The effects of restoration on the structure and function of litter invertebrate communities in New Zealand native forest remnants

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Jessica Anne Costall

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Abstract

Much of New Zealand's remaining lowland forest exists as small, often degraded and heavily disturbed remnants on private farmland. Disturbances, such as livestock grazing and browsing by mammalian pests, are known to have a detrimental effect on native vegetation of these remnants. However, it is unclear what impact these disturbances have on the structure and function of forest floor invertebrate communities. Existing studies of forest fragmentation have predominantly focused on the effects of remnant area and shape, rather than remnant condition. This study examines how litter invertebrate habitat, community structure, and leaf litter decomposition, vary between grazed and ungrazed (fenced) remnants of differing size, and nearby forest reserves. Secondly, I examine how invertebrate community structure and function recover with time since livestock exclusion, with and without additional mammalian pest control.

I found that grazed remnants provide dramatically altered habitat for litter invertebrates, compared to fenced remnants and large forest reserves. Grazed remnants are typified by having higher soil compaction, minimal understorey vegetation, and reduced litter cover. Consequently, grazed remnants have depauperate, yet highly variable invertebrate communities, compared to fenced remnants and forest reserves. Even very small forest remnants can support litter invertebrate communities very similar to that of larger forest reserves, provided they are protected from livestock grazing. Furthermore, invertebrate communities show strong recovery over time since livestock exclusion, particularly when livestock exclusion is combined with mammalian pest control measures. I found that litter decomposition rates did not differ between management treatments in my first observational study. However, in the second observational study, leaf decomposition rates at the edge of remnants increased with time since livestock exclusion, suggesting that restoration actions can lead to changes in ecological functioning.

Small native forest remnants have high ecological value and substantial restoration gains can be made through the relatively simple action of fencing to exclude livestock.

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Many of the staff and fellow postgraduate students in the Ecology Group have provided me with assistance, support (and often welcome distractions!) over the past few years. In particular, I would like to thank the technical and administrative staff, who were always extremely helpful, particularly Erica Dahya, Barbara Just, Paul Barrett, Cleland Wallace, and Tracy Harris. Many of the academic staff, especially Mike Joy, Jill Rapson, Ian Henderson, Murray Potter, Ed Minot, Alastair Roberston, and John Holland, took interest in my research progress, and provided advice and insightful discussion. Doug Armstrong and Yvan Richards deserve special mention for introducing me to the delights of Benneydale. I am very grateful to Doug for allowing me to join the research team at Benneydale, and stay at the "Tutu Road campus".

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My friends, family, and my partner Steve have been very supportive, and I know that I would not have completed this thesis without their patient encouragement (and yes, even simply sharing war stories over a pint at The Celtic Inn at the end of a particularly discouraging week counts as encouragement!). Thank you all for believing in me.

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Preface

Each chapter of this thesis has been written as a stand-alone chapter. As a consequence, there is some repetition of material between chapters, particularly in the methods. Chapters 1-6 are primarily my own work, with guidance from my supervisors and external mentors, as outlined below.

My chief supervisor, Russell Death, provided guidance on methodology and study design, and advice with data analysis, manuscript development and editing for Chapters 1-6. My co-supervisor, Masha Minor, provided helpful advice on methodology and study design, and manuscript editing for Chapters 1-4.

Drs Raphael Didham (University of Western Australia, formerly at University of Canterbury, New Zealand) and Gary Barker (Landcare Research, Hamilton, New Zealand) provided advice on study design, manuscript development and editing for Chapters 5 and 6. Chapter 6 is a more detailed classification and examination of millipede communities that were collected as part of a larger study of invertebrate communities (Chapter 7). Raphael and Gary were primarily responsible for designing the original study. I made a significant contribution to the original study (outlined below), and was solely responsible for all of the laboratory identification work of the millipede specimens. Russell, Raphael, and Gary provided guidance and advice with regards to data analysis and manuscript editing of Chapter 6.

I am the third co-author of Chapter 7, which has been published in the New Zealand Journal of Zoology. Raphael Didham and Gary Barker are the first and second authors of this paper, as they were primarily responsible for designing the study, data analysis, and the writing of the manuscript. I made a significant contribution by coordinating and undertaking fieldwork, laboratory work, and data entry, and provided input on study design, manuscript preparation and editing. Lisa Denmead, Corinne Watts, and Chris Floyd are also co-authors, and made significant contributions towards study design, fieldwork, laboratory work, and manuscript development.

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Introduction

Throughout the world, humans have transformed vast areas of natural habitat into highly modified landscapes in order to meet our needs for resources and land for both settlements and food production. It has been estimated that 40% of the global land area is now devoted to agriculture (Foley et al. 2005). This process of habitat loss, modification and fragmentation continues at a rapid pace, particularly in developing nations (Curran et al. 2004, Foley et al. 2005).

Anthropogenic habitat loss and fragmentation is not a random process. In particular, highly productive lowland ecosystems have been disproportionately affected (Norton 2000, Norton and Miller 2000, Curran et al. 2004). For example, in New Zealand, while around 30% of our total land area is under formal conservation protection, only 18% of land under 500 m in altitude is protected (Norton and Miller 2000). Since human arrival, native forest cover has been reduced from an estimated 84% to 24% of our land area (Ewers et al. 2006). Our lowland forests have been reduced to such an extent that in many areas less than 1% of the original lowland forest cover remains (Ewers et al. 2006). The remaining forest is highly fragmented (Norton 2000), for example in the Waikato region, where native forest cover has declined from 94% to 22%, there are now around 8200 fragments of native forest, with a mean area of 196 ha (Ewers et al. 2006).

There is increasing recognition of the importance of conserving our lowland ecosystems and biodiversity. As such, even very small and degraded habitat remnants are perceived to have conservation value, if only by being all that remains of once continuous ecosystems (Turner and Corlett 1996, Norton and Miller 2000, Tscharntke et al. 2002). However, we have very little understanding of the ecology of small habitat remnants, and how they should be managed to best conserve all facets of biodiversity (Norton 2000).

One particular challenge to the conservation of lowland forest remnants is that many of them remain under private ownership, often on farmland (Norton 2000). Encouragingly, many landowners value highly the native habitat remnants on their properties, and are interested in protecting them (Jay 2005, Durpoix 2010). Organisations such as the Queen Elizabeth II National Trust and regional councils provide some funding towards protective and restorative management actions such as fencing, and pest and weed control, yet landowners are still required to meet much of the costs of managing these remnants themselves. If we are to make reliable recommendations regarding the efficacy of various management actions, we must first have a thorough understanding of how management affects the ecology of remnants (Norton 2000).

There is a large body of literature concerning the impacts of habitat fragmentation on ecological communities. However, compared to studies of plants and vertebrates, few fragmentation studies have assessed the impacts on invertebrates. There is also a taxonomic bias amongst the existing studies, which predominantly considered beetles (Coleoptera), butterflies (Lepidoptera), and ants and bees (Hymenoptera). In contrast, few studies have addressed the impacts of habitat fragmentation on important detritivore groups, such as millipedes (Diplopoda) and woodlice (Isopoda), despite their functional significance (Bardgett 2005, Lavelle et al. 2006).

Many habitat fragmentation studies have taken an island biogeographic approach, whereby remnant area and isolation are deemed to be the most important factors determining remnant community diversity (Cook et al. 2002, Ewers and Didham 2006). Small and isolated habitat remnants were predicted to have the lowest species diversity. However, many organisms in remnants, including invertebrates, do not closely follow the predictions of island biogeographic theory (Debinski et al. 2000). In fact, several studies have shown equivocal results, with some reporting a decline in invertebrate diversity with decreasing remnant size (e.g., Andresen 2003, Bolger et al. 2000, Brühl et al. 2003), some finding no relationship between diversity and remnant size (e.g., Becker et al. 1991, Davies and Margules 1998, Gibb and Hotchuli 2002), and others finding that the relationship between diversity and remnant area was dependent upon which diversity measure was used (Baz and Garcia-Boyero 1995).

The lack of consensus regarding invertebrate response to remnant area can be explained by a number of factors. For one, invertebrates have comparatively small area requirements compared to larger animals and plants, and therefore forest remnant area *per se* is generally not a limiting factor for them. Secondly, and most importantly, studies that examine diversity measures only, rather than species identity, overlook the changes in community composition that ultimately occur in association with habitat fragmentation – habitat fragments typically support communities increasingly dominated by habitat generalists at the expense of specialists (Davies et al. 2004), and also tend to contain higher numbers of invasive species from the surrounding matrix (Cook et al. 2002, Brühl et al. 2003, Ewers and Didham 2006). Other traits, such as body size and trophic level may also influence sensitivity to fragmentation, although there is no strong consensus as to which traits are most important (see Didham et al. 1998, Davies et al. 2000, Gibb and Hotchuli 2002, Driscoll and Weir 2005).

The edges of habitat remnants are ecotones, the boundaries between two distinct ecosystem types, and often support a combination of species from both habitats. Therefore, while forest remnants will typically lose deep-forest specialist taxa, they could potentially support higher diversity than larger remnants. Habitat fragments are clearly not analogous to islands, and the matrix is not a sea (Ewers and Didham 2006).

The conditions at habitat edges can be inhospitable for a variety of invertebrates. The term “edge effects” is used to describe the altered abiotic and biotic conditions at habitat edges. The severity and extent of edge effects will depend on factors such as the size and shape of a remnant, and the degree of contrast between patch and matrix habitat (Murcia 1995); for example, native forest remnants embedded within exotic forestry should experience less severe edge effects than forest remnants surrounded by pasture (Debinski et al. 2000, Denyer et al. 2006). Abiotic edge effects predominantly include climatic changes such as increased light and wind exposure, increased temperatures, and lowered humidity and soil and litter moisture (Murcia 1995, Davies-Colley et al. 2000), which in turn cause a wide range of biotic edge effects. Edge effects alter communities through changes in habitat quality, resource availability, and the strength of species interactions with distance from the edge (Murcia 1995). Changes in the abundance and distribution of one organism with distance to edge can have flow-on effects for other, interacting, organisms (Murcia 1995). Edge effects can penetrate several kilometres into forest, and as a consequence, most small forest remnants will not be able to support populations of edge-sensitive, deep-forest specialist species (Ewers and Didham

2008). For example, in their study of native beech forest fragments in the South Island, Ewers and Didham (2004, 2008) found that almost 90% of the 769 beetle species they collected responded to distance from forest edge, and 12% of the total species pool was restricted to forest fragments >1000 ha. Hence, remnant area and shape can and do influence invertebrate community structure, by determining the edge:interior habitat ratio.

The connectivity of a fragmented landscape is determined not only by the physical distance between fragments, but also by the composition of the matrix, and the dispersal abilities of the taxa concerned. Compared to larger animals and plants, most invertebrates have poor dispersal abilities. While generally speaking, flying insects may be able to disperse greater distances than non-flying invertebrates, studies have shown that even highly mobile flying insects such as bumblebees find roads (Bhattacharya et al. 2005), or gaps as small as 50 m between habitat fragments, strong barriers to dispersal. The main consequence of this is that invertebrates may be unable to escape habitat remnants and relocate to more suitable habitat if conditions are unsuitable, and thus local extinctions of vulnerable invertebrate taxa seem inevitable. We have little knowledge of which particular invertebrates are the most sensitive to fragmentation.

Remnant area and shape alone cannot entirely account for remnant community patterns in fragmented landscapes. Increasingly, it is being recognised that remnant condition may be just as important, or indeed more important, than remnant size and shape (Kupfer et al. 2006). Remnants face continual degradation through a variety of disturbances originating in the surrounding matrix habitat. For example, for forest remnants on farmland, typical disturbances from the agricultural matrix can include unintentional nutrient or chemical inputs from fertiliser

(Stevenson 2004) and pesticide drift, invasion by exotic pests and weeds, and livestock grazing. Disturbances alter the types and severity of edge effects (Murcia 1995). For example, relatively undisturbed forest remnants will often have “sealed” edges, due to high stem densities along their perimeter, whereas disturbances such as livestock grazing create remnants with more open edges, and therefore one might expect altered microclimatic edge effects (Murcia 1995, Didham and Lawton 1999). Disturbances and fragmentation often interact synergistically, so that smaller remnants become much more heavily degraded (e.g. Cochrane 2001, Hobbs 2001, Laurance et al. 2002, Ewers and Didham 2006).

In New Zealand, the most common management actions employed in native forest remnants on farmland are mammalian pest control and fencing to exclude livestock. While these two management actions lead to strong, although often incomplete recovery of native vegetation, little is known about the effects on other aspects of the ecosystem, such as litter invertebrates.

I have recognised four main categories of impact that livestock may have on invertebrates and their habitat; urination and defecation, grazing, trampling, and scratching/rubbing (Figure 1). Firstly, by urinating and defecating within remnants, livestock are altering nutrient inputs to the forest floor (Adams 1975, Braunack and Walker 1985). Their faeces may also represent a novel resource to litter invertebrates, particularly in New Zealand due to the lack of native mammalian herbivores. It is unclear whether any New Zealand native invertebrates will benefit from livestock dung. Secondly, grazing and trampling of seedlings and understorey vegetation severely inhibits regeneration (Aizen and Feinsinger 1994). Grazing livestock not only remove understorey vegetation, but also leaf litter (Abensberg-Traun 1992, pers. obs.), both of which alter the physical structure and also

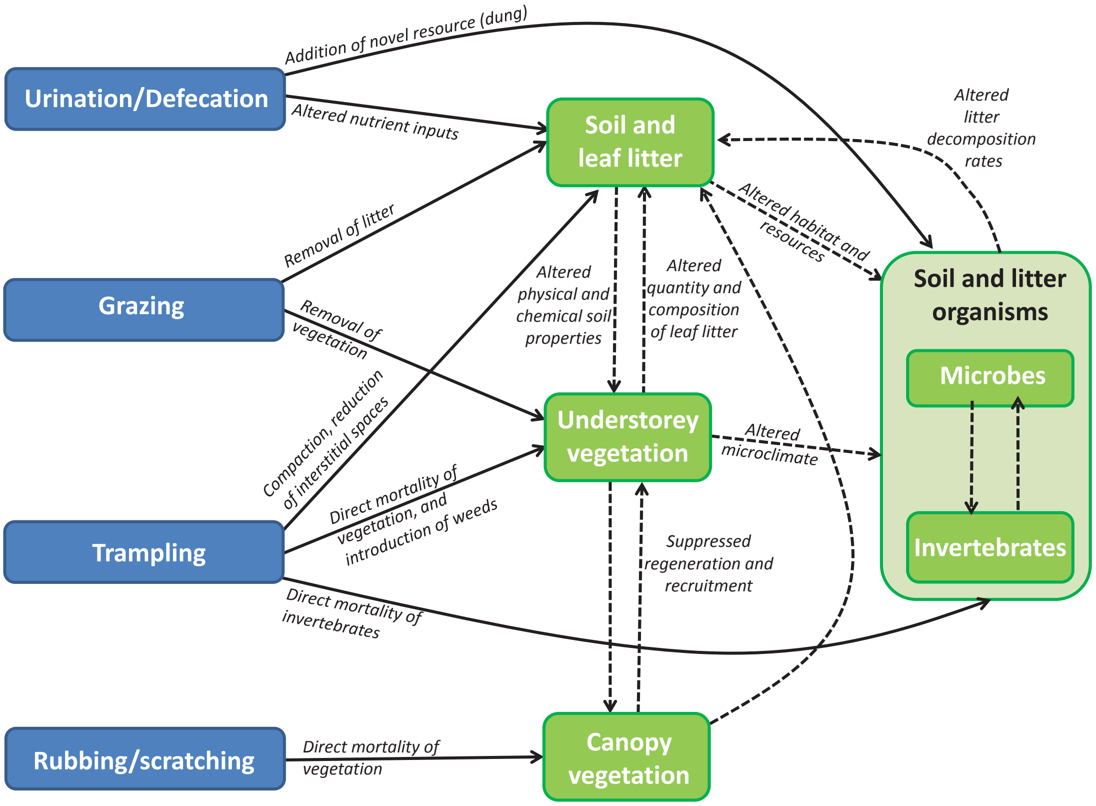

Figure 1. Predicted impacts of livestock grazing on forest floor invertebrates. I identified four main livestock effects: urination/defecation, grazing, trampling, and scratching/rubbing. The direct impacts of these effects on soil and litter, soil and litter organisms, and understorey and canopy vegetation, are indicated with solid arrowed lines, whereas indirect impacts of livestock are indicated with dashed arrowed lines**.**

the microclimate of the forest floor. Specifically, removing vegetation increases light levels, which accompanied with litter removal results in lower humidity, higher temperatures, and greater diurnal fluctuations in microclimatic conditions (Yates et al. 2000). Livestock grazing has also been shown to alter leaf chemistry, and therefore the quality of food resources for litter detritivores (Ashili 2008).

Trampling may result in direct mortality of understorey plants and invertebrates. However, the more serious consequence of trampling, particularly by cattle, is increased soil compaction and pugging, which may reduce soil drainage (Lull 1959, Adams 1975), and also decreases interstitial spaces that are important habitat for many litter and soil invertebrates (Bultman and Uetz 1984). Livestock treading may also facilitate the introduction of weeds from surrounding pasture into remnants (Hobbs 2001). Grazed forest remnants in New Zealand typically have greatly reduced understorey and groundcover vegetation (Smale et al. 2008, Burns et al. 2010).

Finally, livestock also use trees as scratching or rubbing posts, which can increase tree mortality and lead to canopy thinning over time (Adams 1975). Native tree ferns seem to be particularly vulnerable (pers. obs.). Ultimately, livestock can dramatically alter the quantity and quality of habitat, and resource availability for litter invertebrates. For simplicity, I have left organisms from higher trophic levels, such as birds and other introduced mammals, out of the description of livestock impacts illustrated in Fig. 1, but there are studies that show that livestock grazing disturbance has flow-on effects for other vertebrates that are significant predators of invertebrates. For example, rodent tracking rates tend to be much higher in ungrazed forest remnants with dense understorey (Innes et al. 2010).

In New Zealand, we already know that large mammalian herbivores, specifically goats and deer, have a universally negative impact on the abundance of litter invertebrates in areas of continuous forest (Wardle et al. 2001). In addition, New Zealand forest ecosystems are likely to be particularly sensitive to livestock disturbance due to the lack of native mammalian herbivores. Studies conducted in Australian *Eucalyptus* woodlands have found livestock grazing to have a variety of adverse impacts on litter invertebrate abundance and diversity (e.g. Abensperg-Traun et al. 1996, Bromham et al. 1999).

As habitat fragmentation and associated disturbances alters abiotic conditions, resource availability and community structure, all ecological processes are expected to be affected to some degree (Didham *et al.* 1996). However, fragmentation can also alter ecological processes in unpredictable ways. For example, Didham's (1998) study of Amazonian forest fragments found that leaf litter decomposition rates were markedly slower in 1 ha fragments, yet accelerated at the edges of 100 ha fragments, relative to areas of continuous forest. Some authors have neatly linked changes in community composition with accompanying changes in ecological functioning of habitat remnants. For example, declines in the diversity and abundance of dung beetles in Amazonian forest fragments have been linked with declines in the rates of dung decomposition (Klein 1989), and seed burial (Andresen 2003).

The goal of this thesis was to improve our understanding of how restoration management affects the structure and function of invertebrate communities in New Zealand native forest remnants. The specific objectives were as follows:

- To assess the impact that a common disturbance, livestock grazing, has on litter invertebrate habitat in forest remnants (Chapter 1).
- To compare invertebrate community structure in forest remnants of different sizes to that of larger forest areas, and to compare invertebrate structure in small forest remnants under different management conditions. In particular, comparing remnants that had been fenced to exclude livestock with those where livestock were allowed access (Chapters 2, 3), and also remnants where various combinations of livestock exclusion and mammalian pest control had been applied (Chapters 6, 7).

- To assess whether differences in litter invertebrate community structure were accompanied by changes in ecological function, namely litter decomposition (Chapters 4, 5).
- To assess the resilience of litter invertebrate community structure and function following the cessation of livestock disturbance (Chapter 5).

I hypothesised that livestock grazing would have a strong negative influence on forest floor habitat, and would in turn alter the composition of litter invertebrate communities. Small forest remnants, both grazed and fenced, would have different invertebrate communities to that found in larger forest areas, due to the loss of edge-sensitive taxa, and perhaps a greater influx of matrix taxa. I expected that heavily disturbed remnants would also have litter invertebrate communities that were distinct, and depauperate, compared to those from less disturbed remnants, due to the loss of sensitive taxa.

Changes in litter invertebrate communities would be accompanied by changes in associated ecological function, namely litter decomposition, but given the complexity of changes to microclimate, forest floor structure, and invertebrate communities, the direction and extent to which decomposition rates would be altered was impossible to predict. Ultimately, it was expected that small forest remnants that had been protected from livestock grazing and mammalian pests would exhibit a strong recovery in invertebrate community structure and function over time, becoming closer to that of larger forest reserves.

This research should allow me to make several recommendations regarding the conservation of invertebrate communities in native forest remnants, particularly regarding the efficacy of commonly-employed restoration techniques.

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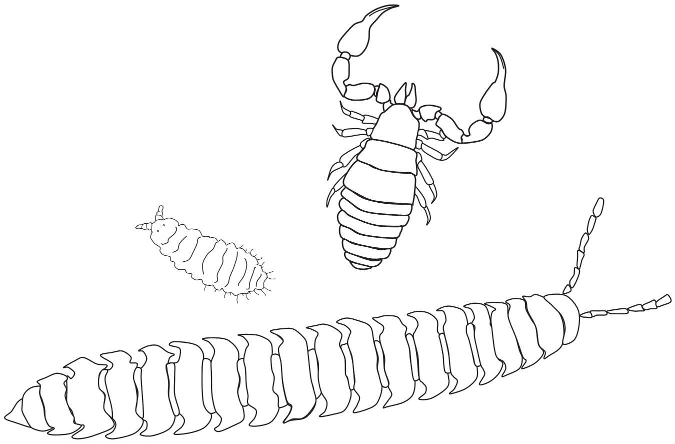
Chapter One

Livestock disturbance and edge effects in native forest remnants alter forest floor habitat for invertebrates



Abstract

Edge effects and the pervasive influence of disturbances from the surrounding matrix are two of the main challenges for the successful conservation management and restoration of habitat remnants. The influence of the edge and livestock disturbance on forest floor habitat for litter invertebrates was assessed by measuring a range of habitat variables at increasing distance from the forest edge at 19 sites. Of these sites five remnants were regularly grazed by livestock, 10 remnants were fenced to exclude livestock, and four were large forest reserves, included as reference sites. The grazed remnants provided markedly different and more variable habitat than both fenced and reserve sites, with higher soil compaction, less understorey vegetation, lower woody stem densities, lower tree species richness, higher bare soil groundcover, and poorer soil drainage. Soil compaction, litter, grass, bryophyte and herb groundcover, vegetation composition, and litter moisture all changed with edge distance, and in the case of soil compaction, litter groundcover, vegetation composition and litter moisture, the nature of the edge response differed between management categories. Biogeographic variables of remnants, such as area, geographic location, slope, aspect and elevation had little influence on habitat compared to the effect of management. Remnant condition, rather than remnant area, was thus a more important determinant of invertebrate habitat quality.

Introduction

Anthropogenic habitat loss and fragmentation has altered the face of the earth, with 40% of the world’s land area now converted for agriculture alone (Foley et al. 2005). Productive, lowland forest and woodland ecosystems have been particularly heavily reduced, both in New Zealand (Norton 2000, Ewers et al. 2006), and around the world (Turner and Corlett 1996, Curran et al. 2004). In many countries, a large proportion of the remaining lowland forest exists as small, degraded remnants, many on private land (Turner and Corlett 1996, Norton and Miller 2000, Ewers and Didham 2006). In heavily fragmented landscapes, even very small remnants have high conservation value, acting as reservoirs of native biodiversity (Turner and Corlett 1996, Norton 2000). Yet, we are still a long way from understanding how to best manage habitat remnants to preserve native biodiversity (Norton 2000).

The two main challenges facing the conservation of small habitat remnants are edge effects and matrix-driven disturbances. Firstly, habitat remnants have much smaller edge: interior ratios than continuous habitat, and therefore the flora and fauna living within habitat remnants are subjected to altered abiotic and biotic conditions, collectively termed edge effects (Murcia 1995). The severity and penetration distance of edge effects vary depending on factors such as the degree of contrast between the remnant habitat and the surrounding matrix, and the physical structure of the edge (Murcia 1995). Ultimately, while remnants will always be affected to some degree by detrimental edge effects, it is hoped that these could be minimised through appropriate management actions that act to “seal” habitat edges, and therefore lessen the severity and/or extent of disturbance.

Secondly, many remnants are also subjected to a variety of disturbances permeating from the surrounding matrix (Hobbs 2001). For example, remnants in agricultural landscapes are typically subjected to disturbances such as unintended nutrient or chemical inputs from fertiliser or spray application (Stevenson 2004), invasion of weeds and pest animals (Hobbs 2001), and incursion by livestock (Hobbs 2001). Edge effects and disturbances interact, often synergistically, so that smaller remnants or remnants with highly complex shapes tend to be more heavily degraded (Hobbs 2001).

Most studies examining forest remnant edge effects have focused on changes to microclimatic variables and vegetation composition and structure (Murcia 1995). Fewer studies have closely examined the flow-on effects for other organisms. We do know that many forest floor invertebrates are likely to be highly sensitive to the altered abiotic and biotic habitat conditions at the forest edges (Didham et al. 1996). Deep forest specialist species, in particular, are likely to be lost from small remnants; for example, Ewers and Didham (2008) found that 12% of the total species pool of beetles collected in their study of New Zealand beech forest were absent from remnants < 1000 ha. However, there are few studies that have explicitly examined forest edge habitat effects from the perspective of their impact on inhabiting invertebrate communities, or how management of forest remnants alters those edge effects for invertebrates.

Livestock grazing has been identified as one of the major disturbances threatening native vegetation remnants embedded in agricultural landscapes in many countries, for example in native podocarp-broadleaf forest remnants in New Zealand (Jay 2005), and the *Eucalyptus* woodlands in Australia (Yates et al. 2000). Small forest remnants on private farmland in New Zealand are often unfenced and used as shelter and grazing areas for livestock (Jay 2005). Most studies of livestock disturbance have focused on the impacts on vegetation. The most visually obvious impact livestock have in forest and woodland remnants is the reduction, and often complete removal, of understorey vegetation (Adams 1975, Bromham et al. 1999, Burns et al. 2010). Livestock grazing is known to severely inhibit tree regeneration (Vasquez 2002, Burns et al. 2010), which has serious consequences for the long-term survival of remnants. However, the potential flow-on effects for other organisms such as forest floor invertebrates have received comparatively little attention, despite evidence for other mammalian herbivore species (predominantly deer and goats) having serious adverse impacts on forest floor invertebrates and their habitat in areas of continuous New Zealand native forest (Wardle et al. 2001).

I have recognised four main categories of impact that livestock may have on invertebrates and their habitat; urination and defecation, grazing, trampling, and scratching/rubbing (as illustrated in Fig. 1 in Introduction). Livestock alter soil nutrient inputs, remove understorey vegetation and leaf litter and inhibit regeneration, alter microclimate, alter leaf chemistry, increase soil compaction and pugging which decreases the number and size of interstitial spaces in the soil and litter (Lull 1959, Adams 1975, Bultman and Uetz 1984, Braunack and Walker 1985, Abensberg-Traun 1992, Aizen and Feinsinger 1994, Yates et al. 2000, Hobbs 2001, Ashili 2008, Smale et al. 2008, Innes et al. 2010, and Burns et al. 2011, as cited in Introduction). Ultimately, livestock can dramatically alter the quantity and quality of habitat, and resource availability for litter invertebrates.

In this study I examine how forest floor invertebrate habitat changes with both distance from the forest edge, and the presence/absence of livestock grazing in native forest remnants in the North Island, New Zealand. I predict habitat characteristics to be more suitable for forest floor invertebrates further from the forest edge and in the absence of grazing livestock. I am, however, unsure how the presence of livestock will interact with edge-related gradients in invertebrate habitat structure.

Methods

Study sites

The study was conducted in the Waitomo District, in the southern Waikato region of the North Island of New Zealand. Prior to human arrival, native forest cover in the district covered an estimated 99% of total land area, but has subsequently been reduced to 30% (Ewers et al. 2006). The area was deforested more recently than many other areas of New Zealand, with logging of native forest occurring up until the late 1970s. The cleared land has largely been converted to pastoral grazing or exotic conifer forestry. Topography in the study area ranges from flat to rolling hills, and elevation ranges from 450 to 580 m a.s.l.

The study sites comprised 19 native forest remnants (Figure 1; Table 1), divided into three management categories: five small privately-owned remnants regularly grazed by livestock, predominantly cattle but also sheep (remnant size range 0.31 ha – 15.05 ha), ten small privately-owned remnants which had been fenced to exclude livestock for a minimum of 10 years (remnant size range 0.88–28.57 ha), and four larger forest blocks managed wholly or in part by the Department of Conservation (DoC), which are the largest remaining forest remnants in the area. These four larger forest reserves comprised a block of Herekawe Scenic Reserve on the southern side of SH30 (hereafter referred to as Hkw, 137.65 ha), the large northern block of Pureora Forest Park (PuN, 30492.13 ha), a smaller central block of Pureora Forest Park near the DoC Field Centre (PFC, 293.56 ha), and Mangapehi Forest Reserve (Mpe, 1655.18 ha), privately-owned but managed in part by DoC.

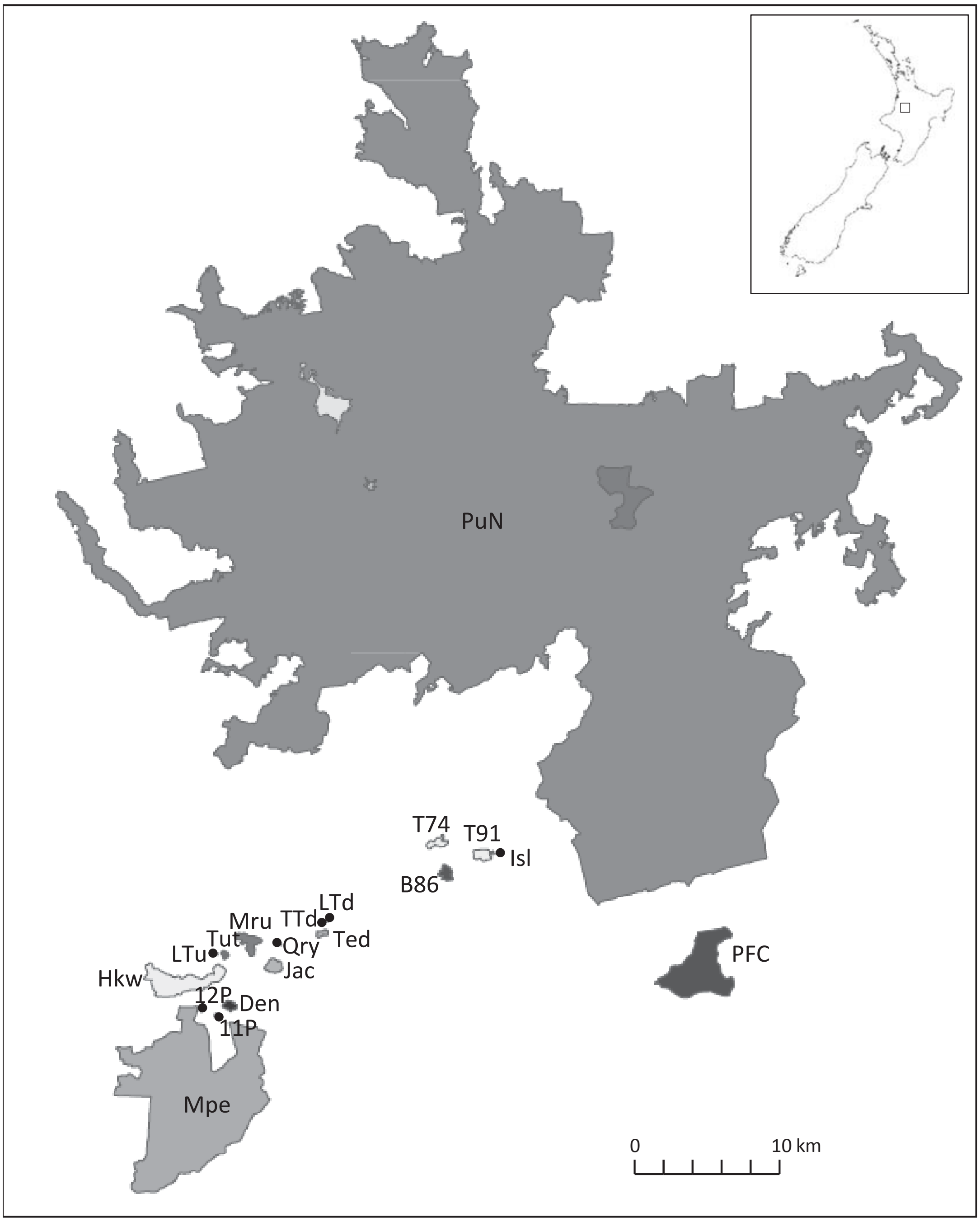


Figure 1. Map of the 19 native forest remnants sampled in this study. Each site is labelled with its code, as listed in Table 1.

Table 1. Characteristics of the 19 native forest remnants sampled in the Waikato region, New Zealand, including remnant area (ha), shape index (SI; Patton 1975), management category (G = grazed remnants, i.e., unfenced remnants which were regularly grazed by livestock at the time of this study , F = fenced remnants, which had been fenced for a minimum of 10 years, R = larger forest reserve sites, representing the largest blocks of forest remaining in the study area), the length of the study transect established at each site, and whether or not a sampling plot was established at the -5 m position along the transect (i.e., outside the remnant in the surrounding pastoral matrix).

Site name	Remnant area (ha)	SI	Management category	Transect length (m)	-5 m plot?
TTd	0.31	1.11	G	10	Y
Qry	1.00	1.58	G	20	Y
11P	1.45	1.22	G	40	Y
12P	1.67	1.39	G	40	Y
T74	15.05	1.79	G	40	Y
Isl	0.88	1.27	F	20	N
LTd	1.15	1.35	F	20	N
LTu	1.42	1.35	F	40	N
Tut	4.51	1.09	F	80	N
Ted	5.86	1.43	F	80	N
Den	10.52	1.15	F	160	Y
B86	15.28	1.37	F	160	N
T91	16.92	1.23	F	160	Y
Jac	18.76	1.19	F	160	Y
Mru	28.57	1.63	F	160	N
Hkw	137.65	1.86	R	320	Y
PFC	293.56	1.51	R	160	Y
Mpe	1655.18	1.84	R	320	Y
PuN	30492.13	5.46	R	320	Y

The forest reserves had never been grazed by livestock. The ungrazed sites were all protected from livestock grazing by high quality fencing which had been in place for a minimum of 10 years, but at most sites much longer. In all of the grazed sites, cattle were regularly observed throughout the remnant interior, i.e., they were not restricted to the edges. Although I was unable to gather specific information regarding the stocking rates for the grazed remnants, all five sites were subjected to a rotational grazing regime throughout the study. Mean stocking rates in the region are estimated at <10.5 stock units (SU) per ha (one stock unit = one dry ewe equivalent, i.e. 55kg, so a stocking rate of <10.5 SU represents less than 2 fullgrown steers per ha), which is comparatively low for the region (Environment Waikato 2011).

The study remnants were selected to have similar canopy composition, composed predominantly of the native tree *Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae). Other common canopy and subcanopy tree species, listed in order of decreasing total basal area, were *Podocarpus totara* G.Benn. ex D.Don var. Totara (Podocarpaceae), *Elaeocarpus dentatus* (J.R.Forst. et G.Forst.) Vahl (Elaeocarpaceae), *Weinmannia racemosa* L.f. (Cunoniaceae), *Dacrycarpus dacrydioides* (A.Rich.) de Laub. (Podocarpaceae), *Melicytus ramiflorus* J.R.Forst. et G.Forst. (Violaceae), *Dacrydium cupressinum* Lamb. (Podocarpaceae), *Knightia excelsa* R.Br. (Proteaceae) and *Hedycarya arborea* J.R.Forst. et G.Forst. (Monimiaceae), and the tree ferns *Dicksonia squarrosa* (G.Forst.) Swartz, *D. fibrosa* Colenso (Dicksoniaceae), and *Cyathea dealbata* (G.Forst.) Sw. (Cyatheaceae). Selective logging of large podocarp trees in the past will have altered the canopy composition of the remnants. The composition, density and condition of understorey vegetation varied considerably between sites, particularly between fenced and unfenced remnants.

Although sheep and cattle were effectively excluded from the fenced remnants and forest reserves, all of the study sites had been adversely affected by a number of other introduced mammal species, including feral goats, pigs, deer, rats, mice, rabbits, and possums. These mammalian pests are ubiquitous throughout the study area and most are not effectively excluded by typical stock fences. Some mammalian pest control, in the form of poisoning and shooting, is undertaken, particularly in the forest reserve sites, but all of the sites are subjected to continual reinvasion.

Habitat characteristics

At each site I established a transect starting from a north-facing edge, leading up to 320 m into the interior of the remnant. I defined the edge (i.e., 0 m along the transect line) by the position of the outermost trunks which formed a continuous canopy. At each transect I established 5 m radius circular sampling plots centred at distances of -5 (i.e., 5 metres outside the remnant in the surrounding pasture matrix), 0, 5, 10, 20, 40, 80, 160 and 320 m, giving a total of 125 sampling plots across the 19 sites. The -5, 0, and 5 m plots overlapped, which meant that the vegetation assessments at each of these near-edge plots were not independent.Transect length was largely determined by remnant area, but was also influenced by remnant shape (i.e., transect length was shorter in irregularly shaped remnants) and was adjusted to avoid canopy gaps or, as in the case of site PFC, a public walking track. I deliberately sampled more intensively at remnant edges because I expected this is where rate of change in habitat would be greatest. I did not establish -5 m plots at fenced sites where the fence was <5 metres from the edge of the remnant, as the -5 m plot would have then been in a different grazing treatment.

I measured a range of variables specific to the habitat requirements of forest floor invertebrates between September and November, 2009. Canopy height (m) was measured using an altimeter held by an observer standing 10 m from the base of a canopy tree at each sampling location. A black and white digital photograph was taken of the canopy directly above each sampling point and an estimate of canopy openness (% sky) calculated by counting the white pixels in Adobe PhotoShop®. I used a pocket penetrometer (ELE Model WF 24950) to measure soil compaction (kgf/cm^2) at 20 randomly generated positions ±5 m perpendicular to the transect line. All soil compaction readings across the 19 sites were undertaken within a two day rain-free period, to minimise variation in soil compaction between sites due to weather. I took five measurements of leaf litter depth (cm), defined as the depth down to the compact soil layer. At three random positions perpendicular to the transect, a 20 x 20 cm quadrat was placed on the ground and all litter, humus and friable material within was collected in a plastic bag. In the laboratory these litter samples were weighed, oven-dried and weighed again. Mean wet litter weight per m^2, mean dry litter weight per m^2, and mean percentage water weight of litter were then calculated for each sampling point.

Vegetation and groundcover composition were assessed within a 5 m radius circular plot centred on each sampling point. I visually assessed percentage ground cover of woody stems, grasses, herbaceous vascular flora, ferns, bryophytes, bare soil, litter, coarse woody debris (logs and branches of over 10 cm diameter), rock, and water within each 5 m radius plot. I measured the diameter at breast height (DBH), and identified to species level, all trees and tree ferns >2 m tall within the 5 m radius circular plot. From this I calculated the total number of trees, tree species richness, and the total basal area within each sampling plot. In addition, the total basal area of *B. tawa* (as the most abundant canopy species) and the total basal area of tree ferns (as tree ferns are indicative of disturbed and/or regenerating forest) were calculated for each sampling plot. In PRIMER (Clarke and Warwick 1994) I created Bray-Curtis resemblance matrices from log(x+1) transformed basal area data, and then calculated two variables of vegetation composition, axes 1 and 2 of a non-metric multidimensional scaling (NMDS) ordination analysis (2D solution stress = 0.19).

The density of all understorey vegetation was visually scored on a scale from 0-3, with values of 0 representing no understorey, and 3 representing very dense understorey. Soil drainage was also visually scored, on a scale of 0-2, with values of 0 representing very poor draining soil (often with standing water puddles), and 2 representing free draining soil.

Remnant area, perimeter, and elevation (m a.s.l) was determined from vector files created in Google Earth™ using satellite imagery. Remnant area was log(x+1) transformed prior to analyses. I calculated the shape index (SI) for each remnant using the formula SI = Perimeter ÷ 200(π.Area)$^{0.5}$ (Patton 1975). Shape index measures deviation from circularity, with a value of 1 representing a perfectly circular remnant, and higher values representing increasingly complex shapes. At each sampling point I also recorded latitude and longitude (listed in Appendix 1), slope and aspect.

Data analysis – individual habitat differences and edge effects

I was interested in whether each individual habitat variable and the slope of its edge effect (if detected) varied between the three remnant management categories (grazed, fenced, and forest reserve). I used one-way ANCOVA, with distance from edge as a covariate, to test whether each habitat variable varied between management categories. Because ANCOVA can only be used for linear relationships, I only included data from 0 – 40 m inclusive in this analysis, as changes in habitat variables appeared to be linear across this range of edge distances. In all instances, I first tested whether there was a significant interaction between management and distance (i.e., whether the assumption of homogeneity of regression was violated), which indicates that the slope of the edge effect varied significantly between management categories.

Where distance was not a significant factor in the ANCOVA model, I proceeded instead with one-way ANOVA with Tukey's posthoc tests on site-mean values of each habitat variable (means calculated across all within-remnant sampling plots) to examine whether there was a significant difference between management categories. Alternatively, where management was not a significant factor in the model, I proceeded by performing logistic regression (see below) of that habitat variable against distance across all sampling points, regardless of management category. Therefore, I was able to categorise each habitat variable as edge-variant, management-variant, both edge and management-variant, or edge and management-invariant.

Continuous curvilinear functions/models can be expected to more accurately model edge effects than linear functions, particularly logistic functions which reach an asymptote at some distance either side of the edge boundary (Ewers and Didham 2006). I fitted four-parameter logistic models to the data to examine change in habitat variables with distance from edge (only including variables previously identified as edge-variant). The model expression had the following form:

$$y = a + \frac{(b - a)}{1 + \left(\frac{x}{c}\right)^{-d}}$$

where *a* is the minimum asymptote, *b* is the maximum asymptote, *c* represents the distance from the forest edge where the rate of change in habitat variable *y* is greatest, *d* is the slope factor or steepness of the edge effect, and *x* is the distance from the forest edge.

For each model I specified sensible upper and/or lower bounds for the model asymptotes, estimated from the collected data. In most cases, the lower bound was >0, and in the case of variables expressed as percentages (for example, ground-cover estimates), the upper bound was ≤100. The distance from forest edge values were log(x+10) transformed prior to the regression as the most dramatic changes were expected closer to the forest edge. In the case of habitat variables that were both edge and management variant (i.e., the variables where I had previously identified a significant interaction between edge and management), I plotted separate logistic models for each of the three management categories, whereas for variables that showed a significant edge response but were apparently management-invariant, I plotted a single logistic function across all sampling plots. In some cases a habitat variable showed a significant edge response in one or two of the management categories, and a seemingly edge-invariant response in the other/s. In this instance I indicated the edge-invariant response in graphs by plotting a straight line of the mean values, ±95% confidence intervals.

Data analysis – overall habitat differences

To examine overall differences in habitat I performed several multivariate analyses in PRIMER 6.1 (Clarke and Warwick 1994), using matrices of Euclidean distances calculated from normalised habitat data (including all measured habitat variables and excluding the biogeographic variables – remnant area, shape index, elevation, latitude, and longitude). I first created a nonmetric multidimensional scaling ordination plot of all sampling plots, and used the ANOSIM (Analysis of Similarities) procedure to test for significant differences in habitat between management categories, and between -5 m plots and all within-remnant plots. The BEST procedure was used to identify which subset of habitat variables best explained the sampling plot pattern. To ensure that observed habitat differences were due to management and not geography, I first calculated centroids for each site, then used the RELATE procedure to test whether there was a significant rank correlation between the matrix of site centroids and a matrix constructed from latitude and longitude. I also correlated habitat ordination axis scores with the geographic variables to examine whether any potential habitat patterns were due to location rather than management.

To compare the extent of variability in overall habitat within each of the three management categories, I calculated the Index of Multivariate Dispersion (IMD) from the site centroids. IMD contrasts the average rank of similarities between sites in one management treatment, against the average rank of similarities between sites in another treatment, and has possible values ranging from -1 to 1. A value of 1 indicates *all* similarities between sites from one treatment are lower than *any* similarities amongst sites from the other treatment, whereas values near 0 indicate no difference in habitat variability between treatments (Clarke and Warwick 1994).

I used one-way analysis of variance (ANOVA) to test whether the extent of change in overall habitat with forest edge changed between management categories, by comparing Euclidean distances between 0 and -5 m, 0 and 10 m, and 0 and 40 m sampling plots for the three management categories. Linear regression was used to examine whether the extent of change in habitat with forest edge changed with log(x+1) remnant area.

Results

Habitat characteristics and edge effects

Soil compaction (kgf/cm^2), litter groundcover (%), litter moisture (%), and vegetation composition (axis 1 scores of NMDS ordination of tree basal areas) all changed significantly with both distance to edge and management category (Table 2). Soil compaction was higher, and litter groundcover was lower at grazed sites than at either fenced or reserve sites (Table 2). Litter moisture (%) was higher at reserve sites than at grazed or fenced sites (Table 2).

Grass, bryophyte and herbaceous groundcover all changed with distance from forest edge, but were management-invariant (non-significant ANCOVA results, not presented). The remaining habitat variables differed by management category, but were apparently edge-invariant over 0-40 m, according to the ANCOVA models (non-significant models not presented). Therefore, I proceeded with one-way ANOVA on site mean data to test for differences between management categories.

Most of the edge-invariant habitat variables differed between management categories (Table 3, Fig. 2). Specifically, grazed remnants had less understorey vegetation, lower woody stem densities, lower tree species richness, higher bare soil groundcover, and poorer soil drainage than either fenced or reserve sites. Grazed remnants also had higher canopy openness than fenced sites, and different vegetation composition to reserve sites (attributable largely to the depauperate nature of tree communities in grazed remnants). In contrast, fenced remnants and forest reserves had much more similar habitat, with the exception of dry litter weights, which were significantly lower at reserve sites than at either grazed or fenced sites (Table 3, Fig. 2). Canopy height, the amount of coarse woody debris, and total tree basal area did not differ significantly between the three management categories (Table 3).

Table 2. ANCOVA results for habitat variables that exhibited a significant response to both distance from forest edge, and management category. Estimated marginal means calculated for distance of 13.83 m. Homogenous management subsets, identified using Tukey’s posthoc tests ($\alpha = 0.05$) are denoted by a and b symbols.

		ANCOVA statistics				Estimated marginal means (SE)		
Habitat variable		F	d.f	*p*	R^2	Grazed	Fenced	Reserves
Soil compaction	Model	18.63	3, 86	<0.01	0.39	1.29 (0.08)^{a}	0.72 (0.06)^{b}	0.66 (0.09)^{b}
	Intercept	303.11	1, 86	<0.01				
	Distance	12.69	1, 86	<0.01				
	Management	20.17	2, 86	<0.01				
Litter % groundcover	Model	7.67	3, 86	<0.01	0.21	62.25 (3.89)^{a}	79.37 (2.63)^{b}	68.24 (4.08)$^{a, b}$
	Intercept	507.97	1, 86	<0.01				
	Distance	7.56	1, 86	0.01				
	Management	7.41	2, 86	<0.01				
Litter moisture %	Model	9.88	3, 86	<0.01	0.26	51.48 (1.94)^{a}	55.10 (1.31)^{a}	63.20 (2.03)^{b}
	Intercept	1410.05	1, 86	<0.01				
	Distance	9.55	1, 86	<0.01				
	Management	9.21	2, 86	<0.02				
VegNMDS Axis 1	Model	6.89	3, 86	<0.01	0.19	-0.50 (0.14)^{a}	0.18 (0.10)^{b}	0.03 (0.15)^{b}
	Intercept	5.43	1, 86	0.02				
	Distance	4.25	1, 86	0.04				
	Management	7.79	2, 86	<0.01				

The logistic models (Table 4) highlighted how certain edge effects varied between management categories. For example, soil compaction was not only higher at grazed sites, but appeared to have a longer penetration distance in grazed sites than in reserve sites, and yet did not change appreciably with distance from edge in fenced sites (Fig. 3). Fenced sites also exhibited a much steeper or abrupt increase in litter groundcover compared to both grazed and reserve sites (Fig. 3), although this result should be interpreted with caution considering the lack of certainty in parameter estimates (Table 4).

Table 3. One-way ANOVA by management category, for habitat variables that did not show a significant edge response. Significant ANOVA tests ($p \leq 0.05$) are indicated in bold.

	Means (SE)			One-way ANOVA by management		
Habitat variable	Grazed	Fenced	Reserves	$F_{(2,16)}$	*p*	R^2
Canopy height (m)	22.14 (1.09)	19.88 (1.75)	17.52 (1.71)	1.14	0.35	0.12
Canopy openness (%)	13.75 (1.27)	11.52 (0.70)	12.79 (0.64)	**5.12**	**0.02**	**0.35**
Understorey vegetation density score (0-3)	0.12 (0.12)	1.78 (0.13)	1.98 (0.26)	**32.46**	**<0.01**	**0.80**
Soil drainage score (0-2)	1.11 (0.25)	1.89 (0.03)	1.60 (0.17)	**9.33**	**<0.01**	**0.54**
Groundcover % - bare soil	13.15 (2.73)	2.12 (0.37)	2.09 (0.62)	**21.74**	**<0.01**	**0.73**
Groundcover % - coarse woody debris	6.06 (0.30)	3.95 (0.56)	6.39 (2.57)	1.79	0.20	0.18
Groundcover % - ferns	2.13 (1.92)	3.08 (0.43)	6.90 (2.69)	2.58	0.11	0.24
Number of woody stems > 2m tall per m^2	0.65 (0.03)	0.72 (0.02)	0.82 (0.04)	**9.99**	**<0.01**	**0.56**
Total tree basal area (m^2) in 5m radius plot	7.13 (1.54)	6.89 (0.52)	6.55 (0.56)	0.08	0.93	0.01
Tree species richness per 5m radius plot	2.73 (0.63)	5.84 (0.36)	7.31 (0.89)	**14.34**	**<0.01**	**0.64**
Leaf litter depth (cm)	1.55 (0.24)	2.73 (0.20)	2.31 (0.38)	**5.72**	**0.01**	**0.42**
Dry litter weight (kgm^{-2})	0.66 (0.03)	0.68 (0.03)	0.49 (0.03)	**6.58**	**0.01**	**0.45**
Vegetation composition (NMDS axis 2 scores)	-0.56 (0.17)	-0.05 (0.13)	0.43 (0.08)	**7.94**	**<0.01**	**0.50**

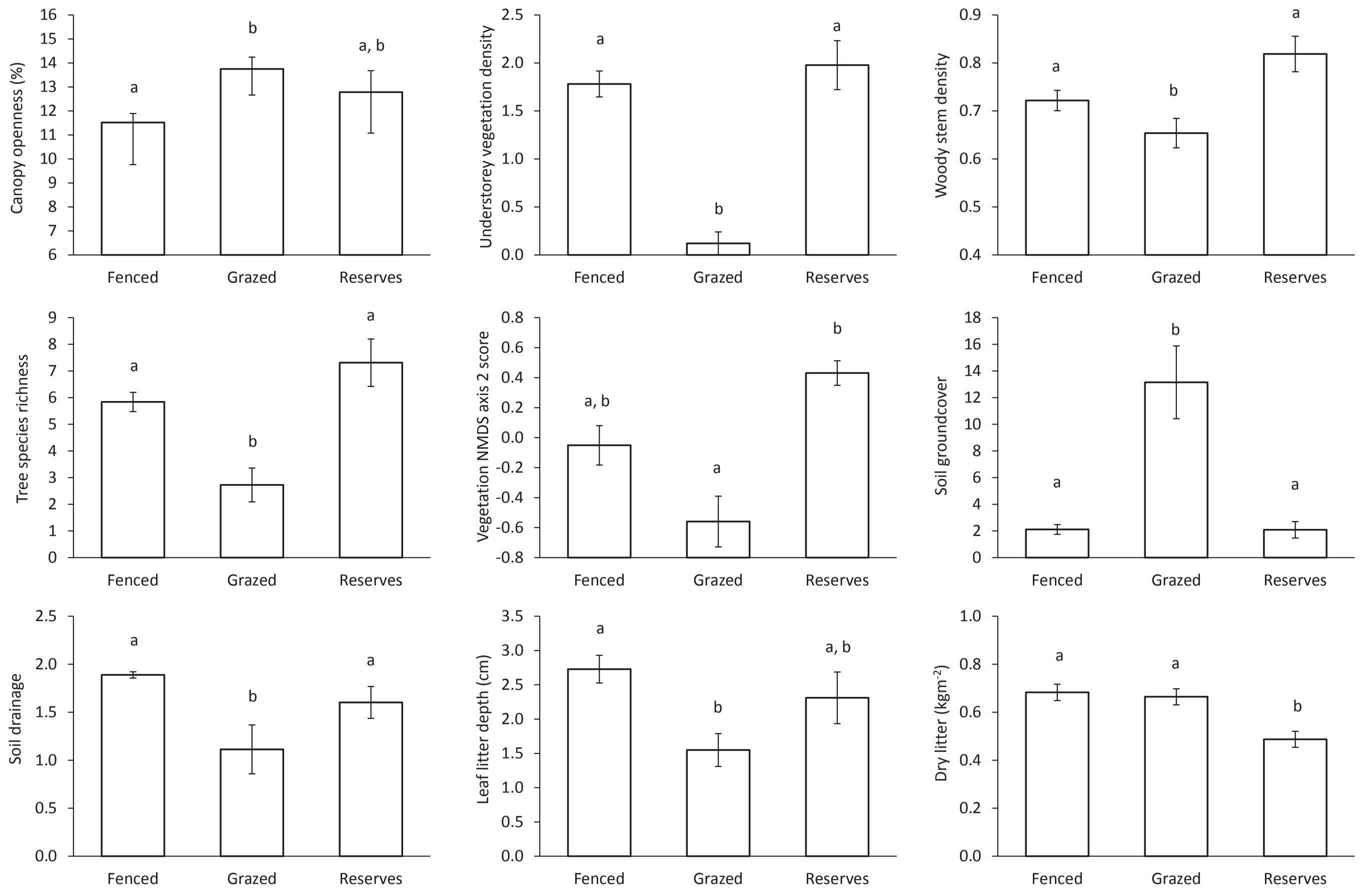


Figure 2. Bar graphs comparing mean values (±1SE) of all edge-invariant habitat variables that differed between the three management categories (calculated from site mean data). Homogenous subgroups identified by Tukey's posthoc tests denoted by a and b symbols. ANOVA results presented in Table 2.

