally comparable to burnt sites, which is consistent with evidence that weather conditions during the fire often eliminated the mitigating effects of topography (Leonard et al., 2014). Most differences arose from the loss of mature trees, since our burnt sites were all severely burnt (crown scorch/burn). Thus, burnt sites had lower canopy and higher understory cover, and since

microclimate appears to be insensitive to these changes in the long-term (Ch. 3), observed effects on detritivores more likely reflect changes to aspects of habitat quality such as detritus input and quality (Croft et al., 2010; Grove et al., 1986; Jakubas et al., 1994). For instance, the relative contribution of leaves, bark and wood have been shown to change over time in eucalypt forest for at least ten years following fire (Fox, 1979). Post-fire litter may be higher in quality due to nutrient release in some systems (Wang et al., 2014), but litter quality is more usually falls immediately following fire and increases gradually over time (Kay et al., 2008; Schafer and Mack, 2014; Stirling et al., 2019). The similarity in leaf litter depth between burnt and unburnt forest reflects the rapid leaf litter accumulation after fire, as is common in eucalypt forests (Birk and Bridges, 1989; Raison et al., 1986b). However, later stages of decomposition and 'mulching' effects on detritus microclimate may not have fully developed (Balch et al., 2008; Raison et al., 1986b). The modest differences in log-dwelling detritivores between burnt and unburnt forest was surprising, given that logs decompose more slowly than litter, which would suggest differences would persist for longer. A more detailed investigation of detritivore habitat requirements in logs may explain this result. However, the lower abundance of litter detritivores in burnt forest, regardless of distance, suggests that litter habitat quality has not reached pre-fire levels.

Detritivores which differed in abundance or occupancy between burnt/unburnt sites generally showed no effect of distance (introduced millipedes excepted), which suggests that some survived *in situ* and re-established post-fire populations. In this study, we considered unburnt patches as refugia and potential source populations for recolonisation. However, because soil is a good insulator, *in situ* survival was likely possible for detritivorous invertebrates. For instance, while temperatures may exceed 700°C aboveground during a prescribed burn, 5 cm below the soil surface they might not reach 45°C (Raison et al., 1986a), and such results are likely to be similar for severe wildfires, since they move so rapidly that heat transfer to the soil is limited (Neary et

al., 1999). An additional reason why the soil may act as *in situ* refugia for detritivores is that many are sensitive to desiccation (see Ch. 3), and may retreat below the soil in summer, when fire is more likely (Glitzenstein et al., 1995; New, 2014). Litter species likely have a greater need to occupy the soil as a refuge during summer, as litter may dry out more extensively than logs. Log species, however, occupy a more buffered environment and may remain in the log, meaning they are more exposed to fires (Ulyshen et al., 2010), so direct fire-caused mortality may be initially greater for log-dwelling detritivores. However, post-fire, the relative benefits of these two microhabitats are likely to be reversed. This is because litter is more temporally variable than logs, having greater temperature (Ch. 1) and humidity fluctuation, relatively rapid decomposition and marked temporal variation in litterfall (Facelli and Pickett, 1991; Pook et al., 1997; Raison et al., 1986b). If the litter environment becomes more variable after fire and thus more stressful, detritivore population growth may be slower than in the more buffered log microhabitat. While the initial impacts of fire could therefore be more severe for log-dwelling detritivores, our results suggest that long-term impacts are more profound for litter-dwelling invertebrates, meaning the post-fire environment limits recovery more than direct mortality, a point worthy of further study.

