

How mammal exclusion using pest-resistant fencing
influences terrestrial invertebrate communities at a
New Zealand ecosanctuary

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Abstract

Despite being such important components of healthy functioning ecosystems, invertebrates are often overlooked in ecosystem restoration research, plants usually being the main focal point. There are many factors that can influence invertebrate communities, and mammalian disturbance is among those factors. Previous research has provided evidence that mammals can influence plant and invertebrate assemblages in a variety of direct and indirect ways. Pest-resistant fencing has been utilized as a strategy for conservation and ecosystem restoration efforts to protect areas of land on the main islands of New Zealand from introduced mammalian pests. The Orokonui Ecosanctuary (Dunedin, South Island) is a 307-hectare mainland reserve and ecosystem restoration project that utilizes pest-resistant fencing, and the vast majority of mammals have been eliminated from within the fence boundary. In the present study, the goal was to investigate how the exclusion of mammals from Orokonui using pest-resistant fencing influenced invertebrate communities by comparing invertebrate abundance and beetle diversity from sites inside the fence to sites outside the fence. How season could potentially interact with fencing was also considered. Three pairs of inside-fence and outside-fence sites for sampling invertebrates were found, where each pair had a distinct composition of plants. Each site had their soil properties analyzed. Ground/litter-dwelling and shallow soil-dwelling invertebrates were sampled from each site, extracted using Tullgren funnels, and categorized into various taxonomic groups for abundance analyses. Beetles were further categorized down to species and recognizable taxonomic units for diversity analyses. Invertebrates deeper down in the soil had their wet weights analyzed. Soil moisture data was also collected alongside the invertebrate data and was included in the analyses as a random effect. Invertebrate and soil moisture sampling occurred once in winter and once in summer. Results showed that the abundance of several invertebrate groups differed significantly inside and outside the fence, but the differences were often not consistent between the pairs of sites. The effect of season had an interaction with the effect of the fence on the abundance of some invertebrates in some pairs. Differences in beetle diversity inside and outside the fence were also evident. No significant differences in soil invertebrate wet weights were found. Ideas for improving the present study and ideas for future research are presented. In conclusion, the exclusion of mammals using pest-resistant fencing at Orokonui does influence invertebrate communities, but the way in which the communities change can depend on the type of habitat being investigated and season.

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Chapter 1: Introduction

In the field of ecology, 'ecosystem' can be defined as a system that involves a biotic community, the interactions within that biotic community, and the interactions by this biotic community with the abiotic environment (Lindeman, 1942; Schmitz et al., 2008). Ecosystem functioning can be described as processes that cause the flow and flux of energy through ecosystems to maintain life (Hooper et al., 2005; Weisser & Siemann, 2008). Living creatures provide functional roles to ecosystems, and these functional roles contribute to 'ecosystem functioning' (Chapin III et al., 1996; Cardinale et al., 2011; Schulze & Mooney, 2012; Powell & Rillig, 2018). Invertebrates play vital roles in ecosystems and ecosystem functioning as they are incredibly numerous and are a source of many key functional roles, which is why invertebrates should not be overlooked in ecosanctuaries and ecosystem restoration projects

1.1. Importance of invertebrates in ecosystems

Invertebrates dominate the planet in terms of global species richness and animal biomass (Stork, 1988; Bar-On *et al.*, 2018). Invertebrates are not just species-rich and numerous but are also incredibly diverse in their functional roles within ecosystems (Stork, 1988; Voigt *et al.*, 2007; Basset *et al.*, 2012; Moretti *et al.*, 2017). Functional roles (or ecosystem functions) are basically activities that living creatures perform in an ecosystem and are typically discussed in terms of trophic interactions (Violle *et al.*, 2007; Bonada *et al.*, 2017). Having a diverse array of functional roles is vital for the maintenance of stable ecosystems (Hulot *et al.*, 2000; Tilman, 2001; Hallett *et al.*, 2017).

The functional roles of terrestrial invertebrates, such as worms (Platyhelminthes, Nematodes, Annelids), Mollusks, and Arthropods, include nutrient cycling (Meyer *et al.*, 2011), decomposing organic matter (Seeber *et al.*, 2008), pollinating (Ollerton *et al.*, 2011), dispersing seeds (O'Rourke *et al.*, 2006), facilitating microbe activity (Cole *et al.*, 2004; Meyer *et al.*, 2011), ecosystem engineering (Wilson, 1987; Lavelle *et al.*, 2006), and are involved in a range of trophic interactions (Saffo, 1992; Lefèvre *et al.*, 2009). Invertebrates are important components

of food webs (Moore *et al.*, 1993; Patrick, 1994; Prather *et al.*, 2013), and food webs are intimately linked with ecosystem functioning (Mikola & Setälä, 1998; Thebault & Loreau, 2003).

1.2. Invasive mammals and their impacts on invertebrates

Mammals are known to be able to modify the habitat structure and functioning of terrestrial ecosystems through processes including feeding, trampling, uprooting, and burrowing (Rooney & Waller, 2003; Miyashita *et al.*, 2004; Campbell & Long, 2009; Holt *et al.*, 2011). The impact of mammals on ecosystems has long been of concern in places where the mammals are introduced outside of their natural historic range (Coblentz, 1978; Clout & Russell, 2008; Dolman & Wäber, 2008), especially on islands with unique ecosystems that have developed in the absence of mammals from the mainland (Simberloff, 1995; Dobson, 1997; Courchamp *et al.*, 2003).

Mammals can directly and indirectly affect invertebrate density and diversity. Direct consumptive interactions can be intentional by insectivores (e.g. rats consuming insect prey) or incidental by herbivores (e.g. deer consuming plant-dwelling invertebrates while feeding on plants) (Ruscoe *et al.*, 2013; Gish *et al.*, 2017). Herbivorous mammals can indirectly impact terrestrial invertebrate density and diversity through habitat modification, especially through changing vegetation structure (Baines *et al.*, 1994; Allombert *et al.*, 2005).

Cervidae (e.g. deer, elk, and caribou) is the mammal family with the highest proportion of successful invasive species (Clout & Russell, 2008). The impact of invasive Cervidae on ecosystems is well documented (Gawel *et al.*, 2018), and there are several studies out there on how they impact invertebrates around the world (Baines *et al.*, 1994; Miyashita *et al.*, 2004; Allombert *et al.*, 2005). High densities of red deer in native pinewoods of Scotland have been shown to reduce Lepidoptera larvae (e.g. butterfly and moth larvae) numbers likely because both the deer and the larvae preferred to feed on the new growth of bilberry bushes, which resulted in incidental ingestion of larvae as well as reduction of habitat for larvae (Baines *et al.*, 1994). In the temperate rainforests of the Haida Gwaii archipelago in Canada, islands with long histories of Sitka black-tailed deer browsing had significantly reduced density of invertebrates that resided in browse-layer (1.5m from the ground), but relatively little effect of browsing

history was observed for litter-dwelling invertebrates (Allombert *et al.*, 2005). Allombert *et al.* (2005) reasoned that deer browsing caused vegetation simplification and/or vegetation removal, which significantly influenced the diversity and density of vegetating-dwelling invertebrates. The less-significant effect of deer browsing on litter invertebrates was proposed to be because although deer browsing can change the quality of litter habitat, the litter habitat still persists, and different invertebrate taxa respond differently to this change in quality (Allombert *et al.*, 2005). In the conifer plantations of Boso Peninsula in Japan with Sika deer present, there was a significant reduction in web spider density and web spider species richness compared to plantations without Sika deer (Miyashita *et al.*, 2004). Miyashita *et al.* (2004) suggested that this was mostly due to fewer scaffolding sites for web spiders in the understory vegetation because of deer browsing, and probably not due to trophic processes as deer presence did not appear to influence prey availability.

Feral goats are another well-known herbivorous mammal in terms of its invasiveness and ability to negatively impact ecosystems, with successful goat eradication projects having occurred on at least 120 islands worldwide (Campbell & Donlan, 2005). Volcán Alcedo of the Galápagos experienced a huge population explosion of feral goats, and a study found that new species of macroinvertebrates (alongside an increase in species diversity) appeared alongside the massive vegetation changes caused by goat activity (Desender *et al.*, 1999). The results suggest that severe vegetation damage by goats can change invertebrate communities by allowing for the colonization of new invertebrate species (and potential loss of old species), probably due to the temporary increase in habitat heterogeneity (Desender *et al.*, 1999; Rosa García *et al.*, 2012).

Wild boar and pigs of the family Suidae are also successful invasive mammals, the wild boar reportedly being the oldest intentionally introduced mammal species for their meat (Sales *et al.*, 2017). As part of their feeding habits, wild boar and feral pigs overturn large areas of soil vegetation through a process called 'rooting' which modifies soil and consequently impacts ecosystems in a variety of ways (Barrios-Garcia & Ballari, 2012). In the hardwood forests of Great Smoky Mountains National Park in the USA, the presence of European wild boar significantly reduced the abundance of macroinvertebrates (but no change in species diversity)

in the soil though a possible reason for this reduction was not given (Howe *et al.*, 1981). In an Australian lowland tropical forest, feral pig disturbance led to decreased macroinvertebrate abundance and diversity, and these effects were mediated by season where there were more significant effects of pig disturbance on macroinvertebrates in the dry season and not the wet season (Taylor *et al.*, 2011). Taylor *et al.* (2011) concluded that disturbance and predation by feral pigs significantly reduced invertebrate abundance, but specific pathways for how pig disturbance affected invertebrate abundance and diversity were not given. Based on their results on litter and plants however, it is likely that the significant changes in litter cover and seedling density that correlated with pig disturbance played a part in influencing invertebrate abundance (Taylor *et al.*, 2011). In a rainforest of Mauna Loa Volcano in Hawaii, the removal of feral pigs from fenced areas resulted in forest regeneration and a significant increase in the abundance of soil micro invertebrates such as endemic springtails (Vtorov, 1993).

Small introduced rodents that are mainly insectivorous can also influence invertebrate communities through direct predation (Chown *et al.*, 2008; Ruscoe *et al.*, 2013). House mice have had their effects on invertebrate populations reported on several island ecosystems (Chown *et al.*, 2008). On the sub-Antarctic Guillou Island where a substantial portion of invertebrate biomass (especially moths and weevils) is consumed by mice, data suggests that mice predation is influencing the size distribution of weevils (Chown & Smith, 1993; Smith *et al.*, 2002). Endangered Achatinellinae snails that are endemic to Hawaii have had their populations heavily suppressed by predation from rats on two different Hawaiian islands (Hadfield *et al.*, 1993; Hadfield & Saufler, 2009).

1.3. Conservation biology and ecological restoration

Conservation biology and restoration ecology share similar goals of preserving natural communities and ecosystems (Soulé, 1985; Jordan *et al.*, 1988; Dobson, 1997; Young, 2000; Aronson *et al.*, 2006). Conservation biology is often about conserving already-intact populations, communities and ecosystems from becoming further degraded by human activity (Jordan *et al.*, 1988; Kleinschroth *et al.*, 2019). Jordan *et al.* (1988) wrote that conservation projects alone cannot necessarily preserve all populations or communities because of rapid

habitat loss from human development. Restoration ecology, on the other hand, is concerned with repairing ecosystems that have already been damaged, degraded, or destroyed (Young, 2000; Davis & Slobodkin, 2004; Aronson *et al.*, 2006; Reif & Theel, 2017).

The recovery of ecosystem functions certainly plays an important part in establishing a stable natural ecosystem (Palmer *et al.*, 1997) and that is where animals, especially invertebrates, can play a huge role because of the important and diverse ecological functions they provide (McAlpine *et al.*, 2016). For example, in the revegetation stage of the ecological restoration of agricultural landscapes investigated by Colloff *et al.* (2010), they found that older revegetated sites showed an increase in the number of holes in the soil created by invertebrates like burrowing bees and spiders compared to younger revegetated sites. This natural colonization of burrowing invertebrates in revegetated pasture thus introduced ecological functions that affected the way in which water could penetrate the soil (Colloff *et al.*, 2010).

Although some invertebrates can easily and quickly colonize restoration sites without human aid, colonization by invertebrates that are rare or have low mobility can take much longer or may not occur at all (Brady *et al.*, 2002; Watts & Didham, 2006). An experiment by Brady *et al.* (2002) demonstrated that without human aid by translocating invertebrates, attempted ecological restoration of a wetland site would be quickly dominated by mobile flying invertebrates, and ultimately result in low species diversity. The invertebrate community structure ended up much more comparable to a nearby natural wetland in terms of species diversity when there was human aid, which involved snail and soil inoculation (Brady *et al.*, 2002). This demonstrates that if ecological restoration focuses mainly on plants, there is no guarantee that the diversity and abundance of appropriate invertebrate taxa will recolonize the area.

1.4. In the context of New Zealand

In New Zealand, invertebrates not only have the role of prey species of the more charismatic macro fauna (such as the Kiwi (Colbourne & Powlesland, 1988), Tuatara (Ussher, 1999), and Grand/Otago skink (Reardon *et al.*, 2012) just to name a few), but they also have biodiversity value themselves as the vast majority of the invertebrates found in New Zealand are native and cannot be found anywhere else in the world (Watt, 1975; McGuinness, 2001). Many native New Zealand invertebrates are endangered (e.g., *Deinacrida* giant weta (Watts & Thornburrow, 2011), *Powelliphanta* snails (Boyer *et al.*, 2013), Katipo spiders (Costall & Death, 2010), and *Prodontria* chafer beetles (Emerson, 1994; Spencer *et al.*, 2017)). There are likely to be many more endangered native invertebrates that we do not know anything about since, in an assessment made in 2010, less than 30% of New Zealand's terrestrial invertebrates have had their threat assessments made (Stringer 2012).

There have been a few studies and reviews looking into how introduced mammals (particularly rodents and small mammals) might be affecting invertebrates in New Zealand. Bremner *et al.* (1984) explored the indigenous invertebrate communities on New Zealand islands and found that 13 out of the 14 groups of indigenous invertebrates studied had lower densities on the island that had been infested with Norway rats for over 100 years compared to the island completely free of mammals. Bremner *et al.* (1984) concluded that rat predation can have negative effects on New Zealand invertebrate communities and among the most vulnerable were large bodied invertebrates like weta. Rickard (1996) explored the diets of various small introduced mammals such as rodents, stoats, and possums, and found that invertebrates were present in the diet of all these mammals and large bodied invertebrates were often preferred. However, it is unclear how invertebrate populations were affected by these mammals (Rickard, 1996). Moreover, while there are no studies on how large mammals like deer, goats, and pigs affect invertebrates in New Zealand, there are many studies on how these mammals degrade native vegetation, damage populations of native vertebrates, and restrict ecosystem recovery (Challies, 1975; Parkes, 1993; Chimera *et al.*, 1995; Wilson *et al.*, 2006; Tanentzap *et al.*, 2009; Tanentzap & Lloyd, 2017).

1.5. Pest-resistant fencing

In New Zealand, specially designed fencing has successfully been used to control the distribution of introduced mammalian pests that negatively affect native species of plants and animals (Burns *et al.*, 2012). These fences which have been employed for ecosystem restoration projects are designed to keep out introduced mammalian pests. Some single-species conservation goals in New Zealand have been met with the help of pest-exclusion fencing, for example the protection of *Powelliphanta* snails in the Marlborough Sounds, the reduction of predation on the flightless Takahē (*Porphyrio mantelli*) at Burwood Bush (Southland, Lat -45.5; Long 168.1), and the population recovery of skinks (*Oligosoma otagense* and *O. grande*) at Macraes (Otago, Lat -45.4; Long 170.42) (Parrish *et al.*, 1995; Scofield *et al.*, 2011; Burns *et al.*, 2012). Pest-resistant fencing has also been considered as vital in protecting not just select species of endangered organisms, but also to help restore biodiversity in a wider ecosystem-centered context, particularly after North Island kokako (*Callaeas cinerea wilsoni*) protection also resulted in positive ecological responses, such as the increase in invertebrate community diversity (Saunders & Norton, 2001; Burns *et al.*, 2012).

1.6. Orokonui Ecosanctuary

The Orokonui Ecosanctuary (hereinafter referred to as "Orokonui", Lat -45.76 ; Long 170.59), is one of the few mainland reserves in New Zealand surrounded by pest-resistant fencing (Burns *et al.*, 2012) and can be characterized as an ecological restoration project (Campbell-Hunt, 2014; Specht, 2016, "Orokonui restoration plan", 2019; Symon *et al.*, 2019). Among the primary objectives of Orokonui is to create a self-sustaining ecosystem and to restore the ecological integrity of the Orokonui Valley ("The Orokonui Story - Orokonui Ecosanctuary," 2019). Orokonui is about a 20km drive north of Dunedin Central in Waitati, Otago, in the South Island of New Zealand (**Figure 1.1**). The 8.7 km long, 2 m tall pest-resistant fence that surrounds 307 hectares of coastal Otago forest was built in July 2007 and pest eradication programmes commenced soon after (Tanentzap & Lloyd, 2017). The forest of Orokonui is dominated by regenerating native New Zealand forest which includes tree species such as Kanuka (*Kunzea ericoides*), native conifer (Podocarp) species, Kotukutuku (*Fuchsia*

excorticata), Kapuka (*Griselinia littoralis*), and Mahoe (*Melicytus ramiflorus*). The eradication of pests including feral goats, brushtail possums, feral cats, mustelids, European hedgehogs, European hares, and rats was completed in 2008 and continuous pest monitoring has since been performed (Tanentzap & Lloyd, 2017). The only pest mammal still detected occasionally are mice, but when they are detected the quick management response lowers mice numbers to near undetectable levels (Tanentzap & Lloyd, 2017). Thanks to various reintroduction programmes as well as continued maintenance of the pest-free nature of Orokonui, it is currently home to many rare, vulnerable, and endangered New Zealand animal species including Haast tokoeka kiwi (*Apteryx australis australis*), kākā (*Nestor meridionalis*), tuatara (*Sphenodon punctatus*), takahe (*Porphyrio hochstetteri*), Otago skinks (*Oligosoma otagense*), jewelled geckos (*Naultinus gemmeus*), and South Island Robins (*Petroica australis australis*) (Bogisch *et al.*, 2016; Kitchin *et al.*, 2017; Tanentzap & Lloyd, 2017; Lloyd *et al.*, 2018).

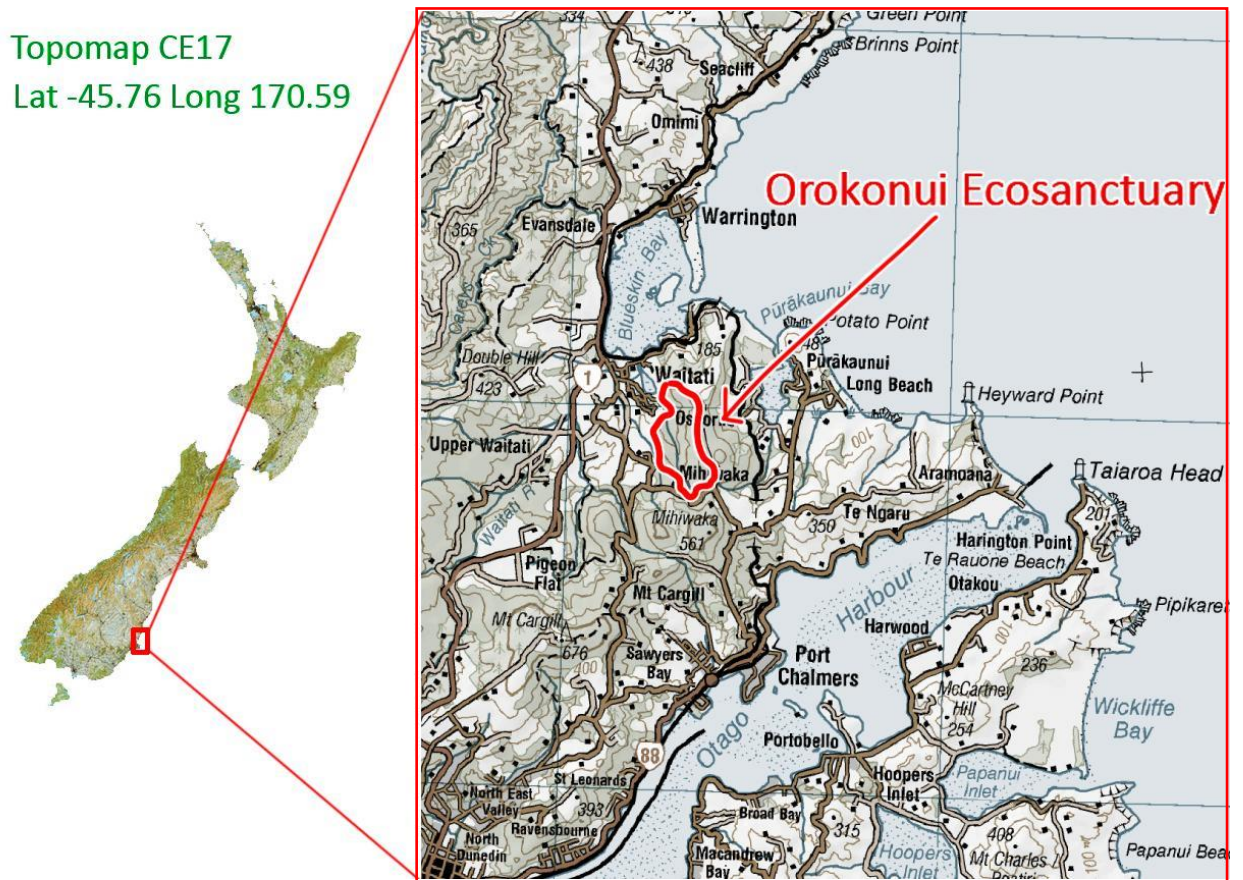


Figure 1.1 Maps showing the location of Orokonui Ecosanctuary in Dunedin, South Island, New Zealand. The approximate edge of the pest-resistant fence is outlined in red in the zoomed-in inset. The images used in creating this figure was taken from topomap.co.nz. The topomap.co.nz reference sheet code is CE17.

1.7. Objectives of the present study

To my knowledge invertebrate surveys were not performed before the installation of the Orokonui fence, so I cannot make comparisons of invertebrate communities between the past (no fence, mammals present), and now (fence erected, most mammals eradicated). However, what I can do is look at what the invertebrate community is like inside and outside the fence in a snapshot of time right now.

In this study I investigate invertebrates at Orokonui to answer this primary question: Does the exclusion of introduced mammals with pest-resistant fencing influence terrestrial invertebrate communities in New Zealand, and if so, are these patterns consistent between seasons?

In order to address this question, I had to first find suitable sites inside and outside the Orokonui fence to collect invertebrate samples from. In chapter 2, I describe how I found pairs of sampling sites inside and outside the fence using plant species presence/absence data. In chapter 2, I also explore the soil properties of the sites selected for sampling. In chapter 3, I compare abundance of terrestrial invertebrate taxa between sites inside and outside the Orokonui fence, and between two seasons (winter and summer). Beetles (Order: Coleoptera) are looked at in finer detail to see how their diversity and proportion of endemic species are affected by mammal exclusion from Orokonui's fencing. In chapter 4, I discuss the results of the present study and provide suggestions for future research in this area.

Chapter 2: The search for sampling sites

2.1. Introduction

Terrestrial invertebrate assemblies are known to correlate with a variety of different biotic and abiotic factors including disturbance by browsing mammals, soil properties, and plant species composition (Gibson *et al.*, 1992; Saunders & Norton, 2001; Boulton *et al.*, 2005; Sylvain & Wall, 2011; Watts *et al.*, 2014).

In ecosystems, soil invertebrates, the soil itself, the microorganisms in the soil, and the plants growing from the soil are linked (De Deyn *et al.*, 2003; Scheu *et al.*, 2005; Wardle, 2006; Frouz *et al.*, 2008; Zagatto *et al.*, 2019). Plant species composition can influence soil and ground-dwelling invertebrate populations in various ways such as through the structural complexity of the vegetation (Oxbrough *et al.*, 2005; Grof-Tisza *et al.*, 2017); the effects plants can have on soil chemistry (Vila *et al.*, 2006); and the consequential effects that soil chemistry can have on invertebrates (van Straalen & Verhoef, 1997; Crisp *et al.*, 1998; Rossi, 2003). In some instances, specific plant assemblages can attract specific specialist invertebrates (Crisp *et al.*, 1998; De Bruyn *et al.*, 2001; Currie *et al.*, 2011).

The ways in which plant species composition affects invertebrate composition and distribution varies amongst the invertebrate taxa. For example, in a study by Sanderson *et al.* (1995) herbivorous true bugs (Order: Hemiptera) were shown to be closely associated with plant species composition, and Gardner (1991) found that distinct carabid beetle (Order: Coleoptera) communities were associated with bogs dominated by *Juncus* and *Sphagnum* (moss) species. However, spiders (Order: Araneae) appeared to have no such association with plant species composition (Sanderson *et al.* 1995).

