Plant invasion down under: Exploring the below-ground impact of invasive plant species and their biological control on soil properties and invertebrate communities in the Central Plateau of New Zealand

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Abstract

With the increase in global trade and environmental disturbances, plant invasion continues to be one of the greatest threats to native ecosystems.

The Central Plateau of New Zealand is of particular interest as it is home to several invasive plant species and biological control agents of these plants. Previous research has focused on the plant community responses of above-ground arthropods to plant invasions, but to my knowledge, no research has investigated soil properties and soil fauna communities at an individual plant level and compared these beneath native and invasive plants. Globally, information on post-release impacts of biological control agents on the below-ground communities and ecological processes is lacking, although we know that organisms such as foliar herbivores can impact the soil ecosystem indirectly, with consequences for control and subsequent recovery.

This research aims to fill in this gap by investigating: 1) the soil properties and soil fauna communities associated with two native plant species (*Leptospermum scoparium* – mānuka, and *Chionochloa rubra* – red tussock) and two invasive species (*Calluna vulgaris* – heather and *Cytisus scoparius* – broom), and 2) how soil properties and soil fauna communities change under heather (*C. vulgaris*) plants at three stages of biocontrol agent (heather beetle) attack (prior, during and following the attack).

In chapter 2, I sampled the soil physicochemical properties and macrofauna communities of two native and two invasive plant species. Rather than finding a difference between native and invasive plants as expected, I found a high degree of similarity between manuka and broom, and between red tussock and heather. This result highlighted the need to understand both the invasive and displaced vegetation when identifying impacts of invasion.

In chapter 3, I sampled the soil ecosystem under heather plants before, during, and after feeding by the heather beetle. As expected, I found that the soil properties under heather differed before and during heather beetle attack. Unexpectedly, I found no difference in soil properties under heather before and after control by heather beetle. I also found that Collembola (springtails) and Oligochaeta (earthworms) were more abundant after heather beetle attack. Interestingly, Thysanoptera (thrips) abundances were highest prior to heather beetle attack, which could potentially have important consequences for biocontrol efficacy.

These results provide some novel insights into the soil ecosystem responses to plant invasion, and the potential soil impacts post-biocontrol release, while highlighting the need for future research into a variety of plant species and control agents.

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Chapter 1: Introduction

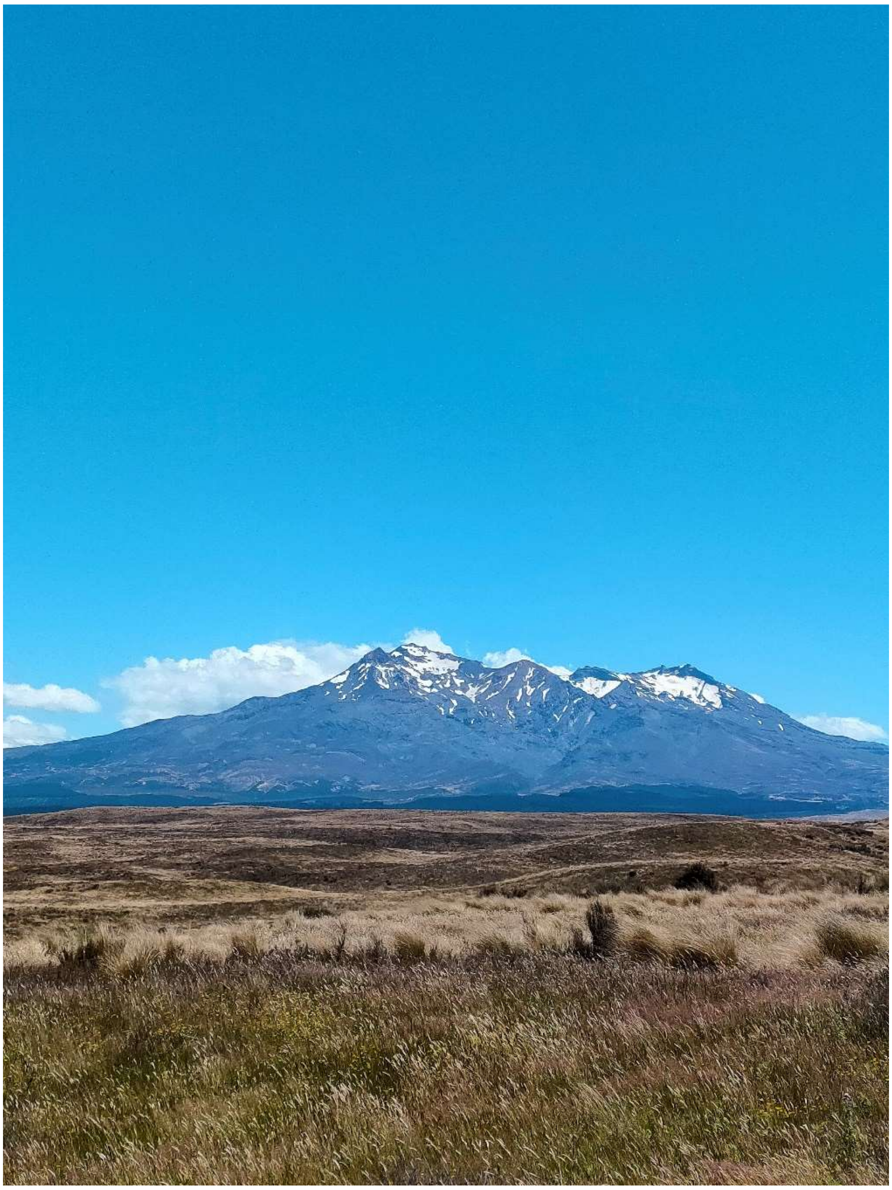

Figure 1. View of Mount Ruapehu from study site 1 (S39.31224°, E175.73932°) in the Waiouru military training area of the North Island Central Plateau, New Zealand.

1.1 Invasive plants in the Central Plateau and their biological control

The North Island Central Plateau (NICP) is a high-altitude desert-like region of the central North Island, New Zealand. NICP is home to Ngauruhoe, Ruapehu and Tongariro volcanoes and the Tongariro National Park (TNP) which was listed as a UNESCO dual heritage site in 1993 because of its natural and cultural significance (UNESCO World Heritage Convention, n.d). Common native vegetation in the area include mānuka *Leptospermum scoparium* (J.R.Forst & G.Forst.), red tussock *Chionochloa rubra* (Zotov), and *Dracophyllum* spp. (Effah et al., 2020). Exotic plant invasion is one of the main risks threatening the assets of TNP and the wider NICP. Two important invasive species of the area are European heather *Calluna vulgaris* (L.) Hull, family Ericaceae; henceforth heather, and Scotch broom *Cytisus scoparius* (L.) Link, family Fabaceae; henceforth broom, both originally from Europe.

From 1912 to 1923, heather was deliberately planted and its spread otherwise facilitated, to provide suitable habitat for exotic game fowl (Bagnall, 1982). After planting ceased, heather continued to spread and is now the most widespread weed species of the area, covering more than 50,000 ha of the TNP and greater NICP (Effah, 2020). Broom was introduced to the area in the 1960s, and while it is not as widespread as heather, its range has expanded in recent years. This species is able to fix nitrogen, and thus has the potential to alter soil nutrients and other soil properties (Landcare Research, 2022).

To manage the spread of heather, hand-pulling and herbicides were initially utilized, with little success (Syrett et al., 2000). Given the extent of the invasion, conventional herbicides were considered no longer a realistic management solution (Peterson et al., 2011). A management programme was initiated in 1990 that included the use of heather beetle *Lochmaea suturalis* (Thomson, 1866) (Coleoptera: Chrysomelidae) as a biocontrol agent of heather (Williams & Keys, 1993). The initial release of the beetle in 1996 was largely unsuccessful, but subsequent introductions of heather beetle have led to self-sustaining populations throughout the central North Island and this biocontrol agent is beginning to significantly impact heather over large areas of TNP (Hayes et al., 2013; Landcare Research, 2021; Peterson et al., 2004; Peterson et al., 2011). Heather beetle populations have dense discrete feeding fronts (Blayney, 2012). This behaviour makes it easy to find heather that is untouched by the heather beetle, live heather that is being fed upon by high densities of heather beetle, and dead heather that has recently been controlled by heather beetle, all in close proximity.

1.2 Invasive plants and their effect on soil properties and invertebrate communities

Invasive species can be defined (and this is the definition used for this thesis) as organisms that establish within a new range where they persist, proliferate and spread, causing environmental and economic harm (Mack et al., 2000; Rejmánek et al., 2005). Invasive plants are becoming increasingly important with the continuing growth of anthropogenic activity (Müller-Schärer et al., 2004). One of the main predictors of successful plant invasions is propagule pressure, which encompasses the number of propagules (such as seeds or reproductively viable individuals) per release and the number of times propagules are released (Williamson & Fitter, 1996). Through increasing global trade and migration, human activity has become a mechanism for enhancing propagule pressure (Mack et al., 2000). As well as being vectors of plant propagules, human activity has increased the susceptibility of native areas to invasions through frequent and large scale disturbances, and has helped many invasive plants to overcome barriers to establishment through deliberate cultivation (Mack et al., 2000). Invasive plants affect their invaded ecosystems in multiple ways, such as by altering plant community composition, aboveground and below-ground arthropod composition, and soil properties (Levine et al., 2003, Litt et al., 2014).

Plants alter soil properties through the uptake of nutrients and water, and through root exudation and decomposition of plant litter which alter nutrient pools and nutrient cycling as well as soil structure (Weidenhamer & Callaway, 2010). Invasive plants appear to alter the soil environment differently compared to native plants, with consequences for ecosystem processes (Stefanowicz et al., 2018; Weidenhamer & Callaway, 2010). In a meta-analysis, Liao et al. (2008) showed that invasive plants are usually associated with increases in soil carbon, nitrogen and phosphorous pools, and increases in decomposition and mineralisation rates, especially for woody and N-fixing invasive species. These trends are likely caused by invasive plants frequently displaying higher plant performance values such as leaf nutrient concentrations and primary productivity, which are linked to soil carbon and nitrogen cycling processes (Stefanowicz et al., 2018). For example, Adams et al. (2016) showed that N-fixing plants in non-agricultural ecosystems consistently had greater nitrogen concentrations in leaf tissue. The effect of invasive plants on soil properties is not consistent, however, and the size as well as the direction of the effect can depend on numerous invader and ecosystem variables. For example, in a study of seven invasive plant species (*Fallopia japonica* (Caryophyllales)*, Heracleum mantegazzianum* (Apiaceae)*, Impatiens glandulifera* (Balsaminaceae)*, Prunus serotina* (Rosaceae)*, Rosa rugosa* (Rosaceae)*,* and *Solidago gigantea* (Asteraceae)) in NW Europe, Dassonville et al. (2008) found positive effects on soil nutrient pools when the initial soil was nutrient poor, and negative effects when the initial soil was nutrient rich.

Invasive plants displace native plants through competition and other mechanisms such as chemical alteration of soil, disruption of native pollinator relationships and allelopathy, often becoming the dominant species in the invaded ecosystem overtime (Effah, 2020; Levine et al., 2003; Vilà et al., 2011). Therefore, it is not surprising that invaded systems are often associated with decreased aboveground arthropod abundance and richness when compared to similar uninvaded systems (Blayney, 2012; Litt et al., 2014). This is often attributed to the decrease in plant biodiversity (Ebeling et al., 2018) and to the replacement of native plant resources by novel plant resources. The success of many invasive plants is attributed to the enemy escape hypothesis, which suggests that invasive species escape the co-evolved antagonistic relationships (such as herbivores) of their native ranges and that this reduced top-down control explains their relative vigour in the new range (Williamson & Fitter, 1996). This hypothesis assumes that native specialists rarely host-shift onto invasive plants and that native generalists have a stronger impact on native plants than on co-existing exotics (Tallamy, 2004). Native herbivores are thought to under-utilize exotic plant resources as they do not share an evolutionary history with them and lack adaptations for incorporating their biomass (Tallamy, 2004). Meijer et al. (2015) tested the assumptions of the enemy escape hypothesis by sampling insect herbivores from 47 woody plant species in the Netherlands and Japan and found that native plants had higher herbivore diversity and herbivore load and more herbivory than the non-native ones. This reduction in herbivores is then thought to drive a reduction in higher trophic levels, as in the predators and parasitoids of native herbivores (Bezemer et al., 2014). Invasive plants can also affect fauna communities by altering plant-arthropod linkages associated with pollination (Muñoz & Cavieres, 2008) or by providing new habitat features that can be utilized by native groups. Though generally negative, the effect of invasive plants on above-ground arthropods can vary in size and direction depending on the specific invader and the recipient habitat, and which arthropod taxa are considered (Effah et al., 2020; Keesing, 1995; Litt et al., 2014).

As well as above-ground, plants can alter below-ground fauna assemblages since plants provide the main input into soil food webs, either through input and subsequent decomposition of leaf litter or through root material and the exudation of organic compounds by the roots (Potapov et al., 2019; Wolfe & Klironomos, 2005). Recent evidence suggests that root material and exudates, rather than leaf litter, supply the greatest proportion of this input (Bluhm et al., 2017; Fu et al., 2017; Pollierer et al., 2007; Sprunger et al., 2019). Studies on the effect of invasive plants on below-ground invertebrates are conflicting and depend on the invasive plant identity and the recipient system. Some studies show positive effects, some show no effect, and some show negative effects such as those reported in gastropods and isopods associated with giant knotweed invasion (Belnap & Phillips, 2001; Kappes et al., 2007; Rudd, 2009; Tanner et al., 2013). However, a meta-analysis reported plant invasion generally favouring soil invertebrates (Meisner et al., 2014). This may be because below-ground herbivore communities typically consist of more generalist taxa than above-ground, which are more likely to utilize a new resource. Therefore, the "enemy escape" phenomenon may be less pronounced or even absent below-ground (van Ruijven et al., 2005).

