Native and adventive detritivores in forests of Manawatu-Whanganui

A thesis presented in partial fulfilment of the requirements for the degree of

Master of Science

in

Ecology

at Massey University, Manawatu, New Zealand

Amie Parker

2013

Abstract

Little is known about many New Zealand invertebrates, including detritivores which have a key role in the functioning of ecosystems and are threatened by habitat modification and the addition of adventive species. Detritivores are an abundant group, and, like many other New Zealand taxa, they contain a high level of endemism that needs conserving. Detritivores are so scarcely studied, that it remains unknown how their forest communities are influenced by changes to New Zealand's forest habitats. This study aimed to increase knowledge on the identity, abundance, and distribution of detritivores in forests of Manawatu-Whanganui. Four main questions were addressed: (1) are adventive detritivores capable of invading native forests?, (2) can pine forests provide an alternative forest habitat for native detritivores?, (3) does proximity to forest edge affect native and adventive detritivores?, (4) are native and adventive detritivores co-occurring in the same habitats? Three detritivore groups (Diplopoda, Isopoda, and Amphipoda) were collected from edge and centre plots in six pine forests and ten native forests (including those that are small and close to urban areas) in Manawatu-Whanganui region of New Zealand.

The results show that a number of adventive taxa have spread throughout native forests in Manawatu-Whanganui, which does not support the hypothesis that native forests are resistant to adventive detritivores. Adventive Diplopoda were actually more abundant in native forests, and abundance of adventive Amphipoda and adventive Isopoda was high in both native and pine forests. Some native taxa were less dominant or absent in pine forests, and forest type influenced the community structure of Diplopoda and possibly Isopoda. The likelihood that a randomly collected detritivore would be an adventive was also influenced by forest type in all three detritivore groups. Human disturbance may have facilitated the invasion and establishment of adventive species, because small, urban, and highly modified native remnants appeared to have higher abundance and diversity of adventive species. Edge proximity had little influence on abundance of detritivores, but did affect the predicted likelihood of encountering an adventive individual in all three groups.

Adventive and native detritivores co-occurred in all forest habitats and it is possible that adventive detritivores will be influencing native species. Native Amphipoda appear to be under the most immediate threat in Manawatu-Whanganui, with adventive Amphipoda having higher abundance and higher probability of being found throughout all investigated forest habitats; there is evidence that adventive *Arcitalitrus* is displacing native species. The presence of adventive species could alter the functioning of native forest ecosystems and further research into the effect of adventive species in native forest is recommended. The data also revealed that for all three investigated taxa pine forests can support as many native detritivores as native forests, suggesting that pine forests contribute to preserving native biodiversity. Pine forests may be used as a tool to conserve native detritivores, but the conditions which promote the establishment of native species need further investigation.

Acknowledgements

Firstly, I would like to thank my thesis supervisor Dr Maria (Masha) Minor for her guidance and help with all aspects of the thesis, including many hours of help in the lab with identification, statistical advice, and finally help with editing. I am thankful to have had a supervisor that was so willing to help with any questions I had throughout the creation of this thesis.

Thanks go to the many helpful land owners and forestry managers who granted me permission to research on their land and provided me with any information I needed: Palmerston North City Council, Department of Conservation, Manawatu District council, Rick Brown, Trish Castle, Peter Wright (Rayonier/Matariki forests), and Pat McCarty (Ernslaw One Limited).

I would also like to thank the Ecology department technicians (Tracy Harris and Cleland Wallace) for providing the equipment needed for field and lab work, Russell Death (Massey University, Ecology – IAE) for statistical advice, and Rick Webber (TePapa Tongarewa Museum) who provided assistance in the identification of amphipods. This thesis was supported by a scholarship from the Ecology Bursary, Massey University.

I am appreciative of the friends that have made the last couple of years a lot more enjoyable and provided me with the support I needed to complete this thesis. Special thanks go to those that even gave up their time to help me with field work, editing, and statistics (Chris Parker, Jess Hiscox, Mike Parker, Leanne Parker, Amanda

Dehoop, Tylee Reedy, Joanne Headly, David Munro, Phoebe Stewart-Sinclair, and Danielle McArley).

Finally, I would like to thank my family not only for the support they have given me throughout the last couple of years (including the many days my mum has given up to spend in the forest helping me) but also for the constant encouragement and support that they have provided me with throughout my life.

Table of contents

List of figures

List of tables

1. Introduction

1.1. Endemism and origins of New Zealand's native invertebrate fauna: an overview

New Zealand's native biota is known to be unique, and New Zealand has been described as being as close as humans will get to studying life on another planet (Diamond, 1990). New Zealand has also been said to have the most interesting and important biota of any island (Diamond, 1990). The levels of endemism in New Zealand's flora and non-marine fauna are very high (Clout, 2011).

High levels of endemism are found in a range of New Zealand's invertebrate taxa (McGuinness, 2001), although there is variation in the amount of endemism at the level of species vs. genera, families, and higher taxa. It has been estimated that approximately 66% of New Zealand's invertebrate species are endemic (Gordon, 2010); however, the endemism levels in some groups can be even higher. Phyla such as Dicyemida (100%), Mollusca (84.6%), Orthonectida (100%), and Nematomorpha (80%) contain more than 80% endemic species (Gordon, 2010). Approximately 75-80% of the 22,000 Arthropoda species in New Zealand have been estimated to be endemic (Landcare Research, 1996; Gordon, 2010), which corresponds to one of the highest endemism levels among invertebrate taxa (Gordon, 2010). Other invertebrate phyla in New Zealand have endemism levels ranging from 0% to 71.8% (Gordon, 2010). Kinorhyncha have six endemic species but no endemic genera (Neuhaus & Blasche, 2006; Neuhaus, Higgins, & Paavo, 2010). Similarly, in Loricicifera there are two endemic species but no endemic genera (Heiner & Neuhaus, 2010); two families of Nematomorpha (horsehair worms) contain no endemic genera but four endemic species (Poinar, 1991; Poinar & Brockerhoff, 2001; Poinar, 2010). Nematoda (roundworms) have four endemic genera and 90 endemic species (Yeates, 2010). There is one endemic family and 25 endemic species of Tardigrada (water bears) (Horning, Palma, & Miller, 2010). In the Onychophora (velvet worms or peripatus) there are nine endemic species and one endemic genus (Gleeson, 1996; Trewick, 1998; Gleeson & Ruhberg, 2010).

Arthropoda is the most specious and abundant animal phylum on the Earth (Chapman, 2009), and in New Zealand there is high endemism at species and generic levels for all four extant sub-phyla (Chelicerata, Myriapoda, Crustacea, and Hexapoda) (Ahyong & Gordon, 2010). In New Zealand Chelicerata there are 245 endemic genera and approximately 2,693 endemic species (Ahyong & Gordon, 2010). In Myriapoda there are about 122 endemic genera and approximately 266 endemic species. Diplopoda has the highest endemism within the Myriapoda (containing 203 endemic species and 12 named endemic genera, along with more than nine endemic unnamed genera) (Johns, 2010). In Crustacea the highest level of endemism can be found in Amphipoda, Isopoda, Cumacea, Thoracica, and Harpacticoida. Amphipoda are the crustaceans with the highest number of endemic genera (58), but Isopoda have the highest number of endemic species (331) (Webber et al., 2010). In Hexapoda there is variation in endemism at genus level between taxa. Those taxa which tend to have the highest number of endemic species also tend to have the highest number of endemic genera (Macfarlane et al., 2010). Lepidoptera (Insecta) have 90% endemism in New Zealand (Dugdale, 1988). Coleoptera (Insecta) also have 90% endemism at the species level, and high endemism at the genus level, with 535 endemic genera proposed, which is the highest number of endemic genera among all New Zealand Hexapoda (Klimaszewski & Watt, 1997; Macfarlane et al., 2010). There is also one endemic family of Coleoptera (Cyclaxyridae) (Leschen, Lawrence, Kuschel, Thorpe, & Wang, 2003). In Protura, Diplura, Arcaeognatha, Isoptera, Mantodea, Dermaptera, Megaloptera, Neuroptera, and Strepsiptera there are endemic species but no endemic genera in New Zealand (Macfarlane et al., 2010). In Hymenoptera, endemism at species level is high, but at genus level endemism values are highly variable between taxa (Macfarlane et al., 2010). The recently described Maamingidae family is only known from New Zealand and highlights the uniqueness of New Zealand's hymenoptera fauna (Derraik et al., 2001). Freshwater aquatic insects Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddis flies), as well as Phasmida (stick insects) have 100% endemism (although there is some uncertainty about the Phasmida) (Early, 2009; Macfarlane et al., 2010). Over 90% of New Zealand's insect and spider species are endemic (Early, 2009). Such dominant endemism is unusual, and only Madagascar and New Caledonia have a similar high proportion of endemic species (Early, 2009).

A number of historical factors have shaped New Zealand's unique biota. New Zealand is one of the most isolated ancient landmasses on Earth (it has been isolated from the continent Gondwana land for over 80 million years); this isolation resulted in evolution of the high levels of endemism we see today (Stevens, 1985; K.-J. Wilson, 2004; Clout, 2011). During the Tertiary age (2-65 mya) the sea flooded large areas of land, increasing isolation of New Zealand, and creating a dispersal barrier to New Zealand from Antarctica and New Caledonia (K.-J. Wilson, 2004). Sea floor spreading separated New Zealand from Australia, creating the Tasman Sea (Stevens & Stevens, 1980). During this time New Zealand's flora and fauna showed an increase in the number of endemic genera and species due to the increased geographic isolation (Cooper & Millener, 1993). During the Tertiary age New Zealand's land mass eroded; the wearing down of the New Zealand ancestral landmass reached its climax in the early Oligocene (35 mya) when the land was worn down to a very low level (Stevens, 1985). During the Oligocene relative sea level rose and there was possibly only about a fifth of the dry land that is present today (Cooper & Millener, 1993; K.-J. Wilson, 2004). The land area was small and low lying, which reduced the range of habitats available (many extinctions and evolution of isolated taxa may have occurred at this time) (Stevens, 1985; Cooper & Millener, 1993; K.-J. Wilson, 2004). The reduced habitat is believed to have created a bottleneck effect (Cooper & Millener, 1993). About 20 mya a period of volcanism and mountain building began, caused by the collision of the Pacific and Indian-Australian tectonic plates (a process which continues today). The land area increased and a more diverse range of habitats became available (Stevens, 1985; K.-J. Wilson, 2004). New habitats influenced the biogeography of invertebrates and plants (but had little influence on vertebrates) (K.-J. Wilson, 2004). The West Wind Drift, which is a current that flows west to east around Antarctica, began to develop in the Ecocene (53 mya). Since the Miocene (24 mya), westerly winds have encircled the globe between 40 and 60 degrees south. Interestingly, New Zealand is only 1800 km downwind of biologically-rich Australia, and should have received a steady flow of wind-blown animals from Australia due to westerly winds; however, there is a paucity of Australian species in New Zealand (K.-J. Wilson, 2004). Some marine organisms, birds, and plant species are believed to have arrived via dispersal from Australia with assistance from the west wind drift (Stevens, 1985; Cooper & Millener, 1993; Trewick, Paterson, & Campbell, 2007). In the Pleistocene (about 2 mya) the Earth's climate cooled and glaciers covered much of the land (Cooper & Millener, 1993; K.-J. Wilson, 2004). In New Zealand, glaciers were particularly widespread in the southern and central parts of major mountain ranges (Trewick, Wallis, & Morgan-Richards, 2000). Each glacial advance caused forest areas to be restricted to small patches; when glaciers retreated, forests expanded to reinvade the land (McGlone, 1985; K.-J. Wilson, 2004). On continents species and habitats moved north or south to escape the glaciers as they advanced (K.-J. Wilson, 2004). In New Zealand, species were limited in northward movement (due to small land area), so forest animals were limited to ice free refuges (Stevens, 1985; K.-J. Wilson, 2004). New Zealand retained a broad habitat range throughout the Pleistocene (Trewick & Wallis, 2001).

The distribution and speciation of New Zealand invertebrates reflect the geographic processes that formed New Zealand into the island it is today. New Zealand's Gondwanan origin can provide some insight into native invertebrate fauna and how it relates to fauna in other parts of the world. There is strong evidence that some invertebrate lineages have been continuously present in New Zealand since it's connection to Gondwana (Giribet & Boyer, 2010). For example, the only two species of the archaic Chilopoda order Craterostigmomorpha are present in New Zealand and Tasmania, one species known from each location. The ancient trans-Tasman distribution was attributed to Gondwana origin based on genetic analysis (Edgecombe & Giribet, 2008; Giribet & Boyer, 2010). The archaic Onychophora (velvet worms) have been described to have a Gondwanan distribution. One family (Peripatidae) is found in the Antilles, Mexico, Central America, northern South America, equatorial West Africa, Assam, and Southeast Asia, and the other family (Peripatopsidae) found in Chile, South

Africa, New Guinea, Australia, and New Zealand (Gleeson, 1996). The presence of both families in Africa suggests divergence before the break up of Gondwana (Gleeson, 1996). There is a close affinity between New Zealand and Tasmanian forms (Gleeson, Rowell, Tait, Briscoe, & Higgins, 1998). Genetic analysis has confirmed that New Zealand Onychophora have an ancient origin which likely corresponds to the separation of New Zealand landmass (Giribet & Boyer, 2010). Diversity and distribution of the richest and most dominant Diplopoda family in New Zealand (Dalodesmidae) also supports a Gondwanan distribution (Johns, 1979). Dalodesmidae have a southern hemispheric distribution (found in New Zealand, New Caledonia, New Guinea, Chile, Madagascar, and southern Africa) but have extremely poor dispersal ability over any water barrier, let alone sea (Johns, 1979).

Glaciation, the refugia available, and the development of mountainous terrain have been identified to have influenced the distribution and evolution of New Zealand’s invertebrates. During the Pleistone the mountains of the South Island were glaciated and the low lands were bare outwash gravels created by rivers; both of these habitats were harmful to the survival of Diplopoda (Johns, 1979). However, there must have been some refugia, for example, Banks Peninsula has been identified as a refuge during this time (Johns, 1979). Evidence based on Diplopoda, ground beetles (Carabidae), and cockroaches (Blattodea) suggests there was also a small refuge in the North of Canterbury; another refuge must have been present in mid-Canterbury for the survival of Diplopoda *Icosidesmus aemulus* Johns, 1979 and *Dityloura dealbata* Johns, 1970 (Johns, 1979). Unique species found in south Canterbury indicate that a refuge must have also been available in this location. As the period of glaciation passed, the refuge areas would have acted as a source area from which populations could expand to recolonize the Island. Glacial periods would have extended the areas that were suitable for alpine species, but as glaciers retreated, habitat for alpine species would have become more limited and some species became restricted to mountain “islands”. Such distribution is evident in Diplopod *Icosidesmus cismontanus* Johns, 1964 which is restricted to mountain “islands” (Johns, 1979). The distribution of apline scree weta *Deinacrida connectens* (Ander, 1939) has also been effected by glaciation (Trewick et al., 2000). *D. connectens* is believed to have radiated in the Pliocene due to mountain building and survived the Pleistocene in discrete mountain range populations, with ice barriers preventing dispersal during glacial periods; this process has resulted in high intraspecific diversity (Trewick et al., 2000). Radiation of alpine species of cicada from the genus *Maoricicada* is thought to have occurred in the late Miocene when there was acceleration in uplift of the Sothern Alps; it is believed that the ancestral *Maoricicada* lived in low to mid altitude habitats (Buckley & Simon, 2007). Distribution of flightless ground beetles (Carabidae) on New Zealand islands indicates that the islands were once connected to the mainland, and the distinctiveness of island taxa reflects the length of time for which islands have been isolated. For example, Carabidae fauna on Three Kings Island and the sub Antarctic is very distinct corresponding to a long isolation from the mainland (Watt, 1974).

Examples illustrate strongly the way in which New Zealand’s geographic history has created a diverse invertebrate fauna. The lack of native terrestrial mammals present elsewhere in the world allowed some invertebrates to become the functional equivalent of mammals (Diamond, 1990; King, 1990). Taxa such as the giant weta (*Deinacrida* spp.) evolved to fill the role of small rodents such as mice and rats

(Diamond, 1990). Many New Zealand invertebrates evolved to become large and flightless. The wëtäpunga, the largest weta species on Little Barrier Island, weighs about 71 g, almost four times as big as some mice (Department of Conservation, 2006). Giant weta were once widespread in North Island lowlands but became extinct through much of the area during European settlement, probably due to the addition of rats which occupy the same niche (Stevens & Stevens, 1980; Early, 2009). Giant weta, tusked weta, giant weevil, kauri snails, flax snails, and Powelliphanta snails, described as "giants of the snail world", are all examples of New Zealand's unique giant invertebrate fauna (Department of Conservation, 2001, 2006). There is a large proportion and variety of flightless insects with reduced or absent wings, found in all major Insecta groups (Parkinson, 2007; Early, 2009). There are more flightless representatives of Insecta in New Zealand than anywhere else in the world (Parkinson, 2007). On the subantartic islands, 40% of Insecta have lost the ability to fly (Early, 2009). Many of New Zealand's endemic invertebrates are cryptic in colouring and nocturnal, as their main predators originally were reptiles and birds which are visual hunters in contrast to effective night hunting introduced mammals with a well-developed sense of smell (Early, 2009). New Zealand is considered to be one of the world's "biodiversity hotspots", partly due to the high level of endemism and partly due to the perceived threat to these endemics (due to loss in habitat and introduced predators). For this reason, New Zealand has been identified as a priority area for conservation work and the protection of endemic species (Myers, Mittermeier, Mittermeier, Da Fonseca, & Kent, 2000).

1.2. Adventive[1] species in New Zealand: an overview and the impacts of adventive invertebrates

Although historical processes can account for New Zealand's distinct native biota, it is the arrival of humans and the many adventive species that came with them that caused the greatest ecological change in New Zealand (K.-J. Wilson, 2004). Introductions of adventive species occur as humans move native species beyond their natural range both deliberately and inadvertently (Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997). The biota in New Zealand is characterised by the high number of adventive species; New Zealand is believed to be one of the most invaded places in the world (Allen & Lee, 2006) and the proportion of adventive species in New Zealand continues to increase (Atkinson & Cameron, 1993).

The large level of invasion of adventive taxa in New Zealand is believed to be due to (i) large areas of human transformed environment (Allen & Lee, 2006), (ii) New Zealand's benign climate, (iii) a European settlers culture dedicated to species introductions, (iv) an economy dependent on global trade (Kelly & Sullivan, 2010) (as regions with a high volume of trade are generally known to have more introduced

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[1] For the purpose of this thesis, an "adventive" species is considered to be one which does not naturally occur in New Zealand. Other publications may also refer to such species as exotic (Dawson, 1958; Brockerhoff et al., 2010; Kelly & Sullivan, 2010), introduced (Johns, 1962; Schubart, 1962; Ward et al., 1999), or alien (Atkinson & Cameron, 1993); sometimes term "invasive" has also been used interchangeably with these terms (Colautti & MacIsaac, 2004). Other authors use the word "invasive" to describe a species with an expanding range (Colautti & MacIsaac, 2004; Brockerhoff et al., 2010), as is done in this thesis.

species (Lövei, 1997)), and (v) the lack of dominant herbivores and predators prior to invasions (Allen & Lee, 2006). For over a century, and long before it was a global issue, non-native species have been the topic of intense public, legislative, management, and research activity in New Zealand. There has been heightened awareness of adventive species present in New Zealand, partly because of the distinct difference that occurs between native and adventive taxa and partly because of the timing of European settlement (New Zealand was one of the last habitable landmasses to be settled by humans) (Allen & Lee, 2006).

The rate of species arrival and loss in New Zealand has increased greatly since the arrival of humans. Dogs (*Canis familiaris* (L.)) and the Polynesian rat kiore (*Rattus exulans* (Peale, 1848)) were the only successful mammals introduced by the Polynesians, most likely along with a few plant species such as kumara (*Ipomoea batatas* (L.) Lam.) and paper mulberry (*Broussonetia papyrifera* (L.) Vent) (King, 1990; McDowall, 1994). However, a great number of new species have arrived in New Zealand since European settlement just over 200 years ago (McDowall, 1994; Kelly & Sullivan, 2010). When Europeans arrived, they found biota that was very different to that of their homeland and it was unsuitable for things such as pasture for stock, edible fruits, or short rotation plantation forests. In an attempt to recreate the resources and recreation opportunities that were present in Europe, thousands of plant and animal species were introduced (McDowall, 1994). Further European introductions continued late into the twentieth century. Introductions were initially from Eurasia and North America but later included species from a wider range of places throughout the world due to increased trade and transportation to other countries, the need for commercial crops, pasture, and forestry species, and a desire for novel garden plants (Allen & Lee, 2006). Since European settlement in 1840, 90 adventive vertebrates (including 32 mammals, 36 birds, and 19 fish) (Clout, 2011) and at least 2200 adventive plant species (resulting in an equal proportion of native and adventive flora in the wild) (Williams & Timmins, 2011) have established in New Zealand. It is believed that the introduction of mammals and birds peaked between 1850 and 1890, reflecting European settlers' attempts to recreate the environment they came from, control pests, and establish farm animals (Atkinson & Cameron, 1993). The number of adventive invertebrate species which have made their way into New Zealand remains unknown, but a value of 2000+ species has been proposed (Cochrane et al., 1997).

Adventive taxa that arrive in New Zealand often represent novel functional groups and have biogeographical and evolutionary histories which greatly differ from New Zealand's native taxa (Allen & Lee, 2006). Adventive species can degrade native environments and threaten native species (Clout, 2011). Adventive species can also alter ecosystem processes such as primary productivity, decomposition, hydrology, nutrient cycling and/or disturbance regimes; they do not simply compete with or consume native species, but change the rules of existence for all species (Vitousek et al., 1997). There is good evidence that biological invasions of adventive species contribute substantially to extinction (Vitousek et al., 1997). Native vertebrates in New Zealand (birds, fish, and reptiles) have suffered disproportionate rates of extinction and endangerment; in most cases the primary cause of this is believed to be predation and competition from adventive species (Clout, 2011). These effects are well documented for introduced plant and vertebrate species, and are becoming clear for invertebrates as well. Mammalian herbivores reduce the native plant understory and have negative impacts on the regeneration of native forest (Atkinson & Cameron, 1993). Adventive mammalian predators have caused much extinction in the native New Zealand fauna (King, 1990; Atkinson & Cameron, 1993). Adventive plants, such as *Tradescantia fluminens* Vell*.,* old man's bed (*Clematis vitalba* L.), and wild ginger (*Hedychium*) can be destructive in New Zealand's native forests (Greer & Sheppard, 1990; Atkinson & Cameron, 1993).

The damage and potential threat caused by adventive species in New Zealand is undeniable. It was predicted that in 2008 over 1500 million New Zealand dollars was spent in attempts to control pests (this includes costs for quarantine, border control, surveillance, research, pest control and eradication attempts) (Giera & Bell, 2009; Clout, 2011). The Biodiversity Act (1993) has been developed to protect New Zealand from the addition of adventive species. It aims to eradicate and effectively manage unwanted adventive organisms by border surveillance and control, early eradication of founding populations of new pests, and development of national and regional strategies by government agencies (Allen & Lee, 2006). However, despite the biosecurity system that has been put in place, hundreds of species continue to arrive and naturalise in New Zealand, fuelled by increase in global trade and by New Zealand's obsession with gardening (Kelly & Sullivan, 2010). The research focus on adventive species in New Zealand has undergone shifts throughout the years. Initially, research on adventive species was due to economic concerns over threats to agro-ecosystems because of early spread of pasture weeds. However, early and rapid decline of native terrestrial birds created awareness of the potential impacts of carnivorous mammals in forest ecosystems (Allen & Lee, 2006). Research priorities on adventive invasive species have now shifted from studying large scale spread and impacts to early detection and surveillance (Allen & Lee, 2006).

There are a large number of adventive invertebrates in New Zealand, including many pests of crops, pasture, forest and timber, livestock, and households (Scott, 1984b). It is unclear exactly how many adventive invertebrate species have made their way into New Zealand; value of about 2000 has been proposed by the Ministry for the Environment (Cochrane et al., 1997); however, it has also been estimated that there are about 2600 species of adventive insects alone (Emberson, 2000). Therefore, while there is uncertainty, it can be concluded that it is likely more than 2000 adventive invertebrate species are present in New Zealand and the naturalised fauna continues to grow (Brockerhoff et al., 2010). For example, 110 species of aphids have been identified in New Zealand, but only 12 species are recorded as being native. It is believed that over the last 130 years on average one aphid species a year has entered New Zealand (Teulon & Stufkens, 2002).

Ecological costs associated with the addition of adventive invertebrate species in New Zealand can be vast. Some adventive invertebrates have been economically beneficial to New Zealand, including Lumbricidae earthworms and the honey bee (*Apis mellifera* L., 1758), which form the basis of profitable farming and export industries. Some of the adventive invertebrates in New Zealand have been introduced as biocontrol agents and are now successfully controlling introduced pests (Fowler & Withers, 2001). However, only about 2.5% of all adventive insects have been introduced for biocontrol purposes (Emberson, 2000). Frequently, adventive invertebrate species have caused negative effects in New Zealand, including creating risks to human health, economic loss, and degrading ecosystem structure and function (Vitousek et al., 1997). The negative impacts associated with the arrival of adventive invertebrate species include damage to economically important crops; in only one year (1988), 267.5 tonnes of insecticide was used in agriculture and plantation forestry to control adventive pests (Holland & Rahman, 1999). A number of species, for example, mites, fleas, human lice, and mosquitos cause annoyance or pain to humans directly and are medically important pests in New Zealand (Scott, 1984b).

The effects that adventive invertebrates have on native communities have been far less evident than the effects on crops or orchards, and have been studied to a much lesser extent (Atkinson & Cameron, 1993). Adventive species may influence native invertebrates by predation, displace natives due to use of the same resources, and could have other indirect effects – for example, interference with natural pollination processes in native plant species. Adventive aphids pose a threat to natural systems by damaging native plants and displacing native aphid species (Teulon & Stufkens, 2002). The native katipo spider (*Latrodectus katipo* Powell, 1871) is being displaced by adventive South African species *Steatoda capensis* Hann, 1990 as both species were found to use the same spatial and trophic resources (Atkinson & Cameron, 1993). The adventive spider can colonise newly vacant habitats more rapidly than the native *L. katipo* can recolonize them, and therefore, the displacement of native species can occur after disturbances (Hann, 1990). *Bombus terrestris* (L., 1758) provides an example of a species which can interfere with the pollination of native plants and lower pollination success of both native and economically beneficial plants in New Zealand. Four *Bombus* species were introduced in an attempt to increase pollination of red clover (Donovan, 1980). Unlike other adventive *Bombus* species, *B.*

terrestris has a short tongue and often robs nectar from flowers with long corollas (for example the native kowhai *Sophora* spp. or red clover flowers) by biting holes near the base and gaining direct access to the nectar (Donovan, 1980). Not only are the flowers robbed of nectar and not pollinated (Donovan, 1980), but nectar robbing can reduce the attractiveness of the flower to other more effective pollinator species which can result in lowered pollination and fertilisation success of the plant (Irwin & Brody, 1999).

Numerous biocontrol agents have implications for native species, either due to direct effects of introduced biocontrol agents not being host-specific and attacking non-target species, or because biocontrol agents were intended to control native species (until the 1980s native species regarded as pests were often targets for biocontrol) (Fowler & Withers, 2001). For example, more adventive natural enemies have been released to control the endemic scarabid grass grub (*Costelytra zealandica* (White, 1846)), a pest of pasture, than any other biological control target (although none of these biocontrol species established) (Cameron & Wigley, 1989; Fowler & Withers, 2001). Biocontrol agents may also have indirect or "knock-on" effects on native species (Fowler & Withers, 2001). *Trigonospila brevifacies* (Hardy, 1934), an adventive parasitoid which was introduced from Australia as a biocontrol agent to control *Epiphyas postvittana* (Walk., 1863), an Australian fruit crop pest, provides an example of a biocontrol agent having both a direct and an indirect effect on native species. *T. brevifacies* has not been restricted to the intended host species - it parasitizes native Tortricidae Lepidoptera and was found to contribute up to 80% of the parasitoid load in native Tortricidea species (Munro & Henderson, 2002). The indirect effect of this is increased competition for hosts for native parasitoids, as *T.*

brevifacies has a host range that overlaps with that of 12 native parasitoid species. It is possibly that the adventive *T. brevifacies* could be competitively excluding native parasitoid species in New Zealand's native forests (Fowler & Withers, 2001).

Some adventive invertebrates are known to have an impact on entire native ecosystems, and can have devastating effects on New Zealand's native fauna – not only by predating native species, but through other further reaching impacts they cause by interfering with natural ecosystem processes (Brockerhoff et al., 2010). The examples are the two *Vespula* species, Argentine ant *Linepithema humile* (Mayr, 1868), ground beetles (Carabidae), and the *Eriococcus* scale insects of *Leptospermum* shrublands (Brockerhoff et al., 2010). Two adventive wasp species, the German wasp *Vespula germanica* (F., 1793) (which arrived in New Zealand in 1945) and the common wasp *Vespula vulgaris* (L., 1758) (which arrived in the 1970s) have invaded *Nothofagus* forests of New Zealand; *V. vulgaris* has displaced *V. germanica* in some beech forests (Thomas, Moller, Plunkett, & Harris, 1990; Beggs, 2001). The approximate biomass (mostly of *V. vulgaris*) is known to be as great, if not greater, than that of native birds, rodents, and stoats combined (Thomas et al., 1990). Honeydew is a resource produced in *Nothofagus* forests by an endemic scale insect and *V. vulgaris* greatly disrupts the native ecosystem by feeding on honeydew. *V. vulgaris* reduces the amount of honeydew by more than 90% for 5 months of the year, competing with native species (such as birds and invertebrates) that also consume honeydew. Behaviour of birds is altered by the reduction in honeydew (Beggs & Wilson, 1991; Beggs, 2001). Wasps also affect nutrient cycling in beech forests by reducing the flow of carbon to micro-organisms (Beggs, 2001). During the second stage of their breeding cycle, wasps predate on invertebrate species and can reduce numbers or completely eradicate some invertebrate populations (Beggs, 2001). The scale insect (*Eriococcus orariensis* Hoy, 1954) is another example of an adventive invertebrate that has impacted native New Zealand systems on a large scale. *E. orariensis* and the associated sooty mould fungus (*Capnodium walteri* Sacc.) invaded native manuka (*Leptospermum*) shrublands where it was responsible for 'manuka blight', the disease which caused the death of large areas of manuka. Photosynthesis was inhibited by the sooty mould, but it is believed that death of the plant was actually due to the removal of plant nutrients by large populations of *E. orariensis* (van Epenhuijsen, Henderson, Carpenter, & Burge, 2000). While the death of manuka associated with *E. orariensis* has now declined, problems associated with *V. vulgaris* are still a pressing issue (van Epenhuijsen et al., 2000; Beggs, 2001). The impact of Argentine ant *L. humile* has not been studied in New Zealand (Brockerhoff et al., 2010), but it is predicted (based on impacts overseas) that not only will it compete for resources and lower diversity of other ants and invertebrates in general, but will also likely influence key ecosystem processes such as pollination, seed dispersal, and decomposition (Harris, 2002).

1.3. Detritivores and the role of soil fauna

Soil and litter detritivores have an important role in an ecosystem and for the purposes of this review are defined as invertebrates which are involved in the decomposition process (Begon, Townsend, & Harper, 2006). The majority of decomposers (including detritivores) are saprotrophs, feeding on dead material; this includes both primary (leaf litter, woody debris) and secondary (predominantly decomposed organic matter, micro-organisms, and microbial residues) detrital resources, as well as animal materials such as skin, hair, and faeces (Begon et al., 2006). Detritivores include a diverse range of invertebrates, such as Isopoda, Amphipoda, Diplopoda, oribatid mites, some insect larvae, Lumbricina (earthworms), Collembola, and others groups (Swift, Heal, & Anderson, 1979; Mikola, Bardgett, & Hedlund, 2002; Paoletti et al., 2007). The key roles of detritivores in the decomposition process is to comminute (reduce resources in size by a physical process), catabolise (a chemical process which causes an energy yielding enzymatic reaction), and mineralise (convert chemical elements from an organic to an inorganic form) (Swift et al., 1979). Soil fauna alter decomposition rates directly, as they consume detritus and release inorganic nutrients, and indirectly by influencing the biomass, activity and composition of soil mircobial communities (J. C. Moore, Walter, & Hunt, 1988; Mikola et al., 2002). Providing a food source to polyphagous predators is another way in which detritivores influence the ecosystem (Paoletti et al., 2007).

Detritivores contribute greatly to the total soil diversity (Mesibov, 1998), which in turn contributes a large proportion to the overall diversity in an ecosystem. One way to classify the diversity of soil animals is by using size classes: micro-, meso-, macro-, and megafauna. For example, the macrofauna are soil animals which have a length of 200 µm to 10 mm; this includes most of large soil and litter decomposers such as Diplopoda, Isopoda, Amphipoda and Insecta, as well as Mollusca and larger Lumbricina. Macrofauna are responsible for the initial shredding of plant remains and redistributing them within the decomposer habitat, and have been recognised to have a dominant role in soil habitat transformation, as opposed to energy flow and nutrient transformation to which microorganisms contribute (Hättenschwiler, Tiunov, & Scheu, 2005).

The presence of macrofauna can significantly alter decomposition pathways and contribute directly to soil structure (Swift et al., 1979). Animals such as Diplopoda have been found to have the biggest influence on decomposition due to the process of shredding leaf litter (Rouifed, Handa, David, & Hättenschwiler, 2010). Studies incorporating the exclusion of detritivores from leaf litter provide some insight into their importance. Leaf litter from deciduous trees in a temperate forest (tree species included *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Acer campestre* L., *Corylus avellana* L., *Quercus robur* L., and *Fagus sylvatica* L.) decomposed faster when macrofauna were present; 22–41% of the total mass loss was attributed to macrofauna (Slade & Riutta, 2012). In a lab experiment, the presence of *Glomeris marginata* (Villers, 1789) (Diplopoda) increased leaf litter loss of four temperate tree species (*Fagus sylvatica* L., *Quercus petraea* (Matt.) Liebl*., Carpinus betulus* L.*, and Tilia platyphyllos* Scop.) by up to 58%, depending on the tree species (Rouifed et al., 2010). Macrofauna were responsible for about 10% of litter loss in temperate mixed forest, although there appeared to be no influence of macrofauna on litter decomposition in beech forest, possibly due to the absence of Diplopoda and low abundance of Cryptostigmata and Isopoda in beech forest (Irmler, 2000). The influence detritivores have on decomposition varies depending on a number of factors: climatic conditions (Wall et al., 2008), species identity of plant(s) being broken down (Slade & Riutta, 2012), site differences (Irmler, 2000), and species identity of detritivores themselves. For example, Isopoda and Diplopoda have been found to affect the mass loss of leaf litter positively, whereas the biomass of Lumbricidae was negatively correlated with mass loss (Irmler, 2000). Macrofauna fragment and consume litter, consume detritus and microbial biomass, and influence microbial communities, although the relative contribution of these mechanisms to decomposition can be difficult to quantify (Mikola et al., 2002; Hättenschwiler et al., 2005).

Macrofauna are often found to have a positive effect on carbon and nitrogen mineralization; however, there are cases in which no influence or a negative effect has been found (Mikola et al., 2002). Detritivore contribution to carbon mineralization is lower (about 10%) than detritivore contribution to nutrient mineralisation (about 30%) (Hättenschwiler et al., 2005). It is estimated that soil fauna overall is responsible for 37% of nitrogen mineralisation (J. C. Moore et al., 1988). Mineralisation is essential for the maintenance of plant production; this is because plant roots are generally impermeable to organic molecules (Swift et al., 1979). Plant growth can be strongly modified by the presence of soil macrofauna. For example, the presence of earthworms (*Aporrectodea caliginosa* (Savigny, 1826) and *Octolasion tyrtaeum* (Savigny, 1826)) in the soil increased shoot and root mass of clover *Trifolium repens* L. by 18% and 6%, respectively, and increased fescue *Poa annua* L. shot and root mass by more than two fold (Scheu, Theenhaus, & Jones, 1999). In New Zealand dairy pastures, earthworms have been estimated to contribute 24–98 kg N/ha/year through mineralization (Schon, Mackay, Hedley, & Minor, 2012).

As well as mineralisation, another key role of detritivores is the formation of soil organic matter. Detritivores contribute to the soil formation process over time as they enhance the incorporation of leaves and litter into the soil (Paoletti et al., 2007) and redistribute the detritus (Begon et al., 2006). Decomposition is a slow process and, in the meantime, partially digested plant and animal materials form the particulate component of the soil organic matter (Swift et al., 1979). Litter displacement, fragmentation, and the conversion of leaf litter to large quantities of faecal pellets by macrofauna disseminates microbial spores, stimulates microbial activity and facilitates decomposition (Hättenschwiler et al., 2005). The transformation of leaf litter into faeces by detritivores can influence decomposition by altering the chemical composition of leaf material after passage through the gut, increasing the bacterial: fungal ratio considerably (David & Gillon, 2002). The amount of woody debris and leaf litter transformed into faecal pellets by soil macrofauna is staggering. Diplopoda *Harpaphe haydeniana* (Wood, 1864) was estimated to consume 720 kg/ha per year of leaf litter, 36% of the estimated aboveground leaf litter input in coastal forests of British Columbia; 90% of this leaf litter was converted to faeces due to assimilation rate being less than 10% for most plant species (Cárcamo, Abe, Prescott, Holl, & Chanway, 2000). Similarly, Diplopoda *G. marginata* was found to consume 14 g of leaf litter (dry weight) per gram of animal (live weight) per year, and had a low assimilation rate of 6% (David & Gillon, 2002). It was estimated that a population of *G. marginata* consumes about 109 g/ m^2 (dry weight) of *Quercus ilex* L. leaves and produces about 103 g/ m^2 (dry weight) of faecal pellets per year; this is a large proportion of the 254 g/m^2 (dry weight) estimated aboveground leaf litter input (David & Gillon, 2002).

Detritivores are abundant in a range of ecosystems in New Zealand. A study on Coleoptera in the Waikato region of New Zealand found that in Kahikatea (*Dacrycarpus dacrydioides* (A. Rich.) de Laubenfels) forest fragments detritivores were the dominant group and in surrounding pasture areas detritivores were also abundant but were found to be co-dominant with predators. Endemic and adventive detritivores made up

15.4% and 25.1% of the Coleoptera fauna respectively in pasture and 64% and 2.1% in Kahikatea forest (Harris & Burns, 2000). Endemic detritivores were also found to be the dominant Coleoptera group in a *Pinus radiata* D. Don forest in Kaingaroa and approximately 60-90% of all Coleoptera collected at each trap were detritivores (Hutcheson & Jones, 1999). However, in another New Zealand study detritivores made up about 50% of individuals in forests (being the most dominant trophic group), about 40% in shrubland (where herbivores were more dominant), about 20% in heathland (where herbivores were dominant), and only about 4% in wetlands (where once again herbivores were dominant) (Hutcheson & Kimberley, 1999). Earthworms and detritivorous mesofauna have been found to occur at 28, 400 mg/m^2 and 200 mg/m^2 (dry weight) respectively in sheep grazed pasture and 15, 200 mg/m^2 and 180 mg/m^2 (dry weight) in dairy grazed pasture (Schon, Minor, Mackay, Yeates, & Hedley, 2010). High abundance of earthworms is an indication of water and air movement by the creation of soil pores, nutrient cycling assisted by litter incorporation, and greenhouse gas regulation by carbon storage (Schon et al., 2010).

In broadleaf forest at Orongorongo Valley, native earthworms contributed more (333 kg/ha) to forest animal biomass than any other group, and total arthropod abundance was 145 kg/ha (Brockie & Moeed, 1986). The weight of Amphipoda, mites, and native Isopoda was higher than in other forests around the world (in Europe, North America, and Japan) (Brockie & Moeed, 1986). A high abundance of leaf litter invertebrates was obtained from Orongorongo Valley from 1975 to 1976 using leaf litter quadrat samples. Collembola total abundance was 8805 ind./0.2m^2 in broadleaf podocarp forest and 9277 ind./0.2m^2 in silver beech forest in Orongorongo Valley, Amphipoda abundance was 2036 ind./0.2m^2 in broadleaf podocarp forest and 639 ind./ 0.2m^2 in silver beech forest, and Diplopoda abundance was 582 ind./0.2m^2 in broadleaf podocarp forest and 320 ind./0.2m^2 in silver beech forest (Moeed & Meads, 1986). A later survey carried out from 1977 to 1978 using cores of hummus and litter found slightly different abundance values. Collembola total abundance was 2200 ind./0.2m^2 in broadleaf podocarp forest and 4726 ind./0.2m^2 in silver beech forest, Amphipoda abundance was 449 ind./0.2m^2 in broadleaf podocarp forest and 180 ind./0.2m^2 in silver beech forest, and Diplopoda abundance was 390 ind./0.2m^2 in broadleaf podocarp forest and 770 ind./0.2m^2 in silver beech forest (Moeed & Meads, 1987). The high abundance of leaf litter fauna in New Zealand forests is believed to be due to the deep leaf litter continuously added through the year, and because the microclimate near the ground is equable and even, providing a permanent, predictable environment, free from extreme temperature or moisture fluctuations (Brockie, 1992).

1.4. Research rationale and questions

1.4.1. How many adventive detritivores are out there, and what are their impacts?

There is a large number of adventive detritivores present in New Zealand (Brockerhoff et al., 2010). The high number of adventive detritivores coming into New Zealand is illustrated by the fact that out of 112 species of adventive Lepidoptera in New Zealand, the majority (36) are detritivore species (Hoare, 2001). Adventive detritivores have gone largely unnoticed in New Zealand, because their effects are less visible than those of crop pests or predators. However, the impacts of adventive detritivores have the potential to be as devastating. There are a number of ways in which the invasion of adventive detritivores could have an impact on native species and/or nutrient cycling (Brockerhoff et al., 2010). Resources such as food and shelter may become unavailable to natives because of interference by adventives (due to agonistic interactions, chemical signals, or crowding); direct competition for resources could occur, which would reduce the available resources for natives; adventive species could change the litter habitat (for example, an increased consumption rate may alter the depth of leaf litter, decomposition rate, or the opportunities available for micro-organisms); high number of adventives may increase the number of predators, diseases, or parasites in the area, increasing the pressure on natives (Griffin & Bull, 1995). An adventive detritivores could cause changes to a community by competing with and displacing native detritivores (Tomlinson, 2007). For example, the adventive Amphipoda *Arcitalitrus sylvaticus* (Haswell, 1880) is believed to displace native Amphipoda species in New Zealand (Duncan, 1994). On the contrary, the decline in the native earthworm fauna (Megascolecidae) is believed to be a result of human induced environmental changes as opposed to direct interaction with the adventive species (K. Lee, 1961).

