The ecosystem effects of the biocontrol of heather (*Calluna vulgaris*) with the heather beetle (*Lochmaea suturalis*).

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Abstract

The biological control of invasive plants has the ability to affect sustainable and targeted control over large areas. Such biological control programs are an important tool in the control of invasive plants in conservation areas. The ultimate aim for these programs is to provide a net ecosystem benefit via the reduction of invasive plant densities. However, whether this aim is fulfilled is rarely evaluated. Invasive plant control results in large scale disturbance to ecosystems by removing the novel but often utilised habitat and resources provided by the invasive plant. Biological control is also complicated by having a novel organism introduced into the ecosystem with potential flow on effects for species and trophic level interactions.

This research evaluated the ecosystem impact of the heather (*Calluna vulgaris*) biological control program using the heather beetle (*Lochmaea suturalis*) on the native tussock grassland in the central North Island of New Zealand. This was achieved by comparing invertebrate communities in a small scale experiment and over three large heather beetle outbreak sites. This work provides an extension to Keesing's (1995) research on the effects of heather invasion on communities.

Heather provides a novel and unsuitable food source to many native phytophagous insects, may disrupt host finding behaviours of these insects, and alter habitat structure and complexity affecting Araneae abundance. Changes in invertebrate community composition following control were related to the removal of these effects. This outcome was consistent with predictions from Keesing (1995) and in both small and large scale studies. Heather beetle presence was found to have a positive effect on Araneae and Collembola abundance.

Heather control also had a positive for the common skink (*Oligosoma nigriplantare polychroma*) Overall the biological control of heather caused invertebrate communities to revert back to a composition resembling more closely those found in non-invaded habitats. This suggests that the biological control of heather provides a net positive conservation benefit to native tussock grasslands.

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Thesis outline

This thesis is broken up into five chapters; general introduction, three research chapters written as individual stand-alone publications, and a general summary & recommendations.

As methods and study sites are often similar between chapters there is overlap and repetition of some aspects of introduction and results in chapters two and three and repetition of methodology throughout all chapters to maintain the stand-alone nature of the research chapters.

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Chapter One

General introduction

Figure 1.0: Mount Ruapehu at sunset on the Central Plateau.

General Introduction

Invasive plants present a difficult problem to management of native biodiversity as they often colonise and become dominant over large tracts of land. These invaded areas, while often vastly changed in structure and microclimate, still provide many resources for native fauna. Control of invasive plants specifically target areas of high weed density, thus there is a significant disturbance to fauna that utilise the habitat (leaving a weed shaped hole). Management techniques must be carefully implemented to ensure the net benefit to the ecosystem being managed.

The biocontrol of invasive plant species is a target specific means of control that has the ability to provide a reduction in density or removal of invasive species over large areas. In comparison, herbicide application is a more generalist control method, and along with mechanical control is unfeasible over large areas. Biocontrol provides a potentially more sustainable way of managing individual invasive plant species, but it also is subject to the same problem of large scale disturbance of utilised habitats with the additional potential flow-on effects on species interactions and food-webs due to the presence of the agent itself.

The main focus of this thesis is to investigate what effect heather (*Calluna vulgaris*) control has on invertebrate communities at three large biological control outbreak sites and one herbicide and insecticide (heather beetle exclusion) trial site in the Tongariro region of the central North Island of New Zealand. The focal control method of this research is biological control by the heather beetle (*Lochmaea suturalis*), with a minimal emphasis on chemical control. This research follows on from the work done by Keesing (1995) in assessing the impacts of heather invasion on invertebrates, by using this research to assess whether post control communities more resemble those found in non-invaded habitats.

Additional to the main focus of this research an unexpected effect of heather control on the endemic common skink (*Oligosoma nigriplantare polychroma*) was identified. This finding is explored in context to the net-benefit to ecosystems of invasive plant management.

This research will provide advice on the sustainability and efficacy of biological control in ecosystem restoration and enable better management of invasive plants to maximise conservation benefit. Furthermore, it will enable decisions on the cost-benefit of novel biological control agent introductions for the purpose of invasive plant control to be made with greater knowledge on the potential ecosystem effects agents can have in the natural ecosystems where they are released.

Chapter Two

Invasive plant control restores invertebrate community composition

Figure 2.0: Heather flowers on the Central Plateau.

Invasive plant control restores invertebrate community composition.

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Abstract

Invasive plants affect the ecosystems they invade in a multitude of ways; displacing native plant communities, altering structure, and disrupting successional processes. These effects not only impact indigenous plant communities but can be wide reaching, affecting all trophic levels. As these effects are so variable depending on the invasive species and its invaded habitat the outcomes of control are difficult to predict. Furthermore, little is known about the impacts of most weeds species on the ecosystems they invade, which can make assessing the success of control programs difficult by reducing our ability to determine whether control techniques restore and/or improve ecosystems to more resemble a pristine habitat. Here we determine the effect of heather (*Calluna vulgaris*) control in native grasslands on invertebrate communities in the central North Island of New Zealand. This was achieved by comparing communities in a herbicide/insecticide/biocontrol experimental trial in an area where a combination of herbicide and biological control using the heather beetle (*Lochmaea suturalis*) were trialled as control methods, with insecticide used in areas to exclude heather beetles and isolate effects of treatments. Areas where heather had been controlled, regardless of method (herbicide or beetle), appeared to contain an invertebrate community more closely resembling that identified by Keesing (1995) as occurring in pre-heather invasion habitat. Thus both chemical and biological control of heather has a net positive effect on invertebrate communities.

Introduction

The effects of invasive plants are far greater than the visually obvious displacement of native vegetation (Chapman & Bannister, 1990; Rogers, 1996; Williams & West, 2000) and may be a greater threat to ecosystem function and indigenous biodiversity than just the displacement of native vegetation (Williams & West, 2000). While there is a growing body of research that details the effects of invasive plants on indigenous animal biodiversity, there still remains a considerable lack of knowledge of the general effects of weed invasion (Martin & Murray, 2011) and whether there is an improvement in indigenous biodiversity following successful control (Owen, 1998; Randall, 1996; Williams & West, 2000; Wotton & McAlpine, 2012). Few studies evaluate whether effects on indigenous biodiversity are reversed or mitigated with the control of an invasive weed (Wotton & McAlpine, 2012) and even fewer that evaluate the impact of weed control on non-plant indigenous biodiversity (see Florens, Mauremootoo, Fowler, Winder, & Baider, 2010; Hanula & Horn, 2011; Standish, Bennett, & Stringer, 2002). Studies that improve our understanding of the mechanisms of how invasive plants affect ecosystems are urgently needed to effectively conserve and manage ecosystems affected by invasive plants.

Invasive weeds can affect animals in one of two principal ways: changes in food availability (Keesing, 1995; Martin & Murray, 2011) and/or habitat suitability (Valentine, 2006; Valentine, Roberts, & Schwarzkopf, 2007; Williams & West, 2000). A major effect of invasive weeds on invertebrates is the influx and often dominance of a novel plant resource unsuitable for many native herbivores (Hanula & Horn, 2011; Keesing, 1995; Martin & Murray, 2011). Not only can this decrease the abundance of herbivores but also the predator taxa which rely on these prey species (Valentine, 2006). Resources other than food can also be affected, such as changes in habitat structure e.g., web sites for spiders (Keesing, 1995) and reduced thermally suitable foraging and basking sites for ectotherms such as lizards (Martin & Murray, 2011; Valentine et al., 2007) (Chapter 3). The effects of plant invasions are highly varied and may result in both increases or decreases in density or diversity depending on taxa (Florens et al., 2010; Garden, McAlpine, Possingham, & Jones, 2007; Hanula & Horn, 2011; Keesing, 1995; Standish et al., 2002; Valentine, 2006) but are generally negative (Valentine et al., 2007).

Heather (*Calluna vulgaris*) is an invasive plant introduced to the Tongariro Plateau region of the central North Island of New Zealand (Chapman & Bannister, 1990; Syrett, 1990; Syrett, Smith, Bourner, Fowler, & Wilcox, 2000). It continues to spread within this area, but is also expanding beyond this range (Chapman & Bannister, 1990). The first record of establishment in New Zealand was in 1910 (Syrett, 1990; Syrett et al., 2000) although it was probably first introduced in the 1860's (Syrett, 1990). Heather infiltrates native plant communities and out competes native plants resulting in a decrease in native plant abundance and diversity as well as altering the function, structure, and successional processes in alpine tussock ecosystems (Keesing, 1995; Rogers, 1996). Heather also negatively impacts recreational activities, military training, and invades pasture (Syrett et al., 2000). Heather's effect on the native fauna is unclear and Keesing's (1995) unpublished study is the only investigation to date of the impact of heather on invertebrate communities. He found that heather invaded invertebrate communities had a greater density of predators (particularly web-spinning spiders), a greater density of pollen feeders (specifically Thysanoptera), and a reduced density of herbivores (particularly Hemiptera) during summer when compared to heather free habitats.

Attempts to control heather have included hand pulling (Syrett, 1990) and herbicide (Rogers, 1996; Syrett, 1990), but these attempts have failed to control the spread of heather (Syrett et al., 2000). Given the extent of heather's invasion conventional herbicide control is no longer viable to control the spread (Peterson et al., 2011; Rogers, 1996). A programme of heather management was initiated in 1990 that included the use of the heather beetle (*Lochmaea suturalis,* Chrysomelidae) as a biological control agent; the heather beetle was introduced to New Zealand in 1992 and was released for the first time in the central North Island in 1996 after several years of quarantine and testing (Fowler, Syrett, & Hill, 2000; Peterson, Fowler, & Barrett, 2004; Syrett et al., 2000). Initial success was poor with only one release establishing (Peterson et al., 2004). This was probably the result of several factors including low plant host nitrogen (Fowler et al., 2000; Peterson et al., 2011), poor climate matching, and a genetic bottleneck (Peterson et al., 2011). However, subsequent releases have led to sustained populations in the central North Island (Peterson et al., 2011).

This study aims to identify whether the goal of improving and/or maintaining indigenous biodiversity is being achieved with the control of heather in the central North Island of New Zealand. This was achieved by experimentally manipulating heather and heather beetle presence with herbicide and insecticide treatments. Treatment regimes consisted of insecticide treatment only (to protect plots from beetle feeding, i.e. no impact on vegetation), herbicide treatment only (to allow for the impact of both beetle feeding and herbicide application), herbicide + insecticide treatment (to allow for the impact of herbicide only), or no treatment (to allow for the impact of beetle feeding only). These treatment regimes provide an opportunity to determine whether the general effects of heather invasion on invertebrate assemblages outlined by Keesing (1995) are reversed as a consequence of its removal and whether this reversal is detectable 2-3 years after the control of heather.

Study area

The study was conducted at a heather beetle outbreak site within the Waiouru Military Training Area (WMTA) bordering Tongariro National Park in the North Island of New Zealand. The site (S39°22' E 175°43') was located at the southern end of the Rangipo desert, approximately 11 km north of Waiouru (Fig. 2.1).

Five hundred heather beetles were released at this site during February 2001 but visible beetle feeding damage to heather was not obvious until the austral summer 2006/2007, with 0.0025 ha of heather killed. The area of feeding damage had increased every season since and by March 2011 approximately 80 ha of heather had been badly damaged or killed (Peterson et al., 2011).

Vegetation at the site had extensive heather growing amongst it until the heather beetle outbreak. As a result of the outbreak it is now largely devoid of live heather and comprises a mixed tussock-shrubland and exotic grass/herb vegetation. Native vegetation includes: red tussock (*Chionochloa rubra*), monoao (*Dracophylum subulatum*), sprawling coprosma (*Coprosma cheesmanii*), cottonwood (*Ozothamnus leptophyllus*), woolly moss (*Racomitrium* sp.), and blue tussock (*Poa colensoi*). Exotic vegetation other than heather is also present at the site with browntop (*Agrostis capillaris*) and mouse-ear hawkweed (*Pilosella officinarum*) the most common.

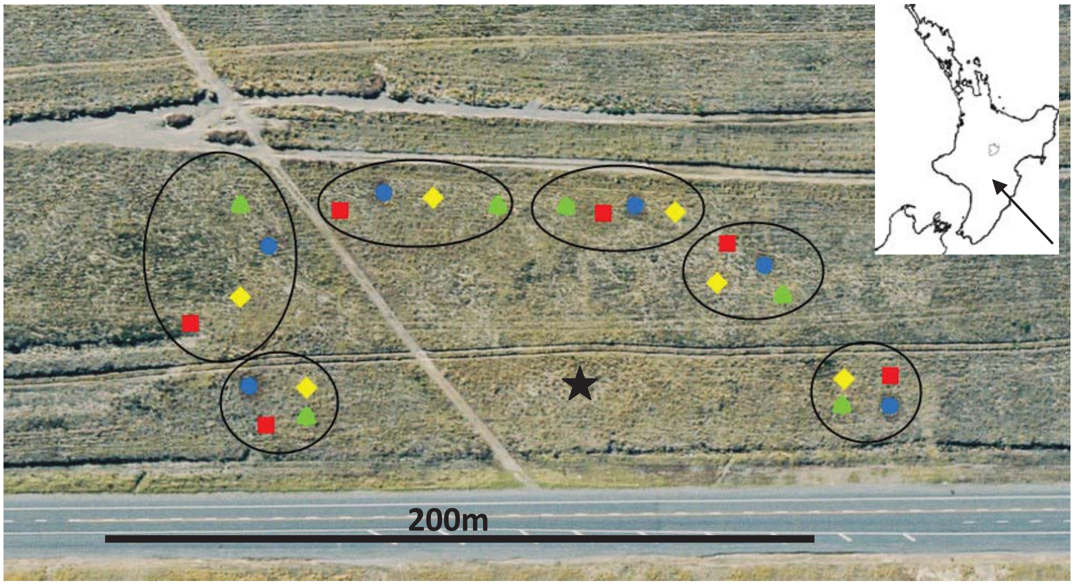

Figure 2.1: Aerial photo of study site in the central North Island. Coloured dots indicate treatment type ●=Insecticide ▲ =Herbicide + Insecticide ♦=Herbicide ■=No treatment. Black circles indicate experimental replication blocks. Star indicates heather beetle release point.

Method

Herbicide and insecticide trial plots

The herbicide/insecticide experiment was initiated in November 2007 and comprised of a randomised block design of 5 x 5 m plots, with 1 m wide treated buffer zones around each plot (total size of treated area 7 x 7 m). All treatments were applied before beetle invasion from the central release point source. Four plots made up each experimental block (Fig. 2.1) and were subject to the following treatment regimes: insecticide (I) treatment only (removal of heather beetle and thus protection of heather), herbicide (H) treatment only (removal of all dicotyledonous plants, including heather), herbicide + insecticide (H+I) treatment (removal of all dicotyledonous plants including heather, plus removal of heather beetle), or no treatment (NT) (heather beetle feeding only). The block design was replicated six times (six plots of each treatment, 24 plots total). Insecticide and herbicide were applied to a schedule (Table 2.1) through the austral spring and summer until October 2010. Monthly sampling to verify insecticide efficacy was undertaken during beetle feeding front movement through the area by using a combination of sweep netting for adults and larvae as well as assessing feeding damage from vegetation samples. While this sampling detected some minor incursion of heather beetle into the insecticide treated plots, the efficacy of insecticide treatment remained sufficient to protect heather from feeding damage. Initially, the insecticide plots were sprayed with the organophosphate diazinon but after the first application in November 2007 the insecticide treatment was switched to the synthetic pyrethroid Karate zeon (1ml/15L) + Vapour guard (0.3 ml/L) for greater efficacy. The herbicide used was 2,4-D ester (Pasture Kleen®) (6.5 ml/L). All chemical was sprayed to run off.

Experimental plots were set outside the reach of the heather beetle feeding front in 2007 and during 2009 beetles spread through the plots and fed on and damaged heather in the plots that were unprotected by insecticide. Herbicide treatment was carried out once a year from the set-up date for two years, while insecticide treatments were carried out approximately once per month (or when heather beetle invasion into plots was detected) when the heather beetle feeding front was moving through the plots, then once a year after the heather beetle feeding front had progressed beyond the plots. The insecticide/herbicide treatment timeline since the trial began is outlined in Table 2.1.

Table 2.1: Treatment timeline for herbicide and insecticide applications, and invertebrate trapping, at the WMTA site between 2007 and 2011. Numbers indicate the day of the month the treatment was applied or day traps were put out/taken in.

	2007		2008								2009						2010		2011	
	Nov	Dec	Jan	Feb	Mar	~	Sep	Oct	Nov	Dec	Jan	Feb	~	Sep	Dec	~	Oct	~	Feb	Mar
Insecticide application	30		11	14	6&27		18	20	20	11	15	18		17			27			
Herbicide application		13								11					22					
Trapping period																			3 Start	3 Finish

Trapping in plots was carried out by placing a flight intercept pitfall (FIP) trap (Fig. 2.2) directly in the middle of each of the 24 5 x 5 m plots (Table 2.1). These traps were set up 3 February 2011 then collected and removed one month later. The FIP trap used in all of the insect monitoring for this project was a modified design of that described by Stevens, McCartney, & Stringer (2007). The modification made to this design was a funnel and catching assembly at the top in place of a flat roof (Fig. 2.2). This top assembly was constructed using plumbing connections and two clear plastic jars (11 x 6 x 6 cm), the lower of which was partially filled with approximately 100 ml of ethylene glycol to catch and preserve specimens. Collection methodology also followed Stevens et al. (2007). The results from the bottom pitfall component and the top flight capture component of this trapping will be discussed separately.

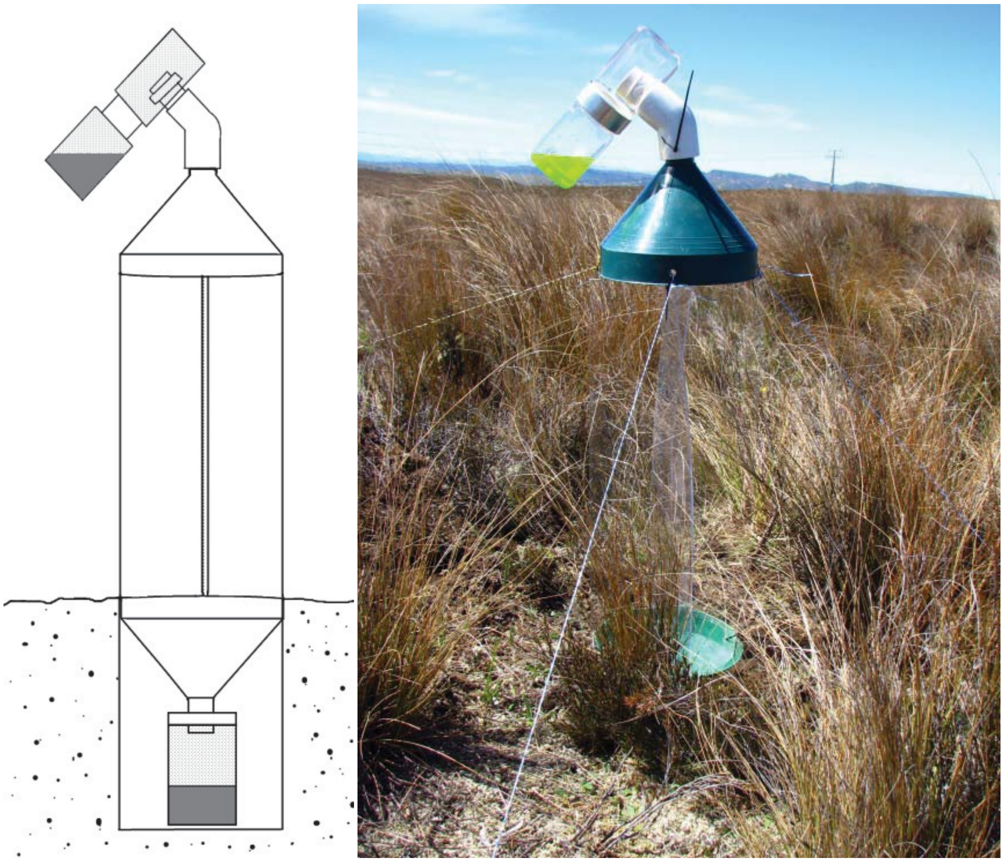

Figure 2.2: Modified flight-intercept-pitfall trap design used for invertebrate trapping at the WMTA site.

Trap area vegetation

Vegetation in each plot was characterised by taking top down photos of a 5 x 5 m area around the trap, using a pole mounted camera to take photos from c.a. 7 m above ground level. The photos were processed using the Digital Sampling Method computer program (Gillingham, 2003) to determine vegetation coverage for each plant species present. As many plots had large areas of dead heather this was included as a vegetation type. Exotic grasses and herbs were considered one category. GPS position, altitude, aspect, a description of vegetation composition and ground cover were also recorded.

Sample processing

Invertebrate samples taken from the herbicide/insecticide trial plots were filtered through a 250 µm sieve, sorted, and counted at the morphospecies level. Spiders (order Araneae) were grouped together as Mygalomorpha or Araneomorphae because of to the difficulty in assigning juveniles to morphospecies. If a morphospecies was particularly abundant in a sample, a subsample for that one taxon was counted and scaled accordingly. A photo of each morphospecies was taken to aid in identification of further specimens.

Data Analysis

Invertebrate samples (both sorted to morphospecies and order) and vegetation composition data were analysed using non-metric multi-dimensional scaling (NMDS) with Bray-Curtis distance measure and no transformation to explore similarities and differences between treatment regime, blocks, and specific plots using Primer 6.1 (Clarke & Gorley, 2007). Abundance, morphospecies richness, rarefied morphospecies richness (calculated using Primer 6.1) differences between treatment regimes were assessed using one-way analysis of variance (ANOVA). These analyses were conducted with Statistix (Statistix 9 Analytical Software, USA).

Two-factor Permutation Multivariate Analysis of Variance (PERMANOVA) to determine the significance of treatment regime and experimental blocks on the invertebrate communities was conducted in PERMANOVA+ (Anderson, Gorley, & Clarke, 2008). Single factor PERMANOVA was used to determine the significance of herbicide, insecticide and heather presence in explaining observed differences. Similarity Percentage (SIMPER) analysis, also in Primer, was used to assess which invertebrate orders were primarily responsible for the differences observed.

Results

A total of 7,974 macroinvertebrates in 18 orders and 194 morphospecies were identified, sorted and counted from collections at the study site during the 2010-11 summer sampling.

Pitfall assemblages

Of the invertebrates caught; 7,541 were caught in the pitfall component of the FIP traps; 45.8% of these were Colllembola, 13.3% Trombidiformes (Acari), 8.8% Hemiptera, 8.7% Araneae, 8.5% Diptera, 3.7% Hymenoptera, 2.5% Thysanoptera, 2.4% Coleoptera, 2.3% Opiliones, 1.8% Orthoptera, and 1.0% Lepidoptera, with no other order comprising more than 1% of the catch.

More invertebrates were caught in plots subject to treatment regimes which did not include insecticide (Fig. 2.3), while richness showed little difference between treatment regimes (Fig.

2.4), although none of these differences between abundance nor richness were significant (p=>0.05).