1.3 Biological control

Classical biological control of invasive plants aims to reduce the population density of a target plant using plant herbivores or pathogens sourced from the plant's native range (Seastedt, 2015). Classical biological control of invasive plants aims to re-establish the antagonistic relationships of invasive plants by establishing one or more of their natural enemies in the invaded range. This is predicted to reduce the competitive advantage of the invasive plant, and ultimately reduce its density and spread (Middleton, 2008). One example of this can be observed in the management of *Lonicera japonica* (Caprifoliaceae) in New Zealand as summarized in Paynter et al. (2017). In the invaded range, the species was shown to support only a small number of weakly antagonistic herbivores and pathogens, while a survey of the native range revealed a rich natural enemy biota, including numerous insect herbivores. The enemy-escape hypothesis was used to explained the relative vigour of the plant in the new range compared to their native range (Schierenbeck et al., 1994). Due to their host-specificity and complimentary damage mechanisms, two of insect herbivores were approved for release in New Zealand. The Honshu white admiral butterfly *Limenitis glorifica*, the first of these agents, was released in 2015 and has become established (Paynter et al., 2017). *L. glorifica* larvae chew the leaves of *L. japonica*. The second agent, the Japanese honeysuckle stem beetle *Oberea shirahatai* was first released in 2018 and will be redistributed once the released populations increase in number (Landcare Research). Larvae of *O. shirahatai* are stem-miners and adults are leaf chewers of *L. japonica*.

Reducing the relative competitive performance reduces invasive plant dominance in local landscapes and the negative impacts associated with them (Gratton & Denno, 2005). Modern classical biological control involves intensive testing to ensure the natural enemy does not cause direct damage to the local habitat by host switching, but indirect effects are less often considered (Pearson & Callaway, 2003). Classical biocontrol can indirectly negatively impact communities when the target plant has become incorporated into the native community, when the control method causes an unexpected plant compensatory response that increases its competitive ability, and when the influx of biomass from the newly establishing biocontrol agent population reshapes the food web (Pearson & Callaway, 2003).

There is little in the literature investigating the effects of biocontrol of invasive plants on soil properties and fauna, however, there is some information about the effects of above-ground invertebrate herbivores, a group commonly implemented in the biological control of invasive plants. Plant processes mediate soil physico-chemical and biological properties of the substrate they inhabit (Zhang et al., 2019). Though highly variable, above-ground herbivory can accelerate nutrient cycling and increase nutrient pools in the rhizosphere and litter (Bardgett et al., 1998; Belovsky & Slade, 2000; Classen et al., 2006; Kristensen et al., 2020). These effects are associated with changes in the quantity and quality of plant inputs into the soil system (Bardgett et al., 1998). Changes to plant resource quantity occur when foliar herbivores induce plant responses that increase root exudation, root carbon allocation and biomass as well as changes in root morphology (Bardgett et al., 1998; Heinze, 2020). The quality of plant inputs into the soil can change when foliar herbivores affect decomposer organisms either directly through deposition of highly labile excreta, or indirectly by inducing plant responses that alter the concentrations of nutrients and secondary metabolites in plant tissues. Increases in nutrient concentrations of leaf tissue will increase litter quality and enhance decomposition and nutrient cycling, whereas the build-up of secondary metabolites in these tissues may have the opposite effect (Bardgett et al., 1998; Wardle & Bardgett, 2008). Root herbivores can be affected by foliar herbivores when they induce changes in root morphology, root carbon allocation and changes in nutrient and secondary metabolite concentrations in root tissue (Blossey & Hunt-Joshi, 2003). For example, Soler et al. (2007) found that foliar herbivory by *Pieris brassicae* L. (Lepidoptera: Pieridae) significantly reduced the survival rate and adult size of the root herbivore *Delia radicum* L. (Diptera: Anthomyidae) on the host plant *Brassica nigra* L. (Brassicaceae). This was thought to be driven by an increase in the root tissue concentrations of indole glucosinolate allelochemicals. Soler et al. (2007) also demonstrated that foliar herbivory can have indirect impacts on members of higher trophic levels, with the survival rate and adult size of *Trybliographa rapae* (Westwood) (Hymenoptera: Figitidae), a natural enemy of *D. radicum*, also being significantly reduced by foliar herbivory. Soil microbial biomass and activity has been shown to increase with increased root exudation (Hamilton & Frank, 2001) and this will presumably have consequences for microbial nutrient cycling, microbivore fauna and higher trophic levels. Some soil fauna groups are sensitive to specific soil properties (Birkhofer et al., 2012; Hoeffner et al., 2021; Singh et al., 2020; Tóth & Hornung, 2020), and indirect and direct effects of aboveground herbivores on soil properties may be expected to also impact upon such groups.

1.4 Research background

Previous work has explored the impact of plant invasions on arthropod communities in the NZ Central Plateau and mainly focused on above-ground effects, while changes in soil properties and the effect of biological control remain poorly explored. In a PhD thesis on heather in Tongariro, Keesing (1995) investigated the above-ground arthropod compositions associated with a variety of common native plant communities with different dominant native plant species and similar communities invaded with heather, as well as communities dominated almost completely by heather. Native communities included those dominated by tussock grass, *Dracophyllum subulatum*, *Gleichenia*, mānuka and flax. The study found an increase in pollen feeders and spider abundance in heather-invaded sites, which Keesing (1995) attributed to the relatively high architectural complexity of heather, as well as a decrease in phytophagous insects. Effah et al. (2020) explored the above-ground arthropod community response to plant invasion in the NZ Central Plateau. Arthropods were collected using several different trapping methods within sites invaded with heather or broom, and uninvaded sites dominated by mānuka or *Dracophyllum*. When compared to uninvaded sites, there was a reduction in arthropod abundance in heather-invaded sites, while arthropod abundance was higher in broom-invaded sites. Overall, Effah et al. (2020) study found no significant effect of broom or heather invasion on arthropod richness. Though Keesing (1995) and Effah et al. (2020) included some soil fauna in their studies, both sampled soil fauna at a plant community level. Keesing (1995) only used one soil fauna sample per plant community type. Effah et al. (2020) only used one sampling method that collected fauna active on the soil surface (pitfall traps).

To assess the ecosystem effects of heather beetle, Blayney (2012) investigated the above-ground arthropod community in plots where heather had been controlled by the heather beetle, plots where heather had been controlled by herbicide and plots where heather was still present and healthy. Blayney (2012) found that community assemblages associated with the heather beetle biocontrol and herbicide control of heather were more closely resembling communities uninvaded by heather as described by Keesing (1995), which implies that the biocontrol agent was partially successful in remedying the effects of plant invasion. The Blayney (2012) study focused on the above-ground plant community scale effects of control of heather, and the results were associated with the removal of negative impacts of heather invasion but did not address soil ecosystem responses to heather beetle attack at the scale of individual plants.

Little is known about the soil properties and fauna associated with invasive plants in the North Island Central Plateau, and how biological control may impact these. As plant invasion and the biocontrol of weeds can have consequences for the soil ecosystem, this thesis aims to explore their effects in this ecosystem.

1.5 Specific Objectives

The objectives of this study were:

1. To investigate soil physicochemical properties and macrofauna assemblages associated with two invasive plants (heather and broom) and two native plants (mānuka and red tussock) in the NZ Central Plateau.

2. To investigate soil physicochemical properties and macro- and mesofauna assemblages associated with heather (*C. vulgaris*) at three stages of heather beetle herbivory (undamaged, alive but being fed upon by populations of heather beetle and having been killed by heather beetle attack).

1.6 Thesis structure

This thesis is made up of four chapters.

Chapter 1 provides general introduction and background information on the key concepts used throughout the thesis, describes the area where research is conducted and presents research aims and thesis structure. The chapter also reviews the current literature on the effect of invasive plants and of above-ground herbivory on soil invertebrate communities.

Chapter 2 is a research-based chapter comparing soil fauna communities under native and invasive plants in the NZ Central Plateau.

Chapter 3 is a research-based chapter comparing soil properties and soil macro- and mesofauna assemblages under heather plants at three stages of heather beetle attack (prior, during and following the attack).

Chapter 4 is a general discussion interpreting the results of the two research chapters and how they fit within the broader field.

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Chapter 2: Soil properties and soil macrofauna communities under broom, heather, mānuka and red tussock plants in the North Island Central Plateau of New Zealand.

2.1 Introduction

Plants influence the physico-chemical properties and fauna compositions of the soil in which they grow (Bezemer et al., 2014; Weidenhamer & Callaway, 2010; Wolfe & Klironomos, 2005). Owing to their different plant traits and novel interactions with the native community members, invasive plants can differently affect the soil environment when compared to native plants (Liao et al., 2008; Meisner et al., 2014).

Plants alter the soil in which they grow through the uptake of nutrients and moisture, the input of root exudation and the deposition of litter (Weidenhamer & Callaway, 2010). Invasive plants are often associated with greater soil pools organic matter and increased rates of litter decomposition and nutrient cycling than native plant species (Liao et al., 2008). This trend is often ascribed to the tendency in invasive plant taxa to present higher values for performance-based plant traits, such as leaf nutrient concentrations and net primary productivity, which are linked to nutrient cycling rates (Stefanowicz et al., 2018). Nitrogen-fixing plant species are disproportionately represented among invasive plants and are associated with higher rates of nitrogen cycling than native taxa and other invasive taxa lacking this trait (Ehrenfeld, 2003; Vilà et al., 2011).

Invasive plants can impact the soil food web through root exudation, root material and litter (Potapov et al., 2019; Wolfe & Klironomos, 2005). However, the impacts of invasive plants on soil fauna communities are not necessarily negative. For example, higher primary productivity and leaf nutrient concentrations, often associated with invasive plants, could stimulate the decomposer groups in the leaf litter. Indeed, a meta-analysis suggests that plant invasion generally favours soil invertebrate abundance (Meisner et al., 2014). In contrast, above-ground, invaded plant communities often have reduced herbivore abundances and richness, and this may be due to the reduced density of native plant species that support more herbivores and/or to a higher number of specialist herbivores unable to adapt to a new plant resource (Litt et al., 2014). The lack of specialist herbivores is the basis of the “enemy-escape hypothesis” used to explain the success of some exotic species in their new ranges.

Two key assumptions of the enemy escape hypothesis are that specialist enemies in the new range will only rarely host-switch to the invading species, and that generalist enemies will have a lesser impact on invasive taxa comparing to the native congeners (Williamson & Fitter, 1996). Combined, these assumptions mean that invasives should have a lower load of enemy organisms, such as herbivores, relative to co-existing native plants (Tallamy, 2004). Although this is generally observed above-ground, the logic should equally apply to the herbivores of the below-ground plant organs. Some soil fauna groups are sensitive to soil properties, such as in Oligochaeta and Diplopoda (Birkhofer et al., 2012; Dunxiao et al., 1999; Hoeffner et al., 2021; Kamin, 2010; Singh et al., 2020; Stašiov et al., 2021; Tóth & Hornung, 2020). By altering soil properties, plants may be expected to indirectly impact these groups.

Previous studies have investigated how invasive plants such as heather and broom affect arthropod communities in the NZ Central Plateau (Effah et al., 2020a; Keesing, 1995), however, these studies mostly focused on above-ground arthropods. Therefore, there is a knowledge gap regarding the impact of these invasive plants on soil invertebrate communities, which I addressed in this work by comparing soil faunal communities underneath two invasive (heather and broom) and two native (red tussock and mānuka) plant species.

Red tussock (*Chionochloa rubra*) is a native grass species common in the central North Island. It was selected for this study partly as a distinctive native character of the area, and partly because it is sensitive to displacement by invasive plants. Mānuka (*Leptospermum scoparium)* is a widespread native New Zealand shrub species of economic interest (Effah et al., 2020b; Hayes et al., 2013; Stephens et al., 2005). Mānuka is a mid-successional plant, playing an important role in disturbed sites and in sites where soil properties prevent succession into forest (Stephens et al., 2005) and is a taonga (treasured) species of cultural value to Māori (Morgan et al., 2019). Broom (*Cytisus scoparium*) and heather (*Calluna vulgaris*) were both introduced to NZ from Europe, and are the most important weed species in the Central Plateau (Effah, 2020). Both are woody shrub species, and broom is an N-fixing plant. Red tussock grassland communities are considered highly at risk due to heather invasion, which resulted in a large decline in red tussock between 1960 and 1984 (Chapman & Bannister, 1990).

In this chapter I investigated differences in soil physico-chemical properties and soil macrofauna communities of the leaf layer and rhizosphere associated with broom, heather, mānuka and red tussock at an individual-plant scale in the North Island Central Plateau.

Based on existing literature, I predicted that:

That soil properties would cluster for invasive and native plants, with separation between these two groups explained by higher soil nutrient concentrations (especially of carbon, nitrogen) under invasive plants. I predicted that soil carbon and nitrogen will be significantly higher for invasive plants compared to native plants, especially for broom, as it is an N-fixing species.

That macrofauna total abundance would be higher for invasive plant species (as generally positive impact on invasive plant on soil invertebrates in the literature). I expected macrofauna community compositions would cluster based on invasive status, with invasives being associated with greater abundances of decomposer groups (due to more labile leaf litter) and lesser abundance of root herbivore groups (due to enemy escape and a lack of shared evolutionary history between native herbivores and invasive plants).

2.2 Methods

Site description

The field sites were located inside the Waiouru military training area (S39.31224°, E175.73932 (site 1); S39.30947°, E175.73894° (site 2); S39.30242°, E175.74498° (site 3)). The region has a Köppen climate classification of “cfb” (temperate oceanic climate) (Kottek, 2006). The mean daily temperature of Wairouru ranges monthly from 5°C to 15°C (Chappell, P.R., 2015). The Rangipo “Desert” has an annual rainfall in excess of 1,500 mm (DOC, n.d). The region has low fertility soils mostly formed from volcanic ash (Effah, 2020). Common soil types of the military training area include tephric recent and orthic allophanic (Hewitt, 2010). The sites were chosen based on the presence of healthy populations of heather, broom, mānuka and red tussock, as well as being reasonably distant from one another while located on the same soil type. To avoid potential effects of above-ground invertebrate herbivory, areas where the heather beetle was present were avoided for this study. At each of the three sites, five individual plants of broom, heather, mānuka and red tussock were selected. Twenty individual plants in total were selected from each site, making up 60 plants over the entire study. Individual plants were selected to have similar phenology within each species. Plants were only selected if they were not in proximity (less than one meter) of any individuals of the other study species.