Table 4. Logistic regression results for habitat variables with significant edge effect. See text for explanation of model parameters (NB: for models where the parameter d is positive, the habitat variable exhibits increasing values with increasing distances into the forest remnant, and vice versa. For soil compaction, litter groundcover, vegetation NMDS axis 1, and litter percentage moisture content a separate model was applied to data from each of the three management categories. As grass, bryophyte, and herbaceous groundcover were management-invariant, I applied a single logistic model to all data. * indicates model parameters for which I was unable to obtain valid estimates.

							Parameter estimates (SE)			
Habitat variable	Site category	Edge response	R^2	F	d.f	*p*	a	b	c	d
Soil compaction (kgf/cm^2)	G	Y	0.36	4.35	4 ,23	0.01	0.00 (10.99)	2.50 (4.68)	1.31 (3.39)	-2.17 (13.86)
	F	N								
	R	Y	0.39	6.59	4, 31	0.001	0.62 (0.09)	1.91 (10.00)	0.71 (1.76)	-6.35 (20.70)
Groundcover (%) - litter	G	Y	0.59	12.7	4, 23	<0.001	3.38 (11.79)	76.79 (15.17)	0.91 (0.14)	4.79 (2.82)
	F	Y	0.87	135.4	4, 59	<0.001	5.00 (3.67)	82.48 (1.42)	*	*
	R	Y	0.62	18.35	4, 31	<0.001	3.87 (11.19)	76.80 (5.70)	0.89 (0.10)	5.63 (2.55)
VegNMDS Axis1	G	N								
	F	Y	0.24	6.1	4, 59	0.001	-3.00 (20.78)	0.43 (0.31)	0.60 (1.77)	3.52 (7.27)
	R	N								
Litter moisture (%)	G	N								
	F	Y	0.36	11	4, 59	<0.001	40.20 (6.34)	62.37 (2.63)	1.11 (0.12)	6.96 (4.17)
	R	Y	0.4	6.75	4, 31	<0.001	*	*	*	*
Groundcover (%) - grass			0.59	58.34	4, 124	<0.001	0.76 (1.69)	50.31 (4.73)	0.95 (0.04)	-12.24 (6.43)
Groundcover (%) - bryophytes			0.24	12.42	4, 124	<0.001	0.70 (0.39)	2.47 (0.80)	1.52 (0.34)	4.06 (3.49)
Groundcover (%) - herbs			0.15	7.02	4, 124	<0.001	*	*	*	*

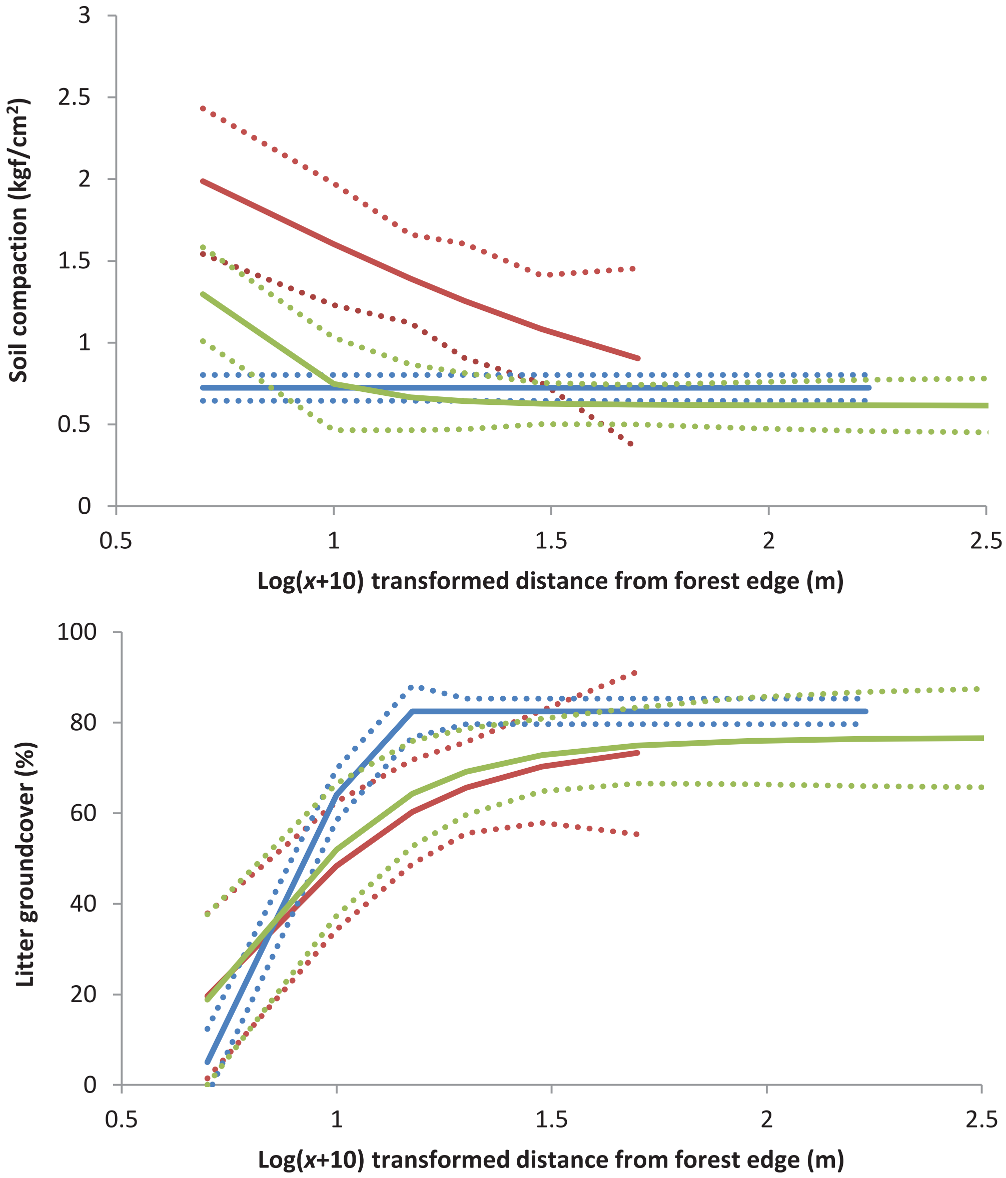


Figure 3. The response of two habitat variables, soil compaction and litter groundcover, to distance from forest edge in different remnant management categories. Solid curvilinear lines are four-parameter logistic regression lines (R^2 values and model parameters provided in Table 2), whereas edge-invariant responses are depicted with horizontal lines of the mean values across all distances. Dashed lines are ± 95% CI lines. Red lines = grazed remnants (sampling plots across 5 sites), blue lines= fenced remnants (sampling plots across 10 sites), green lines = larger forest reserves (sampling plots across 4 sites). Distance to edge is log(*x*+10) transformed, therefore a distance of 1 on the *x*-axis is actually the 0 m point.

Overall habitat change

The NMDS ordination plot of sampling plots (Fig. 4) and related ANOSIM tests revealed that -5 m plots had distinct habitat from all within-remnant plots (Global R = 0.80, *p* = 0.001). Within-remnant sampling plots from the three management categories had significantly different habitat (ANOSIM Global R = 0.37, *p* = 0.001), and all pairwise differences were significant (grazed vs. fenced: R = 0.55, *p* = 0.001; grazed vs. reserves: R = 0.46, *p* = 0.001; fenced vs. reserves: R = 0.21, *p* = 0.001). Specifically, plots from grazed sites tended to have higher axis 2 scores than plots from fenced or reserve sites, and -5 m plots tended to have lower axis 1 scores than within-remnant plots (Fig. 4).

Axis 1 scores were correlated with distance from edge (*r* = 0.37, *p* <0.001), but axis 2 scores were not. The habitat variables that best explained the sampling plot pattern were soil and litter percentage groundcover, litter depth, tree basal area, and vegetation composition (axis 2 scores of an NMDS ordination of tree basal areas) (*r* = 0.73). One sampling plot, the -5 m plot at site PuN, was identified as an outlier. The -5 m plot at PuN had markedly different vegetation composition from all the other plots, with a number of distinct native sapling species present.

NMDS axis 1 scores of sampling plots were not significantly correlated with any of the geographic variables, and axis 2 scores were significantly, albeit weakly, correlated with remnant area (*r* = 0.20, *p* = 0.02). There was no correlation between resemblance matrices constructed from site centroids (Fig. 5) and geographic position (Rho = 0.26, *p* = 0.44). Therefore, although remnant biogeography may have contributed to habitat differences between sampling plots and sites, it could not account for the separation of grazed plots from fenced and reserve plots along axis 1 (Fig. 4), nor the clear separation of sites by management treatment (Fig. 5).

Interestingly, grazed sites exhibited higher variability in overall habitat than fenced or reserve sites (Fig. 5; IMD between grazed and fenced sites was 0.72, between grazed and reserve sites 0.80, and between fenced and reserve sites -0.55).

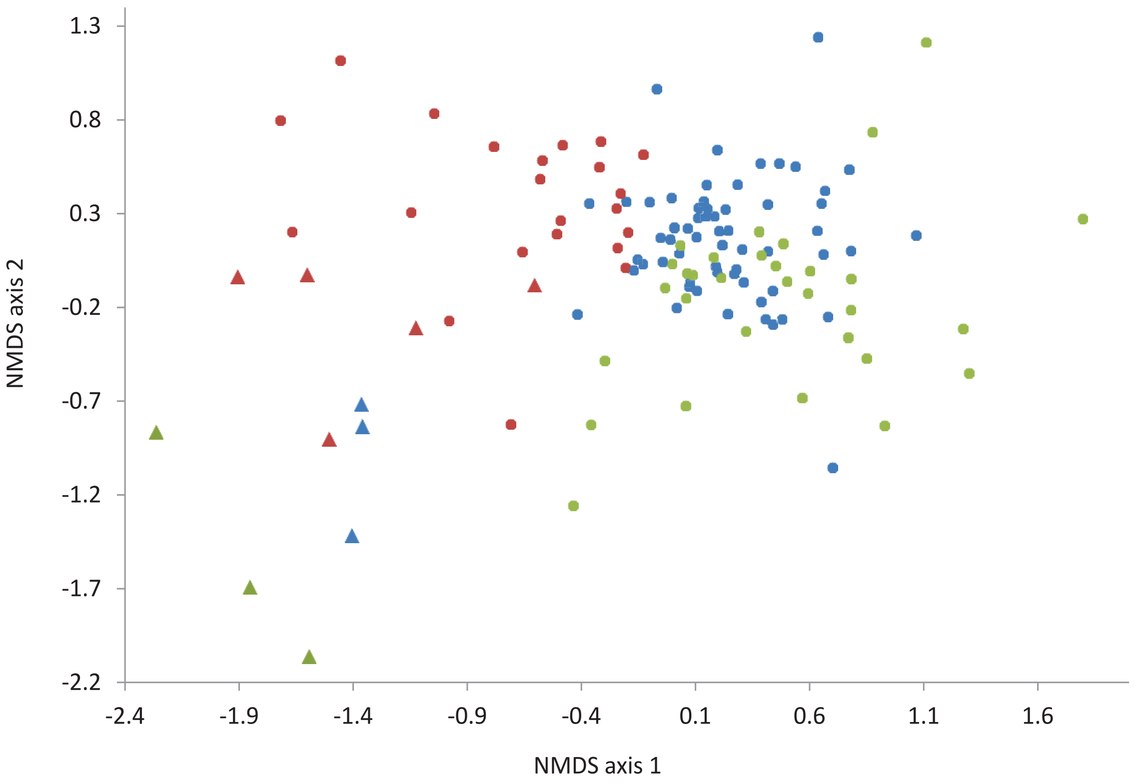


Figure 4. NMDS plot of sampling points, calculated from Euclidean resemblance matrix constructed from normalised habitat variables. Stress = 0.16. Data points are colour coded by management category; red = grazed sites, blue = fenced sites, and green = forest reserve sites. Triangular symbols represent -5 m plots (i.e., sampling plots 5m outside the forest remnants), whereas circular symbols are from all other sampling plots. One outlier with a comparatively low axis 2 value, the -5 m sampling plot at site PuN (2.57, -4.42) is not shown.

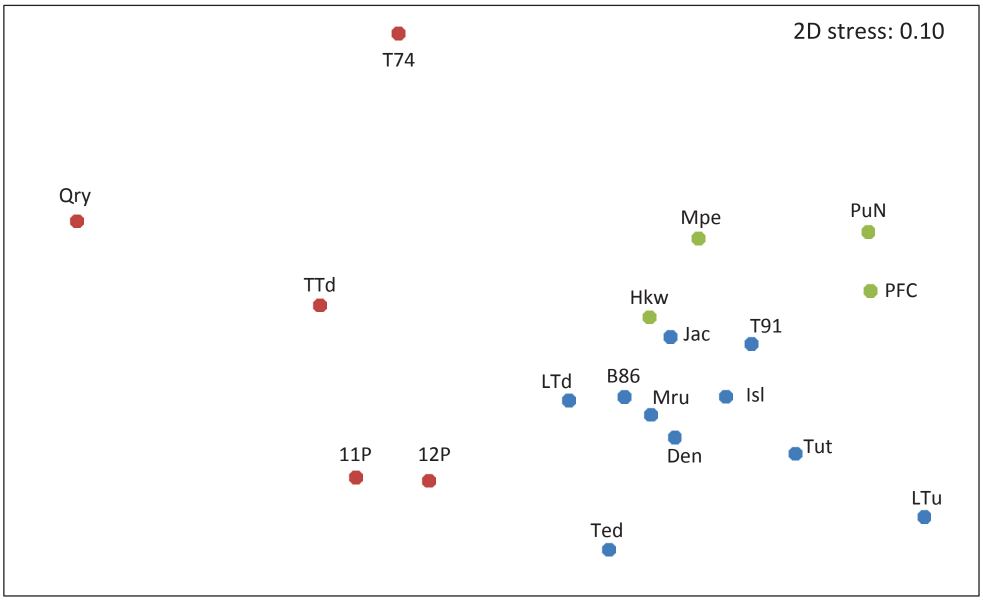


Figure 5. NMDS ordination of centroids calculated for each site from normalised habitat variables**.** Each data point is labelled with its site code (as listed in Table 1), and colour-coded by management; red = grazed sites, blue = fenced sites, and green = forest reserve sites.

While habitat changed with distance from forest edge across all three categories, habitat at fenced sites and reserve sites appeared to converge with increasing edge distance, whereas habitat at grazed sites remained distinct (Fig. 6). I examined whether the extent of change in habitat with distance from edge varied with management, and found that Euclidean distances between -5 m and 0 m sampling plots were significantly lower at grazed sites (mean = 5.18, SE = 0.47) than at fenced sites (mean = 7.59, SE = 0.47), but not forest reserves (mean = 9.26, SE = 1.36; $F_{(2,9)} = 6.12$, $p = 0.02$, $R^2 = 0.58$). While there were no significant differences between management categories in Euclidean similarities over other distance intervals (not presented), the extent of habitat change over 0 – 10 m decreased with increasing remnant area at grazed sites and reserves, but increased at fenced sites (Fig. 7).

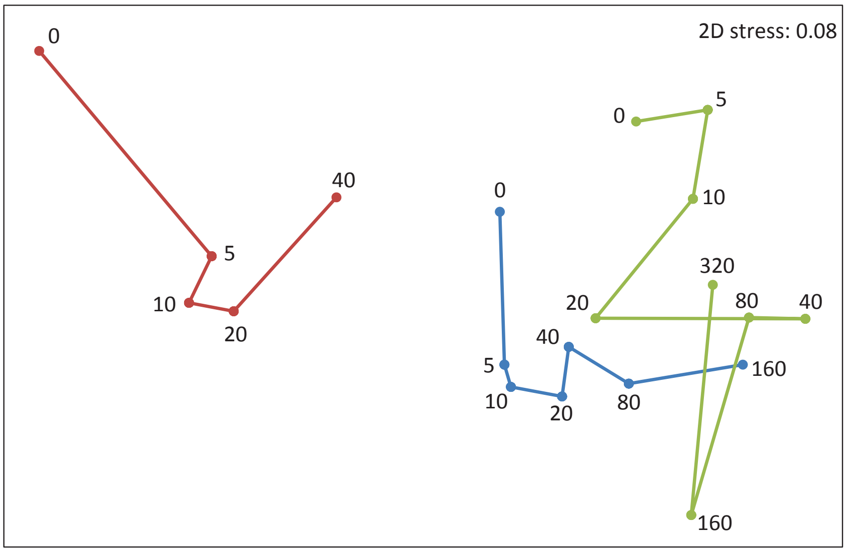


Figure 6. NMDS ordination of centroids calculated for each sampling distance (-5 m sampling points excluded) in each of the three management categories. Lines connect successive sampling distances, and each distance is labelled (in m from forest edge). Red line = grazed sites, blue line = fenced sites, and green line = forest reserve sites.

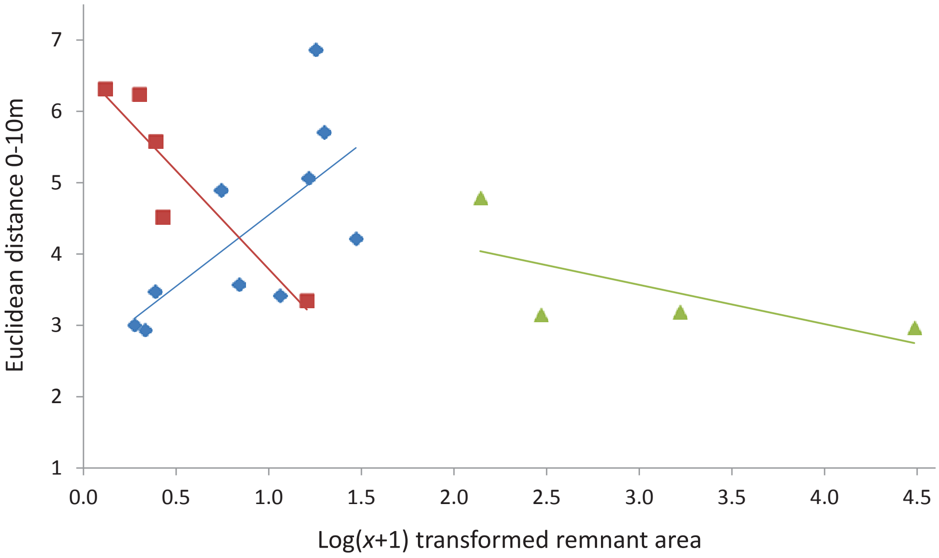


Figure 7. Variation in the Euclidean distance (calculated from normalised habitat variables) between 0 and 10 m sampling plots at each site, as a function of log(x+1) transformed remnant area (ha). Data points and linear regression lines are colour coded by management category; red = grazed sites ($F_{(1,3)} = 15.72$, $p = 0.03$, $R^2 = 0.84$), blue = fenced sites ($F_{(1,8)} = 6.84$, $p = 0.03$, $R^2 = 0.46$), and green = forest reserve sites ($F_{(1,2)} = 1.67$, $p = 0.33$, $R^2 = 0.46$).

Discussion

In fragmented landscapes, it can be difficult to disentangle the effects of remnant geography and management (Hobbs 2001). Remnant geography did affect some habitat characteristics, but grazed sites differed most strongly between fenced and reserve sites along axis 1 of an NMDS ordination of habitat, which was not related to any geographic measures. I am therefore confident that the habitat differences between grazed sites and the other two categories are related to their management, and not their physical location, area or shape.

Grazed remnants provide markedly different habitat for forest floor invertebrates, characterised by poorly draining and compacted soil, shallower litter depths, groundcover comprising proportionally higher bare soil and lower litter cover, sparse understorey vegetation, fewer trees and lower tree species diversity. Fenced remnants and forest reserves provided much more similar habitat to one another. This is encouraging as it suggests that even small forest remnants can provide invertebrate habitat comparable to larger forest reserves, provided they are protected from livestock. Perhaps surprisingly, livestock disturbance did not lead to a homogenising of forest floor habitat, as grazed sites exhibited greater variability in habitat than either fenced sites or reserve sites. However, increased variability can serve as an indicator of increased perturbation or disturbance (Clarke and Warwick 1994).

As predicted, many of the habitat variables changed with distance from the forest edge. Forest edges were highly variable though, and it is difficult to accurately model edge effects because of this. In many cases it was evident that my sampling design did not encompass a wide enough range of edge distances to be able to reach asymptote values on either side of the ecotone. Obviously, it is impossible to extend the range of within-remnant edge distances for small remnants. Hence, the logistic models were characterised by wide confidence intervals, often relatively low R^2 values, and uncertainty in the parameter estimates. Despite this lack of certainty around model fit, these models were still useful in highlighting differences in the edge response between the three management categories. For example, livestock grazing appeared to increase the penetration distance of the soil compaction edge effect, as soil compaction values were still steeply decreasing in grazed remnants at distances where the reserve sites had apparently reached an asymptote.

Fenced sites exhibited a steeper edge response than grazed or reserve sites in litter groundcover, but an apparently edge-invariant response in soil compaction. This could be because the fenced remnants tended to have a ‘harder’ or more abrupt edge than grazed or fenced sites, with densely-vegetated and thus well-sealed edges. The larger forest reserves did not tend to be as densely vegetated at the edges as fenced remnants. The buffering effect of densely-vegetated forest edges has been noted by others (e.g., Murcia 1995, Didham and Lawton 1999). It seems likely that had I sampled at a greater range of distances out into the pasture matrix surrounding fenced sites (i.e., beyond the position of the fence), I would have seen an abrupt change in these seemingly edge-invariant habitat variables, which would perhaps be better modelled as a stepped-response rather than curvilinear.

The habitat changes I have documented will represent altered habitat and resource availability for litter invertebrates. For example, the removal of understorey will alter the microclimate (Didham and Lawton 1999), and by reducing tree species richness, livestock grazing will cause a reduction in the diversity of litter on the forest floor. By reducing litter groundcover and litter depth, livestock grazing reduces habitat quality and spatial complexity for forest floor invertebrates, by flattening and removing interstitial spaces (Bromham et al. 1999, Bultman and Uetz 1984). Leaf litter also represents an important food resource for detritivorous invertebrates. These changes to forest floor habitat can be expected to have a profound impact on invertebrate communities.

Uetz (1979) studied forest floor spider communities in Illinois and Delaware, USA, and found that spider diversity was positively correlated with litter depth, both in sampling an area with naturally-variable leaf litter depth, and in a study where litter depth was experimentally- manipulated. Likewise, Bultman and Uetz (1984) compared invertebrate assemblages in natural and artificial litter of varying structural complexities (i.e., by creating artificial litter mixes with varied proportions of flattened vs. twisted “leaves” they were able to manipulate the structural heterogeneity of litter) and were thus able to disentangle the effects of litter as a food resource and habitat. They found that detritivorous groups such as Collembola, detritivorous Acari, isopods and millipedes, which depend on litter as a food resource, were indeed more abundant in natural litter than artificial litter. However, other invertebrate groups, particularly spiders, showed a strong response to litter structure, increasing significantly in abundance with structural heterogeneity of litter. Likewise, David et al. (1991) showed that experimental litter removal resulted in reduction in abundance of many invertebrate groups, both detritivores and predators.

I predicted that livestock grazing would have strong impacts on invertebrate community composition, perhaps greater than the effects of remnant area or edge distance, a prediction which was confirmed (Chapter 2). Studies undertaken in semi-natural woodlands of Australia have highlighted the detrimental effects of livestock on invertebrate communities. Bromham et al. (1999) attributed the lowered biodiversity in grazed remnants to the reduction in food and habitat resources caused by livestock disturbance. However, Abensberg-Traun (1992) found that while decades of sheep grazing had had detrimental effects on soil and groundcover variables, subterranean termite communities had not been overly adversely affected.

No amount of management intervention can be expected to restore small remnants to the condition of larger forest reserves, because of unavoidable impacts of edge effects. Many taxa can be expected to be highly sensitive to forest edges and will not persist in small remnants. Nevertheless, my results suggest that even very small remnants can provide valuable habitat for forest floor invertebrates, provided they are protected by suitable fences. In further studies in this system I have investigated how forest floor invertebrate community composition responds under these different management categories (Chapter 2), and with edge effects (Chapter 3), and subsequently, how a major ecological process on the forest floor, leaf litter decomposition, is affected (Chapter 4).

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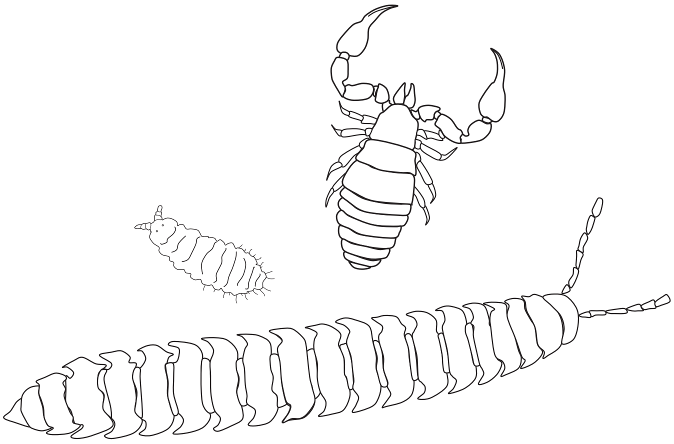
Appendix 1. Geographical locations of 19 forest sampling sites. Coordinates are New Zealand Geodetic Datum 2000 (NZGD2000) values, and indicate the position of the 0 m sampling plot (i.e., forest edge).

Site name	Management category	Latitude	Longitude
TTd	G	38°29.565 S	175°26.817 E
Qry	G	38°29.985 S	175°25.716 E
11P	G	38°31.279 S	175°24.346 E
12P	G	38°31.183 S	175°24.021 E
T74	G	38°28.143 S	175°29.130 E
Isl	F	38°28.399 S	175°30.388 E
LTd	F	38°29.601 S	175°26.700 E
LTu	F	38°30.182 S	175°24.271 E
Tut	F	38°30.189 S	175°24.551 E
Ted	F	38°29.783 S	175°26.618 E
Den	F	38°31.039 S	175°24.623 E
B86	F	38°28.583 S	175°29.372 E
T91	F	38°28.279 S	175°30.236 E
Jac	F	38°30.384 S	175°25.781 E
Mru	F	38°29.917 S	175°25.203 E
Hkw	R	38°30.637 S	175°23.457 E
PFC	R	38°30.592 S	175°35.737 E
Mpe	R	38°31.533 S	175°24.165 E
PuN	R	38°27.248 S	175°31.800 E

Chapter Two

Patch condition is more important than area for litter invertebrate communities: the effects of livestock grazing



Abstract

In heavily fragmented landscapes, even very small remnants of native vegetation can have high conservation value, and yet we know little about how best to manage them to conserve and/or restore biodiversity. Communities in habitat remnants often do not conform to the predictions of island biogeographic theory. A focus on community composition, rather than diversity measures only, is a more informative approach. Remnants in heavily fragmented landscapes are subjected to a variety of disturbances originating from the matrix, including livestock disturbance. Studies that have focused solely on the effects of remnant area on biodiversity may have overlooked the influence of disturbances and remnant condition. I examined how livestock disturbance and remnant area interact to affect the composition of litter invertebrate communities in 19 forest patches: five remnants regularly grazed by livestock, 10 remnants that were fenced to exclude livestock, and four large forest reserves. I found that grazed sites had very different invertebrate communities to either fenced or reserve sites, being both depauperate and highly variable between grazed sites. In contrast, fenced remnants had much more similar communities to those found in large forest reserves. Very few taxa showed a response to remnant area. Overall, remnant condition seems a more important determinant of invertebrate community structure than remnant geography. Even very small forest remnants can support litter invertebrate communities similar to that of larger reserves, provided they are protected from livestock.

Introduction

Humans have reduced global forest cover by 7-11 million km^2 over the past 300 years, driven primarily by our demands for timber, and land for agriculture (Foley et al. 2005). Lowland forest ecosystems have been particularly affected, and once large areas of lowland forest are now represented predominantly by small, isolated, and degraded remnants embedded in agricultural landscapes, throughout developed and developing countries in both temperate (Norton 2000, Armesto et al. 1998), and tropical zones (Turner and Corlett 1996, Curran et al. 2004). While large forest reserves are usually superior to small remnants for conservation, there is increasing recognition of the conservation value of smaller remnants in regions where little native vegetation remains (Turner and Corlett 1996, Armesto et al. 1998, Tscharntke et al. 2002). However, we know little about how best to manage these small forest remnants to protect and/or enhance native biodiversity.

Many studies of animal populations and communities in habitat fragments have taken an island biogeographic approach, and focused on the effects of remnant area, shape and isolation without explicitly examining the effects of remnant condition (Kupfer et al. 2006, Holland and Bennett 2009). Authors such as Kupfer et al. (2006) now recognise that forest fragments in agricultural landscapes often do not conform to the predictions of island biogeography theory, primarily because the agricultural matrix is nothing like a sea – while the matrix represents a formidable dispersal barrier to the majority of forest taxa, it is also an unrelenting source of pervasive physical and biotic disturbances. There can be considerable overlap in forest and matrix communities, particularly at forest edges. Forest and woodland remnants in farmland are threatened by a variety of disturbances from the surrounding agricultural matrix, including weeds and pest animals (Abensperg-Traun et al. 1996, Hobbs 2001), increased nutrient deposition from incidental fertiliser application (Stevenson 1994, Foley et al. 2005), and grazing livestock (Abensberg-Traun et al. 1996). Nevertheless, remnant area can be important even for organisms with small space requirements such as litter invertebrates, as it determines the edge:interior ratio. The altered habitat at the edges of forest fragments is hostile for many invertebrates, and small forest remnants will be unable to support deep forest specialists (Ewers and Didham 2008). However, forest edges can develop densely-sealed vegetation over time, which may partially ameliorate edge effects (Murcia 1995). Remnant area and anthropogenic disturbances may also interact, so that smaller remnants may also be more heavily degraded.

Throughout the world, many small forest and woodland remnants in farmland are unfenced and therefore are deliberately exposed to frequent grazing by livestock, for example the temperate broadleaf-conifer forests of New Zealand (Jay 2005), and Australian woodlands (Abensberg-Traun et al. 1996, Bromham et al. 1999), and there is, of course, a much older history of agricultural conversion and livestock grazing in forests throughout Europe (Vera 2000, Kirby 2004, Gustavsson et al. 2009). Large mammalian herbivores are known to have impacts on litter-dwelling invertebrates even in their natural habitat, for example, Suominen et al. (2003) showed that native reindeer grazing affects the diversity and composition of curculionid and carabid beetle communities in a variety of forest habitats.

While studies like that of Suominen et al. (2003) found that intermediate levels of grazing can be beneficial for beetle diversity, I think that the effects of livestock in New Zealand forests are likely to be largely detrimental, and more severe than elsewhere in the world, because of the lack of native mammalian herbivores (also see Hobbs and Huenneke 1992). In larger tracts of indigenous New Zealand forest, feral goats and deer are known to dramatically reduce abundance of almost all meso- and macro-invertebrate groups (Wardle et al. 2001).

Livestock disturbance in forest results in a substantial reduction in understorey vegetation, and changes to the forest floor include reduction in litter cover and increased soil compaction (Chapter 1, Bromham et al. 1999). Therefore, livestock disturbance would be expected to have a dramatic impact on forest floor invertebrate communities. Indeed, studies from Australian woodlands have shown that livestock disturbance affects invertebrate densities, diversity and community composition (Abensperg et al. 1996, Bromham et al. 1999).

I think that forest remnant condition has been overlooked and may be a more important determinant of litter invertebrate community structure than remnant area *per se*. Some of the community changes attributed to simple area effects in other studies may in fact have been partially attributable to the degraded condition of small remnants, and it is possible that even very small remnants may support assemblages similar to larger forest tracts, provided they are protected from disturbances. In many fragmentation studies, the largest study sites have been larger forest reserves which are part of the public conservation estate, and may be managed more intensively than remnants on private land. Hence, differing management intensities may confound studies at either end of a remnant area range. Here, in order to more objectively assess the conservation value of small forest remnants, and to disentangle the effects of remnant area and management, I investigate how forest floor invertebrate community composition differs, firstly, between small grazed (heavily disturbed) and small ungrazed (less disturbed, hereafter referred to as “fenced”) remnants, and secondly, amongst fenced remnants and larger forest reserves of varying sizes (size range 0.88 – 30492 ha).

Methods

Study area

The study sites comprised 19 native forest remnants in the Waitomo district, in the south of the Waikato region, New Zealand (Table 1; Figure 2 in Chapter 1). Native forest cover in the district has been reduced from 99% prior to human arrival, to around 30% (Ewers et al. 2006), most of which has been converted to pastoral grazing or exotic forestry. Topography in the study area ranges from flat to rolling hills, and elevation ranges from 450-580 m a.s.l.

I assigned the remnant forest patches to one of three management categories: small privately-owned remnants regularly grazed by livestock, predominantly cattle but also sheep (remnant size range 0.31 ha – 15.05 ha, n = 5), small privately-owned remnants which had been fenced to exclude livestock for a minimum of 10 years (remnant size range 0.88–28.57 ha, n = 10), and the largest remaining forest remnants in the area (n = 4), which are all reserves managed wholly or in part by the Department of Conservation (DoC). These larger forest reserves comprised a block of Herekawe Scenic Reserve on the southern side of SH30 (hereafter referred to as Hkw, 137.65 ha), the large northern block of Pureora Forest Park (PuN, 30492.13 ha), a smaller central block of Pureora Forest Park near the DoC Field Centre (PFC, 293.56 ha), and Mangapehi Forest Reserve (Mpe, 1655.18 ha), privately-owned but managed in part by DoC.

The forest reserves had never been grazed by livestock. The ungrazed sites were all protected from livestock grazing by high quality fencing which had been in place for a minimum of 10 years, but at most sites much longer. All five grazed sites were subjected to a rotational grazing regime throughout the study, predominantly cattle but also sheep. Mean stocking rates in the study area are estimated at <10.5

stock units (SU) per ha (one stock unit = one dry ewe equivalent, i.e., 55kg), which is comparatively low for the region (Environment Waikato 2011). In all of the grazed sites, cattle were regularly observed throughout the remnant interior, i.e., they were not restricted to the edges.

Table 1. Characteristics of the 19 native forest remnants sampled in the Waikato region, New Zealand, including remnant area (ha), shape index (SI; Patton 1975), management category (G = grazed remnants – unfenced remnants which were regularly grazed by livestock at the time of this study , F = fenced remnants, which had been fenced for a minimum of 10 years, R = larger forest reserve sites, representing the largest blocks of forest remaining in the study area), the length of the study transect established at each site, and whether or not a sampling plot was established at the -5 m position along the transect (i.e., outside the remnant in the surrounding pastoral matrix).

Site name	Remnant area (ha)	SI	Management category	Transect length (m)	-5 m plot?
TTd	0.31	1.11	G	10	Y
Qry	1.00	1.58	G	20	Y
11P	1.45	1.22	G	40	Y
12P	1.67	1.39	G	40	Y
T74	15.05	1.79	G	40	Y
Isl	0.88	1.27	F	20	N
LTd	1.15	1.35	F	20	N
LTu	1.42	1.35	F	40	N
Tut	4.51	1.09	F	80	N
Ted	5.86	1.43	F	80	N
Den	10.52	1.15	F	160	Y
B86	15.28	1.37	F	160	N
T91	16.92	1.23	F	160	Y
Jac	18.76	1.19	F	160	Y
Mru	28.57	1.63	F	160	N
Hkw	137.65	1.86	R	320	Y
PFC	293.56	1.51	R	160	Y
Mpe	1655.18	1.84	R	320	Y
PuN	30492.13	5.46	R	320	Y

Study remnants had similar canopy composition, composed predominantly of the native tree *Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae). Other common canopy and subcanopy tree species, listed in order of decreasing total basal area, were *Podocarpus totara* G.Benn. ex D.Don var. Totara (Podocarpaceae), *Elaeocarpus dentatus* (J.R.Forst. et G.Forst.) Vahl) (Elaeocarpaceae), *Weinmannia racemosa* L.f. (Cunoniaceae), *Dacrycarpus dacrydioides* (A.Rich.) de Laub. (Podocarpaceae), *Melicytus ramiflorus* J.R.Forst. et G.Forst. (Violaceae), *Dacrydium cupressinum* Lamb. (Podocarpaceae), *Knightia excelsa* R.Br. (Proteaceae), *Hedycarya arborea* J.R.Forst. et G.Forst. (Monimiaceae), and the tree ferns *Dicksonia squarrosa* (G.Forst.) Swartz, *D. fibrosa* Colenso (Dicksoniaceae), and *Cyathea dealbata* (G.Forst.) Sw. (Cyatheaceae). Selective logging of large podocarp trees in the past will have altered the canopy composition of all the remnants. The composition, density and condition of understorey vegetation varied considerably between sites and management categories, the most notable difference being the almost complete lack of native understorey in grazed sites (Chapter 1). Fenced sites tended to have less pronounced edge-related habitat gradients than grazed remnants, due to the buffering effect of dense vegetation at remnant edges (Chapter 1).

Although sheep and cattle were effectively excluded from the fenced remnants and forest reserves, a number of other introduced mammalian species, including feral goats, pigs, deer, rats, mice, rabbits, and possums are ubiquitous throughout the study area and most are not effectively excluded by typical stock fences. Some mammalian pest control, in the form of poisoning and shooting, is undertaken, but all of the sites are subjected to continual reinvasion and hence disturbance.

Field methods

At each remnant I established a transect starting from a north-facing edge, leading up to 320 m into the interior of the remnant. I defined the edge (i.e., 0 m along the transect line) by the position of the outermost trunks which formed a continuous canopy. At each transect I established 5 m radius circular sampling plots centred at distances of -5 (i.e., 5 metres outside the remnant in the surrounding pasture matrix), 0, 5, 10, 20, 40, 80, 160 and 320 m, giving a total of 125 sampling plots across the 19 sites. Transect length was largely determined by remnant area, but was also influenced by remnant shape (i.e., transect length was shorter in irregularly shaped remnants) and was adjusted to avoid canopy gaps or, as in the case of site PFC, a public walking track. I deliberately sampled more intensively at remnant edges because I expected this is where rate of change in invertebrate communities would be greatest. I did not establish -5 m plots at fenced sites where the fence was <5 metres from the edge of the remnant, as the -5 m plot would have then been in a different grazing treatment.

I installed a pitfall trap centred on each sampling point. Each trap comprised a plastic disposable cup (11 cm diameter, 10 cm deep), nested inside a section of polythene pipe dug-in level with the surrounding ground, and covered by a stainless steel lid installed 2 cm above the ground. 70% ethylene glycol was used as a preservative. The traps were set for four-week periods, at three different sampling intervals throughout the year: mid-December 2008 to mid-January 2009 (Summer), mid-April to mid-May 2009 (Autumn), and late October to late November 2009 (Spring). I did not undertake any sampling during winter or early spring, as access to all sites was not possible in winter and during the lambing season. During the final sampling period (Spring) an additional pitfall trap was installed at the innermost sampling point of each site’s transect, 5 m perpendicular to the transect line. After collection, samples were stored in 70% ethanol prior to sorting.

At each sampling point I recorded latitude and longitude (reported in Appendix 1 of Chapter 1), aspect and slope. I also measured a range of other variables specific to the habitat requirements of forest floor invertebrates, to be used as environmental covariates in subsequent analyses, and summarised in Appendix 1. Invertebrate habitat changed markedly between management treatments, and with distance to forest edge, as discussed in detail in Chapter 1. Specifically, grazed remnants had higher soil compaction, less understorey vegetation, lower woody stem densities, lower tree species richness, higher bare soil groundcover, and poorer soil drainage than fenced or reserve sites.

Invertebrate processing

Invertebrate samples were sieved (mesh size = 0.5 mm), then sorted under microscope to Phylum, Class, Order or Family level (as listed in Table 2). Larval and adult forms of holometabolous insect groups were counted separately. Abundances were expressed as mean number of individuals per sample. The abundance of numerically-dominant taxa (i.e., those with abundances exceeding 200 individuals in a single sample) was estimated using sub-sample counts. To do this, the original sample was distributed throughout a tray divided into 10 equal-sized quadrants. The number of individuals was counted in three quadrants, and then the mean count was used to estimate total abundance in the entire sample.

Analysis

Unless stated otherwise, all multivariate analyses were conducted in PRIMER 6.1 (Clarke and Warwick 1994), using log(x+1) transformed invertebrate abundances. I used one-way analysis of similarities (ANOSIM) to test for differences in community composition between the three sampling periods. The RELATE procedure was then used to examine whether samples collected from these sampling periods exhibited the same pattern. Based on this analysis I used seasonal means for all subsequent analysis.

I used one-way ANOSIM to examine differences between samples collected at each of the edge distance intervals. I used the BIO-ENV procedure to identify which subset of measured environmental variables (pertaining to habitat and geography) best explained the pattern of community similarity. I did this for all sampling points, and then for all within-remnant sampling points (-5 m plots excluded), and then separately for sampling points within each management category. I used the SIMPER procedure to identify which taxa contributed the most to differences between the management treatments, and differences between -5 m plots vs. all within-remnant pots. I used multivariate analysis of variance (MANOVA) in SPSS Statistics 17.0 (SPSS Inc.), to examine whether log(x+1) transformed site-mean invertebrate abundances differed overall (only including the 38 taxa with total abundances of more than 150 individuals collected across all within-remnant sampling plots) between management category (Tukey's HSD posthoc tests, with Bonferroni correction, was used to assess differences amongst individual taxa between management categories; Rice 1991). Arithmetic means of untransformed abundance data are presented in graphs and tables.

I calculated a range of community metrics for each site: the mean abundance per sample, ordinal richness (total number of taxa caught per site, at order level or higher), and Berger-Parker dominance. As I used a proportional sampling design, I also calculated rarefied measures of ordinal richness and dominance (900 individuals, 1000 iterations), using the program EcoSim (Entsminger 2004). One-way ANCOVA was used to examine whether these community metrics varied by management category, with log(x+1) transformed remnant area as a covariate.

Studies of various aquatic communities have indicated that community variability increases with increasing disturbance or stress (Warwick and Clarke 1993). Likewise, I was interested in whether grazed sites exhibited greater community variability than fenced and reserve sites. I calculated the Index of Multivariate Dispersion (IMD) between the three management treatments. IMD contrasts the average rank of similarities between sites in one management treatment, against the average rank of similarities between sites in another treatment, and has possible values ranging from -1 to 1. A value of 1 indicates *all* similarities between sites from one treatment are lower than *any* similarities amongst sites from the other treatment, whereas values near 0 indicate no difference in community variability between treatments (Clarke and Warwick 1994).

To examine the response of the invertebrate community to remnant area, I first calculated Pearson correlations between mean community metrics (abundance, rarefied and raw ordinal diversity) and the mean abundance of individual taxa (only those present at more than five sites, and comprising more than 50 individuals) at each site, and the log(x+1) transformed remnant area of each site, first across all sites, and then across the three separate management treatments. Where I have presented significant results, I have also performed simple linear regression against remnant area.

Results

A total of 94 123 invertebrates were collected from 386 samples (8 samples were lost from damage by wind fall or cattle). The most numerically dominant taxa were springtails (Collembola) and mites (Acari), comprising 40 and 32% of all individuals caught, respectively (Table 2). Other common taxa, in order of decreasing abundance, were flies (adult and larval Diptera combined; 8.2%), beetles (adult and larval Coleoptera combined; 5.7%), ants (Formicidae; 2.6%), and spiders (Araneae: 1.6%).

The composition of the samples varied by season (Global R = 0.31, *p* = 0.001), with the greatest difference in community composition between autumn and summer samples. Most of the seasonal differences could be attributed to taxa experiencing increases over the summer sampling period, for example, Poduromorpha springtails were more than three times as abundant in summer than in autumn or spring, and 94% of all Phoridae flies sampled were collected in the summer sampling period. However, as samples from each season revealed similar patterns between sampling points (pairwise RELATE test results: spring vs. summer *Rho* = 0.28, *p* = 0.001; spring vs. autumn *Rho* = 0.32, p = 0.001; summer vs. autumn *Rho* = 0.29, p = 0.001), all subsequent analyses were performed on mean data calculated for each sampling point across all sampling periods.

Table 2. Total and mean abundances of meso- and macro-invertebrate taxa caught in 19 forest remnants in the Waitomo District, Waikato Region, New Zealand, using pitfall traps Data are collated for remnants sampled in each of three management categories, after pooling across all within-remnant sampling plots and collection periods (three 4-week sampling periods in Summer, Autumn, and Spring of 2008-2009). Management categories: Grazed remnants (G, N = 5), regularly grazed by livestock at the time of this study; fenced remnants (F, N = 10), protected from livestock grazing by fencing that had been in place for a minimum of 10 years; and reserve sites (R, N = 4), the four largest forest reserves in the region, managed wholly or in part by the Department of Conservation. Mean abundances across all -5 m (i.e., 5 m outside remnant, in surrounding pasture) sampling plots are also presented.

		Total (% of total)	G	F	R	-5 m plots
ARTHROPODA - Arachnida						
Acari	Mesostigmata	9 635 (10.2)	10.04	30.39	23.47	24.6
	Oribatidae	13 732 (14.6)	39.9	33.55	19.35	83.58
	Prostigmata	5 939 (6.3)	5.69	20.68	15.27	6.78
	Prostigmata -Trombidiidae	407 (0.4)	0.15	1.38	0.73	2.11
	Total mites	29 713 (31.6)	55.78	86	58.82	117.07
Araneae	Araneomorph	1 351 (1.4)	6.64	2.8	2.31	5.43
	Araneomorph - Lycosidae	172 (0.2)	0.25	0.28	0.22	2.68
	Mygalomorph	28 (<0.1)	0.08	0.1	0.04	0
	Total spiders	1 551 (1.6)	6.97	3.18	2.57	8.11
Opiliones	Laniatores	271 (0.3)	1.1	0.72	0.41	0.13
	Eupnoi	78 (0.1)	0.32	0.19	0.19	0.08
	Eupnoi - Caddidae	25 (<0.1)	0.03	0.03	0.09	0.28
	Eupnoi - Phalangiidae	39 (<0.1)	0.14	0.07	0.05	0.4
	Cyphophthalmi	2 (<0.1)	0.03	0	0	0
	Total harvestmen	415 (0.4)	1.61	1	0.75	0.89
Pseudoscorpionida		168 (0.2)	0.01	0.58	0.49	0.31
ARTHROPODA - Insecta						
Archaeognatha		58 (0.1)	0.04	0.22	0.13	0.06
Blattodea		2 (<0.1)	0	0.01	0	0
Dermaptera		9 (<0.1)	0	0.04	0	0
Coleoptera	Carabidae	176 (0.2)	0.31	0.51	0.41	0.57
	Zopheridae	30 (<0.1)	0.02	0.12	0.03	0.04
	Curculionidae	194 (0.2)	0.55	0.52	0.48	0.44
	Elateridae	28 (<0.1)	0.09	0.06	0.07	0.14
	Ptiliidae	19 (<0.1)	0.01	0.06	0.06	0.08
	Staphylinidae	690 (0.7)	2.65	1.41	1.47	3.31
	Scarabaeidae - Melolonthinae	29 (<0.1)	0.08	0.06	0.08	0.17
	Scarabaeidae - Scarabaeinae	974 (1.0)	0.49	3.78	2.41	0.49
	Other Coleoptera	2025 (2.2)	5.7	5.57	4.78	4.21
	Coleoptera larvae	1244 (1.3)	2.5	3.25	3.79	2.28
	Total Coleoptera adults	4165 (4.4)	9.91	12.09	9.79	9.44

…Table 2 continued:

		Total (% of total)	G	F	R	-5 m plots
ARTHROPODA – Insecta (continued)						
Diptera	Calliphoridae	48 (0.1)	0.26	0.1	0.08	0.03
	Cecidomyiidae	444 (0.5)	0.19	1.26	1.71	0.76
	Dolichopodidae	39 (<0.1)	0.34	0.05	0.03	0.1
	Mycetophilidae	107 (0.1)	0.2	0.23	0.37	0.44
	Phoridae	1 932 (2.1)	1.66	2.62	5.79	24.61
	Psychodidae	454 (0.5)	1.01	1.32	1.11	0.81
	Sciaridae	829 (0.9)	4.73	2.07	1.61	1.82
	Sphaeroceridae	832 (0.9)	0.07	2.28	3.69	0.5
	Tipulidae	22 (<0.1)	0.03	0.03	0.13	0.03
	Other Diptera	811 (0.9)	1.68	1.47	2.27	6.14
	Diptera larvae	1950 (2.1)	4.99	5.48	5.01	4.99
	Total Diptera adults	5 518 (5.9)	10.16	11.43	16.8	35.24
Hemiptera	Aphidae	247 (0.3)	0.15	0.64	0.55	2.11
	Aradidae	19 (<0.1)	0	0.04	0.09	0.03
	Cercopidae	19 (<0.1)	0	0.07	0.02	0.06
	Lygaediae	32 (<0.1)	0.08	0.15	0	0
	Coccoidea	966 (1.0)	0.62	0.76	0.8	19.88
	Other Hemiptera	163 (0.2)	0.22	0.37	0.56	0.83
	Total Hemiptera	1 446 (1.5)	1.07	2.04	2.01	22.9
Hymenoptera	Formicidae	2 454 (2.6)	3.97	4.95	6.32	19.88
	Ichneumonidae	25 (<0.1)	0.14	0.03	0.02	0.32
	Pompilidae	24 (<0.1)	0	0.09	0.05	0.06
	Other Hymenoptera	872 (0.9)	2.82	1.8	1.31	6.58
	Hymenoptera larvae	1 (<0.1)	0.02	0	0	0
	Total Hymenoptera adults	3 375 (3.6)	6.93	6.87	7.71	26.83
Isoptera		2 (<0.1)	0	0	0.01	0
Lepidoptera	Lepidoptera adults	45 (<0.1)	0.2	0.12	0.06	0.15
	Lepidoptera larvae	395 (0.4)	0.78	1.2	0.91	0.76
	Psychidae (case moth)	134 (0.1)	0.48	0.37	0.28	0.26
Neuroptera	Neuroptera larvae	5 (<0.1)	0.02	0.02	0.01	0
Orthoptera	Anostostomatidae	93 (0.1)	0.21	0.31	0.19	0
	Gryllidae	127 (0.1)	0	0	0	3.53
	Rhaphidophoridae	421 (0.4)	0.96	1.38	0.66	0.31
	Total Orthoptera	641 (0.7)	1.17	1.69	0.35	3.83
Phasmidae		1 (<0.1)	0	0.01	0	0
Psocoptera		83 (0.1)	0.44	0.21	0.11	0.18
Siphonaptera		37 (<0.1)	0.01	0.16	0.03	0.25
Thysanoptera		246 (0.3)	0.97	0.63	0.38	1.14
Thysanura		1 (<0.1)	0	0	0	0

…Table 2 continued:

		Total (% of total)	G	F	R	-5 m plots
ARTHROPODA - Crustacea						
Amphipoda		1 109 (1.2)	1.89	4.3	2.52	1.21
Isopoda		833 (0.9)	0.28	1.08	0.91	14.44
Copepoda		152 (0.2)	1.77	0.26	0.2	0
Ostracoda		5 (<0.1)	0	0.01	0.03	0
ARTHROPODA -other Hexapoda						
Collembola	Entomobryomorpha	11 484 (12.2)	26.98	26.97	23.32	71.53
	Poduromorpha	20 857 (22.2)	21.22	83.61	30.27	36.63
	Symphypleona	5 530 (5.9)	10.07	16.01	12.14	17.11
	Total Collembola	37 871 (40.2)	58.28	126.6	65.69	125.26
Diplura		27 (<0.1)	0	0.09	0.1	0
ARTHROPODA -Myriapoda						
Chilopoda		103 (0.1)	0.35	0.23	0.2	0.43
Diplopoda	Chordeumatida	25 (<0.1)	0.05	0.06	0.05	0.08
	Julida	109 (0.1)	0.47	0.31	0.06	0.29
	Polydesmida	467 (0.5)	0.26	1.6	1.33	0.6
	Polyzoniida	121 (0.1)	0.11	0.33	0.33	0.64
	Siphonophora	2 (<0.1)	0	0.01	0	0
	Spirostreptida	11 (<0.1)	0.05	0.03	0.02	0.03
	Total Diplopoda	735 (0.8)	0.94	2.34	1.8	1.6
Symphyla		82 (0.1)	0	0.23	0.25	0.06
ANNELIDA - Oligochaeata						
Enchytraeidae		1 019 (1.1)	11.38	0.45	1.64	0.99
Lumbricina		228 (0.2)	1.07	0.44	0.48	1.04
Total Oligochaeata		1 247 (1.3)	12.45	0.89	2.12	2.03
MOLLUSCA - Gastropoda						
Snails		221 (0.2)	0.37	0.66	0.73	0.17
Slugs		145 (0.2)	0.74	0.23	0.19	1.07
Total Mollusca		366 (0.4)	1.1	0.88	0.91	1.24
OTHER PHYLA						
Nematoda		362 (0.4)	3.3	0.39	0.64	0.26
Nematomorpha		4 (<0.1)	0.02	0	0	0.08
Onychophora		1 (<0.1)	0	0	0	0
Platyhelminthes		19 (<0.1)	0	0.06	0.06	0.06
Tardigrada		2 (<0.1)	0	0.01	0	0

The composition of the sampled communities varied with distance to forest edge (Global R = 0.085, $p = 0.001$). Pairwise tests showed that while samples collected from the -5 m sampling points were significantly different ($\alpha \leq 0.05$) from all within-remnant distances, there were only three other significant pairwise differences, all between 0 m plots, and 20, 40, and 80 m plots, respectively. Diptera (specifically Phoridae and “Other flies”, i.e., flies not identified to family level), Oribatid mites, springtails (specifically, Poduromorpha and Symphypleona), ants (Formicidae), Isopoda and wolf spiders (Lycosidae), all of which had markedly higher abundances in samples from -5 m plots, contributed most to the community differences between -5 m plots and all within-remnant plots (average community dissimilarity = 39.0). The community edge response is examined in more detail in Chapter 3.

Understorey vegetation score, soil groundcover, grass groundcover, vegetation composition (NMDSaxis1), and litter moisture content were the variables most closely linked with patterns in invertebrate community composition ($r = 0.53$ for all sampling plots, $r = 0.52$ for all within-remnant sampling plots, i.e., -5 m plots excluded).

The log(x+1) transformed site-mean abundances of the 38 most abundant taxa varied significantly by management category (Wilks’ $\lambda < 0.001$, $F_{(32, 2)} = 398.31$, $p = 0.003$). Subsequent univariate contrasts (using Bonferroni correction) identified that the abundance of four taxa (prostigmatid mites, araneomorph spiders, sphaeoscerid flies, and pseudoscorpions) differed significantly by management category (Appendix 2). Prostigmatid mites, sphaeroscerid flies, and pseudoscorpions had markedly lower abundances at grazed sites, while araneomorph spiders were more abundant at grazed sites than at fenced or reserve sites (Fig. 1).