Soil chemistry and other physical properties of soil (e.g. moisture holding capacity and drainage) can influence invertebrate communities directly (Rickard, 1996; van Straalen & Verhoef, 1997; Fraser *et al.*, 2012), or indirectly because of how soil properties affect plant growth and microorganisms (Roem & Berendse, 2000; Scheu *et al.*, 2005; Sylvain & Wall, 2011; Matkala *et al.*, 2019). Soil pH has been found to influence soil invertebrate and microbe

communities (Paoletti *et al.*, 1996; van Straalen, 1998), and because of this relationship communities of invertebrate species with specific pH tolerance thresholds (such as the springtail (*Tomocerus flavescens*), and the mites (*Platynothrus punctatus* and *Pelops occultus*) have been proposed as bioindicators of soil pH (van Straalen & Verhoef, 1997). Plant species diversity can also be influenced by soil pH (Roem & Berendse, 2000), and invertebrate communities can be influenced by plant species richness and abundance (Crisp *et al.*, 1998; Jonsson *et al.*, 2009), it is therefore possible that soil invertebrates can be indirectly influenced by soil pH because of how pH can influence plant composition..

Phosphorus and nitrogen are essential elements for all living organisms and functioning ecosystems (Brady *et al.*, 2008). Phosphorus content in the soil is correlated with multiple components of ecosystems including plant diversity, soil fungal activity, and soil microbe abundance (Gartlan *et al.*, 1986; Sparling *et al.*, 1987; Doren *et al.*, 1997; Wu *et al.*, 2019). Soil nitrogen has been shown to correlate with nematode and leaf litter arthropod activity in undisturbed forests (Neher *et al.*, 2012). Organic matter content, which consists of many essential trace elements, is an important component of soils and has been linked with invertebrate activity and invertebrate communities (Wolters, 2000; Huerta & van der Wal, 2012).

In this chapter, I will be addressing two questions: (1) **Which sites inside the ecosanctuary are most similar in plant species composition to sites outside the ecosanctuary?** I will be attempting to find pairs of sites inside and outside the fence that have similar plant species composition. After I confirm site pairs, I asked (2) **If we can determine sites with more plant species similarities inside and outside compared to anywhere else in the ecosanctuary, will those sites vary in terms of soil properties?** I investigated the soil properties of the plots, testing the assumption that sites with similar plant species composition would have similar soil properties (Vila *et al.*, 2006).

2.2. Methods

2.2.1. Finding pairs of sampling sites using plant species presence/absence data

In order to establish which sites inside and outside the fence were most similar in plant species composition, I used plant species data to perform a cluster analysis. Tanentzap & Lloyd (2017) investigated whether the pest-resistant fence at Orokonui would result in spillover effects of vegetation outside the fence boundaries. They surveyed plant species (n = 170 species) presence and absence in over 40 permanently marked 10 m x 10 m (100 m²) plots inside (n = 50) and outside (n = 18) (within 500m distance from the fence line) the Orokonui Ecosanctuary, Waitati, Dunedin, NZ (Figure 2.1; Lloyd unpublished data). The plant species in these plots were first surveyed between 2005 and 2007 and then resurveyed between 2013 and 2014 (Tanentzap & Lloyd, 2017).

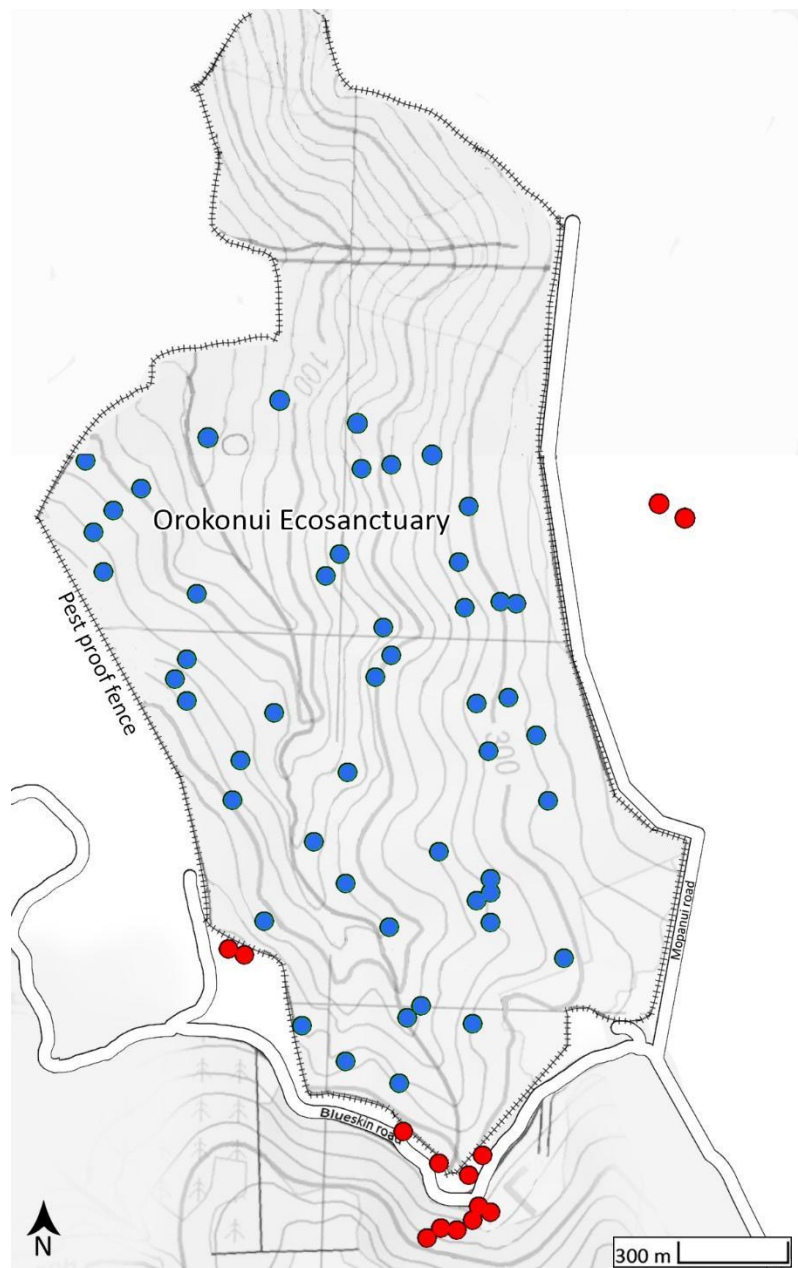


Figure 2.1 Map of the Orokonui Ecosanctuary area, showing the boundary of the pest-resistant fence (hatched lines), main roads (with road names outside the pest-resistant fence), and topography of relevant areas. The dots represent the locations of the 10 m x 10 m marked plots in forest used by Tanentzap and Lloyd (2017) in their research. Blue dots represent plots within the pest-resistant fence, and red dots represent plots outside the pest-resistant fence. Not all the plot locations are shown on this map as some are up to 20km away from this area, and those plots were not utilized in the present study. Reference images used to make the figure are courtesy of Tanentzap & Lloyd (2017) and topomap.co.nz.

I conducted the cluster analysis in R-Studio (R Core Team, 2018). Dissimilarity data (numbers that identify how similar or dissimilar plots are to each other) were produced using 'Euclidean distance' as the distance measure. I clustered the Euclidean dissimilarity data using the 'hclust' function ('average' linkage) from the package 'stats' (R Core Team, 2018). 'Average' linkage has been described as a good compromise between the limitations of the 'single' linkage or 'complete' linkage methods (Yim & Ramdeen, 2015). I plotted this average linkage dissimilarity data into a cluster dendrogram. Forest plot 'pairs' for the purposes of the present study were chosen based on their similarity as derived from the cluster analysis and shown in the dendrogram.

2.2.2. Manual selection of a non-forest grass pair of sampling sites

In addition to the forest plot pairs, a non-forest plot pair dominated by grasses and sedges (graminoids) was also chosen. Open grassy sites with no tree or shrub cover are likely to harbour different types of invertebrates compared to forested sites (Huerta & van der Wal, 2012). To find a non-forest graminoid-dominant pair (referred to here as grass pair), I walked along the edge of the Orokonui fence and took note of locations where there were grassy areas on each side of the fence, and if these grassy areas appeared to have similar graminoid species composition, as well as there being an absence of other tree or shrub cover. I chose one grass pair location where there were similar dominant graminoid species present on both sides of a section (approx. 10 meters) of fencing (Figure 2.6).

2.2.3. Analysis of soil properties

After determining two pairs of forest-dominated (cluster analysis) and one pair of grass (manual selection) sites, on the 12th of September 2018, I collected ten soil core subsamples from all six sites. The soil core subsamples were collected with a hand-auger, a metal cylinder fixed to a metal bar handle which can be pushed into the soil to produce a 7.5cm long x 2.5cm diameter soil core subsample. I took the ten soil core subsamples at random spots within each site in a semi-structured way. I chose ten places evenly spaced from one another to stand, and at each of these places I turned around a few times, and then dropped a marker onto the

ground which indicated the spot for taking a subsample. I rejected sampling spots if it was a steep slope (approximately 30° and above).

Before taking a soil core subsample, I brushed aside the upper layer of litter or plant material until only soil was showing. If the hand-auger could not penetrate the soil to its maximum depth due to underlying rocks or roots, a new random spot for sampling was chosen. I rejected a subsample (and collected a new subsample) if it contained large stones or roots. I combined all 10 soil core subsamples from each site into one labelled 20 x 20cm Ziplock bag. I kept each Ziplock bag containing the subsamples in a 30L chilly bin with two towel-wrapped 1L ice pack bricks while I was still out in the field. When samples were collected for the day, I took the samples to Invermay Agricultural Centre and stored them in a 4°C cold storage room. The samples, still in their Ziplock bags, were shipped on the 13th September 2018 to ARL analytical research laboratories (Napier, NZ) for pH, Olsen soluble phosphorus (Olsen P), anaerobic mineralizable nitrogen (Anaerobic MinN), organic matter, carbon to nitrogen ratio (C/N ratio), and bulk density (dry Weight/volume) soil analyses.

2.3. Results

2.3.1. Sampling site pairs from using plant species presence/absence data

The cluster analysis highlighted two plot pairs (a pair consisting of one inside plot and one outside plot) that contained a plant species composition more similar to each other than to any other plots (Figure 2.2). Based on the woody species common to each pair **Error! Reference source not found.**), these are named Raukaua pair (Figure 2.4) and Hebe/Gorse pair (Figure 2.5) respectively. A full list of plant species documented at each of these sites is in **Appendix A**.

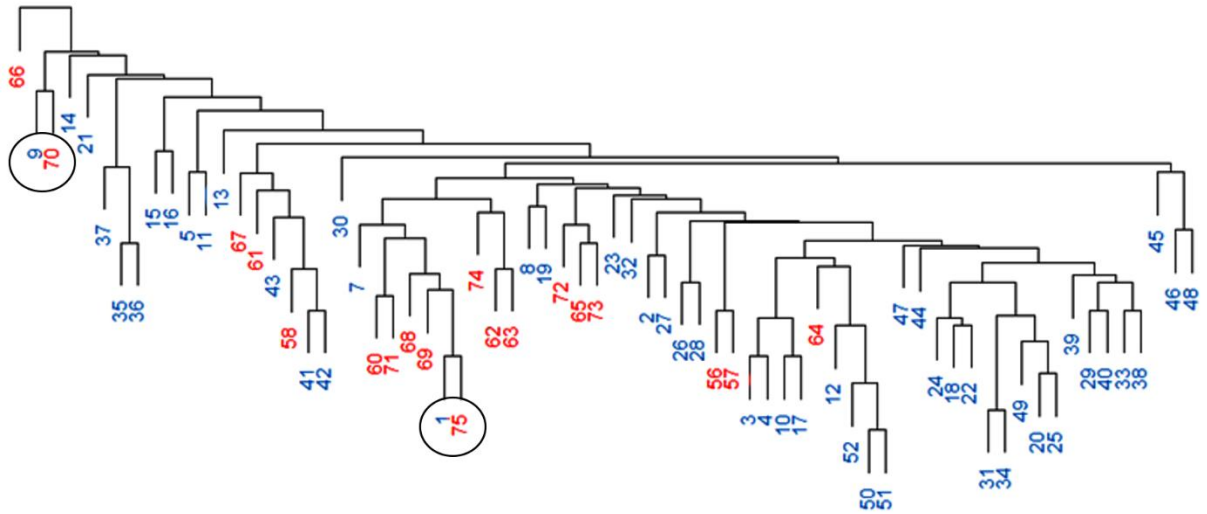


Figure 2.2. The results of the cluster analysis based on plant presence/absence data from 68 plots inside (n=50) and outside (n=18) the Orokonui ecosanctuary Fence. The numbers represent the plot ID number. Blue numbers represent plots that are inside the ecosanctuary fence, red numbers represent plots that are outside the ecosanctuary fence. The inside/outside plot pairs that are closer to one another than they are to any other plot are circled in black.

Table 2.1. Plant species exclusive to each pair of sites with the site pair names and plot ID numbers. The species with a habit of 'Tree/Shrub' are boldened and are the basis for the naming of each pair of sites.

Plant species exclusive to the Raukaua pair (plot 1 and 75)		
Scientific name	Common name	Habit
<i>Asplenium flaccidum</i>	Drooping spleenwort	Ground cover
<i>Blechnum procerum</i>	Small Kio Kio	Ground cover
<i>Rubus cissoides</i>	Bush Lawyer	Ground cover
<i>Raukaua edgerleyi</i>	Raukawa	Tree/Shrub
Plant species exclusive to the Hebe/Gorse pair (plot 9 and 70)		
Scientific name	Common name	Habit
<i>Rubus fruticosus</i>	Blackberry	Ground cover
<i>Muehlenbeckia australis</i>	Pohuehue	Ground cover
<i>Dactylis glomerata</i>	Cocksfoot	Ground cover
<i>Hebe salicifolia</i>	Koromiko	Tree/Shrub
<i>Ulex europaeus</i>	Gorse	Tree/Shrub

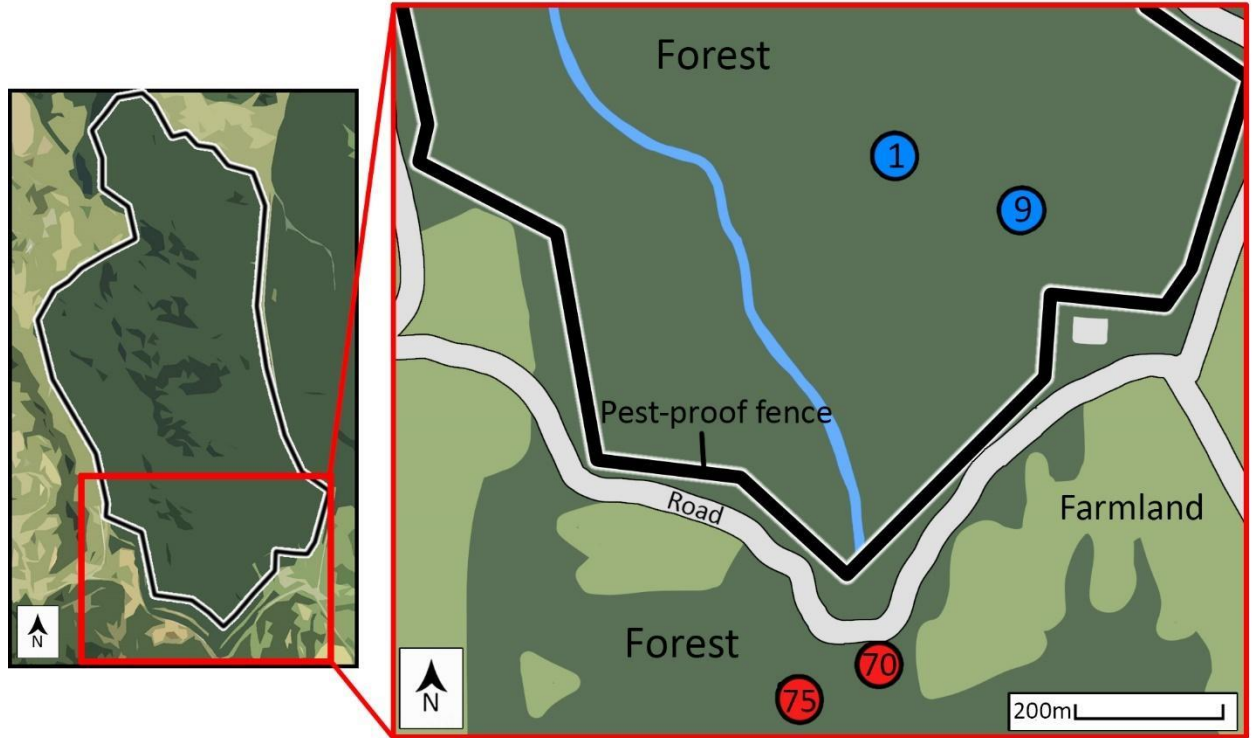


Figure 2.3. Maps displaying the southern section of the Orokonui Ecosanctuary and some of the forest (dark green) and farmland (light green) outside ($45^{\circ}46'S$, $170^{\circ}35'E$). The numbered circles represent the approximate locations of vegetation plots for the Raukaua pair (numbers 1 and 75) and the Hebe/Gorse pair (numbers 9 and 70). Blue dots are inside the Orokonui fence and red dots are outside the Orokonui fence. The blue line inside the fence represents the stream that flows through the Orokonui Ecosanctuary. The plot numbers are the same vegetation plot identification numbers as were used in the study by Tanentzap and Lloyd (2017).

Raukaua pair

Inside

Outside



Figure 2.4 Photographs of the Raukaua pair of sites that were utilized for sampling.

Hebe/Gorse pair

Inside

Outside



Figure 2.5. Photographs of the Hebe/Gorse pair of sites that were utilized for sampling.

Grass pair

Inside

Outside



Figure 2.6. Photographs of the Grass pair of sites that were utilized for sampling.

2.3.2. Manually selected grass pair of sampling sites

A graminoid-dominant pair of sites, named the Grass pair, was located near the fence gate at the northern end of the Orokonui ecosanctuary (Figure 2.6 and Figure 2.7).

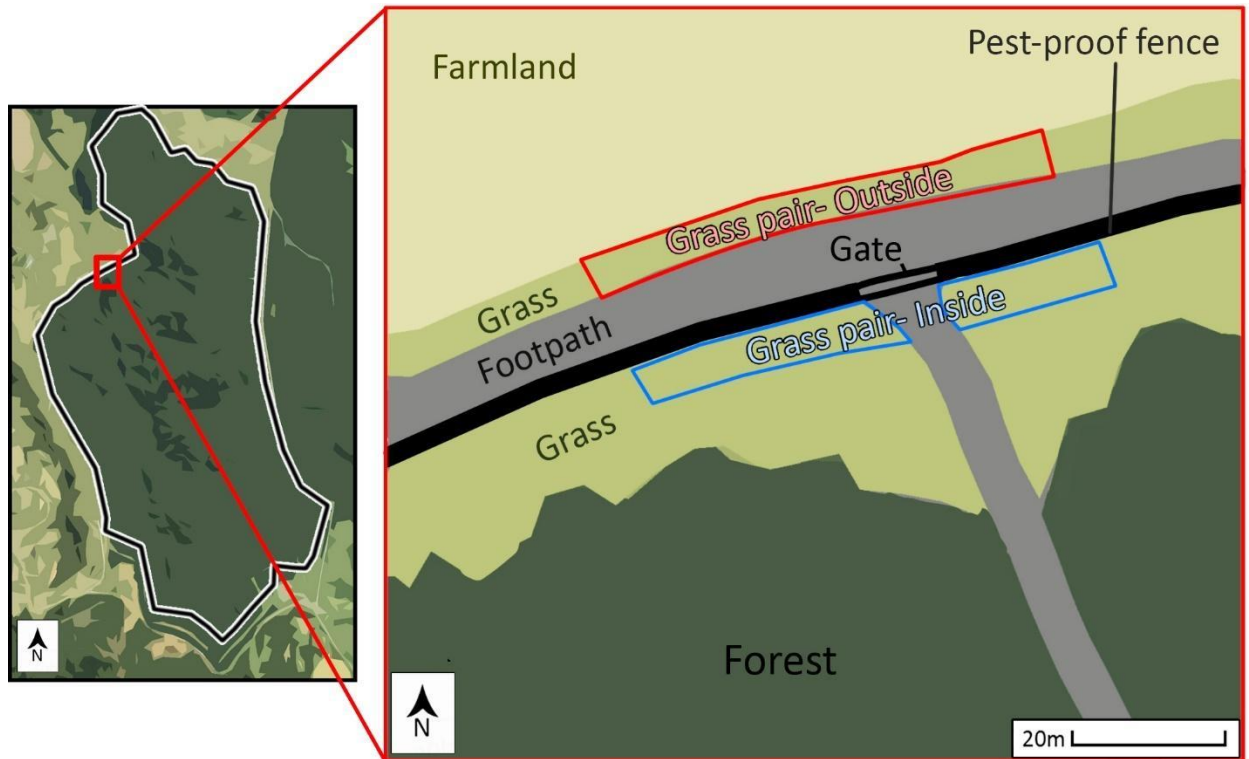


Figure 2.7. Maps displaying the Orokonui ecosanctuary where the northern gate is located (Waitati 45°45'S 170°35'E). The outside site of the grass pair (highlighted in red) is a narrow strip consisting mainly of long uncut grasses, adjacent to pasture. The inside site of the grass pair (highlighted in blue) is a narrow strip consisting of a mix of mowed and unmowed grasses and sedges, adjacent to more graminoids and forest. Only areas of unmowed grasses within the highlighted areas were sampled.

2.3.3. Soil analyses

The Raukaua and Hebe/Gorse pairs had marginally higher values of pH, Olsen soluble phosphorus, anaerobic mineralizable nitrogen, and dry weight/volume inside the fence compared to outside the fence but lower values of organic matter outside the fence compared to inside the fence. The Grass pair showed similar patterns (with greater phosphorus and mineralizable nitrogen differences inside compared to outside the fence) except for in Organic matter content, where there was a higher percentage of soil organic matter inside the fence compared to outside the fence (Table 2.2)

Table 2.2. Soil analysis results for each site as given by analytical research laboratories (ARL). Each result is based off the pooled 10 soil core subsamples per site.

	Raukaua pair		Hebe/Gorse pair		Grass pair	
	inside	outside	inside	outside	inside	outside
pH	5.3	5	5.1	4.9	5.8	5.5
Olsen Sol.P (ug/mL)	10	8	8	6	13	4
Anaerobic MinN (kg/ha)	241	142	181	143	131	46
Organic matter (% w/w)	13.8	24.9	13.1	21.8	8.1	3.3
C/N ratio	17	21	16	18	13	12
Dry Weight/Volume (g/ml)	0.7	0.55	0.72	0.53	0.77	0.88

2.4. Discussion

In this chapter, I set out to answer two questions: (1) **Which sites inside the ecosanctuary are most similar in plant species composition to sites outside the ecosanctuary?** And (2) **If we can determine sites with more plant species similarities inside and outside compared to anywhere else in the ecosanctuary, will those sites vary in terms of soil properties?**

Addressing the first question was successfully accomplished using a cluster analysis to find two pairs of sites dominated by forest species, and by visual manual selection to find one site pair dominated by grass-like (graminoid) plants. These three pairs of sites, named the Raukaua pair, the Hebe/Gorse pair, and the Grass pair were used to survey soil invertebrates. The sites within each forest-dominant pair had a more similar plant species composition to each other than any other site included in the cluster analysis; however, the abundance of each plant species was not taken into account as this information was not available to incorporate into the cluster analysis. It is therefore important to note that the name 'Raukaua pair' for example does not imply that the inside and outside sites of this pair is dominated by *Raukaua edgerleyi*, but rather the sites simply share the presence of the plant. Studies have shown that species diversity and relative abundance of those species (evenness) can work very differently in how they tie in with ecosystems regardless of whether the organisms being studied were plants (Laird *et al.*, 2003) or animals (Dangles & Malmqvist, 2004).

The second question was more challenging to address because as only one value for each soil property was available per site, statistically significant differences could not be calculated for inside sites vs outside sites within each pair. Based on previous work that has shown that soil properties can affect the type of plants that can grow (Roem & Berendse, 2000), and some species of plants can affect soil properties (Vila *et al.*, 2006), I hypothesized that if I found sites with similar plant species composition, the soils at those sites would have similar properties. Regardless, my results show some soil properties were more similar within some pairs for some soil properties but not others.

Soil pH, which is known as a 'master variable' of soils as it influences many other chemical and biological processes (Rengel, 2002), appeared to be very similar within all three pairs of sites (range 4.9 – 5.8), the difference within a pair never exceeded 0.3 units. A study on New Zealand soils by Beets *et al.* (2002) showed a huge variation in soil pH within a section of New Zealand native forest along a 200 - 300 m transect (from ridge crest to gully to opposing ridge crest), which ranged dramatically between a pH of 3.5 and 6.5. Therefore, the pH differences found within the forest and grass pairs in this study are quite small, at least for the forest pairs.

