

Figure 13. k -dominance curves for Coleoptera for each sampling date at Deep Stream (DS) and Mount Benger (MB) pre- and post-burn. A. Deep Stream spring-burnt plots, turf samples; B. Deep Stream spring-burnt plots, tussock samples; C. Deep Stream summer-burnt plots, turf samples; D. Deep Stream summer-burnt plots, tussock samples; E. Mount Benger spring-burnt plots, turf samples; and F. Mount Benger spring-burnt plots, tussock samples.

3.4.5 Community trophic structure and response to treatments

The proportion of Coleoptera species and individuals in each trophic group for both sites, all dates and all treatments is shown in Fig. 14. The most noticeable difference between these findings and those reported in section 3.3 for the invertebrate fauna in general is that the Coleoptera were dominated by carnivores (mainly Staphylinidae), comprising 50% or more of all individuals in most cases. In contrast, there was a more even distribution of herbivores, carnivores and detritivores for the total invertebrates, as indicated in Fig. 6A.

The proportion of species in each trophic group appeared to change little between years and burning treatments, except for the initial (2002) decrease in the proportion of herbivore species in turf and tussock samples from spring-burnt plots at DS (Fig. 14). Similarly, there was little difference between treatments in the proportion of Coleoptera individuals in each trophic group. A restricted maximum likelihood analysis of Coleoptera individuals from both sites (turf and tussock treatments combined) showed that control plots had a significantly lower proportion of carnivores (control = 45%; burnt = 65%; $F = 4.87$, $df = 2, 10$, $P = 0.033$) and a higher proportion of herbivores (control = 47%, burnt = 27%; $F = 6.92$, $df = 2, 10$, $P = 0.013$). However, since there was no significant treatment \times date interaction, these differences were likely to have been present pre-burn, as indicated by Fig. 14.

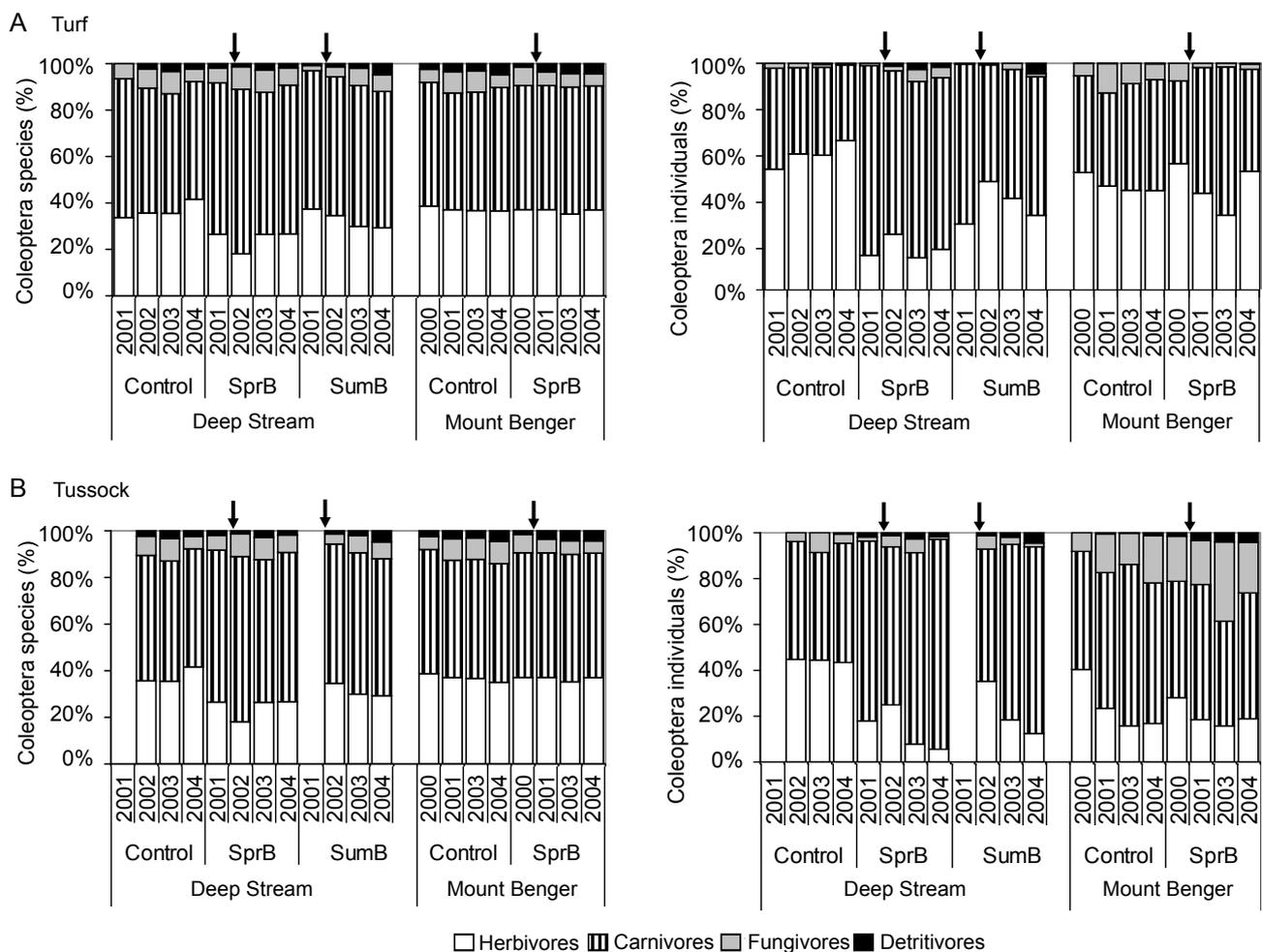


Figure 14. Percentage of Coleoptera species and individuals in each trophic group for each treatment and January sampling date in A. turf and B. tussock samples. The arrows indicate dates between which the burning treatments were carried out. SprB = spring-burnt plots; SumB = summer-burnt plots.

There was a higher proportion of coleopteran fungivores in the MB tussock samples than in the DS tussock samples or the turf samples from both sites (Fig. 14). This group was dominated by the Family Ptiliidae. This family, comprising three species, was present in spring-burnt tussock plots at MB in January 2003 in densities of over 200 individuals/m², but was far less abundant in turf samples or DS tussock samples. Reasons for this positive response to burning in spring are unclear. The small proportion of fungivores that were present in MB turf samples (mainly Ptiliidae and Corylophidae) declined to a very low proportion of the fauna after the spring burn treatment.

The proportion of individual herbivores and carnivores in DS turf and tussock samples in control plots was quite consistent between years, with 55–65% of the fauna comprising herbivores and the majority of the balance being carnivores (Fig. 14). The proportions found in the spring-burnt plots, however, were quite different from the control plots, even pre-treatment, with a much greater proportion of carnivores, attributable mainly to by far the most abundant family, the Staphylinidae. For example, in 2001, the mean density of Staphylinidae individuals in control plot turf samples was 43.3 ± 0.33 individuals/m², compared with 208.7 ± 1.8 individuals/m² in the plots allocated to be burned in spring.

3.4.6 Exotic component of the community

In total, 22 Coleoptera species/morphospecies were classified as exotic (Table 6); five of these were only found at DS, nine at MB, and eight were found at both sites. The proportion of the Coleoptera fauna of exotic origin was 9.2% at DS and 12.6% at MB. Two of the species present were deliberately introduced as biological control agents (Table 6).

At DS, the proportion of species and individuals that were exotic appeared to increase successively between 2001 and 2004 (Fig. 15A & B). However, the proportions increased in both control and burnt plots, suggesting that this was not a treatment effect. At MB, the proportion of exotic species and individuals was generally consistent between years and treatments (Fig. 15A & B).

At both sites, more exotic species were found in turf compared with tussock samples (Table 6), but the mean density of exotic species did not exceed 6 individuals/m² in either sample type (Fig. 15C). The generalised linear model found no significant effects of treatment on the proportion of exotic species or individuals present.

TABLE 6. MAXIMUM DENSITY (NO. INDIVIDUALS/m²) OF EXOTIC COLEOPTERA SPECIES FOUND AT EACH SITE AND SAMPLE TYPE.

'-' = not present.

FAMILY	SPECIES	DEEP STREAM		MOUNT BENGER	
		TURF	TUSSOCK	TURF	TUSSOCK
Anthribidae	<i>Euciodes suturalis</i>	0.5	-	0.5	-
Archeocryptidae	<i>Archeocrypticus topali</i>	-	-	0.5	-
Coccinellidae	<i>Coccinella 11-punctata</i> *	2.0	3.3	0.5	4.4
Coccinellidae	<i>Coccinella leonina</i>	0.5	1.1	0.5	-
Cryptophagidae	<i>Cryptophagus</i> DS sp. 1	0.5	1.1	-	-
Cryptophagidae	<i>Cryptophagus</i> DS sp. 2	-	6.7	0.5	1.1
Curculionidae	<i>Listronotus bonariensis</i>	0.5	-	5.5	3.3
Curculionidae	<i>Otiobrychus ovatus</i>	-	-	0.5	-
Curculionidae	<i>Sitona discoideus</i>	0.5	-	-	-
Curculionidae	<i>Trichosirocalus borridus</i> *	-	-	0.5	1.1
Dermestidae	<i>Anthrenocerus australis</i>	0.5	-	-	-
Dermestidae	<i>Reesa vespulae</i>	0.5	1.1	1.5	-
Latridiidae	<i>Aridius bifasciatus</i>	0.5	1.1	-	1.1
Latridiidae	<i>Cartodere</i> DS sp. 1	2.0	1.1	-	-
Latridiidae	<i>Corticaria serrata</i>	1.0	1.1	0.5	-
Mycetophagidae	<i>Typhaea sterocorea</i>	-	-	0.5	1.1
Scolytidae	<i>Hylastes ater</i>	-	-	0.5	-
Staphylinidae	<i>Pselaphobus atriventris</i>	-	-	-	1.1
Staphylinidae	<i>Pselaphobus</i> MB sp. 1	-	-	-	1.1
Staphylinidae	' <i>Quedius</i> ' DS sp. 1	-	-	0.5	1.1
Staphylinidae	' <i>Quedius</i> ' MB sp. 1	-	-	2.5	2.2
Staphylinidae	<i>Tachyporus nitidulus</i>	0.5	1.1	-	-

* Deliberate introductions for biological control.