While the impacts of adventive detritivores have received little attention in New Zealand, worldwide there is a new awareness that adventive detritivores can have an unforeseen and dramatic impact on ecosystems. Invasive detritivores may alter forest soil carbon levels directly through decomposition or litter consumption, and carbon sequestration indirectly by altering biogeochemical processes and complex interactions with species from other trophic levels (Peltzer, Allen, Lovett, Whitehead, & Wardle, 2010). For example, European earthworms (Lumbricidae) have invaded previously earthworm-free forests in North America and their effects cascade through the ecosystem (Frelich et al., 2006). The presence of adventive earthworms leads to reduced availability and increased leaching of nitrogen and carbon (Bohlen, Pelletier, Groffman, Fahey, & Fisk, 2004; Frelich et al., 2006). Earthworms reduce the thickness of the forest floor (detritus) as leaf litter and hummus is incorporated deeper into the soil (Bohlen et al., 2004; Frelich et al., 2006). As a result, germination of many native plants is disrupted, bulk density of soil is increased and the abundance of native soil dwelling invertebrate species is believed to decreases (Frelich et al., 2006). The changes in soil influence the whole soil food web, including changes to microflora and seedbed conditions for vascular plants (Frelich et al., 2006). Vegetation changes have resulted due to earthworm invasion; the presence of earthworms has led to the decline of forest herbs in the genera *Aralia*, *Botrychium*, *Osmorhiza*, *Trillium*, *Uvularia*, and *Viola,* and earthworm invasion is likely to alter competitive relationships among plant species, possibly facilitating invasion of adventive plant species such as *Rhamnus cathartica* into North American forests (Frelich et al., 2006). Presence of earthworms can create a greater variation of microhabitats and a possible food source for larger organisms which increases the abundance of other soil animals, but this effect is small, transient, and restricted to harsh climates (Migge-Kleian, McLean, Maerz, & Heneghan, 2006). In the long term, invasion of earthworms can have severely negative effects on flora and fauna from a range of trophic levels (Migge-Kleian et al., 2006).

Another earthworm *Dichogaster* nr. *curgensis* Michaelsen, 1921 (originally from Africa) is causing problems in rice fields of the Phillipines and is a widespread pest affecting more than 20,000 ha. *D*. c*urgensis* can cause direct damage to rice roots when earthworms slide past, causing scratching which can tear and sever the roots. At a “low” earthworm density of 140 m^2 injured roots became shorter which reduced plant height but not yield, but at medium and high earthworm density plant injury was more severe and there was lower tiller number and a decline in yield (Barrion & Litsinger, 1997). The burrowing earthworms also interfere with germination by covering up seeds in the seedbed; at high densities, earthworm burrowing covered rice seeds 6 to 10 cm deep in the mud. Some of the buried seeds germinated but did not emerge above the soil level, some seedlings emerged but were shorter than normal, and other seeds decayed and were unable to grow (Barrion & Litsinger, 1997).

There are many naturalised species of invertebrates which may be in their early stage of spread in New Zealand. Obtaining an estimate of the ecological and economic impacts of these species would be beneficial, so priorities can be set and any pre-emptive control can be justified (Kelly & Sullivan, 2010). Before this can be done, however, information on presence, identity and distribution of adventive species needs to be collected, which was one of the objectives of this thesis.

1.4.2. Are New Zealand’s native forests resistant to invasion by adventive invertebrates?

In New Zealand, most adventive invertebrate species are found to be abundant in disturbed habitats, but are thought to be rare or absent in native forests (Berndt, Brockerhoff, & Jactel, 2008; Pawson, Brockerhoff, Meenken, & Didham, 2008). For example, adventive Lumbricidae earthworms have now mostly replaced native Megascolecidae earthworms in areas that have been modified by humans, although in unmodified native forest adventive earthworms are usually absent or rare (K. Lee, 1961). Mammals and social hymenopterans are the only adventive animals known to penetrate through New Zealand’s native forest (Kelly & Sullivan, 2010). Cases of adventive detritivores causing ecosystem-level impact have not been documented in New Zealand forests.

It has been proposed that New Zealand's native forest ecosystems are resistant to invasion by adventive invertebrates (Pawson et al., 2008; Brockerhoff et al., 2010). The reason suggested is that host-specific herbivore invaders encounter New Zealand's endemic flora, which in many cases is phylogenetically distant from their host plant (in which plant defences are overcome due to co-evolution) (Ridley, Bain, Bulman, Dick, & Kay, 2000), which prevents successful invasion and establishment of herbivores in native forests (Brockerhoff et al., 2010). However, this mechanism is unlikely to influence detritivores as they are typically regarded as food generalists (Chahartaghi, Langel, Scheu, & Ruess, 2005). Trophic ecology can affect the success of invasion (Gido & Franssen, 2007). Among trophic guilds, some may be better able to colonise and exploit newly available niches, and detritivores may be one of those guilds (Samways, Caldwell, & Osborn, 1996; Hoare, 2001; Brockerhoff et al., 2010). The success of some invading detritivores has been put down to the fact that detritus is an abundant and easily located resource (Hoare, 2001). It has been proposed that detritivore communities are controlled by top-down processes (such as predation) instead of being regulated by bottom-up control (resource availability) (Mikola & Setälä, 1998; Lensing & Wise, 2006). If this is true, invading detritivores would have large amounts of resources available to them and thus their invasion would not be limited by food availability. However, experimental studies have shown varying results, sometimes suggesting that bottom-up processes dominate; other studies had inconclusive results (Salminen & Sulkava, 1997; Scheu & Schaefer, 1998; Chen & Wise, 1999; Yang, 2006).

In New Zealand, some adventive detritivores have been found to have invaded native forest remnants (Brockerhoff et al., 2010). An adventive Isopoda (*Armadillidium vulgare* Latr.) was present at 17 out of 25 native forest sites sampled (Scott, 1984a). A study of Coleoptera (including many detrivivore groups) in two fragmented kahikatea (*D. dacrydioides*) forests of New Zealand revealed that most species were native, but some adventive species were found (Harris & Burns, 2000). The adventive Diplopoda *Oxidus gracilis* (C.L. Koch, 1847) was found at a high abundance in karaka (*Corynocarpus laevigatus* J.R. Forst. & G. Forst.) litter in the Waitakere Ranges, west of Auckland city (Tomlinson, 2007). *Cylindroiulus britannicus* (Verhoeff, 1891) and *Ophyiulus pilosus* (Newport, 1842) are two other Diplopoda which have been identified in native forests (Dawson, 1958; Johns, 1995). *C. britannicus, O. pilosus,* and the Isopoda *Porcellio scaber* Latreille, 1804 have been found throughout the native Riccarton Bush of Christchurch, being especially common around the edges, in the former oak plantation, and along some of the walking tracks (Johns, 1995). The adventive moth *Opogona omoscopa* (Meyr., 1893) (Tineidae) (which in its larval stages lives in leaf litter and feeds as a detritivore) was found at high abundance in native New Zealand forest (most commonly in puriri (*Vitex lucens* Kirk) litter), and in fact, was the most abundant moth collected from the area (Tomlinson, 2007). Wise (1953) also noted that *O. omoscopa* was the dominant moth in collections made from the Auckland area. While the impact of adventive detritivores on New Zealand's native forests so far appears to be minor (Brockerhoff et al., 2010), their presence, distribution, and abundance in New Zealand forest environments have not been thoroughly investigated.

1.4.3. Pine forests as a new habitat for native and adventive species

One of the unknown variables in the state of detritivore biodiversity is their use of plantation forests. Plantation forestry is now a significant industry in New Zealand, with wood products being the third biggest export behind dairy and meat (Ministry of Agriculture and Forestry, 2011). Exotic plantations cover 1.751 million ha (approximately 7% of New Zealand's land), with the majority of this forest being composed of radiata pine (*P. radiata*) (Ministry of Agriculture and Forestry, 2011). The impacts on native fauna that occur when native vegetation is replaced by exotic plantations can be variable and are often poorly understood (Sax, Kinlan, & Smith, 2005).

There is concern that the establishment of pine plantations will result in a lack of biodiversity, which could lead to change in ecosystem functioning, as ecological processes are often thought to be dependent on the preservation of diversity (Brockerhoff, Ecroyd, & Langer, 2001). In the past, pine plantations have been perceived as "biological deserts" (Brockerhoff et al., 2001). However, New Zealand pine plantations have been found to support native species of birds, bats, and plants, containing more diversity than was initially thought (Maunder, Shaw, & Pierce, 2005). While focus was once placed on large flagship (bird) species in plantation forests, recent work has been extended to include invertebrates (e.g., Ratsirarson, Robertson, Picker, & Van Noort, 2002; Oxbrough, Gittings, O'Halloran, Giller, & Smith, 2005; Callaham, Richter, Coleman, & Hofmockel, 2006). The somewhat scarce existing information suggests that pine plantations in New Zealand can support a number of endemic invertebrates (Hutcheson & Jones, 1999; Brockerhoff, Berndt, & Jactel, 2005;

Pawson et al., 2008). For example, native Coleoptera have been identified from pine plantations in New Zealand (Hutcheson & Jones, 1999; Brockerhoff et al., 2005; Berndt et al., 2008; Pawson et al., 2008). Pawson *et al.* (2008) investigated ground beetles (Carabidae), chafer beetles (Scarabaeidae) and bark beetles (Curculionidae: Scolytinae) in pine forests in the central North Island and the eastern South Island of New Zealand, and found that the proportion of adventive Coleoptera was consistently low. Endemic detritivore species were found to dominate the Coleoptera assemblage across three age classes of pine plantation stands (Hutcheson & Jones, 1999). Pine forests of the Canturbury plains were found to support eight native Carabidae speices, including two species (*Holcaspis brevicula* Butcher, 1984 and *Hypharpax antarcticus* (Castelnau, 1867)) not found in native kanuka (*Kunzea ericoides* (A. Rich) J. Thomps.) forest in the area (Berndt et al., 2008). *H. brevicula* is a critically endangered ground beetle endemic to the Canterbury plains of New Zealand (Brockerhoff et al., 2005; Berndt et al., 2008).

New Zealand research in this subject area appears to be biased towards the study of Coleoptera. However, the presence of endemic Protura in pine plantations has also been documented, although species with an Australian or worldwide distribution were more frequently found in pine forest than endemic species (Minor, 2008). A pine forest's ability to support native species may depend on the age of the stand, with more mature pine forests supporting more native species (Norton, 1998). Recently clear-felled plantations have a lower relative abundance of native Coleoptera species than mature pine forest (Pawson et al., 2008). However, it has also been found that when plantations below five years are excluded, the age of the plantation had no effect on the number of native species present (Bonham, Mesibov, & Bashford, 2002). As well as being influenced by the length of time since the plantation has been established, the presence of native invertebrates in exotic vegetation may be influenced by how far away the plantation is from any similar structured native vegetation patches (Samways et al., 1996; Pawson et al., 2008).

Research from other parts of the world also suggests that native invertebrates are able to persist in exotic pine plantations (Bonham et al., 2002; Gunther & New, 2003; Mesibov, 2005). Car (2010) found that the presence of exotic vegetation instead of native vegetation in a forest did not alter the abundance of native Diplopoda; instead, the immediate microclimate and the disturbance the area is exposed to may have had more influence on native Diplopoda. Native detritivores can be found at high abundance in pine forests (Hutcheson & Jones, 1999; Bonham et al., 2002; Mesibov, 2005; Robson, Baker, & Murray, 2009); this indicates that the native invertebrate community is involved in the break down and recycling of pine debris (Robson et al., 2009).

There is still very little information on soil invertebrates in New Zealand pine plantations (Maunder et al., 2005). It is not clear to what extent adventive detritivores colonise pine plantations, and whether the detritivore community of exotic forests represents a depauperate native community, or a functioning combination of native and adventive species best able to utilise the pine forest resources.

1.4.4. Do edges and closeness to urban areas facilitate advancement of adventive detritivores?

There have been large land use changes in New Zealand's history and New Zealand's landscape has changed significantly from the time prior to the arrival of humans, when 85-90% of New Zealand was covered in native forest (McGlone, 1989). The loss of New Zealand native forest and changes in land use are one of the key issues affecting native decomposer communities in New Zealand (Tomlinson, 2007). The majority of New Zealand's native invertebrates (including detritivores) are forest dwellers, and it is likely that extinctions have already occurred because of land clearance (Cochrane et al., 1997).

Habitat loss is a recognised threat to invertebrates worldwide, with many if not most invertebrates expected to be affected by forest fragmentation. For example, the vast majority of Coleoptera studied in tropical environments were adversely affected by fragmentation, having significantly lower densities near edges or in small forest fragments (Didham, Hammond, Lawton, Eggleton, & Stork, 1998). When compared to undisturbed continuous forest 49.8% of species were absent from samples taken in 1 ha fragments, 29.8% from 10 ha fragments, and 13.8% from 100 ha fragments. However, lower trophic levels may be less susceptible to habitat loss than higher trophic levels such as predators (Didham et al., 1998). Fragmentation of forest can facilitate the invasion of exotic vegetation, which can then replace native vegetation. In a New Zealand study by Standish (2004), plots with invasive *Tradescantia fluminensis* Vell. were compared to plots without, and plots infected with *Tradescantia* had lower Coleoptera richness and abundance. Some Coleoptera detritivores responded to invasion by *Tradescantia* and displayed a clear preference for native habitat, with the exception of *Notoptenidium* spp. which feed on fungus that may thrive in moister *Tradescantia* habitat (Standish, 2004). The decline of native earthworm fauna in areas that have been cleared of native forest and the replacement of the fauna by adventive species also illustrates the threat of native forest loss (K. Lee, 1961).

Habitat fragmentation effects organisms not only by overall loss of forest cover, but also by exposing the organisms in remaining forest to conditions from the outside environment, known as 'edge effects' (Murcia, 1995). Edge effects may influence organisms in three ways: through change in abiotic conditions (such as air temperature, light intensity, and soil moisture), through direct biological interactions (the changes in abundance and distribution of species due to their proximity to the edge of a forest), and through indirect biological effects (which involves a change in species interactions) (Murcia, 1995). There has been few investigations into the effect edge habitats have on animals, comparing with the extensive research into the influence on vegetation and abiotic factors; even less is understood about the response of invertebrates (Norton, 2002). The impact that fragmentation and edges have on invertebrates has been poorly documented (Didham, 1997). While changes in abiotic and biotic parameters across forest edges have been widely documented, there is little consensus on the extent of edge effects (Norton, 2002) and the variation in response of invertebrates reported in the literature highlights this. There is a trend for an increase in abundance and diversity of invertebrates at forest edge and this is put down to the invasion of generalist species from habitats outside the forest fragments (Didham, 1997). However, while some studies have found invertebrate abundance and diversity to increase at the edge, others found an increase towards the forest centre, and some studies have found no response of invertebrates to edge environments (Didham, 1997). Ewers and Didham (2008) found that some Coleoptera species increased in abundance near forest edge, and some species showed a decline in abundance at edge habitat. Almost 90% of Coleoptera responded to edge habitat, and most forest-interior species declined in abundance near forest edges (Ewers & Didham, 2008). The combined abundance of the 80 detritivore species 1 km deep into the forest interior was almost four times greater than at 250 m from the forest edge (Ewers & Didham, 2008). On the other hand, in a lowland forest on the West Coast of New Zealand, forest edges appeared to have little impact on forest floor invertebrates (Norton, 2002). Bolger *et al.* (2000) found the most abundant taxa (Isopoda, Dermaptera, and Blattaria) had no relationship to distance from the edge. However, abundance of Diptera and Coleoptera was positively associated with edge habitat, and Collembolla were negatively associated with edge habitat (Bolger et al., 2000). The distance that edge effects have been found to penetrate into forests is variable, and there is no overall consensus. An Australian study on Coleoptera found two levels of edge effects operating at differing distances into fragments. Species richness increased at fragment edges in response to a shallowly penetrating edge effect about 20 m into fragments. Species relative abundance and composition changed in response to a deeply penetrating edge effect about 100 m into the fragments, which caused an increases in the occurrences of detritivores and fungivores at the edge (possibly in response to an increase of litter, dead wood, and fungal spores on the forest floor) (Davies, Melbourne, & Margules, 2001). Often edge effects are investigated over small scales (from 20 to 250 m), but edge habitat can influence invertebrates at larger scales too. The abundance of 20% of common Coleoptera species was influenced by edge effects that operated more than 250 m into forests and one in eight common species had edge effects that appeared to penetrate as far as 1 km into habitat patches. Large scale edge effects may be driven more by biotic interactions than by environmental variables (Ewers & Didham, 2008). In general, the effects of fragmentation on insects are not well understood and data has been described as diffuse and contradicting (Didham, Ghazoul, Stork, & Davis, 1996). Perhaps when considering edge effects each case should be treated as unique (Murcia, 1995). The only summary that can be drawn about the effects of fragmentation (including edge effects) on invertebrates is that some, if not most, species are probably affected, but not all species will be affected adversely (Didham, 1997).

It has been suggested that the fragmentation of forests creates edge habitat, which in turn promotes the invasion of adventive species into what remains of the native habitat (Hickerson, Anthony, & Walton, 2005). Edge habitats have been described as the key sites for biological invasions into forest remnants (Norton, 2002). Evidence of this can be seen in a study in the USA, which found that an adventive species of Chilopoda (*Lithobius forficatus* (L., 1758)) was more abundant in edge habitat and a native species (*Scolopocryptops sexspinosus* (Say, 1821)) was most abundant in the centre habitat (Hickerson et al., 2005). Although the adventive species was present at the majority of interior sites, the native Chilopoda was rarely found at edge sites (Hickerson et al., 2005). Similarly, the displacement of native ant species by Argentine ant (*L. humile*) follows an edge effect (Holway & Suarez, 2006). *L. humile* was most abundant along urban edges of scrub habitat, with a decrease in density found to be correlated with distance from the urban edge; in larger unfragmented areas *L.*

humile was only found at the edge. The high occurrence of *L. humile* at edge habitats caused the loss of native species, evident as a negative correlation between native ant diversity and the presence of *L. humile* (Suarez, Bolger, & Case, 1998).

Due to increased interest in the impacts of human activity on invasions, there has been a shift in focus from investigating adventive species in natural and rural areas to looking at urban and peri-urban areas (Allen & Lee, 2006). It has always been known that the introduction of adventive species was dependent on humans, but it is now known that humans also play a big part in the naturalisation, establishment and spread of these species. Human population density, intensity of human activity, habitat modification, and human disturbance have all been associated with the success of adventive species (Allen & Lee, 2006).

The above observations suggest that a hypothesis can be formulated – we can anticipate that the adventive soil invertebrates in native New Zealand environments should be more diverse and abundant at the edges and in forest fragments close to urban areas, as both these conditions are expected to promote and facilitate invasion. However, this hypothesis has not been tested for adventive detritivores in native New Zealand environments.

1.5. Summary of research objectives

Knowledge of the invertebrate fauna in New Zealand remains incomplete (Brockerhoff et al., 2010). Despite the important role that detritivores have in an ecosystem, invertebrates (including detritivores) are not frequently studied and well understood in

New Zealand (Maunder et al., 2005; Brockerhoff et al., 2010). Native invertebrates are threatened by loss of forest habitat and by the impacts of adventive species, but lack of information on many species means that many invertebrates are likely threatened without it being known (Cochrane et al., 1997). Given their importance to ecosystem function, high level of endemism, and the high level of threat to New Zealand's fauna (Myers et al., 2000), increased knowledge about New Zealand's detritivores would be of great value.

Invasion by adventive species has played a big role in New Zealand (Allen & Lee, 2006); however, most focus has been directed to vertebrates and plants, with comparatively little interest in adventive detritivores and other invertebrates, except for a few high profile invertebrate invaders (Brockerhoff et al., 2010). There is a shortage of studies which investigate the impacts of adventive invertebrates on native ecosystems and native species in New Zealand (compared to the work done on economically important crops and production ecosystems) (Brockerhoff et al., 2010). Adventive detritivores have altered key ecosystem processes elsewhere in the world (Frelich et al., 2006), but in New Zealand the impact of adventive invertebrates has received little attention (Brockerhoff et al., 2010). One possible impact of adventive detritivores is that they will compete with and displace native detritivore species (Tomlinson, 2007). If the dynamics of the detritivore community change, it is possible that the roles that the detritivores perform will be influenced, and the functioning of the ecosystem may be altered (Peltzer et al., 2010); therefore, any change in the detritivore community would be important to monitor. Forests selected for studying detritivores needed to cover a full range of New Zealand forest types (including pine forests) to get an accurate overview of detritivore distribution. It has been identified that some detritivore studies elsewhere in the world have biased research towards protected forest areas instead of including areas that have undergone human modification (Hornung, Vilisics, & Sólymos, 2008).

While New Zealand's native forests have been proposed as resistant to invasion, detritivores may be more successful at invading than other trophic groups (Brockerhoff et al., 2010), so there is a need for more research to determine which adventive detritivores (along with other invertebrate groups) are already present in native forests of New Zealand (Brockerhoff et al., 2010). The impact that fragmentation (including edge effects) has on soil invertebrates has been poorly documented (Didham, 1997); however, edge habitat has been known to facilitate the invasion of adventive species into native forest (Norton, 1998; Hickerson et al., 2005).

The overall aim of this study was to gain a better understanding of the distribution of native and adventive forest detritivores in Manawatu-Whanganui, and the ways in which they have responded to or have been influenced by changes in forest ecosystems, including introduction of pine plantations in the region. The first hypothesis investigated was that pine plantation forests can provide alternative habitat for native forest detritivores. The second hypothesis investigated was that the native forests in the region are resistant to the invasion of adventive detritivores. Thirdly, the influence of edge effects on the distribution of native and adventive detritivores was analysed. Lastly, investigation was conducted into whether native and adventive species appear to co-exist or if there is evidence for the displacement of native species.

To summarise, the five main objectives were:

1) To identify which detritivores (both native and adventive) from three major macrofauna groups (Isopoda, Amphipoda, Diplopoda) are present in native and pine forests of Manawatu-Whanganui.
2) To find out if native detritivores from these groups are flexible enough to live in exotic pine forests Manawatu-Whanganui.
3) To find out whether adventive detritivores have invaded native forests in Manawatu-Whanganui.
4) To determine whether proximity to forest edge has an influence on detritivore community composition and the presence of adventive species.
5) To find out whether native and adventive detritivore species appear to co-exist in the same habitats in Manawatu-Whanganui.

1.6. Thesis structure

Chapter 1 – Introduction and Background.

Chapter 1 reviews the relevant literature and presents the aims of the thesis as well as an outline of each chapter. The review introduces the rationale behind the thesis by discussing the uniqueness of New Zealand's fauna, the addition of adventive species to the fauna (including adventive invertebrates), detritivores and the important role they play, native forests and possible resistance to adventive invertebrate invasion, pine forests as a habitat for detritivores, and the influence of edge habitat on invertebrates.

Chapter 2 – Methods.

Chapter 2 provides a description of the study sites, sampling, identification, and statistical methods used.

Chapter 3 – Fauna and communities of native and adventive detritivores in the study area.

Chapter 3 provides a description of the detritivore fauna and reports their abundance at the various study sites. Literature on the relevant taxa is reveiwed.

Chapter 4 – Effects of forest type and plot location on adundance and community composition of native and adventive detritivores in the study area.

Chapter 4 investigates the importance of plot location in forests (edge vs. centre) and forest type (pine vs. native) on abundance patterns and community composition. All adventives and all natives are often treated as groups, focusing more on taxa origin (native vs. adventive) and less on taxa identity. A statistical model was used to predict the chance that a randomly chosen detritivore individual would be an adventive one, based on the forest type and plot location. The statistical model was used to predict forest habitat and detritivore groups which were most threatened by adventive species.

Chapter 5 – General discussion and conclusions.

Chapter 5 discusses the importance and the conclusions of the project as well as highlighting areas for future research. Topics discussed include: (1) adventive detritivores and the invasion of native forests – possibly facilitated by disturbance, (2) the suitability of pine forests as a habitat for native detritivores and the factors that may facilitate this, (3) edge effects, (4) project limitations, and (5) further research needed to determine the influence of adventive species on native species and native ecosystem functioning.

2. Methods

2.1. Study sites

To limit the study due to time restrictions, but still cover a broad range of forest types, the study was restricted to Manawatu-Whanganui. Invertebrate samples were collected from ten native and six pine forests in Manawatu-Whanganui region, North Island of New Zealand (Fig. 2.1). Forests in this study range from small urban remnants to larger more isolated native forests to pine forests. GPS coordinates were collected from each plot[2]. See Appendix 1 for a description of the study sites.

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[2] Elevation readings should be interpreted with caution as some inaccuracy can occur (Garmin ltd, 2013).

Figure 2.1. Map of the North Island (New Zealand) displaying sampling sites.

2.2. Sampling and extraction

Sampling took place from March 2012 to October 2012 (the date each site was sampled is reported in Appendix 1). Each forest was sampled within a day. The sampling time frame excluded dry summer months as detritivores are not collected in as high abundance in dry conditions (Maria Minor, personal communication, 2012). Detritivores are known to retreat to moist pockets and bury themselves deeper in the soil during dry conditions (Car, 2010). Samples were not collected during or following heavy rainfall to ensure consistency in sampling conditions between sites.

In each site, one plot was sampled near the edge of the forest and another one in a more central location. Edge plots were placed within 20 m of the start of forest vegetation, as most measured edge effects operate within this zone (Murcia, 1995). Centre plots were placed as central as possible in areas of smaller forest (as could be best determined when in the forest and avoiding very steep slopes). In larger forests the centre plots were at least 100 m away from each edge. However, in Santoft forest centre samples were taken slightly closer to the edge due to hilly terrain within the selected forest area and unsuitability of other forest areas because of dense vegetation or bodies of water. Sampling plots were placed preferentially on flat ground to keep standardisation between samples; if this was not available then a site with only minimal slope was chosen. Within the edge and central locations plot placement was chosen haphazardly once in the forest. A specific randomisation generator or any other method of true random plot selection prior to entering the forest was not used because of the large number of potential sampling sites that could not be accessed due to steep slopes, bodies of water, and dense vegetation. While this could be criticised as a way of introducing biased samples to the study, this is not the first study to use haphazardly chosen invertebrate sampling locations (Bonham et al., 2002).

Two methods of collection were used to gather detritivores. Firstly, detritivores were collected from fallen logs. Within each sampled location (edge or centre plot), a 10 m by 10 m log-sampling quadrate was layed out using a tape measure (Bonham et al., 2002) (see Fig. 2.2b). Fallen logs that were found within each quadrate were placed on a white sheet one at a time. Any Diplopoda, Isopoda, or Amphipoda found on the exterior of the log were collected and placed in a jar of 70% alcohol, as well as any that fell onto the white sheet under the log (see Fig. 2.2c). If the log had bark, then the bark was removed and any of the focus detritivores found under the bark were collected (see Fig. 2.2d). A log was considered to be anything with a circumference over 25 cm, to differentiate logs from any small twigs. If a log had a very large circumference and it was not possible to lift it onto the white sheet, then it was excluded from the study. Logs which were only partly in the quadrat were included in the study if the majority of the log lay within the quadrat.

Secondly, five leaf litter samples were collected from the exterior of each log-sampling quadrat at haphazard locations within 3 m from any edge of the quadrat. Collecting leaf litter from outside the log-sampling quadrat ensured the leaf litter had not been disturbed prior to sampling, as such disturbance can be detrimental to populations of Diplopoda (Car, 2010). Collection of leaf litter samples was achieved by placing a 25 cm by 25 cm metal frame on the forest floor (Gorny & Grum, 1993). Haphazardly selecting sites for leaf litter collection once in the sampling area is a technique that has been previously used to collect invertebrates (Robson et al., 2009).

Leaf litter within the sampling frame was gathered by hand down to 1 cm into the soil layer and then placed in a labelled and sealed plastic bag (see Fig. 2.2a). It was ensured that each sampling frame was placed on a flat surface to limit the variation between samples. All leaf litter samples were stored at 4◦C for up to two weeks until the samples were placed into Berlese extractors at Massey University, Palmerston North. Samples were kept in the Berlese extractors for four to seven days (samples were only removed from Berlese extractors when leaf litter appeared to be completely dry). The invertebrates were collected into containers filled with alcohol. Invertebrates were then kept in 70% alcohol until sorting and identification.

2.3. Sorting and identification

Diplopoda, Isopoda, and Amphipoda were sorted from collected invertebrates and identified (see Fig. 2.3 for some detritivores identified). The level of identification varied between the three detritivore groups. Adventive taxa were identified to species level. Native detritivores were identified to a level that provided differentiation from adventive individuals. Identification of the native taxa to levels beyond family is often very difficult due to poorly developed taxonomy, especially considering the time restraints.

Resources developed elsewhere in the world were used to identify adventive Diplopoda. A ‘Key to millipede groups’ from the ‘Tasmanian Multipedes’ website (Mesibov, 2003) was used in combination with Blower’s (1985) key. Adventive Julida and native Spirostreptida were distinguished from each other using the differences in gnathochilarium as described in Hoffmann (1990). There has been less work done on

New Zealand's natives. Identifying native Diplopoda to order level was achieved using the key by Johns (1962), with taxa names updated due to changes in classification since publication of the key. No updated key on all groups of New Zealand Diplopoda has been developed since 1962. A large number of native species are not described, and it is estimated that there are 200+ species that remain unknown (Johns, 2010). More difficulty was encountered when trying to identify beyond order level for Polydesmida. Both native and adventive species of Polydesmida are present in New Zealand (Johns, 2010) so further identification was needed in this order. There are five species of adventive Polydesmida in New Zealand (Johns, 2010). Polydesmida species can be identified by their gonopods, which are leg-like structures males use to transfer sperm during mating (Blower, 1985; Mesibov, 2003). Mature male Polydesmida were identified by comparing gonopods against illustrations and photos from a Polydesmida key (Mesibov, 2003) and Blower's (1985) illustrations. Individuals were presumed to be native if they did not match the description of the adventive species recorded to be present in New Zealand. The difficulty in using this technique was that only mature males could be identified. Female and juvenile Polydesmida were grouped into morphospecies and compared to mature males that were classified. There was some uncertainty around identifying juveniles and females as adventive or native due to lack of gonopods, but it was the best that could be done considering the scarce work on Diplopoda taxonomy. Difficulties when identifying females and juveniles have been previously been encountered (Bonham et al., 2002; Mesibov, 2003).

Isopoda were identified to family level using an unpublished key by Stefano Taiti (Stefano Taiti, personal communication, 2012). However, the families Styloniscidae (native) and Trichoniscidae (adventive) were indistinguishable using this key. The two families were separated from each other by identifying either the turberculate body surface of Trichoniscidae or the smooth body surface of Styloniscidae (Maria Minor, personal communication, 2012). Individuals from adventive Isopoda families were identified to species using primary descriptions. An adventive species *Cubaris murina* Brandt, 1833 belongs in the Armadillidae family, which also includes many native species. Therefore, Armadillidae were further identified to morphospecies, and each morphospecies compared to the primary description of *C. murina*.

Amphipoda were identified to species level using Fenwick's and Webber's (2008) key, although there was difficulty identifying *Arcitalitrus* past genus level. Samples were then sent to key co-author Rick Webber (TePapa Tongarewa Museum) for confirmation that identification was correct.

Some specimen of Polydesmida (Diplopoda) and Amphipoda were unidentifiable due to damage or due to individuals being too young. For majority of unidentified specimens their origin (native or adventive) could be assumed based on other individuals found in the sample. When both native and adventive Amphipoda individuals were present in the sample, the unknowns were excluded from the analysis. For multivariate analysis and individual taxa ANOVAs all unknown Amphipoda and Polydesmida were excluded from analysis.

Figure 2.2. Methods used to collect detritivores: a) Collection of leaf litter from metal quadrat into plastic bag; b) 10 m by 10 m log sampling quadrat fenced off at Kitchener Park; c) Collection of invertebrates off the exterior of a log placed on a white sheet with bark remaining; d) Log with bark removed for further detritivore collection.

Figure 2.3. Some representative detritivores: a) native mature male Polydesmida (Diplopoda); b) adventive Isopoda *Porcellio scaber* Latreille, 1804; c) native Polyxenida (Diplopoda); d) native Amphipoda *Parorchestia tenuis* (Dana, 1852); e) native Isopoda Armadillidae sp. 3; f) native Polyzoniida (Diplopoda). The black lines and measurements at the top of each image show the scale.

2.4. Statistical analysis

For Chapter 3, abundance values were converted to ind./m^2 to make them more comparable to past and future work (Friend, 1980; Spicer & Tabel, 1996; Fenwick & Webber, 2008). To make the conversion, the total number of individuals collected from five leaf litter samples in each plot was multiplied by 3.2, and the number of individuals collected from all logs in a 10 m by 10 m quadrat was divided by 100. The abundance values used in Chapter 4 were the total number of individuals found in each edge or centre sampling locality, calculated as the sum of individuals collected from five leaf litter samples, plus the individuals from logs within the 10 m by 10 m quadrat. Abundance values for each of the three focus groups (Diplopoda, Isopoda, and Amphipoda) were treated separately.

The statistical software SAS 9.3 was used to determine mean values and standard deviations, perform analysis of variation (ANOVA), and create box plots for pooled groups of native and adventive taxa within Diplopoda, Isopoda, and Amphipoda. Significance level $\alpha = 0.05$ was used for statistical tests, although the possibility of accepting $\alpha = 0.1$ was sometime considered due to the sample size being small. The mean and standard error values for each variable (native Diplopoda, adventive Diplopoda, native Isopoda, adventive Isopoda, native Amphipoda, and adventive Amphipoda) were calculated using the SAS MEANS procedure. Box plots were created for adventive and native individuals of each taxon (Diplopoda, Isopoda, and Amphipoda) to visually display any effects of forest type (pine and native) and plot location (edge and centre) on abundance. ANOVAs were conducted using SAS MIXED procedure to test the effect of forest type (native or pine), plot location (edge or centre), and a possible interaction between the two factors. Forest type and plot location were fixed effects; site identity was considered a random factor. A binary logit model was created using SAS logistic procedure for each taxon (Diplopoda, Isopoda, and Amphipoda) to determine the probability that a randomly selected individual would be adventive based on forest type and plot location (i.e., “adventive” was used as an “event” in the model). A hypothesis test was conducted to determine if forest and plot significantly influenced the probability that a randomly chosen individual would be adventive.

Further analysis was carried out on individual taxa. ANOVA was used to test the effect of forest type, plot location, and a possible interaction between the two factors on individual taxa. Primer v6 was used for multivariate analysis of community composition, and data was transformed by the 4th root to reduce the importance of the most dominant taxa. A Bray-Curtis similarity matrix was created, from which two-way ANOSIMs (analysis of similarity) were used to tests the null hypothesis of ‘no difference’ in community composition between forest types and between plot locations. 999 permutations were run. R value approaching 1 indicates increasing difference between groups (Clarke, 1993). Forest type influenced the composition of Diplopoda, so for this group a non-metric multidimensional scaling (MDS) ordination was created from the Bray-Curtis similarity matrix as visual representation. Vectors were added to the MDS ordination to determine which taxa had the biggest influence on the distribution of sites (based on site similarity); taxa which had a Spearman correlation value >0.5 were included. Bubble plots were added to the MDS ordination to reveal the taxa that had a larger influence over the grouping of pine and native forests. Because plot location had no effect on community composition, edge and centre samples from each forest were pooled in bubble plots to create a clearer picture. For multivariate analysis there was no grouping of taxa and if lower level classification was determined (as was for Polydesmida, Julida, and Armadillidae) then these taxa were included in the analysis separately.

3. Fauna and communities of native and adventive detritivores in the study area

3.1. Introduction

Detritivores encompass a diverse range of groups and add to overall soil diversity (Mesibov, 1998). Many detritivores have been identified to have important roles in an ecosystem, e.g., they greatly contribute to the decomposition process (Swift et al., 1979). Despite recognised importance of detritivores, they are not frequently or sufficiently studied in New Zealand.

There is a lack of information on most species of invertebrates in New Zealand (Cochrane et al., 1997), which is critical given the high rate of endemism recognised in many of New Zealand's invertebrate groups (Gordon, 2010). The distribution of many native detritivores is uncertain. Building on information known on New Zealand's native detritivores would be greatly beneficial, as many invertebrates have been threatened by a vast amount of deforestation in New Zealand (Cochrane et al., 1997). Investigating the distribution and abundance of native detritivores in a range of different native forest remnants could provide an indication on how native detritivores have responded to change in their native forest ecosystem, and whether or not they have been able to adapt in new modified environments. It is possible, for example, that introduced pine plantations will provide an alternative habitat for native forest detritivores – but there has been very little investigation into invertebrates in pine forests (Maunder et al., 2005).

New Zealand's native species and native ecosystems may be threatened by the addition of adventive detritivores. A high number of adventive invertebrates, particularly within Arthropoda, have been detected in New Zealand (Gordon, 2010). Many native invertebrates are possibly threatened by the impact by adventive species, but there is such limited information on many invertebrate species, that it is likely that many invertebrates are threatened without it being known (Cochrane et al., 1997). The vast majority of New Zealand's invertebrates are forest dwellers (Cochrane et al., 1997), and it has been proposed that New Zealand's native forests may be resistant to invasion by adventive invertebrates (Brockerhoff et al., 2010). However, this has not been checked explicitly, and the ability of adventive detritivores to invade native forests is uncertain. Gaining a greater understanding on the presence and contribution of adventive species to detritivore forest communities would be highly beneficial.

This chapter examines fauna and distribution of three focus groups of detritivores – Diplopoda, Isopoda, and Amphipoda – in the study area. The findings were compared to published literature as much as possible; however, the scarce amount of research carried out in New Zealand limited this. The aim of this chapter was to gain an understanding of detritivore fauna, distribution and community composition in Manawatu-Whanganui. This can provide insight into how well adventive species are able to invade New Zealand's native forest, and whether native species are flexible enough to tolerate conditions of pine forests. The chapter also presents summary information on native and adventive species found in the study, and aims to identify where gaps in the knowledge occur.

3.2. Results

3.2.1. Diplopoda

There were a number of Diplopoda orders found in native and pine forests: Julida, Polydesmida, Spirostreptida, Siphonophorida, Chordeumatida, and Polyzoniida were all common and widely distributed. Only three specimen of Polyxenida were found. Diplopoda of the order Julida are all adventive. Polydesmida is a very large order, which in New Zealand includes both native and adventive species – however, all Polydesmida in this study were identified as native. All other orders are native to New Zealand.

3.2.1.1. Adventive Diplopoda

Adventive Diplopoda from the order Julida (*Cylindroiulus britannicus* (Verhoeff, 1891), *Ophyiulus pilosus* (Newport, 1842), *Blaniulus guttulatus* (Fabricius, 1798)*, Nopoiulus kochii* (Gervais, 1847), and *Brachyiulus pusillus* (Leach, 1815)) were found in nine out of ten native forests and in five out of six pine forests investigated in this study. Julida were the dominant Diplopoda order in a number of plots (Fig. 3.1).

C. britannicus was found throughout native forests at both edge and centre plots, but only at the edge of pine forests. It was found in nine out of ten native forests (not found in native forest at Shannon) and in two out of six pine forests (Table 3.1). *C. britannicus* had the highest abundance of any adventive Diplopoda species. It was also more dominant than the majority of native Diplopoda, except native Polydesmida. *C. britannicus* was found at either lower or higher abundance than native Polydesmida depending on the forest and plot sampled. *C. britannicus* was found at higher abundances than native Polydesmida at centre plots in the Gorge, Mt Lees Reserve, Totara Reserve, Santoft, the Esplanade, and the edge in Kitchener Park. The highest abundance of *C. britannicus* found was 224 ind./m^2 in leaf litter at the edge of Kitchener Park. No *C. britannicus* was found in leaf litter at the centre of Bledisloe Park even though individuals had been collected from logs. The highest abundance of *C. britannicus* found on logs was 39 individuals in an area of 100 m^2 at the edge in the Esplanade. No individuals were found on logs in the Gorge, at the edge in Ashhurst Domain, or at the edge in McCrae's Bush even though they were found in leaf litter.

O. pilosus was another very widespread adventive species; it was detected in nine out of ten native forests (Table 3.1). *O. pilosus* was also found in five out of six pine forests in the study (Table 3.1). It was at both edge and centre plots in native and pine forests. However, *O. pilosus* was not found at such high abundances as *C. britannicus* with the highest abundance in leaf litter being 147 ind./m^2 at a centre site in McCrae's Bush. The highest abundance found on logs was 7 individuals in 100 m^2 at the edge in native forest at Kahutarawa. McCrae's Bush was the only site in which *O. pilosus* was the dominant Diplopoda taxon (although abundance of Polydesmida was only slightly lower). *O. pilosus* was not found on logs as commonly as it was found in leaf litter samples. It was absent from logs in a number of areas in which it was identified in the leaf litter (both centre and edge plots in Waitarere, the Hawkey's, Santoft, the Ashhurst Domain, McCrae's Bush; central locations in Kitchener Park, Totara Reserve, the Gorge; and the edge of the Esplanade).

B. guttulatus was found only at two native sites in the study (Table 3.1). It was found at both centre and edge plots, and was never found to be the dominant Diplopoda. The highest density found in leaf litter samples was 32 ind./m^2 and highest abundance found on logs was 6 individuals in 100 m^2, both at a centre plot in Mt Lees Reserve.

Only one specimen of *Nopoiulus kochii* was found throughout the whole study and it was found in leaf litter at the edge of Mt Lees native forest.

B. pusillus was found in two pine forests (edge of the Hawkey's forest and centre plot in Santoft), and in three native forests (Table 3.1). It was not a dominant species of Diplopoda. The highest abundance in the leaf litter was 25.6 ind./m^2 at the edge in the Hawkey's pine forest. The highest abundance on logs was 2 individuals in 100 m^2 at the edge in Kitchener Park, which was the only site where *B. pusillus* was found on logs.