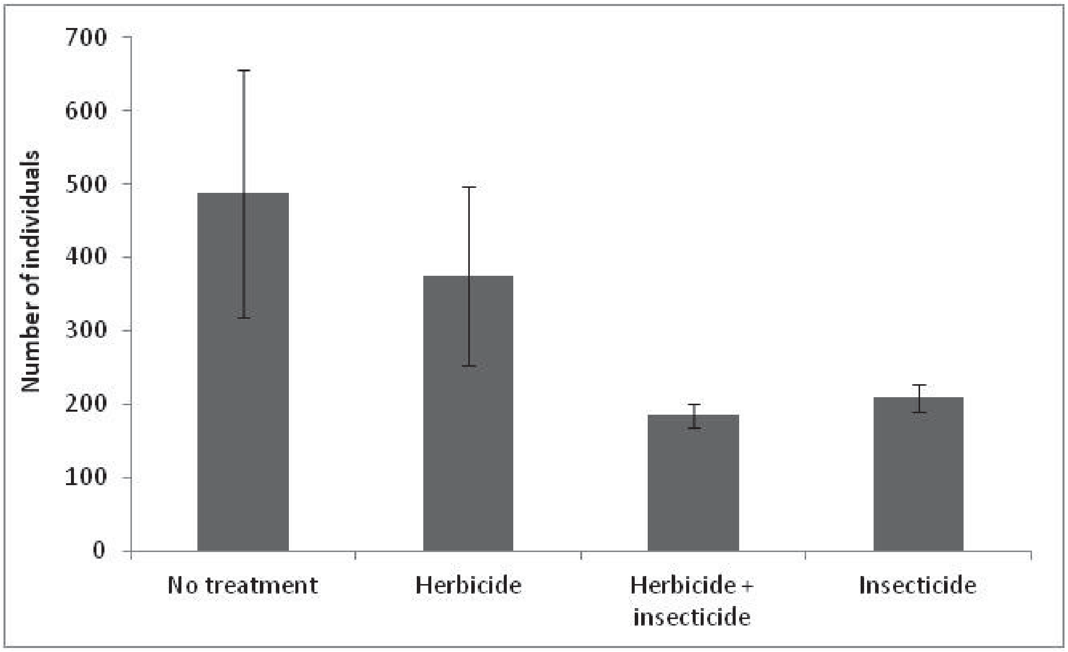

Figure 2.3: Number of individual invertebrates collected in the pitfall component of FIP traps (± 1 SE) in the four experimental treatment regimes at Waiouru 2010/2011.

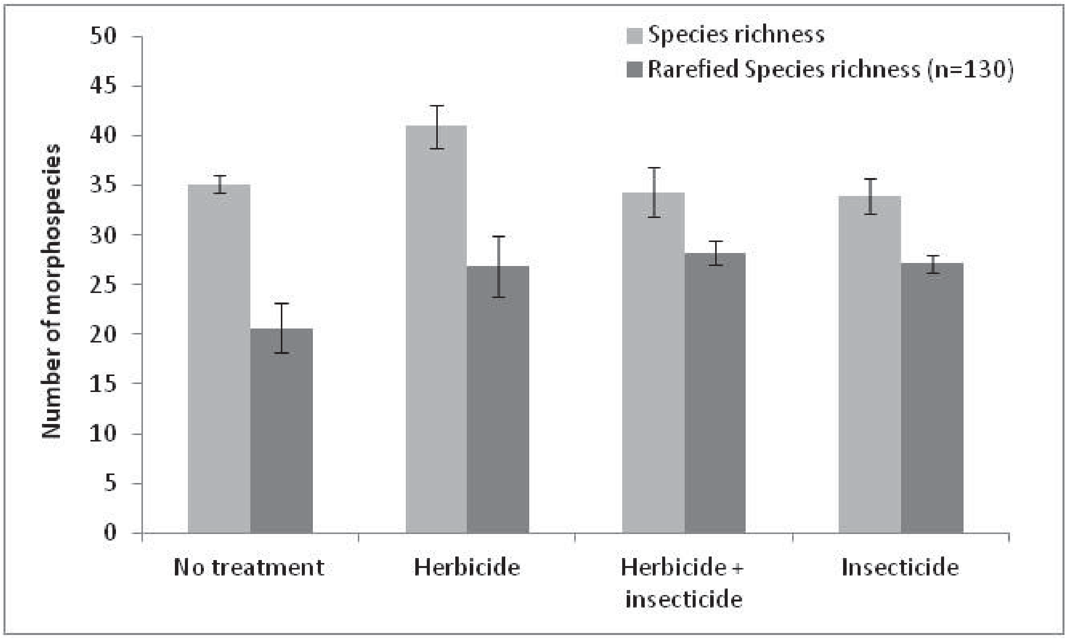

Figure 2.4: Morphospecies richness & rarefied species richness of invertebrates collected in the pitfall component of FIP traps (± 1 SE) in the four experimental treatment regimes at Waiouru 2010/2011.

The invertebrate communities in the pitfall component of the FIP traps were significantly different between treatment regimes (treatment *Pseudo*-$F_{3,15}$= 2.17, p=0.003, block *Pseudo*-$F_{5,15}$ =1.15, p=0.28). There was a significant difference between invertebrate communities in plots with (I and H+I) or without (H and NT) insecticide treatment (*Pseudo*-$F_{1,22}$=3.65 p=0.001), as well as a significant difference between plots with live heather (I) and those without (H+I, H, and NT)(*Pseudo*-$F_{1,22}$=2.00 p=0.047). However, there was no significant difference between plots with (H and H+I) or without (I and NT) herbicide treatment (*Pseudo*-$F_{1,22}$=0.75 p=0.663).

The ordination of invertebrate data sorted to morphospecies (Fig. 2.5) showed that the most pronounced distinction was between plots with and without insecticide, although there was still some overlap. Of the plots that had been treated with insecticide, there was also separation between plots that contained heather (I) and those dominated by native/exotic grasses (H+I).

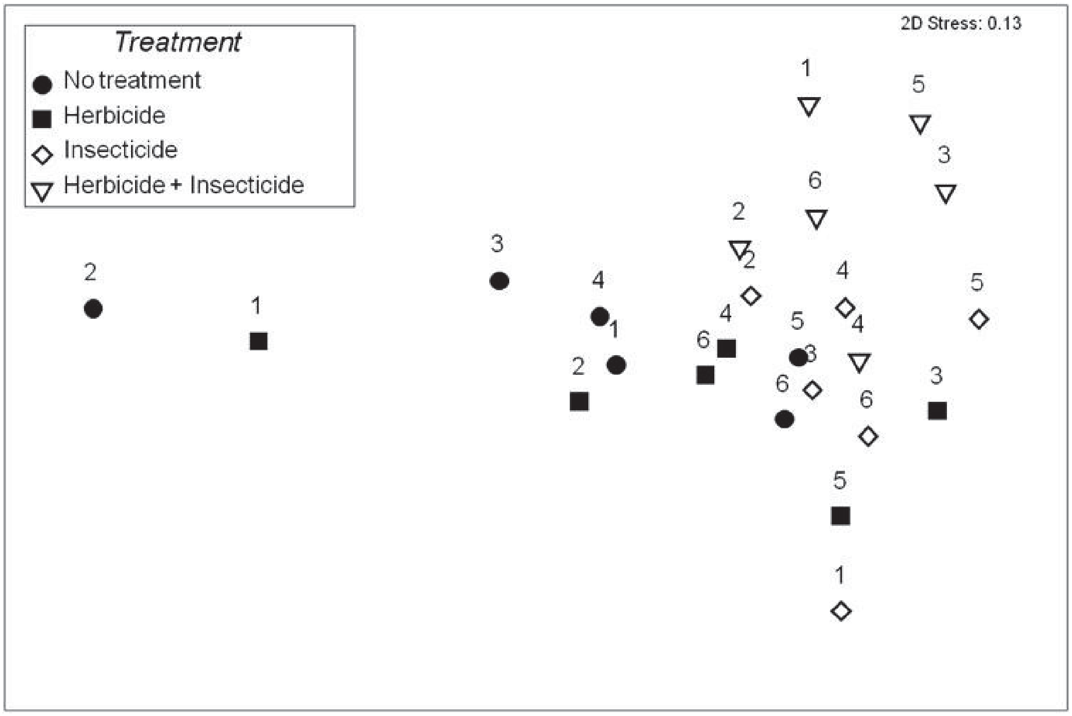

Figure 2.5: NMDS ordination plot of invertebrate data sorted to morphospecies collected in the pitfall component of FIP traps in the four experimental treatment regimes at Waiouru 2010/2011. Numbers above plots indicate experimental block.

Ordination of the data aggregated to order indicated the same pattern (Fig. 2.6). Similarly to the morphospecies data, major differences in community structure were between plots with (I and H+I) or without (H and NT) insecticide treatment (*Pseudo*-$F_{1,22}$=4.31 p=0.001), and plots with (I) or without (H, H+I, and NT) live heather (*Pseudo*-$F_{1,22}$=2.19 p=0.039). There remained no significant difference between plots with (H and H+I) or without (I and NT) herbicide treatment (*Pseudo*-$F_{1,22}$=0.66 p =0.69). Additionally, herbicide had no detectable affect on invertebrate communities (*Pseudo*-$F_{1,10}$=0.43 p=0.69) independent of any insecticide application affect (a comparison of NT and H).

As heather presence could not be separated from the effects of insecticide treatment (plots in the I and H+I treatment regimes), a further two-factor analysis was conducted comparing plots treated with insecticide and those that were not. This analysis indicated that only insecticide treatment (*Pseudo*-$F_{1,21}$=4.00 p=0.001) remained as a significant variable in explaining variance (heather presence *Pseudo*-$F_{1,21}$=1.98 p=0.075). When including only the insecticide treated plots (plots in the I and H+I treatment regimes) in the analysis there was a significant difference between the insecticide only treatment regime (heather present) and the herbicide + insecticide treatment regime (no heather present) (*Pseudo*-$F_{1,10}$=2.83 p=0.004).

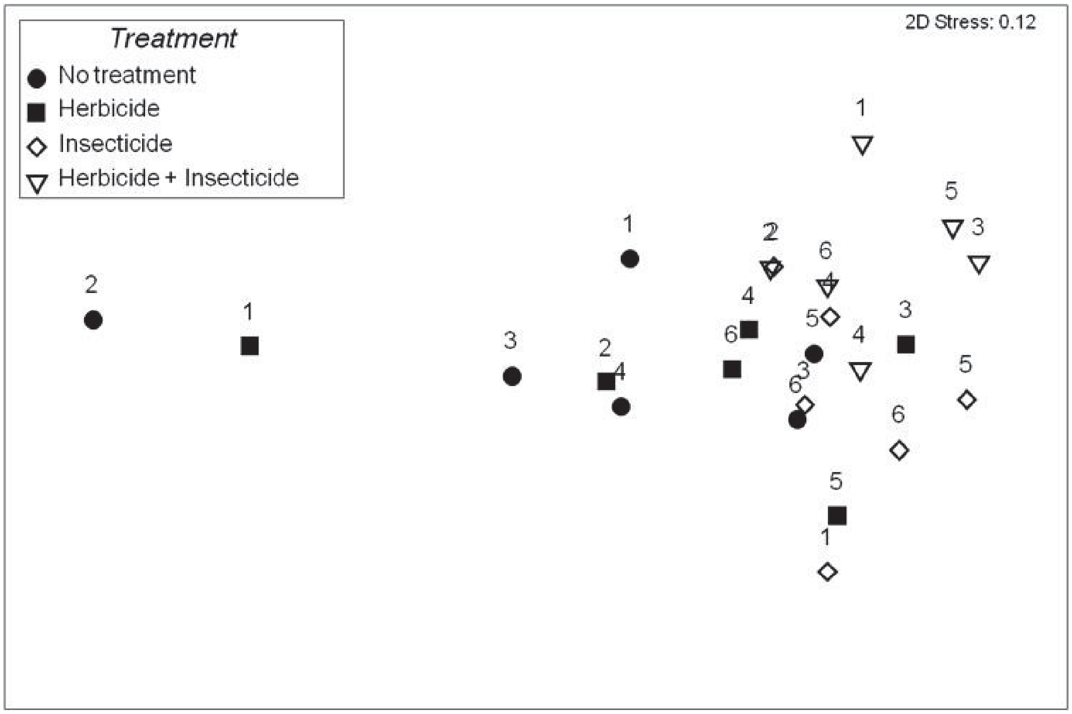

Figure 2.6: NMDS ordination plot of invertebrate data sorted to order collected in the pitfall component of FIP traps in the four experimental treatment regimes at Waiouru 2010/2011. Numbers above plots indicate experimental block.

SIMPER was used to determine the invertebrate orders making the largest contribution to the differences in community composition between the treatment regimes, by comparing no treatment plots to the other treatment regimes (Table 2.2). Collembola had the largest effect on community composition, representing 63%, 50% and 54% contribution to differences between H, H+I and I treatment regimes respectively. Other insect orders that created moderate differences between treatment regimes were Hemiptera (H: 10%, H+I: 14%, and I: 11%) and Trombidiformes (H: 9%, H+I: 12%, and I: 10%). SIMPER analyses were also conducted comparing plots that had been treated with insecticide (I and H+I) and those that had not (NT and H) (Table 2.3) and comparing the insecticide only treatment regime to the herbicide + insecticide treatment regime (Table 2.4). The former analysis again showed Collembola as a major contributor to differences between treatment regimes (49%), with Trombidiformes (13%) and Hemiptera (11%) also having an influence. The comparison of insecticide only treatment regime and herbicide + insecticide treatment regime showed a more even contribution of difference from the insect orders, with Hemiptera (20%), Collembola (17%), Trombidiformes (16%), Thysanoptera (12%) and Areanea (10%) all contributing to at least 10% of the difference between these treatment regimes.

Table 2.2: Average abundance and percentage contribution to Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between no treatment regime and other treatment regimes. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	No treatment	Herbicide only		Herbicide+ Insecticide		Insecticide only		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Collembola	298.50	196.50	63.00	45.83	50.49	34.83	53.70	
Hemiptera	39.00	15.83	9.53	38.33	14.07	17.33	10.74	
Trombidiformes	50.83	54.67	9.09	18.67	11.83	43.00	10.13	
Araneae	34.67	30.00	4.35	14.50	8.68	30.67	4.66	**
Diptera	24.00	28.17	2.94	29.33	4.35	25.83	2.67	
Hymenoptera	14.00	14.33	1.01	10.33	2.48	7.67	2.78	
Thysanoptera	2.00	-	-	-	-	23.33	7.19	***

Table 2.3: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between plots treated with or without insecticide treatment. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Not treated with insecticide (NT & H)	Insecticide treated (HI & I)		
	Avg. abund.	Avg. abund.	Contrib. %	
Collembola	247.5	40.33	49.34	*
Trombidiformes	52.75	30.83	13.19	*
Hemiptera	27.42	27.83	10.97	
Araneae	32.33	22.58	5.90	*
Thysanoptera	2.83	13.08	4.56	*
Diptera	26.08	27.58	4.04	
Hymenoptera	14.17	9.00	3.00	*

Table 2.4. Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between plots treated with insecticide only and those treated with herbicide + insecticide. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Insecticide only	Insecticide + herbicide		
	Avg. abund.	Avg. abund.	Contrib. %	
Hemiptera	17.33	38.33	19.75	
Collembola	34.83	45.83	17.03	
Trombidiformes	43.00	18.67	16.64	
Thysanoptera	22.33	3.83	12.22	**
Araneae	30.67	14.50	10.37	**
Diptera	25.83	29.33	7.11	
Opiliones	6.17	7.00	3.72	
Hymenoptera	7.67	10.33	3.52	

Top flight assemblages

Of the total macroinvertebrates caught only 434 were caught in the top flight component of the FIP traps; 47% of these were Collembola, 14.5% Diptera, 11.5% Hymenoptera, 8.8% Thysanoptera, 7.8% Lepidoptera, 4.4% Araneae, 2.8% Trombidiformes (Acari), 1.8% Hemiptera, with no other order comprising more than 1% of the catch.

More invertebrates were caught in plots subject to the insecticide only treatment regime in comparison to all other treatment regimes (Fig. 2.7). Morphospecies richness showed little difference between the no treatment, herbicide + insecticide and insecticide only treatment regimes with the captures from the herbicide only treatment regime appearing to be higher in richness (Fig. 2.8), although none of these differences between abundance nor richness were significant (p=>0.05).

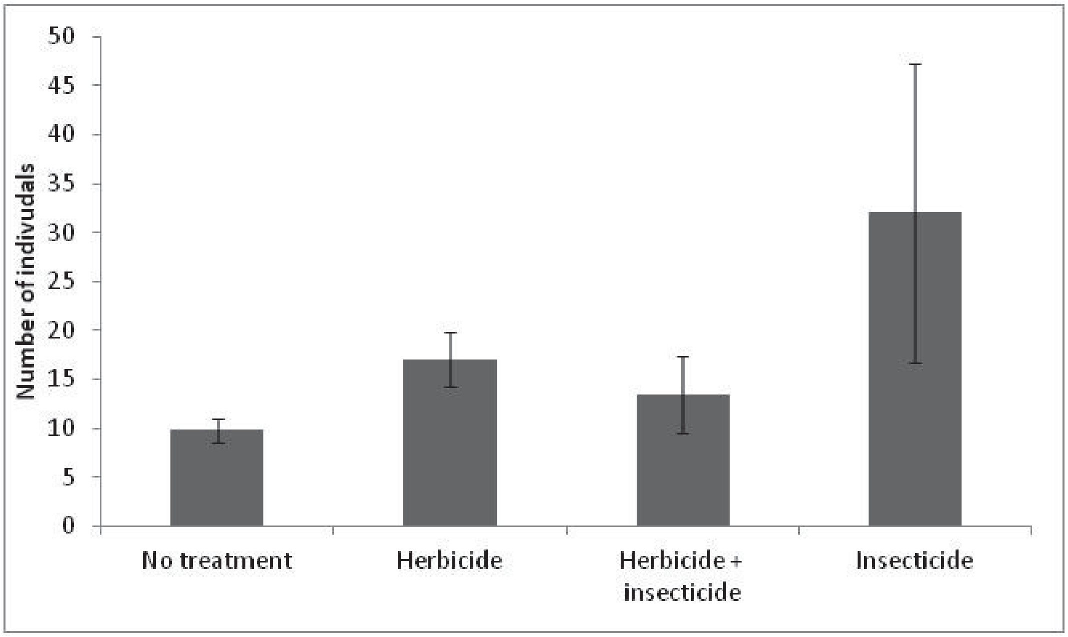

Figure 2.7: Number of individual invertebrates collected in the flight intercept component of FIP traps (± 1 SE) in the four experimental treatment regimes at Waiouru 2010/2011.

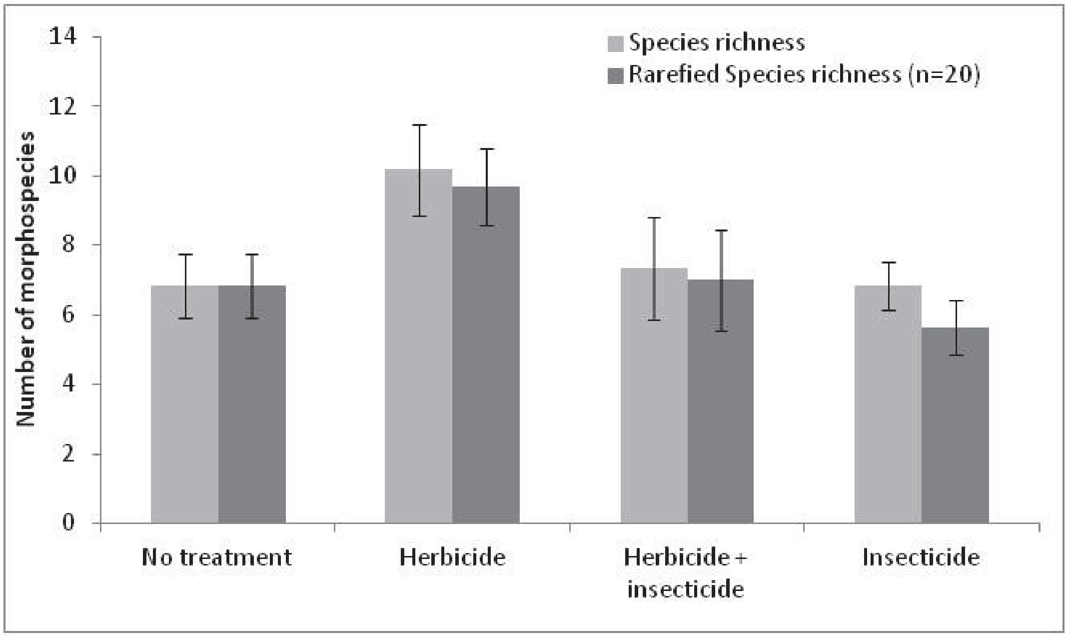

Figure 2.8: Morphospecies richness & rarefied species richness of invertebrates collected in the flight intercept component of FIP traps (± 1 SE) in the four experimental treatment regimes at Waiouru 2010/2011.

The invertebrate communities in the top flight capture component of the FIP traps were not significantly different between treatment regimes or experimental blocks (*Pseudo*-$F_{3,15}$=1.02 p=0.45, Block: *Pseudo*-$F_{5,15}$=1.16 p=0.20). There was no significant difference between invertebrate communities in plots that had been treated with insecticide (I and H+I) and those that had not (H and NT) (*Pseudo*-$F_{1,22}$=1.44 p=0.094). There was no significant difference between plots that had been treated with herbicide (H and H+I) and those that had not (I and NT) (*Pseudo*-$F_{1,22}$=0.57 p=0.94). Invertebrate communities in plots that contained heather (I) were not significantly different to those in plots that did not contain heather (H+I, H, and NT) (*Pseudo*-$F_{1,22}$=1.23 p=0.21).

Ordination of the invertebrate data sorted to morphospecies from the top flight intercept component of the FIP traps showed no grouping or pattern related to any treatment or experimental block variable (Fig. 2.9). Aggregation of data to order had no effect on the outcome of analyses.

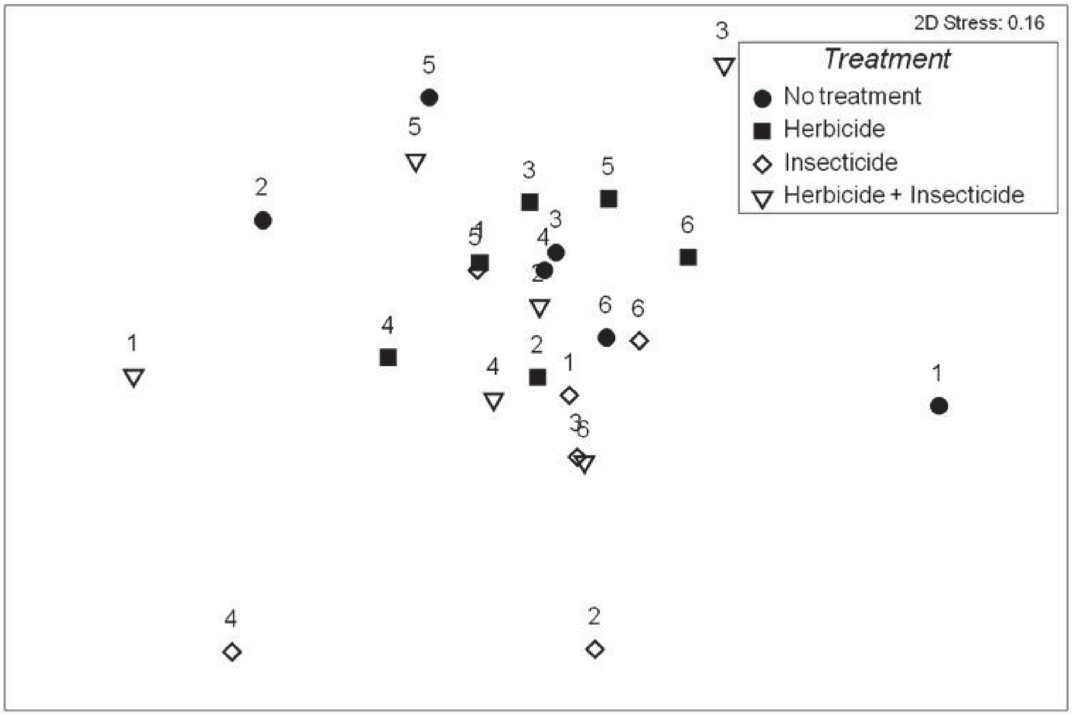

Figure 2.9: NMDS ordination plot of invertebrate data sorted to morphospecies for the top flight intercept component of the FIP traps in the four experimental treatment regimes at Waiouru 2010/2011. Numbers above plots indicate experimental block.