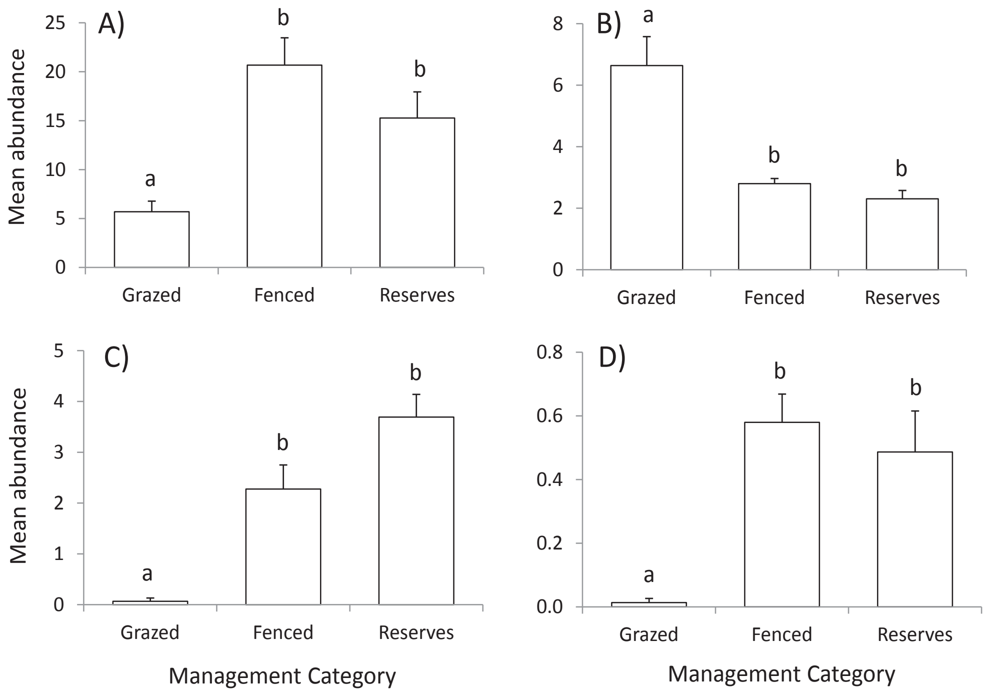


Figure 1. Variation in the site-mean abundance (mean abundance per sample at each site, calculated from all within remnant sampling plots for each site, + 1 SE) of four taxa, across the three remnant management categories (Grazed, N = 5; Fenced, N = 10; Reserves, N = 4). A) Prostigmatid mites ($R^2 = 0.69$, $F_{(2,16)} = 17.82$, $p < 0.001$), B) Araneomorph spiders ($R^2 = 0.79$, $F_{(2,16)} = 30.33$, $p < 0.001$), C) Sphaerocerid flies ($R^2 = 0.71$, $F_{(2,16)} = 19.61$, $p < 0.001$), D) Pseudoscorpions ($R^2 = 0.64$, $F_{(2,16)} = 14.03$, $p < 0.001$). Homogenous subsets identified by Tukey's HSD posthoc tests, are denoted by a and b.

Composition of within-remnant samples varied by management category (Global R = 0.35, $p = 0.001$; Fig. 2). Samples from grazed and fenced remnants were significantly different (R = 0.61, $p = 0.001$), as were samples from grazed sites and forest reserves (R = 0.46, $p = 0.001$). Fenced sites and forest reserves were more similar but still significantly different in composition (R = 0.10, $p = 0.01$). Springtails (Collembola: Symphypleona and Poduromorpha), mites (Acari: Prostigmata and Mesostigmata), beetles (Coleoptera: Scarabaeninae, and "other

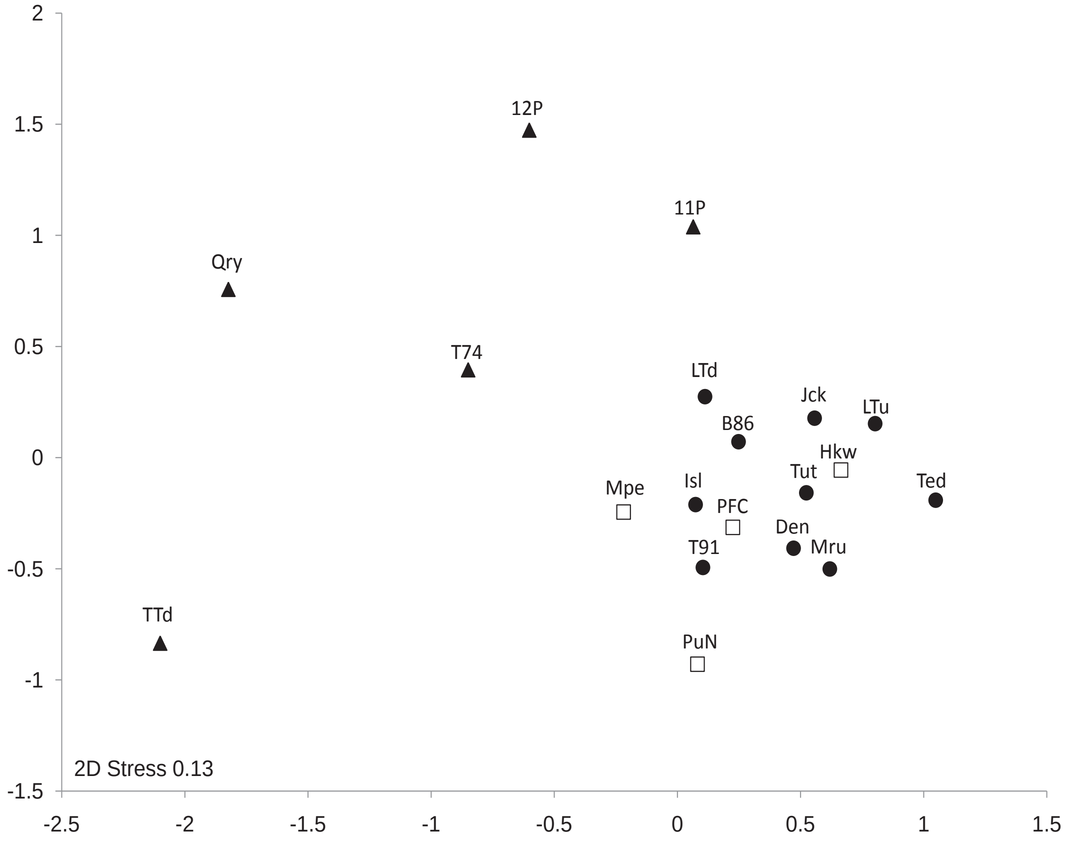


Figure 2. NMDS ordination plot of log(*x*+1) transformed mean invertebrate abundances for each site, calculated from all within-remnant sampling plots (i.e. -5 m sampling plots excluded). Each point labelled with site code, as listed in Table 1. Triangles are grazed sites, circles are fenced sites, and squares are forest reserve sites.

beetles", i.e., beetles not identified to family level), and potworms (Annelida: Enchytraeidae) contributed most to the difference between grazed and fenced sites (average community dissimilarity = 40.8), with potworms having higher abundances, and all the other taxa having lower abundances in grazed sites (Table 2). Springtails (Symphypleona and Poduromorpha), mites (Acari: Prostigmata, Oribatidae, and Mesostigmata), potworms, and Sphaeroceridae flies (Diptera) contributed most to the difference between samples from grazed and forest reserve sites (average community dissimilarity = 41.5), with potworms and oribatid mites having higher abundances at grazed sites, and other taxa lower abundances (Table 2). Springtails (Symphypleona and Poduromorpha), mesostigmatid mites, flies (Phoridae and Sphaeroceridae), ants, and Scarabaeninae beetles contributed most to the differences between samples from fenced and reserve sites (average dissimilarity = 34.6). Phorid and sphaerocerid flies, and ants (Formicidae) had higher abundances in forest reserve sites, while the other taxa were more abundant in fenced sites (Table 2).

The index of multivariate dispersion (IMD), which compares the amount of variability in community structure within treatments was 1 (i.e., the maximum possible value) between grazed and fenced sites, 0.97 between grazed and reserve sites, and -0.49 between fenced and reserve sites. Community composition at grazed sampling plots varied markedly between the five sites (Global R = 0.51, *p* = 0.001). Pairwise tests showed that all grazed sites had significantly different composition from one another, with the exception of TTd and Qry (R = 0.04, *p* = 0.33).

Soil drainage score, coarse wood groundcover, bryophyte cover, number of trees > 2 m, and slope were most closely linked with patterns of community composition at grazed sites (*r* = 0.47). In contrast, the environmental variables that best explained communities of fenced sites were grass and fern groundcover, vegetation composition (NMDS axis1), litter moisture, and remnant area (*r* = 0.42), and for reserve sites, understorey vegetation score, litter groundcover, depth and moisture content, and remnant area (*r* = 0.53).

The abundances of only two of the 63 taxa (with greater than 50 individuals caught across all sites) were correlated with remnant area across the nineteen sites: araneomorph spiders (excluding Lycosidae) (*r* = -0.47, *p* = 0.04; Fig 3a), and oribatid mites (*r* = -0.54, *p* = 0.02; Fig. 3b). However, when grazed sites were excluded, only oribatid mites still showed a correlation with remnant area (*r* = -0.61, *p* = 0.02). When only the ten fenced sites were examined (i.e., both grazed and reserve sites were excluded), none of the individual taxa (those with > 50 individuals sampled) showed a significant relationship with remnant area.

Total ordinal richness was significantly lower at grazed sites than at either fenced or reserve sites, however this difference was not significant when rarefied richness measures were used (Table 3). However, the mean number of orders per sample collected from grazed sites was significantly lower (Table 3), and rarefaction curves also showed that grazed sites tended to have lower ordinal diversity than fenced or forest reserve sites (Fig. 4).

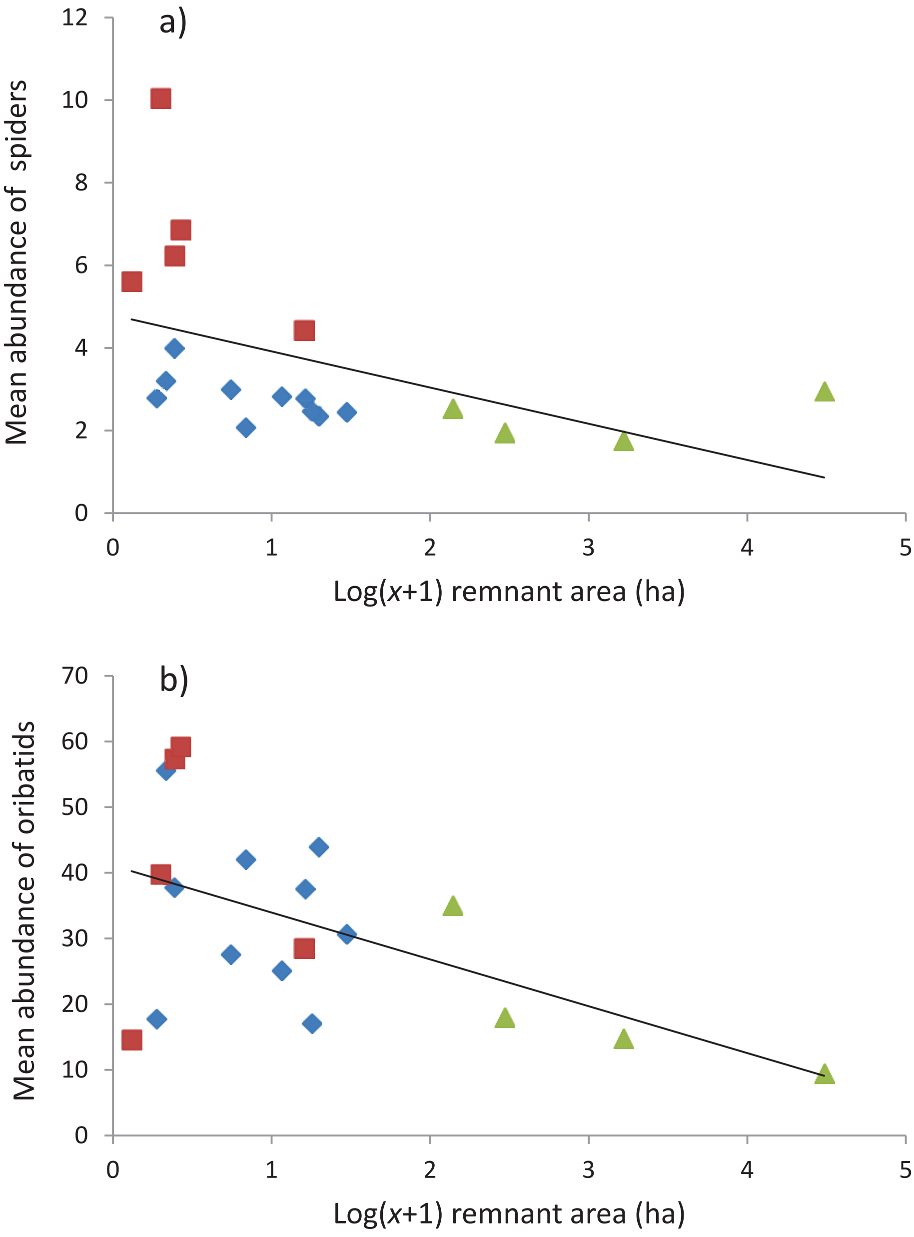


Figure 3. Variation in the site-mean abundance of two taxa, a) araneomorph spiders, and b) oribatid mites, plotted against log(x+1) transformed remnant area. Data points are colour-coded by management category: red = grazed, blue = fenced, green = reserves. Lines are linear regression lines, plotted across all sites; araneomorph spiders ($y = -0.17x + 1.69$), and oribatid mites ($y = -0.27x + 3.72$).

Table 3. Mean values and one-way ANOVA results for community metrics calculated for each management category from site mean abundance data of litter invertebrates, namely mean abundance of individuals per sample, total ordinal richness, rarefied ordinal richness as calculated in EcoSim (Entsminger 2004; parameters = 900 individuals, 1000 iterations), mean ordinal richness per sample, and Berger-Parker dominance (i.e., relative abundance of most abundant taxon). Management categories are denoted as follows: G = grazed remnants (N = 5), F = fenced remnants (N = 10), and R = reserves (N = 4).

	Management category means (SE)						
	G	F	R	-5 m plots	$F_{(2, 16)}$	p	R^2
Mean abundance	180.2 (27.4)	271.1 (53.8)	184.7 (35.19)	386.4 (60.1)	1.14	0.34	0.13
Total ordinal richness	25.8 (0.9)	31.8 (0.5)	31.0 (1.4)	33	17.06	<0.001	0.68
Rarefied ordinal richness	23.6 (0.3)	25.5 (0.7)	26.0 (0.3)	24	2.75	0.09	0.26
Mean ordinal richness	14.7 (0.6)	16.5 (0.3)	15.8 (0.9)	15.9	3.96	0.04	0.33
Berger-Parker dominance	4.0 (0.4)	4.5 (0.6)	4.8 (0.5)	4.6	0.44	0.65	0.05

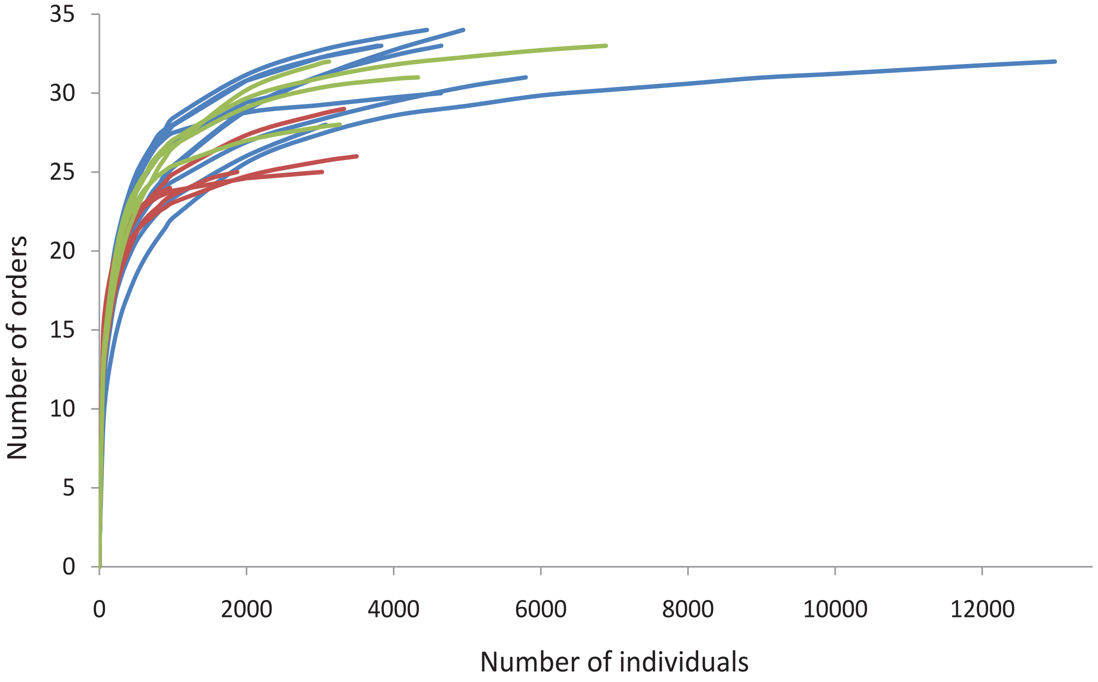


Figure 4. Ordinal richness rarefaction curves, calculated from summed invertebrate abundances in EcoSim (Entsminger 2004). Each line represents one of the 19 remnants, and the lines are colour-coded as follows: blue = fenced sites, red = grazed sites, and green = forest reserve sites.

None of the community metrics (raw, rarefied, and mean ordinal diversity, Berger-Parker dominance, or mean abundance) were significantly correlated with remnant area across all 19 sites (correlations not presented). When grazed sites were excluded, the mean number of orders per sample at each site was negatively correlated with remnant area ($r = -0.55$, $p = 0.04$). When the ten fenced sites only were included, raw ordinal richness was positively correlated with remnant area ($r = 0.77$, $p = 0.01$), unsurprising given our proportional sampling effort.

Discussion

Litter invertebrate community composition in grazed remnants was markedly different to that of either fenced remnants or forest reserves. Grazed remnants contained comparatively depauperate faunal assemblages, with many invertebrate taxa, including prostigmatid mites, pseudoscorpions, and sphaeroscerid flies, among others, adversely affected by grazing disturbance. Conversely, other taxa, such as potworms, araneomorph spiders, and julid millipedes (an introduced taxon) had higher abundances at grazed sites. Ordinal diversity was also lower in grazed sites. Encouragingly, I have found in other studies that livestock exclusion does lead to recovery of invertebrate community composition over time (Chapters 5-7).

Livestock grazing, like the impacts of other large mammalian herbivores (Wardle et al. 2001), clearly has a serious detrimental impact on New Zealand forest floor invertebrates. In countries where large mammalian herbivores have always been present, low intensity, “naturalistic” grazing regimes may be used to promote the maintenance of biodiversity in semi-agricultural landscapes (Kirby 2004). In contrast, mammals were absent from primeval New Zealand forests, and large mammalian herbivores have very different effects to that of the now extinct avian herbivores, moa (Forsyth et al. 2010).

Litter invertebrates contribute to several important ecological functions within forest ecosystems, namely litter decomposition, soil formation, and hence, nutrient cycling (Bardgett 2005). Disturbances, such as livestock grazing, that cause substantial shifts in community composition, are likely to have strong flow-on effects on ecological functioning, and interactions with other organisms which depend on litter invertebrates, for example as a food source, or as pollinators or seed dispersers.

Interestingly, there was greater variability in invertebrate assemblages between the five grazed remnants than between the other management categories. Despite the depauperate communities grazing disturbance appears to have caused divergence rather than convergence in community composition. Laurance et al.

(2007) describe their landscape-divergence hypothesis for forest fragment communities, stating that “fragments that experience similar matrix, disturbance, and environmental conditions are predicted to converge in composition”. The five grazed fragments in our study have clearly divergent communities, and given the low dispersal capabilities of many litter invertebrate groups, it seems unlikely that community composition in these remnants will become more similar over time.

Increased variability in community structure with disturbance has been documented by Warwick and Clarke (1993), who examined community variability between control and stressed sites in four different case studies of marine communities, each experiencing different environmental stressors, namely organic enrichment, oil pollution, a severe El Niño season, and mining. Indeed, there are numerous examples of disturbance leading to increased variability in community structure across a range of ecosystem types, yet few studies have explicitly examined variability as a community response to disturbance (Fratterrigo and Rusak 2008).

The variability in communities from grazed sites can be partially explained by variability in overall habitat, as grazed sites exhibited greater variability in habitat structure than the other sites (the IMD calculated from a Euclidean resemblance matrix of habitat variables was 0.72 between grazed and fenced sites, 0.80 between grazed and reserve sites, and -0.55 between fenced and reserve sites; Chapter 1).

Two specific habitat variables that may have had a strong influence are soil drainage and soil compaction. The response of soil to livestock treading is largely dependent upon pre-existing soil moisture – in wet soils, pugging or poaching occurs, whereby the substrate becomes pock-marked with well-defined hoofprints, but in drier soils simple compaction occurs without well-defined surface irregularities (Greenwood and McKenzie 2001). There was a clear compositional difference between poorly-draining grazed sites and grazed sites with good drainage, as the sites with particularly poor drainage (T74 and TTd) had much higher abundances of potworms, and lower abundances of prostigmatid mites and centipedes than the other grazed sites, or in fact, any of the other sites.

Remnant area was identified as an environmental covariate of invertebrate communities in fenced remnants and in forest reserves, but not in grazed sites. However, like Abensperg et al. (1996), I found that remnant management, and hence condition, seemed a far more important determinant of invertebrate community structure than remnant area. I think that previous studies that have found a significant influence of remnant area may have actually been confounded by the poorer habitat condition of small degraded sites, and future habitat fragmentation studies should be carefully designed so that the effects of area and condition can both be examined separately. In my study, the response of araneomorph spiders provides an excellent example of why failure to include consideration of patch condition may lead to erroneous conclusions regarding importance of remnant area – across all sites there appeared to be a decline in abundance (and less variation in abundance) of spiders with increasing remnant area, but in fact this was because heavily disturbed grazed sites had markedly higher abundances of spiders.

Even very small fenced remnants support invertebrate communities that are similar to those found in the edges of larger forest reserves. Fencing to exclude livestock is currently prioritised as a management action for privately-owned native forest remnants in New Zealand. This study supports the assertion that fencing to prevent livestock access is one of the most effective conservation management actions for forest remnants. Small forest remnants have high conservation value for litter invertebrates, provided they are protected from livestock disturbance.

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Appendix 1. List of habitat variables measured at each sampling plot or site, and used as environmental covariates in analyses.

Habitat variable	Units	Description
Sampling plot-level:		
Canopy height	m	Measured using an altimeter held by an observer standing 10 m from the base of the canopy tree closest to the sampling plot.
Canopy openness	% sky	A black and white digital photograph taken of sky directly above each pitfall trap, and the white pixels (i.e., sky), were later counted in Adobe Photoshop®, and then expressed as a percentage of total pixels.
Soil compaction	kgf cm^{-2}	Pocket penetrometer (ELE Model WF 24950) was used to take 20 measurements at randomly generated positions ±5 m perpendicular to transect line.
Soil drainage score		Soil drainage was visually scored on a scale of 0-2, with values of 0 representing very poor drainage (often with standing water puddles), and 2 representing free-draining soil.
Litter depth	cm	Five measurements of litter depth, down to compact soil layer, taken at randomly generated position perpendicular to transect line.
Wet litter weight	g m^{-2}	Three 20 x 20 cm quadrat samples of all friable material and humus down to compact soil layer were collected at each sampling point. Samples were transported back to laboratory, weighed, dried, then weighed again, to calculate mean wet weight, dry weight, and moisture content.
Dry litter weight	g m^{-2}	
Litter moisture content	%	
Groundcover - woody stems	%	I visually estimated percentage groundcover of woody stems, grasses, herbaceous vascular flora, ferns, bryophytes, bare soil, litter, coarse woody debris (defined as logs and branches >10 cm diameter), rock, and water, within a 5 m radius plot centred on each pitfall trap. Groundcover estimates totalled 100% at each sampling plot.
Groundcover - grasses	%	
Groundcover - herbs	%	
Groundcover - ferns	%	
Groundcover - bryophytes	%	
Groundcover - bare soil	%	
Groundcover - litter	%	
Groundcover - coarse woody debris	%	
Groundcover - rock	%	
Groundcover - water	%	

…Appendix 1 continued

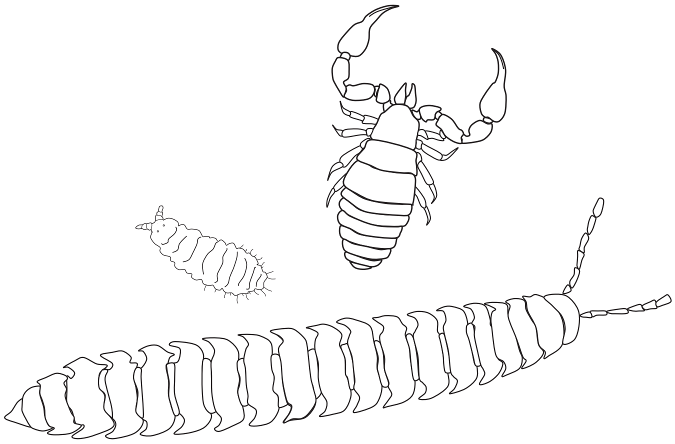
Habitat variable	**Units**	**Description**
Number of trees > 2 m		I measured the diameter at breast height (DBH), and identified to species level, all woody trees and tree ferns >2 m tall within the 5 m radius circular plot. From this I calculated the total number of trees, tree species richness, and basal areas within each sampling plot.
Tree species richness		
Total tree basal area	m^{-2}	
B. tawa basal area	m^{-2}	
Veg. composition - NMDSaxis1		In PRIMER (Clarke and Warwick 1994) I created Bray-Curtis resemblance matrices from log (x+1)-transformed tree basal area data, and then calculated two variables of vegetation composition, axes 1 and 2 of a non-metric multidimensional scaling (NMDS) ordination analysis (2D solution stress = 0.19).
Veg. composition - NMDSaxis2		
Understorey vegetation score		The density of all understorey vegetation was visually scored on a scale from 0-3, with values of 0 representing no understorey, and 3 representing very dense understorey.
Site-level:		
Remnant area		Remnant area, perimeter, and elevation (m a.s.l) were determined from vector files created in Google™ Earth using satellite imagery. Remnant area was log(x+1) transformed prior to analyses.
Elevation		
Remnant shape index (SI)		I calculated the shape index (SI) for each remnant using the formula $SI = \text{Perimeter} \div 200(\pi.\text{Area})^{0.5}$ (Patton 1975).

Appendix 2. One-way ANOVA by management category, on log(*x*+1) transformed abundances of 15 taxa with total abundances over 150 individuals, that also exhibited a change in mean abundance of more than 50% between any two management categories. Significant univariate tests (after Bonferroni correction) are in bold.

Taxa	One-way ANOVA, by Management Category		
	$F_{(2, 16)}$	*p*	Bonferroni-corrected *p*
Acari - Mesostigmata	4.95	0.021	0.798
Acari - Oribatida	2.96	0.081	1.000
Acari - Prostigmata	**17.82**	**0.000**	**0.003**
Acari - Trombidiidae	6.33	0.009	0.359
Araneae - Araneomorph	**30.33**	**0.000**	**0.000**
Opiliones - Laniatores	0.46	0.639	1.000
Pseudoscorpionida	**14.03**	**0.000**	**0.011**
Crustacea - Amphipoda	0.38	0.688	1.000
Crustacea - Isopoda	5.87	0.012	0.467
Crustacea - Copepoda	0.632	0.544	1.000
Coleoptera - Carabidae	0.89	0.429	1.000
Coleoptera - Curculionidae	0.06	0.940	1.000
Coleoptera - Staphylinidae	3.06	0.075	1.000
Coleoptera - Scarabaeinae	4.18	0.035	1.000
Coleoptera - other	0.62	0.550	1.000
Coleoptera larvae	0.59	0.565	1.000
Diptera - Cecidomyiidae	4.86	0.022	0.854
Diptera- Phoridae	1.82	0.193	1.000
Diptera - Psychodidae	0.04	0.965	1.000
Diptera - Sciaridae	0.68	0.519	1.000
Diptera - Sphaeroceridae	**19.61**	**0.000**	**0.002**
Diptera - other	0.76	0.484	1.000
Diptera larvae	0.07	0.937	1.000
Hemiptera - Aphidae	0.57	0.578	1.000
Hemiptera - Coccoidea	0.06	0.944	1.000
Hymenoptera - Formicidae	0.34	0.715	1.000
Hymenoptera - other	3.02	0.077	1.000
Lepidoptera larvae	1.27	0.308	1.000
Orthoptera - Rhaphidophoridae	1.63	0.227	1.000
Thysanoptera	1.31	0.296	1.000
Collembola - Entomobryomorpha	0.18	0.839	1.000
Collembola - Poduromorpha	1.97	0.172	1.000
Collembola - Symphypleona	2.55	0.110	1.000
Diplopoda - Polydesmida	3.32	0.062	1.000
Annelida - Enchytraeidae	5.61	0.014	0.541
Annelida - Lumbricina	4.52	0.028	1.000
Mollusca - snails	1.98	0.171	1.000
Nematoda	5.75	0.013	0.499

Chapter Three

Living on the edge: forest remnant management changes the edge responses of forest floor invertebrates.



Abstract

Forest edge effects can include marked changes to forest floor habitat, and litter invertebrates within forest fragments often exhibit strong edge- related changes in abundance as a result. However, forest edges can be highly variable in their structure. In particular, heavily disturbed fragments tend to have more ‘open’ edges than less disturbed fragments. Here I examine how varying the management of forest fragments with regards to livestock disturbance affects the edge responses of the litter invertebrate community. I found that most taxa had highly variable, somewhat idiosyncratic edge responses. There was also evidence that remnant management can alter the edge response of some taxa, for example, Entomobryomorpha springtails and Mycetophilidae flies exhibited steeper edge responses at grazed remnants than in remnants from other management categories. Overall community change was greatest between comparatively closely spaced sampling plots at the forest edge, than at widely spaced sampling plots further into the forest interior.

Introduction

Widespread anthropogenic habitat fragmentation is one of most pressing global conservation issues (Foley et al. 2005). Fragmentation not only reduces the total area of habitat, but also increases the extent of habitat edge, thus increasingly exposing biota to the conditions of the surrounding habitat matrix (Murcia 1995). The altered abiotic and biotic conditions at the edges of habitat remnants are referred to collectively as edge effects. Edge effects can have strong impacts on species diversity, community composition, species interactions and ecosystem functioning (Laurance et al. 2007).

The extent to which forest fragments will be influenced by edge effects depends on fragment size, shape, degree of contrast between the matrix and fragment habitat, disturbances from the surrounding matrix, and the physical structure of the edge (Murcia 1995, Barbosa and Marquet 2002, Norton 2002). Penetration distances of individual edge effects vary, but may extend several kilometres into the forest, thus, small fragments, or fragments with complex shapes, may be entirely composed of highly-modified edge habitat (Murcia 1995, Ewers et al. 2007). Ewers et al. (2007) studied beetle communities in New Zealand *Nothofagus* forest fragments and found that very small fragments exhibited little or no edge gradient and were dominated by matrix fauna because of the absence of forest-like conditions, whereas larger fragments had much stronger edge-related changes in beetle community composition.

The greater the contrast between matrix and fragment habitat, the greater the magnitude and extent of the edge gradient (Murcia 1995, Kupfer et al. 2006). Therefore, native forest fragments surrounded by the typically low-stature, low-complexity vegetation of agricultural landscapes suffer from a greater contrast between matrix and fragment habitat than native forest remnants embedded in exotic plantation forest (Denyer et al. 2006), or in regenerating secondary native forest (Laurance et al. 2007). In addition, human-caused external disturbances related to the surrounding landuse, such as fire and livestock grazing, may alter or amplify the magnitude and extent of edge effects (Ewers and Didham 2006a).

For forest remnants, the principal abiotic changes that occur with edges are associated with microclimate, with edges typically experiencing higher temperatures, lower humidity, and increased light penetration (Murcia 1995). This can have flow-on effects for litter invertebrate habitat, for example reducing litter moisture content

(Chapter 1). Forest remnants in agricultural landscapes may also be subjected to additional abiotic edge effects from physical disturbances related to agricultural practices, such as increased nutrient inputs from fertiliser drift (Murcia 1995, Stevens 1994) or contamination by pesticides.

Biotic edge effects are manifested as changes in the abundance or distribution of organisms with distance from forest edge. The most obvious direct biotic edge effect in forest remnants is altered vegetation structure (Murcia 1995). While some forest plants are unable to cope with edge conditions and suffer increased mortality, others respond to the increased light levels with prolific growth, and as a result, forest edges often exhibit high stem densities and basal areas (Murcia 1995). This dense vegetation can act as a buffer and lessen the severity of microclimatic edge effects (Murcia 1995). However, vegetation structure at forest edges can also be altered by disturbances from the surrounding matrix. For example, Didham and Lawton (1999) showed that the penetration distance and magnitude of edge effects was greater in fragments with open, fire-encroached edges, than in fragments with closed, undisturbed edges. Likewise, while forest fragments that are fenced to exclude livestock tend to have densely-vegetated edges, grazed fragments typically have very open edges, with greatly reduced understorey and tree density (Chapter 1). Therefore, how forest fragments are managed with regard to disturbances such as livestock grazing has the potential to alter the severity and extent of the vegetation edge effects. In turn, this is likely to affect other organisms, such as invertebrates.

The response of invertebrates to forest edges is not as well studied as the responses of plants and vertebrates. Invertebrates may have small area requirements, but many are highly sensitive to the altered conditions that can occur at forest edges, hence forest fragmentation may lead to dramatic changes in community composition.

Specifically, deep forest invertebrates are predicted to be lost from the edge community. For example, Ewers and Didham (2004) found that 102 beetle species, representing 12% of the total beetle species pool collected in their study of New Zealand *Nothofagus* forest fragments, were restricted to forest fragments of >1000 ha in size, and of those, 43 species were only collected in a deep forest site located more than 2 km from the nearest forest edge. Meanwhile, the abundance of habitat-generalist, early-successional, edge-adapted, or invasive invertebrate species from the matrix could be expected to be higher at forest edges (Murcia 1995). Forest edges often support higher invertebrate diversity because of the mixing of matrix and forest taxa (Ewers et al. 2007).

In Chapter 1 I found that forest floor habitat changes with both distance to forest edge, and remnant management category. Specifically, grazed remnants exhibit several habitat changes resulting from the impacts of grazing livestock, including greatly reduced understorey vegetation, reduced litter groundcover, and higher soil compaction. Grazed remnants and forest reserves exhibited more extensive edge gradients than fenced sites. In contrast, fenced forest remnants typically exhibit a much more abrupt change in habitat between matrix and interior. In Chapter 2, I found that forest floor invertebrate communities are markedly different in grazed remnants compared to fenced remnants and forest reserves, and that remnant condition appears to be a more important determinant of forest floor invertebrate community structure than remnant area. However, I did not specifically examine the effect of distance from the forest edge. In this chapter I examine whether remnant management affects the edge response of the forest floor invertebrate community. I was also interested in how the edge responses of individual taxa, including known exotic invasive taxa, varied between remnants under different management regimes.

Methods

Study area

The study sites comprised 19 native forest remnants in the Waitomo district, in the south of the Waikato region, New Zealand (Table 1; Figure 2 in Chapter 1). Native forest cover in the district has been reduced from 99% prior to human arrival, to 30% (Ewers et al. 2006), and largely converted to pastoral grazing and exotic forestry (the study remnants were all bordered by pasture). Topography in the study area ranges from flat to rolling hills, and elevation ranged between 450-580 m a.s.l.

The remnants were separated into three management categories: five small privately-owned remnants regularly grazed by livestock, predominantly cattle but also sheep (remnant size range 0.31ha – 15.05ha), ten small privately-owned remnants which had been fenced to exclude livestock for a minimum of 10 years (remnant size range 0.88–28.57 ha), and the four largest remaining forest remnants in the area, which are all reserves managed wholly or in part by the Department of Conservation (DoC). These four larger forest reserves comprised a block of Herekawe Scenic Reserve on the southern side of SH30 (hereafter referred to as Hkw, 137.65 ha), the large northern block of Pureora Forest Park (PuN, 30492.13 ha), a smaller central block of Pureora Forest Park near the DoC Field Centre (PFC, 293.56 ha), and Mangapehi Forest Reserve (Mpe, 1655.18 ha), privately-owned but managed in part by DoC.

Table 1. Characteristics of the 19 native forest remnants sampled in the Waikato region, New Zealand, including remnant area (ha), shape index (SI; Patton 1975), management category (G = grazed remnants – unfenced remnants which were regularly grazed by livestock at the time of this study , F = fenced remnants, which had been fenced for a minimum of 10 years, R = larger forest reserve sites, representing the largest blocks of forest remaining in the study area), the length of the study transect established at each site, and whether or not a sampling plot was established at the -5 m position along the transect (i.e. outside the remnant in the surrounding pastoral matrix.

Site name	Remnant area (ha)	SI	Management category	Transect length (m)	-5 m plot?
TTd	0.31	1.11	G	10	Y
Qry	1.00	1.58	G	20	Y
11P	1.45	1.22	G	40	Y
12P	1.67	1.39	G	40	Y
T74	15.05	1.79	G	40	Y
Isl	0.88	1.27	F	20	N
LTd	1.15	1.35	F	20	N
LTu	1.42	1.35	F	40	N
Tut	4.51	1.09	F	80	N
Ted	5.86	1.43	F	80	N
Den	10.52	1.15	F	160	Y
B86	15.28	1.37	F	160	N
T91	16.92	1.23	F	160	Y
Jac	18.76	1.19	F	160	Y
Mru	28.57	1.63	F	160	N
Hkw	137.65	1.86	R	320	Y
PFC	293.56	1.51	R	160	Y
Mpe	1655.18	1.84	R	320	Y
PuN	30492.13	5.46	R	320	Y

The forest reserves had never been grazed by livestock. The ungrazed sites were all protected from livestock grazing by high quality fencing which had been in place for a minimum of 10 years, but at most sites much longer. All five grazed sites were subjected to a rotational grazing regime throughout the study, predominantly cattle. Mean stocking rates in the study area are estimated at <10.5 stock units (SU) per ha (one stock unit = one dry sheep equivalent, i.e., 55 kg), which is comparatively low for the region (Environment Waikato 2011). Feral deer, pigs and goats were present throughout the study area.

In all of the grazed sites, cattle were regularly observed throughout the remnant interior, i.e., they were not restricted to the edges. Some livestock impacts, such as soil compaction, appeared to decline in severity with increasing edge distances, while others such as understorey vegetation removal, were discernable throughout grazed remnants yet did not vary appreciably with distance from the edge (Chapter 1).

The study remnants were selected to have similar canopies, composed predominantly of the native tree *Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae). Other common canopy and subcanopy tree species, listed in order of decreasing total basal area, were *Podocarpus totara* G.Benn. ex D.Don var. totara (Podocarpaceae), *Elaeocarpus dentatus* (J.R.Forst. et G.Forst.) Vahl) (Elaeocarpaceae), *Weinmannia racemosa* L.f. (Cunoniaceae), *Dacrycarpus dacrydioides* (A.Rich.) de Laub. (Podocarpaceae), *Melicytus ramiflorus* J.R.Forst. et G.Forst. (Violaceae), *Dacrydium cupressinum* Lamb. (Podocarpaceae), *Knightia excelsa* R.Br. (Proteaceae) and *Hedycarya arborea* J.R.Forst. et G.Forst. (Monimiaceae), and the tree ferns *Dicksonia squarrosa* (G.Forst.) Swartz, and *D. fibrosa* Colenso (Dicksoniaceae), and *Cyathea dealbata* (G.Forst.) Sw. (Cyatheaceae). Selective logging of large podocarp trees in the past will have altered the canopy composition of the remnants. The composition, density and condition of understorey vegetation varied considerably between sites and management categories, the most notable difference being the almost complete lack of native understorey in grazed sites. While livestock disturbance was not limited to forest edges, I found that edge gradients in invertebrate habitat had greater penetration distances in grazed remnants than in fenced remnants (Chapter 1).

Field methods

At each remnant I established a transect leading up to 320 m into the interior of the remnant. As penetration of edge effects may vary with orientation (Murcia 1995), all transects began on a north-facing edge. I defined the edge (i.e., 0 m along the transect line) by the position of the outermost trunks which formed a continuous canopy. At each transect I established sampling plots centred at distances of -5 (i.e., 5 metres outside the remnant in the surrounding pasture matrix), 0, 5, 10, 20, 40, 80, 160 and 320 m, giving a total of 125 sampling plots across the 19 sites. Transect length was largely determined by remnant area, but was also influenced by remnant shape (i.e. transect length was shorter in irregularly shaped remnants) and was adjusted to avoid canopy gaps or, as in the case of site PFC, a public walking track. I deliberately sampled more intensively at remnant edges because I expected that this is where rate of change in invertebrate communities would be greatest (as per Ewers et al. 2007, Didham et al. 2009). I did not establish -5 m plots at fenced sites where the fence was <5 metres from the edge of the remnant, as the -5 m plot would have then been in a different grazing treatment.

A pitfall trap was installed centred on each sampling point. Each trap comprised a plastic disposable cup (11 cm diameter, 10 cm deep), nested inside a section of polythene pipe dug-in level with the surrounding ground, and covered by a stainless steel lid installed 2 cm above the ground. 70% ethylene glycol was used as a preservative. The traps were set for four-week periods, at three different sampling intervals throughout the year: mid-December 2008 to mid-January 2009 (Summer), mid-April to mid-May 2009 (Autumn), and late October to late November 2009

(Spring). I did not undertake any sampling during winter or early spring as access to all sites was not possible in winter and during lambing season. After collection, samples were stored in 70% ethanol prior to sorting. During the final sampling period (Spring) an additional pitfall trap was installed at the innermost sampling point of each site's transect, 5 m perpendicular to the transect line. This allowed me to compare the community dissimilarity between Spring samples collected from two traps installed 5 m apart at the remnant edge (i.e. the 0 and 5 m samples), and two traps installed 5 m apart at the remnant interior. A paired t-test was used to see if the observed difference in community similarity was significant.

At each sampling point, latitude, longitude, aspect and slope were recorded. I also measured a range of other variables specific to the habitat requirements of forest floor invertebrates, to be used as environmental covariates in subsequent analyses (summarised in Appendix 1 of Chapter 2). Invertebrate habitat changed markedly between management treatments and with distance to forest edge, and is discussed in detail in Chapter 1.

Invertebrate processing

Invertebrate samples were sieved (mesh size = 0.5 mm), then sorted under microscope to Phylum, Class, Order or Family level. Larval and adult forms of holometabolous insect groups were counted separately. Abundances were expressed as number of individuals per sample. The abundance of numerically-dominant taxa (i.e., those with abundances exceeding 200 individuals in an individual sample) was estimated using sub-sample counts. To do this, the original sample was distributed throughout a tray divided into 10 equal-sized quadrants. The number of individuals was counted in three quadrants, and then the mean count was used to estimate total abundance in the entire sample.

Analysis

I first calculated mean abundances of taxa at each sampling plot across the three sampling seasons (Chapter 2). To test whether community composition changed in a predictable linear fashion with distance from edge at each site, I created Bray-Curtis resemblance matrices of log(x+1) transformed mean abundances, and model matrices based on distance (m) between each sampling point, in PRIMER 6.1 (Clarke and Warwick 1994), and then used the RELATE procedure to calculate the extent of agreement between the physical distance matrix and sampling point matrix, for each site. I performed NMDS ordinations from log(x+1) transformed sampling point mean abundances for each site. To examine whether the community edge response varied between management categories, I calculated the mean Bray-Curtis similarity between the 0 m sampling plots, and each subsequent sampling plot distance, for each management category.

To examine the edge response of individual taxa, I calculated the simple linear regression of the log(x+1) transformed mean invertebrate abundances against log(x+10) transformed distance from forest edge (m), for each site, for all taxa with total abundances (i.e., summed across all sites) of over 100 individuals (as listed in Table 3). Many edge responses are best modelled by sigmoidal functions, with asymptotes at some distance either side of the edge boundary (Ewers and Didham 2006b). However, as I sampled invertebrates over a fairly small range of edge distances the abundances did not approach asymptotes on either side of the edge boundary and hence linear models were appropriate for modelling the edge responses. I used the slope values of the regression lines as a measure for the edge response of each taxon at each site (an edge response or slope of 0 was specified in the case of non-significant regressions). Then, I used Kruskall-Wallis non-parametric tests to examine whether the edge responses of individual taxa varied between the three management treatments (for taxa that exhibited significant edge responses at a minimum of three sites). I also examined and compared the penetration distances of three exotic taxa known to be abundant in the pastoral matrix, namely julid millipedes (Diplopoda: Julida), field crickets (Orthoptera: Gryllidae) and field slugs (*Deroceras reticulum*).

The strength of edge effects may be affected by remnant area, and the ability to detect edge effects may also depend on total transect length. I calculated Pearson correlations first between the area and transect length of each site, and the number of taxa that exhibited significant edge responses, and also between area and transect length and the mean strength of edge responses (i.e. mean absolute slopes of edge regressions across all taxa, first with only significant regressions, then across all taxa, i.e., including 0 slope values). I used one-way ANOVA to test whether the number of taxa exhibiting significant edge responses, or the mean strength of significant edge responses, varied significantly between different management categories.

Results

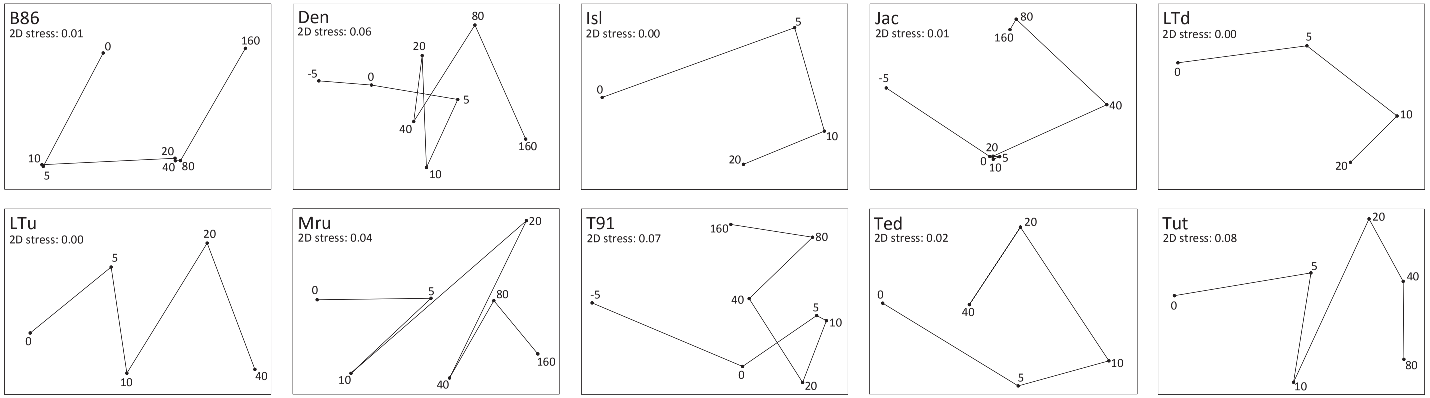
Community similarity between sampling points was positively correlated with the physical distance between sampling points at four of the sites (11P, B86, Den, and Ltu) (Table 2). However, at five of the sites (Isl, PFC, PuN, Ted, and TTd), the biological and distance matrices were negatively correlated (though not significant), indicating that community similarity tended to be greater between more widely-spaced sampling plots (Table 2). Indeed, the ordination plots for each site reveal that in many cases, communities exhibited more marked changes between the closely-spaced -5, 0 and 5 m plots, than between subsequent sampling plots, despite plots being progressively further apart (Fig. 1). Grazed sites exhibited a greater change in community over the first 5 m of the transect, compared to fenced or reserve sites (Fig. 2).

Table 2. RELATE statistics, testing for extent of agreement between community similarity and physical distance between sampling points. Positive Rho values indicate that communities became less similar with increasing physical distance between traps, whereas negative values indicate communities became more similar with increasing physical distance between traps. Significant ($p \leq 0.05$) values are indicated in bold.

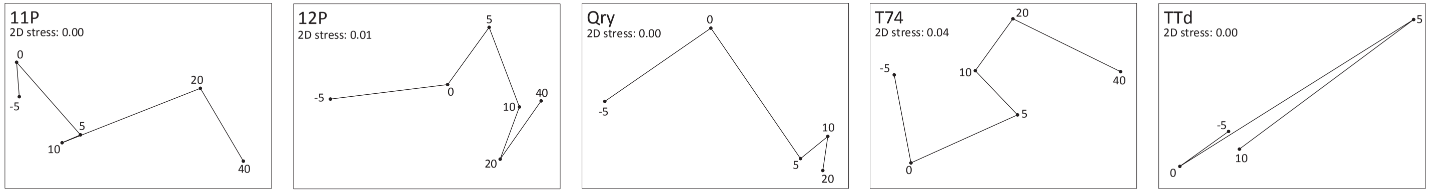
Site	Rho	*p*
11P	**0.82**	**0.00**
12P	0.20	0.28
B86	**0.73**	**0.00**
Den	**0.51**	**0.01**
Hkw	0.19	0.23
Isl	-0.03	0.54
Jac	0.40	0.09
LTd	0.09	0.37
LTu	**0.75**	**0.01**
Mpe	0.37	0.05
Mru	0.10	0.38
PFC	-0.35	0.89
PuN	-0.04	0.53
Qry	0.49	0.07
T74	0.45	0.11
T91	0.21	0.22
Ted	-0.27	0.84
TTd	-0.62	1.00
Tut	0.18	0.32

Figure 1: NMDS ordinations for each site, calculated from mean invertebrate abundances at each sampling plot, showing community change with distance from edge (sampling points labelled with distance).

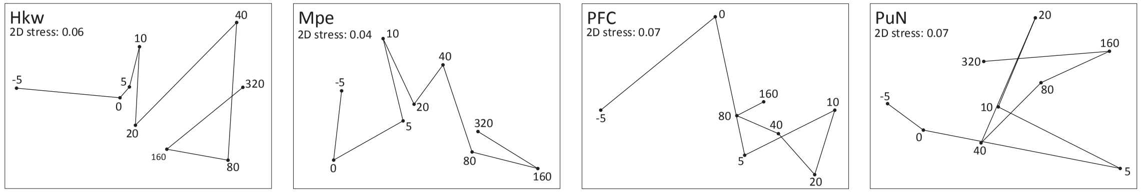
A) Fenced sites



B) Grazed sites



C) Forest reserve sites



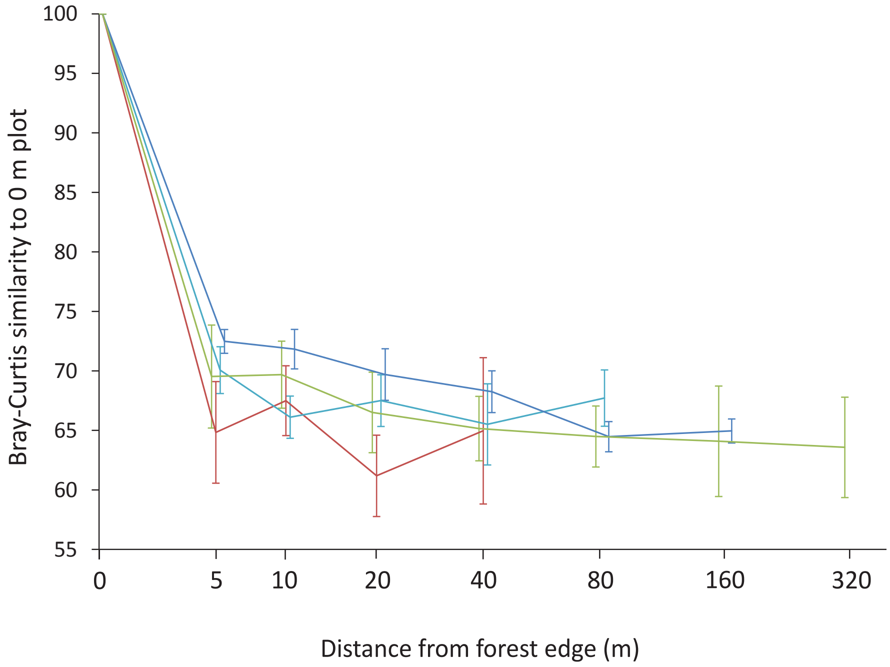


Figure 2. Change in community with distance from forest edge, expressed as mean (+/- SE) Bray-Curtis similarities between 0 m sampling plot and subsequent sampling points. Red = grazed sites, light blue = small fenced sites (Isl, LTd, Ltu, Tut, and Ted; all < 6 ha), dark blue = larger fenced sites (Den, B86, T91, Jack, Mru; all > 10 ha), green = forest reserve sites. The *x*-axis was plotted using log(*x*+6) transformed edge distances, but labels are expressed in absolute distances (m) for ease of interpretation. Data points from the three management treatments are jittered slightly along the *x*-axis to assist interpretation.

In the Spring sampling period, when we added an additional pitfall trap at the innermost sampling point of each remnant (5 m from existing trap, perpendicular to transect line), community similarity between the 0 and 5 m sampling points was lower than the community similarity between the two remnant interior traps (installed 5 m apart) at 14 of the 19 sites (mean difference in Bray-Curtis community similarity = -4.04%, t = -2.25, $p = 0.04$).

Most taxa did not exhibit strong edge responses at any of the sites, particularly in the fenced management sites (Table 3). Notable exceptions included oribatid mites, araneomorph spiders (this appeared to be largely, but not entirely, driven by the response of lycosid spiders, hence they were also analysed separately), and phorid flies, which exhibited significant edge responses at 9 of the 19 sites. The distribution of edge responses of some taxa varied significantly between the three management treatments (Table 3). Notably, araneomorph spiders showed steeper edge responses at grazed and reserve sites than at fenced sites (Table 3, Figure 3). Entomobryomorph springtails exhibited significant negative edge responses at three grazed sites, but at none of the other sites. Likewise, mycetophilid flies exhibited negative edge responses at three out of the four grazed sites they were collected from, but no discernable edge response at any other site.

Introduced field crickets (Orthoptera: Gryliidae) were limited to pasture matrix habitat as they were only caught in -5 m traps. There are native crickets in New Zealand but none were collected in this study. The common introduced grey field slug (*Deroceras reticulatum)* only extended up to 20 m into forest remnants. Julid millipedes (an introduced group that is often very abundant in the agricultural matrix), were much more abundant at grazed sites (Chapter 2), and were caught throughout grazed remnants (i.e., at 0 – 40 m sampling plots), but did not extend more than 10 m in from the forest edge at fenced sites, or beyond 0 m at reserve sites.

Table 3. Variation in the edge responses (expressed as the slope of linear regression lines for log(*x*+1) transformed abundances plotted against log(*x*+10) transformed distance from forest edge) of individual taxa with total abundances >100, for each management category. For each taxon the table reports the number of sites in each management category where the taxon was collected, the number of sites where it exhibited a significant edge response (i.e., where regression line was significant at α= 0.05 level), the range of edge response values (non-significant responses reported as 0), and the results of a Kruskall-Wallis test examining whether the distribution of edge responses varied significantly between management categories. Where a particular taxon was present at fewer than 3 sites within a particular management category (as denoted by *), that management category was excluded from the Kruskall-Wallis test.

