

**The Effects of Seabirds, Rats, and Ecosystem
Restoration on Invertebrate Food Webs.**

Joshua Jeffrey Thoresen

PhD

2016

The Effects of Seabirds, Rats, and Ecosystem Restoration on Invertebrate Food Webs.

Joshua Jeffrey Thoresen

A thesis submitted to Auckland University of Technology in fulfilment
of the requirements for the degree of
Doctorate of Philosophy (PhD)

2016

School of Science

Auckland University of Technology

Abstract

Burrowing seabirds that nest on islands transfer nutrients from the sea, disturb the soil through burrowing, damage tree foliage when landing, and thereby modify the surface litter. One of the greatest effects seabirds may have on their recipient ecosystems may be via the nutrient subsidies they transfer onto islands from the sea. How these nutrients effect their recipient ecosystems however, depends on many factors such as water availability. However, seabirds are in decline worldwide, as are their community- and ecosystem-level impacts, primarily due to invasive predatory mammals. Seabird islands are vulnerable to the invasion of predatory mammals such as rats, which can have lasting effects even after these pests are eradicated. Once these islands are restored and seabirds start to return the ecosystems can recover quickly, returning to a pre-disturbance state within as little as 20 years. However, legacy effects of the invasive mammals may occur meaning ecosystems may revert to alternate stable states. The direct and indirect effects of seabirds, their decline and recolonisation on ecosystems are inherently complex. I employed network analysis of invertebrate food webs, as a means of simplifying ecological complexity, to better understand the effects seabirds, their loss, and recolonization, may have on island invertebrate communities. I found that on rat-invaded islands the invertebrate food webs were smaller and less complex than on their seabird-dominated counterparts, likely due to the suppression of seabird derived nutrients and consequent effects on trophic cascades. There was also an interplay between nutrient subsidies and water availability, where invertebrate food webs were larger and more complex as litter water increased and soil C: N slightly decreased. When comparing a restored island to invaded islands and those never invaded I found that the restored island supported some areas that were virtually indistinguishable from an invaded island and it

demonstrated strong environmental gradients indicative of a recovering island. Finally when comparing the family richness and missing common families between islands I found that the restored islands had a similar number of missing families to invaded islands and were missing more family groups than islands that had never been invaded when controlling for covariates. Seabird and rat effects on island ecosystems are manifested throughout entire food webs. As seabirds spread across restored islands the areas similar to invaded islands will become fewer as the island starts to fully resemble a burrowing seabird island ecosystem. A key finding was the resilience of the invertebrate food webs, which shrunk to a fraction of their full potential complexity during arid periods then reconstructed themselves with increased water availability. However, the invertebrate food webs were unable to reconstruct fully on restored islands due to the legacy effects of invasive mammal suppression. This may have had negative effects on the nutrient cycling of at least one of the restored islands. I finally conclude that more effort is needed to understand and integrate invertebrate communities into ecosystem restoration in the future.

Table of Contents

Cover page page.....	i
Title page.....	ii
Abstract.....	iii
Acknowledgements.....	xi
Chapter one: Introduction	1
1.1 Literature review	2
1.1.1 The effects of seabirds on island ecosystems.....	4
1.1.2 The effects of seabird loss or invasive species on island ecosystems	7
1.1.3 The application of network analysis of food webs.....	9
1.2 Research questions	13
1.3 Thesis layout	15
1.4 Methods summary	15
1.4.1 Study sites and field methods.....	15
1.4.2 Invertebrate identification and food web description.....	23
Chapter two: Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure.....	28
2.1 Abstract	29
2.2 Introduction	30
2.3 Methods.....	34
2.3.1 Study sites	34
2.3.2 Sampling methods.....	35
2.3.3 Network description.....	36
2.3.4 Network analysis metrics	38
2.3.4 Statistical methods	39
2.4 Results	40
2.5 Discussion	43
2.6 Supplementary materials	48
Chapter three: Effects of litter water and nutrient subsidies on invertebrate food webs in an island ecosystem	51
3.1 Abstract	52
3.2 Introduction	53
3.3 Methods.....	57
3.3.1 Study site.....	57
3.3.2 Experimental set up.....	57
3.3.3 Food web methods	59
3.3.4 Statistical methods	60

3.4 Results	61
3.5 Discussion	70
3.6 Conclusion.....	75
3.7 Supplementary materials	77
Chapter four: Network analysis of food webs defines the restoration status of a seabird island ecosystem	79
4.1 Abstract	80
4.2 Introduction	81
4.3 Methods.....	84
4.3.1 Study areas	84
4.3.2 Field methods.....	86
4.3.3 Food web methods	88
4.3.4 Statistical methods	91
4.4 Results	92
4.5 Discussion	101
4.6 Conclusion.....	106
Chapter five: The legacy effects of invasive predatory mammals on invertebrate families on restored seabird islands	108
5.1 Abstract	109
5.2 Introduction	110
5.3 Methods.....	113
5.3.1 Study sites	113
5.3.2 Field methods.....	115
5.3.3 Statistical methods	117
5.4 Results	118
5.5 Discussion	122
5.6 Conclusion.....	127
Chapter six: Discussion.....	130
6.1 Introduction	131
6.2 The effects of seabirds and rats	133
6.3 The interplay between nutrient subsidies and water	136
6.4 The effects of restoration	140
6.5 The legacy effects of rats	144
6.6 Conclusion.....	146
6.7 Management recommendations.....	149
References	151
Appendix A: The niche model	181
Appendix B: Invertebrate identification.....	188

Appendix C: Mercury Islands and their role in understanding seabird island restoration	192
---	-----

Table of Tables

Table 1.1 Summary table of study islands	21
Table 2.1 ANCOVAs between food webs and island status, size and isolation, and soil N...43	43
Table 2.2 Traits of islands used in Chapter 2	48
Table 2.3 Environmental variables on seabird and non-seabird islands	49
Table 2.4 Food webs on seabird and non-seabird islands	49
Table 3.1 Multilevel ANOVAs for environmental variables	62
Table 3.2 Multilevel ANOVAs for food webs	64
Table 3.3 Multiple linear models between food webs and environmental variables	68
Table 3.4 Amounts of fertilizer used for each treatment.....	77
Table 4.1 Linear discriminant analyses comparing Korapuki and Ruamaahuanui	96
Table 5.1 Chao2 asymptotic species richness estimations	122
Table A1 Comparisons of empirical and niche model food webs for chapter 2	183
Table A2 Comparisons of empirical and niche model food webs for chapter 3	183
Table A3 Comparisons of empirical and niche model food webs for chapter 4	184
Table B1 Invertebrate identification and feeding strategies.....	189

Table of Figures

Figure 1.1 Correlation matrix heat map of food web metrics	12
Figure 1.2 A conceptual diagram of the research questions and flow of this thesis	14
Figure 1.3 Map of the nineteen islands used in this study	17
Figure 1.4 Map of an enlargement of the Mercury, Noises and Alderman Island groups	18
Figure 1.5 Map of an enlargement of the Western Coromandel and Poor Knights Island groups.....	19
Figure 2.1 The most and least complex food webs on seabird and non-seabird islands	41
Figure 3.1 Boxplots of environmental variables between the three sampling trips	63
Figure 3.2 Three dimensional regression plot of entropy vs. litter dry weight and soil C:N ..	66
Figure 3.3 Three dimensional regression plot of saprophagivores vs. litter dry weight and soil C:N	67
Figure 3.4 Food webs of the highest and lowest entropy per trip	69
Figure 4.1 Boxplots comparing invertebrate functional group abundances between four island groups	93
Figure 4.2 Boxplots comparing the food webs between four island types.....	95
Figure 4.3 The least complex food webs for Korapuki and Ruamaahuanui	97
Figure 4.4 The most complex food webs for Korapuki and Ruamaahuanui.....	97
Figure 4.5 Linear models of food webs against environmental variables	100
Figure 5.1 Adjusted mean family richness and missing families for three island types	119
Figure 5.2 Proportions of invertebrates in different functional groups between islands	120
Figure 5.3 Family accumulation curves for each island and the three trips on Motuhoropapa	121
Figure 6.1 A summary of each thesis chapter	132
Figure 6.2 A simplified conceptual diagram of the effects of seabirds and rats	135

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

Joshua Thoresen

A handwritten signature in black ink, appearing to read 'Joshua Thoresen', with a stylized, cursive script.

Acknowledgements

First and foremost, I want to thank my supervisory team; Dave Towns, Sebastian Leuzinger, and John Robertson. Dave you have been the best supervisor I could have possibly wanted, supportive, knowledgeable, an amazing editor but most of all kind, caring, and understanding; there is no way I could have done this without your continual support. Sebastian, likewise you have been incredibly supportive and caring as well as providing a wonderful resource for statistical knowledge. I have learnt so much about statistics with your guidance and knowledge continually on hand. John, while we have not talked much over the last few years you were a great support for me while I was trying to get my head around all the chemistry at the start of this thesis, thank you.

To my intern Lusanne Brand I must say thank you for all of your hard work. You were an amazing help in an especially hard time for me during this thesis. Thank you for all of the tedious work you did identifying invertebrates and grinding soil samples and for all the good times we had during field work.

To all my family and friends who supported me both emotionally and financially during the last four years thank you. I am not exaggerating when I say I would have utterly fallen apart without this support. I'd especially like to thank my parents and grandparents for all of your loving, continual support. To my parents I wouldn't be who I am today without all of the amazing things we did and places you took us as children. You absolutely fostered my love of nature and challenged me to face my fears, nurturing my love of adventure (yep it is totally your fault I risk my life somewhat frequently). Amber and Scott, you were slightly annoyed I did not acknowledge you in my MSc thesis (I remember) so here it is now! I am seriously grateful for the support you showed me throughout this journey, especially at a particularly hard time. Both of you understood and really helped (even if you still don't know what I actually do).

Thank you.

Francis Wheeler (and his parents Christine and Malcolm) thanks for giving me a second home and always being happy to see me. Francis Wheeler (again), Bodie Johnson and Aislynn Rogers thank you for your amazing support during an especially hard time. To all of the Rosehill squad thanks for including me. All my

fellow PhDs (especially Becs, Tim and Jarrod) thanks for all the coffee and drinks, for listening and sympathising (and understanding better than anyone else). All of my rock climbing friends (Brendon, Rene, Edwin, Owen, Pet... too many to name) thanks for helping to foster my new passion and for all the belays and stress release.

