Impact of fire on tussock grassland invertebrate populations

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Cover: A smouldering summer burn plot at Mount Benger. *Photo: Barbara Barratt.*

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ABSTRACT

The invertebrate fauna of tussock grassland in New Zealand has not been well studied, and the effect of burning on the biodiversity of the ecosystem is poorly understood by land managers. The impacts of burning on two tussock grassland invertebrate communities in Otago, New Zealand, were investigated between 1998 and 2006. At each site, three replicate 1-ha plots that were unburned (control), or burned in spring or summer were sampled. Pre- and post-burn sampling compared invertebrate densities and trophic group structure in inter-tussock (turf) and tussock samples, and recovery after treatment. Most groups were initially reduced in density post-burn. In the 1–2 year period following treatment, Thysanoptera and Hemiptera 'rebounded' and reached significantly higher population densities than before the fires. By the end of the study, Amphipoda had not recovered to pre-burn densities. In general, herbivore population densities recovered over a 2–3 year period, and litter-dwelling invertebrate population densities were most negatively impacted. Season of treatment had no major impact on invertebrate responses. Coleoptera were chosen as a representative group for more detailed investigations of responses at species level. Coleoptera species richness was reduced by about 50% at 2–3 months post-burn, but recovered to pre-burn levels 3 years later. There was no evidence of a change in the density of exotic Coleoptera following the burning treatments. Invertebrate data from these sites should be considered as case studies, rather than applicable to tussock grassland in general. However, these findings have several implications for the management of tussock grassland: fire treatments that remove the litter layer are likely to reduce litter-dwelling invertebrate populations for 3 years or more; summer fires do not appear to be more detrimental to the invertebrate community than burning in spring, based upon the limited seasonal data available to us; and the exotic component of the fauna does not increase in response to fire in the first 3–4 years after burning.

Keywords: tussock grassland, invertebrates, Coleoptera species, burning, fire, diversity, recovery, exotic species, New Zealand

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1. Introduction

Grasslands of indigenous tussock species are characteristic of the lower rainfall hill and high country areas in the South Island of New Zealand, and are used for extensive pastoralism (Floate 1992). Since European settlement in the late 19th century, fire has been used extensively to facilitate movement of grazing animals and to convert tussock grassland into improved pasture. Burning promotes new tussock growth, which is palatable to stock. It also removes litter to increase the success of aerial over-sowing with introduced legumes and grasses (Lowther & Douglas 1992). For pasture management, burning is usually carried out in spring, when conditions are relatively cool and the soil and vegetation are moist. Accidental fires tend to occur in late summer, when conditions are usually drier, and hence the damage to vegetation and litter would be expected to have a more severe impact on invertebrates.

There are concerns that fire damages native biota, allows weeds to establish and promotes soil erosion (Payton & Pearce 2001). Overuse of fire in tussock grassland has been recognised as causing loss of tall tussock species, with their replacement by short tussock species or invasive weeds such as *Hieracium* (Aspinal 2001). Local agencies with responsibility for promoting sustainable land use have pointed out that the burning of tussock grassland can accelerate soil erosion and reduce soil quality, change vegetation characteristics, reduce conservation values and habitats for flora and fauna, and reduce water yield (Otago Regional Council 2002).

Since 1983, considerable areas of tussock grassland have been retired from grazing and formally protected as a result of the Protected Natural Area Programme, which sought to protect representative vegetation types from 85 biogeographic areas (ecological regions) across the country (McEwen 1987). As a result of the crown pastoral tenure review under the Crown Pastoral Land Act 1998, areas of rangeland, particularly at higher altitudes, are currently being retired from grazing and managed so that their natural character and the indigenous biodiversity will be retained, and in some cases restored. In order to maintain conservation values of these areas, an improved understanding of the biodiversity and dynamics of grassland ecosystems is required.

Land managers need information about the impact of fire on the conservation values of tussock grassland to make appropriate management decisions for these areas. Hunt (2007) expressed the view that the Department of Conservation (DOC) needs to improve monitoring of changes to ecosystems after fire. Hunt's report acknowledged the research outlined in this study, but recommended that continued research on impacts of fire on ecosystems and biodiversity be given a high priority, 'especially invertebrates before and after fires'.

1.1 BACKGROUND

Worldwide, research into the impacts of fire on invertebrates in grassland environments have shown few consistent patterns (Tscharntke & Greiler 1995; Friend 1996; Blanche et al. 2001). Responses to fire depend upon seasonal and environmental factors and their interaction with the micro-habitat requirements of the fauna. Warren et al. (1987) and Webb (1994) attributed reductions in densities of some arthropods to the reduced levels of soil moisture and changes in microclimate that follow removal of the litter layer. Fire intensity is important in determining impacts on invertebrates (Swengel 2001), and this is influenced by several factors, including fuel load, vegetation moisture content, weather conditions and topography. However, even after very hot and 'complete' burns, mortality of invertebrates has rarely been reported to be 100% (Swengel 2001). The size and uniformity of the burnt area naturally influences the rate of recolonisation from surrounding unburnt areas, or unburnt patches within the burnt area. The impact of fire can also vary for different invertebrate life-cycle stages; for example, a soil-dwelling stage is likely to be less immediately affected by fire than a surface-dwelling stage.

Warren et al. (1987) reviewed literature on the impact of fire on each major taxonomic group found in grassland. Studies investigating the effect of fire on invertebrates are full of conflicting and variable data. This is partly because the studies have been carried out using different methods, with widely differing treatment intensities and regularities, and in areas with different climates. Furthermore, many studies reported in the literature have been carried out in ecosystems that are fire-adapted, and thus are likely to have different responses from essentially non-fire-adapted environments such as New Zealand tussock grassland. Warren et al. (1987) found that litter-dwelling invertebrates such as mites and Collembola are generally adversely affected by fire as a result of loss of the litter layer where they live and feed. Miriapods, such as millipedes and centipedes, were less susceptible to acute impacts because of their cryptic behaviour, but it was found that post-burn habitat modification could reduce populations. Impacts on some of the larger groups, such as Coleoptera, Diptera and Hemiptera, were found to be very variable, depending upon their trophic group and the seasonal characteristics of the fire. Ants, which are common in most grassland environments, usually survived the acute impacts of fires, and generally recolonised burnt areas rapidly.

Several studies in New Zealand have investigated the impact of tussock burning on plant communities (e.g. O'Connor & Powell 1963; Mark 1965; Payton et al. 1986), but comparatively little has been published on the effect of indigenous grassland burning on invertebrates. Yeates & Lee (1997) found that 18 months after a spring burn densities of both mites and Collembola in litter and in up to 2 cm soil depth were about 50% of those in an adjacent unburnt area; however, after 30 months, the densities of these groups in the burnt areas were < 10% of the unburnt areas. Henig-Sever et al. (2001) found, not unexpectedly, that litter-dwelling invertebrates are more severely affected by fire than those living deeper in the soil profile and suggested that inhabitants of the litter layer might be useful ecological indicators of fire intensity on ecosystems.

In 1960, the Tussock Grasslands and Mountain Lands Institute (TGMLI) was set up to assist farming in tussock grassland, and Graeme White, employed by the TGMLI, emphasised the importance of understanding insect population dynamics if management was to be successful (White 1972). Invertebrate biodiversity and ecology in tussock grassland in Otago is not well known, although the body of knowledge is steadily increasing. As for the New Zealand invertebrate fauna in general, studies have indicated that the fauna exhibits a high degree of endemism. One of the earliest papers on tussock grassland insects reported on a study in Canterbury, where damage to tussock plants from noctuids and other Lepidoptera was described, and *Odontria* (Coleoptera: Scarabaeidae) larvae were found to be killing patches of grasses (Dick 1940). The author noted that run-holders believed that burning tussock in spring reduced the numbers of caterpillars found in tussock plants.

In 1978, the senior author was appointed to work on tussock grassland entomology in Otago. The work, as in Canterbury, was mainly applied with emphases on the ecology and management of the striped chafer (*Odontria striata* White), and pests of white clover (*Trifolium repens* L.) seedlings oversown into tussock. Research on these two topics was prompted by the concerns of farmers and researchers, respectively, and the studies resulted in a series of publications (Barratt 1982a, b, 1983; Barratt & Campbell 1982; Barratt & Johnstone 1984; Barratt & Lauren 1984). However, it was Brian Patrick, a well-known lepidopterist, who really laid the foundation for our current knowledge of tussock grassland insect biodiversity and ecology, by instigating a series of collecting trips with colleagues to tussock grassland sites throughout Otago and Southland, which resulted in a series of reports and publications (Patrick et al. 1984, 1985a, b, 1986, 1993a, b, 1987; Barratt & Patrick 1987; Patrick & Barratt 1988, 1989; Patrick 1991, 1994; Dickinson et al. 1998).

Since then, there have been a number of students at the University of Otago, Dunedin, under the guidance of Prof. Katherine Dickinson, who have focussed their ecological studies on tussock grassland, some of whom have used the sites that are the topic of this report (Derraik et al. 2001, 2002, 2003; Murray 2001; Goodman 2002; Murray et al. 2003, 2006; Dixon 2004; Rate 2005; Scott 2007). Recently, a student at Lincoln University, Christchurch, has initiated a PhD study of spiders at the Deep Stream site.

Since we still know so little about the composition of tussock grassland invertebrate communities, we use Coleoptera as a surrogate group in this report. Coleoptera are a suitable group for this because they are speciose, they include representatives of all trophic groups and they are reasonably well known taxonomically (Hutcheson et al. 1999). Furthermore, Bulan & Barrett (1971), working in cereal plots in Ohio, USA, found that the responses of Coleoptera to fire were representative of the rest of the arthropod community, and reported that changes in biomass and species diversity were good measures for evaluating the impact of fire.

1.2 OBJECTIVES

The objective of the project was to provide information to assist in the future management of natural grassland ecosystems. This included information on:

- The short- to medium-term (3 months up to 4 years) impacts of burning on the density of tussock grassland invertebrates
- The short- to medium-term impacts of burning on Coleoptera species density, species richness, species diversity and trophic structure
- The time frame over which the invertebrate fauna in tussock grassland is able to recover to an equilibrium density after burning
- The time frame over which the Coleoptera fauna is able to recover to pre-burn species densities, species richness and species diversity after burning
- The comparative short- to medium-term impact of tussock burning in moist spring conditions compared with those in hot, dry summer conditions
- The extent to which exotic Coleoptera species have established in native tussock grassland and their responses to burning

2. Methods

2.1 SITES

Two sites in the Otago region of the South Island of New Zealand were chosen for this study: Deep Stream (DS) and Mount Benger (MB) (Fig. 1). These sites are part of a multi-disciplinary study of fire modelling (Scion study), and the impacts of tussock burning on plant (Payton & Pearce 2009) and invertebrate (present study) communities. They were chosen as representatives of higher (MB) and lower (DS) altitude tussock grassland environments in Otago. They were selected on the basis of their relatively undisturbed soils (no history of cultivation) and relatively unmodified vegetation. Both sites had experienced fires since European settlement, but had not been burned for at least 10 years before these experimental burns. Site details are given in Table 1.