Plot vegetation composition

Vegetation composition within the plots was strongly affected by the treatment applied, with a major division between insecticide only regime plots and all others (Fig. 2.10).

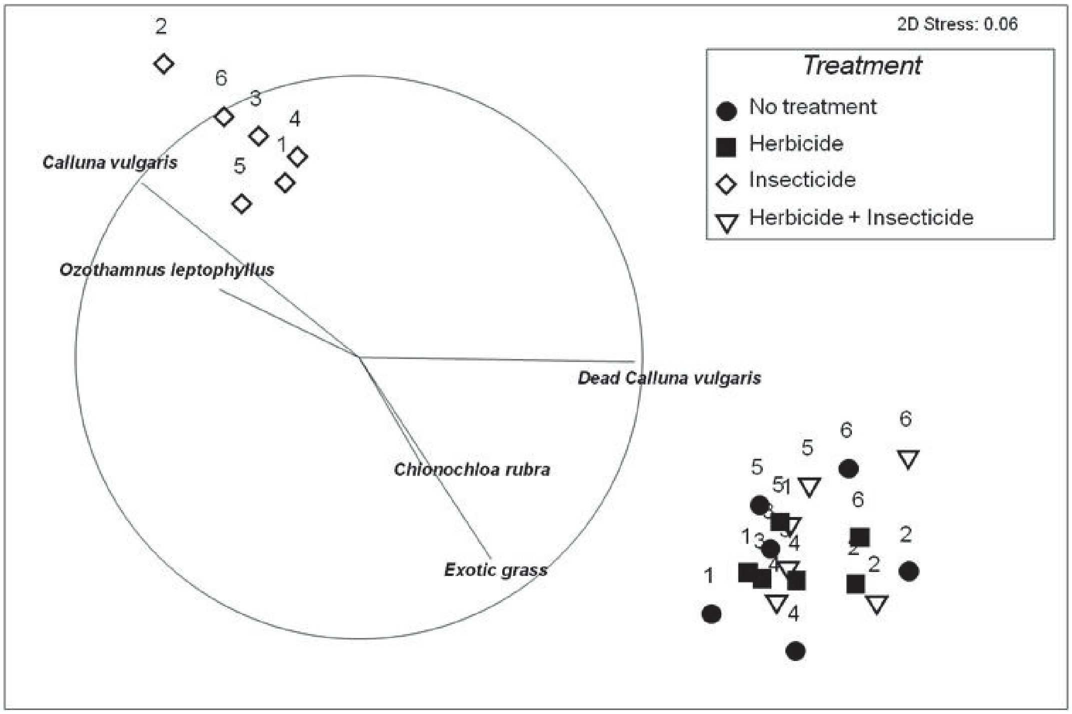

Figure 2.10: NMDS plot of vegetation composition of all plots from the herbicide/insecticide trial in Tongariro 2010/2011.

Herbicide only and herbicide + insecticide treatment regimes were characterised by an absence of dicotyledonous plants (e.g. heather and native shrubs like monoao and sprawling C*oprosma*) (Fig. 2.11b & c). Plots under the no treatment regime likewise had no heather, but contained small amounts of native dicotyledonous shrubs (Fig. 2.11a). Plots subject to the insecticide only treatment regime were dominated by heather, with some native shrubs (Fig. 2.11d).

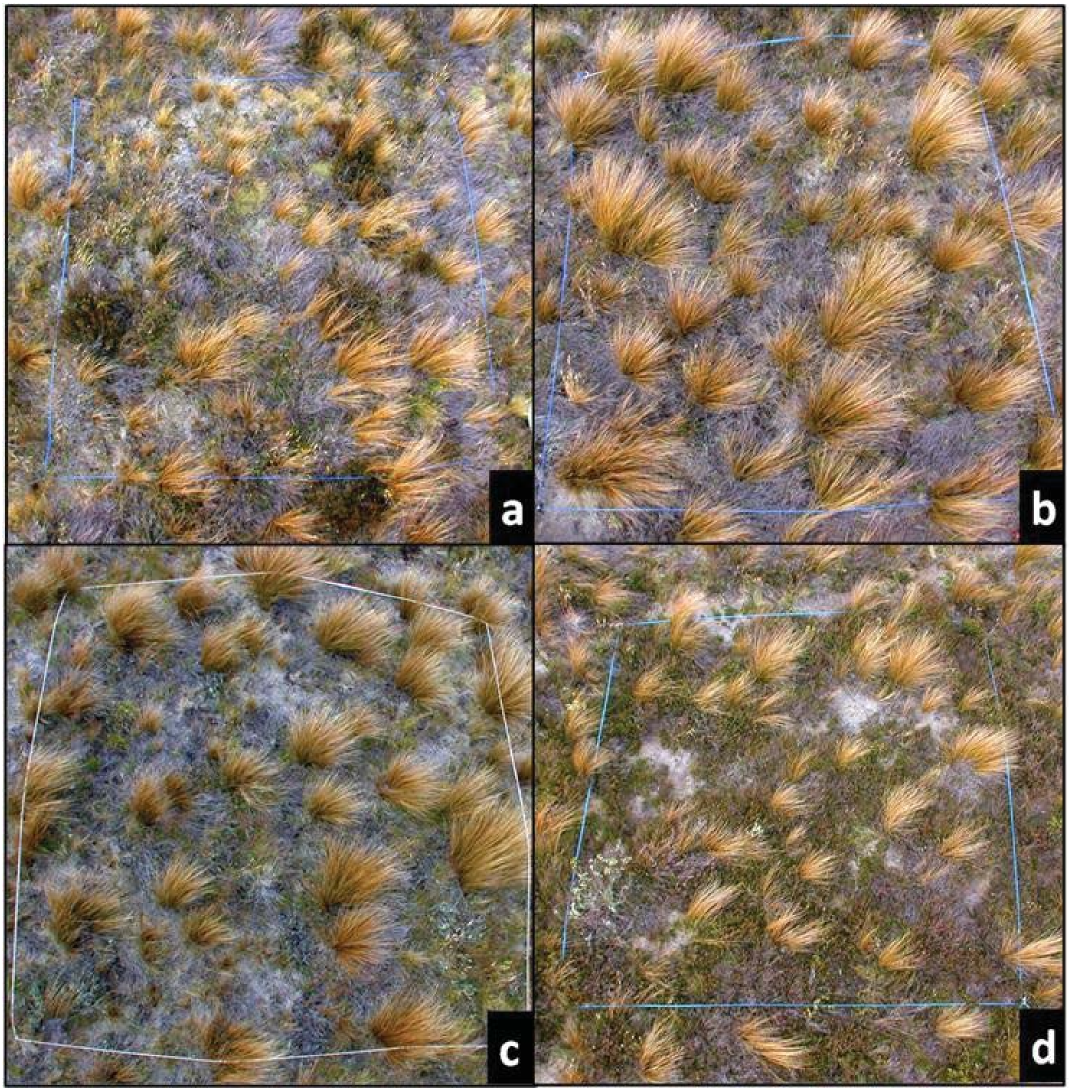

Figure 2.11: Top down view of herbicide/insecticide trial plots in Tongariro 2010/2011 with the four different treatment regimes, showing the different a; no treatment regime, b; herbicide only treatment regime, c; herbicide + insecticide treatment regime, d; insecticide only treatment regime.

Two-factor analysis revealed significantly different vegetation composition between treatment regimes (*Pseudo*-$F_{3,15}$=60.52 p=0.001) and experimental blocks (*Pseudo*-$F_{5,15}$=10.75 p=0.001). No treatment, herbicide only, and herbicide + insecticide treated plots (that contained no live heather) were significantly different from insecticide only treated plots (that contained live heather) (*Pseudo*-$F_{1,22}$=52.67 p=0.001). Two-way analyses showed there was no significant difference between treatment regimes when insecticide only plots were excluded (*Pseudo*-

$F_{2,10}$=2.09 p=0.09, block: *Pseudo*-$F_{5,10}$=7.30 df=5 p=0.001) and only experimental block was significantly different .

SIMPER analysis indicated that the presence of live heather was the major driver of dissimilarity between insecticide only treated plots and all others with a contribution to dissimilarity of 46%, 46.5%, and 45.2% when compared to no treatment, herbicide, and herbicide + insecticide treatments respectively.

Discussion

The major differences between invertebrate communities caught in the pitfall component of the FIP traps were between the treatment regimes that included insecticide application and those that did not. A comparison between the insecticide only (heather present) and herbicide + insecticide (heather absent) treatment regimes was performed to remove the effect of insecticide application confounding the effect of heather presence; this comparison revealed a significant effect of heather, isolated from the effect of insecticide application, on invertebrate communities.

In contrast, the invertebrate communities collected from the top-flight intercept traps did not differ between the treatment regimes, probably as a result of low number of animals collected. Another possible explanation for the lack of difference between the flight intercept traps with different treatment regimes is that they potentially caught invertebrates moving above the vegetation that were not directly influenced by the vegetation present or treatment regime applied.

Vegetation composition in the plots was influenced by both treatment regime and block. The major difference between treatment regimes was the large percentage of live heather in the plots that were treated with the insecticide only regime. When insecticide only treated plots were removed from the analysis treatment regime was no longer a significant factor in explaining vegetation composition. The influence of experimental block remained and while this had the potential to affect the invertebrates caught it had no influence on the invertebrate composition.

The effect of insecticide application on invertebrate communities.

As would be expected, the captures from the treatment regimes that included insecticide treatment (I & H+I) caught fewer invertebrates than those treatment regimes did not. Species richness appeared unaffected.

The specific invertebrate orders affected by insecticide treatment (within I and H+I treatment regimes) were; Collembola, Trombidiformes, Hemiptera, Araneae, Thysanoptera, Diptera, and Hymenoptera. Of these; Collembola, Trombidiformes, Araneae, and Hymenoptera were less abundant in insecticide treated plots, Hemiptera and Diptera were largely unchanged in average abundance (but still contributed to the difference between treatments) and Thysanoptera were more abundant.

The differences in presence and abundance of specific invertebrates orders three months after insecticide treatment of these plots may be the result of different dispersal abilities (As, 1984; Duffield & Aebischer, 1994; Jepson & Thacker, 1990; Sherratt & Jepson, 1993) or resource availability (Jepson & Thacker, 1990). Invertebrates have a wide range of dispersal abilities (Kremen et al., 1993) related to their locomotive abilities as well as their directional perception (Ojala & Huhta, 2001). Among many invertebrate taxa locomotive ability has been shown to positively correlate with body size (Gathmann, Greiler, & Tscharntke, 1994; Juliano, 1983; Ojala & Huhta, 2001) as well as other physical factors such as flighted species having greater dispersal ability than non-flighted species (Gillespie & Roderick, 2002).

In insecticide treated plots (I and H+I) a reduction of Collembola, Trombidiformes, and Araneae may be due to their poor dispersal ability; they are flightless, small bodied organisms. In those orders with a greater or unchanged density within insecticide treated plots wind dispersal (Bengtsson, Hedlund, & Rundgren, 1994; Bonte, Baert, Lens, & Maelfait, 2004; Hutson, 1980; Ojala & Huhta, 2001) or the ability to fly could have affected catch rates or sped colonisation. The intercept panes of the traps could catch windblown or flying invertebrates so it is unknown whether the densities found are related to active invasion or passive wind dispersal. A reduction in Hymenoptera, an invertebrate order made up of mostly winged taxa within the trap captures (pers. obs.), is not explained by limited capacity for flight but small body size could be a contributing factor.

Dispersal ability cannot be considered in isolation from resource availability as these two factors will be linked in the recovery of invertebrate taxa in insecticide treated patches.

Resource availability within the insecticide treated plots will initially be high for herbivores, fungivores (primary consumers), and detritivores following treatment due to the lack of competitors. Gradually abundance of these groups will increase over time due to invasion, resurgence, and colonisation, resulting in an equilibrium between resources and invertebrate abundance (Duffield & Aebischer, 1994; Hutson, 1980). Prey for predatory organisms will also be lower, thus they will follow a similar trend (Van den Berg, Hassan, & Marzuki, 1998). The indiscriminate removal of all invertebrates from plots also gives early invaders a predator free-window in which to colonise (Duffield & Aebischer, 1994). Given this resource availability dichotomy, predators are predicted to exhibit invasion mediated recovery from the edge of treated plots (Duffield & Aebischer, 1994) or a numerical response to initially reduced prey density (Van den Berg et al., 1998) and primary consumers are expected to follow a pattern analogous to the pesticide-induced resurgence problem in agriculture arising from a release from predators (Duffield & Aebischer, 1994).

The orders at the same or very similar densities in insecticide versus non-insecticide treated plots (Hemiptera and Diptera) could be explained by pesticide-induced resurgence through escaping predation as well as an abundance of unutilized resources within the plots, which allowed quick recovery of these orders to an abundance similar to before insecticide treatment. However, given these orders are at similar densities as those found in non-treated plots and contain taxa that are not primary consumers, the observed densities are likely a result of a combination of dispersal ability and resource availability for primary consumers. Thysanoptera density is likely to be high because of the provision of a large pollen resource by heather (Keesing, 1995) in insecticide only treated plots .

Of the invertebrate orders at lower densities within insecticide plots; Araneae are generalist predators (Riechert & Lockley, 1984), Trombidiformes (of which all were Trombidiidae) are all predators (Zhang, 1998), and Hymenopterans are predominantly predacious/parasitoid taxa (LaSalle & Gauld, 1993). These lower densities are consistent with reinvasion mediated recovery from the edge (Duffield & Aebischer, 1994) and/or a numerical response to reduced prey density (Van den Berg et al., 1998). Collembola are not predators but are a mixture of microbivores and detritivores (Bengtsson et al., 1994; Ojala & Huhta, 2001; Ponge, 1991) that are not likely to be limited by resources, but are more likely restricted by their limited dispersal ability.

It is also possible that some invertebrate taxa, trophic level, and life stages respond differentially to insecticide (Dennett, Bernhardt, & Meisch, 2003; Lawler, Dritz, Christiansen, &

Cornel, 2007) as well as insecticide efficacy being affected by vegetation structure and spray distribution (Hoy, Head, & Hall, 1998); this may have had an unknown influence on the results presented.

The effect of heather control on invertebrate communities.

While the presence of heather may have a significant effect on invertebrate communities its influence was confounded by the use of insecticide, as live heather was only found within plots of the insecticide only regime. However, there was still a significant difference between invertebrate communities in plots within the insecticide only (insecticide treated, heather present) regime and plots under the insecticide + herbicide treatment regime (insecticide treated, heather absent).

The difference between these two treatment regimes allows us to explore the effect of heather control on invertebrate recolonisation into either heather dominated vegetation or tussock/exotic grass dominated vegetation over the 3 month period between the most recent insecticide application and the beginning of trapping. The type of control (heather beetle or herbicide) is largely irrelevant for this comparison as there was no significant difference between the invertebrate communities found in herbicide only treated plots (dicotyledonous plants absent) and no-treatment plots (dicotyledonous plants present, heather controlled by the heather beetle). Thus the absence of dicotyledonous plants in herbicide + insecticide treated plots presents a realistic comparison with heather dominated plots when compared to no-treatment plots and the larger surrounding area which has had heather killed by the heather beetle.

The invertebrate orders identified as being the most significant drivers of dissimilarity between heather and tussock/ exotic grass dominated vegetation within this study were: Hemiptera, Collembola, Trombidiformes, Thysanoptera, Araneae, Diptera, Opiliones, and Hymenoptera. Of these orders the average abundance of; Hemiptera, Collembola, Diptera ,and Hymenoptera were less abundant plots subjected to the insecticide only treatment regime, Opiliones were largely unchanged and Trombidiformes, Thysanoptera, and Araneae were more abundant.

Keesing's (1995) also found heather dominated plots had higher abundances of Araneae. Keesing (1995) found that spider abundance was higher in heather during summer due to an increase in orb-web spiders caught during sweep netting. In contrast, in this study pitfall trapping collected largely hunting spiders and the flight interception trap caught ballooning juveniles rather than orb-web spiders. This increase in largely non-web spinners may have an analogous explanation to Keesing's findings in that the higher habitat complexity found within heather invaded areas provides resources than benefit both web-spinning and hunting spiders (Halaj, Ross, & Moldenke, 2000). Web-spinning spiders prefer a structurally complex habitat for web-attachment sites (Mcnett & Rypstra, 2000), while non-web spinning spiders require structurally complex habitats as they provide suitable sites to construct retreats used for moulting, egg laying/brooding, and predator avoidance (Halaj et al., 2000), although this effect may be weaker for hunting spiders than web-spinners (Buddle, 2001).

Trombidiformes (all Trombidiidae), another predacious group, were also found at much higher densities within heather dominated plots and were a major contributor to dissimilarity between vegetation types. This group was omitted in Keesing's thesis (1995) but still fits the general observation of greater predator numbers found in heather. The reasons for this increase of Trombidiid mites are unknown; their widely varied terrestrial habitat requirements, life histories, and environmental requirements (Zhang, 1998) mean that further research and/or taxonomic resolution would be required to identify the factors that cause greatly increased Trombidiid mite density within heather dominated habitats.

Thysanoptera were found at far greater densities within heather dominated plots and were a moderate driver in the dissimilarity between vegetation types, a finding congruent with Keesing's (1995) findings. This is a consequence of the greatly increased resources of pollen and nectar provided during heather's prolific flowering period in summer (Keesing, 1995). This may also explain the high abundance of invertebrates caught in the flight intercept component of the FIP traps in the insecticide only treatment regime as the flowers attract more flying invertebrates.

The largely herbivorous order Hemiptera were at markedly lower densities within heather dominated plots and had a major contribution to the dissimilarity between these plots and those dominated by tussock/ exotic grass. This finding was consistent with Keesing's general observations, namely that invasion of an exotic plant outcompetes native vegetation and thus native invertebrates' food sources.

Collembola were at lower densities within heather dominated plots; the reason for this is unknown but may have an analogous explanation to the decrease of herbivores. Detritus, fungi, and other microbes within heather dominated plots may be less favoured by/suitable for native collembolans. The large amount of dead and decomposing heather within the herbicide + insecticide treated plots may also provide a food source for collembolans. Alternatively, it may simply be that Collembola are slow to reinvade the plot, or heather may change the microclimate or habitat structure (Keesing, 1995; Rogers, 1996).

Diptera and Hymenoptera were also found to be at slightly lower densities in heather dominated plots. The cause of this lower density may be as above for Hemiptera and Collembola or, in the case of predators or parasitoids within these orders, as a result of the reduction in native prey items such as Hemiptera.

The insect communities within heather are at odds with the expected increased abundance of primary consumers as a result of a predator free window (Duffield & Aebischer, 1994) and a lower density of predators due to initially diminished prey availability (Van den Berg et al., 1998) after insecticide treatment. Instead, the invertebrate communities found within heather dominated plots are largely opposite to that expected; this can be explained by the dichotomy of resource suitability for native invertebrate herbivores and predators. Heather as a novel food source is unsuitable for native phytophagous insects but its structural complexity provides valuable resources for Araneae which are generalist predators (Keesing, 1995). This deviation from the expected outcome of insecticide application further highlights the potential impacts of an invasion exotic weed on the composition of native invertebrate communities.

Conclusion

This study found that with the control of heather there are broad changes in invertebrate communities, resulting in a move to more closely resemble those found within native non-invaded communities. These differences were detected only three months after insecticide treatment of the 5 x 5 m plots but we predict the same to occur over a large scale as the heather beetle spreads and continues to damage heather. The effect of insecticide treatment on certain invertebrate taxa was more pronounced than others with some responding positively and others negatively to the treatment. These differences were likely to be explained by variations in dispersal ability and resource requirements between these taxa; this raises uncertainties as to whether observed differences are part way through a transition or are longer term differences in stable invertebrate communities. The effect of heather was isolated in a comparison between the herbicide + insecticide (heather absent) and insecticide only treatment (heather present) regimes. Heather was found to cause a deviation from the expected invertebrate community after insecticide treatment by containing a lower density of primary consumers. Heather presence, being a novel and unsuitable host for many native phytophagous insects, was the most likely explanation and further highlights the differing effects an invasive exotic weed can have on the composition of invertebrate communities.

Chapter Three

Invasive plants reduce endemic lizard abundance: effects and implications of weed control

Figure 3.0: Common skink intrigued by the reflections off a camera lens.

Invasive plants reduce endemic lizard abundance: effects and implications of weed control.

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Abstract

Following its introduction to New Zealand, heather (*Calluna vulgaris*) has become an aggressive invasive weed in the central North Island, particularly within the native tussock grasslands of Tongariro National Park. A biological control program, using the foliage feeding heather beetle (*Lochmaea suturalis*) was initiated in 1992, with the first releases in 1996. We had been investigating the effects on invertebrate communities of the subsequent reduction in heather density over the 2010/2011 summer. This research identified an unexpected deleterious effect of heather on the native common skink (*Oligosoma nigriplantare polychroma*); in replicated blocks where heather density was experimentally manipulated we found skinks were almost completely absent from areas of high heather density. Heather may exclude skinks by shading basking sites, by posing a barrier to foraging activities, or by reducing their ability to avoid predators. This finding makes it clear that the effects of invasive weeds extend beyond the obvious, direct impacts we can easily observe.

Introduction

Invasive weeds pose a significant risk to the native ecosystems they invade and are one of the greatest threats to conservation in New Zealand (Williams & West, 2000) and internationally (Randall, 1996). The most visible effect of environmental weeds is the displacement of native plant communities and their associated fauna (Chapman & Bannister, 1990; Rogers, 1996; Williams & West, 2000). However, invasive weeds also have many indirect effects that may not be so obvious, such as altering habitat structure, suitability for native fauna, disturbance regimes, and affecting ecosystem functioning (Buckley, Bolker, & Rees, 2007; Williams & West, 2000).

Invasive weeds can affect both invertebrates and vertebrates in two principal ways, by either changes in resource availability (Keesing, 1995; Martin & Murray, 2011) and/or habitat suitability (Valentine, 2006; Valentine et al., 2007; Williams & West, 2000). A major effect of invasive weeds on invertebrates is the influx and often dominance of a novel plant resource unsuitable for many native herbivores (Hanula & Horn, 2011; Keesing, 1995; Martin & Murray, 2011). Not only can this decrease the abundance of herbivores, but may also affect the predator taxa which rely on these species (Valentine, 2006). Non-food resources can be affected, such as increases in habitat complexity providing increased web sites for spiders (Keesing, 1995), reduced availability of spatial niches such as basking sites (Martin & Murray, 2011), and thermally suitable foraging areas for lizards (Valentine et al., 2007). The effects of weed invasions are highly varied within both invertebrates and vertebrates (Martin & Murray, 2011) and may result in increases or decreases in density or diversity depending on taxa (Florens et al., 2010; Garden et al., 2007; Hanula & Horn, 2011; Keesing, 1995; Standish et al., 2002; Valentine, 2006) but are generally negative (Valentine et al., 2007).

Heather (*Calluna vulgaris*) is an invasive plant which has been introduced to the Central Plateau region of the North Island of New Zealand (Chapman & Bannister, 1990; Syrett, 1990; Syrett et al., 2000). It continues to spread within this area but is also expanding beyond this range (Chapman & Bannister, 1990). The first record of it being established in the wild was in 1910 (Syrett, 1990; Syrett et al., 2000), although it was probably first introduced in the 1860's (Syrett, 1990). Heather invades native plant communities and outcompetes native plants resulting in a decrease in native plant abundance and diversity as well as altering the function, structure, and successional processes in these alpine tussock ecosystems (Keesing, 1995; Rogers, 1996). Heather also negatively impacts recreational activities, military training, and invades pasture (Syrett et al., 2000). However, heather's effect on native fauna is unclear and only Keesing's (1995) unpublished study identified the impact of heather on native invertebrate communities. He found that invertebrate communities within heather invaded areas had a greater density of predators (particularly web-spinning spiders), a greater density of pollen feeders (specifically Thysanoptera), and a reduced density of herbivores (particularly Hemiptera) during summer when compared to more pristine habitats.