I would like to acknowledge the Department of Conservation New Zealand, Manaaki Whenua Landcare Research, and the JS Watson Trust Forest and Bird for providing scholarships and grants. Many people helped with field work who I would like to thank including: Lusanne Brand, Francis Wheeler, Rose Benns, Phil Wainwright, Rebecca Jarvis, Emma and Matt Betty, Steph Borrelle and Sonya Popoff. For permission to work on the islands they own, I thank the following iwi: Ngati Hako, Ngati Hei, Ngati Manuhiri, Ngati Paoa, Ngati Puu, Ngati Rehua, and Ngatiwai, as well as the Aldermen Islands Trust, John McCallum, and Bryce Rope. I would like to thank the Neureuter family, especially Rod, Sue and Zoe for giving me access to their Islands and Dr James Russell for restoring the hut on Motuhoropapa Island. Finally, many thanks to Professor Jason Tylianakis who provided a thorough review on an early draft of the first paper/chapter and advice on network analysis.

Chapter one: Introduction

1.1 Literature review

Before the arrival of Polynesians and invasive mammals, New Zealand's terrestrial fauna and flora were influenced by extraordinarily high densities of seabirds on parts of the mainland (Craig et al. 2000; Mulder & Keall 2001; Holdaway et al. 2001). As a result, terrestrial ecosystems, watersheds and subsequent marine systems would have been exposed to high inputs of nutrients such as nitrogen and phosphorus. This seabird fauna has now largely been lost from mainland New Zealand; however, populations have survived on some offshore islands and after the removal of introduced predators are now spreading on others (Fukami et al. 2006; Towns et al. 2009; Bellingham et al. 2010). These island ecosystems are strongly influenced by nutrient transfer from the sea via seabirds, with extremely high concentrations of nutrients sequestered within soils (Furness, 1991; Anderson & Polis, 1999; Bancroft, 2004; Mulder et al. 2011a; Caut et al. 2012). Over 100 offshore islands around New Zealand are currently undergoing restoration, with pest species eradicated and bare areas afforested (Towns et al. 2013). It is therefore important to understand in depth how these ecosystems might change as they are restored and as seabirds return.

Understanding the manner in which various factors influence species interactions in food webs is a central goal of current ecological research (Spiller et al. 2010), especially when attempting to conserve or restore an ecosystem in its entirety. A growing body of research has focused on the flow of material and organisms across ecosystem boundaries (i.e. allochthonous subsidies), which can potentially have considerable influence on food web dynamics in recipient ecosystems (Polis et al. 1997; Gende et al. 2002; Marczak et al. 2007; Fariña et al. 2008; Mellbrand 2009; Spiller et al.

2010). The allochthonous subsidies of nutrients via biotic vectors such as seabirds (Ellis et al. 2006; Caut et al. 2012), reptiles (Bouchard & Bjordal 2000; Hannan et al. 2007; Fariña et al. 2008), mammals (Hilderbrand et al. 1999; Fariña et al. 2003; Villegas-Amtmann et al. 2008), invertebrates (Nakano et al. 1999; Mellbrand 2009) and fish (Gende et al. 2002; Drake et al. 2005) can have a major influence on recipient food web dynamics (Myrcha & Tatur 1991; Towns et al. 2009) and have long been recognised as vital links in ecosystem processes between habitats. Many abiotic vectors may also influence the flow of nutrients across ecosystem boundaries; these include winds, flooding, leaching, coastal upwelling and wave action (Bildstein 1992; Polis & Hurd 1996; Polis et al. 1997; Spiller et al. 2010). Nutrient transport across ecosystems is especially important, and simplest to study in ostensibly closed systems such as islands (Caut et al. 2012).

Seabirds show particularly dramatic examples of biotic allochthonous nutrient transfer because they have been found to transform terrestrial (Anderson & Polis, 1999; Bancroft, 2004; Bancroft et al 2005a; Ellis 2005; Fukami et al. 2006; Caut et al. 2012), freshwater (Marion et al. 1994; Izaguirre et al. 1998; Harding et al. 2004) and coastal marine ecosystems (Bosman et al. 1986; Bosman & Hockey 1988; Keatley et al. 2009). Foraging at sea, seabirds drop prey items on terrestrial colonies, either whole or in stomach oils as well as via guano and shed feathers (Myrcha & Tatur 1991). Additionally, nutrients are added when adults or chicks die on the colony or when eggs are abandoned or destroyed (Mulder et al. 2011b). Of all this input, guano is considered the most important influence on recipient ecosystems. Through guano, burrowing

species may increase nitrogen subsidies by 100 times and phosphorus by 400 times (Furness 1991).

1.1.1 The effects of seabirds on island ecosystems:

Numerous publications now demonstrate how primary producers are enriched via the nutrients in seabird guano (Erksine et al. 1998; Wainright et al. 1998; Mulder & Keall 2001; Markwell & Daugherty 2003; Bancroft et al. 2005a & 2005b; Ellis et al. 2006; Kolb et al. 2010; Ellis et al. 2011; Mulder et al. 2011a). Guano deposition can increase the primary productivity of plants, thus indirectly benefitting consumers of plant tissue, detritus and seeds; which in turn benefit the predators of these consumers (Ellis et al. 2006; Fukami et al. 2006; Wardle et al. 2009; Mulder et al. 2009; Kolb et al. 2010; Kolb et al. 2011; Caut et al. 2012). Additionally, seabirds influence food webs in a more direct way, benefitting scavengers, parasites and predators that feed directly on live birds, carcasses and eggs (Mulder & Keall 2001; Towns et al. 2009; Mulder et al. 2011b). Finally, seabirds are great drivers of physical disturbance. The effects of nesting and other behaviours decrease soil stability, community diversity, and plant productivity and water retention (Gillham 1956; Furness 1991; Bancroft et al. 2005a & 2005b; Ellis et al. 2011; Mulder et al. 2011a).

Stable isotopes of $\delta^{15}\text{N}$ have been used to demonstrate the direct effect of guano deposition and seabird derived nutrient subsidies on these recipient ecosystems. Many studies have used these isotopes to demonstrate that oceanic derived nitrogen (via seabirds) effectively enters island food webs and moves up higher trophic levels via sequential consumption events (Markwell & Daugherty 2002; Stapp & Polis 2003a & 2003b; Barrett et al. 2005; Kolb et al. 2010; Caut et al. 2012).

An extensive literature demonstrates the increase in abundance of consumers across many aspects of island food webs when seabird dominated islands are compared with islands devoid of birds. Seabird islands in the Stockholm Archipelago, Sweden, had more abundant aphids, ladybirds, lacewings, lepidopteran larvae, flies, midges and parasitic hymenopterans, although lycosid spiders and collembolans were less abundant (Kolb et al. 2010). In Cook Strait, New Zealand, seabird islands had higher abundances of collembolans, hymenopterans, spiders, and lizards (Markwell & Daugherty 2002). On seabird islands in north-eastern New Zealand 8 of 19 litter-dwelling invertebrate orders were significantly more abundant (Towns et al. 2009). However, in areas where seasonality is strong the effects of seabirds vary according to numerous abiotic factors, with an important and prevalent factor being rainfall. On the arid islands in the Gulf of California, seabird derived nutrient subsidies support only ectoparasites and detritivores until wet years when there is a veritable explosion of life. On these islands, wet years lead to higher primary productivity due to a combination of highly available nutrients and water, resulting in periodic nutrient-rich plant growth (Polis and Hurd 1996; Polis et al. 1997; Anderson and Polis 1999; Anderson et al. 2008). These nutrient rich plants support a high diversity and abundance of herbivorous invertebrates resulting in extremely high densities of orb-web spiders, lizards and mice (Polis and Hurd 1995; Sánchez-Piñero and Polis 2000; Stapp and Polis 2003a; Barrett et al. 2005).

Seabirds have also been shown to cause changes in the survivability and physiology of consumers while not always increasing their abundance. This influence may be due to confounding effects such as competition or the top down pressure of predators (Kolb et al. 2011). For example, in Australia an endangered insectivorous

marsupial, the dibbler (*Parantechinus apicalis*) increased male post-breeding survivability and body condition on seabird islands (Wolfe et al. 2004). These differences were likely due to the increase in prey items such as Orthoptera, Blattodea, Coleoptera, Diptera and Isoptera (Miller et al. 2004). Additionally, on an island off the coast of Scotland, red deer (*Cervus elaphus*) living in proximity to gull colonies had increased reproductive success over their lifetime, which was argued to be a result of the increased nutrient content of vegetation (Iason et al. 1986).

Several studies have also demonstrated the influence of seabirds on vegetation community structure and growth patterns. Burrow nesting seabirds have generally been shown to reduce habitat complexity, plant density, species richness (Crooks 2002) and cause plant dwarfism (Gillham 1956; Bancroft et al. 2004). In addition, seabirds can cause regular soil disturbance that favours smaller annual plants that can rapidly grow and reproduce in the brief periods between disturbance events (Grime 2002; Rippey & Rowland 1995). The combination of burrowing and trampling can also result in extensive root damage, decreasing the stability of trees (Cameron 1990) and reducing seed germination and seedling survival (Mulder and Keall 2001; Grant-Hoffman et al. 2010a & 2010b). Birds may also cause disturbance to vegetation as they climb trees to take off and crash through the canopy when they land (Brooke 2004; McKechnie 2006). Bancroft et al. (2005b) demonstrated that with decreasing distance towards the centre of a burrowing seabird colony there were fewer species, lower diversity, more annuals, exotics and succulents, shorter and denser growth patterns, an increase in productivity and more patches of bare earth. In sum, seabirds are nutrient vectors as well as drivers of disturbance, which is why they are regarded as ecosystem engineers (McKechnie, 2006;

Mulder et al. 2011a; Orwin et al. 2016); species that directly or indirectly modulate the availability of resources to other species (Jones et al. 1994).