Soil sampling

Date and time of day were recorded immediately prior to sampling the soil underneath individual plants. At each individual sampling point, soil temperature and soil volumetric water content were recorded. A digital soil thermometer was used to collect three measurements around the target plant which were then averaged. A TDR soil moisture meter was used to collect three measurements of soil volumetric water content around the target plant that were then averaged. Soil samples (5 cm length x 5 cm width x 8 cm depth) were taken from the base of every plant in this study, kept on ice in the field and then sent to Hill Laboratories in Hamilton, New Zealand for “basic soil profile” and “organic soil profile” analysis, which included pH, Olsen phosphorous, anaerobically mineralizable nitrogen, total nitrogen, organic matter, carbon/nitrogen ratio, potassium (percentage of base saturation, i.e., %BS), calcium (%BS), magnesium (%BS), sodium (%BS), cation exchange capacity (me/100g), total base saturation, and volume weight (g/mL).

Macrofauna sampling

Another lot of soil samples (30 cm length, 20 cm width x 15 cm depth) were collected with a shovel directly against the base of each target plant. Samples were bagged and put on ice in the field and stored at 4°C in the lab until sorting. A total of 60 macrofauna samples were collected and sorted for this study. Macrofauna were hand-sorted from the samples and stored in 70% ethanol until being identified to order level. For this study, macrofauna were defined as any organism larger than 2 mm on its longest axis.

Data analysis

All data analysis was performed in R (version 4.1.3).

Soil property data was first standardized to unit variance (standardized value = value-mean/standard deviation) prior to Principal component analysis (PCA). PCA using "FactoMineR" and "factoextra" packages was performed on the standardized soil property data. The PCA biplot and corresponding table of variable contributions were then used to identify clusters and visualise differences in soil properties between vegetation types (heather, broom, mānuka and red tussock). To test for differences in the composition of soil properties between vegetation types, permutational multivariate analysis (PERMANOVA) was done using the "adonis" function in the "vegan" package. Soil property data was first standardized to unit variance to prevent bias from properties with naturally higher levels of variation and different units of measurement. PERMANOVA was performed using Euclidean distance for soil properties. When a significant difference was detected, multiple comparisons were performed for each plant species pairing individually. Data was then grouped by the clusters identified from the PCA ordination and a PERMANOVA was then used to compare the soil property compositions of the clusters.

Generalized linear models (GLMs) were used to test differences in specific soil properties between vegetation types. For each property, a GLM with normal, gamma or inverse-gaussian distribution family was generated, and the model with the best fit to the data (lowest AIC value) was used. The "LRTest" function from the "lmtest" package was used to assess the significance of the predictor variable for each of the chosen models. When the model was significant, Tukey's honestly significant difference test was performed using "TukeyHSD" function for post-hoc pairwise analysis.

Soil macrofauna data were then analysed. Invertebrate taxa that were not present in more than two samples were omitted from the data set. Total macrofauna abundance for each sample was calculated by summing the counts from all orders. For each sample, order richness was calculated using the "specnumber" function. Simpson's diversity and Shannon's diversity indices (Morris et al., 2014) were calculated using the "diversity" function from the "vegan" package. Generalized linear models were used to compare abundance and diversity variables among vegetation type (heather, broom, mānuka and red tussock). For total abundance and order richness, GLMs with poisson and negative-binomial distributions were generated, and the best fitting models selected for each. For Simpson's index and Shannon's index, GLMs with normal, gamma or inverse-gaussian distribution family were generated and the model with the best fit to the data was selected for each. The "LRTest" function was used to assess the significance of the predictor variable for each of the chosen models. When the model was significant, a Tukey's HSD test was performed for post-hoc pairwise analysis.

To visualise the differences in community composition and to identify specific groups likely to contribute to them, linear discriminant analysis (LDA) was performed on the soil macrofauna data. For this analysis, counts of Diplura, Blattodea and Achatinoidea were combined into the group "Other" to reduce the number of zeros and the dataset was square roottransformed. PERMANOVA with Bray-Curtis distance was performed on this dataset to test if the composition of the soil macrofauna community varied significantly among vegetation types. When significant results were detected, multiple comparisons for each vegetation pairing were performed using PERMANOVA with Bray-Curtis distance. Individual groups were then compared between plant species using GLMs (selected by AIC from poisson and negative-binomial distributions) and likelihood ratio test. When models were significant, TukeyHSD were performed for post-hoc pairwise analysis.

2.3 Results

2.3.1 Soils

The PCA ordination showed overlap between soil properties under mānuka and broom as well as between red tussock and heather, forming two distinctive clusters, mānuka/broom and red tussock/heather (Fig. 2). The first and second principal components (PC1 and PC2) collectively explained 58.3% of the variation in soil properties between vegetation types (Appendix 1.1). PC1 was characterized by potentially available nitrogen, anaerobically mineralizable nitrogen, total nitrogen, cation exchange capacity and total base saturation. PC2 was characterized by pH, organic matter, calcium, magnesium and total base saturation (Appendix 1.2). PCA ordination (Fig. 2) suggests that red tussock and heather are associated with acidic and nutrient-poor soils, whereas broom and mānuka are associated with higher soil pH and higher soil nutrient availability.

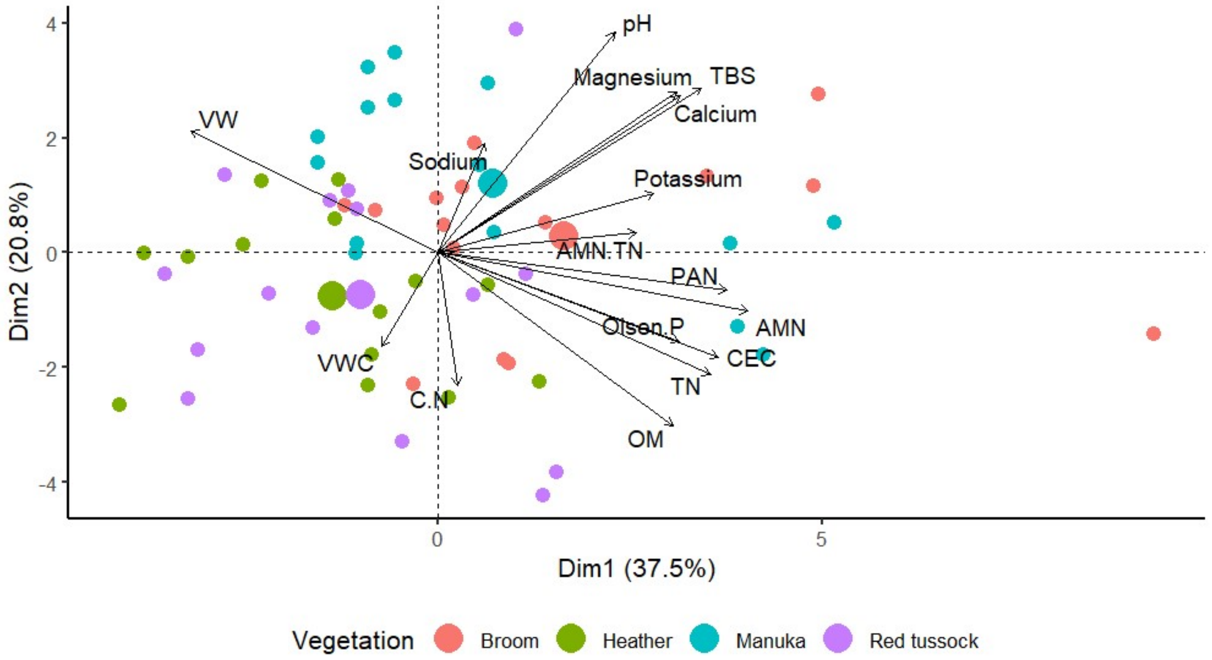

Figure 2. PCA biplot showing the soil properties under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Dim1 represents PC1 and Dim2 represents PC2. Large circles indicate the centroids of the respective groups. Abbreviations/acronyms/units: Volume weight in g/mL (VW), Volumetric water content (VWC), Olsen phosphorous (Olsen P), Potentially available nitrogen (PAN), Anaerobically mineralizable nitrogen (AMN), Total nitrogen (TN), Organic matter (OM), carbon/nitrogen ratio (C.N), Potassium in %base saturation (i.e., %BS), calcium %BS, magnesium %BS, sodium %BS, Cation exchange capacity (CEC), Total base saturation (TBS).

The overall composition of soil properties was significantly different among the plant species (PERMANOVA; Pseudo-$F_{3,56} = 4.52$, $P = 0.001$). Specifically, differences in soil properties were detected between broom and heather (PERMANOVA; Pseudo-$F_{1,28} = 6.76$, $P = 0.001$), broom and mānuka (PERMANOVA; Pseudo-$F_{1,28} = 3.42$, $P = 0.006$), broom and red tussock (PERMANOVA; Pseudo-$F_{1,28} = 5.43$, $P = 0.001$), heather and mānuka (PERMANOVA; Pseudo-$F_{1,28} = 6.18$, $P = 0.001$), and mānuka and red tussock (PERMANOVA; Pseudo-$F_{1,28} = 5.61$, $P = 0.001$). Soil property composition was significantly different between heather/red tussock and broom/mānuka clusters (PERMANOVA; Pseudo-$F_{1,58} = 9.37$, $P = 0.001$).

Among the four plant species, there were significant differences in pH (LRTest; $P < 0.001$), Olsen phosphorous ($P = 0.036$), potentially available nitrogen ($P = 0.041$), anaerobically mineralizable nitrogen ($P = 0.037$), total nitrogen ($P < 0.001$), C:N ratio ($P = 0.001$), potassium ($P < 0.001$), calcium ($P = 0.001$), magnesium ($P < 0.001$), sodium ($P < 0.001$) and total base saturation ($P < 0.001$) (Table 1).

Table 1 summarizes the soil properties associated with the four tested plant species. The mean soil pH values were slightly acidic for all treatments but were significantly more acidic in the soil associated with heather and red tussock than with broom and mānuka. Mean Olsen P was highest under broom, but not significantly different among treatments. The mean PAN was significantly higher under broom than heather. Mean TN and potassium were significantly higher and C/N ratio was significantly lower under broom than under all other treatments. Mean calcium was highest under mānuka (significantly higher than under heather). Mean magnesium was significantly higher under mānuka than heather or red tussock and significantly higher under broom than red tussock. Mean sodium was significantly higher under mānuka than other plants and significantly higher under broom than red tussock. Mean total base saturation was significantly higher under mānuka than under heather or red tussock and significantly higher under broom than heather.

Table 1. Soil properties under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Overall comparisons between plant species were performed using generalized linear models and likelihood ratio tests. Different letters indicate significant differences of the means within each row (Tukey's HSD, α=0.05). Abbreviations/acronyms/units: Volume weight in g/mL (VW), Volumetric water content (VWC), Olsen phosphorous (Olsen P), Potentially available nitrogen (PAN), Anaerobically mineralizable nitrogen (AMN), Total nitrogen (TN), Organic matter (OM), carbon/nitrogen ratio (C.N), Potassium in %base saturation (i.e., %BS), calcium %BS, magnesium %BS, sodium %BS, Cation exchange capacity (CEC), Total base saturation (TBS).

	Broom			Heather			Mānuka			Red tussock			χ^2	*P*-value
	Mean	SE		Mean	SE		Mean	SE		Mean	SE			
VW	0.61	0.02		0.63	0.02		0.62	0.01		0.63	0.01		1.84	0.606
VWC	10.94	1.21		13.23	1.65		10.54	1.46		11.66	0.99		2.44	0.487
pH	5.71	0.07	A	5.39	0.05	B	5.63	0.04	A	5.40	0.07	B	19.33	**<0.001**
Olsen P	4.33	0.23	A	3.60	0.16	B	3.87	0.27	AB	3.60	0.16	AB	8.57	**0.036**
PAN	98.47	9.15	A	67.67	7.20	B	73.60	7.20	AB	73.53	6.97	AB	8.25	**0.041**
AMN	4.43	0.54	A	3.20	0.21	A	5.57	0.29	A	2.93	0.31	A	8.49	**0.037**
TN	0.51	0.02	A	0.37	0.01	B	0.39	0.03	B	0.41	0.02	B	18.67	**<0.001**
AMN/TN	2.15	0.18		1.99	0.25		2.07	0.17		1.92	0.16		0.85	0.839
OM	18.32	1.02		16.01	0.91		16.47	1.56		17.79	1.42		2.36	0.501
C/N	20.87	0.92	B	24.67	0.59	A	23.82	0.67	A	24.88	0.90	A	15.7	**0.001**
Potassium	4.02	0.39	A	2.13	0.12	B	2.67	0.15	B	2.25	0.13	B	41.03	**<0.001**
Calcium	17.67	2.07	AB	11.33	1.14	A	22.40	1.72	B	14.13	2.47	AB	15.79	**0.001**
Magnesium	4.43	0.54	AB	3.20	0.21	BC	5.57	0.29	A	2.93	0.31	C	26.81	**<0.001**
Sodium	0.44	0.05	B	0.34	0.03	BC	0.61	0.03	A	0.31	0.02	C	34.48	**<0.001**
CEC	18.87	1.14		17.27	0.90		19.87	1.32		16.53	0.91		6.44	0.092
TBS	26.67	2.69	AB	16.60	1.49	C	31.33	1.92	A	19.53	2.76	BC	22.89	**<0.001**

2.3.2 Soil macrofauna

Order richness, Simpson’s and Shannon’s indices for soil macrofauna showed no significant difference among the vegetation types. Total macrofauna abundance was significantly different among the four plant species of this study (LRTest; $\chi^2 = 13.64$, $P = 0.003$). Total macrofauna abundance was lower under mānuka than under red tussock (TukeyHSD; $P < 0.001$), but there was no significant difference between any other vegetation pairing (Fig. 3).

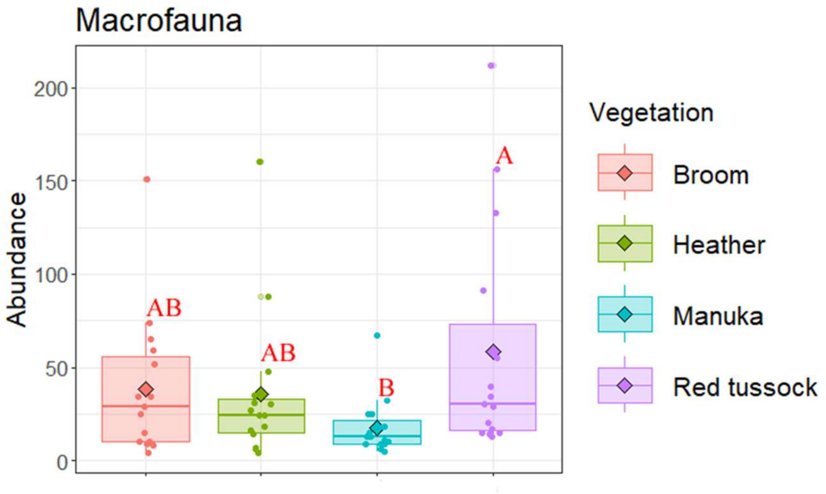

Figure 3. Total soil macrofauna abundances (individuals per sample) under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. The median for each plant species is indicated by the line across the box. The mean is indicated by a diamond. Different letters indicate significant differences of the means (Tukey’s HSD, α=0.05).