		Fenced sites			Grazed sites			Reserve sites			Kruskall-Wallis		
Taxon		Sites present	Sig. responses	Range of edge responses	Sites present	Sig. responses	Range of edge responses	Sites present	Sig. responses	Range of edge responses	H	d.f	p
ARTHROPODA - Arachnida													
Acari	Mesostigmata	10	3	-0.61 - 0.68	5	2	-0.54 - 0	4	1	-0.39 - 0	0.68	2	0.71
	Oribatidae	10	5	-0.22 - 0.1	5	2	-0.10 - 0	4	3	-0.05 - 0	0.43	2	0.81
	Prostigmata	10	3	-0.10 - 0.09	5	1	0 - 0.07	4	1	0 - 0.06	0.07	2	0.96
	Prostigmata -Trombidiidae	10	3	-0.26 - 0.20	4	0	0	4	0	0	0.30	2	0.86
Araneae	Araneomorph	10	2	-0.11 - 0	5	4	-0.20 - 0	4	3	-0.11 - 0	**6.73**	2	**0.02**
	Araneomorph - Lycosidae	9	2	-0.11 - 0	5	5	-0.18 - -0.04	4	3	-0.09 - 0	**9.31**	2	**0.00**
Opiliones	Eupnoi	10	3	-0.11 - 0.09	5	1	-0.09 - 0	4	1	-0.05 - 0	1.47	2	0.61
Pseudoscorpionida		10	3	-0.16 - 0.15	1*	0	0	4	0	0	0.16	1	0.95
ARTHROPODA - Crustacea													
Amphipoda		10	3	-0.25 - 0.13	5	1	0 - 0.10	4	0	0	1.19	2	0.55
Isopoda		10	2	0.16 - 0.26	5	1	-0.10 - 0	4	1	0 - 0.05	2.85	2	0.36

… Table 3 continued

Taxon		Fenced sites			Grazed sites			Reserve sites			Kruskall-Wallis		
		Sites present	Sig. responses	Range of edge responses	Sites present	Sig. responses	Range of edge responses	Sites present	Sig. responses	Range of edge responses	H	d.f	p
ARTHROPODA - Hexapoda													
Collembola	Entomobryomorpha	10	0	0	5	3	-0.16 - 0	4	0	0	**9.39**	**2**	**0.01**
	Poduromorpha	10	2	-0.08 - 0.13	5	2	0 - 0.10	4	3	-0.10 - 0	**7.54**	**2**	**0.01**
	Symphypleona	10	4	-0.07 - 0.30	5	1	-0.17 - 0	4	0	0	2.21	2	0.30
ARTHROPODA -Myriapoda								4	4	0			
Chilopoda		9	3	-0.06 - 0	4	1	-0.04 - 0	3	0	0	0.22	1	0.77
Diplopoda	Julida	5	3	-0.18 - 0	5	1	-0.07 - 0	2*	0	0	1.68	1	0.29
	Polyzoniida	9	2	-0.13 - 0	2	0	0	4	2	-0.10 - 0	0.89	1	0.43
ARTHROPODA - Insecta													
Coleoptera	Carabidae	10	2	-0.20 - 0	5	1	-0.09 - 0	4	0	0	0.89	2	0.79
	Staphylinidae	10	2	-0.16 - 0	5	1	-0.08 - 0	4	0	0	0.89	2	0.79
	Coleoptera larvae	10	2	-0.12 - 0	5	1	-0.14 - 0	4	0	0	0.92	2	0.72
Diptera	Cecidomyiidae	10	2	0 - 0.21	5	0	0	4	1	0 - 0.09	1.20	2	0.56
	Mycetophilidae	10	0	0	4	3	-0.11 - 0	4	0	0	**11.78**	**2**	**0.01**
	Phoridae	10	3	-0.19 - 0	5	4	-0.22 - 0	4	2	-0.19 - 0	4.22	2	0.12
	Psychodidae	10	1	0 - 0.11	5	0	0	4	2	0 - 0.07	3.87	2	0.15
	Sphaeroceridae	10	4	0 - 0.17	2*	1	-0.03 - 0	4	2	0 - 0.08	0.10	1	0.83
	Other Diptera	10	2	-0.08 - 0	5	0	0	4	3	-0.15 - 0	3.92	2	0.13
	Diptera larvae	10	2	0 - 0.15	5	0	0	4	1	-0.07 - 0	3.58	2	0.14
Hemiptera	Aphidae	8	1	-0.05 - 0	5	2	-0.25 - 0	4	1	-0.09 - 0	1.75	2	0.55
	Coccoidea	10	2	-0.36 - 0	5	1	-0.39 - 0	4	0	0	0.92	2	0.72
	Other Hemiptera	10	1	0 - 0.14	5	0	0	4	2	-0.06 - 0.05	0.34	2	0.95
Hymenoptera	Formicidae	10	3	-0.30 - 0	5	0	0	4	1	-0.10 - 0	1.86	2	0.42
	Other Hymenoptera	10	2	-0.13 - 0	5	1	-0.26 - 0	4	1	-0.08 - 0	0.08	2	0.98
Lepidoptera	Lepidoptera larvae	10	0	0	5	2	-0.13 - 0	4	1	0 - 0.06	1.39	2	0.51
	Rhaphidophoridae	10	2	0 - 0.10	5	2	0 - 0.10	4	0	0	1.90	2	0.39
MOLLUSCA - Gastropoda													
Slugs		5	2	-0.10 - 0	5	1	-0.09 - 0	2*	1	-0.10 - 0	0.10	1	0.84

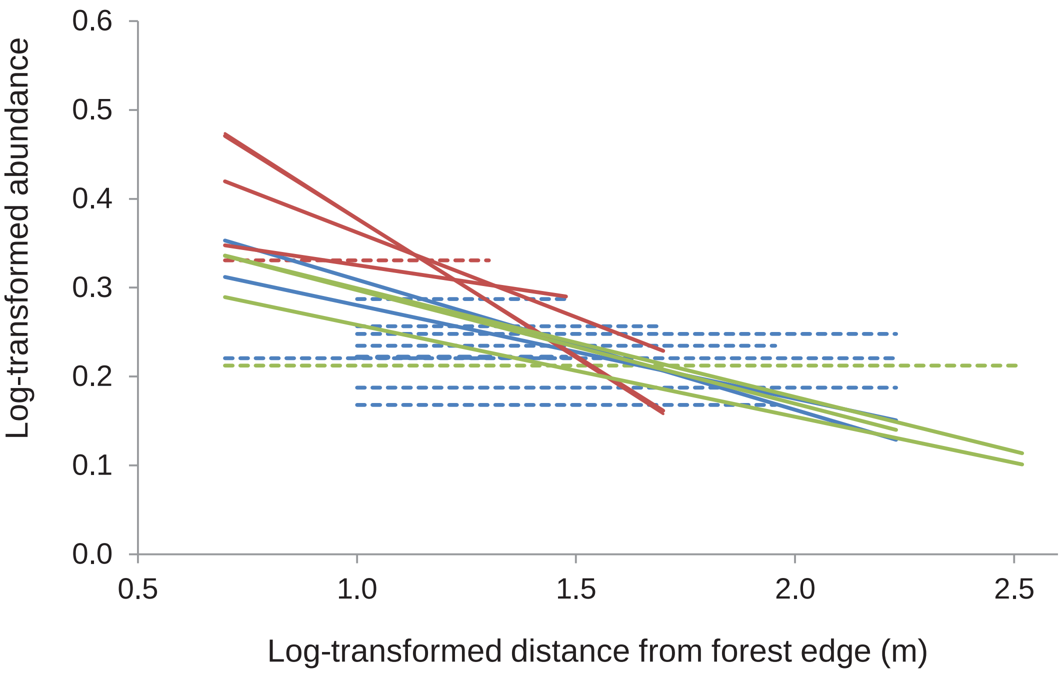


Figure 3. Variation in the edge response of araneomorph spiders. Linear regression line for each site, of log(*x*+1) transformed mean abundance, against log(*x*+10) transformed distance from forest edge (i.e., a value of 1 corresponds with the 0 m transect distance). Each line represents one of the 19 forest remnant sites, colour-coded by management (red = grazed, blue = fenced, green = reserve sites). Solid lines are linear regression lines (all sig. at α = 0.05), dashed horizontal lines are mean values, used for sites where no significant edge response was apparent. The edge response (i.e., the slope of the regression lines) of araneomorph spiders varied significantly between the three management categories (H = 6.73, d.f = 2, p = 0.02).

The mean slope of significant edge responses varied between management categories ($F_{2,16}$ = 5.65, p = 0.01), being significantly lower in reserve sites (mean = 0.08, SE = 0.01) than at fenced sites (mean = 0.14, SE = 0.01), but neither reserve or fenced sites were significantly different from grazed sites (mean = 0.13, SE = 0.01.) The number of taxa exhibiting significant edge responses at each site was not correlated with either remnant area or transect length, and did not vary with management category. However, the mean slope of all taxa that exhibited significant edge responses was negatively correlated with remnant area (r = -0.59, p = 0.01), i.e., smaller remnants exhibited steeper edge gradients (Fig. 4a). This result may be partly attributable to sampling artefacts (i.e., it is easier to detect edge effects with lesser slopes over longer transect distances), as the mean slope of significant edge effects at each site was negatively related to the transect length at each site (R^2 = 0.44, $F_{1,18}$ = 13.25, p <0.01; Fig. 4b).

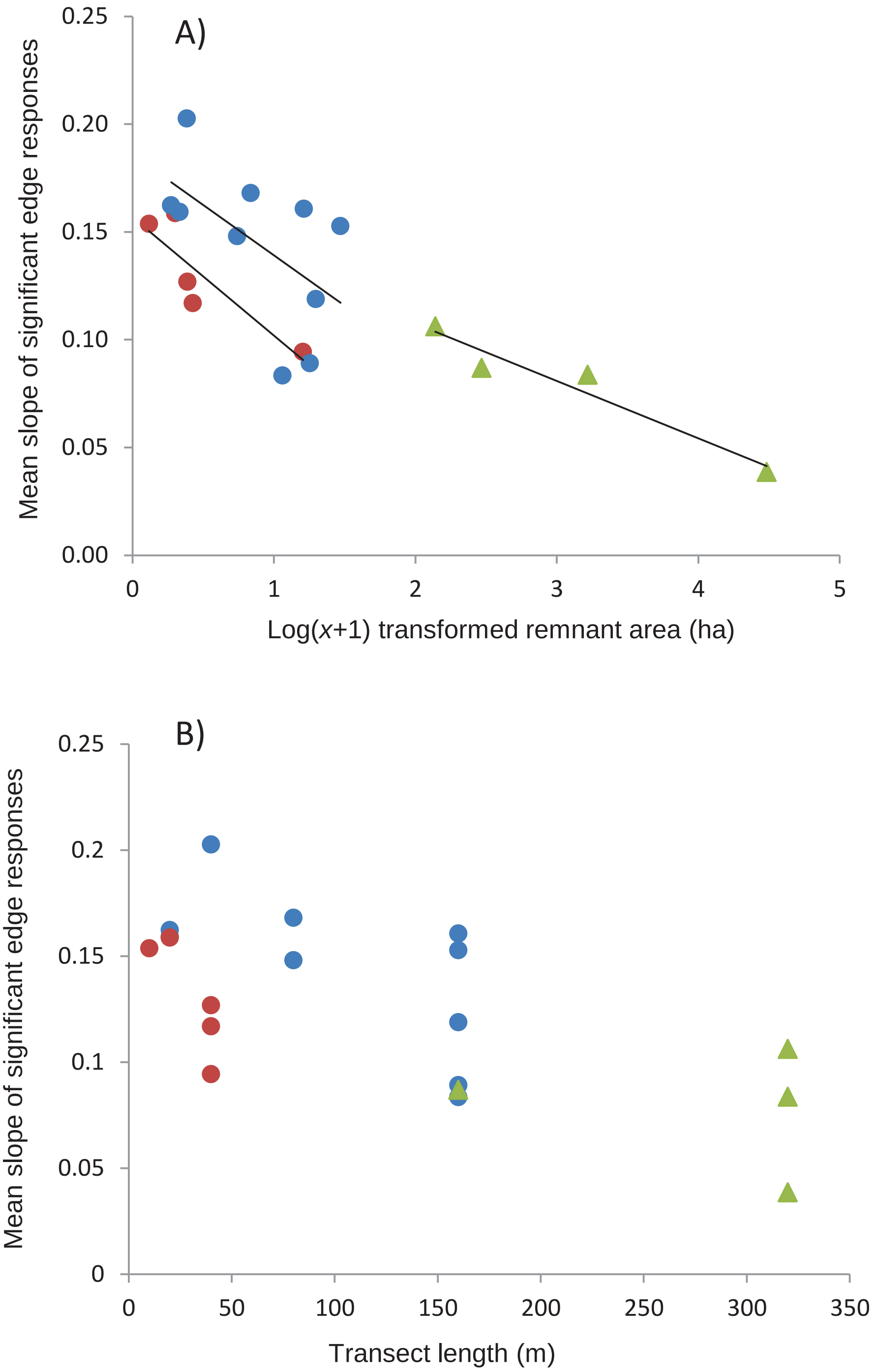


Figure 4. Variation in the mean slope of significant edge regressions with A) remnant area, and B) transect length at each site. Each data point is one of 19 sites, and points are colour-coded by management category (red = grazed, blue = fenced, and green = reserve sites). Each management category is fitted with a linear regression line. A) Grazed sites; $y = -0.06x + 0.16$ ($R^2 = 0.63$, $F_{1, 4} = 5.10$, $p = 0.11$). Fenced sites; $y = -0.05x + 0.19$ ($R^2 = 0.18$, $F_{1, 9} = 1.75$, $p = 0.22$). Reserve sites; $y = -0.03x + 0.16$ ($R^2 = 0.90$, $F_{1, 3} = 17.67$, $p = 0.05$).

Discussion

As expected, overall community composition changed markedly with distance from forest edge, particularly over the first 10 metres of each site’s transect. Generally, edge-related changes in invertebrate community composition were steeper in smaller remnants than in larger tracts of forest, and also steeper in fenced remnants compared to forest reserves. However, when the responses of individual taxa were examined, it was clear that most did not exhibit strong edge -related gradients in abundance. The taxa which did show consistently strong responses to forest edges included araneomorph spiders, oribatid mites, and phorid flies, which all tended to decline in abundance with increasing distance into forest. This was presumably in response to one or several edge-related gradients in habitat, resource availability, or altered interactions with other taxa, but it is difficult to disentangle the exact mechanisms involved.

A few taxa exhibited edge responses that differed between the three remnant management categories. Livestock grazing disturbance leads to several habitat changes, including dramatically reduced understorey vegetation and increased soil compaction (Chapter 1). Grazed remnants also tend to exhibit steeper edge-related habitat gradients than fenced remnants (Chapter 1), which might explain why taxa such as entomobryomorph springtails and Mycetophilidae flies exhibited steeper edge responses at grazed remnants than in remnants from other management categories. Fences that exclude livestock may in fact partially ameliorate or lessen the severity of edge effects for invertebrate communities in small forest fragments, by allowing a dense “buffer” of understorey vegetation to establish. This buffering effect seems to at least partially override the influence of remnant area on edge structure. Vegetation densities, rather than distance from edge per se, may be a more important determinant of invertebrate densities (Jokimaki et al. 1998).

One of the most serious implications of invertebrate edge responses relates to the invasion of exotic invertebrates from the surrounding pastoral matrix. Invasive invertebrates may displace native taxa, and therefore lower the natural biodiversity of remnants. The response of introduced taxa such as julid millipedes suggests that heavily-disturbed, grazed remnants are more susceptible to invasion by exotic invertebrates than fenced or forest reserve sites. Julid millipedes are found throughout New Zealand, and are particularly abundant in pasture (Johns 1962), as well as being present in native forest (Chapter 6). Remnant condition seemed to be a more important determinant than remnant area for the presence of julid millipedes, because julid millipedes did not penetrate more than 10 m into even very small fenced fragments, but were found throughout grazed sites at much higher densities. Several studies have already shown that heavily disturbed habitat remnants are more susceptible to exotic plant invasions than less-disturbed forest (for example, Ross et al. 2002, Bustamante et al. 2003), so it is possible that invasive invertebrates would show a similar trend. Many invasive species have the potential to create serious adverse flow-on effects for the ecosystem they invade. Invasive invertebrates can have serious impacts on the composition and diversity of native invertebrate communities, as is the case with Argentine ant-invaded scrub fragments in coastal California, USA, which support lower native ant diversity than uninvaded habitat (Suarez et al. 1998). Invasive invertebrates can also impact ecological functioning, for example, invasive earthworms in North American hardwood forest have been shown to disrupt nutrient cycling and plant regeneration (Bohlen et al. 2004).

The main purpose of this study was to assess whether forest fragments under different management regimes exhibited different invertebrate edge-effects. I should stress that because I examined the community response at a comparatively coarse taxonomic level, the edge responses of individual species will have been masked. Closely related invertebrate species can exhibit markedly different responses to forest edges (Ewers 2004). Although higher-order taxonomic studies are often criticised (e.g., see Majer 2009), I think this approach was best for this study as it allowed me to examine the response of the invertebrate community in its entirety. Other studies have shown that patterns of invertebrate abundance and diversity measured at higher taxonomic levels have been found to be good predictors of responses at species level (Williams and Gaston 1994, Pik et al. 2002). The taxonomy of most invertebrate groups in New Zealand is very poorly resolved. A species-level approach would have inevitably meant I would have had to focus on a subset of taxa, with very little prior knowledge of which taxa are most sensitive to forest edge effects. Another potential constraint of this study is the comparatively small range of edge distances sampled. Abiotic edge effects can penetrate kilometres into forest, and despite their small area requirements, invertebrates are highly sensitive to edge effects. Kilometre-scale edge effects have been previously observed for New Zealand beetles (Ewers and Didham 2004).

Fencing to exclude livestock has already been shown to be important for maintaining natural vegetation and allowing canopy regeneration (e.g., Burns et al. 2011). This study suggests that the benefits of livestock exclusion extend beyond vegetation effects, to include protection of litter invertebrate communities. Native forest remnants that are fenced to exclude livestock support invertebrate communities that are much more similar to nearby larger forest reserves (Chapter 2).

Additionally, by allowing a dense buffer of edge vegetation to establish, fencing partially ameliorates the severity and penetration distances of invertebrate edge effects.

Acknowledgments

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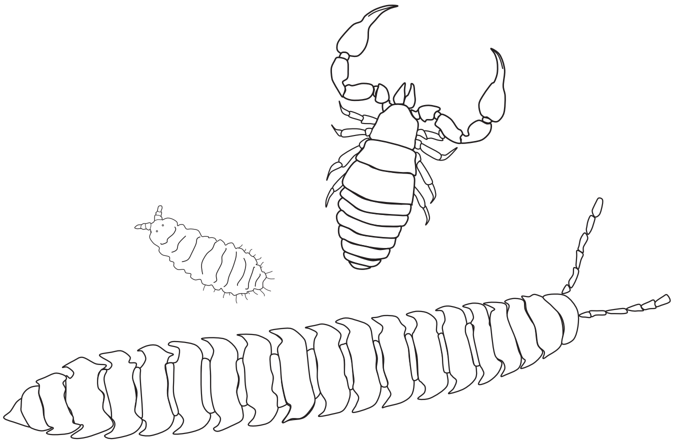
Chapter Four

Ecosystem function consequences of habitat fragmentation and disturbance: leaf and wood litter decomposition in grazed and fenced native forest remnants



Abstract

Habitat remnants often support biological communities markedly different to those in larger areas of intact habitat due to pervasive edge effects and disturbances from surrounding land use, such as livestock grazing. However, few studies have examined the consequent effects for ecological function, particularly for remnants under differing management regimes. I used litter bags to examine leaf and wood decomposition rates at a variety of edge distances in grazed and fenced native forest remnants and nearby large forest reserves. Leaf litter decomposition rates were initially slower (for bags collected after 140 days) in grazed remnants compared to fenced remnants and forest reserves, but after 350 days leaves from grazed remnants exhibited the fastest decomposition rates. Leaf decomposition rates were associated with changes in a suite of environmental variables, particularly the density of understorey vegetation, percentage litter moisture, and litter macroinvertebrate community composition. Woody decomposition rates were much slower than leaf decomposition rates, and were seemingly idiosyncratic with regards to edge distance, remnant management, and environmental variables.

Introduction

Natural habitat remnants in highly-modified human landscapes are subjected to a variety of disturbances and pervasive edge effects, and as a consequence often support markedly different ecological communities than areas of more intact habitat (Turner 1996, Andresen 2003). How such remnants are managed also has a strong influence on the integrity of remnant communities. Communities in heavily disturbed remnants are often dominated by habitat generalists, and have a greater number of invasive species (Kupfer et al. 2006). In Chapter 2, I showed that small native forest fragments that are grazed by livestock support depauperate and variable litter invertebrate communities, whereas small remnants fenced to exclude livestock support litter invertebrate communities which are much more similar to those found in larger forest reserves.

Several authors have highlighted the need for more studies that consider not only the direct effects of habitat fragmentation and modification on the structure of communities, but also the flow-on effects for important ecological functions (e.g., Didham et al. 1996, Andresen 2003). Invertebrates contribute towards numerous critical ecological processes, including, but not limited to; decomposition, soil formation, plant pollination and seed dispersal, and also interact with species from higher trophic levels (Didham et al. 1996).

Litter decomposition is a crucial component of nutrient cycling, and is a commonly-examined function of forest floor systems. Litter decomposition rates are known to be influenced by a variety of abiotic and biotic factors, including macro- and microclimate, physical and chemical parameters of soil and litter (such as soil drainage, soil and litter chemistry, litter quantity and diversity), and the composition of the microbial and invertebrate communities (Aerts 1997, Bardgett 2005, Bradford et al. 2002, Vos et al. 2011). Soil meso- and macro-fauna are thought to make a relatively small contribution towards litter decomposition compared to microbes (Bardgett 2005), and subsequently their role has often been ignored in decomposition studies (see Vos et al. 2011). However, studies such as those by Zimmer et al. (2005) and Vos et al. (2011) indicate that macrodetritivores can strongly influence the decomposition process.

Litter decomposition consists of two distinct processes; the physical and chemical breakdown of litter. Litter detritivores directly contribute to decomposition by consuming leaf and woody litter, and physically fragmenting litter into smaller pieces. They also indirectly contribute to decomposition because the fragmentation of litter and subsequent gut passage facilitates the establishment and action of microbial decomposers (Ausmus 1977, Bradford et al. 2002, Bardgett 2005, Vos et al. 2011).

Little is known about how invertebrate diversity and community composition influence litter decomposition rates. While it has been suggested that there is a high level of functional redundancy among soil and litter decomposers (Bardgett 2005), other studies have shown that combinations of litter fauna species can act synergistically on litter decomposition (Zimmer et al. 2005). While the studies to date have focused on the effects of macroinvertebrate *diversity* on decomposition, many authors have stressed that species *identity* is likely to be a more critical determinant of decomposition (Vos et al. 2011, Zimmer et al 2005). Hence, it should be more informative to examine links between community composition and ecological functions, rather than simple measures of taxonomic richness (Bengstton 1998). Another limitation to our understanding is that few field-based experiments have been carried out. Laboratory mesocosm studies, such as those of Zimmer et al (2005) and Vos et al. (2011) are useful for generating predictions, but are unlikely to accurately reflect what occurs in nature.

We know that forest fragmentation can alter litter decomposition rates. Didham (1998) found that leaf decomposition rates in tropical forest remnants in Brazil changed with distance from the forest edge, and with forest fragment area; in particular, decomposition rates at the centres of 1 ha fragments were much slower than in 100 ha remnants and continuous forest. Disturbances such as livestock grazing tend to exacerbate edge effects (Chapters 1 and 3), and it follows that forest remnants that are subjected to additional disturbances are likely to exhibit more marked changes in decomposition rates than less disturbed remnants. Although studies of forest fragmentation are prolific, Lindsay and Cunningham (2009) appears to be one of the few studies that have examined how the management of forest fragments with regard to disturbance affects ecological communities and functioning. They found that Australian *Eucalyptus* remnants that had been fenced to exclude grazing livestock for a minimum of six years had invertebrate communities characterised by higher abundances of beetles and "opportunist" ants (functional group), and a faster rate of leaf decomposition than sites that were still grazed by livestock.

While livestock grazing may be used elsewhere as a tool to manage or even promote native biodiversity in systems with a long history of herbivorous mammalian grazing (Bugalho et al. 2011), introduced mammalian grazers and browsers in New Zealand forest are highly detrimental to vegetation, forest floor habitat (Chapter 1) and litter invertebrate communities (Chapters 2 and 3, Wardle et al. 2001, Didham et al. 2009). This is not surprising given that forest-dwelling browsing and grazing mammals were absent from New Zealand prior to human arrival (Wardle et al. 2001).

Disturbance from livestock grazing is likely to alter litter decomposition rates through changes to forest floor microclimate, soil and litter structure, and decomposer community composition. Large browsing mammals have been shown to influence litter decomposition rates in large continuous forest areas in New Zealand, mostly through their direct effects on vegetation, e.g., selective browsing reduces the abundance of plants that produce rapidly-decomposing litter (Wardle et al. 2002). The effects of herbivorous mammals can be even more subtle, as livestock grazing can also alter leaf chemistry. Ashili (2008) showed that some litter macroinvertebrate species show a preference for leaves collected from ungrazed areas to those from grazed forest.

Clearly, livestock grazing and remnant area and edge effects are likely to directly and indirectly alter decomposition rates, but how these factors interact to control this ecosystem function is, however, unclear. Litter turnover will also be altered by fragmentation and the presence of livestock. The amount of standing litter on the forest floor is affected not only by litter decomposition rates, but also by litter removal (cattle consume fallen litter) and by potentially reduced litterfall. In this chapter I examine how forest remnant area and management (specifically, livestock exclusion) affect rates of leaf and fine woody debris decomposition and litterfall in podocarp-broadleaf forest remnants in the Waikato region of New Zealand.

Methods

Study area

The study sites were 19 native forest remnants in the Waitomo district, in the south of the Waikato region, New Zealand (see Chapter 1 for map and list of study sites). Native forest cover in the district has been reduced from 99% prior to human arrival, to 30% (Ewers et al 2006), and largely converted to pastoral grazing and exotic forestry. Topography in the study area ranges from flat to rolling hills, and elevation ranges from 450 to 580 m a.s.l.

Remnants were assigned into three management categories: five small privately-owned remnants regularly grazed by livestock, cattle and sheep (remnant size range 0.31 – 15.05 ha), ten small privately-owned remnants which had been fenced to exclude livestock for a minimum of 10 years (remnant size range 0.88 –

28.57 ha), and four large forest remnants, which are all reserves managed wholly or in part by the Department of Conservation (DoC). These four larger forest reserves comprised a block of Herekawe Scenic Reserve on the southern side of State Highway 30 (hereafter referred to as Hkw, 137.65 ha), the large northern block of Pureora Forest Park (PuN, 30492.13 ha), a smaller central block of Pureora Forest Park near the DoC Field Centre (PFC, 293.56 ha), and Mangapehi Forest Reserve (Mpe, 1655.18 ha), privately-owned but managed in part by DoC.

The forest reserves had never been grazed by livestock. The ungrazed sites were all protected from livestock grazing by high quality fencing which had been in place for a minimum of 10 years, but at most sites much longer. All five grazed sites were subjected to a rotational grazing regime, predominantly cattle, throughout the study. Mean stocking rates in the study area are estimated at <10.5 stock units (SU) per ha (one stock unit = one dry ewe equivalent, i.e. 55kg), which is comparatively low for the region (Environment Waikato 2011). In all of the grazed sites, cattle were regularly observed throughout the remnant interior, i.e., they were not restricted to the edges.

The study remnants were selected to have similar canopy composition, composed predominantly of the native tree *Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae). Other common canopy and subcanopy tree species, listed in order of decreasing total basal area, were *Podocarpus totara* G.Benn. ex D.Don var. Totara (Podocarpaceae), *Elaeocarpus dentatus* (J.R.Forst. et G.Forst.) Vahl (Elaeocarpaceae), *Weinmannia racemosa* L.f. (Cunoniaceae), *Dacrycarpus dacrydioides* (A.Rich.) de Laub. (Podocarpaceae), *Melicytus ramiflorus* J.R.Forst. et G.Forst. (Violaceae), *Dacrydium cupressinum* Lamb. (Podocarpaceae), *Knightia excelsa* R.Br. (Proteaceae), *Hedycarya arborea* J.R.Forst. et G.Forst.

(Monimiaceae), and the tree ferns *Dicksonia squarrosa* (G.Forst.) Swartz and *D. fibrosa* Colenso (Dicksoniaceae), and *Cyathea dealbata* (G.Forst.) Sw. (Cyatheaceae). Selective logging of large podocarp trees in the past will have altered the canopy composition of the remnants. The composition, density and condition of understorey vegetation varied considerably between sites and management categories, the most notable difference being the almost complete lack of native understorey in grazed sites (Chapter 1).

Field methods

At each remnant I established a transect starting from a north-facing edge, leading up to 320 m into the interior of the remnant. I defined the edge (i.e., 0 m along the transect line) by the position of the outermost trunks which formed a continuous canopy. At each transect I established 5 m radius circular sampling plots centred at distances of -5 (i.e., 5 metres outside the remnant in the surrounding pasture matrix), 0, 5, 10, 20, 40, 80, 160 and 320 m, giving a total of 125 sampling plots across the 19 sites. Transect length was largely determined by remnant area, but was also influenced by remnant shape (i.e., transect length was shorter in irregularly shaped remnants) and was adjusted to avoid canopy gaps or, as in the case of site PFC, a public walking track. I deliberately sampled more intensively at remnant edges because I expected this is where rate of change in invertebrate community composition and litter decomposition rates would be greatest. I did not establish -5 m plots at fenced sites where the fence was <5 metres from the edge of the remnant, as the -5 m plot would have then been in a different grazing treatment.

At each sampling point I recorded latitude, longitude, aspect and slope. I also measured a range of other variables to be used as environmental covariates in subsequent analyses (Chapter 2; Appendix 1).

Leaf and woody litter decomposition

Litter bag studies have been widely used to examine litter decomposition rates, although there are some concerns with the technique (see Bradford et al. 2002). Many of these focus on the mesh size of the bags used – finer mesh sizes exclude many of the macroinvertebrate fauna which consume leaf litter, but may also create an altered microclimate within the bags. Conversely, if coarse mesh bags are used, leaf decomposition rates may be overestimated due to the loss of leaf fragments from the bag. However, the loss of small leaf fragments from coarse mesh bags will also reflect the level of macroinvertebrate activity, e.g., through burrowing and fragmenting the leaf litter within.

Freshly abscised *B. tawa* leaves were collected from the forest floor within Pureora Forest Park. The leaves were then transported back to the laboratory, and oven dried at 50°C to constant weight. Mesh leaf bags were constructed out of coarse (8 mm) and fine mesh (0.5 mm). The fine mesh was used to assess decomposition in the absence of macroinvertebrates, whereas the coarse mesh bags allowed invertebrate access. Two grams of dry tawa litter (approximately 25 individual leaves) were placed inside each mesh bag. Ten coarse mesh bags were installed on the forest floor at each of the -5, 0, 10, 40, 80, 160 and 320 sampling plots, and at the 20 m plots at sites where the transect only extended 20 m (Qry, Isl, LTd). In addition, five fine mesh bags were installed at the 0 m and innermost sampling plots at sites 12P, Hkw, Jck, and Ltu, and at all sampling plots at site PuN. The litter bags were secured in place with steel pegs. Five of the coarse mesh bags were collected after

140 days (20 weeks), and the remaining packs were collected after 350 days (50 weeks). The remaining leaf material within each bag was cleaned by hand to remove dirt, frass and other debris, and then the leaves were dried at 50°C to constant weight. As macroinvertebrates contribute primarily to the physical aspect of decomposition, I focused solely on mass loss, rather than changes in leaf chemistry. Unless stated otherwise, all subsequent references to leaf litter decomposition refer to coarse mesh bags.

To measure woody decomposition rates, I used popsicle sticks made from untreated birchwood as analogues for naturally-occurring fine woody litter. Sticks were oven-dried at 50°C to constant weight. Five sticks of known weight were sealed inside individual coarse mesh bags (same dimensions as leaf bags). Two stick bags (i.e., ten sticks total) were installed at each of the aforementioned sampling plots. One bag was collected after 140 days, and the other bag was collected after 350 days. The sticks were cleaned by hand and then dried and weighed, as per leaf litter bags.

Litter decomposition

I calculated the mean total proportion of leaf and wood mass lost, and the mean daily proportion mass lost after 140 and 350 days for each sampling plot. Paired sample t-tests were used to examine whether there was a significant difference between daily proportion mass lost over the first 140 days, compared with the daily proportion mass lost over the next 210 days. I fitted both linear and exponential regression lines to the leaf and wood mass loss data from each sampling plot to model decomposition, as appropriate, but proceeded with linear models only as they had better fit (as per R^2 values).

I calculated mean mass losses from both the leaf and stick bags for each site, across all within-remnant sampling plots (i.e., excluding the -5 m plots), and then used one-way analysis of variance (ANOVA), both with and without log(x+1) transformed remnant area included as a covariate, to examine whether there were significant site-level differences in decomposition between remnant management categories.

Invertebrate communities

I installed a pitfall trap centred on each sampling point. Each trap comprised a plastic disposable cup (11 cm diameter, 10 cm deep), nested inside a section of polythene pipe dug-in level with the surrounding ground, and covered by a stainless steel lid installed 2 cm above the ground; 70% ethylene glycol was used as a preservative. The traps were set for four-week periods, at three different sampling intervals throughout the year: mid-December 2008 to mid-January 2009 (Austral Summer), mid-April to mid-May 2009 (Autumn), and late October to late November 2009 (Spring). The pitfall trapping dates coincided with the dates when I first installed litter bags (Summer), the collection of litter bags after 140 days (Autumn), and the final litter bag collection (Spring). After collection, invertebrate samples were stored in 70% ethanol prior to sorting.

Invertebrate samples were sorted to Phylum, Class, Order or Family level. In PRIMER 6.1 (Clarke and Warwick 1994) Bray-Curtis resemblance matrices of log(x+1) transformed mean abundances at each sampling plot were ordinated with NMDS. The three axis scores of the ordinations at each of the three sampling periods, and mean abundance of taxa across all three sampling periods, were used as measures of invertebrate community composition in analyses examining links between litter decomposition and invertebrate community composition (Table 2). I also calculated mean invertebrate abundance, and the mean absolute and relative abundance of detritivorous taxa at each sampling plot.

Determinants/Correlates of litter decomposition

I first calculated Pearson correlations between remaining leaf masses, and a suite of environmental variables (as listed in Appendix 1 of Chapter 2), and report all significant correlations ($\alpha = 0.05$). I then used regression tree analysis (CART) in WEKA 3.6.1 (The University of Waikato, Hamilton, New Zealand), to identify which subset of environmental and invertebrate community composition variables best explained percentage leaf and wood mass remaining at sampling plots, both after 140 and after 350 days separately. Each leaf of an M5P regression tree consists of a distinct multivariate linear regression model.

Litter turnover – standing litter and litter fall

The amount of standing litter on the forest floor reflects the net effect of litter fall and litter decomposition. To examine this relationship I measured standing leaf litter mass, and rates of litter fall at each site. At each sampling plot I collected three samples of the naturally occurring litter layer, at random distances, up to 5 m either side and perpendicular to the transect line. A 20 x 20 cm quadrat was placed on the ground, and all friable material and humus down to compact soil layer were collected and sealed inside plastic bags. Samples were transported back to the laboratory, weighed, dried, and weighed again, to calculate mean wet weight, dry weight, and moisture content.

I measured litter fall rates at the innermost sampling plot of each site, in both Autumn and Spring (coinciding with invertebrate and litter bag collections). Four plastic buckets were placed on the forest floor at four equidistant points in a 5m radius from the centre of the plot. The buckets had two small holes drilled in the bottom, which served as drainage holes, and allowed the buckets to be secured in place with metal pegs. The buckets were left in place for a period of 4 weeks in both Autumn and Spring. Litter within the buckets was collected at least twice during each four-week period, placed in plastic bags, and transported back to the laboratory. Samples were then weighed, dried, and weighed again, as per standing leaf litter samples. The litter samples were sorted into leaf, wood, and all other plant material (fruit, seeds, and flowers), and each component was weighed separately. For each site I calculated mean litterfall, expressed as g per m^2 per day. I calculated Pearson correlations between each site's spring and autumn values of total, leaf, wood and fruit litterfall, leaf mass losses, and amounts of standing leaf litter.

Results

Leaf and wood decomposition

Simple linear regression modelled the leaf mass data at all sampling plots (R^2 values ranged from 0.82-0.99, mean = 0.96). While there was little variation in the mass lost from replicate leaf bags at each sampling plot, there was considerable variation in mean leaf litter mass losses amongst sampling plots (mean percentage mass remaining at each sampling plot after 140 days = 74%, SE = 0.4, range = 63-81%; mean percentage mass remaining after 350 days = 18%, SE = 0.3, range = 13-24%). Daily percentage mass losses were lower over the first 140 days (mean = 0.19% mass lost per day, SE = 0.003), than over the subsequent 210 days (mean = 0.26%, SE = 0.003; $t = 13.68$, d.f = 87, $p < 0.001$). There was a significant negative relationship between the mean percentage mass remaining in leaf packs collected from each sampling plot after 140 days and the mean mass remaining in leaf packs after 350 days, i.e., the sampling plots that experienced the fastest daily mass losses in the first 140 days, experienced slower decomposition over the subsequent 210 days (Fig. 1).

The mean mass lost from fine mesh leaf bags was higher than that lost from the coarse mesh bags at all but one (Jck 0 m) of the 15 sampling plots (mean percentage mass remaining in fine mesh bags after 350 days = 18.7%, SE = 0.7, mean difference in mass loss between fine and coarse mesh bags at each sampling plot = 2.2%, SE = 0.6%). This meant that the fine mesh bags could not be used as a reliable measure of decomposition in the absence of macroinvertebrates.

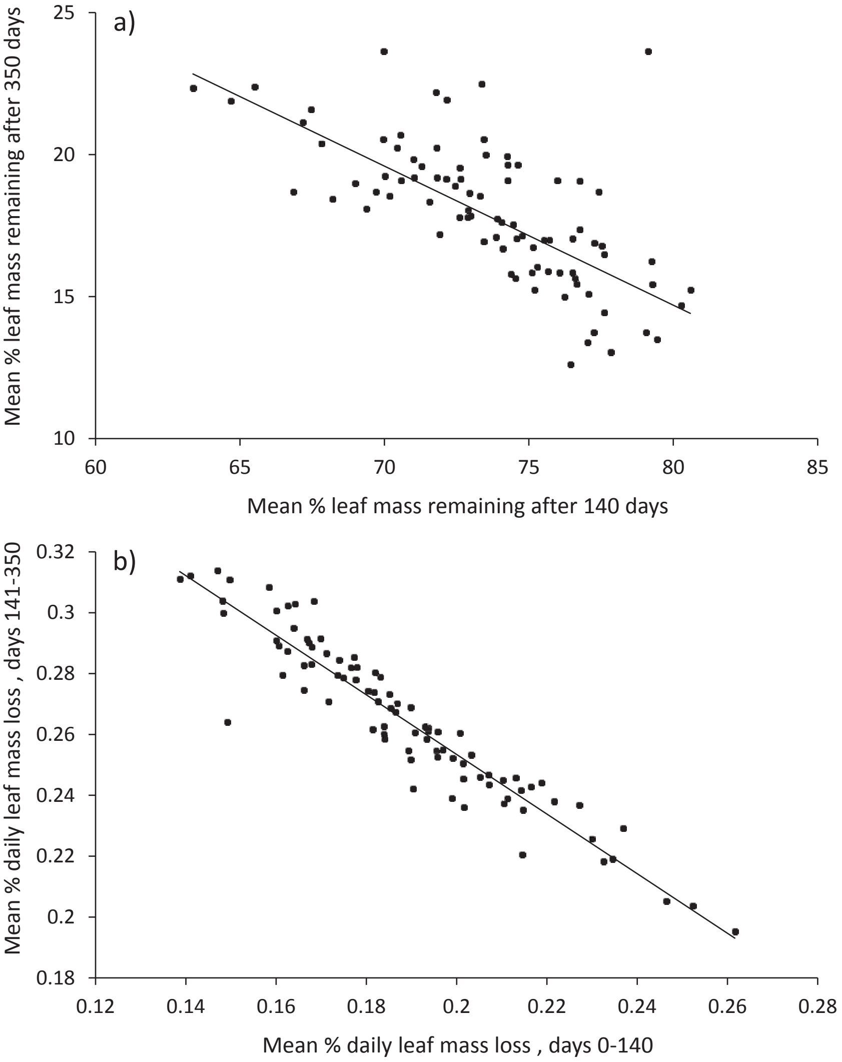


Figure 1. a) Variation in the mean percentage leaf mass remaining after 140 days at each sampling plots, plotted against the mean percentage leaf mass remaining after 350 days. Each point represents one sampling plot. Data fitted with a linear regression line, $y = -0.47x + 0.53$ ($R^2 = 0.45$, $F_{(1,86)} = 69.64$, $p < 0.001$, N = 88). b) Variation in the mean daily percentage leaf mass lost (c.f. to original weight at day 0) over the first 140 days, plotted against the mean daily percentage leaf mass lost over the subsequent 210 days, at each sampling plot, and fitted with a linear regression line, $y = -0.98x + 0.45$ ($R^2 = 0.90$, $F_{(1,86)} = 760.92$, $p < 0.001$, N = 88).

The mean percentage leaf mass remaining after 140 days declined with increasing distance from forest edge ($R^2 = 0.14$, $F_{(1, 86)} = 14.21$, $p < 0.001$) across all sampling plots. However, mean leaf mass remaining after 350 days exhibited a much weaker, and opposite relationship to distance from forest edge ($R^2 = 0.03$, $F_{(1, 86)} = 3.03$, $p = 0.09$; Fig. 2). When data from the sampling plots from each site were examined separately, there was only a significant change in mass lost after 140 days with distance from forest edge at three sites (Den, Mru, and Qry, all exhibiting a decline in mass remaining with distance), and after 350 days only at two sites (Ltu and Ted, both exhibiting an increase in mass remaining with distance; individual regressions not presented).

There was a weak relationship between site mean leaf mass remaining after 140 days, and remnant area ($R^2 = 0.17$, $F_{(1,17)} = 3.39$, $p = 0.08$; Fig. 3). However, this relationship did not hold when remnants from each management category were examined separately (Fig. 3). There was no apparent change in leaf mass losses with remnant area at fenced sites, and while leaf mass losses tended to increase with remnant area at grazed and forest reserve sites, this was not significant. The mean mass remaining in leaf bags collected from grazed sites (mean = 75.33%, SE = 0.78) after 140 days was higher than that of reserve (mean = 72.62%, SE = 1.56) and fenced sites (mean = 73.32%, SE = 0.76; Fig. 2a), though not significantly different ($F_{(2,16)} = 1.63$, $p = 0.23$). Conversely, after 350 days, the mean mass remaining in bags from grazed sites (mean = 17.09%, SE = 0.84) was lower than that of reserve (mean = 18.10%, SE = 0.84) and fenced sites (mean = 18.37%, SE = 0.54; Fig. 4), though again not significantly different ($F_{(2,16)} = 1.00$, $p = 0.39$). Including remnant area as a covariate did not improve the models, so here I have reported results of a one-way ANOVA without remnant area.

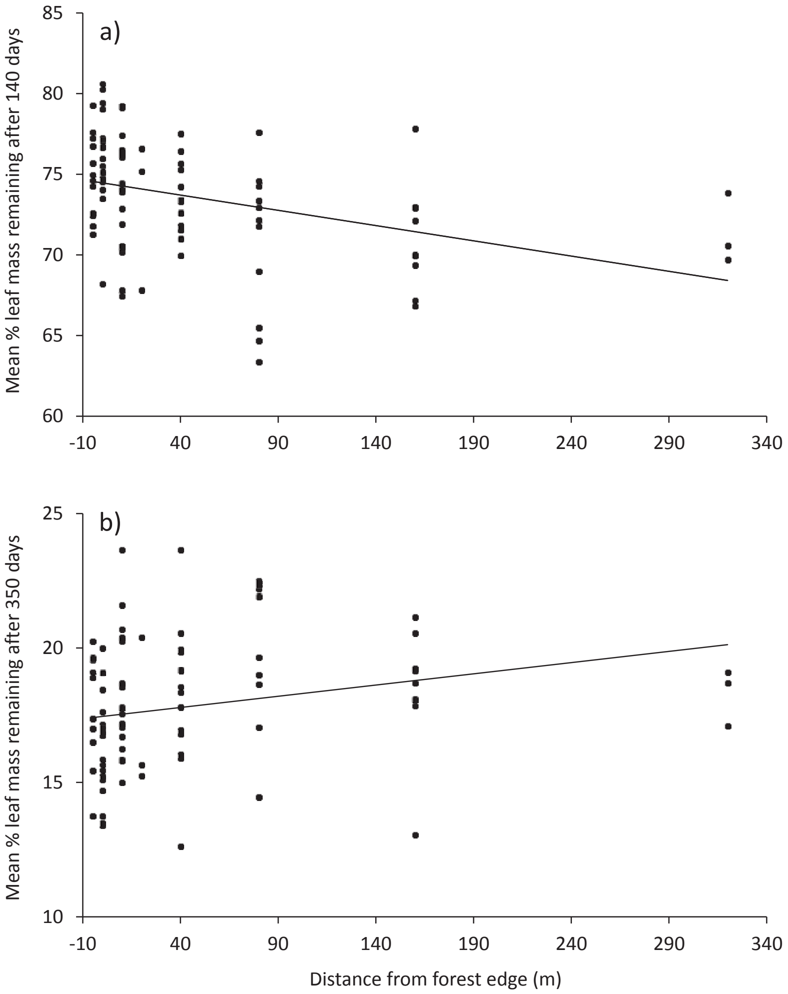


Figure 2. Variation in the mean percentage leaf mass remaining at each sampling plot with distance from forest edge, after a) 140 days ($R^2 = 0.14$, $F_{(1,\,86)} = 14.21$, $p < 0.001$, fitted with linear regression line $y = -0.02x + 74.46$), and b) 350 days ($R^2 = 0.03$, $F_{(1,\,86)} = 3.03$, $p = 0.09$, fitted with linear regression line $y = 0.01x + 17.45$).

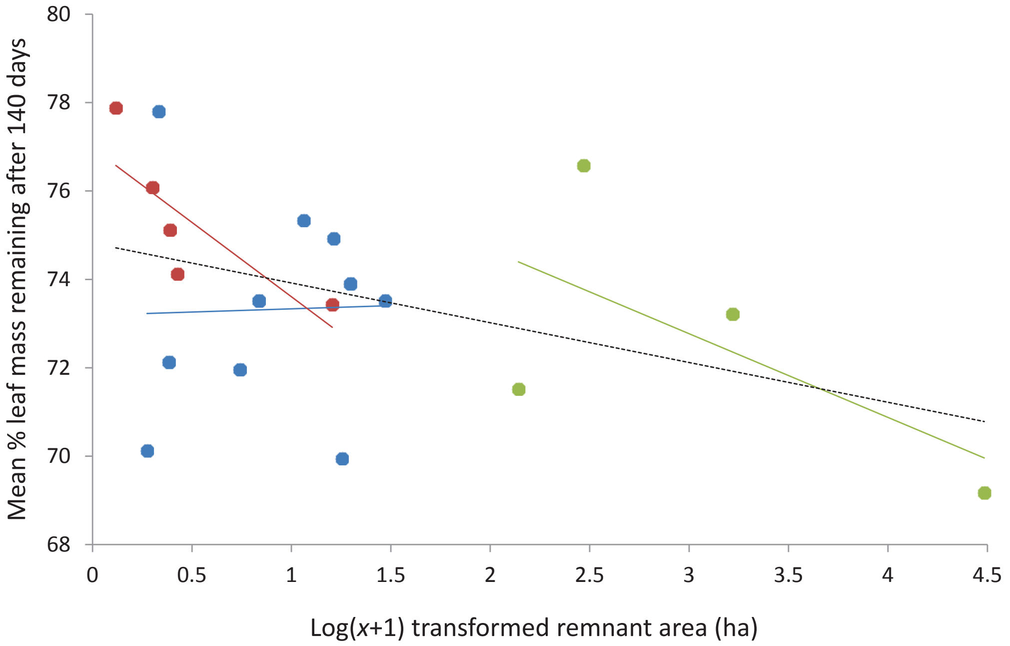


Figure 3. Site-level mean percentage leaf mass remaining after 140 days, plotted against log(x+1) transformed remnant area. Data points are colour-coded by remnant management category: red = grazed sites ($R^2 = 0.65$, $F_{(1,3)} = 5.57$, $p = 0.10$, $y = -3.36x + 76.97$), blue = fenced sites ($F_{(1,8)} = 0.01$, $p = 0.94$, $y = 0.15x + 73.19$), and green = reserve sites ($R^2 = 0.40$, $F_{(1,2)} = 1.33$, $p = 0.37$, $y = -1.89x + 78.46$). Black dotted line is a linear regression of all sites ($R^2 = 0.17$, $F_{(1,17)} = 3.39$, $p = 0.08$, $y = -0.90x + 74.82$).

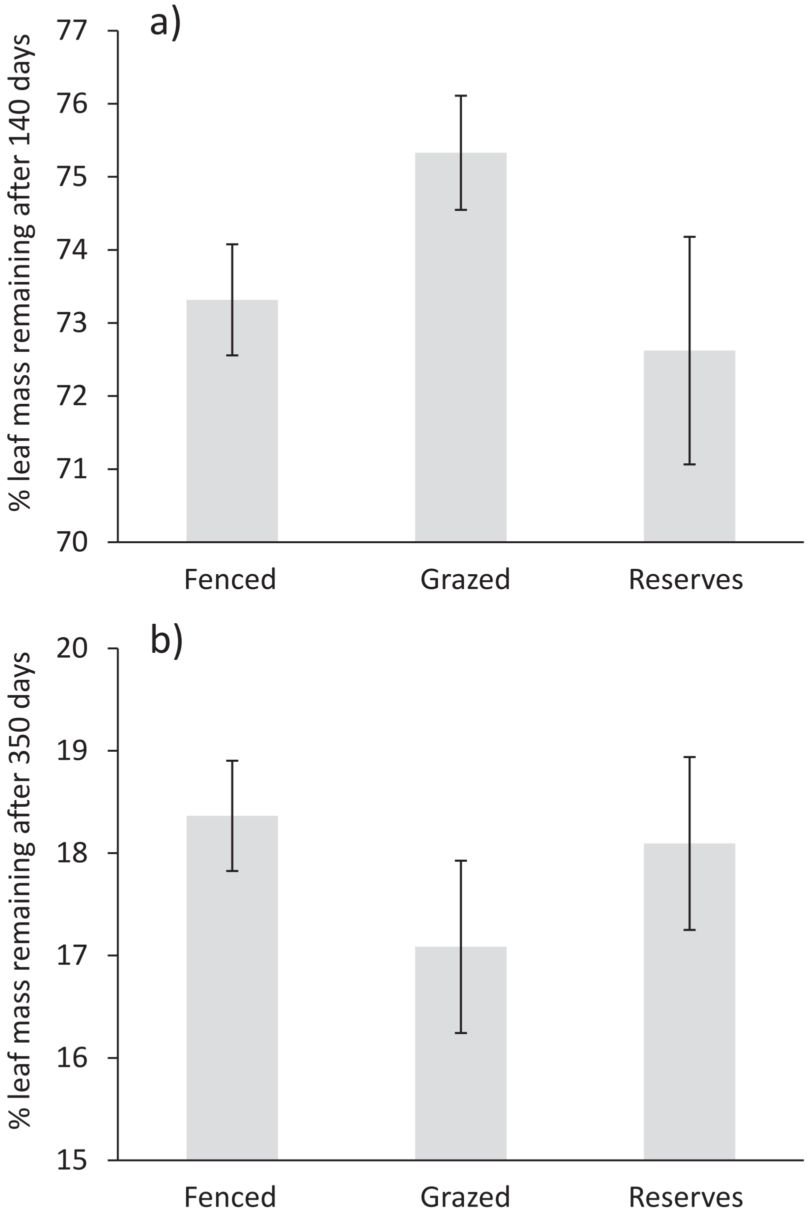


Figure 4. Mean site-mean mass (+/- SE) remaining after (a) 140 days, and (b) 350 days in each of the three management categories. Site means were calculated from all within-remnant sampling plots, i.e., with -5 m plots excluded. Site-mean leaf mass remaining did not vary significantly between management categories after 140 days ($F_{(2,16)} = 1.63$, $p = 0.23$), nor after 350 days ($F_{(2,16)} = 1.00$, $p = 0.39$).

Not surprisingly, wood decomposition was much slower than that for leaf litter, and five of the sticks collected after 140 days and one of the sticks collected after 350 days actually gained weight (presumably due to fungal colonisation). The mean percentage wood mass remaining at each sampling plot after 140 days ranged from 91% to 97% (mean = 94%, SE = 0.15). After 350 days, the mean percentage mass remaining at each sampling plot ranged from 22% to 97% (mean = 88%, SE = 1.19). There was noticeably accelerated wood decomposition at four of the sampling plots (the 0 and 40 m plots at Tut, the 20 m plot at Isl, and the 160 m plot at Mpe), but this seemed idiosyncratic with regards to site, management, or distance from edge. The mean mass remaining in stick bags collected from grazed sites (mean = 90.04%, SE = 0.89) after 350 days was higher than that of reserve (mean = 85.89%, SE = 2.88) and fenced sites (mean = 87.38%, SE = 2.82), but this was not significant ($F_{(2,16)} = 0.40$, $p = 0.68$).

At seven sampling plots, the mean mass of sticks collected after 350 days was higher than the mean mass of sticks collected after 140 days. Daily percentage mass losses were higher over the first 140 days (mean = 0.04% mass lost per day, SE = 0.001), than over the subsequent 210 days (mean = 0.03%, SE = 0.006; $t = 2.01$, d.f = 83, $p = 0.048$). There were no significant correlations between leaf pack and stick pack mass losses at sampling plots, either after 140 or 350 days.

Fifty three leaf bags (5% of total deployed) were lost, mostly due to cattle interference. However, I recovered at least some of the replicate leaf bags from all sampling plots except the 0 and 10 m plots at site T74. Similarly, eight stick packs (3% of total deployed) were also lost, including all of the stick packs from the 40 m plot at site 12P, and the 10 m plot at site T74.

Relationship between litter decomposition and environmental covariates

The mean leaf mass remaining at each sampling plot after 140 days was positively correlated with soil compaction ($r = 0.37$), soil, grass and herbaceous plant percentage groundcover estimates (0.28, 0.26, and 0.22, respectively), and latitude (0.31), and negatively correlated with understorey vegetation density (-0.21), litter and fern percentage groundcover (-0.27, and -0.29), woody stem density (-0.35), tree species richness (-0.23), canopy composition (axis 2 of NMDS ordination of tree species basal areas; $r = -0.36$), percentage litter moisture (-0.52), slope (-0.22), remnant area (-0.29), and distance from forest edge (-0.38). The mean leaf mass remaining at each sampling plot after 140 days was also correlated with several measures of invertebrate community composition (NMDS axis scores of invertebrate communities collected in Summer, Autumn, and overall community composition across all seasons).