1.1.2 The effects of seabird loss or invasive species on island ecosystems:

Invasive predatory mammals are now the most common global threat to seabirds (Howald et al. 2007; Mulder et al. 2011b; Croxall et al. 2012). Species such as rats (*Rattus* spp.) and house mice (*Mus musculus*) are the most prevalent invaders, and the introduction of these species to seabird islands has often been followed by severe reduction or extinction of seabird nesting populations (Fukami et al. 2006; Howald et al. 2007; Jones et al. 2008; Jones et al. 2016). With this decline comes the loss of the ecosystem engineering and nutrient subsidies provided by seabirds (Croll et al. 2005; Fukami et al. 2006), with the added pressure of a new top predator to the ecosystem. Comparative studies of islands with seabirds and invasive mammals, largely rats; *Rattus rattus*, *R. norvegicus* and *R. exulans*, show that rat dominated islands have less C, N, P and $\delta^{15}\text{N}$ in soils, fewer plants and animals, higher soil pH and more leaf litter (Fukami et al. 2006; Wardle et al. 2007 & 2009; Mulder et al. 2009; Jones 2010a; Towns et al. 2009; Orwin et al. 2016). The indirect effect of rats on these islands included reduced forest soil, foliage and leaf litter fertility and reduced litter decomposability as a result of interrupted seabird-derived nutrient subsidies (Fukami et al. 2006; Wardle et al. 2009; Mulder et al. 2009). The loss of these nutrients contributes to the decline in both above and below-ground invertebrate diversity and abundance (Fukami et al. 2006; Towns et al. 2009); the declines include many smaller animals such as nematodes, mites and springtails, which are too small to be directly consumed by rats (Towns et al. 2006). Some of these species may be heavily suppressed but still recover after invasions, but

others may be lost completely, and incapable of recovering without human intervention (e.g. Towns et al. 2016; Appendix C). Such losses could be termed a ‘legacy effect’ although there is little research demonstrating whether these effects exist on species too small to be directly affected by invasive species.

When invasive mammals are removed, seabirds should recolonise, thus reinstating their engineering effects. Worldwide, there are now more than 300 examples of successful invasive mammal eradications from seabird islands (Rauzon 2007; Keitt et al. 2011) and on many of these islands seabirds have indeed begun to recolonise (Rauzon 2007; Buxton et al. 2014; Borrelle et al. 2015). Chronosequences of recovering seabird islands have shown that $\delta^{15}\text{N}$ and C:N ratios of soils, plants and spiders take two to three decades to recover to seabird influenced levels even after a century of rat infestation (Jones 2010b). However, the full extent to which invasive predators effect these ecosystems, whether they might have legacy effects, and how ecosystems might change as invasive species are removed, is not fully understood, especially in terms of the resident food webs.

While the effects of seabirds and predator invasion on consumers and primary producers have been extensively studied, there have been few studies of the effects of seabirds on the food webs that make up these ecosystems. The recent development of metrics that use network analysis to quantify food webs (Bersier et al. 2002; Bascompte et al. 2005 & 2006; Tylianakis et al., 2010) enables us to study the effects of seabirds on the entire food web as opposed to selected components. This thesis will use network analysis to analyse invertebrate food webs in order to determine the effects invasive predatory mammals, seabirds and ecosystem restoration have upon these food webs.

1.1.3 The application of network analysis of food webs:

Research has increasingly become focused on determining the extent of ecosystem recovery on seabird islands (e.g. Mulder et al. 2009; Jones et al. 2011; Buxton et al. 2014; Orwin et al. 2016; Jones et al. 2016). However, when studying communities this research largely focuses on structural aspects of biodiversity, such as species richness and abundance. An alternative is to emphasize functional aspects such as patterns of interactions between species (Forup et al. 2008) which is achievable through network analysis. Network analysis is a method of simplifying the complexity found in food webs and describes trophic interactions among species; it may also be capable of reconciling the structure and function of biodiversity (Polis et al. 1997; Thompson et al. 2012). To date, network approaches have not been used to study the effects of seabirds or their loss (i.e. due to predator invasion) on invertebrate communities, or how these communities might recover as seabirds return.

Using network analysis in ecosystem restoration, in conjunction with other methods, will help to further our understanding of restoration ecology. All species interact with each other in complex antagonistic or mutualistic networks (Tylianakis et al. 2010). Using network analysis, these food webs can be visualised using binary matrices of ones and zeros, where a 1 denotes an interaction between two species and a 0 denotes no interaction. The types of interactions can then be used to analyse the structural attributes of a food web, which can indicate their capacity for self-reconstruction after disturbance events. However, research using network analysis to determine the extent of ecosystem change or recovery is rare, presumably due to its novelty. The only comparable research to date was carried out by Forup et al. (2008),

who compared pollinator networks between ancient and restored British heathlands. They found that the pollinator networks were significantly more complex in ancient sites.

Numerous metrics can be used to describe food webs using network analysis. In this thesis I used general metrics including: (1) species diversity (i.e. trophic group diversity); (2) generalist diversity (i.e., the number of species where the number of items a species feeds on (i.e. in-degree) is equal to or greater than the maximum in-degree of the least complex network); (3) specialist diversity (i.e., the number of species with an in-degree greater than zero but less than the average first quartile of all empirical networks); (4) the maximum food chain length per network (FCL); (5) generality (i.e., the mean number of consumed species per consumer); (6) vulnerability (i.e., the mean number of consumers per consumed species); and (7) the Omnivory Index, a measurement of the number of species feeding across numerous trophic levels (Dunne et al. 2002; Post 2002; Kondoh & Ninomiya 2009; Tylianakis et al. 2010).

Other, more complex metrics can be used, which can characterise entire food webs. I used two measures in this thesis: the metrics nestedness (Ings et al. 2009; Tylianakis et al. 2010; Thompson et al. 2012; Zeng et al. 2014) and entropy (Allesina and Pascual 2009; Gauzens et al. 2015). Nestedness, or community cohesiveness, is a metric that characterises the generalist-specialist balance in ecological networks (Araujo et al. 2010). High nestedness is associated with a greater degree of generalisation within the network, reduced competition within trophic levels, and an increase in the number of coexisting species (Bascompte & Jordano 2006 & 2007; Araujo et al. 2010; Tylianakis et al. 2010 Rezende et al. 2007; Dattilo et al. 2013). Network entropy is a quantitative

measure of resistance (Demetrius and Manke 2005), defined as a network's capacity to remain functional in the face of random perturbations (Gauzens et al. 2015). In network analysis, entropy measures the diversity of pathways of energy flow between species in the trophic network (Gauzens et al. 2015). For a binary matrix, entropy is the logarithm of the dominant eigenvalue of the matrix (after the matrix has been corrected for energy circulation) (Allesina and Pascual 2009; Gauzens et al. 2015, also see Chapters 2-5). Entropy increases with species richness and maximal entropy is obtained when all matrix entries equal one.

The caveat must be made that some of these network metrics are correlated. Figure 1.1 demonstrates the correlation matrix of all the metrics used. Strong positive correlations exist between the metrics: entropy, species diversity, generality, vulnerability and total generalists (correlation coefficient (r) > 0.5 , p -value < 0.05). The remaining metrics (FCL, specialist diversity, omnivory index, and nestedness) are not strongly correlated with any other metric, excluding the negative correlations between specialists and omnivory, and nestedness and species diversity ($r < -0.4$, p -value < 0.05). These correlated metrics were all included as they each tell a slightly different story about the food webs. Generality and Vulnerability for example are strongly correlated and this should be expected as one shows the mean predators per prey and the other the mean prey per predator. However if only one variable was used then only half the story would have been told. Entropy is strongly correlated with four other variables but this again should be expected as entropy characterises the overall complexity of the food webs. The key aspects that contribute to this complexity such as species or generalist diversity will then influence entropy. Finally specialist diversity and omnivory are

moderately and negatively correlated, again this makes sense, food webs with more specialists will be characterised by low omnivory. However this does not mean these metrics can be used interchangeably, they each describe two distinct characteristics of a food web. The opposite would be expected of the relationship between generalists and omnivory too, but this was not the case. This then reflects the difference between omnivory (feeding across many trophic levels) and generalism (feeding widely within one trophic level).

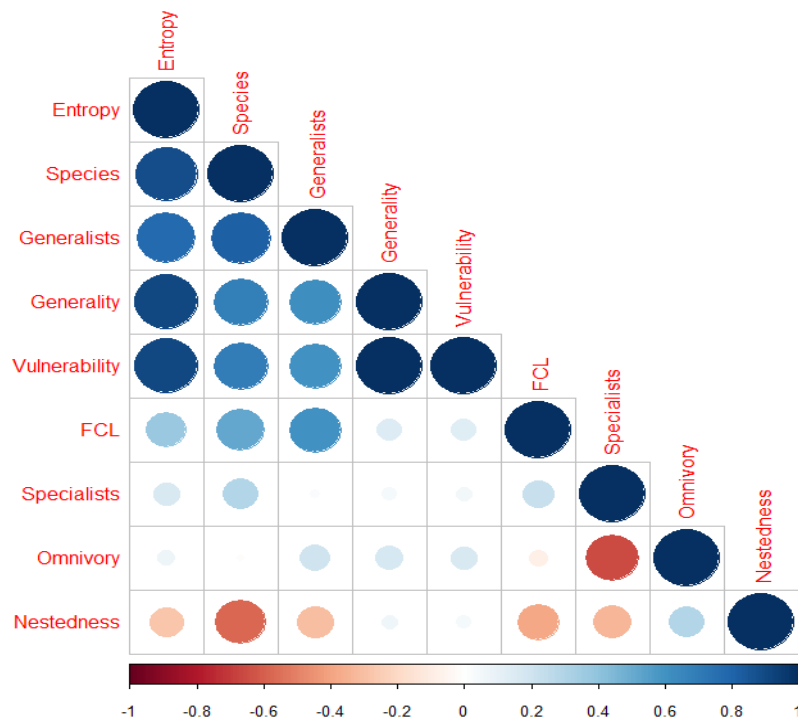


Figure 1.1 Correlation matrix heat map of the different network metric used in this study. Size and colour of the circle denote the strength and direction of the correlation respectively.

By determining the way that environmental changes driven by rats, seabirds and seabird recolonisation on islands can alter trophic interactions in food webs, I will illustrate the differences in the composition and structure of island communities. I will also provide insight into why these communities might change as well as how, and

describe the possible consequences of these changes. For example, ecosystems with more generalists and high entropy are less susceptible to random extinction events because if one food source disappears there are many others available (Saint-Béat et al. 2015). Food webs characterised by low generality and vulnerability will have few consumers feeding on fewer resources. In areas with food web characterised by low vulnerability there will be less options for consumers. This would mean that resource switching to avoid competition would be infrequent and the benefits gained to those species consumed from high competition between consumers (e.g. apparent mutualisms) would be less apparent. In my thesis, network analysis is used to investigate the indirect effects of predator invasion on litter invertebrate food webs, the effects of nutrient subsidies on invertebrate food webs, and to compare and contrast the food webs on recovering islands with those on uninvaded islands.