TABLE 1. A. SITE AND B. SOIL CHARACTERISTICS AT DEEP STREAM AND MOUNT BENGER STUDY SITES.

A

SITE CHARACTERISTIC	DEEP STREAM	MOUNT BENGER
Tenure	Dunedin City Council water reserve	Benger Pastoral Lease
Altitude	640–700 m a.s.l.	1100–1180 m a.s.l.
Map reference	45°44′S 169°54′E	45°58′S 169°26′E
Dominant vegetation*	*Chionochloa rigida* *Gaultheria nana* *Poa pratensis* *Poa colensoi*	*Chionochloa rigida* *Poa colensoi* *Polytrichum juniperinum* *Agrostis capillaris*
Slope and aspect	< 10° predominantly N	2 plots flat; 1 plot < 20° S
Mean annual rainfall†	993 mm	1264 mm
Soil type‡	Wehenga silt loam Allophanic brown soils	Carrick Allophanic brown soils

* Espie & Barratt (2006).

† Payton & Pearce (2009).

‡ Hewitt (1992).

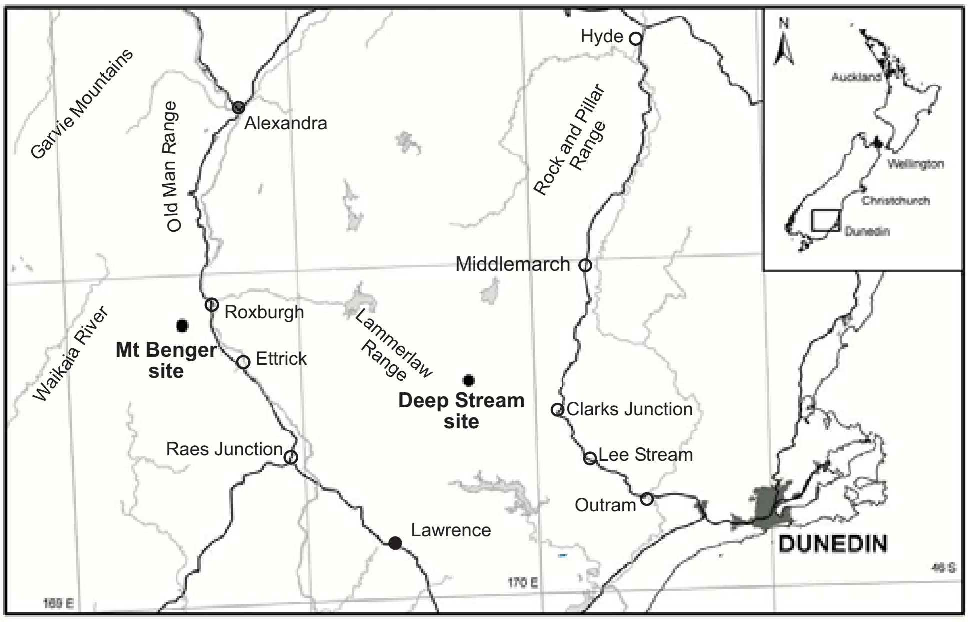
B

SOIL CHARACTERISTIC*	DEEP STREAM		MOUNT BENGER	
	TURF	TUSSOCK	TURF	TUSSOCK
% organic C	7.1	7.9	7.7	7.3
% organic matter	12.2	13.6	13.3	12.6
Total % N	0.38	0.42	0.43	0.47
C:N ratio	19	19	18	16
pH	4.6	4.6	4.6	4.5
Ca (me/100g)†	125	125	125	125
P (µg/g)	8	8	7	8
K (me/100g)†	80	100	60	60
Mg (me/100g)†	45	55	35	40
Na (me/100g)†	15	20	15	15

* Sarathchandra et al. (2005).

† Milli equivalents per 100 g soil.

Figure 1. Map of the study sites at Deep Stream and Mount Benger (from Payton & Pearce 2009).



2.2 TREATMENTS

At each site, nine 1-ha plots were randomly allocated to three replicates of three treatments: control (unburnt), burned in spring or burned in summer/autumn (these will be referred to as spring-burnt and summer-burnt plots, respectively). Each plot was marked out into twenty-five 20×20 m sub-plots. One of these sub-plots in each main plot was randomly selected for invertebrate sampling, excluding the outer sub-plots, which served as a buffer to reduce 'edge effects'. For simplicity, the sub-plots designated for invertebrate sampling will henceforth be called invertebrate plots.

Fire treatments were coordinated, carried out and supervised by DOC staff according to best practice guidelines. Timing was based on information from the national Rural Fire Authority network of fire weather stations. Data from these stations were used to calculate a number of indices using the New Zealand Fire Weather Index System (Van Wagner 1987), which were then used to determine optimum times for burns. The burn dates, between November 2000 and April 2006, are shown in Table 2. More details of the indices used in relation to the fires for this trial are given in a report by Forest Research (NZ Fire Research 2001). The summer burn treatment at MB was delayed until March 2006 because of restrictions on burning in a prohibited fire season. The data from this treatment are not included in this report.

TABLE 2. TREATMENT AND SAMPLING DATES AT DEEP STREAM AND MOUNT BENGER.
× = pre-burn sample; ✕ = post-burn sample.

TREATMENT/ SAMPLE	DATE	PLOT 1	2	3	4	5	6	7	8	9
Deep Stream										
Control		×					×	×		
Spring burn	2 Oct 2001			×	×				×	
Summer burn	7 Mar 2001		×			×				×
Samples	3 Apr 1998	×	×	×	×	×	×	×	×	×
	19 Aug 1998	×		×	×		×	×	×	
	11 Jan 1999	×	×	×	×	×	×	×	×	×
	14 Sept 1999	×		×	×		×	×	×	
	6 Jan 2000	×	×	×	×	×	×	×	×	×
	18 Sept 2000	×		×	×		×	×	×	
	12 Jan 2001	×	×	✕	✕	×	×	×	✕	×
	9 Mar 2001	×	✕			✕	×	×		✕
	24 Sept 2001	×		✕	✕		×	×	✕	
	5 Oct 2001	×		✕	✕		×	×	✕	
	11 Jan 2002	×	✕	✕	✕	✕	×	×	✕	✕
	17 Jan 2003	×	✕	✕	✕	✕	×	×	✕	✕
	6 Jan 2004	×	✕	✕	✕	✕	×	×	✕	✕
	11 Jan 2005	×	✕	✕	✕	✕	×	×	✕	✕
Mount Benger										
Control			×		×			×		
Spring burn	3 Nov 2000	×					×			×
Summer burn	31 Mar 2006			×		×			×	
Samples	15 Apr 1998	×	×	×	×	×	×	×	×	×
	26 May 1998	×	×	×	×	×	×	×	×	×
	13 Jan 1999	×	×	×	×	×	×	×	×	×
	20 Sept 1999	×	×		×		×	×		×
	7 Jan 2000	×	×	×	×	×	×	×	×	×
	20 Sept 2000	×	×		×		×	×		×
	10 Nov 2000	✕	×		×		✕	×		✕
	15 Jan 2001	✕	×	×	×	×	✕	×	×	✕
	14 Jan 2002	✕	×	×	×	×	✕	×	×	✕
	8 Jan 2003	✕	×	×	×	×	✕	×	×	✕
	16 Jan 2004	✕	×	×	×	×	✕	×	×	✕
	Jan 2005	✕	×	×	×	×	✕	×	×	✕
	Apr 2006		×	✕	×	✕		×	✕	

2.3 INVERTEBRATE SAMPLING

Invertebrate sampling dates for each site are shown in Table 2. Not all invertebrate plots were sampled on each sampling date; for example, where a spring burn had been carried out, only the control and spring-burnt plots were sampled, and not the plots to be burned in summer. Invertebrates were sampled quantitatively using a 320 × 320 mm quadrat (0.1 m^2) as a guide and cutting turves with a spade to a depth of approximately 50 mm. The invertebrates extracted from these samples (see below) provided a measure of density (number/m^2). For each sample date (Table 2), twenty 0.1-m^2 inter-tussock ('turf') samples were taken by throwing the quadrat and cutting turves in a general pattern of four rows of five turves from within the invertebrate plots. In addition, in each invertebrate plot, nine samples (three rows of three) were taken as above, but which included a tussock (*Chionochloa rigida*) plant ('tussock samples'). Thus, on a date when all plots were sampled, a total of 180 turf samples and 81 tussock samples were taken from each site. Care was taken to avoid resampling areas that had been sampled previously.

All samples were individually bagged, transported to AgResearch Invermay, and stored at 4°C for a maximum of 3 weeks before processing (Bremner 1988).

2.4 INVERTEBRATE EXTRACTION AND PROCESSING

In the laboratory, invertebrates were extracted from each turf sample over a 7-day period using modified Tullgren funnel heat extractors (Crook et al. 2004). Sample extraction was arranged to avoid differential storage of treatments and plots. After extraction from turves, the invertebrates were stored in 70% ethanol at 4°C until sorting.

Samples were washed through fine muslin, which retained all invertebrates but allowed fine silt to pass though. The 'cleared' samples were then sorted and invertebrates counted under a 6.3–40× binocular microscope. A list of the 55 taxonomic groups into which invertebrates were identified is shown in Appendix 1, which also gives common names where possible. The only groups not identified and counted for each sampling date were Collembola and Acari, although for some dates these have been further subsampled and identified to family (Barratt et al. 2006); the Collembola and Acari from all other dates have been retained for future study.

Coleoptera were identified to species, so that further analysis at species level (species richness/diversity) could be carried out on a representative insect group. Adult Coleoptera were identified to morphospecies (recognisable taxonomic units) or, where possible, to species level. Larval Coleoptera were identified to family, but identification beyond this was rarely possible. In the Coleoptera species analyses, larval morphospecies are included as separate taxa even though this is likely to over-estimate species numbers. This is because it is impossible in most cases to match larvae with adults, and this also allows for the fact that larvae and adults are sometimes in different trophic groups, occupying different niches and in general performing different functions in the community.

The higher taxonomic groups were allocated to the functional categories of herbivores, carnivores, fungivores and detritivores. Carrion-feeders (Coleoptera: Dermestidae) were also present, but at densities too low to be worthwhile including in the analyses. In some cases where taxa comprised either sub-groups that varied in feeding characteristics (e.g. Lepidoptera larvae can be herbivores or detritivores), or where adults and larvae belonged in different groups (e.g. Lepidoptera again, where adults are often nectar feeders), a judgement was made on the predominant function for the particular taxon. Trophic group could not always be allocated with complete confidence, but the literature was consulted as far as possible to assist (e.g. Klimaszewski & Watt 1997).

A species list for Coleoptera from both sites is shown in Appendix 2, along with their native/adventive status and allocation to trophic group. The higher taxonomic classification of Leschen et al. (2003) was used for guidance on native/exotic status, although this was not available at the species level.

The January 2001 tussock Coleoptera samples for DS were identified for the spring-burnt plots but not for the control and summer-burnt plots. Regrettably, this omission was discovered too late to be rectified and limits our scope for data analysis for that date.