Attempts to control heather have included hand pulling (Syrett, 1990) and herbicide (Rogers, 1996; Syrett, 1990), but these attempts have failed to control the spread of heather (Syrett et al., 2000). Given the extent of heather's invasion conventional herbicide control is no longer viable to control the spread of heather (Peterson et al., 2011; Rogers, 1996). A heather management plan was initiated by the Department of Conservation in 1990 that included the use of the heather beetle (*Lochmaea suturalis,* Chrysomelidae) as a biological control (biocontrol) agent (Syrett et al., 2000).

The heather beetle was introduced to New Zealand in 1992 and was released for the first time in the central North Island in 1996 after several years of quarantine and testing (Fowler et al., 2000; Peterson et al., 2004; Syrett et al., 2000). Initial success was poor with only one release establishing (Peterson et al., 2004). This was probably the result of several factors including low nitrogen within the host plant (Fowler et al., 2000; Peterson et al., 2011), poor climate matching, and a genetic bottleneck (Peterson et al., 2011). Subsequent releases have led to sustained populations in the central North Island (Peterson et al., 2011).

While investigating the effects of the subsequent reduction in heather density from biocontrol or herbicide application on invertebrate communities in a herbicide-insecticide experimental trial we were also able to observe the effect of the experimental removal of heather plants. It was during this research we revealed an unexpected effect of heather invasion on the endemic common skink (*Oligosoma nigriplantare polychroma*). The aim of this paper was to evaluate this effect and explore the possible factors that may cause it.

Species overview

Common skinks are small lizards (maximum snout-vent-length = 77mm) endemic to New Zealand and are diurnal heliotherms (Lettink, O'Donnell, & Hoare, 2011; Spencer, Thomas, Mason, & Dugdale, 1998). Their colouration is variable with some populations exhibiting speckled patterning and others being striped (Freeman, 1997) (Fig. 3.1). Preferred habitats for this species are dry and open with low vegetation or suitable refugia such as rocks and logs for cover (Lettink et al., 2011). The common skink is an active forager consuming a wide variety of prey of which insects and arachnids are major components (Freeman, 1997). They are also known to consume fleshy fruits of divaricating shrubs when available (Lettink et al., 2011).

Figure 3.1: Common skink found near the study area showing the distinctively striped body pattern.

Study area

The study was undertaken at one heather beetle outbreak site within the Waiouru Military Training Area (WMTA) bordering Tongariro National Park in the North Island of New Zealand. The site (S39°22' E 175°43') was located at the southern end of the Rangipo desert, approximately 11 km north of Waiouru (Fig. 3.2).

Five hundred heather beetles were released at this site during February 2001 but visible beetle feeding damage to heather was not obvious until the austral summer 2006/2007, with 0.0025 ha of heather killed. The area of feeding damage had increased every season since and by March 2011 approximately 80 ha of heather had been badly damaged or killed (Peterson et al., 2011).

Vegetation at the site had extensive heather growing amongst it until the heather beetle outbreak. As a result of this outbreak it is now largely devoid of live heather and comprises a mixed tussock-shrubland and exotic grass/herb vegetation. Native vegetation includes: red tussock (*Chionochloa rubra*), monoao (*Dracophylum subulatum*), sprawling coprosma (*Coprosma cheesmanii*), cottonwood (*Ozothamnus leptophyllus*), woolly moss (*Racomitrium* sp.), and blue tussock (*Poa colensoi*). Exotic vegetation other than heather is also present at the site with browntop (*Agrostis capillaris*) and mouse-ear hawkweed (*Pilosella officinarum*) being the most common.

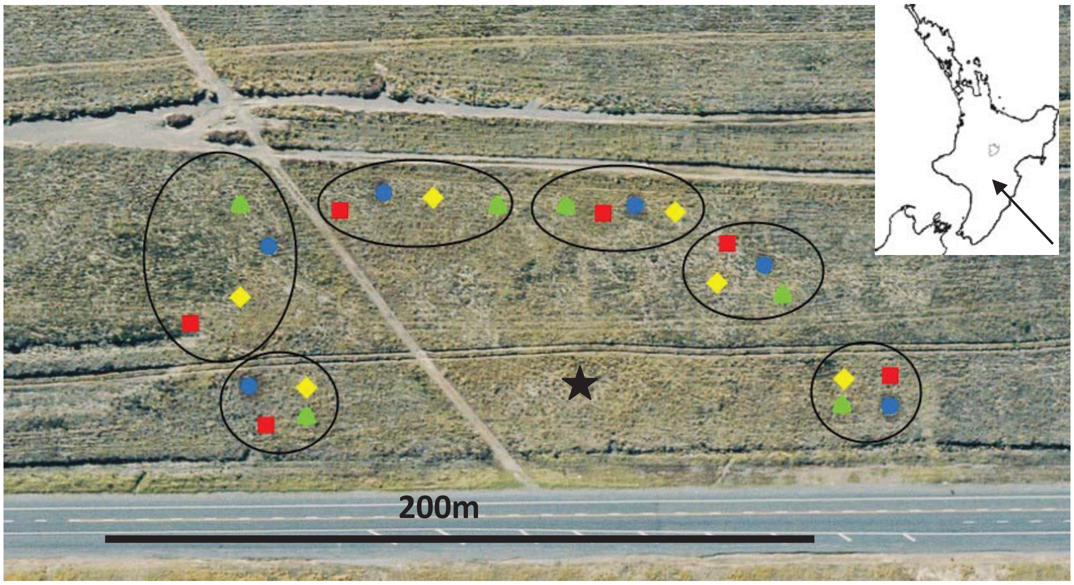

Figure 3.2: Aerial photo of the WMTA study site. Coloured dots indicate treatment type ●=Insecticide ▲ =Herbicide + Insecticide ◆=Herbicide ■=No treatment. Black circles indicate experimental replication blocks. Star indicates heather beetle release point.

Method

Herbicide and insecticide trial

The herbicide/insecticide experiment was initiated in November 2007 and comprised of a randomised block design of 5 x 5 m plots, with 1 m wide treated buffer zones around each plot (total size of treated area 7 x 7 m). All treatments were applied before beetle invasion from the central release point. Four plots made up each experimental block (Fig. 3.2) and were subject to the following treatment regimes: insecticide (I) treatment only (removal of heather beetle and thus protection of heather), herbicide (H) treatment only (removal of all dicotyledonous plants, including heather), herbicide + insecticide (H+I) treatment (removal of all dicotyledonous plant including heather, plus removal of heather beetle), or no treatment (NT) (heather beetle feeding only). The block design was replicated six times (six plots of each treatment, 24 plots total). Insecticide and herbicide were applied to a schedule (Table 3.1) through the austral spring and summer until October 2010. Monthly sampling to verify insecticide effectiveness was undertaken during beetle feeding front movement through the area by using a combination of sweep netting for adults and larvae as well as assessing feeding damage from vegetation samples. While this sampling detected some minor incursions of heather beetle into the insecticide treated plots, the efficacy of insecticide treatment remained sufficient to protect heather from feeding damage. Initially, the insecticide plots were sprayed with the organophosphate diazinon but after the first application in November 2007 the insecticide treatment was switched to the synthetic pyrethroid Karate zeon (1ml/15L) + Vapour guard (0.3 ml/L) for greater efficacy. The herbicide used was 2,4-D ester (Pasture Kleen®) (6.5 ml/L). All chemical was sprayed to run off.

Experimental plots were set outside the reach of the heather beetle feeding front in 2007 and by 2009 beetles spread had through the plots, with plots unprotected by insecticide showing heather damage. Herbicide treatment was carried out once a year from the set-up date for two years, while insecticide treatments were carried out approximately once per month when the heather beetle feeding front was moving through the plots, then once a year after the heather beetle feeding front had progressed beyond the plots or when heather beetle invasion into plots was detected. The insecticide/herbicide treatment timeline since the trial began is outlined in Table 3.1.

Table 3.1: Treatment timeline for insecticide/herbicide trial plots between 2007 and 2010. Numbers indicate the day of the month the treatment was applied or traps were put out/taken in.

	2007		2008								2009					2010			2011	
	Nov	Dec	Jan	Feb	Mar	~	Sep	Oct	Nov	Dec	Jan	Feb	~	Sep	Dec	~	Oct	~	Feb	Mar
Insecticide application	30		11	14	6&27		18	20	20	11	15	18		17			27			
Herbicide application		13								11					22					
Trapping period																			3 Start	3 Finish

Trapping in plots was carried out by placing a flight intercept pitfall (FIP) trap (Fig. 3.3) directly in the middle of each of the 24 5 x 5 m plots. These traps were set up 3 February 2011 then collected and removed one month later. The FIP trap used in all of the insect monitoring for this project was a modified design of that described by Stevens, McCartney, & Stringer (2007).

The modification made to this design was a funnel and catching assembly at the top in place of a flat roof (Fig. 3.3). This top assembly was constructed using plumbing connections and two clear plastic jars (11 x 6 x 6 cm), the lower of which was partially filled with approximately 100 ml of ethylene glycol to catch and preserve specimens. Collection methodology also followed Stevens et al. (2007).

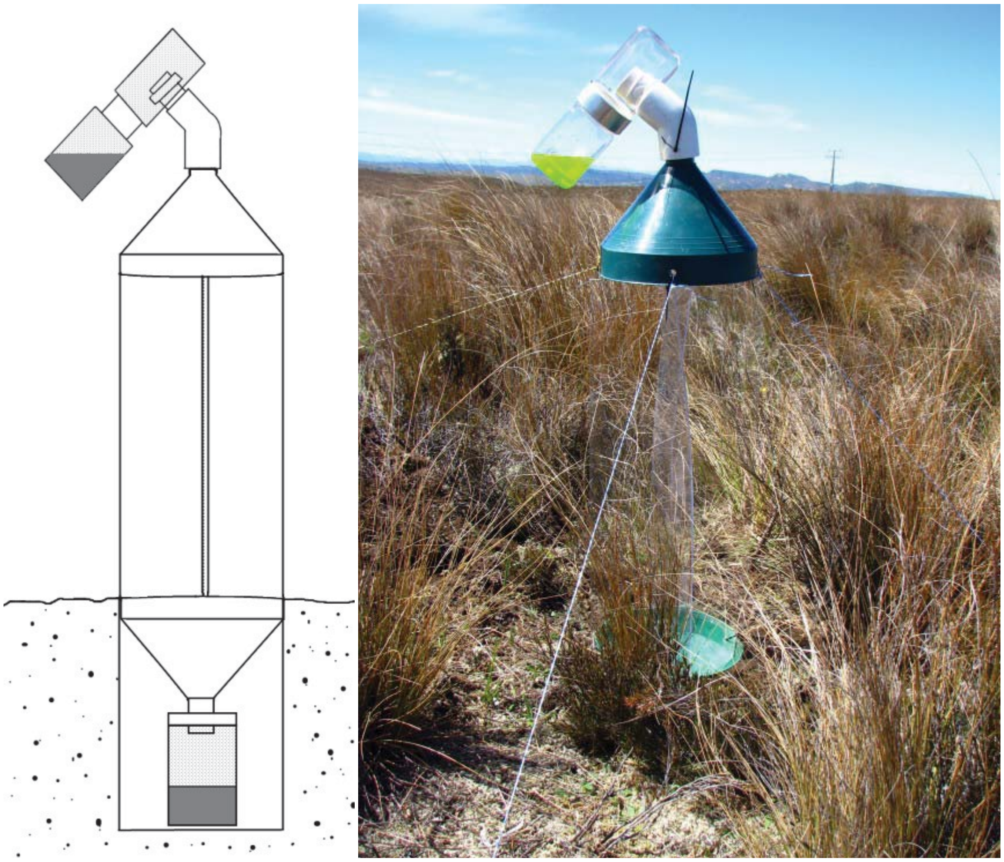

Figure 3.3: Modified flight-intercept-pitfall trap design used for invertebrate trapping at the WMTA site.

Trap area vegetation

Vegetation in each plot was characterised by taking top down photos of a 5 x 5 m area around the trap, using a pole mounted camera to take photos from c.a. 7 m above ground level. The photos were processed using the Digital Sampling Method computer program (Gillingham, 2003) to determine vegetation coverage for each plant species present. As some plots had large areas of dead heather this was included as a vegetation type. Exotic grasses and herbs were considered one category. GPS position, altitude, aspect, and a description of vegetation composition and ground cover were also recorded.

Sample processing

Skinks accidentally caught and killed in pitfall traps were placed in 70% ethyl alcohol. Invertebrate samples taken from the herbicide trial plots were filtered through a 250 µm sieve, sorted, and counted at the morphospecies level. Spiders (order Araneae) were grouped as Mygalomorpha or Araneomorphae because of difficulty in assigning juveniles to morphospecies. If a morphospecies was particularly abundant in a sample a subsample for that one taxon was counted and scaled accordingly. A photo of each morphospecies was taken to aid in identification of further specimens. Collembola, Thysanoptera and Acari were not included in this analysis because they were considered unsuitable as prey items for skinks.

Data Analysis

Two-way Friedman's nonparametric analysis of variances (ANOVA) was used to test for differences in skink captures, invertebrate abundance, and invertebrate species richness between treatments and blocks. To separate the effect of heather presence a one-way ANOVA analysis was used to compare no treatment (NT), herbicide (H), and herbicide + insecticide (H+I) treatment with the insecticide (I) treatment plots.

These analyses were conducted with Statistix (Statistix 9 Analytical Software, USA). Effect sizes when listed are Cohen *d* statistic, calculated using the pooled within group standard deviation, as outlined in Arthur, Bennett, & Huffcutt (2001).

Vegetation and invertebrate prey community composition was analysed using non-metric multidimensional scaling (NMDS) with Bray-Curtis distance measure and no transformation to explore relationships between treatments and blocks. Vegetation composition was analysed using two-factor Permutation Multivariate Analysis of Variance (PERMANOVA) using Primer and PERMANOVA+ (PRIMER 6 software; PRIMER-E Ltd, Plymouth, UK) to test the significance of differences between treatments and experimental blocks. To separate the effect of heather presence a single-factor PERMANOVA analysis was used to compare no treatment (NT), herbicide (H), and herbicide + insecticide (H+I) treatment plots grouped together versus insecticide (I) treatment for both invertebrate prey community and vegetation composition. Invertebrate composition was also analysed using single-factor PERMANOVA to determine whether there was a difference between plots that caught skinks and those that had not. Similarity Percentage (SIMPER) was used to assess which taxa were responsible for the observed differences.

Results

Skink captures

Twenty common skinks were caught in the 24 traps (Fig. 3.4). There was no significant difference between all four treatment regimes (F_3=4.47 *p*=0.22, block: F_5=2.04 *p*=0.84). Comparing plots that contained heather (I treatment regime) and plots that no longer contained live heather (NT, H, and H+I treatment regimes) revealed a significant difference in skink captures (F_1=4.96 *p*= 0.04). This difference represents a large effect size (*d*=1.29) with an average of 1.06 (SE= 0.22) skinks per trap month^{-1} in plots with no heather and 0.17 (SE= 0.17) skinks per trap month^{-1} in plots with heather present.

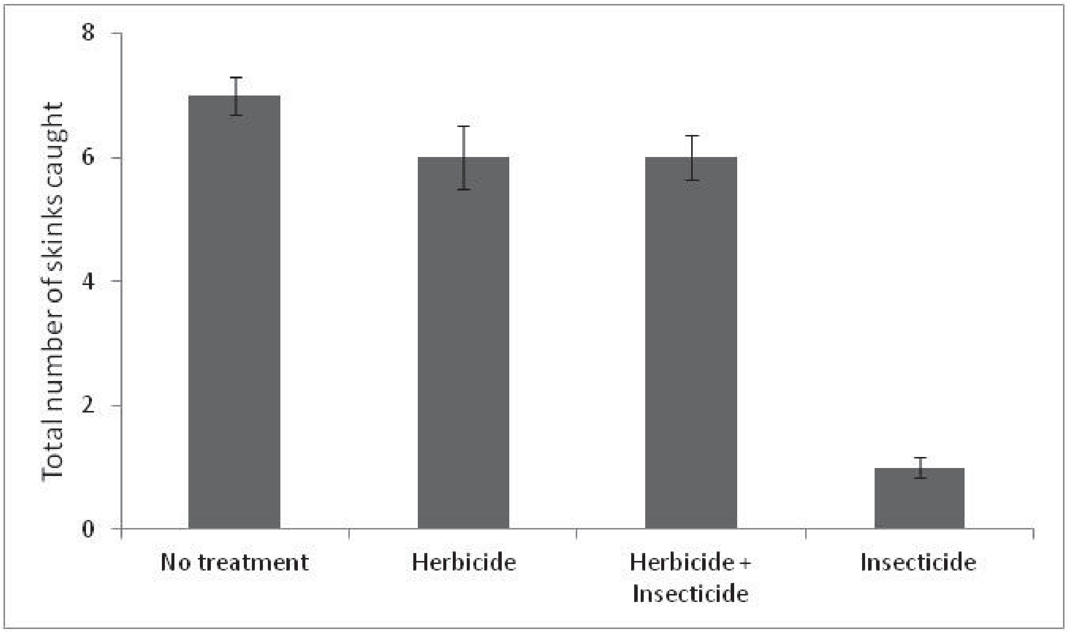

Figure 3.4: Total skink captures (± 1 SE) in each treatment type during sampling of herbicide-insecticide trial plots from 3rd February to 3rd March 2011.

Plot vegetation composition

Vegetation composition within the plots was strongly affected by the applied treatment regime, with the major division between the insecticide only treated plots and all others (Fig. 3.5).

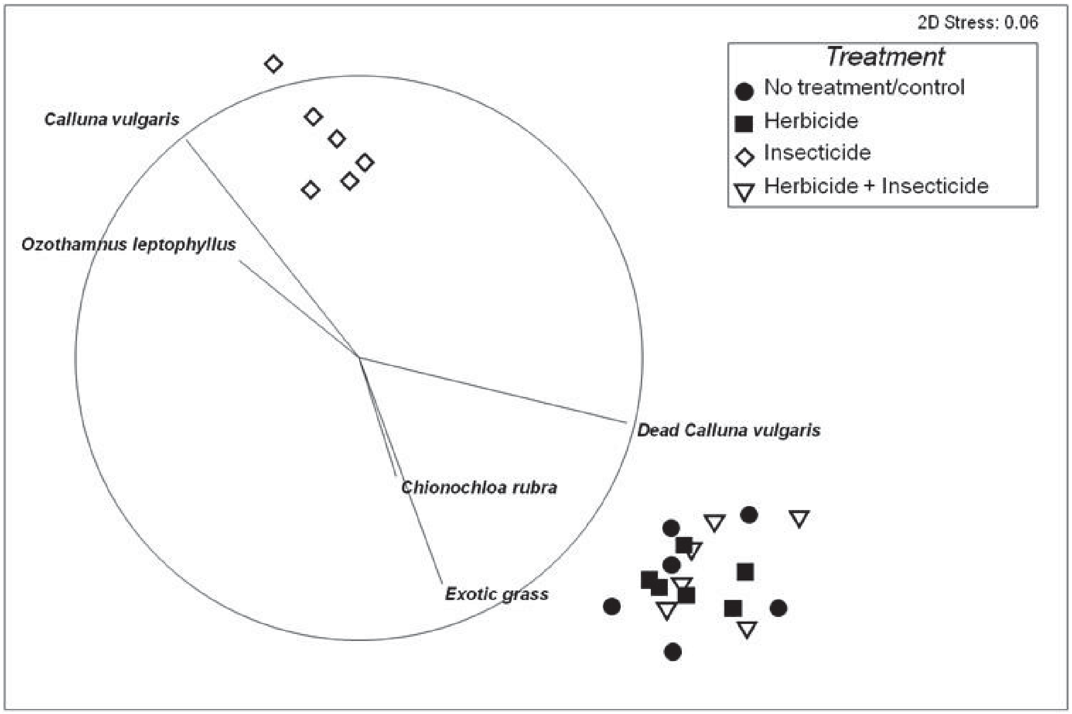

Figure 3.5: NMDS plot of vegetation composition of all plots from the herbicide/insecticide trial in Tongariro 2010/2011.

Herbicide only and herbicide + insecticide treatment regimes were characterised by an absence of dicotyledonous plants (e.g., heather and native shrubs like monoao and sprawling C*oprosma*) (Fig. 3.6b & c). Plots under the no treatment regime likewise had no heather, but contained small amounts of native dicotyledonous shrubs (Fig 3.6a). Plots subject to the insecticide only treatment regime were dominated by heather, with some native shrubs (Fig 3.6d).

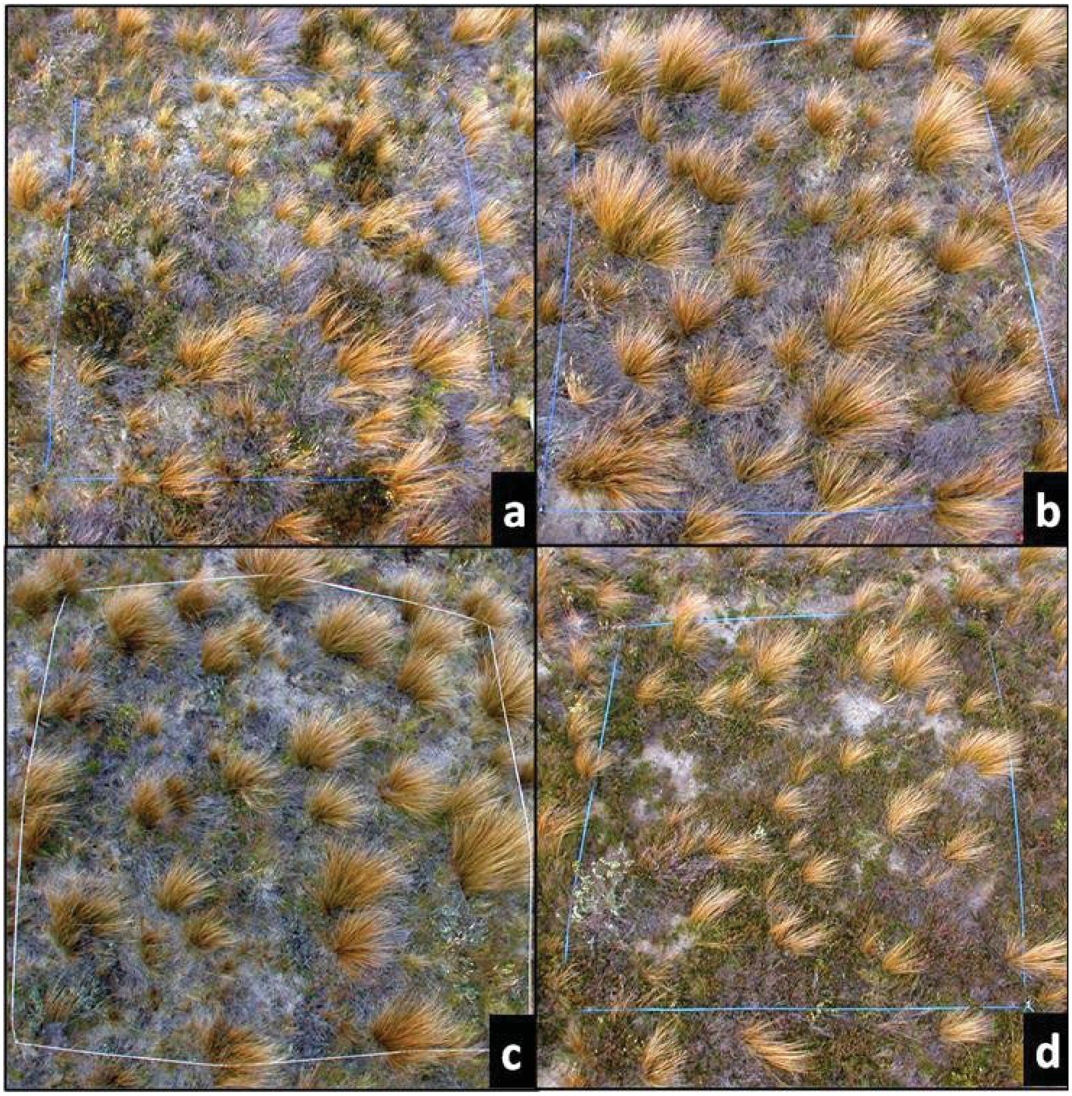

Figure 3.6: Top down view of herbicide/insecticide trial plots in Tongariro 2010/2011 with the four different treatment regimes, showing the different a; no treatment regime, b; herbicide only treatment regime, c; herbicide + insecticide treatment regime, d; insecticide only treatment regime.