3.2.1.2. Native Diplopoda

There were a number of native Diplopoda orders found in native and pine forests. Native Polydesmida, Spirostreptida, Siphonophorida, Chordeumatida, and Polyzoniida were all common and widely distributed in the study. Only three specimen of Polyxenida were found, and they all came from a single log at the centre plot in the Gorge.

Native Polydesmida were found in five out of six pine forests and in all ten native sites (Table 3.1). They were not restricted to centre or edge habitats.

Polydesmida were the most abundant order of Diplopoda found (Fig. 3.1), although, in some sites the order was found at lower abundance than adventive *C. britannicus* (e.g., centre plots at the Gorge, Mt Lees Reserve, Totara Reserve, Santoft, the Esplanade, and the edge of Kitchener Park). Highest abundance of Polydesmida in leaf litter was 425.6 ind./m^2 at the edge in Ashhurst Domain. At the edge in Waitarere and Whanganui pine forest, Polydemsida were found on logs but not in leaf litter. Highest abundance found on logs was 33 individuals on all logs in a 100 m^2 area at the edge in native forest at Kahutarawa. In McCrae's Bush, the edge in the Esplanade, and a centre plot in Totara Reserve, Polydesmida were found in leaf litter but not on logs. Fifteen different morphospecies of native Polydesmida were distinguished. Highest abundance of a single morphospecies (morphospecies 7) was 326.4 ind./m^2 in leaf litter at the edge in Ashhurst Domain. Highest abundance on logs was 17 individuals of morphospecies 5 on all logs in 100 m^2 at the edge in native forest at Kahutarawa. Different morphospecies were found to co-occur, with up to eight morphospecies present in the same forest.

Chordeumatida were also very commonly found, being present in all study sites except pine forest at Waitarere (Table 3.1). However, they were never collected in very large abundances. The highest density of Chordeumatida found in leaf litter was 44.8 ind./m^2 at the edge in pine forest at Shannon, where Chordeumatida was the dominant Diplopoda taxon (Fig. 3.1); Polydesmida was the only other group present in that plot. The highest abundance of Chordeumatida found on logs was 10 individuals found on all logs in 100 m^2 at the centre plot in Mt Lees Reserve.

Spirostreptida were not found in any pine forests in the study, but they were found at eight of the native sites (Table 3.1). Spirostreptida were only found in low abundance, more commonly on logs than in leaf litter. The highest abundance found in leaf litter was 12.8 ind./m^2 at the centre plot in the Gorge. The highest abundance found on logs was 12 individuals found on all logs in 100 m^2 at the edge of the Gorge.

Siphonophorida were found in eight out of ten native sites, but in only two pine forests (Table 3.1). Siphonophorida were the dominant Diplopoda group in leaf litter at the edge in native forest at Kahutarawa (corresponding to a density of 246.4 ind./m^2 in the area). However, this abundance was uncharacteristically high, and that plot was the only locality where Siphonophorida was dominant (Fig. 3.1). Highest abundance found on logs was 5 individuals on all logs in an area of 100 m^2 at the edge in Totara Reserve.

Polyzoniida were found in nine out of ten native forests sampled but were not common in pine forests (only present in pine at Kahutarawa, which has dense native understory vegetation) (Table 3.1). The highest abundance of this Diplopoda order (92.8 ind./m^2) was in leaf litter at the edge in Ashhurst Domain, where Polyzoniida were the second dominant group after native Polydesmida, and were more dominant than adventive Diplopoda (Fig. 3.1). Highest abundance on logs was 11 individuals in an area of 100 m^2 at the edge in Mt Lees Reserve.

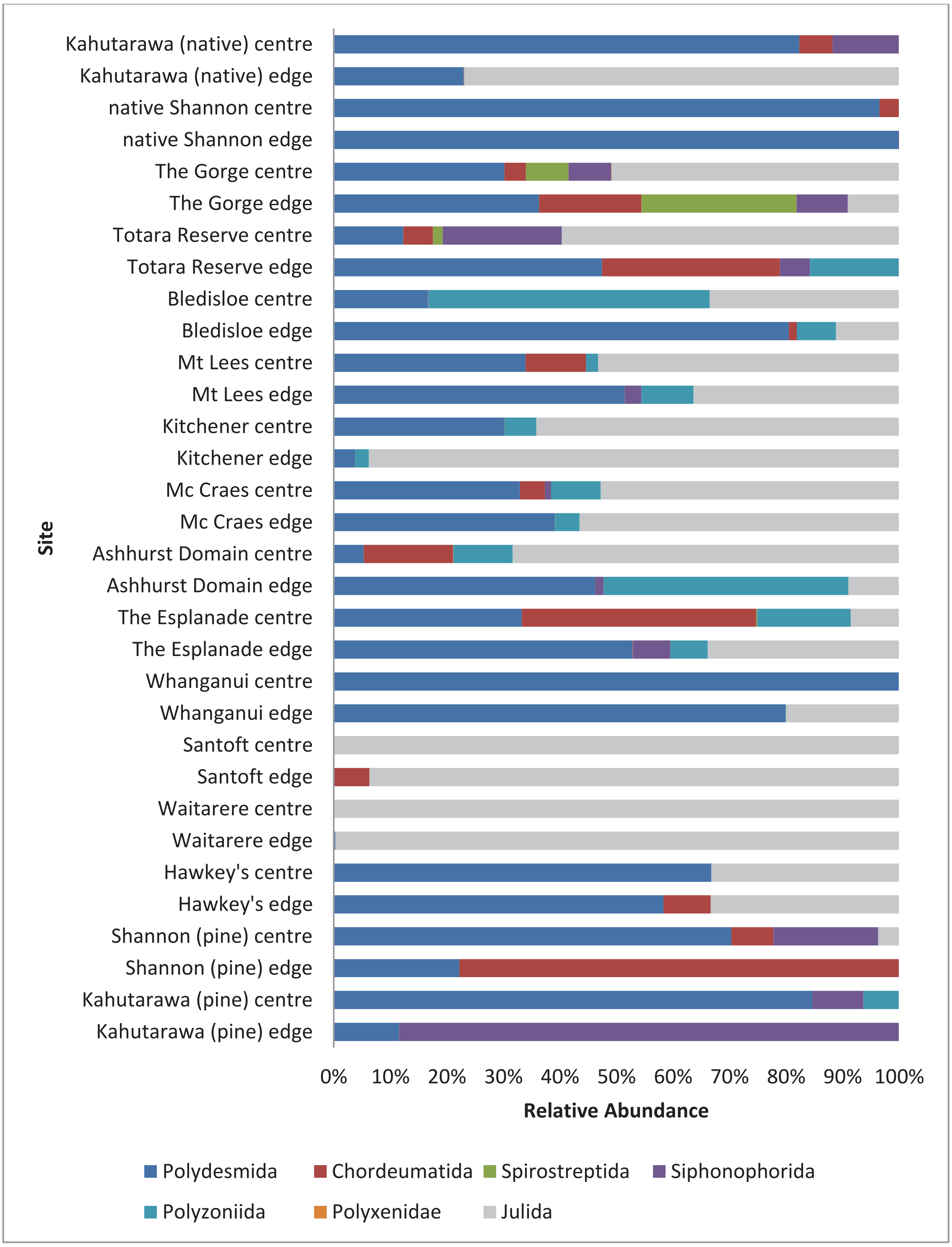

Figure 3.1. Relative abundance of Diploploda in sampled forest plots, Manawatu-Whanganui, 2012. Relative abundance percentages are based on ind./m^2 data collected from logs and from five leaf litter samples in each plot. Julida is an order comprised entirely of adventive species in New Zealand.

3.2.2. Isopoda

3.2.2.1. Adventive Isopoda

Three species of adventive Isopoda were found in the study – *Armadillidium vulgare* (Latreille, 1804); *Porcellio scaber* Latreille, 1804; and *Haplophthalmus danicus* Budde-Lund, 1885[3].

A. vulgare (family Armadillidiidae*)* was found as a single specimen in leaf litter at the edge of the McCraes Bush. Four specimen of *P. scaber* (family Porcellionidae*)* were found in two pine forests (Table 3.1), they were all found on logs at the edge of the forest. *H. danicus*[3] (family Trichoniscidae) was the most dominant adventive species (Fig. 3.2), found in four native forests and in one pine forest (at the edge in pine forest at Shannon) (Table 3.1). It was usually in edge plots, and only found at a centre plot in Mt Lees Reserve. *H. danicus* was more commonly found on logs than in leaf litter (only found in leaf litter in three plots). The highest density in leaf litter was 19.2 ind./m^2 at the edge in Kitchener Park. On logs, *H. danicus* was found at abundances from 1 (at the edge in Bledisloe Park and Kitchener Park) to 35 (at the edge of the Esplanade) individuals on logs within 100 m^2. The highest numbers of *H. danicus* were found at the Esplanade, Mt Lees Reserve, and Bledisloe Park.

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[3] Since the submission of this thesis, it has come to my attention that the Isopoda identified in this thesis as adventive *H. danicus* is an undescribed native species. The results of statistical analysis for Isopoda may be biased by this fact, and the conclusions should be treated with caution. The manuscript based on this thesis is in preparation to be published as a research paper, and the Isopoda material will be reviewed and re-analysed for the upcoming publication.

3.2.2.2. Native Isopoda

More diversity was seen in native Isopoda than in adventive Isopoda. Four native families of Isopoda were found in the study – Oniscidae, Philosciidae, Armadillidae, and Styloniscidae.

Oniscidae were not found in any of the pine forests but were found in six native forests (Table 3.1). The highest density of Oniscidae found in leaf litter was 28.8 ind./m^2 at the edge in Bledisloe Park. Oniscidae weren't found on logs at the centre sites in Ashhurst Domain and Kitchener Park even though they had been found in leaf litter in those locations. The highest density of Oniscidae on logs was 6 individuals on all logs in 100 m^2, at a centre plot in The Esplanade.

Philosciidae were found in seven native forests and at the edge in four pine forests (Table 3.1). The highest abundance in leaf litter was 198.4 ind./m^2 at a centre plot in Mt Lees Reserve. This was the highest abundance found for any Isopoda family. Philosciidae were not found as commonly on logs as they were in leaf litter, and were absent from logs at many locations in which they were identified in leaf litter (Kahutarawa, the Ashhurst Domain, Waitarere, Santoft, the Esplanade, McCrae's Bush, and the Gorge). The highest number of Philosciidae found on logs was 7 individuals on all logs within 100 m^2 at the edge in pine forest at Kahutarawa.

Four morphospecies of Armadillidae were found and none were a dominant group (Fig. 3.2). Only one Armadillidae species (morphospecies 4) was found in pine forests (Table 3.1) and only Armadillidae morphospeceis 3 and morphospecies 4 were found in leaf litter, the rest of native Armadillidae were restricted to native forests and only found on logs. Armadillidae morphospecies *Cubaris* sp. 1 was found in four native forests (Table 3.1), at edge and centre plots, with maximum abundance of 5 individuals on logs in 100 m^2 at the edge in Kitchener Park. Morphospecies *Cubaris* sp. 2 was found at centre plots in two native forests (the Esplanade, and Kahutarawa) and at both centre and edge locations in Kitchener Park. The highest abundance found was 9 individuals on logs in 100 m^2 at the centre in Kitchener Park. Armadillidae morphospecies 3 was found on both logs and in leaf litter in seven native forests (Table 3.1). The highest abundance of Armadillidae morphospecies 3 in leaf litter was 9.6 ind./m^2 at edge in Kitchener Park and Mt Lees Reserve; the highest abundance on logs was 14 individuals on logs in 100 m^2 at the edge in Kitchener Park. Armadillidae morphospecies 4 was found in leaf litter, with an abundance of 12.8 ind./m^{2,} at the edge in pine forest at Kahutarawa. It was also found at the centre in native forest at Shannon with 2 individuals being found on all logs within 100 m^2.

Styloniscidae were the most commonly encountered family of native Isopoda, and were found present at all sampled sites, both native and pine (Table 3.1). Styloniscidae were often the most numerous Isopoda group at a site (Fig. 3.2). The highest abundance of Styloniscidae in leaf litter was 147.2 ind./m^2 at the edge in Bledisloe Park. The highest density of Styloniscidae on logs was discovered at the centre in Whanganui in which 43 individuals were on logs in a 100 m^2 area. On many occasions Styloniscidae were not found on logs even though they had been identified from leaf litter in the area (Bledisloe Park, pine forest at Shannon, Kitchener Park, the Esplanade, McCraes Bush, and a number of other plots). Conversely, no Styloniscidae were found in the leaf litter at the edge in Whanganui and the Esplanade, even though they were on logs in the areas.

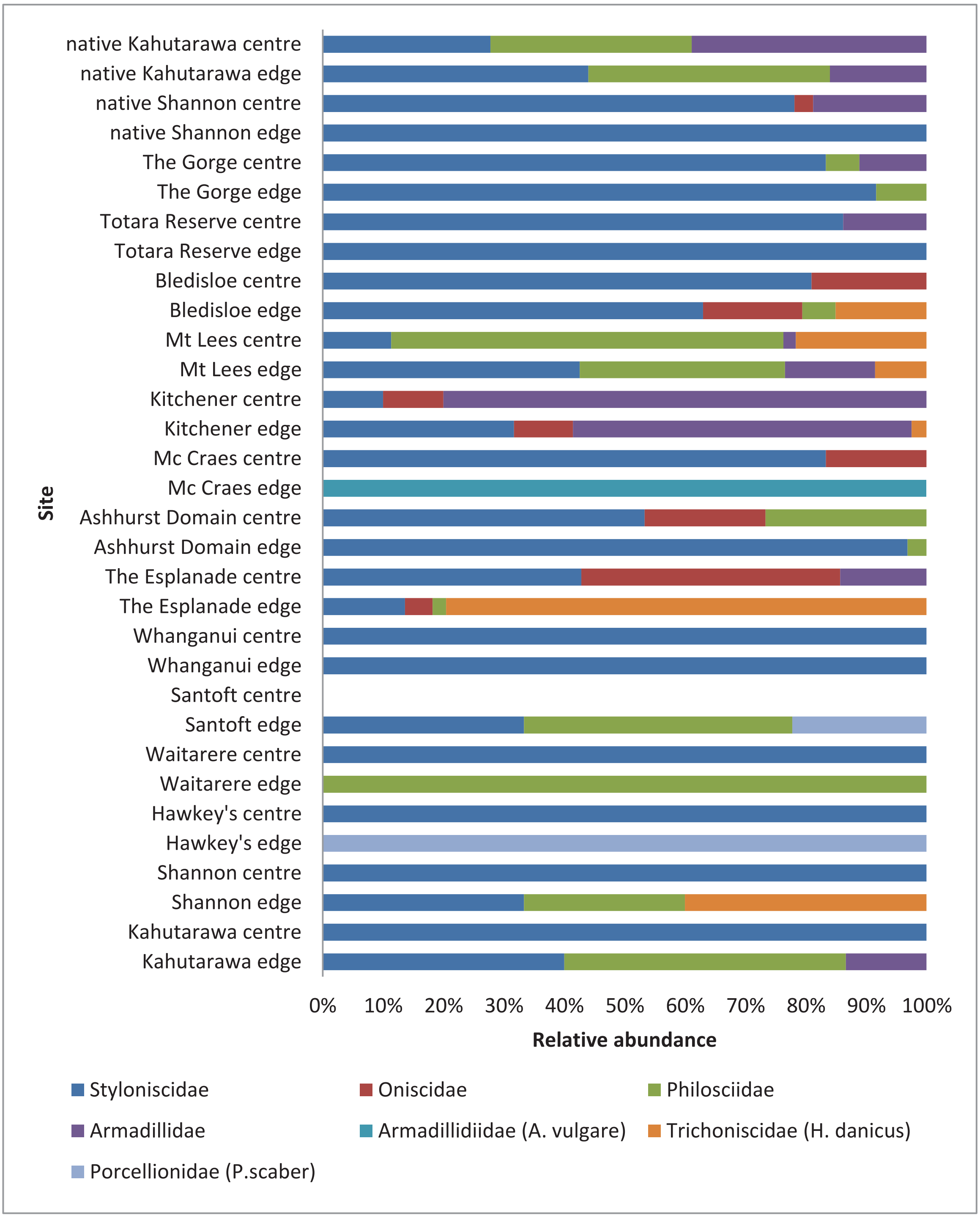

Figure 3.2. Relative abundance of Isopoda in sampled forest plots, Manawatu-Whanganui, 2012. Relative abundance percentages are based on ind./m^2 data collected from logs and from five leaf litter samples in each plot. In New Zealand Armadillidiidae, Porcellionidae, and Trichoniscidae contain only adventive species.

3.2.3. Amphipoda

Amphipoda of the adventive genus *Arcitalitrus* were found in five out of six pine forests and no other Amphipoda were found in these forests (Table 3.1). There are two closely related species of *Arcitalitrus* present in New Zealand, *Arcitalitrus sylvaticus* (Haswell, 1880) and *Arcitalitrus dorrieni* (Hunt, 1925) (Fenwick & Webber, 2008) and they are not easily distinguished (Rick Webber, personal communication, 2013). *Arcitalitrus* were also found in nine out of ten native forest sites in this study, and were the only Amphipoda present in five of those native forests (Table 3.1). At the other four native forests *Arcitalitrus* co-occurred with native species, but with very low abundance (only 1-3 individuals were collected). When present, *Arcitalitrus* were found at a range of densities from 3.2 ind./m^2 (at centre locations in the Gorge, The Esplanade, and McCrae's Bush) to 867.2 ind./m^2 (at the edge in Bledisloe Park) in leaf litter samples. *Arcitalitrus* were also found on fallen logs, with up to 42 individuals being found on all the logs that occur within 100 m^2 (at the edge in Bledisloe Park). Often no individuals were found on logs even though they were in leaf litter (e.g., at centre and edge locations in the Gorge, native forest at Kahutarawa, native forest at Shannon, Santoft, McCraes Bush, and the centre in Whanganui and the Hawkey's forest). *Arcitalitrus* were only found at the edge in Whanganui forest, the Hawkey's forest, native forest at Kahutarawa, and native forest at Shannon. Only one individual was found at the centre in McCraes Bush and the Gorge.

Two species of native Amphipoda were found – *Puhuruhuru aotearoa* Duncan, 1994 and *Parorchestia tenuis* (Dana, 1852). *P. aotearoa* was found in five native forests and *P. tenuis* was found in three native forests (Table 3.1). *P. aotearoa* and *P. tenuis* were found in only one pine forest – at Kahutarawa (where no adventive species were found). In leaf litter, *P. aotearoa* was found to have densities from 3.2 ind./m^2 (centre plot in native forest at Kahutarawa) to 89.6 ind./m^2 (the edge of the Gorge). *P. aotearoa* was also found to be present on logs with up to 21 individuals being found on logs in 100 m^2 (native forest at Kahutarawa). In some sites (the edge in pine forest at Kahutarawa, and the centre in the Gorge) *P. aotearoa* was absent from logs even though it was in the area. For *P. tenuis,* density in leaf litter samples ranged between 6.4 ind./m^2 (at the centre in native forest at Kahutarawa) and 128 ind./m^2 (at the centre in pine forest at Kahutarawa). The highest abundance on logs was 12 individuals found on logs in an area of 100 m^2 at the centre in native forest at Shannon. *P. tenuis* was only found on logs at the centre plots in native forest at Kahutarawa and Shannon.

P. tenuis was never found in the absence of *P. aotearoa,* but *P. aotearoa* was sometimes the only species at a site or co-occured with adventive *Arcitalitrus* (Table 3.1). All three species co-occurred at the edge in native forests at Kahutarawa, where adventive *Arcitalitrus* was found at low abundance (Fig. 3.3).

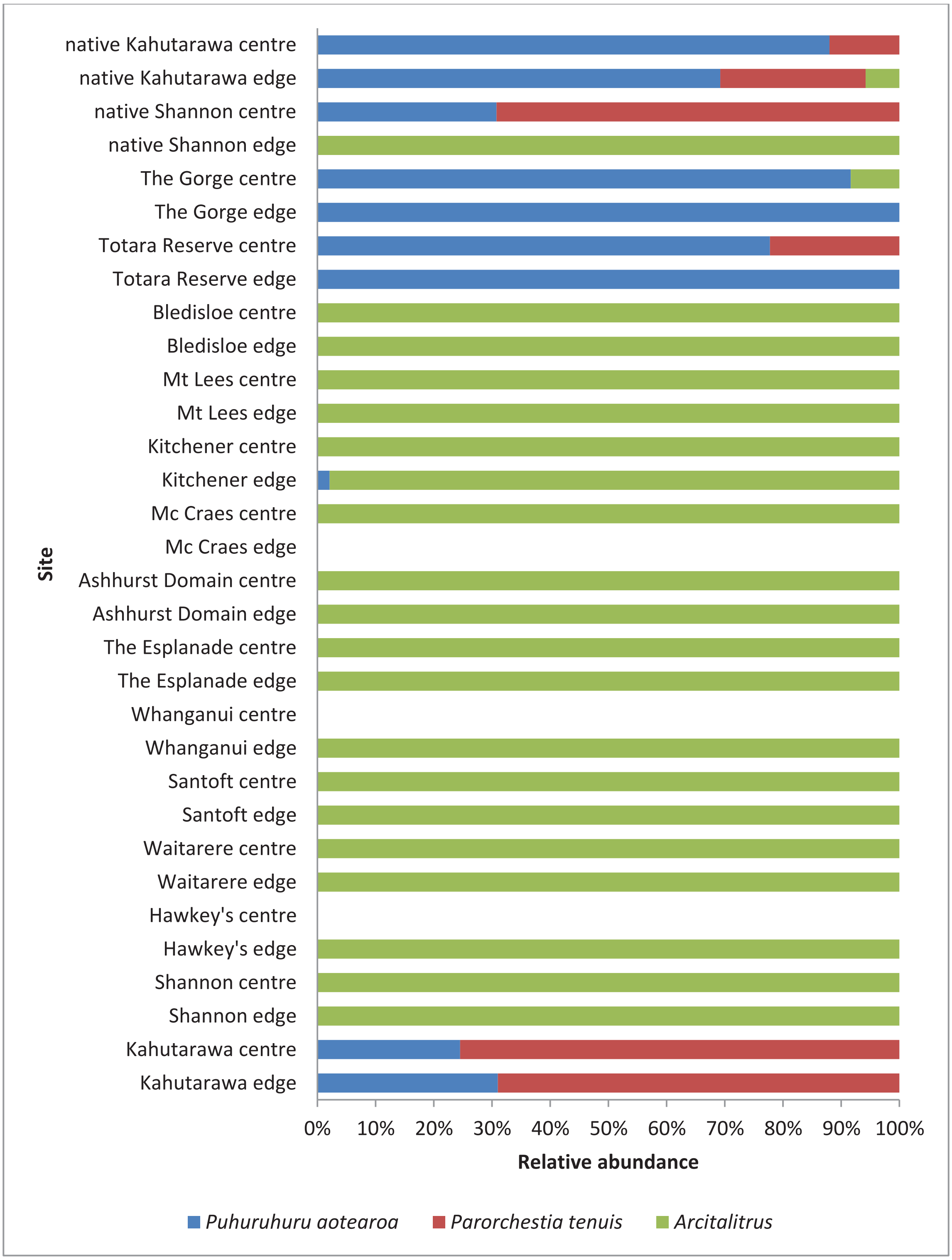

Figure 3.3. Relative abundance of Amphipoda in sampled forest plots, Manawatu-Whanganui, 2012. Relative abundance percentages are based on ind./m^2 data collected from logs and from five leaf litter samples in each plot. *Arcitalitrus* is adventive.

Table 3.1. Detritivore taxa found in forests of Manawatu-Whanganui. Forests are displayed along the top with a black vertical line separating pine and native forests. Adventive taxa are shaded in grey. See Appendix 1 for GPS coordinates of sites.

		Native (N) or Adventive (A) taxon?	The Esplanade	Ashhurst Domain	Mc Craes	Kitchener	Mt Lees	Bledisloe	Totara Reserve	The Gorge	Shannon	Kahutarawa	Kahutarawa	Shannon	Hawkey's	Waitarere	Santoft	Whanganui
Forest type- Native (N) or Pine (P)			N	N	N	N	N	N	N	N	N	N	P	P	P	P	P	P
Diplopoda	Polydesmida sp. 1	N	✓	✓	✓	✓		✓	✓	✓		✓	✓					
	Polydesmida sp. 2	N	✓															
	Polydesmida sp. 3	N	✓															
	Polydesmida sp. 4	N	✓	✓	✓		✓	✓	✓	✓		✓						
	Polydesmida sp. 5	N	✓	✓	✓		✓	✓	✓	✓	✓	✓						✓
	Polydesmida sp. 6	N	✓			✓	✓	✓		✓		✓	✓					✓
	Polydesmida sp. 7	N		✓			✓	✓		✓	✓	✓	✓	✓				
	Polydesmida sp. 8	N		✓	✓	✓	✓	✓	✓	✓			✓	✓	✓	✓		✓
	Polydesmida sp. 9	N			✓													
	Polydesmida sp. 10	N				✓	✓	✓		✓			✓	✓				
	Polydesmida sp. 11	N					✓						✓	✓	✓	✓		✓
	Polydesmida sp. 12	N						✓										
	Polydesmida sp. 13	N							✓				✓		✓			
	Polydesmida sp. 14	N							✓									✓
	Polydesmida sp. 15	N									✓	✓	✓					
	Chordeumatida	N	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓
	Spirostreptida	N	✓	✓	✓	✓		✓	✓	✓		✓						
	Siphonophorida	N	✓	✓	✓		✓	✓	✓	✓		✓	✓	✓				
	Polyzoniida	N	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓					
	Polyxenidae	N								✓								
	Julida (*Cylindroiulus britannicus*)	A	✓	✓	✓	✓	✓	✓	✓	✓		✓					✓	✓
	Julida (*Ophyiulus pilosus*)	A	✓	✓	✓	✓	✓	✓	✓	✓		✓		✓	✓	✓	✓	✓
	Julida (*Brachyiulus pusillus*)	A		✓	✓		✓								✓		✓	
	Julida (*Nopoiulus kochii*)	A					✓											
	Julida (*Blaniulus guttulatus*)	A				✓		✓										
Isopoda	Styloniscidae	N	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Oniscidae	N	✓	✓	✓	✓		✓			✓							
	Philosciidae	N	✓	✓	✓		✓	✓		✓		✓	✓	✓		✓	✓	
	Armadillidae *Cubaris* sp. 1	N				✓			✓		✓	✓						
	Armadillidae *Cubaris* sp. 2	N	✓			✓						✓						
	Armadillidae sp. 3	N	✓			✓	✓		✓	✓	✓	✓						
	Armadillidae sp. 4	N									✓		✓					
	Armadillidiidae *(Armadillidium vulgare)*	A			✓													
	Trichoniscidae (*Haplophthalmus danicu* s)	A	✓			✓	✓	✓						✓				
	Porcellionidae (*Porcellio scaber*)	A													✓		✓	
Amphipoda	*Puhuruhuru aotearoa*	N				✓			✓	✓	✓	✓	✓					
	Parorchestia tenuis	N							✓		✓	✓	✓					
	Arcitalitrus	A	✓	✓	✓	✓	✓	✓		✓	✓	✓		✓	✓	✓	✓	✓

3.3. Discussion

3.3.1. Diplopoda

Diplopoda (Arthropoda: Myriapoda), commonly referred to as millipedes, are a diverse and species-rich group worldwide (with over 7500 species). There are 13 families of Diplopoda in New Zealand from nine different orders, and 203 known native species (Johns, 2010). All native species are endemic to New Zealand (Johns, 2010). Diplopoda are known to be an ecologically important group. They help breakdown leaf litter by shredding leaf litter and transforming it into a large amount of faeces (Cárcamo et al., 2000; David & Gillon, 2002; Rouifed et al., 2010), which stimulates microbial activity and facilitates decomposition (Hättenschwiler et al., 2005).

Very little is known about the distribution, biology, and ecological importance of Diplopoda in New Zealand, and a greater amount of work on classification and distribution of native Diplopoda is needed. Some of the current knowledge relating to taxa found in Manawatu-Whanganui is summarised below.

3.3.1.1. Adventive Diplopoda

Thirteen adventive Diplopoda species occur in New Zealand (Johns, 2010). Most of these species were probably introduced in the nineteenth century and are now well established, but the ecological effect of adventive Diplopoda in New Zealand is not known (Johns, 1962). Generally, adventive Diplopoda present in New Zealand have not been reported to be of economic importance, but occasionally they have been a nuisance in homes and gardens (Johns, 1966). It is important that adventive Diplopoda are monitored for further spread (Dawson, 1958).

Dawson (1958) believed that in some parts of New Zealand adventive Dipolopoda could be abundant in native forests and that belief was confirmed by this study. Adventive Diplopoda were found throughout native and pine forests in Manawatu-Whanganui. Of the 13 adventive species recognised in New Zealand, five Julida species were found in this study - *C. britannicus, O. pilosus*, *B. guttulatus, N. kochii, and B. pusillus*. Of these, *C. britannicus* and *O.pilosus* were widely distributed and found at high abundance.

C. britannicus was the adventive species found in the highest abundance throughout the study (up to 224 ind./m^2 in leaf litter), and was more dominant than the majority of native Diplopoda orders (except native Polydesmida). *C. britannicus* originates from Europe, and is reported as being present in New Zealand from 1919 (Johns, 1966). It is known to be a successful invader worldwide as it is now widespread outside Europe (in Azores, Maderia, South Africa, USA, Newfoundland, Australia, and New Zealand) (Blower, 1985; Mesibov, 2000). In Tasmania it has been reported as invasive and is widely distributed (Mesibov, 2000). *C. britannicus* has been found throughout New Zealand as one of the dominant species in agricultural and urban habitats (Johns, 1976), with records from Christchurch, Banks Peninsula, Hokitika, Reefton, Otakaike, Queenstown, Wellington, Taranaki, and Chatham Islands (Dawson, 1958; Johns, 1966). It is found underneath bark of dead tree trunks (a habitat not occupied by related species), close to dead wood, or in leaf litter (Blower, 1985). *C. britannicus* is believed to prefer synanthropic and disturbed habitats such as agricultural and horticultural environments, household gardens (where it can occasionally become a pest), coastal dune vegetation, urban forest reserves, and forests and shrubs grazed by stock (Dawson, 1958; Johns, 1966; Mesibov, 2000). It is not surprising that *C. britannicus* was commonly found in pine forests in this study, as it has been described as the dominant Diplopoda associated with exotic forests in New Zealand (Johns, 1976). The frequency with which *C. britannicus* was found in native forests is more surprising; however, there have been previous records of this species in native forests. It has been found in native forest at Chandler's Mill near Reefton (Dawson, 1958), in Hinewai reserve (although Hinewai does contain small patches of pasture along with native forest) (Ward et al., 1999), and throughout native Riccarton Bush of Christchurch, especially common around the edges, in the former oak plantation, and along some of the walking tracks (Johns, 1995). Johns (1976) reported *C. britannicus* to only be in native forest or scrub where there has been large interference by sheep, cattle or development of roads. However, this study found *C. britannicus* in almost all sampled native habitats, including both edge and central locations in larger native forests further from urban environments (although many of the centre plots were close to paths due to limited access into dense forest and steep slopes). Therefore, *C. britannicus* can invade deep into native forest, and may become one of the most dominant Diplopoda in some native forests. *C. britannicus* has previously been believed to have no effect on endemic Spirostreptida (Johns, 1962), but this has not been investigated.

O. pilosus was not discovered at abundances as high as *C. britannicus*, but was the most widespread adventive Diplopoda, found at both centre and edge plots in most native and pine forest, more commonly in leaf litter samples than on logs. *O.*

pilosus originated from Europe, and its association with human activities is the reason it has dispersed to a number of distant countries (Canada, United States, New Zealand, and Australia) (Blower, 1985; Mesibov, 2000). In its native range in Britain, it is present in gardens as well as in and around farmland, but also reaches high density in forests (Blower, 1985). *O. pilosus* has been described throughout New Zealand, with records from Christchurch, Banks Peninsula, New Plymouth, Wellington, Whanganui, the Hawke's Bay, Auckland, and Chatham Islands (Dawson, 1958; Johns, 1966, 1995). It was first recorded in New Zealand in 1914, but was probably introduced much earlier than this due to it being found around gold diggings, old coaching stations, and early homesteads in high country (Johns, 1962). In New Zealand *O. pilosus* is an important inhabitant of household gardens and can sometimes be a problem as it invades homes (Johns, 1966). The density of *O. pilosus* in a vegetable garden in Christchurch was estimated at 21.53-107.34 ind./m^2 (Johns, 1966), which is lower than the highest leaf litter abundance of 147 ind./m^2 found in the native forest remnant (McCrae's Bush) in this study. *O. pilosus* has previously been reported to occur in native forests in New Zealand. It has been recorded throughout native Riccarton Bush (Christchurch), especially around the edges, in the former oak plantation, and along some of the walking tracks (Johns, 1995). *O. pilosus* has been found in native forests in the Waikato (including smaller forest remnants as well as larger forest reserves), where it comprised 45% of all Diplopoda individuals (Costall, 2012). It was found in native forests in Otago (Derraik et al., 2001) and at Chandler's Mill near Reefton (Dawson, 1958). Unlike *C. britannicus, O. pilosus* is believed to be restricted to Europeanised habitats in Tasmania (Mesibov, 2000). However, in this study it was in nine out of ten native forests surveyed and not restricted to smaller, more disturbed, urban sites or pine plantations, as could have been expected. It is not evident that *O. pilosus* has an effect on endemic Diplopoda populations (Johns, 1962). However, due to the frequency with which *O. pilosus* was found in forests, it should not be ruled out as a threat to native species.

B. guttulatus was found only in two small, urban native forest remnants. This adventive species has been introduced from Europe (Johns, 2010). It has been present in New Zealand from at least 1962 when it was recorded in Christchurch (Johns, 1966) and is now widespread in gardens and orchards (Johns, 2010). At large density, it can cause damage to vegetables and tubers in gardens (Johns, 1966). *B. guttulatus* was also introduced to Tasmania where it is believed to be restricted to modified environments (Mesibov, 2000). In Europe *B. guttulatus* is occasionally a pest of potato crops and is also a problem in beets, beans, cucumber, and gourde (Chamberlin, 1921). It is common in woodlands and open areas in Britain, where it is native (Blower, 1985). In this study the highest abundance of *B. guttulatus* in forest leaf litter was 32 ind./m^2, which is much lower than 322.9 ind./m^2 observed in a vegetable garden in Christchurch where *B. guttulatus* was one of the dominant species (Johns, 1966). In this study *B. guttulatus* was not dominant compared to other Diplopoda. Based on the results of this study, it is likely that *B. guttulatus* may not be as successful as other adventive species at invading into forest habitat, may be more restricted to human modified environments in New Zealand, and may be more of a threat to agriculture than to native ecosystems.

Only one individual of *N. kochii* was found in this study. It was identified from Mt Lees reserve which, while still containing remnants of native forest, is essentially a garden with a large native flora component. In New Zealand, this adventive species is found in gardens, but is usually restricted to gardens in the North Island (Johns, 2010). Blower (1985) states that *N. kochii* has been misclassified as *Nopoiulus minutus* (Brandt, 1841) in the past, so New Zealand records for *N. minutus* may be records for *N. kochii*. *N. minutus* has been recorded in New Zealand since 1921, and is distributed in Wellington, Whanganui, Auckland, and Temuka (Canturbury) (Johns, 1966). It was recorded at high abundance in a South Canturbury garden and was found to always co-exist in gardens with *B. pusillus* (Johns, 1966); however, in this study *N. kochii* was absent from a few sites where *B. pusillus* was found. Based on the results of this study, *N. kochii* does not appear to commonly invade either native or pine forests.

B. pusillus was present in three native forest areas, all of which are small remnants close to urban areas and show evidence of human disturbance and/or weed invasion. *B. pusillus* was also found in two pine forests. It was not abundant at any site (max abundance 25.6 ind./m^2). Originally from Europe, *B. pusillus* has been in New Zealand for a long time, as there are records from Chatham Island in 1923 and from the mainland in 1924 (Johns, 1966). In Britain, *B. pusillus* is commonly found in costal habitats as well as inland (usually on arable land or grassland), but it is not common in forests (Blower, 1985). In Tasmania, where it is adventive, *B. pusillus* is restricted to Europeanised habitats and is not believed to be invasive (Mesibov, 2000). In New Zealand, *B. pusillus* is almost as widespread as *C. britannicus,* but is restricted to coastal areas and areas that have undergone intense modification, such as towns, cities, and gardens (Johns, 1976). It has been found in Chatham Islands, Norfolk Islands, New Plymouth, Whanganui, Wellington, and Christchurch (Johns, 1966). Despite *B. pusillus'* widespread distribution in New Zealand, its presence in only three urban forests, low abundance, and information on its distribution elsewhere in the world indicate that it may not invade less disturbed patches of native forest which occur further from urban centres.

Julida were the only order of adventive Diplopoda found in this study. Five adventive species of the Polydesmida order have also been recorded in New Zealand (Johns, 2010). Of these, three species - *Akamptogonus novarae* (Humbert & Saussure 1869)*, Brachydesmus superus* Latzel 1884*,* and *"Polydesmus kochii"* [4] are all known to be widespread in the North Island of New Zealand (Johns, 2010). It is not clear whether these species are absent from Manawatu-Whanganui, or were not encountered because forest habitat was not a suitable environment for them. Elsewhere, adventive Polydesmida have been found in native New Zealand forests. *Oxidus gracilis* (C.L. Koch, 1847) was found to be at a high abundance in karaka (*Corynocarpus laevigatus*) litter in the Waitakere Ranges, west of Auckland city (Tomlinson, 2007) and at low abundance in a native forest in the Waikato region (Costall, 2012). "*P. kochii"* is present in modified shrublands in Nelson (Johns, 2010).

3.3.1.2. Native Diplopoda

Few advances in the knowledge of New Zealand Diplopoda fauna have been made since Johns (1962) published his "introduction", and little is still known on New

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[4] Information on "*Polydesmus kochii"* (not the same species as *Nopiulus kochii* (Gervais, 1847)) was discussed by Johns (2010), but such species is absent from Diplopoda taxonomic record. In the same publication (Johns, 2010) the only *Polydesmus* species included on the species list is *Polydesmus inconstans* Latzel, 1884. It is possible that a mistake was made, and "*Polydesmus kochii"* is actually *Polydesmus inconstans* Latzel, 1884.

Zealand's Diplopoda fauna. There appears to be more known about adventives in New Zealand than natives. This may be partially due to the paucity of taxonomic knowledge on natives, making them difficult to study. Additionally, interest in studying adventives could be due to their perceived threat. Some progress is being made on native Diplopoda. For example, two new species (*Eumastigonus hallelujah* Korsos & Johns, 2009 and *E. waitahae* Korsos & Johns, 2009) of native Spirostreptida order have recently been described (Korsós & Johns, 2009). More descriptions of native Diplopoda are in preparation (Korsós & Johns, 2009). The distribution of many native species is unclear. Most of the knowledge on the distribution comes from the locality information from the original descriptions of species.

There are nine native orders of Diplopoda in New Zealand (Johns, 2010) and five of those (Polydemida, Spirostreptida, Siphonophorida, Chordeumatida, and Polyzoniida) were found in forests in Manawatu-Whanganui.

Polydesmida were the dominant native Diplopoda group in this study, diverse (15 morphotypes were recorded) and widely distributed throughout the study area (present in all native forests and in most pine forests). However, at some sites Polydesmida were found at lower abundances than the adventive *C. britannicus* (Julida). The same situation has been observed previously in some New Zealand native forests, where Polydesmida were the second most abundant order after the dominant adventive Julida (Costall, 2012). In New Zealand, Polydesmida are more diverse than all other Diplopoda orders (Johns, 2010). Most diversity is in family Dalodesmidae, which contains 50 described species and 61 undescribed and unnamed species from 11 genera, 10 of those genera are endemic to New Zealand (Johns, 2010). Dalodesmidae have a southern hemispheric distribution; they are present in New Zealand, Australia, New Caledonia, New Guinea, Chile, Madagascar, and southern Africa (Johns, 1979). There has been a high level of speciation in this group, and species have limited distributions (Johns, 1962). No information on described species present in Manawatu-Whanganui could be found, but it is believed that at least seven species are restricted to the lower North Island, south of Otaki and Masterton (Johns, 1962). *Icosidesmus olivaceus* Carl 1902, *Icosidesmus hochstetteri* Humbert & Saussure, 1869 (Auckland), *Icosidesmus wheeleri* Chamberlin, 1920 (Wellington), *Icosidesmus falcatus* Johns 1964 (Wellington), *Icosidesmus collinus* Johns 1964 (Lake Waikarimoana and West Taupo), *Pseudoprionopeltis haastii* (Humbert & Saussure, 1869) (Auckland), and *Pseudoprionopeltis elaphrus* Johns 1964 (central volcanic plateau) have all been found in the North Island (Chamberlin, 1920; Johns, 1964). *P. elaphrus* is known to be moderately widespread in the North Island (Johns, 1979). *I. falcatus* has been reported to be capable of invading pine forests (Johns, 1964). Many of the described species of Dalodesmidae have not been recorded from the North Island, and no species of the genera *Erythrodemus*, *Dityloura*, *Notonaia*, *Notnesiotes*, and *Blysmopeltis* are recorded from the mainland North Island of New Zealand (Johns, 1970). Based on the high abundance and wide distribution throughout forests of Manawatu-Whanganui, there is no indication that Polydesmida are highly threatened by the presence of adventive species or human modification to native habitat.

Chordeumatida were widely distributed in both native and pine forests of Manawatu-Whanganui. Order Chordeumatida has an Austro-Malayan distribution (Johns, 1962). They are known to be very common in New Zealand forests (Johns, 1962; Minor & Robertson, 2006). There is only one endemic genus (*Schedotrigona*) in

New Zealand, containing five described species, and there are another 11 undescribed and unnamed species (Johns, 2010). Access could not be gained to original description of majority of described species, so it is unknown if any species have been described from the North Island. Chordeumatida have been found to tolerate a wide range of forest conditions; a study in Tasmania found Chordeumatida in both native and pine forests, although not in high numbers (Bonham et al., 2002).