1.2 Research questions

In light of the afore-mentioned gaps in the literature, this thesis sets out to answer the following research question: how do seabirds, rat invasion, and ecosystem restoration effect the food webs of invertebrates on offshore islands? This questions will be answered using four sub-questions: 1) Are food webs on invaded islands different from uninvaded islands? 2) How do nutrient subsidies and water availability effect food web structure? 3) Do recovering island food webs differ from invaded or uninvaded islands? And 4) is there a legacy of indirect rat suppression on invertebrate food web composition on recovering islands? A conceptual diagram of how this thesis is set out and hypotheses for each of the research questions is presented below (Figure 1.2).

How do seabirds, rat invasion, and ecosystem restoration effect the food webs of invertebrates on offshore islands?

Question 1, Chapter 2
Are food webs on invaded islands different from uninvaded islands?

Hypothesis:
On invaded islands invertebrate food webs will be smaller and less complex as a result of lower soil nutrients.

If so, then...

Question 2, Chapter 3
How do nutrient subsidies and water availability effect food web structure?

Hypotheses:

- 1) Artificial nutrient subsidies will have a positive effect on food web structure and function with larger, more complex food webs in areas of higher subsidies.
- 2) Water availability will increase food web complexity and size across all subsidy treatments but higher complexity will be found in areas of higher nutrient subsidies.

If so, then...

Question 3, Chapter 4
Do recovering island food webs differ from invaded or uninvaded islands?

Hypotheses:

- 1) The food webs metrics from Korapuki Island (recovering) will be typical of Ruamahuanui Island (uninvaded).
- 2) There will be areas on Korapuki where the food webs are typical of an uninvaded island.
- 3) There will be differences in the way environmental and food web metrics interact on Korapuki compared with Ruamahuanui.

Question 4, Chapter 5

Is there a legacy of indirect rat suppression on invertebrate food web composition on recovering islands?

Hypotheses:

- 1) Family groups will be missing from the recovering and invaded islands due to rat invasion and/or the legacy of invasion.
- 2) Family groups will be missing from recovering islands which are common on uninvaded islands.
- 3) If more samples were taken on the recovering islands the missing family groups would not have been found.

If so, then...

Figure 1.2 A conceptual diagram of the research questions and hypotheses for each chapter, and the flow of the thesis.

1.3 Thesis layout

In order to answer the above questions, the following thesis is divided into six chapters. Four of these are stand-alone, publishable papers (Chapters 2-5) followed by a final discussion. Despite the fact that each stand-alone chapter is distinct, there is overlap in methodologies and themes which necessitates some repetition within the introduction and methods sections of each chapter. A reference section is provided at the end where all references are collated for each chapter.

1.4 Methods summary

1.4.1 Study sites and field methods

The methods used are thoroughly described in each chapter, so I only briefly summarise them here. Data were provided for this study from previous field research for chapters two, four and five. The data were in the form of raw environmental variables and coarsely or non-identified invertebrates. I then identified the invertebrates to family level and their feeding habits in order to describe food webs. Chapter three used data that I gathered during the course of the research. The studies that have previously used the data are Fukami et al. (2006), Wardle et al. (2009), Towns et al. (2009) and Mulder et al. (2009) for the data first used in chapter two (comparing eighteen invaded and uninvaded islands) and Orwin et al. (2016) for the data first used in chapter four (comparing one uninvaded island with an island that had has pests eradicated). Table 1.1 provides a summary of the islands and data.

Of the nineteen islands used in this study, nine had been invaded by the rats *Rattus rattus* and *R. norvegicus* introduced by Europeans 50 to 150 years ago and support few or no seabirds. Nine others had never been invaded (supporting high seabird densities) and two were invaded but have subsequently had all invasive mammals eradicated from them; one supporting mid to high seabird densities (Korapuki Island) and one supporting low seabird densities (Motuhoropapa Island). Maps of the area of north-eastern New Zealand and five island groups are provided in Figures 1.2 – 1.4. Only uninhabited islands were used that contained coastal forest and lacked farm stock. The islands were constrained in geographical range (35°25'S to 37°12'S) to avoid variation in the species pool of native plants and seabirds (Mulder et al. 2009; Towns et al. 2009). The soil types across the islands varied, with the majority being of volcanic origin. It was assumed that seabird effects on soil would override variations in soil properties, with previous studies throughout New Zealand supporting this assumption (Atkinson, 1964; Hawke et al. 1999; Mulder and Keall, 2001; Markwell and Daugherty, 2003).

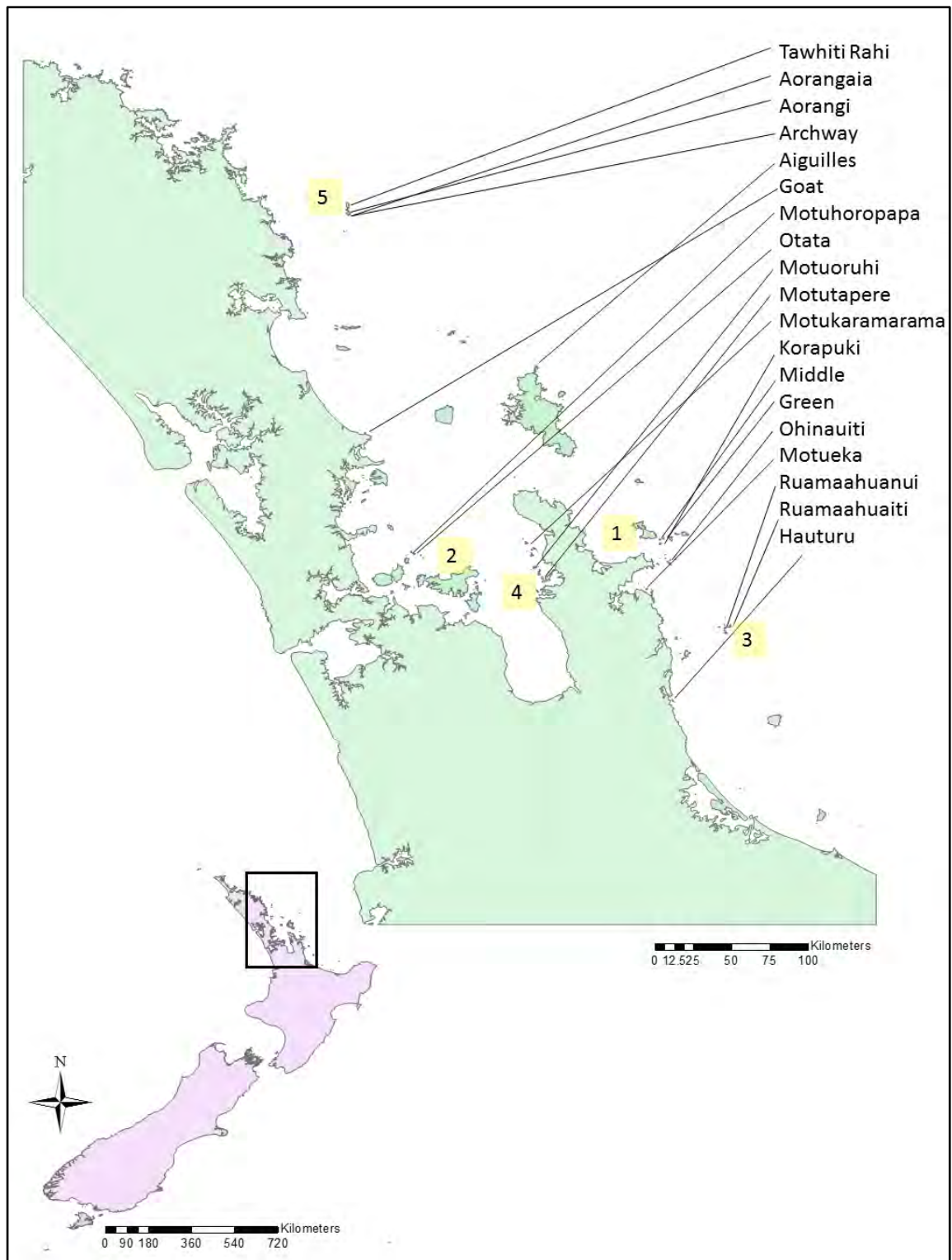


Figure 1.3 The nineteen islands used in this study spread across north-eastern New Zealand.