The exotic species that reached highest densities in individual samples at DS were *Cartodere* DS sp. 1 (Latridiidae) and *Coccinella 11-punctata* (Coccinellidae) in turf samples; and *Cryptophagus* DS sp. 2 (Cryptophagidae) and *C. 11-punctata* in tussock samples. At MB, the exotic species that reached highest densities were *Listronotus bonariensis* (Curculionidae) and '*Quedius*' MB sp. 1 (Staphylinidae) in turf samples; and *C. 11-punctata* and *L. bonariensis* in tussock samples. Of the herbivores, *L. bonariensis* (Argentine stem weevil) was the most commonly found, with 11 being collected from a single turf sample at MB in January 2000.

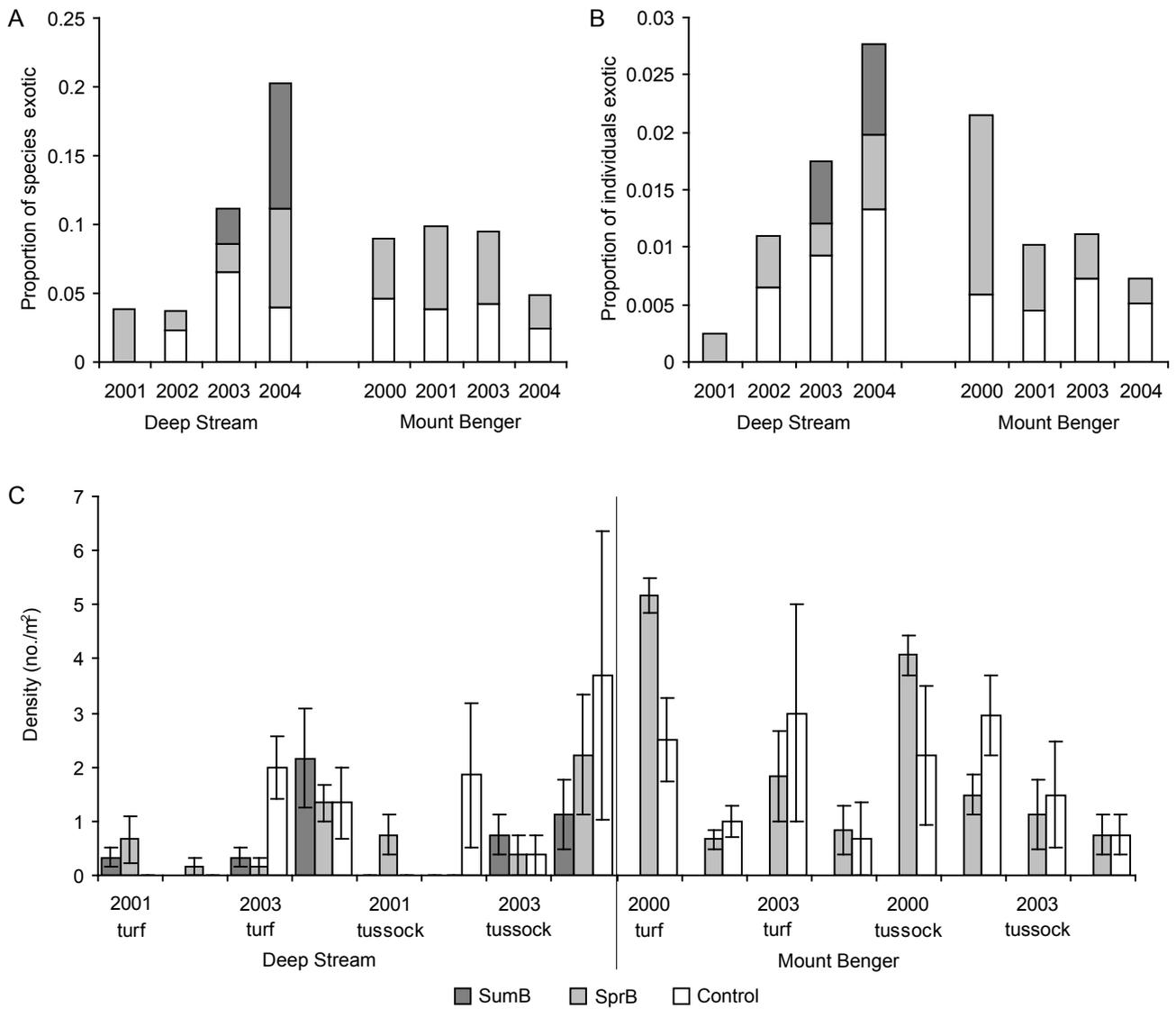


Figure 15. Composition of Coleoptera community for both sites and treatments across all annual January sampling dates. A. Proportion of species that were exotic; B. proportion of individuals that were exotic; and C. mean density of exotic species. SumB = summer-burnt plots; SprB = spring-burnt plots.

4. Discussion

4.1 COMPARISONS BETWEEN DEEP STREAM AND MOUNT BENDER INVERTEBRATE COMMUNITIES

The two sites at DS and MB, which were chosen to represent examples of lower and higher altitude tall tussock grassland, respectively, were both dominated by *Chionochloa rigida*. Soil types are similar, although geological history of the areas is probably quite different, with evidence of glaciation at higher altitudes in the MB area (McEwen 1987). At the time of this study, both areas had been retired from grazing and had not been burned for 10 years or more. DS has a higher average temperature (6.8 °C cf. 4.9°C) and lower rainfall (993 mm/year cf. 1264 mm/year) than MB (Payton & Pearce 2009).

The composition of the invertebrate communities at these sites has been influenced by combinations of physical and biotic factors. However, our understanding of these relationships is currently insufficiently advanced to be able to explain spatial differences in density and community composition. Previous management history (burning and grazing) for these sites is poorly known further back than 10–20 years, and this will certainly have influenced the invertebrate faunas that we see today.

The total density of the invertebrate fauna (excluding the microarthropods) was considerably higher at DS than at MB, which might be attributable to the higher altitude and cooler average temperature at MB. However, this needs to be considered in the context of the total invertebrate fauna (including microarthropods). Barratt et al. (2006) found that microarthropod (Collembola and Acari) densities in control turf plots at DS and MB averaged over 2001–2003 were 18 579 and 20 413 individuals/m², respectively, comprising about 80–90% of the total invertebrate fauna.

4.1.1 Taxonomic composition

At both sites, over 75% of the invertebrate community (in terms of density) comprised Hymenoptera (mainly Formicidae), Myriapoda (mainly Chilopoda), Hemiptera (mainly Pseudococcidae), Crustacea (mainly Amphipoda), Coleoptera (mainly Curculionidae and Staphylinidae beetles) and Arachnida (mainly Araneae). In a previous study, the taxonomic structure of the invertebrate communities at DS and MB were compared with two other tussock grassland sites at Cass (Canterbury) and Tukino (central North Island) (Barratt et al. 2005). Barratt et al. (2005) found that the mean rank of the most abundant taxa (Formicidae (Hymenoptera), Coleoptera and Pseudococcidae (Hemiptera)) were consistent at all sites. These data suggest that, in general, these taxa are amongst the dominant invertebrate components of tussock grassland environments in New Zealand.

The far greater density of Formicidae at DS compared with MB, particularly in turf samples, was one of the most striking differences in the taxonomic composition of the invertebrate fauna between the two sites. Reasons for this are not clear, but it could be the result of altitude-related climatic or biotic variables. Support

for this comes from a study carried out at a higher altitude (about 1600 m a.s.l.) on the Old Man Range (part of the same mountain massif as MB), where ants were found to be very scarce (Scott 2007).

4.1.2 Trophic composition

Despite differences in the density of invertebrates at DS and MB, the trophic structure of the communities at the two sites was quite similar. However, the proportions reported (Fig. 6A) apply only to meso- and macroinvertebrates, and exclude the soil and litter-dwelling microarthropods, such as Collembola and Acari, where fungivores predominate (Barratt et al. 2006). If biomass had been measured, yet another picture would emerge (Saint-Germain et al. 2007). A summary of studies of trophic composition of invertebrates in grassland based on biomass was presented by Curry (1994). Three different studies showed that decomposers comprised 40–96%, herbivores up to 52% and carnivores up to 19%. In general, Curry (1994) found that decomposers (fungivores and detritivores) were the dominant trophic group in grassland, except in very arid environments. These findings are comparable to those from the current study—approximately 42% decomposers (detritivores and fungivores), 35% herbivores and 22% carnivores (Fig. 6A).