Olsen phosphorus values also appeared to be similar within the forest-dominant pairs, with differences of 2 µg/ml, which is within the standard error found by Sparling and Schipper (2004) for 58 different indigenous forest types in New Zealand. Olsen phosphorus values tend to be much higher in grassy pastures compared to indigenous forest (Sparling & Schipper, 2004), so the highest Olsen P value of 13 µg/ml found in the Grass pair-inside site is not unusual. However, the value of 4 µg/ml found in the Grass pair-outside site is unusually low, being even lower than what is expected in indigenous forest.

According to what is usually observed with soil anaerobic mineralizable nitrogen, the inside site of the Raukaua pair had a very high anaerobic mineralizable nitrogen value at 241 kg/ha, and the outside site of the Grass pair had a very low value at 46 kg/ha. The only pair with a somewhat similar anaerobic mineralizable nitrogen value within a pair is the Raukaua pair, where the difference is 38 kg/ha which is within a normal range (which is about 50 kg/ha for

pasture according to ARL who analyzed my samples). It was difficult to compare the mineralizable nitrogen ranges found in this study to the ranges found in other studies, as the units measured were different (e.g. my values are based on volume, not weight of soil) and the incubation methods/times used to attain mineralizable nitrogen values may differ (Mariano *et al.*, 2013).

Organic matter content was lower inside the fence compared to outside the fence for the forest pairs, but higher inside the fence compared to outside the fence for the grass pair. The difference in organic matter content inside and outside the fence appear to be quite different (the organic matter difference inside and outside the fence being 11.1 % , 8.7 % , and 4.8 % for the Raukaua, Hebe/Gorse and Grass pair respectively), especially considering the usual ranges of organic carbon percentages that were found in soils under a variety of vegetation in a study by Sparling (1992) and under fir and grassland in a study by Alfredsson (1998). In the study by Sparling (1992), the organic carbon content only ranged from 5.2 % to 7.2 % in soils (to 5 cm depth) under vastly different vegetation types including native beech, gorse, radiata pine, weedy pasture, and fertilized pasture. In the study by Aldredsson (1998), there was a significant difference in organic carbon content in soils (to 5 cm depth) under Douglas fir trees and adjacent grassland, where their organic carbon contents were 7% and 11.9% respectively. It is unclear whether the apparent patterns showing differences inside and outside the fence for organic matter especially are due to mammal activity, plant species dominance, the activity of soil invertebrates and microorganisms, or other complex ecological interactions. For instance, the higher soil organic matter content outside the fence in the forest-dominant pairs compared to inside could be due to how large mammals influence invertebrate decomposer communities or organic carbon input into soils through processes such as grazing, digging, and defecation (Sankaran & Augustine, 2004; Mohr *et al.*, 2005).

The C/N ratio did not appear to be very different inside and outside the fence for all three pairs as the difference fell within the ranges that are normally observed in New Zealand based on data by Sparling & Schipper (2004) and Stevenson *et al.* (2010). The C/N ratio also seemed more similar within plot pairs than between plot pairs which fits with what was hypothesized. In the Stevenson *et al.* (2010) study, even when comparing soils in forestry

forest with a mean C/N ratio of 18.2 (standard error of 0.7) with indigenous forest with a mean C/N ratio of 16.8 (standard error of 0.5), the difference in C/N ratio was not considered to be significantly different.

The bulk density of soil between the inside and outside sites within pairs were only slightly different according to the quality classes and 'target ranges' described in a report by Lilburne et al. (2004). In the Lilburne et al. report, organic soils categorized at 'loose' ranged from 0.2 to 0.4 g/ml, organic soils categorized as 'adequate' ranged from 0.4 to 0.6 g/ml, and compact ranged from 0.6 to 1.0 g/ml. In this study, the highest dry weight per volume was observed in the outside site of the Grass pair, and I attribute this value to the fact that I observed many tiny stones in the soil of this site during soil core sampling, and some of these stones may have been in the soil samples that I sent to ARL for analyses.

In conclusion, three pairs of sites were found based on similarity of plant species composition, namely the Raukaua pair, the Hebe/Gorse pair, and the Grass pair. Soil properties were documented from one aggregated sample from each site in each pair and these data provided an indication of the similarity and variability within the pairs of sites. There could be differences in a few soil properties such as organic matter and mineralizable nitrogen, but I could not confirm this statistically, and questions regarding these potential differences could be answered in future research.

Chapter 3: The influence of fencing and season on invertebrate communities

3.1. Introduction

Soil and other ground-dwelling invertebrates are important for the healthy functioning of ecosystems (Cole *et al.*, 2004; Lavelle *et al.*, 2006; O'Rourke *et al.*, 2006; Seeber *et al.*, 2008). The functional roles of terrestrial invertebrates include nutrient cycling (Hartley & Jones, 2008), decomposing organic matter (Hartley & Jones, 2008; Bachmann & Simmons, 2010), pollinating (Ollerton *et al.*, 2011), seed predation (O'Rourke *et al.*, 2006; Lewis & Gripenberg, 2008), ecosystem engineering (Wilson, 1987; Cornelissen *et al.*, 2016) are also involved in a range of trophic interactions (Schoenly *et al.*, 1991). Because invertebrates provide such a diverse array of functional roles, they are vital for the maintenance of functional ecosystems (Tilman, 1999; Ueda *et al.*, 2008; Weisser & Siemann, 2008) and are an important source of food for some endangered insectivorous New Zealand vertebrates (Colbourne & Powlesland, 1988; Reardon *et al.*, 2012; Kitchin *et al.*, 2017). Terrestrial invertebrates in New Zealand also have diversity value in and of themselves where the vast majority of them cannot be found anywhere else in the world (Watt, 1975; McGuinness, 2001, chapter 1 section 1.4).

Beetles (Order: Coleoptera) are among the most species-rich order of animals on earth (Leschen *et al.*, 2003; Ponomarenko, 2003; Jäch & Balke, 2008) and New Zealand beetles boast a rate of over 90% for species endemism (Klimaszewski, 1997). Many beetles are important components of soil and litter ecosystems and they perform a wide variety of functional roles (Petersen & Luxton, 1982; Pizzolotto *et al.*, 2018). Even just beetles that feed on dung (evolved several times in the Scarabaeoidea superfamily) for example, cycle nutrients from dung back into the soil, suppress or disperse parasites found in dung, mix sediment particles (bioturbation), disperse seeds, predate on maggots and ants, and even pollinate flowers (Nichols *et al.*, 2008). Species diversity usually has a positive correlation with functional diversity, however there have been rare cases where species diversity had had an inverse relationship with functional diversity, for example in ground beetles (family: Carabidae) where

there was an increase in species diversity but a decrease in functional diversity after flood disturbance (Gerisch *et al.*, 2012).

Many factors can negatively impact invertebrate communities and consequently overall ecosystem health, and one of those is mammalian disturbance. The impact of mammals on ecosystems has long been of concern in places where the mammals are introduced outside of their natural historic range (Coblentz, 1978; Clout & Russell, 2008; Dolman & Wäber, 2008), especially on islands with distinctive ecosystems that have evolved and developed in the absence of mammals (Simberloff, 1995; Dobson *et al.*, 1997; Courchamp *et al.*, 2003). Mammals can modify the habitat structure and functioning of terrestrial ecosystems through processes including feeding, trampling, uprooting, and burrowing (Rooney & Waller, 2003; Miyashita *et al.*, 2004; Campbell & Long, 2009; Holt *et al.*, 2011). Mammals can directly and indirectly affect invertebrate assemblages via deliberate or incidental predation (Ruscoe *et al.*, 2013; Gish *et al.*, 2017), and herbivorous mammals can indirectly impact invertebrate density and diversity through habitat modification, especially through changing vegetation structure (Baines *et al.*, 1994; Allombert *et al.*, 2005; Ueda *et al.*, 2008).

Different types of invertebrate taxa may respond differently to the direct and indirect pressures from mammals (Allombert *et al.*, 2005). For example, Allombert *et al.* (2005) found that browsing pressure by Sitka black-tailed deer significantly reduced Gastropoda (slug and snail) abundance but significantly increased Curculionidae (weevil beetle) abundance on island forests in Canada. Mammalian impacts on invertebrates could also vary across seasons because of the way different invertebrate taxa respond to seasons, for example due to seasonal availability of food, seasonal changes in phenology, and abiotic environmental changes such as moisture levels and temperature (Recher *et al.*, 1996; Southwood *et al.*, 2004; Harris, 2013). The way in which invertebrates respond to seasonal changes can also depend on the local climate. For example, invertebrates living in the canopy of eucalyptus forests in eastern and western Australia respond differently to season, even though the vegetation stayed constant, where invertebrate taxa tended to be most abundant in spring in the eastern forests, but most abundant in autumn in the western forests (Recher *et al.*, 1996). There could be complex

interactions between mammalian pressure and the pressures of seasonal changes on invertebrate communities, which I will explore in the present study.

Pest-resistant fencing is argued to be important for preserving functional native ecosystems (Scofield et al., 2011) by keeping out unwanted introduced mammalian pests from areas of protected land (Burns et al., 2012). In the present study, the focus is on the Orokonui Ecosanctuary which is a mainland reserve in New Zealand surrounded by pest-resistant fencing (Burns et al., 2012). The Orokonui fence not only keeps mammals outside of its border, but also keeps vulnerable New Zealand flora and fauna inside of its border (Bogisch et al., 2016; Kitchin et al., 2017; Tanentzap & Lloyd, 2017; Lloyd et al., 2018). Predation by introduced mammals such as stoats, cats, dogs, and rats are arguably among the primary reason for the decline in populations of native animals such as the kiwi and tuatara in mainland areas around the country, so it stands to reason that the densities of these native animals will be higher within the boundary of the Orokonui fence (Cree et al., 1995; Robertson et al., 2016; Tanentzap & Lloyd, 2017; Lloyd et al., 2018). The situation that the fencing presents could mean that the invertebrates inside the fence will be facing a set of pressures from a higher density of flightless native vertebrates compared to invertebrates outside the fence facing a different set of pressures from a higher density of mammals.

In this chapter, I want to address three main questions on the role that the Orokonui's pest-resistant fence may be having on the terrestrial soil and leaf-litter-dwelling invertebrate biodiversity. (1) **Does soil and litter invertebrate abundance vary inside compared to outside the Orokonui Ecosanctuary fence?** The inside of the fence represents an environment where threatened native animals are protected and mammals are absent except small rodents (which are being controlled year-round), and the outside of the fence is an environment rich in free roaming introduced mammals and a presumably lower density of threatened native animals. If the exclusion of introduced mammals and the inclusion of native animals affects invertebrate abundance, I expect to see differences in invertebrate abundance within my pairs of sites (one site inside the fence and one site outside the fence) that were found in chapter 2. (2) **Does season affect soil and litter invertebrate abundance differentially inside and outside the Orokonui Ecosanctuary fence?** If the abundance of invertebrates responds differently to

season depending on if they are exposed to pressures from mammals or not, I would expect to see an interaction between the effects of mammal exclusion (the fence) and the effects of season. (3) **What is the difference in soil and litter Coleoptera diversity/endemism inside and outside the Orokonui Ecosanctuary fence?** Coleoptera are now widely used as indicators of ecological health because of their species and functional diversity. Even single families of beetles such as Carabidae are used in this manner because of their diversity and ease of identification (Bowie *et al.*, 2019). I have thus chosen this order of insects to investigate in finer detail for the present study. If mammal exclusion affects species and functional diversity (represented here with Coleopterans), I would expect to see a difference in Coleoptera diversity inside and outside the fence. I predict that there will be higher diversity inside the fence compared to outside the fence as the Coleoptera communities inside the fence will be facing fewer direct and indirect pressures from many introduced mammals which they have likely evolved in the absence of (Worthy *et al.*, 2006).

3.2. Methods

3.2.1. Sampling

Based on the results from chapter 2, there were three pairs of sites (six sites in total) for sampling: “Raukaua pair”, “Hebe/Gorse pair”, and “Grass pair”. Invertebrate sampling was performed once for each site in winter (between the 2nd May to the 18th of July 2018) and once for each site in summer (between the 30th of November and the 23rd of December 2018) (Table 3.1). A sampling unit consisted of three samples: a turf sample for surface-dwelling invertebrates, a hand-sorted sample for invertebrates deeper in the soil, and a soil moisture sample to document moisture conditions at the time (Figure 3.1). In the Raukaua and Hebe/Gorse pair sites, I randomly selected eight spots to collect sampling units. In the Grass pair sites, I randomly selected six spots to collect sampling units (Table 3.2). The random location of each sampling spot was determined by throwing a 15x15cm quadrat onto the ground after turning around twice with my eyes closed. If the quadrat landed on a steep slope (~30° and above) or if there were obstacles like large roots and rocks, the quadrat was moved to the closest amenable area for collecting a sampling unit.

Table 3.1. Sampling dates for the collection of sampling units, which include turf, hand-sorted, and moisture samples.

	Raukaua pair		Hebe/Gorse pair		Grass pair	
	Inside	Outside	Inside	Outside	Inside	Outside
Winter	30/05/18	21/05/18	2/05/18	9/05/18	18/07/18	18/07/18
Summer	23/12/18	23/12/18	30/11/18	30/11/18	5/12/18	5/12/18

Table 3.2. Pairs, the sites within that pair, and the number of sampling units collected per site.

Pairs	Sites	Sampling units collected
Raukaua pair	Raukaua pair- inside	8
	Raukaua pair- outside	8
Hebe/Gorse pair	Hebe/Gorse pair- inside	8
	Hebe/Gorse pair- outside	8
Grass pair	Grass pair- inside	6
	Grass pair- outside	6



Figure 3.1. Drawings visualizing the protocol for collecting a sampling unit in the field. A) Spade was used to cut into the ground around a 15x15cm quadrat. B) The upper surface of the cut ground (turf sample) was removed and stored in a paper bag. The soil in the remaining hole was dug down to 12cm. C) The soil to 12cm depth was placed on a tarp, then hand-sorted for invertebrates which were placed live into a plastic pottle (hand-sorted sample). D) Approximately 250ml of the remaining soil that was previously hand-sorted was stored into a Ziplock plastic bag for soil moisture analyses (moisture sample). E) The three types of samples collected per 'sampling unit'.

3.2.2. Turf samples

A turf sample was taken by using a sharp square-point spade to cut around the quadrat (15x15cm), and then pulling this soil up by sliding the shovel 4cm deep underneath this square so the resulting sample would be a 15x15x4cm tile of dirt with litter/vegetation on top (Figure 3.1 **A**).

Each turf sample was placed into a labelled paper bag (Figure 3.1 **B**) and taken to Invermay Agricultural Research Centre on the day of collection. Turf samples were kept in a 4°C refrigerated room for one or two days before being put into Tullgren funnels. The Tullgren funnels were large lidded metal cylinders with funneled exits at the bottom, a 150-watt bulb suspended at the roof of the cylinder and grating to hold the turf samples (Figure 3.2). Illustrations showing the external (A) and internal (B) structure of the Tullgren funnels used to extract invertebrates from the turf samples. (A) Shows the housing of the Tullgren funnels which is a large wooden lidded box on legs. Each of these boxes houses six metal Tullgren funnels surrounded by insulation. (B) Shows internal details about each of the Tullgren funnels including the position of the collection pot under the Tullgren funnel exit. (Figure 3.2). Six of these Tullgren funnels were housed in a large raised wooden box and insulated with wool. Up to 24 of these Tullgren funnels (in four boxes) were available for use at Invermay.

I placed the turf samples litter-side-down onto the funnel grating and replaced excess material that fell through the grating back on top of the turf samples (Figure 3.2 **B**). Invertebrate extraction involved keeping the lights within the funnels turned on for one week. After extraction, I sieved the invertebrates out of the collecting pots using fine mesh and stored them in cylindrical plastic containers (6cm height, 3.5cm diameter) with 70% alcohol.

I counted and identified all the invertebrates extracted from the turf samples in a petri dish under a dissecting microscope. The invertebrates were identified down to taxonomic levels based on how easily I could identify them within a reasonable timeframe, and where ecological functional differences varied (Figure 3.3). For example, the subphylum Myriapoda was identified to class level because there are clear feeding habit differences between e.g. centipedes (Class: Chilopoda) and millipedes (Class: Diplopoda). I avoided counting springtails

(Collembola) and mites (Acari) as there was an overabundance of them, making it near impossible to count (see also discussion in Chapter 4, section 4.2) Once I identified and recorded an invertebrate in the petri dish, that invertebrate was stored in a pottle containing 70% alcohol so that invertebrates were not recorded multiple times.

Coleoptera were pinned and labelled with the date and location of collection and identified down to species level where possible with the help of Barbara Barratt at Invermay Agricultural Centre. If a specimen could not be identified down to the level of species, they were identified down to recognizable taxonomic units (RTUs) (Oliver & Beattie, 1993; Barratt *et al.*, 2003).

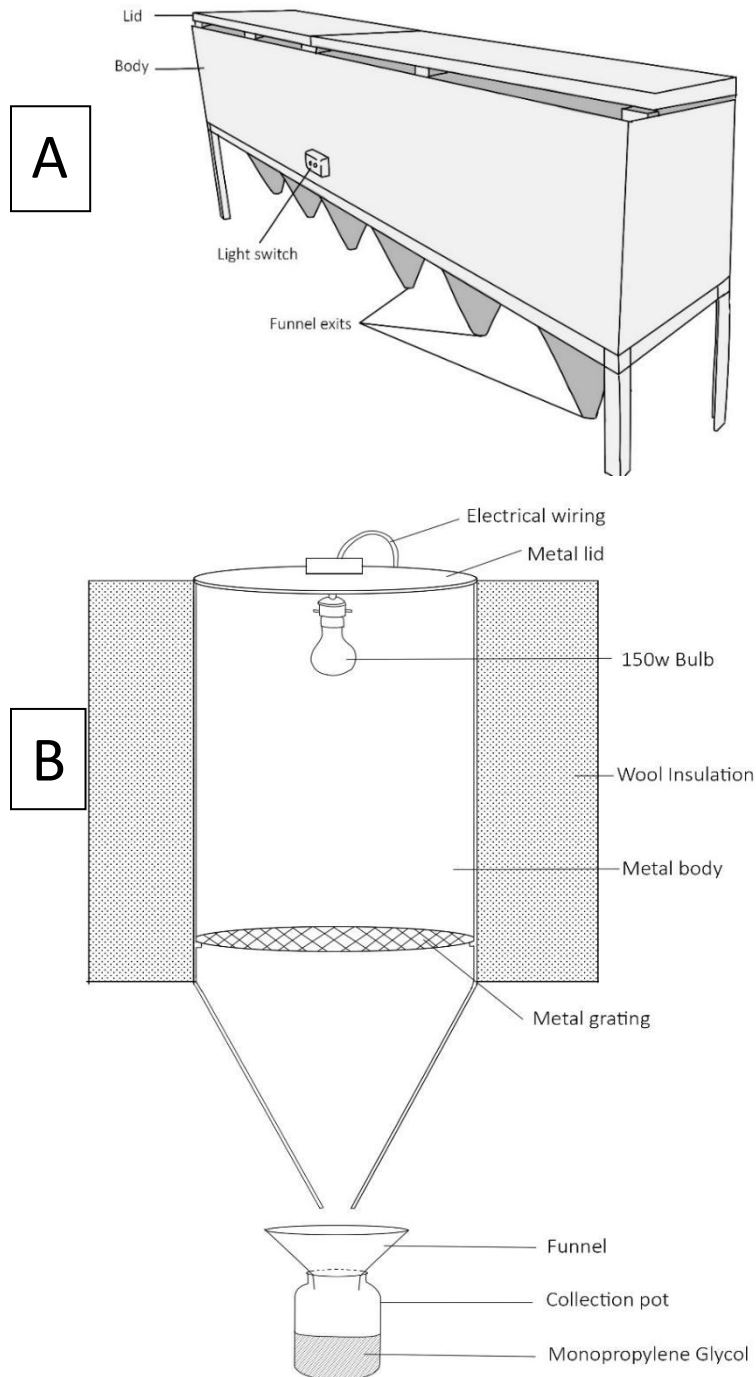


Figure 3.2. Illustrations showing the external (A) and internal (B) structure of the Tullgren funnels used to extract invertebrates from the turf samples. (A) Shows the housing of the Tullgren funnels which is a large wooden lidded box on legs. Each of these boxes houses six metal Tullgren funnels surrounded by insulation. (B) Shows internal details about each of the Tullgren funnels including the position of the collection pot under the Tullgren funnel exit.

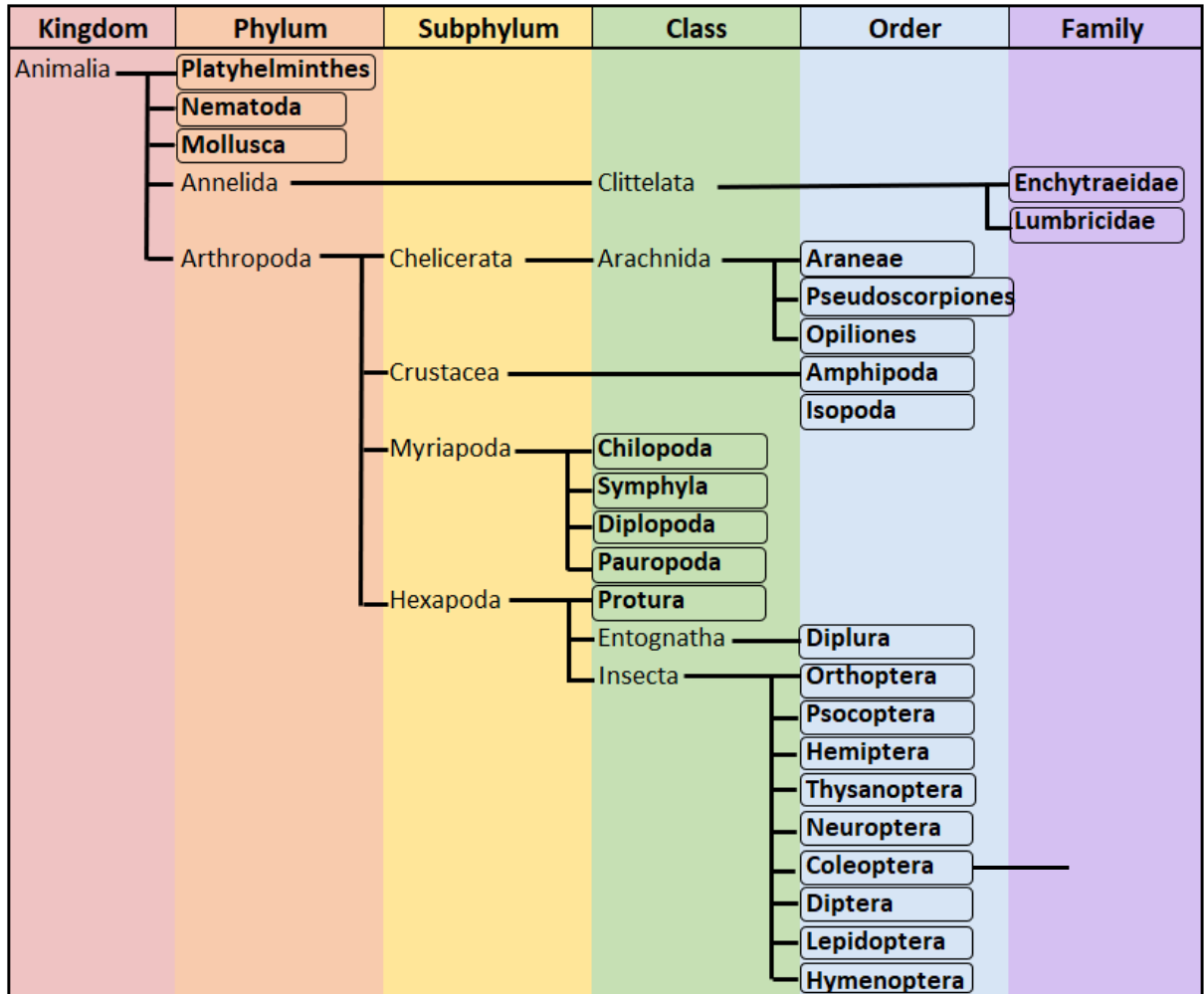


Figure 3.3. A taxonomic tree with a focus on the invertebrate groups I have identified for this study. The boldened and outlined taxa were ones that were identified and recorded for this study. Note that Coleoptera were classified down to lower taxonomic levels that are not shown in this figure.

3.2.3. Hand-sorted samples

After the collection of a turf sample in the field, I placed the dug-up soil that was underneath that turf sample (to 12cm depth) onto a tarpaulin and sorted through that soil by hand (Figure 3.1 C). Kiwi at the Ecosanctuary are thought to forage down to a depth of about 12cm using their beaks as probes (Elton Smith, Orokonui Conservation Manager, Pers Comm). The soil sorting process involved breaking up the soil by hand and looking carefully for invertebrate movement with the help of a headlamp. I placed all the invertebrates I found live into a cylindrical plastic container (6cm high, 3.5cm diameter), one container for each hand-sorted sample. I brought the hand-sorted invertebrate samples back to Invermay Agricultural

Centre to be weighed on the same day as their collection. For each sample I recorded the wet weight of all invertebrates and took note of the taxonomic groups that were present (Figure 3.3). I washed the invertebrate with tap water and patted the invertebrate dry before weighing if it was covered in debris.