Litter-dwelling Lepidoptera, and some isopods and amphipods seemed to be most affected by the post-fire environment. Moths (Lepidoptera) showed no effect of distance from edge, indicating they can recolonise after fire, consistent with their ability to fly. Their lower abundance at burnt sites thus appears to be mainly a response to reduced food/habitat quality or availability. Psychidae moths were an exception to this result, as they tended to be absent from burnt sites, which may reflect the fact that females of many species are flightless and are thus unable to recolonise rapidly (Zborowski and Edwards, 2007). Similarly, some amphipods and isopods (Styloniscidae sp. 3 & Armadillidae sp. 1) had lower abundances at burnt sites regardless of distance, and since they are not good dispersers, this suggests they survived *in situ*. Similar taxa

appear capable of *in situ* survival during prescribed burns (Ch. 2), although we acknowledge that this wildfire was of far greater severity. In contrast, other isopod species and one diplopod (Porcellionidae sp. 1, Armadillidae sp. 2, unidentified Armadillidae & *Victoriocambala buffalensis*) were absent at some burnt sites, indicating they tended to be eliminated by fire and had not yet recolonised. Such a difference in the ability of flightless detritivores to survive *in situ* may be due to differences in their microhabitat occupancy. Amphipods and Styloniscidae are more sensitive to temperature than Armadillidae and *Victoriocambala buffalensis* (Ch. 3), and may thus inhabit more sheltered environments during summer when the fire occurred. However, since Armadillidae sp. 1 appears to have survived *in situ*, and Porcellionidae sp. 2 was as sensitive to temperature as amphipods (Ch. 3), this conclusion is somewhat tentative. Together, our results suggest that microhabitat occupancy interacts with dispersal ability and habitat quality to determine post-fire detritivore abundance. However, further investigation of what aspects of habitat change drive these responses, especially with regards to microclimate, litter quality and decomposition stage, is needed to more fully explain these results.

Although distance from unburnt forest is considered an important factor for invertebrate recolonisation after fire, few studies have measured recovery over distances as great as five kilometres (e.g. Arnold et al., 2017). Grasshopper abundances may decline over shorter distances from the fire edge, while snails, in contrast, may persist irrespective of distance (Kiss and Magnin, 2006; Knight and Holt, 2005). However, these studies are likely complicated by edge effects, meaning it is not possible to separate the effects of changing habitat from those of increasing distance. A different study at the same sites used for this project showed that one cockroach species declined with distance, but that others responded more to habitat variables (Arnold et al., 2017). In this study, diplopods were the only taxa that declined with distance in both litter and logs, and for most morphospecies, both occupancy and abundance declined. Some amphipods

and isopods, and the rare Chordeumatida millipedes increased in abundance with distance from the edge, though this was a weaker trend. Given the substantial overlap in habitat occupancy among these taxa (Ch. 1), this increase may be due to declining competition for habitat from millipedes, as there is some evidence that competition for space between Amphipod species drives niche partitioning (Friend and Richardson, 1977; Richardson and Devitt, 1984; Sutherland and Dickman, 1999). Our results suggest that some millipede morphospecies did not survive *in situ* and were eliminated, but are recolonising slowly. The lack of habitat change with distance further suggests millipede population growth is influenced by increased immigration from unburnt patches, since abundance is greater near the fire edge.

Millipedes are less sensitive to desiccation than isopods and amphipods (Ch. 3; Cloudsley-Thompson, 1962), which should increase their dispersal potential, so our results were somewhat surprising. Amphipods have strong genetic population structuring in this system, indicating poor dispersal abilities (Menz et al., 2016), which agrees with our results showing no negative impact of distance from edge, indicating they survive fire *in situ*. One explanation for this result is that, in comparison to the other taxa studied (Lepidoptera, Amphipoda and Isopoda), Diplopoda could be expected to require a longer time to reach maturity, which may slow population growth, thus explaining why they showed the most pronounced effects of distance (David and Gillon, 2009; Friend, 1986; Hopkin and Read, 1992; Hornung, 2011; Kight, 2009; Kime and Golovatch, 2000; Zborowski and Edwards, 2007). The decline in both introduced millipede species (*Ommatoiulus moreleti*, the Portuguese millipede, and *Brachyiulus pusillus*) may reflect their reliance on human-assisted dispersal. Although this can be quite rapid, such dispersal may have been slowed in our system because the sites are somewhat remote (Baker, 1978; Baker, 1985). In addition, these two species may not be well adapted to persist through severe fires and are thus more likely to be strongly impacted. A further potential explanation for the decline of native millipedes with