4.2 INVERTEBRATE RESPONSES TO BURNING

As expected, most invertebrate groups were initially adversely affected by the burning treatments, with often significant reductions in population density. Some of the groups most severely affected were those dependent upon the litter layer for feeding and for the habitat that it provides. Removal of the litter layer by fire at these sites was reported by Payton & Pearce (2009). The pre-burn above-ground vegetation biomass was similar at DS and MB, at about 27 000–29 000 kg/ha, of which about 60% and 68%, respectively, was litter (Payton & Pearce 2001). The spring burn (November 2000) at MB removed an average of 32% of the above-ground biomass and left much of the ground-cover vegetation intact. However, the spring burn at DS removed 70% of the above-ground biomass, including most of the litter and ground-cover vegetation. This difference was attributed to the lower moisture content of tussock bases and upper soil layers at DS compared with MB (Payton & Pearce 2001). The summer burn at DS caused a similar amount of damage as the spring burn, removing 74% of the above-ground biomass and most of the litter; however, the recovering vegetation was also exposed to winter frosts soon after the burning treatment (Payton 2003).

The Duff Moisture Code (DMC) is one of the Fire Weather Index measurements (Van Wagner 1987) of particular significance to litter-dwelling invertebrates. It is an index of the moisture content of the layer of partially and fully decomposed organic materials lying below the undecomposed litter layer and immediately above the mineral soil. A DMC range of 0–30 denotes minimal to high fire risk. The DMC for the MB spring burn was 6, compared with 14 for the DS spring burn and 26 for the DS summer burn. The greater loss of ground cover at DS following both burns and the higher DMC at DS probably contributed to the more significant impacts of the fires on litter-dwelling invertebrate densities at

DS than at MB. Henig-Sever et al. (2001) found a negative correlation between fire intensity and microarthropod density and community composition. A more intense fire would be expected during summer than spring at DS (and in comparison with the MB spring burn), using plant biomass removal and DMC as indicators; however, it appears that the spring burn at DS was probably more intense than would generally be expected at this time of year.

Table 4 shows that the effects of burning were most prolonged for five taxa and were probably most pronounced for the Amphipoda. These 'land-hoppers' were substantially reduced in density at both sites and vegetation types, and little recovery was observed by January 2005. Terrestrial amphipods are litter dwellers, feeding on decaying organic material and dependent upon a moist, humid habitat. Duncan (1969) found a relationship between litter thickness and amphipod density. Similar burning experiments in Tasmania in button grass vegetation showed a very similar effect, with substantial reductions in density and very slow recovery of Amphipoda (M. Driessen, Department of Primary Industries, Tasmania, pers. comm. 2007). In the current study, the destruction of the litter layer is likely to have caused a collapse in amphipod populations, and it is likely that previous densities would not be restored until the litter layer has had time to re-establish. Psocoptera (at DS) and Diplopoda (at MB) are other litter-feeding invertebrates that also suffered longer-term population density reductions after fire.

Densities of Hymenoptera (mainly ants) declined after burning, particularly in DS turf samples, and densities remained low. In grassland ecosystems that are well adapted to fire, the ant fauna appears to be comparatively resilient to burning. For example, in African savannah, Parr et al. (2004) found that 8 months after a fire there was no significant change in relative ant abundance measured by pitfall trapping; and harvester ants (*Pogonomyrmex rugosus*) appear to be well-adapted to cope with wildfires in the desert grassland of New Mexico, with no measurable change in abundance (Zimmer & Parmenter 1998). It would be expected that in the event of fire, population survival in subterranean nests (to which the highly mobile individuals would most likely retreat) might be quite high. Therefore, the post-burn population density reduction measured in the current study could be attributable to reduced prey and seed availability.

Invertebrate groups that were negatively impacted by fire but recovered by January 2005 were represented mainly in DS turf samples. These included the myriapod orders Symphyla and Chilopoda. The latter are carnivorous, probably feeding on microarthropods such as Collembola and Acari, which were reduced in density after the fire but mostly recovered in the following 2-3 years (Barratt et al. 2006). Post-burn reductions in chilopod densities have also been observed in Illinois prairie (Rice 1932) and in grassland in Spain (Garcia-Ruiz 2001).

Annelid densities were also significantly reduced by fire, but had recovered in DS turf by January 2005. Lumbricidae in tallgrass prairie in Kansas (Callahan Jr. et al. 2003) and prairie in Illinois (Rice 1932) also exhibited declines in density in 0.1-m² turf samples after burning. The annelid fauna in this study was dominated by Enchytraeidae. Yeates & Lee (1997) recorded reductions in density of Enchytraeidae in a tussock grassland similar to that reported here 16 months after fire, but the differences were not significant, possibly because of lower sample replication.

Lepidoptera densities at MB were reduced after the spring burn, but recovered to pre-burn and control densities between 2001 and 2003 (Appendix 5). Lepidoptera larvae are either herbivores or litter-feeders, and are probably very susceptible to the high temperatures and acute effects of fire. However, adults are relatively mobile and likely to recolonise quite quickly, especially once plant regrowth occurs and the litter layer re-establishes. In a review of impacts of fire on invertebrates, Warren et al. (1987) found that impacts of fire on Lepidoptera were varied and dependent on habitat and food source, and the way in which these resources were affected by fire (host plant decline, litter removal, etc.).

Invertebrate groups that demonstrated immediate post-burn population impacts followed by rapid recovery were Coleoptera, Pseudococcidae, Diptera and Thysanoptera. Coleoptera will be discussed in more detail below. Declines in pseudococcid (mealybug) densities after burning may have resulted from their generally soft-bodied structure, and hence susceptibility to increased temperature, as well as their immobility and inability to move quickly away from the higher temperatures. However, many mealybugs are found on plant roots in the soil and would have been protected; therefore, other environmental changes following the fires may have resulted in population reduction. Thysanoptera were initially reduced in density but then recovered quite rapidly to achieve densities that were higher than found pre-burn, especially at DS (Table 4). This group is not only very mobile, but has the capacity to increase population density quite quickly.

Changes in invertebrate community structure in the longer term will be influenced by changes in plant species composition. The vegetation in the DS burnt plots became browntop (*Agrostis capillaris* L.) dominant after burning (Payton & Pearce 2001) and native plant species diversity was reduced by about 50% 3 years post-burn (Espie & Barratt 2006).

Substantial loss of litter is likely to delay recovery of litter-dwelling species through altered food and habitat conditions. Loss of tussocks will also potentially reduce biodiversity, since 6-8% of the species at the sites were found only in samples containing *Chionochloa rigida*. The spring burn at DS killed 21-70% of tussock plants (Payton & Pearce 2009).

4.3 SEASONAL EFFECT OF BURNING ON INVERTEBRATES

In general, seasonality of the burning treatments, which could only be compared at DS, did not appear to be a major factor influencing the immediate and longer-term recovery of most invertebrate groups. Irrespective of season, the immediate impact of fire on invertebrate faunas depends upon the intensity and duration of the fire (Curry 1994). At DS, the spring burn was more intense than would be expected, since both spring and summer burns removed much of the litter (Payton & Pearce 2009). Other factors that are likely to result in seasonal difference in invertebrate responses to fire include seasonal diapause, presence of different stages of the life cycle (e.g. surface-dwelling cf. soil-dwelling stages) and differential removal of vegetation (Swengel 2001).

4.4 EFFECT OF BURNING TREATMENTS ON COMMUNITY TROPHIC STRUCTURE

It is well recognised that management practices such as grazing, burning, etc. that change the composition of the sward will inevitably change invertebrate species composition in grassland (Curry 1987). Change in botanical composition can potentially have the most profound effects on monophagous herbivore species (those that eat only one species of plant). However, herbivores in general are dependent upon the standing crop of vegetation, which was severely depleted in the first few months after the fire (NZ Fire Research 2001). The changes that occurred in invertebrate abundance 2-3 months after burning are likely to have been responses to the changed environment of reduced litter and drier soil surface conditions. After 3 years, however, botanical changes had probably influenced the community structure. A discussion of trophic structure and changes brought about by a disturbance such as burning can at best be superficial without data on biomass and energy flow (which was beyond the scope of this study). Nevertheless, our speculative interpretations of some of the major responses seen are discussed in the following sections.

4.4.1 Herbivore response

The massive reduction in herbivore densities 2-3 months after treatment (Fig. 7), especially at DS, probably resulted from the direct effect of the fire causing mortality of invertebrates, as well as indirect effects as a result of the large reduction in available plant material. The relationship between plant biomass and invertebrate biomass was demonstrated by Andrzejewska (1979a). From data collected in Polish grasslands, he calculated that for every 1000 kg DM (dry matter)/ha there is an increase of 20 kg DM/ha of invertebrates. While this clearly cannot be directly applied to New Zealand tussock grassland, especially since invertebrate biomass data are not available for our sites, it could be indicative of the scale of invertebrate biomass loss that might accompany the large plant biomass losses of approximately 13 600 and 25 500 kg DM/ha that were calculated after the spring burns at MB and DS, respectively (Payton & Pearce 2009).

The 'rebound' in herbivore densities measured for Thysanoptera and Lepidoptera (Table 4) following an initial dramatic decline was almost certainly related to the flush of vegetation regrowth. A study carried out close to the MB site showed that 1.5 years after a tussock fire, the level of phosphorus in burnt plots was twice the value of that in control plots, and 2 years after the fire, higher concentrations of nitrogen and phosphorus were available to plants (Ross et al. 2001). In addition, the level of total nitrogen and phosphorus in *Chionochloa rigida* leaves was significantly higher in burnt plots than control plots after 2 years. These increased nutrient levels would contribute to improved plant growth and the nutrient value of vegetation for herbivorous invertebrates.