3.2.4. Soil moisture samples

After the collection of a hand-sorted sample in the field, I put approximately 250ml of the soil that was already hand-sorted for invertebrates in Ziplock plastic bags (Figure 3.1 D). I measured the wet weight of soil moisture samples on the same day as collection at Invermay Agricultural Centre using a digital scale. After recording the wet weight, I dried the soil in large drying ovens at 65 °C for 28 hours over a 48-hour period (ovens automatically turned on for 14 hours at night and turned off for 10 hours in the day), after which the dry weight was recorded. With the wet and dry soil weight data I calculated the percentage of weight lost (percent moisture as % wet weight) for each soil sample.

3.2.5. Data analyses

3.2.5a Soil moisture

The soil moisture data were collected and processed first. I ran separate analyses for each pair of locations in R (R Core Team, 2018), using a logit GLM with a binomial distribution, where the percent of soil moisture was included as the response variable, and fence (inside/outside) and season (winter/summer) were included as fixed effects [*'% soil moisture ~ fence + season'*]. Note that 'Fence' as a factor throughout the study is the comparison between two different areas that may have multiple confounding factors and does not test for a more specific effect.

3.2.5b Invertebrates from turf samples

To address whether the fence (inside/outside), season (summer/winter), and/or the interaction of the fence and season correlated with invertebrate counts, I performed likelihood ratio tests on GLMM (General Linear Mixed Model) Poisson models in R (R Core Team, 2018)

using the 'lme4' package (Bates *et al.*, 2015). Soil moisture data were included in all GLMM models as a random effect. For each invertebrate group, I compared a full model with both fence and season included as fixed effects [*Invertebrate~ fence*season+(1|moisture)*] with a reduced null model with fence [*Invertebrate~ season+(1|moisture)*] or season [*Invertebrate~ fence+(1|moisture)*] excluded using the 'anova()' function. Comparing a full model with a reduced model was done to determine if fence or season as stand-alone fixed effects influenced the abundance of the invertebrate group in question. To see if the fence and season were interdependent of each other in how they influenced invertebrate abundance, I compared models with an interaction between fence and season [*Invertebrate~fence*season+(1|moisture)*] with models without an interaction [*Invertebrate~fence+season+(1|moisture)*] for each invertebrate group individually.

3.2.5c Diversity indices

With the Coleoptera data, I calculated number of species/RTUs, Shannon-Wiener diversity, and effective Shannon diversity. Shannon-Wiener diversity indices were calculated using the Coleoptera species and RTUs found at each site in both seasons using the diversity function from the 'vegan' package (Oksanen *et al.*, 2019) in R (R Core Team, 2018). The Shannon-Wiener indices, which have non-linear relationships with species richness, were then transformed into a linear relationship called 'effective Shannon diversity' (also known as Hill numbers) by using the function 'exp' (which computes exponential values) on the Shannon-Wiener indices. By transforming the entropic diversity indices into effective diversity numbers, the values of diversity are more intuitive.

3.2.5d Soil invertebrate wet weights

The wet weights of invertebrates from the hand-sorted samples were compared inside and outside the fence and between the seasons for each of the three pairs using a Mann-Whitney U test in R (R Core Team, 2018) with the 'wilcox.test()' function as the data were not normally distributed.

3.3. Results

3.3.1. Soil moisture differences within pairs

No differences in soil moisture within any of the pairs were found based on the Bonferoni corrected alpha of $P = 0.017$ which was based on having three pairs of sites to address the hypothesis (Table 3.3).

Table 3.3. Mean and standard deviation for the percent soil moisture (expressed as a % of moisture) is shown for each site in both seasons.

Percent soil moisture per location (Mean \pm SD)				
Raukaua pair				
	inside		outside	
Winter	32.12	± 3.61	32.96	± 3.50
Summer	32.38	± 1.92	37.50	± 3.28
Hebe/Gorse pair				
	inside		outside	
Winter	33.76	± 2.98	29.05	± 2.75
Summer	35.87	± 2.45	33.82	± 2.29
Grass pair				
	inside		outside	
Winter	25.88	± 6.19	32.00	± 5.84
Summer	31.95	± 6.26	24.99	± 3.14

3.3.2. Turf sample invertebrates

The total number of invertebrates identified and counted was 8158 individuals, 4190 from winter samples and 3968 from summer samples (Table 3.4Table 3.5Table 3.6Table 3.7). The sum of invertebrates counted per site per season, separated into taxonomic groups, is shown in **Appendix B** and **Appendix C**.

Table 3.4. The counts of invertebrates from all taxonomic groups are shown per site per season.

	Raukaua pair		Hebe/Gorse pair		Grass pair	
	Inside	Outside	Inside	Outside	Inside	Outside
Winter	1160	745	363	365	849	708
Summer	797	701	405	606	901	558

Table 3.5. The median invertebrate counts (in bold) and the range of invertebrate counts (in parentheses) is shown for the Raukaua pair for both seasons. These results are based on eight samples per site per season.

	Raukaua pair			
	Winter		Summer	
	Inside	Outside	Inside	Outside
Platyhelminthes	0 (0-1)	0 (0-0)	0 (0-0)	0 (0-0)
Nematoda	19 (0-38)	8 (0-109)	2 (0-9)	19 (4-100)
Mollusca	1 (0-3)	1 (0-3)	0 (0-1)	0 (0-2)
Enchytraeidae	57 (4-177)	12 (0-43)	21 (3-52)	14 (2-83)
Lumbricidae	1 (0-2)	0 (0-1)	0.5 (0-3)	0 (0-2)
Araneae	6 (2-16)	1 (0-4)	2 (0-6)	1 (0-5)
Opiliones	2 (0-3)	0.5 (0-5)	0 (0-5)	0 (0-0)
Pseudoscorpiones	1 (0-3)	2 (0-7)	1 (0-3)	0 (0-1)
Amphipoda	8.5 (2-20)	7.5 (2-15)	17 (7-36)	12 (3-16)
Isopoda	6.5 (3-24)	9.5 (2-31)	4.5 (0-57)	0 (0-8)
Chilopoda	1 (0-5)	4 (0-14)	4 (2-11)	0 (0-4)
Symphyla	0 (0-2)	0 (0-9)	0 (0-1)	0 (0-0)
Diplopoda	1 (0-12)	3 (0-21)	2 (0-7)	1.5 (1-4)
Pauropoda	0 (0-0)	0 (0-0)	0 (0-1)	0 (0-1)
Protura	0 (0-0)	0 (0-1)	0 (0-0)	0 (0-0)
Diplura	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Orthoptera	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Psocoptera	0 (0-0)	0 (0-0)	9 (1-25)	7 (1-23)
Hemiptera	1 (0-4)	0.5 (0-1)	0 (0-1)	0 (0-5)
Thysanoptera	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Neuroptera	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Coleoptera (adult)	4.5 (1-9)	4 (1-10)	1 (0-8)	1.5 (0-6)
Coleoptera (larvae)	0 (0-3)	1 (0-4)	2 (0-6)	1 (0-7)
Diptera (adult)	0 (0-0)	0 (0-1)	1 (0-5)	0.5 (0-4)
Diptera (larvae)	9 (2-22)	7 (0-25)	6.5 (0-34)	5 (0-9)
Lepidoptera (adult)	0 (0-0)	0 (0-0)	0 (0-1)	0 (0-2)
Lepidoptera (larvae)	0 (0-1)	0 (0-0)	0 (0-2)	0 (0-0)
Hymenoptera	0 (0-3)	0 (0-1)	0 (0-1)	0 (0-0)

Table 3.6. The median invertebrate counts (in bold) and the range of invertebrate counts (in parentheses) is shown for the Hebe/Gorse pair for both seasons. These results are based on eight samples per site per season.

	Hebe/Gorse pair			
	Winter		Summer	
	Inside	Outside	Inside	Outside
Platyhelminthes	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Nematoda	0 (0-6)	1 (0-2)	2 (0-10)	0 (0-4)
Mollusca	0 (0-1)	0 (0-1)	0.5 (0-3)	0.5 (0-2)
Enchytraeidae	3 (0-29)	0 (0-7)	8.5 (1-17)	1 (0-4)
Lumbricidae	0 (0-1)	0 (0-1)	0 (0-1)	0.5 (0-6)
Araneae	4 (0-8)	4 (2-8)	5 (2-12)	2 (0-3)
Opiliones	1 (0-4)	0 (0-3)	1 (0-2)	0 (0-1)
Pseudoscorpiones	0 (0-1)	2 (0-8)	0 (0-1)	1 (0-3)
Amphipoda	13 (0-44)	4 (0-17)	6 (0-15)	4.5 (3-42)
Isopoda	3 (0-20)	8 (0-23)	4 (1-9)	1.5 (0-15)
Chilopoda	1 (0-7)	5 (2-21)	2 (0-5)	2.5 (0-6)
Symphyla	0 (0-0)	0 (0-2)	0 (0-1)	0 (0-0)
Diplopoda	3 (0-12)	2 (0-9)	2.5 (1-7)	1 (0-4)
Pauropoda	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Protura	0 (0-0)	0 (0-1)	0 (0-2)	0 (0-0)
Diplura	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Orthoptera	0 (0-0)	0 (0-2)	0 (0-0)	0 (0-2)
Psocoptera	0 (0-0)	0 (0-0)	0.5 (0-3)	1 (0-2)
Hemiptera	0 (0-1)	1 (0-13)	1 (0-6)	2.5 (1-5)
Thysanoptera	0 (0-0)	0 (0-1)	0 (0-1)	0 (0-1)
Neuroptera	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)
Coleoptera (adult)	2 (0-7)	2 (0-4)	3.5 (0-10)	1 (1-4)
Coleoptera (larvae)	0 (0-4)	1 (0-3)	0.5 (0-10)	4.5 (0-11)
Diptera (adult)	0 (0-1)	1 (0-3)	1.5 (0-3)	1 (0-3)
Diptera (larvae)	1 (0-8)	4 (0-16)	1.5 (0-4)	6.5 (4-224)
Lepidoptera (adult)	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-1)
Lepidoptera (larvae)	1 (1-4)	1 (0-2)	0 (0-4)	0 (0-1)
Hymenoptera	1 (0-2)	0 (0-1)	0.5 (0-2)	0.5 (0-1)

Table 3.7. The median invertebrate counts (in bold) and the range of invertebrate counts (in parentheses) is shown for the Grass pair for both seasons. These results are based on six samples per site per season.

	Grass pair			
	Winter		Summer	
	Inside	Outside	Inside	Outside
Platyhelminthes	0 (0-1)	0 (0-1)	0 (0-1)	0 (0-2)
Nematoda	2 (0-11)	2 (0-12)	5.5 (1-61)	7 (0-16)
Mollusca	0 (0-1)	0 (0-0)	0 (0-2)	0.5 (0-4)
Enchytraeidae	8 (4-29)	26 (3-127)	8.5 (0-81)	8 (5-88)
Lumbricidae	0 (0-1)	0 (0-2)	0 (0-2)	0 (0-6)
Araneae	11 (2-23)	13 (0-35)	12 (5-27)	6 (0-16)
Opiliones	3 (1-13)	3 (0-7)	0 (0-1)	0 (0-1)
Pseudoscorpiones	1 (0-3)	0 (0-0)	0 (0-0)	0 (0-0)
Amphipoda	1 (1-2)	1 (0-5)	2.5 (0-9)	1.5 (0-5)
Isopoda	1 (0-9)	0 (0-1)	0 (0-1)	0 (0-0)
Chilopoda	11 (0-34)	6 (0-21)	14 (0-26)	7.5 (1-16)
Symphyla	0 (0-0)	0 (0-0)	0 (0-3)	0 (0-0)
Diplopoda	6 (0-21)	1 (0-21)	12 (5-31)	1.5 (0-9)
Paupoda	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-2)
Protura	0 (0-0)	1 (0-4)	1 (0-11)	0.5 (0-6)
Diplura	0 (0-5)	0 (0-0)	0 (0-0)	0 (0-0)
Orthoptera	0 (0-0)	0 (0-0)	0 (0-1)	0 (0-0)
Psocoptera	0 (0-0)	0 (0-0)	0 (0-5)	1 (0-3)
Hemiptera	22 (15-127)	15 (4-38)	19 (8-53)	5.5 (2-30)
Thysanoptera	10 (2-21)	6 (3-26)	2.5 (0-41)	12 (7-38)
Neuroptera	0 (0-0)	0 (0-0)	0 (0-1)	0 (0-0)
Coleoptera (adult)	8 (1-17)	2 (0-9)	2 (1-4)	0.5 (0-2)
Coleoptera (larvae)	1 (0-3)	1 (0-2)	2.5 (0-11)	0.5 (0-3)
Diptera (adult)	0 (0-1)	1 (0-2)	7 (2-15)	3.5 (0-10)
Diptera (larvae)	19 (3-49)	6 (2-18)	5.5 (0-30)	3 (1-5)
Lepidoptera (adult)	0 (0-1)	0 (0-0)	0 (0-1)	0.5 (0-2)
Lepidoptera (larvae)	0 (0-1)	0 (0-1)	1 (0-1)	0 (0-1)
Hymenoptera	2 (1-3)	1 (0-2)	1.5 (0-5)	0 (0-1)

3.3.3. Invertebrates from turf samples

The following invertebrates were not observed at a high enough frequency for data analysis: Platyhelminthes, Lumbricidae, Symphyla, Pauropoda, Protura, Diplura, Orthoptera, Neuroptera, and adult Lepidoptera (**Appendix B and C**)

3.3.3a Nematoda

In the Raukaua pair, fence and season as stand-alone main effects did not have significant effects on Nematoda abundance (fence $\chi^2 = 2.86$, $df = 1$, $P > 0.05$; season $\chi^2 = 0.33$, $df = 1$, $P > 0.05$) but there was a significant interaction between the two main effects on Nematoda abundance ($\chi^2 = 9.12$, $df = 1$, $P < 0.01$). In the Hebe/Gorse pair there was no evidence that the fence, season, or the interaction of the two had a significant effect on Nematoda abundance (fence $\chi^2 = 1.83$, $df = 1$, $P > 0.05$; season $\chi^2 = 2.14$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 1.60$, $df = 1$, $P > 0.05$). In the Grass pair, season had a significant effect on Nematoda abundance, where there was a lower abundance of Nematoda in winter compared to summer ($\chi^2 = 3.94$, $df = 1$, $P < 0.05$). There was no evidence that the fence or an interaction between fence and season significantly affected Nematoda abundance (fence $\chi^2 = 0.21$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 0.48$, $df = 1$, $P > 0.05$) (Figure 3.4).

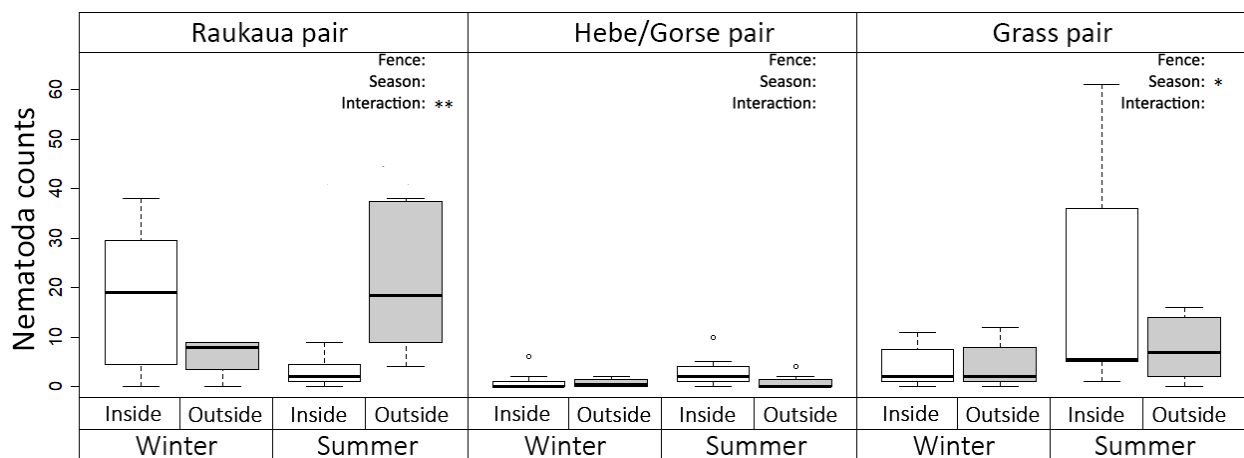


Figure 3.4. Box and whisker plots based on the counts of Nematoda found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$, and '**' is significant at $P < 0.01$.

3.3.3b Mollusca

In the Raukaua pair there was no evidence that the fence, season, or the interaction of the two affected Mollusca abundance (fence $\chi^2 = 0.04$, df= 1, $P > 0.05$; season $\chi^2 = 3.65$, df= 1, $P > 0.05$; interaction $\chi^2 = 0.46$, df= 1, $P > 0.05$). Season had a significant effect on Mollusca abundance in the Hebe/Gorse (fence $\chi^2 = 4.38$, df= 1, $P = 0.04$) and in the Grass pair (fence $\chi^2 = 4.68$, df= 1, $P = 0.03$) where there was a lower abundance of Mollusca in winter in both pairs. There was no evidence that the fence or the interaction between fence and season influenced Mollusca abundance in the Hebe/Gorse pair (fence $\chi^2 = 0$, df= 1, $P > 0.05$; interaction $\chi^2 = 0.43$, df= 1, $P > 0.05$) or in the Grass pair (fence $\chi^2 < 0.001$, df= 1, $P > 0.05$; interaction $\chi^2 = 1.43$, df= 1, $P > 0.05$) (Figure 3.5).

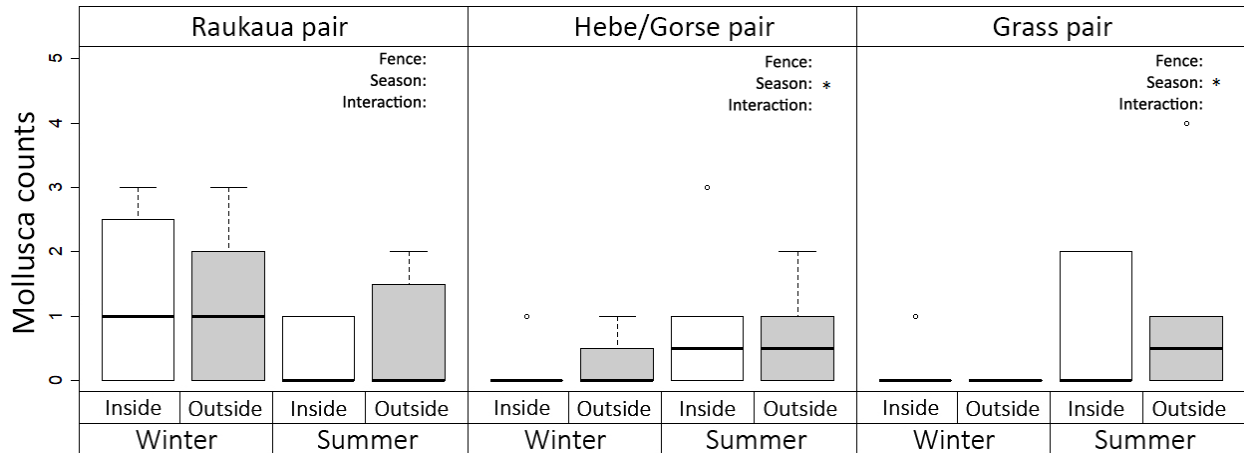


Figure 3.5. Box and whisker plots based on the counts of Mollusca found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$.

3.3.3c Enchytraeidae

There was no evidence that the fence, season, or the interaction of the two affected Enchytraeidae abundance in the Raukua pair (fence $\chi^2 = 3.00$, $df = 1$, $P > 0.05$; season $\chi^2 = 1.32$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 1.32$, $df = 1$, $P > 0.05$) nor in the Grass pair (fence $\chi^2 = 1.63$, $df = 1$, $P > 0.05$; season $\chi^2 = 0.21$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 0.25$, $df = 1$, $P > 0.05$). In the Hebe/Gorse pair the fence had a significant effect on Enchytraeidae abundance ($\chi^2 = 10.33$, $df = 1$, $P = 0.001$) where there was a higher abundance of Enchytraeidae inside the fence compared to outside the fence, but there was no evidence that season or the interaction between fence and season had an effect (season $\chi^2 = 1.04$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 1.31$, $df = 1$, $P > 0.05$) (Figure 3.6).

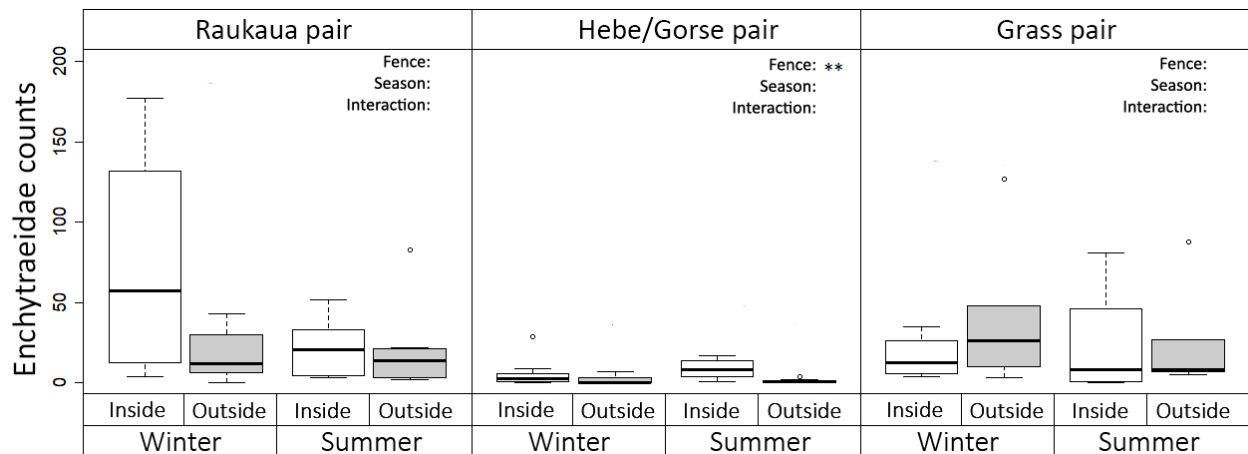


Figure 3.6. Box and whisker plots based on the counts of Enchytraeidae found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '**' is significant at $P < 0.01$.

3.3.3d Lumbricidae

There was no evidence that the fence, season, or the interaction of the two had a significant effect on Lumbricidae abundance in the Raukua pair (fence $\chi^2 = 1.70$, $df = 1$, $P > 0.05$; season $\chi^2 = 0.20$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 1.19$, $df = 1$, $P > 0.05$), the Hebe/Gorse pair (fence $\chi^2 = 1.79$, $df = 1$, $P > 0.05$; season $\chi^2 = 0.60$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 1.53$, $df = 1$, $P > 0.05$), and the Grass pair (fence $\chi^2 = 0.92$, $df = 1$, $P > 0.05$; season $\chi^2 = 0.40$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 0.23$, $df = 1$, $P > 0.05$).

3.3.3e Araneae

In the Raukaua pair, the fence and season had a significant effect on Araneae abundance, where there was a higher abundance of Araneae inside the fence compared to outside the fence ($\chi^2 = 10.14$, $df= 1$, $P= 0.0015$), and a higher abundance of Araneae during winter compared to summer ($\chi^2= 5.97$, $df= 1$, $P= 0.015$). There was no significant interaction between fence and season on Araneae abundance the Raukaua pair ($\chi^2= 3.82$, $df= 1$, $P> 0.05$). In the Hebe/Gorse pair, fence and season as stand-alone main effects did not have significant effects on Araneae abundance (fence $\chi^2 = 3.64$, $df= 1$, $P> 0.05$; season $\chi^2 = 0.55$, $df= 1$, $P> 0.05$) but there was a significant interaction between the two main effects on Araneae abundance ($\chi^2 = 5.96$, $df= 1$, $P= 0.015$). There was no evidence that the fence or season (or the interaction of the two) had a significant effect on Araneae abundance in the Grass pair (fence $\chi^2 = 1.56$, $df= 1$, $P> 0.05$; season $\chi^2 = 0.32$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 1.17$, $df= 1$, $P> 0.05$) (Figure 3.7).