distance may be that some are dietary specialists, relying on specific fungal species or decomposition stages that are affected by fire (Scheu and Simmerling, 2004; Zuo et al., 2014). Although pyrophilous fungi sprout fruiting bodies in response to fire, other species are found at long-unburnt sites (M. McMullan-Fisher et al., 2011). Fungal growth and recolonisation after fire may thus take some time depending on the species, since fungi can be eliminated by high severity fire and recolonise slowly from less severely burnt patches, especially through hostile habitat (Aylward et al., 2015; Edman et al., 2004; M. McMullan-Fisher et al., 2011). At least one of our affected diplopod species (Siphonotidae sp. 1) appears to have a specialised diet, as indicated by its unusual 'sucking mouthparts', though it is unknown whether this includes fungi (Black, 1997). If this species depends on the growth of specific dispersal-limited fungus, for example, populations may show signs of isolation by distance, even if individuals survive fire *in situ*.

In conclusion, we used a relatively rare, large-scale fire event to determine how large distances affected invertebrate detritivore recovery 7-8 years after wildfire. Our study shows that even if most taxa survive *in situ*, high fire severity has lasting impacts on their populations. The effects of fire were strongly taxon-dependent, and were greater in litter microhabitats than for logs, possibly due to the greater buffering afforded by log microclimate post-fire. Our results suggest that recovery is likely to be partly contingent on the recovery of trees and associated litter-fall, since even good dispersers persist at lower abundance relative to unburnt sites. While some flightless taxa (amphipods and isopods) appeared to survive *in situ*, distance limited the recovery of millipedes, indicating their recolonisation is slow after being eliminated by fire or the fire aftermath. Finally, our results suggest recovery times for detritivores in this system may have exceeded eight years following severe fire. This is of some concern, given the predicted increase in fire extent under climate change and the probable effects of distance on recovery. We suggest



that exempting unburnt forest patches from prescribed burning following a severe fire may be an appropriate management strategy that favours the recovery of detritivores in this system.

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## Chapter 4: Appendix

**Table 1.** Loadings of each environmental variable in each principal component axis. Only burnt sites were included. Darker cells indicate a stronger contribution to the axis. Blue cells indicate a positive and red cells a negative association.

Variable	Litter			Log		
	PC1	PC2	PC3	PC1	PC2	PC3
% Canopy cover	0.01	0.25	0.18	0.02	0.03	0.33
% Understory cover	-0.14	-0.20	-0.16	-0.04	0.02	-0.40
% Bare ground cover	0.19	-0.16	-0.15	-0.03	-0.30	-0.02
% Plant cover	-0.01	-0.01	-0.26	0.09	-0.28	0.18
% Litter cover	-0.15	0.13	0.29	-0.06	0.40	-0.12
Litter depth	-0.06	0.00	0.12	-0.08	0.09	-0.07
Soil volumetric water content	-0.23	-0.07	0.02	0.22	0.05	0.02
Log number	-0.01	-0.27	0.28	0.00	-0.05	-0.22
Dead trees	0.00	-0.37	0.26	-0.02	0.07	-0.41
Live trees	-0.08	0.26	0.39	0.08	0.32	0.14
PADIR	0.03	-0.19	-0.10	-0.01	-0.05	-0.19
Altitude	-0.06	-0.07	0.44	0.06	0.30	-0.17
Site slope	0.09	-0.38	-0.22	-0.11	-0.28	-0.25
No. days<1°C	-0.13	0.24	0.09	0.12	0.24	0.17
No. days>35°C	0.25	0.18	-0.07	-0.28	0.11	0.14
No. days>95%RH	-0.25	0.22	-0.20	0.28	0.05	0.09
No. days<20%RH	0.26	0.19	0.04	-0.27	0.12	0.16
Absolute min %RH	-0.24	-0.20	-0.09	0.26	-0.19	-0.13
Average max %RH	-0.24	0.24	-0.19	0.27	0.05	0.11
Average day %RH	-0.29	-0.02	-0.12	0.28	0.04	-0.17
Average night %RH	-0.28	0.17	-0.17	0.29	0.08	0.03
Absolute min °C	0.23	-0.10	0.04	-0.15	-0.25	0.02
Absolute max °C	0.25	0.19	-0.16	-0.04	-0.16	-0.02
Average max °C	0.25	0.19	-0.16	-0.27	0.03	0.10
Average day °C	0.30	0.09	0.04	-0.31	0.02	0.16
Average night °C	0.30	0.01	0.06	-0.31	-0.02	0.07
Log burn score				0.08	0.11	0.16
Log decomposition				-0.02	0.24	-0.16
Log length				0.16	-0.09	0.19
Log length on ground				0.17	-0.05	0.20
Log width				-0.10	0.27	-0.10
Log volume				-0.04	0.07	0.02
Log volume on ground				-0.06	0.09	0.03