4.4.2 Carnivore response

Although there was a reduction in carnivore densities in the 1–2 years after spring burning, especially at DS in turf samples (Fig. 7), the response was not large. This perhaps reflects the ability of carnivores to switch to alternative prey items when there are fluctuations in density of the other trophic groups. There was no evidence of a ‘rebound’ in numbers as the carnivore populations recovered.

4.4.3 Detritivore response

At MB, there was no evidence of a reduction in detritivore densities following burning. However, at DS there was a pronounced decline and then ‘rebound’ in detritivore densities in both turf and tussock samples after the spring burn, and in tussock samples after the spring and summer burns (Fig. 7). The initial decline could have resulted from reduced litter and more variable temperatures and humidity. The increase in January 2005, however, is more difficult to interpret. Andrzejewska (1979b) emphasised the importance of herbivore faeces as a highly nutritious substrate for saprophagous feeders (here called detritivores), affecting the fecundity of this group. It is conceivable, therefore, that the large increase in herbivore density recorded in January 2004 and 2005 in particular provided the mechanism for the recovery; indeed the observed ‘rebound’ was mirrored by herbivore densities, despite the herbivores largely comprising Thysanoptera and Pseudococcidae.

4.4.4 Fungivore response

Fungivore densities were very low at both sites and vegetation types (Fig. 7). This is somewhat misleading, since microarthropods, which were not included in this investigation, contribute a large component of the fungivore fauna. However, the ‘rebound’ of fungivore densities at MB, especially in tussock samples, might be explained by their response to a possible flush of fungal activity on dead organic material and litter that had begun to accumulate in the system after being removed by fire. This effect was far less pronounced at DS, where litter removal by the spring and summer burns was more complete.

4.5 COLEOPTERA: A DETAILED STUDY

Coleoptera were identified to species/morphospecies in this study with an endeavour to include larval stages. However, this presented some major challenges. In all cases, identification to family at least was attempted for larvae. Inevitably, there will have been some errors in our taxonomy for immature stages, which it may be possible to correct in the future, since all specimens have been retained in storage. Taxonomic assignment was particularly demanding for Staphylinidae in the subfamily Aleocharinae, where several species were distinguished as adults but species-level diagnostic characters could not readily be assigned to larvae with the available resources. This subfamily would lend itself well to a molecular approach to linking larvae with adults.

The coleopteran families with the highest recorded number of species were the Curculionidae and Staphylinidae at both sites. This was also found to be the case at 1600 m a.s.l. on the Old Man Range, close to MB (Scott 2007).

The pre-treatment MDS ordination data (Fig. 8A) illustrated the variability in density of individual species between the treatment replicates, varying from close agreement in DS control plots to widely variable in MB plots designated to be burned in spring. This illustrates the heterogeneous nature of the Coleoptera population densities at the sites.

4.5.1 Effect of treatments on species richness

Pre-treatment Coleoptera species richness was higher at MB than at DS, and in both cases was higher in turf than tussock samples, possibly as a result of greater plant species diversity in turf samples. Burning reduced coleopteran species richness substantially in turf samples, especially at DS, where it did not recover to pre-burn levels until 2004 for both spring and summer burn treatments. A similar pattern was observed for tussock samples. The similarity of impact for the spring and summer burn treatments probably resulted from the similarity of intensity of the two fires. Both fires removed much of the ground cover layer of plants and the litter layer (Payton & Pearce 2009), reducing food resources for herbivorous families such as Curculionidae, and shelter for many litter-dwelling families such as the Staphylinidae. Furthermore, the spring burn at DS was followed by a period of dry weather (Payton & Pearce 2009), which would have further reduced survival of litter-dwelling species. Conditions following the spring burn at MB were more favourable to Coleoptera species survival, as snow covered the sites a few days after treatment (Payton & Pearce 2009), which would have buffered communities against frost, from which they would have found difficulty in sheltering, and against dehydration.

Fadda et al. (2007) found that species richness of Coleoptera was higher in disturbed sites than undisturbed steppe in southern France because the vegetation contained more early colonising plant species, which supplied vegetation of a higher nutritive value to herbivores and a more diverse supply of prey items for carnivores. They argued that cultivation created soil conditions that were beneficial for Coleoptera with soil-dwelling stages. Although disturbance by burning is unlikely to alter the soil environment substantially, it is known to produce a 'flush' of vegetative regrowth as a result of increased levels of phosphorus and nitrogen available to plants after fire (Ross et al. 2001), which is likely to be beneficial to herbivorous invertebrates.

In a semi-arid shortgrass steppe in New Mexico, USA, Ford (2007) recovered 29 families of Coleoptera (by pitfall trapping) and identified 115 species. Ford (2007) investigated the effect of burning on Coleoptera by comparing 2-ha plots burned in spring with plots burned in summer and unburnt plots. Coleoptera species 'abundance' was not significantly changed 1 year after burning, but species richness significantly increased in the spring-burnt plots; the summer fire treatment had no effect on species richness. This contrasts with our data, where Coleoptera species richness declined significantly at both sites and after both treatments. However, the sampling method used by Ford (2007) might have influenced the results in his study: pitfall traps are a better measure of activity than abundance, and burnt plots with less vegetation and litter might have allowed increased activity of Coleoptera.

4.5.2 Species diversity and rank abundance patterns

The Shannon-Wiener species diversity indices calculated were found to mirror to some extent the decline in Coleoptera species richness and density. This might be expected, since the Shannon-Wiener index takes account of both these variables. However, *k*-dominance curves for the coleopteran community under different treatments encompass species richness and evenness of spread of individuals between species (Platt et al. 1984). If the *k*-dominance curves intersect (e.g. as seen for the curves for January 2002 and January 2003 DS spring-burnt turf samples in Fig. 13A), this suggests that the Coleoptera species assemblages are not comparable in terms of intrinsic diversity and that Shannon-Wiener is not necessarily reliable (Platt et al. 1984). Furthermore, the difference in the shape (steepness) of the curves for the pre-spring-burn treatment in the two vegetation types at DS suggests that the evenness of spread of individuals between species is greater for the turf samples than the tussock samples.

If the Shannon-Wiener plots (Fig. 11) are compared with the *k*-dominance curves for DS spring- and summer-burnt plots for turf samples (Fig. 13A & C), then both indicate a substantial reduction in species diversity in 2002 (3 months post-burn), and to a lesser extent in 2003 (1 year later). However, the Shannon-Wiener indices for 2004 have returned to pre-burn values for both treatments, whereas the *k*-dominance curve remained distinctly separated, at least for the spring-burnt plots.

For the DS tussock samples, the pattern suggested by the *k*-dominance curves closely reflects the Shannon-Wiener index values, with diversity decreasing from 2002 to 2003, then returning further towards the pre-burn values by 2004. The summer burn tussock *k*-dominance curves (Fig. 13D) indicate a large reduction in diversity in 2002 (as do the Shannon-Wiener indices, although the pre-burn values are not available). For the following years, a substantial increase in diversity is indicated by both methods.

For MB, there was generally good agreement between the two methods of species diversity assessment. Apart from a clear separation of the *k*-dominance curves for 2001 turf samples (Fig. 13E) and significant reduction in Shannon-Wiener values, there is little difference in the following years. The tussock data also suggest little difference in Coleoptera species assemblages (Fig. 13F).

With the exception of a single inconsistency noted above, the Shannon-Wiener and *k*-dominance approaches give consistent findings, providing a reasonable degree of confidence in the comparative assessment of spring and summer burning treatments on Coleoptera species diversity.

4.5.3 Trophic structure and response to treatments

The trophic structure in the Coleoptera community observed in our study was similar to that found by Fadda et al. (2007) in steppe grassland in southern France, with herbivores comprising about 35% of species in both studies, carnivores about 50% (cf. 30% in France) and the remaining 15% fungivores, detritivores and coprophagous species (cf. 35% in France).

Burning brought about few changes in the trophic structure of the coleopteran community, either in proportion of species or individuals (Fig. 14). However, the analysis of these data did highlight the differences in the proportions of

herbivores and carnivores that occurred between the DS plots before the spring burns took place, particularly with regard to the dominance of carnivores. The effect of burning was, however, evident in MB tussock samples, where the proportion of fungivores increased in 2003, 2 years after treatment.

4.5.4 Exotic component of the community

A large number of exotic organisms have become established in New Zealand, and some represent a threat to native ecosystems. In a recent international review of literature, it was found that about 20% of all exotic insects accidentally or deliberately introduced into semi-natural or natural ecosystems are Coleoptera (C.B. Phillips, AgResearch, unpubl. data 2008).

Exotic Coleoptera have become established in the relatively undisturbed tussock grassland environments at both DS and MB, although at both sites the proportion of exotic species (and individuals) was low. There was no significant or consistent effect from the burning treatments at the two sites. While it might be expected that disturbance by burning would lead to an increase in the exotic component of the fauna, especially if the diversity and abundance of exotic plants increases, the time scale of this study was probably too short to measure such changes. There is very little, if any, comparable data from New Zealand with which to compare these findings.