Spirostreptida were found in most native forest sites in this study, but not found in any pine forests; they occurred in low abundance compared with other Diplopoda, and were most commonly on logs. Spirostreptida are reported as being abundant in New Zealand's native forests and are common in rotting logs (Korsós & Johns, 2009). They are important in the breakdown of litter in forests, native shrub, and grassland (Korsós & Johns, 2009). There are 11 described species in New Zealand, all classified under the genus *Eumastigonus,* and a further 21 undescribed and unnamed species (Johns, 2010). *Eumastigonus maior* Chamberlin, 1920; *Eumastigonus parvus* Chamberlin, 1920; *Eumastigonus insulanis* (Attems, 1903); *Eumastigonus ater* (Chamberlin, 1920); *Eumastigonus hemmingseni* Mauries, 1983; and *Eumastigonus distinctior* Chamberlin, 1920 have all been found in Wellington (Chamberlin, 1920; Korsós & Johns, 2009) and may occur in Manawatu-Whanganui. The morphology and ecological function of Spirostreptida are similar to members of the order Julida (Korsós & Johns, 2009). In this study Spirostreptida and Julida were found to co-occur, and it is very possible that abundant Julida (especially C*. britannicus* and *O. pilosus*) could compete with native Spirostreptida fauna and displace them. However, other authors found no indication of this occurring (Johns, 1962; Costall, 2012).

Siphonophorida were widely distributed in native forests of the Manawatu-Whanganui, and were found in two pine forests. In one pine forest (Kahutarawa) Siphonophorida were found in high abundance (246.4 ind./m^2) and were the dominant Diplopoda in leaf litter. Siphonophorida are capable of building up large populations, and have been observed to have large populations in pine plantations (Johns, 1966). There is only one described species of Siphonophorida in New Zealand – *Siphonophora zelandica* Chamberlin, 1920 described from Days Bay, near Wellington, but six other undescribed and unnamed species have also been discovered (Johns, 2010).

Polyzoniida were not a dominant Diplopoda group in this study, although they are capable of building up very large populations (Johns, 1966). Only in one site (the edge of Ashhurst Domain) were Polyzoniida more abundant than adventive Diplopoda species. There are three species known in New Zealand (all of the genus *Siphonethus*) (Johns, 2010). Two species – *Siphonethus bellus* Chamberlin, 1920 (from Day's Bay near Wellington) and *S. enotatus* Chamberlin, 1920 (from Taumarunui) have been reported in the North Island of New Zealand (Chamberlin, 1920). In Tasmania, native Polyzoniida often congregate in small single-species groups under bark or fallen wood; this tendency to cluster makes them difficult to find (Mesibov, 2000). Clustering behaviour may be present in endemic New Zealand species, which would explain why observed abundances were not as large as could be expected.

Only three specimens of Polyxenida were found in this study, collected from a log in a native forest. Polyxenidae are uncommon in New Zealand (Johns, 1962; Minor & Robertson, 2006). There is only one described species in New Zealand, *Propolyxenus forsteri* Conde, 1951, known to occur in dry *Nothofagus* forest in Canturbury. It (along with any other undescribed species) is an important member of the native tussock community (Johns, 1962). One other undescribed *Propolyxenus* species has been discovered (Johns, 2010).

3.3.2. Isopoda

Terrestrial Isopoda (sub order Oniscidea, class Crustacea) are the large crustacean group that has been successful at competing with other Arthropoda on land. These terrestrial Isopoda are sometimes referred to as slaters, woodlice, or pill bugs (Webber et al., 2010). There are six families of truly terrestrial Isopoda in New Zealand, containing 72 described species (including a number of littoral species). The majority of species are native and only six species are adventive. Of the native species there are four non-endemic species (Webber et al., 2010). Species most commonly found in urban environments in New Zealand (*P. scaber* and *A. vulgare*) are introduced from Europe (Webber et al., 2010). Terrestrial Isopoda can be found in garden litter, rotting grass, under rotting wood, and are particularly common in leaf litter and decaying undergrowth of the bush (Hurley, 1950). Most species feed on dead plant litter (Webber et al., 2010).

Hurley (1950) published a key on terrestrial Isopoda in New Zealand. Members of the family Styloniscidae were more recently revised (Green, 1971). Hurley's (1950) key provides use for the identification of some species (only 48 species of Oniscidea were known at the time of publication). The knowledge of native Oniscidea in New Zealand is incomplete and is in urgent need of taxonomic revision. More complete identification keys would be beneficial. It would also be useful to record known distribution of species, as this information is not easily sourced.

3.3.2.1. Adventive Isopoda

There are six species of adventive Isopoda known to occur in New Zealand (Webber et al., 2010). Three adventive species (*H. danicus*, *A. vulgare,* and *P. scaber*) were identified in forests of Manawatu-Whanganui*. A. vulgare* and *P. scaber* (both introduced from Europe) have been in New Zealand for over one hundred years (Chilton, 1910a). They are particularly common in New Zealand (Webber et al., 2010), yet they were only rarely found in forests in Manawatu-Whanganui. This is in contrast to *H. danicus,* which was commonly found in forests in this study (in native and pine forest), yet, while being reported from New Zealand (Webber et al., 2010), was not found to be discussed in any New Zealand studies.

P. scaber and *A. vulgare* are cosmopolitan species, which were accidently introduced into New Zealand (Chilton, 1905). *P. scaber* occurs in Europe, America, Asia, and Australia (Chilton, 1905)*. P. scaber* is found in great abundance throughout New Zealand, usually around buildings, in greenhouses (Chilton, 1901), along roads, and in coastal dune habitats of the North and South Island (Maria Minor, personal communication, 2013). It has spread far from inhabited places, but is not often found in native forest (Chilton, 1901, 1910a). Only four specimen of *P. scaber* were found in this study, all at the edge of pine forest. However, there have been some records of *P. scaber* in native forest and it can sometimes penetrate considerable distances into the bush (Chilton, 1905). *P. scaber* has been found throughout the native Riccarton Bush of

Christchurch, being especially common around the edges, in the former oak plantation, and along some of the walking tracks (Johns, 1995). It was also found in native shrubland in Otago and in Hinewai reserve in Canterbury (which consist largely of native forest or shrubland, but also contain areas not covered with native vegetation) (Ward et al., 1999; Derraik et al., 2001).

A. vulgare is recorded from Europe, Asia, Africa, and Australia (Chilton, 1905). Only one specimen of *A. vulgare* was found in this study, collected at the edge of a native forest. *A. vulgare* is known to occur in areas of native forest in New Zealand. For example, *A. vulgare* was found to be present in the majority of native forest sites (17 out of 25 sites) sampled in the Auckland area, although only once did it make up more than 10% of the Isopoda fauna (Scott, 1984a). It was also identified in a survey of invertebrates on Kapiti Island (which consists mostly of native forest) (Sinclair et al., 2005).

3.3.2.2. Native Isopoda

There is very scarce information available on native terrestrial Isopoda in New Zealand. Four native Isopoda families (Oniscidae, Philosciidae, Armadillidae, and Styloniscidae) were identified from forests in Manawatu-Whanganui. Any knowledge on the distribution of native Isopoda in New Zealand could often only be gained from original species descriptions, which could not always be obtained.

Family Oniscidae were found in six native forests in Manawatu-Whanganui, although never in high numbers, and not in any pine forests. There is one genus (*Phalloniscus*) of Oniscidae present in New Zealand, containing 13 species (Webber et al., 2010). *Phalloniscus punctatus* (Thomson, 1879) is common throughout New Zealand (Chilton, 1901), but many records may be misidentifications (Maria Minor, personal communication, 2013). *Phalloniscus lamellatus* Vandel, 1977, *Phalloniscus bowleyi* Vandel, 1977, *Phalloniscus bifidus* Vandel, 1977, and *Phalloniscus armatus* Bowley, 1935 occur in New Zealand and their distribution could include locations in the North Island (Schmalfuss, 2003).

Philosciidae were widely distributed in forests in Manawatu-Whanganui in both native and pine forests, and were the dominant Isopoda taxon at a number of sites. Philosciidae contains a number of different genera in New Zealand (*Adeloscia*, *Okeaninoscia*, *Papuaphiloscia, Paraphiloscia, Philoscia*, and *Stephenoscia*). *Adeloscia*, *Okeaninoscia*, and *Stephenoscia* are genera endemic to New Zealand (Webber et al., 2010). There are eight described species in New Zealand (Webber et al., 2010). *Paraphiloscia brevicornis* (Budde-Lund, 1912), *Paraphiloscia fragilis* (Budde-Lund, 1904), *Philoscia novaezelandiae* Filhol, 1885, *Philoscia pubescens* (Dana, 1853) (near Bay of Islands and Auckland), and *Adeloscia dawsoni* Vandel, 1977 all occur in the North Island of New Zealand (Chilton, 1901; Schmalfuss, 2003). *Stephenoscia bifrons* Vandel, 1977 and *Papuaphiloscia hurleyi* Vandel, 1977 were described to be present in New Zealand without the exact distribution specified. However, they were not described exclusively from the South Island or outlying New Zealand Islands as many taxa were (Schmalfuss, 2003). *Papuaphiloscia proxima* Vandel 1977 is also described vaguely to occur “in New Zealand” (Schmalfuss, 2003). However, it was not included on a recent list of New Zealand taxa (Webber et al., 2010).

Four native Armadillidae morphospecies were identified from forests of the Manawatu-Whanganui. Two of these morphospecies were identified as genus *Cubaris*. Armadillidae were more common on logs than in leaf litter, and not found in high abundance. There are 26 described species of Armadillidae in New Zealand (including the adventive *Cubaris murina* which was not found in this study); there is some uncertainty around their generic classification (Webber et al., 2010). *Acanthodillo spinosus* (Dana, 1853) (near Bay of Islands); *Spherillo brevis* Budde-Lund, 1904; *Spherillo danae* Heller, 1865 (Auckland); *Spherillo marginatus* Budde-Lund, 1904; *Spherillo monolinus* Dana, 1853 (near Bay of Islands); *Spherillo setaceus* Budde-Lund, 1904; *Spherillo speciosus* (Dana, 1853) (Auckland and near Bay of Islands); *Coronadillo hamiltoni* (Chilton, 1901) (near Napier); *Coronadillo milleri* (Chilton, 1917); *Coronadillo suteri* (Chilton, 1915); and *Cubaris ambitiosa* (Budde-Lund, 1885) (widely distributed around the North Island including Whanganui) all occur in the North Island of New Zealand (Schmalfuss, 2003). *Cubaris tarangensis* (Budde-Lund, 1904) was described simply as occurring in New Zealand, but could have been described from North Island specimen (Schmalfuss, 2003). *A. spinosus* has been found on the bark of pine trees (Chilton, 1901).

Styloniscidae were the most commonly encountered family of native Isopoda in this study, present at all sites that were sampled (both native and pine). On most occasions it was also the family of Isopoda found at the greatest abundance. Styloniscidae is made up of two genera in New Zealand (*Notoniscus* and *Styloniscus*), neither genus is endemic to New Zealand (Webber et al., 2010). Styloniscidae has previously been recognised as inhabiting damp forest leaf litter (Green, 1971). *Styloniscus commensalis* (Chilton, 1910) is widely distributed around the North Island

(Chilton, 1910b); no other species have been described from individuals collected from the North Island (Chilton, 1901; Green, 1971; Schmalfuss, 2003).

3.3.3. Amphipoda

There is only one group of Amphipoda (class Crustacea) – family Talitridae – that has colonised terrestrial habitats worldwide (Webber et al., 2010). Talitridae have been described as a successful group, mostly due to their very abundant detrital food source (Duncan, 1994). Terrestrial Amphipoda (otherwise known as landhoppers) live in litter, under trees and rocks, or in burrows which they construct themselves (Webber et al., 2010). Terrestrial Amphipoda are a conspicuous part of the macrofauna in New Zealand, and make up a large part of the soil and leaf litter fauna in forest, grassland, and other damp habitats (Fenwick & Webber, 2008). Some species can thrive equally well in streams as they do in terrestrial habitats (Fenwick & Webber, 2008). Often, terrestrial Amphipoda can occur at large densities (this includes adventive species), indicating that they play a significant role in ecosystems (Fenwick & Webber, 2008). Despite their ecological importance, terrestrial Amphipoda have not been well researched in New Zealand (Fenwick & Webber, 2008).

Terrestrial Amphipoda from 36 species and nine genera are known in New Zealand (excluding a few possible freshwater species) (Webber et al., 2010). There is some uncertainty about the presence of genus *Austrotroides*, which only contains one unnamed species (Fenwick & Webber, 2008). Most New Zealand Amphipoda are native but there are at least three adventive species from two genera (Webber et al., 2010), believed to have been introduced with plants brought into New Zealand; more adventive Talitridae are likely to be discovered (Fenwick & Webber, 2008). All native species in New Zealand are endemic (Fenwick & Webber, 2008; Webber et al., 2010).

Duncan (1994) produced a key to New Zealand Talitridae (which requires both a male and female for identification), described characteristics used to identify many native species, and included some ecological information on the species and their known distributions. Duncan's (1994) work made terestrial Talitridae relatively well known compared to other groups of Amphipoda in New Zealand (Webber et al., 2010). Fenwick and Webber's (2008) key further added seven unnamed native species and two adventive species (*Arcitalitrus dorrieni* (Hunt, 1925) and *Talitroides topitotum* Burt, 1934). Compared to other detritivores in New Zealand, taxonomy and general knowledge on terrestrial Amphipoda is advancing. However, there is still progress to be made and many gaps in knowledge on terrestrial Amphipoda still occur; there may be species that have not yet been discovered (including adventive species) and a number of species remain unnamed (Fenwick & Webber, 2008). Densities of terrestrial Amphipoda in New Zealand are largely unreported, but they are expected to be similar to those elsewhere (Fenwick & Webber, 2008). The status of some Amphipoda species in New Zealand is uncertain (Fenwick & Webber, 2008) – for example, it is believed that some species of the genus *Waematu* may already be extinct, but this is not certain (Duncan, 1994).

3.3.3.1. Adventive Amphipoda

Two species of *Arcitalitrus* have been introduced into New Zealand from Australia (Fenwick & Webber, 2008). *A. sylvaticus* is usually found in abundance in urban and disturbed environments, commonly in parks and gardens of human settlements in the North Island (Duncan, 1994). It is known to be aggressive and is now the most common Amphipoda in modified habitats of the North Island, where it has displaced native species in many environments, especially around Auckland and Wellington (Duncan, 1994). In New Zealand its distribution is from Nelson upwards; it is rare in Christchurch and Greymouth (Fenwick & Webber, 2008). *A. sylvaticus* is believed to be still actively expanding its range (Duncan, 1994). The second species, *A. dorrieni*, has been described as being present in Northland, Auckland, Waikato, central Canterbury and Otago lakes (Fenwick & Webber, 2008). It is difficult to distinguish between the two known *Arcitalitrus* species (Rick Webber, personal communication, 2013), so they were not separated in this study. Based on known distribution, *Arcitalitrus* in this study is probably *A. sylvaticus,* because *A. dorrieni* has not been identified in the lower North Island (Fenwick & Webber, 2008).

Adventive *Arcitalitrus* were found throughout Manawatu-Whanganui in this study, and were very common in pine forests (in all sites except one) and in native forests (in all sites except two). *Arcitalitrus* were the only Amphipoda found at half of the native forest sites. This may be an indication that adventive *Arcitalitrus* has displaced native species in these forest areas. *Arcitalitrus* had a tendency to be more common in sampled native forests which were smaller in size, more modified, and located in urban areas (McCraes Bush, Ashhurst Domain, Bledisloe Park, Kitchener Park, Mt Lees Reserve, and The Esplanade).

The preference for disturbed habitats provides some explanation as to why *Arcitalitrus* were found in pine forests, which are known to contain disturbance (Lozon

& MacIsaac, 1997; Pawson et al., 2008). *Arcitalitrus* also occurs in native forests in New Zealand – *A. sylvaticus* was found in a survey of Hinewai reserve (Ward et al., 1999), and Duncan (1994) reported *A. sylvaticus* in areas of native vegetation (although majority of these native forest sites had been altered by the presence of invasive plants or had severely damaged undergrowth). Other studies done in native New Zealand forests have found only endemic Amphipoda species (Moeed & Meads, 1985; Derraik et al., 2001).

This appears to be the first study to highlight the dominance of adventive Amphipoda in native forest remnants in in a region of New Zealand. *Arcitalitrus* has previously been thought to show little capability of invading into native habitats around the world (Richardson, 1990); although some research revealed that *Arcitalitrus* has been invading native forests (P. Moore & Spicer, 1986).

3.3.3.2. Native Amphipoda

A number of New Zealand species and genera are restricted in their distribution in New Zealand. For example, *Kanikania motuensis* Duncan, 1994 occurs only on Stewart Island and *Parorchestia longicornis* Stephensen, 1938 occurs only on Stewart Island and in Bluff (Duncan, 1994; Fenwick & Webber, 2008). There are often species from several different genera occurring together but species from the same genus have not been found together (Duncan, 1994).

Two native species of Talitridae (*P. aotearoa* and *P. tenui*s) were found in Manawatu-Whanganui. Except for *Parorchestia lesliensis* Hurley, 1957, which is found in Wellington, *P. tenuis* and *P. aotearoa* are the only species (along with the adventive

A. sylvaticus) known to occur in the lower North Island (Duncan, 1994; Fenwick & Webber, 2008). *P. tenuis* and *P. aotearoa* are the two most widely distributed New Zealand species (Duncan, 1994). In Manawatu-Whanganui *P. tenuis* and *P. aotearoa* were found in leaf litter at densities up to 128 ind./m^2 and 89.6 ind./m^2, respectively. These densities are not high for terrestrial Amphipoda, considering that native *Makawe hurleyi* (Duncan, 1968) has been found to occur at 1230–2670 ind./m^2 (Fenwick & Webber, 2008)[5] and a Tasmanian study found a native forest species (*Keratroides angulosus* (Friend, 1979)) at densities as high as 6185 ind./m^2 (Friend, 1980).

P. aotearoa, one of New Zealand's most common Amphipoda, may be considered to be one of New Zealand's most numerous native terrestrial animals (Duncan, 1994). It has been known to reach high densities in lowland forests (both podocarp/hardwood and beech) and is abundant in bush remnants (even those where the soil has been disturbed by stock), as well as in regenerating forests (Duncan, 1994). Moss and leaf litter are known habitats for *P. aotearoa* (Duncan, 1994) and findings of this study revealed fallen logs as an additional habitat. *P. aotearoa* is present on Three Kings Island, North and South Islands, as well as Stuart Island and has been described as abundant on islands around the Cook Straight (Duncan, 1994; Fenwick & Webber, 2008). *P. aotearoa* was the only Amphipoda found in a native shrubland in the South Island (Brookdale Convenant) (Derraik et al., 2001). It is known to commonly co-occur with other native species, often with *P. tenuis* (as it did in this study) (Duncan, 1994). *P. aotearoa* is found from sea level to at least 1000 m; at higher altitudes and low

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[5] Fenwick and Webber (2008) cite Duncan (1994) but I could not find that information in Duncan (1994).

conductivity soils it is known to be partially replaced by *P. tenui*s (Duncan, 1994). In this study, *P. tenui*s was at higher abundance than *P. aotearoa* at the centre in native forest at Shannon and in pine forest at Kahutarawa; both these sites were at higher altitude than sites where *P. tenui*s was found to be less abundant.

*P. tenui*s is also one of New Zealand's most common Amphipoda (Duncan, 1994). *P. tenui*s occurs in the North Island, the West coast of the South Island, Steward Island, and possibly on Campbell Island (Duncan, 1994; Fenwick & Webber, 2008). The only record from Campbell Island has been described as dubious due to the small size of the specimens and the fact that they were from freshwater where *P. tenui*s is not known to be found (Duncan, 1994). It has been found from sea level to up to 2000 m in all kinds of native forest but is less common in beech forests and manuka/kanuka scrubland; it is also less common in grasslands and in suburban gardens (Duncan, 1994). *P. tenui*s is believed to be an opportunistic coloniser which disperses rapidly (Duncan, 1994). In Manawatu-Whanganui *P. tenui*s was only found in larger, less disturbed native forests, further from urban areas (Shannon, Totara Reserve, and Kahutarawa) with absence or low abundances of *Arcitalitrus.* It was typically not found in pine forests (except for Kahutarawa).

Both *P. aotearoa* and *P. tenui*s have been displaced by adventive *A. sylvaticus* in urban and agricultural areas in New Zealand (Duncan, 1994) and based on the results of this study it seems that they are also being displaced by *Arcitalitrus* in native forests. *Arcitalitrus* was the dominant Amphipoda in small native forest remnants that were in urban locations or suffered from high levels of human disturbance. Generally, native

Amphipoda were only found in sites where *Arcitalitrus* was either not found or present at low density (only a few specimens of *Arcitalitrus* were found).

Some native Amphipoda, such as *P. aotearoa,* are able to invade modified habitats, including introduced pine plantations (Duncan, 1994). However, based on the results of this study, pine plantations do not appear to be a common habitat for native Amphipoda. Native Amphipoda were not in the majority of forests in Manawatu-Whanganui, their absence from most pine forests and half of the native forests indicates that the habitat of native Amphipoda may be limited.

3.4. Summary

The results of this study highlight a widespread presence of adventive detritivores in the forests of Manawatu-Whanganui. Another significant result is the importance of combining several sampling methods when studying detritivores, as different species/groups are better collected by different sampling methods.

Among Diplopoda, two adventive species (*C. britannicus* and *O. pilosus*) were found to readily invade native environments, were very abundant in numerous native forests in Manawatu-Whanganui, and were not restricted to smaller, more disturbed urban sites, or pine plantations, as may have been expected. Another group of adventive Diplopoda from the order Julida (*B. guttulatus, N. kochii,* and *B. pusillus*) are associated with urban habitats and gardens (Johns, 1976, 2010), and were less commonly found in forests. Native Spirostreptida were restricted to native forest, found at low abundance, and co-occurred with adventive Julida, and it is very possible that abundant Julida (especially *C. britannicus* and *O. pilosus*) could compete with native Spirostreptida and displace them. The low abundance of Siphonophorida (despite knowledge that they are capable of reaching high abundance (Johns, 1966)) may at least partially be due to the presence of adventive species. Polydesmida were the dominant native Diplopoda group in this study, although sometimes found at lower abundances than the adventive *C. britannicus.* Based on their high abundance and wide distribution, there is no indication that Polydesmida are threatened by the presence of adventive species or human modification to native forests of Manawatu-Whanganui. Further work is needed to identify any impacts of adventive Diplopoda on native species.

Styloniscidae were the most commonly encountered family of native Isopoda, present in all sites that were sampled. Styloniscidae and Philosciidae were dominant groups in Manawatu-Whanganui. Very scarce information is available on native taxa, and there is great need for further research on terrestrial Isopoda in New Zealand.

Adventive *Arcitalitrus* was the dominant Amphipoda in small native forest remnants that were in urban locations or suffered from high levels of human disturbance; it was the only Amphipoda in majority of pine forests sampled in Manawatu-Whanganui. This is the first study to highlight the dominance of adventive Amphipoda in native forest remnants in New Zealand. Native species *P. aotearoa* and *P. tenuis* are displaced by *A. sylvaticus* in urban and agricultural areas (Duncan, 1994), and based on results of this study they are likely being displaced by *Arcitalitrus* in native forests. Therefore, evidence suggests that Amphipoda should be further studied to clarify the negative impacts adventive detritivores may have on native species.

4. Effects of forest type and plot location on abundance and community composition of native and adventive detritivores in the study area

4.1. Introduction

It has been proposed that New Zealand's native forests are resistant to invasion by adventive invertebrates (Pawson et al., 2008; Brockerhoff et al., 2010), and that adventive invertebrate species are abundant in disturbed habitats, but are rare or absent in native forests (Berndt et al., 2008; Pawson et al., 2008). However, multiple studies have reported adventive detritivores in New Zealand's native forests (Johns, 1995; Harris & Burns, 2000; Tomlinson, 2007), and a number of adventive Diplopoda, Isopoda, and Amphipoda species have been found to occur in native forests of Manawatu-Whanganui (Chapter 3).

Another concept that has been proposed is that pine plantations are "biological deserts" which contain little biodiversity (Brockerhoff et al., 2001). While this concept is no longer considered accurate, and pine forest are known to contain a number of native species (O'Loughlin, 1995; Brockerhoff et al., 2001; Maunder et al., 2005), there is very little information on invertebrates in New Zealand pine plantations (Maunder et al., 2005). The somewhat scarce information that has been collected suggests that pine plantations in New Zealand can support a number of endemic invertebrates (Hutcheson & Jones, 1999; Brockerhoff et al., 2005; Pawson et al., 2008), and, indeed, a number of native taxa of Diplopoda, Isopoda, and Amphipoda have been found in pine forests of Manawatu-Whanganui (Chapter 3).

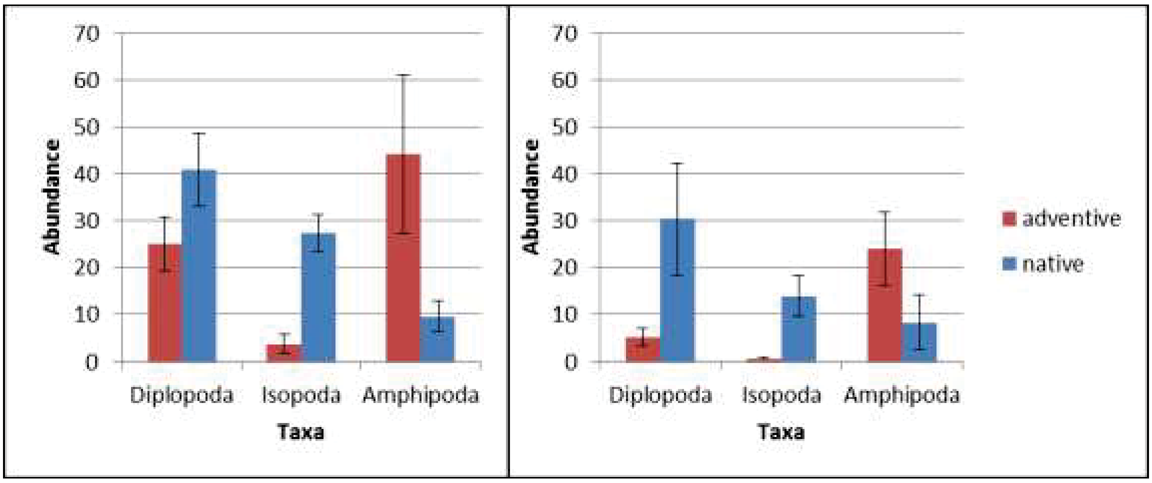
Proximity to the edge of the forest may also influence abundance patterns of detritivores. Edge effects have been found to influence invertebrate abundance (Didham, 1997; Davies et al., 2001; Norton, 2002; Ewers & Didham, 2008). Edge habitat may facilitate the invasion of adventive species (Norton, 2002), which can result in a higher abundance of adventive invertebrates at edge habitats and the displacement of native species, restricting them to more central locations in the forest (Suarez et al., 1998; Hickerson et al., 2005).

The overall aim of this Chapter was to investigate whether forest type (native/pine) and plot location (edge/centre) influence the abundance and community composition of native and adventive detritivores (Diplopoda, Isopoda, and Amphipoda) in the region. Within each of the three detritivore groups the effect of plot location and forest type was investigated at all taxonomic levels, in case combining the taxa was masking any effects. Taxa included all identified levels of diversity – orders of Diplopoda, morphospecies of order Polydesmida (Diplopoda), species of adventive Diplopoda, families of Isopoda, morphospecies of family Armadillidae (Isopoda), species of adventive Isopoda, and species of Amphipoda. ANOVA was used to compare abundance values between the two forest types and plot locations, to identify if either factor influenced detritivore abundances. A binary logistic regression model predicting the likelihood of encountering an adventive individual depending on forest type and plot location was used for each of the three focus groups. Multivariate analysis was used to determine if plot location and forest type influenced community composition. See Chapter 2 (section 2.4) for more information on the statistical analyses used. The analysis of detritivore abundances can reveal how dominant adventive taxa are in respect to native taxa, provide further insight into the suitability of pine forest as an alternative forest habitat for native detritivores, and identify the forest habitats and native detritivore groups most threatened by adventive detritivores.

4.2. Results

4.2.1. Overall detritivore abundance patterns

The mean abundance of detritivores in native forests was higher than that in pine forests. In both forest types, adventive Amphipoda were more abundant than natives, and native Diplopoda and Isopoda were more abundant than adventives, although the abundance of adventive Diplopoda in native forests was very high (Fig. 4.1).



a) Native forests b) Pine forests

Figure 4.1. Mean abundance of detritivores in a) native forests and b) pine forests. Error bars represent standard error of the mean. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter quadrats, plus the sum of individuals from logs found in a 10 m x 10 m quadrat, at each forest plot.

4.2.2. Diplopoda

There were slightly more native Diplopoda in native forests, although ANOVA found this pattern not significant. There was no relationship between abundance of native Diplopoda and plot location (edge vs. centre) (Fig. 4.2, Table 4.1). Native taxa of Diplopoda were not affected by forest type or plot location, except Polydesmida morphospecies 11, which was significantly more abundant in pine forests (Table 4.1). Adventive Diplopoda were significantly more abundant in native forests compared to pine forests; no pattern was seen for plot location except that samples from edge plots had a greater range in results (Fig. 4.2, Table 4.1). Higher abundance of adventive Diplopoda in native forests was a reflection of the distribution of *Cylindroiulus britannicus,* which was the only adventive Diplopoda species influenced by forest type, and was significantly more abundant in native forests (Table 4.1).

Diplopoda community structure was influenced by forest type (Fig. 4.3) (R value = 0.511, level of significance = 0.001) but not plot location (R value = -0.094, level of significance = 0.97). Six taxa had the strongest correlation (>0.5) with the MDS ordination axes (*C. britannicus*, *Ophyiulus pilosus*, Polydesmida morphospecies 5, 8, 11, and 15) (Fig. 4.3). Based on the bubble plots (Figs. 4.4-4.9), *C. britannicus*, Polydesmida morphospecies 5, and Polydesmida morphospecies 11 appear to be the taxa most responsible for the difference in the Diplopoda community between native and pine forests.

Logistic regression model suggests that both forest type and plot location influence the probability of a randomely collected Diplopoda individual being adventive (see Apendix 3 for SAS output). It is more likely that any Diplopoda found would be adventive if it was found in a central location instead of the edge (Wald Chi-square = 12.3926, p-value = <.0001). It is also more likely that a Diplopoda would be adventive if it was found in a native forest compared to a pine forest (Wald chi-square = 75.9162, p-value = <.0001), this is due to higher overall abundance of adventive Diplopoda in native forests. The highest probability (0.514) that any collected Diplopoda individual would be an adventive species is at the centre of a native forest, and the lowest probability (0.048) of a Diplopoda being adventive is at the edge of a pine forest (Fig. 4.10).

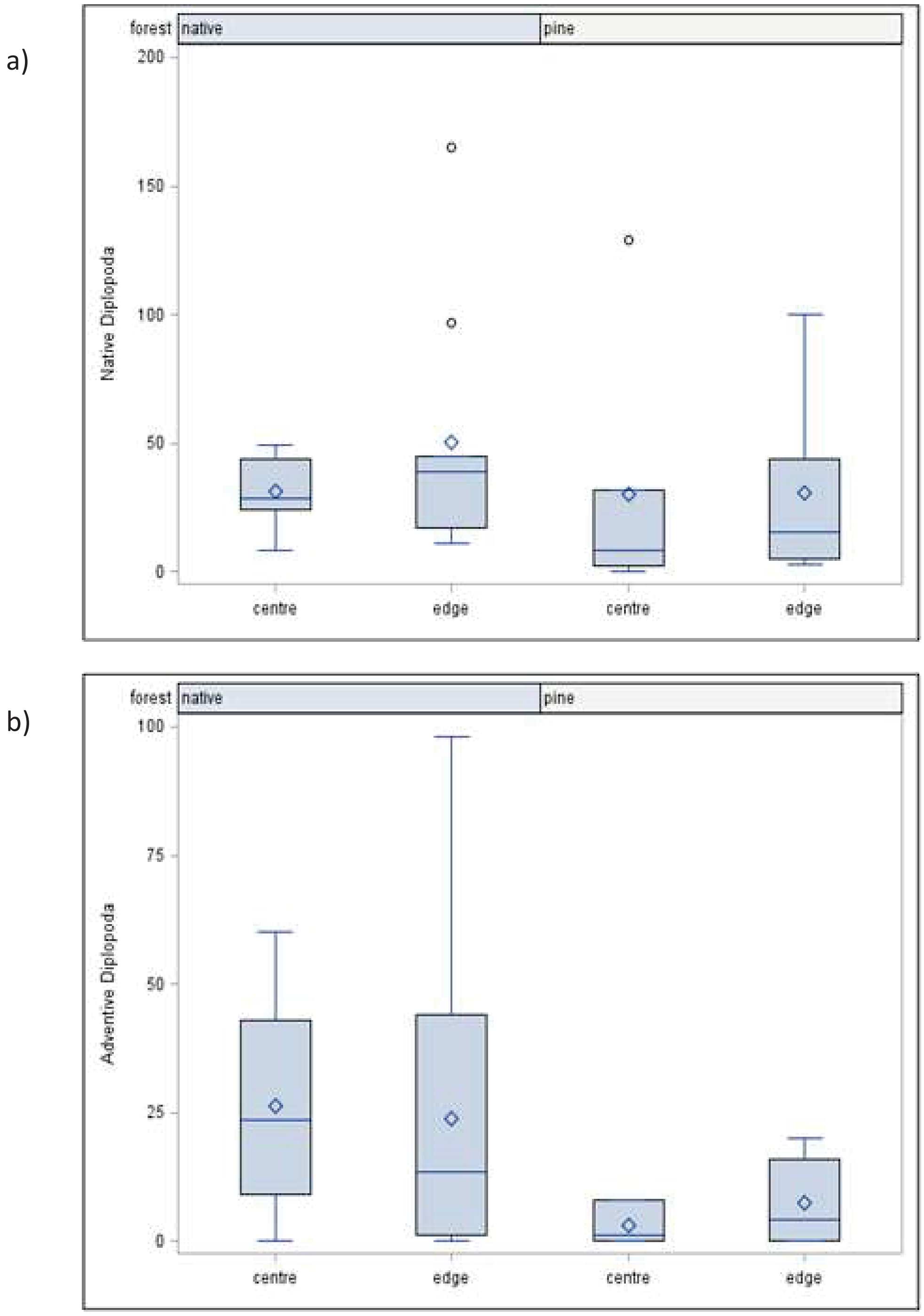


Figure 4.2. Box plot showing abundance of a) native Diplopoda and b) adventive Diplopoda in native and pine forests, in plots at the edge and centre of forests. Median (represented by a line across the box), mean (represented by a diamond), upper and lower quartiles (box represents interquartile range), and the highest and lowest values are shown. Outlying values have been included. The Y-axis shows abundance (sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat, at each forest plot).

Table 4.1. The effect of forest type (pine and native), plot location (edge and centre), and interaction between the two factors on Diplopoda abundance (ANOVA, n = 32). ** indicates a significant value ($\alpha = 0.05$). See Appendix 4 for SAS output for total native and total adventive Diplopoda.

	Effect	**F-value**	**Degrees of freedom**	**p-value**
Native Diplopoda				
Polydesmida total	Forest Plot Forest* plot	0.87 0.14 2.00	28 28 28	0.3591 0.7153 0.1687
Polydesmida sp. 1	Forest Plot Forest* plot	1.25 1.51 1.10	24 15.6 15.6	0.2754 0.2378 0.3111
Polydesmida sp. 2	Forest Plot Forest* plot	0.58 0.58 0.58	10.7 10.7 10.7	0.4615 0.4615 0.4615
Polydesmida sp. 3	Forest Plot Forest* plot	0.18 0.63 0.63	24.4 15 15	0.6743 0.4413 0.4413
Polydesmida sp. 4	Forest Plot Forest* plot	3.82 0.60 0.60	28 28 28	0.0607 0.4462 0.4462
Polydesmida sp. 5	Forest Plot Forest* plot	3.55 0.83 0.52	28 28 28	0.0700 0.3711 0.4765
Polydesmida sp. 6	Forest Plot Forest* plot	2.19 0.71 0.71	27.2 15 15	0.1507 0.4115 0.4115
Polydesmida sp. 7	Forest Plot Forest* plot	1.63 0.42 0.53	23.5 13.3 13.3	0.2140 0.5271 0.4788
Polydesmida sp. 8	Forest Plot Forest* plot	0.38 1.66 0.02	27.9 14.1 14.1	0.5404 0.2187 0.8775
Polydesmida sp. 9	Forest Plot Forest* plot	0.58 0.58 0.58	10.7 10.7 10.7	0.4615 0.4615 0.4615
Polydesmida sp. 10	Forest Plot Forest* plot	1.05 0.02 0.02	28 28 28	0.3136 0.8897 0.8897
Polydesmida sp. 11	Forest Plot Forest* plot	12.75 0.80 0.56	28 28 28	0.0013** 0.3797 0.4585
Polydesmida sp. 12	Forest Plot Forest* plot	0.58 0.58 0.58	10.7 10.7 10.7	0.4615 0.4615 0.4615

Polydesmida sp. 13	Forest	1.11	28	0.3003
	Plot	0.20	28	0.6546
	Forest* plot	0.20	28	0.6546
Polydesmida sp. 14	Forest	0.65	22.2	0.4292
	Plot	0.70	13.3	0.4175
	Forest* plot	2.42	13.3	0.1437
Polydesmida sp. 15	Forest	1.28	26.3	0.2677
	Plot	1.88	21.9	0.1848
	Forest* plot	1.69	21.9	0.2075
Chordeumatida	Forest	0.00	28	1.0000
	Plot	0.09	28	0.7644
	Forest* plot	3.87	28	0.0591
Spirostreptida	Forest	0.82	23.7	0.3748
	Plot	0.03	14.8	0.8587
	Forest* plot	0.03	14.8	0.8587
Siphonophorida	Forest	1.67	26.1	0.2079
	Plot	1.06	20.6	0.3144
	Forest* plot	1.29	20.6	0.2690
Polyzoniida	Forest	3.71	28	0.0642
	Plot	0.06	28	0.8012
	Forest* plot	0.69	28	0.4146
Polyxenida	Forest	0.58	10.7	0.4615
	Plot	0.58	10.7	0.4615
	Forest* plot	0.58	10.7	0.4615
Total native Diplopoda	Forest type	0.29	25.1	0.5980
	Plot	0.56	17.5	0.4654
	Forest* plot	0.52	17.5	0.4805
Adventive Diplopoda				
Cylindroiulus britannicus	Forest	5.40	28	0.0277**
	Plot	0.27	28	0.6080
	Forest* plot	0.02	28	0.8874
Ophyiulus pilosus	Forest	1.08	23.4	0.3083
	Plot	0.70	15.1	0.4149
	Forest* plot	1.09	15.1	0.3129
Brachyiulus pusillus	Forest	0.01	23.7	0.9341
	Plot	2.92	14.6	0.1087
	Forest* plot	0.00	14.6	0.9811
Nopoiulus kochii	Forest	0.58	10.7	0.4615
	Plot	0.58	10.7	0.4615
	Forest* plot	0.58	10.7	0.4615
Blaniulus guttulatus	Forest	0.97	20.5	0.3365
	Plot	0.50	11.3	0.4917
	Forest* plot	0.50	11.3	0.4917
Total adventive Diplopoda	Forest type	5.67	24.3	0.0254**
	Plot	0.03	15.8	0.8733
	Forest* plot	0.17	15.8	0.6835

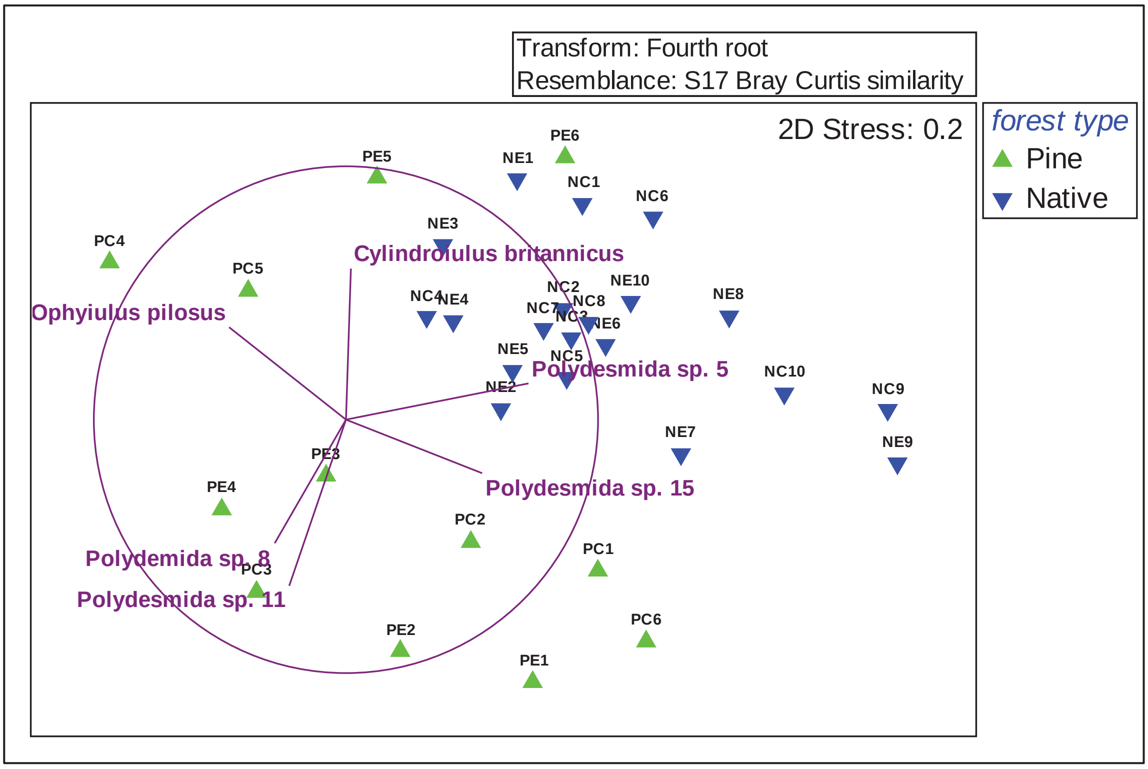


Figure 4.3. Non-metric multidimensional scaling ordination representing Diplopoda community composition in native and pine forest plots. See appendix for a list of sites that correspond to site labels. Vectors of taxa with a Spearman correlation value >0.5 have been included.