The mean leaf mass remaining at each sampling plot after 350 days was positively correlated with fern percentage groundcover (0.30), woody stem density (0.25), canopy composition (axis 2 of NMDS ordination of tree species basal areas; $r = 0.28$), and percentage litter moisture (0.33), and negatively correlated with soil compaction (-0.27), soil groundcover (-0.26), tree basal area (-0.30), and latitude (-0.23). The mean leaf mass remaining at each sampling plot after 350 days was also correlated with several measures of invertebrate community composition (NMDS axis scores of invertebrate communities collected in Summer, Autumn, Spring, and overall community composition across all seasons). Hence, the relationships between leaf mass losses and several environmental variables at 140 days, were reversed by 350 days.

Modelling percentage mass remaining after 140 days with CART resulted in a relatively simple one-branch regression model. The model (correlation coefficient = 0.40) used the distance (m) from forest edge (regression coefficient -0.01), the percentage ground cover of coarse woody debris (0.15), total tree basal area (m^2) (0.14), percentage litter moisture (-0.13), the axis 2 scores of an NMDS ordination of invertebrate community composition during the Autumn sampling period (1.13) and a constant (80.01). The CART model explaining mass remaining after 350 days also consisted of a one-branch regression model (correlation coefficient = 0.31), which used the percentage open sky above the sampling plot (0.02), percentage fern groundcover (0.09), total tree basal area (-0.14), mean dry litter mass (g) (0.01), percentage litter moisture (0.07), the axis 2 scores of an NMDS ordination of invertebrate community composition during the Autumn sampling period (-1.03), and a constant (13.03). No useful models could be found for the woody decomposition data.

Litter turnover – standing litter and litter fall

Total litterfall was slightly higher in Spring (mean across 19 sites = 0.15 gm^{-2} per day, SE = 0.04) than in Autumn (mean = 0.13 gm^{-2} per day, SE = 0.04). The composition of litterfall also changed between the two seasons (Autumn: 80.1% leaves, 7.6% wood, and 12.3% fruit, flowers and seeds; Spring: 61.2% leaves, 37.2% wood, and 1.6% fruit, flowers and seeds).

There was no correlation between the percentage cover, depth, or dry weight of litter at each sampling plot, and litter fall rates (data not presented). Litter fall rates were also not correlated with the number of woody stems >2 m tall in each plot, nor the total basal area of woody stems in the plots (data not presented). There was very little evidence that litterfall was affected by distance from forest edge, as only the amount of Spring woody litter fall was correlated with the distance from forest edge ($r = 0.46$, $p = 0.05$). Leaf and wood litterfall was not correlated with leaf and wood decomposition rates at each plot (data not presented).

Discussion

In Chapters 1 and 2 I found that small grazed forest remnants had much more variable habitat and litter invertebrate communities than fenced remnants and larger forest reserves (Chapters 1 and 2), and I expected that litter decomposition rates would be affected as a consequence. However, it is very difficult to predict the direction and extent of change in any given ecosystem function. A commonly-held assumption is that ecological structure and function are linearly related (Cortina et al. 2006), and yet this is not necessarily the case.

Laurance (2002) predicts that the majority of ecological processes will become hyperdynamic in habitat fragments, meaning that they will both accelerate and increase in amplitude, particularly in small and disturbed fragments. Leaf litter decomposition rates are predicted to respond to changes in microclimate, decomposer community structure and litter chemistry. However, despite finding strong effects of fragmentation and livestock disturbance on forest floor habitat (Chapter 1), and invertebrate communities (Chapters 2 and 3), litter decomposition rates did not change strongly between management treatments, with distance from forest edge, or with remnant area, although subtle effects were apparent. At plot-level I found that litter decomposition rates were significantly correlated with a number of environmental covariates.

I also detected an unexpected compensatory effect, whereby sampling plots that exhibited the slowest decomposition rates over days 0-140, exhibited the fastest decomposition rates over days 141-350. This suggests that different environment variables have varying influences at different stages of decomposition. For example, there was a strong positive correlation between litter moisture content, and leaf mass losses over days 0-140, which presumably relates to rapid mass losses via leaching (Aerts 1997). Yet, at the later collection period (350 days) leaf mass losses were negatively correlated with litter moisture. Hence grazed remnants, which due to the absence of native understorey have significantly lower litter moisture than fenced remnants or forest reserves (Chapter 1), experienced slower leaf decomposition over days 0-140, and faster leaf decomposition over days 141-350. Temperature may have also played a role, as litter bags would have been exposed to warmer temperatures over the first 140 days (Summer-Autumn), then over the following 210 days (Winter-Spring). Decomposition may have been initially moisture-limited, so that wetter sites (e.g., fenced remnants and reserves) experienced faster decomposition, to later become temperature-limited, so that warmer sites (e.g., grazed sites) experienced faster decomposition. This highlights how critical timing is for litter bags studies. Ideally, litter bag studies should employ multiple widely spaced collection periods to avoid drawing spurious conclusions regarding environmental variables driving decomposition rates.

Even though grazed remnants support depauperate invertebrate communities (Chapter 2), diversity loss is not always accompanied by a functional decline, or at least not at the same rate (Cortina et al. 2006). This could very well apply to leaf litter decomposition, if indeed there is a high level of functional redundancy amongst litter macroinvertebrates. Alternatively, factors that I was unable to assess, such as microbial community composition, may be more important determinants of litter decomposition rates than habitat variables and macro invertebrate community composition.

In this type of observational study it is impossible to disentangle causative effects, as many of the environmental variables are highly related. Likewise, any correlation between litter invertebrate community composition and leaf mass losses, cannot be necessarily attributed to invertebrate community composition driving decomposition effects, as it is possible that invertebrate communities are simply responding to the same environmental gradients that drive litter decomposition. Indeed, litter moisture content was strongly associated with litter invertebrate community composition (Chapter 2).

Litterfall seemed largely idiosyncratic and unrelated to the amount of standing litter or leaf decomposition rates at each plot. I had expected that litterfall rates may have been related to distance from forest edge (due to edge-related changes in wind exposure, changes in stem density, etc.), or to the number and basal area of trees present in the plot, but did not find this to be the case.

I found that habitat fragmentation and matrix-driven disturbances have a strong influence on invertebrate habitat, and hence habitat communities, but effects on one aspect of ecological functioning are less apparent. The length of time litter bags are deployed can have a large influence on the results, as I had almost opposite effects between samples collected after 140 days and 350 days.

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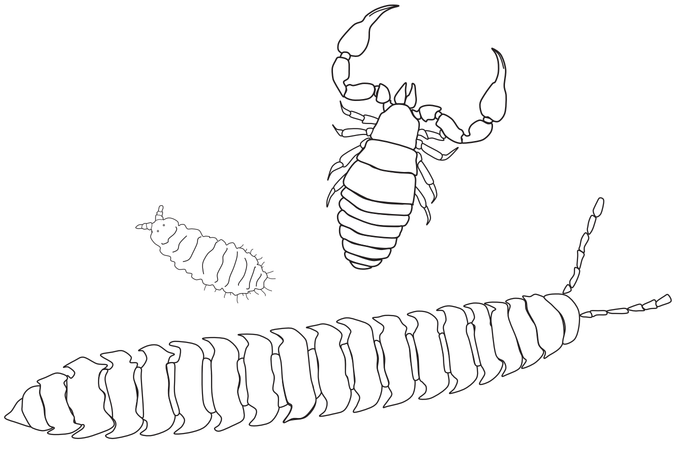
Chapter Five

Recovery of invertebrate community structure and function with time since livestock exclusion from native forest remnants in New Zealand



Abstract

In agricultural landscapes, small degraded remnants of native vegetation are often all that remain of once continuous ecosystems. Livestock grazing in forest remnants is a common disturbance that can have severe impacts on understorey vegetation and forest floor habitats. Although land managers are often interested in conserving and restoring remnants, there is limited information available on the efficacy of restoration techniques for taxa other than plants. I used a space-for-time substitution approach to test the effects of livestock exclusion on the reassembly of leaf-litter invertebrate community structure, and associated changes in leaf-litter decomposition rates in degraded forest remnants. In an agricultural landscape in the Waikato region, New Zealand, 10 small native forest remnants were selected to represent the full range of available time since remnants had been fenced to exclude livestock, from 0 to 48 years, either with or without additional conservation management actions aimed at controlling other feral mammals. Invertebrate community composition changed substantially with increasing time since livestock exclusion, with several taxa (Isopoda, Collembola, Diptera larvae, and Pseudoscorpionida) increasing in abundance through time. Community recovery was long term, with many taxa still increasing in abundance decades after fencing. These long-term livestock exclusion impacts were seemingly unaffected by additional feral mammal pest control. There was also a consequent effect of livestock exclusion on at least one measure of invertebrate-mediated ecosystem functioning. Leaf-litter decomposition rates at the edge of remnants increased with time since livestock exclusion. Fencing to exclude livestock has ecological benefits beyond vegetation recovery.

Introduction

Humans have transformed the earth's surface through widespread destruction and fragmentation of natural ecosystems. One of the primary drivers of habitat loss has been the expansion of agriculture, to the extent that croplands and pastures currently comprise greater than 40% of the global land area (Foley et al. 2005). Throughout the world, much of the remaining native vegetation now exists as small, isolated, and degraded remnants embedded in agricultural landscapes. Many of these small habitat remnants have little or no formal protection, and yet they can have high conservation values, especially in landscapes with a low total amount of remaining natural vegetation cover (Abensperg-Traun and Smith 1999, Tscharntke et al. 2002). We are still a long way from understanding how forest remnants should be managed to retain or restore near-natural ecological communities and processes.

As landscape modification and land-use intensity increase, not only does the total area of natural habitat decrease, but the remaining patches of native vegetation are increasingly influenced by disturbances from the surrounding matrix (McIntyre and Hobbs 1999). These effects are numerous and diverse in anthropogenically-fragmented landscapes, including altered fire regimes (Gill and Williams 1996), drought-susceptibility (Laurance and Williamson 2001), nutrient deposition (Stevenson 2004) and invasion by exotic organisms (Hobbs 2001). One of the most important disturbances is livestock grazing. In many regions of the world, domestic cattle (*Bos taurus)*, sheep (*Ovis aries*), goats (*Caprus hircus*) and horses (*Equus ferus caballus*) are allowed free access to habitat remnants and, consequently, livestock have been identified as one of the major threats to native vegetation remnants (McIntyre and Hobbs 1999, Yates et al. 2000, Vasquez 2002, QEII National Trust 2011).

Although there is now an extensive literature on livestock impacts in natural and semi-natural grasslands, there are comparatively few studies of livestock encroachment in forests. The most visible effects of livestock in forests are the impacts of grazing, trampling and other physical disturbance to the structure, density and composition of understorey vegetation (Adams 1975, Chapter 1), but also include long-term suppression of plant regeneration (Burns et al. 2011), alteration of soil structure and chemistry, namely increased soil compaction (Chapter 1) and reduced water infiltration (Adams 1975, Braunack and Walker 1985, Yates et al. 2000), reduced soil organic matter (Braunack and Walker 1985), reduced litter mass and cover (Yates et al. 2000), as well as altered microclimate (Yates et al. 2000), and facilitation of exotic plant invasion (Hobbs 2001). Livestock impacts are consistently more severe in ecosystems where large mammalian herbivores are historically rare or absent, as is the case on many oceanic islands (Courchamp et al. 2003).

There is clearly great potential for livestock to adversely impact forest floor invertebrates, not only through direct-mortality effects of trampling, but also indirectly by changing habitat, resource availability and microclimate (Abensperg-Traun et al. 1996, Bardgett 2005). Yet the effects of livestock on forest invertebrate communities have received little attention (Vasquez 2002), despite their high biomass, biodiversity and importance in ecosystem functioning (Didham et al. 1996, Bardgett 2005).

In the few studies that have been conducted, livestock encroachment into forest has been found to have adverse impacts on invertebrate communities. For example, studies in Australian woodland remnants show that livestock grazing causes a significant change in invertebrate densities (Abensperg-Traun et al 1996, Abensperg-Traun and Smith 1999) and diversity (Abensperg-Traun et al 1996, Bromham et al. 1999), and strongly influences community composition (Abensperg-Traun et al. 1996). Similarly, in New Zealand, Wardle et al. (2001) showed that the browsing impacts of feral goats and deer have led to substantial reductions in the densities of almost all forest floor meso- and macroinvertebrate taxa. Didham et al. (2009; Chapter 7) showed that in the Waikato region of New Zealand, both grazed and recently-fenced remnants typically have invertebrate densities an order of magnitude lower than recorded in nearby large forest reserves that have never been subjected to livestock grazing. In Chapters 2 and 3, I found that invertebrate communities were depauperate, and highly variable, in grazed forest remnants, compared to fenced forest remnants and forest reserves.

Fencing to exclude livestock from forest remnants has been recognised by conservation groups as a priority for the restoration of understorey plant communities (QEII National Trust 2011). The key question is whether the slowing (see Spooner et al. 2002, Burns et al. 2011) or reversal (Smale et al. 2005, Briggs et al. 2008) of vegetation decline commonly observed following livestock exclusion will be influential in the successful restoration of invertebrate community structure.

There is also scant knowledge of how livestock impacts on remnant invertebrate communities influences invertebrate-mediated ecosystem processes, such as pollination, herbivory, or leaf-litter decomposition rates (Vazquez 2002). Lindsay and Cunningham (2009) conducted one of the few studies to examine the impacts of livestock disturbance on both invertebrate community composition and function, in the grassy woodland remnants of south-eastern Australia. They found that grazed sites had lower abundances of beetles and ants in pitfall traps, and slower decomposition rates of artificial filter paper and lettuce-leaf substrates, than sites where livestock had been excluded for >6 years. However, it is unclear what the full time-course of community reassembly and ecosystem recovery is following livestock exclusion.

Here, I test the effects of time since livestock exclusion on the reassembly of leaf-litter invertebrate community structure, and associated changes in leaf-litter decomposition rates, across a 48-year chronosequence of remnant forest restoration in the Waikato region of New Zealand. Although fencing has been identified as a priority for forest remnant restoration (QEII National Trust 2011), it is still a costly investment for land managers. An increased understanding of the flow-on benefits of vegetation recovery for faunal biodiversity and ecosystem functioning would support greater emphasis being placed on policies and incentives to mitigate livestock impacts in remnant natural ecosystems.

Methods

Study area

In New Zealand, native forest cover has been reduced from an estimated 82%, to 24% of New Zealand’s land area since human arrival around 730 years ago (Ewers et al. 2006). Most of that has been converted for agricultural use. The study was conducted in a matrix of mixed sheep and cattle grazing pasturelands within the Te Miro district of the Waikato region, North Island, New Zealand. Deforestation in the region began in the late 1800s and was mostly completed by the early 1900s (Burns et al. 2011). Topography of the area ranges from flat to rolling hills, with elevation between 179-356 m a.s.l.

Forest remnants in the study area have intact native canopies dominated by the native trees tawa (*Beilschmiedia tawa*), rewarewa (*Knightia excelsa*), mangeao (*Litsea calicaris*), and pukatea (*Laurelia novae-zealandiae*), and sub-canopies dominated by kawakawa (*Macropiper excelsum)*, mahoe (*Melicytis ramiflorus*), pigeonwood (*Hedycarya arborea),* and the tree fern *Cyathea dealbata* (Burns et al. 2011). Fragmentation and ongoing disturbance have altered plant community composition (Burns et al. 2011).

In addition to livestock, native forest remnants in the study area often support high population densities of introduced omnivorous mammalian pests, namely brushtail possums (*Trichosurus vulpecula*), and rodents (*Mus musculus* and *Rattus rattus*), which may impact invertebrate populations (Innes et al. 2010). Pest control methods in these remnants included shooting, trapping and/or poisoning, and targeted brushtail possums.

Study design

I used a space-for-time substitution approach to investigate the response of invertebrate communities following livestock exclusion. I selected 10 forest remnants that had been fenced for between 0 (i.e., remnant was unfenced and grazed at time of this study) and 48 years to exclude livestock (principally sheep and beef cattle) present in the surrounding farmland, representing the full range of available time since livestock exclusion (Table 1). Five of the forest remnants received sporadic, and/or low-intensity mammalian pest control, and the other five remnants received intensive, sustained pest control (i.e., involving continual use of poison or trapping stations for at least 2 years prior, with a minimum of annual repeats, using at least 1 trap/bait station per hectare, across the entire remnant) (Table 1). Forest remnants were selected so that there was no confounding correlations between time since livestock exclusion and remnant area (r = 0.28, n = 10, p = 0.44) or geographic location (latitude: r = -0.19, n = 10, p = 0.61; longitude: r = 0.01, n = 10, p = 0.98).

Within each forest remnant I established two sampling plots, with one on the north-facing edge, as defined by the position of the trunks of the outermost trees that formed an unbroken canopy, and the second in the remnant core. I expected that invertebrate communities at the edge and core of remnants might respond differently to livestock exclusion, with edge plots predicted to show a greater degree of recovery in response to increasing time since livestock exclusion because of the greater magnitude of livestock disturbance experienced at the edges of unfenced fragments. The position of the core plot varied from 35 – 75 m from the edge, largely dependent on remnant area, but also adjusted according to remnant shape, and to avoid anomalies such as canopy gaps (Table 1).

The understorey vegetation in the remnants was highly modified, and the current state was largely a reflection of how long each site had been fenced to exclude livestock. At sites fenced for 0-3 years, understorey vegetation was dominated by exotic pastoral grasses and herbaceous perennials, whereas sites fenced for longer periods had increasing densities of native shrubs, woody saplings and seedlings, and ground ferns. The vegetation changes following livestock exclusion in remnants is discussed in greater detail in Burns et al. (2011).

Remnant and environmental covariates

A range of remnant- and plot-level variables were used to characterise remnants, which had previously been recorded as part of other studies on the same remnants (Didham et al. 2009, Burns et al. 2011). Remnant-level variables were remnant area, perimeter, shape index (a measure of deviation from circularity, with a value of 1 representing a perfectly circular remnant, and higher values representing increasingly complex shapes; calculated using the formula

SI = Perimeter ÷ $200(\pi.\text{Area})^{0.5}$, see Patton 1975), latitude, longitude, elevation (m above sea level), 5kforest (the proportion of native forest cover within a 5 km radius of the core plot), MDClimate (axis 1 scores of a multidimensional scaling ordination on nine climatic variables: mean annual temperature, mean temperature of the coldest month (July), mean temperature in driest Month (March), mean annual solar radiation, mean solar radiation during winter (June), vapour pressure deficit in the windiest month (October), mean annual rainfall, absolute variation in annual rainfall, and the ratio of mean annual rainfall to potential evapotranspiration, with all estimates of solar radiation and rainfall corrected for slope and aspect; MDS stress = 0.076), MDSoil (Axis 1 scores of an MDS ordination on 10 edaphic variables calculated from a bulked soil sample collected at each remnant’s core plot; pH, total carbon, total nitrogen, available phosphorus, and exchangeable calcium, potassium, magnesium and sodium, total exchangeable cation capacity, and base saturation; MDS stress = 0.085), tree basal area (total tree basal area in 11.3 m radius plot at the remnant core), vegetation richness (total plant species richness in 11.3 m radius plot at the remnant core), and vegetation composition (Axis 1 scores of a MDS ordination on the basal areas of 38 woody plant species, >3 cm DBH; MDS stress = 0.164).

The plot-level variables were plot type (i.e., edge or core), aspect (°), slope (°), canopy openness (proportion of open canopy above plot, photographed using a hemispherical camera at the centre of the core plot), and litter mass (mean dry weight coarse litter mass from three replicate 33 cm-diameter samples).

Data loggers (HOBO Pro Series Temp, RH (C) 1998 ONSET) were installed just above ground level at the edge and core plots in each remnant to record temperature (C°) and relative humidity (%) at 30 minute intervals. There were insufficient data loggers to monitor all remnants simultaneously, so loggers were moved between remnants in a randomly-determined sequence, ensuring a minimum of 14 days data collection at each site. Thus I can only compare the magnitude of edge-core differences in microclimate between remnants.

Experimental leaf bags

Leaf bags measuring 16 x 16 cm were constructed from 8 mm plastic mesh secured at the sides by steel staples, and lined on one side by a sheet of finer fibreglass mesh (2 mm) to prevent loss of small leaf fragments. Fresh leaves of two common native tree species, mahoe (*M. ramiflorus*) and tawa (*B. tawa*) were used to fill the leaf bags. I used fresh leaves as both mahoe and tawa are evergreen, and thus large quantities of freshly abscised litter are difficult to obtain. I selected these two species because mahoe is known to have a particularly rapid rate of decomposition and tawa is known to have a slower rate of decomposition (Hicks and Laboyrie 1999), which was important as I had no advance knowledge of the likely relative treatment effects on average leaf-litter decomposition over the time-course of the study. Leaves were oven-dried at 50 °C until constant weight was achieved, and 4 g dry weight of each species was placed into each leaf bag.

In early January 2008, 16 leaf bags were placed on the forest floor at each of the edge and core plots in each forest remnant (i.e., 320 leaf bags in total). The bags were placed with the fine mesh side facing down, and secured with metal pegs. Three bags were collected from each of the edge and core sampling plots at 2, 4, 10, and 20 weeks. After 30 weeks the remaining four bags were collected from each of the sampling points. Three of the 320 bags were lost, one each from the edge and core plots at remnant N8 and one from the core plot at remnant N0, which meant that three instead of four bags were collected from these plots at the 30 week collection period.

Leaf bags were transported to the laboratory within individual cloth bags and placed in individual Berlese funnels, which were operated using 60w incandescent lightbulbs for 48 hours (see Southwood 1978 for detailed description of Berlese extraction). The extracted invertebrate samples were preserved in 70% ethanol, prior to sorting. Leaves were cleaned by hand, oven-dried at 50 °C to constant weight, and weighed. Residual tawa and mahoe leaves were sorted and weighed separately for the 30 week samples only.

Invertebrates in experimental leaf bags and natural leaf litter

To assess if the leaf bag colonists were a distinct subset of the existing leaf litter communities of each remnant, invertebrate communities in natural leaf litter were also sampled, in addition to the experimental leaf bag invertebrate samples. Thirty natural leaf litter samples were collected from each forest remnant between December 2007 and January 2008, as part of a complementary study (Didham et al. 2009; Chapter 7). Sampling points were randomly offset ±10 m either side of a transect line running from the edge to core, and at random distances within each of six set distance intervals in from the forest edge (–2.5 to 2.4 m, 2.5–7.4 m, 7.5–14.9 m, 15–29.9 m, 30–59.9 m and 60 m–core). Smaller remnants with shorter transect lengths had higher numbers of samples collected within each near-edge distance interval. At each sampling point, a 33 cm diameter frame was placed on the ground and all leaf litter and friable humus was scraped into a large bag-sieve. The collected material was immediately sieved through a 10 mm diameter mesh to remove coarse organic material. Invertebrates were later extracted from the fine material as for the leaf bags using Berlese funnels, and preserved in 70% ethanol.

Invertebrates extracted from leaf bags and natural leaf litter were sorted to Phylum, Class or Order depending on the particular taxon (see Appendix 1). Larval and adult forms of the holometabolous insect groups Coleoptera, Lepidoptera, Diptera and Neuroptera were counted separately. Ants (Formicidae) and other Hymenoptera were counted separately. The total abundance of Acarina and Collembola in leaf bags was estimated using sub-sample counts in samples with more than 200 individuals in either group. I did not count Acarina or Collembola from natural leaf litter. As sample area and methodology differed between samples from natural leaf litter and experimental leaf bags I used the relative proportions of individual taxa, excluding Acarina and Collembola, to compare community composition.

Differences in habitat structure between the edge and core of remnants

From the data loggers I calculated daily mean temperature and absolute humidity, and daily fluctuation in temperature and humidity for each plot. I used simple linear regression to examine whether the extent of edge-core differences in the microclimatic variables, and the plot-level variables canopy openness, and mean leaf litter dry weight, changed with time since livestock exclusion.

Variation in leaf-litter and leaf bag invertebrate assemblages

I calculated mean invertebrate abundances across all sampling periods. I used exploratory regression tree analysis in WEKA 3.6.1 (The University of Waikato, Hamilton, New Zealand) to examine whether any combination of the continuous remnant and plot-level variables predicted mean total invertebrate abundance, and the mean abundance of individual taxa. Two-way ANOVA was used to see if mean invertebrate abundances differed between pest control treatments.

I used remnant-level mean relative abundance data (excluding Acarina and Collembola), to compare invertebrate composition in leaf bags versus natural leaf litter. Non-metric multidimensional scaling (NMDS), on Bray-Curtis similarity matrices, in PRIMER 6.1 (Clarke and Warwick 1994) was used to examine differences in faunal composition between leaf bags and natural leaf litter samples. Analysis of similarities (ANOSIM) was used to test whether the observed differences were significant. ANOSIM is a nonparametric procedure that evaluates whether the average similarities between samples within groups are higher than the average similarities of pairs of samples between groups.

The rest of the analyses were carried out on leaf bag data only. NMDS plots were created from Bray-Curtis similarity matrices, using mean $\log(x+1)$ transformed invertebrate abundances at the plot and remnant level, to examine patterns in community composition. The BIOENV procedure in PRIMER was used to identify which remnant and plot-level environmental variables best explained the observed faunal pattern.

Variation in leaf litter decomposition rates

Exponential decay curves (equation $y = 8e^{-kt}$, where y = mass (g) remaining after number of days, t) were fitted to litter mass data separately for each of the 20 sampling plots. I calculated the mean weight loss of tawa and mahoe leaves after 30 weeks for each sampling plot. Analysis of covariance (ANCOVA) in SPSS Statistics 17.0 (SPSS Inc.) was used to examine whether the mean weight after 30 weeks at edge and core plots responded differently to the number of years fenced. Regression tree analysis, using the M5P algorithm in WEKA (Hall et al. 2009) was used to examine whether mean weight loss from leaf bags after 30 weeks, or the exponential decay rate, *k*, were related to any combination of continuous plot- and remnant-level environmental variables.

To investigate the strength of the association between faunal composition and leaf decomposition rates in experimental leaf bags, I calculated Pearson correlations between plot ordination axis scores, and mean *k*, and proportion mahoe and tawa weight lost after 30 weeks. ANOSIM was used to examine if invertebrate communities were different between the two pest-control treatments, and plot type (edge vs. core).

Results

Differences in habitat structure between the edge and core of remnants

Edge plots were warmer than corresponding core plots at all remnants except N8. The mean temperature difference ranged from -0.12°C between the edge and core plots at N8, to a 1.37°C difference at P48. Edge plots also experienced greater daily temperature fluctuations than their corresponding core plot, but the magnitude of difference ranged from 0.29°C/day at N8, to 8.59°C/day at P3. Edge-core differences in absolute humidity and daily humidity fluctuation exhibited no consistent pattern between remnants (Table 1). The extent of the edge-core difference in temperature increased with the number of years a remnant had been fenced, although only at the 10% level ($F_{(1,8)} = 4.14$, $p = 0.08$, $R^2 = 0.34$). All other edge-core differences in microclimate were not related to the number of years fenced, remnant size or transect length.

Edge and core plots did not differ significantly in aspect ($F_{(1,8)} = 0.74$, $p = 0.41$), or slope ($F_{(1,8)} = 0.002$, $p = 0.97$). Not surprisingly canopy openness was greater at the edge plot than the core plot at all of the remnants, except N11 and P16. There was a trend for edge-core difference in canopy openness to decline with years fenced, but this was not significant ($F_{(1,8)} = 2.28$, $p = 0.17$, $R^2 = 0.22$,). All remnants except N28 and P48 had lower standing leaf litter weights at the edge than at the core. Mean standing leaf litter weights increased with years fenced at edge plots ($F_{(1,8)} = 17.68$, $p = 0.003$, $R^2 = 0.69$), but not at core plots ($F_{(1,8)} = 1.59$, $p = 0.24$, $R^2 = 0.17$).

Table 1. Characteristics of the 10 native forest remnants sampled in the Te Miro District, Waikato, New Zealand. This includes remnant area, shape index, mean absolute daily core versus edge temperature and humidity differences, and mean differences in daily core versus edge temperature and humidity fluctuations (i.e., edge plot value minus core plot value). Remnant codes incorporate pest control category (N = no pest control, P = sustained, intensive pest control), and number of years remnant has been fenced to exclude livestock. * = missing data.

Remnant code	Area (ha)	SI	Transect length (m)	Abs. Temp. Diff. (SE) °C	Abs. Humidity Diff. (SE)	Temp. Fluc. Diff. (SE)°C	Humidity Fluc. Diff. (SE)
N0	4.2	1.8	55	0.55 (0.03)	-0.81 (0.03)	2.31 (0.45)	-0.25 (0.20)
P1	0.8	1.3	35	0.42 (0.03)	0.34 (0.02)	3.51 (0.37)	2.31 (0.35)
P2	1.7	1.3	40	0.31 (0.01)	0.11 (0.01)	1.07 (0.25)	0.14 (0.08)
P3	3.3	1.6	40	0.80 (0.09)	-0.81 (0.04)	8.59 (1.29)	0.31 (0.32)
N8	3.1	1.9	40	-0.12 (0.01)	-0.06 (0.01)	0.29 (0.17)	-0.04 (0.21)
N11	2.4	1.1	65	0.83 (0.04)	-0.80 (0.03)	3.55 (0.41)	0.12 (0.25)
P16	2.4	1.6	65	0.32 (0.02)	0.19 (0.01)	1.02 (0.25)	0.57 (0.11)
N28	10.4	1.8	75	0.26 (0.01)	0.19 (0.01)	0.57 (0.17)	0.32 (0.10)
N40	4.9	1.5	50	0.75 (0.04)	0.56 (0.05)	2.66 (0.47)	1.66 (0.32)
P48	1.5	1.3	55	1.34 (0.02)	*	2.21 (0.25)	*

Variation in leaf-litter and leaf bag invertebrate assemblages

In total, 96 022 invertebrates were extracted from the leaf bags (mean number of individuals per bag was 320±19; Appendix 1). Acarina (49 098 individuals, 51.1%) and Collembola (27 701 individuals, 28.8%) were numerically the most abundant taxa, followed by Coleoptera (larvae = 7 897 or 8.2%, adults = 2 037 or 2.1%), and Psocoptera (2 425, 2.5%). Invertebrate abundance was lowest in Week 2 leaf bags (mean per sample = 184.6± 21.0), and highest at Week 20 (mean = 454.7, SE = 68.9), with a change in composition as the leaves decayed (Figure 1).

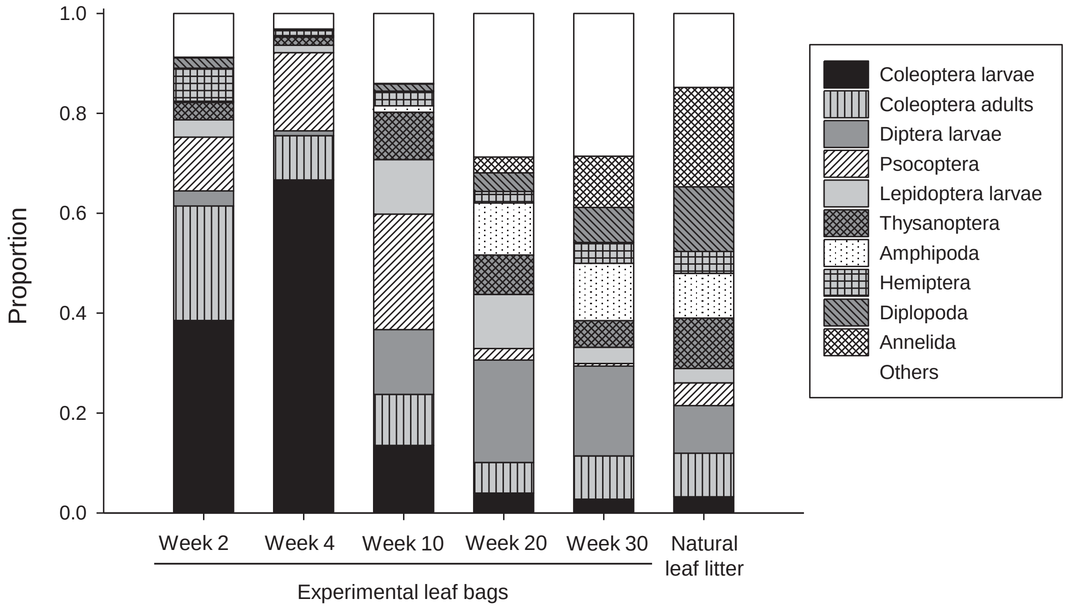


Figure 1. Variation in the mean proportions of the 10 most abundant invertebrate taxa (excluding Acarina and Collembola), extracted from experimental leaf bags over a 30-week period of litter decomposition (January – September 2008). Proportions are compared with invertebrate samples from naturally-occurring leaf litter collected between December 2007 and January 2008. Mean proportions are calculated across all samples, from all plots and remnants. “Others” = all other taxa combined (Araneae, Archaeognatha, Blattodea, Chilopoda, Diptera adults, Formicidae, Isopoda, Mollusca, Lepidoptera, Nematoda, Neuroptera adults, Neuroptera larvae, Opiliones, Orthoptera, Platyhelminthes, Pseudoscorpionida, Siphonaptera and Symphyla).

Almost all of the invertebrate taxa that were extracted from natural leaf litter were also present in the leaf bags at each remnant. The exceptions were Dermaptera, Diplura, Protura and Pauropoda, which were found in the natural leaf litter but not the experimental leaf bags (each comprised less than 0.05% of individuals extracted from litter). The relative abundance of the leaf bag assemblages differed from the natural leaf litter samples (natural leaf litter samples versus all leaf bags: Global R = 0.70, p = 0.001), but composition of leaf bags became more similar to the leaf litter communities over subsequent collection periods.

Ordination of mean leaf bag assemblages from each plot (2D solution stress = 0.16) revealed that although the edge and core plots at each remnant had distinct invertebrate composition, there was not a consistent compositional difference between the edge and core plots across all remnants (Global R = -0.009, p = 0.48; Fig. 2a). None of the individual taxa exhibited a consistent change in mean abundance between the edge and core plots across the ten remnants (results not presented). Invertebrate assemblages did not differ significantly between the two pest control treatments (Global R = 0.068, p = 0.26). The three plot and remnant level variables that best explained the observed invertebrate assemblage pattern were number of years fenced, longitude, and a vegetation ordination axis (MDveg) (*Rho* = 0.61, p = 0.01). NMDS Axis 1 scores decreased over time since livestock exclusion at both core and edge plots (Fig. 2b).

Regression tree analysis found that simple linear regression against the number of years fenced was the best predictor of the remnant-level mean abundance of key taxa, and as none of the other remnant and plot level variables explained significant amounts of variation in invertebrate abundances I have not presented regression tree models. The mean abundance of Collembola, Diptera larvae, Isopoda, and Pseudoscorpionida increased with years fenced (Fig. 3). The only taxon which showed an apparent decline with years fenced was Araneae, although this was not significant (Fig. 3a).

Variation in leaf litter decomposition rates

After 30 weeks, plant material within the leaf bags had a mean total weight of 2.73 g (SE = 0.41, range = 1.49 – 3.49 g), or 34.0% of their initial weight. Mahoe leaves (mean remaining = 0.27 g or 6.7% of initial weight, SE = 0.02, range = 0.001- 0.85 g) broke down faster than tawa (mean = 2.46 g, 61.4% of initial weight, SE = 0.04, range = 1.46 – 3.40 g).

Exponential curves fitted total litter mass remaining against time at all sampling plots, with R^2 values ranging from 0.83 to 0.98 (mean = 0.93, SE = 0.01). There was little variation in decay rate, k, across the twenty plots (mean = 5.17×10^{-3} d-1, CV = 0.12). There was a significant difference in the edge and core y-intercepts (p <0.001), and plot type ($p = 0.02$), but neither years fenced (p = 0.42) nor plot type*years fenced ($p = 0.14$) explained significant amounts of variation in the exponential decay rate, k ($R^2 = 0.33$, $F_{(3, 16)} = 2.56$, $p = 0.09$). However, I felt that the rapid decomposition of the mahoe leaves may have meant that the decay rate, k, masked treatment effects, so I also analysed mean tawa and mahoe weight loss after 30 weeks separately.

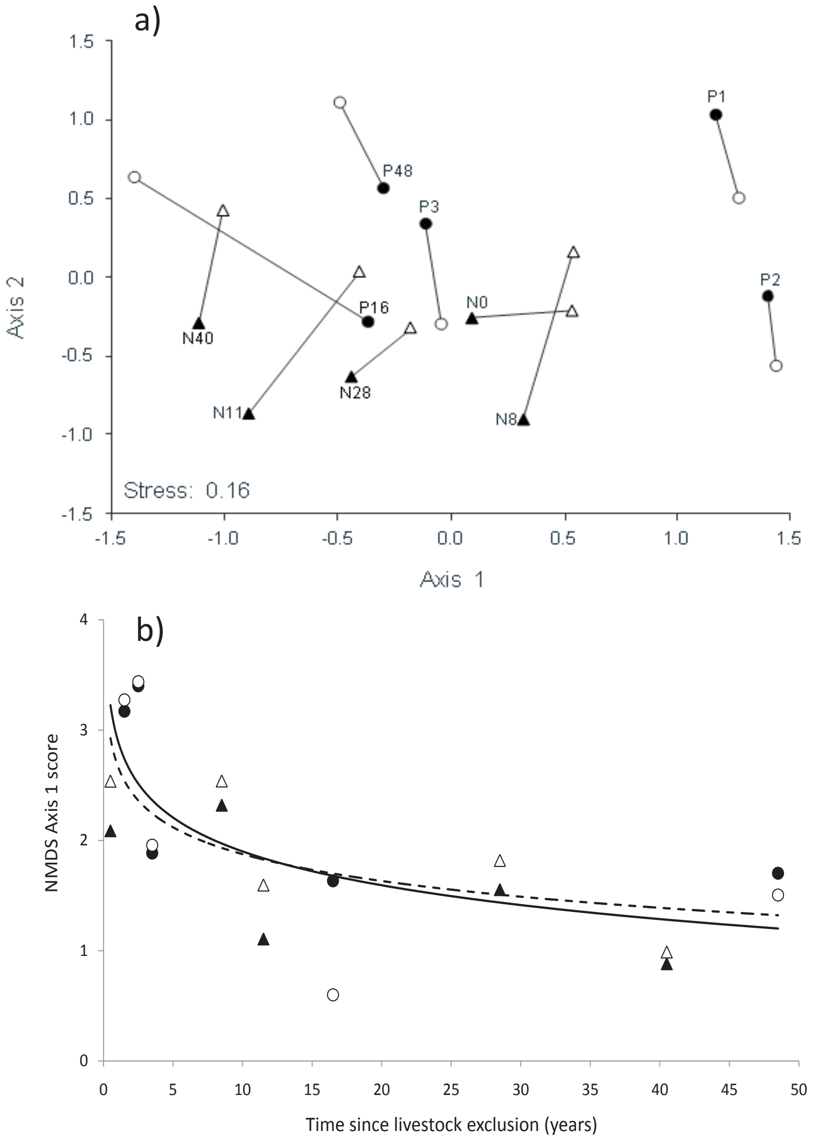


Figure 2. Variation in invertebrate community composition between edges (open symbols) and interiors (closed symbols) of forest fragments with varying time since livestock exclusion and feral mammal pest control. (a) NMDS ordination (2D stress = 0.16) of invertebrate relative abundance for samples extracted from experimental leaf-litter bags over a 30-week period of litter decomposition (January – September 2008, combined). A line is drawn between the core and edge plot of each forest remnant for ease of interpretation. Circles indicate remnants receiving additional mammalian pest control and triangles indicate remnants not receiving pest control. Remnant codes incorporate pest control category (N = no pest control, P = sustained, intensive pest control), and number of years remnant has been fenced to exclude livestock. (b) Axis 1 scores of the NMDS ordination (2D stress = 0.16) of invertebrate communities + constant value of 2, plotted against the number of years each site had been fenced to exclude livestock + constant value of 0.5. Equations of the fitted lines are as follows. Edge plots (solid line): $y = -0.44\ln(x) + 2.92$ ($F_{(1,9)} = 8.86$, $p = 0.02$, $R^2 = 0.53$). Core plots (dashed line): $y = -0.35\ln(x) + 2.68$ ($F_{(1,9)} = 6.01$, $p = 0.04$, $R^2 = 0.43$). Constants of 0.5, and 2, were added to years and NMDS axis scores respectively, to enable logarithmic regression to be fitted.

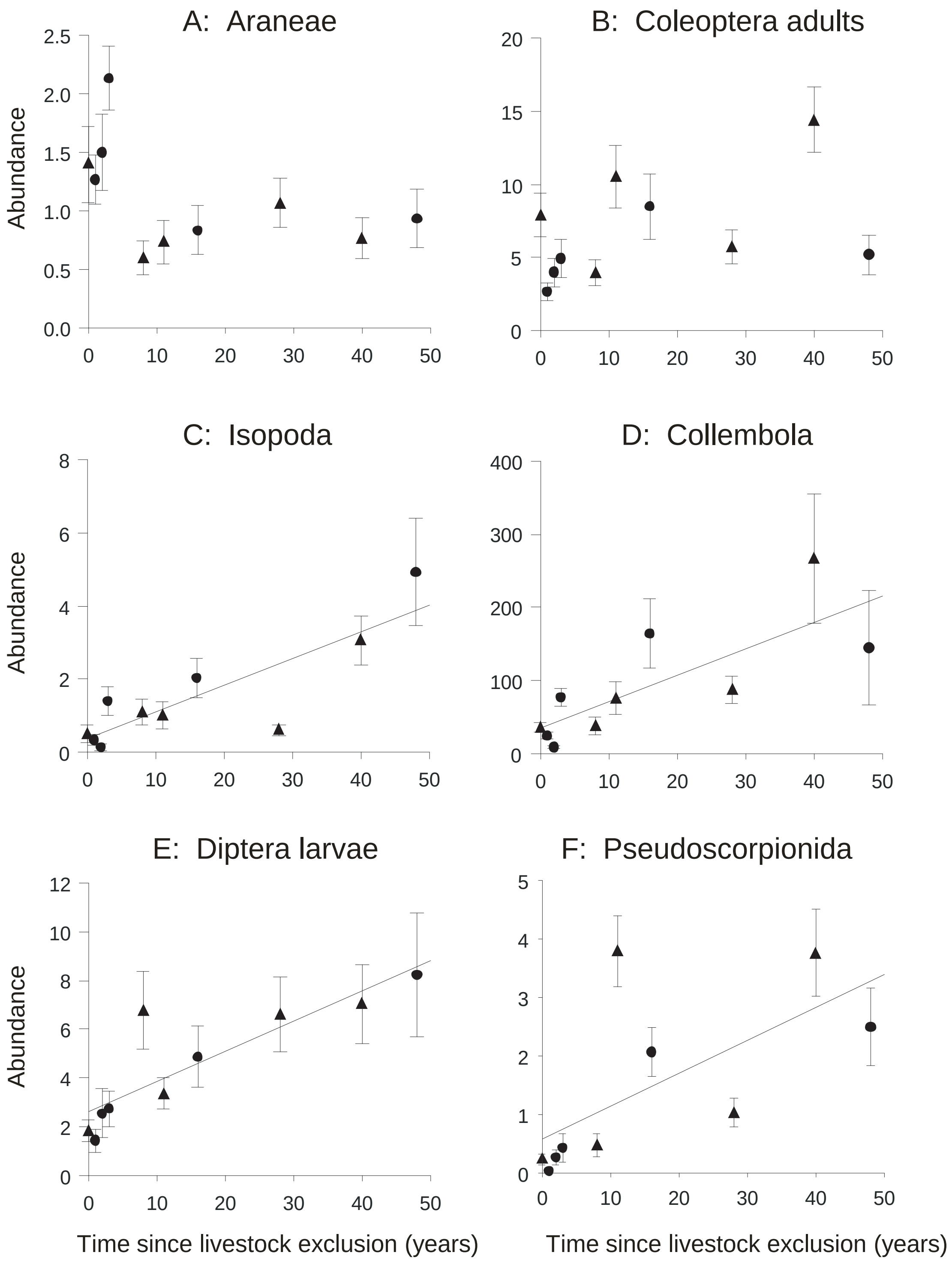


Figure 3. Variation in mean (± 1SE) abundance of selected invertebrate taxa with increasing time since livestock exclusion from forest remnants. A: Araneae ($y = 1.32 - 0.01x$; $F_{(1, 9)} = 2.32$, $p = 0.17$), B: Coleoptera adults ($y = 5.44 + 0.09x$; $F_{(1, 9)} = 1.64$, $p = 0.24$) , C: Isopoda ($y = 0.36 + 0.07x$; $F_{(1, 9)} = 20.59$, $p < 0.01$, $R^2 = 0.72$), D: Collembola ($y = 35.90 + 3.60x$; $F_{(1, 9)} =12.45$, $p = 0.01$, $R^2 = 0.61$) , E: Diptera larvae ($y = 2.59 + 0.12x$; $F_{(1, 9)} = 24.28$, $p < 0.01$, $R^2 = 0.75$), F: Pseudoscorpionida ($y = 0.58 + 0.06x$; $F_{(1, 9)} = 6.22$, $p = 0.04$, $R^2 = 0.44$).

There was an interaction between plot type and years fenced for mean proportion weight lost for tawa after 30 weeks ($F_{(1,16)} = 5.20$, $p = 0.04$). There was no significant relationship between mean proportion tawa weight lost at core plots and years fenced ($F_{(1, 8)} = 0.001$, $p = 0.98$, $R^2 < 0.001$,), but at edge plots the proportion tawa weight lost increased with years fenced ($F_{(1, 8)} = 8.76$, $p = 0.02$, $R^2 = 0.52$; Fig. 4). There was also higher variance in proportion tawa weight lost at edge plots than at core plots (Fig. 4).

While the edge and core y-intercepts were significantly different (p <0.001), neither plot type, years fenced or plot type*years fenced explained significant amounts of variation in the proportion of mahoe weight lost ($F_{(3, 16)} = 0.79$, $p = 0.52$, $R^2 = 0.13$). None of the other remnant and plot level variables explained significant amounts of variation in tawa or mahoe weight lost, or k (regression tree models are not presented).

There was a weak correlation between plot Axis 1 scores from the leaf bag invertebrate assemblage NMDS ordination and k (r = -0.434, p = 0.056), otherwise there were no significant correlations between each plot's NMDS axis scores nor the summed abundance of detritivorous taxa (either when natural litter or leaf bag invertebrate data was used), and k, or mean mahoe or tawa leaf mass loss.

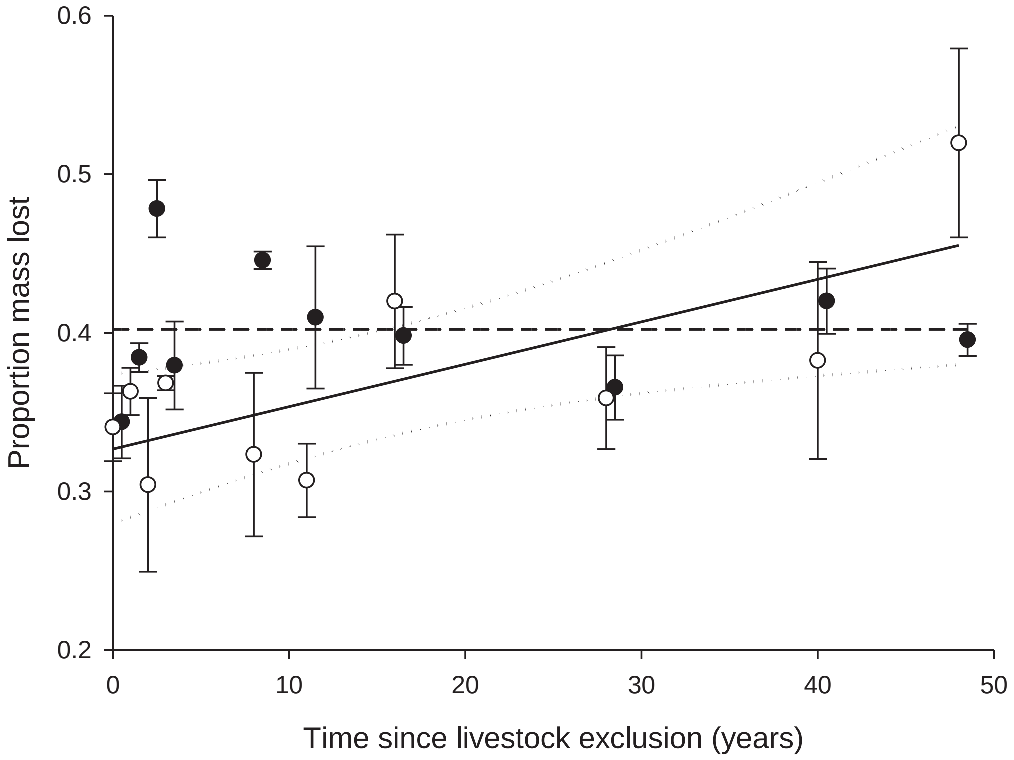


Figure 4: Proportion tawa (*Beilschmiedia tawa*) leaf mass lost after 30 weeks at edge versus core plots in forest remnants of varying time since livestock exclusion and feral mammal pest control (mean +/- SE). Symbols as in Figure 3. Equations of the fitted lines are as follows. Edge plots (solid line +/- 95% CI): $y = 0.003x + 0.327$ ($F_{(1,9)} = 8.756$, $p = 0.018$, $R^2 = 0.523$). Core plots (dashed line): $y = 0.403$ (i.e., intercept-only model; $F_{(1,9)} = 0.001$, $p = 0.980$). Overlapping data points are offset for clarity.

Discussion

In restoration ecology, linear relationships between changes in community structure and ecological functioning are widely-assumed, yet poorly supported by evidence from field studies (Cortina et al. 2006). This study showed both a strong community structure change and a change in a corresponding ecological function following livestock exclusion, although community and process changes were only weakly linked.

Livestock have a variety of adverse impacts on the vegetation, soil and groundcover of remnants (Chapter 1). Studies such as that of Braunack and Walker (1985), Smale et al. (2005), and Burns et al. (2011) have shown that many of these changes are reversible following livestock exclusion. Likewise, in this study I had predicted that variables related to forest floor habitat would change with time since livestock exclusion and that the response may vary between the edges and centre of the remnant. I found that the edge-core difference in temperature, and mean standing litter weights at edge plots increased with the number of years fenced.

It follows that livestock exclusion would also lead to changes in invertebrate community composition. The apparent edge-core differences in forest floor habitat did not strongly influence invertebrate community composition, as although the edge and core plots at each remnant had distinct invertebrate communities, there was not a consistent compositional change between edge and core plots. However, there was an overall change in invertebrate community composition with time since livestock exclusion, with four Orders increasing significantly in abundance over time. These results also highlight the long term nature of invertebrate recovery. Changes in community composition were most pronounced in the first decade following livestock exclusion, yet some taxa had responses across greater time scales. For example, Pseudoscorpionida only showed an appreciable increase in abundance more than 10 years post-fencing, and groups such as Isopoda and Diptera larvae were still increasing sharply after 48 years.

A distinct subset of the leaf litter fauna colonised the leaf bags. The most likely explanation for differing composition is that as fresh leaves rather than naturally-abscised leaves were used in the bags, the leaf bags provided a different quality resource in terms of nutrients and microflora than surrounding natural leaf litter. Indeed, invertebrate composition in leaf bags became more similar to that of natural leaf litter over time, as the leaves within the bags broke down.

There was very little variation in the exponential decay rate of leaf bags across the 20 sampling plots. However, the decomposition rate of tawa leaves at remnant edges increased with the number of years fenced, suggesting that livestock exclusion led to a change in this ecological function.

One of my aims was to examine specific links between the invertebrate fauna and leaf decomposition. Litter detritivores, such as millipedes and amphipods, assist the decomposition process through mechanical fragmentation of the litter they digest, and facilitating microbial decomposers (Bardgett 2005). Yet I only found weak associations between faunal composition and leaf decomposition. The level of taxonomic resolution I used may have been too broad to identify specific links. Also, detritivorous macroinvertebrates may make a relatively small contribution to decomposition compared to microbial decomposers (Bardgett 2005, but see Vos et al. 2011).

Bardgett (2005) and Dodd et al. (2011) identify the main mechanisms by which large herbivores influence decomposer organisms and processes; altering resource quantity (i.e., changes to the amount of litter present, and microhabitat parameters like soil macroporosity and microclimate), resource quality (e.g., altering nutrient balance of soils and litter) and changing vegetation composition (often towards unpalatable species, which in turn may reduce litter quality). Arthropods are thought to be more susceptible to the physical disturbances caused by mammalian herbivores, such as trampling, than smaller microbial decomposers (Bardgett 2005). It is possible therefore that leaf decomposition didn’t respond strongly to stock exclusion if microbial decomposers are relatively unaffected by grazing, although the limited studies of the effect of land management on microbial community composition suggest this is not the case (Steenwerth et al. 2002). It is worth noting, however, that livestock may contribute to the decomposition process by consuming leaf litter, and trampling leaf litter into smaller fragments.

Without management intervention, the outlook for unfenced native forest remnants in the study area is grim. However, this study, and others carried out in the same system (Didham et al. 2009, Innes et al. 2010, Burns et al. 2011) provide evidence that both livestock exclusion and mammalian pest control can greatly improve the resilience of forest remnants. Although I found no effect of mammalian pest control on invertebrate community composition or leaf litter decomposition, another study (Didham et al. 2009; Chapter 7) carried out in the same system has shown pest control to be beneficial for invertebrates, but only when combined with long-term livestock exclusion. Although they are unlikely to ever achieve the ecological quality of larger tracts of forest, small forest remnants remain valuable from a conservation perspective, and should be protected from livestock disturbance.

Acknowledgements

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Appendix 1. Mean abundance data for invertebrates extracted from leaf bags collected 2, 4, 10, 20, and 30 weeks after placement in January 2008, and natural leaf litter samples collected between December 2007 and January 2008, in ten native forest remnants in the Te Miro district, Waikato, New Zealand. Mean absolute abundance calculated across all leaf bag samples (30 per remnant). Pearson correlation coefficients of mean absolute abundances per remnant plotted against the number of years each remnant had been fenced are presented, with bold values indicating significant (p <0.05) relationships.