4.6 LIMITATIONS OF THIS STUDY

The delay in carrying out the MB summer burn treatment reduced the potential for a robust analysis of the effect of season (spring or summer) on the impact of fire and recovery of invertebrate populations and community structure. However, annual sampling of all plots has continued, so further analysis will be possible in the future. Similarly, the discontinuation of processing samples after 2005 has limited our ability in this report to discuss recovery of some taxa that had not returned to pre-burn population densities. Furthermore, the absence of invertebrate data from the DS January 2001 tussock control and summer-burnt plots has limited our ability to fully analyse these data, but again this could be addressed in the future. Finally, it must be remembered that the treated plots were 1 ha in size, and so recolonisation from the surrounding unburnt vegetation is likely to have occurred more rapidly than it would from a large-scale burning programme or from a wild fire. This recolonisation is also likely to occur differentially amongst invertebrates, depending upon their relative mobility.

5. Conclusions

This research has provided data on invertebrate density and trophic structure using two case studies in Otago tussock grassland. For Coleoptera, it was possible to make additional measurements of species richness and diversity, trophic structure and the exotic component.

Since the study reported here was limited by a lack of site replication, the DS and MB sites need to be considered as case studies, limiting the ability to extrapolate the findings to other sites. The study was also limited by the relatively short time scale for post-burn analysis of impacts. However, where clear and substantial short- to medium-term effects have been observed at both sites, it is probably reasonable to cautiously generalise about effects.

The data obtained for Coleoptera in this study are probably the most informative for assessing the impacts of fire on biodiversity, assuming that Coleoptera are a good surrogate for the invertebrate fauna. These data indicate that species richness was initially substantially reduced, but that this returned to pre-burn levels 2–3 years post-burn at both sites and treatments, and the exotic component of the fauna did not change at these sites in the time frame of the study. Species diversity, measured by the Shannon-Wiener index and also presented as k -dominance plots, returned to pre-burn levels within the study period, with the possible exception of the spring-burnt turf samples at DS, as indicated (quite strongly) by the k -dominance curves.

The rest of the invertebrate fauna was not analysed at the species level, and there were no indications that entire groups were removed by the fire treatments. However, there were clear and sometimes severe impacts on elements of the fauna, some of which did not return to pre-burn status within the study period, a case in point being the Amphipoda. Given that Coleoptera was not one of the most severely impacted groups, the impacts on the rest of the fauna need to be considered. As other higher taxa are further analysed at species level, it will be valuable to include these in an analysis of the impact of fire on species richness and diversity.

The comparison of the impact of spring and summer fires on the invertebrate fauna indicated that there were no major differences, at the level of detail possible in this investigation, either for the full range of taxa or for Coleoptera species. Similarly, there were no substantial differences between seasons in the effect on any of the trophic groups within the community. It is unfortunate that the MB summer burn data were not available for analysis in this report, so that the comparison was restricted to a single site. An analysis of individual species in the future might unearth differential effects on taxa of the timing of burning treatments.

6. Recommendations

The authors make the following recommendations, including topics for further research:

- Continue annual sampling and storage of specimens for at least another 5 years to develop a resource of collected material. This has been carried out for 2007, 2008 and 2009. This will allow for longer term effects of burning to be analysed at some stage in the future.
- Store one complete set of unsorted material from both sites (e.g. January 2008 sample) in deep freeze to preserve DNA for future study. This would allow DNA extraction to be carried out for taxa where molecular methods are required to solve taxonomic or systematic problems. Improve standard of curation of remaining collected material to museum standard.
- Integrate invertebrate and plant data, and work towards using data on fire characteristics, and effects on the flora and invertebrates to develop a predictive model that can be tested.
- Encourage students to make use of the material and the data to add value to the information reported so far. Such studies could include:
 - Estimation of treatment impacts on biomass of invertebrate taxa and trophic groups, which is often considered more ecologically meaningful than density.
 - Determination of consequences to native flora of post-burn outbreaks of Pseudococcidae, Thysanoptera and Homoptera, as found in the current study, and the potential for these taxa to transmit plant pathogens.
 - Molecular studies to match larvae with adult stages. This may be limited by the quality of DNA that can be extracted for longer-term alcohol-stored specimens unless stored in deep freeze. This would be particularly valuable for species-rich groups such as Staphylinidae, where morphology is particularly challenging.
 - Testing of consistent results from these case study sites to determine whether they apply more universally.

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Appendix 1

TAXONOMIC GROUPS AND COMMON NAMES OF INVERTEBRATES IDENTIFIED

PHYLUM	SUBPHYLUM	CLASS	ORDER	FAMILY	COMMON NAME
Platyhelminthes		Turbellaria			Flatworms
Annelida		Oligochaeta	Clitellata		Earthworms, potworms
Mollusca		Gastropoda	Pulmonata		Slugs
Mollusca		Gastropoda	Pulmonata		Snails
Arthropoda	Chelicerata	Arachnida	Araneae		Spiders
Arthropoda	Chelicerata	Arachnida	Opiliones		Harvestmen
Arthropoda	Chelicerata	Arachnida	Pseudoscorpionida		Pseudoscorpions
Arthropoda	Crustacea	Malacostraca	Amphipoda		Bush hoppers
Arthropoda	Crustacea	Malacostraca	Isopoda		Woodlice/slaters
Arthropoda	Myriapoda	Chilopoda			Centipedes
Arthropoda	Myriapoda	Diplopoda			Millipedes
Arthropoda	Myriapoda	Symphyla			
Arthropoda	Myriapoda	Pauropoda			
Arthropoda	Hexapoda		Diplura		
Arthropoda	Hexapoda	Entognatha	Protura		
Arthropoda	Hexapoda	Insecta	Orthoptera	Blattidae	Cockroaches
Arthropoda	Hexapoda	Insecta	Orthoptera	Stenopelmatidae	Weta
Arthropoda	Hexapoda	Insecta	Orthoptera	Acrididae	Grasshoppers
Arthropoda	Hexapoda	Insecta	Orthoptera	Gryllidae	Crickets
Arthropoda	Hexapoda	Insecta	Dermaptera		Earwigs
Arthropoda	Hexapoda	Insecta	Psocoptera		Book-lice
Arthropoda	Hexapoda	Insecta	Hemiptera	Homoptera	Aphids and others
Arthropoda	Hexapoda	Insecta	Hemiptera	Pseudococcidae	Mealybugs
Arthropoda	Hexapoda	Insecta	Hemiptera	Heteroptera	True bugs
Arthropoda	Hexapoda	Insecta	Hymenoptera	Formicidae	Ants
Arthropoda	Hexapoda	Insecta	Hymenoptera	Other Hymenoptera	Bees, wasps
Arthropoda	Hexapoda	Insecta	Lepidoptera		Butterflies, moths
Arthropoda	Hexapoda	Insecta	Neuroptera		Lacewings
Arthropoda	Hexapoda	Insecta	Trichoptera		Caddis flies
Arthropoda	Hexapoda	Insecta	Coleoptera	Anthicidae	Ant beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Anthribidae	Fungus weevils
Arthropoda	Hexapoda	Insecta	Coleoptera	Byrrhidae	Moss beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Carabidae	Ground beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Cerambycidae	Longhorn beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Chrysomelidae	Leaf beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Coccinellidae	Ladybirds
Arthropoda	Hexapoda	Insecta	Coleoptera	Corylophidae	Minute fungus beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Cryptophagidae	Silken fungus beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Curculionidae	Weevils
Arthropoda	Hexapoda	Insecta	Coleoptera	Dermestidae	Carrion beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Elateridae	Click beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Latridiidae	Mildew beetles

Continued on next page

Appendix 1—continued

PHYLUM	SUBPHYLUM	CLASS	ORDER	FAMILY	COMMON NAME
Arthropoda	Hexapoda	Insecta	Coleoptera	Leiodidae	Small carrion beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Melandryidae	False darkling beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Melyridae	Leaping beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Mycetophagidae	Hairy fungus beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Oedemeridae	Lax beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Ptiliidae	Feather-winged beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Scarabaeidae	Scarabs
Arthropoda	Hexapoda	Insecta	Coleoptera	Scirtidae	Marsh beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Scydmaenidae	Stone beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Staphylinidae	Rove beetles
Arthropoda	Hexapoda	Insecta	Coleoptera	Tenebrionidae	Darkling beetles
Arthropoda	Hexapoda	Insecta	Diptera		True flies
Arthropoda	Hexapoda	Insecta	Thysanoptera		Thrips

Appendix 2

COLEOPTERA TAXA FOUND AT DEEP STREAM AND MOUNT BENGER

Native/adventive status, trophic group and presence at Deep Stream (DS) and Mount Benger (MB) are indicated.