All invertebrate material has been stored fully labelled in 70% ethanol. The material identified to major groups has been separated and stored in vials. Collembola (springtails) and Acari have been stored together with the material retained by the muslin after filtering.

2.5 STATISTICAL ANALYSES

Invertebrate density data and the proportion of individuals in each trophic group were analysed for each site using restricted maximum likelihood (REML, which is a method for fitting linear mixed models producing unbiased estimates of variance) to model the effect of treatments and dates and their interactions on the $\log_e$ counts of number of individuals (Payne et al. 2006).

For the more detailed analyses of coleopteran species density data, a similarity matrix for the nine plots from DS and six plots (three replicates of control and spring-burnt plots) from MB was calculated using a Euclidean metric (which was considered appropriate since distance measures are on a continuous rather than a discontinuous scale). From this, a distance matrix (using distances between the individual plot data points) was obtained as $(2(1 - \text{similarity}))^{0.5}$. This was used for non-metric multidimensional scaling (MDS) using two dimensions (Payne et al. 2006) for Coleoptera species density data to obtain a visual assessment of the degree of similarity between the sites, and the treatment plots within the sites.

Coleopteran species richness (number of species present per plot) was calculated for the turf and tussock samples for each plot at each site on each date. Restricted maximum likelihood was used to model the effect of site, treatment and date and their interactions on the $\log_e$ species richness counts (Payne et al. 2006).

Coleopteran species diversity was examined by calculating Shannon-Wiener indices of diversity (*H*) for each plot at each site on each date. This index is probably the most commonly used measure of biodiversity, and takes into account the number of species and the number of individuals of each species in the sample. Restricted maximum likelihood was used to model the effect of site, treatment and date and their interactions on the indices (Payne et al. 2006). Changes in coleopteran species diversity following burning treatments were also investigated using *k*-dominance plots. These plots were used in addition to the Shannon-Wiener index because they give a good visual appreciation of the data showing all data points and the shape of the curve provides an indication of dominance (steep plots) or evenness (shallow curves) of species assemblages. Log_{10} density was ranked for Coleoptera species and plotted against cumulative percentage density. This produced curves in which the most diverse samples appear on the lower part of the plot. The pre-burn and post-burn data were compared for the same plots for DS and MB spring-burnt turf plots and for DS summer-burnt turf plots. Comparisons were not possible for DS summer-burnt tussock plots, as the pre-burn data were not available. There are no pre-burn and post-burn comparisons for the MB summer-burnt plots because of the late date (31 March 2006) of the MB summer burn.

The percentage of Coleoptera in each of five trophic groups and the percentage of exotic Coleoptera species were calculated for each plot at each site on each date. Restricted maximum likelihood was used to model the effect of site, treatment and date and their interactions.

3. Results

Between April 1998 and April 2006, a total of 6177 0.1-m^2 samples were taken from the nine 1-ha treatment plots at DS and MB. Approximately 1.26 million invertebrates were extracted, identified and counted from the samples collected.

Two burn treatments were successfully undertaken on treatment plots at DS in March (summer burn) and October (spring burn) 2001. At MB, the spring burning treatment was carried out in November 2000. However, as noted above, it was not possible to conduct the summer burn at MB until March 2006.

3.1 DEEP STREAM VERSUS MOUNT BENGER INVERTEBRATE COMMUNITIES

At DS, the mean density of all invertebrates in control plots over the study period was 4018 individuals/m^2 in turf samples and 3059 individuals/m^2 in tussock samples. The equivalent mean values at MB were 2309 individuals/m^2 and 2644 individuals/m^2, respectively.

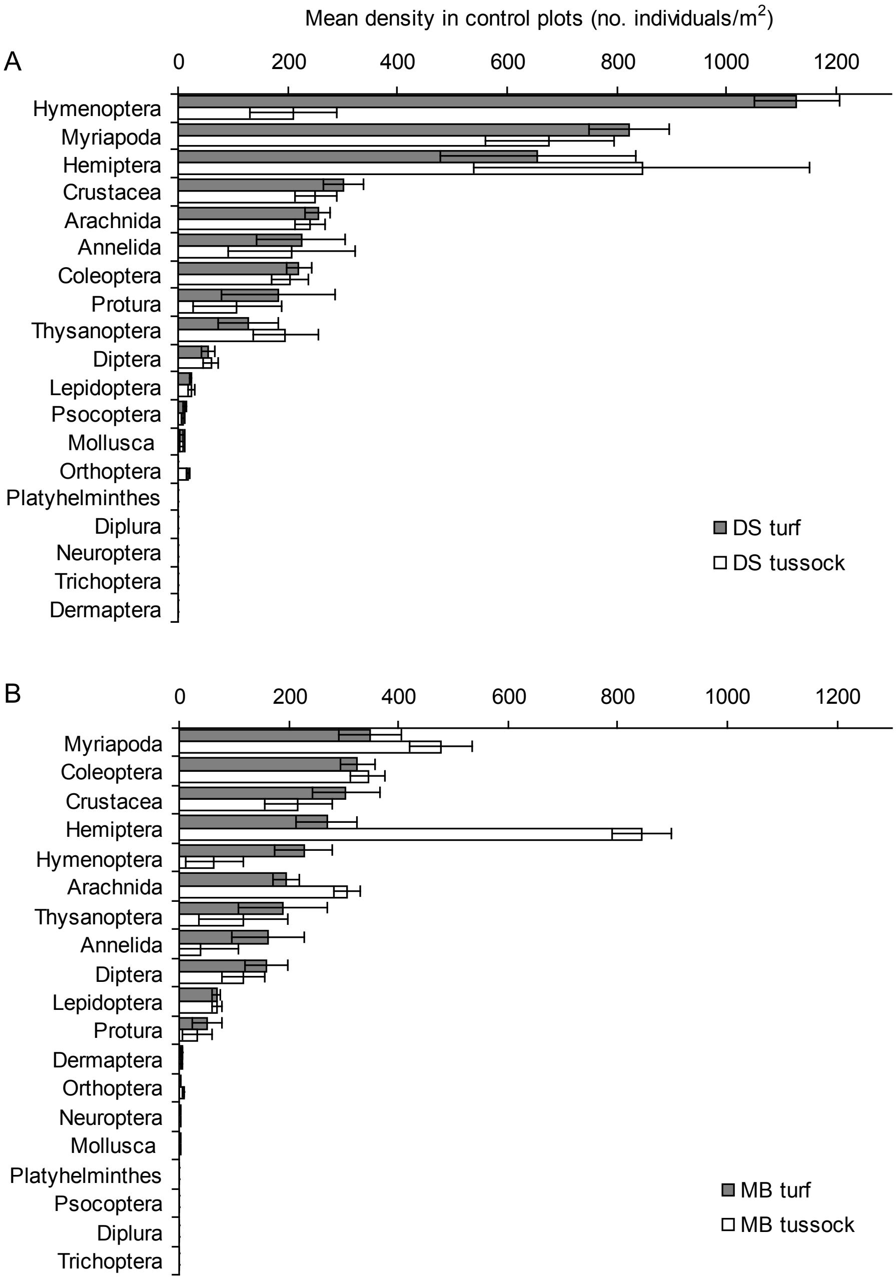
3.1.1 Taxonomic composition

At the higher taxonomic levels (i.e. order and above), the composition of the communities at the two sites was similar, with the exception of Hymenoptera (mainly ants), which were present at a higher density at DS than at MB (Fig. 2). Hymenoptera occurred at a higher density than any other group at DS, with their mean density in turf samples (averaged across all control plot samples throughout the study) reaching > 1100 individuals/m^2. This was almost 30% of all the invertebrates present in the DS turf samples. At MB, the hymenopteran population was ranked at the fifth highest density; the Myriapoda were recorded at the highest density (348 individuals/m^2), although densities here were lower than at DS (Fig. 2).

At DS, turf and tussock samples contained similar densities of the different invertebrate groups, with the exception of Hymenoptera, which were present at a far greater density in the turf than the tussock samples. Myriapoda densities were higher than other groups in tussock samples at DS. At MB, the greatest difference between turf and tussock samples was in the density of Hemiptera; the Pseudococcidae was by far the largest family in this group in terms of number of individuals, and their density was higher in the tussock samples than in turf samples.

Notes on a few of the taxa collected and their ecology are given in Appendix 3.

Figure 2. Mean density of invertebrates (no. individuals/m[2]) at Order level or above in control plots for all sample dates shown for turf and tussock samples. A. Deep Stream; B. Mount Benger. Error bars represent 2 SEMs.



3.1.2 Trophic composition

The mean density of each of the four recognised trophic groups was calculated for each site and vegetation sample type for control plots as an average of all sample dates. Formicidae (ants) were excluded from this analysis because they are generalist feeders. For each site and vegetation type, herbivores comprised 30–40% of the total invertebrate density, carnivores 20–25%, detritivores 30–40%, and fungivores about 5% (see section 3.3).

3.2 EFFECT OF BURNING TREATMENTS ON INVERTEBRATE DENSITY

The effect of the spring and summer tussock fires on total invertebrate density and on Coleoptera density is shown in Fig. 3 (DS) and Fig. 5 (MB) in the sections that follow. Effects on other taxa that were present at high densities and are discussed in the sections below can be found in Appendices 4 and 5. The probabilities calculated for the restricted maximum likelihood model for treatment effects (Chi *P*) are shown in Table 3, and comments on significant differences for individual dates are provided where they occurred. Data for Platyhelminthes, Neuroptera, Mollusca, Trichoptera and Dermaptera are not shown in Table 3 because in most cases densities were too low ($< 1/m^2$) for reliable analysis in the

TABLE 3. PROBABILITIES (CHI *P*) FOR TREATMENT EFFECTS FOR DEEP STREAM (DS) AND MOUNT BENGER (MB) TURF AND TUSSOCK SAMPLES FOR MAIN INVERTEBRATE TAXA.

Where main effects were not significant, differences for individual dates are shown. 'id' = insufficient data for analyses.