Variance explained by each axis for litter are: PC1 38%, PC2 12%, PC3 11%, and for logs: PC1

27%, PC2 12%, PC3 10%

**Table 2.** Results of manylm analysis testing the difference in abiotic variables between burnt and unburnt sites, for variables measured for two microhabitats. Post-hoc results indicate whether variables were higher or lower in burnt sites relative to unburnt sites. Significant p-values are in bold.

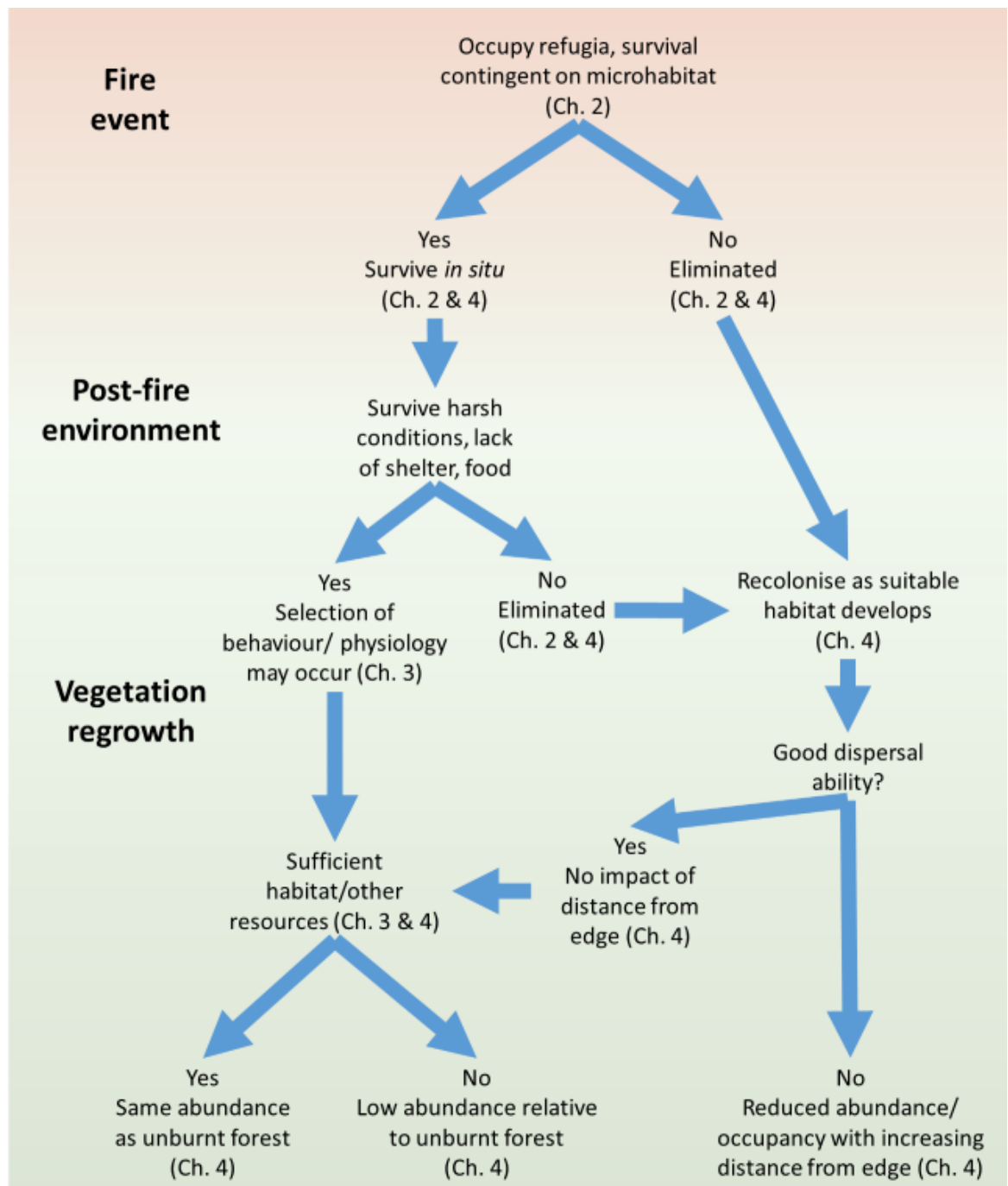
Variable	Litter			Log		
	Df	F	p	Df	F	p
Burning	(1, 139)	282.4	<b>&lt;0.001</b>	(1, 85)	20.5	<b>0.029</b>
Season	(2, 137)	2905.7	<b>&lt;0.001</b>	(2, 83)	35.2	<b>0.001</b>
Year	(2, 135)	56.9	<b>0.008</b>	(2, 81)	116.8	<b>&lt;0.001</b>
Site	(5, 130)	655.9	<b>&lt;0.001</b>	(5, 77)	12.9	<b>0.014</b>
Post hoc results						
	F	Lower	Higher	Summary	Lower	Higher
Burning	282.4	Canopy *** Live trees * Log number *	Understory *** Dead trees *** Altitude *	20.5		Log burn severity ** Log decomposition *