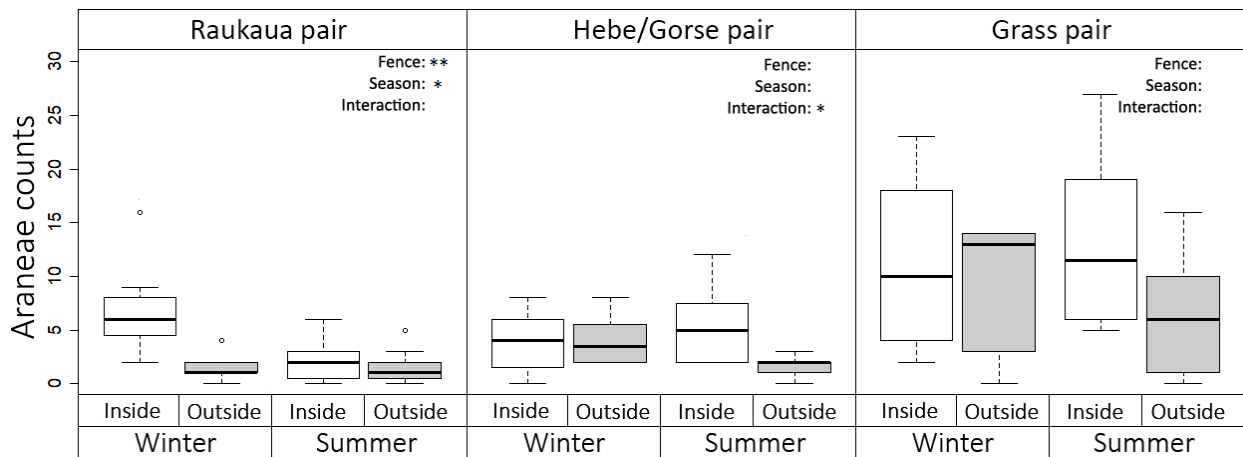


Figure 3.7. Box and whisker plots based on the counts of Araneae found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P<0.05$ and '**' is significant at $P<0.01$.

3.3.3f Pseudoscorpiones

In the Raukaua pair, there was no evidence that the fence, season, or the interaction of the two had a significant effect on Pseudoscorpiones abundance (fence $\chi^2 = 0.01$, df= 1, $P > 0.05$; season $\chi^2 = 3.84$, df= 1, $P > 0.05$; interaction $\chi^2 = 2.68$, df= 1, $P > 0.05$). In the Hebe/Gorse pair, the fence had a significant effect on Pseudoscorpiones abundance ($\chi^2 = 9.70$, df= 1, $P = 0.002$), where there was a lower abundance of Pseudoscorpiones inside the fence compared to outside the fence. There was no evidence that season ($\chi^2 = 3.84$, df= 1, $P > 0.05$) or the interaction between fence and season ($\chi^2 = 0.11$, df= 1, $P > 0.05$) influenced Pseudoscorpiones abundance in the Hebe/Gorse pair. In the Grass pair there were too many zeroes in the data for Pseudoscorpiones counts for the analysis to be performed (Figure 3.8).

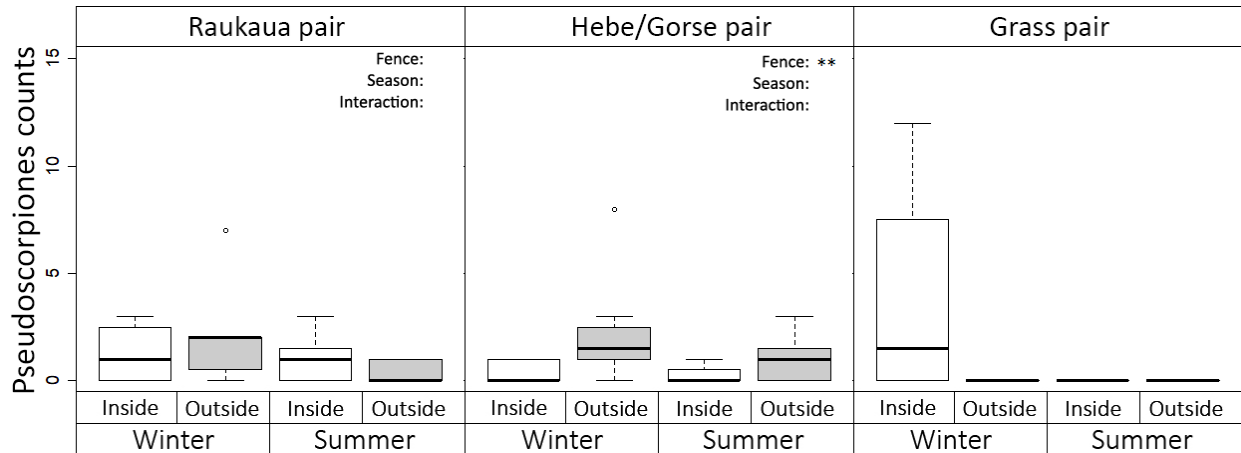


Figure 3.8. Box and whisker plots based on the counts of Pseudoscorpiones found at each of the three pairs of sites for both seasons. The significance of the main effects ‘fence’ and ‘season’ as well as their ‘interaction’ are shown. ‘***’ is significant at $P < 0.01$. Analyses were not available for the Grass pair.

3.3.3g Opiliones

In the Raukaua pair, the fence ($\chi^2 = 4.21$, $df = 1$, $P = 0.04$), season ($\chi^2 = 5.72$, $df = 1$, $P = 0.017$), and the interaction of the two ($\chi^2 = 4.31$, $df = 1$, $P = 0.038$) had a significant effect on Opiliones abundance, where there was a higher abundance of Opiliones inside the fence compared to outside the fence and a higher abundance of Opiliones in winter compared to summer. In the Hebe/Gorse pair there was no evidence that the fence or season (or the interaction of the two) influenced Opiliones abundance (fence $\chi^2 = 2.55$, $df = 1$, $P > 0.05$; season $\chi^2 = 1.30$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 0.01$, $df = 1$, $P > 0.05$). In the Grass pair, season had a significant effect on Opiliones abundance ($\chi^2 = 19.27$, $df = 1$, $P < 0.0001$), where there was a higher abundance of Opiliones in winter compared to summer. There was no evidence that the fence ($\chi^2 = 1.52$, $df = 1$, $P > 0.05$) or the interaction between fence and season ($\chi^2 = 0.01$, $df = 1$, $P > 0.05$) influenced Opiliones abundance in the Grass pair (Figure 3.9).

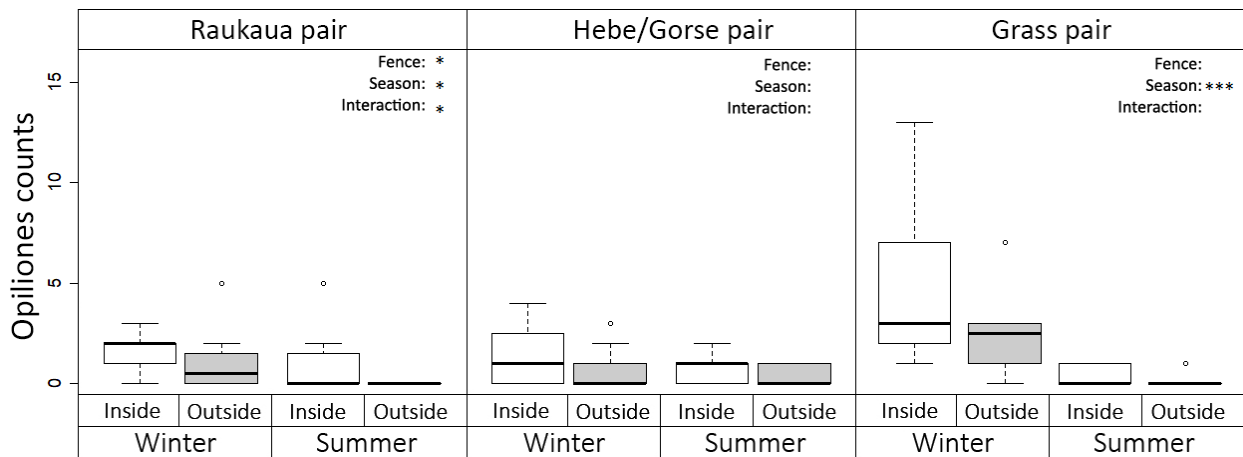


Figure 3.9. Box and whisker plots based on the counts of Opiliones found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$ and '**' is significant at $P < 0.001$.

3.3.3h Amphipoda

In the Raukaua pair, the fence and season had a significant effect on Amphipoda abundance, where there was a higher abundance of Amphipoda inside the fence compared to outside the fence ($\chi^2 = 3.85$, $df= 1$, $P= 0.049$), and a lower abundance of Amphipoda in winter compared to summer ($\chi^2 = 5.72$, $df=1$, $P= 0.017$). There was no significant interaction between fence and season on Amphipoda abundance the Raukaua pair ($\chi^2= 1.52$, $df= 1$, $P> 0.05$). There was no evidence that the fence, season, or the interaction of the two affected Amphipoda abundance in the Hebe/Gorse pair (fence $\chi^2 = 0.60$, $df= 1$, $P> 0.05$; season $\chi^2 = 0.05$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 2.88$, $df= 1$, $P> 0.05$) and in the Grass pair (fence $\chi^2 = 0.53$, $df= 1$, $P> 0.05$; season $\chi^2 = 2.35$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 0.52$, $df= 1$, $P> 0.05$) (Figure 3.10).

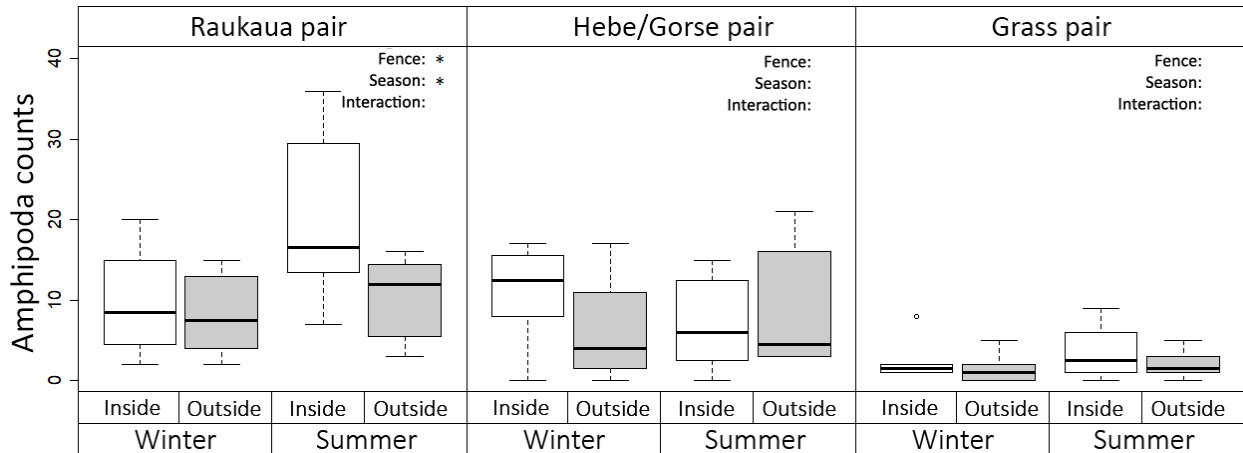


Figure 3.10. Box and whisker plots based on the counts of Amphipoda found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P<0.05$.

3.3.3i Isopoda

In the Raukaua pair, season ($\chi^2 = 8.26$, $df = 1$, $P = 0.004$) and the interaction between fence and season ($\chi^2 = 7.75$, $df = 1$, $P = 0.005$) had a significant effect on Isopoda abundance, where there was a significantly higher abundance of Isopoda in winter compared to summer. There was no evidence that the fence influenced Isopoda counts in the Raukaua pair ($\chi^2 = 3.10$, $df = 1$, $P > 0.05$). In the Hebe/Gorse pair, there was no evidence that the fence, season, or the interaction of the two influenced Isopoda abundance (fence $\chi^2 < 0.01$, $df = 1$, $P > 0.05$; season $\chi^2 = 0.04$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 2.62$, $df = 1$, $P > 0.05$). In the Grass pair, the fence had a significant effect on isopoda counts ($\chi^2 = 4.87$, $df = 1$, $P = 0.027$), where there was a higher abundance of Isopods inside the fence compared to outside the fence. There was no evidence that season ($\chi^2 = 2.63$, $df = 1$, $P > 0.05$) or the interaction between fence and season ($\chi^2 = 0.29$, $df = 1$, $P > 0.05$) influenced Isopoda abundance in the Grass pair (Figure 3.11).

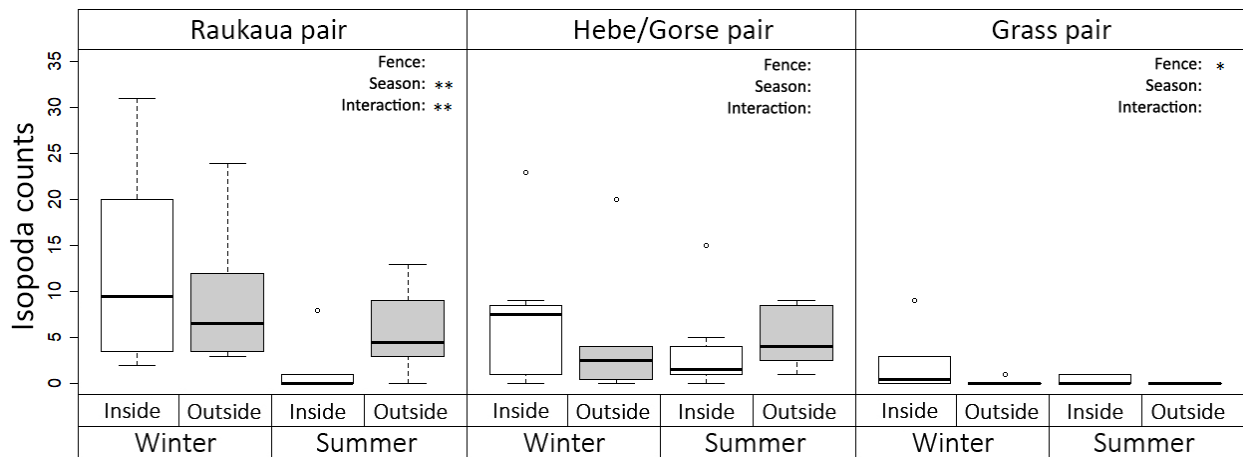


Figure 3.11. Box and whisker plots based on the counts of Isopoda found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$ and '**' is significant at $P < 0.01$.

3.3.3j Chilopoda

In the Raukua pair, fence and season as stand-alone main effects did not have significant effects on Chilopoda abundance (fence $\chi^2 = 0.16$, $df= 1$, $P> 0.05$; season $\chi^2 = 0.28$, $df= 1$, $P> 0.05$) but there was a significant interaction between the two main effects on Chilopoda abundance ($\chi^2 = 12.70$, $df= 1$, $P= 0.00036$). In the Hebe/Gorse pair, the fence had a significant effect on Chilopoda abundance ($\chi^2 = 5.70$, $df= 1$, $P= 0.017$), where there was a lower abundance of Chilopoda inside the fence compared to outside the fence. There was no evidence that season ($\chi^2 = 1.22$, $df= 1$, $P> 0.05$) or the interaction between fence and season ($\chi^2 = 3.12$, $df= 1$, $P> 0.05$) influenced Chilopoda abundance in the Hebe/Gorse pair. In the Grass pair, there was no evidence that the fence, season, or the interaction of the two influenced Chilopoda abundance (fence $\chi^2 = 0.42$, $df= 1$, $P> 0.05$; season $\chi^2 = 0.01$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 0.24$, $df= 1$, $P> 0.05$) (Figure 3.12).

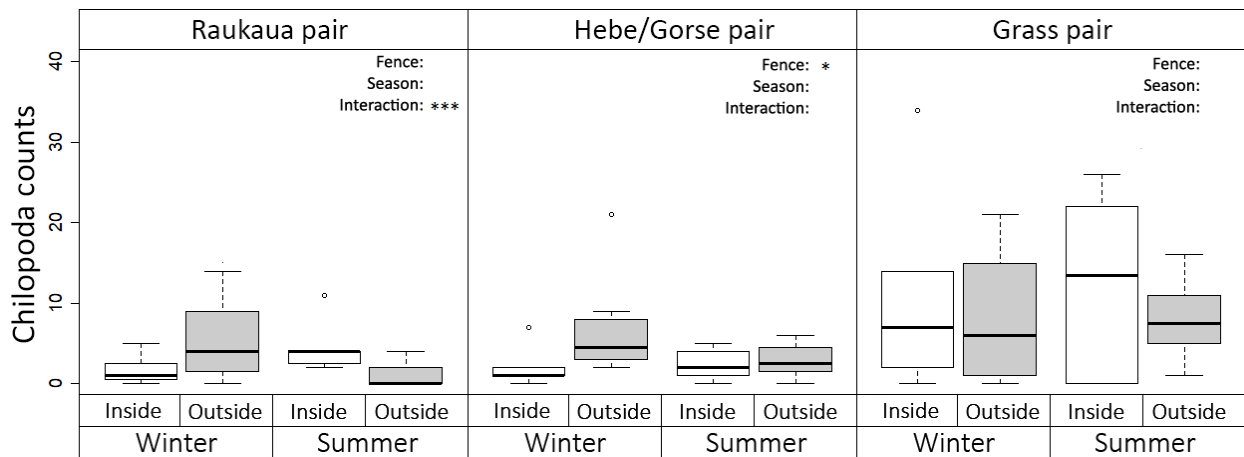


Figure 3.12. Box and whisker plots based on the counts of Chilopoda found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P<0.05$ and '***' is significant at $P<0.001$.

3.3.3k Diplopoda

In the Raukaua pair, there was no evidence that the fence, season, or the interaction of the two influenced Diplopoda abundance (fence $\chi^2 = 0.18$, df= 1, $P > 0.05$; season $\chi^2 = 1.28$, df= 1, $P > 0.05$; interaction $\chi^2 = 1.00$, df= 1, $P > 0.05$). The fence had a significant effect on Diplopoda abundance in the Hebe/Gorse pair ($\chi^2 = 5.82$, df= 1, $P = 0.016$) and the Grass pair ($\chi^2 = 7.18$, df= 1, $P = 0.0074$) where there was a higher abundance of Diplopoda inside the fence compared to outside the fence in both cases. There was no evidence that season and the interaction between fence and season influenced Diplopoda counts in the Hebe/Gorse pair (season $\chi^2 = 1.78$, df= 1, $P > 0.05$; interaction $\chi^2 = 0$, df= 1, $P > 0.05$) and the Grass pair (season $\chi^2 = 0.36$, df= 1, $P > 0.05$; interaction $\chi^2 = 1.24$, df= 1, $P > 0.05$) (Figure 3.13).

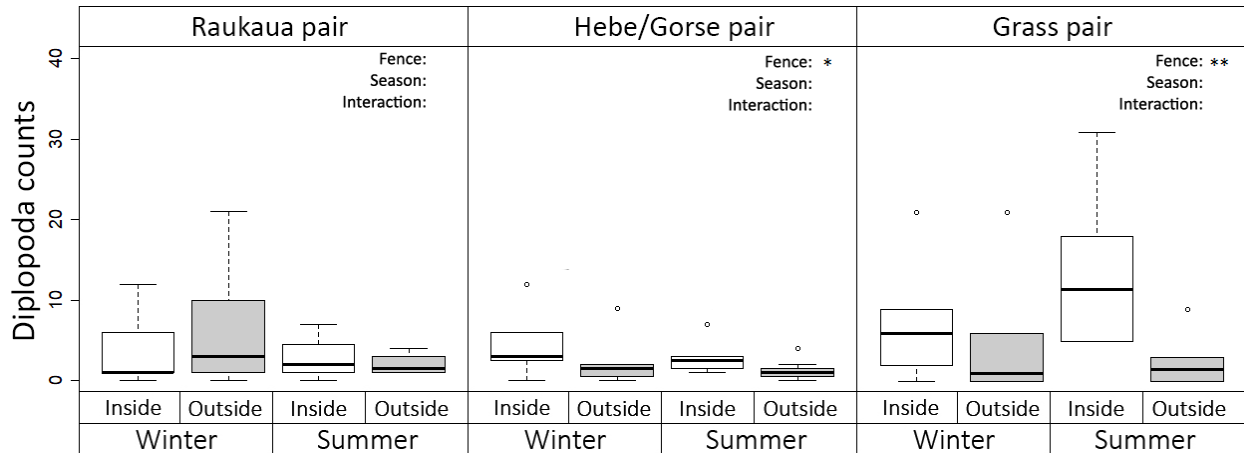


Figure 3.13. Box and whisker plots based on the counts of Diplopoda found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$ and '**' is significant at $P < 0.01$.

3.3.3| Psocoptera

Season had a significant effect on Psocoptera counts in the Raukaua pair ($\chi^2 = 50.04$, $df= 1$, $P= 1.5e^{-12}$), the Hebe/Gorse pair ($\chi^2 = 16.77$, $df= 1$, $P= 4.2e^{-5}$), and the Grass pair ($\chi^2 = 9.20$, $df= 1$, $P= 0.0024$). In all three cases Psocoptera abundance was higher in summer compared to winter. There was no evidence that the fence or the interaction between fence and season influenced Psocoptera abundance in the Raukaua pair (fence $\chi^2 = 0.03$, $df= 1$, $P > 0.05$; interaction $\chi^2 = 0$, $df= 1$, $P = 1$), the Hebe/Gorse pair (fence $\chi^2 = 0.29$, $df= 1$, $P > 0.05$; interaction $\chi^2 = 0$, $df= 1$, $P = 1$), and the Grass pair (fence $\chi^2 = 0.09$, $df= 1$, $P > 0.05$; interaction $\chi^2 = 0$, $df= 1$, $P = 1$) (Figure 3.14).

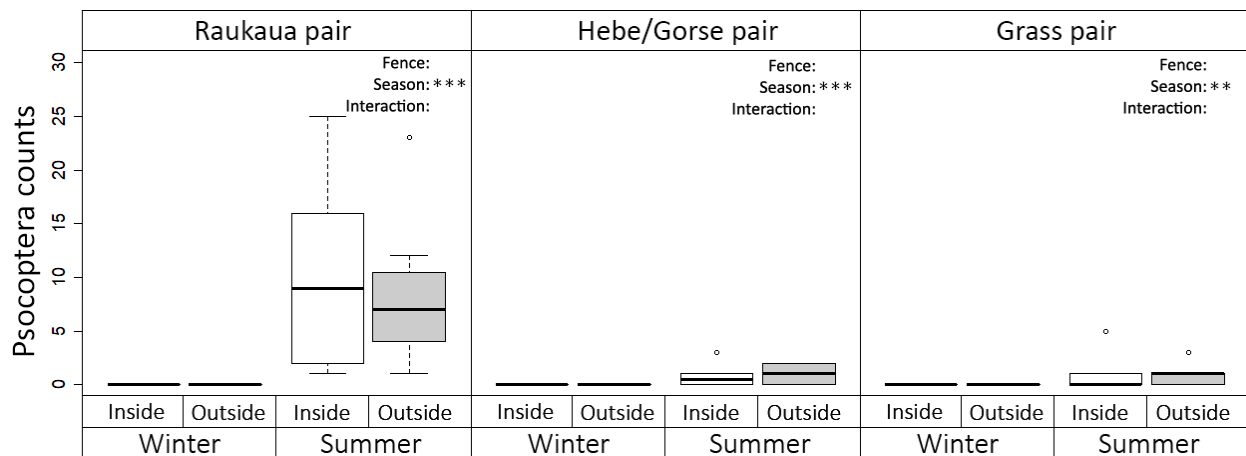


Figure 3.14. Box and whisker plots based on the counts of Psocoptera found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '**' is significant at $P < 0.01$ and '***' is significant at $P < 0.001$.

3.3.3m Hemiptera

In the Raukaua pair, there was no evidence that the fence, season, or the interaction of the two influenced Hemiptera abundance (fence $\chi^2 = 0.56$, df= 1, $P > 0.05$; season $\chi^2 = 1.39$, df= 1, $P > 0.05$; interaction $\chi^2 = 0.61$, df= 1, $P > 0.05$). In the Hebe/Gorse pair, the fence ($\chi^2 = 4.11$, df= 1, $P = 0.043$) and season ($\chi^2 = 7.01$, df= 1, $P = 0.008$) had a significant effect on Hemiptera abundance, where there was a lower abundance of Hemiptera inside the fence compared to outside the fence and a lower abundance in winter compared to summer. There was no evidence of an interaction between the fence and season on Hemiptera counts in the Hebe/Gorse pair ($\chi^2 = 1.17$, df= 1, $P > 0.05$). In the Grass pair, the fence had a significant effect on Hemiptera abundance ($\chi^2 = 6.50$, df= 1, $P = 0.011$), where there was a higher abundance of Hemiptera inside the fence compared to outside the fence. There was no evidence that season or the interaction between the fence and season influenced Hemiptera abundance in the Grass pair (season $\chi^2 = 3.30$, df= 1, $P > 0.05$; interaction $\chi^2 = 0.61$, df= 1, $P > 0.05$) (Figure 3.15).