CLASS	ORDER	DEEP STREAM		MOUNT BENGER		TREATMENT DIFFERENCES
		TURF	TUSSOCK	TURF	TUSSOCK	FOR INDIVIDUAL DATES
Platyhelminthes		0.385	0.411	0.231	0.832	
Annelida	Oligochaeta	<0.001	0.003	0.177	0.217	
Mollusca		0.251	0.555	0.018	0.620	
Arachnida	Total	<0.001	0.01	0.002	0.074	
Arachnida	Araneae	<0.001	0.055	0.012	0.143	
Arachnida	Opiliones	<0.001	0.001	<0.001	<0.001	
Crustacea	Total	<0.001	<0.001	<0.001	0.009	
Crustacea	Amphipoda	<0.001	<0.001	<0.001	0.004	
Crustacea	Isopoda	<0.001	<0.001	0.426	0.803	
Myriapoda	Total	<0.001	0.011	<0.001	0.934	
Myriapoda	Chilopoda	<0.001	0.022	0.046	0.239	
Myriapoda	Diplopoda	0.028	0.418	<0.001	<0.001	
Myriapoda	Symphyla	<0.001	0.022	0.019	0.465	
Insecta	Diplura	id	id	id	id	
Insecta	Protura	0.062	0.745	0.537	0.902	
Insecta	Orthoptera (total)	0.051	<0.001	0.169	0.001	
Insecta	Dermaptera	id	id	<0.001	0.721	
Insecta	Psocoptera	<0.001	0.087	–	–	
Insecta	Hemiptera (total)	0.007	0.044	0.208	0.279	MB turf post-burn < pre-burn
Insecta	Hemiptera (Pseudococcidae)	0.002	0.508	0.027	0.174	DS tussock spring and summer post-burn < pre-burn
Insecta	Hymenoptera	<0.001	0.409	<0.001	0.135	
Insecta	Lepidoptera	0.734	0.05	<0.001	0.012	DS turf spring and summer post-burn < pre-burn
Insecta	Neuroptera	id	id	id	id	
Insecta	Trichoptera	id	id	id	id	
Insecta	Coleoptera (total)	<0.001	0.064	<0.001	0.677	DS tussock spring and summer post-burn < pre-burn
Insecta	Diptera	0.467	0.400	0.032	0.062	DS turf spring and summer post-burn < pre-burn
Insecta	Thysanoptera	<0.001	<0.001	0.029	0.072	
Total invertebrates		0.002	0.175	<0.001	0.244	DS tussock spring and summer post-burn < pre-burn

study area in both turf and tussock samples. Table 4, which is presented at the end of this section, summarises the findings for each invertebrate group reported below.

3.2.1 Deep Stream

Total invertebrate density in control plots remained quite consistent throughout the sampling period for both turf and tussock samples (Fig. 3A & B). The immediate effect of the spring and summer burns in 2001 was to reduce the number of invertebrates to about 8% and 5%, respectively, of pre-burn densities in turf samples (Fig. 3A), and to about 12% and 18% of pre-burn densities in tussock samples (Fig. 3B). The treatment effects were significant for turf samples (Table 3).

Coleoptera densities were less variable between replicate plots than many other taxa, and remained quite consistent in control plots throughout the study period in both turf and tussock samples (Fig. 3C & D). There were significant reductions in density after both burn treatments in turf samples, but not in tussock samples (Table 3). Recovery was evident for the family as a whole within 1 year after the burn.

Annelid densities in control plots varied considerably between dates, but the treatment effects were significant for both turf and tussock samples (Table 3). In both treatments, there was some recovery of annelid numbers during the year following treatment, but they then declined substantially in January 2003. By 2005, the population had recovered to levels similar to the control plots.

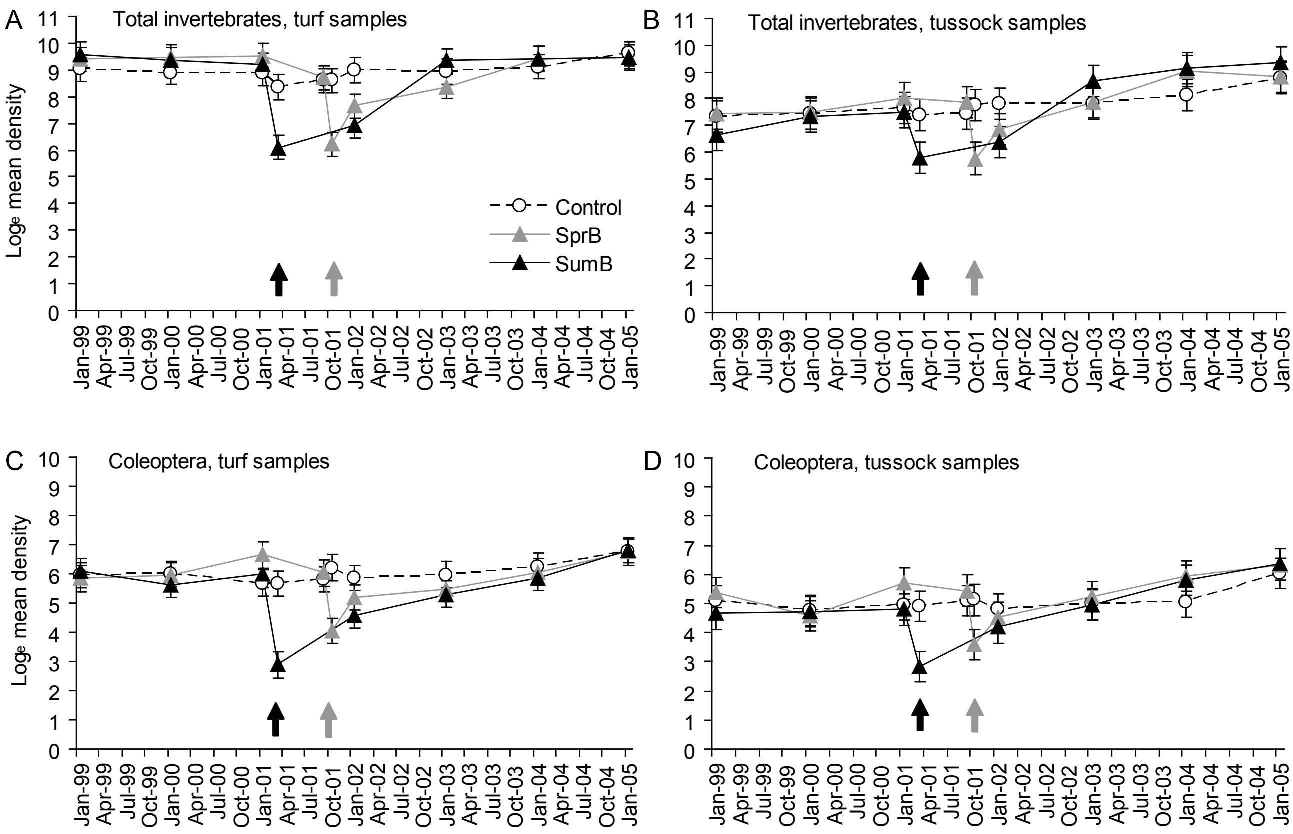


Figure 3. Mean density (no. individuals/m^2) of A. total invertebrates in turf; B. total invertebrates in tussock; C. Coleoptera in turf; and D. Coleoptera in tussock at Deep Stream in control, spring-burnt (SprB) and summer-burnt (SumB) plots. Density is expressed as log$_e$ mean density throughout the study period. Error bars represent 2 SEMs. Arrows indicate summer (black arrow) and spring (grey arrow) burn dates.

Arachnid densities were reduced significantly in both turf and tussock samples (Table 3). Burn treatments reduced density in turf samples for Araneae, and in turf and tussock samples for Opiliones. Recovery of the Araneae appeared to be more rapid than for the Opiliones. Opiliones densities became very low in January 2003, but showed signs of recovery in the following years.

Crustacea were represented mainly by Amphipoda and Isopoda. Amphipoda densities were dramatically reduced by the burning treatments in both turf and tussock samples (Table 3). In the spring-burnt plots, there was no evidence of recovery by the 2005 sample date. Control plot densities remained quite consistent over the sampling period. Isopoda were also significantly reduced in density by the burning treatments in turf and tussock samples and, like the Amphipoda, the spring-burnt plot densities remained low to 2005.

Myriapoda were represented by Chilopoda, Diplopoda and Symphyla. Overall, Myriapoda density was reduced significantly in turf and tussock samples at both sites (Table 3), but this reduction was observed mainly during the 2–3 years after the burns. Chilopoda were significantly reduced in density in both turf and tussock samples for all treatments when sampled in 2003 and 2004, but recovery was evident by 2005. Diplopoda densities were very variable between the replicate plots, but there was a significant reduction in density in turf samples immediately post-burn. Symphyla densities declined in turf samples in the 2–3 years post-burn.

Orthoptera were present at low density at DS, although higher densities were observed in the tussock samples than in the turf samples. Densities in turf samples were very variable, but in tussock samples the densities after the spring burn remained very low compared with control plots and pre-burn densities.

Following burning, densities of Psocoptera (detritivores that did not occur at MB) were significantly reduced in the turf samples (Table 3), where their density was initially higher than in tussock. In both turf and tussock samples, densities post-burn remained very low.

Hemiptera densities were dominated by Pseudococcidae. Numbers of individuals in 0.1-m^2 samples ranged from 0 to over 1000, which suggested that these are very aggregated in the field. A significant reduction was found only in post-burn turf samples (Table 3). Mean density was very variable even in control plots, but both spring and summer burns reduced densities to low levels. There was evidence of recovery by January 2003.

Hymenoptera densities were dominated by Formicidae. Densities were very high and consistent in control turf samples for all sample dates, and there was a significant treatment effect (Table 3). Hymenoptera density was lower and more variable in tussock samples, and there were no significant treatment effects.

Lepidoptera, present mainly as larvae in samples, were significantly reduced in density in tussock samples post-burn (Table 3), but populations had recovered by 2003, and appeared to exceed densities in the control plots by 2004. This increase was not significant, but occurred in both turf and tussock samples.

Diptera, present mainly as larvae in the samples, showed no significant treatment effects (Table 3).

Thysanoptera density was dramatically reduced after spring and summer burns in both turf and tussock samples. However, for both vegetation types, the densities in the summer-burnt plots recovered to densities that were substantially higher than those in the control plots. For example, in the summer-burnt plots, pre-burn density (January 2001) in turf samples was approximately 70 individuals/m^2, which was reduced to less than 1 individual/m^2 immediately post-burn, but reached about 5000 individuals/m^2 by January 2003. A similar pattern was observed in tussock samples.

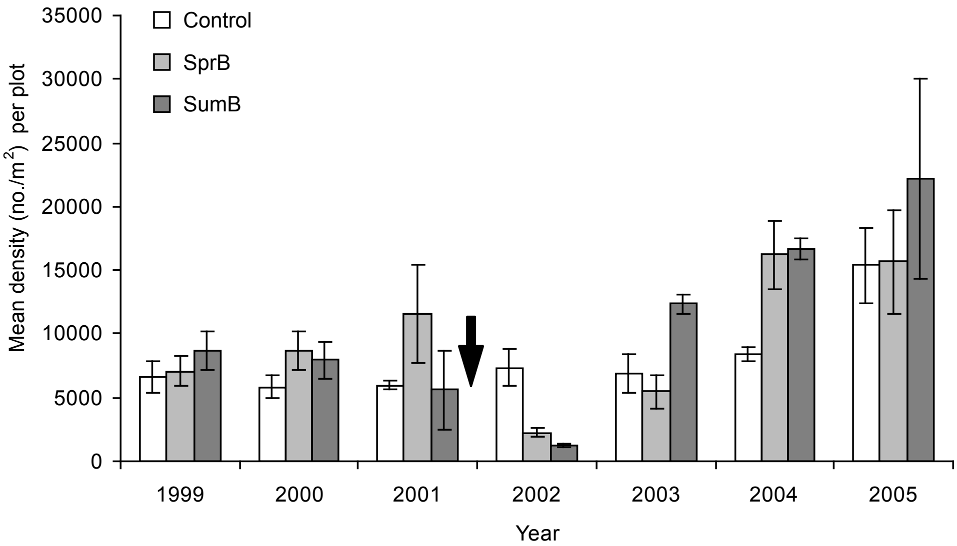
Spring versus summer burn at Deep Stream

The mean density of invertebrates per plot for each January sampling date is shown in Fig. 4. Densities in control plots were consistent from year to year until 2005, when they increased significantly, largely as a result of greatly increased densities of Protura.