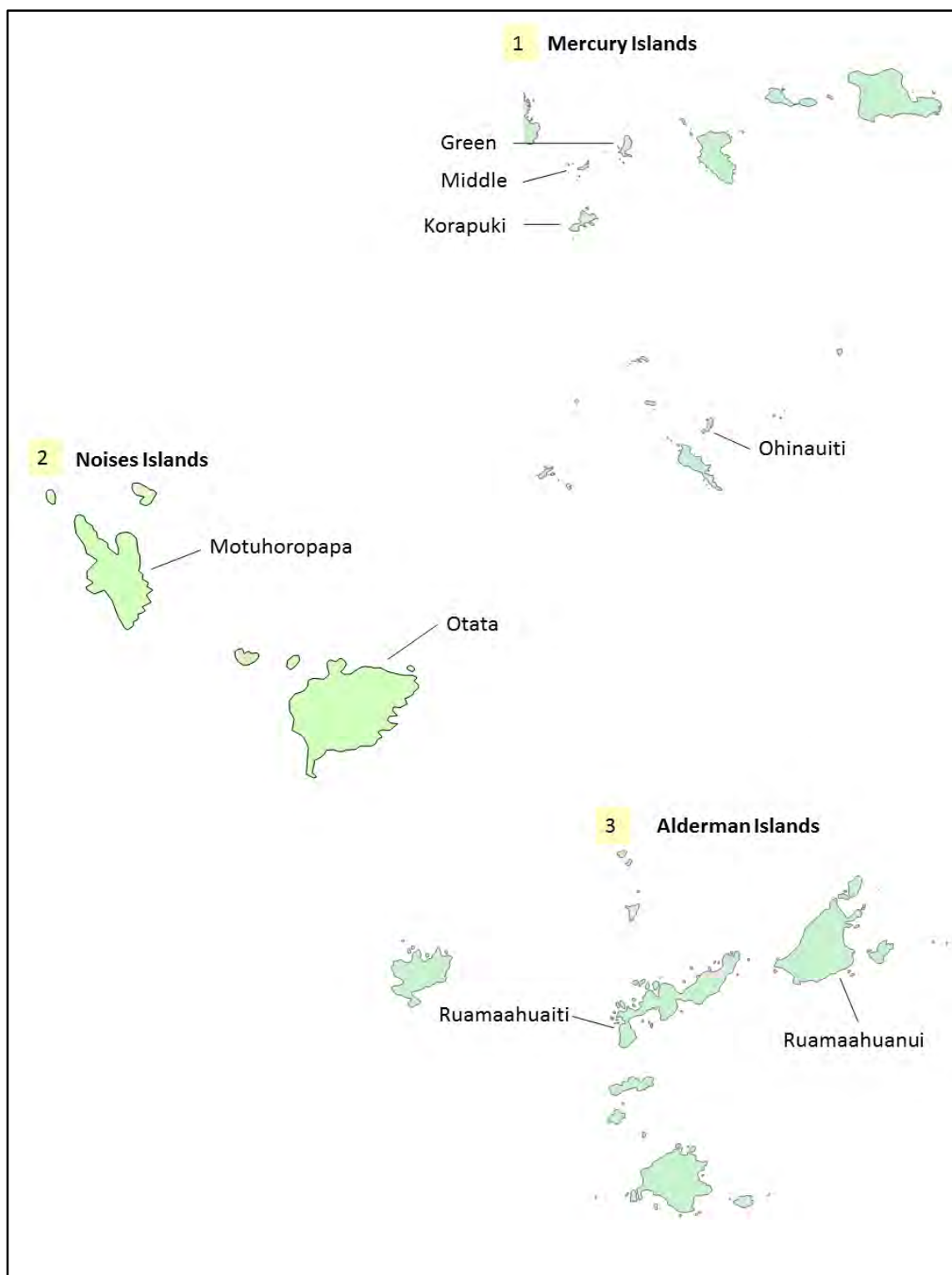


Figure 1.4 An enlargement of the Mercury, Noises and Alderman Island groups (islands not to scale)

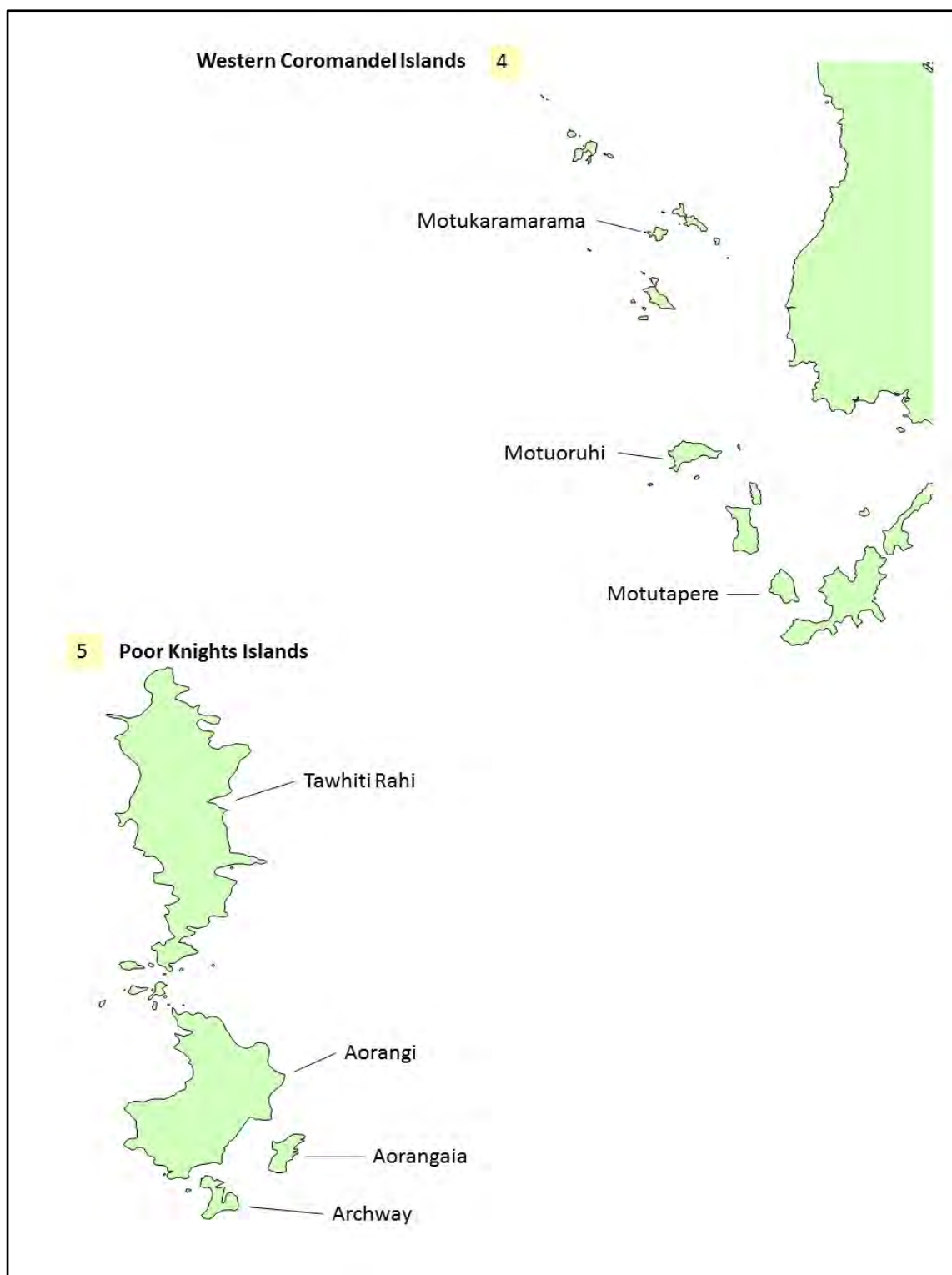


Figure 1.5 An enlargement of the Western Coromandel and Poor Knights Island groups (islands not to scale).

All of the islands in this study were burned by humans about 50 to 800 years ago (Atkinson 2004). The effects of fire on island ecosystems are varied and each of the islands have had varying histories of burn-off with some islands almost burnt entirely and others only burnt partially. Near total burn-offs would result in the island ecosystem being dominated by pioneer species such as pohutakawa (*Metrosideros excelsa*), kanuka (*Kunzea ericoides*), manuka (*Leptospermum scoparium*) and bracken fern (*Pteridium esculentum*) which is largely the case for all of these islands (Atkinson 2004). Islands that have not burnt entirely or have not burnt for hundreds of years would instead be dominated by broadleaf forest with species including; kohekohe (*Dysoxylum spectabile*), puriri (*Vitex luciens*) and mahoe (*Melicactus ramiflorus*), many of these islands have remnant patches of these broadleaf forests. The effects of near total burn-off would have been significant on the invertebrate fauna of the islands as well. It is possible entire species were lost during these fire events, species that would have not had the time to recolonise for the islands burnt more recently. In order to attempt to control for the effects of fire on these islands the sampling was confined to well-developed multi-tree species secondary forest to maximize comparability across islands (Fukami et al. 2006). However, fire may still have had an effect on islands with more recent or total burn offs.

In order to address the hypotheses for Chapter 2, 18 islands were sampled with nine of them invaded, supporting high abundances of rats (and other invasive mammals) and few to no seabirds, and nine uninvaded supporting high abundances of seabirds and no invasive mammals. Two plots of 10 by 10m were subjectively assigned on each island under forest canopy and on slopes of $< 30^\circ$ to ensure potential litter accumulation (Townes et al. 2009). The field work was carried out during February and March 2004.

The data for the two plots were combined so that each island served as a unit of replication. Within each plot seabird burrow densities were counted and soil and leaf litter samples collected using the methods described in Towns et al (2009).

Table 1.1 Summary table of all the islands used in this study, what time they were sampled, their invasion history, size, chapters the island was used for and whether the raw data was provided or gathered.

Island name	Data provided?	Chapter used	Year sampled	Island status	Longitude Latitude	Area (ha)	Elevation (m)	Rat invasion
Tawhiti Rahi	Provided	2,4,5	2004	Uninvaded	174.71°E 35.45°S	158.2	191	Never
Aorangaia	Provided	2,4,5	2004	Uninvaded	174.74°E 35.48°S	5.6	102	Never
Aorangi	Provided	2,4,5	2004	Uninvaded	174.72°E 35.48°S	107.1	216	Never
Archway	Provided	2,4,5	2004	Uninvaded	174.74°E 35.49°S	6.3	97	Never
Middle	Provided	2,4,5	2004	Uninvaded	175.84°E 36.60°S	13.5	85	Never
Green	Provided	2,4,5	2004	Uninvaded	175.85°E 36.64°S	2.5	50	Never
Ohinauiti	Provided	2,4,5	2004	Uninvaded	175.88°E 36.71°S	5.9	40	Never
Ruamaahuanui	Provided	2,4,5	2004 & 2011	Uninvaded	176.09°E 36.95°S	32.4	160	Never
Ruamahuaity	Provided	2,4,5	2004	Uninvaded	176.06°E 36.97°S	25.3	180	Never
Aiguilles	Provided	2,4,5	2004	Rat Invaded	175.39°E 36.03°S	72.7	120	<i>R. rattus</i>
Goat	Provided	2,4,5	2004	Rat Invaded	174.8°E 36.26°S	13.4	60	<i>R. rattus</i>
Motukaramarama	Provided	2,4,5	2004	Rat Invaded	175.37°E 36.68°S	10.1	71	<i>R. norvegicus</i>
Motuhoropapa	Provided (2004) Gathered (2014)	2,3,4,5	2004 & 2014	Rat Invaded (2004), Rats eradicated (2014)	174.96°E 36.69°S	8.6	50	<i>R. norvegicus</i>
Otata	Provided	2,4,5	2004	Rat Invaded	174.97°E 36.69°S	16.8	67	<i>R. norvegicus</i>

Motuoruhi	Provided	2,4,5	2004	Rat Invaded	175.38 °E 36.73 °S	58.0	169	<i>R. norvegicus or R. rattus</i>
Motutapere	Provided	2,4,5	2004	Rat Invaded	175.4 °E 36.78 °S	45.6	175	<i>R. rattus</i>
Motueka	Provided	2,4,5	2004	Rat Invaded	175.8 °E 36.82 °S	6.2	46	<i>R. norvegicus or R. rattus</i>
Hauturu	Provided	2,4,5	2004	Rat Invaded	175.89 °E 37.21 °S	10.3	85	<i>R. norvegicus</i>
Korapuki	Provided	4,5	2011	Rats eradicated	175.83 °E 36.62 °S	18	40	<i>R. exulans</i>

Chapter 3 used one island that was heavily sampled, with 90 samples taken over five months during December 2014 to April 2015. Thirty 2m² plots were set up on the recovering Motuhoropapa Island using a GIS randomised block study design. The plots were organised in six replicate blocks of five treatments that were placed at least 50m apart. In each block, five fertilisation treatments were randomly assigned: (1) control (no fertiliser), (2) low seabird density (1 burrow/m²), (3) medium seabird density (3 burrows/m²), (4) medium-high seabird density (5 burrows/m²), and (5) high seabird density (10 burrows/m²) (Jones 2010a). I used a mixture of marine based fertiliser; Verteflow 8.3.6 (a liquid fish-based fertilizer; Fertilizer New Zealand, Nelson, New Zealand) supplemented with uric acid, ammonium nitrate and time-release fertiliser to simulate seabird guano following the methods of Jones (2010a). The fertiliser mixture was applied twice during the austral summer (once in December 2014 and once more in January 2015). Leaf litter and soil samples were collected from each plot once in December 2014 and January 2015 (before fertilisers were applied) and a final time in April 2015.