Two-factor analysis revealed significantly different vegetation composition between treatment regimes (*Pseudo*-$F_{3,15}$=60.52 p=0.001) and experimental blocks (*Pseudo*-$F_{5,15}$=10.75 p=0.001). No treatment, herbicide only, and herbicide + insecticide treated plots (that contained no live heather) were significantly different from insecticide only treated plots (that contained live heather) (*Pseudo*-$F_{1,22}$=52.67 p=0.001). Two-way analyses showed there was no significant difference between treatment regime when insecticide only plots were excluded and only experimental block was significantly different (*Pseudo*-$F_{2,10}$=2.09 p=0.09, block: *Pseudo*-$F_{5,10}$=7.30 df=5 p=0.001).

SIMPER analysis indicates that the presence of live heather was the major driver of dissimilarity between insecticide treated plots and all others with a contribution to dissimilarity of 46%, 46.5%, and 45.2% when compared to no treatment, herbicide, and herbicide + insecticide treatments respectively.

Invertebrate prey community

Abundance and species richness

There was no significant difference in invertebrate prey abundance between all treatment regimes (F_3=1.80 p=0.62, block: F_5=7.88 p=0.16) nor between plots with (I) or without (H, H+I, and NT) live heather (F_1=1.32 p=0.26). Invertebrate prey species richness showed no significant difference between treatments (F_3=4.24 p=0.24, block: F_5=4.36 p=0.50) and no significant difference between plots with (I) or without (H, H+I, and NT) live heather (F_1=1.42 p=0.25) (Fig. 3.7).

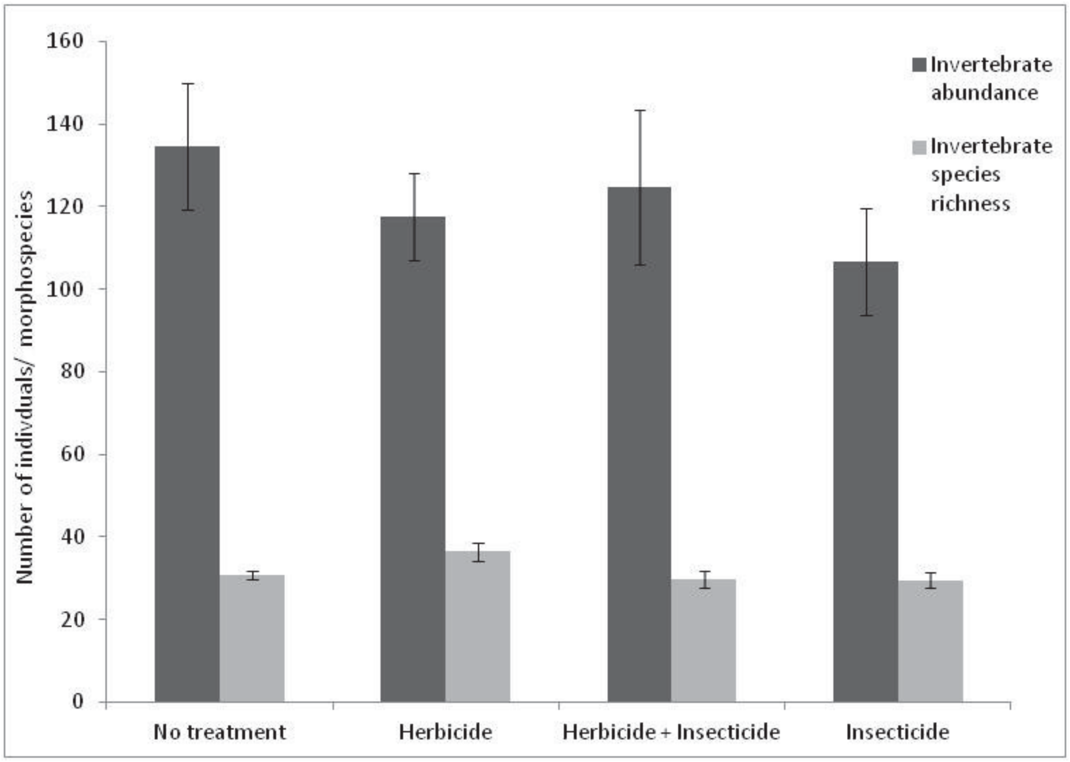

Figure 3.7: Bar graph showing both mean invertebrate prey abundance & richness for plots over the four treatment types (± 1 SE) for trap captures in the herbicide/insecticide trial from 3rd February to 3rd March 2011.

Community composition

Multivariate analysis of potential invertebrate prey community data also failed to provide a direct explanatory factor for skink abundance; NMDS plot of invertebrate prey communities did not show a distinction between plots where skinks were or were not caught (Fig. 3.8).

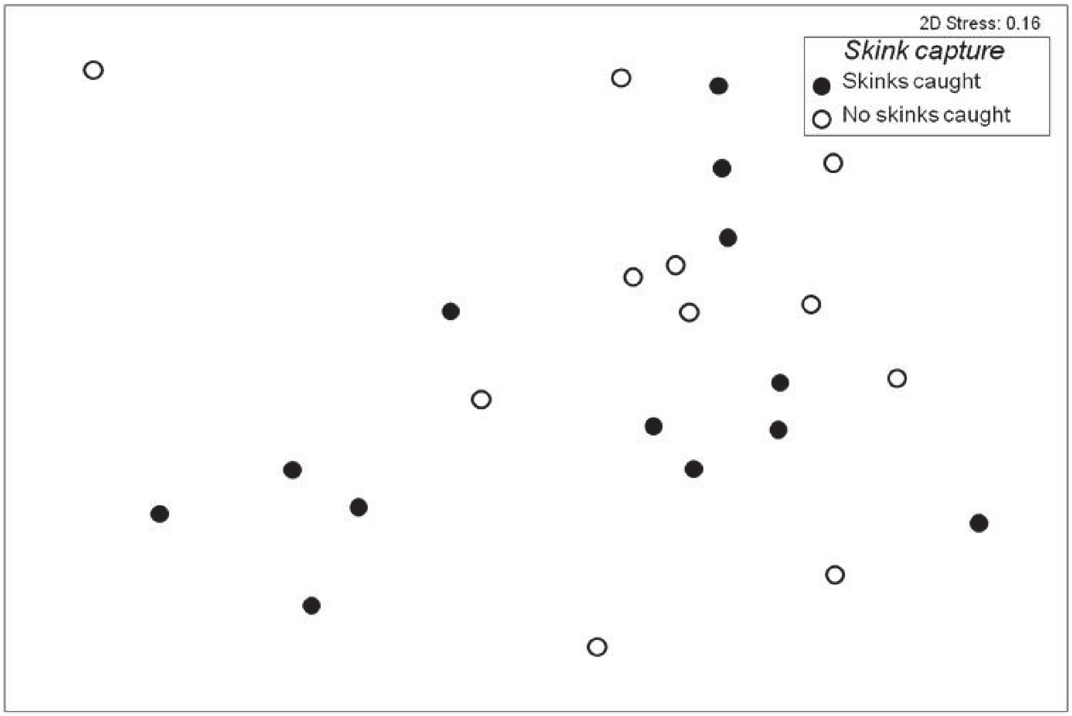

Figure 3.8: NMDS plot of invertebrate prey community data from FIP traps in herbicide/insecticide trial plots from 3rd February to 3rd March 2011.

Single-factor PERMANOVA indicated no difference in invertebrate prey samples from plots with and without skink captures (*pseudo*-$F_{1,22}$=1.10 *p*= 0.32). There was also no significant difference between plots that contained heather (I treatment regime) and plots that no longer contained live heather (NT, H, and H+I treatment regime) (*pseudo*-$F_{1,22}$= 0.82 *p*= 0.64).

Discussion

Common skink abundance was lower in plots that had been experimentally manipulated to protect heather from heather beetle feeding (insecticide only treated plots) compared with plots where heather was controlled with herbicide, beetle feeding, or a combination. Not surprisingly, vegetation composition differed between treatment regimes. In contrast, available invertebrate prey communities did not appear to differ between treatment regimes, thus the observed difference in skink abundance was not a result of invertebrate prey availability or composition.

The reasons for the observed distribution of common skinks and the detrimental effect of heather on skink abundance were not clear. The main difference between tussock/exotic grass dominated plots and heather dominated plots was that heather is architecturally more complex, thus its stems and foliage take up more space than grasses and native shrubs (Keesing, 1995). This structural complexity in conjunction with high density means heather dominated plots are much less open and have less light reaching through the canopy than tussock/exotic grass dominated plots. As small, actively foraging, diurnal heliotherms (Lettink et al., 2011; Spencer et al., 1998), common skinks need to be able to bask to maintain body temperature (Lettink et al., 2011), feed, avoid predators, and tolerate or avoid abiotic stressors (Martin & Murray, 2011).

Changes in habitat structure and complexity as a result of exotic weed invasion have been identified by Martin & Murray (2011) as factors that can have a dramatic effect on reptiles. In fact, changes in habitat structure have been identified in several studies to be more important than changes in actual vegetation composition (Garden et al., 2007).

Habitat selection by individuals is based on an optimisation of numerous competing requirements (Ahnesjö & Forsman, 2006; Hill, Holwell, Goth, & Herberstein, 2004; Law & Bradley, 1990), which vary with the organisms physiological and morphological needs (Adolph, 1990; Huey, 1991). Therefore the observed variation of common skink abundance may have arisen due to either the changes in habitat structure as described above or biotic changes such as the presence of predators or competitors (Patterson, 1985). As any potential biotic changes (such as predator densities) due to heather presence or absence are not known this factor will not be discussed in this paper.

Thermoregulation

A unique and key habitat requirement of heliothermic species is they need suitable basking sites within their chosen microhabitats, thus their distribution is often dependent on this requirement (Klingenböck, Osterwalder, & Shine, 2000; Law & Bradley, 1990). For both large and small skinks the availability of basking sites is important (Martin & Murray, 2011); large skinks take a long time to heat thus requiring a long basking period, while smaller species such as common skinks heat and cool quickly due to their smaller body size and less efficient physiological adaptations to prevent cooling (Klingenböck et al., 2000). Often ectotherms have narrow temperature ranges in which they perform optimally (Ahnesjö & Forsman, 2006; Stevenson, Peterson, & Tsuji, 1985) and to maintain this optimal temperature range ectotherms shuttle between sunny and shady areas or bask in intermediately sunny areas (Adolph, 1990; Baling, 2003; Garden et al., 2007; Martin & Murray, 2011). Given this need for thermoregulation an ideal habitat for common skinks is one that provides a heterogeneous mix of both sun and shade to allow thermoregulation with little movement necessary for shuttling between areas (Adolph, 1990). Heather dominated plots do not provide this because of high structural complexity which shades much of the plots. In contrast, tussock/exotic grass dominated plots provide a heterogeneous mix of shady and sunny areas, with native shrubs and tussock providing shade and large areas of open and low growth dominated spaces between tussocks.

This pattern of high skink abundance within habitats that provide more basking/thermoregulation opportunities has been found to explain the patchy distribution of several lizard species. The water skink (*Eulamprus quoyii*) was found to be present at higher densities in sites that contained open rocky areas than in cool closed forests with few rocks (Law & Bradley, 1990). Klingenböck et al. (2000) found that land mullet (*Egernia major*) distribution relied on the presence of three habitat variables; large hollow logs, relatively thick vegetation, and enough open areas for behavioural thermoregulation. Juvenile land mullet were restricted to close proximity of basking areas compared to the larger adults. Behavioural thermoregulation was also found to be an important predictor of habitat use by two *Sceloporus* lizards that occupy overlapping altitudinal ranges (Adolph, 1990). The lizards altered their microhabitat use with change in altitude such as occupying lower perches and more often coming to the ground as altitude increases. The teiid lizard *Ameiva ameiva* is also an actively foraging heliotherm that is restricted to habitats which provide basking sites that allow it to bask during much of the day (Sartorius, Vitt, & Colli, 1999).

Foraging efficiency

The efficiency in which an animal can forage is influenced by prey availability, the time needed to find prey, and the time spent handling prey (Gotceitas, 1990). Availability of prey appears not to vary between habitats in this study. However, secondary plant compounds sequestered by invertebrates feeding on heather may make them unpalatable to common skinks, as was suggested for Australian skinks that appeared to avoid invertebrates that had fed on the introduced rubber vine (*Cryptostegia grandiflora*) (Valentine et al., 2007).

The ability of a common skink to find its prey could be an important factor in its habitat choice. High structural complexity of a habitat, such as with heather patches, has been found to decrease predator foraging success and increase time needed for foraging (Diehl, 1988; Gotceitas, 1990; Hill et al., 2004). This is a result of highly complex habitats offering refuge to prey by restricting predator vision and movement thus making prey more difficult to detect and capture (Hill et al., 2004). This may also contribute to the preference of tussock/exotic grass dominated habitats by common skinks because they are primarily active predators (Freeman, 1997).

Predator avoidance

The ability of common skinks to avoid predators may also be a factor in their preference for tussock/exotic grass dominated habitats. Related to heather's effect of increasing habitat complexity, common skinks may not only be restricted in movement and vision for foraging but also increased difficulty escaping from predators (Hill et al., 2004). Conflicting with this is that high structural complexity in a habitat provides cover and decreases predation risk (Hill et al., 2004). However, amount of cover is not the only determining factor regarding predation risk; a species which relies on crypsis to avoid detection by predators must match its habitat in colour and pattern (Lillywhite, Friedman, & Ford, 1977; Valentine et al., 2007). As common skinks spend long periods basking in the open to maintain body temperatures, crypsis to avoid detection rather than being hidden by vegetation is necessary for them to avoid predation.

Patterson (1985) found when studying the common skink species complex in central Otago that dorsal patterning appeared to camouflage the skinks in their preferred habitats. Skinks with speckled dorsal patterning (now *Oligosoma maccanni*) were found to occupy shrub and schist habitats and skinks with stripped patterning (now *O. n. polychroma*) were found in grassland habitats. The same relationship between dorsal patterning and habitat preference was found at Birdlings flat by Freeman (1997) despite a switch of dorsal patterns between the two species, with the striped McCann's skinks preferring grassland habitats and the speckled common skinks preferring shrubland habitats. The relationship between habitat preference and skink body pattern may help with crypsis by matching background pattern to avoid avian predators hunting principally by vision. Skinks found in our study area all had markedly striped dorsal and side patterning. This would suggest a preference for tussock/exotic grass dominated habitats, with the striped pattern assisting crypsis in grassland habitats. Native scincid lizards in Australia also avoid an invasive weed, the rubber vine (Valentine, 2006) because it is less cryptic in invaded environments as leaf size, colour and shape make the skink more vulnerable to predation (Valentine et al., 2007). Being cryptic may not only limit detection by predators but may also give skinks an advantage in avoiding detection by their prey thus increasing foraging efficiency (Patterson, 1985).

Implications

This previously unknown effect of heather invasion on the native common skink further reinforces the importance of controlling heather, also highlighting the need to be aware of potential ecological effects of heather and other invasive weeds beyond that of displacing native plant communities. The large areas of ideal common skink habitat being created by the continued success and spread of the heather beetle may mean a subsequent increase in skink abundance in controlled areas. The future of this preferred common skink habitat is uncertain with indigenous shrubby vegetation regenerating in areas where the heather beetle has killed heather (Peterson et al., 2011), meaning a future increase in habitat complexity, canopy cover (although much less than that previously present with heather (Keesing, 1995)), and heterogeneity with an unknown affect on habitat suitability for common skinks.

Further research is needed to investigate the effects of invasive plants on native fauna to better prioritise weed control in the future to maximise conservation benefits. Care must be also taken when controlling weeds that may provide suitable habitat for native fauna. For example; marram grass (*Ammophilia arenari*) dominated dunes provide better habitat for invertebrates and common skinks when compared with restored duneland vegetation (Jamieson, 2010). In such instances conservation goals and expected outcomes must be clear and be made with an understanding of potential effects on both fauna and flora.

Martin & Murray (2011) provided a framework for predicting these effects on reptiles and amphibians which may be useful in identifying weeds that many pose a significant risk to native herpetofauna as well as identifying native species that may be particularly sensitive to habitat modification from plant invasion. The use of life history traits and properties of invasive weeds to predict effects as outlined by Martin & Murray (2011) could be used beyond that of predicting effects on herpetofauna to identify native species and exotic weeds that research attention may be best spent on. For example; the ability of heather to invade inter-tussock gaps in place of and outcompeting native dwarf shrubs and herbs (Chapman & Bannister, 1990) means the habitat structure changes from typically low growth forms to heather's higher growth form (Keesing, 1995). This change in canopy height could have negative impacts on the nest site suitability of the native Australasian pipit (*Anthus novaeseelandiae*) as they have a strong nest site preference for vegetation <30cm in height (Norment & Green, 2004).

Conclusion

Heather appears to have a deleterious effect on common skink abundance, perhaps because heather changes habitat structure reducing the common skinks ability to thermoregulate, forage, and avoid predation. The biological control of heather by the heather beetle appears to be opening up large areas of preferred common skink habitat. However, the effect of regeneration of native vegetation over time in these controlled areas for habitat suitability of common skinks is unclear.

Chapter Four

The direct and indirect effects of the biocontrol of heather (*Calluna vulgaris*) with heather beetle (*Lochmaea suturalis*) on invertebrate communities

Figure 4.0: Two heather beetles in the Tongariro National Park.

The direct and indirect effects of the biocontrol of heather (*Calluna vulgaris*) with the heather beetle (*Lochmaea suturalis*) on invertebrate communities

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Abstract

Biological control of invasive plants has many potential effects on ecosystems, related to the decrease in invasive plant density as well as direct effect of the agent itself on food-webs and species/trophic level interactions. These potential effects are highly variable, difficult to predict, and often subtle, making it difficult to quantify the net effect on ecosystems post invasive plant control. It is important to quantify and isolate the ecosystem effects of biological control to advise on the most effective management of invasive plants for the future. This research followed from an evaluation of invertebrate community changes in a small scale experimental manipulation of heather (*Calluna vulgaris*) density (Chapter two) and Keesing's (1995) research on the effects of heather invasion on invertebrate communities. The research investigated the invertebrate communities before, during, and after biological control of heather using the heather beetle (*Lochmaea suturalis*); it assessed whether the changes observed at this large scale were consistent with those found in the experimental manipulation, and whether identified effects of heather invasion are reversed following control. The biocontrol of heather does appear to restore invertebrate communities to resemble more closely the community found in non-invaded habitats and these findings suggest the biological control of heather contribute a conservation and ecosystem net benefit to the tussock grasslands in the study area. Two orders were found to respond positively to heather beetle presence; Collembola which may have responded to the increase in frass, cadavers, and detritus and Araneae which may have responded to heather beetles providing a food subsidy.

Introduction

When managing invasive species in a natural ecosystem, net benefit to that system should be the ultimate goal (Buckley, 2008). Yet this remains one of the hardest things to quantify because the effects of invasive species are wide ranging and can affect community structure, food-webs, and ecosystem function (Davis, Thompson, & Grime, 2001; Keesing, 1995; Shea & Chesson, 2002; Strayer, Eviner, Jeschke, & Pace, 2006). Efforts to control invasive species, although generally beneficial (Zavaleta, Hobbs, & Mooney, 2001), will affect ecosystem structure and function and may present a significant disturbance to ecosystems (Buckley et al., 2007).

When attempting to control an invasive plant with a biological control (biocontrol) agent, quantification of net-benefit becomes even more complicated because in addition to the significant disturbance caused by removal of the invasive plant, there may also be a myriad of potential effects of the agent itself on the ecosystem (Pearson & Callaway, 2003). Furthermore, the often patchy distribution of invasive plants (Fagan, Lewis, Neubert, & Van Den Driessche, 2002; Groenendael, 1988; Waage et al., 1988) and biocontrol agents can make research difficult to undertake.

Understanding potential impacts of biocontrol agents is especially important in natural ecosystems because agents have the potential to control weeds over large areas and possibly have indirect impacts on non-target species over these large areas (Louda & Stiling, 2004; Simberloff, 2012; van Driesche, 2012). Indirect impacts are extremely difficult to predict *a priori* as they can be complex, varied and often subtle (Simberloff, 2012). Thus risk-benefit analyses can never fully predict all potential effects of what is essentially a planned, facilitated invasion of an exotic species (Louda & Stiling, 2004; Simberloff & Stiling, 1996; van Driesche, 2012). Despite these difficulties, classical biocontrol is an important component of invasive species control in conservation and ecological restoration (van Driesche, 2012) and research into the non-target impacts of already established biocontrol agents will assist in better risk-benefit assessments of proposed new agents.

Current progress of the heather (*Calluna vulgaris*) biological control programme in New Zealand lends itself to investigations into the non-target impacts of the biocontrol agent heather beetle (*Lochmaea suturalis*) on the natural ecosystem. The heather beetle feeds in a discreet, dense feeding front which radiates from release sites creating three distinct zones; the regenerating zone behind the feeding front where the heather has been removed, a narrow feeding front where the heather beetles are high in abundance and controlling heather, and a live heather zone where the vegetation is a mixture of native vegetation and live heather. This discreet feeding front behaviour enables sampling in areas of intact heather invaded habitat, and habitat where the heather has been controlled, as well as a narrow area of high heather beetle density all within a small area; ideal for research on effects of biocontrol on ecosystems. The heather biological control programme has recently progressed to a stage where we can sample from these three zones at three outbreak sites to help establish the specific impacts of heather biocontrol on flora and fauna.

This study aims to quantify, at a landscape scale, some of the direct and indirect impacts of biocontrol with the heather beetle on plant and invertebrate communities. We also compare these impacts with those found in the smaller scale experimental study in chapter two and previous research done by Keesing (1995) to see if they are consistent. In general Keesing (1995) found that with the invasion of heather came an increase of generalist predators (specifically Araneae), pollen feeders (specifically Thysanoptera), and a decrease in phytophagous insects (specifically those in the order Hemiptera).

Study areas

The study was conducted at three sites with sustained heather beetle outbreaks located in the Tongariro region in the North Island of New Zealand; sites one and two were located in the Waiouru Military Training Area (WMTA) bordering Tongariro National Park (Fig. 4.1). Two sites (S39°22’ E 175°43’ and S39°16’ E 175°43’) were located at the southern end of the Rangipo desert, approximately 11 and 12.3 km north of Waiouru at an altitude ranging between 1000 m and 1030 m asl. Site three was located in the Erua Conservation Area which borders the north-western corner of the Tongariro National Park (Fig. 4.2). The site (S39°09’ E 175°23’) was located 1.6 km north of the National Park township at an altitude of 800 m asl on a large frost flat/ wetland area.