For the 3 years pre-burn (1999–2001), there was no significant difference in invertebrate density between plots, although the variability in 2001 was higher than previous years. In January 2002, 3 months after the spring burn and 10 months after the summer burn, the density of invertebrates in both treatments was significantly reduced compared with the control plots. However, compared with means from the same plots in the previous year, invertebrate densities were significantly reduced for only the spring-burnt plots, as the large variability between the summer-burnt plots in 2001 obscured any differences.

By 2003, invertebrate densities in the spring-burnt plots had returned to levels similar to those before treatment, and those in the summer-burnt plots had increased significantly. In 2004, invertebrate densities in both burnt plots significantly exceeded those in control plots, and this was still the case in 2005. This reflects the increased densities of some of the herbivorous taxa (see section 3.3).

Figure 4. Mean (±SEM) total density (no. individuals/m^2) per plot of invertebrates in each treatment from 1999 to 2005 at Deep Stream. Arrow indicates sampling dates between which the burning treatments occurred. SprB = spring-burnt plots; SumB = summer-burnt plots.



3.2.2 Mount Benger

As for DS, total invertebrate density in control plots at MB remained quite consistent throughout the sampling period for both turf and tussock samples (Fig. 5A & B). The immediate effect of the spring burn in 2000 was less pronounced than at DS, although invertebrate density was still significantly reduced by 40% and 19% of pre-burn densities in 2001 and 2002, respectively.

For total invertebrate density, the generalised linear model showed that there was a significant interaction between treatment and vegetation type. The density of invertebrates (c. 2000 individuals/m^2 before the spring burn) was reduced to about 400 individuals/m^2 in January 2002, just over 1 year after the spring burn (Fig. 5A). No such reduction was observed in the tussock samples (Fig. 5B).

Coleoptera densities were quite consistent between replicate control plots and between dates throughout the study period (Fig. 5C & D). After the spring burn, numbers were reduced significantly in turf samples (Fig. 5C), but there were no significant changes in density in the tussock samples (Fig. 5D).

Annelid density was variable over the study period. There were no significant effects of the spring fire treatment.

Total Arachnida were significantly reduced only in turf samples in January 2002. Araneae densities showed a significant treatment effect only in turf samples (Table 3), but the density of Opiliones was substantially reduced in both turf and tussock samples (Table 3).

A significant treatment effect was found for total Crustacea in turf and tussock samples (Table 3). The fauna was dominated by Amphipoda, which were significantly reduced by the spring burn in both sample types in January 2002; as at DS, there was no evidence of recovery of the population by the end of the study. Isopoda at MB were not significantly affected by the burning treatment, whereas they were at DS.

Total Myriapoda were significantly reduced in density by the spring burn, particularly Diplopoda, which showed no sign of recovery by the end of the study in either turf or tussock samples. Symphyla and Chilopoda showed significant treatment effects in turf samples only (Table 3).

Orthoptera densities were significantly reduced in tussock samples from immediately post-burn to the end of the study period. As at DS, this reduction was mainly attributable to Blattidae densities being reduced to almost zero in tussock samples after the burn.

Hemiptera densities were dominated by Pseudococcidae, as they were at DS. However, at MB the spring burn reduced densities significantly only in turf

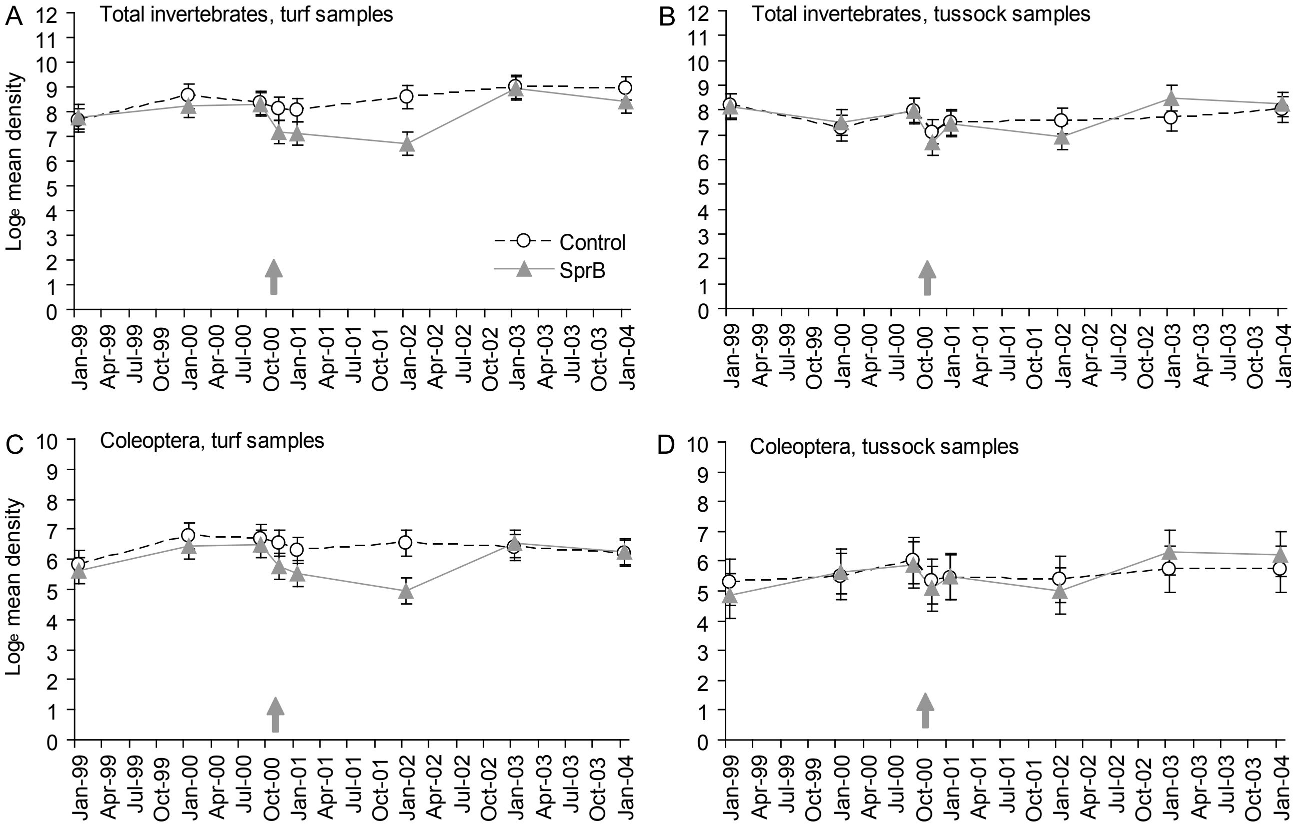


Figure 5. Mean density (no. individuals/m^2) of A. total invertebrates in turf; B. total invertebrates in tussock; C. Coleoptera in turf; and D. Coleoptera in tussock at Mount Benger in control and spring-burnt (SprB) plots. Density is expressed as $\log_e$ mean density throughout the study period. Error bars represent 2 SEMs. The grey arrow indicates the spring burn date.

samples. At this site there was also a large post-burn increase in numbers of Aphididae (not shown) observed in January 2003.

Hymenoptera densities, dominated by Formicidae, were very variable in turf samples, but there was a significant treatment effect (Table 3). Densities were less variable in tussock samples, but there was no significant treatment effect.

Lepidoptera densities were significantly reduced in 2001 after the spring fire in both turf and tussock samples, but populations appeared to have recovered by January 2003.

Thysanoptera densities were significantly reduced only in turf samples (Table 3), but recovered rapidly. In both sample types, densities in January 2003 exceeded pre-burn and control densities, although variability between plots was high.

3.2.3 Summary

The responses of invertebrate taxa found at Deep Stream and Mount Benger to burning treatments are summarised in Table 4.

TABLE 4. SUMMARY OF RESPONSES OF INVERTEBRATE TAXA TO BURNING TREATMENTS AT DEEP STREAM (DS) AND MOUNT BENGER (MB).

RESPONSE	TAXA	WHERE APPLICABLE
No significant treatment effect	Platyhelminthes	Both sites and sample types
	Protura	Both sites and sample types
	Coleoptera	Both sites tussock
	Pseudococcidae	Both sites tussock
	Hymenoptera	Both sites tussock
	Isopoda	Both sites tussock
	Orthoptera	Both sites turf
	Diptera	DS both sample types
	Mollusca	DS both sample types
	Araneae	MB both sample types
	Annelida	MB both sample types
Density reduced but recovered rapidly	Pseudococcidae	Both sites and sample types
	Coleoptera	Both sites turf
	Diptera	DS
Density reduced but recovered by Jan 2005	Annelida	DS turf
	Isopoda	DS turf
	Chilopoda	DS turf
	Araneae	DS turf
	Symphyla	DS turf
	Lepidoptera	MB
Density reduced and little if any recovery by Jan 2005	Amphipoda	Both sites and sample types
	Psocoptera	DS turf
	Hymenoptera	DS turf
	Orthoptera (Blattidae)	DS spring burn and MB tussock
	Diplopoda	MB
Density reduced but then 'rebounded'	Thysanoptera	DS in particular
	Lepidoptera	DS summer burn
Differences between sites	Annelida	Greater impact DS turf than MB turf
	Myriopoda	Greater impact DS turf than MB turf
	Hemiptera	Faster recovery MB than DS both sample types
	Coleoptera	Greater impact DS than MB both sample types
Differences between vegetation sample types	Myriopoda	Main effects in turf
	Orthoptera (Blattidae)	Main effects in tussock
	Hymenoptera	Main effects in turf

3.3 EFFECT OF BURNING TREATMENTS ON COMMUNITY TROPHIC STRUCTURE

Short-term (2–3 months post-burn) and medium-term (36 months post-burn) changes in the trophic group composition of the invertebrate fauna are discussed below. The trophic structure of the invertebrate communities was similar for the two sites and vegetation types pre-burn (Fig. 6A), with herbivores and detritivores present at similar densities and comprising similar proportions of the invertebrate fauna. Carnivores were slightly less well represented and fungivores comprised a small proportion of the invertebrate fauna. However, as mentioned previously, Collembola, which are primarily fungivores, have not been included in this study.

3.3.1 2–3 months post-burn

Figure 6B suggests that 2–3 months post-burn, densities were reduced for all groups and the proportional structure of the community had changed, particularly at DS.

At DS, the data indicate that the proportion of herbivores in the community was reduced to about 10% of the total, whereas the proportion of detritivores increased to 70% (turf) and 55% (tussock). A comparison of Fig. 6A and 6B suggests that these proportional changes were attributable mainly to the substantial decline in the density of herbivores (mainly Pseudococcidae, Curculionidae and Thysanoptera) and a lesser decline in detritivore densities after burning.