p =\* <0.05 \*\*<0.01 \*\*\* <0.001

## Synthesis

Detritivores are among the central drivers of Australian fire regimes through their impact on fuel load decomposition. However, such species are vulnerable to the negative effects of fire, due to their generally low physiological tolerance and dispersal abilities. Given the ever-increasing efforts by humans to control fire regimes, and predicted changes in fire frequency, severity and extent due to altered climate, the mechanisms that drive detritivore recovery after fire are of great interest. If detritivore species are not adapted to novel fire regimes, the potential for detrimental long-term effects increases, including the possibility of a negative feedback loop favouring future fires through slower decomposition and resulting increases in fuel load (Dale et al., 2000; Koltz et al., 2018). This is especially true with respect to probability of severe fires, but such fires are unpredictable and therefore difficult to study, though this may change in the future. This project used the opportunity provided by the severe, landscape-level 'Black Saturday' wildfires to extend our knowledge of detritivore recovery over a significant period in three areas: *in situ* survival, post-fire persistence and recolonisation (Fig. 1). These three aspects are discussed in divine comedic sequence below.





*Figure 1.* Conceptual diagram of the recovery process for detritivores following fire, with references to chapters where supporting evidence is provided.

### ***Inferno: In situ survival***

Measuring *in situ* survival of detritivores during a fire event is particularly difficult for logistical and safety reasons. Nevertheless, knowing whether an animal can survive *in situ* in refugia is critical for predicting their recovery after fire (Robinson et al., 2013). Severe wildfires leave few refuges, whether as unburnt forest patches or thermally insulated microhabitats (Bassett et al., 2017; Cruz et al., 2012; Leonard et al., 2014). In the present study, I found that distinct microhabitats appear to provide different levels of protection from hostile conditions. Specifically, detritivore abundance was reduced in leaf litter, consistent with it being the most exposed microhabitat to fire, while soil detritivores increased in abundance, likely reflecting the good insulating ability of the soil (Ch. 3). Further evidence of *in situ* survival was reported in chapter 4, as both isopod and amphipod species generally showed little effect of distance from unburnt sites, although the data was 8 years post-fire. Nonetheless, given their lack of wings and the extent of the fire, it is more plausible to suggest that individuals of these groups survived *in situ* rather than recolonised. This fits with previous genetic work indicating that amphipods have highly genetically structured populations, which is unlikely if they recolonised and did not survive *in situ* (Menz et al., 2016). Overall, these results generally concur with the few studies that directly address invertebrate *in situ* survival during fire, suggesting that it is possible for a minority of individuals to survive using refugia (Brennan et al., 2011; Neumann and Tolhurst, 1991; Wikars and Schimmel, 2001). More broadly, they support the conclusions of Robinson et al. (2013) in highlighting the importance of microhabitats as refugia from fire. It is also worth noting that the effectiveness of these refuges, including soil, was noticeably reduced by increasing burn severity, as in other studies (Bogorodskaya et al., 2011; Wikars and Schimmel, 2001).