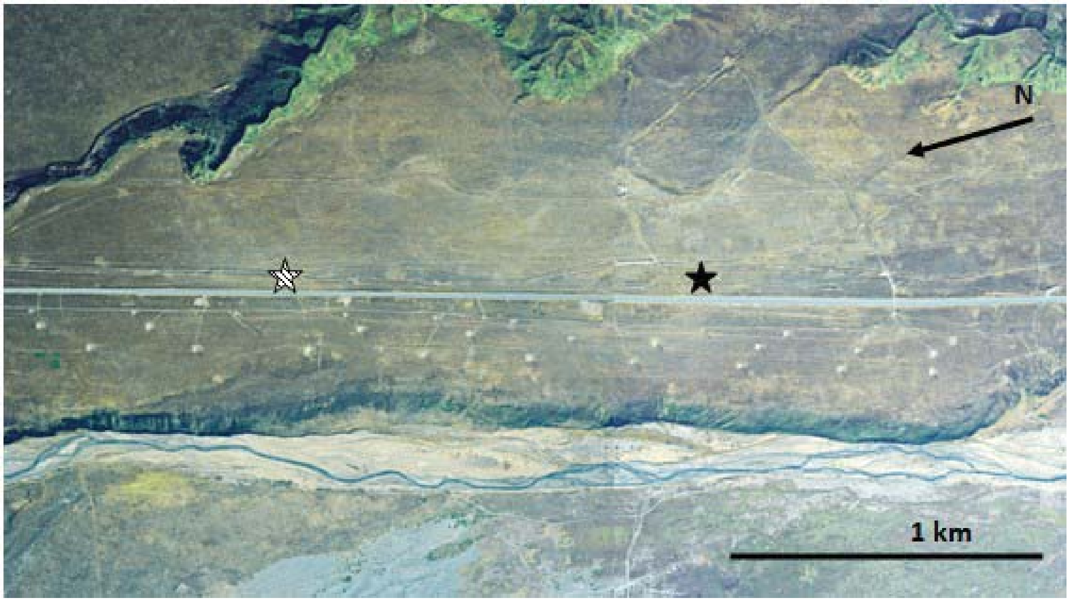


Figure 4.1: Aerial photo of the WMTA study sites in the central North Island of New Zealand, heather beetle release points indicated by stars (site 1; solid coloured, site 2; striped fill).

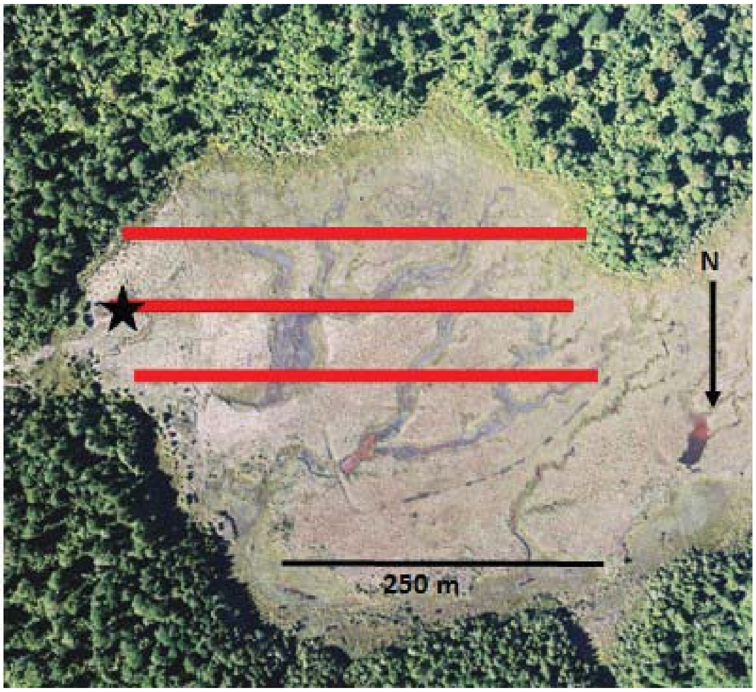


Figure 4.2: Aerial photo of Erua Conservation Area site in the central North Island of New Zealand (site 3). Star indicates heather beetle release point. Red lines indicate an example of the layout of transects.

Vegetation at all sites had extensive heather growing throughout prior to heather beetle release. As a result of heather beetle outbreaks the sites were largely devoid of live heather behind the feeding front but beyond the feeding front the vegetation comprised mixed native and heather vegetation.

Native vegetation at sites one and two included: red tussock (*Chionochloa rubra*), monoao (*Dracophylum subulatum*), sprawling coprosma (*Coprosma cheesmanii*), cottonwood (*Ozothamnus leptophyllus*), woolly moss (*Racomitrium* sp.), and blue tussock (*Poa colensoi*). Exotic vegetation other than heather was also present at the sites with browntop (*Agrostis capillaris*) and mouse-ear hawkweed (*Pilosella officinarum*) being the most common. Site three's native vegetation comprised: red tussock, monoao, sprawling coprosma, woolly moss, flax (*Phormium tenax*), tangle fern (*Gleichenia dicarpa*), coral lichen (*Cladia retipora*), and wire rush (*Empodisma minus*). No exotic vegetation besides heather was recorded at site 3.

Five hundred heather beetles were released at site one during February 2001. It took until the 2006-2007 season (austral spring to autumn) until beetle feeding damage to heather was visible, with 0.0025 ha of heather killed. The area of feeding damage had increased every season since and by March 2011 approximately 80 ha of heather had been heavily damaged or killed. Five hundred and twenty five beetles were released at site two during February 2001, and although it was not as closely monitored as the other earlier and larger outbreaks, by 2012 the outbreak had killed or heavily damaged approximately 12 ha of heather. Two hundred and fifty beetles were released at site three during December 2001. It took until the 2006-2007 season (austral spring to autumn) until beetle feeding damage to heather was visible, with 0.01 ha of heather killed. The area of feeding damage had increased every season since and by March 2011 approximately 12 ha of heather had been heavily damaged or killed.

Methods

Invertebrate trapping was carried out by placing 18 modified flight-intercept-pitfall (FIP) traps (Stevens et al., 2007) (Fig. 4.3) along three parallel transects at each site. The distance between traps and transects was determined by the extent of heather beetle spread at the time of trap installation. As a result of the variation in heather beetle outbreak size the transect length was set to be twice the distance the heather beetle had spread from the original release point. The traps were then spread evenly along these transects, and transects placed one trap distance apart from one another with the first trap of the middle transect located at the heather beetle release point of the site (Fig. 4.2). The traps remained in place for three months with collections occurring approximately once a month (Table 4.1).

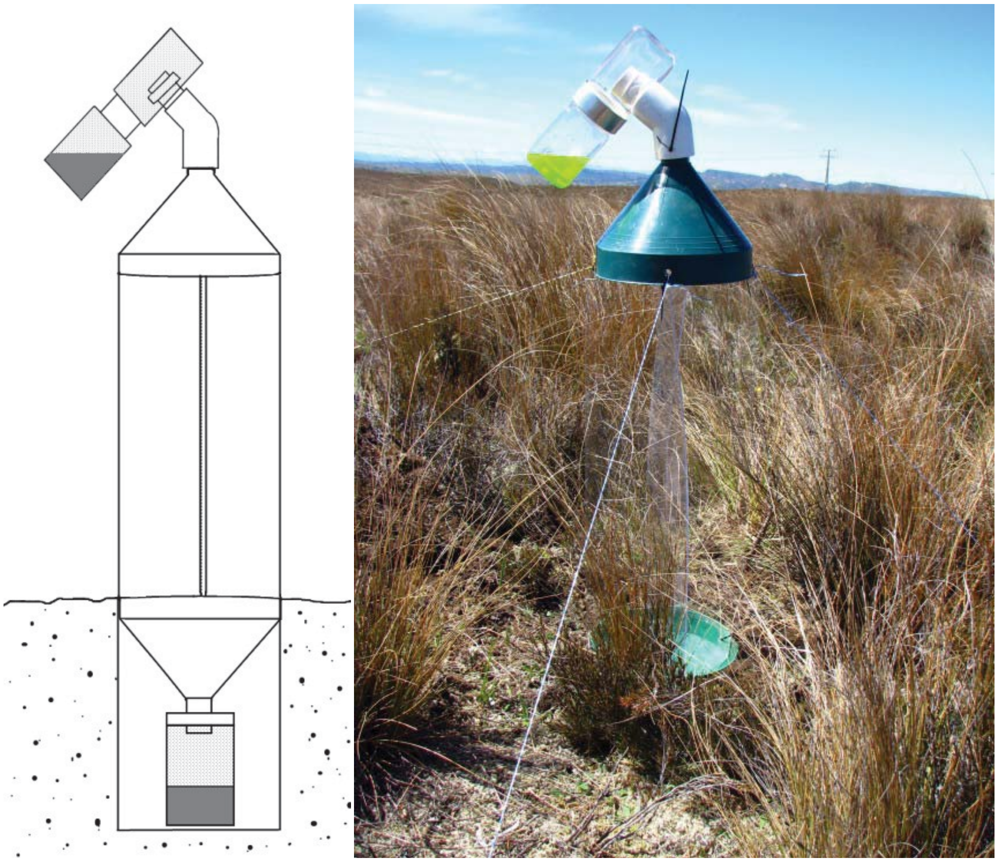


Figure 4.3: Modified flight-intercept-pitfall trap design used for invertebrate trapping at Tongariro.

Table 4.1: Invertebrate trapping transects details and timeline, Tongariro 2010-2011 (austral summer). * *Collection and removal delayed as a flooded river prevented access to site*.

Site	Transect extent (m)	Distance between traps and transects (m)	Bearing (°MAG)	Date of trap placement	Date of first collection	Date of second collection	Date of third collection and removal
One	400	80	92	8th Dec 2010	4th Jan 2011	2nd Feb 2011	4th Mar 2011
Two	250	50	92	10th Dec 2010	4th Jan 2011	2nd Feb 2011	3rd Mar 2011
Three	400	80	270	11th Dec 2010	5th Jan 2011	4th Feb 2011	10th Mar 2011*

As a consequence of consistently poor capture rates (Chapter two) data from the top capture component of the FIP traps was not used in this study. Following unintentional capture of common skinks (*Oligosoma nigriplantare polychroma*) at sites one and two during the first trapping period we added mesh to prevent skink capture (Fig. 4.4). However, the mesh proved ineffective and was removed after the second sample collection and consultation with the Department of Conservation.

Figure 4.4: Pitfall element of trap design used for invertebrate trapping at Tongariro with mesh used in the second trapping period to attempt to prevent common skink captures.

Invertebrate sample processing

Invertebrate samples taken from the traps installed at the three sites were filtered through a 250 µm sieve, sorted to order, and counted. If a morphospecies was particularly abundant in a sample a subsample for that one order was counted and scaled accordingly. Heather beetle adults and larvae were counted separately from other Coleoptera.

Trap area descriptions

Vegetation in each plot was characterised by taking top down photos of a 5 x 5 m area around the trap, using a pole mounted camera to approximately 7 m above ground level. The photos were processed using the Digital Sampling Method computer program (Gillingham, 2003) to determine vegetation coverage for each plant species present. As some plots had large areas of dead heather this was included as a vegetation type and used to determine presence/absence of live heather at each trap site. Exotic grasses and herbs were considered one category. GPS position, altitude, aspect, and a general description of vegetation composition and ground cover were also recorded.

Distance from the initial heather beetle release site was recorded upon the installation of each trap and the position relative to the heather beetle feeding front was recorded at the time of trap placement as native regenerating, heather beetle feeding belt, or heather zones. However, as the beetle feeding front was highly mobile during the trapping period these zones are only useful for vegetation type characterisation and not heather beetle presence/density; pitfall traps were used for this. Furthermore, as a result of the patchy nature of heather in some areas beyond the heather beetle feeding front some traps were not surrounded by heather despite being in the 'heather zone'.

Data analysis

Individual sites

All multivariate analyses was conducted using Primer 6.1 (Clarke & Gorley, 2007) and PERMANOVA+ (Anderson et al., 2008).

Vegetation composition data was analysed individually for each site using non-metric multi-dimensional scaling (NMDS) with Bray-Curtis distance measure and no transformation to explore similarities and differences between vegetation zones. Single factor Permutation Multivariate Analysis of Variance (PERMANOVA) was used to determine the significance of differences between vegetation zones and Similarity Percentage (SIMPER) was used to characterise the plant species which were the main drivers of these differences.

Invertebrate community data from each site was also analysed using NMDS and single-factor PERMANOVA to test the significance of; collection period (month), vegetation zone, heather presence, and heather beetle presence/density (heather beetle density was characterised as a binomial factor for each collection; heather beetles present or absent, greater than or less than 100 heather beetles, and greater than or less than 500 heather beetles) as significant factors in explaining observed variation. As sites one and two had mesh applied in the second trapping period, month for these sites was tested with a two-factor PERMANOVA with mesh presence as a factor to investigate if mesh had any effect on invertebrate captures.

SIMPER analysis was used to explore which insect orders were driving dissimilarity when significant factors were found. Invertebrate orders found to be drivers of dissimilarity between factors were analysed using single-factor ANOVA to test for significant difference between factors using Statistix 9 to perform the analyses.

All sites combined

Datasets from all three sites were combined to explore general effects over the three sites as a whole. Analysis followed that described above for both vegetation and invertebrate composition data, except for the analysis of mesh effects.

Results

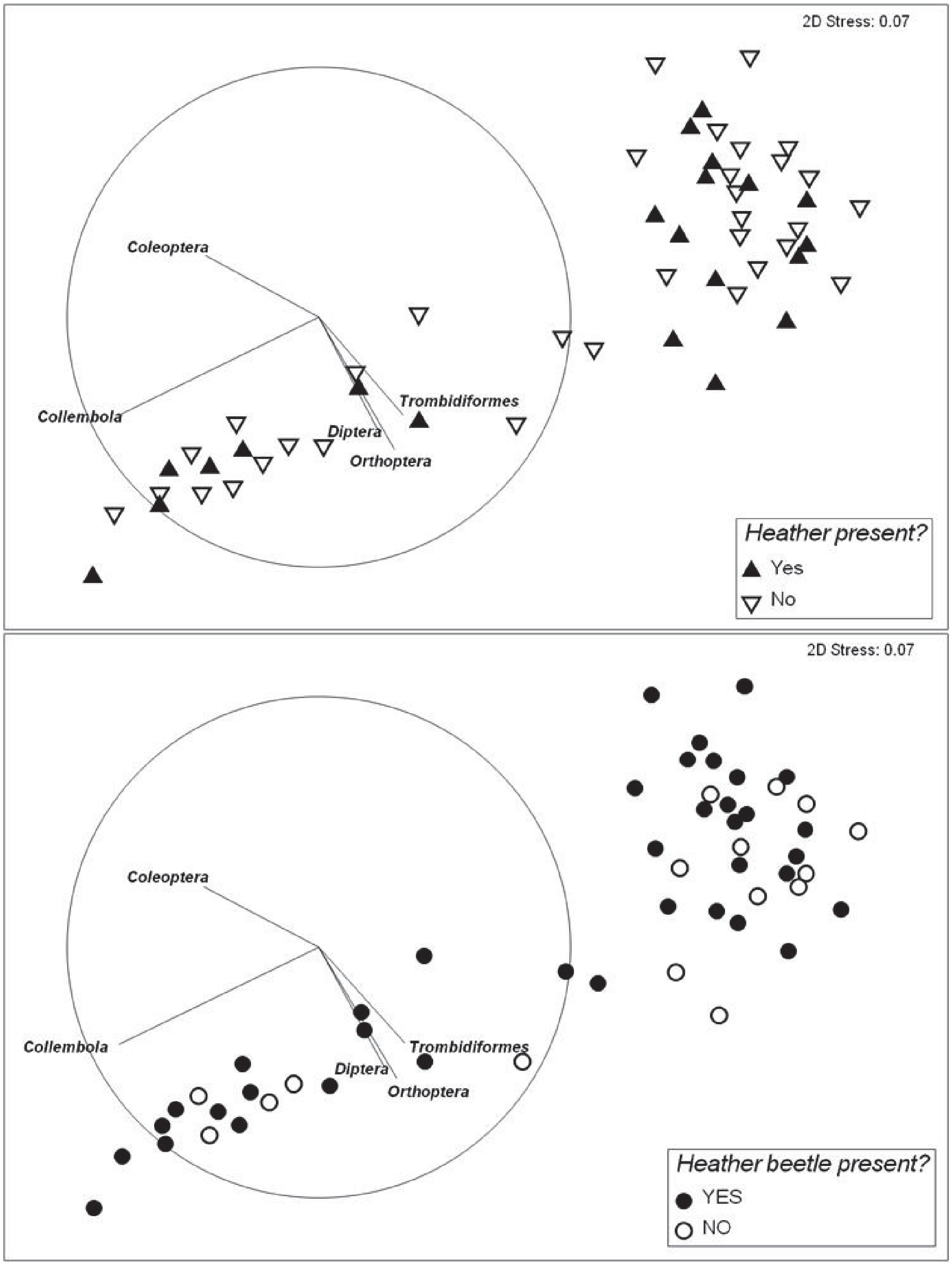
Site one

Invertebrate composition

A total of 44,343 macroinvertebrates of 21 orders were collected over the 2010-2011 austral summer at site one, of which 82% were Collembola, 4% Araneae, 4% Trombidiformes, and the rest made up of orders comprising less than 4% of total abundance. Along with these macroinvertebrates 8,675 heather beetles were caught (adults and larvae combined).

Ordination of the data indicated no distinct grouping between plots with and without live heather (Fig. 4.5), or between traps that did and did not catch heather beetles (Fig. 4.6).

There was no difference between invertebrate captures in vegetation zones (*Pseudo*-$F_{2,51}$=0.73 p=0.59), trap sites with or without live heather (*Pseudo*-$F_{1,52}$=0.31 p=0.87), traps with or without heather beetles (*Pseudo*-$F_{1,52}$=0.72 p=0.48), traps that caught at least 100 heather beetles and those that caught less (*Pseudo*-$F_{1,52}$=0.59 p=0.58), and traps that caught at least 500 heather beetles and those that caught less (*Pseudo*-$F_{1,52}$=1.44 p=0.22). Two-factor analysis showed that while there were significant differences between invertebrate captures in different months (*Pseudo*-$F_{2,50}$=1.95 p=0.051) there was no effect of the usage of mesh on invertebrate captures (*Pseudo*-$F_{1,50}$=0.88 p=0.53).



Figures 4.5 & 4.6: NMDS ordination plots of invertebrate data collected during the austral summer 2010-2011 at site one in the WMTA, central North Island. Symbols indicate whether either live heather (top plot) or heather beetles (bottom plot) are present. Vectors are Pearson correlations (>0.5).

Vegetation composition

Vegetation composition at site one was strongly affected by the trap site's zone characterisation with the major division between the native regenerating zone and the live heather zone. The feeding belt zone remained more variable (Fig. 4.7).

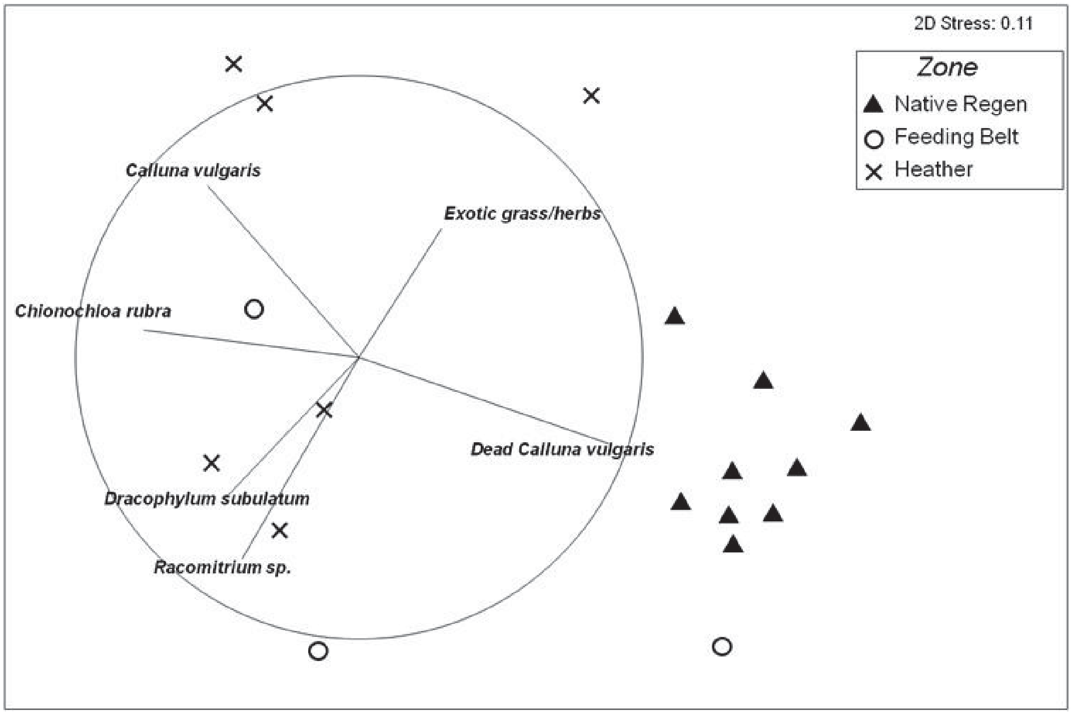


Figure 4.7: NMDS ordination plot of vegetation data collected during the austral summer 2010-2011 at site one in the WMTA, central North Island. Symbols indicate characterised zone of trap area. Vectors are Pearson correlations (>0.5).

There was a significant difference in vegetation composition between characterised vegetation zones (*Pseudo*-$F_{2,15}$=7.05 p=0.001). As expected the main driver in the difference between the regenerating native zone and heather zones was the presence of live and dead heather. However, there was much less live heather in the heather zone than what had been in the native regenerating zone prior to beetle feeding, as indicated by the large abundance of dead heather in the native regeneration zone. The heather beetle feeding zone was more variable containing mixtures of live and dead heather (Table 4.2).

Table 4.2: Average abundance and percentage contribution to the Bray-Curtis dissimilarity (SIMPER analysis) of plant species between characterised vegetation zones reported against the regenerating native zone at site one with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

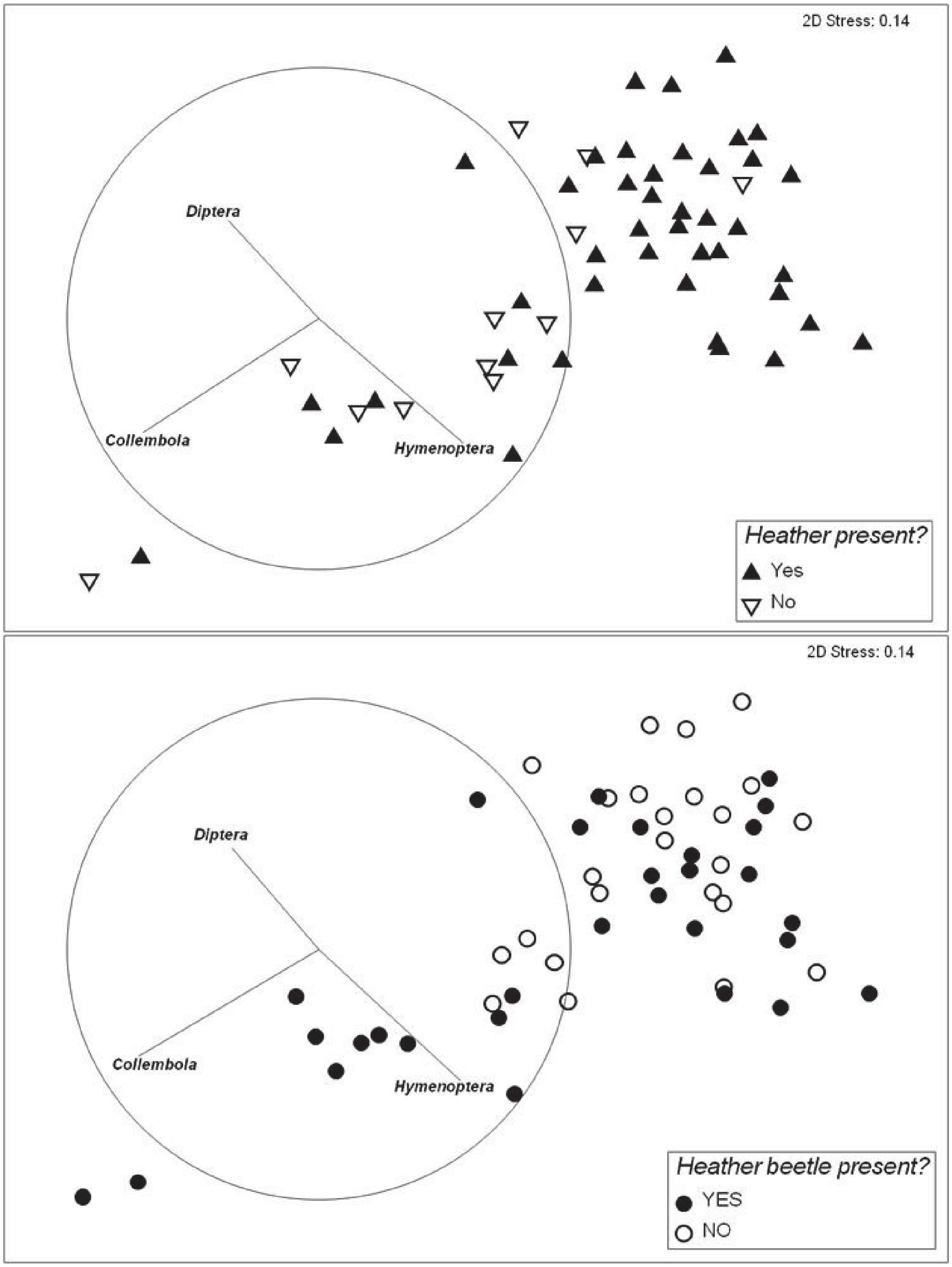
Plant species	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Dead heather	109.56	0	40.27	32	36.72	***
Heather	0.56	50	18.34	18.00	8.28	***
Exotic grass/herb	23.22	29.83	13.40	15.33	9.22	
Red tussock	42.56	76.33	12.46	59.33	16.03	***
Woolly moss	17.89	29.83	9.01	54	18.02	***
Monoao	1.33	-	-	21.33	9.51	**

Site two

Invertebrate composition

A total of 13,403 macroinvertebrates of 17 orders were collected over the 2010-2011 austral summer at site two, of which 49% were Collembola, 10% Hymenoptera, 7% for each of; Araneae, Diptera, and Trombidiformes, 6% Hemiptera, and the rest made up of orders comprising less than 5% of total abundance. Along with these macroinvertebrates 7,107 heather beetles were caught (adults & larvae combined).