At MB, the community trophic structure was little changed following burning, except that fungivores were almost totally removed (Fig. 6B). This may have mainly been due to reductions in the density of Protura in the spring-burnt plots. Unlike at DS, by the January following the spring burn, the density of Pseudococcidae in the tussock plots at MB had already recovered almost to pre-burn densities.

3.3.2 3 years post-burn

After 3 years, the picture in the burnt plots was even more different from the long-term averages of the control plots, with much greater densities of herbivores, largely resulting from the huge 'rebound' response of Pseudococcidae and other Hemiptera, and Thysanoptera (Fig. 6C). At DS, the increase in the proportion of carnivores in turf samples was a result mainly of the recovery of Araneae (Appendix 4). At MB, the reappearance of fungivores was represented mainly by Protura and Pauropoda (data not presented).

Figure 7 shows the mean densities of invertebrates in the major trophic groups (excluding Hymenoptera) each year for the years preceding and following the spring-burn treatments at DS and MB (Fig. 7A & C); and for the years preceding and following the summer-burn treatment at DS (Fig. 7B). The figure shows that the density of some of the functional groups was quite variable between years before treatments were applied. For example, there were higher densities of detritivores (mainly Annelida, Amphipoda and Diptera larvae) in turf (but not tussock) at MB in January 2000 compared with 1999; conversely, there was a greater density of herbivores in tussock at MB in January 1999 compared with 2000, almost entirely due to a greater density of Pseudococcidae. Generally however, apart from these exceptions, the pre-treatment densities of each of the trophic groups were quite similar.

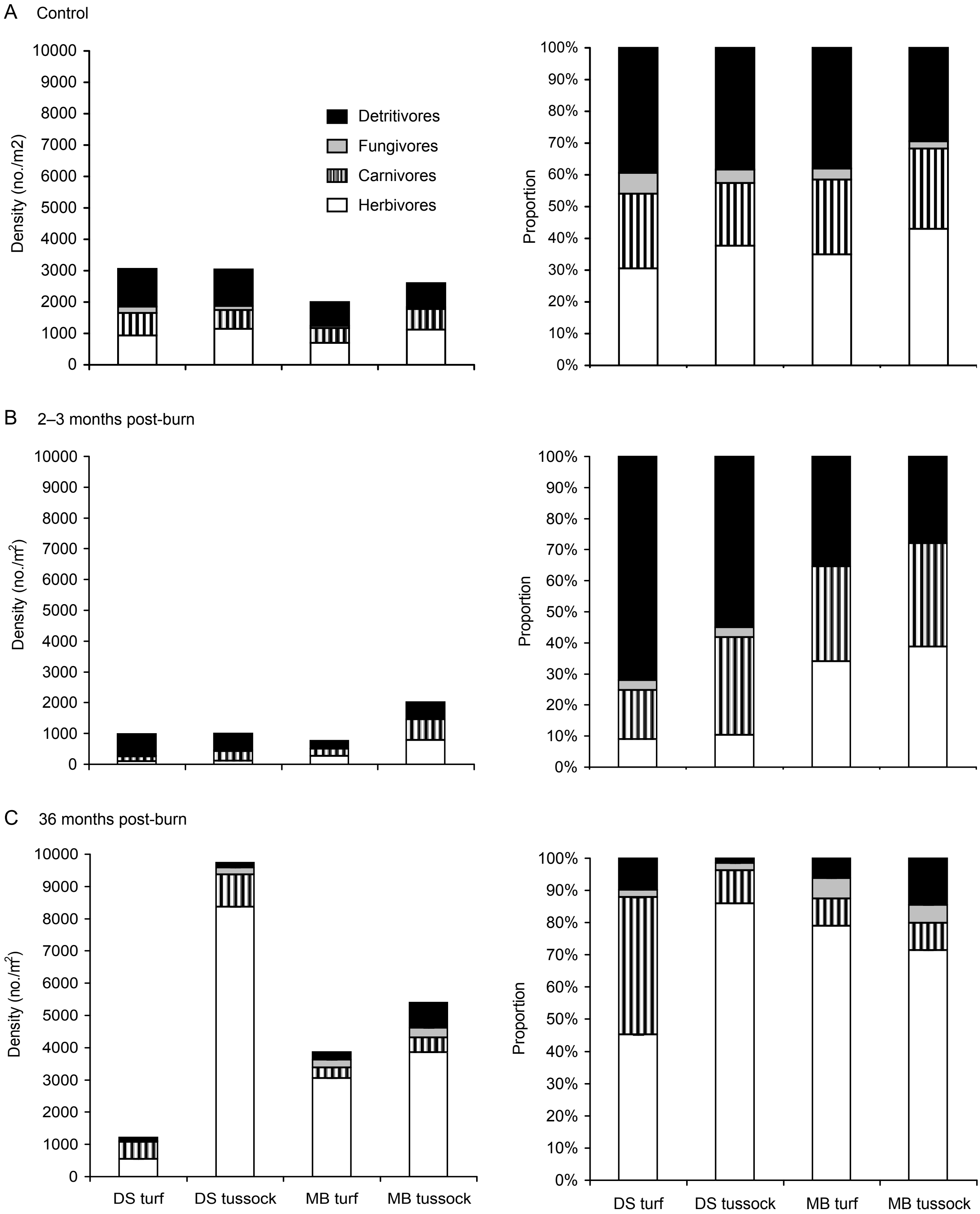
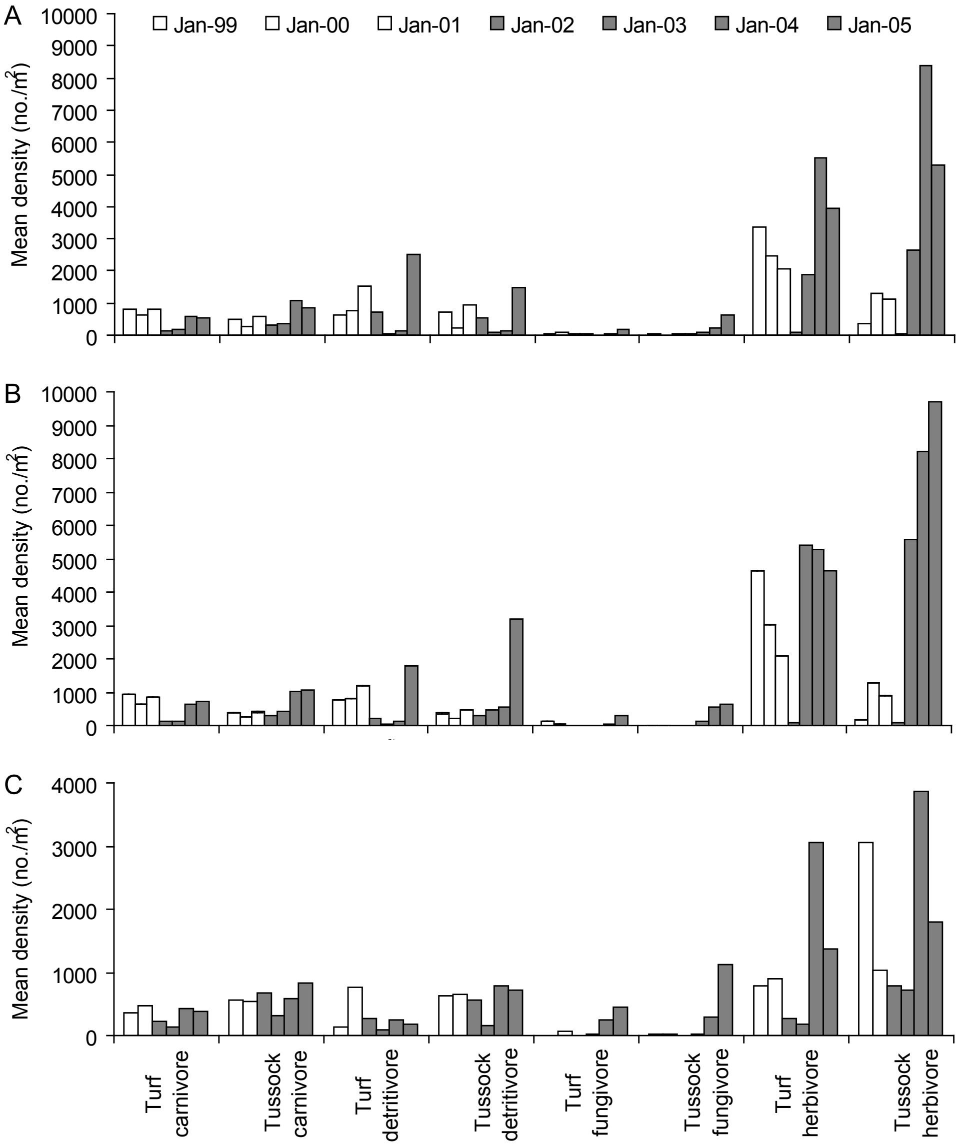


Figure 6. Mean density (no. individuals/m^2) and proportion (%) of invertebrate fauna in each trophic group A. in control plots; B. 2–3 months post-burn; and C. 36 months post-burn.

Figure 7. Mean density of invertebrates (excluding Hymenoptera) in each trophic group shown for consecutive January samples. A. Deep Stream—spring burn (1999–2005); B. Deep Stream—summer burn (1999–2005); and C. Mount Benger—spring burn (1999–2004). Open bars are pre-burn (all plots) and grey bars are post-burn in consecutive January samples.



After treatment, herbivores were most severely and immediately reduced in abundance at both sites and vegetation types, but particularly at DS for both spring and summer-burns. However, in the subsequent years, the abundance of herbivores increased and in most cases exceeded pre-burn densities, attributable mainly to Hemiptera (especially Pseudococcidae) and Thysanoptera, as discussed above.

The post-burn response in detritivore density differed between the two sites, particularly for the fourth year. At DS, detritivore densities in turf and tussock samples exceeded pre-burn levels by 2005. In the spring-burnt turf samples, detritivores comprised mainly Diptera larvae, Annelida and Symphyla. However, in the summer-burnt tussock samples, it comprised mainly Annelida and Diplopoda (data not presented). Detritivores exhibited a delayed response to burning, suggesting that environmental change rather than the direct effects of the fire precipitated their decline; e.g. it may have been caused by a reduction in litter, which provides a food source, habitat and insulation from temperature and humidity changes.

The density of fungivores at MB appeared to increase progressively following the spring fire (Fig. 7C). This response also occurred at DS, but less significantly (Fig. 7A). As noted above, this was attributable mainly to Pauropoda and Protura (data not presented).

3.4 COLEOPTERA: A DETAILED STUDY

3.4.1 Density, species composition and effect of burn treatments

The mean density (no. individuals/m^2) of Coleoptera in control plots is shown in Fig. 2. At DS, the mean density for control plots for all sample dates was 221 ± 23 individuals/m^2 in turf samples and 203 ± 34 individuals/m^2 in tussock samples. At MB, the equivalent densities were 325 ± 32 and 344 ± 30 individuals/m^2.