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPHIC GROUP	PRESENCE	
				DS	MB
Anthicidae	<i>Anthicus otagoensis</i> Bates	Native	Carnivore	×	
Anthicidae	<i>Anthicus</i> sp. cf. <i>minor</i> Broun	Native	Carnivore	×	
Anthribidae	<i>Euciodes suturalis</i> Pascoe	Adventive	Herbivore	×	
Archeocryptidae	<i>Archeocrypticus topali</i> Kaszab	Adventive	Fungivore		×
Byrrhidae	Byrrhidae MB larva sp. 1	Native	Herbivore	×	×
Byrrhidae	Byrrhidae MB larva sp. 2	Native	Herbivore		×
Byrrhidae	Byrrhidae MB larva sp. 3	Native	Herbivore	×	×
Byrrhidae	Byrrhidae MB larva sp. 4	Native	Herbivore		×
Byrrhidae	<i>Microchaetes</i> DS sp. 1	Native	Herbivore	×	×
Byrrhidae	<i>Microchaetes</i> MB sp. 1	Native	Herbivore		×
Byrrhidae	<i>Synorthus</i> DS sp. 1	Native	Herbivore	×	×
Byrrhidae	<i>Synorthus</i> MB sp. 1	Native	Herbivore		×
Byrrhidae	<i>Synorthus</i> MB sp. 2	Native	Herbivore		×
Cantharidae	<i>Asilis subnuda</i> Broun	Native	Carnivore	×	
Cantharidae	Cantharidae DS larva sp. 1	Native	Carnivore	×	×
Carabidae	<i>Anchonemus otagoensis</i> (Bates)	Native	Carnivore	×	×
Carabidae	<i>Bembidion</i> MB sp. 1	Native	Carnivore		×
Carabidae	Carabidae DS larva sp. 1	Native	Carnivore	×	
Carabidae	Carabidae DS larva sp. 2	Native	Carnivore	×	×
Carabidae	Carabidae DS larva sp. 3	Native	Carnivore	×	
Carabidae	Carabidae DS larva sp. 4	Native	Carnivore	×	×
Carabidae	Carabidae DS larva sp. 5	Native	Carnivore	×	
Carabidae	Carabidae MB larva sp. 1	Native	Carnivore		×
Carabidae	Carabidae MB larva sp. 2	Native	Carnivore	×	×
Carabidae	Carabidae MB larva sp. 3	Native	Carnivore	×	×
Carabidae	Carabidae MB larva sp. 4	Native	Carnivore	×	×
Carabidae	Carabidae MB larva sp. 5	Native	Carnivore	×	×
Carabidae	<i>Demetrida moesta</i> Sharp	Native	Carnivore	×	×
Carabidae	<i>Dicrochile novaezelandiae</i> (Fairmaire)	Native	Carnivore	×	
Carabidae	<i>Holcaspis placida</i> Broun	Native	Carnivore	×	
Carabidae	<i>Holcaspis punctigera</i> Broun	Native	Carnivore	×	×
Carabidae	<i>Mecodema minax</i> Britton	Native	Carnivore		×
Carabidae	<i>Mecyclothorax rotundicollis</i> (White)	Native	Carnivore	×	
Carabidae	<i>Megadromus fultoni/meritus</i>	Native	Carnivore	×	
Carabidae	<i>Notagonum</i> sp. cf. <i>feredayi</i> (Bates)	Native	Carnivore	×	
Carabidae	<i>Oopterus</i> DS sp. 1	Native	Carnivore	×	
Carabidae	<i>Oopterus</i> MB sp. 1	Native	Carnivore		×
Carabidae	<i>Oregus aereus</i> White	Native	Carnivore	×	×
Carabidae	<i>Pelodiaetus</i> MB sp. 1	Native	Carnivore		×

Continued on next page

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPIC GROUP	PRESENCE	
				DS	MB
Carabidae	<i>Scopodes cognatus</i> Broun	Native	Carnivore		×
Carabidae	<i>Scopodes edwardsi</i> Bates	Native	Carnivore	×	
Carabidae	<i>Scopodes fossulatus</i> (Blanchard)	Native	Carnivore	×	×
Cerambycidae	Cerambycidae DS larva sp. 1	Native	Herbivore	×	
Cerambycidae	<i>Ptinostoma spinicolle</i> Broun	Native	Herbivore	×	
Cerambycidae	<i>Somatidia</i> DS sp. 1	Native	Herbivore	×	
Chrysomelidae	<i>Adoxia pygidialis</i> (Broun)	Native	Herbivore	×	×
Chrysomelidae	<i>Allochbaris</i> DS sp. 1	Native	Herbivore		×
Chrysomelidae	<i>Allochbaris limbata</i> Broun	Native	Herbivore		×
Chrysomelidae	<i>Allochbaris</i> MB sp. 1	Native	Herbivore	×	×
Chrysomelidae	<i>Chaetocnema</i> DS sp. 1	Native	Herbivore	×	×
Chrysomelidae	<i>Chaetocnema</i> DS sp. 2	Native	Herbivore	×	
Chrysomelidae	<i>Chaetocnema</i> MB sp. 1	Native	Herbivore		×
Chrysomelidae	<i>Chaetocnema</i> MB sp. 2	Native	Herbivore		×
Chrysomelidae	Chrysomelidae DS larva sp. 1	Native	Herbivore	×	
Chrysomelidae	Chrysomelidae DS sp. 2	Native	Herbivore	×	
Chrysomelidae	Galerucinae MB larva sp. 1	Native	Herbivore	×	×
Chrysomelidae	Galerucinae MB larva sp. 2	Native	Herbivore	×	×
Coccinellidae	? <i>Rbizobius</i> MB sp. 2	Native	Carnivore	×	
Coccinellidae	? <i>Rbizobius</i> MB sp. 3	Native	Carnivore		×
Coccinellidae	? <i>Rbizobius</i> MB sp. 4	Native	Carnivore		×
Coccinellidae	<i>Coccinella 11-punctata</i> L.	Adventive	Carnivore	×	×
Coccinellidae	<i>Coccinella leonina</i> F.	Adventive	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 1	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 2	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 3	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS larva sp. 4	Native	Carnivore	×	
Coccinellidae	Coccinellidae DS larva sp. 5	Adventive	Carnivore	×	×
Coccinellidae	Coccinellidae DS sp. 1	Native	Carnivore	×	
Coccinellidae	Coccinellidae DS sp. 2	Native	Carnivore	×	×
Coccinellidae	Coccinellidae DS sp. 3	Native	Carnivore	×	
Coccinellidae	Coccinellidae MB larva sp. 1	Native	Carnivore		×
Coccinellidae	Coccinellidae MB sp. 1	Native	Carnivore		×
Coccinellidae	Coccinellidae MB sp. 4	Native	Carnivore		×
Coccinellidae	<i>Veronicobius</i> sp. cf. <i>tristis</i>	Native	Carnivore	×	×
Corylophidae	Corylophidae DS larva sp. 1	Native	Fungivore	×	
Corylophidae	Corylophidae MB larva sp. 1	Native	Fungivore		×
Corylophidae	<i>Holopsis</i> DS sp. 1	Native	Fungivore	×	×
Corylophidae	<i>Holopsis</i> DS sp. 2	Native	Fungivore	×	×
Cryptophagidae	<i>Antarcticotectus silvanus</i>	Native	Fungivore	×	×
Cryptophagidae	Cryptophagidae DS larva sp. 1	Native	Fungivore	×	
Cryptophagidae	<i>Cryptophagus</i> DS sp. 1	Adventive	Fungivore	×	
Cryptophagidae	<i>Cryptophagus</i> DS sp. 2	Adventive	Fungivore	×	×
Curculionidae	? <i>Crisius</i> MB sp. 2	Native	Herbivore		×
Curculionidae	<i>Athor arcifer</i> Broun	Native	Herbivore	×	
Curculionidae	<i>Baeosomus amplus</i> Broun	Native	Herbivore	×	×
Curculionidae	<i>Baeosomus</i> DS sp. 4	Native	Herbivore	×	×
Curculionidae	<i>Baeosomus</i> DS sp. 6	Native	Herbivore	×	×
Curculionidae	<i>Baeosomus</i> MB sp. 1	Native	Herbivore	×	×