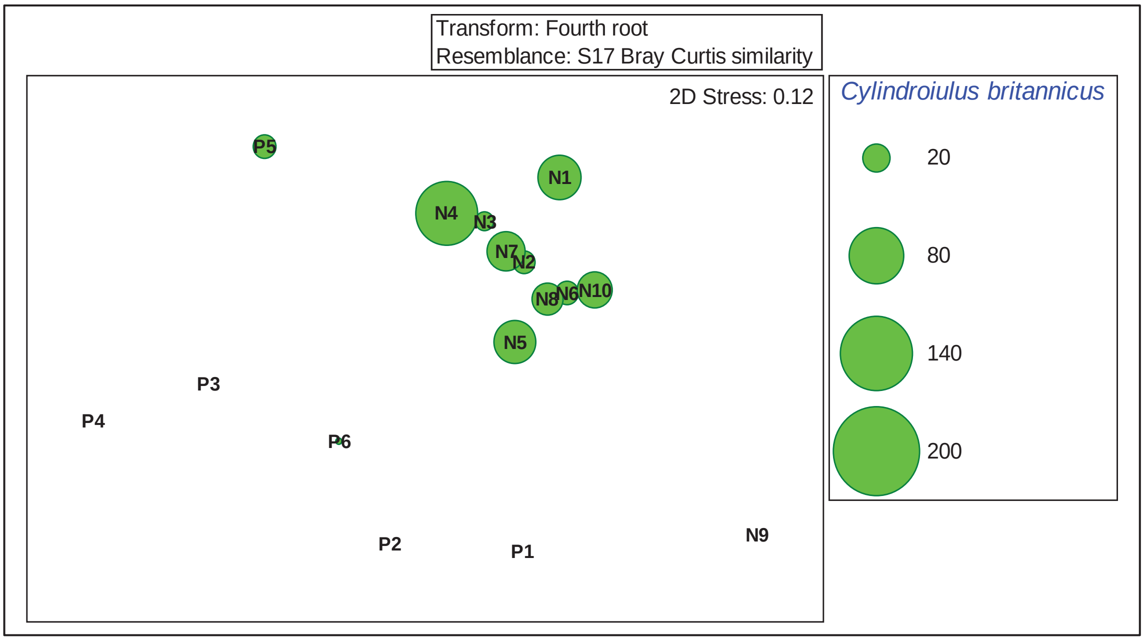


Figure 4.4. Non-metric multidimensional scaling ordination (bubble plot) displaying the abundance of *C. britannicus* (Diplopoda) in sampled forests. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat at each forest plot. Data from edge and centre plots were pooled. N = native forest, P = pine forest. For site codes see Appendix 3.

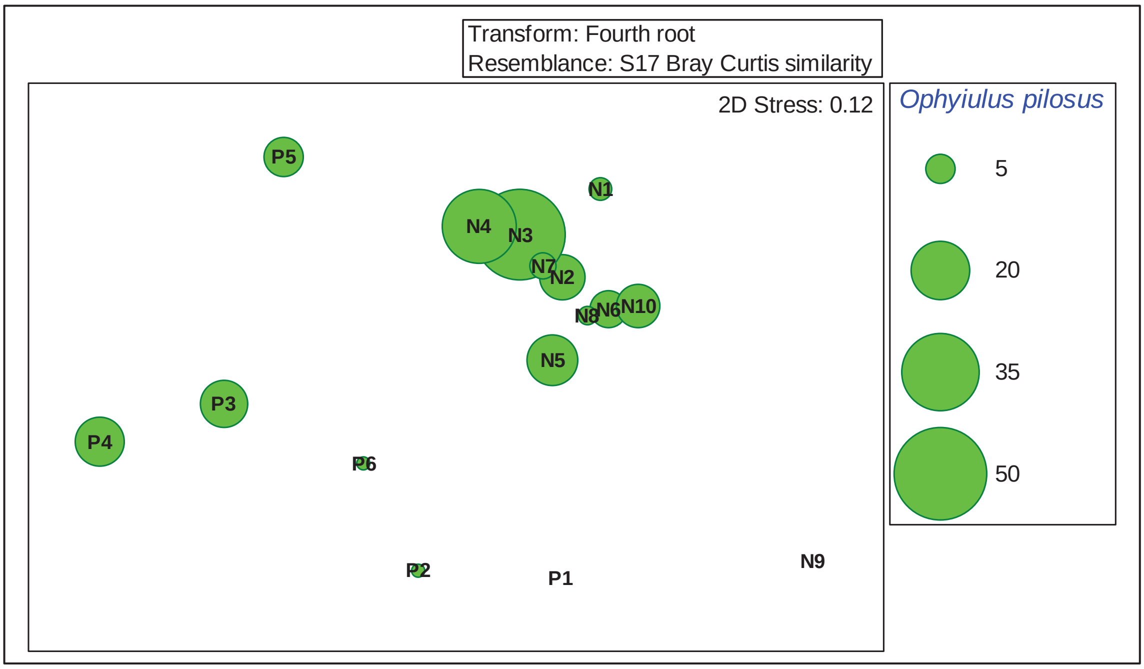


Figure 4.5. Non-metric multidimensional scaling ordination (bubble plot) displaying the abundance of *O. pilosus* (Diplopoda) in sampled forests. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat at each forest plot. Data from edge and centre plots were pooled. N = native forest, P = pine forest. For site codes see Appendix 3.

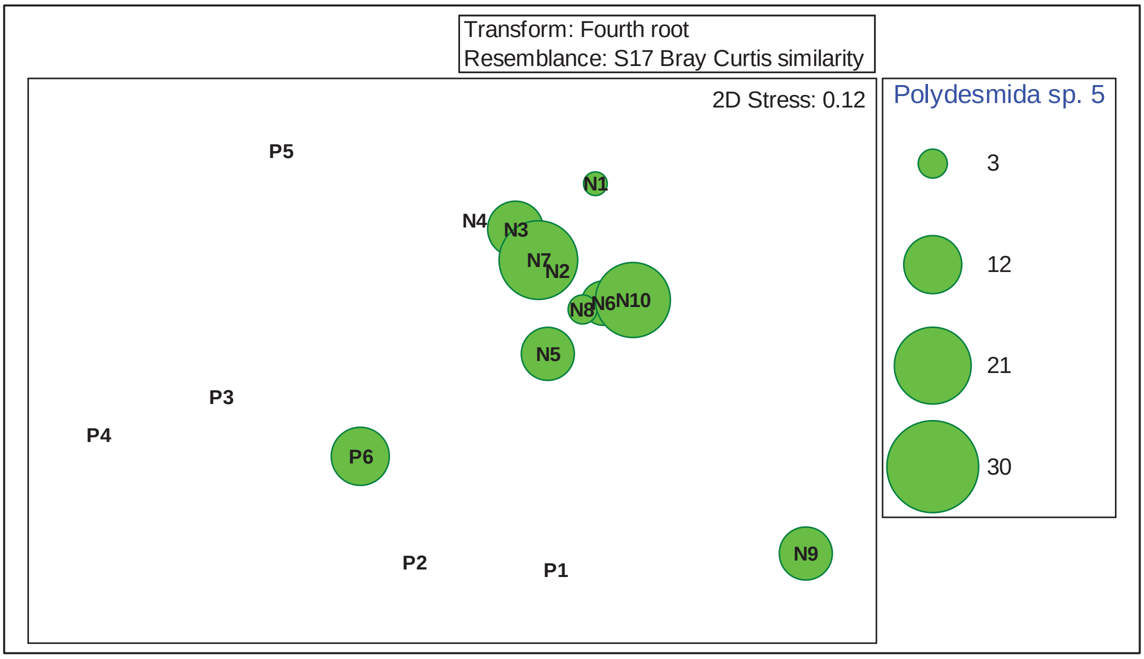


Figure 4.6. Non-metric multidimensional scaling ordination (bubble plot) displaying the abundance of Polydesmida morphospecies 5 (Diplopoda) in sampled forests. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat at each forest plot. Data from edge and centre plots were pooled. N = native forest, P = pine forest. For site codes see Appendix 3.

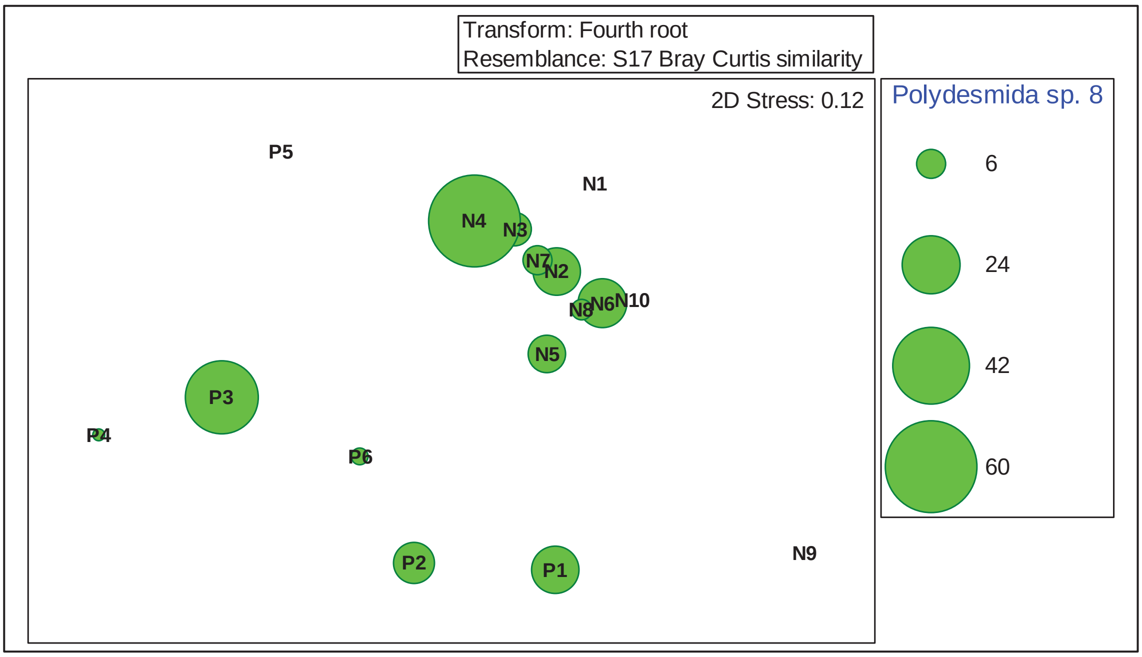


Figure 4.7. Non-metric multidimensional scaling ordination (bubble plot) displaying the abundance of Polydesmida morphospecies 8 (Diplopoda) in sampled forests. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat at each forest plot. Data from edge and centre plots were pooled. N = native forest, P = pine forest. For site codes see Appendix 3.

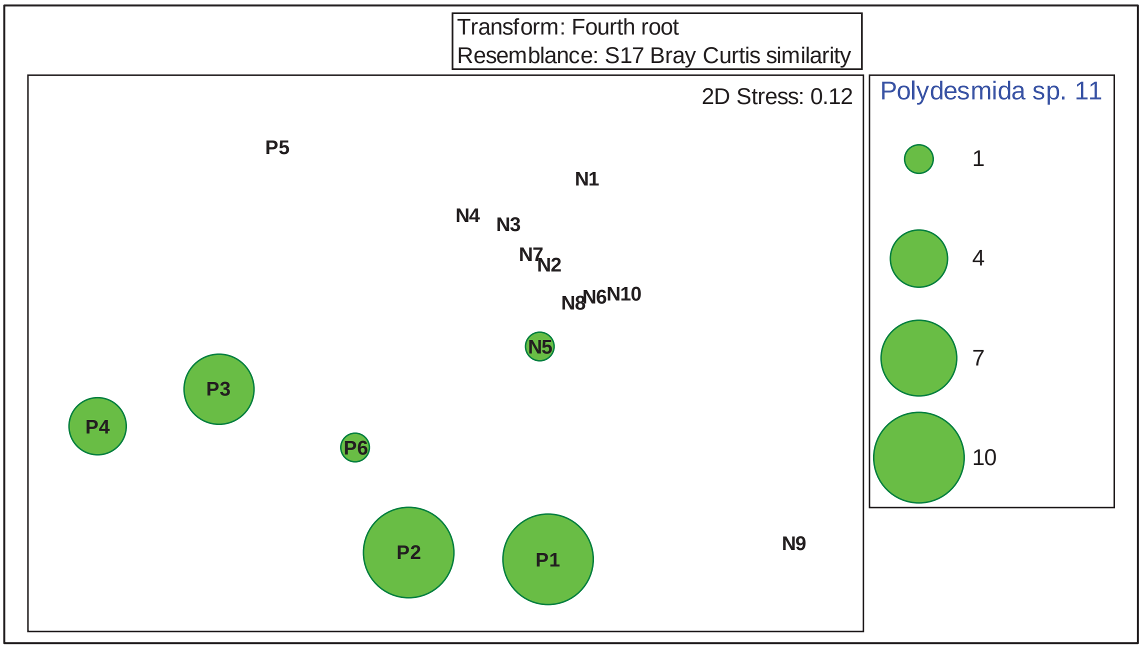


Figure 4.8. Non-metric multidimensional scaling ordination (bubble plot) displaying the abundance of Polydesmida morphospecies 11 (Diplopoda) in sampled forests. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat at each forest plot. Data from edge and centre plots were pooled. N = native forest, P = pine forest. For site codes see Appendix 3.

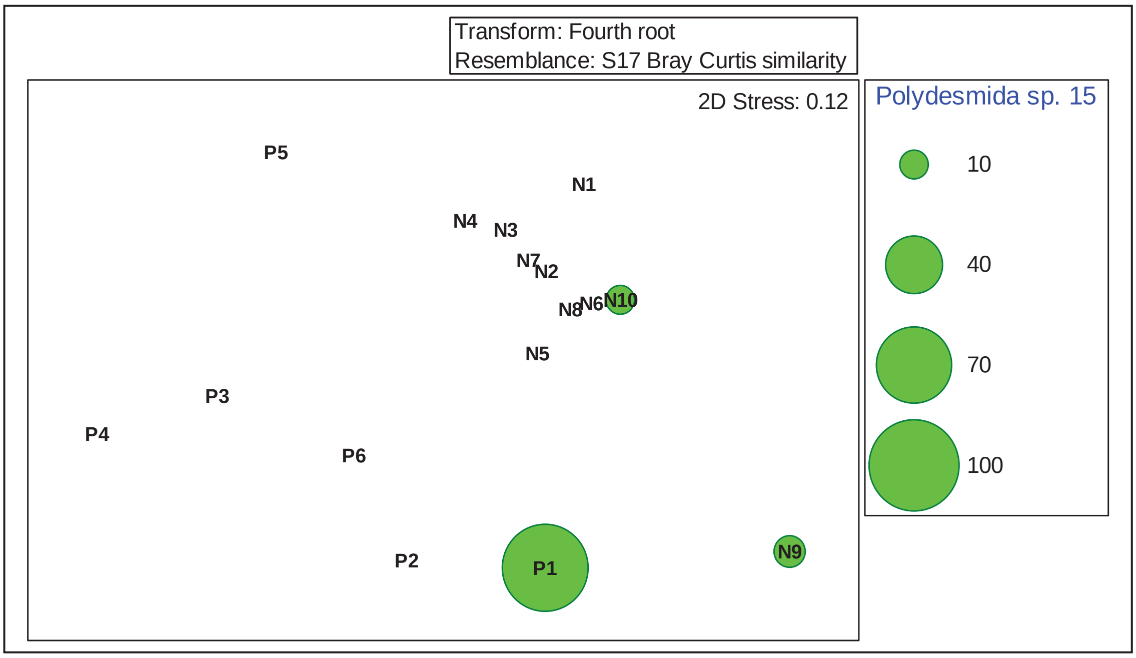


Figure 4.9. Non-metric multidimensional scaling ordination (bubble plot) displaying the abundance of Polydesmida morphospecies 15 (Diplopoda) in sampled forests. Abundance is the sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat at each forest plot. Data from edge and centre plots were pooled. N = native forest, P = pine forest. For site codes see Appendix 3.

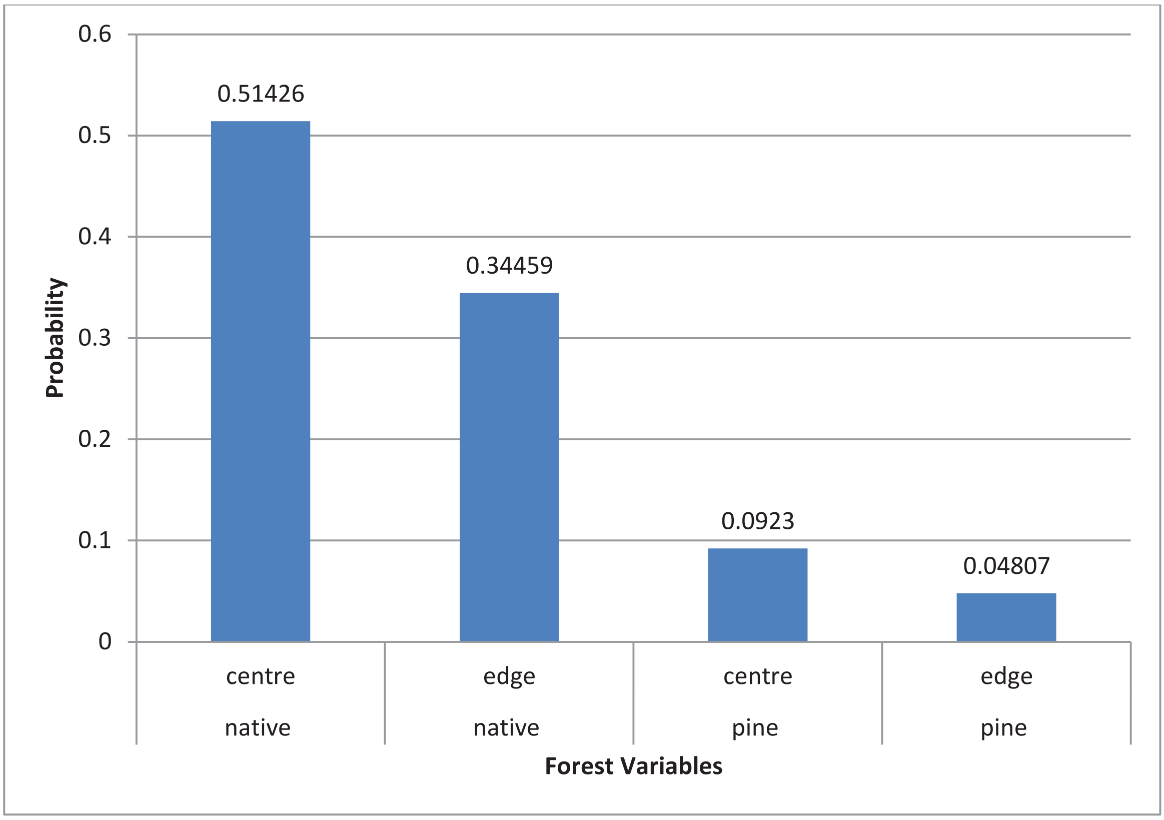


Figure 4.10. The probabilities that a randomly collected Diplopoda individual would be adventive depending on forest type (native forest or pine forest) and plot location (forest edge or centre) (logistic regression, p-value = <.0001 for both forest type and plot location).

4.2.3. Isopoda[6]

There was a trend that higher abundances of native Isopoda were found in native forests; however, this trend was not significant (Fig. 4.11, Table 4.2). There was no indication that native Isopoda were more abundant at either the centre or edge of forests (Fig. 4.11, Table 4.2). Overall, there was a low number of adventive Isopoda

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[6] Since the submission of this thesis, it has come to my attention that the Isopoda identified in this thesis as adventive *H. danicus* is an undescribed native species. The results of statistical analysis for Isopoda may be biased by this fact, and the conclusions should be treated with caution. The manuscript based on this thesis is in preparation to be published as a research paper, and the Isopoda material will be reviewed and re-analysed for the upcoming publication.

found. Adventive Isopoda seemed more abundant in edge habitats, although this pattern was not significant, and were not influenced by forest type (Fig. 4.11, Table 4.2). Among individual Isopoda families and morphospecies, none were influenced by plot location (Table 4.2). Native Armadillidae were the only family significantly influenced by forest type, and were more abundant in native forests, but the influence of forest type was not evident for individual morphospecies (Table 4.2). Forest type (R value = 0.131, level of significance = 0.062) and plot location (R value = 0.048, level of significance = 0.186) had no significant influence on Isopoda community structure, although forest type would be significant if a lower significance level was accepted (α = 0.1).

Both forest type and plot location influenced the probability that a randomly collected Isopoda individual would be adventive (see Apendix 3 for SAS output). It is more likely that any Isopoda found would be adventive if it was found at the edge of a forest (Wald Chi-square = 19.6119, p-value = <.0001). Similar to Diplopoda, it is also more likely that an Isopoda would be adventive if it was found in a native forest (Wald chi-square = 4.9420, p-value = 0.0256). The highest probability (0.171) that any located Isopoda would be an adventive species would be at the edge of a native forest, and the lowest probability (0.029) that an Isopoda would be adventive is at the centre of a pine forest (Fig. 4.12), but overall the probabilities of encountering an adventive species are very low (<20%) everywhere.

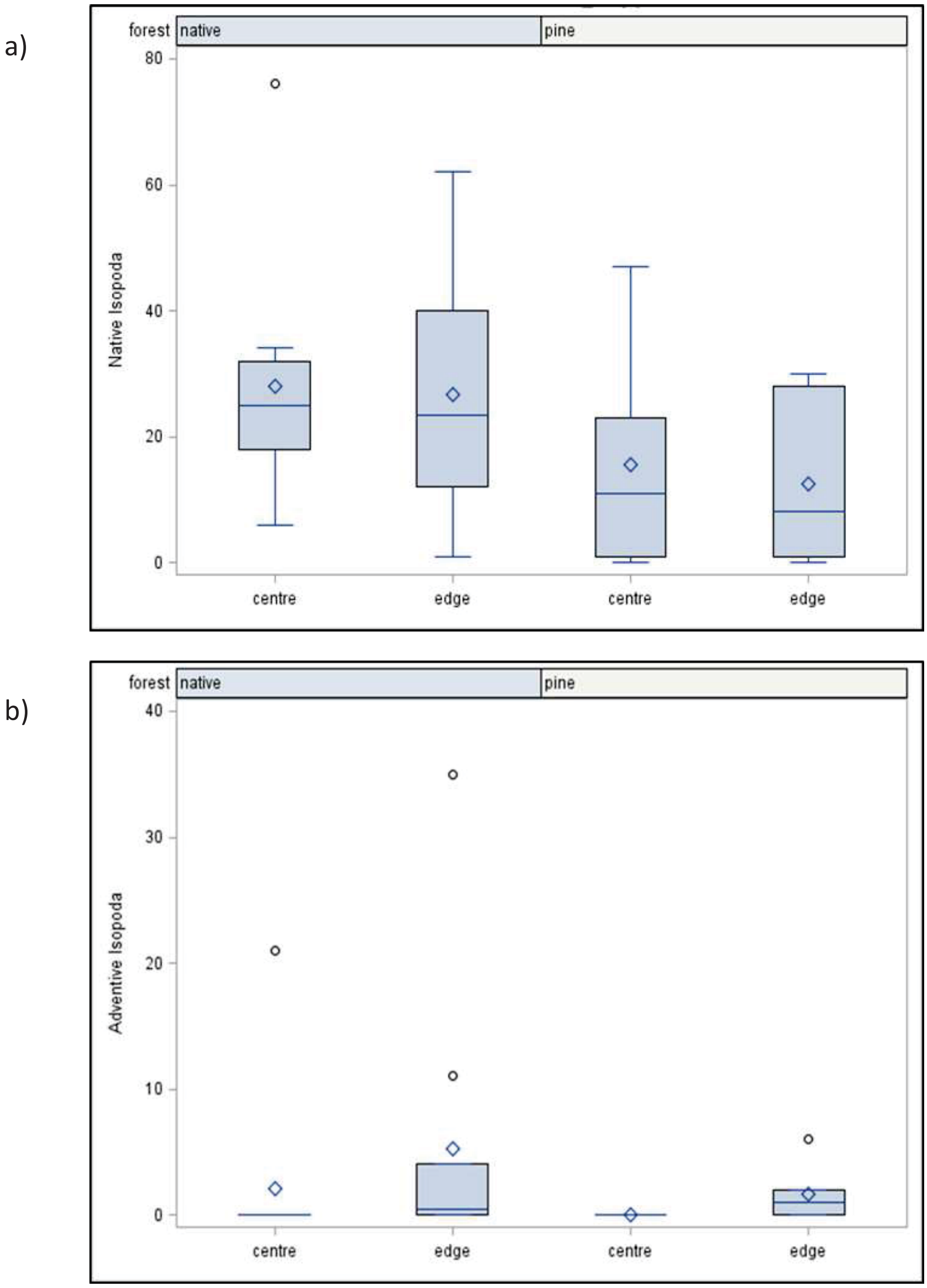

Figure 4.11. Box plot showing abundance of a) native Isopoda and b) adventive Isopoda in native and pine forests, in plots at the edge and centre of forests. Median (represented by a line across the box), mean (represented by a diamond), upper and lower quartiles (box represents interquartile range), and the highest and lowest values are shown. Outlying values have been included. The Y-axis shows abundance (sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat, at each forest plot).

Table 4.2. The effect of forest type (pine and native), plot location (edge and centre), and interaction between the two factors on Isopoda abundance (ANOVA, n=32). ** indicates a significant value (α = 0.05). See Appendix 4 for SAS output for total native and total adventive Isopoda.

	Effect	**F-value**	**Degrees of freedom**	**p-value**
Native Isopoda				
Styloniscidae	Forest Plot Forest* plot	0.81 0.28 3.27	27.9 15.1 15.1	0.3773 0.6024 0.0904
Oniscidae	Forest Plot Forest* plot	2.23 0.02 0.02	27.1 14.3 14.3	0.1466 0.8956 0.8956
Philosciidae	Forest Plot Forest* plot	0.31 0.01 1.69	27.8 14.8 14.8	0.5836 0.9300 0.2139
Armadillidae total	Forest Plot Forest* plot	5.32 0.00 0.65	23.3 15.2 15.2	0.0304 ** 0.9846 0.4334
Armadillidae *Cubaris* sp. 1	Forest Plot Forest* plot	2.08 0.15 0.15	28 28 28	0.1601 0.6969 0.6969
Armadillidae *Cubaris* sp. 2	Forest Plot Forest* plot	1.79 1.45 1.45	24.3 15.9 15.9	0.1932 0.2460 0.2460
Armadillidae sp. 3	Forest Plot Forest* plot	1.89 0.24 0.24	27.7 14.9 14.9	0.1804 0.6287 0.6287
Armadillidae sp. 4	Forest Plot Forest* plot	0.68 0.68 2.33	28 28 28	0.4182 0.4182 0.1382
Total native Isopoda	Forest Plot Forest* plot	2.95 0.18 0.03	27.7 14.7 14.7	0.0972 0.6748 0.8760
Adventive Isopoda				
Armadillidiidae	Forest Plot Forest* plot	0.58 0.58 0.58	10.7 10.7 10.7	0.4615 0.4615 0.4615
Trichoniscidae	Forest Plot Forest* plot	1.32 0.55 0.14	28 28 28	0.2605 0.4649 0.7138

Porcellionidae	Forest Plot Forest* plot	4.38 4.38 4.38	14.6 14.6 14.6	0.0543 0.0543 0.0543
Total adventive Isopoda	Forest Plot Forest* plot	1.10 0.79 0.07	28 28 28	0.3037 0.3829 0.7918

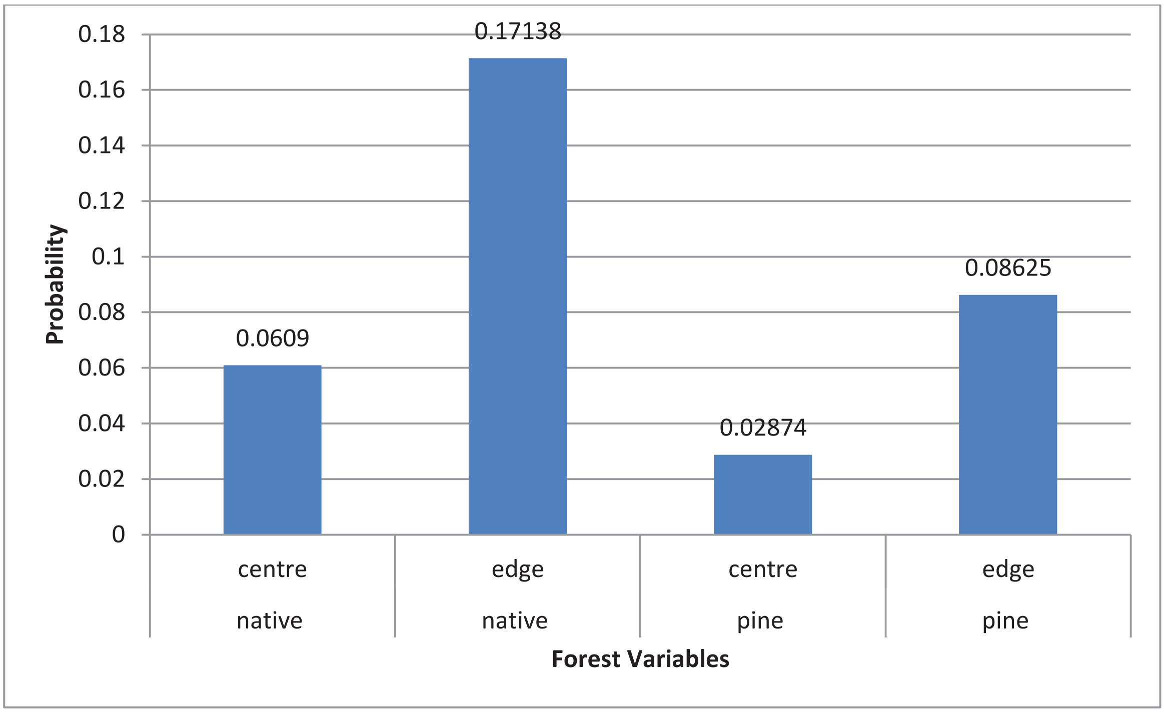

Figure 4.12. The probabilities that a randomly collected Isopoda individual would be adventive depending on forest type (native forest or pine forest) and plot location (forest edge or centre) (logistic regression, p-value = 0.0256 for forest type, p-value = <.0001 for plot location).

4.2.4. Amphipoda

Native Amphipoda were more abundant in native forests than in pine forests; however, this was not significant in the ANOVA due to one outlying value (Fig. 4.13, Table 4.3). This is because although native Amphipoda were only found in one pine forest, they were found there at high abundance. *Puhuruhuru aotearoa* was significantly more abundant in native forests, while *Parorchestia tenuis* was not influenced by forest type (Table 4.3). Plot location did not influence the total number of native Amphipoda, or the abundance of *P. tenuis* or *P. aotearoa* when they were considered separately (Table 4.3). Adventive Amphipoda were found at higher abundances than natives across all habitat types; neither forest type nor plot location had any influence on the abundance of adventive Amphipoda *Arcitalitrus* (Fig. 4.13, Table 4.3). Forest type (R value = -0.067, level of significance = 0.786) and plot location (R value = -0.034, level of significance= 0.605) had no influence on Amphipoda community structure.

The results of logistic regression suggest the probability that a randomly collected Amphipoda individual would be adventive is significantly higher if it was found in a native forest (Wald chi-square = 8.5429, p-value = 0.0035) (see Apendix 3 for SAS output), this is due to higher abundance of adventive Amphipoda in native forests overall. If alpha = 0.1 is accepted, it is more likely that any Amphipoda found would be adventive if it was found at the edge of a forest (Wald Chi-square = 3.3263, p-value = 0.0682). The highest probability (0.837) that any located Amphipoda would be an adventive species is if it was found at the edge of a native forest and the lowest probability (0.726) of an Amphipoda being adventive is at the centre of a pine forest (Fig. 4.14); but overall the chances of finding an adventive species are very high (>70%) everywhere.

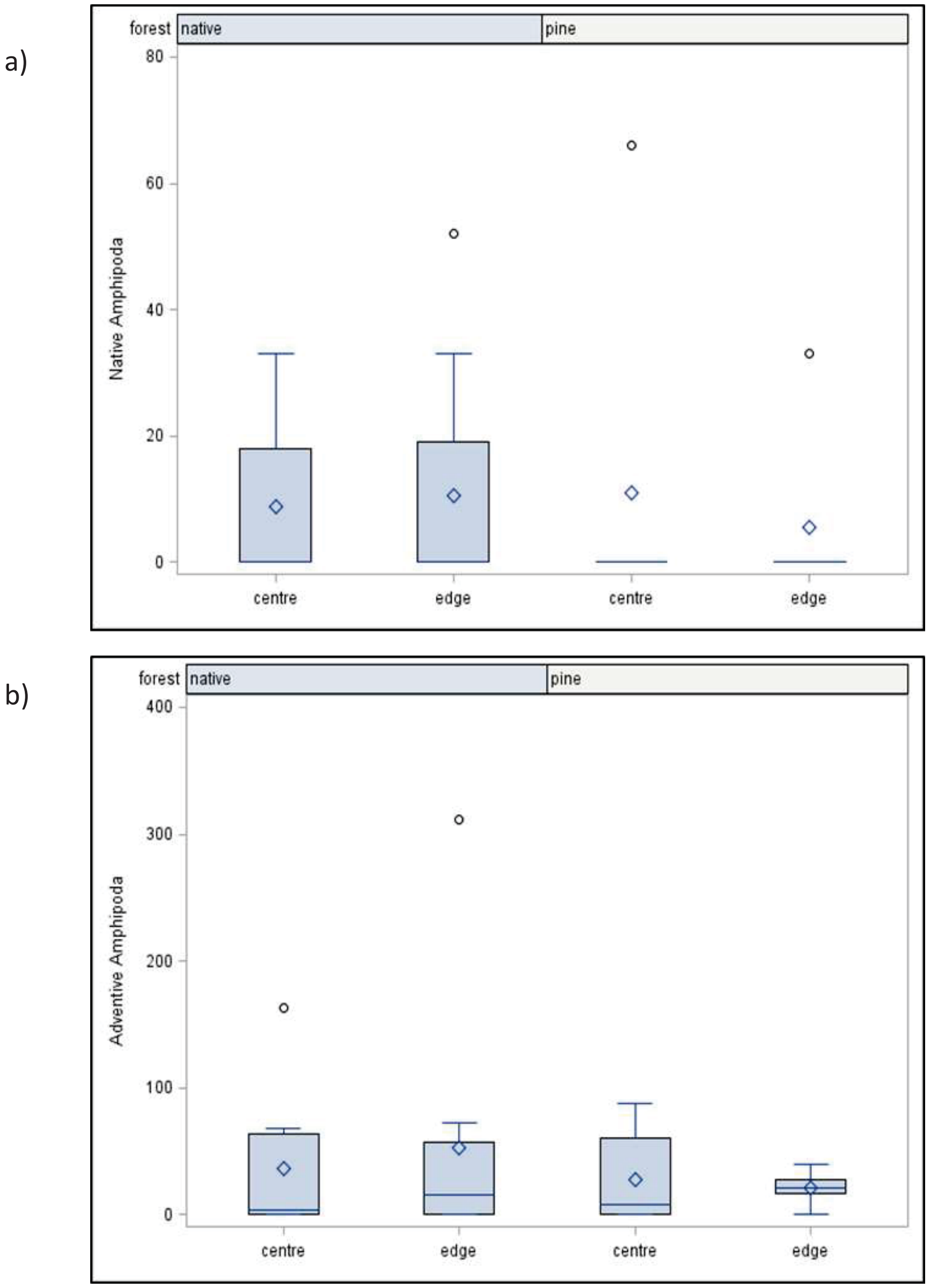

Figure 4.13. Box plot showing abundance of a) native Amphipoda and b) adventive Amphipoda in native and pine forests, in plots at the edge and centre of forests. Median (represented by a line across the box), mean (represented by a diamond), upper and lower quartiles (box represents interquartile range), and the highest and lowest values are shown. Outlying values have been included. The Y-axis shows abundance (sum of individuals collected from five 25 cm x 25 cm leaf litter samples and from logs found in a 10 m x 10 m quadrat, at each forest plot).

Table 4.3. The effect of forest type (pine and native), plot location (edge and centre), and interaction between the two factors on Amphipoda abundance (ANOVA, n=32). ** indicates a significant value (α = 0.05). See Appendix 4 for SAS output for total native and total adventive Amphipoda.

	Effect	F-value	Degrees of freedom	p-value
Puhuruhuru aotearoa	Forest Plot Forest* plot	7.33 0.40 0.91	25.5 14.8 14.8	0.0119 ** 0.5392 0.3542
Parorchestia tenuis	Forest Plot Forest* plot	1.18 0.79 0.17	27 19.6 19.6	0.2865 0.3860 0.6810
Total native Amphipoda	Forest Plot Forest* plot	0.19 0.21 0.83	28 17.5 17.5	0.6631 0.6492 0.3736
Adventive Amphipoda (*Arcitalitrus*)	Forest Plot Forest* plot	0.17 0.06 0.35	26.8 14.5 14.5	0.6810 0.8164 0.5647

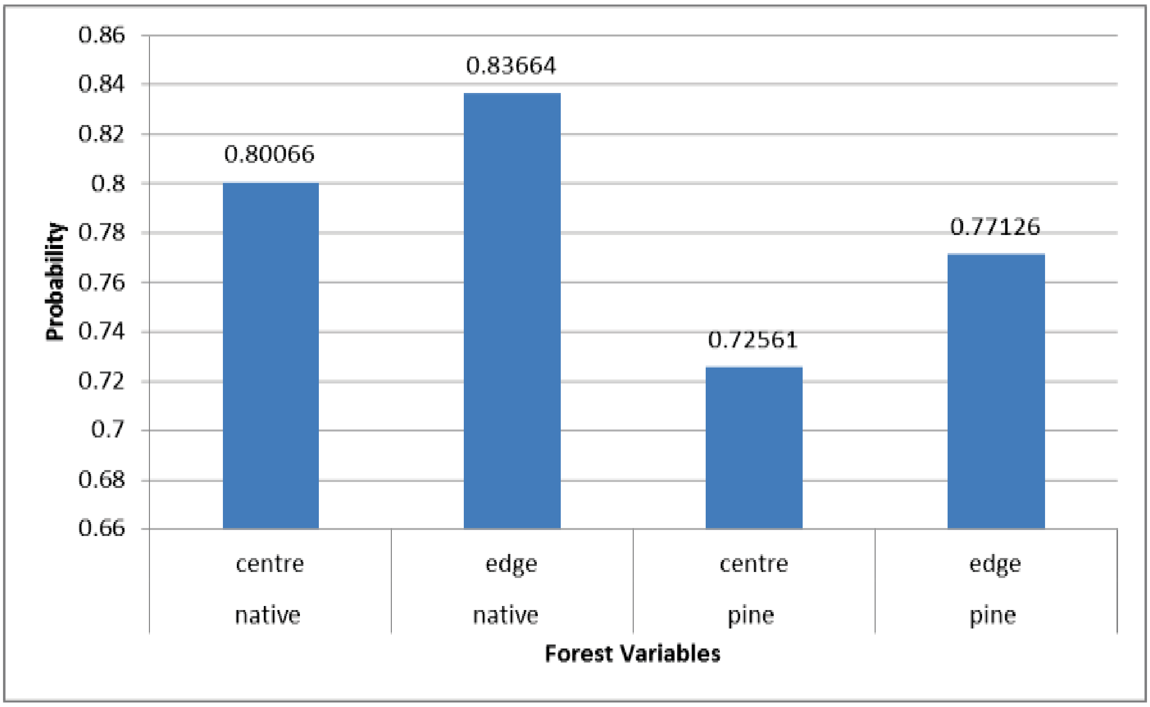

Figure 4.14. The probabilities that a randomly collected Amphipoda individual would be adventive depending on forest type (native forest or pine forest) and plot location (forest edge or centre) (logistic regression, p-value = 0.0035 for forest type, p-value = 0.0682 for plot location).

4.3. Discussion

4.3.1. Native and adventive detritivore abundance patterns and the effect of forest type

Overall, native Diplopoda in this study were as abundant in pine forests as they were in native forests, and native Polydesmida morphospecies 11 was more abundant in pine forests. The abundance of adventive Diplopoda was higher in native forests, due to the higher abundance of *C. britanicus*. Car (2010) found that in Australia pine plantations could support as many native Diplopoda (both in abundance and species richness) as native forests, although only the family Paradoxosomatidae were sampled. However, for this to occur it was recognised that pine plantations should be close to native forest for colonisation and be free from leaf litter disturbance (Car, 2010). In another Australian study, native Diplopoda of the of the orders Chordeumatida, Polyzonidae, and Polydesmida were also found to be as abundant in pine plantations as they were in native forests (Bonham et al., 2002).

In general, abundance of terrestrial Isopoda (whether taxa are native or adventive was not specified) is believed to be lower in intensively managed forests (Paoletti & Hassall, 1999). However, in this study Armadillidae was the only taxon found to be lower in managed pine forests, and this trend was not observed in individual Armadillidae morphospecies. Adventive Isopoda abundance did not differ between forest types in this study, and while there was a trend for lower abundance of native Isopoda in pine forest, this trend was not significant. It should be noted that the decrease in Isopoda abundance found in earlier work was partially due to the direct effects of pesticides that are often applied in managed plantation forests (Paoletti & Hassall, 1999). In this study, the only pesticides used in the pine forests were laid out in bait stations and similar bait stations were also used in a number of native forests (personal observation); therefore, pesticide could not be responsible for any difference between the two forest types. In a study in the Mediterranean basin, Isopoda were the only Arthropoda group found not to have a lower abundance in *Eucalyptus* plantations compared with native woodland, and this was attributed to the fact that Isopoda are detritivores which would benefit from the abundance of leaf litter present (Zahn, Rainho, Rodrigues, & Palmeirim, 2009).