These results have practical application in land management, as my results suggest conducting prescribed burns such that some refuges, like logs, are left intact. Nonetheless, further investigation is required. For example, separating the immediate effects of burning from those of

the post-fire environment is likely to be a challenging but promising topic. This may be achieved by intensive sampling of detritivores and habitat variables very soon and for several months after burning, to determine if species are lost immediately after fire or decline in response to habitat changes. Finally, sampling multiple habitats following fire proved especially rewarding in this study, in demonstrating that the response of various taxa depended on microhabitat, and so I recommend expanding the range of microhabitats under consideration in future work in order to achieve a full understanding of how post-burn communities may arise. For example, detritivore abundance in the soil was generally very low, but was higher in soil hollows where litter collects (pers. ob.), suggesting this microhabitat is worth investigating for its potential as an *in situ* refuge.

#### ***Purgatorio: post-fire persistence***

The post-fire environment immediately introduces new stressors that detritivores must be able to survive. These include a loss of food, especially those provided by later stages of decomposition, loss of shelter, resulting from the destruction of detritus, and hotter and dryer climate due to loss of canopy and ground cover. All of these factors may contribute to elevated mortality rates and possible elimination of some taxa (Auclerc et al., 2019; Coyle et al., 2017; Ehbrecht et al., 2019; Ray and Bergey, 2014; Sileshi and Mafongoya, 2006). These challenges are particularly acute following severe fires, as there is no post-fire litter-fall, as can occur with lower-severity fires, to mitigate microclimate changes (Alexis et al., 2010; Christensen and Abbott, 1989; Majer, 1984; Penman and York, 2010). The impact of severe fire may thus be felt for some time and, even when habitat differences have disappeared, may persist as legacy elements as post-fire habitats develop (Koltz et al., 2018; Thompson, 1998). In this study, differences in microclimate were no longer evident eight years after severe fire, though detritivore distributions and abundance had been determined by the interaction of site microclimates and species traits (Ch. 3). More broadly, while it is clear that latitudinal gradients predict broad-scale distributions, local distributions are thought

to broadly reflect site microclimates (Chown and Terblanche, 2006), and my results support this conclusion. However, I found that detritivores from burnt sites had behavioural preferences for lower humidities and higher temperatures, provoking the tentative suggestion that selection in the post-fire environment has left a legacy. Rather than negatively affecting abundance (although genetic diversity may have been reduced), this change allowed log-dwelling detritivores to mitigate the impacts of the post-fire environment through selection of behavioural preferences. Burn status did not apparently affect detritivore abundance through the four physiological traits measured. Thus, the capacity to recover from fire appears partly contingent on how rapidly a species can adjust its behaviour at the population level (Hoffmann and Sgro, 2011; Koltz et al., 2018; Thompson, 1998). Evidence of physiological adjustments have also been found for (other or these) litter-dwelling detritivores in the same system, where invertebrates from burnt sites were larger (Buckingham et al., 2015). However, I found no such effect of burning on the weight of log-dwelling invertebrates, and attribute the difference to the greater thermal buffering of the log habitat which reduced the need for physiological adaptation. These results, along with evidence of the highly structured populations of some dispersal-limited detritivores in this system (Menz et al., 2016), suggest fire may influence detritivore evolution through behavioural selection in the post-fire environment (Banks et al., 2013). Thus, while the ability to make physiological adjustment could limit recovery in the short-term, it does not affect long-term recovery. Conducting a similar study immediately after severe wildfire could confirm if short-term recovery is indeed limited by physiological traits.