Continued on next page

FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPIC GROUP	PRESENCE	
				DS	MB
Curculionidae	<i>Baeosomus rugosus</i> Broun	Native	Herbivore	×	×
Curculionidae	<i>Baeosomus</i> sp. cf. <i>angustus</i> (Broun)	Native	Herbivore	×	×
Curculionidae	<i>Baeosomus</i> sp. cf. <i>crassipes</i> (Broun)	Native	Herbivore	×	×
Curculionidae	<i>Catoptes cuspidatus</i> (Broun)	Native	Herbivore	×	×
Curculionidae	<i>Catoptes dispar</i> Broun	Native	Herbivore		×
Curculionidae	<i>Catoptes</i> DS sp. 1	Native	Herbivore	×	×
Curculionidae	<i>Catoptes robustus</i> Sharp	Native	Herbivore	×	
Curculionidae	Cryptorhynchini MB sp. 1	Native	Herbivore		×
Curculionidae	Curculionidae DS larva sp. 2	Native	Herbivore	×	
Curculionidae	Curculionidae MB larva sp. 1	Native	Herbivore	×	×
Curculionidae	Curculionidae MB larva sp. 2	Native	Herbivore	×	×
Curculionidae	Curculionidae MB larva sp. 3	Native	Herbivore	×	×
Curculionidae	Curculionidae MB larva sp. 4	Native	Herbivore		×
Curculionidae	<i>Eugnomus dispar</i> (Broun)	Native	Herbivore	×	
Curculionidae	<i>Eugnomus durvillei</i> Schonherr	Native	Herbivore	×	×
Curculionidae	<i>Gromilus</i> DS sp. 1	Native	Herbivore	×	
Curculionidae	<i>Gromilus</i> DS sp. 2	Native	Herbivore	×	
Curculionidae	<i>Gromilus impressus</i> (Broun)	Native	Herbivore	×	
Curculionidae	<i>Gromilus</i> MB sp. 1	Native	Herbivore		×
Curculionidae	<i>Gromilus</i> MB sp. 2	Native	Herbivore		×
Curculionidae	<i>Irenimus curvus</i> Barratt & Kuschel	Native	Herbivore	×	×
Curculionidae	<i>Irenimus posticalis</i> (Broun)	Native	Herbivore	×	
Curculionidae	<i>Irenimus stolidus</i> Broun	Native	Herbivore	×	×
Curculionidae	<i>Listronotus bonariensis</i> (Kuschel)	Adventive	Herbivore	×	×
Curculionidae	<i>Nestrius</i> DS sp. 1	Native	Herbivore		×
Curculionidae	<i>Nestrius</i> MB sp. 1	Native	Herbivore		×
Curculionidae	<i>Nestrius</i> MB sp. 2	Native	Herbivore		×
Curculionidae	<i>Nestrius</i> MB sp. 3	Native	Herbivore		×
Curculionidae	<i>Nestrius</i> MB sp. 4	Native	Herbivore		×
Curculionidae	<i>Nicaeana cinerea</i> Broun	Native	Herbivore	×	×
Curculionidae	<i>Otiobrychus ovatus</i> L.	Adventive	Herbivore		×
Curculionidae	<i>Peristoreus ?sexmaculatus</i> (Broun)	Native	Herbivore	×	
Curculionidae	<i>Peristoreus insignis</i> (Broun)	Native	Herbivore	×	×
Curculionidae	<i>Peristoreus</i> MB sp. 2	Native	Herbivore		×
Curculionidae	<i>Peristoreus veronicae</i> (Broun)	Native	Herbivore	×	
Curculionidae	<i>Rhopalomerus alternans</i> (Broun)	Native	Herbivore		×
Curculionidae	<i>Sitona discoideus</i> Gyllenhal	Adventive	Herbivore	×	
Curculionidae	<i>Tanysoma angustulum</i> Broun	Native	Herbivore	×	
Curculionidae	<i>Trichosirocalus horridus</i> (Panzer)	Adventive	Herbivore		×
Curculionidae	<i>Trinodicalles</i> MB sp. 1	Native	Herbivore		×
Dermestidae	<i>Antbrenocerus australis</i> (Hope)	Adventive	Carrion	×	
Dermestidae	Dermestidae DS larva sp. 2	Native	Carrion	×	
Dermestidae	Dermestidae DS larva sp. 3	Native	Carrion	×	
Dermestidae	Dermestidae MB larva sp. 1	Native	Carrion	×	×
Dermestidae	<i>Reesa vespulae</i> (Milliron)	Adventive	Carrion	×	×
Elateridae	<i>Betarmonides</i> DS sp. 1	Native	Herbivore	×	
Elateridae	Elateridae DS larva sp. 1	Native	Herbivore	×	
Elateridae	Elateridae DS sp. 1	Native	Herbivore	×	
Elateridae	Elateridae MB larva sp. 1	Native	Herbivore	×	×

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FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPIC GROUP	PRESENCE	
				DS	MB
Elateridae	Elateridae MB larva sp. 2	Native	Herbivore	×	×
Elateridae	Elateridae MB sp. 1	Native	Herbivore	×	×
Elateridae	Elateridae MB sp. 2	Native	Herbivore		×
Elateridae	<i>Elasticbrosis</i> sp. cf. 'castanea' (Broun)	Native	Herbivore	×	×
Erotylidae	<i>Loberus anthracinus</i> (Broun)	Native	Fungivore		×
Latridiidae	? <i>Corticaria</i> DS sp. 4	Native	Fungivore	×	×
Latridiidae	<i>Aridius bifasciatus</i> (Reitter)	Adventive	Fungivore	×	×
Latridiidae	<i>Cartodere</i> DS sp. 1	Adventive	Fungivore	×	
Latridiidae	<i>Corticaria formicaeophila</i> (Broun)	Native	Fungivore	×	×
Latridiidae	<i>Corticaria serrata</i> (Paykull)	Adventive	Fungivore	×	×
Latridiidae	Latridiidae DS larva sp. 1	Native	Fungivore	×	
Latridiidae	<i>Melanoptbalma</i> DS sp. 2	Native	Fungivore	×	
Latridiidae	<i>Melanoptbalma gibbosa</i> (Herbst)	Native	Fungivore	×	×
Leiodidae	<i>Inocatops compactus</i> (Broun)	Native	Fungivore	×	×
Leiodidae	<i>Isocolon modestum</i> Broun	Native	Fungivore	×	
Leiodidae	Leiodidae DS larva sp. 1	Native	Fungivore	×	
Melandryidae	<i>Hylobia</i> MB sp. 1	Native	Fungivore		×
Melyridae	<i>Arthracanthus</i> DS sp. 1	Native	Herbivore	×	×
Melyridae	Melyridae DS larva sp. 1	Native	Carnivore	×	×
Mycetophagidae	Mycetophagidae DS sp. 1	Native	Fungivore	×	
Mycetophagidae	Mycetophagidae MB larva sp. 1	Native	Fungivore		×
Mycetophagidae	Mycetophagidae MB larva sp. 2	Native	Fungivore		×
Mycetophagidae	<i>Typhaea stercorea</i> L.	Adventive	Fungivore		×
Oedemeridae	<i>Thelyphassa nemoralis</i> (Broun)	Native	Fungivore		×
Ptiliidae	<i>Ptinella</i> DS sp. 1	Native	Fungivore	×	×
Ptiliidae	<i>Ptinella</i> DS sp. 2	Native	Fungivore	×	×
Ptiliidae	<i>Ptinella</i> MB sp. 1	Native	Fungivore	×	×
Scarabaeidae	<i>Costelytra zealandica</i> (White)	Native	Herbivore	×	
Scarabaeidae	<i>Odontria striata</i> White	Native	Herbivore	×	
Scarabaeidae	<i>Odontria striata</i> White larva	Native	Herbivore	×	×
Scarabaeidae	<i>Pyronota</i> DS larva sp. 1	Native	Herbivore	×	
Scarabaeidae	<i>Pyronota festiva</i> (F.)	Native	Herbivore	×	×
Scirtidae	Scirtidae MB sp. 1	Native	Herbivore		×
Scirtidae	Scirtidae MB sp. 2	Native	Herbivore		×
Scolytidae	<i>Hylastes ater</i> (Paykull)	Adventive	Herbivore		×
Scraptiidae	<i>Notbotelus</i> DS sp. 1	Native	Herbivore	×	
Scydmaenidae	Scydmaenidae DS larva sp. 1	Native	Carnivore	×	×
Scydmaenidae	Scydmaenidae DS larva sp. 2	Native	Carnivore	×	
Scydmaenidae	Scydmaenidae DS sp. 1	Native	Carnivore	×	
Scydmaenidae	Scydmaenidae DS sp. 2	Native	Carnivore	×	×
Scydmaenidae	Scydmaenidae DS sp. 3	Native	Carnivore	×	
Scydmaenidae	Scydmaenidae MB larva sp. 1	Native	Carnivore		×
Staphylinidae	<i>Agnostethus</i> DS sp. 1	Native	Carnivore	×	
Staphylinidae	<i>Agnostethus</i> DS sp. 2	Native	Carnivore	×	
Staphylinidae	<i>Agnostethus</i> MB sp. 1	Native	Carnivore		×
Staphylinidae	Aleocharinae Cass sp. 1	Native	Carnivore	×	×
Staphylinidae	Aleocharinae DS sp. 1	Native	Carnivore	×	×
Staphylinidae	Aleocharinae DS sp. 10	Native	Carnivore		×
Staphylinidae	Aleocharinae DS sp. 13	Native	Carnivore	×	

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FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPIC GROUP	PRESENCE	
				DS	MB
Staphylinidae	Aleocharinae DS sp. 2	Native	Carnivore	x	x
Staphylinidae	Aleocharinae DS sp. 3	Native	Carnivore	x	
Staphylinidae	Aleocharinae DS sp. 4	Native	Carnivore	x	
Staphylinidae	Aleocharinae DS sp. 5	Native	Carnivore	x	
Staphylinidae	Aleocharinae DS sp. 6	Native	Carnivore	x	x
Staphylinidae	Aleocharinae DS sp. 7	Native	Carnivore	x	
Staphylinidae	Aleocharinae DS sp. 8	Native	Carnivore	x	
Staphylinidae	Aleocharinae DS sp. 9	Native	Carnivore	x	x
Staphylinidae	Aleocharinae MB sp. 1	Native	Carnivore	x	x
Staphylinidae	Aleocharinae MB sp. 2	Native	Carnivore		x
Staphylinidae	Aleocharinae MB sp. 3	Native	Carnivore		x
Staphylinidae	Aleocharinae MB sp. 4	Native	Carnivore	x	x
Staphylinidae	Aleocharinae MB sp. 5	Native	Carnivore		x
Staphylinidae	Aleocharinae MB sp. 6	Native	Carnivore		x
Staphylinidae	<i>Anabaxis</i> Tukino sp. 1	Native	Carnivore	x	x
Staphylinidae	<i>Eupines</i> DS sp. 1	Native	Carnivore	x	x
Staphylinidae	<i>Eupines</i> MB sp. 1	Native	Carnivore		x
Staphylinidae	Habrocerinae DS sp. 1	Native	Carnivore	x	
Staphylinidae	<i>Hyperomma</i> DS sp. 1	Native	Carnivore	x	x
Staphylinidae	<i>Maorotbitus</i> DS sp. 1	Native	Carnivore	x	
Staphylinidae	<i>Microsilpha</i> DS sp. 2	Native	Carnivore	x	
Staphylinidae	<i>Microsilpha</i> DS sp. 3	Native	Carnivore	x	
Staphylinidae	<i>Paraphytopus</i> DS sp. 1	Native	Carnivore	x	x
Staphylinidae	<i>Protopristus</i> DS sp. 1	Native	Carnivore	x	x
Staphylinidae	<i>Protopristus</i> DS sp. 2	Native	Carnivore	x	x
Staphylinidae	<i>Protopristus</i> DS sp. 3	Native	Carnivore	x	x
Staphylinidae	<i>Protopristus</i> MB sp. 1	Native	Carnivore	x	x
Staphylinidae	<i>Pselaphaulax</i> DS sp. 1	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS larva sp. 1	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS sp. 1	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS sp. 2	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS sp. 3	Native	Carnivore	x	
Staphylinidae	Pselaphinae DS sp. 4	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS sp. 5	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS sp. 6	Native	Carnivore	x	
Staphylinidae	Pselaphinae DS sp. 7	Native	Carnivore	x	x
Staphylinidae	Pselaphinae DS sp. 9	Native	Carnivore	x	
Staphylinidae	Pselaphinae MB larva sp. 1	Native	Carnivore	x	x
Staphylinidae	Pselaphinae MB larva sp. 2	Native	Carnivore	x	x
Staphylinidae	Pselaphinae MB sp. 1	Native	Carnivore		x
Staphylinidae	Pselaphinae MB sp. 2	Native	Carnivore		x
Staphylinidae	Pselaphinae MB sp. 3	Native	Carnivore		x
Staphylinidae	Pselaphinae MB sp. 4	Native	Carnivore	x	x
Staphylinidae	Pselaphinae MB sp. 5	Native	Carnivore	x	x
Staphylinidae	Pselaphinae Tukino sp. 2	Native	Carnivore	x	
Staphylinidae	<i>Pselaphobus atriventris</i> (Westwood)	Adventive	Carnivore		x
Staphylinidae	<i>Pselaphobus</i> MB sp. 1	Adventive	Carnivore		x
Staphylinidae	' <i>Quedius</i> ' DS sp. 1	Adventive	Carnivore		x
Staphylinidae	' <i>Quedius</i> ' MB sp. 1	Adventive	Carnivore		x