Ordination of the data showed little distinction between plots with and without live heather (Fig. 4.8), and little distinction between traps with or without heather beetles (Fig. 4.9). However, there appears to be loose groupings of both factors.



Figures 4.8 & 4.9: NMDS ordination plots of invertebrate data from site two collected during the austral summer 2010-2011 at site two in the WMTA, central North Island. Symbols indicate whether either live heather (top plot) or heather beetles are present (bottom plot). Vectors are Pearson correlations (>0.5).

There was a significant difference between invertebrate captures in vegetation zones (*Pseudo*-$F_{2,51}$=4.42 p=0.001), trap sites with or without live heather (*Pseudo*-$F_{1,52}$=5.18 p=0.003), traps with or without heather beetle (*Pseudo*-$F_{1,52}$=2.49 p=0.03), and traps that caught greater or less than 100 heather beetles (*Pseudo*-$F_{1,52}$=5.45 p=0.002). Traps that caught at least 500 heather beetles and those that caught less were found not be significantly different from each other (*Pseudo*-$F_{1,52}$=1.84 p=0.084). Two-factor analysis indicated that while there was a significant difference between invertebrate captures in different months (*Pseudo*-$F_{2,50}$=2.69 p=0.008) there was no effect of the usage of mesh on invertebrate captures (*Pseudo*-$F_{1,50}$=1.31 p=0.22).

The main invertebrate orders contributing to the difference between characterised vegetation zones were; Collembola which were abundant at both the regenerating native zone and heather beetle feeding belt zone but low in the live heather zone, and Hemiptera which were five times more abundant in the regenerating native zone than the other two zones (Table 4.3).

Both Collembola and Hemiptera were significantly less abundant in areas where live heather was present (Table 4.4) and so were the main drivers of dissimilarity between sites with or without live heather.

Collembola were the main drivers of dissimilarity of invertebrate communities; they were caught at significantly higher densities in traps which caught heather beetles, an effect that appeared amplified with ≥100 heather beetles caught (Tables 4.5 & 4.6). In addition; Diptera were approximately twice as abundant and Trombidiformes were caught at greater abundance in traps that caught ≥100 heather beetles. Hymenoptera were more abundant where <100 beetles were caught (Table 4.6).

Table 4.3: Average abundance and percentage contribution to the Bray-Curtis dissimilarity (SIMPER analysis) of invertebrate orders between characterised vegetation zones reported against the regenerating native zone at site two with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Collembola	172.44	27.79	53.13	208.29	58.21	
Hemiptera	42.44	8.54	11.83	8.67	9.77	**
Hymenoptera	23.56	20.79	5.85	28.10	7.05	
Trombidiformes	13.00	17.46	5.10	19.52	3.77	
Diptera	19.22	12.96	4.52	21.29	5.81	
Coleoptera	15.00	9.75	3.48	-	-	
Orthoptera	8.78	4.00	3.40	8.78	3.23	
Araneae	17.22	14.21	3.28	18.62	3.47	

Table 4.4: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites with or without live heather at site two with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Live heather absent	Live heather present		
	Avg. abund.	Avg. abund.	Contrib. %	
Collembola	273.42	78.86	55.10	*
Hemiptera	34.42	8.48	8.84	**
Hymenoptera	20.42	25.14	6.62	
Diptera	19.92	16.48	5.72	
Trombidiformes	15.67	18.05	5.08	
Araneae	19.00	15.69	4.26	
Orthoptera	8.17	5.19	3.36	
Coleoptera	13.17	9.90	2.96	

Table 4.5: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites with or without heather beetle catches at site two with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Heather beetle present	Heather beetle absent		
	Avg. abund.	Avg. abund.	Contrib. %	
Collembola	193.23	33.17	44.07	*
Hymenoptera	25.70	22.08	10.80	
Trombidiformes	17.93	17.00	7.24	
Diptera	18.77	15.33	7.13	
Hemiptera	14.87	13.46	6.06	
Araneae	17.73	14.79	4.09	
Orthoptera	4.97	6.96	3.91	
Thysanoptera	8.47	5.46	3.90	
Coleoptera	11.60	9.42	3.72	

Table 4.6: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites that caught at least 100 heather beetles and those that caught less at site two with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	At least 100 heather beetles	Less than 100 heather beetles		
	Avg. abund.	Avg. abund.	Contrib. %	
Collembola	478.44	50.82	62.41	***
Diptera	32.00	14.29	8.52	*
Hymenoptera	10.56	26.80	5.69	*
Trombidiformes	26.44	15.73	5.20	*
Araneae	17.11	16.29	3.74	
Hemiptera	8.33	15.42	2.95	
Orthoptera	6.89	5.64	2.68	

Vegetation composition

Vegetation composition at site two was strongly affected by the trap site's zone characterisation with the major division between the native regenerating zone and the live heather zone, even with few native regenerating zone traps. The feeding belt zone remained more variable across the other two zones (Fig. 4.10).

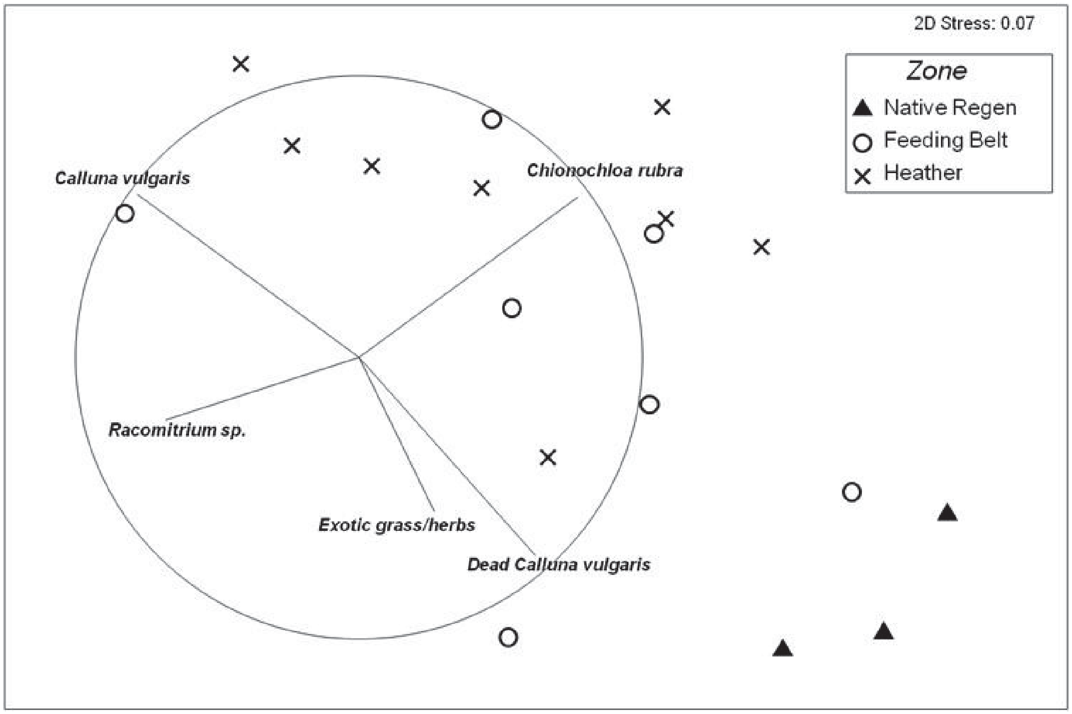


Figure 4.10: NMDS ordination plot of vegetation data from site two collected during the austral summer 2010-2011 at site two in the WMTA, central North Island. Symbols indicate characterised zone of trap area. Vectors are Pearson correlations (>0.5).

There was a significant difference in vegetation composition between characterised vegetation zones (*Pseudo*-$F_{2,15}$=4.47 p=0.007). As expected the main driver in the difference between the regenerating native and heather zones was the presence of live and dead heather. The density of heather in the heather zone was similar to that of dead heather in the native regenerating zone and the heather beetle feeding zone was more variable containing mixtures of live and dead heather. The native regenerating zone contained higher densities of exotic grass/herbs than other zones (Table 4.7).

Table 4.7: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of plant species between characterised vegetation zones reported against the regenerating native zone at site two with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

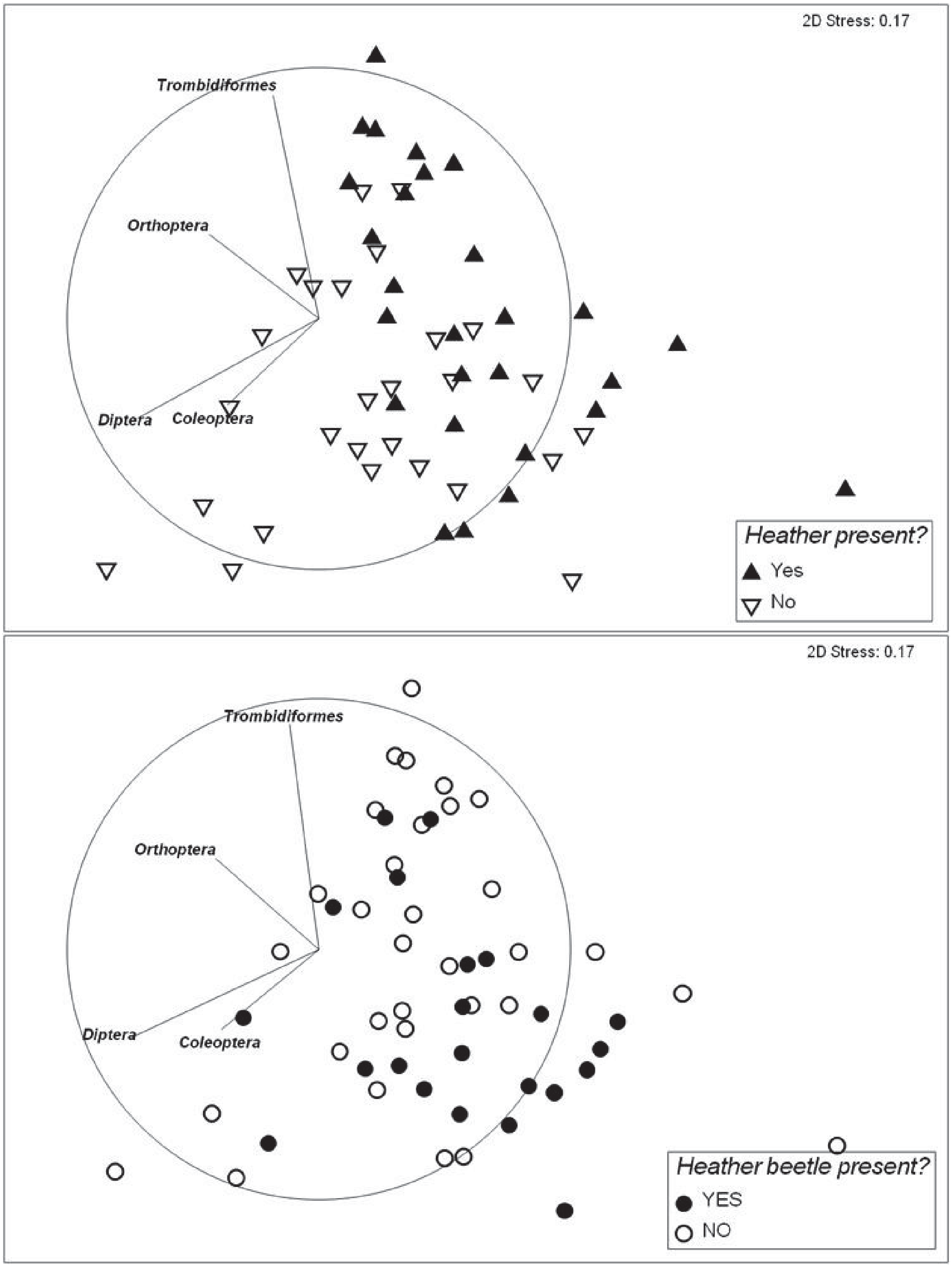
Plant species	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Heather	0	79.5	36.32	57.14	30.57	***
Dead heather	89.33	22.75	30.41	44.29	26.08	***
Exotic grass/herb	31	0.63	14.07	0.86	16.43	***
Red tussock	68.67	73.88	9.15	64.14	11.28	
Woolly moss	7	18.63	6.95	27.43	12.2	**

Site three

Invertebrate composition

A total of 10,325 macroinvertebrates of 23 orders were collected over the 2010-2011 austral summer at site three of which 30% were Trombidiformes, 16% Diptera, 13% Collembola, 9% each of Hymenoptera and Araneae, 7% Coleoptera and the rest made up of orders comprising less than 5% of total abundance . Along with these macroinvertebrates 1,581 heather beetles were caught (adults and larvae combined).

Ordination of the data showed grouping and distinction between plots depending on live heather presence/absence (Fig. 4.11), grouping and distinction between traps due to heather beetle presence/absence (Fig. 4.12).



Figures 4.11 & 4.12: NMDS ordination plots of invertebrate data from site three collected during the austral summer 2010-2011 at site three in the Erua conservation area, central North Island. Symbols indicate whether either live heather (top plot) or heather beetles are present (bottom plot). Vectors are Pearson correlations (>0.5).

There was a significant difference between invertebrate captures in vegetation zones (*Pseudo*-$F_{2,51}$=3.68 p=0.001), trap sites with or without live heather (*Pseudo*-$F_{1,52}$=4.18 p=0.003), and traps with or without heather beetles (*Pseudo*-$F_{1,52}$=2.30 p=0.026). There was no significant difference between traps that caught at least 100 heather beetles and those that caught less (*Pseudo*-$F_{1,52}$=1.46 p=0.165) or traps that caught at least 500 heather beetles and those that caught less (*pseudo*-$F_{1,52}$=0.58 p=0.787).

The main invertebrate orders contributing to the difference between invertebrate communities in characterised vegetation zones were Trombidiformes, Diptera, Collembola, Araneae, and Hymenoptera. Trombidiformes were at higher abundance in the heather zone than the other zones. Diptera were at least three times more abundant in the native regenerating zone than the others. Collembola were least abundant in the heather beetle feeding belt but at similar abundance in the other two zones. Araneae and Hymenoptera were almost equally abundant in the heather beetle feeding belt and live heather zone but at a lower abundance in the native regenerating zone (Table 4.8).

Trombidiformes and Diptera were significantly different in abundance between sites with or without live heather, with Trombidiformes in much higher abundance where live heather was present and Diptera more abundant where live heather was absent. Other important taxa were Collembola with little change in abundance, and Araneae which were twice as abundant where live heather was present (Table 4.9).

The invertebrate orders that were the main drivers of dissimilarity between traps with or without heather beetles were Trombidiformes, Diptera, Collembolla, Araneae, and Hymenoptera. All of these orders were more abundant in traps that did not catch heather beetles, with Trombidiformes significantly so (Table 4.10).

Table 4.8: Average abundance and percentage contribution to the Bray-Curtis dissimilarity (SIMPER analysis) of invertebrate orders between characterised vegetation zones reported against the regenerating native zone at site three with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Trombidiformes	39.95	75.22	29.07	34.17	19.11	
Diptera	55.10	14.67	21.29	18.17	23.26	***
Collembola	23.95	26.48	9.49	17.50	8.24	
Araneae	10.24	21.81	8.21	20.83	9.54	
Hymenoptera	13.86	20.48	6.14	22.50	7.74	
Oribatida	11.90	4.33	6.06	0.67	6.25	
Coleoptera	18.14	12.89	5.35	6.67	7.50	**
Orthoptera	8.10	4.11	3.67	2.50	4.26	
Amphipoda	8.57	4.70	3.58	-	-	*
Hemiptera	8.52	-	-	4.83	4.34	

Table 4.9: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites with or without live heather at site three with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Live heather absent	Live heather present		
	Avg. abund.	Avg. abund.	Contrib. %	
Trombidiformes	38.67	75.22	30.66	*
Diptera	46.89	14.67	18.53	***
Collembola	22.52	26.48	9.68	
Araneae	12.59	21.81	9.65	
Hymenoptera	15.78	20.48	6.50	
Coleoptera	15.59	12.89	5.39	
Oribatida	9.41	4.33	5.31	
Orthoptera	6.85	4.11	3.44	
Hemiptera	7.70	4.85	3.34	

Table 4.10: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites with or without heather beetle catches at site three with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Heather beetle present	Heather beetle absent		
	Avg. abund.	Avg. abund.	Contrib. %	
Trombidiformes	35.23	71.88	31.01	*
Diptera	24.91	34.81	16.65	
Collembola	22.68	25.75	9.77	
Araneae	16.00	18.03	9.69	
Hymenoptera	16.09	19.53	6.56	
Coleoptera	12.95	15.13	5.69	
Oribatida	6.27	7.28	5.34	
Orthoptera	4.68	6.03	3.57	
Amphipoda	4.68	6.75	3.53	

Vegetation composition

Vegetation composition at site three was strongly affected by the trap site's zone characterisation with the major distinct division between the native regenerating and heather beetle feeding belt zones to the live heather zone. The heather zone was also far more variable than either of the other two zones (Fig. 4.10).

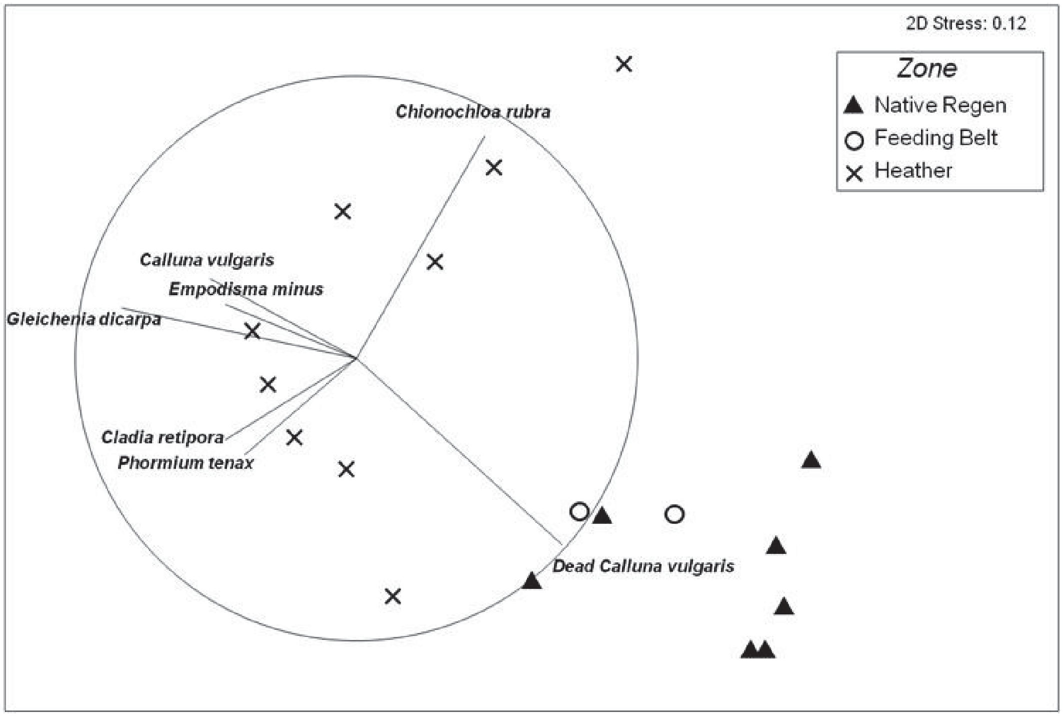


Figure 4.13: NMDS ordination plot of vegetation data collected during the austral summer 2010-2011 at site three in the Erua conservation area, central North Island. Symbols indicate characterised zone of trap area. Vectors are Pearson correlations (>0.5).

There was a significant difference in vegetation composition between characterised vegetation zones (*Pseudo*-$F_{2,15}$=8.41p=0.001), with the main driver of difference between the regenerating native and heather zones being the presence dead heather in the native regenerating zone. The density of (dead or alive) heather in the live heather zone was far lower than what was in the native regenerating zone, while the heather beetle feeding zone was more variable containing mixtures of live and dead heather (Table 4.11).