LDA ordination showed good separation between soil macrofauna assemblages under mānuka vs. both red tussock and heather, and a lot of overlap among other vegetation types (Fig. 4). Similar to the ordination of soil properties (Fig. 2), the macrofauna data in Fig. 4 forms clusters of mānuka/broom and red tussock/heather. Based on the LDA, mānuka and broom appear to be associated with higher abundances of Diplopoda, Chilopoda, Oligochaeta and Diptera, and with lower abundances of Hemiptera than heather and red tussock. Because of the high portion of variance explained by LD1 (76.03%), the groups contributing the most to this axis (Diptera, Oligochaeta, Hemiptera, Diplopoda and Chilopoda) were identified as drivers of dissimilarity (Appendix 1.3).

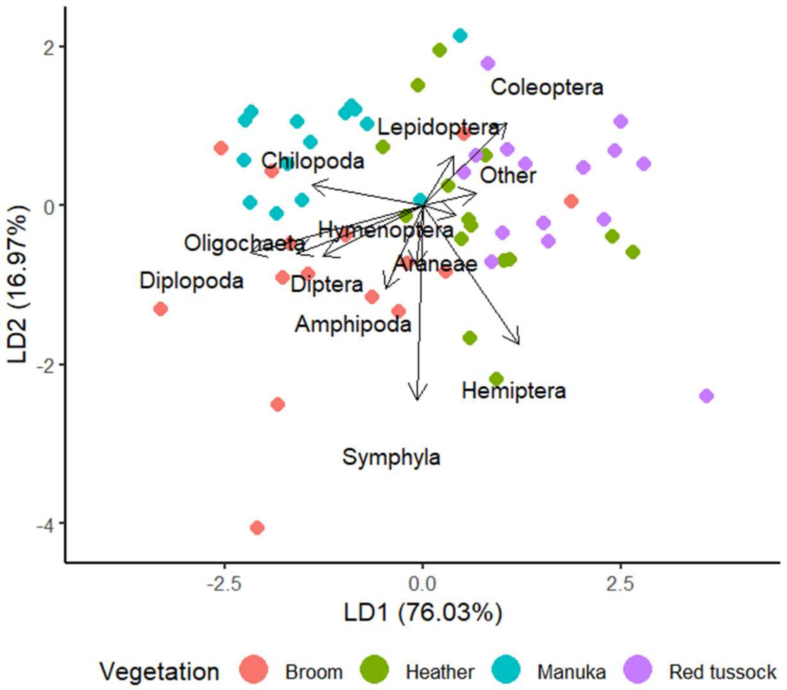

Figure 4. LDA biplot showing the macrofauna community composition under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021.

I found that the soil macrofauna community composition significantly differed among plant species (PERMANOVA; Pseudo-$F_{3,56} = 3.66$, $P = 0.001$). Significant differences in community composition were detected between broom and mānuka (PERMANOVA; Pseudo-$F_{1,28} = 2.17$, $P = 0.038$), broom and red tussock (PERMANOVA; Pseudo-$F_{1,28} = 3.87$, $P = 0.004$), heather and mānuka (PERMANOVA; Pseudo-$F_{1,28} = 5.03$, $P = 0.001$) and between mānuka and red tussock (PERMANOVA; Pseudo-$F_{1,28} = 8.42$, $P = 0.001$). Macrofauna community composition significantly differed between the clusters of mānuka/broom and red tussock/heather (PERMANOVA; Pseudo-$F_{1,58} = 7.66$, $P = 0.001$). Hymenoptera were the most common order, with 1241 individuals over all treatments and sites. Among plant species, I found significant differences for Oligochaeta, Diplopoda, Symphyla, Hymenoptera and Hemiptera (Fig. 5 and Table 2).

Table 2 Soil macrofauna abundances under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Overall comparisons between plant species were performed using generalized linear models and likelihood ratio tests. Different letters indicate significant differences of the means within each row (Tukey's HSD, α =0.05).

	Broom			Heather			Mānuka			Red tussock			χ^2	*P*-value
	Mean	SE		Mean	SE		Mean	SE		Mean	SE			
Diptera	2.27	0.48		2	0.47		1.73	0.45		1.6	0.35		1.36	0.716
Lepidoptera	0.87	0.48		0.87	0.31		0.6	0.19		0.73	0.35		0.47	0.926
Oligochaeta	4.53	0.77	A	1.73	0.40	BC	3.60	0.77	AB	1.20	0.38	C	17.69	**<0.001**
Coleoptera	3	0.91		3.47	0.73		3	0.74		6	1.46		5.42	0.144
Amphipoda	1.67	1.15		0.07	0.07		0.13	0.09		0.13	0.13		6.12	0.106
Chilopoda	2.67	0.72		1.8	0.37		3.8	1.12		1.53	0.39		7.06	0.070
Diplopoda	0.87	0.35	A	0.13	0.09	A	0.93	0.49	A	0.07	0.07	A	9.91	**0.019**
Symphyla	1.13	0.63	A	0.00	0.00	A	0.13	0.09	A	0.07	0.07	A	12.32	**0.006**
Araneae	0.4	0.19		0.53	0.24		0.07	0.07		0.6	0.27		5.20	0.158
Opiliones	1.4	1.08		0.13	0.09		0.13	0.09		0.07	0.07		6.79	0.079
Hymenoptera	17.73	7.87	AB	19.80	9.84	A	2.93	2.65	B	42.27	14.97	A	9.93	**0.019**
Achatinoidea	0.4	0.34		0.07	0.07		0.33	0.16		0.2	0.2		1.95	0.583
Blattodea	0	0		0.07	0.07		0	0		0.2	0.11		6.59	0.086
Hemiptera	1.60	0.41	B	4.80	1.58	A	0.13	0.09	C	3.53	1.17	AB	31.52	**<0.001**
Diplura	0.07	0.07		0	0		0.27	0.21		0.07	0.07		3.89	0.274
Total abundance	38.6	9.93	AB	35.47	10.38	AB	17.8	4.04	B	58.27	15.94	A	12.78	**0.005**
Order richness	6.67	0.53		6.13	0.50		5.2	0.37		5.93	0.36		5.7	1.27
Shannon's index	1.45	0.09		1.31	0.11		1.33	0.08		1.12	0.12		5.73	0.126
Simpson's index	0.68	0.04		0.62	0.05		0.67	0.03		0.53	0.06		6.46	0.091

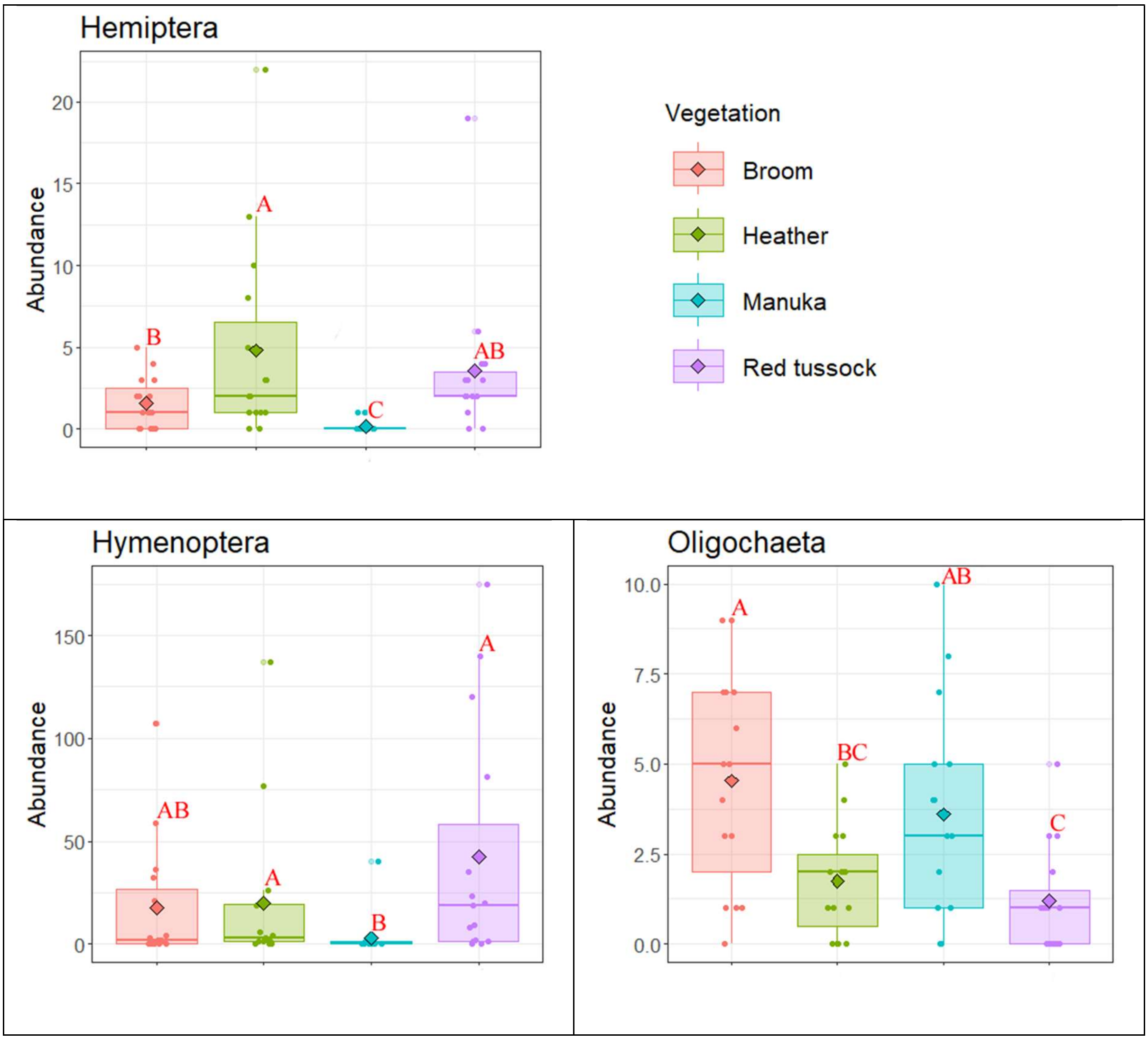

Figure 5. Abundance of selected soil macrofauna taxa under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021 (see Table 2 for the full list of taxa). Values are total abundances. The median for each plant species is indicated by the line across the box. The mean is indicated by a diamond. Different letters indicate significant differences of the means (Tukey's HSD, α=0.05).

2.4 Discussion

Invasive plants are often associated with increases in soil nutrients, such as carbon, nitrogen and increases in decomposition and mineralisation rates when compared to native plant species (Liao et al., 2008). This pattern is often linked to a tendency for invasive plants to have higher values for ecophysiological traits such as primary productivity and leaf nutrient concentrations which are linked to soil carbon and nitrogen cycling processes (Castro-Díez et al., 2014; Liao et al., 2008; Stefanowicz et al., 2018). A study by Rothstein et al. (2004) showed that leaf litter of invasive plants decomposed faster than that of native taxa, owing to the increased litter quality of invasive plants, which lead to increased nutrient cycling rates of nitrogen and phosphorous (likely due to a species-specific high concentration of leaf phosphorous).

Contrary to this, I found that soil properties clustered for red tussock and heather and for mānuka and broom, and that soil property composition significantly differed between these two clusters. Mānuka and broom were associated with less acidic, more nutrient-rich soils, whereas soils under heather and red tussock were more acidic and nutrient-poor. The soil properties contributing most to the dissimilarity between plant species were: Potentially available nitrogen (PAN), anaerobically mineralizable nitrogen (AMN), total nitrogen (TN), cation exchange capacity (me/100g), total base saturation (TBS), pH, organic matter (OM), calcium, magnesium and carbon/nitrogen ratio (C/N). Despite being identified as contributors to dissimilarity, models for soil cation exchange capacity and organic matter between individual plant species were not significant.

The association of our study plants with their soil property compositions may be driven by the plant species being differently able to utilize patches of pre-existing soil properties, rather than, or as well as, engineering them (van der Putten et al., 2013). In my study, broom was associated with higher soil nutrient concentrations and has significantly higher soil total nitrogen and soil potassium than all other study plant species. This could be due to broom having eco-physiological traits common to invasive plants and associated with higher rates of nutrient cycling (Castro-Díez et al., 2014; Stefanowicz et al., 2018). Liao et al. (2008) showed that woody N-fixing invasives have greater impacts on soil carbon and nitrogen cycling. N-fixing invasives are associated with greater impacts on soil nitrogen cycles than non-N-fixing invasives (Ehrenfeld, 2003; Vilà et al., 2011). Indeed, I found that broom was associated with the highest soil concentrations of potentially available nitrogen and significantly higher total nitrogen than any other study plant species.

Different plant species are adapted to occupy different soil habitats, and some species will have competitive advantages under certain soil condition. In its natural range, heather is an early succession species and generally establishes in nutrient-poor soils (Keesing, 1995). I found that heather (along with red tussock) was associated with lower soil nutrients relative to mānuka and broom. Here, the adaptations that allow heather to exploit its habitat in its native range could allow it to utilize patches of low nutrient soil, as well as facilitating its success in the generally poor soils of NICP. I found that mānuka was associated with relatively nutrient-rich soil. Mānuka is a mid-successional plant, playing an important role in disturbed sites and in sites where soil properties prevent succession into forest (Stephens et al., 2005). Mid successional plant species generally colonize sites with moderate soil nutrient richness, and so mānuka may be exclusively establishing in patches of soil that are already relatively nutrient rich.