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FAMILY	TAXON	NATIVE/ ADVENTIVE	TROPIC GROUP	PRESENCE	
				DS	MB
Staphylinidae	<i>Sagola</i> DS sp. 1	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 1	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 2	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 3	Native	Carnivore	×	
Staphylinidae	Staphylinidae DS larva sp. 6	Native	Carnivore	×	×
Staphylinidae	Staphylinidae DS larva sp. 8	Native	Carnivore	×	
Staphylinidae	Staphylinidae MB larva sp. 1	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 2	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 3	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 4	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 5	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 6	Native	Carnivore	×	×
Staphylinidae	Staphylinidae MB larva sp. 7	Native	Carnivore	×	×
Staphylinidae	Staphylininae DS sp. 1	Native	Carnivore	×	
Staphylinidae	Staphylininae DS sp. 2	Native	Carnivore	×	
Staphylinidae	Tachyporinae MB sp. 1	Native	Carnivore		×
Staphylinidae	<i>Tachyporus nitidulus</i> (F.)	Adventive	Carnivore	×	
Staphylinidae	<i>Zealandius</i> DS sp. 1	Native	Carnivore	×	×
Staphylinidae	<i>Zealandius</i> DS sp. 2	Native	Carnivore	×	×
Tenebrionidae	<i>Loirelus tarsalis</i> Broun	Native	Herbivore	×	
Tenebrionidae	Tenebrionidae DS larva sp. 1	Native	Herbivore	×	×
Tenebrionidae	Tenebrionidae DS larva sp. 2	Native	Herbivore	×	×
Tenebrionidae	<i>Zeadelium aeratum</i> (Broun)	Native	Herbivore	×	
Tenebrionidae	<i>Zeadelium chalmeri</i> (Broun)	Native	Herbivore		×
Tenebrionidae	<i>Zeadelium budsoni</i> (Broun)	Native	Herbivore	×	×
Tenebrionidae	<i>Zeadelium senile</i> Watt	Native	Herbivore	×	×
Tenebrionidae	<i>Zeadelium</i> sp. cf. <i>nigritulum</i> (Broun)	Native	Herbivore		×
Trogossitidae	Trogossitidae MB sp. 1	Native	Fungivore		×
Zopheridae	<i>Bitoma morosa</i> (Broun)	Native	Fungivore	×	
Zopheridae	<i>Notocoxellus</i> MB sp. 1	Native	Fungivore		×
Zopheridae	<i>Pristoderus</i> DS sp. 1	Native	Fungivore	×	
Zopheridae	<i>Pristoderus</i> MB sp. 3	Native	Fungivore	×	

Appendix 3

NOTES ON IDENTIFICATION AND ECOLOGY OF SOME SPECIES

A3.1 Mollusca

The snail fauna has been examined by Frank Climo (c/- Te Papa Museum). Despite being relatively low in abundance, the fauna was of great interest, possibly because it has been so poorly collected from tussock grassland areas such as our sites in the past. The collection has extended the range of some species and added considerably to the quantity of known specimens for some species. Notably, *Flammulina* n. sp. (Amphodoxinae) was known previously from only two specimens from Governor's Bush, Mt Cook; this species was found to be well represented in the material from Deep Stream.

A3.2 Amphipoda

Terrestrial amphipods are litter dwellers, feeding on decaying organic material, and dependent upon a moist, humid habitat. It has been noted by Friend & Richardson (1986) that only the hardiest groups of terrestrial amphipods have extended their range from forest into grassland environments. The talitrid *Makawe* (= *Orchestia*) *burleyi* (Duncan) is known to have successfully colonised eastern South Island grassland and can reach densities of 300/m² in disturbed grassland (Duncan 1969), although it is limited to areas where rainfall is above about 600 mm per annum. Identification of the species most commonly found in the current study has not been confirmed, but is likely to be *Parorchestia tenuis* (Dana), given the characteristics described by Duncan (1994).

A3.3 Hymenoptera: Formicidae

In our study, the ant fauna was represented by three species, which were present at both sites. The predominant species found was the widespread endemic *Monomorium antarcticum* (Fr. Smith), which is a generalist feeder, preying on small insects, harvesting small seeds, and 'milking' homopterans (Don 2007). The population density reduction following fire could be attributable to reduced prey items and seed availability, since it would be expected that in the event of fire, population survival in subterranean nests (to which the highly mobile individuals would most likely retreat) might be quite high. The other two species found were the endemic *Huberia striata* (Fr. Smith), and the adventive species *Prolasius advena* (Fr. Smith), both of which were present in comparatively low numbers.

A3.4 Hemiptera: Pseudococcidae

Although a full identification of all pseudococcid material has not been carried out, a subsample was examined, within which three species were identified (Rosa Henderson, Landcare Research, pers. comm. 2000). These were *Ventrispina otagoensis* (Brittin), *Laminicoccus eastopi* Cox, and *Balanococcus danthoniae* (Morrison). *Ventrispina otagoensis* is found throughout New Zealand and has been associated with Poaceae, Rosaceae and mosses. *Laminicoccus eastopi* has been recorded from *Chionochloa* spp., and *B. danthoniae* from a number of grass species where it feeds in the leaf sheaths.

A3.5 Thysanoptera

At Deep Stream, the predominant species of Thysanoptera found was *Aptinothrips rufus* (Haliday), an exotic, cosmopolitan species known as the grass thrips. This species has a wide plant host range (Mound & Walker 1982) and was mainly responsible for the 'outbreak' in thrips densities that occurred 1–2 years post-burn. Also present but far less abundant were *Aptinothrips stylifer* Trybom, which is well known from South Island tussock grassland; *Chirothrips manicatus* (Haliday), known as Timothy thrips, which is associated with exotic and native grasses; the exotic tubuliferan spore-feeding *Nesothrips propinquus* (Bagnall), which is also well known from tussock grassland; and the long-tailed tubuliferan *Baenothrips moundi* (Stannard), another exotic species from Australia that feeds on fungal hyphae in leaf litter (Mound & Walker 1982). At Mount Benger, the same *Aptinothrips* species were present, as well as two Australian species that were recorded from sub-alpine tussock grass bases, *Carientothrips badius* (Hood) and *Emprosthiotrips* sp. The New Zealand flower thrips, *Thrips obscuratus* (Crawford), was also present; this is a New Zealand native species found in inflorescences of a wide range of species and sometimes considered a pest. Lawrence Mound (CSIRO, Canberra), who examined some of the thrips material from these sites, commented that he was surprised to see so few native species.

A3.6 Coleoptera: Ptiliidae

Taxonomy of the Ptiliidae, a family of minute beetles commonly known as feather-wing beetles, was revised in 1982 (Johnson 1982). To date, 56 species in 13 genera have been recognised from New Zealand. Very little information is given in the revision about the biology or ecology of the group, but they are believed to be fungivores, feeding on fungal spores and hyphae (Lawrence & Britton 1994; Klimaszewski & Watt 1997). Published observations have shown that ptiliids tend to be found in very moist environments (haystack bottoms, compost, litter, moss, under bark, etc.). One species has been found only in deeply set pitfall traps, suggesting that it lives in the soil. In the current study, the species found were mainly present in tussock samples at the two sites and seem best to fit the genus *Ptinella*, which is a large genus with species that are typically difficult to differentiate. No members of this genus seem to have been associated previously with *Chionochloa* species. However, Johnson (1975) had recorded species occurring on *Poa* tussock bases and extracted from tussock leaf mould on subantarctic islands.