Table 4.11: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of plant species between characterised vegetation zones reported against the regenerating native zone at site three with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

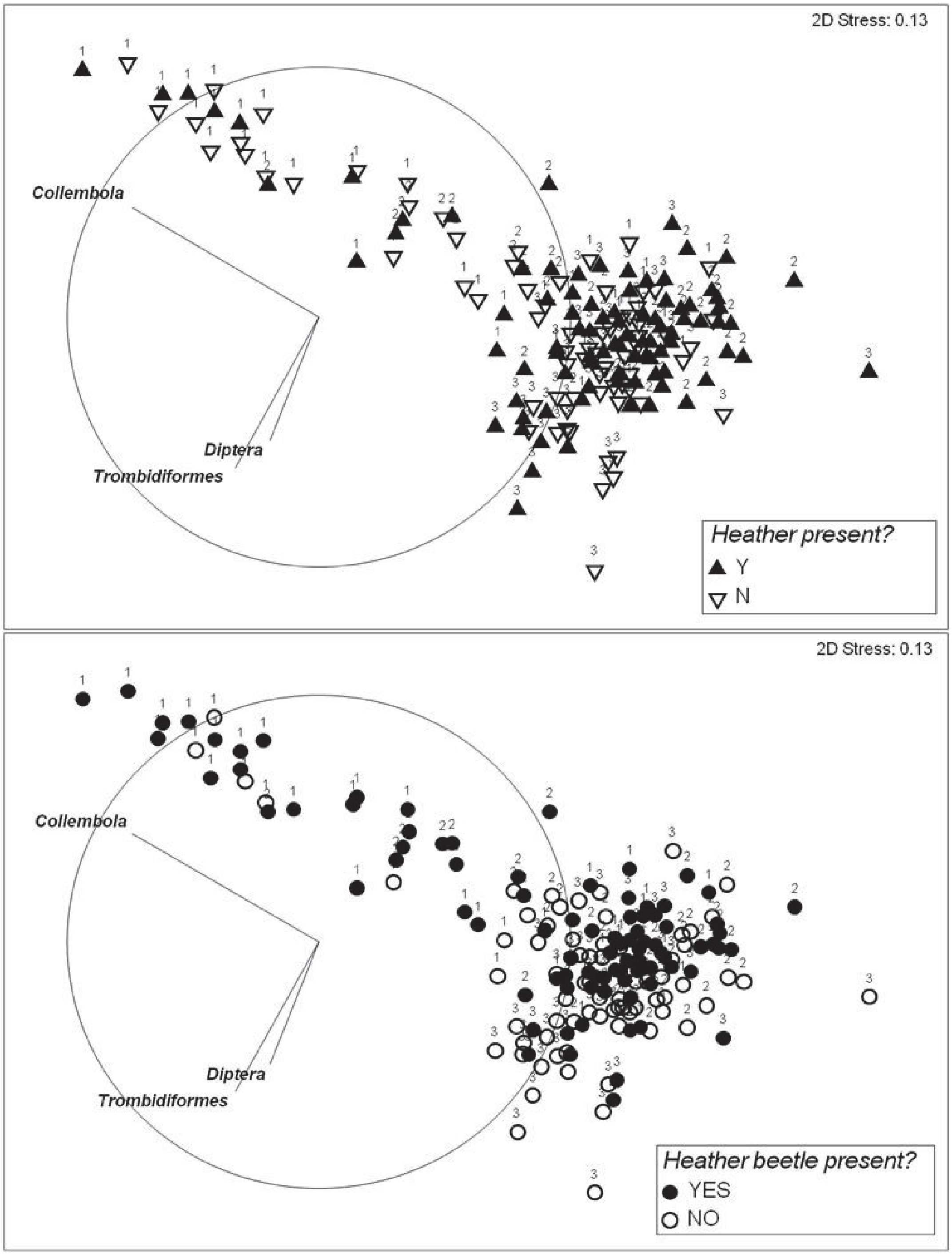
Plant species	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Dead heather	122.71	11	38.76	107	25.13	***
Tangle fern	25.57	73.22	17.60	62.5	34.42	***
Heather	0	40	13.88	-	-	***
Red tussock	21.57	30.67	10.97	18	12.44	
Coral lichen	13.57	17.89	6.19	6.5	11.22	
Wire rush	3.86	11.44	4.54	0	3.46	
Monoao	4.71			6	6.15	

All sites combined

Invertebrate composition

Overall, 68,071 macroinvertebrates were caught at all three sites during the 2010-2011 austral summer, excluding 17,363 heather beetles (adults and larvae combined) caught in addition to these macroinvertebrates.

Ordination of the data revealed little obvious distinction or grouping between plots with or without live heather (Fig. 4.14), as well as little distinction or grouping between traps with or without heather beetles (Fig. 4.15).



Figures 4.14 & 4.15: NMDS ordination plots of invertebrate data from all sites collected during the austral summer 2010-2011 from all sites in the central North Island. Symbols indicate whether either live heather or heather beetles are present. Vectors are Pearson correlations (>0.5) and numbers above plots indicate site.

There was a significant difference between invertebrate captures in different vegetation zones (*Pseudo*-$F_{2,159}$=3.38 p=0.001), trap sites with or without live heather (*Pseudo*-$F_{1,160}$=3.52 p=0.009), traps with or without heather beetles (*Pseudo*-$F_{1,160}$=4.03 p=0.003), and traps that caught at least 500 heather beetles and those that caught less (*Pseudo*-$F_{1,160}$=2.26 p=0.034). Traps that caught at least 100 heather beetles and those that caught less were not significantly different from each other (*Pseudo*-$F_{1,160}$=1.57 p=0.147).

The main invertebrate orders contributing to the difference between invertebrate communities in characterised vegetation zones were Collembola, Diptera, Trombidiformes, and Araneae. Collembola and Diptera were at high abundance in the native regenerating zone, with a decrease of density through the heather beetle feeding belt and a further decrease in the live heather zone. Trombidiformes were abundant in the live heather zone and at a lower abundance in the other two zones. Araneae were at highest abundance in the live heather and heather beetle feeding zones (Table 4.12).

In the comparison of invertebrate communities between trap sites with or without live heather invertebrate orders that were drivers of dissimilarity were Collembola, Diptera, Trombidiformes, Hymenoptera, and Hemiptera. Collembola and Diptera were approximately 50% more abundant in trap sites not containing live heather, while Trombidiformes were more abundant where live heather was present. Additionally, while being minor drivers of dissimilarity, Hymenoptera were significantly more abundant where live heather was present and Hemiptera were significantly less abundant (Table 4.13).

In a comparison of invertebrate communities between traps with or without heather beetle catches, Collembola and Araneae were more abundant in traps that caught heather beetles, while Trombidiformes and Diptera were slightly less abundant in traps that caught heather beetles (Table 4.14). In a comparison between trap sites that caught ≥500 heather beetles and those that caught less, Collembola and Diptera were major drivers of dissimilarity at about twice the abundance when ≥500 heather beetles were caught, compared with Trombidiformes which were less abundant (Table 4.15).

Table 4.12: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between characterised vegetation zones reported against the regenerating native zone using combined data with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Collembola	390.56	184.86	45.96	261.83	50.48	
Trombidiformes	29.47	43.99	13.44	24.72	8.06	*
Diptera	31.47	16.51	9.30	21.36	9.91	*
Araneae	18.72	22.88	6.13	21.22	5.34	
Hymenoptera	14.07	20.81	4.80	23.56	6.26	**
Hemiptera	18.42	7.71	4.69	8.31	4.68	**
Coleoptera	15.46	14.14	3.68	9.64	3.34	*
Oribatida	5.07	3.49	2.70	-	-	
Orthoptera	6.86	-	-	6.47	2.84	

Table 4.13: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites with or without live heather using combined data with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Live heather absent	Live heather present		
	Avg. abund.	Avg. abund.	Contrib. %	
Collembola	335.35	225.53	46.70	
Trombidiformes	29.67	38.54	12.50	
Diptera	29.07	17.88	9.03	*
Araneae	21.44	20.73	6.35	
Hymenoptera	15.25	22.09	5.66	**
Hemiptera	14.82	9.04	4.20	*
Coleoptera	14.92	12.56	3.55	
Orthoptera	6.53	5.22	2.61	

Table 4.14: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites with or without heather beetle catches using combined data with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	Heather beetle present	Heather beetle absent		
	Avg. abund.	Avg. abund.	Contrib. %	
Collembola	389.13	130.85	44.90	*
Trombidiformes	25.66	45.78	13.82	**
Diptera	21.52	24.51	8.64	
Araneae	24.00	17.36	6.68	*
Hymenoptera	18.86	19.29	5.91	
Hemiptera	11.31	11.99	4.12	
Coleoptera	13.93	13.19	3.60	
Orthoptera	5.27	6.47	2.69	

Table 4.15: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of invertebrate orders between trap sites that caught at least 500 heather beetles and those that did not using combined data with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Invertebrate order	At least 500 heather beetles present	Less than 500 heather beetles	
	Avg. abund.	Avg. abund.	Contrib. %
Collembola	680.50	253.24	61.71
Diptera	41.13	21.90	10.52
Trombidiformes	23.88	35.16	7.32
Araneae	16.88	21.27	3.88
Hymenoptera	13.13	19.36	3.53
Orthoptera	11.38	5.51	2.79
Coleoptera	12.25	13.68	2.27

Vegetation composition

Vegetation composition in all sites combined was strongly affected by the trap site's zone characterisation with the major distinct division between the native regenerating and the live heather zone. The heather beetle feeding belt zone was far more variable than either of the other two zones. There was also a distinction between the site located within the Erua conservation area (site 3) and the sites located within the WMTA (sites 1 and 2); despite this difference in vegetation between areas the distinction between the native regenerating zone and the live heather zone was maintained (Figs. 4.16 & 4.17)

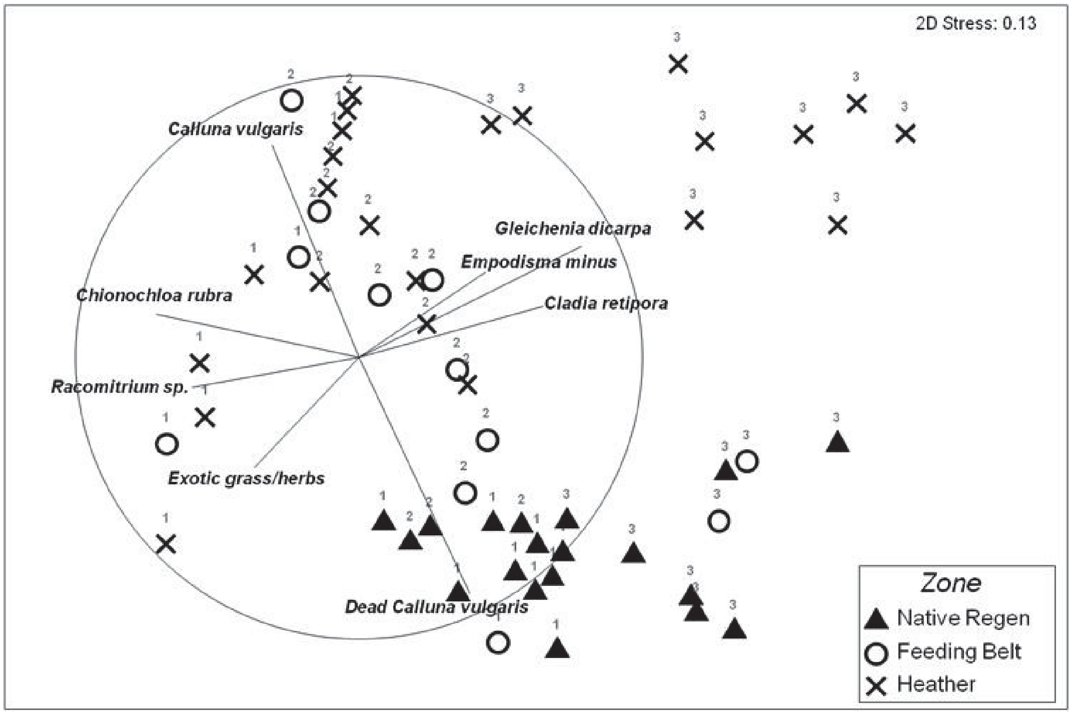


Figure 4.16: NMDS ordination plot of vegetation data collected during the austral summer 2010-2011 from all sites in the central North Island. Numbers above plots indicate site number. Vectors are Pearson correlations (>0.5).

There was a significant difference in vegetation composition between characterised vegetation zones (*Pseudo*-$F_{2,159}$=12.33 p=0.001). The main driver in the difference of vegetation composition between the regenerating native and heather zones was the presence of dead heather in the native regenerating zone. The density of heather in the live heather zone was also far lower than in the native regenerating zone.

Table 4.16: Average abundance and percentage contribution to the Bray-Curtiss dissimilarity (SIMPER analysis) of plant species between characterised vegetation zones reported against the regenerating native zone using combined data with a cut off of 90% cumulative contribution. Asterisk indicates significance of differences (*=p<0.05, **=p<0.01, & ***=p<0.001).

Plant species	Regenerating native zone	Live heather zone		Heather beetle feeding belt zone		
	Avg. abund.	Avg. abund.	Contrib. %	Avg. abund.	Contrib. %	
Dead heather	111.21	12.22	33.67	51.67	29.57	***
Heather	0.26	56.35	19.08	37.83	17.28	***
Red tussock	38.95	57.61	13.00	55.25	15.52	**
Tangle fern	9.42	28.65	10.59	10.42	7.68	***
Exotic grass/herbs	15.89	8.00	7.05	4.33	7.70	*
Woolly moss	10.26	14.26	5.61	29.50	12.05	***
Coral lichen	5.00	7.00	3.41	-	-	*
Monoao	2.37	-	-	7.00	3.69	

Discussion

The effects of heather, vegetation zones, and heather beetles were only obvious at site two and three. A combined analysis of data from all sites indicated invertebrate communities were affected by heather presence, heather beetle presence, and heather beetle densities over 500 individuals.

The effect of heather control on invertebrate communities

There were several invertebrate orders affected by the control of heather by the heather beetle. Collembola, Diptera, and Hemiptera were all more abundant after heather control. Trombidiformes and Araneae were more abundant in areas where heather was still intact.

The effects of heather presence/absence on invertebrate orders observed at this larger scale were consistent with the findings of the small scale experimental manipulation (Chapter two) and could be due to the same processes and factors hypothesised in chapter two. The results are also consistent with what would be expected after heather control based on the findings of Keesing (1995) on the effect of heather invasion on invertebrate communities. Heather appears to be an unsuitable food source for many herbivores (within Hemiptera and Diptera) and detritivores (such as Collembola), is a poor supporter of prey species for predators and parasitoids (including some Hemiptera and Diptera), and results in a more structurally complex habitat (resulting in an increase in Araneae abundance).

Trombidiformes were less abundant within heather free plots; this may be a result of the soil receiving greater exposure to sunlight, resulting in increased temperature fluctuations, reduced humidity, and increased likelihood of desiccation. However, Trombidiformes are a diverse order and resolving the driver for this change in density will require further investigation. In contrast to the experimental manipulation (Chapter two), Hymenoptera abundance was higher in this study in areas of intact heather. This may have an analogous explanation to the increased Thysanoptera abundance observed in chapter two and Keesing (1995); i.e. the result of heather providing a large nectar and pollen resource during flowering.

Heather dominated zones support few herbivores probably in part because of the low native vegetation density (Chapter two and Keesing (1995)), as the native regenerating zone is still recovering from very high heather density. When heather beetles were introduced they were released into the area of highest heather density and consequently lowest native vegetation density. Despite this low density of native vegetation in this zone (probably due to lack of recovery time), invertebrate herbivores are at greater densities within this zone than the heather zones. This may be a result of heather not only having a negative effect on native food sources, but also disrupting host finding behaviour of invertebrate herbivores by physical disruption, visual camouflage of host plant, masking of host odours, repellent chemicals, and increasing the number of inappropriate landings during host plant finding (Finch & Collier, 2000). Another possible cause was the increase in exotic grasses and herbs (at sites one and two) after the disturbance of biocontrol provided suitable resources for invertebrate herbivores. Exotic pasture grasses can be an unsuitable habitat for native invertebrates but their abundance and richness can nevertheless be higher in exotic pasture (Derraik, Rufaut, Closs, & Derraik, 2005). As this study was restricted in taxonomic resolution, whether or not this invasion of exotic grasses and herbs after biocontrol provides habitat for native invertebrate herbivores or facilitates invasion by an exotic invertebrate assemblage is not clear.

This study found that the broad changes in invertebrate communities in heather invaded habitats outlined by Keesing (1995) were reversed when heather was controlled to more closely resemble that of native non-invaded invertebrate communities. This finding, suggests that the large scale biological control of heather provides an ecosystem and conservation benefit to native tussock grasslands as it facilitates restoration to an invertebrate community resembling more closely what would occur in tussock-grassland not invaded by heather.

The effect of heather control on vegetation composition

As mentioned in the previous section, there was a higher heather density (as shown by the high density of dead heather) within the native regenerating zone before biological control than what is now in the live heather zone. This appeared to result in a greater proportion of native vegetation within the live heather zone than the native regenerating zone. The lower density of heather in the live heather zone may have been a contributing factor for the lack of clear differences in invertebrate communities between evaluated factors, although this situation of relatively low heather density within the live heather zone also occurred at site three where invertebrate communities, in contrast, did clearly differ between feeding zones.

At sites one and two exotic grass/herbs were at far high densities in the native regenerating zone than in the live heather zone suggesting that heather removal may be facilitating a secondary weed invasion, perhaps as a result of a "weed shaped-hole" being created (Buckley et al., 2007). However, there may be several contributing factors such as the previous land use of the site, which included grazing and attempts to oversow with exotic grass until the 1980s (John Mangoes pers comm.). Additionally, this invasion of exotic grasses and herbs may be a result of nutrient influx following biocontrol (discussed below). Further studies are being conducted to determine whether or not the invasion of exotic grass will be short lived as soil nutrients become depleted. Whether exotic grass/herb invasion is of benefit or detriment to the native ecosystem when compared to the previous invasion of heather is unknown. Unlike heather invasion, exotic grass/herb invasion does not facilitate habitat succession from grassland to shrubland (Keesing, 1995; Rogers, 1996) nor perhaps prohibit native revegetation (Dickinson & Mark, 1994; Dickinson, Mark, & Lee, 1992), thus exotic grass/herbs may have less of an impact than heather.

The indirect effect of the heather beetle on invertebrate communities

In comparisons between trap sites with or without heather beetle captures there were several invertebrate orders that appeared affected by heather beetle presence. When heather beetles were caught Collembola and Araneae showed an increase in abundance, while Trombidiformes showed a decrease in abundance. The effect on Diptera was more varied; depending on site they either reduced or increased in abundance in response to heather beetle presence.

The driver of the decrease in Trombidiforme abundance in the presence of heather beetles is unknown and further research is needed to explore how this invertebrate order is affected by the biocontrol of heather.

The presence of heather beetles could have a range of direct effects beyond reducing heather density, including an increase in the deposition of beetle frass, cadavers, and an increase in prey food items for generalist predators. An increase in herbivory increases nutrient deposition to the soil (Frost & Hunter, 2004; Hunter, 2001) through frass, insect cadavers, and dying plant material, thus the dense, mobile beetle feeding front would provide a sudden increase of food resources for detritivores and decomposers. Increases in deposition of frass to the soil are often accompanied by increases in soil arthropods like Collembola that respond to the associated microbial activity (Hunter, 2001). This would explain the observed greater abundances of Collembola in areas where heather beetles were present; the increase of Diptera may also have an analogous explanation as they may respond to the increase in decomposing matter for feeding, oviposition, and larval feeding sites.

The superabundance of heather beetles in the mobile feeding front may provide a food-subsidy to generalist predators and this short term food subsidy may disrupt natural food webs and community interactions (Pearson & Callaway, 2003), but perhaps only briefly. The super abundance of heather beetles is ephemeral as the front moves on after the heather has been consumed. The increase in Araneae abundance may be a result of food-subsidy by feeding on heather beetles. If this increase in a generalist predator's abundance is in fact a numerical response it may have the ability to spill over on to native invertebrates, food-webs and community structure (Pearson & Callaway, 2003), but these questions are beyond the scope of this work.

Conclusion

The biocontrol of heather using the heather beetle appears to restore invertebrate communities to one more closely resembling what Keesing (1995) found to occur in un-invaded habitats. This finding was consistent with the experimental manipulations in chapter two. Increased Hemiptera abundance in the native regenerating zone despite a lower abundance of native vegetation is believed to be a result of two non-mutually exclusive factors; the exotic grasses and herbs provide herbivores with a suitable resource and/or heather's effect on native herbivores goes beyond displacement of food sources and extends to it disrupting host finding behaviours. The disturbance caused through biocontrol appears to facilitate the invasion of exotic grasses and herbs but it is possible this invasion could be short-lived and caused by a pulse of nutrients from the impacts of heather beetle feeding. Two indirect effects of biocontrol on invertebrate communities were an increase in detritivores and decomposers (probably as a result of an increase in frass deposition, heather beetle cadavers, and dying heather), and the super abundance of heather beetles potentially providing a food-subsidy to Araneae, both of which may have further food-web community impacts. This study does not demonstrate net-benefit of biocontrol but does suggest an ecosystem and conservation benefit to native tussock grasslands through evidence for restoration of the invertebrate community. Ultimately though, more time will be required to assess longer-term changes including whether or not a short-term nutrient pulse is driving the invasion of exotic grass and if native plants recover along with their associated invertebrate communities.

Chapter Five

General Summary & Recommendations

Figure 5.0: Stream flowing from the slopes of Mount Ruapehu.

General Summary & Recommendations

General summary

This research, conducted in the tussock grasslands of the central North Island of New Zealand, was able to show that controlling heather (*Calluna vulgaris*) results in a net positive effect on communities. This was demonstrated regardless of the method of control and beyond the effects on the indigenous plant communities, showing conservation benefit to macroinvertebrate communities as well as native lizard abundance.

The effect of heather control

Invertebrates

The effect of heather control on invertebrate communities remained largely consistent between small experimental scale and large, landscape scale studies. Hemiptera were at higher density in areas where heather was controlled. This effect may be a result of heather providing a novel and unsuitable food source for native phytophagous insects. Furthermore, heather may pose a disruption to the host finding and acceptance behaviours of Hemiptera, preventing the utilisation of food resources located within heather dominated areas. Hymenoptera and Diptera increased following heather control, possibly as a result of an increase of phytophagous prey such as Hemiptera.

Araneae were less abundant in heather controlled areas. This effect was likely a result of the reduced structural complexity following heather removal. High structural complexity in heather dominated habitats provides greater web attachment, retreat, and brooding sites.

Thysanoptera were less abundance in areas where heather had been controlled. This effect may be due to the large amounts of pollen and nectar provided during heather’s prolific flowering period being no longer being available.

Trombidiid mites were lower in abundance where heather had been controlled. This was possibly a result of the opening up of the vegetation canopy and more exposure of the soil to sunlight, causing greater desiccation and temperature fluctuations rendering the soil less suitable as habitat.

These effects of heather control all remained consistent with a reversal of the effects of heather invasion Keesing (1995) identified. Namely heather presence caused an increase in the abundance of Araneae, pollen feeders such as some Thysanoptera, and a decrease in abundance of phytophagous insects (Keesing 1995). Thus heather control represents a reversion to an invertebrate community that more closely resembles those found within non-invaded habitats.

Common skink (*Oligosoma nigriplantare polychroma*)

Heather control appeared to have a positive effect on common skink abundance in small scale experimental manipulations of heather abundance. This effect was so pronounced that common skinks were almost completely absent in areas where heather cover remained intact. This effect was suggested to be a result of heather shading basking sites, posing a barrier to foraging activities, or by reducing their ability to avoid predators.

Vegetation composition

While noth herbicide and biological control methods effectively removed heather, biocontrol did not have any obvious direct non-target impacts on native vegetation like herbicide application did. Heather control in two sites where this research was undertaken appeared to facilitate the invasion of exotic grasses and herbs in the weed shaped hole left after control. Whether this is a short-term response to the influx of detritus and nutrient to the soil as a result of heather beetle feeding and heather decomposition is unknown. The ecosystem effects of this secondary invasion and the effect on the revegetation of native plants are also unknown.

The effect of the heather beetle on non-plant communities

Two orders were indentified that were positively impacted by the heather beetle’s presence. Collembola showed marked increases in abundance in the presence of heather beetles; this effect was more than likely a result of the increased deposition of frass, cadavers, and detritus from dead and dying heather. Araneae also increased in abundance in the presence of heather beetles; this was most likely a result of the super abundance of heather beetles providing a readily available food source that acted as a food subsidy. The effect of these observed effects of heather beetle presence on ecosystem function and species/trophic level interactions is unknown but may only be short-term.

Recommendations

- Continue to promote, use, and develop biological control programs for invasive plant control in conservation areas for sustainable, effective, and targeted weed control for conservation gains.
- Undertake more research on the direct and indirect effects of biological control in other biocontrol programs to increase the understanding of the effects of agents in the environment and to better inform future biocontrol programs.
- Continue post control monitoring to determine whether the findings of this research (apparent restoration of invertebrates to that resembling invertebrate communities found in non-invaded habitats) remain true following the recolonisation and increase in density of native vegetation.
- Undertake research to isolate and identify the reasons for heathers apparent detrimental effect on common skink abundance and investigate the effect of native revegetation on the abundance of common skinks in the Waiouru military training area.
- Investigate the persistence and ecosystem effects of increased Araneae and Collembola abundance post heather beetle feeding to expand current knowledge on the indirect effects of biological control and possible effects on species/trophic level interactions.

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