For Amphipoda, previous studies have concluded that both native and adventive species can be present in native and pine forests, and the abundance patterns between forest types were inconsistent (Ratsirarson, Robertson, Picker, & Van Noort, 2002; Borkin, Goodman, Mayhew, & Smith, 2007). A New Zealand study found Amphipoda abundance to be similar between *Pinus radiata* plantations and native kanuka-manuka (*Kunzea ericoides - Leptospermum scoparium*) forests, but the abundance was greater in plantations of Douglas fir (*Pseudotsuga menziesii*); however, it was not determined if Amphipoda were native or adventive species (Borkin et al., 2007). The native *P. aotearoa* (the only species to be influenced by forest type in this study) was less abundant in pine forests. Similarly, a native Amphipoda (*Talitriator setosa* (Barnard, 1940)) in South Africa had lower abundance in *Eucalyptus* and pine plantations than in native forest (Ratsirarson et al., 2002). A study conducted in Britain found the abundance of adventive Amphipoda (*Arcitalitrus dorrieni*) in coniferous forests to be lower than in native deciduous forests (Spicer & Tabel, 1996). In this study, ANOVA analysis showed no significant difference in abundance of native

Amphipoda in pine and native forests. However, this was more of a reflection of the lack of native Amphipoda in native forest remnants (only found in half of the native forest sites) than the abundance in which they were found in pine forests. In fact, Kahutarawa was the only pine site that contained native Amphipoda.

My original expectation was that the abundance and diversity of adventive species would be higher in pine plantations than in native forests, because it is believed that disturbance is more frequent and intense in plantation forests compared with native forests, and disturbance is known to facilitate the establishment of adventive species (Lozon & MacIsaac, 1997; Pawson et al., 2008). The difference in abundance of adventive species between forest types would be further exaggerated if native forests in New Zealand were resistant to the invasion of adventives. Disturbance and the resistance of native forests to invasion provided an explanation for why more adventive beetles were found in pine forests than in native forests in New Zealand (Pawson et al., 2008). However, in this study higher abundance of adventives in pine forests was not found for any of the three detritivore groups, and adventive Diplopoda were actually more abundant in native forests. While the combined abundance values reveal that pine forests can support as many native detritivore taxa as native forests, when the analysis was done at a lower taxonomic level, it showed that forest type had a significant influence on the Diplopoda (and perhaps Isopoda) community structure. Forest type also significantly influenced the probability that a randomly collected individual of Diplopoda, Isopoda or Amphipoda would be an adventive species. Some taxa (Oniscidae, Polyxenidae and Spirostreptida) were found in native forests but never found in pine forests (Chapter 3). If we accept an alpha value of 0.1, total native Isopoda, Polyzoniida, and Polydesmida morphospecies 4 and 5 were also more abundant in native forests and adventive Porcellionidae were more abundant in pine forests. Native forests have previously been found to contain different invertebrate communities with a wider range of taxa than pine plantations (Robson et al., 2009). In California, exotic plantations of *Eucalyptus* had a different invertebrate community composition to that of native forest (49% of invertebrate species sampled did not occur in both forest types) (Sax, 2002). Previous work found that species abundant in one forest type (either native or plantation) were usually abundant in the other and it was the rare species that tend to only be present in one forest type (Sax, 2002). The most dominant response of ground-living invertebrates to vegetation of exotic origin has been found to occur at species level, although a response due to structural difference can be evident at order and family level (Samways et al., 1996). Many taxa in this study were only identified to order or family level and in this case a response at species level may have been masked. However, the taxa that were identified to species level (Amphipoda, Polydesmida, Julida, and Armadillidae) did not show more of a response to forest type (except for *P. aotearoa* and Polydesmida morphospecies 11) than the groups at higher classification.

Overall, my results are not too surprising, as response of invertebrates to the development of pine plantations is poorly understood (Sax et al., 2005). Although adventive detritivore species have often been described as dominant in disturbed environments such as intensively managed forests (Paoletti et al., 2007), other authors (e.g., Mesibov, 2005) suggested that there is likely to be considerable variation in the ability of different invertebrates to persist in farmed landscapes such as plantation forests. Therefore, results from comparing invertebrate fauna between native and plantation forests may be expected to differ depending on the detritivore group sampled. Bonham *et al.* (2002) found that many invertebrate taxa (including Diplopoda) were as abundant in pine forests as they were in native forests, and the only differential response was seen in adventive snails, which had higher abundance in pine plantations. Robson *et al.* (2009) found that total invertebrate abundance in Jenolan Caves area of New South Wales was higher in pine plantations compared to neighbouring native forests, but mainly due to the aggregation of Acari and Collembola. While the higher abundance of adventive Diplopoda in native forests compared to pine forests in this study may seem a surprising result, the response of invertebrates has been described as “idiosyncratic” when comparing between native and pine forest habitat (Car, 2010).

It is possible that the lack of effect of forest type on detritivores in this study was because a number of native forests sampled were close to urban areas and have suffered from high disturbance. Native forest disturbance was mainly due to recreational use by the public, this was particularly high for the small urban remnants (personal observation). Human activity is a disturbance factor which has commonly been identified to encourage the establishment of adventive animals (Lozon & MacIsaac, 1997). It is also possible that disturbance actually has little to do with the invasion of adventives. In a review, disturbance was found to facilitate the establishment of adventive animals only 28% of the time and may be less important for the invasion of animals than it is for plants (Lozon & MacIsaac, 1997). Parameters other than anthropogenic disturbance are believed to be responsible for the success of adventive invertebrate species on the Canary Islands (although these parameters have not been identified) (Arndt & Perner, 2008). While it is believed that much of New Zealand’s native biota is better adapted to a low disturbance regime than adventive species, because a large number of New Zealand native taxa are k-selected species with long lives and low reproductive rates (Kelly & Sullivan, 2010), New Zealand's native detritivores may be no longer-lived than adventive species. Adventives are not always found to be more abundant in planted or disturbed forests – as previously mentioned, a British study found the abundance of adventive Amphipoda *Arcitalitrus dorrieni* to be higher in native deciduous forests compared to coniferous forests (Spicer & Tabel, 1996). Adventive Diplopoda had a higher abundance in what was perceived as less disturbed forest habitat in Arndt and Perner's (2008) study on the Canary Islands.

Overall, adventive detritivores were not found to be any less abundant in native forests compared to pine in this study, suggesting that native forests do not provide a barrier to invasion by adventive detritivores. Similarly, the abundance of many native detritivore taxa did not vary between native and pine forests. Ratsirarson *et al*. (2002) expected that native detritivores would occupy plantation forests more readily than herbivorous invertebrates, because, despite the differences in leaf-litter composition, plant matter in a decomposed state is expected to be more similar between native forests and plantations than when in a fresh state, due to breakdown of complex secondary compounds. Detritivores are known to be more successful at colonising and exploiting newly available niches than other trophic groups (Samways et al., 1996; Hoare, 2001; Brockerhoff et al., 2010); this provides an explanation as to why no resistance of native forests to detritivore invasion was evident in this study.

4.3.2. Edge effects

There was no significant effect of plot location (edge vs. centre) on abundance of any of the detritivore groups investigated in this study. The only evidence for response to edge habitat found in this study was an increase in abundance of adventive Isopoda at edge habitat and this was not found to be significant. However, if an alpha value of 0.1 had been accepted, Porcellionidae would have been significantly more abundant in edge habitat.

Although invertebrates exhibit a variety of responses to edge effects (Didham, 1997), some previous New Zealand studies also found that edge effects had little impact on the abundance of forest floor invertebrates (Norton, 2002). Out of 13 orders of invertebrates sampled by Bolger *et al.* (2000) in California, all orders except the native Diptera and non-ant Hymenoptera (which increased in abundance towards the edge of the forest), and Collembola (which increased in abundance toward the forest centre) showed no response to the edge. The abundance of terrestrial Isopoda (dominated by adventive species) was unaffected by proximity to the edge of scrub remnant patches (Bolger et al., 2000). A common response of invertebrates is that there will be an increase in abundance and diversity at forest edge. This is due to an influx of species from human-modified areas outside of the forest into the disturbed forest edge (Didham, 1997). One study even described the invertebrate community in a native woodland forest edge as more similar to that in the surrounding fields than to that in internal forest habitat (Bedford & Usher, 1994). An Australian study on Coleoptera identified an edge effect which penetrated 100 m into fragments and caused an increase in the occurrences of detritivores and fungivores at the edge (this may have been in response to an increase in litter and dead wood on the forest floor, and also an increase in fungal spores) (Davies et al., 2001). It has been noted that there are a range of responses of invertebrates to forest edge, and it is site- and taxon-dependent (Didham, 1997). Higher trophic levels are often considered to be more sensitive to fragmentation and edge effects (Bolger et al., 2000). Detritivores in general, being a low trophic level, may not be sensitive to the effects of fragmentation including edge effects; this has been demonstrated for detritivorous Coleoptera (Didham et al., 1998).

While plot location did not significantly affect the abundance of detritivores in this study, it did influence the prediction that any collected Diplopoda, Isopoda, and possibly Amphipoda would be adventive. For Isopoda and Amphipoda (if the alpha value is increased to 0.1), the probability of an individual being an adventive was higher at the edge of a forest. For Isopoda, edge habitat was a more influential predictor of origin (native or adventive) than forest type. In contrast, the probability of encountering an adventive individual of Diplopoda was lower in edge habitats; this is due to high overall abundance of adventive Diplopoda in centre plots.

Edge habitats could promote the invasion of adventive species into what remains of the native habitat (Norton, 2002; Hickerson et al., 2005). As previously mentioned, there is often an influx of species from human-modified areas outside of the forest into the edge habitat (Didham, 1997). Evidence of this was provided by a USA study which found that an adventive species of Chilopoda was more abundant in the edge habitat and a native species was more abundant in the forest centre. Although the adventive species was present at the majority of interior sites, the native

Chilopoda was rarely found at edge sites (Hickerson et al., 2005). Invasion of Argentine ants (*Linepithema humile*) into native scrub provides another example of higher abundance of adventive species in edge habitat. *L. humile* was most abundant along edges of scrub habitat with decreased densities found with distance from the edge and in larger unfragmented areas *L. humile* was only found at the edge. Native ant diversity was negatively correlated with the presence of *L. humile* (Suarez et al., 1998) and the displacement of native ant species from the exterior of shrub fragments was classified as an edge effect (Holway & Suarez, 2006). In my study there was some evidence that adventive Isopoda species more easily invade, or prefer, edge habitats; adventive and native Diplopoda co-occurred throughout forests.

The uncertainty that surrounds edge effects makes testing for them a difficult task. Firstly, there could be one or more unidentified factors operating on the abundance of detritivores, and response to edge may be undetectable due to an interaction between two or more confounding variables that obscure or neutralize each other (Murcia, 1995; Didham, 1997). For example, Bolger *et al*. (2000) showed Diptera and Coleoptera tend to increase in abundance closer to the edge, but this effect was cancelled out due to their aversion to argentine ants, which had higher abundance towards edges of forests. Secondly, scale is of crucial importance when studying fragmentation effects (including edge effects), as it can influence perceptions of patterns and processes (Murcia, 1995; Didham, 1997), yet there is still much uncertainty surrounding the way edge effects should be measured (Murcia, 1995). It is possible, that what my study deems to be ‘edge’ or ‘centre’ habitat might not be the edge or centre habitat that detritivores are responding to. This may especially be the case within smaller urban forests, where it is possible that the entire forest should be considered an edge habitat. Bolger *et al.* (2000) considered fragments (usually long and thin in shape) of a size of less than 9 ha to be all edge. If forest fragments of less than 9 ha should in fact be considered all edge, then forests of less than this size (the Esplanade, Bledisloe Park, McCraes Bush) should not have contained a centre plot. It is also difficult to assume the distance which edge effects would penetrate into forests, because of the inconsistencies that have been found in previous studies (Murcia, 1995). Therefore, my study doesn't necessarily conclude that Isopoda, Diplopoda, and Amphipoda are not affected by edge effects, even though only limited response to edge was detected.

4.3.3. Implications for invertebrate biodiversity conservation

The probabilities of encountering an adventive individual summarise the results from all investigated forests to provide a better understanding of where adventive detritivores are common or even dominant. This information could be used to predict where adventive taxa would be most common and highlight the areas in which native detritivores may be suffering the most from the impacts of adventive species; although, at this point the results are based on data from Manawatu-Whanganui only, and should not be extrapolated to other areas.

For all three detritivore groups there was always a higher probability that a detritivore would be an adventive individual in native forest compared to pine. While this reflects the fact that all detritivores (both native and adventive) were more abundant in native forests, it also provides supporting evidence that adventives invade native forest. The higher probability that a detritivore would be adventive in a native forest habitat corresponds to a higher likelihood that a detritivore would be native in pine forest, providing further evidence that pine forests can provide alternative habitat for native detritivores. This suggests that native detritivores that live in native forests may be more exposed to possible threats from adventive species than native detritivores that are able to adapt to living in pine forests.

No matter the forest conditions, the probability of a randomly collected Amphipoda being an adventive was always very high (>70%). This high probability of encountering an adventive individual (especially in native forest) indicates a serious threat to native species, and adventive Amphipoda of the *Arcitalitrus* genus found in this study have been known to displace native Amphipoda (Duncan, 1994). The probabilities of encountering an adventive Diplopoda are not as high as they are for Amphipoda, with most habitats having a value of below 50%, corresponding to the expectation that more native Diplopoda than adventive Diplopoda would be found in every forest habitat, provided a large enough sample was collected. The probability of an Isopoda being adventive was found to be below 20% in every forest habitat type considered (which is well below the probability found for Diplopoda and Amphipoda). Therefore, out of the three detritivore taxa investigated in this study, the native Isopoda may be the least vulnerable to the immediate threat of adventive species in forest habitats (especially away from the forest edge).

For all three detritivore groups investigated, pine forests supported similar total abundance of native detritivores as native forests, proving that pine forests do have value in preserving native biodiversity and are most definitely not biological deserts. Native Polydesmida morphospecies 11 was more abundant in pine forests than in native forests. The relative abundance of native detritivores did not appear to be influenced by forest type, and native Diplopoda and Isopoda were more abundant in pine forests than adventive species. Previous work also discovered that the majority of Diplopoda found in a pine forest were native (with native species composing 83% of the total) (Mesibov, 2005).

One result that should be highlighted is that native Amphipoda abundance was lower than the abundance of adventives throughout investigated forests in Manawatu-Whanganui. This suggests that native Amphipoda are the group under the most immediate threat due to adventive species, which is also supported by the suggestion that adventive Amphipoda are most likely displacing native species (Duncan, 1994). Kahutarawa pine forest (the only pine forest where native Amphipoda were found) provides valuable information on the ability of pine plantations to support native detritivore taxa, highlights the impact one unusual site can have when only 12 sites are sampled, and provides hope that pine plantations could be an alternative habitat for native Amphipoda. Due to the scarcity of native Amphipoda in native forests, pine plantations that do provide a suitable habitat would be extremely beneficial to protect native species. Evidence suggests that while pine plantations are not a replacement for native forests in terms of the native detritivore biodiversity they support, they do provide a suitable environment for some native taxa. This is still beneficial for native biodiversity due to the fact that at this point in time most native forests have already been cleared.

4.4. Summary

The data presented in this Chapter provide evidence that native detritivores are flexible enough to live in the habitat created by pine forests, and that adventive detritivores are able to invade native forests. The expectation that the abundance and diversity of adventive species would be higher in pine plantations than in native forests was not confirmed. Forest type did not significantly affect the overall abundance of any of the three detritivore groups, except for adventive Diplopoda, which were actually more abundant in native forests. At a finer taxonomic resolution, forest type had a significant influence on Diplopoda (and perhaps Isopoda) community structure, and significantly influenced the probability that a randomly collected individual of Diplopoda, Isopoda or Amphipoda would be an adventive species. Some native taxa (Armadillidae and *P. aotearoa*) were more abundant in native forests, but one (Polydesmida morphospecies 11) was more abundant in pine forests. The conclusion is that adventive detritivores in Manawatu-Whanganui have spread throughout native forests, which further supports that native forests have no resistance to adventive detritivores. The data also revealed that for all three investigated taxa pine forests can support as many native detritivores as native forests, suggesting that pine forests contribute to preserving native biodiversity.

There was little indication that adventive and native detritivores were living in different habitat types or responded to edge effects, therefore, it is very possible that the presence of adventive detritivores will negatively influence native species. Native Amphipoda are particularly threatened in Manawatu-Whanganui, with adventive Amphipoda having higher abundance and higher probability of being found throughout all investigated forest habitats; evidence of displacement of native Amphipoda by adventives has already been found (Chapter 3). It is unknown if the invasion of adventive detritivores into native forests has altered ecosystem function. The influence that adventives may have on native detritivores and ecosystem function needs further investigation.

5. General discussion and conclusions

5.1. Importance of the study

There is limited knowledge on New Zealand's invertebrates (Johns, 1962; Brockerhoff et al., 2010; Webber et al., 2010); therefore, gaining greater understanding of distribution and abundance patterns of adventive and native species would be very beneficial. While this study only covers detritivores in Manawatu-Whanganui, it could give an indication of other New Zealand areas, and undertaking similar studies in other areas of New Zealand could provide additional insight into New Zealand detritivores.

Conserving biodiversity is of huge importance, considering New Zealand is recognised as a priority area for conservation work and the protection of endemic species, due to the high level of endemism and the perceived threat to these endemic species (Myers et al., 2000). Biodiversity loss must be one of the most serious issues to confront human beings (Morrison, 2010). Minimising the loss to New Zealand's biodiversity requires knowledge on smaller and often less well known groups (Morrison, 2010). Many native invertebrates are threatened by the loss of forest habitat and the impact by adventive species, but there is such limited information on invertebrates that it is likely that many invertebrates are threatened without it being known (Cochrane et al., 1997). No Amphipoda, Isopoda, or Diplopoda are on the list for New Zealand's most threatened invertebrates (Cochrane et al., 1997), but it is possible this is simply due to the lack of knowledge.

This study investigates the way detritivores may be influenced by changes to their native forest habitat. Anthropogenic influences, such as areas of human settlement, clearance of native forest habitat, and the establishment of plantations are known to threaten biodiversity (Arndt & Perner, 2008), but the way these factors influence New Zealand detritivores has not been recognised. The invasion of adventive species can also threaten biodiversity (Arndt & Perner, 2008); therefore, the distribution of adventive species and identification of their co-occurrence with native species are important to monitor.

Having a greater understanding of New Zealand detritivores is important not only for the conservation of biodiversity, but also for the conservation of ecosystem function, because dertitivores carry out a number of ecosystem processes and are important for nutrient recycling. To conserve the functioning of ecosystems, the components of ecosystems and the roles of those components must also be known (Morrison, 2010). Information on presence, identity, and distribution of adventive species needs to be collected before their impact can be assessed.

5.2. Improved knowledge of the fauna

This study has identified that adventive detritivores make up a large part of the detritivore community in forests of Manawatu-Whanganui. A number of adventive Diplopoda, Isopoda and Amphipoda were found throughout forests of Manawatu-Whanganui, and were found to co-occur with a number of native detritivores.

Chapter 3 provided increased knowledge on the distribution of forest detritivores in Manawatu-Whanganui, and highlighted the need for further developments in Diplopoda and Isopoda taxonomy and ecology; without information on the distribution of native species any changes in distribution cannot be detected. At the moment, distribution records are very scant and often could only be obtained from original species descriptions.

5.3. Adventive detritivores and the invasion of native forests

Biodiversity suffers when adventive species expand their ranges at the expense of native species (Hickerson et al., 2005). It has been proposed that New Zealand's native forest ecosystems are resistant to invasion by adventive invertebrates (Pawson et al., 2008; Brockerhoff et al., 2010), and if this were true, native forest remnants would provide a refuge for native species. However, for all detritivore groups investigated in this study – Diplopoda, Isopoda, and Amphipoda – adventive species were found in native forests. The mechanisms that could have facilitated the invasion of adventive species were discussed thoroughly in Chapter 4 and are mentioned again in the following paragraphs.

It was hypothesised that there would be more adventive species in pine forests than native forests, due firstly to the resistance of native forests to invasion, and secondly, because pine forests are known to suffer frequent disturbance (Pawson et al., 2008). However, adventive Isopoda and Amphipoda in my study were found at similar abundance between the two forest types, and adventive Diplopoda were less common in pine forests than in native forests. This provides more evidence that native New Zealand forests are not resistant to invasion by adventive species, and perhaps indicates that native forest remnants in urban environments are no less disturbed than pine forests. The results of this study do not support the hypothesis that New Zealand's native forests (in Manawatu-Whanganui) are resistant to invasion by adventive detritivores.

Results indicate that disturbance to native forest remnants and development of surrounding urban areas may have facilitated the invasion of adventive species, despite anthropogenic disturbance previously being rejected as the factor which contributes to the success of adventive invertebrates (Arndt & Perner, 2008). Large areas of human-transformed environments are believed to be responsible for the high level of adventive taxa in New Zealand (W. G. Lee, Allen, & Tompkins, 2001). Human activity creates disturbance which can encourage the establishment of adventive animals (Lozon & MacIsaac, 1997). Human disturbance was apparent in forest remnants in this study, especially in small forest remnants surrounded by urban areas (personal observation). A number of adventive species (*B. guttulatus, N. kochii,* and *B. pusillus* (Diplopoda), *A. vulgare* and *H. danicus* (Isopoda)) preferred small native remnants that showed evidence of high human disturbance. Of the native forests sampled, it was small disturbed fragments closer to urban centres that had dominance of adventive Amphipoda. Therefore, as hypothesised, adventive detritivores appear to be more abundant and diverse in native remnants close to urban populations and/or small remnants that show clear evidence of human modification. Anthropogenic habitat alteration can cause a reversal of the competitive advantage that well-adapted native species may have over adventive species, and in extreme cases it may result in extinction of native species (Hickerson et al., 2005). Human disturbance is important in maintaining dominance of adventive species (W. G. Lee et al., 2001). Anthropogenic change may have added to the competitive advantage of the adventive *Arcitalitrus,* because it was found at higher abundance than native Amphipoda in all forest habitats. Further investigation into the role of disturbance in the establishment of adventive detritivores would be valuable.

The presence of adventive Diplopoda, Isopoda, and Amphipoda in native forests confirms the view that detritivores are a guild which is more successful at colonising and exploiting newly available niches than other trophic groups (Samways et al., 1996; Hoare, 2001; Brockerhoff et al., 2010). Unlike herbivores, which are often host-specific and unable to overcome the defences of New Zealand's endemic flora, which in many cases is phylogenetically distant from their host plant (Ridley et al., 2000), preventing their successful invasion and establishment in native forests (Brockerhoff et al., 2010), detritivores utilise plant matter in a decomposed state, which will be more similar between forest types due to the breakdown of complex secondary compounds (Ratsirarson et al., 2002). A future research option would be to carry out a similar study based on other trophic group(s), to further investigate the level of resistance New Zealand forests have to invasion by adventive invertebrates.

5.4. Pine forests as alternative habitat for detritivores

Pine forests may enhance the chance of survival of native species and help to protect New Zealand's biodiversity (Bonham et al., 2002; Brockerhoff et al., 2005; Maunder et al., 2005). The planting of pine plantation on intensely farmed landscapes for the conservation of invertebrates has been proposed as an alternative to establishing native bush. This is because of the commercial appeal it holds, which may result in increased acceptance by landowners (Mesibov, 2005). Investigating pine forests as alternative habitat for native detritivores provided an indication whether pine forests could be used as a tool in the preservation of New Zealand's biodiversity. The overall abundance of native Diplopoda, Isopoda, and Amphipoda did not vary between native and pine forests, indicating that pine forests are a suitable habitat for some native taxa. One native species (Polydesmida morphospecies 11) was more common in pine forests than in native forests. High abundance of native detritivores in pine forests could be explained by the ability of detritivores to invade newly available niches and the fact that once leaf litter starts to decompose it is more similar between forest types. The suitability of pine forests to support native taxa has benefits for the preservation of biodiversity, and understanding factors which promote the establishment of native species would be of further value.

While a diverse invertebrate fauna may be found in pine plantations, it is still important to remember that some native invertebrates may be restricted to native vegetation (Samways et al., 1996; Pawson et al., 2008; Robson et al., 2009; David & Handa, 2010). Pine plantations do not support as much native detritivore biodiversity as native forests, but they do provide a suitable environment for some native taxa. At the same time, abundance of *P. aoteroa* and native Armadillidae was lower in pine forests compared to native forests, and some native taxa were not found in pine forests. Pine forests also contained a different Diplopoda community than native forests, and possibly a different community of Isopoda. Therefore, based on the results of this study, while pine forests can provide a habitat for some native species, they cannot be considered an equal habitat to native forests. The native taxa that do live in pine forests will not be exempt from threat due to adventive species. While not all taxa are equal in their ability to tolerate conditions in pine forests, pine forests are still beneficial for native biodiversity because such a high proportion of native forests have already been cleared.

While some native taxa may be capable of living in a wide range of forests, the presence of more sensitive native taxa may be facilitated by the presence of a diverse understory of plants (like that in pine forest at Kahutarawa) and close proximity to native forest (like at Kahutarawa and Shannon). Many native understory plants in pine plantations are likely to support a variety of native invertebrates (Gunther & New, 2003). Robson *et al.* (2009) believed a rich and abundant native plant understory provides increased habitat heterogeneity and explains the richer invertebrate assemblage found in native remnant *Eucalyptus* woodland compared with pine forests. Establishing a native understory in pine plantations has been proposed as an approach to increase invertebrate biodiversity (Robson et al., 2009). While a dense native understory may influence what detritivores are present, it is unclear whether detritivores are responding to the origin of the vegetation (native or exotic), or whether it is the difference in structure that the detritivores are responding to. The majority of pine forests sampled had a scarce number of understory plants with little diversity in vegetation, but the pine forest at Kahutarawa had a diverse understory of native plants (personal observation). Leaf litter fauna are thought to respond to structural diversity rather than the taxonomy of vegetation (Richardson, 1990). In many cases habitat choice by animals is not based on vegetation alone; animals will respond indirectly to a change in vegetation type due to changes in the structure of the vegetation or physical changes to the habitat, as well as a change in mircoclimate, or changes in hydrological conditions (Richardson, 1990). Invertebrates have been identified to respond to the origin of vegetation at species level but the structure of vegetation at family and order level (Samways et al., 1996).

Native invertebrates may extend their range from native forest remnants into adjoining pine plantations, and pine plantations may provide a suitable habitat once colonisation has occurred (Bonham et al., 2002; Car, 2010). Pawson *et al.* (2008) found that proximity to native forest was an important factor for controlling species composition of Coleoptera and the number of native species. Maintaining native forest remnants in plantation landscapes is important to preserve native biodiversity (Mesibov, 2005; Pawson et al., 2008).

A pine forest's ability to support native species may depend on the age of the stand, with more mature pine forests supporting more native species (Norton, 1998). The native diversity found in pine forest a Kahutarawa could be partially explained by the age of the pine plantation, because trees at Kahutarawa are 38-41 years old (Palmerston North City Council, n.d.-a). Individual stands are clearfelled about every 28 years in New Zealand (Pawson et al., 2008), placing the stands of pine trees at Kahutarawa at an age older than the average. Recently clear-felled plantations have a lower relative abundance of native Coleoptera species than mature pine forest (Pawson et al., 2008). However, when plantations below five years are excluded, the age of the plantation has been found to have no effect on the number of native invertebrate species present (Bonham et al., 2002).

Although further investigation is needed, proximity to native forest and ensuring a diverse native plant understory could be used in plantation management to enhance native biodiversity. Extending the rotation time could also have an influence on the number of native detritivores in a plantation. However, for native Amphipoda the absence of adventive species may be the most important factor. The importance of developing pine plantations which can support native detritivores is increasingly important due to abundance of adventive detritivores in native forests and the potential threats this has for native taxa. Due to time restrictions only six pine forests were included in this study. It would be beneficial to sample a greater number of pine forests including pine forests which cover a range of ages, degree of vegetative understory diversity, and proximity to native forest to further investigate the influence these factors have on native detritivores.

5.5. Edge effects

Significant loss of native forest habitat has occurred in New Zealand (a 71% loss) with remainder of native forest divided into small fragments (Ewers et al., 2006). Fragmentation of native forest creates more edge habitat which can facilitate the invasion of adventive species; this may result in a higher abundance of adventive species at forest edges and a higher abundance of native species in the centre (Hickerson et al., 2005). A greater understanding of edge effects could be used to enhance conservation efforts (Didham, 1997). In this study, proximity to edge had no significant effect on detritivore abundance or community composition, although the probability of a detritivore being an adventive was higher at edge habitats for Isopoda, Diplopoda, and possibly Amphipoda (see Chapter 4 for more discussion on edge effects). Native and adventive detritivores co-occurred at both edge and centre locations in each forest type. Due to recognised difficulties when studying edge effects (especially regarding the scale at which to study edge effects or confounding factors) (Bolger et al., 2000), it is possible edge habitats have a stronger influence on detritivores than what was detected in this study. Further research into the effect that edge habitat has on detritivores could be investigated using different methods.

5.6. Threat to native species

Adventive and native detritivores co-occurred in all forest habitats investigated in this study, and it is possible that adventive detritivores could have a negative influence on native species. The impact on native detritivore communities due to adventive invertebrates has received little attention (Tomlinson, 2007). Adventive detritivores could affect native detritivores in a number of ways: resources such as food and shelter may become unavailable due to interference by adventives, this may be due to agonistic interactions, chemical signals, crowding, or direct competition; adventive species could change the litter habitat (for example, an increased consumption rate may alter the depth of leaf litter, decomposition rate, or the opportunities available for micro-organisms); high number of adventives may increase the number of predators, disease, or parasites in the area, increasing the pressure on natives (Griffin & Bull, 1995). Competition may result in displacement of native detritivores (Tomlinson, 2007).

The probabilities of encountering an adventive individual summarised the results from all forests to provide a better understanding of where adventive detritivores were common or even dominant. This information was used to predict where adventive taxa would be most common and highlighted the taxa and forest habitats which are most threatened by the presence of adventive species. While the probability of a Diplopoda being adventive was usually below 50% and the probability of encountering an adventive Isopoda was always below 20%, the probability that any collected Amphipoda would be adventive was above 70% in all sampled forests in Manawatu-Whanganui. This suggests that any potential threat imposed by adventive species may be exceptionally large for native Amphipoda. The facts that the adventive genus *Arcitalitrus* has been previously known to displace natives in modified environments (Duncan, 1994), that native Amphipoda were not present where *Arcitalitrus* occured (unless adventives were only found in low abundance), and that native Amphipoda were found at high abundances in all native forests without *Arcitalitrus* suggests that adventive Amphipoda are out competing and displacing native Amphipoda in Manawatu-Whanganui.

Adventive Amphipoda are likely to present a huge threat to natives; however, adventive Diplopoda and Isopoda may pose a threat too. Even though no impacts may have been noticed, it does not mean they are not occurring. Many invaders go through an extended lag phase in which their impacts are not easily recognised, until they become more abundant and create more damage (Brockerhoff et al., 2010). Adventive

Isopoda were found at very low abundance compared to natives, but it is possible that the abundance of adventive Isopoda could increase overtime. *C. britannicus* can invade deep into native forest and can be one of the most dominant Diplopoda in native environments. While less abundant, *O. pilosus* was also widespread in Manawatu-Whanganui. It is possible that adventive Diplopoda could be influencing native taxa such as Spirostreptida. *C. britannicus* and *O. pilosus* are believed to have no effect on the endemic Spirostreptida (Johns, 1962), but this (and their influence on other native taxa) has not been investigated. Studying the ecology of endemic species following an invasion is important (Griffin & Bull, 1995) and is a possible direction of future research.

5.7. Limitations of this study

There were some limitations to this project. Because it was carried out as a Master's project, both time and money were limited. If more time was available, I would have liked to analyse microhabitat factors that detritivores respond to. It is possible that forest type is irrelevant to detritivores due to the similar microhabitat conditions that can occur between native and pine forests. Car (2010) believed that Diplopoda were not responding to forest type but were responding to factors at the microhabitat scale in native and pine forests in Australia (Car, 2010). Small scale disturbance, moisture, and temperature are believed to influence the distribution of detritivores (Crawford, 1992; Car, 2010). While it was not an objective of this study (due to time restrictions), investigation into how the abundance and distribution of adventive and native detritivores are affected by microhabitat conditions should be a future priority for study. Microhabitat conditions that promote the establishment of native detritivores could be used to manage pine forests in a way which enhances native biodiversity. It would have been interesting to investigate the extent to which microhabitat conditions changed between edge and centre plots despite the limited response of detritivores to plot location.

Ideally, more samples would have been collected from each forest to improve the accuracy of results, but due to the large amount of time required to sort through samples it was not possible. Gathering samples from multiple edge and centre locations within each forest could have provided further insights. Extending the study to include a greater number of forests (especially pine forests) may also have provided further insights. The sample size used in this study may be considered small, and for this reason accepting an alpha value of 0.1 was sometimes considered. Increasing the sample size would increase confidence in using an alpha value of 0.05 to test the significance of effects. Another limitation was that samples were generally only gathered close to paths and not deeper into forest due to steep terrain or dense vegetation limiting access in larger forests. It is possible that adventive fauna may not have penetrated deep into undisturbed native forests further away from areas easily accessed by humans.

Due to lack of identification keys for Diplopoda and Isopoda, native species were only identified to a level in which they could be distinguished from adventive species. This meant that generally native Diplopoda were only identified to order and native Isopoda to family. Gaining a more thorough understanding of detritivore distribution at species level would be valuable, but due to the poor taxonomic knowledge and the large amounts of time required to identify morphospecies it was not possible.

5.8. Future research

5.8.1. Investigating competition between native and adventive detritivores

One possibility for further research (which due to time restrictions could not be carried out in this study) is using stable isotope analysis to investigate if native and adventive detritivores compete for the same niche. It would be beneficial for the isotope study to be based on taxa in New Zealand's native forest, because this is where all three taxa are predicted to be most threatened. It is possible that there is an overlap in resource use between native and adventive detritivores which will result in competition; stable isotope analysis offers one way to identify if native and adventive detritivores are competing for the same food resources. An animal's isotopic signature reflects both the food source and position in the food chain (Tiunov, 2007). Using stable isotopes of carbon and nitrogen are a common choice in soil and leaf litter ecological studies (Tiunov, 2007; Maraun et al., 2011; Semenyuk & Tiunov, 2011). Carbon isotopes are little fractured, therefore the carbon isotope ratio changes little up the food chain and can be used to identify the main food source of an animal (McCutchan, Lewis, Kendall, & McGrath, 2003; Tiunov, 2007). The amount of heavy nitrogen isotope accumulates up the trophic food chain and can be used to identify the trophic position of an animal (Ponsard & Arditi, 2000; Tiunov, 2007; Semenyuk & Tiunov, 2011). Using stable isotope analysis to study resource use of detritivores is beneficial for a couple of reasons. Firstly, invertebrates are small and cryptic and their behaviour can be difficult to observe in the field (Tiunov, 2007; Maraun et al., 2011). A second benefit is that stable isotope ratios of animal tissue reflect nutrition over long periods of time (providing more than just a snap shot in time of consumption); this is in contrast to molecular gut content analysis (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004; Maraun et al., 2011). Detritovores are regarded as food generalists (Chahartaghi et al., 2005); however, detailed analysis into feeding structure using stable isotopes has revealed that differentiation can exist between species within a detritivore taxonomic group (Schmidt, Scrimgeour, & Handley, 1997; Schneider et al., 2004; Chahartaghi et al., 2005; Erdmann, Otte, Langel, Scheu, & Maraun, 2007). When differentiation occurs, species can co-exist without having to face competition with each other. As far as I am aware, stable isotope analysis has not been used specifically to investigate competition between native and adventive leaf litter dwelling species; however, the potential is there.

5.8.2. Investigating threat to ecological function

The presence of adventives may influence the functioning of the native forest ecosystems. If the dynamics of the detritivore community change, it is possible that the roles that detritivores perform will be influenced and functioning of the ecosystem may be altered (Peltzer et al., 2010). Perturbation of the decomposer community has far-reaching impacts on nutrient supply and retention, and hence, on the stability of the ecosystem (Didham et al., 1996). The long-term effects of adventive species in groups known to invade native forests, e.g., Diplopoda, are not known (Hickerson et al., 2005). While native diversity is important to consider, abundance values may be most relevance to the functioning of the ecosystem, and it is debatable whether the origin of detritivores (native or adventive) will influence ecosystem function. Adventive and native species of Isopoda play an important role in litter breakdown (Paoletti et al., 2007). Native Spirostreptida (Diplopoda) have a similar ecological function to adventive Julida (Korsós & Johns, 2009). However, some species may be far more important than others to decomposition because decomposition rates have been found to only be weakly correlated with total abundance of detritivores (Didham et al., 1996). It is possible that adventive taxa will decompose native litter at a slower rate because they have not adapted to the breakdown of New Zealand leaf litter. The effect that soil biodiversity has on the functioning of the ecosystem is poorly understood; little is known about how it effects mineralisation and soil-organic matter formation and there is need to further investigate this (Hättenschwiler et al., 2005). In the case of Amphipoda, the number of species present (which may be influenced by the presence of a dominant adventive species) is known to influence ecosystem functioning (Richardson & Morton, 1986). The displacement of native Amphipoda species by the adventive *Arcitalitrus* could alter ecosystem function. An additional species can increase the functioning of an ecosystem (the soil respiration rate) even if the overall abundance of Amphipoda remains unchanged (Richardson & Morton, 1986). Multiple native species of Amphipoda can co-occur in the same location (providing they are not from the same genus) (Duncan, 1994) and in this study it was common for two native species to co-exist (*Puhuruhuru aotearoa* and *Parorchestia tenuis*). Therefore, if *Arcitalitrus* displaces native species, over time forests may change from having multiple native species to one adventive species. An invasive detritivore may impact key ecosystem processes with the potential to have far reaching impacts on the ecosystem (Brockerhoff et al., 2010).

Change in native ecosystems due to adventive detritivores is very possible. European earthworms (Lumbricidae) invaded previously earthworm free forests in North America and their effects cascaded through the ecosystem (Frelich et al., 2006), although the consequences may be not be as severe if native taxa from the detritivore group are already present. Detritivores can contribute to ecosystem function in a number of ways. The presence of macrofauna can significantly alter decomposition pathways and contribute directly to soil structure (Swift et al., 1979). Detritivores influence the mineralisation of carbon and nitrogen (Swift et al., 1979; Mikola et al., 2002) and can influence plant growth (Scheu et al., 1999). Litter displacement, fragmentation, and the conversion of leaf litter to large quantities of faeces by macrofauna stimulates microbial activity and facilitates decomposition (Hättenschwiler et al., 2005). Adventive invertebrate species can alter soil carbon, nitrogen and phosphorus pools as well as affecting the distribution and function of roots and mirco-organisms (Arndt & Perner, 2008). A high abundance of adventive detritivores have been found in native forests in New Zealand and the crucial next step would be to investigate the influence they have on ecosystem function. Ecosystem services (such as litter consumption and transformation, and plant growth) performed by detritivores in the presence and absence of adventive species should be monitored to determine any influence of adventive species.

5.9. Summary

1) A diverse group of detritivores were present in forests of Manawatu-Whanganui. New data on abundance and distribution of many adventive and native Diplopoda, Isopoda and Amphipoda are provided. The results highlight the urgent need for more research on taxonomy and ecology of native detritivore species, and the importance of combining several sampling methods when studying detritivores.
2) Adventive detritivores were widespread throughout native forests in Manawatu-Whanganui, sometimes at higher abundance than native species, suggesting that native forests have no resistance to invasion by adventive detritivores. The effect of adventive detritivore species on native forest ecosystems remains unknown. Determining any effect that adventive detritivores may have on the function of New Zealand's native forests should be a priority for research.
3) This is the first study to highlight the dominance of adventive Amphipoda in native forest remnants in New Zealand. The probability that any collected Amphipoda would be adventive *Arcitalitrus* was above 70% in all sampled forests in Manawatu-Whanganui. Native Amphipoda were not present where *Arcitalitrus* occured (unless adventives were only found in low abundance), but were found at high abundances in all native forests

without *Arcitalitrus,* providing evidence that adventive Amphipoda are out competing and displacing native Amphipoda in Manawatu-Whanganui.

4) The expectation that the abundance and diversity of adventive species would be higher in pine plantations than in native forests was not confirmed. Forest type did not significantly affect the overall abundance of any of the three detritivore groups, except for adventive Diplopoda, which were actually more abundant in native forests. At a finer taxonomic resolution, forest type had a significant influence on Diplopoda (and perhaps Isopoda) community structure, and significantly influenced the probability that a randomly collected individual of Diplopoda, Isopoda or Amphipoda would be an adventive species.
5) Proximity to forest edge did not significantly influence detritivore community composition or the abundance of adventive species, although it did impact the predicted probability that a randomly collected detritivore would be adventive.
6) Native detritivores were flexible enough to live in pine forests in Manawatu-Whanganui. Pine forests can provide an alternative forest habitat for a high abundance of native detritivores and provide potential for preservation of native detritivores, although it appears that some native taxa are more suited to living in conditions created by pine forests than others. Investigating the factors which encourage the establishment of native taxa in pine forests has benefits for the conservation of biodiversity and would be worthwhile research to undertake in the future.

7) Native and adventive detritivores co-existed in the same habitats in forests of Manawatu-Whanganui. Wherever native and adventive detritivores co-occur, adventive detritivores could be influencing natives, and determining any effects adventive species have on native species should be a priority for future research.

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Appendix 1: site descriptions

Lists of dominant plant species identified at each plot are included. It should be noted that this was not used in analysis and was only recorded to give some background information on the sites. Therefore, vegetative surveys were not thorough and the list of vegetation is by no means a comprehensive list of all species in a forest.