Rather than seeing a reduced soil macrofauna abundance for invasive plants, my results showed no significant difference in total abundance between invasive and native plants. Instead, I found that the mean total abundance of macrofauna was significantly higher under one native plant species (red tussock) when compared to another native species (mānuka). Soil macrofauna assemblages did not cluster by invasive status as predicted, but instead clustered into red tussock and heather vs mānuka and broom, with significant differences in the community compositions between the two clusters. The mānuka-broom cluster tended towards more Diptera, Oligochaeta, Diplopoda and Chilopoda and fewer Hemiptera compared to the red tussock-heather cluster. Oligochaeta mean abundance was significantly higher for broom than for heather and red tussock and significantly higher for mānuka than for red tussock. Mean abundance of Hymenoptera was significantly higher for red tussock and heather than for mānuka. Mean abundance of Hemiptera was significantly higher for heather than for broom or mānuka and significantly higher for broom and red tussock than mānuka.

I found more Oligochaeta under broom compared to red tussock, which matched our predictions of invasive plants (and especially N-fixing invasives) being associated with greater abundances of decomposers. I also found more Oligochaeta under broom than heather. This could be due to the increased impact on leaf litter quality of N-fixing invasives even relative to other non-N-fixing invasives. I also found more Oligochaeta under mānuka than red tussock. Some soil fauna groups, such as Oligochaeta and Diplopoda, are sensitive to soil physico-chemical properties (Birkhofer et al., 2012; Hoeffner et al., 2021; Singh et al., 2020; Tóth & Hornung, 2020). Oligochaeta are linked to numerous soil properties, including soil organic matter, pH and moisture (Baker et al., 1998; Baker & Whitby, 2003; De Wandeler et al., 2016; Hoeffner et al., 2021; Jiménez et al., 2011; Perreault & Whalen, 2006; Singh et al., 2020). De Wandeler et al. (2016) showed that Oligochaeta abundance increased with pH as it moved from acidic to neutral. Diplopoda have been linked to soil properties such as soil texture and soil concentrations of calcium and magnesium (Kime & Wauthy, 1984; Tóth & Hornung, 2020). Diplopoda require calcium for the development of their exoskeletons (Tóth & Hornung, 2020). Our LDA ordination of soil macrofauna and our PCA ordination of soil properties both show clustering of red tussock and heather and of mānuka and broom, with separation between these two clusters. This may suggest that there is a strong relationship between soil fauna and soil properties in our study. In the LDA, mānuka and broom were associated with higher abundances of Oligochaeta and Diplopoda than red tussock and heather, and our PCA soil property ordination showed mānuka and broom were associated with higher pH (closer to neutral) and greater magnesium and calcium concentrations. As pH, magnesium, and calcium have been linked to the distribution of these two groups, the soil properties associated with our study plants may be driving the soil fauna community compositions.

2.5 Limitations

As discussed above, different plant species can affect soil properties differently, and pre-existing soil properties can also differently facilitate the germination and success of different plant species (van der Putten et al., 2013). An observational study does not allow us to determine if plant species are driving soil property composition patterns, or if soil properties are driving plant species distributions, or both. It is therefore only with caution that I interpret such results as the higher soil nitrogen concentrations of broom as a response rather than a driver of broom invasion.

Our study looked exclusively at the order level of taxonomic resolution of soil macrofauna. If there were competing patterns for different groups among the same order, they may have cancelled each other out and been unobservable at the order level. Higher taxonomic resolution would also allow us to better interpret the drivers of changes.

I have only observed a small subset of the native and invasive plants of the Central Plateau. Though I did not observe a separation of soil properties and fauna based on invasive and native plant species, this does not disprove the trends of invasive and native plants in literature, but rather highlights the limitations in using these trends alone in predicting the traits of an invasive and native subset.

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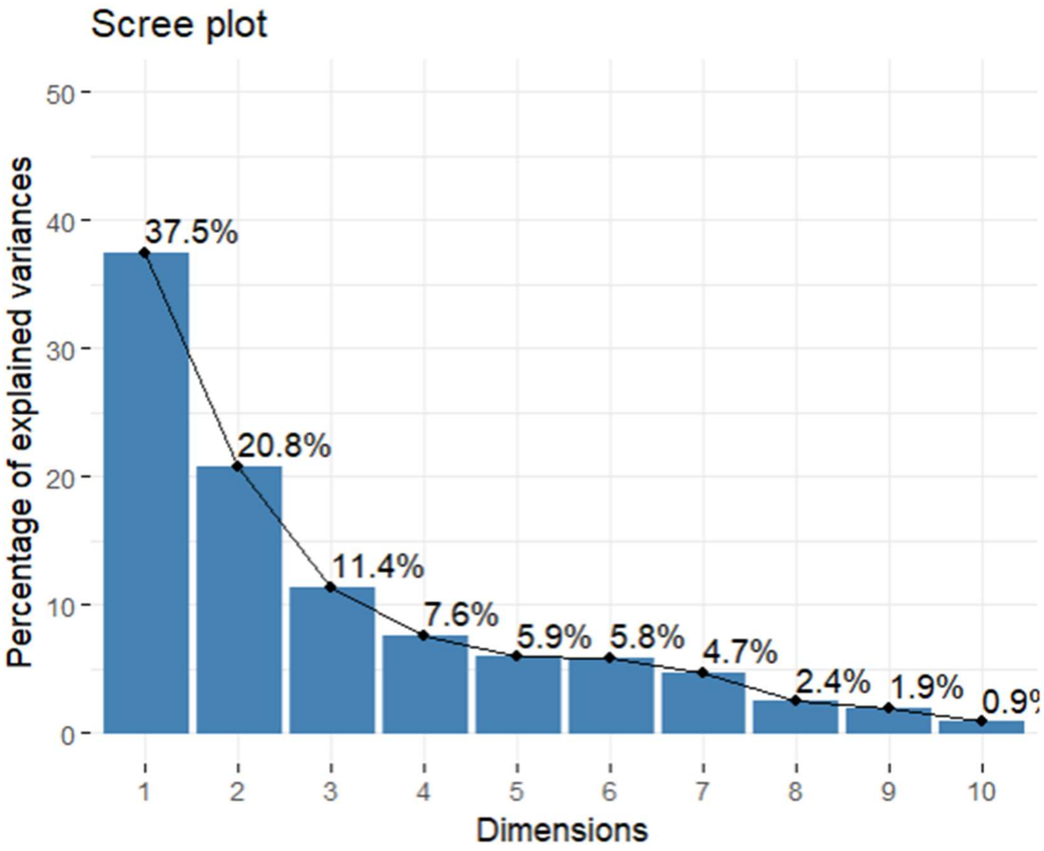
2.7 Appendix 1: Supplementary information

Appendix 1.1



Scree plot showing the relative contributions of the first ten principal components of PCA on the soil properties under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021.

Appendix 1.2

Variable contributions for the first five dimensions (principal components) of PCA on the soil property composition under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Values representing high contributions to respective principal component highlighted in bold for the first two principal components. Abbreviations/acronyms/units: Volume weight in g/mL (VW), Volumetric water content (VWC), Olsen phosphorous (Olsen P), Potentially available nitrogen (PAN), Anaerobically mineralizable nitrogen (AMN), Total nitrogen (TN), Organic matter (OM), carbon/nitrogen ratio (C.N), Potassium in % base saturation (i.e., %BS), calcium %BS, magnesium %BS, sodium %BS, Cation exchange capacity (CEC), Total base saturation (TBS).

	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5
VW	7.44205	5.928214	2.906241	0.456727	1.426061
VWC	0.381266	3.453655	0.576955	0.388306	74.08305
pH	3.846302	**19.35362**	0.131956	0.874392	0.009468
Olsen.P	7.141544	3.137743	0.152887	16.642	0.000594
PAN	**10.22563**	0.542485	17.55032	1.196343	0.778618
AMN	**11.79928**	1.357134	11.38982	1.298608	0.07317
AMN.TN	4.821622	0.156946	25.79244	12.2384	3.395124
OM	6.790096	**11.85617**	6.065634	0.043959	0.822271
TN	**9.130162**	5.875686	1.02785	11.05583	2.0965
C.N	0.048469	7.009694	7.739095	26.17349	0.083043
Potassium	5.710417	1.386358	0.137512	21.56388	3.007809
Calcium	7.204726	**9.759784**	2.201435	4.414401	0.764393
Magnesium	7.010589	**10.28741**	7.103185	0.26048	0.712827
Sodium	0.272508	4.769895	9.265045	0.087537	12.29825
CEC	**9.663435**	4.314623	5.442223	1.939611	0.435319
TBS	**8.511902**	**10.81058**	2.517407	1.366047	0.013504

Appendix 1.3

Variable contributions for the three LDA components (LD1, LD2 and LD3) for LDA of the soil macrofauna composition under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Values representing high contributions to LD1 highlighted in bold.

	LD1	LD2	LD3
Diptera	**-0.50375**	-0.25231	-0.17218
Lepidoptera	0.151148	0.248775	-0.42746
Oligochaeta	**-0.63986**	-0.23964	0.041934
Coleoptera	0.422319	0.418741	0.311948
Amphipoda	-0.19086	-0.41859	-0.09112
Hymenoptera	0.161774	-0.04612	0.144731
Araneae	-0.03416	-0.30517	-0.34861
Hemiptera	**0.483597**	-0.69652	-0.38724
Chilopoda	**-0.56283**	0.107616	-0.2699
Diplopoda	**-0.8713**	-0.23617	-0.28207
Symphyla	-0.02775	-0.97672	1.244734
Other	0.26644	0.065122	0.683453

Chapter 3: Soil properties and soil fauna communities of heather *Calluna vulgaris* prior, during and following attack by heather beetle *Lochmaea suturalis*.

3.1 Introduction

While biocontrol agents have a great deal of pre-release research to predict their efficacy and the risk of direct effects from host swapping, post-release assessment of efficacy and indirect effects is much less common (Blayney, 2012). Even less common are studies of biocontrol consequences for the soil ecosystem of target plants. Plant processes mediate soil physicochemical and biological properties of the substrate they inhabit through the uptake of nutrients an water and the input of live plant material, root exudates and litter (Zhang et al., 2019). While there is little in the way of knowledge regarding biocontrol impacts on these processes, it may be expected that the response will depend on the individual biocontrol agent and its mode of action.

Specialist foliar herbivores are commonly used as biocontrol agents. Foliar herbivores can cause changes to plant resource quantity when induce plant responses that alter root exudation, root carbon allocation and biomass as well as changes in root morphology (Bardgett et al., 1998; Heinze, 2020). The quality of plant inputs into the soil can change when foliar herbivores deposit highly labile excreta or when they induce plant responses that alter the concentrations of nutrients and secondary metabolites in plant tissues (Bardgett et al., 1998). Increases in nutrient concentrations of leaf tissue may increase litter quality and enhance decomposition and nutrient cycling, where-as the build-up of secondary metabolites in these tissues may have the opposite effect (Bardgett et al., 1998).

For repair and compensatory growth, plants can increase the uptake of soil nutrients following defoliation, with consequences for soil nutrient pools (Wallace & Macko, 1993), and soil carbon and nitrogen mineralization can be enhanced (Kristensen et al., 2020; Wardle & Bardgett, 2008). Thanks to decomposer groups responding to leaf litter quality and microbial communities responding to root exudation shifts, above-ground herbivory is often associated with increased soil pools of carbon and nitrogen and variable effects on other nutrient pools (Bardgett et al., 1998).

By altering the quality and quantity of plant inputs into the soil system, aboveground herbivory can also alter the composition of soil fauna. Decomposer groups are stimulated by increases in the quality and quantity of leaf litter and the deposition of insect excreta (Kristensen et al., 2020). Root herbivores may respond to the induced changes in root carbon allocation and morphology and changes in secondary metabolite concentrations (Blossey & Hunt-Joshi, 2003). Soil microbial biomass and activity have been shown to increase with increased root exudation (Hamilton & Frank, 2001) and this will presumably have consequences for microbial nutrient cycling, microbivore fauna and higher trophic levels. Some soil fauna groups are likely to be more sensitive to specific soil properties than others (Birkhofer et al., 2012; Hoeffner et al., 2021; Singh et al., 2020; Tóth & Hornung, 2020). Indirect and direct effects of aboveground herbivores on soil properties may be expected to also impact upon such groups.

To help control the spread of heather, heather beetle was introduced to the Central Plateau of New Zealand's North Island (CPNZ) as a biological control agent from 1995 (Fowler et al., 2015). Heather beetle is a natural enemy of heather in its native European ranges, feeding on foliage and having population outbreaks that cause serious damage to large areas of the plant (Fowler et al., 2015). In one study conducted in New Zealand (Blayney, 2012), the outcome of the heather beetle as a biocontrol agent was assessed by investigating the above-ground arthropod community in plots where heather had been controlled by the beetle, plots where heather had been controlled by herbicide and plots where heather was still present and healthy. Blayney (2012) found that community assemblages of above-ground arthropods associated with the heather beetle and herbicide control were closer to those of habitats uninvaded by heather, such as described in (Keesing, 1995), which suggests that the biocontrol agent was undoing some of the impacts of heather invasion.

Despite the known mechanisms through which heather beetle (as a foliar herbivore) could influence the soil community, these associations have yet to be investigated in the NZ Central Plateau heather beetle program scenario. This chapter aimed to investigate the differences in soil properties as well as macro- and mesofauna communities associated with heather that is healthy and not infested with heather beetle (D0), live heather that is being actively fed upon by heather beetle (D1), and heather that has been heavily damaged by heather beetle (D2) in the North Island Central Plateau. Because above-ground herbivory can directly and indirectly impact soil fauna and the soil processes they mediate, I hypothesized that different soil properties and fauna community compositions would be associated with different levels of damage caused by heather beetle biocontrol agent. This information will help expand our current understanding of the immediate indirect outcomes of biocontrol in the North Island Central Plateau.

Predictions:

Though effects of foliar herbivory are highly variable between plant species, herbivore species and system variables, I expected that there would be some consistent effects for a single study plant species exposed to a single study herbivore species within a single system.

Predicting the direction of the effect is more challenging, but I expected that the compositions of soil fauna and soil properties would differ between D0, D1 and D2. Because foliar herbivory can both indirectly enhance and reduce leaf litter quality (Bardgett et al., 1998), I expected that decomposer groups would also differ between D0, D1 and D2. In addition to this, I expected that decomposer groups would be directly stimulated by the increased deposition of frass associated with the heather beetle infestation, leading to decomposer organisms being stimulated over-all and groups dominated by decomposers being more abundant in D1 and D2, than D0.