Chapter 4 used data from Chapter 2 along with new data from Korapuki and Ruamaahuanui Islands. Fifteen plots (placed at least 50m apart) of 10 by 10m were randomly assigned on these two islands using ArcGIS 10 software (ESRI, Redlands, CA, USA), and field work was carried out in March 2011. Steep inaccessible parts of the islands, or areas without forest were excluded. Within each plot the number of burrow entrances was recorded and soil and litter samples collected. Four litter samples per plot were collected and subsequently bulked into one following the methods described by Orwin et al. (2016).

Chapter 5 collated the data from Chapters 2 to 4, so no new field or lab methods were used for this section of research.

1.4.2 Invertebrate identification and food web description

For all fieldwork, invertebrates were extracted from leaf-litter using Tullgren funnels run over seven days, then sorted, counted and classified to family-level using a dissection microscope. Litter invertebrates were used for the network analysis because of their abundance and diversity within small areas, their sensitivity to both direct and indirect environmental effects (e.g. Towns et al. 2009; Orwin et al. 2016) and the complex trophic structure of their communities (e.g. Kolb et al. 2011). Taxa were identified to family; however, most of the organisms identified belonged to only one undetermined genus or (occasionally) species within the family. For families where the larval feeding strategy differed from that of the adults, they were classified into separate categories. I aggregated the invertebrates to family-level in order to reduce methodological bias related to uneven resolution of taxa within and among the food webs (Williams and Martinez 2000; Dunne et al. 2002). There were 128 invertebrate

families identified in total (including separately identified larval groups) for this thesis. A list of each group identified from class to family, including functional groups and feeding links is included in Appendix B.

Trophic links were determined from the literature (Digel et al. 2014; Gauzens et al. 2015) and through communication with experts. Where there was little information on feeding habits, I estimated feeding category through taxonomic similarities, i.e. groups from similar families were assumed to have similar feeding methods, or only slight modifications due to size effects (Gauzens et al. 2015). In addition, morphological similarity within families led me to infer that feeding strategies are also similar. All plant species were split into three nodes; leaves, woody material, and vegetation fluids (i.e. those in the xylem and phloem), detritus was also added to the networks. Three extra nodes that were not measured during the sampling process (bacteria, and micro and macroscopic fungi) were included as food source nodes because of the presence of their consumers and their ubiquity in forest ecosystems. I then used this information to describe the food web networks where each family group is a node, or point, in the network that is connected to other points through their feeding interaction links.

Because I measured invertebrates from a single collection of leaf forest litter at one time of the year (Towns et al. 2009), I recognize that these food webs do not fully represent the types of leaf litter invertebrate communities found throughout the year. Further, they represent only a defined component of the overall food webs of these island ecosystems (which include large invertebrates, reptiles and birds). Despite this, and in line with other comparable studies (Towns et al. 2009; Kolb et al. 2011), I do believe that the invertebrate food webs developed here are sufficiently comprehensive to

enable informative conclusions about the effects of seabirds, invasive mammals and ecosystem restoration on food web structure.

Research using network analysis is usually very precise in quantifying the feeding interactions between species and in identifying the components of the food web. Generally, feeding interactions are identified using a combination of stable isotopes, behavioural observation, gut content analyses, and DNA profiling. Food web components are usually identified to species level. This research, by necessity could not be so precise and so a way of proving the accuracy of the described food webs was needed in order to show that the overall findings were valid. I did this by comparing the empirical networks for each chapter to those constructed using the niche model. The niche model has been used to draw conclusions on how the structure and function of real-world food webs may change in relation to external stimuli and has been published in top-tier journals such as *Nature* (Williams and Martinez 2000; Dunne et al. 2002; Williams and Martinez, 2008; Williams et al. 2010; Thompson et al. 2012). The niche model uses species diversity and connectance to develop networks based on simple parameters. Each ‘species’ is assigned a randomly drawn niche value from the interval of 0 – 1. The species are then constrained to consume all prey species within one range of values whose randomly chosen centre is less than the consumer’s niche value (Williams and Martinez, 2000). In this way, a model can be created that accurately predicts many network metrics (Dunne et al. 2002; Williams and Martinez, 2008; Williams et al. 2010; Thompson et al. 2012). I rationalised that if my networks were as accurate as networks constructed using the niche model then I could draw conclusions at least as informative as those drawn by the theoretical studies that have used this model.

Appendix A details the comparisons between the empirical and model food webs for each relevant chapter. I concluded from these comparisons that the metrics describing my food webs were largely as accurate, and in some cases more accurate than those described using the niche model. However, from the results of these comparisons I also found that the methods used in describing the food webs may have caused some metrics to be inaccurate (i.e. specialist diversity) but they still change in consistent ways; as such, I was confident in using them to predict changes in the food webs.

Chapter two: Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure.

2.1 Abstract

Burrowing seabirds that nest on islands transfer nutrients from the sea, disturb the soil through burrowing, damage tree foliage when landing, and thereby modify the surface litter. However, seabirds are in decline worldwide, as are their community- and ecosystem-level impacts, primarily due to invasive predatory mammals. The direct and indirect effects of seabird decline on communities and ecosystems are inherently complex. Here I employed network analysis, as a means of simplifying ecological complexity, to better understand the effects seabird loss may have on island invertebrate communities. Using data on leaf litter communities, I described invertebrate food webs for each of eighteen offshore oceanic islands in north-eastern New Zealand, nine of which have high seabird densities and nine of which were invaded by rats. Ten network topological metrics (including entropy, generality and vulnerability) were compared between rat invaded and uninvaded (seabird dominant) islands. I found that on rat-islands the invertebrate food webs were smaller and less complex than on their seabird-dominated counterparts, which may be due to the suppression of seabird derived nutrients and consequent effects on trophic cascades. This decreased complexity of food webs due to the presence of rats is indicative of lower ecosystem resistance via lower trophic redundancy. My results show that rat effects on island ecosystems are manifested throughout entire food webs, and demonstrate how network analysis may be useful to assess ecosystem recovery status as these invaded islands are restored.

2.2 Introduction

Understanding how indirect abiotic factors influence species interactions in food webs is a central goal of current ecological research (Spiller et al. 2010). A growing number of studies have focused on the flow of material and organisms across ecosystem boundaries (i.e. allochthonous subsidies), which can potentially have considerable influence on food web dynamics in recipient ecosystems (Polis et al. 1997; Fariña et al. 2008; Mellbrand, 2009; Spiller et al. 2010; Wright et al. 2010). For example, allochthonous subsidies of nutrients via biotic vectors such as seabirds (Ellis et al. 2006; Caut et al. 2012) can have a major influence on island food webs (Myrcha and Tatur, 1991; Towns et al. 2009) and have long been recognised as important in linking ecosystem processes between habitats. Likewise, the loss of these subsidies, through the extirpation of seabirds from their nesting islands by predators, can have major influences on those food webs the seabirds once supported (Croll et al. 2005; Fukami et al. 2006). Invasive predatory mammals are now the most common global threat to seabirds (Howald et al. 2007; Mulder et al. 2011; Croxall et al. 2012). Species such as rats (*Rattus sp.*) and house mice (*Mus musculus*) are the most prevalent invaders, causing the decline and often local extinction of seabird breeding populations (Howald et al. 2007; Jones et al. 2008; Jones et al. 2016). Invasive mammals are increasingly being removed from islands worldwide (Howald et al. 2007), which will enable seabirds to recolonize (Mulder et al. 2009; Jones 2010; Croxall et al. 2012; Jones et al. 2016). However, the extent to which invasive predators indirectly influence food web structure on seabird islands, either through the suppression of nutrient subsidies, or through other factors, is still largely unknown.

Seabird-derived subsidies generate a variety of direct and indirect responses in island food web dynamics. The nutrients from guano have direct effects on soil bacteria, fungi, and plant growth (Fukami et al. 2006; Wright et al. 2010). These effects then flow up the trophic system through microbivores and herbivores to primary and secondary predators (Ellis et al. 2011; Kolb et al. 2011). Seabirds and their products (i.e. guano, feathers, carcasses and eggshells) are consumed directly by predators and scavengers (Fukami et al. 2006; Wardle et al. 2009). Seabirds also support a wide array of ectoparasites which can act as food sources for other invertebrate predators (Morbey, 1996; Marcogliese and Cone, 1997). An extensive literature has demonstrated that these seabird-driven subsidies can be major drivers of consumer populations on island ecosystems (Polis and Hurd 1995; Sánchez-Piñero and Polis 2000; Markwell and Daugherty 2002; Stapp and Polis 2003; Barrett et al. 2005; Towns et al. 2009; Kolb et al. 2010).