The need to adapt will depend on how extreme habitat changes are. Detritivores may be more vulnerable to changes caused by fire than other communities, because they do not immediately benefit from the post-fire flush of new growth as do, for instance, herbivores and pollinators (Campbell et al., 2007; Pryke and Samways, 2012). My results (Ch 4) showed that Lepidoptera and

Isopoda were less abundant at burnt than unburned sites, regardless of distance from fire edge, suggesting that habitat limited the recovery of these taxa. This is generally consistent with results of other studies in underscoring that succession of invertebrates after fire depends on vegetation regrowth and changes in soil surface properties (Auclerc et al., 2019). More detailed understanding of the nature of microhabitats and their extent would clarify what factors best predict detritivore abundance and thus their response to post-fire habitat changes. For example, the amount of fine fuel is reduced by wildfire for at least six years (Birk and Bridges, 1989), which represents a structural change to an important microhabitat for detritivores. Similarly, fire can promote rapid fungal growth (McMullan-Fisher et al., 2011), which may provide a valuable resource in the post-fire environment. Thus, some detritivores may have persisted because they were able to use rapidly responding resources, such as fungi, following fire, while others that could not were eliminated. By measuring variables like litter structure and fungal growth over a chronosequence after fire, along with describing the associated detritivore community, it would be possible to determine if these habitat changes predict survival in the post-fire environment. This may also explain why behavioural traits responded to burning, but apparently strictly physiological traits did not. For example, fire could reduce the extent of preferred microhabitats, so that behavioural adjustments increase available habitat post-fire.

### ***Paradiso: Recolonisation***

Disturbance, especially its tendency to fragment a landscape, is recognised as a major ecological factor that interacts with dispersal ability to determine species distributions (Schowalter, 2012; Sousa, 1984). Thus, if a species is eliminated by fire or its aftermath, the probability of which increases with fire severity, as my results show (Chapter 2), it must recolonise to be included in post-fire communities. Dispersal ability is critical to predicting recolonisation after disturbance (Sousa, 1984), which agrees with my results, since the one winged taxa included

(Lepidoptera) showed no effect of distance from burn edge, while wingless taxa were either eliminated or survived *in situ* (Ch. 4). These results partly agree with those from other work on this system, which showed that distance from edge limits the recovery of some detritivorous cockroaches, but differ in that dispersal ability had no effect (Arnold et al., 2017). Thus, in order to persist in an area, detritivores have two basic responses to wildfire disturbance: *in situ* survival or elimination and recolonisation. This supports general theory, which indicates that invertebrates are usually either intolerant of disturbance and are eliminated (and potentially recolonise), or are able to make use of the changed environment and persist (Schowalter, 2012). Thus, if poor dispersers are eliminated, my study indicates they may become locally extinct (Ch. 4), as is true in other systems (Schowalter, 2012). However, this study does not completely clarify why some flightless detritivores were eliminated and recolonised slowly, while others survived *in situ*. It is possible that differences in habitat occupancy or requirements explain why some species were eliminated, as outlined in the previous sections. However, study of the largely unknown life history aspects of these detritivores may reveal the detailed mechanisms behind the different recovery strategies displayed here (Driscoll et al., 2010; Hopkin and Read, 1992; Malmström, 2012; New, 2014). For example, considering the life history traits of butterflies, such as voltinism, improved the accuracy of dispersal estimates based on wing size by up to five times (Stevens et al., 2013). In this study, I only considered whether taxa were winged or not, so measuring life history traits particular to detritivores may further explain the trends observed. For example, sampling these animals continuously for at least a year, coupled with rearing experiments to provide information on lifespan, fecundity, parity and other life history traits likely to influence dispersal tendency and population growth (Bonte et al., 2012; Stevens et al., 2013) may potentially explain the trends observed in detritivore dispersal rates and population growth after fire. In conjunction with genetic analysis, this approach might further clarify whether the patterns observed were indeed the result of *in situ* survival or of recolonisation (Banks et al., 2013).