3.2 Methods

Site description

The sites used in this chapter were located in the Waiouru military training area at 39.42755°S, 175.7198°E (site 1), and 39.42437°S, 175.721°E (site 2). Sites were chosen based on patches of different heather beetle invasion and damage. Heather beetle populations feed in dense fronts that radiate out from release sites (Blayney, 2012). Ideally, this would allow for discrimination of patches of heather that had been recently killed by a given heather beetle population, patches that were currently being fed upon by said population, and patches yet to be infested. Presence of heather beetle was determined by beating tray method. Distinct patches of heather existed in close proximity at site 1, where heather was healthy and heather beetle was not present on the plants (damage level 0, henceforth D0), and where heather beetles were present and were causing visible damage to the plants (damage level 1, henceforth D1). Heather that was killed by heather beetle could not be found close to D0 and D1 and was instead found at Site 2 (350 m) from the D0; heather beetle at site 2 had caused apparently total above ground destruction of individual heather plants (damage level 2, henceforth D2) (Fig. 6). Eight individual heather plants were selected from each damage level, making a total of 24 individual plants used for this study. Individual plants were selected to have similar phenology between damage levels.

Figure 6. Heather plants under three levels of heather beetle induced damage: (A) D0, where heather appears healthy and heather beetle is not present based on beating tray method; (B) D1 where heather is being visibly damaged by heather beetle herbivory; (C) D2, where heather is apparently killed (inferred from above-ground plant parts) by heather beetle herbivory.

Soil properties and Macrofauna

At each individual plant in this chapter, soil for soil properties and macrofauna was sampled following the methods detailed in Chapter 2, section 2.2. Before soil property cores were sent to Hill Laboratories, they were used to extract mesofauna as detailed below.

Mesofauna

Mesofauna were extracted from the soil property cores using a modified Berlese-Tullgren apparatus for ten days using a mesh size of ~2mm. Mesofauna were extracted into 70% ethanol. Following mesofauna extraction, soil cores were resealed in their original zip-lock bags and sent to Hill Laboratories for soil analysis. To make collecting and counting the Collembola from the samples easier, several drops of diethyl ether were added to each sample to dissolve their cuticle wax and allow them to sink. Samples were sorted under a dissection microscope and the following groups were counted: mites (Acari) including Oribatida, Gamasida, Uropodina, Bdellidae; Collembola (springtails); insects, including Coleoptera, Lepidoptera, Hemiptera, Thysanoptera, Diptera; and other taxa including Oligochaeta, Chilopoda, Diplura and Araneae.

Data analysis

For soil properties and macrofauna community, data analysis was performed following the same methods detailed in Chapter 2, section 2.2. Soil mesofauna were analysed following the same methods as those used for soil macrofauna. For analysis, mesofauna were aggregated to reduce the number of zeros in the data set: Uropodina and Bdellidae counts were combined into "other Acari", Oligochaeta, Diptera, Chilopoda, Diplura and Araneae counts were combined into "other mesofauna".

3.3 Results

3.3.1 Soil

PCA ordination showed an overlap between the soil properties under all three damage levels (Fig. 7). The first and second principal components (PC1 and PC2) collectively explained 58.8% of the total variation (Appendix 2.1). Though heavily overlapping, D1 tends towards the negative side of PC1 while D0 and D2 towards the positive side. D0 tends towards the positive side of PC2 compared to D1 and D2 which tend towards the negative side. PC1 is characterized by anaerobically mineralizable nitrogen, total base saturation, magnesium, organic matter, and cation exchange capacity and PC2 is characterized by pH, anaerobically mineralizable nitrogen/total nitrogen ratio, organic matter, cation exchange capacity, total nitrogen, and Olsen phosphorous (Appendix 2.2). Based on their high contributions to the first two principal components, these properties were identified as potential drivers of dissimilarity between treatments.

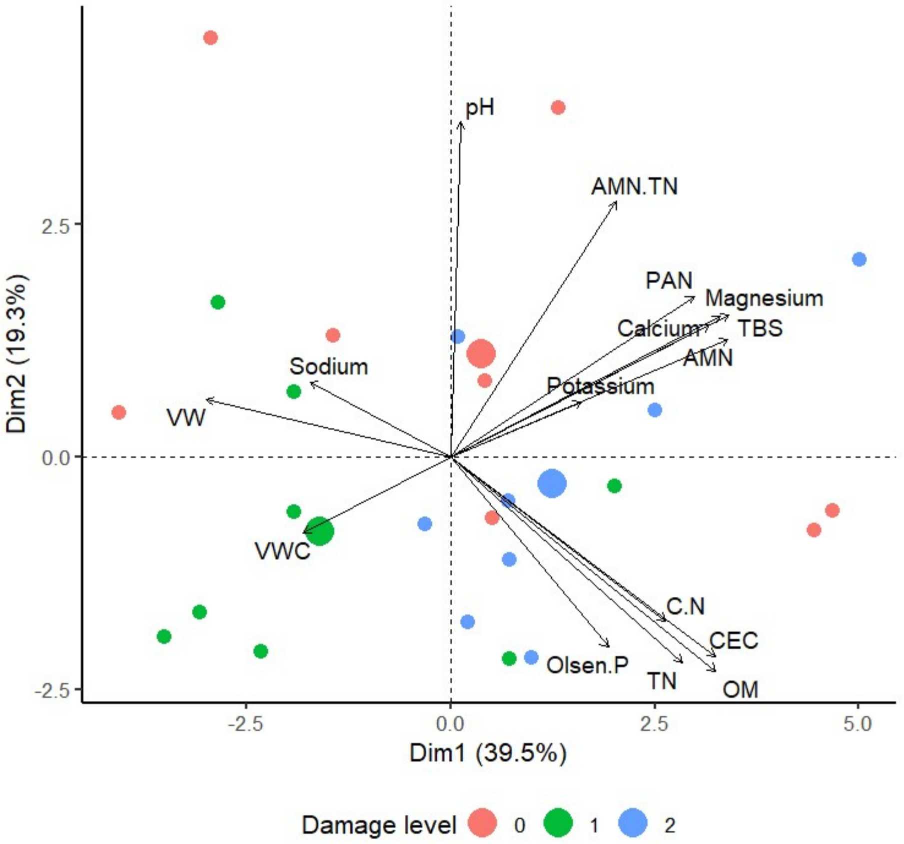


Figure 7. PCA biplot showing the soil property composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Dim1 represents PC1 and Dim2 represents PC2. Large circles indicate the centroid of the respective groups. Abbreviations/acronyms/units: Volume weight in g/mL (VW), Volumetric water content (VWC), Olsen phosphorous (Olsen P), Potentially available nitrogen (PAN), Anaerobically mineralizable nitrogen (AMN), Total nitrogen (TN), Organic matter (OM), carbon/nitrogen ratio (C.N), Potassium in %base saturation (i.e., %BS), calcium %BS, magnesium %BS, sodium %BS, Cation exchange capacity (CEC), Total base saturation (TBS).

The overall composition of soil properties significantly differed among damage levels (PERMANOVA; Pseudo-$\mathrm{F}_{2,21} = 2.78$, $P = 0.012$). Specifically, differences were detected between D0 and D1 (PERMANOVA; Pseudo-$F_{1,14} = 2.81$, $P = 0.025$) and between D1 and D2 (PERMANOVA; Pseudo-$F_{1,14} = 3.9$, $P = 0.002$).

Various soil properties were found to differ between the different damage levels (Table 3). Volumetric water content was significantly lower, and pH was significantly higher in D0 than in other treatments. Calcium was lower in D1 than D2. Magnesium and total base saturation were lower in D1 than in the other treatment. Olsen P was also significantly higher for D2 than for D0. Total nitrogen did not significantly differ between any of the treatment.

Table 3 Soil properties under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Overall comparisons between plant species were performed using generalized linear models and likelihood ratio tests. Different letters indicate significant differences of the means within each row (Tukey's HSD, α=0.05). Abbreviations/acronyms/units: Volume weight in g/mL (VW), Volumetric water content (VWC), Olsen phosphorous (Olsen P), Potentially available nitrogen (PAN), Anaerobically mineralizable nitrogen (AMN), Total nitrogen (TN), Organic matter (OM), carbon/nitrogen ratio (C.N), Potassium in %base saturation (i.e., %BS), calcium %BS, magnesium %BS, sodium %BS, Cation exchange capacity (CEC), Total base saturation (TBS).

	D0			D1			D2			χ^2	P value
	Mean	SE		Mean	SE		Mean	SE			
VW	0.68	0.03		0.70	0.02		0.68	0.001		0.28	0.869
VWC	9.45	0.48	B	13.86	0.73	A	12.96	0.52	A	23.23	**<0.001**
pH	5.83	0.04	A	5.70	0.03	B	5.73	0.02	B	10.43	**0.005**
Olsen P	4.13	0.30	B	4.25	0.25	AB	5.13	0.30	A	7.35	**0.025**
PAN	109.13	9.66		93.25	7.97		113.88	12.05		2.78	0.249
AMN	108.25	11.76		91.88	11.22		112.13	12.98		2.04	0.361
TN	0.49	0.04		0.48	0.02		0.50	0.01		0.58	0.747
AMN/TN	2.26	0.22		1.94	0.20		2.24	0.25		1.53	0.466
OM	15.93	1.70		14.98	0.78		16.66	0.47		1.26	0.532
C/N	18.58	0.77		18.15	0.40		19.23	0.24		2.50	0.287
Potassium	2.95	0.16		2.60	0.15		2.75	0.17		2.67	0.264
Calcium	25.38	1.53	AB	22.25	0.65	B	26.88	1.14	A	7.88	**0.019**
Magnesium	7.18	0.40	A	5.60	0.25	B	7.33	0.29	A	15	**0.001**
Sodium	0.65	0.07		0.51	0.04		0.53	0.03		5.81	0.055
CEC	17.75	1.47		17.88	1.06		20.5	0.66		3.65	0.161
TBS	36.25	1.86	A	31.00	0.91	B	37.75	1.18	A	11.79	**0.003**

3.3.2 Soil macrofauna

Total macrofauna abundance, order richness and Simpson’s and Shannon’s diversity indices did not differ between damage levels (Table 4).

LDA ordination showed much overlap of the soil macrofauna assemblages of D0 and D1, but apparent separation of D2 from both of these groups (Fig. 8). This separation is apparent along LD1, which explains 96.88% of the total variation in the dataset and is characterized by Oligochaeta, Araneae and Opiliones (Appendix 2.3). It was therefore these groups that were most indicative of the change in fauna between D2 and both D0 and D1.

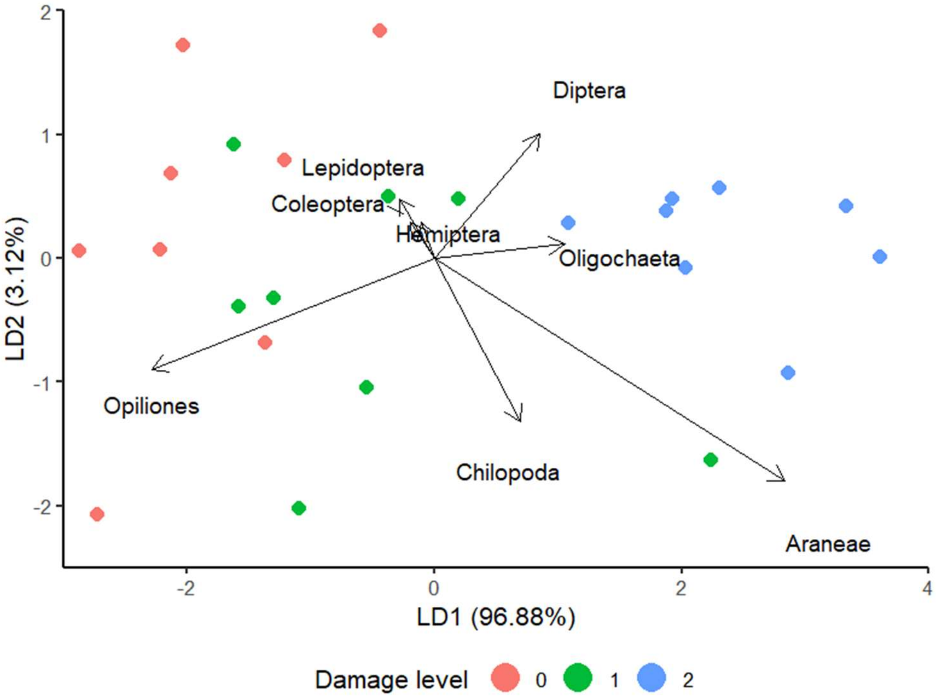


Figure 8. LDA biplot showing the macrofauna community composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021.

Overall, soil macrofauna community composition significantly differed among damage levels (PERMANOVA; Pseudo-$F_{2,21}$ = 3.14, P = 0.001). Significant differences in composition were found between D0 and D2 (PERMANOVA; Pseudo-$F_{1,14}$ = 6.03, P = 0.002) and between D1 and D2 (PERMANOVA; Pseudo-$F_{1,14}$ = 3.54, P = 0.009), but not between D0 and D1. This confirms the structure seen in the LDA ordination. The mean abundance of Oligochaeta was significantly higher for D2 than for either D0 or D1 and the mean abundance of Araneae was significantly higher for D2 than D0 (Table 4 and Fig 9).

Table 4. Soil macrofauna abundances under heather exposed to three levels of heather beetle damage (D1, D2 and D3), NZ Central Plateau, 2021. Overall comparisons between plant species were performed using generalized linear models and likelihood ratio tests. Different letters indicate significant differences of the means within each row (Tukey's HSD, α =0.05).