Seabirds can be ecosystem engineers due to their physical disturbance of ecosystems, primarily through nest building and, for many seabird species, associated burrowing (McKechnie, 2006; Mulder et al. 2011; Orwin et al. 2016). Disturbance through burrowing reduces soil integrity and alters soil porosity, temperature, bulk density, strength, water content and repellency, hydraulic conductivity, nutrient distribution, organic matter and pH (Bancroft et al. 2005). Disturbance through burrowing also increases vertical soil mixing (Furness 1991; Hawke and Newman 2004), leading to incorporation of surface litter into lower soil horizons (Mulder and Keall 2001; Fukami et al. 2006; McKechnie 2006). These disturbances can create

unfavourable microenvironments for larger invertebrates living within the soil or leaf litter (Fukami et al. 2006).

The introduction of invasive predators to seabird islands has often been followed by severe reduction or extinction of seabird nesting populations (Atkinson 1985; Blackburn et al. 2004; Fukami et al. 2006; Jones et al. 2008). With this decline comes the loss of the ecosystem engineering and nutrient subsidies provided by seabirds, with the added pressure of a new apex predator to the system. The direct and indirect effects of predator invasion have numerous different outcomes on these island ecosystems. Research has shown that the indirect effects of rats are prevalent on seabird islands; introduced rats reduce forest soil, foliage and leaf litter fertility and reduce litter decomposability by interrupting seabird derived nutrient subsidies (Fukami et al. 2006; Wardle et al. 2009; Mulder et al. 2009). The loss of these nutrients contributes to the decline in both above and below-ground invertebrates (Fukami et al. 2006; Towns et al. 2009), including many smaller animals such as nematodes, mites and springtails which are too small to be directly consumed by rats (Towns et al. 2006). The management implications for these results are clear: rats must be removed from these ecosystems before they can be expected to recover (Mulder et al. 2011). However, if rats are removed without seabirds recolonising then these ecosystems may not revert to their previous state (Mulder et al. 2009). It is therefore important to further understand how these ecosystems change during the processes of rat invasion and subsequent rat eradications in order to predict the need for and outcomes of ecological restoration.

Many studies have shown the changes in abundance of consumers comparing seabird and invaded islands, fewer have examined differences in diversity and none have

focused on structural changes in food webs. Here I use network analysis to investigate the indirect effects of predator invasion on litter invertebrate food webs on seabird islands. Food web studies describe trophic interactions among species and are capable of reconciling the structure and function of biodiversity (Polis et al. 1997; Thompson et al. 2012). To date, network approaches have not been used to study these environmental changes. Using network analysis in ecosystem restoration, in conjunction with other methods, will help to further our understanding of restoration ecology. For example, determining how the environmental changes driven by rats on these islands alter trophic interactions will illustrate the differences in the composition and structure of island food webs between invaded and uninvaded islands and also provide points of reference in the process of ecosystem reconstruction. Moreover, network analysis can be used to identify whether an ecosystem cleared of invasive species is reverting to a previous unmodified state or entering a novel alternative stable state (e.g. Mulder et al 2009).

I use litter invertebrates for the network analysis because of their abundance and diversity within small areas, their sensitivity to both direct and indirect environmental effects (e.g. Towns et al. 2009; Orwin et al. 2016) and the complex trophic structure of their communities (e.g. Kolb et al. 2011). In addition, the invertebrates in this study were generally too small to be affected by rats directly through predation (Towns et al. 1997; Green 2002; Fukami et al. 2006); as such, any differences between invaded and uninvaded islands will be due to the indirect effects of rats.

Due to past studies showing the indirect effects of rats on the ecosystems of seabird islands, I postulate that the major effects of rat invasion on leaf litter invertebrate food webs will be via the loss of nutrient subsidies. I hypothesise that on invaded islands

invertebrate food webs will be smaller and less complex as a result of lower soil nutrients. To test this hypothesis, I described food webs from different taxa of leaf-litter invertebrates on each of nine islands in north-eastern New Zealand that have high densities of seabirds and nine that do not. I identified a range of metrics from network analyses that can be used to characterize the differences between invertebrate communities on islands with and without rats. I then evaluated the potential for rat-driven changes in soil chemistry and disturbance measured on these islands to explain these network metrics.

2.3 Methods

2.3.1 Study sites

I used invertebrate and environmental data from published research by Fukami et al. (2006); Wardle et al. (2009); Towns et al. (2009) and Mulder et al. (2009) on eighteen islands in north-eastern New Zealand (ranging in size from around 10 to 158 ha). Nine islands were invaded by the rats *Rattus rattus* and *R. norvegicus* introduced by Europeans 50 to 150 years ago and support few or no seabirds, while the other nine have never been invaded and support very high seabird densities (Fukami et al. 2006; Wardle et al. 2009). Only uninhabited islands were used that contained coastal forest and lacked farm stock. The islands were constrained in geographical range (35°25'S to 37°12'S) to avoid variation in the species pool of native plants and seabirds (Mulder et al. 2009; Towns et al. 2009). Since portions of these islands were burned by humans from about 800 to 50 years ago, the sampling was confined to well-developed multi-tree species

secondary forest to maximize comparability across and within islands (Fukami et al. 2006). Fukami et al. (2006) demonstrated that there were no significant differences between the invaded and uninvaded islands with regard to longitude, latitude, area, elevation, disturbance history, distance to mainland, distance to nearest larger island or distance from plots to shore within islands. The soil types across the 18 islands varied, with the majority being of volcanic origin. It was assumed that seabird effects on soil would override variations in soil properties, with previous studies throughout New Zealand supporting this assumption (Wright, 1961; Atkinson, 1964; Hawke et al. 1999; Mulder and Keall, 2001; Markwell and Daugherty, 2003). Finally, Durrett et al. (2014) found little spatial collinearity between soil properties on islands within my study system, demonstrating that seabird burrow density affected different soil properties in multiple ways. The properties of all eighteen islands and comparisons between invaded and uninvaded islands are presented in Supplementary material: Tables 2.2 and 2.3 respectively; also see Mulder et al. (2009).

2.3.2 *Sampling methods*

All 18 islands were sampled within a 67-day period between February and April 2004 to minimise potential seasonal effects. On each island, two 10×10 m plots were set up within forested areas and on slopes of $< 30^\circ$ to ensure potential litter accumulation (Towns et al. 2009). The data for the two plots on each island were combined so that each island served as the unit of replication to avoid pseudoreplication. Entrances of seabird burrows were used as a proxy of seabird density (Fukami et al. 2006); within each plot they were counted by systematically walking along predetermined belt transects covering the entire area. A sample of surface mineral soil (depth layers: 0-10cm) was collected from a 0.5×0.5 m subplot within each plot and analysed for %N,

%P, %C, Olsen P and pH (data from Fukami et al. 2006 and Mulder et al. 2009). Fukami et al. (2006) has previously tested these environmental variables using ANCOVAs and found no change in the significance of the differences between island types when considering island isolation or size. From each plot a single 2 litre sample of leaf litter was collected to the soil surface level and stored in a cloth bag. Invertebrates from this litter were extracted into ethanol within three days of sampling using Tullgren funnels running for seven days (Towns et al. 2009). After invertebrate extraction the litter was then oven dried (60°C until constant weight) and weighed. The invertebrates were then sorted, counted (data from Towns et al. 2009) and classified to family level using a dissection microscope.

2.3.3 *Network description*

Taxa were identified to family; however, most of the organisms identified belonged to only one undetermined genus or (occasionally) species within the family. For families where the larval feeding strategy differed from that of the adults, they were classified into separate categories. Appendix B provides a full list of the families identified and their feeding strategies. I aggregated the invertebrates by family into trophic groups in order to reduce methodological bias related to uneven resolution of taxa within and among the food webs (Williams and Martinez 2000; Dunne et al. 2002).

Trophic links were determined from the literature (Digel et al. 2014; Gauzens et al. 2015) and through communication with experts. Where there was little information on feeding habits, I estimated feeding category through taxonomic similarities, i.e. groups from similar families were assumed to have similar feeding methods, or only slight modifications due to size effects (Gauzens et al. 2015). In addition,

morphological similarity within families led us to infer that feeding strategies are also similar. I then used trophic groups and their feeding habits to describe 18 food web networks (one for each of the 18 islands) where each trophic group is a node, or point, in the network that is connected to other points through their feeding interaction links. All plant species were split into three nodes; leaves, woody material, and vegetation fluids (i.e. those in the xylem and phloem), detritus was also added to the networks based on the presence of vegetation and detritus in the plots. Four extra nodes that were not measured during the sampling process (bacteria, microscopic fungi, macroscopic fungi and nematodes) were included as food source nodes because of the presence of their consumers and their ubiquity in forest ecosystems. This information for invertebrates and their feeding categories was then used to describe a binary food web matrix for each island.

Because I measured invertebrates from a single collection of leaf forest litter at one time of the year (Towns et al. 2009), I recognize that these food webs do not fully represent the types of leaf litter invertebrate communities found throughout the year. Further, they represent only a defined component of the overall food webs of these island ecosystems (which include large invertebrate, reptiles and birds). Despite this, and in line with other comparable studies (Towns et al. 2009; Kolb et al. 2011), I do believe that the invertebrate food webs developed here are sufficiently comprehensive to enable informative conclusions about the effects of seabirds and invasive mammals on food web structure. I verified the effectiveness of my approach by comparing my empirical networks to those constructed using the niche model (Williams and Martinez 2000; Dunne et al. 2002; Williams and Martinez, 2008; Williams et al. 2010; Thompson et al.

2012) (see Appendix A for detailed explanation of niche model construction and analyses used). Seven of the ten metrics I used to compare these webs were not significantly different from the niche model; the other three (food chain length, generalists and specialists) were different but in those instances the niche model showed unrealistic values (Williams and Martinez, 2008; Borrelli and Ginzburg 2014). I thus conclude that not only are my webs as accurate as the widely used niche model, but that they are also realistic representations of true food webs.