The taxonomic composition of the Coleoptera communities at DS and MB is summarised in Appendix 6. Overall, 24 families of Coleoptera were represented at DS and 28 familes at MB, and in total 111 genera and 202 species were found, excluding larvae. The number of Coleoptera species in each genus and family was similar for both sites, although species richness (excluding larvae) was a little higher at DS (142 species) compared with MB (135 species). If larvae are included, 270 taxa in total were identified. However, since some larvae would also be represented by adults this is certainly an overestimate.

The overlap of species between the two sites was about 40%. Exactly 33% of all species were found only at DS, and slightly fewer (25–29%) were found only at MB (Table 5). To assess the similarity of Coleoptera communities between sites and between plots within sites, non-metric MDS ordinations were carried out for coleopteran data pre-burn and 2–3 month post-burn (Fig. 8A & B). Both MDS ordinations show complete faunal separation between the two sites, suggesting that the coleopteran species abundance patterns were quite different at DS and MB. For the pre-burn data, the replicate plots within sites varied from close faunal similarity (DS control plots) to wide variability (MB spring-burnt plots) (Fig. 8A). For the post-burn data, there is very close faunal similarity between the DS spring- and summer-burnt plots, and the MB spring-burnt plots were also quite closely clustered in comparison with the control plots (Fig. 8B). The stress values (a measure of 'goodness of fit') for the coordinates for both pre- and post-burn MDS ordinations indicated a high level of confidence; it is generally

TABLE 5. SUMMARY OF NUMBER (AND %) OF COLEOPTERA SPECIES AT DEEP STREAM (DS) AND MOUNT BENGER (MB) IN DIFFERENT SAMPLE TYPES.

SITE	SAMPLE	NUMBER OF SPECIES/MORPHOSPECIES (%)	
		INCLUDING LARVAE	EXCLUDING LARVAE
DS only	Turf only	42 (15.5)	32 (15.8)
	Tussock only	22 (8.2)	17 (8.4)
	Total	89 (33.0)	67 (33.2)
MB only	Turf only	41 (15.2)	34 (16.8)
	Tussock only	17 (6.3)	13 (6.4)
	Total	68 (25.2)	59 (29.2)
Both DS and MB	Turf only	6 (2.2)	5 (2.5)
	Tussock only	1 (0.4)	1 (0.5)
	Total	113 (41.9)	76 (37.6)
Total DS		202 (74.8)	142 (70.3)
Total MB		181 (67.0)	135 (66.8)
Total DS and MB		270	202

accepted that values below 0.1 suggest an excellent fit, whereas values above 0.15 are unacceptable.

Non-metric MDS ordinations using species presence-absence data also gave complete separation of points for the two sites (Fig. 9). For the pre-burn data, there was a similar degree of spread across plots designated for the treatments at DS, but more clustering of plots at MB (Fig. 9A). Post-burn, the DS plots clustered more closely, especially the spring-burnt plots, suggesting that Coleoptera species composition was more similar after treatment than before (Fig. 9B).

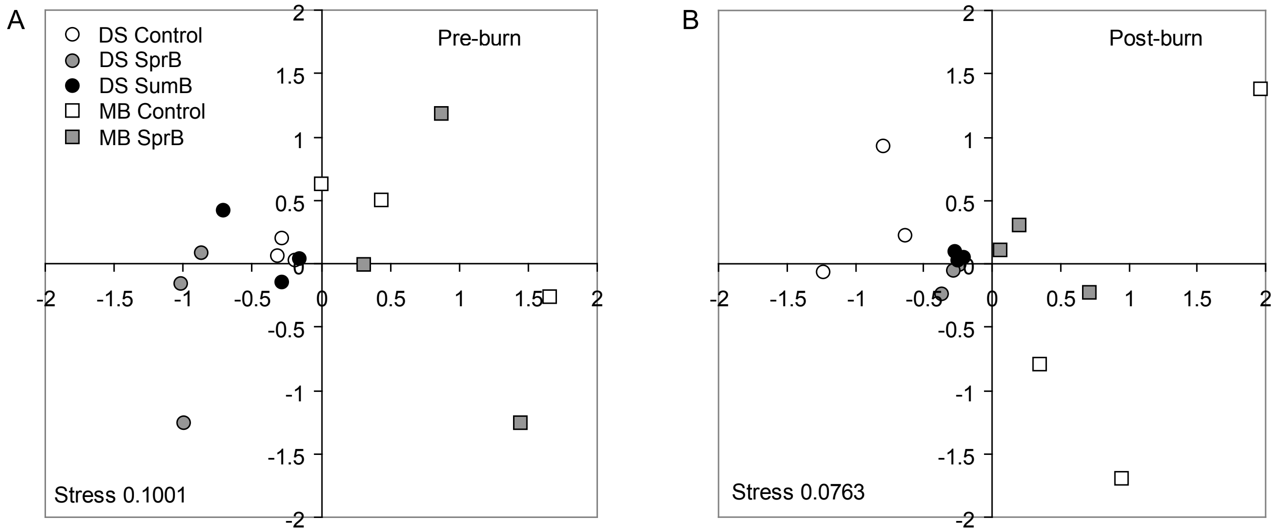


Figure 8. Multidimensional scaling (MDS) ordinations for Coleoptera species density for each of the replicate field plots at each site. A. Pre-burn samples and B. 2–3 months post-burn samples for Deep Stream (DS; circles) and Mount Benger (MB; squares), showing control, spring-burnt (SprB) and summer-burnt (SumB) plots. The closer the points, the more similar are the densities of each species.

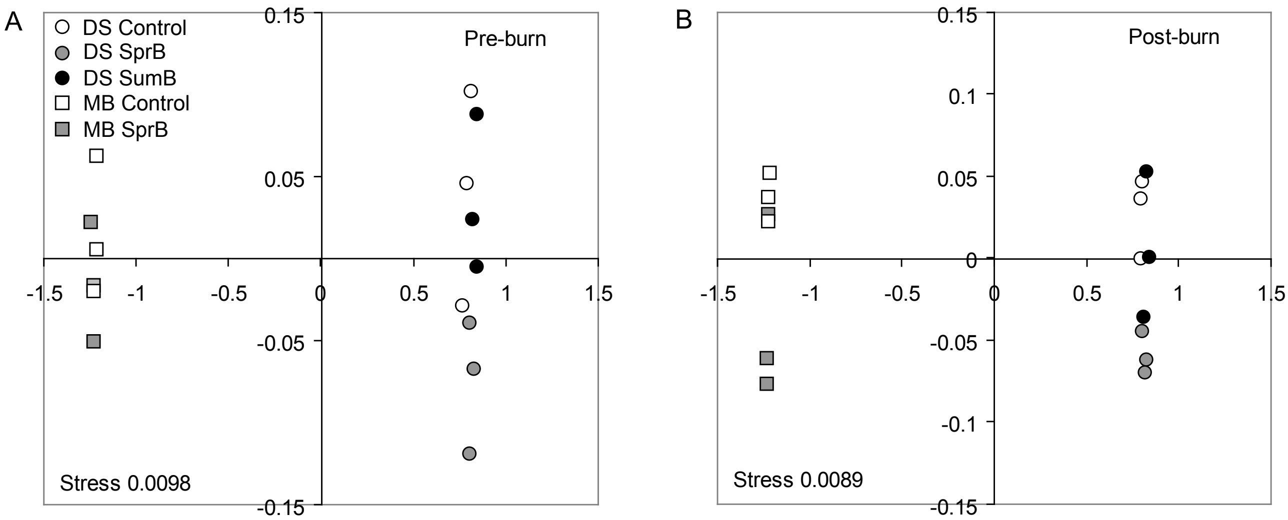


Figure 9. Multidimensional scaling (MDS) ordinations for Coleoptera species presence/absence data for each of the replicate field plots at each site. A. Pre-burn samples and B. 2–3 months post-burn samples for Deep Stream (DS; circles) and Mount Benger (MB; squares), showing control, spring-burnt (SprB) and summer-burnt (SumB) plots. The closer the points, the more similar the species composition of each plot.

3.4.2 Species richness

Analysis of species richness data (number of species) for total Coleoptera species (i.e. pooled for all turf plus tussock samples) showed that site and treatment had significant effects on species richness. Over the study period, species richness in control plots at DS and MB was significantly different (Wald statistic = 11.69, df = 1, $P < 0.001$), with means of 51 species and 71 species, respectively (back-transformed $\log_e$ values).

The effect of the burning treatments on species richness is illustrated in Fig. 10, which shows mean species richness $\log_e$-transformed with the back-transformed means (i.e. no. species/m^2) superimposed.

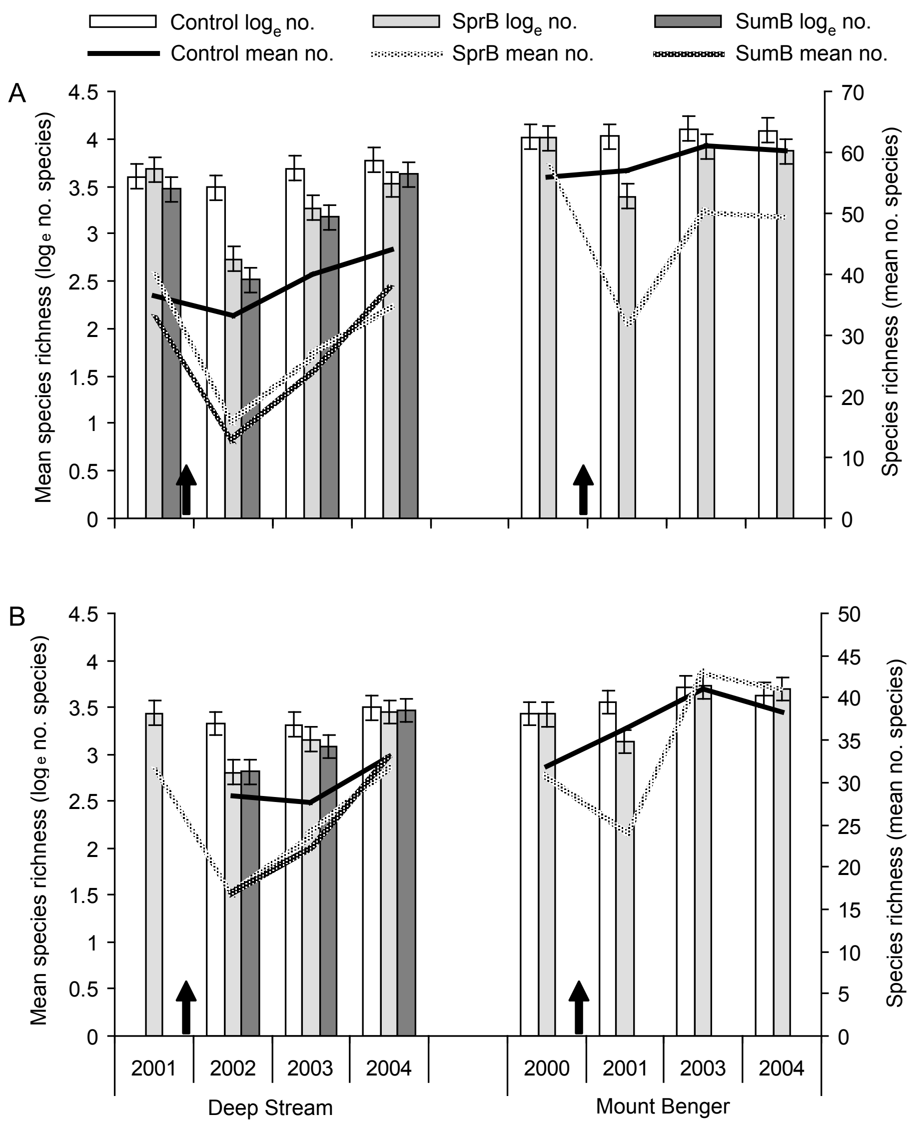
For turf samples at DS, there was no significant difference between the control and treatment plots prior to treatment in January 2001, with a range of 31–39 species/m^2 recorded (Fig. 10A). In January 2002, species richness dropped significantly by about 50% in spring- and summer-burnt plots to a mean of about 15 and 12 species, respectively, while species richness in control plot species richness remained at 33 species. By the following year, species richness in spring- and summer-burnt plots had recovered to 26 and 24 species, respectively, and by January 2004, no significant differences remained between treatments.