Kitchener Park

Date sampled: 24/04/2012

Edge plot coordinates: S 40◦ 14.786’, E 175◦ 32.380’, elevation: 26 m

Centre plot coordinates: S 40◦ 14.800’, E 175◦ 32.333’, elevation: 25 m

Edge plot vegetation: karaka (*Corynocarpus laevigatus* J.R. Forst. & G. Forst.), kawakawa (*Macropiper excelsum* (G. Forst.) Miq.), titoki (*Alectryon excelsus* Gaertn.), matai (*Prumnopitys taxifolia* (D. Don) de Laub.)

Centre plot vegetation: kawakawa (*M. excelsum*), whiteywood (*Melicytus ramiflorus* J.R. Forst. & G. Forst.), titoki (*A. excelsus*), matai (*A. excelsus*), kahikaitea (*Dacrycarpus dacrydioides* (A. Rich.) de Laub.), karaka (*C. laevigatus*)

Kitchener Park (Fig. A1.1), located only a few minutes from Feilding on Kawakawa road, is 7.112 ha and makes up part of a larger reserve of 13.9868 ha that is owned by the Manawatu District Council (Manawatu District Council, 2009). It was purchased, in attempts to preserve the native bush, in 1915 from the Riddiford family (Manawatu

District Council, 2009). Kitchener Park contains kahikatea, matai, and totara and is also known for having a kowhai (*Sophora microphylla* Aiton) tree believed to be the tallest kowhai tree in New Zealand (Manawatu District Council, 2009). Kawakawa was dominant in the understory of the sampling sites (personal observation).

There are a number of disturbances that could affect the dynamics at Kitchener Park. One disturbance is the frequent flooding and ponding of water due to stop banks restricting drainage (Manawatu District Council, 2009). Especially flooding that occurred in 2004 creating lasting damage (Sutton, 2010). There has also been grazing and infestation of weeds (particularly *Tradescantia fluminensis* Vell.) during the reserves history (Standish, 2002; Manawatu District Council, 2009). In 1991 an extensive restoration and weed eradication program was undertaken by the council and the community (Manawatu District Council, 2009). The bush is open to the public with a car park and walkways throughout (personal observation).

Figure A1.1. Kitchener Park: a) and b) edge plot; c) centre plot.

Mt Lees Reserve

Date sampled: 12/07/2012

Edge plot coordinates: S 40◦ 11.284’, E 175◦ 27.103’, elevation: 95 m

Centre plot coordinates: S 40◦ 11.303’, E 175◦ 26.983’, elevation: 94 m

Edge plot vegetation: titoki (*A. excelsus*), kawakawa (*M. excelsum*), rangiora (*Brachyglottis repanda* J.R. Forst. & G. Forst.), kowhai (*Sophora*), *Agapanthus*, manuka (*Leptospermum scoparium* J.R. Forst. & G. Forst.), unidentified shiny fern

Centre plot vegetation: kawakawa (*M. excelsum*), kahikitea (*D. dacrydioides*), titoki (*A. excelsus*), unidentified shiny fern, totara (*Podocarpus totara* G. Benn. ex D. Don), whiteywood (*M. ramiflorus*), bamboo, *Agapanthus*, kowhai seedlings (*Sophora*)

Mt Lees reserve (Fig. A1.2) is on Ngaio Road between Sanson and Bulls (Teahan & Teahan, n.d.). Sampling took place in the bush gully which is 16 ha (Graham Teahan, personal communication, 2013). The bush gully has been developed as a garden that contains some native remnant vegetation as well as a number of both adventive and native species that were planted (O. Wilson, 1985). Remnant native vegetation includes giant kahikatea, totara, and pukatea trees as well as other trees (tawa, totara, and matai) and a number of vines (*Clematis*, *Muuhlenbeckia*, laywer, and supplejack); whiteywood also established in the understory (O. Wilson, 1985).

In 1951 fencing around the bush gully was complete, until this point there was nothing to stop stock from grazing in the area (O. Wilson, 1985). The reserve was established and maintained by Ormond Wilson, who purchased the land in 1873, until 1972 when it was gifted to the crown and is now owned by the Mawanwatu District Council (O. Wilson, 1985). The reserve is now open to the public from nine to five seven days a week and has paved walkways throughout (Teahan & Teahan).

Figure A1.2. Mt Lees Reserve: a) and b) edge plot; c) centre plot.

McCraes Bush

Figure A1.3. McCraes Bush: a) centre plot; b) and c) edge plot.

Date sampled: 8/05/2012

Edge plot coordinates: S 40◦ 17.005′, E 175◦ 45.929′, elevation: 52 m

Centre plot coordinates: S 40◦ 17.028′, E 175◦ 45.867′, elevation: 54 m

Edge plot vegetation: kawakawa (*M. excelsum*), titoki (*A. excelsus*), supplejack (*Ripogonum scandens* J.R. Forst. & G. Forst.), whiteywood (*M. ramiflorus*)

Centre plot vegetation: supplejack (*R. scandens*), titoki (*A. excelsus*), totara (*P. totara*), kawakawa (*M. excelsum*)

McCraes Bush in Ashhurst (Fig. A1.3) is 45,654 m^2 (0.0046 ha) of land which is owned by the Palmerston North City Council (Palmerston North City Council, 2011). It can be accessed by River road (Palmerston North City Council, 2011). The small area of urban remnant contains a walking track and is open to the public. There has been work recently undertaken by the community to improve the quality of the remnant, with willows cleared and a recent clean up including rata planting, which took place on the 25th of August 2012 (Palmerston North City Council, 2011; RECAP, 2012). High weed infestations are being managed in McCraes bush (Palmerston North City Council, 2011). There are plans to fence off the area from stock and plant vegetation to provide a buffer to the native bush remnant (Palmerston North City Council, 2011).

The Victoria Esplanade

Date sampled: 6/03/2012

Edge plot coordinates: S 40◦ 22.316’, E 175◦ 36.755’, elevation: 14 m

Centre plot coordinates: S 40◦ 22.330’, E 175◦ 37.196’, elevation: 14 m

Edge plot vegetation: silver fern (*Cyathea dealbata* (G. Forst.) Swartz), wheki (*Dicksonia squarrosa* (G. Forst.) Sw.), whiteywood (*M. ramiflorus*), tawa (*Beilschmiedia tawa* (A. Cunn.) Benth. & Hook. f. ex Kirk)

Centre plot vegetation: lemonwood (*Pittosporum eugenioides* A.Cunn.), whiteywood (*M. ramiflorus*), kawakawa (*M. excelsum*), and seven-finger (*Schefflera digitata* J.R. Forst. & G. Forst.)

The Victoria Esplanade (Fig. A1.4) is a popular public park owned by the Palmerston North City Council, and within the 23.5 ha of the Victoria Esplanade lies 7.5 ha of native forest remnant (Palmerston North City Council, 2011). It is located in an urban area, alongside side the Manawatu River in Palmerston North. Access can be gained via Manawaroa Street, Fitzherbert Avenue, and Park Road.

Figure A1.4. The Victoria Esplanade: a) centre plot; b) edge plot.

Bledisloe Park

Date sampled: 7/03/2012

Edge plot coordinates: S 40◦ 23.000’, E 175◦ 37.180’, elevation: 44 m

Centre plot coordinates: S 40◦ 22.980’, E 175◦ 37.180’, elevation: 45 m

Centre plot vegetation: broadleaf (*Griselinia litoralis* Raoul), lemonwood *(P. eugenioides)*, puriri (*Vitex lucens* Kirk), seven-finger (*S. digitata*), soft tree fern (*Cyathea smithii* Hook. F.), whiteywood (*M. ramiflorus*), kawakawa (*M. excelsum*), rangiora (*B.*

repanda), gully fern (*Pneumatopteris pennigera* (G. Forst.) Holttum), common maidenhair fern (*Adiantum cunninghamii* Hook.)

Edge plot vegetation: lemonwood (*P. eugenioides*), karaka (*C. laevigatus*), whiteywood (*M. ramiflorus*), kawakawa (*M. excelsum*)

Bledisloe Park (Fig. A1.5) is an urban area of remnant native forest on the Massey University campus in Palmerston North. Access to the 86,127 m^2 bush can be gained off Tennent drive (Brenkley, Brown, Way, & Phillips, 2008; Palmerston North City Council, 2013b). The area is open to the public with walking tracks on both flat and steep terrain. Bledisloe Park is owned by Palmerston North City Council (Palmerston North City Council, 2011).

Figure A1.5. Bledisloe Park: a) centre plot; b) and c) edge plot.

The Ashhurst Domain

Date sampled: 9/03/2012

Edge plot coordinates: S 40◦ 18.138’, E 175◦ 45.475’, elevation: 45 m

Centre plot coordinates: S 40◦ 18.210’, E 175◦ 45.526’, elevation: 26 m

Edge plot vegetation: kawakawa (*M. excelsum*), karaka (*C. laevigatus*), lemonwood (*P. eugenioides*), whiteywood (*M. ramiflorus*), titoki (*Alectryon excelsus* Gaertn.)

Centre plot vegetation: wineberry (*Aristotelia serrate* Oliv.), kawakawa (*M. excelsum*), whiteywood (*M. ramiflorus*), *T. fluminensis*.

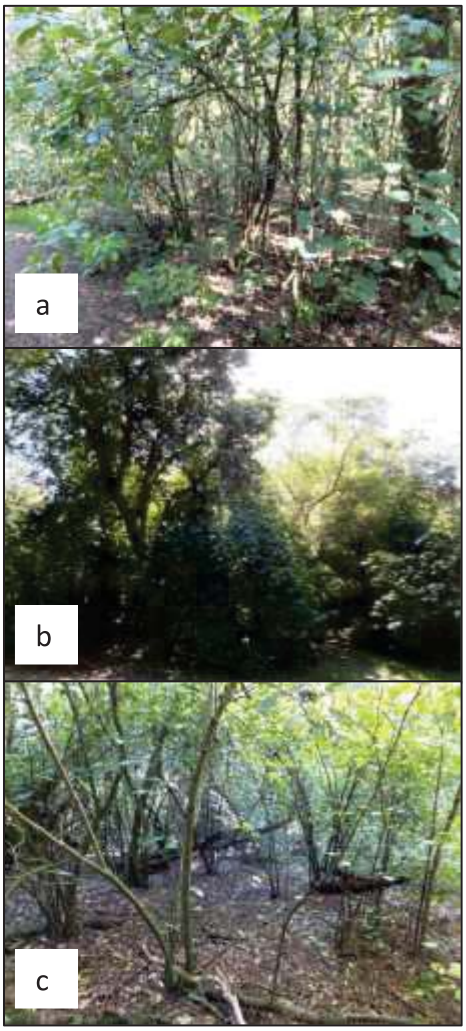

Figure A1.6. Ashhurst domain: a) and b) edge plot; c) centre plot.

The Ashhurst Domain (Fig. A1.6) is located off Napier Rd (SH 3) (Palmerston North City Council, 2013a). It is popular with the public and provides a number of facilities including sheltered family picnic area, a BBQ shelter, a children's playground, walking tracks (this is a popular area for dog walking), and sports fields (Palmerston North City Council, 2013a). Part of the 27.4 ha of land which is open for public use contains native forest (Palmerston North City Council, 2011). While very close to Ashhurst, the native forest is considered a rural forest remnant (Palmerston North City Council, 2011). The mature native forest area is known to contain a number of both introduced and native birds and is located near by a restored wetland (Ashhurst dot org, 2013). Ashhurst domain's native forest area has been identified as having ecological significance (Palmerston North City Council, 2011). It has been included in the Gorge Biodiveristy Project (a community project aimed to promote biodiversity, scenic, and recreational values) which has increased its status as a significant area (Brenkley et al., 2008).

Totara Reserve

Date sampled: 2/09/2012

Edge plot coordinates: S 40◦ 09.102', E 175◦ 50.598', elevation: 139 m

Centre plot coordinates: S 40◦ 08. 824', E 175◦ 50.638', elevation: 164 m

Edge plot vegetation: mapau (*Myrsine australis* (A. Rich.) Allan), supplejack (*R. scandens*), hen and chicken fern (*Asplenium bulbiferum* G. Forst.), tawa (*B. tawa)*, kawakawa (*M. excelsum*), lancewood (*Pseudopanax crassifolius* (Sol. ex A. Cunn.) C. Koch), hanging spleenwort (*Asplenium flaccidum* G. Forst.), kahikatea (*D. dacrydioides*), cabbage tree (*Cordyline australis* (Forst. f.) Endl.), juvenile karaka (*C. laevigatus*)

Centre vegetation: kawakawa (*M. excelsum*), supplejack (*R. scandens*), tawa (*B. tawa)*, kahikatea (*D. dacrydioides*), unidentified tree fern with skirt, pigeonwood (*Hedycarya arborea* J.R.Forst. & G.Forst), hen and chicken fern (*A. bulbiferum*)

Totara Reserve (Fig. A1.7) is located in the Pohangina Valley and is approximately 338 ha (Martyn, 2012). The reserve is open to the public and provides a number of recreational activities such as bush walking, camping, picnicking, wildlife observation, swimming, and fishing (Martyn, 2012). Totara Reserve covers land ranging from river flats to hills up to 600 m high (Knight, 2008). Podocarp forest made up of totara, matai, rimu and kahikatea covers the hills and valleys (Martyn, 2012).

Sampling was done in the fern walk area of the bush which contains mature native forest, although there may be some exotic species in the area (Martyn, 2012). The fern walk area was once a major kahikatea forest until 1936 when a cyclone destroyed the area. The area is now covered by tawa, totara, rimu, pukatea, and rata (Martyn, 2012).

While Totara Reserve may have suffered from the impact of fire, wandering stock, or destruction and modification for milling purposes, it is still considered to be the finest native forest remnant in the Manawatu ecological district (Martyn, 2012). However, the reserve does have a number of pests and weeds that require eradication. Weeds include banana passionfruit (*Passiflora molissima* Bailey*)*, wandering willy (*T. fluminensis)*, and old man's beard (*Clematis vitalba* L*.*) (Martyn, 2012). Pests in the reserve include possums, deer, mustelids, sulphur crested cockatoos, rodents and feral cats (Martyn, 2012). The river that runs through Totara Reserve is prone to flooding and has been known to cause damage to areas on the river flats (Martyn, 2012).

Figure A1.7. Totara Reserve: a) centre plot; b) edge plot.

The Manawatu Gorge

Date sampled: 12/07/2012

Edge plot coordinates: S 40◦ 20.392’, E 175◦ 49.068’, elevation: 86 m

Centre plot coordinates: S 40◦ 20.203’, E 175◦ 48.740’, elevation: 118 m

Edge plot vegetation: kawakawa (*M. excelsum*), tawa (*B. tawa)*, juvenile lancewood (*P. crassifolius*), hanging spleenwart (*A. flaccidum*), giant maiden hair fern (*Adiantum formosum* R. Br.), supplejack (*R. scandens*)

Centre plot vegetation: kawakawa (*M. excelsum*), tawa (*B. tawa)*, hanging spleenwart (*A. flaccidum*), supplejack (*R. scandens*), nikau palm (*Rhopalostylis sapida* H.Wendl. & Drude), *Phittosporum*, hen and chicken fern (*A. bulbiferum*), filmy fern (*Hymenophyllum*)

The Manawatu Gorge (Fig. A1.8) is located 20 minutes (approximately 12 km) from Palmerston North between Ashhurst and Woodville (Department of Conservation, 2011). The vegetation in the Gorge scenic reserve is mainly tawa and podocarp although there are a significant number of broadleaved trees (Department of Conservation, 2011). The native forest remnant also contains the giant maidenhair Fern which is only found in the Manawatu in New Zealand (Department of Conservation, 2011). The forest remnant covers steep hilly terrain but there is a 10 km walking track that has been developed to encourage public use of the area (Department of Conservation, 2011).

The Manawatu Gorge has been identified as an important area to protect and the Gorge Biodiversity project is a project developed for the area which aims to preserve, sustain and enhance the biodiversity, scenic and recreational values. The focus of this project is to use a number of agencies and community involvement to control pest animals and plants, replant native vegetation, and upgrade recreational facilities (Department of Conservation, 2011).

Figure A1.8. Manawatu Gorge: a) centre plot; b) edge plot.

Waitarere forest

Date sampled: 25/06/2012

Centre plot coordinates: S 40◦ 31.209’, E 175◦ 13.169’, elevation: 9 m

Edge plot coordinates: S 40◦ 31.279’, E 175◦ 13.247’, elevation: 15 m

Edge plot vegetation: *Pinus radiata* D. Don, occasional ground fern (including bracken, *Pteridium esculentum* (G. Forst.) Cockayne)

Centre plot vegetation: *P. radiata*, occasional ground fern

Waitarere forest (Fig. A1.9) is 2500 ha of costal pine forest with the main entrance located on Waitarere Beach Road (Peter Wright, personal communication, 2012). It is flat terrain owned by the forestry company Rayonier/Matariki. Waitarere forest has intensive use from the public; pedestrians and cyclists are permitted in the forest but vehicles must have a permit to entre (Peter Wright, personal communication, 2012). Planting of pine trees began in 1936 as an attempt to stabilise sand dunes, and the plot in which sampling took place was most recently planted in 1997 (Peter Wright, personal communication, 2012).

Figure A1.9. Waitarere forest, edge plot.

Santoft forest

Date sampled: 21/09/2012

Edge plot coordinates: S 40◦ 06.849’, E 175◦ 11.809’, elevation: 10 m

Centre plot coordinates: S 40◦ 06.799’, E 175◦ 11.806’, elevation: 38 m

Edge plot vegetation: *P. radiata*, grass, blackberry (*Rubus fruticosus* L. agg.), dandelions (*Taraxacum officinale* F.H. Wigg), *Mulenbekia*

Centre plot vegetation: *P. radiata*, grass, blackberry (*R. fruticosus*), dandelions (*T. officinale*)

Santoft forest (Fig. A1.10) is owned by forestry company Ernslaw One and is located off Knottingly Road or Beamish Road, Santoft, Bulls (Pat McCarthy, personal communication, 2012). Santoft forest is planted on flat sandy terrain. The area is 4478 ha in total and 3832 ha is stocked with *P. radiata* (Ernslaw One, 2011). The first planting of pine at Santoft took place in the 1950's as a sand stabilisation project (Ernslaw One, 2011). Before the area was planted in pine it was farmland but it was overgrazed and sand drifts resulted in large sandy areas (Pat McCarthy, personal communication, 2012). Harvesting began in 1988, and after areas were harvested they were replanted in the winter following (Ernslaw One, 2011). The plot where sampling took place was planted in 1994 (Pat McCarthy, personal communication, 2012).

Santoft pine forest, being close to both Palmerston North and Whanganui, is a popular recreation area. It is used for hunting, game shooting, firewood collecting, motor sport, mountain biking, firewood collecting, tramping, white baiting, dog-sledding, researching, and orienteering (Ernslaw One, 2011).

Figure A1.10. Santoft forest, centre plot.

Hawkey's forest

Date sampled: 7/05/2012

Edge plot coordinates: S 40◦ 13.415', E 175◦ 49.131', elevation: 215 m

Centre plot coordinates: S 40◦ 13.424', E 175◦ 49.177', elevation: 232 m

Edge plot vegetation: *P. radiata*

Centre plot vegetation: *P. radiata*, a few small ground ferns

Located in the Pohangina Valley, the pine forest is privately owned by the Hawkey family. It is a small pine forest of approximately 15 ha and is surrounded in farm land (Fig. A1.11). The forest has been planted on sloped land, and there is no public access. The forest was planted in 1990 and until this point it was farmland. The forest is fenced, but sheep and deer are let in to graze (Trish Hawkey, personal communication, 2012).

Figure A1.11. Hawkey's pine forest, the edge.

Whanganui forest

Date sampled: 19/10/2012

Coordinates: S 39◦ 48.803', E 175◦ 1.972' [7]

Edge plot vegetation: *P. radiata*, blackberry (*R. fruticosus*)

Centre plot vegetation: *P. radiata*, gorse (*Ulex europaeus* L.), blackberry (*R. fruticosus*)

The pine forest in Whanganui (Fig. A1.12) covers hilly and flat terrain but the area sampled area was flat. The pine planation is 1400 ha in total and it is owned by different partners. Rick Brown, the owner of the site where research took place, owns

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[7] Due to problems with the GPS at the Whanganui pine forest coordinates were gained from Google Earth after sampling took place. Therefore, coordinates reflect location of the forest but not the exact sampling locations, and elevation was not recorded.

250 ha of the total forest. The plot where sampling took place was 1.8 ha and the trees were eight years old, having been harvest only once previously. There is wild fallow deer in the area and, while it is fenced from bordering farmland, there is the occasional escaped sheep found in the forest. The land is privately owned but permission is granted for some recreational use which includes horse trekkers, mountain bikers, hunters, and those searching for firewood (Rick Brown, personal communication, 2012).

Figure A1.12. Whanganui forest, edge plot.

Shannon forest

Dates sampled: 11/10/2012 (native) and 25/08/2012 (pine)

Edge plot coordinates (native forest): S 40◦ 35.088’, E 175◦ 25.781’, elevation: 140 m

Centre plot coordinates (native forest): S 40◦ 36.299’, E 175◦ 25.640’, elevation: 433 m

Edge plot coordinates (pine forest): S 40◦ 35.224’, E 175◦ 25.774’, elevation: 162 m

Centre plot coordinates (pine forest): S 40◦ 35.309’, E 175◦ 25.932’, elevation: 184 m

Edge plot vegetation (native forest): macrocapa (*Cupressus macrocarpa* Hartw. ex Gordon), fox glove (*Digitalis)*, whiteywood (*M. ramiflorus*), gorse (*U. europaeus*), palm leaf fern (*Blechnum novae-zelandiae* T.C. Chambers & P.A. Farrant), creek fern (*Blechnum fluviatile* (R. Br.) Lowe ex Salomon), rough tree fern (*Dicksonia squarrosa* (G. Forst.) Sw.), seven-finger (*S. digitata*)

Centre plot vegetation (native forest): bush lawyer (*Rubus cissoids* A. Cunn.), supplejack (*R. scandens*), hen and chicken fern (*A. bulbiferum*), tawa (*B. tawa)*, rangiora (*B. repanda*), seven-finger (*S. digitata*), rewarewa (*Knightia excels* R. Br.), wheki (*D. sqarrosa*), filmy fern (*Hymenophyllum*)

Edge plot vegetation (pine forets): *P. radiata*, foxglove (*Digitalis*), bracken (*P. esculentum*), gorse (*U. europaeus*), manuka (*L. scoparium*), grass

Centre plot vegetation (pine forest): *P. radiata*, foxglove (*Digitalis)*, gorse (*U. europaeus*), manuka (*L. scoparium*), either *Scripus* or *Carax* grass species, bush lawyer (*R. cissoides*)

The forest at Shannon (Fig. A1.13) is owned by Ernslaw One and lies 5 km south-east of Shannon. The forest is used by interest groups such as hunters (including possum trappers), mountain bikers, trampers, orienteers, and horse riders (Ernslaw One, 2011); although the forest is locked so permission for these activities would have to be granted (personal observation).

There are 366 ha of stocked pine forest in the area (Pat McCarthy, personal communication, 2012). The forest is planted on moderate to steep ex-pasture or reverting farmland and majority of the forest was established by Carter Holt Harvey, between 1974 and 1981 (Ernslaw One, 2011). Harvesting began in 2004 and ceased in 2007 (Ernslaw One, 2011). There is some variation in the age of the forest, with majority of trees ranging from zero to ten years, but areas sampled contained seven year old trees (Pat McCarthy, personal communication, 2012).

The remainder of the Ernslaw one forest has been left as native forest and the majority of this forest can be found on very steep terrain.

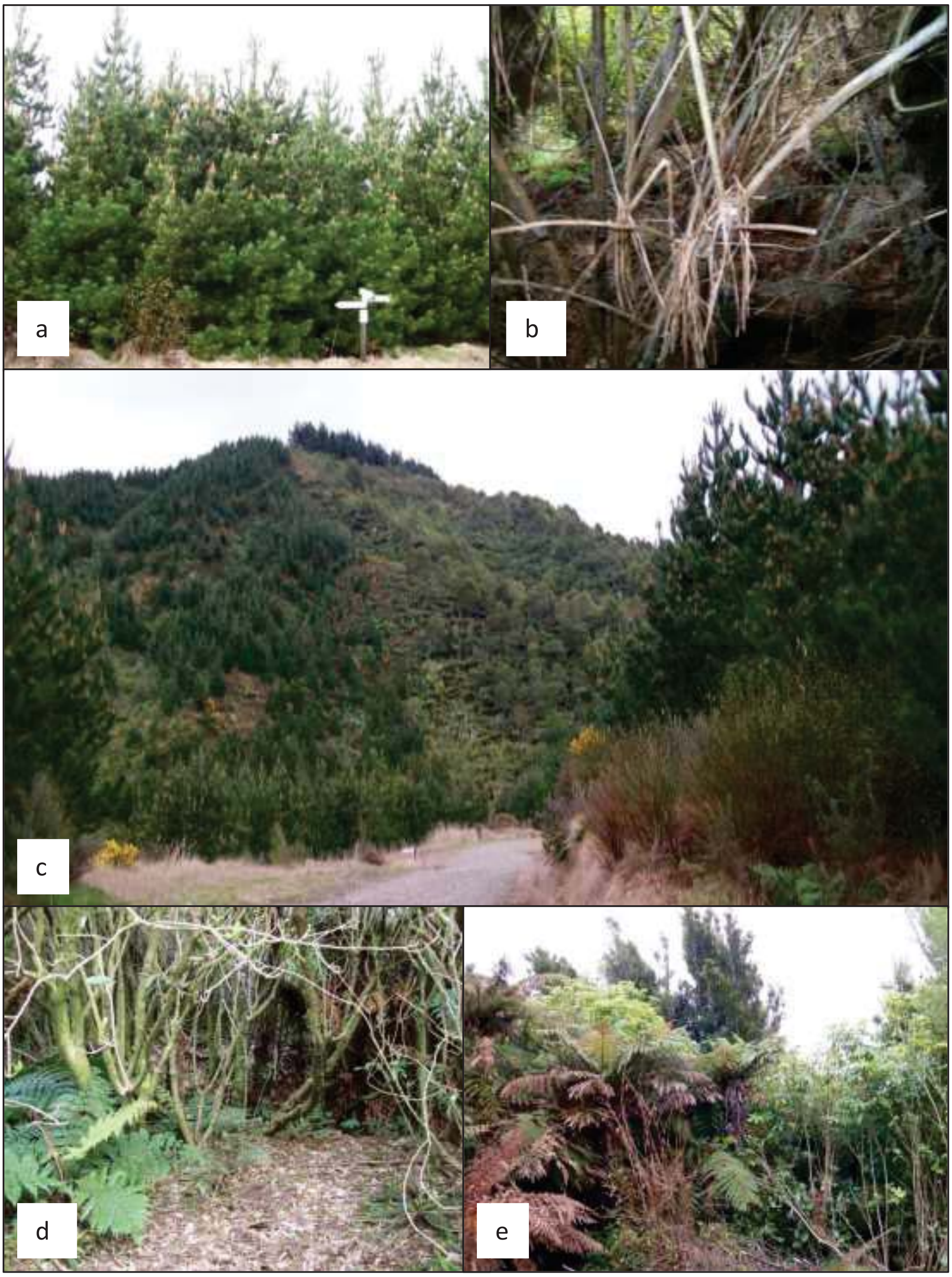

Figure A1.13. Shannon forest: a) the exterior of the centre plot; b) the dense vegetation within the centre plot; c) native and pine forest near the edge of Shannon forest; d) native forest at the edge plot; e) native forest, centre plot.

Kahutarawa

Dates sampled: 14/06/2012 (pine) and 30/09/2012 (native)

Edge plot coordinates (pine forest): S 40◦ 28.264’, E 175◦ 36.712’, elevation: 173 m

Centre plot coordinates (pine forest): S 40◦ 28.434’, E 175◦ 36.644’, elevation: 278 m

Edge plot coordinates (native forest): S 40◦ 28.247’, E 175◦ 36.801’, elevation: 97 m

Centre plot coordinates (native forest): S 40◦ 28.458’, E 175◦ 36.259’, elevation: 92 m

Figure A1.14. Kahutarawa native forest, centre plot.

Edge plot vegetation (pine): unidentified tree fern with skirt, seven-finger (*S. digitata*), whiteywood (*M. ramiflorus*)

Centre plot vegetation (pine): rangiora (*B. repanda*), unidentified tree ferns

Edge plot vegetation (native): black tree fern (*Cyathea medullaris* (G. Forst) Sw.), parataniwha (*Elatostema rugosum*), kawakawa (*M. excelsum*), five-finger (*Pseudopanax arboreus* (Murr.) Philipson)

Centre plot vegetation (native): hen and chicken fern (*A. bulbiferum*), rangiora (*B. repanda*), supplejack (*R. scandens*), fiver finger (*P. arboreus*), rewarewa (K. excels), wheki (*D. sqarrosa*), parataniwha (*E. rugosum*), kawakawa (*M. excelsum*)

Figure A1.15. Kahutarawa native forest, edge plot.

The Kahutarawa outdoor recreation area is currently owned by the Palmerston North City Council and it is located on Kahuterawa Road, just a short distance from Palmerston North (Palmerston North City Council, n.d.-a). Part of this recreation area is Radiata pine forest known as Woodpecker Forest, which includes both steep terrain and flattens out near the top of the forest (Palmerston North City Council, n.d.-a). A distinctive feature of the Kahutarawa pine forest was the diverse native understory of plants that occur throughout the forest (personal observation) (Fig. A1.16). There are a number of walking and mountain bike tracks that run through the forest; mountain bikers and other members of the public have used the facilities for a number of years even though it was privately owned until 2006 (Palmerston North City Council, n.d.-b). The woodpecker forest is a 130 ha plot which was planted between the years of 1975 and 1978 (making the trees 38-41 years old) (Palmerston North City Council, n.d.-a). Harvesting is currently underway Monday to Friday in the summer months (Palmerston North City Council, 2013c). Woodpecker forest is generally un-pruned and has been thinned to waste to produce structural timber in the forest (Palmerston North City Council, n.d.-a).

Part of the Kahutarawa outdoor recreation centre is 63 ha of naturally regenerating native forest found on steeper slopes and margins of the stream (Fig.

A1.14 and A1.15); there are also walking tracks through this area (Palmerston North City Council, n.d.-b). There is another patch of native forest nearby which is known as 'Hardings Bush' and is over 800 ha (however, sampling did not take place in this area) (Palmerston North City Council, n.d.-a).

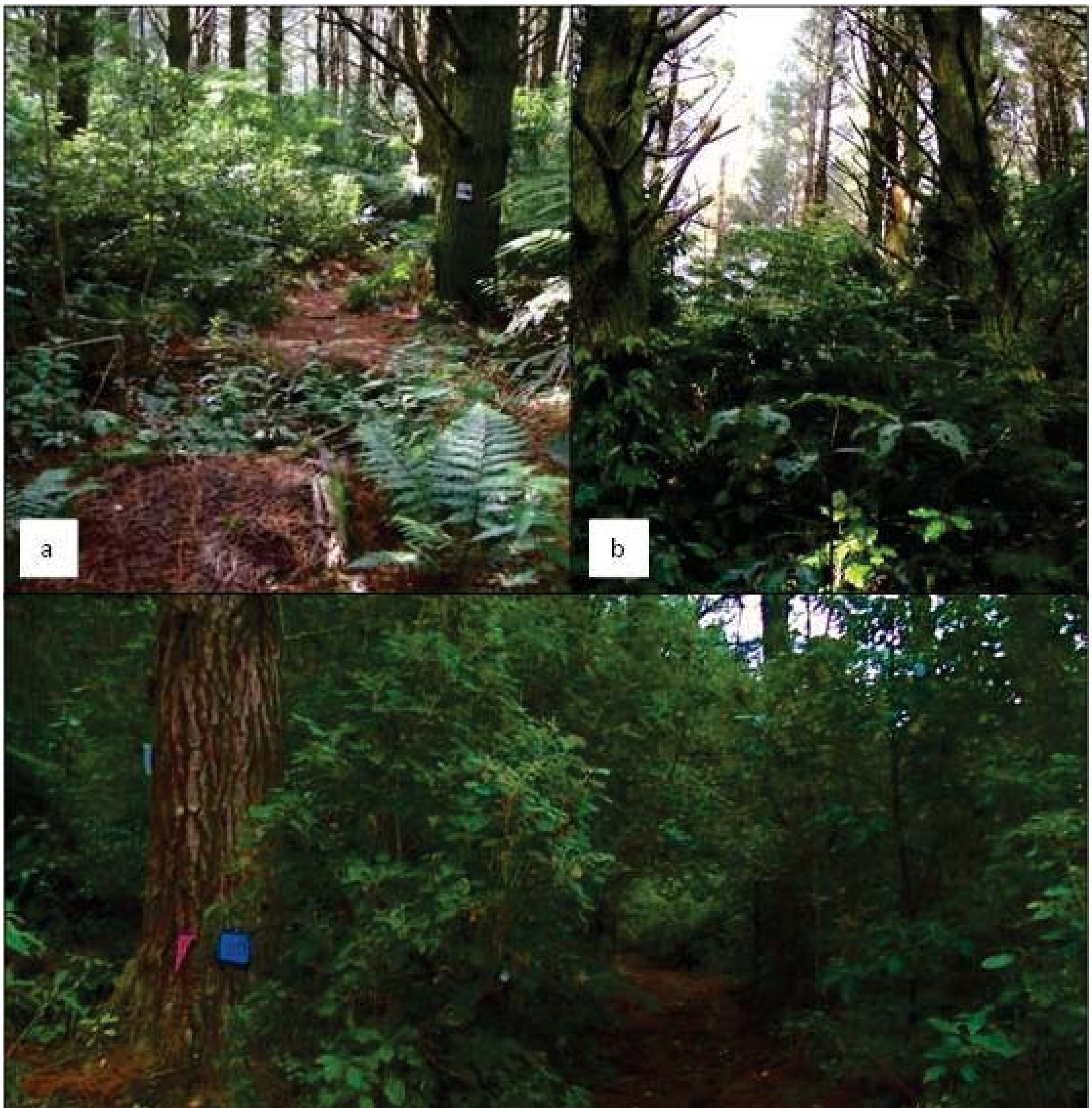

Figure A1.16. Kahutarawa pine forest, the diverse understory of native plants: a) and b) centre plot; c) edge plot.

Appendix 2: data sheet

Abundance of detritivore taxa from leaf litter and log samples at centre and edge forest plots. Abundance from leaf litter is the sum of individuals collected from five 25 cm x 25 cm samples at each forest plot. Abundance from log samples is the sum of all individuals collected from logs found in a 10 m x 10 m quadrat, at each forest plot. Identification and taxa origin (native vs adventive) is stated but sometimes origin is assumed if damged or young individuals can not be identified, based on other detritivores in the sample.

Site	**Forest type**	**Taxa**	**Identification**	**Taxa origin (native vs adventive)**	**Edge log**	**Edge leaf litter**	**Centre log**	**Centre leaf litter**
The Victoria Esplanade	native	Diplopoda	Mature male polydemida sp. 6	native	0	0	1	0
The Victoria Esplanade	native	Diplopoda	Polydesmida sp. 1	native	0	0	1	0
The Victoria Esplanade	native	Diplopoda	Polydesmida sp. 2	native	0	1	0	0
The Victoria Esplanade	native	Diplopoda	Polydesmida sp. 3	native	0	7	1	2
The Victoria Esplanade	native	Diplopoda	Polydesmida sp. 4	native	1	0	0	0
The Victoria Esplanade	native	Diplopoda	Polydesmida sp. 5	native	0	0	0	2
The Victoria Esplanade	native	Diplopoda	Polydesmida (juvenile too young to id)	assumed native	0	0	0	1
The Victoria Esplanade	native	Diplopoda	Polydesmida sp. 6	native	2	0	0	0
The Victoria Esplanade	native	Diplopoda	Spirostreptida	native	0	0	4	0
The Victoria Esplanade	native	Diplopoda	Siphonophorida	native	0	1	0	0
The Victoria Esplanade	native	Diplopoda	Chordeumatida	native	4	0	0	5
The Victoria Esplanade	native	Diplopoda	Polyzoniida	native	0	1	0	2
The Victoria Esplanade	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	39	3	7	1
The Victoria Esplanade	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	2	1	0
The Victoria Esplanade	native	Isopoda	Oniscidae	native	1	1	6	0
The Victoria Esplanade	native	Isopoda	Philosciidae	native	0	1	0	0
The Victoria Esplanade	native	Isopoda	Armadillidiidae species 3	native	0	0	0	1
The Victoria Esplanade	native	Isopoda	Armadillidiidae *Cubaris* species 2	native	0	0	1	0
The Victoria Esplanade	native	Isopoda	Styloniscidae	native	6	0	0	6
The Victoria Esplanade	native	Isopoda	Trichoniscidae	adventive	35	0	0	0

The Victoria Esplanade	native	Amphipoda	*Arcitalitrus*	adventive	14	13	4	1
The Ashhurst Domain	native	Diplopoda	Mature male polydemida sp. 7	native	0	8	0	0
The Ashhurst Domain	native	Diplopoda	Mature male polydemida sp. 1	native	0	0	1	0
The Ashhurst Domain	native	Diplopoda	Mature male polydemida sp. 8	native	0	0	0	1
The Ashhurst Domain	native	Diplopoda	Polydesmida sp. 8	native	1	14	0	0
The Ashhurst Domain	native	Diplopoda	Polydesmida sp. 5	native	0	0	2	0
The Ashhurst Domain	native	Diplopoda	Polydesmida (juvenile too young to id)	assumed native	0	0	0	1
The Ashhurst Domain	native	Diplopoda	Polydesmida sp. 7	native	0	94	2	10
The Ashhurst Domain	native	Diplopoda	Polydesmida sp. 4	native	0	17	0	0
The Ashhurst Domain	native	Diplopoda	Chordeumatida	native	1	0	2	3
The Ashhurst Domain	native	Diplopoda	Spirostreptida	native	0	0	3	0
The Ashhurst Domain	native	Diplopoda	Siphonophorida	native	0	1	0	0
The Ashhurst Domain	native	Diplopoda	Polyzoniida	native	0	29	0	2
The Ashhurst Domain	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	0	1	7	5
The Ashhurst Domain	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	4	0	8
The Ashhurst Domain	native	Diplopoda	Julida (*Brachyiulus pusillus*)	adventive	0	1	0	0
The Ashhurst Domain	native	Isopoda	Philosciidae	native	1	0	0	8
The Ashhurst Domain	native	Isopoda	Oniscidae	native	0	0	0	6
The Ashhurst Domain	native	Isopoda	Styloniscidae	native	11	20	5	11
The Ashhurst Domain	native	Amphipoda	*Arcitalitrus*	adventive	17	55	21	43
McCraes Bush	native	Diplopoda	Spirostreptida	native	1	0	2	0

McCraes Bush	native	Diplopoda	Siphonophorida	native	0	0	1	1
McCraes Bush	native	Diplopoda	Mature male polydemida sp. 8	native	0	2	0	6
McCraes Bush	native	Diplopoda	Mature male polydemida sp. 4	native	0	0	0	2
McCraes Bush	native	Diplopoda	Polydesmida (juvenile too young to id)	assumed native	0	0	0	5
McCraes Bush	native	Diplopoda	Polydesmida sp. 9	native	0	0	0	8
McCraes Bush	native	Diplopoda	Polydesmida sp. 5	native	0	4	0	7
McCraes Bush	native	Diplopoda	Polydesmida sp. 1	native	0	0	0	1
McCraes Bush	native	Diplopoda	Polydesmida sp. 8	native	0	3	0	6
McCraes Bush	native	Diplopoda	Chordeumatida	native	0	0	0	4
McCraes Bush	native	Diplopoda	Polyzoniida	native	0	1	0	8
McCraes Bush	native	Diplopoda	Julida (*Brachyiulus pusillus*)	adventive	0	7	0	0
McCraes Bush	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	0	4	3	2
McCraes Bush	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	2	0	46
McCraes Bush	native	Isopoda	Oniscidae	native	0	0	1	0
McCraes Bush	native	Isopoda	Philosciidae	native	0	1	0	0
McCraes Bush	native	Isopoda	Armadillidiidae	adventive	0	1	0	0
McCraes Bush	native	Isopoda	Styloniscidae	native	0	0	0	5
McCraes Bush	native	Amphipoda	*Arcitalitrus*	adventive	0	0	0	1
Kitchener Park	native	Diplopoda	Mature male polydemida sp. 1	native	2	0	0	0
Kitchener Park	native	Diplopoda	Mature male polydemida sp. 6	native	1	1	0	0
Kitchener Park	native	Diplopoda	Mature male polydemida sp. 8	native	12	5	1	9
Kitchener Park	native	Diplopoda	Mature male polydemida sp. 4	native	1	0	0	0
Kitchener Park	native	Diplopoda	Polydesmida sp. 1	native	0	0	0	2
Kitchener Park	native	Diplopoda	Polydesmida sp. 8	native	2	16	0	15
Kitchener Park	native	Diplopoda	Polydesmida sp. 6	native	1	0	0	2
Kitchener Park	native	Diplopoda	Polydesmida sp. 10	native	0	1	0	10
Kitchener Park	native	Diplopoda	Chordeumatida	native	1	0	4	0
Kitchener Park	native	Diplopoda	Spirostreptida	native	0	0	2	0
Kitchener Park	native	Diplopoda	Polyzoniida	native	0	2	1	3
Kitchener Park	native	Diplopoda	Julida (*Brachyiulus pusillus*)	adventive	2	3	1	0