	D0			D1			D2			χ^2	*P*-value
	Mean	SE		Mean	SE		Mean	SE			
Diptera	1.13	0.85		1.38	0.90		3	0.71		2.58	0.276
Lepidoptera	7.63	2.43		8.88	4.54		8.63	3.65		0.08	0.961
Oligochaeta	1.88	0.77	B	3	1.72	B	8	1.67	A	14.04	**0.001**
Coleoptera	9.38	1.84		8.38	2.30		5	1.20		4.20	0.122
Chilopoda	2.13	1.46		1.25	0.41		0.25	0.16		4.99	0.082
Araneae	0.13	0.13	B	1	0.56	AB	1.88	0.30	A	14.70	**0.001**
Opiliones	0.25	0.16		0.38	0.16		0.13	0.13		1.05	0.593
Hemiptera	0.38	0.26		0.38	0.27		0.5	0.27		0.19	0.907
Total abundance	22.88	5.02		24.63	3.87		27.38	4.27		0.52	0.773
Order richness	4.38	0.68		5.13	0.45		5.5	0.42		10.7	0.587
Shannon's index	1.1	0.1		1.19	0.13		1.37	0.09		4.36	0.113
Simpson's index	0.60	0.03		0.59	0.06		0.69	0.03		3.05	0.218

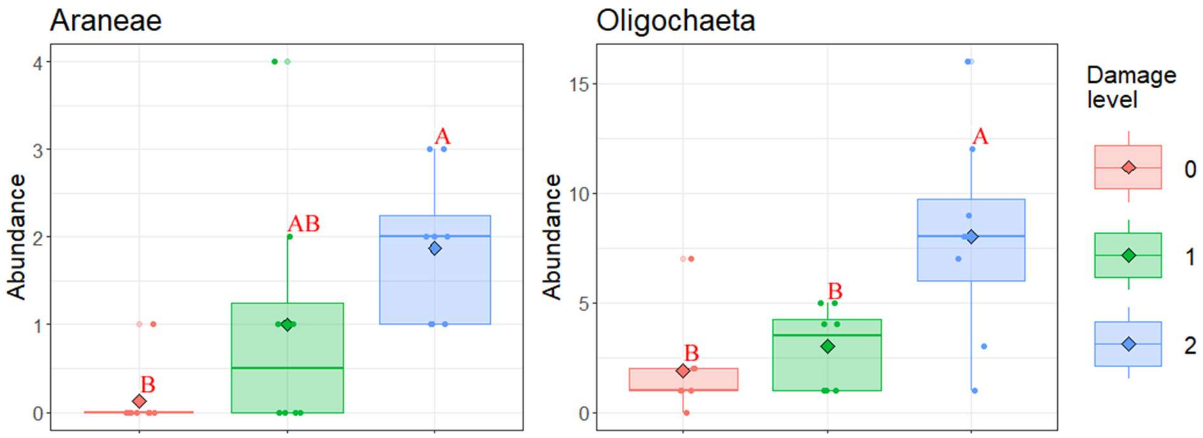


Figure 9. Araneae and Oligochaeta abundances under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Values are counts per sample. The median is indicated by the line across the box. The mean is indicated by a diamond. Different letters indicate significant differences of the means (Tukey's HSD, $\alpha = 0.05$).

3.3.3 Mesofauna

Total mesofauna abundance, order richness and simpson's and shannon's indices did not differ among damage levels (all $P > 0.05$) (Table 5).

LDA showed an overlap between the mesofauna community composition of the three heather damage levels (Fig. 10). LD1 (56.6%) was characterized by Thysanoptera, other mites and Collembola (Appendix 2.6).

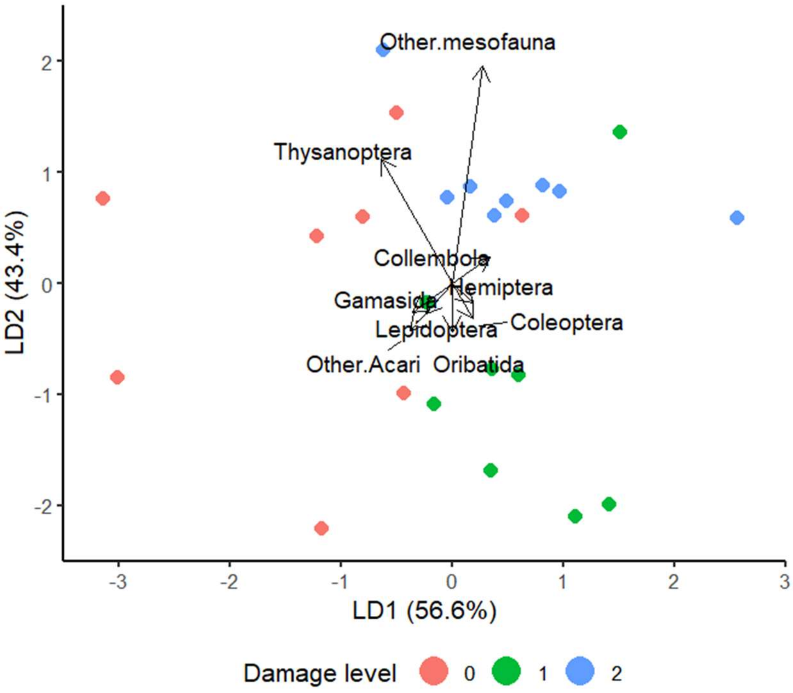


Figure 10. LDA biplot showing the mesofauna community composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021.

The overall mesofauna community composition did not significantly differ among the three damage levels (PERMANOVA; Pseudo-$F_{2,21}$ = 1.57, P = 0.121). Mean abundances were significantly different between damage levels for Collembola (LRTest; χ^2= 6.12, P = 0.047) and for Thysanoptera (LRTest; χ^2 = 10.77, P = 0.005) (Fig. 11), but not for any other group (Table 5). The mean abundance of Collembola was significantly higher for D2 than for D0, and the mean abundance of Thysanoptera was significantly lower for D1 and D2 than D0.

Table 5. Soil mesofauna abundances under heather exposed to three levels of heather beetle damage (D1, D2 and D3), NZ Central Plateau, 2021. Overall comparisons between plant species were performed using generalized linear models and likelihood ratio tests. Different letters indicate significant differences of the means within each row (Tukey's HSD, α =0.05).

	D0			D1			D2			χ^2	*P*-value
	Mean	SE		Mean	SE		Mean	SE			
Oribatida	84.00	22.15		86.75	12.06		62.75	14.62		1.7	0.427
Gamasida	20.88	6.25		11.38	2.75		16.38	2.2		4.94	0.085
Other Acari	4.13	2.15		1.88	0.6		1.13	0.48		4.5	0.105
Collembola	13.25	3.21	B	35.00	14.01	AB	37.50	14.95	A	6.12	**0.047**
Hemiptera	3.00	0.91		10.25	3.96		7.13	5.33		2.66	0.265
Lepidoptera	4.25	1.42		3.38	0.93		2.13	0.77		1.79	0.408
Thysanoptera	7.50	3.24	A	0.88	0.89	B	1.75	0.96	B	10.77	**0.005**
Coleoptera	0.88	0.35		0.75	0.31		0.88	0.23		0.1	0.95
Other Mesofauna	0.75	0.37		0.75	0.49		1.75	0.45		4.6	0.1
Total abundance	138.63	27.3		151.00	21.28		131.38	28.03		0.36	0.837
Order richness	7.63	0.38		6.88	0.59		7.25	0.53		0.31	0.856
Shannon's index	1.25	0.08		1.10	0.07		1.26	0.06		3.52	0.172
Simpson's index	0.58	0.04		0.54	0.04		0.64	0.02		4.71	0.095

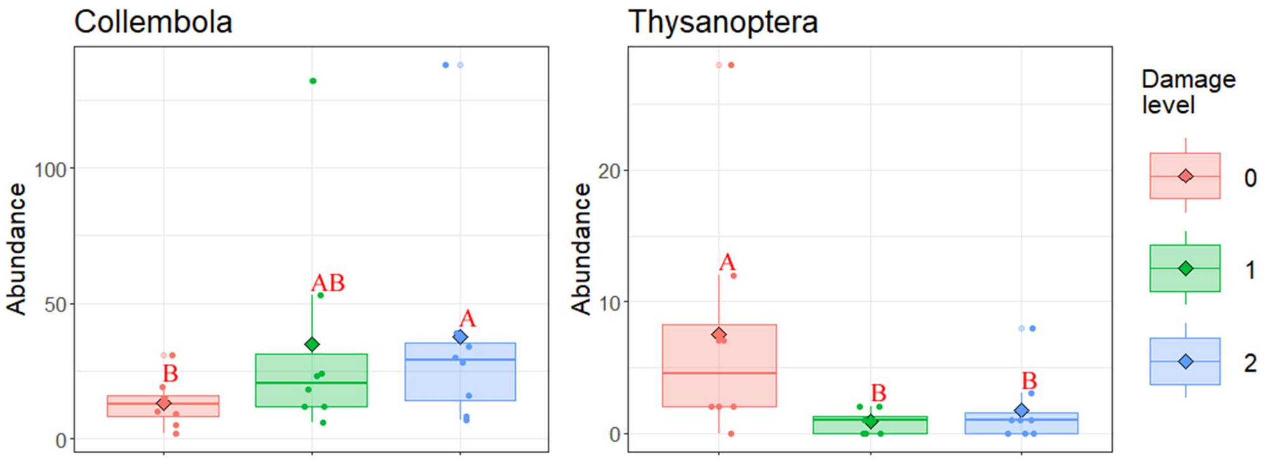


Figure 11. Collembola and Thysanoptera abundances under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Values are abundances. The median for each plant species is indicated by the line across the box. The mean is indicated by a diamond. Different letters indicate significant differences of the means (Tukey's HSD, α =0.05).

3.4 Discussion

I found significant differences in the overall composition of soil properties between D0 and D1. Soil properties were expected to vary in predictable ways associated with changes in decomposition fauna. Although I did not test the full range of decomposer organisms in the soil, in the groups I did test there was no significant difference between D0 and D1. The lack of observed differences could explain the lack of change in the composition of soil nutrients, especially for carbon and nitrogen measures. VWC was significantly higher in D1. Soil pH, magnesium and TBS were significantly lower in D1.

I found no difference in the composition of soil macrofauna between D0 and D1, nor did I find any significant differences in total abundance, order diversity, or mean abundance of any individual order. Similarly, there was no difference in the soil mesofauna community compositions of D0 and D1. The mean abundance of Collembola was higher in D1 than D0, but this result was not significant. Though not significant, the greater mean abundance of Collembola in D1 compared to D0 matches our expectation of decomposer groups being stimulated by foliar herbivory. There were significantly fewer Thysanoptera in D1 than D0. As soil Thysanoptera are often root herbivores, that D1 has a lower mean abundance of this group could tentatively support the theory that foliar herbivory may inhibit root herbivores.

It might be expected that D2 will be exposed to similar mechanisms as D1, but over a longer (though not consistent or defined) period. For example, foliar herbivory may be slow to alter root biomass and therefore resource quantity for root herbivores (Bardgett et al., 1998). Therefore, root herbivore fauna of D2 may differ more from D0 than D1 does. D2 will also have a longer history of deposition by invertebrates, though also a reduction in recent depositions, as the decreasing aboveground biomass supports less. Additionally, the individuals of D2 have been killed by heather beetle, and plant death is expected to have additional effects. This should result in an increase in resources for decomposer groups from dead plant material, and a decrease in resources for plant feeding groups (above- and below-ground).

There was no significant difference in the composition of soil properties between D0 and D2, but there was a significant difference between D2 and D1. Specific significant differences were detected for VWC, pH, Olsen P, Ca, Mg and TBS. D2 had lower pH and higher VWC and Olsen P than D0. D2 had higher Ca, Mg, and TBS than D1. That the composition differed between D0 and D1, but not between D0 and D2 may suggest that differences are caused by active plant responses to herbivory, and that these effects cease upon plant death.

There was a significant difference in macrofauna community composition of D2 compared to D0 or D1, with D2 being positively associated with Oligochaeta and Aranea and negatively with Opiliones. Specifically, Oligochaeta were significantly more abundant in D2 than D0 or D1 and Araneae were significantly more abundant in D2 than D0. The increase in Oligochaeta in D2 supports my theory of increased decomposer organisms.

The community composition of soil mesofauna did not significantly differ between D2 and either D0 or D1. For specific groups, Collembola were significantly more abundant for D2 than D0 and Thysanoptera were significantly less abundant for D2 than D0. The increase in Collembola echoes the increase in Oligochaeta in support of the theory that plant death following foliar herbivory will stimulate decomposer fauna, as Collembola are primarily decomposers in leaf-litter and soil (Christiansen et al., 2009). Like the decrease in Thysanoptera seen in D1 compared to D0, the decrease in Thysanoptera in D2 compared to D0 could be indicative of foliar herbivory (and in this case, plant death) negatively impacting root herbivores. With no understanding of the composition of feeding guilds represented in the Thysanoptera of this study, it would be difficult to suggest a mechanism driving the observed pattern.

In conclusion, this study shows that heather during heather beetle attack and after being killed by heather beetle damage are associated with an increase in the largely decomposer groups Collembola and Oligochaeta and a decrease in the soil Thysanoptera. This in agreement to the initial predictions of foliar herbivory stimulating decomposer groups and may agree with predictions of foliar herbivory impacting root herbivore groups. Given the paucity of the literature it is difficult to contrast the results of this study with other work. Therefore, I encourage additional studies exploring the impact of other weed biocontrol agents, especially those with different modes of action, on soil properties and fauna.

3.5 Limitations

As with chapter 2, here I am performing an observational study where I can only cautiously infer the direction of causality. I interpreted any change in soil properties and fauna as a response to aboveground herbivory and death there-from, but there is also the possibility that differences detected were there prior to heather beetle herbivory, and that certain soil properties and soil fauna effect the presence and success of the heather beetle.

Taxonomic resolution was as limitation in the same capacity as it was for chapter 2. Patterns that occurred at higher resolutions (level of genera or species) could have been ecologically important. Higher taxonomic resolution would have allowed us to more confidently infer the mechanism of impact, especially for the taxa such as Thysanoptera, which include multiple functional groups.

Due to the uneven distribution of the heather beetle invasion front, it was not possible to equally space the three treatments of this study. Therefore, treatment D2 where the heather beetle has killed heather was located further from the D0 (undamaged treatment) than from D1 where heather beetle was actively feeding on heather. Due to the distance decay of similarity, I would expect D2 to be more different to D0 than to D1 is, regardless of any other variable. Separating the effect of distance from the treatment effect is not possible here, so interpretation of differences needs to be cautious.

D1 was infested by heather beetle sometime in the past and I do not have data on exactly when, and D2 was presumably infested further in the past. If heather and soil response to foliar herbivory varies with the season, then D2 may not be simply a later stage of the same treatment as D1, but the later stage of a response to a treatment in a different season, which could yield different results.