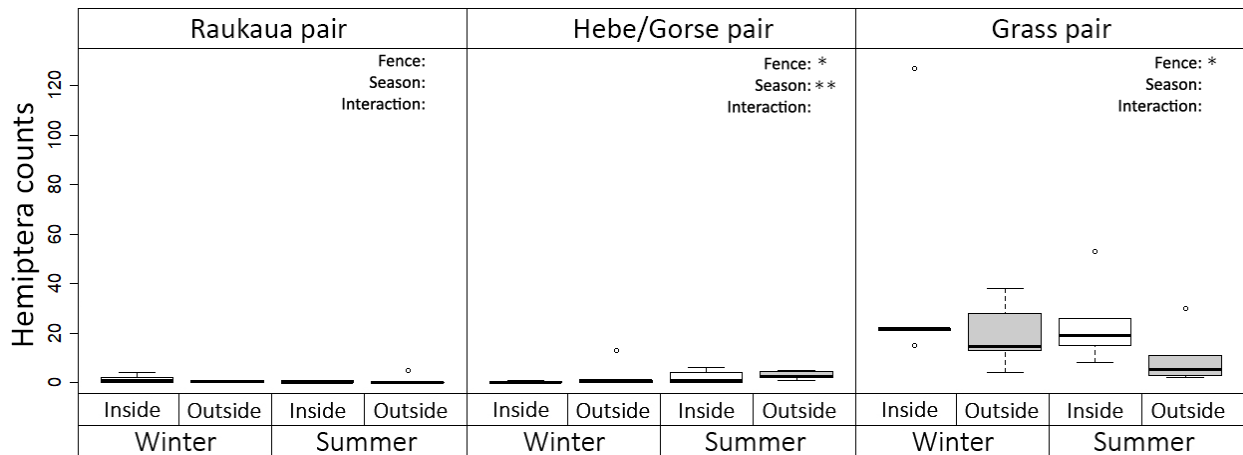


Figure 3.15. Box and whisker plots based on the counts of Hemiptera found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$ and '**' is significant at $P < 0.01$.

3.3.3n Thysanoptera

In the Raukaua pair and the Hebe/Gorse pair, there were too many zeroes in the data for Thysanoptera counts for the analyses to be performed. There was no evidence that the fence, season, or the interaction of the two influenced Thysanoptera counts in the Grass pair (fence $\chi^2 = 1.78$, $df = 1$, $P > 0.05$; season $\chi^2 = 0$, $df = 1$, $P > 0.05$; interaction $\chi^2 = 3.43$, $df = 1$, $P > 0.05$) (Figure 3.16).

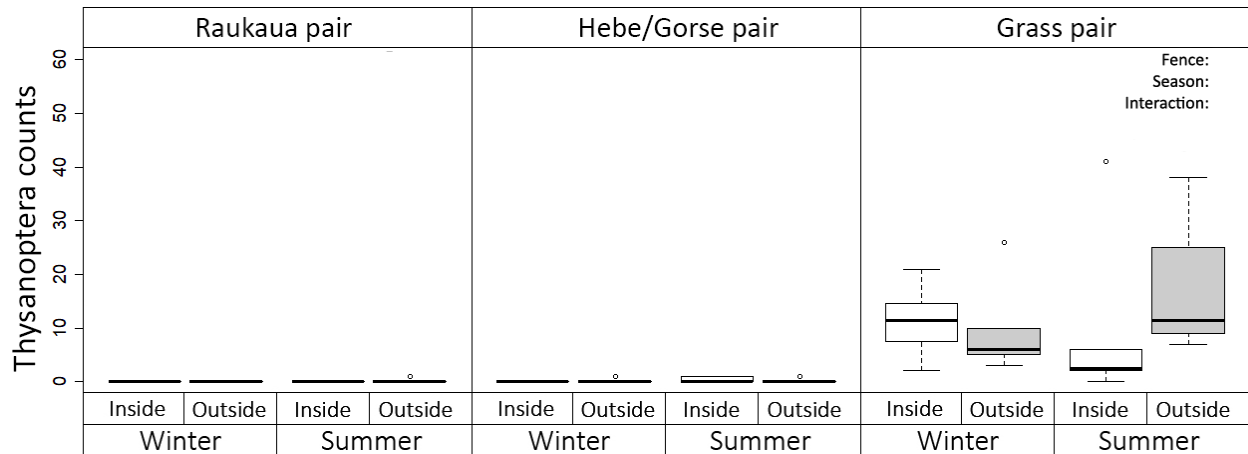


Figure 3.16. Box and whisker plots based on the counts of Thysanoptera found at each of the three pairs of sites for both seasons. There was no significance of the main effects or their interaction. Analyses were not available for the Raukaua pair and the Hebe/Gorse pair.

3.3.3o Coleoptera (adult)

In the Raukaua pair, season had a significant effect on adult Coleoptera abundance ($\chi^2 = 4.17$, $df= 1$, $P= 0.041$) where there was a higher abundance of adult Coleoptera in winter compared to summer. There was no evidence that the fence or the interaction between the fence and season influenced adult Coleoptera abundance in the Raukaua pair (fence $\chi^2 = 0.04$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 0.20$, $df= 1$, $P> 0.05$). There was no evidence that the fence and season (or the interaction of the two) influenced adult Coleoptera abundance in the Hebe/Gorse pair (fence $\chi^2 = 1.33$, $df= 1$, $P> 0.05$; season $\chi^2 = 1.35$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 1.13$, $df= 1$, $P> 0.05$). In the Grass pair, the fence and season had a significant effect on adult Coleoptera abundance, where there was a higher abundance of adult Coleoptera inside the fence compared to outside the fence and a higher abundance in winter compared to summer (fence $\chi^2 = 6.00$, $df= 1$, $P= 0.014$; season $\chi^2 = 8.19$, $df= 1$, $P= 0.0042$). There was no evidence of an interaction between the fence and season on adult Coleoptera counts in the Grass pair ($\chi^2 = 0.57$, $df= 1$, $P> 0.05$) (Figure 3.17).

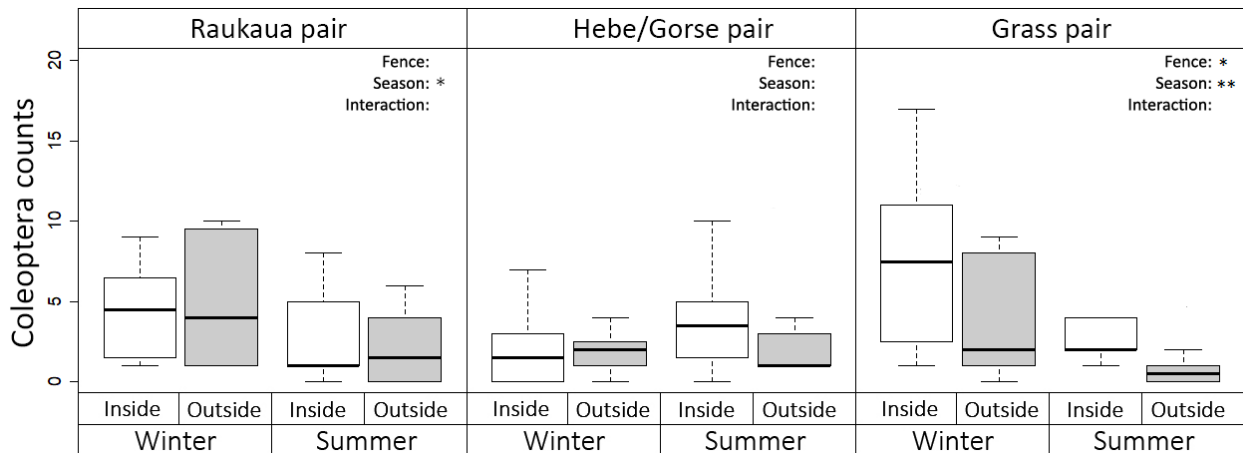


Figure 3.17. Box and whisker plots based on the counts of adult Coleoptera found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P<0.05$ and '**' is significant at $P<0.01$.

3.3.3p Coleoptera (larvae)

In the Raukaua pair, season had a significant effect on Coleoptera larvae abundance ($\chi^2 = 4.27$, $df= 1$, $P= 0.039$) where there was a higher abundance of Coleoptera larvae in summer compared to winter. There was no evidence that the fence or the interaction between fence and season influenced Coleoptera larvae abundance (fence $\chi^2 = 0.68$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 0.73$, $df= 1$, $P> 0.05$). There was no evidence that the fence, season, or the interaction of the two influenced Coleoptera larvae abundance in the Hebe/Gorse pair (fence $\chi^2 = 2.80$, $df= 1$, $P> 0.05$; season $\chi^2 = 3.37$, $df= 1$, $P> 0.05$, interaction $\chi^2 = 0.33$, $df= 1$, $P> 0.05$) and the Grass pair (fence $\chi^2 = 2.24$, $df= 1$, $P> 0.05$; season $\chi^2 = 2.24$, $df= 1$, $P> 0.05$, interaction $\chi^2 = 1.18$, $df= 1$, $P> 0.05$) (Figure 3.18).

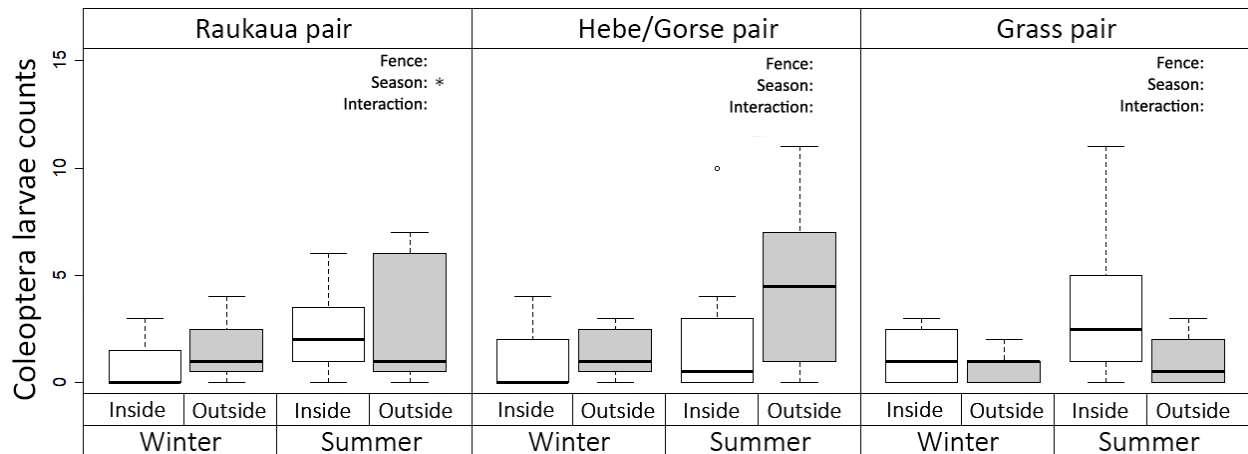


Figure 3.18. Box and whisker plots based on the counts of Coleoptera larvae found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P<0.05$.

3.3.3q Diptera (adult)

Season had a significant effect on adult Diptera abundance in the Raukaua pair ($\chi^2 = 12.23$, $df= 1$, $P= 0.0004$) and the Grass pair ($\chi^2 = 22.41$, $df= 1$, $P= 2.2e^{-6}$) where there was a lower abundance of adult Diptera in winter compared to summer in both cases. There was no evidence that the fence or the interaction between fence and season influenced adult Diptera abundance in the Raukaua pair (fence $\chi^2 = 0.08$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 1.61$, $df= 1$, $P> 0.05$) and the Grass pair (fence $\chi^2 = 0.83$, $df= 1$, $P> 0.05$; interaction $\chi^2 = 1.64$, $df= 1$, $P> 0.05$). In the Hebe/Gorse pair, the interaction between fence and season had a significant effect on adult Diptera abundance ($\chi^2 = 7.45$, $df= 1$, $P= 0.006$) where adult Diptera abundance was lower inside the fence in winter, and higher inside the fence in summer. There was no evidence that fence or season as stand-alone main effects influenced adult Diptera abundance in the Hebe/Gorse pair (fence $\chi^2 = 2.34$, $df= 1$, $P> 0.05$; season $\chi^2 = 3.49$, $df= 1$, $P> 0.05$) (Figure 3.19).

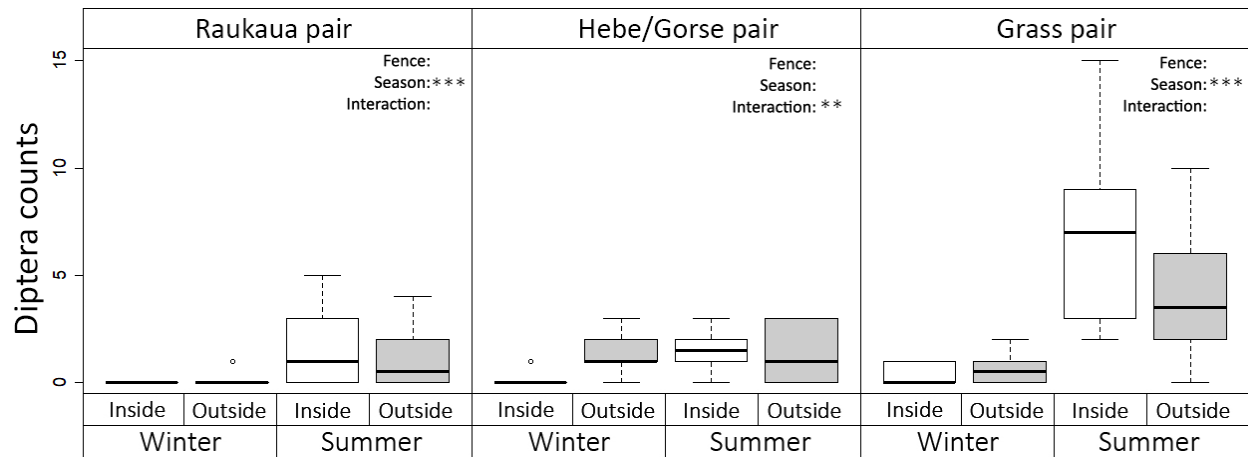


Figure 3.19. Box and whisker plots based on the counts of adult Diptera found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '***' is significant at $P<0.01$ and '****' is significant at $P<0.001$.

3.3.3r Diptera (larvae)

In the Raukaua pair, there was no evidence that fence, season, or the interaction of the two influenced Diptera larvae abundance (fence $\chi^2 = 0.93$, df= 1, $P > 0.05$; season $\chi^2 = 1.23$, df= 1, $P > 0.05$; interaction $\chi^2 = 0.49$, df= 1, $P > 0.05$). The fence had a significant effect on Diptera larvae abundance in the Hebe/Gorse pair ($\chi^2 = 15.10$, df= 1, $P = 0.0001$) and the Grass pair ($\chi^2 = 5.46$, df= 1, $P = 0.019$). There was a lower abundance of Diptera larvae inside the fence compared to outside the fence in the Hebe/Gorse pair and a higher abundance of Diptera larvae inside the fence compared to outside the fence in the Grass pair. Season had a significant effect on Diptera larvae abundance in the Hebe/Gorse pair ($\chi^2 = 4.00$, df= 1, $P = 0.047$) and the Grass pair ($\chi^2 = 7.15$, df= 1, $P = 0.0075$). There was a lower abundance of Diptera larvae in winter compared to summer in the Hebe/Gorse pair and a higher abundance of Diptera larvae in winter compared to summer in the Grass pair. There was no evidence that the interaction between fence and season influenced Diptera larvae abundance in the Hebe/Gorse pair ($\chi^2 = 0.58$, df= 1, $P > 0.05$) and the Grass pair ($\chi^2 = 0.18$, df= 1, $P > 0.05$) (Figure 3.20)

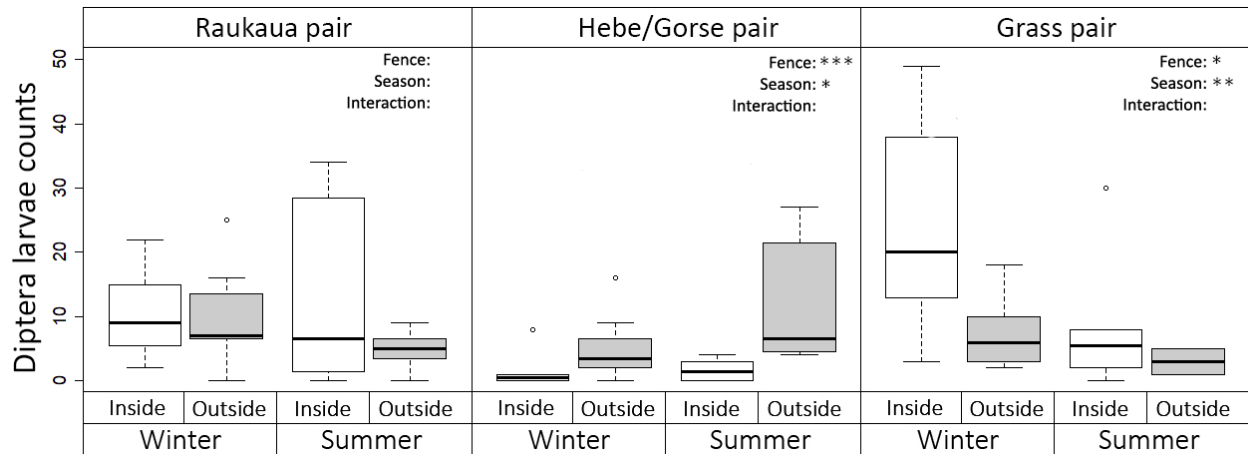


Figure 3.20. Box and whisker plots based on the counts of Diptera larvae found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P < 0.05$, '**' is significant at $P < 0.01$, and '***' is significant at $P < 0.001$.

3.3.3s Lepidoptera (larvae)

In the Raukaua pair and the Grass pair, there were too many zeroes in the data for Lepidoptera larvae counts for the analyses to be performed correctly. There was a significant effect of the fence ($\chi^2 = 4.50$, $df= 1$, $P= 0.034$) and season ($\chi^2 = 6.33$, $df= 1$, $P= 0.012$) on Lepidoptera larvae abundance in the Hebe/Gorse pair, where there was a higher abundance of Lepidoptera larvae inside the fence compared to outside the fence and a higher abundance of Lepidoptera larvae in winter compared to summer. There was no evidence of an interaction between fence and season on Lepidoptera larvae abundance in the Hebe/Gorse pair ($\chi^2 = 1.78$, $df= 1$, $P> 0.05$) (Figure 3.21)

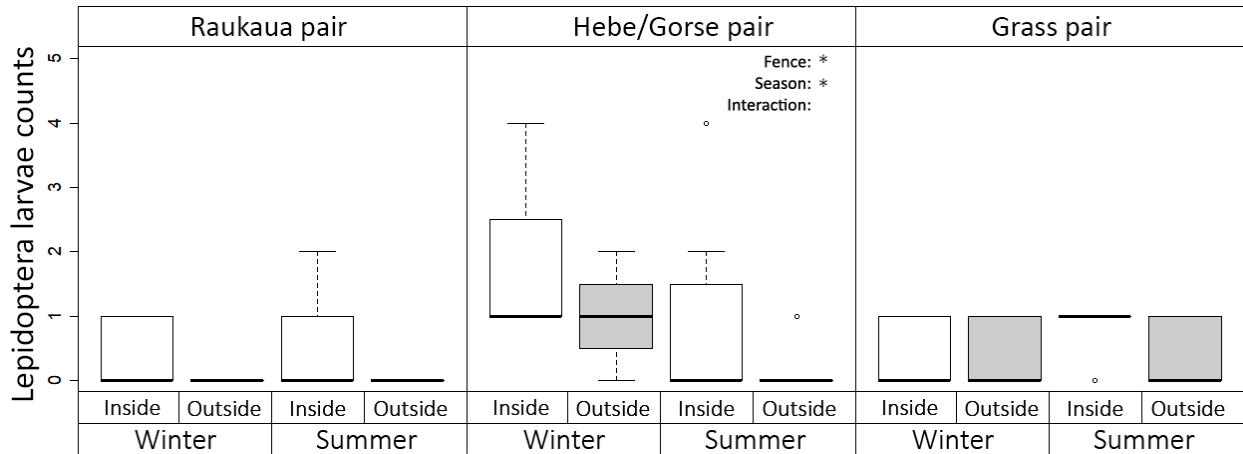


Figure 3.21. Box and whisker plots based on the counts of Lepidoptera larvae found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at $P<0.05$. Analyses were not available for the Raukaua pair and the Grass pair.

3.3.3t Hymenoptera

There was no evidence that the fence, season, or the interaction of the two influenced Hymenoptera abundance in the Raukaua pair (fence $\chi^2 = 1.35$, df= 1, P> 0.05; season $\chi^2 = 1.35$, df= 1, P> 0.05; interaction $\chi^2 = 0.35$, df= 1, P> 0.05). The fence had a significant effect on Hymenoptera abundance in the Hebe/Gorse pair ($\chi^2 = 5.23$, df= 1, P= 0.022) and the Grass pair ($\chi^2 = 6.87$, df= 1, P= 0.0087) where there was a higher abundance of Hymenoptera inside the fence compared to outside the fence. There was no evidence that season or the interaction between fence and season influenced Hymenoptera abundance in the Hebe/Gorse pair (season $\chi^2 = 0.20$, df= 1, P> 0.05; interaction $\chi^2 = 1.80$, df= 1, P> 0.05) and the Grass pair (season $\chi^2 = 0.01$, df= 1, P> 0.05; interaction $\chi^2 = 0.72$, df= 1, P> 0.05) (Figure 3.22).

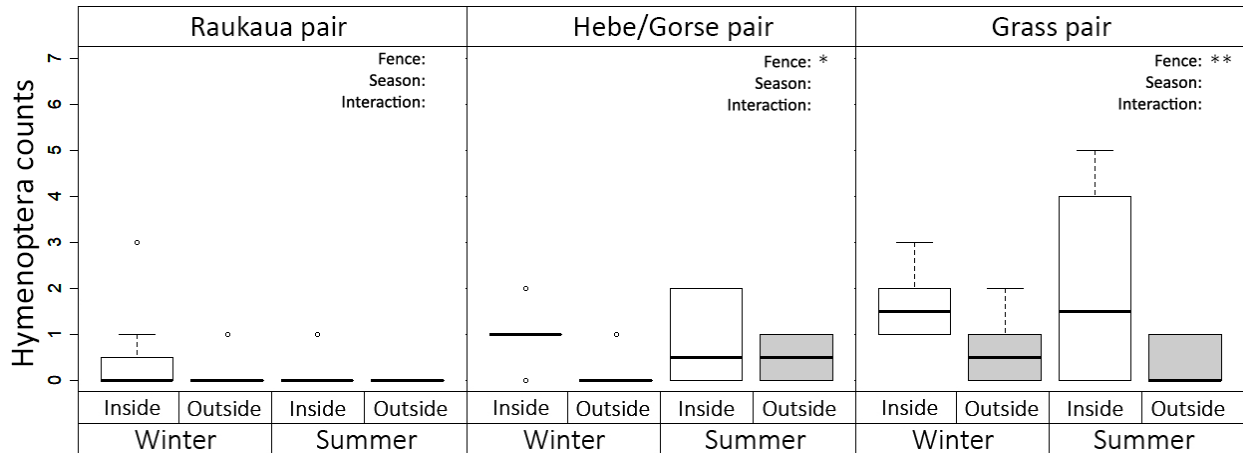


Figure 3.22. Box and whisker plots based on the counts of Hymenoptera found at each of the three pairs of sites for both seasons. The significance of the main effects 'fence' and 'season' as well as their 'interaction' are shown. '*' is significant at P<0.05 and '**' is significant at P<0.01.

3.3.4. Soil invertebrate wet weights

There was no evidence to suggest that the fence or season had a significant influence on the wet weight of invertebrates hand-sorted from the soil to 12cm deep below the turf samples (Table 3.13). The heaviest sample which weighed in at 21.35 grams from the Hebe/Gorse pair-outside site contained a partial piece of a native earthworm which had a length of about 13cm and a diameter of about 1.8cm (Table 3.14).

3.3.5. Beetle diversity indices

Out of the 291 adult Coleoptera counted from the turf samples (Table 3.8), 261 individuals were sufficiently intact for identification, which were identified down to 18 species and 45 recognizable taxonomic units (RTUs) (Table 3.10). Fifteen out of the 18 identified species were identified as being native to New Zealand and three were identified as being exotic. Out of the 45 RTUs, 17 were identified as being native, none were identified as being exotic, and the origin of the remaining 28 RTUs was not determined. See **Appendix D** for example photographs of all these specimens.

Table 3.8. The abundance of Coleoptera per site per season is shown.

	Raukahu pair		Hebe/Gorse pair		Grass pair	
	inside	outside	inside	outside	inside	outside
Winter	35	40	16	30	60	22
Summer	22	17	15	15	15	4

Coleoptera species under the families Curculionidae and Staphylinidae were most commonly found. A higher number of Curculionidae species were found inside the fence than outside for all three pairs when combining data from both seasons. There was no such consistency with Staphylinidae species (Table 3.9)

Table 3.9. The number of Curculionidae, Staphylinidae, and Other Coleoptera species found per site. Data for winter and summer are combined.

	Raukaua pair		Hebe/Gorse pair		Grass pair	
	inside	outside	inside	outside	inside	outside
Curculionidae	10	8	7	4	3	2
Staphylinidae	3	6	6	5	10	4
Other	5	7	9	6	14	2

Table 3.10. List of Coleoptera species and recognizable taxonomic units (RTUs) identified for this study. The species and RTUs are colour coded to indicate whether they are native (blue), exotic (red), or if their status was not determined (yellow). ‘Counts’ indicate the number of times they found throughout the entire study.