Kitchener Park	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	18	70	8	7
Kitchener Park	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	2	3	0	27
Kitchener Park	native	Isopoda	Oniscidae	native	4	0	0	2
Kitchener Park	native	Isopoda	Armadillidiidae species 3	native	14	3	6	1
Kitchener Park	native	Isopoda	Armadillidiidae *Cubaris* species 1	native	5	0	0	0
Kitchener Park	native	Isopoda	Armadillidiidae *Cubaris* species 2	native	1	0	9	0
Kitchener Park	native	Isopoda	Styloniscidae	native	0	13	1	1
Kitchener Park	native	Isopoda	Trichoniscidae	adventive	0	1	0	0
Kitchener Park	native	Amphipoda	*Arcitalitrus*	adventive	12	34	13	55
Kitchener Park	native	Amphipoda	*Puhuruhuru aotearoa*	native	1	0	0	0
Kitchener Park	native	Amphipoda	Unidentified Amphipoda	unknown	0	1	0	1
Mt Lees Reserve	native	Diplopoda	Mature male polydemida sp. 8	native	0	3	0	1
Mt Lees Reserve	native	Diplopoda	Mature male polydemida sp. 4	native	0	2	0	1
Mt Lees Reserve	native	Diplopoda	Mature male polydemida sp. 6	native	0	1	0	0
Mt Lees Reserve	native	Diplopoda	Mature male polydemida sp. 7	native	0	4	2	0
Mt Lees Reserve	native	Diplopoda	Polydesmida sp. 11	native	0	0	1	0
Mt Lees Reserve	native	Diplopoda	Polydesmida sp. 5	native	0	0	2	8
Mt Lees Reserve	native	Diplopoda	Polydesmida sp. 7	native	0	4	0	2
Mt Lees Reserve	native	Diplopoda	Polydesmida sp. 8	native	0	2	1	3
Mt Lees Reserve	native	Diplopoda	Polydesmida sp. 4	native	0	0	0	1
Mt Lees Reserve	native	Diplopoda	Polydesmida sp. 10	native	1	1	0	0
Mt Lees Reserve	native	Diplopoda	Chordeumatida	native	0	0	10	5
Mt Lees Reserve	native	Diplopoda	Siphonophorida	native	0	1	1	0
Mt Lees Reserve	native	Diplopoda	Polyzoniida	native	11	3	5	1
Mt Lees Reserve	native	Diplopoda	Julida (*Blaniulus guttulatus*)	adventive	0	0	6	10
Mt Lees Reserve	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	5	5	27	10
Mt Lees Reserve	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	2	6	2	5
Mt Lees Reserve	native	Diplopoda	Julida (*Nopoiulus kochii*)	adventive	0	1	0	0
Mt Lees Reserve	native	Isopoda	Philosciidae	native	2	14	1	62
Mt Lees Reserve	native	Isopoda	Armadillidiidae species 3	native	4	3	1	1
Mt Lees Reserve	native	Isopoda	Styloniscidae	native	6	14	1	10

Mt Lees Reserve	native	Isopoda	Trichoniscidae	adventive	4	0	15	6
Mt Lees Reserve	native	Amphipoda	*Arcitalitrus*	adventive	14	43	14	149
Bledisloe Park	native	Diplopoda	Mature male polydemida sp. 7	native	1	5	0	1
Bledisloe Park	native	Diplopoda	Mature male polydemida sp. 1	native	3	0	0	0
Bledisloe Park	native	Diplopoda	Mature male polydemida sp. 4	native	1	0	0	0
Bledisloe Park	native	Diplopoda	Mature male polydemida sp. 8	native	1	1	0	0
Bledisloe Park	native	Diplopoda	Mature male polydemida sp. 6	native	0	1	0	0
Bledisloe Park	native	Diplopoda	Polydesmida sp. 1	native	3	22	1	0
Bledisloe Park	native	Diplopoda	Polydesmida sp. 8	native	0	17	0	0
Bledisloe Park	native	Diplopoda	Polydesmida sp. 10	native	0	4	0	0
Bledisloe Park	native	Diplopoda	Polydesmida sp. 12	native	0	1	0	0
Bledisloe Park	native	Diplopoda	Polydesmida sp. 5	native	6	0	1	0
Bledisloe Park	native	Diplopoda	Polydesmida sp. 7	native	14	7	0	0
Bledisloe Park	native	Diplopoda	Spirostreptida	native	1	0	0	0
Bledisloe Park	native	Diplopoda	Siphonophorida	native	3	0	1	0
Bledisloe Park	native	Diplopoda	Polyzoniida	native	0	5	1	3
Bledisloe Park	native	Diplopoda	Chordeumatida	native	0	1	0	0
Bledisloe Park	native	Diplopoda	Julida (*Blaniulus guttulatus*)	adventive	0	3	0	2
Bledisloe Park	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	8	2	4	0
Bledisloe Park	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	2	3	3	0
Bledisloe Park	native	Isopoda	Oniscidae	native	3	9	4	0
Bledisloe Park	native	Isopoda	Philosciidae	native	4	0	0	0
Bledisloe Park	native	Isopoda	Styloniscidae	native	0	46	0	17
Bledisloe Park	native	Isopoda	Trichoniscidae	adventive	10	1	0	0
Bledisloe Park	native	Amphipoda	*Arcitalitrus*	adventive	40	271	11	51
Totara Reserve	native	Diplopoda	Mature male polydemida sp. 1	native	1	0	0	0
Totara Reserve	native	Diplopoda	Mature male polydemida sp. 8	native	0	0	0	1
Totara Reserve	native	Diplopoda	Mature male polydemida sp. 13	native	1	0	0	0
Totara Reserve	native	Diplopoda	Mature male polydemida sp. 14	native	1	0	0	0
Totara Reserve	native	Diplopoda	Polydesmida sp. 8	native	1	0	0	4
Totara Reserve	native	Diplopoda	Polydesmida sp. 4	native	3	0	0	1

Totara Reserve	native	Diplopoda	Polydesmida sp. 5	native	12	9	0	1
Totara Reserve	native	Diplopoda	Chordeumatida	native	1	6	0	3
Totara Reserve	native	Diplopoda	Spirostreptida	native	1	0	0	1
Totara Reserve	native	Diplopoda	Siphonophorida	native	5	1	0	12
Totara Reserve	native	Diplopoda	Polyzoniida	native	0	3	1	0
Totara Reserve	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	0	0	9	30
Totara Reserve	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	0	0	4
Totara Reserve	native	Isopoda	Armadillidiidae *Cubaris* species 1	native	0	0	2	0
Totara Reserve	native	Isopoda	Armadillidiidae species 3	native	0	0	2	0
Totara Reserve	native	Isopoda	Styloniscidae	native	9	12	0	25
Totara Reserve	native	Amphipoda	*Puhuruhuru aotearoa*	native	10	7	5	9
Totara Reserve	native	Amphipoda	*Parorchestia tenuis*	native	0	0	0	4
Totara Reserve	native	Amphipoda	Unidentified Amphipoda	assumed native	2	0	0	0
The Manawatu Gorge	native	Diplopoda	Mature male polydemida sp. 4	native	1	0	2	0
The Manawatu Gorge	native	Diplopoda	Mature male polydemida sp. 8	native	0	0	0	2
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 8	native	0	0	0	1
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 5	native	1	1	1	0
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 7	native	1	1	1	11
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 1	native	0	1	0	0
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 6	native	0	0	0	2
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 4	native	2	0	3	0
The Manawatu Gorge	native	Diplopoda	Polydesmida sp. 10	native	0	1	0	0
The Manawatu Gorge	native	Diplopoda	Chordeumatida	native	1	2	1	2
The Manawatu Gorge	native	Diplopoda	Spirostreptida	native	12	3	5	4
The Manawatu Gorge	native	Diplopoda	Siphonophorida	native	0	1	0	4

The Manawatu Gorge	native	Diplopoda	Polyzoniida	native	0	0	1	0
The Manawatu Gorge	native	Diplopoda	Philosciidae	native	0	2	0	2
The Manawatu Gorge	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	0	1	0	25
The Manawatu Gorge	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	0	0	2
The Manawatu Gorge	native	Isopoda	Polyxenidae	native	0	0	3	0
The Manawatu Gorge	native	Isopoda	Armadillidiidae species 3	native	0	0	4	0
The Manawatu Gorge	native	Isopoda	Styloniscidae	native	7	15	7	23
The Manawatu Gorge	native	Amphipoda	*Puhuruhuru aotearoa*	native	5	28	0	11
The Manawatu Gorge	native	Amphipoda	*Arcitalitrus*	adventive	0	0	0	1
The Manawatu Gorge	native	Amphipoda	Unidentified Amphipoda	unknown	0	0	0	3
Kahutarawa	native	Diplopoda	Mature male polydemida sp. 7	native	1	0	0	0
Kahutarawa	native	Diplopoda	Mature male polydemida sp. 4	native	1	0	1	0
Kahutarawa	native	Diplopoda	Polydesmida sp. 1	native	13	1	0	0
Kahutarawa	native	Diplopoda	Polydesmida sp. 6	native	0	2	0	0
Kahutarawa	native	Diplopoda	Polydesmida sp. 4	native	1	0	2	0
Kahutarawa	native	Diplopoda	Polydesmida sp. 15	native	0	1	0	9
Kahutarawa	native	Diplopoda	Polydesmida sp. 5	native	17	0	0	3
Kahutarawa	native	Diplopoda	Polydesmida sp. 7	native	0	1	0	2
Kahutarawa	native	Diplopoda	Chordeumatida	native	1	0	0	1
Kahutarawa	native	Diplopoda	Spirostreptida	native	1	0	0	0
Kahutarawa	native	Diplopoda	Siphonophorida	native	4	0	0	2
Kahutarawa	native	Diplopoda	Polyzoniida	native	0	1	0	6
Kahutarawa	native	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	20	13	0	0
Kahutarawa	native	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	7	4	0	0
Kahutarawa	native	Isopoda	Philosciidae	native	2	8	0	6
Kahutarawa	native	Isopoda	Armadillidiidae *Cubaris* species 1	native	2	0	0	0
Kahutarawa	native	Isopoda	Armadillidiidae species 3	native	2	0	0	0
Kahutarawa	native	Isopoda	Armadillidiidae *Cubaris* species 2	native	0	0	7	0
Kahutarawa	native	Isopoda	Styloniscidae	native	5	6	0	5
Kahutarawa	native	Amphipoda	*Puhuruhuru aotearoa*	native	21	15	21	1

Kahutarawa	native	Amphipoda	*Parorchestia tenuis*	native	0	13	1	2
Kahutarawa	native	Amphipoda	*Arcitalitrus*	adventive	0	3	0	0
Kahutarawa	native	Amphipoda	Unidentified Amphipoda	native	0	3	0	0
Shannon forest	native	Diplopoda	Chordeumatida	native	1	0	0	1
Shannon forest	native	Diplopoda	Polydesmida sp. 15	native	1	7	0	4
Shannon forest	native	Diplopoda	Polydesmida sp. 5	native	8	0	1	1
Shannon forest	native	Diplopoda	Polydesmida sp. 7	native	0	0	0	23
Shannon forest	native	Isopoda	Oniscidae	native	0	0	1	0
Shannon forest	native	Isopoda	Armadillidiidae *Cubaris* species 1	native	0	0	2	0
Shannon forest	native	Isopoda	Armadillidiidae species 3	native	0	0	0	2
Shannon forest	native	Isopoda	Armadillidiidae species 4	native	0	0	2	0
Shannon forest	native	Isopoda	Styloniscidae	native	5	7	1	24
Shannon forest	native	Amphipoda	*Puhuruhuru aotearoa*	native	0	0	8	0
Shannon forest	native	Amphipoda	*Parorchestia tenuis*	native	0	0	12	6
Shannon forest	native	Amphipoda	*Arcitalitrus*	adventive	0	4	0	0
Shannon forest	native	Amphipoda	Unidentified Amphipoda	native	0	0	0	7
Hawkey's forest	pine	Diplopoda	Chordeumatida	native	0	5	0	0
Hawkey's forest	pine	Diplopoda	Mature male polydesmida sp. 13	native	0	0	1	0
Hawkey's forest	pine	Diplopoda	Mature male polydesmida sp. 8	native	0	4	0	1
Hawkey's forest	pine	Diplopoda	Polydesmida sp. 8	native	0	31	1	1
Hawkey's forest	pine	Diplopoda	Polydesmida sp. 11	native	4	0	2	0
Hawkey's forest	pine	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	12	0	1
Hawkey's forest	pine	Diplopoda	Julida (*Brachyiulus pusillus*)	adventive	0	8	0	0
Hawkey's forest	pine	Isopoda	Porcellionidae (*Porcellio scaber*)	adventive	2	0	0	0
Hawkey's forest	pine	Isopoda	Styloniscidae	native	0	0	0	1
Hawkey's forest	pine	Amphipoda	*Arcitalitrus*	adventive	1	26	0	0
Kahutarawa	pine	Diplopoda	Siphonophorida	native	1	77	1	10
Kahutarawa	pine	Diplopoda	Polyzoniida	native	0	0	0	7
Kahutarawa	pine	Diplopoda	Mature male polydesmida sp. 7	native	1	0	0	0
Kahutarawa	pine	Diplopoda	Mature male polydesmida sp. 8	native	3	0	4	2
Kahutarawa	pine	Diplopoda	Mature male polydesmida sp. 6	native	0	0	1	0
Kahutarawa	pine	Diplopoda	Polydesmida sp. 15	native	0	6	0	91

Kahutarawa	pine	Diplopoda	Polydesmida sp. 11	native	2	2	6	0
Kahutarawa	pine	Diplopoda	Polydesmida 8	native	3	0	3	1
Kahutarawa	pine	Diplopoda	Polydesmida sp. 1	native	2	1	0	1
Kahutarawa	pine	Diplopoda	Poldesmida sp. 10	native	0	1	0	0
Kahutarawa	pine	Diplopoda	Poldesmida sp. 13	native	0	1	0	0
Kahutarawa	pine	Diplopoda	Chordeumatida	native	0	0	2	0
Kahutarawa	pine	Isopoda	Philosciidae	native	7	7	0	0
Kahutarawa	pine	Isopoda	Armadillidiidae species 4	native	0	4	0	0
Kahutarawa	pine	Isopoda	Styloniscidae	native	1	11	2	9
Kahutarawa	pine	Amphipoda	*Puhuruhuru aotearoa*	native	0	9	1	12
Kahutarawa	pine	Amphipoda	*Parorchestia tenuis*	native	0	20	0	40
Kahutarawa	pine	Amphipoda	Unidentified Amphipoda	assumed native	0	4	1	12
Waitarere forest	pine	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	6	0	8
Waitarere forest	pine	Diplopoda	Polydesmida sp. 11	native	4	0	0	0
Waitarere forest	pine	Diplopoda	Polydesmida sp. 8	native	1	0	0	0
Waitarere forest	pine	Isopoda	Philosciidae	native	0	1	0	0
Waitarere forest	pine	Isopoda	Styloniscidae	native	0	0	0	23
Waitarere forest	pine	Amphipoda	*Arcitalitrus*	adventive	1	38	3	85
Shannon forest	pine	Diplopoda	Mature male polydemida sp. 10	native	0	0	0	1
Shannon forest	pine	Diplopoda	Mature male polydemida sp. 7	native	0	0	0	3
Shannon forest	pine	Diplopoda	Polydesmida sp. 8	native	0	4	4	4
Shannon forest	pine	Diplopoda	Polydesmida sp. 7	native	0	0	0	1
Shannon forest	pine	Diplopoda	Polydesmida sp. 11	native	0	0	0	10
Shannon forest	pine	Diplopoda	Chordeumatida	native	1	14	2	2
Shannon forest	pine	Diplopoda	Siphonophorida	native	0	0	0	5
Shannon forest	pine	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	0	0	1
Shannon forest	pine	Isopoda	Philosciidae	native	4	0	0	0
Shannon forest	pine	Isopoda	Styloniscidae	native	0	5	1	9
Shannon forest	pine	Isopoda	Trichoniscidae	adventive	6	0	0	0
Shannon forest	pine	Amphipoda	*Arcitalitrus*	adventive	1	24	3	57
Santoft forest	pine	Diplopoda	Chordeumatida	native	2	1	2	0
Santoft forest	pine	Diplopoda	Julida (*Brachyiulus pusillus*)	adventive	0	0	0	1
Santoft forest	pine	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	0	2	0	7
Santoft forest	pine	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	1	13	0	0

Santoft forest	pine	Diplopoda	Unknown polydesmida	assumed native	0	6	0	2
Santoft forest	pine	Isopoda	Philosciidae	native	0	4	0	0
Santoft forest	pine	Isopoda	Porcellionidae (*Porcellio scaber*)	adventive	2	0	0	0
Santoft forest	pine	Isopoda	Styloniscidae	native	0	3	0	0
Santoft forest	pine	Amphipoda	*Arcitalitrus*	adventive	0	16	0	16
Whanganui forest	pine	Diplopoda	Chordeumatida	native	2	2	1	0
Whanganui forest	pine	Diplopoda	Mature male polydesmida sp. 14	native	0	0	0	1
Whanganui forest	pine	Diplopoda	Polydesmida sp. 6	native	1	0	0	0
Whanganui forest	pine	Diplopoda	Polydesmida sp. 5	native	7	0	2	3
Whanganui forest	pine	Diplopoda	Polydesmida sp. 8	native	0	0	1	1
Whanganui forest	pine	Diplopoda	Polydesmida (juvenile, too young to id)	assumed native	0	0	0	1
Whanganui forest	pine	Diplopoda	Polydesmida sp. 11	native	0	0	0	1
Whanganui forest	pine	Diplopoda	Polydesmida sp. 14	native	0	0	0	1
Whanganui forest	pine	Diplopoda	Julida (*Ophyiulus pilosus*)	adventive	1	0	0	0
Whanganui forest	pine	Diplopoda	Julida (*Cylindroiulus britannicus*)	adventive	1	0	0	0
Whanganui forest	pine	Isopoda	Styloniscidae	native	28	0	43	4
Whanganui forest	pine	Amphipoda	*Arcitalitrus*	adventive	4	13	0	0

Appendix 3: key to sites presented on figures in Chapter 4[8]

Native forests

NE1= The Esplanade edge
NC1=The Esplanade centre
NE2=The Ashhurst Domain edge
NC2= The Ashhurst Domain centre
NE3=McCraes Bush edge
NC3=McCraes Bush centre
NE4=Kitchener Park edge
NC4=Kitchener Park centre
NE5= Mt Lees edge
NC5= Mt Lees centre
NE6= Bledisloe Park edge
NC6= Bledisloe Park centre
NE7=Totara Reserve edge
NC7=Totara Reserve centre
NE8= The Gorge edge
NC8= The Gorge centre
NE9=Shannon edge
NC9=Shannon centre
NE10=Kahutarawa edge
NC10 = Kahutarawa centre

Pine forests

PE1=Kahautarawa edge
PC1=Kahutarawa centre
PE2=Shannon edge
PC2=Shannon centre
PE3=Hawkey’s edge
PC3=Hawkey’s centre
PE4=Waitarere edge
PC4= Waitarere centre
PE5= Santoft edge
PC5=Santoft centre
PE6= Whanganui edge
PC6=Whanganui centre

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[8] In figures 4.4- 4.9 edge and centre plots were pooled; therefore the letters ‘E’ and ‘C’, which denote edge and centre locations, are removed from the codes.

Appendix 4: logistic regression model (SAS output)

Diplopoda

Model Information		
Data Set	WORK.AMIE2	
Response Variable (Events)	mill_a	mill_a
Response Variable (Trials)	mill_total	
Model	binary logit	
Optimization Technique	Fisher's scoring	

Number of Observations Read	32
Number of Observations Used	32
Sum of Frequencies Read	1744
Sum of Frequencies Used	1744

Response Profile		
Ordered Value	**Binary Outcome**	**Total Frequency**
1	Event	563
2	Nonevent	1181

Class Level Information			
Class	**Value**	**Design Variables**	
forest	**native**	1	0
	pine	0	1
plot	**centre**	1	0
	edge	0	1

Model Convergence Status
Convergence criterion (GCONV=1E-8) satisfied.

Model Fit Statistics

Criterion	Intercept Only	Intercept and Covariates	With Constant
AIC	2195.874	2098.840	707.486
SC	2201.338	2115.232	723.878
-2 Log L	2193.874	2092.840	701.486

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	101.0337	2	<.0001
Score	91.8575	2	<.0001
Wald	84.4162	2	<.0001

Type 3 Analysis of Effects

Effect	DF	Wald Chi-Square	Pr > ChiSq
forest	1	75.4056	<.0001
plot	1	11.8994	0.0006

Analysis of Maximum Likelihood Estimates

Parameter		DF	Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq
Intercept		1	-1.9486	0.1487	171.8408	<.0001
forest	**native**	1	1.2957	0.1492	75.4056	<.0001
forest	**pine**	0	0	.	.	.
plot	**centre**	1	0.3644	0.1056	11.8994	0.0006
plot	**edge**	0	0	.	.	.

Odds Ratio Estimates

Effect	Point Estimate	95% Wald Confidence Limits	
forest native vs pine	3.654	2.727	4.895
plot centre vs edge	1.440	1.170	1.771

Association of Predicted Probabilities and Observed Responses

Percent Concordant	47.7	**Somers' D**	0.277
Percent Discordant	20.1	**Gamma**	0.408

Association of Predicted Probabilities and Observed Responses

Percent Tied	32.2	**Tau-a**	0.121
Pairs	664903	**c**	0.638

The SAS System

Obs	site	forest	plot	substrate	mill_n	mill_a	mill_total	advents
1	McCraes	native	centre	all	41	51	92	0.42836
2	bledisloe	native	centre	all	8	9	17	0.42836
3	domain	native	centre	all	27	20	47	0.42836
4	esplanade	native	centre	all	19	9	28	0.42836
5	gorge	native	centre	all	45	27	72	0.42836
6	kahutarawa	native	centre	all	26	0	26	0.42836
7	kitchener	native	centre	all	49	43	92	0.42836
8	mt_lees	native	centre	all	44	60	104	0.42836
9	shannon	native	centre	all	30	0	30	0.42836
10	totara_reserve	native	centre	alla	24	43	67	0.42836
11	McCraes	native	edge	all	11	9	20	0.34233
12	bledisloe	native	edge	all	97	18	115	0.34233
13	domain	native	edge	all	165	6	171	0.34233
14	esplanade	native	edge	all	17	44	61	0.34233
15	gorge	native	edge	all	30	1	31	0.34233
16	kahutarawa	native	edge	all	45	44	89	0.34233
17	kitchener	native	edge	all	45	98	143	0.34233
18	mt_lees	native	edge	all	33	19	52	0.34233
19	shannon	native	edge	all	17	0	17	0.34233
20	totara_reserve	native	edge	all	45	0	45	0.34233
21	Hawkeys	pine	centre	all	6	1	7	0.17019
22	kahutarawa	pine	centre	all	129	0	129	0.17019
23	santoft	pine	centre	all	2	8	10	0.17019
24	shannon	pine	centre	all	32	1	33	0.17019
25	waitarere	pine	centre	all	0	8	8	0.17019
26	whanganui	pine	centre	all	11	0	11	0.17019
27	Hawkeys	pine	edge	all	44	20	64	0.12470
28	kahutarawa	pine	edge	all	100	0	100	0.12470
29	santoft	pine	edge	all	3	16	19	0.12470
30	shannon	pine	edge	all	19	0	19	0.12470

Obs	site	forest	plot	substrate	mill_n	mill_a	mill_total	advents
31	waitarere	pine	edge	all	5	6	11	0.12470
32	whanganui	pine	edge	all	12	2	14	0.12470

Isopoda

Model Information		
Data Set	WORK.AMIE2	
Response Variable (Events)	slat_a	slat_a
Response Variable (Trials)	slat_total	
Model	binary logit	
Optimization Technique	Fisher's scoring	

Number of Observations Read	32
Number of Observations Used	31
Sum of Frequencies Read	798
Sum of Frequencies Used	798

Response Profile

Ordered Value	Binary Outcome	Total Frequency
1	Event	83
2	Nonevent	715

Note: 1 observation with an invalid response value has been deleted. Either the number of trials was less than or equal to zero or less than the number of events, or the number of events was negative.

Class Level Information

Class	Value	Design Variables	
forest	**native**	1	0
	pine	0	1
plot	**centre**	1	0
	edge	0	1

Model Convergence Status

Convergence criterion (GCONV=1E-8) satisfied.

Model Fit Statistics

Criterion	Intercept Only	Intercept and Covariates	With Constant
AIC	534.754	510.521	258.056
SC	539.436	524.567	272.102
-2 Log L	532.754	504.521	252.056

Testing Global Null Hypothesis: BETA=0

Test	Chi-Square	DF	Pr > ChiSq
Likelihood Ratio	28.2331	2	<.0001
Score	26.4474	2	<.0001
Wald	24.3361	2	<.0001

Type 3 Analysis of Effects

Effect	DF	Wald Chi-Square	Pr > ChiSq
forest	1	4.9799	0.0256
plot	1	19.2976	<.0001

Analysis of Maximum Likelihood Estimates

Parameter		DF	Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq
Intercept		1	-2.3604	0.3362	49.2928	<.0001
forest	**native**	1	0.7845	0.3515	4.9799	0.0256
forest	**pine**	0	0	.	.	.
plot	**centre**	1	-1.1598	0.2640	19.2976	<.0001
plot	**edge**	0	0	.	.	.

Odds Ratio Estimates

Effect	Point Estimate	95% Wald Confidence Limits	
forest native vs pine	2.191	1.100	4.365
plot centre vs edge	0.314	0.187	0.526

Association of Predicted Probabilities and Observed Responses			
Percent Concordant	48.8	**Somers' D**	0.322
Percent Discordant	16.6	**Gamma**	0.493
Percent Tied	34.6	**Tau-a**	0.060
Pairs	59345	**c**	0.661

The SAS System

Obs	site	forest	plot	substrate	slat_n	slat_a	slat_total	advents
1	McCraes	native	centre	all	6	0	6	0.06090
2	bledisloe	native	centre	all	21	0	21	0.06090
3	domain	native	centre	all	30	0	30	0.06090
4	esplanade	native	centre	all	14	0	14	0.06090
5	gorge	native	centre	all	34	0	34	0.06090
6	kahutarawa	native	centre	all	18	0	18	0.06090
7	kitchener	native	centre	all	20	0	20	0.06090
8	mt_lees	native	centre	all	76	21	97	0.06090
9	shannon	native	centre	all	32	0	32	0.06090
10	totara_reserve	native	centre	all	29	0	29	0.06090
11	McCraes	native	edge	all	1	1	2	0.17138
12	bledisloe	native	edge	all	62	11	73	0.17138
13	domain	native	edge	all	32	0	32	0.17138
14	esplanade	native	edge	all	9	35	44	0.17138
15	gorge	native	edge	all	22	0	22	0.17138
16	kahutarawa	native	edge	all	25	0	25	0.17138
17	kitchener	native	edge	all	40	1	41	0.17138
18	mt_lees	native	edge	all	43	4	47	0.17138
19	shannon	native	edge	all	12	0	12	0.17138
20	totara_reserve	native	edge	all	21	0	21	0.17138
21	Hawkeys	pine	centre	all	1	0	1	0.02874
22	kahutarawa	pine	centre	all	12	0	12	0.02874
23	santoft	pine	centre	all	0	0	0	0.02874

Obs	site	forest	plot	substrate	slat_n	slat_a	slat_total	advents
24	shannon	pine	centre	all	10	0	10	0.02874
25	waitarere	pine	centre	all	23	0	23	0.02874
26	whanganui	pine	centre	all	47	0	47	0.02874
27	Hawkeys	pine	edge	all	0	2	2	0.08625
28	kahutarawa	pine	edge	all	30	0	30	0.08625
29	santoft	pine	edge	all	7	2	9	0.08625
30	shannon	pine	edge	all	9	6	15	0.08625
31	waitarere	pine	edge	all	1	0	1	0.08625
32	whanganui	pine	edge	all	28	0	28	0.08625

Amphipoda

Model Information		
Data Set	WORK.AMIE2	
Response Variable (Events)	amph_a	amph_a
Response Variable (Trials)	amph_total	
Model	binary logit	
Optimization Technique	Fisher's scoring	

Number of Observations Read	32
Number of Observations Used	29
Sum of Frequencies Read	1463
Sum of Frequencies Used	1463

Response Profile		
Ordered Value	**Binary Outcome**	**Total Frequency**
1	Event	1172
2	Nonevent	291

Note: 3 observations with invalid response values have been deleted. Either the number of trials was less than or equal to zero or less than the number of events, or the number of events was negative.

Class Level Information			
Class	**Value**	**Design Variables**	
forest	**native**	1	0
	pine	0	1
plot	**centre**	1	0
	edge	0	1

Model Convergence Status
Convergence criterion (GCONV=1E-8) satisfied.

Model Fit Statistics			
Criterion	**Intercept Only**	**Intercept and Covariates**	**With Constant**
AIC	1461.730	1452.120	1419.100
SC	1467.019	1467.984	1434.965
-2 Log L	1459.730	1446.120	1413.100

Testing Global Null Hypothesis: BETA=0			
Test	**Chi-Square**	**DF**	**Pr > ChiSq**
Likelihood Ratio	13.6107	2	0.0011
Score	14.0035	2	0.0009
Wald	13.8469	2	0.0010

Type 3 Analysis of Effects			
Effect	**DF**	**Wald Chi-Square**	**Pr > ChiSq**
forest	1	8.5429	0.0035
plot	1	3.3263	0.0682

Analysis of Maximum Likelihood Estimates						
Parameter		**DF**	**Estimate**	**Standard Error**	**Wald Chi-Square**	**Pr > ChiSq**
Intercept		1	1.2155	0.1432	72.0628	<.0001
forest	**native**	1	0.4180	0.1430	8.5429	0.0035
forest	**pine**	0	0	.	.	.

Analysis of Maximum Likelihood Estimates

Parameter		DF	Estimate	Standard Error	Wald Chi-Square	Pr > ChiSq
plot	**centre**	1	-0.2430	0.1332	3.3263	0.0682
plot	**edge**	0	0	.	.	.

Odds Ratio Estimates

Effect	Point Estimate	95% Wald Confidence Limits	
forest native vs pine	1.519	1.148	2.010
plot centre vs edge	0.784	0.604	1.018

Association of Predicted Probabilities and Observed Responses

Percent Concordant	41.3	**Somers' D**	0.123
Percent Discordant	29.0	**Gamma**	0.175
Percent Tied	29.7	**Tau-a**	0.039
Pairs	341052	**c**	0.562

The SAS System

Obs	site	forest	plot	substrate	amph _n	amph _a	amph _total	advents
1	McCraes	native	centre	all	0	1	1	0.80066
2	bledisloe	native	centre	all	0	62	62	0.80066
3	domain	native	centre	all	0	64	64	0.80066
4	esplanade	native	centre	all	0	5	5	0.80066
5	gorge	native	centre	all	11	1	12	0.80066
6	kahutarawa	native	centre	all	25	0	25	0.80066
7	kitchener	native	centre	all	0	68	68	0.80066
8	mt_lees	native	centre	all	0	163	163	0.80066
9	shannon	native	centre	all	33	0	33	0.80066
10	totara_reserve	native	centre	all	18	0	18	0.80066
11	McCraes	native	edge	all	0	0	0	0.83664
12	bledisloe	native	edge	all	0	311	311	0.83664
13	domain	native	edge	all	0	72	72	0.83664
14	esplanade	native	edge	all	0	27	27	0.83664

Obs	site	forest	plot	substrate	amph _n	amph _a	amph _total	advents
15	gorge	native	edge	all	33	0	33	0.83664
16	kahutarawa	native	edge	all	52	3	55	0.83664
17	kitchener	native	edge	all	1	46	47	0.83664
18	mt_lees	native	edge	all	0	57	57	0.83664
19	shannon	native	edge	all	0	4	4	0.83664
20	totara_reserve	native	edge	all	19	0	19	0.83664
21	Hawkeys	pine	centre	all	0	0	0	0.72561
22	kahutarawa	pine	centre	all	66	0	66	0.72561
23	santoft	pine	centre	all	0	16	16	0.72561
24	shannon	pine	centre	all	0	60	60	0.72561
25	waitarere	pine	centre	all	0	88	88	0.72561
26	whanganui	pine	centre	all	0	0	0	0.72561
27	Hawkeys	pine	edge	all	0	27	27	0.77126
28	kahutarawa	pine	edge	all	33	0	33	0.77126
29	santoft	pine	edge	all	0	16	16	0.77126
30	shannon	pine	edge	all	0	25	25	0.77126
31	waitarere	pine	edge	all	0	39	39	0.77126
32	whanganui	pine	edge	all	0	17	17	0.77126

Appendix 5: the mixed procedure (SAS output)

Adventive Diplopoda

Model Information	
Data Set	WORK.AMIE2
Dependent Variable	mill_a
Covariance Structure	Variance Components
Estimation Method	REML
Residual Variance Method	Profile
Fixed Effects SE Method	Model-Based
Degrees of Freedom Method	Satterthwaite

Class Level Information

Class	Levels	Values
forest	2	native pine
plot	2	centre edge
site	14	Hawkeys McCraes bledisloe domain esplanade gorge kahutarawa kitchener mt_lees santoft shannon totara_reserve waitarere whanganui

Dimensions	
Covariance Parameters	2
Columns in X	9
Columns in Z	14
Subjects	1
Max Obs Per Subject	32

Number of Observations	
Number of Observations Read	32
Number of Observations Used	32
Number of Observations Not Used	0

Covariance Parameter Estimates

Cov Parm	Estimate
site	44.8012
Residual	431.82

Fit Statistics	
-2 Res Log Likelihood	260.1
AIC (smaller is better)	264.1
AICC (smaller is better)	264.6
BIC (smaller is better)	265.4

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
Forest	1	24.2	5.59	0.0264
plot	1	15.9	0.02	0.8951
forest*plot	1	15.9	0.19	0.6679

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		25.1655	5.0958	16.1	4.94	0.0001
forest	**pine**		5.9450	6.5654	17.2	0.91	0.3777
plot		**centre**	15.0469	5.6939	26	2.64	0.0138
plot		**edge**	16.0636	5.6939	26	2.82	0.0090

Differences of Least Squares Means

Effect	forest	plot	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		**pine**		19.2205	8.1263	24.2	2.37	0.0264
plot		**centre**		**edge**	-1.0167	7.5879	15.9	-0.13	0.8951

Native Diplopoda

Model Information	
Data Set	WORK.AMIE2
Dependent Variable	mill_n
Covariance Structure	Variance Components
Estimation Method	REML
Residual Variance Method	Profile
Fixed Effects SE Method	Model-Based
Degrees of Freedom Method	Satterthwaite

Class Level Information

Class	Levels	Values
forest	2	native pine
plot	2	centre edge
site	14	Hawkeys McCraes bledisloe domain esplanade gorge kahutarawa kitchener mt_lees santoft shannon totara_reserve waitarere whanganui

Dimensions

Covariance Parameters	2
Columns in X	9
Columns in Z	14
Subjects	1
Max Obs Per Subject	32

Number of Observations

Number of Observations Read	32
Number of Observations Used	32
Number of Observations Not Used	0

Covariance Parameter Estimates

Cov Parm	Estimate
site	165.70
Residual	1285.20

Fit Statistics

-2 Res Log Likelihood	291.2
AIC (smaller is better)	295.2
AICC (smaller is better)	295.7
BIC (smaller is better)	296.5

Type 3 Tests of Fixed Effects-Diplopoda native

Effect	Num DF	Den DF	F Value	Pr > F
forest	1	25.1	0.29	0.5946
plot	1	17.5	0.57	0.4618
forest*plot	1	17.5	0.51	0.4845

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		39.1676	8.9647	17.7	4.37	0.0004
forest	**pine**		31.5025	11.5400	19	2.73	0.0133

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
plot		**centre**	30.4100	9.9524	26.2	3.06	0.0051
plot		**edge**	40.2600	9.9524	26.2	4.05	0.0004

Differences of Least Squares Means

Effect	forest	plot	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		**pine**		7.6651	14.2211	25.1	0.54	0.5946
plot		**centre**		**edge**	-9.8500	13.0904	17.5	-0.75	0.4618

Adventive Isopoda

Model Information

Data Set	WORK.AMIE2
Dependent Variable	slat_a
Covariance Structure	Variance Components
Estimation Method	REML
Residual Variance Method	Profile
Fixed Effects SE Method	Model-Based
Degrees of Freedom Method	Satterthwaite

Class Level Information

Class	Levels	Values
forest	2	native pine
plot	2	centre edge
site	14	Hawkeys McCraes bledisloe domain esplanade gorge kahutarawa kitchener mt_lees santoft shannon totara_reserve waitarere whanganui

Dimensions

Covariance Parameters	2
Columns in X	9
Columns in Z	14
Subjects	1
Max Obs Per Subject	32

Number of Observations

Number of Observations Read	32
Number of Observations Used	32
Number of Observations Not Used	0

Covariance Parameter Estimates	
Cov Parm	**Estimate**
site	0
Residual	54.2083

Fit Statistics	
-2 Res Log Likelihood	199.4
AIC (smaller is better)	201.4
AICC (smaller is better)	201.6
BIC (smaller is better)	202.1

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
forest	1	28	1.10	0.3037
plot	1	28	0.79	0.3829
forest*plot	1	28	0.07	0.7918

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		3.6500	1.6463	28	2.22	0.0349
forest	**pine**		0.8333	2.1254	28	0.39	0.6980
plot		**centre**	1.0500	1.9010	28	0.55	0.5851
plot		**edge**	3.4333	1.9010	28	1.81	0.0817

Differences of Least Squares Means

Effect	forest	plot	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		**pine**		2.8167	2.6885	28	1.05	0.3037
plot		**centre**		**edge**	-2.3833	2.6885	28	-0.89	0.3829

Native Isopoda

Model Information	
Data Set	WORK.AMIE2
Dependent Variable	slat_n
Covariance Structure	Variance Components
Estimation Method	REML
Residual Variance Method	Profile
Fixed Effects SE Method	Model-Based

Model Information

Degrees of Freedom Method	Satterthwaite

Class Level Information

Class	Levels	Values
forest	2	native pine
plot	2	centre edge
site	14	Hawkeys McCraes bledisloe domain esplanade gorge kahutarawa kitchener mt_lees santoft shannon totara_reserve waitarere whanganui

Dimensions

Covariance Parameters	2
Columns in X	9
Columns in Z	14
Subjects	1
Max Obs Per Subject	32

Number of Observations

Number of Observations Read	32
Number of Observations Used	32
Number of Observations Not Used	0

Covariance Parameter Estimates

Cov Parm	Estimate
site	146.01
Residual	173.92

Fit Statistics

-2 Res Log Likelihood	245.2
AIC (smaller is better)	249.2
AICC (smaller is better)	249.6
BIC (smaller is better)	250.4

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
forest	1	27.8	2.88	0.1011
plot	1	14.7	0.20	0.6618
forest*plot	1	14.7	0.03	0.8623

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		26.7808	4.6640	15.6	5.74	<.0001
forest	**pine**		15.6456	5.8037	19.9	2.70	0.0139
plot		**centre**	22.2882	4.7681	20.3	4.67	0.0001
plot		**edge**	20.1382	4.7681	20.3	4.22	0.0004

Differences of Least Squares Means

Effect	forest	plot	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		**pine**		11.1352	6.5668	27.8	1.70	0.1011
plot		**centre**		**edge**	2.1500	4.8155	14.7	0.45	0.6618

Adventive Amphipoda

Model Information

Data Set	WORK.AMIE2
Dependent Variable	amph_a
Covariance Structure	Variance Components
Estimation Method	REML
Residual Variance Method	Profile
Fixed Effects SE Method	Model-Based
Degrees of Freedom Method	Satterthwaite

Class Level Information

Class	Levels	Values
forest	2	native pine
plot	2	centre edge
site	14	Hawkeys McCraes bledisloe domain esplanade gorge kahutarawa kitchener mt_lees santoft shannon totara_reserve waitarere whanganui

Dimensions

Covariance Parameters	2
Columns in X	9
Columns in Z	14
Subjects	1
Max Obs Per Subject	32

Number of Observations	
Number of Observations Read	32
Number of Observations Used	32
Number of Observations Not Used	0

Covariance Parameter Estimates	
Cov Parm	**Estimate**
site	1514.04
Residual	2675.69

Fit Statistics	
-2 Res Log Likelihood	318.7
AIC (smaller is better)	322.7
AICC (smaller is better)	323.2
BIC (smaller is better)	324.0

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
forest	1	26.8	0.17	0.6810
plot	1	14.5	0.06	0.8164
forest*plot	1	14.5	0.35	0.5647

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		42.6662	16.5098	15.2	2.58	0.0206
forest	**pine**		32.5978	20.8151	18.9	1.57	0.1340
plot		**centre**	35.3987	17.1857	21.7	2.06	0.0516
plot		**edge**	39.8653	17.1857	21.7	2.32	0.0302

Differences of Least Squares Means

Effect	forest	plot	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		**pine**		10.0684	24.2292	26.8	0.42	0.6810
plot		**centre**		**edge**	-4.4667	18.8880	14.5	-0.24	0.8164

Native Amphipoda

Model Information	
Data Set	WORK.AMIE2
Dependent Variable	amph_n

```
                 Model Information
Covariance Structure          Variance Components
Estimation Method             REML
Residual Variance Method      Profile
Fixed Effects SE Method       Model-Based
Degrees of Freedom Method     Satterthwaite
```

```
                              Class Level Information
Class   Levels  Values
forest       2  native pine
plot         2  centre edge
site        14  Hawkeys McCraes bledisloe domain esplanade gorge kahutarawa kitchener mt_lees santoft
                shannon totara_reserve waitarere whanganui
```

```
        Dimensions
Covariance Parameters    2
Columns in X             9
Columns in Z            14
Subjects                 1
Max Obs Per Subject     32
```

```
          Number of Observations
Number of Observations Read        32
Number of Observations Used        32
Number of Observations Not Used     0
```

```
Covariance Parameter Estimates
Cov Parm              Estimate
site                    149.59
Residual                119.81
```

```
           Fit Statistics
-2 Res Log Likelihood        238.2
AIC (smaller is better)      242.2
AICC (smaller is better)     242.6
BIC (smaller is better)      243.4
```

```
           Type 3 Tests of Fixed Effects
Effect     Num DF   Den DF   F Value    Pr > F
forest          1       28      0.19    0.6631
```

Type 3 Tests of Fixed Effects

Effect	Num DF	Den DF	F Value	Pr > F
plot	1	17.5	0.21	0.6492
forest*plot	1	17.5	0.83	0.3736

Least Squares Means

Effect	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		8.0350	4.3581	18.4	1.84	0.0814
forest	**pine**		5.4796	5.3287	22.6	1.03	0.3147
plot		**centre**	7.6823	4.3892	21.2	1.75	0.0946
plot		**edge**	5.8323	4.3892	21.2	1.33	0.1981

Differences of Least Squares Means

Effect	forest	plot	forest	plot	Estimate	Standard Error	DF	t Value	Pr > |t|
forest	**native**		**pine**		2.5554	5.8045	28	0.44	0.6631
plot		**centre**		**edge**	1.8500	3.9969	17.5	0.46	0.6492