Tussock samples at DS (Fig. 10B) are missing data for the control and summer-burnt plots in 2001 (see section 2.4). However, estimates of species richness in control plots were consistent between 2002 and 2003, increasing in 2004. In the spring-burnt plots, a similar pattern was observed in turf and tussock samples, with a reduction from pre-burn species richness in 2002, which then recovered over the following 2 years. The summer-burnt plots followed a very similar pattern to the spring-burnt plots between 2002 and 2004.

For turf samples at MB, estimates of species richness in January 2000 was about 56 species in control plots and 57 species in plots allocated to be burned in spring (Fig. 10A). Two months after the spring burn, mean species richness in the spring-burnt plots was 32 species, and subsequently rose to about 50 species in 2003 and 2004.

Tussock samples at MB followed a similar pattern to turf samples, with an initial reduction in species richness, followed by recovery by January 2003 (Fig. 10B).

Figure 10. Coleoptera species richness in A. turf and B. tussock samples from both sites each year. The histograms show $\log_e$ mean number of species ± SEM on the left y-axis. The superimposed lines show back-transformed mean numbers of species on the right y-axis. Data for 2000 and 2001 are pre-burn for Mount Benger and Deep Stream, respectively. The arrows indicate dates between which the burning treatments were carried out. 2001 data for the burnt tussock treatments at Deep Stream were unavailable.



3.4.3 Species diversity

Shannon-Wiener indices of coleopteran species diversity were calculated for each site, sample date, sample type (turf and tussock) and treatment. These data are shown in Fig. 11. The Shannon-Wiener indices calculated for overall species diversity in control plots and combining both vegetation types was significantly higher at MB than DS ($H = 3.245$ and 2.769, respectively; $F = 15.3$, df = 11.8, $P < 0.002$).

At DS in January 2001 (pre-treatment), there was no significant difference in the Shannon-Wiener indices between the plots selected for the three treatments as calculated for turf samples (Fig. 11A). For DS control turf samples, there was some variability in species diversity from year to year. However, there was a clear decrease in species diversity in the burnt plots in the January following both the spring and summer fire treatments (January 2002). There was an indication of some recovery in the burnt plots in 2003, and there was no significant difference between the control and burnt plots by 2004.

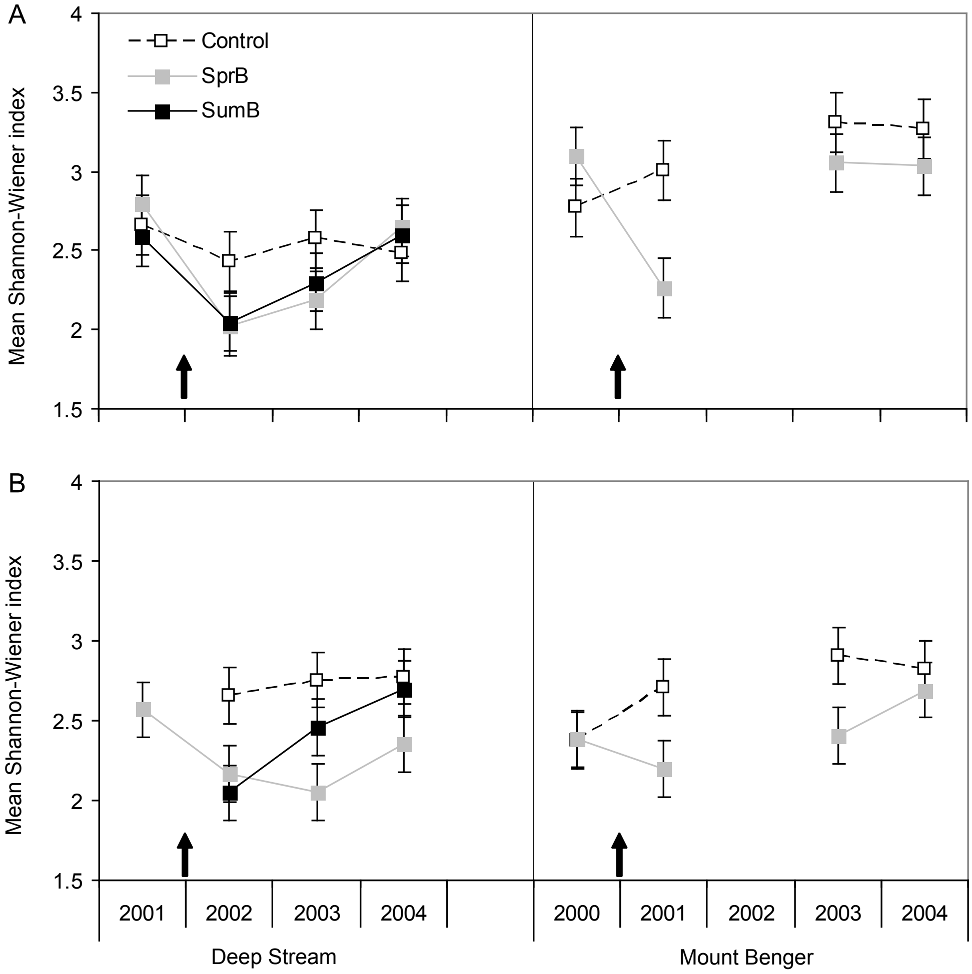


Figure 11. Mean (per plot ± SEM) Shannon-Wiener indices for Coleoptera for both sites and January sampling dates in A. turf and B. tussock samples. The arrows indicate dates between which the burning treatments were carried out. 2001 data for the burnt tussock treatments at Deep Stream were unavailable.

The index values for the tussock samples from the control plots at DS were consistent between 2002 and 2004, whereas values were significantly lower for the burnt plots in 2002 (Fig. 11B). The Shannon-Wiener indices calculated in subsequent years indicated recovery of species diversity. This recovery was more rapid during 2003–2004 in the summer-burnt tussock samples; index values for the spring-burnt plots remained significantly lower than those of the control plots in 2004 ($F = 15.6$, df = 2, 8, $P < 0.05$), although was not significantly lower than the pre-burn index.

For the turf samples at MB, the Shannon-Wiener indices were a little higher (but more variable) than at DS (Fig. 11A). In January 2000, the mean values for the control and the intended spring-burnt plots were similar, but in 2001 there was a significant reduction in the Shannon-Wiener index for the spring-burnt turf samples. However, by 2003 and 2004 no differences remained between treatments.

The indices for the tussock samples at MB were very similar for both treatments pre-burn in 2000, but reduced significantly in the burnt plots in 2001 and 2003 (Fig. 11B). By 2004, species diversity has recovered to a similar level to that of control plots.

3.4.4 Rank-abundance patterns

The *k*-dominance curves for DS and MB control plots (averaged across years) give an indication of the inherent species diversity at the two sites for turf and tussock (Fig. 12A & B). The lower the curves on the plot, the more diverse are the species assemblages. The *k*-dominance curves indicate that species diversity is generally higher at MB than DS, but this is more pronounced for the turf Coleoptera community than for tussock. This supports the Shannon-Wiener index data (section 3.4.3). Curves for each site, date and sample vegetation type have been plotted in Fig. 13.

For DS spring-burnt plots, the *k*-dominance curves for turf samples indicate that the Coleoptera species assemblage was more diverse in the pre-burn samples taken in 2001 than in any of the post-burn samples (Fig. 13A). For the tussock samples, the curves are less spread and show a similar pattern to each other in successive years (Fig. 13B). For the summer burn treatment, the *k*-dominance curves for turf samples show a similar pattern to the spring burn data, except that the pre-burn and 2004 curves are almost superimposed (Fig. 13C), suggesting that the Coleoptera species assemblage recovered to a greater extent following the summer burn treatment than following the spring burn treatment. The tussock data for summer-burnt plots in 2001 were not available, but the 2002 curve indicates a large reduction in diversity compared with the 2003 and 2004 curves, which were very similar (Fig. 13D).

For MB spring-burnt plots, the *k*-dominance curves for turf samples in 2001 (2 months post-burn) is clearly separated out; however, the 2003 and 2004 curves are very close to the pre-burn curve (Fig. 13E). As at DS, the curves for the tussock samples are less separated between sample dates (Fig. 13F).

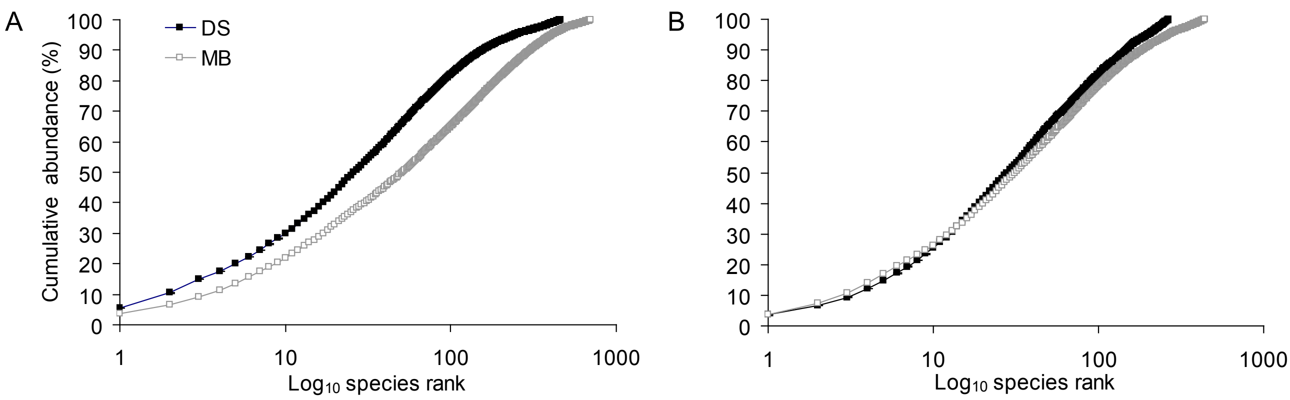


Figure 12. *k*-dominance curves for Coleoptera at Deep Stream (DS) and Mount Benger (MB) in A. turf and B. tussock samples.

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