		Per leaf bag			**Mean relative abundance % across remnants***		
Taxon	**Total**	**Mean**	**SE**	**Years fenced (*r*)**	**Leaf litter**	**Week 2 leaf bags**	**All leaf bags**
Class Insecta							
Archaeognatha	2	0.01	0	0.30	<0.1	0	<0.1
Blattodea	2	0.01	0	0.13	<0.1	<0.1	<0.1
Coleoptera - adults	2 037	6.79	0.52	0.41	11.0	22.5	10.4
Coleoptera - larvae	7 897	26.32	3.47	0.43	4.1	32.5	38.8
Collembola	27 701	92.34	13.7	**0.78**	-	-	-
Diptera - adults	119	0.40	0.06	-0.18	0.4	2.4	0.7
Diptera - larvae	1 362	4.54	0.44	**0.87**	13.0	3.5	7.7
Hemiptera	490	1.63	0.19	-0.15	5.6	7.5	2.8
Hymenoptera - adults							
Formicidae	164	0.55	0.12	-0.31	6.7	3.7	1.1
Other families	158	0.53	0.06	-0.14	2.1	0.8	0.9
Lepidoptera - adults	4	0.01	0.01	-0.53	<0.1	<0.1	<0.1
Lepidoptera - larvae	814	2.71	0.32	-0.39	4.1	4.3	4.8
Neuroptera - adults	1	0	0	-0.26	<0.1	0	<0.1
Neuroptera - larvae	15	0.05	0.02	0.05	<0.1	<0.1	<0.1
Orthoptera	2	0.01	0	**0.66**	<0.1	0	<0.1
Pscocoptera	2 425	8.08	1.22	-0.29	2.2	11.9	13.4
Siphonaptera	1	0	0	-0.32	<0.1	<0.1	<0.1
Thysanoptera	783	2.61	0.29	0.36	16.1	4.1	4.8
Other Arthropoda							
Acarina	49 098	163.66	9.47	-0.01	-	-	-
Amphipoda	561	1.87	0.26	-0.10	5.4	0.3	2.8
Araneae	337	1.12	0.08	-0.47	2.7	2.4	1.9
Chilopoda	13	0.04	0.02	-0.28	0.2	0	0.1
Diplopoda	363	1.21	0.30	0.43	13.7	1.8	1.6
Isopoda	453	1.51	0.20	**0.85**	1.8	1.0	2.2
Opiliones	23	0.08	0.02	-0.01	0	0	0.1
Pseudoscorpionida	438	1.46	0.15	**0.66**	1.7	0.6	2.0
Symphyla	44	0.15	0.08	**0.66**	0.1	0	0.2

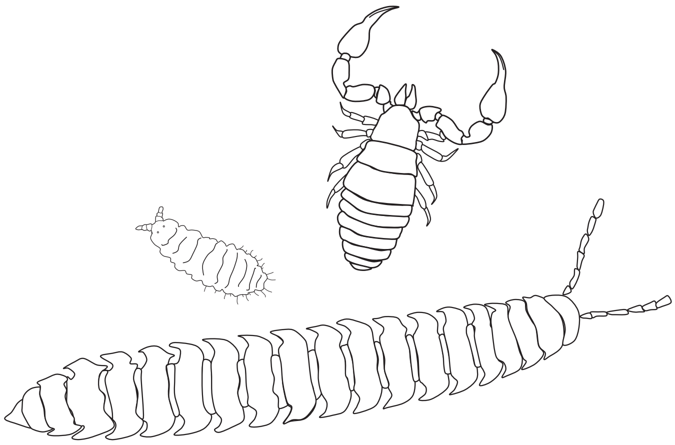
…Appendix 1 continued

Taxon	**Total**	**Mean**	**SE**	**Years fenced (*r*)**	**Leaf litter**	**Week 2 leaf bags**	**All leaf bags**
Non-Arthropod Taxa							
Oligochaeta	322	1.07	0.36	0.13	6.4	0.2	1.3
Gastropoda	240	0.80	0.10	0.10	1.4	0.2	1.3
Nematoda	152	0.51	0.08	**0.89**	1.0	0.3	0.8
Platyhelminthes	1	0	0	**0.66**	0	0	<0.1
Total abundance	96 022	320.07	19.3	-0.07			

* Acarina and Collembola excluded

Chapter Six

Restoration of millipede communities in native forest remnants: the role of livestock exclusion and mammalian pest control



Abstract

Invertebrates remain under-represented in ecological restoration studies, despite their functional significance and sensitivity to changes in environmental conditions. Millipedes are ideal indicator taxa for use in forest restoration studies, as they are numerically abundant, and play an important role in litter decomposition, but yet still have specific habitat requirements, and poor dispersal capabilities. I examined the response of millipede communities to two restoration actions, exclusion of livestock grazing and mammalian pest control, in 30 forest remnants and three larger forest reserve “reference sites” in the Waikato region in the North Island of New Zealand. A single introduced julid millipede species, *Ophyiulus pilosus*, comprised 45% of all individuals collected, and was present at all sites. Remnants that received both long term livestock exclusion and pest control had assemblage composition most similar to that of forest reserves. Sensitivity to mammalian disturbances may be related to millipede body size, as small millipede morphospecies had a more dramatic response to time since fencing at pest control sites.

Introduction

There has been increasing emphasis placed on the role of fauna in ecological restoration over the past few decades (Majer 2009). However, invertebrates remain relatively understudied in restoration ecology, despite recognition of their diversity and functional significance (Lavelle et al. 2006, Snyder and Hendrix 2008). When invertebrates are considered in restoration studies there is strong taxonomic bias with almost all studies on groups such as beetles, butterflies and/or ants (Majer 2009). In forest restoration, however, it seems sensible that our attention should be on the invertebrate fauna which inhabit the soil and litter of the forest floor, given their contribution towards healthy forest functioning through litter decomposition, and nutrient cycling (Bardgett 2005).

Millipedes (Class Diplopoda) are one of the most diverse and abundant macroinvertebrate groups, with an estimated global diversity of approximately 80,000 species (Hoffman et al. 2002, in Sierwald and Bond 2007). Millipedes are also some of the most abundant macroinvertebrate taxa in forest floor invertebrate communities in New Zealand (Brockie and Moeed 1986, Didham et al. 2009), and elsewhere (Hopkin and Read 1992). Most millipedes are forest-dwelling stratobionts, i.e., they are limited to litter and upper soil layers (Kime and Golovatch 2000). The vast majority of millipedes are detritivores, feeding on dead leaves and wood (Blower 1985, Hopkin and Read 1992, Barker 2000). Their role in decomposition is thought to be primarily mechanical, with comminution and gut passage of litter by millipedes facilitating subsequent bacterial colonisation and decomposition (Blower 1985, Cárcamo et al. 2000).

The contribution of millipedes to litter decomposition and nutrient cycling can be substantial. Although Hopkin and Read (1992) state that there are few habitats in which millipedes consume more than 5-10% of annual litter fall, Dangerfield and Telford (1991) found that millipedes comprised 36% of the total litter fauna density in Zimbabwean woodlands, and estimated that millipedes consumed over 30% of annual leaf litter production. Similarly, Cárcamo et al. (2000) combined abundance estimates with the results of laboratory feeding trials and calculated that a single millipede subspecies, *Harpaphe haydeniana haydeniana* (Polydesmida), had the potential to consume at least 36% of annual litter production in coastal conifer forest in British Columbia.

Although the biology and ecology of millipedes is poorly known (David 2009), studies of individual millipedes have shown that they are sensitive to a wide range of environmental variables, particularly microclimatic factors such as humidity and temperature as millipedes are particularly vulnerable to desiccation (Hopkin and Read 1992, Barker 2000, David 2009). Kime and Golovatch (2000) state that millipedes are "conservative in their habitat requirements", and, "when limited by a single edaphic factor, e.g., soil texture, litter thickness, millipedes generally fail to overcome it". Despite their ecological importance and apparent environmental sensitivity, few ecological restoration studies have examined the response of millipedes to that restoration (Snyder and Hendrix 2008). One exception is the study by Redi et al. (2005). They examined the response of millipede communities to active rehabilitation efforts in South African coastal dune forest regeneration post-mining operations. They found that rehabilitation accelerated and enhanced restoration compared to naturally-occurring, spontaneous regeneration, and encouragingly the composition of millipede communities in restored forest became more similar to that of intact forest over time, rather than diverging to form an "artificial" or man-made community.

The native and introduced millipede fauna of New Zealand contains representatives from seven orders: Chordeumatida, Julida, Polydesmida, Polyzoniida, Siphonophora, Spirostreptida, and Sphaerotheriida**.** Millipedes are thought to originally be a forest-floor dwelling group (Kime and Golovatch 2000, Barker 2002), and the majority of New Zealand native millipedes seem to be limited to forest habitat. This is exemplified by the two "juliform" orders (Julida and Spirostreptida), which are characteristically elongated, cylindrical, smooth-bodied millipedes. Despite their marked similarity in body form, the native juliform millipedes

(Spirostreptida) are fundamentally limited to native forest habitat, although some species occupy alpine herb fields and coastal dune vegetation (Korsos and Johns 2009), whereas the introduced juliforms (Julida) are found in native forest along with pastoral and urban areas (Johns 1962). In other countries, juliforms are the most prevalent millipede group in open habitats such as grasslands, which has been attributed to their ability to avoid harsh environmental conditions by burrowing deeper into soil (Kime and Golovatch 2000).

In New Zealand, and throughout the world, lowland native forest ecosystems have been disproportionately affected by habitat loss and conversion to agricultural land, and are poorly represented in conservation land. Much of the remaining native podocarp-broadleaf lowland forest in New Zealand consists of small, degraded remnants on privately-owned pastoral land. These small remnants have high conservation value by simple virtue of being all that remains of once continuous ecosystems. Encouragingly, many private landowners are interested in protecting and restoring remnants, and local government agencies (e.g., regional councils) and non-governmental agencies (e.g., Queen Elizabeth II National Trust) provide some financial assistance towards ecological restoration.

Two of the most commonly applied restoration techniques for forest remnants in New Zealand are fencing to exclude livestock, and mammalian pest control. Most pest control is aimed at controlling the introduced Australian brushtail possum, *Trichosurus vulpecula*. Possums are controlled largely due to their role as vectors of bovine tuberculosis (Barlow 1991), but they are known to cause substantial damage to native vegetation through selective browsing of palatable species (Allen et al. 1997, Burns et al. 2010), and are also significant nest predators of native passerines (Brown et al. 1996). Livestock grazing has a variety of impacts on the forest understorey, including suppression of regeneration (Burns et al. 2010), soil compaction, and almost complete removal of understorey vegetation (Chapter 1). The recovery of forest remnant vegetation following livestock exclusion has been documented (e.g., Burns et al. 2010, Smale et al. 2005).

I predicted that pest control and livestock exclusion would have its strongest influence on millipedes via *indirect* effects on vegetation, and soil and litter parameters (Berg and Hemerik 2004). However, possums may also have direct impacts by opportunistically feeding on invertebrates (Cowan and Moeed 1987), and pest control aimed at possums may also affect rodents (*Rattus* spp. and *Mus. musculus*), that also feed on invertebrates. Some invertebrates may feed on poison baits aimed at controlling mammals, but this is unlikely to have long-term impacts on invertebrate populations (Spurr and Drew 1999). Trampling by livestock may also increase mortality of forest floor invertebrates.

This study is one of several carried out in the same system with the overall aim of compiling a comprehensive assessment of how commonly applied restoration techniques enhance the resilience of lowland forest remnants (Dodds et al. 2010). Other studies in the same system have examined the effects of livestock exclusion and mammalian pest control on the vegetation of remnants (Burns et al. 2010), the population dynamics and meta-dispersal of a mammalian pest, the ship rat (*Rattus rattus*) (Innes et al. 2010), leaf litter decomposition (Chapter 5; Barker, Watts and Didham, unpubl.) and ordinal-level invertebrate community composition (Chapter 5, Chapter 7; Didham et al. 2009). In this study I focus on one component of the invertebrate community; the millipedes, by examining the effects of time since livestock exclusion and mammalian pest control, on density, diversity, and assemblage structure.

Methods:

Study area

The study area was in the central districts of the Waikato region, in the North Island of New Zealand, where only 9% of the original native forest area remains, and is highly fragmented (Ewers et al. 2006). Most of the approximately 5000 native forest remnants in the lowlands and rolling hill country of the Waikato are on private farmland, and 96% of these are less than 25 ha in area, with little or no legal protection (Didham et al. 2009).

I studied 30 forest remnants, which were clumped in three main geographical districts; Whatawhata, Te Miro and Maungatautari-Te Waotu. Remnant size ranged from 0.84 ha to 27.29 ha. In addition to the 30 remnants, three larger forest reserves, which represent some of the largest remaining areas of native forest left in the region, and have been subjected to lower levels of anthropogenic disturbance than the remnants, were also sampled. These three reserves are Te Miro Scenic Reserve (402.8 ha) in the Te Miro area, Karakariki Scenic Reserve (5500 ha) in the Whatawhata area, and Maungatautari Scenic Reserve (3363 ha) in the Maungatautari–Te Waotu area. The study remnants and forest reserves were all surrounded by open pasture matrix habitat, and had similar canopy species composition, dominated by the native evergreen tree tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk; Lauraceae). The vegetation of the study remnants is discussed in more detail by Burns et al. (2010).

The remnants have experienced differing types and intensity of management. In this study I restricted my attention to fencing to exclude grazing livestock (cattle and sheep), and mammalian pest control, which are the two most commonly applied management actions for small forest remnants in New Zealand (Dymond et al. 2007).

Fencing periods ranged from 0 years (i.e., remnant was unfenced and therefore subjected to livestock grazing), to 67 years. Only remnants that had high quality fences that had been continuously maintained to avoid livestock incursions were selected. Mammalian pest control in the study remnants was aimed primarily at controlling the introduced brushtail possum, *Trichosurus vulpecula* (Kerr), but may have also impacted other introduced omnivorous mammals such as rats (*Rattus* sp.), which are abundant in remnants (Innes et al. 2010). The remnants were assigned to two pest-control categories: N, no or sporadic, and/or low-intensity pest control; and P, intensive, sustained pest control (i.e., involving continual use of poison or trapping stations for a minimum of the previous 2 years, but usually >10 years, with at least annual repeats, and at least 1 trap/bait station per hectare, with full coverage of the remnant).

Invertebrate sampling

Thirty leaf litter samples were collected from each site, along a transect leading from the northern edge into the interior, or “core” of the remnant. The forest edge (0 m) was defined by the position of the trunks of the outermost trees that formed an unbroken canopy. Sampling points were selected at random distances from the forest edge, with approximately equal number of samples taken within each of six fixed distance intervals centred at 0, 5, 10, 20, 40 m and “core” distances from edge; i.e., within distance intervals of –2.5 to 2.4 m, 2.5–7.4 m, 7.5–14.9 m, 15–29.9 m, 30–59.9 m and 60 m–core. In order to give a good degree of spatial separation between samples, each sampling point was also randomly offset parallel to the forest edge, within ±10 m of the transect line. Transect length varied with patch area, from 15 to 200 m from the edge. As sampling effort was equal at the patch level (n = 30 sampling points), small remnants in which the core was less than 60 m from the edge had a greater number of samples collected within the near-edge distance intervals. Sampling intensity was deliberately higher closer to the forest edge, because the rate of change in invertebrate abundance and composition was predicted to be greatest near the edge (Didham et al. 1998, Ewers et al. 2007).

Each site was sampled on a single occasion between early December 2007 and mid February 2008. At each sampling point, a 33 cm diameter circular metal frame was placed on the ground, and all litter and friable humus within was rapidly scraped into a cloth bag-sieve. The sample was then immediately sieved through 10 mm mesh by vigorously shaking the bag-sieve. The fine, sieved litter containing invertebrates was transported to the laboratory in individual cotton bags, whilst the coarse (>10 mm) litter fraction was placed in a plastic bag to be later dried and weighed to obtain a combined sample litter mass.

Each sieved litter sample was placed into an individual Berlese funnel (BioQuip® collapsible bag design #2832, Rancho Dominguez, California) (Wheeler and McHugh 1987), which were operated for a 72-h period. The extracted invertebrates were preserved in 70% ethanol, and the remaining fine litter was dried and weighed. Invertebrates were initially sorted to phylum, class or order level. The results from the analysis of these higher order groups are presented in Chapter 7 (Didham et al. 2009). Millipedes (Class Diplopoda) were the second most numerically-abundant group after Coleoptera, comprising 17.7% of the macro-invertebrates collected (Acarina and Collembola excluded) (Didham et al. 2009).

Genus and species-level millipede taxonomy is very poorly resolved (Sierwald and Bond 2007). Traditional classification is based on genitalic structures and other morphological characters, but there is high potential for cryptic species within the group (Sierwald and Bond 2007). Reliance on genitalic structures also requires mature specimens, yet field collections yield high numbers of juveniles (pers. obs.). Given the degree of taxonomic uncertainty, and difficulty in sorting to species level, I sorted the millipedes first to order level, then to morphospecies. I think that sorting based on phenotypic characters should give a reasonable indication of the functional diversity of millipedes in a given area. New Zealand has a modest introduced millipede fauna of 12 recorded species (Johns 1966), which are well described and can be readily distinguished from native species.

Millipedes were sorted first into the orders Chordeumatida**,** Polydesmida, Polyzoniida, Siphonophorida**,** Sphaerotheriida, and “Juliform” (this group includes two orders comprising the introduced Julida species, and native Spirostreptida millipedes, which are very similar at a gross morphological level, but can be readily distinguished with microscopic examination (Korsós and Johns 2009)). I was able to separate most “Juliform” millipedes into Julida and Spirostreptida, with the exception of some early instar juveniles and damaged specimens. Millipedes were subsequently sorted to morphospecies, based on morphological features such as presence of eyes, segmentation, setation, shape of telson, leg length, body shape and texture, size and shape of paranota, markings and pigmentation, etc. I did not use genitalic characters to distinguish individuals, as most of the specimens were immature. Representative mature specimens of introduced species were identified using the keys and notes of Johns (1962), Blower (1985), and Korsos and Johns (2009).

Body size is an important anatomical trait as it can be linked directly to function, as food consumption and metabolic rates are proportional to body size of forest floor arthropods (Reichle 1968), and body size is also related to lifestyle in millipedes, particularly burrowing habit (Kime and Golovatch 2000). The body length of each specimen was also recorded within 5 mm interval categories, i.e., 0-4.9 mm, 5-9.9 mm, 10-14.9 mm, etc. I calculated body-length weighted abundances to use in ordination analyses. I also calculated the mean length for each morphospecies, and then assigned each morphospecies to one of three size categories: "small" millipedes were morphospecies with mean body length < 5mm, "medium" millipedes had a mean body length 5-9.9 mm, and "large" > 10 mm. Pooled abundances of small, medium and large millipedes were used to see if millipedes of different body sizes responded differently to the restoration treatments.

Environmental covariates

A range of variables pertaining to vegetation, soil, and ecological condition were recorded at each site, to be used as potential covariates in subsequent analyses. Patch area (range: 0.9–27.3 ha for remnants, and 402.8–5500.0 ha for forest reserves) was determined from a GIS analysis of the Land Cover Database (LCDB2) (Terralink 2004). The shape index (SI) was calculated for each remnant using the formula SI = Perimeter ÷ $200(\pi.\text{Area})^{0.5}$ (Patton 1975). Shape index measures deviation from circularity, with a value of 1 representing a perfectly circular remnant, and higher values representing increasingly complex shapes. At each sampling point latitude, longitude, slope and aspect were also recorded.

A range of topographic, climatic, edaphic and vegetation variables were measured at the core plots only. First, elevation (range: 99–356 m a.s.l.) was derived from the New Zealand 25 m resolution digital elevation model. I used a composite measure of overall variation in climate among remnants (hereafter referred to as "MDSclim"), obtained from the axis 1 scores of a semi-strong hybrid multidimensional scaling ordination, as used by a prior study of higher-level invertebrate community composition (Chapter 7). The climate ordination had a good fit to the data (stress = 0.08), and of the nine measured variables (mean annual temperature, mean temperature of the coldest month, mean temperature in driest month, mean annual solar radiation, mean solar radiation during winter, vapour pressure deficit in the windiest month, mean annual rainfall, absolute variation in annual rainfall, and the ratio of mean annual rainfall to potential evapotranspiration) the gradient in ordination scores was most strongly correlated with mean annual temperature (r = 0.95), variation in solar radiation in winter (r = 0.94), mean temperature in the driest month (r = 0.95), mean temperature of the coldest month (r = 0.94) and mean annual solar radiation (r = 0.94).

I also used a composite measure of variation in edaphic parameters (hereafter referred to as “MDSsoil”), calculated from a single bulked sample collected at the core plot of each site, namely the axis 1 scores of a SSH-MDS ordination, using the Gower dissimilarity metric (see Chapter 7). The edaphic ordination had a good fit to the data (stress = 0.09), and of the 10 measured variables (pH, total nitrogen, total carbon, available phosphorus, exchangeable calcium, exchangeable potassium, exchangeable magnesium, exchangeable sodium, total exchangeable cation capacity, and base saturation), the gradient in ordination scores was most strongly correlated with variation in total carbon (r = –0.92), total nitrogen (r = –0.86), base saturation (r = 0.71), pH (r = 0.71) and exchangeable cation capacity (r = –0.66).

Vegetation structure and composition were assessed in one 11.3 m radius plot (400 m^2) at the “core” plot at each site. Total tree basal area (range: 42.2–151.9 m^2 ha^{-1}), the basal area of each of 38 woody plant species (>3 cm DBH), total plant species richness (range: 20–55 species per plot), and the proportion of open canopy (range: 0.05–0.17). A composite measure of variation in vegetation composition among remnants (hereafter referred to as "MDSveg") was obtained from the axis 1 scores of a SSH-MDS ordination on the basal areas of the 38 tree species, using the Bray & Curtis (1957) dissimilarity metric (Chapter 7). The vegetation ordination had a moderate fit to the data (stress = 0.16), and the gradient in ordination scores was most strongly correlated with variation in *B. tawa* cover ($r = 0.60$), *Podocarpus totara* cover ($r = 0.52$), *Pseudopanax crassifolius* (Sol. ex A.Cunn.) C. Koch cover ($r = 0.51$), *Macropiper excelsum* (G.Forst.) cover ($r = 0.44$) and *Dacrycarpus dacrydioides* cover ($r = 0.42$).

The number of woody plant seedlings (15 cm < height < 1.4 m) was recorded in a 0.5 m radius area (0.79 m^2) (range: 0–40) and the number of woody plant saplings (>0.5 m in height and <3 cm DBH) was recorded in a 2.5 m radius area (19.6 m^2) (range: 0–55), at up to six distance intervals (0, 5, 10, 20, 40 m and "core") along the transect at each site. Standing mass of leaf litter on the forest floor was estimated by collecting two leaf-litter samples with a 33 cm diameter circular frame from within the 0.5 m radius plots. The samples were dried at 80°C for 24 hours, and then weighed, to obtain a mean dry mass (range: 64.7–6219.4 g m^{-2}) for each site.

Data analysis

Millipede abundances per sample were converted to densities per square metre. Mean density values were calculated for each site, and used in all analyses except those examining edge responses. I calculated total morphospecies richness (number of species) and Berger-Parker's dominance, for each site. As the number of individuals caught per site varied considerably, I also calculated rarefied morphospecies richness and dominance for each site using the species diversity procedure in EcoSim (Entsminger 2004).

I carried out ordination in PRIMER (Clarke and Warwick 1994) to examine how livestock exclusion and pest control affected assemblage composition. I calculated Bray-Curtis resemblance matrices from log(x+1) transformed mean abundance data, for morphospecies (for all morphospecies, and then native morphospecies only) and orders. I also calculated a Euclidean distance resemblance matrix between sites from normalised environmental variables, and a matrix of the geographical (straight line) distance between sites. The RELATE procedure was used to examine whether the order and morphospecies-level resemblance matrices revealed the same site pattern. The BEST-BIOENV procedure was used to identify which subset of environmental variables best explained the site-mean and sample patterns. ANOSIM was used to test for significant differences in assemblage composition between management treatments.

To examine the extent of change in assemblage composition between the edge and centre of each remnant, I calculated mean abundances from samples collected within each distance interval, and then calculated Bray-Curtis similarities between the edge and core distance intervals, i.e., between the outermost and innermost distance intervals for each site.

I examined the response of the seven most common morphospecies (i.e., species >400 individuals, comprising 1 Chordeumatida, 1 Julida, 1 Spirostreptida and 4 Polydesmida species) to forest edge, by plotting the $\log_{10}$ (x+1) transformed abundance against the distance from edge and calculating separate simple linear regression lines for each site. Slopes of the regression lines were used in subsequent analyses.

I carried out ANCOVA on the non-reserve sites to determine whether millipede assemblage metrics (i.e., mean densities of orders, diversity measures, assemblage and common morphospecies edge responses, and assemblage similarity to nearest reserve) varied significantly with pest control or fencing, using pest control category and geographic district as fixed factors, and years fenced as a covariate. I first tested for homogeneity of regression slopes, before proceeding with full-factorial two-way ANCOVA. Where regression slopes were significantly different, I did not proceed with ANCOVA and instead report separate linear regressions against years fenced for the two pest control categories. Additionally, if the ANCOVA model only identified fencing as significant, and not pest control or region, I report a pooled linear regression against years fenced across all sites.

Results

Millipede densities

A total of 15 656 millipedes were sorted. Juliforms were the most numerically abundant group, consisting of 8 711 individuals. The juliforms were subsequently split into Julida (7 113 individuals, 2 morphospecies), Spirostreptida (1 455, 2 species), and 143 juveniles which were too immature to be identified to order. The densities of the two juliform orders were positively correlated at both the sample (r = 0.47, p <0.001, N = 974) and site (r = 0.74, p <0.001, N = 33) level.

The order Polydesmida (5 322, 10 species) was the second most abundant millipede group, followed by Chordeumatida (643, 4 species) and Polyzoniida (641, 5 species). The orders Siphonophora and Sphaerotheriida were minor components of the millipede fauna (10 and 13 individuals respectively, with 1 morphospecies identified from each order). The remaining 2% of millipedes (313) were immature or damaged specimens that could not be reliably identified to order. The total number of millipedes collected at individual sites ranged from 22 to 2139, and millipede densities from individual samples ranged from 0 – 425.6 m^{-2} (mean = 18.8, SE = 1.2). Mean millipede densities (individuals m^{-2}) were at least twice as high across sites with pest control than sites without pest control (Table 1).

Three morphospecies were identified as introduced species. The most numerically abundant exotic species, *Ophyiulus pilosus* (Julida), comprised 45% (7111) of all millipedes collected. This species was present at all sites, with site mean densities ranging from 0.35 – 68.1 individuals m^{-2}. It should be noted that juveniles allocated to this morphospecies could not be keyed definitely, and may have belonged to other exotic juliform millipede species such as *Cylindroiulus britannicus*. The two other exotic millipede species were identified as *Blaniulus guttulatus* (Julida; 2 individuals), and *Oxidus gracilis* (Polydesmidae; 1 individual). All other morphospecies were presumed to be native, as they did not key out as known exotics.

Mean total millipede densities increased with years since livestock exclusion ($F_{(1,28)} = 7.74$, $p = 0.01$, $R^2 = 0.22$), as did chordeumatid abundances ($F_{(1,28)} = 8.63$, $p = 0.01$, $R^2 = 0.24$), and the pooled densities of native morphospecies ($F_{(1,28)} = 10.31$, $p = 0.003$, $R^2 = 0.27$). After controlling for number of years fenced, there was no effect of pest control category, geographic district, or pest control*region on site-mean chordeumatid, native or total millipede densities (non significant models not presented).

Table 1: Mean millipede densities and diversity metrics by pest control category (N = no pest control, P = pest control). Mean values calculated from the site-mean data from across all sites within a category, with standard errors in parentheses. Values for the three forest reserve sites also presented.

	Forest reserve sites			Pest control category	
	KarRes	MauRes	TMRes	N	P
Mean densities (individuals per m^2)					
Chordeumatida	0.23	1.01	1.13	0.50 (0.22)	1.02 (0.27)
Julida	1.25	0.82	1.4	5.53 (1.20)	12.72 (4.18)
Polydesmida	2.34	13.25	15.94	4.39 (1.20)	7.28 (1.98)
Polyzoniida	0.74	8.81	0.12	0.14 (0.04)	0.84 (0.28)
Siphonophora	0	0	0.04	0.003 (0.003)	0.019 (0.017)
Sphaerotheriida	0	0.04	0	0.011 (0.009)	0.028 (0.022)
Spirostreptida	0	0.04	0.04	0.71 (0.22)	3.10 (0.86)
All exotic morphosp.	1.25	0.82	1.4	5.53 (1.20)	12.72 (4.18)
All native morphosp.	3.31	23.34	17.58	6.35 (1.45)	12.84 (2.81)
Total	4.56	24.16	18.98	11.88 (2.24)	25.55 (5.80)
Morphospecies diversity					
Richness (raw)	10	13	14	9.93 (0.66)	9.75 (0.92)
Richness (rarefied)	8.04	7.27	7.01	5.76 (0.34)	5.66 (0.44)
Dominance (raw)	0.27	0.33	0.37	0.49 (0.04)	0.47 (0.04)
Dominance (rarefied)	0.32	0.36	0.39	0.51 (0.04)	0.49 (0.04)

Polydesmid density did not change with years fenced at non pest control sites ($F_{(1, 12)} = 0.43$, $p = 0.53$, $R^2 = 0.04$), but increased with years fenced at pest control sites ($F_{(1, 12)} = 10.78$, $p = 0.01$, $R^2 = 0.44$). Mean polyzoniid density per site increased with the number of years fenced ($F_{(1, 28)} = 5.13$, $p = 0.03$, $R^2 = 0.16$), and varied between districts ($F_{(2, 24)} = 4.09$, $p = 0.03$), being higher in Maungatautari-Waotu sites (mean = 1.46 per m^2, SE = 0.47) than both Te Miro (0.18 per m^2, SE = 0.07) and Whatawhata (0.13 per m^2, SE = 0.05) sites. There was no effect of pest control category or pest control*district on mean polyzoniid abundance after controlling for number of years fenced. There was no effect of years fenced, pest control or district on julid, spirostreptid, or exotic millipede abundances.

Diversity

Raw morphospecies richness per site increased with number of years fenced ($F_{(1, 28)}$ = 6.12, p = 0.02, R^2 = 0.18), and also differed between districts ($F_{(2, 24)}$ = 4.92, p = 0.02), being higher at Maungatautari-Waotu sites (mean = 11.38, SE = 0.86) than at Whatawhata sites (6.50, SE = 1.44) but not at Te Miro sites (9.89, SE = 0.71). Rarefied species richness per site also varied by district ($F_{(2, 24)}$ = 3.95, p = 0.03), being higher in Te Miro sites (mean = 6.09, SE = 0.31) than Whatawhata sites (4.01, SE = 0.60) but not Maungatautari-Waotu sites (5.69, SE = 0.60). There was no effect of pest control category or pest control*region on raw or rarefied species richness after controlling for number of years fenced. There was no effect of fencing, pest control category, district, or pest control*region on raw or rarefied Berger-Parker dominance.

Assemblage composition

The morphospecies and order-level resemblance matrices had very similar site patterns (Rho = 0.92, p = 0.001), so only the morphospecies level NMDS plot is presented (Fig. 1). Resemblance matrices generated from body length-weighted abundance data produced virtually identical site patterns to matrices generated from abundance data alone (Rho >0.95, whether morphospecies or ordinal level matrices were compared). Resemblance matrices constructed from overall millipede assemblage data, and data from native species only, also revealed very similar site patterns (Rho = 0.90, p = 0.001), hence I proceeded with overall assemblage data for subsequent analyses.

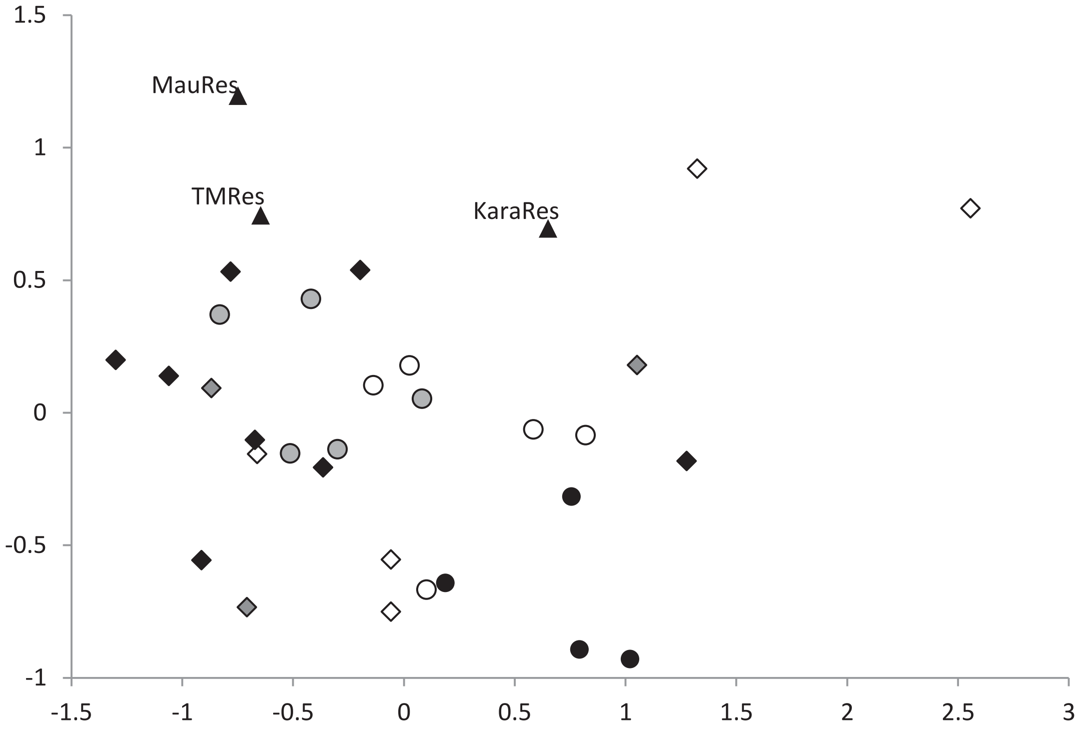


Figure 1. NMDS ordination plot of Bray-Curtis resemblance matrix from log(*x*+1) transformed site-level mean morphospecies abundance data. Circles = non pest control sites (P0), diamonds = pest control sites (P1), triangles = forest reserve sites. White fill = fenced 0-2 years, grey fill = fenced 3-10 years, black fill = fenced for more than 10 years. Stress = 0.14.

ANOSIM on site mean abundance data (log(*x*+1) transformed), indicated that sites from different management categories differed in morphospecies and ordinal composition (Table 2). Pest control sites that had been fenced to exclude livestock for over 10 years had a composition similar to that of the forest reserve sites, whereas the composition of non-pest control sites fenced for more than 10 years differed from forest reserve sites. Pest control and non pest control sites had significantly different ordinal composition (Global $R = 0.09$, $p = 0.05$),

Table 2: Pairwise ANOSIM *R* statistics between different management categories, from Bray-Curtis resemblance matrices constricted from log(x+1) transformed mean morphospecies and ordinal abundances. Management categories are coded as follows: FR = the three larger forest reserves, P indicates sites receiving mammalian pest-control, N indicates sites with no pest control, and values in parentheses indicate the number of years each remnant had been fenced to exclude livestock. Management categories with significantly different assemblage composition ($p \leq 0.05$) are indicated in bold. Morphospecies composition differed significantly between pestcontrol*fencing treatments (Global R = 0.28, p = 0.001), and between pest control treatments only (Global R = 0.13, p = 0.03). Ordinal composition differed significantly between pestcontrol*fencing treatments (Global R = 0.27, p = 0.002), and between pest control treatments only (Global R = 0.15, p = 0.02).

	ANOSIM *R* statistics							
Management Category	P (0-2)	P (3-10)	P (>10)	N (0-2)	N (3-10)	N (>10)	P	N
Morphospecies level								
FR	0.29	0.26	0.30	**0.73**	**0.55**	**0.85**	0.13	**0.48**
P(0-2)		-0.06	**0.29**	0.08	**0.25**	0.06		
P(3-10)			-0.02	0.48	**0.40**	0.39		
P(>10)				**0.35**	-0.05	**0.60**		
N(0-2)					**0.33**	**0.39**		
N(3-10)						**0.86**		
N(>10)								
P								0.07
Ordinal level								
FR	0.23	0.30	0.34	**0.84**	**0.60**	**0.59**	0.17	**0.46**
P (0-2)		-0.08	**0.25**	0.10	0.17	0.11		
P (3-10)			-0.07	**0.49**	0.32	0.28		
P (>10)				**0.30**	0.00	**0.56**		
N (0-2)					0.21	**0.45**		
N (3-10)						**0.84**		
N (>10)								
P								**0.09**

The environmental variable resemblance matrix correlated with morphospecies (Rho = 0.22, $p = 0.02$) and ordinal level (Rho = 0.21, $p = 0.03$) resemblance matrices. There was no correlation between the geographical distance matrix and the morphospecies (Rho = 0.14, $p = 0.06$) and ordinal level resemblance matrices (Rho = 0.12, $p = 0.06$).

The morphospecies site pattern was best explained by remnant area, elevation, MDScli, plant species richness, and slope ($r = 0.28$). The ordinal site pattern was best explained by area, longitude, and mean litter mass ($r = 0.25$). However, when the three forest reserve sites were excluded from the analysis, remnant area was no longer important. Instead, the morphospecies site pattern was best explained by the variables elevation, MDScli, total basal area, plant species richness, and slope ($r = 0.25$), whereas the ordinal site pattern was best explained by elevation, total basal area, plant species richness, mean litter mass, and slope ($r = 0.22$).

There was a significant interaction between pest control and years fenced for assemblage similarity to nearest forest reserve ($F_{(1,21)} = 5.31$, $p = 0.03$). However, assemblage similarity to nearest forest reserve did not change significantly with years fenced in either pest control category.

There was some evidence that restoration treatments affected millipedes of each size category differently, as there was a significant interaction between pest control category and years fenced for the total abundance of “small” millipedes (i.e., morphospecies with mean body length <5mm) (Fig. 2). The density of “small” millipedes did not change with years since fencing at non-pest control sites ($F_{(1,12)} = 0.40$, $p = 0.54$, $R^2 = 0.03$), but increased significantly at pest control sites ($F_{(1,14)} =$

12.63, $p = 0.003$, $R^2 = 0.47$). No effect was observed for medium (5-10 mm) or large millipedes (>10 mm).

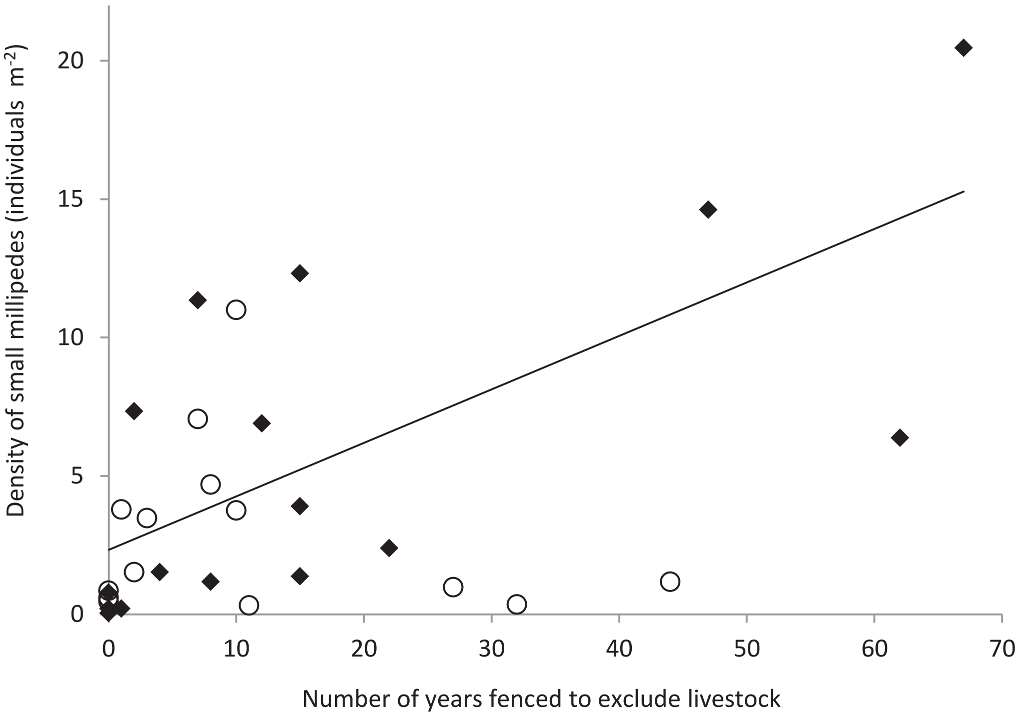


Fig. 2: Changes in the mean density (number of individuals m^{-2}) of small millipedes (summed abundance of all millipede morphospecies with a mean body length of <5mm), with time since fencing to exclude livestock. Pest control categories are plotted separately; circles are non-pest control sites, diamonds are pest control sites. The density of "small" millipedes did not change with years since fencing at non-pest control sites ($R^2 = 0.03$, $F_{(1,12)} = 0.40$, $p = 0.54$), but increased significantly at pest control sites $R^2 = 0.47$, $F_{(1,14)} = 12.63$, $p = 0.003$; solid line is simple linear regression, $y = 0.19x +2. 33$).

Edge responses

Edge responses varied between individual species, and the edge response of individual species varied between sites. For example, the most abundant morphospecies, identified as *Ophyiulus pilosus,* showed a significant positive response to distance from edge at five sites, a significant negative response to distance at seven remnants and at Karakariki Reserve, and no significant edge responses at the remaining 18 remnants and two forest reserves. After accounting for the effect of years fenced, the edge response of *O. pilosus* varied by pest control category ($F_{(1, 24)} = 8.91$, $p = 0.01$), district ($F_{(2, 24)} = 6.44$, $p = 0.01$), and the interaction of these two factors ($F_{(1, 24)} = 5.99$, $p = 0.02$). Specifically, *O. pilosus* had a steeper edge response at non-pest control sites (mean slope = -0.003, SE = 0.002) than at pest control sites (mean slope = -0.001, SE = 0.003). Post-hoc Tukey’s tests indicated that the edge response of *O. pilosus* was significantly different at Maungatautari-Waotu sites (mean slope = -0.006, SE = 0.003) to that at Whatawhata sites (mean slope = 0.007, SE =0.007).

The morphospecies *Polydesmid1* showed a significant positive edge response at four sites, and a significant negative edge response at one site. The edge response of *Polydesmid1* also varied with pest control ($F_{(1, 24)} = 9.75$, $p = 0.01$), district ($F_{(2, 24)} = 4.89$, $p = 0.02$), and the interaction of these two factors ($F_{(1, 24)} = 5.71$, $p = 0.03$) after controlling for the effect of years fenced. *Polydesmid1* exhibited an almost negligible edge response at non-pest control sites (mean slope = -0.0003, SE = 0.001), and a positive edge response (i.e. an increase in density with increasing distances into remnants) at pest control sites (mean slope = -0.003, SE = 0.002). Post-hoc tests showed that *Polydesmid1*also had steeper edge response at

Whatawhata sites (mean slope = 0.008, SE = 0.01), than at Te Miro sites (mean slope = 0.0003, SE = 0.001).

The most common Spirostreptida morphospecies, *Spirostreptida1*, showed a significant response to transect distance at six sites, with its abundance declining with transect distance at five of these sites. The edge response of this morphospecies did not vary by pest control category, region, or years fenced. However, the edge responses of *Julida1*, *Spirostreptida1*, and *Polydesmid1* from each site were significantly positively intercorrelated, suggesting they have a similar response to edge-related environmental gradients.

Bray-Curtis similarities in assemblage structure between the edge and core distance intervals varied from 0 (at 3 sites) to 74.1% at one site (*Bdle16*). There was a significant interaction between years fenced and pest control category in edge-core assemblage similarity ($F_{(1,24)} = 6.32$, $p = 0.02$). At pest control sites, millipede assemblage similarity between the edge and core increased with time since fencing ($R^2 = 0.28$, $F_{(1, 14)} = 5.31$, $p = 0.04$), but at non-pest control sites, millipede assemblage similarity between remnant edge and core decreased ($R^2 = 0.25$, $F_{(1, 14)} = 3.97$, $p = 0.07$); Fig. 3).

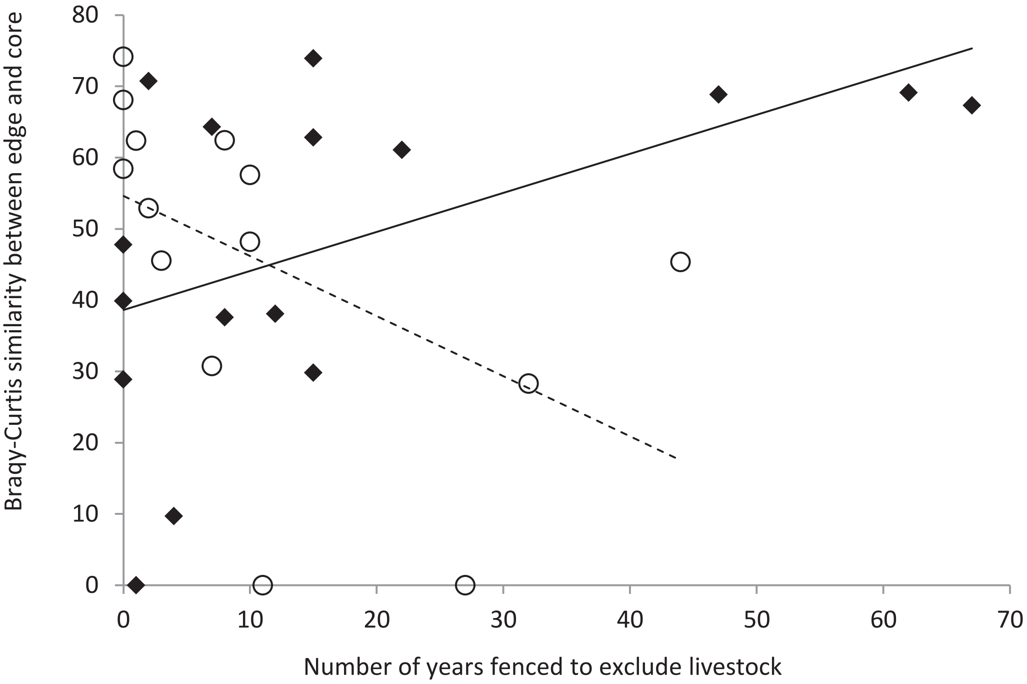


Figure 3. Millipede morphospecies assemblage similarity between the edge and core of each remnant, with time since fencing. Assemblage similarity is Bray-Curtis similarity measure, calculated from mean log(x+1) transformed morphospecies abundances at remnant edges and cores (i.e., samples collected within the –2.5 to 2.4 m "edge" distance interval, were compared to those collected from innermost or "core" distance interval – see Methods). Pest control categories are plotted separately with linear regression lines; circles are non-pest control sites (dashed line; $y = -0.84x + 54.60$), and diamonds are pest control sites (solid line; $y = 0.33x + 39.10$).

Discussion

The millipede orders exhibited a variety of responses to restoration. Fencing to exclude livestock resulted in an increase in chordeumatid and polyzoniid millipedes, whereas polydesmid millipedes required both livestock exclusion and mammalian pest control to increase, and juliform millipedes (Julida and Spirostreptida), showed no significant response to either restoration action.

Livestock exclusion alone is clearly not sufficient to restore all the components of millipede communities, despite its strong effect on recovery of the vegetation (Burns et al. 2010), and other invertebrate groups (Chapter 5, Chapter 7). Remnants that had been subjected to pest control and long-term livestock exclusion (>10 years) have assemblage composition most similar to that of forest reserve sites. Conversely, the assemblage composition of non-pest control sites apparently becomes more divergent from forest reserves as time since livestock exclusion increases.

Body size of millipedes also influenced their sensitivity to restoration treatments. Small millipedes increased in abundance with time since fencing only at pest control sites. Smaller millipedes are more likely to exhibit burrowing behaviour (Kime and Golovatch 2000), and may be much more adversely affected by impacts such as soil compaction associated with livestock grazing. However, this does not satisfactorily explain why they only exhibited recovery in pest-control sites.

The pest control methods used in the study remnants targeted possums (*T. vulpecula*), which are not known to have strong direct effects on litter invertebrates. Cowan and Moeed (1987) describe possums as opportunistic predators of invertebrates, yet millipedes do not feature in their list of taxa identified from possum gut contents. Therefore, we assume that the effects of possum control on litter invertebrates must be almost exclusively indirect effects. These indirect effects could include changes to vegetation composition and palatability, and/or changes in other mammalian pest populations. Possums are known to change canopy composition over time through preferential grazing (Allen et al. 1997), which would presumably reduce litter quality for forest floor detritivores. Pest control targeting possums may benefit litter invertebrates if it also leads to population declines of other mammalian pests, particularly rodents which are known to feed extensively on invertebrates. Unfortunately, we did not examine the effect of possum control on rodent population densities, but Sweetapple and Nugent (2007) report an *increase* in rodents following possum control. Therefore we should not discount this link between millipedes and possum pest control. Despite being unable to elucidate the actual mechanism involved, it is clear that pest control aimed at possums has a strong benefit for millipede communities.

The effects of livestock grazing on millipedes (and other litter invertebrates) are comparatively more straightforward. Firstly, livestock remove leaf litter, and compact the soil and litter layers (Chapter 1), removing interstitial spaces that provide habitat for burrowing invertebrates, and altering microclimatic conditions. Secondly, livestock completely remove understorey vegetation, supress regeneration of canopy trees, and hence alter canopy composition. Secondary plant succession occurring as a result of livestock exclusion can affect soil and litter detritivores by changing the quantity and quality of leaf litter inputs (Berg and Hemerik 2004). Leaf litter is generally a low quality food resource, and millipedes are vulnerable to reductions in litter quality, as it has been shown to affect their reproductive output (David 2009). Furthermore, feeding trials conducted by Ashili (2008) showed that millipedes are able to distinguish leaves from grazed and fenced sites, and that they will preferentially feed on leaves from fenced sites, presumably because plant chemical defences released in response to grazing make leaves less palatable to millipedes. Finally, livestock removal impacts rodent populations. Ship rat densities in this study system are actually markedly higher in fenced remnants than in unfenced remnants, and this is thought to be because the dense understorey vegetation in fenced remnants provides ideal habitat and abundant food resources for rats (Innes et al. 2010).

Therefore, for greatest efficacy fencing to exclude livestock might be best combined with pest control methods that target both rodents *and* possums. However, rodents successfully reinvade forest remnants within days or weeks of eradication (Innes et al. 2010), and therefore pest control requires on-going investment from land managers. Also, little evidence exists to suggest that rodent reduction or eradication in New Zealand forests has a strong effect on millipede densities (see Sinclair et al. 2005, Rate 2009). This may simply be because the control of pest mammals in New Zealand forest tends to lead to population increases of native insectivorous birds, which could mask any rodent effects. Clearly, more work is needed to elucidate the net benefit of rodent control and possum control for litter invertebrate restoration.

The two restoration actions also altered the nature of edge responses of individual taxa, and the extent of edge-core difference in assemblage composition. Remnants become more densely vegetated with native understorey with time since fencing (Burns et al. 2010), and the edges of fenced remnants become particularly densely vegetated, and hence have more leaf litter. Yet, millipede communities at the edge and centre of remnants became more similar with time since fencing at pest control sites only. In contrast, at sites without pest control, millipede communities at the edge and centres of remnants became less similar with time since fencing. Possum browsing in these remnants alters canopy composition and reduces overall canopy cover, while allowing increased abundance of lianes and epiphytes (Burns et al. 2010). Forest-dwelling possums routinely venture out into pasture to forage (Green and Coleman 1986) and their browsing impacts could be much stronger at remnant edges than centres as a result.

Majer (2009) was critical of order-level analyses of invertebrate communities, as different species within an order may show substantial variation in their ecological role. However, I think for these millipede communities this was suitable, as ordinal and morphospecies level analyses revealed almost identical patterns in response to environmental variables and restoration actions. Others have also found this to be true for millipede communities (Nakamura et al. 2003; Snyder and Hendrix 2008). Additionally, Manton (1977) divided millipedes into distinct ecomorphological or functional groups at approximately order level. Therefore, for this group of invertebrates at least, ordinal analysis is appropriate for assessing restoration effects.

Millipedes also seem a useful indicator group of restoration effects as they were relatively unaffected by geographical differences (e.g., remnant area, latitude, longitude) between forest patches. David (2009) suggested millipedes may not be as sensitive to the area of forest remnants as other invertebrate taxa, and that small remnants (<1 km^2) may be adequate to protect and support millipede richness. Báldi (2008) similarly found in a study of terrestrial invertebrate diversity across 16 nature reserves in Hungary, that there was no species-area relationship for Diplopoda. It is encouraging that even very small forest remnants can support millipede assemblages similar to nearby reference sites, and are therefore viable targets for restoration actions.

Didham et al. (2009), examined the response of the entire invertebrate community at a higher taxonomic level than this study (phylum, class and order), and found that livestock exclusion resulted in strong increases in the densities of many key taxa, whereas pest control by itself had limited benefit for invertebrates, and led to community composition becoming more divergent from that of forest reserve sites. In another study carried out in the same system, I also found that pest control had little discernable effect on invertebrate colonists of leaf litter packs, instead the abundance of selected invertebrate groups responded primarily to livestock exclusion, with increasing abundances with time since fencing (Chapter 5). The results from these studies all carried out in the same system suggest that both fencing and pest control are needed to successfully restore remnants.

I was unable to explain variation in the abundance of the two introduced juliform millipede groups and the native Spirostreptida. In the case of the Julida, which is also known to be abundant in farmland (Blower 1985), the characteristics of the surrounding agricultural matrix may have been a more important determinant of their abundance then the characteristics of the remnants themselves. Introduced julids are thought to have arrived in NZ in the nineteenth century, and are now common in native forests and grasslands (Johns 1962). The presence of *O. pilosus* at all sites, and the fact that it comprised 45% of all individuals, is a concern if this introduced species presents serious competition for native millipede fauna. However, Johns (1962) states that introduced julids do not appear to have any effect on native julid species, despite their overlap in ecomorphology. I also found no evidence that introduced julids are having a negative impact on native julids, as the densities of Julida and Spirostreptida were strongly positively correlated.

This study clearly demonstrates the usefulness of millipedes as potential bioindicators of forest restoration success, as they are sensitive to restoration efforts. Other traits which make them ideal indicator taxa are that they are unitrophic, predominantly forest-specialists with poor dispersal ability, and make a direct contribution to an important ecosystem function, leaf litter decomposition (Nakamura et al. 2003). Encouragingly, New Zealand millipede fauna also show strong responses to management at order level, which also makes them a comparatively straightforward group to study, without the need for specialised taxonomic knowledge.