The elimination of species with recolonisation constrained by poor dispersal abilities may impact ecosystem functioning. Although decomposition rates are apparently unaffected by burn severity in this system (Buckingham et al., 2015), changes to fire regime can depress microbial decomposition rates, and detritivores appear to be essential in compensating for this shortfall (Brennan et al., 2009; Butler et al., 2019). If the recolonisation of detritivores is slowed by the extent of severe fire, this compensatory effect may be diminished (Arnold et al., 2017). Therefore, ensuring that unburnt forest patches are left intact following large-scale, severe fires (i.e. not burned in hazard reduction burns) can be recommended as a conservation strategy to promote recolonisation.

### ***Conclusions***

Taken together, the results of this project show that detritivore recovery after severe bushfire is a complex process (Fig. 1). Although the detritivore community was quite temporally variable, emphasising the value of long-term studies, some general patterns could be detected. Along with other studies of invertebrates in this system (Arnold et al., 2017; Buckingham et al., 2015; Menz et al., 2016), my results show that some taxa do recover after even the most severe fires, overcoming the challenges of the fire event and its aftermath. Despite their high physiological sensitivity, the detritivores considered here appear capable of surviving hot and xeric conditions post-fire and recovering over the long-term. Microhabitats seem critical to the resilience shown by such detritivores, ensuring their survival during and after fire, thus eliminating the need to recolonise from unburnt patches. However, other wingless taxa appear to be eliminated and recolonise more slowly than winged taxa (Ch. 4). In addition, persistent habitat differences between burnt and unburnt sites are likely to be responsible for lower abundance eight years after fire, a point that may be addressed by continuous, longer-term sampling of detritivores and more detailed habitat measurements. This study bears out the recommendations of Teasdale et al.

(2013) who pointed out that determining responses depends on sampling method (in this study, different microhabitats) and taxonomic resolution.

More generally, the results of this project agree with other studies of the ecological consequences of the catastrophic Black Saturday fires. For small mammals, survival *in situ* was the dominant source of recovering populations (Banks et al., 2011), as I also found for some detritivore taxa. Robinson et al. (2014); (and other fauna; Robinson et al., 2013), highlighted the importance of unburnt refuges for recovery of bird (and other) populations after fire and some detritivores in this study (notably millipedes) also displayed this trend. The predicted increase in the extent of high severity fires is therefore concerning, since they leave few refugia (Bassett et al., 2017; Cruz et al., 2012). The recovery process of detritivores outlined in Fig. 1 is conceptually similar to the recruitment and survival of *Eucalyptus regnans* seedlings post-fire, in that their survival depends on the ability to pass through several site-dependent filters (Smith et al., 2016). Finally, loss of mature trees was well-documented as extensive, as I also found, and may potentially result in ecosystem transformation to more open forest (Bennett et al., 2016; Benyon and Lane, 2013; Nolan et al., 2014), thus explaining why the ability of some detritivores to recover appeared to be limited by extent of habitat recovery.

This project clarified the recovery process of detritivorous invertebrates, laying out a series of potential responses that are highly taxon-dependent (Fig. 1), leading to some suggestions for management, as well as identifying specific areas for future investigation. I adopted an approach designed to identify mechanisms driving responses to fire (Driscoll et al., 2010), which revealed that detritivore recovery is first determined by whether they are eliminated by fire or the post-fire environment, after which post-fire habitat changes may affect abundance or alter behaviour, while dispersal traits will limit recolonisation. It follows that managing prescribed burning regimes



to retain both small- (e.g. logs) and larger-scale refuges (e.g. unburnt forest patches) would promote detritivore recovery after burns and wildfire. Finally, I suggest four general areas of research that may further develop our understanding of post-fire recovery of detritivores: work to determine 1) if taxa are lost predominately during the fire event or by post-fire habitat change; 2) if habitat alteration or population growth limits abundance after fire; 3) if genetic information can be used to separate recolonisers from *in situ* survivors; and 4) obtaining basic life-history and ecological information of species and how these affect response to fire.

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