3.6 References

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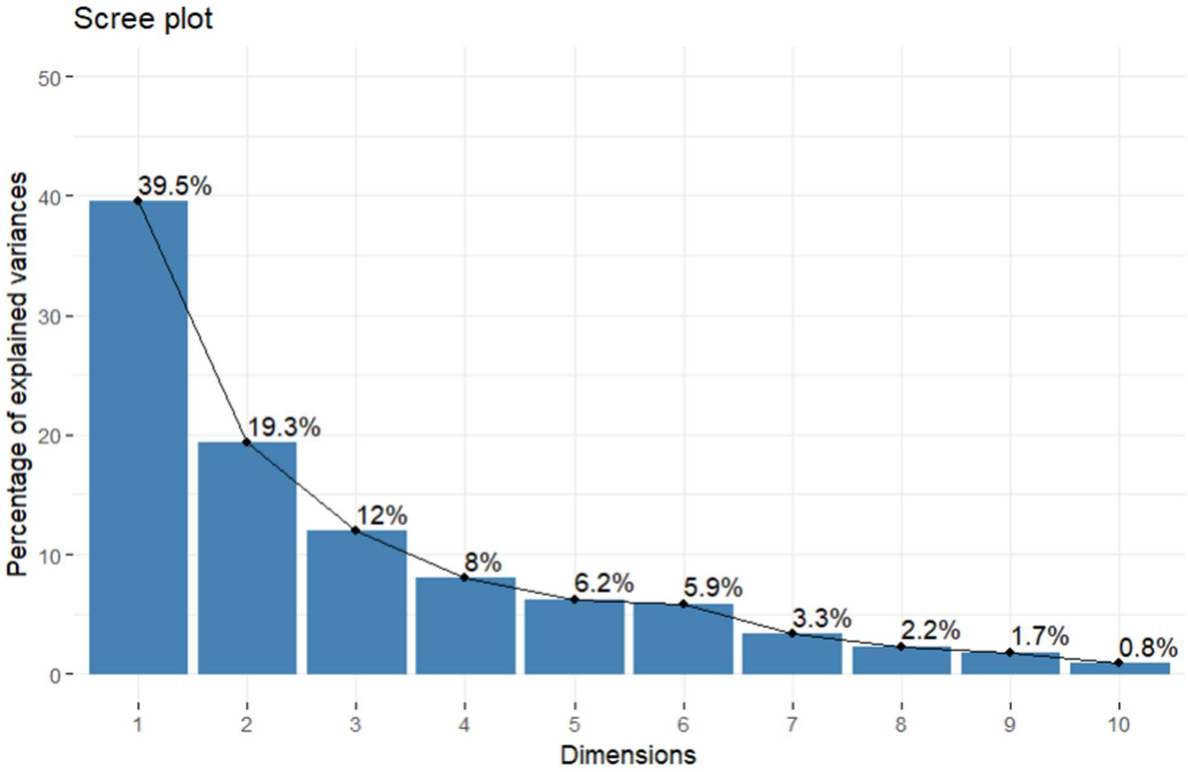
3.7 Appendix 2: Supplementary information

Appendix 2.1



Scree plot showing the relative contributions of the first ten principal components of PCA on the soil property composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021.

Appendix 2.2

Variable contributions for the first five dimensions (principal components) of PCA on the soil property composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Values representing high contributions to respective principal component highlighted in bold for the first two principal components. Abbreviations/acronyms/units: Volume weight in g/mL (VW), Volumetric water content (VWC), Olsen phosphorous (Olsen P), Potentially available nitrogen (PAN), Anaerobically mineralizable nitrogen (AMN), Total nitrogen (TN), Organic matter (OM), carbon/nitrogen ratio (C.N), Potassium in %base saturation (i.e., %BS), calcium %BS, magnesium %BS, sodium %BS, Cation exchange capacity (CEC), Total base saturation (TBS).

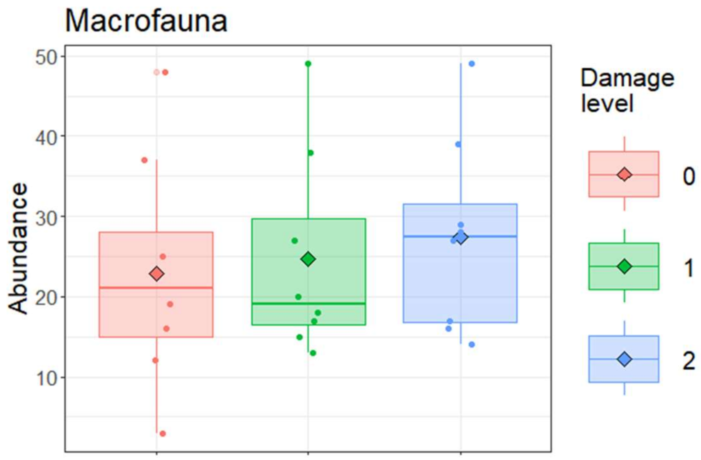
	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5
VW	7.832254	0.690188	1.053955	0.006372	15.38039
VWC	2.85597	1.196017	12.55835	1.520778	16.43693
pH	0.012226	**23.22594**	9.062932	0.216588	2.103652
Olsen.P	3.244602	**7.483716**	0.092867	8.367385	2.940482
PAN	7.743969	5.351598	9.991047	7.036506	2.1943
AMN	**10.05309**	2.84821	9.88479	5.399951	0.015547
AMN.TN	3.603057	**13.47547**	15.86928	2.115323	0.039379
OM	**9.183591**	**9.501025**	3.263549	0.045152	0.029276
TN	7.016662	**8.765542**	3.704901	4.965408	0.047047
C.N	6.041726	5.599802	0.627459	11.23777	0.450379
Potassium	2.247774	0.634522	9.211935	8.652462	44.5393
Calcium	**8.717**	3.588891	0.496653	17.38654	2.856309
Magnesium	**9.541374**	4.086137	8.036597	0.002204	0.024844
Sodium	2.614875	1.159184	9.230105	25.17954	10.80613
CEC	**9.165034**	**8.217762**	4.026966	0.339793	1.249711
TBS	**10.12679**	4.175998	2.888619	7.528215	0.886337

Appendix 2.3

Variable contributions for the two LDA components (LD1 and LD2) for LDA of the soil macrofauna composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Values representing high contributions to LD1 highlighted in bold.

	LD1	LD2
Diptera	**0.609848**	0.714692
Lepidoptera	-0.20094	0.342754
Oligochaeta	**0.751261**	0.085014
Coleoptera	-0.13987	0.208652
Hemiptera	-0.07845	0.205554
Chilopoda	0.498644	-0.93962
Araneae	**2.022568**	-1.28731
Opiliones	**-1.63298**	-0.63977

Appendix 2.4



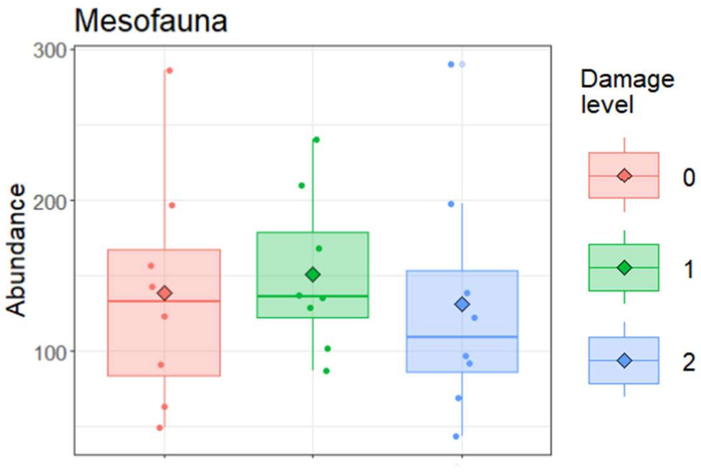
Total soil macrofauna abundances under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Values are total abundances. The median for each plant species is indicated by the line across the box. The mean is indicated by a diamond.

Appendix 2.5

Variable contributions for the two LDA components (LD1 and LD2) for LDA of the soil mesofauna composition under heather exposed to different levels of heather beetle induced damage (0,1 and 2), NZ Central Plateau, 2021. Values representing high contributions to LD1 highlighted in bold.

	LD1	LD2
Oribatida	-0.00314	-0.33516
Gamasida	**-0.27514**	-0.19697
Other.Acari	**-0.29209**	-0.32402
Collembola	**0.259496**	0.186687
Hemiptera	0.143813	-0.13499
Lepidoptera	-0.18545	-0.20699
Thysanoptera	**-0.49168**	0.863263
Coleoptera	0.139175	-0.24522
Other.Mesofauna	0.212551	1.502906

Appendix 2.6



Total soil mesofauna abundances under broom, heather, mānuka and red tussock, NZ Central Plateau, 2021. Values are total abundances. The median for each plant species is indicated by the line across the box. The mean is indicated by a diamond.

Chapter 4: Synthesis

The Central Plateau of the North Island of New Zealand is home to numerous invasive plant species and biological control agents there-of. Studies have focused on the plant community level response of above-ground arthropod communities to plant invasion, but nothing yet has explicitly investigated the individual plant level soil properties and soil fauna associated with invasive plants compared to native plants. More-over, while pre-release research on biocontrol agents is common, research on post-release impacts is scarce (Blayney, 2012). In the Central Plateau, Blayney (2012) investigated the long-term plant-community scale arthropod community response to heather beetle, but nothing is known about the short-term, individual-plant level response of soil properties and soil fauna to this biocontrol agent. This thesis documents some of the differences in soil properties and soil fauna communities associated with 1) native red tussock and mānuka and invasive broom and heather and 2) heather plants prior, during and following biological control by the heather beetle biocontrol agent.

In chapter 2, soil properties and fauna compositions did not differ predictably according to plant invasive status. Instead, I found that soil under mānuka had soil properties and macrofauna community composition similar to broom, and that soil under red tussock had soil properties and macrofauna compositions similar to heather. My findings for soil properties are inconsistent with the trends in invasive plant traits, which suggest that invasives tend to have higher rates of nutrient cycling, as they tend to have higher values for performance-based plant traits relative to native plants (Liao et al., 2008; Stefanowicz et al., 2018). My findings for soil fauna communities are inconsistent with literature that suggests decomposer groups could be stimulated by invasive plants relative to native plants due to their relatively high performance-based traits, and with the enemy escape hypothesis, that suggests root herbivores should be reduced on invasive plants relative to native plants due to their lack of shared evolutionary history with native herbivores (Stefanowicz et al., 2018, Williamson & Fitter, 1996). These findings are consistent with conclusions from a previous study by Effah et al. (2020), where he suggested that individual plant identity, rather than invasive status, was important in predicting an invasive plants effect on the above-ground arthropod community in the Central Plateau. Below-ground, this appears to be true of both soil properties and soil fauna.

Our findings highlight the need to consider plant species, rather than simply the invasive status when predicting the impact of plant invasion on the soil biotic and abiotic factors. As broom is associated with high soil nutrients (and is likely engineering these conditions through its N-fixing ability and high plant fitness traits (Liao et al., 2008)), it may have a greater impact on the native habitat of this area relative to heather, which was associated with low soil fertility, as is red tussock. By increasing the nutrient richness of the soil, broom may facilitate secondary invasion by disproportionately benefitting other non-native plants suited to nutrient rich soils and reducing the advantage of the native plants of the area which are adapted to very low nutrient soils. As well as secondary invasion, this could accelerate the rate of succession of the Central Plateau tussock grassland ecosystems. The similarity in the soil properties under broom and mānuka could, however, bode well for the revegetation by mānuka following broom removal, especially if management encourages such establishment. On the other hand, habitat heterogeneity is an important aspect of the Central Plateau plant communities, so the preservation of low nutrient soil habitats may be threatened by the spread of broom.

The relatively low nutrient soils associated with heather in our study could imply a relatively tame impact upon the soil ecosystem. Since heather has a similar composition of soil properties as red-tussock, I might predict that the removal of this invasive plant could be followed by revegetation by red-tussock and other native plants that are adapted to the naturally low soil fertility of the area.

In chapter 3, I found that the composition of soil properties differed between D0 and D1 and D1 and D2. I found no difference between the compositions of soil fauna (macro- or meso-) between undamaged heather and live heather being actively fed upon by heather beetle. The observed reduction in Thysanoptera in D1 could be in line with the literature that shows foliar herbivory can negatively influence root herbivores. There was a greater abundance of Collembola in D1 than D0 (though not a statistically significant effect), which is in line with expectations of foliar herbivores stimulating decomposer groups with their frass deposition (Wardle & Bardgett, 2008). Oligochaeta and Collembola were more abundant in D2 than D0, which was similarly in line with what I might expect from an influx of decomposing plant material following plant death.

If Thysanoptera in our study represent root herbivores, then the biocontrol agent may be associated with a significant decrease in root herbivory. This is observed in the literature where aboveground herbivores can reduce belowground herbivore success as reviewed by Blossey & Hunt-Joshi (2003) and demonstrated in Soler et al. (2007), where foliar herbivory reduced root herbivore survival and size, seemingly by stimulating the build-up of allelochemicals in root tissue. The biocontrol agent should be increasing the top-down pressure on the invasive plant species, but if the biocontrol agent reduces the efficacy of other antagonists, the total level of control achieved could be less than predicted. Plant responses to biocontrol can also condition the soil and facilitate secondary invasion. The composition of soil properties did not significantly differ between D0 and D2, which could indicate the plant death caused by heather beetle biocontrol damage did not cause any significant soil conditioning that might further facilitate secondary invasion.

Altogether, the findings in this study highlight the need for future research into a variety of plant species. With invasive status failing to predict the soil properties and fauna of the study plants, there may instead be good cause to investigate the plant traits of each important invasive plant and of a range of native plants susceptible to displacement. To better quantify the magnitude of the effect invasive plants can have on the soil system, longitudinal studies should be conducted to include the pre-invasion soil properties, as well as measurements of the soil over the plants life cycle and the changes throughout various control measures. Due to broom having a greater capacity to alter the soil ecosystem, focus should be placed on this species (and other weedy species sharing plant traits such as N-fixation, which is associated with greater effects on soil nitrogen cycling (Ehrenfeld, 2003; Vilà et al., 2011)). The relative capacity of native plants to germinate in soils before and after broom has conditioned them should be investigated. Future studies should also consider the impact of biological control agents on soil properties and below-ground communities. The post-release response of ecosystems to biocontrol agents is rarely investigated, but biological control agents have a huge potential to cause cascading effects on the ecosystems where they are introduced that extend far beyond their direct impact on the invasive plants. An ecosystem approach involving multiple trophic levels is highly encouraged for future studies.

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