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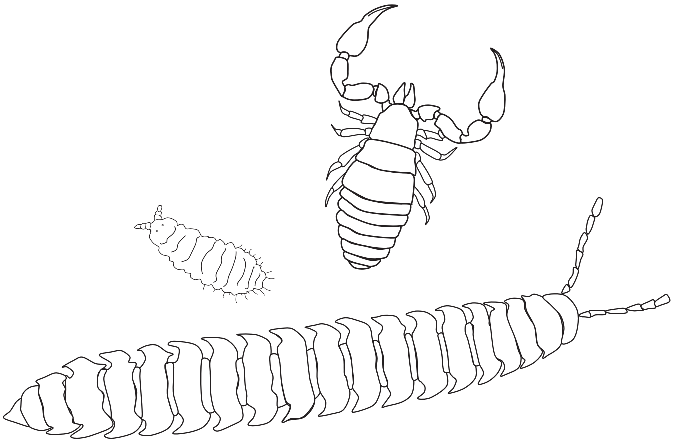
Chapter Seven

The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants



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Abstract

In many agricultural landscapes, significant biodiversity gains can be made by improving the ecological condition of degraded remnants of semi-natural habitat. Recent emphasis has been on the level of management intervention required to initiate vegetation recovery in small forest remnants, but no comparable emphasis has been placed on benefits for invertebrate communities. In the Waikato region, New Zealand, we tested the effects of livestock exclusion, mammalian pest control, and their interaction, on leaf-litter invertebrate communities in 30 forest remnants, using a space-for-time substitution approach. A total of 87 376 invertebrates were extracted from 964 leaf-litter samples. Invertebrate density was an order of magnitude lower in remnants than in nearby large forest reserves. For key taxa, such as Diplopoda, Isopoda, Coleoptera and Mollusca, 10- to 100-fold lower densities were recorded in remnants with no pest control, particularly where livestock were not excluded. By contrast, other taxa such as Thysanoptera and Formicidae (Hymenoptera) had up to 100-fold greater densities in remnants with recent stock exclusion and pest control. These changes led to a significant livestock exclusion × pest control interaction effect on the degree of invertebrate community dissimilarity between forest remnants and forest reserves. Using structural equation modelling, we found that treatment effects were largely mediated by a cascading series of indirect causal paths involving altered soil chemistry, vegetation composition, and litter mass relative to large forest reserves, although the livestock exclusion × pest control interaction was inadvertently confounded with differing slopes and areas of remnants in different treatments. Livestock exclusion and mammalian pest control have significant, but contrasting, effects on invertebrates in the first 10–20 years following

livestock exclusion from forest remnants, with mammalian pest control having limited benefit for the leaf-litter invertebrate fauna without livestock exclusion.

Introduction

New Zealand justifiably celebrates its place among the world's top 25 "biodiversity hotspots" (regions harbouring more than 1% of the world's endemic plants; Myers et al. 2000). Yet, by and large, we choose to ignore the fact that these are also hotspots of extinction threat, defined equally by Myers' second criterion of severe (>70 %) habitat loss (Myers et al. 2000). Nearly half of the administrative districts of New Zealand have less than 10–15% remaining native habitat cover, and most of that is heavily fragmented (Ewers et al. 2006). This is particularly true of the once extensive lowland forests of New Zealand (Thompson et al. 1983, MfE 2000). The non-random pattern of severe native habitat loss in fertile lowland regions (Ewers et al. 2006), combined with a protected areas network built on the acquisition of high-elevation land of low commercial value (Norton 1999, Park 2000), has greatly exacerbated conservation threats in "the other 70%" of the country used for agricultural production. Across wide swathes of our lowland agricultural landscapes the extent of indigenous biodiversity loss is unparalleled anywhere in the world (Norton and Miller 2000).Correspondingly, the conservation value of even the smallest remnants of semi-natural habitat in these landscapes is extremely high.

Recognition that lowland forests are poorly represented in the conservation estate has prompted calls to shift the balance of protection and management towards small, under-represented forest remnants in landscapes that have suffered the highest amounts of deforestation (Leathwick et al. 2003a). Over the past decade, however, it has become clear that conservation management on private land brings with it a unique set of challenges for conservation managers (Norton and Miller 2000, Newburn et al. 2005). For instance, the rich ecological debates over reserve selection and design criteria in the 1980s and 1990s (e.g., Simberloff and Abele 1982, Saunders et al. 1991) are moot when there is little alternative but to accept the remaining habitat in the landscape, regardless of spatial location or configuration (Schwartz 1999, Tscharntke et al. 2002b).

Recent evidence suggests that the relative conservation value of small remnants on private land can be substantial (Abensperg-Traun and Smith 1999, Oliver et al. 2006, Arroyo-Rodríguez et al. 2009). Even small areas of remnant forest can sustain diverse assemblages of native plants (Whaley et al. 1997) and animals (Harris and Burns 2000), compared to the surrounding agricultural landscape (Harris and Burns 2000, Derraik et al. 2005, Ewers et al. 2007). Furthermore, c. 20% of New Zealand’s threatened vascular plants are confined to private land, and for an additional 60% of species private land constitutes a significant proportion of their habitat (Norton 2000). Nevertheless, it must be acknowledged that the small size of many of the remaining lowland forest remnants limits the number of species they contain (Ogle 1987, Saunders et al. 1991), and the total population sizes of remaining species (Connor et al. 2000), particularly where species are sensitive to edge effects (Ewers and Didham 2007, Ewers et al. 2007). To complicate matters, the effects of these fragmentation processes may only become fully evident in small remnants after considerable lag-times (the so-called “extinction debt”, Tilman et al. 1994), with an estimated half-life of species decline of 25–100 years for birds (Brooks et al. 1999, Ferraz et al. 2003) and 50–100 years for prairie-dwelling plants (Leach and Givnish 1996). Some long-term studies of vegetation dynamics in small isolated forest remnants in New Zealand paint a grim picture with regard to the maintenance of native plant diversity. For example, Whaley et al. (1997) recorded the local extinction of one-third of the 122 native species from a single 5.2 ha forest remnant (Claudelands Bush) in the Waikato region between 1956 and 1980. As a result, plant species which occupied habitats that have undergone the greatest reductions in area are more likely to have become rare or been extirpated than species in habitats that were already sparsely distributed (Duncan and Young 2000). Clearly, the legacy of historic habitat loss still very much influences current populations (Ewers and Didham 2006b, Ewers et al. 2006, Ewers and Didham 2007), notwithstanding recent statements that “classical problems of ecosystem loss and fragmentation have largely been countered in some regions by reservation of 30% of total land area” (Craig et al. 2000, p. 61).

Historical habitat loss can have further indirect effects on native species in forest remnants by altering the relative magnitude of effects of a wide range of other threatening processes. For example, the impact of intermittent livestock browsing and soil disturbance (Jane 1983, Buxton et al. 2001, Miller 2006), anthropogenic fertiliser inputs (Stevenson 2004), altered hydrological regimes (Burns et al. 2000), and the impact of exotic mammals (Atkinson 2001, Wardle et al. 2001) and plant pests (Timmins and Williams 1991) are all likely to be exacerbated in small remnants with a high proportion of edge habitat (Ewers and Didham 2006b). Recent work has provided compelling evidence for synergistic interactions between multiple drivers of global environmental change, including land-use intensification and species invasion (Didham et al. 2005, Didham et al. 2007, Tylianakis et al. 2008). For example, Wiser et al. (1998) found that the invasive exotic herb *Hieracium lepidulum* (Stenstroem) Omang (Asteraceae) had the highest probability of occurrence near forest edges, and Timmins and Williams (1991) noted the invasion of a wide range of exotic plants into forest remnants with greater levels of anthropogenic disturbance. Invasion of the exotic *Tradescantia fluminensis* Vell. (Commelinaceae) into forest remnants caused a significant reduction in species richness, abundance and survival rates of native forest seedlings (Standish et al. 2001), and a significant change in the diversity and composition of terrestrial invertebrate communities (Toft et al. 2001, Yeates and Williams 2001, Standish 2004), with substantial flow-on effects for litter decomposition rates and nutrient availability (Standish et al. 2004). Clearly, in the face of severe threats from multiple, interacting drivers of ecological change, preservation alone is not likely to be sufficient to stem the loss of biodiversity from forest remnants without management intervention (Leathwick et al. 2003a, Chazdon 2008).

Land managers now recognise these issues more widely in New Zealand, and recent initiatives explicitly address the need for and importance of nature conservation on private land (Norton 2000). Small privately-owned remnants are a key focus of territorial local authorities in the management of biodiversity, and in the development of guidelines for regional biodiversity protection. Open space covenants through the New Zealand Queen Elizabeth II National Trust (QEII Trust 1984) allow landowners to protect parts of their property in perpetuity, and the government has provided funds for the purchase or protection of native remnants on private land through the Nature Heritage Fund and Nga Whenua Rahui Trust (Norton and Miller 2000). These initiatives have been matched by increases in community involvement in conservation and restoration projects (MfE 2000, Ritchie 2000, PCE 2001, MfE 2002). The remnants managed by >63 000 rural land owners (Statistics NZ 2008) provide unparalleled opportunities to address local-scale restoration of lowland forests, while at the same time achieving high-level national goals for conservation. Most important of all, there is a steadily growing desire by landowners to maintain and improve the condition of biodiversity on their land (Davis and Cocklin 2001, MfE 2002). For example, as of November 2008, QE II National Trust had over 3500 registered covenants, with active management of threats to over 100 000 ha of privately-owned remnants (Anon. 2008).These initiatives recognise that management actions such as fencing will often be required to prevent grazing and trampling by livestock (Burns et al. 2000), and exotic weeds and pests may need to be controlled (Porteus 1993) in order to reduce threats to native biodiversity within remnants. These figures are encouraging and reflect the enthusiasm New Zealanders have for the protection of their natural heritage. However, the degree to which this enthusiasm has translated into significant conservation gains in small remnants has not been tested.

In this context, the goal of our study was to test whether livestock exclusion and mammalian pest control, the two management actions most commonly applied in the conservation management of forest remnants on private land (QEII Trust 1984, Porteus 1993), are sufficient to promote the recovery of terrestrial invertebrate abundance and composition towards the condition observed in the few relatively large forest reserves remaining in the landscape. Although there have been no previous attempts to test the potential conservation benefits of management intervention for the restoration of native invertebrate communities in severely degraded forest remnants, recent studies testing the effects of livestock exclusion on plant community dynamics and physical soil properties in forest remnants (Burns et al. 2000, Smale et al. 2005, Dodd and Power 2007, Dodd et al. 2008, Smale et al. 2008) suggest that strong responses might also be expected among soil- and litter-dwelling invertebrates.

We test for direct effects of time since livestock exclusion and mammalian pest control on litter invertebrate density and community structure, highlighting in particular the antagonistic interaction effects that can occur between management treatments. We also attempt to tease apart the indirect mechanisms by which management treatments might affect invertebrates via altered soil structure and geochemistry due to trampling, altered plant structure and composition due to browsing, and altered litter structure and biomass resulting from more complex feedbacks between soil, vegetation and litter processes (Milchunas and Lauenroth 1993, Wardle et al. 2001). Here, we present the first phase in our investigation, in which we take a higher taxonomic approach to the detection of the key invertebrate taxa responding to habitat fragmentation and subsequent conservation management intervention. In doing so, we adopt the approach of Biaggini et al. (2007) and others (Kremen et al. 1993, Pik et al. 1999, Andersen et al. 2002, Nakamura et al. 2007) in identifying general trends across the entire invertebrate fauna, laying the foundation for species-level analyses testing management effects on detritivorous invertebrates and their role in litter decomposition processes (Barker, Watts and Didham, unpubl.).

Methods

Study area

The study was conducted in the Waikato region of the central North Island of New Zealand (Fig. 1). In the central portions of the region (the Waikato, Waipa, Matamata-Piako and South Waikato administrative districts) surrounding the city of Hamilton, only 9% of the original 800 000 ha forest area has survived human settlement (Ewers et al. 2006). Much of the remaining forest consists of small forest remnants dominated by tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex

Kirk; Lauraceae) on moderate hill country from 100–400 m a.s.l. (Land Environments of New Zealand, LENZ, classification D2, F1, F6, F7; Leathwick et al. 2003b). Most of the 5000 or so separate remnants in the lowlands and rolling hill country of the Waikato region are on private land, and 96% of these are less than 25 ha in area, with little or no conservation protection.

In addition to the significant component of tawa in the canopy and subcanopy at all sites sampled in this study, other important tree species in one or more remnants included *Knightia excelsa* R.Br. (Proteaceae), *Laurelia novae-zealandiae* A.Cunn. (Atherospermataceae), *Litsea calicaris* (A.Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae), *Dysoxylum spectabile* (G.Forst.) Hook.f. (Meliaceae), and *Melicytis ramiflorus* J.R.Forst. et G.Forst. (Violaceae), as well as several other canopy species found predominantly at the forest reserve sites, including *Elaeocarpus dentatus* (J.R.Forst. et G.Forst.) Vahl (Elaeocarpaceae), *Metrosideros robusta* A.Cunn. (Myrtaceae), *Weinmannia racemosa* L.f. (Cunoniaceae) and the conifers *Prumnopitys taxifolia* (D.Don) de Laub., *Prumnopitys ferruginea* (D.Don) Laubenf. (Prumnopityaceae), *Dacrydium cupressinum* Lamb., *Dacrycarpus dacrydioides* (A.Rich.) de Laub., and *Podocarpus totara/hallii* G.Benn. ex D.Don (Podocarpaceae) (Smale et al. 2008, Burns et al. 2011).

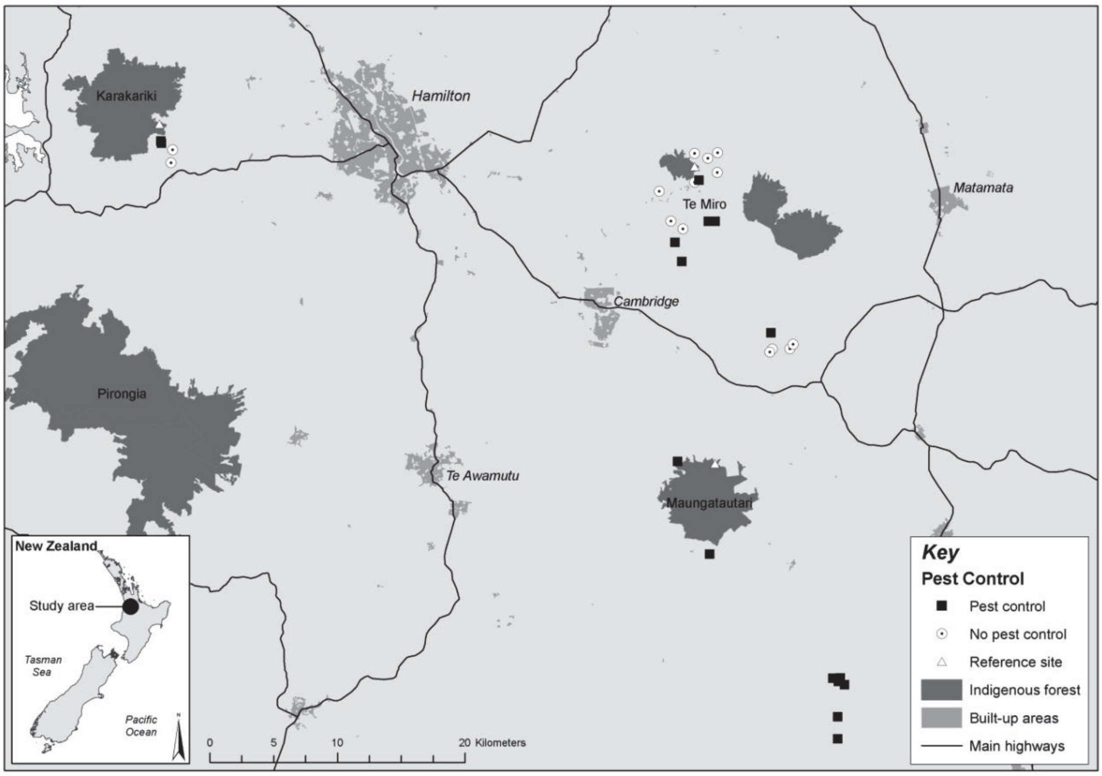

Figure 1. Map of the study area in the Waikato region, North Island, New Zealand, showing the spatial locations of the 30 forest remnants and three forest reserves (Te Miro Scenic Reserve, Maungatautari Mountain Scenic Reserve and Karakariki Scenic Reserve) in which leaf-litter invertebrates were sampled.

Sampling design

A Geographic Information System (GIS) analysis was used to identify all forest remnants in LE NZ classes D2, F1, F6 and F7 in the Waikato, Waipa, Matamata-Piako and South Waikato administrative districts. Subsequently, extensive phone interviews and site visits with landowners were conducted for over 100 forest remnants in the c. 0.5–50 ha size range, in order to select a final subset of 47 remnants that had been subject to a factorial combination of differing types and intensities of management action: (1) four levels of livestock exclusion (fencing), crossed with (2) two levels of control of introduced mammalian omnivores (pest control). In the livestock exclusion treatment, remnants were selected based on four nominal classes of time since livestock exclusion: F0, fenced 0–1 years ago (i.e., no fence or livestock excluded by fencing within the past year); F6, fenced 2–9 years ago; F12, fenced 10–15 years ago; and F42, fenced 22–67 years ago. A remnant was assigned to a livestock exclusion treatment class only if it was known that a high quality fence had been present, and had evidently excluded livestock grazing for the entire treatment period. Within each nominal time since livestock exclusion class, remnants were subsequently selected on the basis of mammalian pest control treatments: P0, no or little (sporadic, and/or low-intensity) pest control; and P1 intensive, sustained pest control (i.e., involving continual use of poison or trapping stations for a minimum of the previous 2 years, but usually >10 years, with at least annual repeats using at least 1 trap/bait station per hectare, with full coverage of the remnant). Pest control was predominantly targeted at brushtail possums (*Trichosurus vulpecula* (Kerr); Phalangeridae), but may also have impacted other omnivorous species such as ship rats (*Rattus rattus* (Linnaeus); Muridae) which are abundant in forest remnants (Innes et al. 2010). Due to the limited availability of remnants that had been subject to some combinations of pre-existing management treatments, the number of remnant replicates varied from 3 to 8 within the eight livestock exclusion × pest control treatment combinations. Because of their clumped spatial distribution in the landscape, remnants tended to be clustered in three major areas (Te Miro, Whatawhata, and Maungatautari–Te Waotu; Fig. 1), and there was potentially confounding spatial autocorrelation of remnant location across treatments (particularly due to widespread, landscape-scale possum culling for tuberculosis control in the Maungatautari–Te Waotu area), and this was explicitly factored into multivariate analyses.

The effects of livestock exclusion and pest control treatments on plant community structure (Burns et al. 2011) and leaf-litter decomposition rates (Barker, Watts and Didham, unpubl.) were tested across all 47 remnants, but it was not logistically feasible to sample invertebrates at all sites. Therefore, invertebrates were sampled from leaf litter in 30 forest remnants selected from the full set of 47 remnants, based on accessibility, while ensuring the inclusion of three or four replicates in each treatment combination. As a reference point for changes in invertebrate community composition in forest remnants, invertebrate communities were also sampled in three forest reserves, representing some of the largest available reference sites classified in the same LENZ categories as the forest remnants throughout the study area: Te Miro Scenic Reserve (402.8 ha) in the Te Miro area, Karakariki Scenic Reserve (5500 ha) in the Whatawhata area, and Maungatautari Mountain Scenic Reserve (3363 ha) in the Maungatautari–Te Waotu area (Fig. 1). The reserves had larger areas and lower intensities of recent anthropogenic disturbance than remnants.

In each of the 30 remnants and three forest reserves, 30 sampling points were selected along a matrix-to-forest interior gradient using a fully-randomised block design. The forest edge (0 m) was defined by the position of the trunks of the outermost trees that formed an unbroken canopy. Negative distances from edge were assigned to sites outside the forest edge, while positive distances were assigned to sites within the forest. All edges were selected on the northern side of the remnant, and were adjacent to open pasture matrix habitat. Sampling points were selected at five random distances from the forest edge, within each of six fixed distance intervals centred at 0, 5, 10, 20, 40 m and “core” distances from edge; i.e., within distance intervals of –2.5 to 2.4 m, 2.5–7.4 m, 7.5–14.9 m, 15–29.9 m, 30–59.9 m and 60 m–core. Each sampling point was randomly offset by ±10 m perpendicular to the edge-to-interior gradient (i.e., parallel to the forest edge) in order to give a good degree of spatial separation between samples. The distance to the remnant core varied with patch area, from 15 to 200 m from the edge. As sampling effort was equal at the patch level (n = 30 sampling points), small remnants in which the core was less than 60 m from the edge had a greater number of replicates allocated (proportionally) into the near-edge distance intervals. Sampling intensity was purposely higher close to the forest edge than in the forest interior, because the rate of change in invertebrate abundance and composition is known to be greatest near the forest edge (Didham et al. 1998, Ewers et al. 2007).

Sampling leaf-litter invertebrates

One leaf-litter sample was collected in a 33 cm diameter circular frame (0.086 m^2) at the 30 selected sampling distances in each of the 30 remnants and three forest reserves, giving a total of 990 leaf-litter samples collected from 4 December 2007 to 19 February 2008. At each remnant all 30 leaf-litter samples were collected on the same day so that putative edge gradients in invertebrate density or composition were reliably captured, without introducing potential bias from sampling different parts of the edge gradient on different days. Within logistical constraints of researcher movement throughout the study area, daily sampling was randomly allocated between different treatment classes to prevent bias arising from seasonal variation in activity patterns of invertebrates (variation in the seasonal spread of sampling dates within a given livestock exclusion by pest control treatment combination ranged from 3 to 8 weeks). All leaf litter and friable humus was scraped rapidly from the frame and placed in a large bag-sieve to minimise invertebrate escape. The material was immediately sieved over a 10 mm mesh by vigorously shaking the bag-sieve for approximately 5 min. The fine, sieved litter containing invertebrates was then transported to the laboratory in individual cotton bags. After the sieving process, the coarse “top fraction” of remaining litter was placed in a plastic bag and later dried and weighed to obtain a combined estimate of sample litter mass.

Invertebrates were extracted from the sieved leaf litter over a 72-h period using Berlese funnels (BioQuip® collapsible bag design #2832, Rancho Dominguez, California) (Wheeler and McHugh 1987). We operated 60 Berlese funnels continuously for 3 months. Subsequently, invertebrates were sorted and identified to invertebrate Phylum, Class and Order, and counted. Two samples were excluded due to labelling error, and 24 samples were not sorted due to time constraints, giving a total of 964 samples sorted (with four sites having 20, 21, 25 and 28 samples sorted out of 30).

Measurement of explanatory variables

In addition to nine treatment variables imposed by the study design (livestock exclusion, pest control, distance from forest edge and their interactions with each other and with patch area), we measured 10 potential confounding variables and 17 sample-, plot-, and patch-level environmental variables to identify potential determinants of invertebrate response to management action (Table 1).

Treatment variables

To test for potential interaction effects, three variables were calculated representing livestock exclusion × pest control, livestock exclusion × distance from edge, and pest control × distance from edge interactions. In addition, three interaction variables were calculated between the treatment design variables and patch area (livestock exclusion × patch area, pest control × patch area, and distance from edge × patch area). To avoid problems of linear dependency and collinearity in multivariate analyses, the interaction terms were calculated by multiplying deviation scores (i.e., each of the values minus their respective grand mean), rather than the raw score cross-products (Kline and Dunn 2000).

Table 1. Treatment variables, potential confounding variables and sample-level, plot-level and fragment-level environmental correlates used in the ordination analyses and structural equation model. NZMG = New Zealand Metric Grid mapping system. SSH-MDS = semi-strong hybrid multidimensional scaling. † = variable removed in ordination analysis due to multicollinearity.

Code	Explanation	Units
Treatment variables and associated interaction effects		
LvExcl	Number of years since livestock were excluded from the fragment (0 = not excluded)	years
PstCtr	Presence (P1) or absence (P0) of pest control	binary
LxP	Livestock exclusion × pest control interaction (cross-product of deviance scores)	
Edge	Distance from forest edge into forest interior	m
LxE	Livestock exclusion by Distance from edge interaction (cross-product of deviance scores)	
PxE	Pest control by Distance from edge interaction (cross-product of deviance scores)	
AxE	Fragment area by Distance from edge interaction (cross-product of deviance scores)	
LxA	Livestock exclusion by Fragment area interaction (cross-product of deviance scores)	
PxA	Pest control by Fragment area interaction (cross-product of deviance scores)	
Potential confounding variables		
Date	Sampling date	
x	Modified spatial coordinate representing longitude (eastings in NZMG units/1000) (see text)	
y	Modified spatial coordinate representing latitude (northings in NZMG units/1000) (see text)	
xy	Linear component of spatial trend surface	
†x^2	Quadratic longitudinal component of spatial trend surface	
†y^2	Quadratic latitudinal component of spatial trend surface	
†x^2y	Quadratic latitudinal and longitudinal component of spatial trend surface	
†xy^2	Quadratic latitudinal and longitudinal component of spatial trend surface	
†x^3	Cubic longitudinal component of spatial trend surface	
†y^3	Cubic latitudinal component of spatial trend surface	
Environmental correlates		
Sample-level variables		
SmpLit	Dry-weight litter mass of the sample from which invertebrates were extracted	g
Plot-level variables		
PltSdl	Number of seedlings in a 0.5-m radius plot	
PltSpl	Number of saplings in a 2.5-m radius plot	
PltAsp	Aspect at each seedling plot (absolute deviations from North)	º
PltSlp	Slope at each seedling plot	º
PltLit	Average dry-weight litter mass in the vicinity of each seedling plot	g.m^{-2}
Fragment-level variables		
LgArea	Log$_{10}$ Fragment area	ha
† SI	Shape index (see text for formula)	
5kCore	Proportion of indigenous forest cover within a 5-km radius of the ‘core’ vegetation plot	
Elev	Elevation above mean sea level	m
MDScli	Axis 1 scores of an SSH-MDS ordination on 9 climate variables (see text)	
MDSsoi	Axis 1 scores of an SSH-MDS ordination on 10 edaphic variables (see text)	
Basal	Total tree basal area in an 11.3-m radius plot at the fragment 'core'	m^2.ha^{-1}
VegRic	Total plant species richness in an 11.3-m radius plot at the fragment 'core'	
OpCan	Proportion of open canopy above an 11.3-m radius plot at the fragment 'core'	
MDSveg	Axis 1 scores of an SSH-MDS ordination on the basal areas of 38 plant species (see text)	
MDShis	Dissimilarity of axis 1 and 2 scores of current versus historical predicted vegetation composition in SSH-MDS ordination	

Potential confounding variables

Although every effort was made to randomise the order of sampling of treatment replicates across dates, the potential confounding effect of sampling date on invertebrate community composition was explicitly taken into account in multivariate analyses. Further, a cubic trend surface approach was used to remove potentially confounding spatial autocorrelation from the data (Borcard et al. 1992, Davies et al. 2003). This approach utilises nine variables representing linear, quadratic, and cubic combinations of New Zealand Metric Grid (NZMG) northing and easting values (x, y, xy, x2, y2, x2y, xy2, x3, y3) of the interior sampling site at each remnant or reserve. The NZMG coordinates were expressed relative to the minimum northing and easting values within the dataset, and divided by 1000 prior to analysis. The use of fitted trend surfaces is a conservative approach to dealing with potentially autocorrelated data (see Ewers et al. 2007).

Sample-level correlates

For each of the 964 leaf-litter samples, the coarse top fraction of litter removed during the sieving process in the field, and the fine sieved fraction of litter returned to the laboratory for invertebrate extraction, were both oven dried at 80°C for 24 h and the resulting dry mass values combined to give a single measure of sample litter mass (range: 13.2–1402.5 g).

Plot-level correlates

At (up to) six distance intervals (0, 5, 10, 20, 40 m and “core”) into the 30 remnants and three forest reserves (184 plots in total), the number of woody plant seedlings (15 cm < height < 1.4 m) was recorded in a 0.5 m radius area (0.79 m^2) (range: 0–40) and the number of woody plant saplings (>0.5 m in height and <3 cm DBH) was recorded in a 2.5 m radius area (19.6 m^2) (range: 0–55). In addition, the aspect (recorded as absolute deviations from North) (range: 0–180°) and the slope (range: 0–45°) were recorded at each plot, and standing mass of leaf litter on the forest floor was estimated by collecting two leaf-litter samples with a 33 cm diameter circular frame, and drying them (80°C, 24 h) to obtain a single average value of dry mass (range: 64.7–6219.4 g m^{-2}).

Patch-level correlates

For each of the 30 remnants and three forest reserves, patch area (range: 0.9–27.3 ha for remnants, and 402.8–5500.0 ha for forest reserves) was determined from a GIS analysis of the Land Cover Database (LCDB2) (Terralink 2004), and patch shape index (SI) was calculated using the formula $SI = Perimeter \div 200(\pi.Area)^{0.5}$ (Patton 1975), where patch perimeter (m) was determined from LCDB2. The SI provides a measure of deviations from circularity, with a perfectly circular remnant having an SI value of 1.0, and remnants with increasingly more complex shapes having greater SI values (range: 1.1–23.0). A 5 km radius circular buffer around the core of each remnant and reserve was created in the GIS, and the proportion of the landscape in indigenous forest cover was calculated within this buffer area (range: 0.03–0.52).

At the “core” plots, a range of topographic, climatic, edaphic and vegetation variables were also measured, or derived from spatial databases of environmental attributes maintained as GIS grids for geographic locations in NZMG coordinates. First, elevation (range: 99–356 m a.s.l.) was derived from the New Zealand 25 m resolution digital elevation model. Next, climate parameters for each remnant and reserve were derived from 100 m resolution GIS surfaces interpolated from meteorological station climate data (30-year period 1950–80) (Leathwick and Stephens 1998): mean annual temperature (range: 7.0–3.9°C); mean temperature of the coldest month (July) (range: 0.4–4.6°C); mean temperature in driest month (March) (range: 10.7–17.1°C); mean annual solar radiation (range: 74.8–165.6 MJ m^{-2} day^{-1}); mean solar radiation during winter (June) (range: 4.5–75.0 MJ m_{-2} day^{-1}); vapour pressure deficit in the windiest month (October) (range: 27.0–34.0 kPa); mean annual rainfall (range: 1339–1613 mm); absolute variation in annual rainfall (range: 148– 153 mm); and the ratio of mean annual rainfall to potential evapotranspiration (range: 2.7–3.0). The meteorological stations were predominantly on flat terrain, whereas actual solar radiation on hilly terrain is strongly influenced by topography (Antonic 1998), so the estimates of solar radiation and temperature for each location were corrected for slope and aspect using an empirical method developed for the North Island, New Zealand (McAneney and Noble 1976). Similarly, since increasing slope reduces soil moisture status (Radcliffe and Lefever 1981), the estimates of rainfall received at sites were adjusted by the cosine of the slope angle. A composite measure of overall variation in climate among remnants was obtained from the axis 1 scores of a semi-strong hybrid multidimensional scaling ordination (Belbin 1991), using the Gower (1971) dissimilarity metric, implemented in the PATN software package (Belbin 1995). The climate ordination had a good fit to the data (stress = 0.076), and of the nine measured variables the gradient in ordination scores was most strongly correlated with mean annual temperature (r = 0.95), variation in solar radiation in winter (r = 0.94), mean temperature in the driest month (r = 0.95), mean temperature of the coldest month (r = 0.94) and mean annual solar radiation (r = 0.94).

Edaphic parameters were measured in a single bulked soil sample taken from the “core” in each remnant and forest reserve with a 25 mm diameter Hoffer soil-corer (0–10 cm depth), using standard analytical procedures (Blakemore et al. 1987; see www.landcareresearch.co.nz/services/laboratories/eclab/eclabmethods_soils): pH (range: 3.8–6.3); total nitrogen (range: 0.2–1.8%); total carbon (range: 3.6–29.8%); available phosphorus (Olsen, range: 2.7–139.7 mg/kg); exchangeable calcium (range: 2.9–24.2 cmol/kg); exchangeable potassium (range: 0.4–2.7 cmol/kg); exchangeable magnesium (range: 1.2–7.2 cmol/kg); exchangeable sodium (range: 0.1–0.8 cmol/kg); total exchangeable cation capacity (range: 16.2–54.9 cmol/kg); and base saturation (range: 13.7–80.6%). A composite measure of overall variation in edaphic conditions among remnants was obtained from the axis 1 scores of a SSH-MDS ordination, using the Gower dissimilarity metric, implemented in PATN. The edaphic ordination had a good fit to the data (stress = 0.085), and of the 10 measured variables the gradient in ordination scores was most strongly correlated with variation in total carbon (r = –0.92), total nitrogen (r = –0.86), base saturation (r = 0.71), pH (r = 0.71) and exchangeable cation capacity (r = –0.66).

Vegetation structure and composition were measured in one 11.3 m radius plot (400 m^2) at the “core” distance inside each remnant and forest reserve. Combined measures of total tree basal area (range: 42.2–151.9 m^2 ha^{-1}), total plant species richness (range: 20–55 species per plot), and proportion open canopy (range: 0.05–0.17) were recorded in each plot, as well as basal areas of each of 38 woody plant species (>3 cm DBH). A composite measure of overall variation in tree species composition among remnants was obtained from the axis 1 scores of a SSH-MDS ordination on the basal areas of the 38 tree species, using the Bray and Curtis (1957) dissimilarity metric, implemented in PATN. The vegetation ordination had a moderate fit to the data (stress = 0.164), and of the 38 measured variables the gradient in ordination scores was most strongly correlated with variation in *B. tawa* cover ($r = 0.60$), *P. totara* cover ($r = 0.52$), *Pseudopanax crassifolius* (Sol. ex A.Cunn.) C.Koch cover ($r = 0.51$), *Macropiper excelsum* (G.Forst.) cover ($r = 0.44$) and *D. dacrydioides* cover ($r = 0.42$).

As a measure of the long-term history of canopy disturbance at each site, current tree species composition observed in the "core" plot was compared with the predicted tree species composition at that location, estimated from 100 m resolution spatial predictions of the potential natural vegetation of each site derived from generalised additive regression models (Leathwick 2001, J. Overton and C. Dischinger unpubl.; www.derivedbd.landcareresearch.co.nz). For the same 38 tree species as observed in current vegetation plots, we compared variation in predicted basal area (m^2) of tree species among remnants using a SSH-MDS ordination, with the Bray-Curtis dissimilarity metric, implemented in PATN. From the biplot of SSH-MDS axes 1 and 2 scores, we estimated the historical change in vegetation composition in each remnant as the euclidean distance between observed and predicted vegetation composition in ordination space.

Analyses

Variation in invertebrate density within and among forest remnants

The number of individual invertebrates per quadrat was converted to no. m^{-2} prior to analysis. We tested two *a priori* expectations for variation in invertebrate density within and among forest remnants. First, we expected that the impact of livestock encroachment and mammalian omnivores should be greatest at forest edges, and in small remnants, due to spatial subsidisation in the surrounding landscape matrix, resulting in positive slopes of edge effects on invertebrate abundance in the absence of livestock exclusion or pest control (F0P0); i.e., edges might be degraded relative to remnant interiors. Therefore, we expected that the greatest immediate response to management action would be observed at edge locations, resulting in a decreasing slope of edge effect on invertebrate abundance with increasing time since livestock exclusion and commencement of intensive pest control (although disturbance-adapted taxa might show the opposite response compared to forest-dependent taxa). Consequently, slopes of edge effects were calculated using simple least squares regression on $\log_{10}(x + 1)$ transformed no. m^{-2}, with distance from edge on a linear scale, and the slopes were compared across treatment classes.

We also expected that management actions should improve "ecological condition" within remnant interiors over time. Differences in invertebrate density in the interiors of forest remnants subject to different livestock exclusion and pest control treatments were best compared using the fitted edge response functions to calculate standardised, model-predicted abundances at a nominally-selected distance of 40 m from the forest edge (which was the maximum core distance of many of the remnants). Predicted values were derived from the best-fit edge response function (null or linear in all cases) (Ewers and Didham 2006a), in order to overcome the differing sizes of forest remnants and the differing edge responses of different taxa at different sites. Negative predicted density values were assigned a zero value.

Variation in invertebrate community composition among remnants

Variation in the relative abundance of invertebrate Classes and Orders between the 30 remnants and three forest reserves was quantified using a constrained Canonical Correspondence Analysis (CCA) ordination on $\log_{10}(x + 1)$ transformed sample-level abundance data. First, an unconstrained Detrended Correspondence Analysis (DCA) ordination was carried out to confirm that the gradient lengths in the species-abundance data were appropriate to the unimodal (chi-square) distance metric underlying the CCA (DCA axis 1: 3.858). We next assessed collinearity among the 36 treatment, environmental and potential confounding variables using a correlation matrix, and found that there were seven pairs of variables that were highly intercorrelated ($r > 0.9$). One of each pair of intercorrelated variables was removed (the spatial variables x^2, y^2, x^2y, xy^2, x^3, y^3, and the shape index, SI), leaving a total of 29 variables in the analysis. Sampling date and spatial autocorrelation among sites (x, y, xy) had significant confounding effects on invertebrate composition and were included as covariables in a subsequent partial CCA (pCCA) analysis. We used a forward selection procedure to rank the measured variables in order of their importance in explaining invertebrate composition (ter Braak and Verdonschot 1995). This process is analogous to forward stepwise regression, and significance was tested at each step using a Monte Carlo permutation test with 999 random permutations. The overall significance of the final pCCA ordination was also tested with a Monte Carlo permutation test, using 999 permutations. All ordination analyses were conducted using CANOCO version 4.02 (ter Braak and Smilauer 1997).

Although the pCCA ordination provides a useful comparison of invertebrate composition between forest remnants and the large-area reference sites, it does not allow a direct test of the effects of management actions on the remnants themselves, because the inclusion of the reference sites in the ordination alters the relative weighting of treatment and environmental correlations. Therefore, treatment effects were more effectively discriminated in subsequent analyses utilising patch-level dissimilarity values calculated from the ordination. From the pCCA biplot of axes 1 and 2 sample scores, the degree of dissimilarity in invertebrate community composition was calculated between each of the 30 remnants and their geographically nearest continuous forest reference site. To do this, we calculated the mean and 95% confidence limits of the euclidean distance between the weighted average (WA) sample scores for each leaf-litter sample in a given remnant and the average (centroid) of the WA sample scores for the geographically nearest large forest area that acted as a local-area reference point.

Discriminating the direct and indirect effects of management actions

We used structural equation modelling (SEM) to discriminate the relative direct, indirect and total effects of livestock exclusion, pest control, and a livestock exclusion × pest control interaction on invertebrate community dissimilarity, using Amos version 16.0 (Arbuckle 2007). From the pCCA ordination analysis it was clear that there was not only a significant interaction effect between the livestock exclusion and pest control treatments, but the treatment effects also covaried with the effects of patch area and slope, and were intercorrelated with multiple environmental variables. In situations such as this, structural equation modelling offers a superior alternative for discriminating the underlying mechanisms of effect, as it allows variables in each model to be specified as both a potential predictor variable and a potential response variable, enabling the causal structure of a composite path model to be tested (Kline 2005). In our SEM, we recognised three causal pathways of treatment effects: (1) indirect effects mediated by environmental variables, (2) indirect effects via shared correlations with patch slope and area, and (3) direct effects (of unknown mechanism). First, we were primarily interested in determining the relative importance of the indirect factors mediating the influence of livestock exclusion, mammalian pest control and their interaction on invertebrate community dissimilarity. Because the number of potential indirect mediating variables that we measured was much larger than the number of degrees of freedom available to test multiple paths in the model, we started from the premise of selecting only one variable to represent each of the soil, vegetation and litter structural variation in the system. We compared the raw correlations between environmental variables and invertebrate dissimilarity as an initial indicator of the variables most likely to mediate treatment effects in the SEM model, testing correlations of both absolute values of the environmental variables, as well as relative values calculated as dissimilarity to the nearest continuous forest reference site (as was done for invertebrate dissimilarity). The three variables selected to have the greatest explanatory power were a soil variable represented by the absolute values of axis 1 scores from the soils SSH-MDS ordination, a vegetation variable represented by relative dissimilarity values calculated between axis 1 and 2 scores of forest remnants and their nearest continuous forest reference site in the plant species SSH-MDS ordination, and a litter structure variable represented by absolute values of average sample litter mass. Second, in addition to indirect mediated pathways in the SEM, the total effects of the treatment variables may also be influenced by indirect effects via joint correlations with underlying spatial or topographic characteristics of the remnants that may also influence invertebrate composition. Moderately strong correlations were observed between the treatment variables and patch slope and patch area, so these variables were entered into the model with all possible combinations of their effects on invertebrate dissimilarity via soil chemistry, vegetation dissimilarity and litter mass. Third, there could also be residual direct effects of livestock exclusion and pest control that represent variance in unmeasured proximate mechanisms of effect, such as the provision of dung resources by livestock (Abensperg-Traun et al. 1996, Hanski et al. 2008), or the direct predation of invertebrates by introduced mammals (Daniel 1973, Cowan and Moeed 1987, Dugdale 1996, Fitzgerald and Gibb 2001). The full SEM model was tested using a maximum likelihood (ML) approach (Kline 2005). Of the nine variables in the full SEM, time since livestock exclusion, patch area, patch slope and litter mass were $\log_{10}$-transformed prior to analysis to meet the assumptions of ML and multivariate normality. The SEM determines standardised path coefficients among variables, which are equivalent to standardised regression coefficients, and these are used to quantify the direct effects of an independent variable on a dependent variable, while controlling for the effects of other independent variables (Mitchell 2001). To find the most parsimonious SEM model with the minimum adequate suite of paths necessary to explain variation in invertebrate composition among forest remnants, we compared multiple hierarchical models using a stepwise specification search in Amos 16.0.1 (Arbuckle 2007), where all paths directly and indirectly affecting composition were fixed as optional. To select the best fitting model from the stepwise specification search results, we used the minimum discrepancy function ($\hat{C}_{MIN}$), adjusted for sample size, $\hat{C}_{MIN}$ /d.f. (Grace 2006). Lower $\hat{C}_{MIN}$/d.f. values indicate good model fit, where $\hat{C}_{MIN}$ /d.f. ≤ 2 is an acceptable minimum value (Bollen 1989). A probability value of $P \geq 0.05$ indicates that the null hypothesis cannot be rejected and the predicted correlations and covariances of the model equal their observed counterparts (Kline 2005). Finally, we used bootstrapping with 1000 random samples generated from the observed covariance matrix to estimate 90th percentile confidence intervals and significance values for the standardised direct, indirect and total effects (Kline 2005) in the final, most parsimonious model.

Results

Variation in invertebrate density within and among forest remnants

A total of 87 376 invertebrates in 31 higher taxonomic groups (not including Acari or Collembola) were extracted from the 964 leaf-litter samples (range: 1-2518 individuals per sample) (Table 2). The fauna was numerically dominated by the Phylum Annelida (6011), the myriapod Class Diplopoda (15 429), the crustacean Orders Amphipoda (7351) and Isopoda (2739), and by the insect Orders Coleoptera (11 880 adults, 3837 larvae), Thysanoptera (11 671), Diptera (352 adults, 10 140 larvae), Hymenoptera (2783 Formicidae, 1290 other families) and Hemiptera (3842). The average densities of most taxa varied widely across sites, with some taxa varying in density by up to two orders of magnitude between the 30 forest remnants and the three forest reserves, and by one to two orders of magnitude between remnants in the different livestock exclusion and pest control treatment classes (Table 2). For total invertebrate density, there was no strong evidence of significant edge effects in either the forest reserves (except a weakly significant positive edge effect at Maungatautari Mountain SR), or in the 30 forest remnants (except for weakly significant negative edge effects in four remnants) (Fig. 2A). Consequently, there was no evidence that livestock exclusion or pest control treatments had any influence on the slope of edge effects in total invertebrate density (Fig. 2A). However, total invertebrate density in the “remnant interior” (i.e., density predicted by the best-fit null or linear edge-model at a standardised distance of 40 m from the edge) was dramatically lower in many of the forest remnants compared with the forest reserves (Fig. 2B), and there was a clear indication that this was related to the absence of pest control in these remnants (squares indicate no pest control, circles indicate pest control in Fig. 2B).

Table 2. Mean (± 1 S.D.) densities (no. m^{-2}) of terrestrial invertebrates (excluding Acari and Collembola) extracted from 33-cm diameter leaf-litter samples in the Waikato Region, New Zealand, using Berlese funnels. Data are collated for multiple forest fragments sampled in each of eight livestock exclusion by mammalian pest control treatment classes (P0, no pest control; P1, pest control) (F0 – F42, time since livestock exclusion, indicating the median number of years since livestock were excluded from fragments in each class). TMRes = Te Miro Scenic Reserve; MauRes = Maungatautari Mountain Scenic Reserve; KaraRes = Karakariki Scenic Reserve. 'Other taxa' comprises Protura (n = 39), Symphyla (24), Isoptera (16), Diplura (14), Neuroptera adults (2) and larvae (11), Archaeognatha (10), Orthoptera (9), Blattodea (7), Dermaptera (7), Hymenoptera larvae (3), Platyhelminthes (3), Trichoptera (3), Pauropoda (2), Siphonaptera (2), Cladocera (1) and unknown (4).

Pest control:	P0				P1				Reference sites			Total
Livestock exclusion:	F0	F6	F12	F42	F0	F6	F12	F42	TMRes	MauRes	KaraRes	count
No. forest fragments:	4	4	3	3	4	4	4	4	1	1	1	33
No. samples:	120	120	88	90	120	115	110	111	30	30	30	964
Phylum Arthropoda												
Insecta												
Coleoptera adults	94.6 (149.6)	128.2 (154.8)	129.9 (246.1)	72.7 (155.2)	62.2 (76.8)	118.4 (128.1)	196.5 (253.4)	194.3 (202.3)	454.4 (428.1)	326.6 (292.8)	215.9 (176.1)	11880
Coleoptera larvae	31.2 (39.8)	30.0 (53.4)	29.5 (37.6)	24.0 (30.2)	72.4 (114.1)	45.2 (96.0)	58.2 (134.2)	73.4 (87.1)	60.8 (38.0)	62.0 (79.2)	21.0 (29.8)	3837
Diptera adults	1.9 (5.7)	4.2 (8.1)	5.4 (14.9)	1.7 (7.1)	2.3 (6.5)	6.7 (13.9)	2.7 (6.7)	6.7 (16.7)	3.9 (7.1)	7.8 (13.5)	10.1 (27.8)	352
Diptera larvae	75.7 (131.8)	103.3 (123.5)	190.0 (274.7)	67.8 (76.4)	75.0 (133.9)	132.8 (173.9)	102.7 (96.4)	184.9 (227.2)	215.5 (222.4)	227.6 (231.1)	162.5 (125.9)	10140
Hemiptera	19.4 (32.7)	32.2 (44.2)	29.1 (49.6)	30.8 (48.5)	61.2 (82.5)	71.2 (121.8)	34.5 (47.5)	53.8 (92.7)	144.2 (120.2)	95.9 (132.8)	30.0 (27.2)	3842
Hymenoptera - Formicidae	20.5 (39.6)	25.7 (79.7)	24.6 (47.9)	5.3 (15.5)	140.9 (323.8)	28.3 (59.5)	15.7 (68.9)	15.8 (32.8)	3.1 (7.5)	17.9 (40.9)	2.7 (5.0)	2783
Hymenoptera - Other	13.8 (20.4)	14.2 (19.2)	9.6 (13.6)	10.8 (25.5)	26.6 (34.6)	21.4 (27.7)	10.9 (18.5)	14.2 (20.2)	16 (18.5)	30.4 (23.7)	2.7 (5.0)	1290
Lepidoptera adults	0.1 (1.1)	0.5 (2.3)	0.4 (2.1)		0.3 (1.8)	0.2 (1.5)	0.3 (1.9)	0.1 (1.1)	0.8 (3.0)	1.2 (4.7)	2.3 (8.9)	29
Lepidoptera larvae	23.4 (29.2)	15.1 (24.6)	15 (19.7)	29.0 (29.2)	62.3 (80.4)	43.2 (71.9)	13.3 (15.2)	46.2 (44.3)	35.1 (29.8)	23 (25.8)	6.6 (11.4)	2525
Psocoptera	18.0 (36.0)	6.3 (18.7)	5.6 (14.6)	4.8 (10.4)	46.5 (121.8)	17.3 (38.8)	7.0 (15.6)	7.2 (16.1)	4.3 (8.4)	3.9 (11.2)	1.6 (5.1)	1135
Thysanoptera	43.6 (72.3)	85.5 (128.3)	45.2 (54.7)	131.3 (237.2)	261.3 (295.2)	193.3 (214.9)	165.4 (459.6)	291.3 (339.8)	4.7 (9.0)	27.3 (43.5)	3.1 (6.1)	11671

…Table 2 continued

Pest control:	P0				P1				Reference sites			Total
Livestock exclusion:	F0	F6	F12	F42	F0	F6	F12	F42	TMRes	MauRes	KaraRes	count
No. forest fragments:	4	4	3	3	4	4	4	4	1	1	1	33
No. samples:	120	120	88	90	120	115	110	111	30	30	30	964
Myriapoda												
Chilopoda	0.8 (3.3)	2.5 (7.6)	1.9 (4.7)	0.3 (1.7)	0.6 (2.6)	2.2 (7.2)	2.0 (6.3)	4.1 (9.9)	1.2 (3.6)	10.9 (14.4)	2.3 (5.7)	173
Diplopoda	80.6 (119.7)	168.7 (245.5)	170.3 (216.0)	60.3 (203.2)	65.7 (143.5)	204.9 (287.8)	210.5 (350.6)	544.1 (747.1)	212.4 (198.2)	243.6 (453.9)	46.8 (42.4)	15429
Crustacea												
Amphipoda	45.1 (86.9)	113.1 (142.7)	186.4 (282.0)	8.8 (23.3)	55.2 (131.9)	61.0 (152.7)	153.1 (241.3)	147.6 (303.5)	18.7 (23.5)	75.6 (67.7)	2.3 (4.8)	7351
Isopoda	7.6 (12.9)	40.5 (109.3)	34.4 (78.7)	6.8 (19.0)	2.8 (11.7)	18.2 (37.4)	39.5 (90.9)	37.1 (64.7)	125.5 (146.3)	242.0 (207.0)	23.0 (26.7)	2739
Arachnida												
Araneae	13.8 (20.0)	20.9 (23.4)	20.1 (25.4)	18.1 (23.3)	36.7 (48.0)	75.2 (132.5)	20.5 (46.4)	31.3 (36.1)	23.4 (21.9)	30.8 (24.7)	17.9 (19.4)	2438
Opiliones					0.1 (1.1)			4.0 (41.1)	0.4 (2.1)	2.3 (4.8)	0.4 (2.1)	47
Pseudoscorpiones	6.8 (12.1)	9.1 (14.7)	27.9 (54.9)	8.3 (10.8)	7.3 (19.5)	7.5 (15.4)	9.9 (19.9)	30.0 (36.7)	48.3 (51.4)	76.4 (74.3)	36.6 (35.5)	1378
Other Phyla												
Annelida	16.8 (43.1)	50.0 (151.2)	28.0 (55.0)	1.6 (7.9)	31.4 (117.4)	45.1 (99.4)	330.1 (2486.9)	111.5 (310.5)	2.3 (5.7)	60.8 (69.4)	3.9 (15.1)	6011
Mollusca	12.9 (24.7)	9.7 (17.8)	10.6 (16.9)	16.1 (23.9)	8.1 (16.9)	18.8 (27.9)	17.3 (26.6)	17.7 (24.2)	20.3 (35.8)	104.1 (181.7)	25.3 (23.4)	1419
Nematoda	26.0 (141.9)	17.6 (56.6)	1.6 (15.0)	0.5 (3.0)	1.1 (6.9)		2.4 (21.6)	19.2 (93.4)	1.2 (3.6)	24.6 (43.4)	1.6 (5.1)	750
'Other taxa'	0.4 (2.1)	1.5 (4.4)	0.5 (3.0)	2.5 (6.9)	0.6 (2.6)	2.1 (10.6)	0.7 (2.9)	2.6 (11.9)	2.7 (5.9)	16.4 (24.3)	2.7 (7.9)	157
All taxa combined	552.9 (418.7)	878.8 (639.1)	966.0 (1028)	501.4 (562.6)	1020.5 (731.3)	1113.1 (861.4)	1393.5 (2998.8)	1837.3 (1430.4)	1399.1 (936.2)	1710.9 (1191.3)	621.6 (365.3)	87376

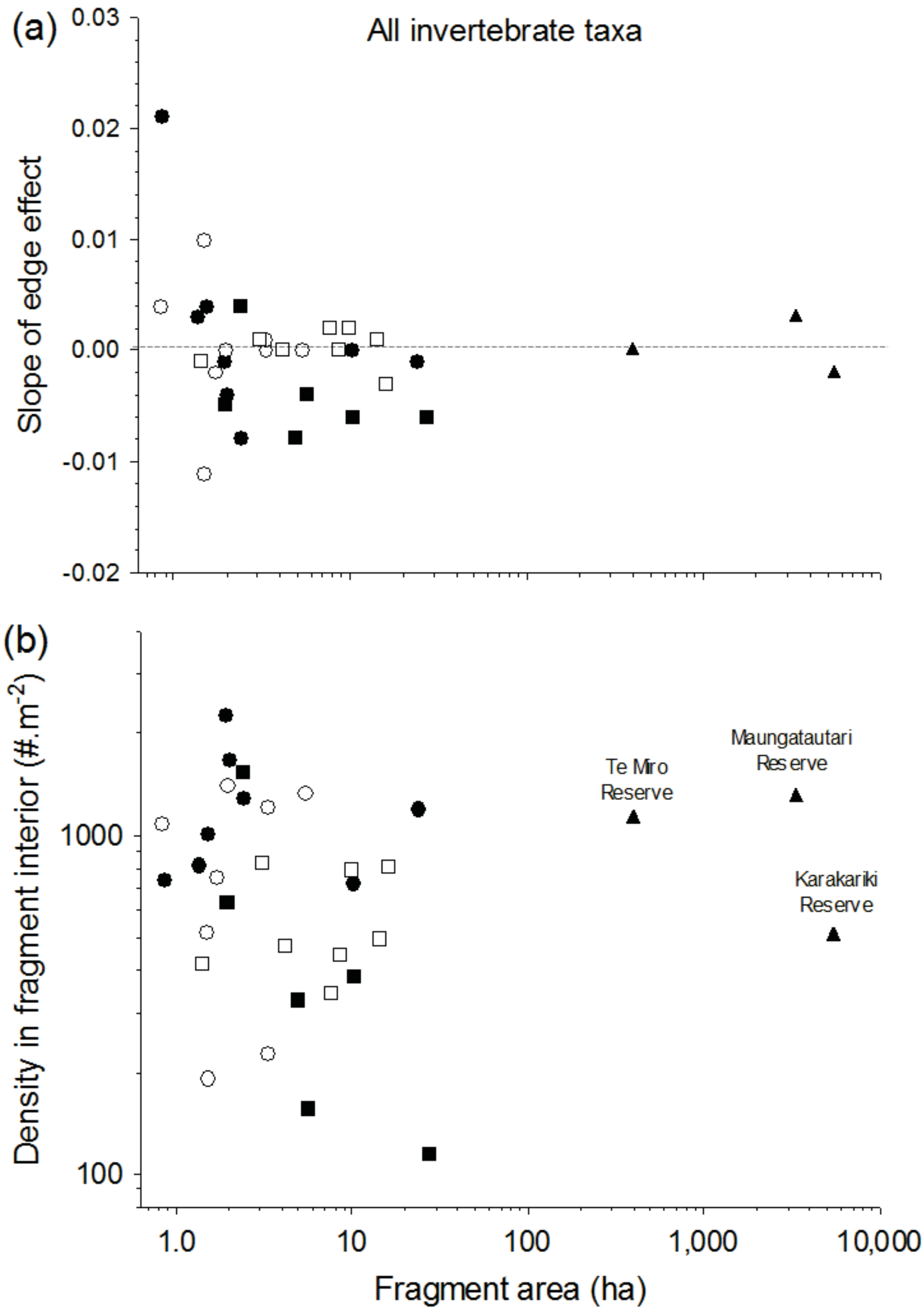

Figure 2. Variation in total leaf-litter invertebrate density (excluding Acari and Collembola) in forest remnants of differing sizes and management treatments: (**A**) slopes (±1 SE) of edge effects calculated using simple least squares regression on $\log_{10}(x + 1)$ transformed invertebrate no. m–2, with distance from edge on a linear scale; and (**B**) mean (±1 SE) invertebrate density in the "remnant interior" (i.e., density predicted by the best-fit null or linear edge-model at a standardised distance of 40 m from the edge). Open symbols = unfenced or recently-fenced remnants (livestock exclusion categories F0 and F6); solid symbols = remnants fenced for a moderately-long to long period of time (F12 and F42). Squares = no pest control; circles = pest control; triangles = forest reserves. Note: a slope of edge effect of 0.01 on a $\log_{10}$ scale of invertebrate density indicates an order of magnitude change in density for every 100 m distance along the edge-to-interior gradient, and a slope of 0.02 indicates an order of magnitude change in density every 50 m.