Family	Subfamily	Genus	Species	Counts		
Carabidae	Trechinae	<i>Zeanillus</i>	<i>sp.</i>	1		
		<i>Pelodietus</i>	<i>sp.</i>	1		
	Pterostichinae	<i>Holcaspis</i>	<i>placida</i> (Broun)	2		
	Harpalinae	<i>Lecanomerus</i>	<i>latimanus</i> (Bates)	1		
	Psydrinae	<i>Mecyclothorax</i>	<i>rotundicollis</i> (White)	1		
	Broscinae	<i>Oreagus</i>	<i>aereus</i> (White)	1		
Cerambycidae	Lamiinae	<i>Somatidia</i>	<i>sp.</i>	1		
Clambidae	Clambinae	-	<i>sp.</i>	1		
		<i>Sphaerotherax</i>	<i>suffusus</i> (Broun)	2		
		<i>Clambus</i>	<i>sp.</i>	1		
Cleridae	-	-	<i>sp.</i>	1		
Coccinellidae	Coccinellinae	<i>Coccinella</i>	<i>11-punctata</i> (Linnaeus)	1		
Corticoriidae	Corticariinae	<i>Melanophthalma</i>	<i>qibbosa</i> (Herbst)	3		
Corylophidae	Corylophinae	? <i>Holopsis</i>	<i>sp.</i>	1		
Curculionidae	?Cyclominae	-	<i>sp.</i>	1		
	Cossoninae	? <i>Pentarthrum</i>	<i>sp.</i>	1		
	Cryptorhynchinae	<i>Allanacis</i>	<i>sp.</i>	1		
		<i>Cryptorhynchine</i>	<i>sp.</i>	1		
	Curculioninae	<i>Abantiadinus</i>	<i>nodipennis</i> (Broun)	26		
		-	<i>sp.1</i>	1		
		<i>Peristoreus</i>	<i>sp.2</i>	1		
		-	<i>sp.3</i>	1		
		Cyclominae	<i>Listronotus</i>	<i>bouriensis</i> (Kuschel)	2	
			<i>Brachyolus</i>	<i>baoooides</i> (Sharp)	29	
	Entiminae	<i>Catoptes</i>	<i>cuspidatus</i> (Broun)	1		
		-	<i>ensorius</i> (Pascoe)	1		
	Molytinae	? <i>Lithocia</i>	<i>sp.</i>	16		
<i>Erymneus</i>		<i>sp.</i>	9			
<i>Etheophanus</i>		<i>sp.</i>	6			
<i>Phrynixus</i>		<i>astutus</i> (Pascoe)	13			
Histeridae	Histerinae	<i>Histerid</i>	<i>sp.</i>	2		
Latridiidae	Latridiinae	<i>Aridius</i>	<i>bifasciata</i> (Reitter)	3		
Leiodidae	Camiarinae	<i>Inocatops</i>	<i>sp.</i>	3		
		<i>Zelodes</i>	<i>sp.</i>	1		
Ptiliidae	Ptiliinae	<i>Ptinella</i>	<i>sp.1</i>	9		
		-	<i>sp.2</i>	2		
		-	<i>sp.3</i>	2		
		-	<i>sp.4</i>	9		
Scarabaeidae	Melolonthinae	<i>Odontria</i>	<i>Striata</i> (White)	1		
		-	<i>sp.1</i>	11		
		-	<i>sp.2</i>	1		
		-	<i>sp.3</i>	16		
		-	<i>sp.4</i>	3		
		-	<i>sp.5</i>	6		
		-	<i>sp.6</i>	1		
		-	<i>sp.7</i>	2		
		-	<i>sp.8</i>	2		
		-	<i>sp.9</i>	6		
		Euasthetinae	-	<i>sp.</i>	6	
		Pselaphinae	-	<i>sp.1</i>	3	
			-	<i>sp.2</i>	18	
			-	<i>sp.3</i>	2	
		Scydmaenidae	-	<i>sp.1</i>	3	
			-	<i>sp.2</i>	1	
		Staphylininae	-	<i>sp.1</i>	4	
			-	<i>sp.2</i>	2	
		Tenebrionidae	Lagriinae	<i>Pheloneis</i>	<i>aeratus</i> (Broun)	1
		Zopheridae	Colydiinae	<i>Pristoderus</i>	<i>sp.1</i>	5
-	<i>sp.2</i>			2		
Zopherinae	<i>Pycnomerus</i>		<i>sp.1</i>	2		
	-		<i>sp.2</i>	1		

	Native
	Exotic
	Uncertain

Exotic Coleoptera were found in two locations, both only during winter collections: the Hebe/Gorse pair-inside, and the Grass pair-outside (Table 3.11). The individuals that appeared in the Hebe/Gorse pair consisted of *Aridius bafasciata* (Reitter) (n = 3) and *Coccinella 11-punctata* (Linnaeus) (n = 1). Those that found in the Grass pair were *Listronotus bouriensis* (Kuschel) (n = 2).

Table 3.11. Counts of Coleoptera per site for both seasons are categorized into native New Zealand taxa or exotic taxa. Coleoptera that could not be categorized are excluded.

Raukaua pair					
		Winter		Summer	
		Inside	Outside	Inside	Outside
Native		27	20	14	17
Exotic		0	0	0	0

Hebe/Gorse pair					
		Winter		Summer	
		Inside	Outside	Inside	Outside
Native		14	5	15	5
Exotic		4	0	0	0

Grass pair					
		Winter		Summer	
		Inside	Outside	Inside	Outside
Native		20	3	3	0
Exotic		0	2	0	0

In the Raukaua pair, Coleoptera diversity was higher outside the fence in winter, but did not differ inside compared to outside in summer. In the Hebe/Gorse pair, Coleoptera diversity was higher inside the fence during summer but did not differ inside compared to outside in winter. In the Grass pair Coleoptera diversity was higher inside the fence for winter and summer (Table 3.12).

Table 3.12. Species richness, Shannon-Wiener index, and Effective Shannon diversity for Coleoptera for all sites in both seasons. Effective Shannon diversity is transforming the relationship between species richness and Shannon-Wiener index from a non-linear relationship into a linear relationship.

	Raukaua pair			
	Winter		Summer	
	Inside	Outside	Inside	Outside
Species richness	12	15	9	9
Shannon-Wiener index	2.21	2.48	2.15	2.12
Effective Shannon diversity	9.07	11.89	8.62	8.32

	Hebe/Gorse pair			
	Winter		Summer	
	Inside	Outside	Inside	Outside
Species richness	9	9	15	8
Shannon-Wiener index	2.09	2.87	2.59	1.99
Effective Shannon diversity	8.08	8.04	13.29	7.33

	Grass pair			
	Winter		Summer	
	Inside	Outside	Inside	Outside
Species richness	22	6	9	2
Shannon-Wiener index	2.87	1.23	2.10	0.69
Effective Shannon diversity	17.63	3.43	8.12	2.00

Table 3.13. Results from the Mann-Whitney U test on whether there were differences in soil invertebrate wet weight inside and outside the fence and between winter and summer within each pair.

Mann-Whitney U test results						
	Raukaua pair		Hebe/Gorse pair		Grass pair	
	W	p	W	p	W	p
inside/outside	121.0	0.81	82.5	0.09	63.5	0.64
season	131.5	0.91	174.0	0.09	74.0	0.93

Table 3.14. Numbers show the median and range (min-max) of the hand-sorted invertebrate wet weights in grams at each site for both seasons.

	Winter		Summer	
	inside	outside	inside	outside
Raukaua pair	2.10g (0.00-6.07g)	1.00g (0.00-5.48g)	0.53g (0.28-1.48g)	1.77g (0.00-6.52g)
Hebe/Gorse pair	0.17g (0.00-1.08g)	0.31g (0.14-3.51g)	0.79g (0.00-1.98g)	2.09g (0.00-21.35g)
Grass pair	0.08g (0.00-0.38g)	0.23g (0.00-1.10g)	0.12g (0.00-1.56g)	0.12g (0.00-1.32g)

3.4. Discussion

3.4.1. Turf sample invertebrates

3.4.1a Fence: Inside vs Outside

Here, I asked three questions: (1) **'Does soil and litter invertebrate abundance vary inside compared to outside the Orokonui Ecosanctuary fence?'**, (2) **'Does season affect soil and litter invertebrate abundance differentially inside and outside the Orokonui Ecosanctuary fence?'**, and (3) **'What is the difference in soil and litter Coleoptera diversity/endemism inside and outside the Orokonui Ecosanctuary fence?'**. I found evidence that for some invertebrate groups, there was a significant difference in their abundance inside compared to outside the fence, often with higher abundance inside the fence compared to outside. This was expected as invertebrate abundance tends to decline, not increase, in the presence of mammals (Howe *et al.*, 1981; Baines *et al.*, 1994; Suominen *et al.*, 1999; Miyashita *et al.*, 2004; Allombert *et al.*, 2005; Taylor *et al.*, 2011). However, there did not appear to be a consistent pattern between the three pairs of sites as oftentimes statistical significance was only found in one of the three pairs. The most consistent pattern for the effect of the fence on invertebrate abundance was found for Diplopoda and Hymenoptera, where their abundance increased inside the fence in two out of three pairs, and for both groups their abundance increased inside the fence. The fence had a significant effect on Hemiptera in two out of three pairs as well, but the direction of the effect occurred in opposite directions: abundance of Hemiptera decreased inside the fence in the Hebe/Gorse pair but increased inside the fence in the Grass pair.

The two invertebrate groups that only showed a higher abundance outside the fence compared to inside the fence were pseudoscorpions (Order: Pseudoscorpiones) and centipedes (Family: Chilopoda). This finding is contrary to the results in a study by Wardle *et al.* (2001) which investigated how introduced browsing mammals influenced litter-dwelling invertebrates inside and outside 30 different fenced browsing mammal enclosure plots in New Zealand. Wardle *et al.* (2001) found that where there was a significant difference in pseudoscorpion and centipede abundance, there was always a significantly higher abundance of these invertebrates inside the fence. However, the difference between the fenced areas investigated by Wardle *et*

al. (2001) compared to the Orokonui fenced area investigated in the present study is that the Orokonui fence is specially designed to exclude all invasive mammals including rats and brushtail possums, but the browser-exclusion fences Wardle et al. investigated only restricted the movement of large browsing mammals (Wardle *et al.*, 2001; Tanentzap & Lloyd, 2017).

Inconsistencies in results among the three pairs of sites could be due to the difference in invertebrate communities at the species level because of the difference in habitat structure, though I cannot be sure of this as I did not record all taxa to species level. The study by Suominen et al. (1999) investigated how ground-dwelling invertebrates responded to the presence of moose in two different areas called 'Sunnas' and 'Furudal' in Sweden. Suominen et al. (1999) found that moose browsing affected invertebrates in different ways in the two areas, where the invertebrate response to browsing often occurred in opposite directions. For example, nematode abundance was significantly higher in unbrowsed (compared to browsed) plots at Sunnas, but significantly lower in unbrowsed plots at Furudal. Suominen et al. (1999) ultimately concluded that invertebrate communities changed in the presence (or absence) of moose browsing, likely indirectly by how moose browsing can change vegetation structure, vegetation density, and the amount of deciduous leaf litter. Suominen et al. (1999) suggest that inconsistencies in results between the two areas could be due to any number of things including the potentially different composition of invertebrate species present at each area. Suominen et al (1999) suggested that more consistent results may have been seen if the analyses were extended to the species level as invertebrates are incredibly ecologically diverse, and the different species of invertebrates within a general taxonomic group would be responding to changes in their environment in different ways (Suominen *et al.*, 1999). Spitzer et al. (2008) similarly found inconsistency in the direction of invertebrate abundance in response to large mammal presence in two different types of oak woodland: sparse and dense. Carabid beetles were more abundant in the absence of deer in the sparse forest, but less abundant in the absence of deer in the dense forest. This contrasting result found by Spitzer et al. was discussed as likely being due to the different abundances of different types of carabid beetles in the two different areas, where small-bodied carabids that fed on small prey were more abundant in the dense forest and larger carabids that fed on larger prey were more abundant in

the sparse forest (Spitzer *et al.*, 2008). Overall, the preexisting literature suggests that the reason why there were inconsistent responses of invertebrate groups to mammals between the three pairs of sites in this study is likely because the sites in this study contain different species communities of invertebrates.

3.4.1b Season: Winter vs Summer

I found evidence that invertebrate abundance in some of the invertebrate groups differed between the seasons of winter and summer, but like the results for the effect of the fence, this effect was not always consistent between the three pairs. Wood lice (Order: Psocoptera) was the only invertebrate group that showed consistency in results for the effect of season, where they were completely absent in winter but present in summer for all three pairs. Contradictory results were present when examining the results for fly (Order: Diptera) larvae, where their abundance was lower in winter compared to summer in the Hebe/Gorse pair but higher in winter compared to summer in the Grass pair. These contradictory results for season on fly larvae abundance could be due to dominant fly taxa being different in the different habitats (Richards & Goff, 1997), and not all fly larvae having the same seasonal pattern of abundance in soil (Frouz *et al.*, 2008).

3.4.1c Interaction: Fence and Season

Significant interdependence of the effect of the fence and season occurred five times in one of the three pairs for five different invertebrate groups, being the spiders (Order: Araneae), centipedes (Family: Chilopoda), flies (Order: Diptera), Isopoda, and harvestmen (Order: Opiliones). For the spiders, centipedes, flies, and harvestmen, the interaction made it so that there was a lower abundance of these invertebrates inside the fence compared to outside the fence during winter, but a higher abundance of these invertebrates inside the fence compared to outside the fence during summer. Only Isopoda showed a different pattern where their abundance was higher inside the fence compared to outside the fence during winter, but lower inside the fence compared to outside the fence during summer. All five cases of a significant interaction ($p < 0.05$) between fence and season occurred in one of the forested pairs of sites

(the Raukaua pair or the Hebe/Gorse pair). These results suggest that the way in which introduced mammals could influence the abundance of spiders, centipedes, Isopoda, and harvestmen in native New Zealand forest habitats can differ between the summer months and the winter months.

These interaction patterns could occur due to a variety of factors including that communities of these invertebrate groups can have seasonal changes in diet (Smithers, 2005), can grow to a larger size as time passes (Cheong *et al.*, 2015), can have seasonal changes in microhabitat selection (Sinclair *et al.*, 2001), and/or can display seasonal changes in behavior (Adams, 1984). All of the aforementioned changes could interact with disturbance by introduced mammals, for example larger bodied invertebrates are more likely to be selected as prey by rodents compared to smaller bodied invertebrates (St Clair, 2011). Therefore populations of invertebrates that grow in size over time through ecdysis (molting) may be more likely to be impacted by rodents as they grow larger and become increasingly preferred as prey by mammalian insectivores (St Clair, 2011). Another example of how season can interact with trophic interactions is demonstrated in a study by Pennuto (2003) who found that the mortality of mayflies and caddisflies as a result of predation changed significantly between different seasons, where mayflies had a lower mortality rate than caddisflies in summer but mayflies had a higher mortality rate than caddisflies in winter (Pennuto, 2003).

Just like how there could be variation in species composition in different habitats, there could be variation in species composition in different seasons, and these species compositions react differently to mammalian pressure. It is documented that the species composition of invertebrates in an area can change dramatically between the seasons (Driessen *et al.*, 2013; Xu *et al.*, 2016), so this change in composition could also be what causes the interaction between mammal presence and season to occur.

3.4.2 Beetle diversity indices

There was a statistically significant difference in beetle abundance inside compared to outside the fence in the grass pair only. Like with invertebrates in general, this could be because the different pairs of sites host different beetle species assemblages, and something about the

beetle assemblages in the grass pair sites exacerbated the potential effect of fencing/mammal exclusion. Iida et al. (2016) investigated how the abundance and species diversity of three beetle groups were affected by high densities of sika deer (*Cervus nippon*) in Japan. The different beetle groups responded to sika deer density in different ways, where ground beetles showed decreased abundance/diversity with increased deer density, but dung and carrion beetles showed increased abundance/diversity (Iida et al., 2016). The direction of the effects were further divided when accounting for the size of the beetles, where large sized beetles were affected differently compared to small sized beetles. This again demonstrates that changes in beetle assemblages in response to mammalian pressure can depend on a variety of factors, including the taxonomic group of the beetles, functional group of the beetles, or even the body size of the beetle species involved.

Based on the information gathered and the sample sizes, I cannot statistically conclude that beetle diversity was different inside and outside the fence within each pair of sites. However the diversity indices of beetles were generally higher inside the fence compared to outside the fence regardless of season except for in the Raukaua pair, where beetle diversity appeared to be higher outside the fence in winter and did not appear to have any substantial difference inside and outside the fence in summer. The most abundant family of beetles counted were weevils (Family: Curculionidae) which are herbivorous (Fuentes et al., 2017), followed by rove beetles (Family: Staphylinidae) which are a part of the most biologically diverse beetle families in the world with a multitude of different dietary habits (Klimaszewski et al., 1996). More Curculionidae species were found inside the fence compared to outside the fence in all three pairs, but this consistency in pattern was not seen in Staphylinidae species. For Staphylinidae, more species were found outside the fence in the Raukaua pair, but more outside the fence in the Hebe/Gorse and Grass pair. This difference may be due to the different families of beetles having different functional roles, and previous literature has shown that the abundance of different varieties of beetles changes in various ways to deer disturbance (Iida et al., 2016).

The functional diversity of beetles could vary inside the fence compared to outside the fence in the absence of mammals. An increase in species diversity often (but not always) results

in the increase of functional diversity (Bihn *et al.*, 2010; Gerisch *et al.*, 2012). Further analysis of functional groups is desirable for accuracy. Preliminary analyses of functional diversity based only on beetle diet indicated that functional diversity was higher inside the fence for the Hebe/Gorse and Grass pairs (no difference in Raukaua pair), but the diet data were not robust enough to include in the body of this thesis (**Appendix E**).

There were more native than exotic beetles identified in this study as only six out of the 261 intact beetle individuals throughout the present study were identified as being exotic. This was expected as in New Zealand, native beetle species tend to make up a high proportion of the beetle community even in habitats with a relatively high proportion of exotic vegetation (Crisp *et al.*, 1998). The six exotic beetle individuals found in this study were found from both inside and outside the fence, so it does not appear that, at least for the Orokonui area, that mammalian pressure increases the incidence of exotic beetles. These results might suggest that the beetle species present at Orokonui before the fence was installed were predominantly native species, that the proportion of beetle species being native isn't greatly affected by introduced animals, or that the conservation benefits of the sanctuary (ie: maintaining a high proportion of native beetles within its fenced boundary) is spilling out into the surrounding area. This 'halo effect' has been studied by Tanentzap and Lloyd at the Orokonui Ecosanctuary where they found that the effect of protecting mammal-sensitive trees (and the frugivorous birds that feed on these trees) by the pest-resistant fence of the ecosanctuary spilt over into the immediate wider landscape outside the sanctuary through seed dispersal (Tanentzap & Lloyd, 2017).

3.4.3 Hand-sorted soil invertebrates

There was no evidence based on the results in this study to suggest that mammal exclusion with the fence or season influenced the wet weight of macroinvertebrates in soil down to a depth of 12cm at Orokonui. Most of the wet weight data came from earthworms (Family: Lumbricidae) and beetle larvae. The results are unsurprising as previous studies have shown that mammal disturbance does not necessarily decrease earthworm abundance, even when mammal disturbance was shown to decrease overall soil macroinvertebrate abundance

(Taylor *et al.*, 2011). In fact, soil disturbance from large mammals like deer and feral pigs sometimes correlates with an increase in the biomass of earthworms, particularly non-native earthworms (Rearick *et al.*, 2011; Lincoln, 2014; Wehr *et al.*, 2019). That being said, abundance does not necessarily tell us the same thing as weight, because one large heavy earthworm in one sample could be nutritionally equivalent to several smaller earthworms. A motivation for measuring the wet weight of soil invertebrates was to investigate whether mammal exclusion appeared to have affected soil invertebrate prey availability for Haast tokoeka kiwi (*Apteryx australis australis*) at Orokonui. These results imply that excluding mammals has not significantly influenced the wet weight of soil invertebrate prey that is available for the kiwi.

3.4.4 Conclusion

My results suggest that the way in which restricting animal movement with fencing and season influences invertebrate abundance is nuanced. Based on my results, I can conclude that the way in which mammal exclusion and flightless native animal inclusion (using pest-resistant fencing) influences invertebrates can depend on the habitat, the season, and the invertebrate taxa being investigated. How large vertebrates influence invertebrates differently in a variety of habitats is probably due to the varying invertebrate species assemblages that inhabit those habitats. Different invertebrate taxa will respond to disturbance in different ways. The ways in which season and the fencing interact with each other in how they influence invertebrates could be because of a variety of temporal changes that occur in individual invertebrate species (e.g. growth or behavioral changes) and/or their species composition. Overall, evidence here suggests that pest-resistant fencing can influence invertebrate assemblages (though the exact mechanisms behind these effects needs further study), and this can have implications for the conservation of the invertebrates themselves and potentially for insectivorous native animals that live in and around a fenced mainland sanctuary.

Chapter 4: Discussion

4.1. Summary and discussion

The purpose of this study was to address the primary question: Does the exclusion of introduced mammals and the inclusion of flightless native animals using pest-resistant fencing influence terrestrial invertebrate communities in New Zealand, and if so, are these patterns consistent between seasons? I wanted to address this question by comparing terrestrial invertebrate samples taken from sites inside and outside the boundary of the Orokonui Ecosanctuary pest-resistant fence, where the primary purpose of the pest-resistant fence was to keep introduced mammals from getting past the boundary of the ecosanctuary. The Orokonui fence does not only limit animal movement by excluding mammals, as there are also threatened native New Zealand animals such as Kiwi (*Apteryx australis australis*), Tuatara (*Sphenodon punctatus*), and Otago skinks (*Oligosoma otagense*) that are restricted to the inside of the fence (Bogisch *et al.*, 2016; Kitchin *et al.*, 2017; Tanentzap & Lloyd, 2017). This means that the potential difference in vertebrate pressure on invertebrate communities inside and outside the Orokonui fence are different not only because of the animals it excludes, but also because of the animals it includes. However, the pressures from introduced mammals are the main focus of this study as there is plenty of documented evidence in the literature about how much these mammals can influence not only invertebrate communities, but habitats as a whole (e.g. Baines *et al.*, 1994; Miyashita *et al.*, 2004; Allombert *et al.*, 2005).

To begin answering the primary question, I identified three pairs of sites to collect samples from, namely the Raukaua pair, the Hebe/Gorse pair, and the Grass pair (chapter 2). The Raukaua pair and the Hebe/Gorse pair consisted of one site inside the Orokonui fence and one site outside the Orokonui fence that had a similar plant species composition. These pairs were selected based on a cluster analysis utilizing plots and vegetation data from a previous study that was performed at Orokonui. The Grass pair consisted of graminoid-dominant sites inside and outside the fence that were manually selected by visual appearance. I also analyzed the soil properties at each of the six sites. Though I did not observe significant differences in any of the

soil properties, differences inside and outside the fence could be expected given the difference in animal (especially mammal) activity. The higher values of soil organic matter content I saw outside the fence for all three pairs for example could be because of mammalian activity as they have been found to be able to influence soil organic matter content through grazing, digging, and defecation (Sankaran & Augustine, 2004; Mohr *et al.*, 2005). How mammals influence the soil, and how the changes in soils could consequently influence invertebrate communities could be a topic of future research in connection to how pest-resistant fencing (in ecosystem restoration projects or otherwise) limits the movement of mammals.

To answer my primary question, I collected and compared invertebrate and soil moisture from each pair of sites (chapter 3). Most of the invertebrate information was collected from samples consisting of the upper layer of soil and everything on top of that (litter and vegetation) in the form of 'turf samples'. In many cases there was inconsistency when looking at the effect of the fence (inside the fence compared to outside the fence) on invertebrate abundance, as usually only one out of the three pairs of sites showed a significant difference in the abundance of an invertebrate group. In some studies that found evidence that mammals affect the abundance of invertebrate taxa, the type of invertebrate taxa affected, and the direction of the effects were different depending on the habitat being sampled from (Suominen *et al.*, 1999; Spitzer *et al.*, 2008). For example in the study by Suominen *et al.* (1999), fly (Order: Diptera) abundance increased in the absence of moose in the area called Sunnas, but decreased in the absence of moose in another area called Furudal. Sunnas and Furudal had different densities and compositions of tree species. This opposite direction of the effect of mammals on fly abundance is comparable to what I found in my study, where fly larvae abundance decreased in the absence of mammals in the Hebe/Gorse pair but increased in the absence of mammals in the Grass pair. The inconsistencies in patterns between pairs suggest that, assuming no other factors were playing a significant role in these patterns, the different habitats present in each of the pairs had an influence on how mammal presence affected invertebrate abundance. Despite the inconsistencies, oftentimes where there was a significant effect of the fence, there were significantly more invertebrates inside the fence compared to outside the fence.