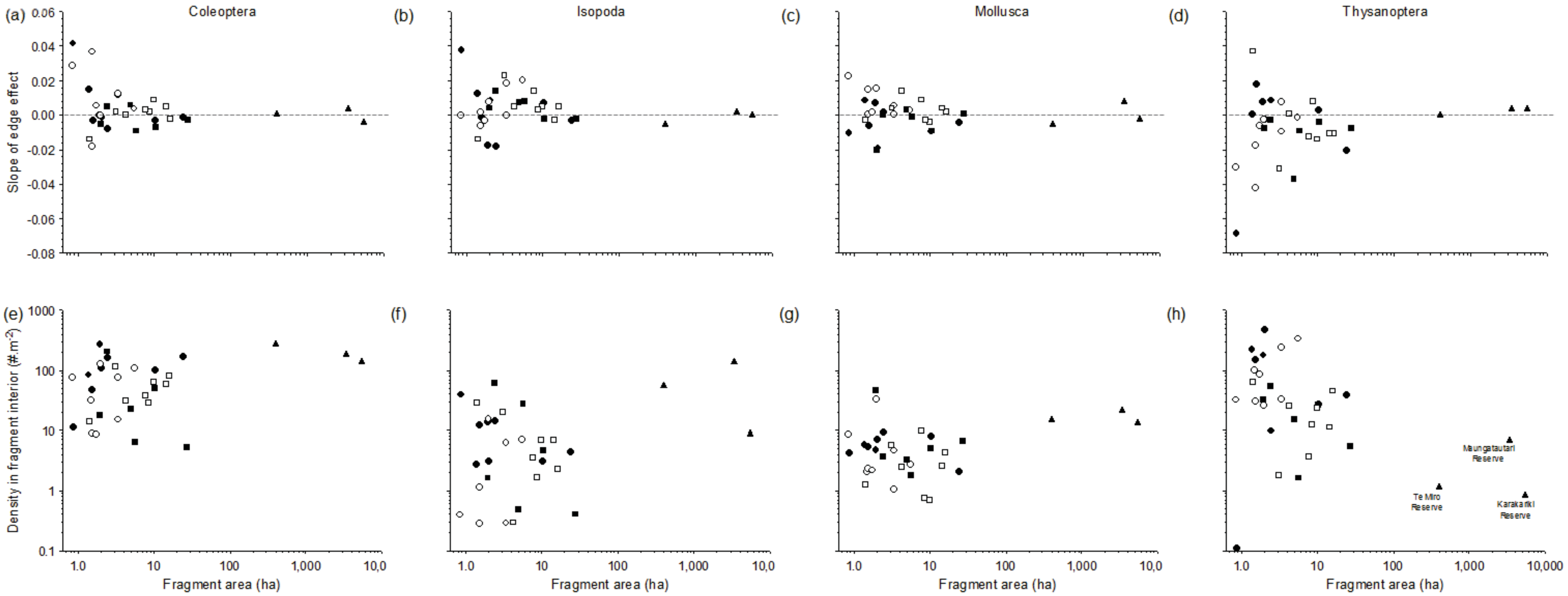

Figure 3. Variation in the densities of selected leaf-litter invertebrate taxa in forest remnants of differing sizes and management treatments: (**a-d**) slopes (±1 SE) of edge effects for Coleoptera, Isopoda, Mollusca and Thysanoptera, respectively; and (**e-h**) mean (±1 SE) density in the "remnant interior" for Coleoptera, Isopoda, Mollusca and Thysanoptera, respectively (see text and Fig. 2 for explanation of how slopes and interior values were calculated). Symbols as in Fig. 2.

Eight out of the 10 remnants with the lowest total invertebrate densities (100–500 m^{-2}) were in the no pest control treatment, whereas nine out of the 10 remnants with the highest invertebrate densities (1000–2500 m^{-2}) were in the pest control treatment (Fig. 2B). By contrast, there was no clear indication of an effect of time since livestock exclusion on total invertebrate density (Fig. 2). As observed for total invertebrate density, there were predominantly non-significant or relatively weak edge effects on the densities of most individual taxa in the majority of forest remnants and forest reserves (representative examples shown in Fig. 3A–D). However, when significant edge effects were detected, these were almost invariably observed in the smallest forest remnants (indicating an interaction between patch area and distance from forest edge), and these also tended to be remnants in the P1 pest control treatment class. Positive edge effects indicated more degraded edge habitat for taxa such as Coleoptera (Fig. 3A), Isopoda (Fig. 3B), Mollusca (Fig. 3C) and Diplopoda (not shown), and an increase in suitable habitat near edges for taxa such as Thysanoptera (Fig. 3D) and Formicidae (not shown), in the smallest forest remnants. Only for Mollusca (Fig. 3C) was there also some indication that time since livestock exclusion had a detectable effect on the slopes of edge effects for invertebrate taxa, with weak positive slopes for recently-fenced remnants (F0 and F6) and weak negative slopes for long-fenced remnants (F12 and F42). In contrast to the weak evidence for edge effects on invertebrate density, there was strong evidence for substantial changes in the densities of invertebrate taxa in the interiors of most forest remnants, compared to densities at the same distance from the edge of forest reserves (Fig. 3E–H). For example, Coleoptera (Fig. 3E) and Mollusca (Fig. 3G) showed a 10-fold decline in density in forest remnants, and Isopoda (Fig. 3F), Hemiptera (not shown) and Diplopoda (not shown) had up to a 100-fold decline in density compared to the interior of the forest reserves. Meanwhile, Formicidae (not shown) had up to a 10-fold increase in density in forest remnants, and Thysanoptera (Fig. 3H) had up to a 100-fold increase in density compared to the forest reserves. These extremely low fragment-interior densities of Coleoptera, Hemiptera and Diplopoda, in particular, were observed predominantly in remnants in the P0 pest control treatment class, and the extremely high densities of Thysanoptera were observed predominantly in remnants in the P1 pest control treatment class (Fig. 3E–H). Again, only Mollusca showed a substantial time since livestock exclusion effect on densities in the remnant interior, with the lowest densities observed for recently-fenced remnants (F0 and F6) (Fig. 3 G). These contrasting patterns of variation in the abundance of individual taxa are indicative of a significant shift in both the overall density (Fig. 2) as well as the composition of invertebrate communities (Fig. 3) in forest remnants.

Variation in invertebrate community composition among remnants

In an initial CCA ordination, all four variables considered to be potential confounding factors in the analysis had significant effects on invertebrate community composition, with substantial variance explained by spatial autocorrelation in latitude ($\lambda = 0.009$, $F = 10.05$, $P = 0.001$), longitude ($\lambda = 0.020$, $F = 21.31$, $P = 0.001$) and the linear component of latitude × longitude ($\lambda = 0.010$, $F = 10.40$, $P = 0.001$) of sampling locations, and to a lesser extent by sampling date ($\lambda = 0.010$, $F = 10.97$, $P = 0.001$). These variables were entered as covariables into a partial CCA, in which they collectively explained 5.9% of the variance in invertebrate composition. After partialling out the covariables, the first four pCCA axes explained 14.1% of the remaining variance in invertebrate composition among leaf-litter samples ($\lambda_1 =$

0.072, λ_2 = 0.022, λ_3 = 0.018 and λ_4 = 0.009 for axes 1.4, respectively; Table 3), with the forward selection procedure identifying patch area, vegetation richness, time since livestock exclusion and a livestock exclusion × pest control interaction as the major predictors of invertebrate composition, explaining more than half of the total effect (Table 3).

Table 3. (a) Results of a forward selection procedure to determine which of the 25 treatment and environmental variables in a partial Canonical Correspondence Analysis (pCCA) explained significant variation in invertebrate community composition among the 964 leaf litter samples (see Fig. 4). Effects were calculated after first partialling out the confounding effects of sampling date and spatial autocorrelation among sampling locations. (b) Interset correlations between variation in the environmental variables and variation in invertebrate community composition on each of the three canonical pCCA axes. Variables are ordered from most to least significant in the forward selection procedure (all with a Bonferroni corrected *P*-value of $P < 0.002$). λ_a represents the additional variance explained by environmental variables as they are sequentially added into the model. Correlations in **bold** are significant at $P < 0.001$. Codes for environmental variables as in Table 1.

	(a) Forward selection			(b) Interset correlations			
Variable	λ_a	*F*	*P*	Axis 1	Axis 2	Axis 3	Axis 4
LgArea	0.042	49.560	0.001	**-0.535**	0.188	0.068	0.052
VegRic	0.018	21.300	0.001	0.122	**0.317**	**0.220**	-0.089
LvExcl	0.010	12.180	0.001	**-0.436**	0.066	**-0.227**	0.023
LxP	0.009	10.830	0.001	**-0.471**	-0.003	0.107	0.046
PltSpl	0.009	11.120	0.001	**-0.206**	-0.026	0.076	0.131
OpCan	0.006	7.230	0.001	0.021	0.114	-0.110	-0.041
Basal	0.005	5.740	0.001	**-0.323**	-0.108	**0.217**	-0.008
MDShis	0.009	11.750	0.001	0.040	0.101	0.123	0.032
MDSsoi	0.007	8.710	0.001	0.148	-0.026	**0.279**	-0.125
PxA	0.005	6.120	0.001	**-0.542**	0.115	0.062	0.034
MDSveg	0.005	6.100	0.001	**0.378**	-0.061	0.125	0.014
PstCtr	0.005	6.580	0.001	-0.051	0.188	**-0.209**	-0.013
Elev	0.005	6.050	0.001	**-0.265**	-0.105	0.036	0.192
5kCore	0.004	5.910	0.001	**-0.439**	0.151	-0.167	0.014
LxA	0.003	4.560	0.001	**-0.395**	0.185	0.107	0.097
SmpLit	0.003	4.130	0.001	**-0.210**	0.018	-0.003	0.037
Dist	0.002	2.710	0.001	-0.176	0.081	0.090	0.041
LxE	0.003	4.540	0.001	-0.024	0.103	-0.050	0.074
PltSdl	0.003	3.650	0.001	-0.048	-0.023	-0.040	0.144
MDScli	0.003	3.350	0.002	-0.152	0.077	-0.026	0.127
$\Sigma(\lambda_a)$:	0.156						
Total	0.911		*Eigenvalue:*	0.072	0.022	0.018	0.009
		Species-environment correlation:		0.734	0.540	0.535	0.433

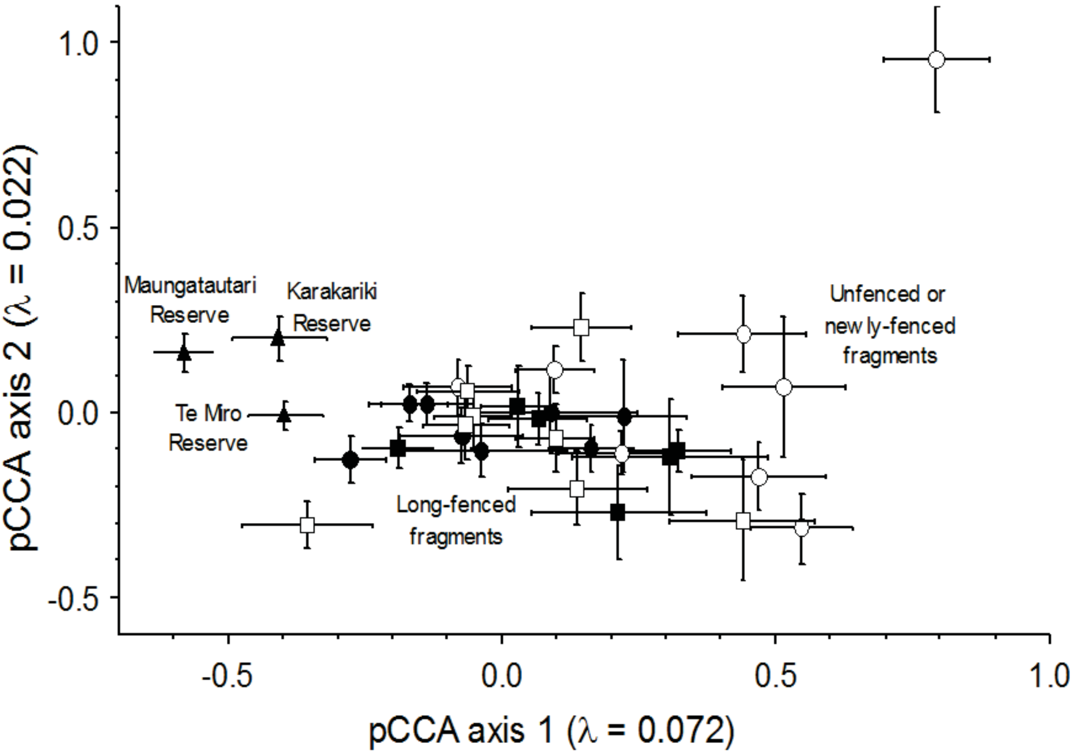

Figure 4. Partial Canonical Correspondence Analysis (pCCA) ordination biplot showing variation in invertebrate community composition among 964 leaf-litter samples collected from 30 forest remnants and three forest reserves (Te Miro Scenic Reserve, Maungatautari Mountain Scenic Reserve and Karakariki Scenic Reserve) in the Waikato region, North Island, New Zealand. Symbols as in Fig. 2. For clarity, variation in invertebrate composition among the individual leaf-litter samples within each remnant or forest reserve is represented as 95% confidence limits around the mean (centroid) of the axis 1and 2 scores for that site. Weighted average sample scores were derived from the pCCA analysis after first partialling out the confounding effects of sampling date and spatial autocorrelation (x, y, and xy) among sampling locations. Lambda (λ) is a measure of the variance explained by site ordering along the ordination axes (see Table 3).

Site ordering along pCCA axes 1 and 2 (Fig. 4) shows the strong dissimilarity in invertebrate composition between forest remnants and the forest reserves, with the relative densities of Isopoda (r = .0.45), Pseudoscorpiones (*r* = .0.40), Coleoptera (*r* = .0.37), Amphipoda (*r* = .0.28) and Diplopoda (*r* = .0.25) strongly negatively correlated with axis 1, and the relative densities of Psocoptera (*r* = 0.29), Lepidoptera (*r* = 0.25), Thysanoptera (*r* = 0.22) and Formicidae (*r* = 0.22) strongly positively correlated with axis 1 (all $P < 0.001$). Only Formicidae density was strongly positively correlated with axis 2 ($r = 0.50$, $P < 0.001$).

The strong patch area gradient was also closely aligned with the effects of time since livestock exclusion and the livestock exclusion × pest control interaction on invertebrate composition (Table 3). Unfenced or recently-fenced remnants (F0 and F6; open symbols in Fig. 4) tended to have higher dissimilarity to the forest reserves than did the long fenced remnants (F12 and F42; closed symbols in Fig. 4), but this was only evident for forest remnants with pest control (P1; circles in Fig. 4) and not in remnants without pest control (P0; squares in Fig. 4). Plotting the livestock exclusion × pest control interaction effect on invertebrate dissimilarity between the 30 forest remnants and their (geographically) nearest forest reserve (Fig. 5A), it is clear that the reason for the treatment intercorrelation with patch area along pCCA axis 1 is because the pest control treatment was inadvertently confounded with patch area in the study design (Fig. 5B; see also Fig. 6). The highest invertebrate dissimilarity values were observed in remnants in the youngest time since livestock exclusion class with good pest control (Fig. 5A), but these were also the smallest of all the forest remnants sampled (Fig. 5B), making it difficult to discriminate the relative treatment effects from the patch area effect. Finally, interset correlations between environmental variables and site ordering along axis 1 were also high for various components of vegetation change (particularly tree basal area and plant species composition) and sample litter mass (Table 3), suggesting further complex interdependencies among treatment and environmental variables.

Discriminating the direct and indirect effects of management actions

To discriminate the direct and indirect causal relationships among these variables, a stepwise specification search was used to select the most parsimonious structural equation model (SEM) explaining variation in invertebrate community dissimilarity (Fig. 6). The reduced model (Fig. 6) had an acceptable minimum discrepancy function, $\hat{C}_{MIN}$ /d.f. = 0.543, and no significant difference between the predicted covariance structure of the model and the observed covariance structure in the data ($P = 0.933$). In this final reduced model, three correlations among variables and 16 causal paths were found to make significant contributions to overall model fit (Fig. 6), although these paths varied in their strength and the statistical significance of their partial regression or covariance coefficients. The major proximate mechanisms affecting invertebrate community dissimilarity were a negative effect of litter mass on invertebrate dissimilarity (i.e., lower litter mass in the remnant led to a greater dissimilarity of invertebrate composition between the remnant and the nearest forest reserve), a positive effect of vegetation dissimilarity on invertebrate dissimilarity (i.e., the more dissimilar the vegetation composition was to the nearest forest reserve, the more dissimilar the invertebrate composition was), as well as a cascading series of causal paths between altered soil chemistry (higher pH and base saturation, and lower total carbon, nitrogen and exchangeable cation capacity), increased vegetation dissimilarity, and lower litter mass (Fig. 6), with substantial total effect sizes for vegetation dissimilarity and litter mass in particular (Table 4). Livestock exclusion and pest control influenced these proximate relationships via weak to moderate effects of time since livestock exclusion and the livestock exclusion × pest control interaction on soil chemistry, and via strong significant effects of pest control on vegetation dissimilarity (Fig. 6, Table 4). In addition, the pest control treatment had further indirect effects on invertebrate dissimilarity via joint correlations with underlying remnant attributes of both slope and area (Fig. 6). The patch slope effect (i.e., remnants with pest control were typically on shallower slopes) was mediated by a strong influence on soil chemistry parameters, and by a significant negative effect on litter mass (Fig. 6). Meanwhile, the patch area effect (i.e., remnants with pest control were typically smaller) was mediated by a strong positive influence (somewhat surprisingly) on vegetation dissimilarity, which affected invertebrate dissimilarity both directly and indirectly via its effect on litter mass (Fig. 6).

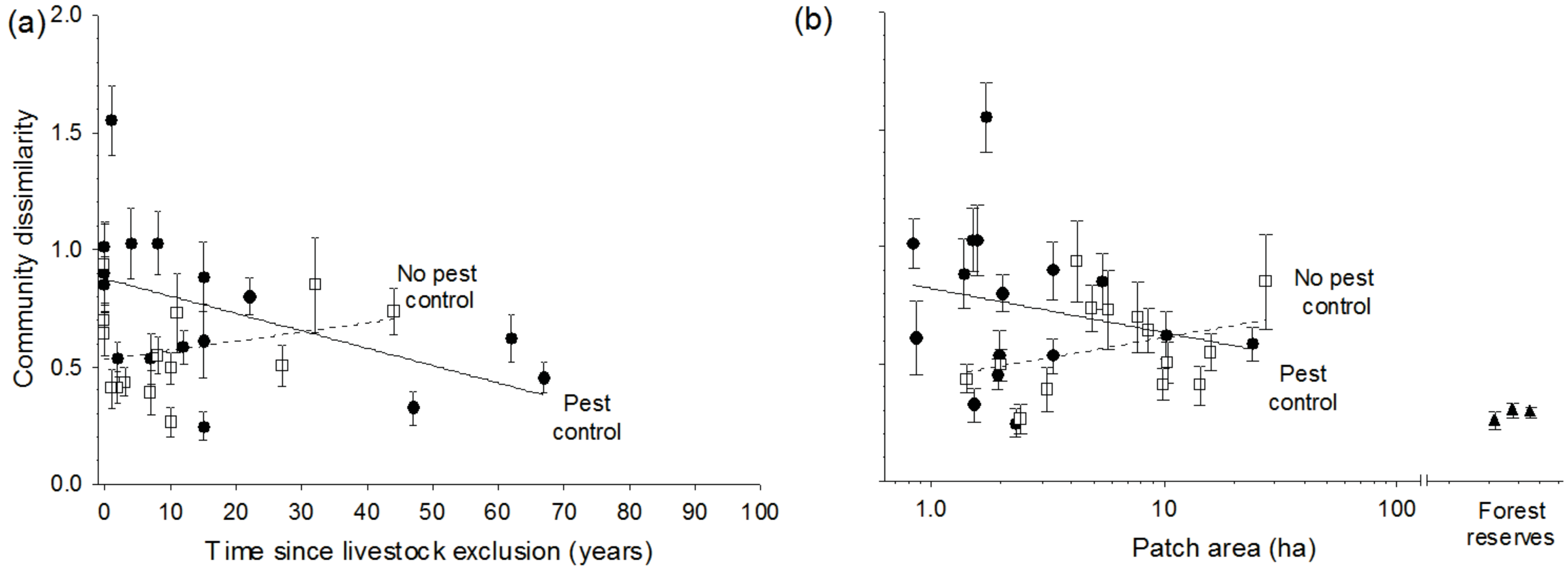

Figure 5. Dissimilarity of invertebrate community composition between each of the 30 forest remnants and their (geographically) nearest forest reserve, plotted with respect to (a) time since livestock exclusion, and (b) patch area. Mean dissimilarity (± 95 % confidence limits) was calculated from the pCCA analysis in Fig. 4, using the euclidean distance between the weighted average (WA) sample scores for each leaf litter sample in a given remnant and the average (centroid) of the WA sample scores for the nearest forest reserve that acted as a local-area reference point. Mean dissimilarity values (± 95 % confidence limits) are also shown for all possible pairwise comparisons among (not within) forest reserve sites in (b). Symbols as in Fig. 2. Overlapping data points offset for clarity.

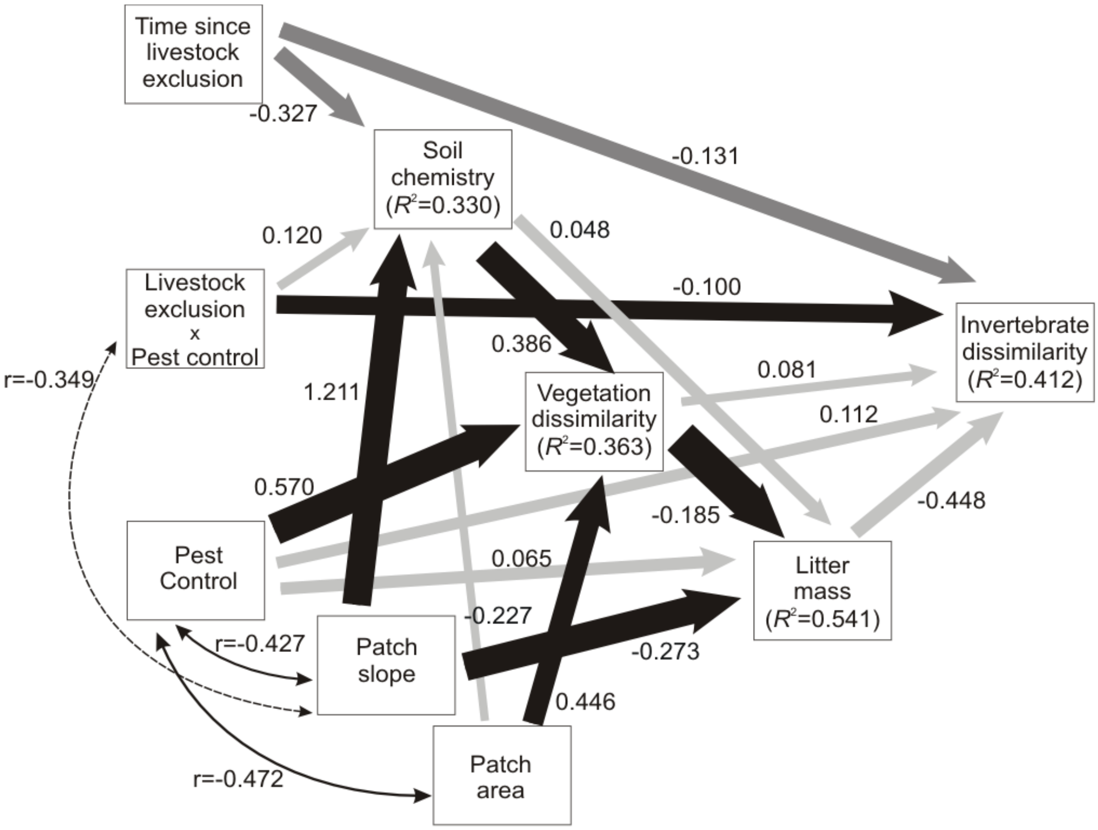

Figure 6. Final reduced structural equation model testing the direct and indirect effects of the livestock exclusion and mammalian pest control treatments on the dissimilarity of invertebrate community composition between each of the 30 forest remnants and their (geographically) nearest forest reserve. Single-headed arrows represent causal paths from predictor to response variables, and the number on each path is the value of the unstandardised partial regression coefficient, indicating whether the relationship is positive or negative. The statistical significance of individual regression coefficients is indicated by the colour of the line (black, $P \leq 0.05$; dark grey $0.05 > P \leq 0.10$; light grey, $P > 0.10$). The thickness of the line indicates the magnitude of the standardised path coefficients, which relates to the effect sizes presented in Table 4. Double-headed arrows indicate covariance between variables, with solid lines indicating significant covariance ($P \leq 0.05$) and dashed lines indicating non-significant covariance ($P > 0.05$) which nevertheless improves the overall model fit. Correlation coefficients, r, are shown for covariance paths. For the four endogenous variables in the model, squared multiple correlations (R^2) are given to represent the variance explained by all the associated pathways linking that variable. Note that vegetation dissimilarity is not the absolute vegetation composition of the site, but is instead the dissimilarity of vegetation composition between each remnant and the nearest forest reserve.

Finally, time since livestock exclusion, pest control, and the livestock exclusion × pest control interaction all had direct effects on invertebrate dissimilarity that could not be explained by the indirect mediating pathways incorporated in the model (although only the direct effect of the livestock exclusion × pest control interaction was strongly significant). These direct effects represented the dominant components of the total effect sizes of the treatment variables (Table 4).

Overall, the SEM model indicates that the longer the period of time that livestock have been excluded from a remnant the greater the reduction in invertebrate community dissimilarity between the remnant and the forest reserves (LvExcl, total effect = –0.320; Table 4). Meanwhile, the direct and indirect effects of pest control on vegetation dissimilarity, combined with the inadvertent confounding of the pest control treatment with patch area and slope, led to a significant increase in invertebrate community dissimilarity in remnants with pest control compared to remnants without pest control (PstCtr, total effect = 0.332; Table 4), but this effect only appears to be significant for unfenced or recently fenced remnants (LxP, total effect = –0.318; Table 4) (see Fig. 5A).

Discussion

The impact of habitat fragmentation on leaf-litter invertebrate communities in managed versus unmanaged remnants.

In the heavily fragmented lowland forests of the Waikato region, New Zealand, the density and composition of leaf-litter invertebrate communities varied significantly between managed and unmanaged forest remnants, suggesting that management intervention can lead to substantial conservation gains in even the most degraded forest remnants. We identified three broad trends in the response of leaf-litter invertebrate communities to habitat fragmentation and subsequent restoration management: (1) the leaf-litter invertebrate fauna is severely degraded in unmanaged forest remnants; (2) management intervention generally increases the density of leaf litter invertebrates and reduces the dissimilarity of community composition between remnants and nearby forest reserves, but different management actions have contrasting effects on the recovery of leaf-litter invertebrate communities; and (3) even the most intensive management intervention in forest remnants does not result in complete convergence of community composition with that found in forest reserves, over the time period studied here.

First, unmanaged forest remnants (i.e., unfenced remnants without significant management intervention) exhibited the lowest invertebrate densities and a substantial shift in overall community composition compared to forest reserves, even when composition was measured as total counts of invertebrates within higher taxonomic units. The higher taxon approach taken here thus provides strong evidence of widespread restructuring of litter-dwelling invertebrate communities in small remnants, involving in particular key detritivore taxa such as Mollusca, Diplopoda, Isopoda and Coleoptera. There have been surprisingly few comparable studies of the degree to which habitat fragmentation affects overall invertebrate community composition in New Zealand (Ewers et al. 2002, Norton 2002, Ewers 2004), but elsewhere similar levels of effect have been widely reported (reviewed in Didham 1997 and Ewers and Didham 2006b). Given that invertebrates comprise the largest component of biomass and biodiversity in terrestrial systems (Wilson 1987), these effects are likely to have a significant impact on ecosystem functioning in forest remnants (e.g., Didham et al. 1996, Larsen et al. 2005, Snyder and Hendrix 2008).

Of course, we recognise that the use of higher taxon data will inevitably leave some questions unresolved until the corresponding species-level data become available. For instance, here we interpret the observed trends in higher taxon abundance as being indicative of a general decline in many, if not most, dominant species within each of these Orders, but this could easily mask contrasting species-specific variation in the densities of rarer species (Ewers and Didham 2006b). For example, at the Hope River Forest Fragmentation Project in the South Island, New Zealand, trends in the abundance of higher taxa in forest remnants (Ewers and Didham 2006a) were consistent with declining abundances of the majority of individual species (e.g., Ewers and Didham 2008), and yet a substantial number of rarer species showed contrasting responses (Ewers et al. 2007). Furthermore, contrasting species-specific responses to habitat fragmentation have been recorded for a range of other invertebrate species in New Zealand (Ogle 1987, Burns et al. 2000, Harris and Burns 2000, Bach and Kelly 2004) and elsewhere (see reviews in Foggo et al. 2001, Tscharntke et al. 2002a, Ewers and Didham 2006b).

Second, although management intervention was generally beneficial for invertebrate communities inhabiting remnants, different management actions had contrasting effects on the densities of different invertebrate taxa. In some treatments there was a significant reduction in community dissimilarity between remnants and their nearest forest reserve (convergence, or recovery, in community structure), whereas in other treatments there was a significant increase in invertebrate community dissimilarity in remnants (divergence in community structure). For instance, time since livestock exclusion had a consistently positive effect on the densities of most taxa, particularly Isopoda, Pseudoscorpiones, Coleoptera, Amphipoda, Diplopoda and Mollusca, but the magnitude of the effect was strongly dependent on the level of mammalian pest control applied. In unfenced or recently-fenced remnants, pest control actually had an adverse effect on invertebrate communities, with intensive pest control associated with an increase in invertebrate dissimilarity compared to the nearest large forest area. In particular, intensive pest control in recently-fenced forest remnants promoted unusually high densities of Thysanoptera and Formicidae (Hymenoptera) that were atypical of the densities normally found in forest reserves.

There was no consistent evidence that these contrasting management effects on invertebrate communities were mediated by altered edge response functions of different taxa. We had expected the impact of livestock encroachment and feral mammalian omnivores to be greater at forest edges than in the forest interior (e.g., Bach and Kelly 2004), and therefore predicted that the greatest immediate response to management action would be observed at edge locations. In general, though, we found that the densities of most invertebrate taxa were not significantly related to distance from forest edge in most remnants, despite recent evidence of the large magnitude and extent of edge effects for many invertebrate taxa (Ewers and Didham 2006a,b, 2008; but see Kotze and Samways 2001, Dangerfield et al. 2003). In the relatively few cases where significant edge effects were detected, they did tend to be in the direction expected, with a decrease in the slopes of edge effects for forest-dependent invertebrates, and an increase in the slopes of edge effects for disturbance-adapted invertebrates, with increasing time since livestock exclusion in the intensive pest control treatment. However, a more parsimonious explanation for the observed edge responses is that there was an inadvertent bias in the selection of forest remnants across management treatment classes, with recently-fenced remnants in the intensive pest control treatment tending to have the smallest patch areas of all the remnants sampled. The greater slopes of edge effects in the smallest remnants (typically <1.5 ha) are consistent with recent evidence that non-linear interactions between patch area and edge effects (Ewers et al. 2007; Fletcher et al. 2007) exacerbate the impact of habitat fragmentation on invertebrate community decline in very small remnants.

The confounding effect of patch area on invertebrate community structure was pronounced, even though remnants were selected to have only a narrow range of patch areas (from c. 1–30 ha) reflecting the real range of remnant sizes that are typically considered for conservation management on private land (QEII Trust 1984, Porteus 1993, Anon. 2008). As a generality, larger remnants (greater than c. 4–5 ha) tended to have densities of most invertebrate taxa that were more similar to forest reserves than those in smaller remnants, regardless of management treatment. The smallest remnants (less than c. 1.5 ha) were most dissimilar in community composition and appeared to exhibit divergent trajectories of community change in response to pest control treatment.

Third, even in forest remnants with the greatest level of management intervention (i.e., a long period of livestock exclusion and a history of intensive mammalian pest control), there was still a significant residual difference in invertebrate community composition compared to that observed in forest reserves. This most likely represents the inevitable change in composition associated with a dramatic reduction in habitat area (i.e., this is “as good as it gets” for a forest remnant), but it might also be that 67 years of livestock exclusion is still not enough time for complete community recovery. Deforestation and land-use intensification in the surrounding landscape may have forced remnant communities over some significant biotic or abiotic thresholds, suggesting that there might still be some component of “recoverable” variation in community composition in remnants that requires more extreme management intervention (such as faunal translocations or improvement of habitat quality) (Hobbs and Cramer 2008).

Discriminating the interactive effects of livestock exclusion and mammalian pest control on invertebrate community recovery in degraded forest remnants

Our most striking finding was the degree to which the recovery in invertebrate abundance and community composition towards the condition observed in nearby forest reserves was influenced by a complex, antagonistic interaction between livestock exclusion and mammalian pest control. Using structural equation modelling to discriminate the direct and indirect drivers of management effects, we found that livestock exclusion and pest control affected litter invertebrate communities via a cascading series of changes in soil geochemistry, leading to altered vegetation composition and significant variation in leaf-litter mass among remnants, with the strongest relative effects mediated by the direct and indirect effects of vegetation dissimilarity on invertebrate dissimilarity. Interestingly, both the main effect of time since livestock exclusion and the main effect of pest control, had an almost identical magnitude of total (direct and indirect) effects, but with opposite signs. The livestock exclusion × pest control interaction was itself of equivalent magnitude of total effect to the main effects of the two separate treatment variables, with a net effect in the same direction as the time since livestock exclusion treatment. This suggests that although the two management actions had contrasting effects in the short term, it appears that long-term livestock exclusion results in the greatest recovery of invertebrate composition (lowest dissimilarity), irrespective of whether intensive pest control is applied or not.

In terms of the livestock exclusion treatment, it is surprising that there have been only anecdotal studies investigating the effects of livestock trampling and browsing on invertebrate communities in New Zealand forests (Burns et al. 2000; but see Scrimgeour and Kendall 2003, Doledec et al. 2006, Schon et al. 2008 for studies of New Zealand grassland ecosystems, and Abensperg-Traun et al. 1996, Bromham et al. 1999, Woinarski et al. 2002 for a range of similar studies in forest ecosystems elsewhere). Furthermore, we are aware of no studies that that have explicitly tested the effects of livestock exclusion on invertebrate communities in native forest remnants in New Zealand. Even for plant communities, there have been remarkably few studies of the effects of livestock grazing in New Zealand forests (Burns et al. 2000, Buxton et al. 2001, Timmins 2002, Miller 2006, Dodd et al. 2008, Smale et al. 2008) despite the severe damage caused by livestock in the forest understorey. Of these, we know of only two previous studies that have measured the long-term recovery of plant communities following livestock exclusion from forest remnants (Smale et al. 2005, Dodd and Power 2007; but see also Pettit et al. 1995, Spooner et al. 2002, Close et al. 2008 and Dodd et al. 2008 for short-term temporal studies of livestock exclusion from forest remnants in New Zealand and Australia). In both kahikatea-dominated forests in the Waikato Basin (Smale et al. 2005) and tawa-dominated forests in the Rotorua Basin (Dodd and Power 2007), time since livestock exclusion had a significant positive effect on litter cover (up to 10–15 years) and native vegetation recovery (up to 30–35 years), and a significant negative effect on populations of exotic plants in Waikato remnants. Smale et al. (2008) concluded that the outlook for plant communities was bleak in the absence of management intervention, and they argued that livestock exclusion is the single most important measure that managers can take to improve the long-term viability of plant communities in forest remnants.

For invertebrates, our principal knowledge of the potential effects of browsing mammals on native forests comes from the landmark study by Wardle et al. (2001) comparing the community- and ecosystem-level effects of introduced browsing mammals (predominantly feral deer, goats and pigs) inside and outside fenced exclosures throughout New Zealand. Wardle et al. (2001) found very strong increases in the abundances of all dominant leaf-litter invertebrate taxa following browser exclusion. Unlike our study, though, the response of most leaf-litter invertebrates to browser exclusion in Wardle et al. (2001) was not significantly related to the effect of browsers on vegetation density or composition, or to the age of fenced exclosure. Instead, variation in invertebrate density was better explained by combinations of variables reflecting soil geochemistry and litter structure (Wardle et al. 2001). In particular, invertebrate community dissimilarity inside versus outside browser exclosures was most strongly correlated with measures of litter quality and heterogeneity (Wardle et al. 2001).

Wardle et al. (2001) concluded that browsing mammals clearly induced changes in the structure and community composition of dead leaves in the litter layer that must ultimately have resulted from changes in the composition of aboveground vegetation, yet they could not detect a significant cascading series of causal links between soil, vegetation and litter structural effects on litter invertebrates. In the present study, we did observe a weak direct effect of plant community dissimilarity on invertebrate community dissimilarity across remnants, and a strong association between vegetation dissimilarity and litter mass, that together represent the major indirect pathways mediating mammalian browser effects on invertebrate dissimilarity in forest remnants. These changes in invertebrate abundance and composition may result from the negative effect of browsers on plant properties allowing increased light incidence at the ground layer (Suominen et al. 1999) and from adverse microclimatic changes in the ground layer (Kielland and Bryant 1998). However, it is more likely that these effects operate primarily through alteration of litter structure and resource availability. Unfortunately, our measure of litter mass is only a weak surrogate for more complex changes in litter quality, litter structure and litter heterogeneity. With no direct effect of soil geochemistry on invertebrate dissimilarity, and in the absence of appropriate measures of litter resource quality and heterogeneity, we follow Wardle et al. (2001) in considering that adverse effects of browsing mammals on leaf-litter invertebrates might have more to do with the physical trampling and scuffing effects of browsers, than the indirect effects via vegetation change. Wardle et al. (2001) consider that the intensity of scuffing and treading (and resultant disturbance, compaction, and reduced substrate porosity) caused by hoof pressure from deer and goats can be considerable (see also Duncan and Holdaway 1989), and the intensity of these effects by domestic livestock is likely to be even greater because of their larger mass and greater density. Similarly, Dodd and Power (2007) attribute the effects of livestock exclusion on plant community recovery in tawa-dominated forest remnants to the reduction in trampling and soil compaction, and to the reduction in browsing effects on removal of leaves and subsequent litter inputs and soil geochemistry.

In terms of the mammalian pest control treatment, the SEM results indicate an increase in invertebrate dissimilarity in remnants with pest control compared to remnants without pest control, mediated largely by the indirect effects of pest control on vegetation dissimilarity. The exact mechanism underlying this adverse effect of pest control is uncertain (Burns et al. 2011.), but as it is observed only in remnants with continued livestock browsing, or very recent livestock exclusion, it is possible that it is associated with differing successional trajectories resulting from the differential susceptibility of plants to livestock versus omnivore (predominantly possum) browsing. For example, across the larger set of 47 tawa-dominated remnants sampled as a component of the present study, Burns et al. (2011) found that the P1 pest control treatment was associated with an increase in exotic plant species richness. It may also be that a primary focus on reducing possum numbers in the pest control operations unintentionally caused an increase in other omnivorous mammals, such as mice and rats (e.g., Tompkins and Veltman 2006, Sweetapple and Nugent 2007). Certainly, in some of the same forest remnants that we sampled, Innes et al. (2010) found very high densities of ship rats. Once again, the exact mechanism by which the changes in plant community dissimilarity might have resulted in the observed changes in invertebrate community dissimilarity is unknown. The most striking change in invertebrate composition in small remnants with P1 pest control management was a massive increase in the densities of Thysanoptera (thrips) and Formicidae (ants) in the leaf litter. Whether this results from direct changes in plant resource availability, or is only indirectly associated with other soil, vegetation or litter properties remains to be tested.

Lastly, the SEM was also able to tease out the degree to which management effects were confounded with inadvertent differences in the area and slope of remnants in different treatments. Both patch area and patch slope had significant indirect effects on invertebrate dissimilarity via their influence on soil geochemistry, vegetation dissimilarity and litter mass, but the magnitude of these indirect effects was substantially smaller than either of the management treatments or their interaction. Of course, there is only a limited capacity for statistical analyses to overcome the inherent bias in remnant sizes among treatments (Grace 2006), and these conclusions will inevitably remain somewhat speculative in this study.

Trajectories of invertebrate community recovery in heavily fragmented landscapes

Careful management consideration needs to be given to the strikingly divergent short term trends in both plant and invertebrate composition exhibited in unfenced or recently-fenced forest remnants with intensive pest control compared to remnants with no pest control. For plants, short-term trajectories of weed invasion and the succession of a non-random subset of native species persisting in forest remnants could drive these dynamics (Smale et al. 2005, Burns et al. 2011). For invertebrates, initial indications are that the unusually high densities of Thysanoptera and Formicidae in these treatments might represent high levels of invasion of disturbance-adapted taxa when intensive pest control is applied without first having 10–20 years of recovery from livestock exclusion, and this warrants further species-level investigation. The irony would be if mammalian pest control promoted an increase in invertebrate pest abundance, whether as an indirect result of pest control effects on vegetation structure, or due to the confounding effects of patch area on invertebrate community structure.

Finally, it is interesting to speculate whether the confounding of intensive pest control treatments with recent livestock exclusion from remnants of smaller average area, on shallower average slopes, was due solely to an inadvertent bias in remnant selection from a moderately small subsample of available forest remnants in this study, or whether it actually stems from a genuine trend in the degree to which management actions covary with remnant attributes in real landscapes. Both livestock exclusion and pest control appear to be applied intentionally to non-random subsets of remnants in order to maximise conservation gain, and perhaps the more intensive and costly the management action, the greater the bias in the selection of the remnants deemed to be of greatest value. Whether the criteria used by land managers to select appropriate remnants for management action actually matches the degree of improvement in ecological condition of the fragment, or even whether this correlates with any wider perceived benefits for conservation, is an open question. Certainly, our data suggest that intensive pest control had unexpected, adverse short term effects on the trajectory of invertebrate community recovery, both independently of patch area via changes in plant community structure (Burns et al. 2011) and also because most of the unfenced and recently-fenced remnants with intensive pest control happened to be of small average area (in our dataset).

Conclusion

Not only is livestock exclusion from native forest remnants an important management tool for the recovery of vegetation structure and composition, it also has substantial positive effects on the recovery of invertebrate community composition on the forest floor. However, the relative effects of livestock exclusion are strongly dependent on the level of mammalian pest control. There appears to be a significant adverse effect of mammalian pest control on invertebrate community composition in unfenced remnants, and for the first 10–20 years following livestock exclusion, although a significant component of this livestock exclusion × pest control interaction is confounded with differing patch slopes and patch areas among treatments. Partitioning of the apparent pest control effect on invertebrate composition using structural equation modelling suggests that it operates primarily through an alteration of vegetation biomass or vegetation successional trajectories, leading to unusually high densities of taxa such as Thysanoptera and Formicidae, without substantive recovery of populations of taxa such as Isopoda, Diplopoda, Coleoptera and Mollusca that are typical of relatively undisturbed forests. In the longer term, recovery trajectories following livestock exclusion converge on similar levels of “effectiveness” at about 30 years after livestock exclusion, whether intensive pest control is applied or not. Nevertheless, given that there are also likely to be substantial species-specific benefits of pest control for the recovery of individual invertebrate (as well as plant and vertebrate) taxa that are not captured by our higher-taxon approach, we cannot discount the possibility that a combination of these management actions may be most effective in the long term. With the available evidence, though, priority should be given to livestock exclusion when conservation management is targeted at leaf-litter invertebrate communities.

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MASSEY UNIVERSITY
GRADUATE RESEARCH SCHOOL

STATEMENT OF CONTRIBUTION
TO DOCTORAL THESIS CONTAINING PUBLICATIONS

(To appear at the end of each thesis chapter/section/appendix submitted as an article/paper or collected as an appendix at the end of the thesis)

We, the candidate and the candidate's Principal Supervisor, certify that all co-authors have consented to their work being included in the thesis and they have accepted the candidate's contribution as indicated below in the *Statement of Originality*.

Name of Candidate: Jessica Anne Costall

Name/Title of Principal Supervisor: Russell Death

Name of Published Research Output and full reference:

Didham, R. K., G. M. Barker, J. A. Costall, L. H. Denmead, C. G. Floyd, and C. H. Watts. 2009. The interactive effects of livestock exclusion and mammalian pest control on the restoration of invertebrate communities in small forest remnants. *New Zealand Journal of Zoology 36*: 135-163.

In which Chapter is the Published Work: Chapter 7

Please indicate either:

- **The percentage of the Published Work that was contributed by the candidate:** ______

  and / or

- **Describe the contribution that the candidate has made to the Published Work:**

Raphael Didham and Gary Barker are the first and second authors of this paper, as they were primarily responsible for designing the study, data analysis, and the writing of the manuscript. I made a significant contribution by coordinating and undertaking fieldwork, laboratory work, and data entry, and provided input on study design, manuscript preparation and editing. Lisa Denmead, Corinne Watts, and Chris Floyd are also co-authors, and made significant contributions towards study design, fieldwork, laboratory work, and manuscript development.

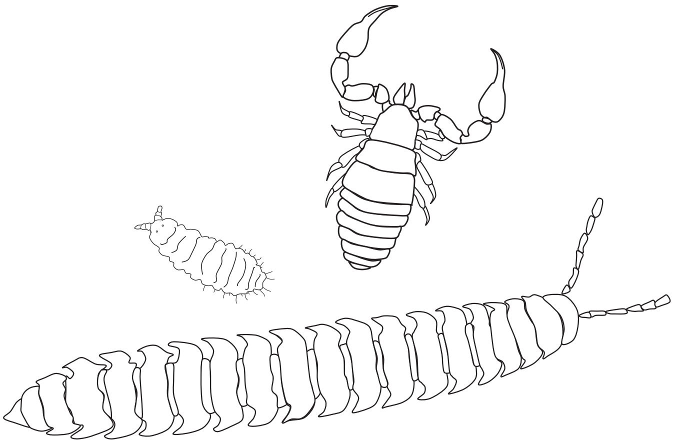
Jessica Costall
Candidate's Signature

29/9/2012
Date

Principal Supervisor's signature

29/9/2012
Date

Synthesis and Recommendations



The purpose of my research was to extend current knowledge of the structure and function of litter invertebrate communities in native forest remnants. Specifically, I investigated how both remnant geography and condition (i.e., the presence or absence of livestock) affected these communities, and subsequently, whether commonly employed restoration techniques such as fencing to exclude livestock, and possum control, could lead to a recovery of community structure and function. I conducted observational studies in two distinct fragmented native forest/pastoral landscapes in the Waikato region, in the North Island of New Zealand. Prior to these studies, little information on the relative importance of forest remnant area and condition existed for invertebrates. It had been established that livestock grazing was detrimental for native remnant vegetation but the effects on forest floor invertebrates had not been investigated.

Livestock impacts, from grazing, trampling, rubbing, defecation and urination, had both direct and indirect impacts on invertebrate habitat. Grazed remnants had markedly different, and more variable habitat to that of fenced remnants or forest reserves; for example, they had higher soil compaction, reduced understorey vegetation, reduced tree basal area and diversity, and higher bare soil groundcover (Chapter 1). Thus grazed remnants provide highly altered habitat for litter invertebrates, in terms of microclimate, interstitial spaces, and resource quality and quantity (particularly for detritivores which rely on leaf litter). However, fenced remnants can provide forest floor habitat similar to that in larger forest reserves (Chapter 1). Habitat changed with distance from forest edge, with habitat in fenced and forest reserve sites becoming more similar with increasing distance from the edge, yet habitat in grazed sites remained distinct from fenced and reserve sites at all distances (Chapter 1).

These dramatic changes in forest floor habitat lead to markedly distinct invertebrate communities in grazed remnants (Chapter 2). Specifically, grazed remnants had depauperate communities, with several taxa, particularly prostigmatid mites, sphaeroscerid flies, and pseudoscorpions, exhibiting markedly lower abundances in grazed remnants compared to fenced and reserve sites. Some taxa, such as araneomorph spiders, had higher abundances in grazed remnants than in fenced or reserve sites (Chapter 2). Invertebrate communities in grazed remnants were much more variable than in fenced or reserve sites. Community variability may be an indicator of high levels of disturbance or stress.

The nature of the edge responses also varied between management categories, with taxa such as entomobryomorph springtails and mycetophilid flies exhibiting steeper edge responses at grazed remnants than in remnants from other management categories (Chapter 3). However, most taxa had highly variable, seemingly idiosyncratic edge responses. Fences that exclude livestock may in fact partially ameliorate or lessen the severity of edge effects for invertebrate communities in small forest fragments, by allowing a dense “buffer” of understorey vegetation to establish. This buffering effect seems to at least partially override the influence of remnant area on edge structure (Chapter 3).

It is important to know whether ecological restoration actions, such as fencing to exclude livestock and pest control, have any benefit for litter invertebrates. These restoration actions have clear benefits for the native vegetation of remnants, but prior to my research little was known about the flow-on effects for invertebrates. I found that invertebrate communities showed a strong recovery with time since fencing, with several taxa increasing in abundance with time since fencing (Chapter 5). The recovery of invertebrate community structure is long-term, with some taxa only responding more than a decade following livestock exclusion, and other taxa still increasing in abundance fifty years post-fencing. Millipede community structure also responds strongly to livestock exclusion, but also appears to require sustained possum control, as remnants with long-term fencing and possum control supported millipede communities most similar to nearby large forest reserves (Chapter 6). The findings of a larger collaborative study support this (Chapter 7).

Changes in community structure are predicted to have flow-on effects for ecological functions, but as yet this has been little studied in fragmented landscapes. Invertebrates are known to make important contributions to several important ecological functions. However, despite strong effects of livestock grazing on invertebrate habitat and community structure, the effects on one key ecological function, litter decomposition, was more muted (Chapter 4, Chapter 5). Leaf and wood decomposition rates did not vary between grazed, fenced and forest reserve sites. Instead, decomposition rates seemed to be determined by variables at the sampling plot-scale only, with the density of understorey vegetation, percentage litter moisture, and litter macroinvertebrate community composition being particularly important. However, in another study I found that leaf decomposition rates at the edge of forest remnants increased with time since livestock exclusion (Chapter 5), suggesting that remnant condition, and restoration actions can influence ecological functioning of remnants.

Invertebrate conservation and restoration studies are comparatively rare. This is partly a result of a lack of researchers with the required taxonomic skills. However, my research indicates that restoration success for invertebrates can be adequately assessed at the ordinal taxonomic level. It is my hope that my research has highlighted some useful taxa for further study at a more resolved taxonomic level. For example, taxa such as millipedes and pseudoscorpions are little-studied, yet are clearly highly sensitive to remnant condition and restoration actions, and warrant further study.

Many studies of terrestrial invertebrate communities have focused on using simple community metrics, such as diversity indices. Studies that have examined patterns in community composition are comparatively rare, though they are clearly more informative. Species-area relationships are notoriously difficult to apply in fragmented landscapes, due to the invasion of generalist matrix species into habitat fragments.

My research has shown that the benefits of commonly-employed restoration actions extend beyond protecting native vegetation of remnants. Fencing to exclude livestock is clearly the single-most effective restoration action for native forest remnants on farmland. Even very small remnants can have high ecological value if they are protected by high-quality fencing. However, it appears that additional restoration actions, such as long-term sustained possum control, are also required to effectively restore litter invertebrate communities to approach that of larger forest reserves. I suspect that other restoration actions, such as replacement/supplementary planting of native trees, weed control, and sustained control of other pest mammals, particularly rodents, would also benefit litter invertebrate communities in forest remnants. Since these management actions require substantial financial investment from land-owners, research should be undertaken to assess the efficacy of these actions.

My specific recommendations for the restoration of native forest remnants in New Zealand are as follows:

- Restoration of forest remnants on farmland should prioritise livestock exclusion first and foremost. Even small remnants (i.e., < 3 ha) can retain high ecological (and social/lifestyle) value if fenced. Livestock are extremely destructive to native vegetation, and without effective fences, native forest remnants will eventually degrade into pasture.
- Livestock exclusion is most effective when combined with long-term, sustained possum control. As possums are known vectors of bovine tuberculosis, many rural landowners already carry out possum control on their properties. As mammalian pests are known to rapidly reinvade areas following control, sustained, landscape-scale control programs will be most effective.
- Restoration actions represent a substantial cost to private landowners. Organisations such as regional councils and QEII National Trust already provide some financial assistance to landowners, but this could be improved.

My recommendations for future ecological research:

- I observed higher variability in community structure amongst highly disturbed (grazed) remnants, as opposed to less disturbed (fenced and reserve) sites. Studies in aquatic systems have also found this relationship, and have suggested increased community variability can be used as an indicator of increase stress. However, this relationship has been poorly explored for terrestrial invertebrate communities.

- Invertebrates remain understudied in the fields of habitat fragmentation and ecological restoration. Additionally, there is a strong taxonomic bias in existing invertebrate restoration, so that taxa such as beetles, butterflies, and ants have received the bulk of attention. My research has identified several other invertebrate taxa that are highly sensitive to remnant condition, and restoration actions, and warrant further attention.
- More research is needed to investigate the efficacy of additional restoration actions, such as rodent control and supplementary planting, for litter invertebrates, and the ecological condition of remnants as a whole.

Most conservation and restoration actions are directed towards the conservation of native plant and vertebrate populations. We still tend to overlook the invertebrates, despite their important roles as “the little things that run the world” (Wilson, 1987). New Zealand was once blanketed in forest, but regrettably, most of that forest has been cleared in the comparatively short time since human arrival. All of our lowland native forest remnants, no matter how small or degraded, have high conservation value and the potential to support diverse native invertebrate communities. Encouragingly, the greatest conservation gains can be made from arguably one of the most simple and cost-effective restoration actions, that is, fencing to exclude livestock. However, if we do not act to protect our forest remnants from livestock they could be lost forever within the space of a few decades.

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