Although I could not make statistical conclusions from the beetle diversity data, the way in which the fence affected beetle diversity also did not appear to be consistent between the pairs. For example, from the winter samples there was a lower diversity of beetles inside compared to outside the fence in the Raukaua pair, but a higher diversity of beetles inside compared to outside the fence in the Grass pair. More inconsistencies between pairs were found when looking at just one family of beetles, the Staphylinidae, where there were fewer RTUs of Staphylinidae inside compared to outside the fence in the Raukaua pair, but more RTUs of Staphylinidae inside compared to outside the fence in the Grass pair. This phenomenon has also been found in the literature, where the composition of beetle species size can differ between habitats, and different beetle families and/or size groups have been shown to react differently to mammalian pressure (Spitzer *et al.*, 2008; Iida *et al.*, 2016). In the study by Iida *et al.* (2016), carabid beetle abundance decreased in response to high densities of sika deer, but dung and carrion beetle abundance increased in response to high densities of sika deer. Another example is in the study by Spitzer *et al.* (2008), where carabid beetle abundance reacted differently to the presence of deer in two different forest densities (sparse and dense), and this difference was attributed to the sizes of the different carabid beetle species that were inhabiting the sparse and dense forest.

There were season and fence interactions but only in a few invertebrate groups, those being the spiders (Order: Araneae), centipedes (Class: Chilopoda), adult flies (Order: Diptera), woodlice (Order: Isopoda), and harvestmen (Order: Opiliones). The interaction between season and fence could be because the species or size/age composition of these invertebrate groups might have varied between the seasons (Sinclair *et al.*, 2001; Pennuto, 2003; Driessen *et al.*, 2013; Xu *et al.*, 2016). This would be a similar phenomenon to how invertebrates in different habitats react differently to mammal presence, but this time invertebrates in different seasons react differently to mammal presence.

4.2. Recommendations for future application of this research

(1) Count springtails and mites.

Initially when counting the invertebrates for this study, I decided to avoid counting the springtails and mites to save time because they were incredibly numerous, with probably over a thousand individuals per sample. However, I could have estimated these numbers by either counting individuals in small areas of the petri dish and extrapolating that number or counting all the individuals in the petri dish with the help of counting software. Such software already exists for counting ants, mosquitoes (Marois *et al.*, 2012), live springtails, and other small invertebrates (Mallard *et al.*, 2013). Springtails and mites are the most abundant and diverse arthropods in soil and leaf litter, are important components of soil ecosystems, and have been referred to as 'important knots in the food web of soils' (Larink, 1997; Filser, 2002; Greenslade, 2007).

(2) Include standardized sampling spots

Invertebrate populations can be patchy and very sensitive to microhabitats in their environment. Even within a 10mx10m plot, the invertebrates found in a sample taken from next to a rock compared to a sample taken from under plant cover can be very different. I think it could be a good idea to standardize where samples are taken. For example, prickly shield fern (*Polystichum vestitum*) were abundant in all my native forest sampling sites, so taking samples from underneath the foliage of this fern would have helped to standardize the sampling process. I could also have included several other standardized sampling spots (e.g. next to rocks or on ground without vegetation cover) to represent a variety of micro ecology. Wehr (2018) looked at how invertebrates responded to feral pig removal by taking samples 1m from the base of tree ferns (*Cibotium spp.*). By doing this Wehr could confidently conclude how feral pig removal influenced invertebrate communities near the base of tree ferns, but not how feral pig removal influenced invertebrate communities within other micro habitats. The benefit of my sampling method was that my samples represented invertebrates collected from a variety of different microhabitats, but only the microhabitats that my quadrat just happened to randomly

land on. I also did control for some level of microclimate by including soil moisture as a random factor in my statistical models.

(3) Include community-level analyses

Here, I investigated invertebrate groups as individual separate entities, but in the future, I might consider diversity-type analyses that look at all invertebrate groups together as a whole. I would attempt to identify all invertebrates to the same taxonomic level before applying these statistics. In the present study I identified invertebrates to different taxonomic levels including class, order, and family; therefore, it would have been inappropriate to apply diversity statistics to all invertebrates. Diversity indices have been used in invertebrate studies at higher taxonomic levels such as order (Bromham *et al.*, 1999) and family (Hoback *et al.*, 1999) level. Hughes (1978) found that when comparing community differences between sites, diversity indices applied up to order level can work but only if the same taxonomic level has been used. However, I did identify Coleoptera to species/RTU level here, and they can be considered a good surrogate for the overall invertebrate fauna.

(4) Use dry weight instead of wet weight when analyzing invertebrate weight from hand-sorted samples

I weighed hand-sorted invertebrates in this study to assess prey availability for soil-probing insectivores, particularly the Haast Tokoeka Kiwi. However, by measuring the dry weight of invertebrates I would have been able to assess the weight of nutritionally important components such as protein and fat (Rolff & Joop, 2002; Knapp & Knappová, 2013). Wet weight of invertebrates can also be highly variable, changing based on environmental conditions like moisture; therefore, dry weight would be a more reliable estimate of nutrient availability (Bennett *et al.*, 2005). Water content of invertebrates may be more relevant in regions where insectivores rely on the water content of their prey to survive (Cloudsley-Thompson, 2001), which is not necessarily the case in the region of Orokonui.

(5) Protect Tullgren funnel collection pots from contamination

It is possible that some of the adult Diptera and adult Lepidoptera collected in the collection pots underneath the Tullgren funnels were not actually from their respective turf samples. The collection pots that were positioned several inches below the Tullgren funnels and were illuminated by the light coming from within the funnels. The light likely attracted the flying invertebrates from the room, or from other turf samples, causing them to fall into the monopropylene glycol of the collection pots. I confirmed this by positioning a collection pot underneath a Tullgren funnel that did not contain a turf sample, and some adult Diptera did appear in this pot. For future Tullgren invertebrate extractions, I recommend surround the gap between the Tullgren funnels and the collection pots with extra card or netting to prevent samples being contaminated by invertebrates from the wrong samples, or from areas not relevant to the study.

(6) Beetle functional diversity analyses

In the present study, all beetles were identified to species or RTUs, and I calculated species diversity indices. For functional diversity indices, each species or RTU would need to be assigned functional traits such as e.g., diet, body size, breeding season, dispersal ability, length of life cycle, and most active time of day (Cole *et al.*, 2012). I attempted to perform functional diversity analyses on my beetles in the present study, but only using diet as a functional trait as I ended up running out of time (**Appendix E**). The functional diversity of beetles inside compared to outside the fence of Orokonui could also be an entire study on its own as beetle identification as well as determining the functional traits of each beetle species/RTU would take a considerable amount of time.

(7) Include plant dominance as a factor when selecting site pairs

I recommend that for future work in comparing the invertebrate communities of one site to another to also consider what the dominant plant species are at those sites because dominant plant species play key roles in structuring communities (Angelini *et al.*, 2011; Crawford & Rudgers, 2013). In the present study when finding site pairs, I only relied on whether plant species were either present or absent.

(8) Check for critical P value corrections with multiple comparisons

Because I analyzed each taxon and pair separately, each of my hypotheses (eg: difference in invertebrate abundance inside vs outside the fence) were tested many times. I should have applied a correction for my alpha P value from 0.05 to something much lower to avoid type 1 errors. This can be done using several methods, one of the simplest and conservative being the Bonferroni method which would give me an alpha P value of less than 0.002, and as a result would make many of the significant results at $P < 0.05$ in this study non-significant. Because of the highly conservative nature of the Bonferroni method, using it results in greatly diminished power to detect differences among pairs of samples although type 1 errors are greatly reduced (Eichstaedt *et al.*, 2013). A 'q-value' analysis or changing the study design entirely by reducing the number of separate tests by using a multivariate approach instead of analyzing each individual taxon separately can get around the Bonferroni method being conservative (Storey, 2003). Many other methods less conservative than the Bonferroni method are also available, such as the Holm Bonferroni method (Abdi, 2010). In the end, by not correcting for multiple comparisons, there is a risk of reporting irreproducible results.

(9) Moisture should be a fixed variable

Moisture was included as a random effect to the analyses in this study based on advice that I did not completely understand. I have since been advised that continuous covariates are not suitable to use as random effects, and so soil moisture should have been included in the models as a fixed covariate instead. Random effects are more suited to dependent categorical variables such as sites that are measured repeatedly (Grafen & Hails, 2002).

4.3. Future work

During the present study, a few ideas for future research in this field arose:

(1) Repeat the invertebrate survey (chapter 3) at Orokonui with invertebrates but use a range of non-quantitative methods inside and outside the fence. For example, the focus could be on aerial invertebrates collected using suction, window or malaise traps (e.g. Moeed &

Meads, 1987), vegetation-dwelling invertebrates collected using vegetation beating (e.g. Memmott *et al.*, 2000), or aquatic invertebrates from streams/ponds collected using kick nets (Frost *et al.*, 1971). Invertebrates in each of these habitat types may also be influenced by mammals and/or be important prey species for the protected vertebrates inside the fence.

(2) Investigate the feces of insectivorous Orokonui inhabitants to see what they are eating, and compare these diets to the invertebrates available at Orokonui. Comparing the diets of insectivores at Orokonui to the insectivores at other sanctuaries and wild locations would be useful because it would give us insight into what prey these animals prefer given prey availability. Information about this could be used as guidelines for invertebrate inoculations/introductions in ecosystem restoration projects to ensure preferred invertebrate prey at appropriate densities will be available.

(3) Repeat soil sample collections to determine if differences in soil properties inside and outside the fence at Orokonui are significant. If there are differences, it would be important to understand whether mammals are causing the soil property differences, and determine if these differences cause or correlate with differences in invertebrate communities.

4.4. Concluding statement

Overall, the control of mammals from areas of land using pest-resistant fencing can influence invertebrate communities within the fence boundary, but the types of invertebrates being affected, and the direction of the effect, can depend on the habitat and the season. Invertebrate communities are incredibly complex, and even communities of invertebrates that fall under a single taxonomic group (even down to family level) can respond very differently to mammalian disturbance depending on the species composition of that community. There are many opportunities to further understand the important role invertebrates play in ecosystems and ecosystem restoration projects in New Zealand, and how invasive mammals also play a part in influencing these ecosystems through changing the soil, vegetation, and even directly affecting the invertebrates.

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APPENDIX

Appendix A. Table showing the presence absence matrix of plant species and their habit (Ground cover or Tree/shrub) for the two pairs found using a cluster analysis.

Species	Habit	Raukaua pair		Hebe/Gorse pair	
		Inside	Outside	Inside	Outside
<i>Acaena anserinifolia</i>	Ground cover			1	
<i>Agrostis capillaris</i>	Ground cover				1
<i>Agrostis stolonifera</i>	Ground cover			1	
<i>Anthoxanthum odoratum</i>	Ground cover			1	
<i>Asplenium bulbiferum</i>	Ground cover	1	1	1	1
<i>Asplenium flaccidum</i>	Ground cover	1	1		
<i>Astelia fragrans</i>	Ground cover	1	1	1	1
<i>Blechnum chambersii</i>	Ground cover	1			1
<i>Blechnum discolor</i>	Ground cover	1	1		1
<i>Blechnum fluviatile</i>	Ground cover	1	1		1
<i>Blechnum procerum</i>	Ground cover	1	1		
<i>Blechnum vulcanicum</i>	Ground cover				1
<i>Cardamine debilis</i>	Ground cover		1		
<i>Carex forsteri</i>	Ground cover				1
<i>Carex geminata</i>	Ground cover			1	
<i>Carex inopinata</i>	Ground cover				
<i>Cerastium fontanum</i>	Ground cover			1	
<i>Clematis marata</i>	Ground cover				
<i>Clematis paniculata</i>	Ground cover	1	1	1	1
<i>Ctenopteris heterophylla</i>	Ground cover				1
<i>Dactylis glomerata</i>	Ground cover			1	1
<i>Dryopteris filix-mas</i>	Ground cover			1	
<i>Festuca rubra</i>	Ground cover			1	
<i>Galium aparine</i>	Ground cover			1	
<i>Grammitis billardierei</i>	Ground cover	1			
<i>Histiopteris incisa</i>	Ground cover			1	
<i>Holcus lanatus</i>	Ground cover			1	
<i>Hypolepis millefolium</i>	Ground cover			1	
<i>Hypochaeris radicata</i>	Ground cover				1
<i>Lagenophora strangulata</i>	Ground cover	1	1	1	1
<i>Metrosideros diffusa</i>	Ground cover				1
<i>Microsorium pustulatum</i>	Ground cover	1	1	1	1
<i>Muehlenbeckia australis</i>	Ground cover			1	1
<i>Nertera villosa</i>	Ground cover	1	1	1	1
<i>Parsonsia heterophylla</i>	Ground cover	1	1		1
<i>Polystichum vestitum</i>	Ground cover	1	1	1	1
<i>Prunella vulgaris</i>	Ground cover				1

Appendix A. (continued).

<i>Ranunculus acris</i>	Ground cover			1	
<i>Ranunculus repens</i>	Ground cover			1	
<i>Ripogonum scandens</i>	Ground cover	1			
<i>Rubus cissoides</i>	Ground cover	1	1		
<i>Rubus fruticosus</i>	Ground cover			1	1
<i>Senecio minimus</i>	Ground cover			1	
<i>Stellaria parviflora</i>	Ground cover		1	1	1
<i>Uncinia</i> sp.	Ground cover				1
<i>Uncinia gracilentata</i>	Ground cover	1			
<i>Uncinia uncinata</i>	Ground cover	1	1	1	1
<i>Aristolelia serrata</i>	Tree/shrub	1	1	1	1
<i>Berberis darwinii</i>	Tree/shrub		1		1
<i>Carpodetus serratus</i>	Tree/shrub	1	1	1	1
<i>Coprosma dumosa</i>	Tree/shrub	1	1	1	1
<i>Coprosma foetidissima</i>	Tree/shrub	1	1	1	1
<i>Coprosma linariifolia</i>	Tree/shrub				1
<i>Coprosma propinqua</i>	Tree/shrub	1	1	1	1
<i>Coprosma rhamnoides</i>	Tree/shrub	1	1	1	1
<i>Coprosma robusta</i>	Tree/shrub				1
<i>Coprosma rotundifolia</i>	Tree/shrub	1	1	1	1
<i>Coprosma Xrobusta</i> hybrid	Tree/shrub				1
<i>Crataegus monogyna</i>	Tree/shrub				1
<i>Cyathea smithii</i>	Tree/shrub	1	1		1
<i>Elaeocarpus hookerianus</i>	Tree/shrub	1			
<i>Fuchsia excorticata</i>	Tree/shrub	1	1	1	1
<i>Griselinia littoralis</i>	Tree/shrub	1	1	1	1
<i>Hebe salicifolia</i>	Tree/shrub			1	1
<i>Kunzea robusta</i>	Tree/shrub		1	1	1
<i>Leptospermum scoparium</i>	Tree/shrub		1		1
<i>Meliccytus ramiflorus</i>	Tree/shrub	1	1	1	1
<i>Myrsine australis</i>	Tree/shrub	1	1	1	1
<i>Myrsine divaricata</i>	Tree/shrub		1	1	1
<i>Pennantia corymbosa</i>	Tree/shrub	1	1	1	1
<i>Pittosporum eugenioides</i>	Tree/shrub	1	1	1	1
<i>Pittosporum tenuifolium</i>	Tree/shrub	1	1	1	1
<i>Pseudopanax colensoi</i>	Tree/shrub	1	1	1	1
<i>Pseudopanax crassifolius</i>	Tree/shrub	1	1	1	1
<i>Pseudowintera colorata</i>	Tree/shrub	1	1	1	1
<i>Raukaua edgerleyi</i>	Tree/shrub	1	1		
<i>Schefflera digitata</i>	Tree/shrub	1	1	1	1
<i>Ulex europaeus</i>	Tree/shrub			1	1
Number of species		39	40	48	53




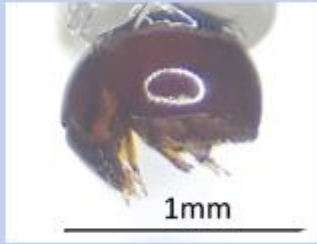

Appendix B. Table showing the total counts of invertebrate groups for each of the sampling sites in winter. Total counts are all invertebrates counted from all 8 samples per site for the Raukaua pair and Hebe/Gorse pair, and from all 6 samples per site for the grass pair.

Total invertebrate counts per sampling location in winter						
	Raukaua pair		Hebe/Gorse pair		Grass pair	
	inside	outside	inside	outside	inside	outside
Platyhelminthes	2	0	0	0	2	1
Nematoda	144	150	8	6	32	25
Mollusca	10	9	1	2	1	0
Enchytraeidae	584	140	47	14	128	240
Lumbricidae	7	2	2	1	3	4
Araneae	55	12	31	32	89	78
Opiliones	13	9	11	5	56	16
Pseudoscorpiones	10	16	3	18	37	0
Amphipoda	78	66	116	50	18	9
Isopoda	71	99	34	57	31	1
Chilopoda	13	43	15	54	80	49
Symphyla	3	12	0	2	1	0
Diplopoda	28	49	35	17	47	29
Paupoda	0	0	0	0	0	0
Protura	0	1	0	1	0	6
Diplura	0	0	0	0	8	0
Orthoptera	0	0	0	2	0	0
Psocoptera	0	0	0	0	0	0
Hemiptera	10	4	2	17	452	112
Thysanoptera	0	0	0	1	90	56
Neuroptera	0	0	0	0	0	0
Coleoptera (adult)	35	40	16	15	60	22
Coleoptera (larvae)	6	12	8	11	10	5
Diptera (adult)	0	1	1	11	3	4
Diptera (larvae)	83	79	11	40	194	45
Lepidoptera (adult)	0	0	0	0	1	0
Lepidoptera (larvae)	3	0	14	8	10	2
Hymenoptera	4	1	8	1	11	4






Appendix C. Table showing the total counts of invertebrate groups for each of the sampling sites in summer. Total counts are all invertebrates counted from all 8 samples per site for the Raukaua pair and Hebe/Gorse pair, and from all 6 samples per site for the grass pair.

Total invertebrate counts per sampling location in summer						
	Raukaua pair		Hebe/Gorse pair		Grass pair	
	inside	outside	inside	outside	inside	outside
Platyhelminthes	0	0	0	1	1	2
Nematoda	24	234	24	7	114	46
Mollusca	3	5	6	5	4	6
Enchytraeidae	171	162	70	9	145	143
Lumbricidae	6	5	2	9	3	7
Araneae	17	12	43	13	80	39
Opiliones	8	0	6	3	2	1
Pseudoscorpiones	8	3	2	8	0	0
Amphipoda	162	83	57	92	21	12
Isopoda	90	10	40	28	2	0
Chilopoda	34	8	19	23	75	48
Symphyla	1	0	1	0	4	0
Diplopoda	22	16	22	10	82	15
Paupoda	1	1	0	1	0	2
Protura	0	0	2	0	15	10
Diplura	0	0	0	0	0	0
Orthoptera	0	0	0	3	2	0
Psocoptera	80	67	6	8	6	6
Hemiptera	3	5	16	24	140	57
Thysanoptera	0	1	3	1	54	102
Neuroptera	0	0	0	0	2	0
Coleoptera (adult)	22	17	30	15	15	4
Coleoptera (larvae)	19	22	17	36	22	6
Diptera (adult)	13	9	12	11	43	25
Diptera (larvae)	107	39	13	293	51	18
Lepidoptera (adult)	1	2	0	1	1	5
Lepidoptera (larvae)	4	0	7	1	5	2
Hymenoptera	1	0	7	4	12	2






Appendix D. Table with example pictures of the Coleopteran recognizable taxonomic units. Question marks denote uncertainty of assignment.

Family	Subfamily	Genus	Species	Photo
Carabidae	Trechinae	<i>Pelodietus</i>	<i>sp.</i>	
		<i>Zeanillus</i>	<i>sp.</i>	
Cerambycidae	Lamiinae	<i>Somatidia</i>	<i>sp.</i>	
Clambidae	Clambinae	-	<i>sp.</i>	
		<i>Clambus</i>	<i>sp.</i>	




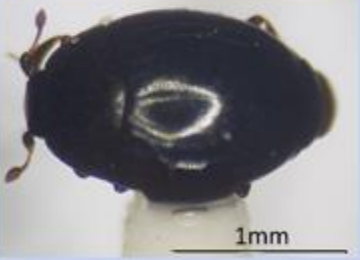

Appendix D. (continued)

Cleridae			sp.	
Corylophidae	Corylophinae	?Holopsis	sp.	
Curculionidae	Cossoninae	?Pentarthrum	sp.	
	Cryptorhynchinae	Allanalcis	sp.	
	Cryptorhynchinae	Cryptorhynchine	sp.	


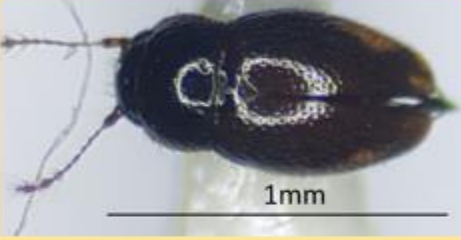


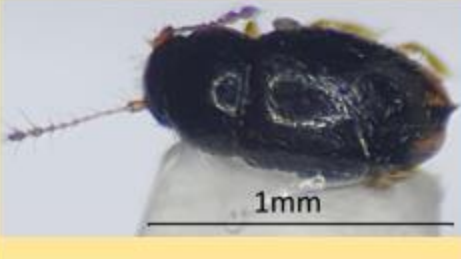
Appendix D. (continued)

	?Cyclominae	-	sp.	
	Molytinae	<i>Erymneus</i>	sp.	
		<i>Etheophanus</i>	sp.	
		<i>Phrynixus</i>	?thoracicus	
		?Lithocia	sp.	


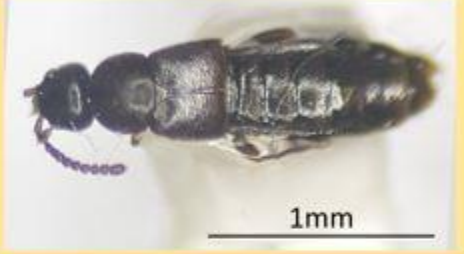

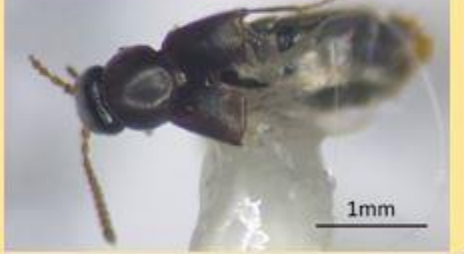

Appendix D. (continued)

	Curculioninae	<i>Peristoreus</i>	<i>sp.1</i>	
			<i>sp.2</i>	
			<i>sp.3</i>	
Histeridae	Histerinae	<i>Histerid</i>	<i>sp.</i>	
Leiodidae	Camiarinae	<i>Inocatops</i>	<i>sp.</i>	






Appendix D. (continued)

		<i>Zelodes</i>	<i>sp.</i>	
Ptiliidae	Ptiliinae	<i>Ptinella</i>	<i>sp.1</i>	
			<i>sp.2</i>	
			<i>sp.3</i>	
			<i>sp.4</i>	






Appendix D. (continued)

Staphylinidae	Aleocharinae	-	sp.1	
		-	sp.2	
		-	sp.3	
		-	sp.4	
		-	sp.5	




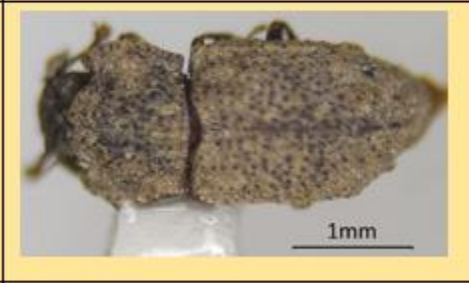

Appendix D. (continued)

	-	<i>sp.6</i>	
	-	<i>sp.7</i>	
	-	<i>sp.8</i>	
	-	<i>sp.9</i>	
Euasthetinae	-	<i>sp.</i>	



Appendix D. (continued)

	Pselaphinae	-	<i>sp.1</i>	
		-	<i>sp.2</i>	
		-	<i>sp.3</i>	
	Scydmaenidae	-	<i>sp.1</i>	
		-	<i>sp.2</i>	

Appendix D. (continued)

		-	<i>sp.2</i>	
	Staphylininae	-	<i>sp.1</i>	
		-	<i>sp.2</i>	
Zopheridae	Colydiinae	? <i>Pristoderus</i>	<i>sp.1</i>	
			<i>sp.2</i>	

Appendix D. (continued)

	Zopherinae	<i>Pycnomerus</i>	<i>sp.1</i>	
			<i>sp.2</i>	

Appendix E. Beetle functional diversity indices based on general information about diet. Beetle information from both seasons were combined. Table includes functional diversity, functional evenness, and Rao’s quadratic entropy. Analyses were performed in R using the package ‘FD’ and the function ‘dbFD()’.

	Raukua pair		Hebe/Gorse pair		Grass pair	
	inside	outside	inside	outside	inside	outside
Functional richness	5.9	5.9	8.0	2.9	8.0	5.9
Functional evenness	0.2	0.1	0.3	0.1	0.2	0.4
RaoQ	2.5	2.5	3.2	2.5	4.2	3.0