2.3.4 Network analysis metrics

General metrics and Nestedness

Using the 18 food webs I calculated nine general metrics to characterise each island network. These metrics include total ‘species’ (i.e. trophic groups) (S_T), links (L), generalists (G ; i.e., the number of species where the number of items a species feeds on (i.e. in-degree) is equal to or greater than the maximum in-degree of the least complex network), specialists (S_P ; i.e., the number of species with an in-degree greater than zero but less than the average first quartile of all empirical networks), and the maximum food chain length per network (FCL) (Dunne et al. 2002; Post 2002; Kondoh and Ninomiya 2009; Tylianakis et al. 2010). In addition, generality (G_q ; i.e., the mean number of consumed species per consumer), vulnerability (V_q ; i.e., the mean number of consumers per consumed species), and nestedness (Ings et al. 2009; Tylianakis et al. 2010; Thompson et al. 2012; Zeng et al. 2014). Nestedness, or community cohesiveness, is a useful metric that characterises the generalist-specialist balance in ecological networks (Araujo et al. 2010). In highly nested networks generalist species are organised in a dense core of interactions while a large number of specialists coexist with a few super

generalists (Araujo et al. 2010; Tylianakis et al. 2010). To estimate nestedness I used the Nestedness Temperature calculator in the R (version 3.0.0) package ‘vegan’ (Oksanen et al. 2015). To assess if the values observed were higher than expected by random interaction patterns I tested the nestedness of each network using null models generated using the R package EcoSimR (Gotelli and Ellison 2013). I used the package ‘NetIndices’ (Kones et al. 2009) to calculate all other general network metrics.

Food-web complexity

In order to characterise food-web complexity I used entropy as defined by Kolmogorov-Sinai (Billingsley 1965). In network analysis, entropy measures the diversity of pathways of energy flow between species in the trophic network (Gauzens et al. 2015); I followed the methods of Allesina and Pascual (as referenced in Gauzens et al. 2015). To account for the circulation of energy (Allesina and Pascual 2009) a root node is attached to the network with links pointing to all the basal nodes (i.e. primary producers and detritus) and all other nodes are connected to this root node. In this way the root node acts to represent the build-up of detritus that is in turn partially recycled into the food web (Allesina and Pascual 2009). For a binary matrix, entropy is the logarithm of the dominant eigenvalue of the matrix. Entropy increases with species richness and maximal entropy is obtained when all matrix entries are 1.

2.3.5 Statistical methods

The comparisons of the environmental variables between seabird and invaded islands have been published previously in Fukami et al. (2006), Towns et al. (2009) and Mulder et al. (2009), and as such are included in Supplementary material: Table 2.3. I

conducted ANCOVAs (using type III sum of squares) to identify the effects of invasion status of the islands and soil N on the food web metrics when controlling for variation among islands in size and isolation. After initial data exploration to determine the best predictors I used island status (i.e. invaded or uninvaded) as a discrete factor, and soil N, island area and isolation (i.e., distance to mainland or nearest larger island) as per Fukami et al. (2006) as covariates.

2.4 Results

Across the eighteen islands, the number of species involved in the ecological networks ranged from 21 (an invaded island) to 56 (a seabird island), with a total of over 3,500 interactions across all islands. The networks on rat invaded islands were smaller and less complex (Figure 2.1) and had the lowest number of species and links between them. The most complex network of the invaded islands was approximately as complex as the least complex network of the seabird islands (Figure 2.1). Invaded islands also had a lower number of core generalist species reflected in large, central nodes with a

lower number of links compared with seabird islands (Figure 2.1

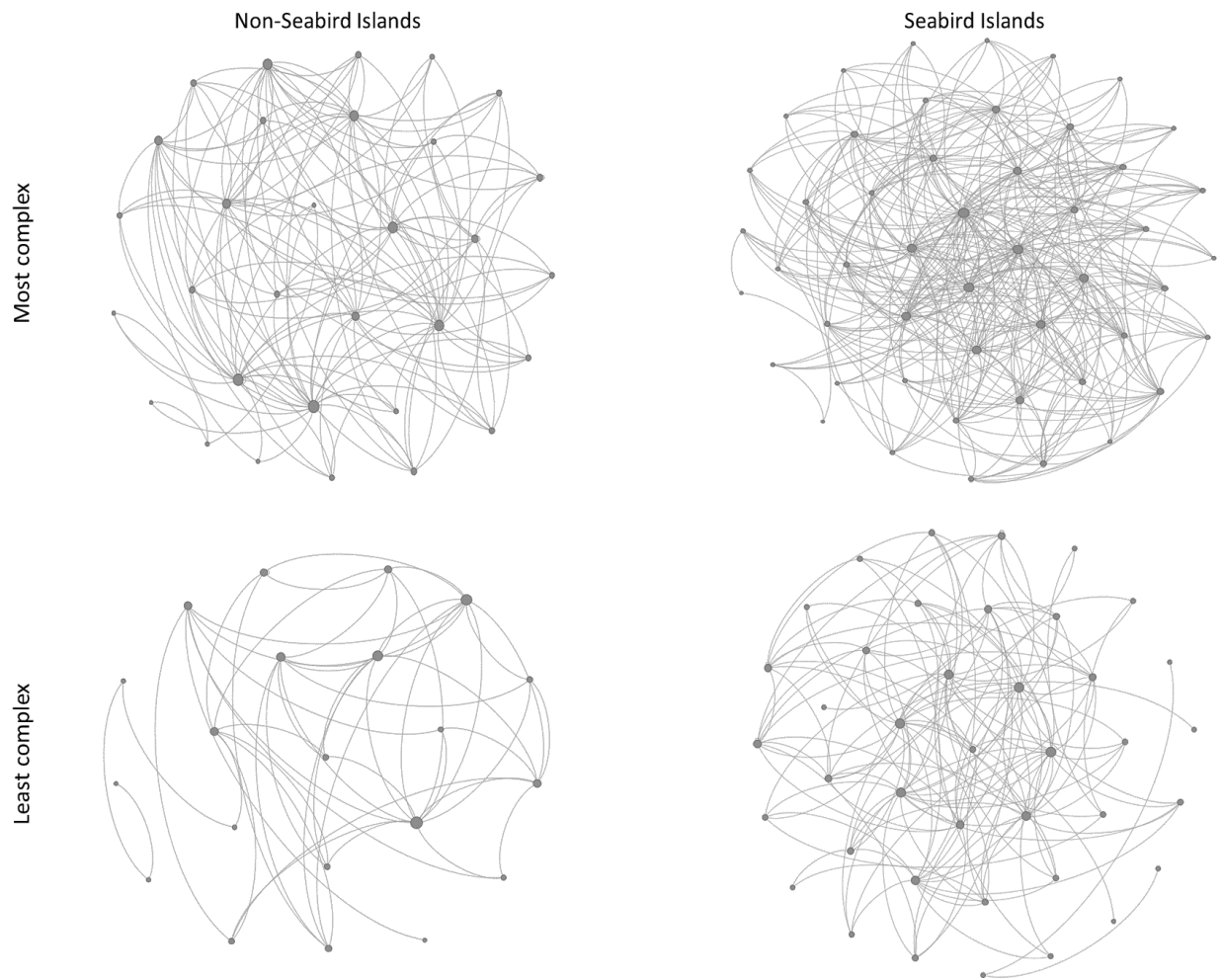


Figure 2.1 The most (upper) and least (lower) complex networks (as measured by entropy) of the seabird and non-seabird category islands, where each node represents a trophic species and each edge a directed feeding link. Node size demonstrates the number of links per node. Generalist species are situated within the core of each network, while specialists are in the periphery. Networks were designed using the open-source social network analysis software Gephi (Bastian et al. 2009).

Most of the effects of island status (rat dominated versus seabird) on food web metrics remained significant when controlling for island size or degree of isolation (Supplementary material: Table 2.3). However, when soil N was added to the models island status was largely no longer significant (Table 2.1), which is likely because these

variables correlated with high soil N apparent on seabird islands (Supplementary material: Table 2.4). Food chain length was found to be affected by the distance to the mainland ($F_{(1,13)} = 10.6$, $p < 0.01$), while nestedness and total specialists both had no significant relationship with any variable. Overall the linear models were strong with adjusted R^2 values ranging from 0.50 to 0.77 with the exception of nestedness and specialists for which R^2 was 0.31 and 0.11 respectively (Table 2.1). For five of the seven significant models soil N was a significant predictor, whereas island size was significant three times and island isolation, twice. Nestedness and specialists were not significantly related to any predictor, while FCL showed a strong model but only with island isolation as a predictor. The generalists variable showed a strong model overall but was marginally insignificant ($p < 0.1$) for all predictors (Table 2.1). Average links between species and entropy showed the strongest models; average links had soil N and island size as predictors while entropy had soil N and island isolation. Soil N was the only significant predictor of the average number of species (Table 2.1).

Table 2.1 ANCOVAs (using type III sum of squares) testing the relationships of the ten network metrics with island status (i.e. invaded vs. uninvaded), soil N, island size, and island isolation. The results show the beta coefficient ‘Est’ (or Estimate), the F-value and the significance. The results of the overall models are given in the two far right columns, where the adjusted R² ‘Adj R²’ and F-values are given and the significance (the degrees of freedom for each model = 3 and 13). P-value symbols: ns = non-significance, NS = near significant ($p < 0.10$), * < 0.05 , ** < 0.001 , *** < 0.0001 .

Network metric	Island status		N		Island size		Island isolation		Full model	
	Est	F	Est	F	Est	F	Est	F	Adj R ²	F
FCL	0.06	2.20 _{ns}	-0.00	0.00 _{ns}	-0.01	0.33 _{ns}	0.04	6.69*	0.50	5.35**
S_T	3.24	1.44 _{ns}	10.30	5.20*	1.23	0.85 _{ns}	2.41	4.31 _{NS}	0.65	9.03**
L	32.79	2.35 _{ns}	134.38	14.17**	25.27	5.78*	15.61	2.89 _{ns}	0.77	15.87***
T	-0.88	0.23 _{ns}	-0.95	0.23 _{ns}	0.07	0.01 _{ns}	-0.58	1.32 _{ns}	0.31	1.66 _{ns}
G_q	0.40	1.48 _{ns}	1.69	9.47**	0.36	5.06*	0.18	1.71 _{ns}	0.69	10.55***
V_q	0.38	1.44 _{ns}	1.68	9.83**	0.35	5.03*	0.18	1.77 _{ns}	0.69	10.74***
G	1.48	3.82 _{NS}	2.58	5.17 _{NS}	0.70	3.61 _{NS}	0.46	2.00 _{NS}	0.67	9.81***
S_P	0.60	0.47 _{ns}	1.13	0.58 _{ns}	0.10	0.06 _{ns}	0.31	0.70 _{ns}	0.11	1.54 _{ns}
E	0.02	0.60 _{ns}	0.18	10.00**	0.03	4.65 _{ns}	0.03	6.46*	0.74	13.2***

Where FCL = food chain length, S_T = average species (families), L = average links, T = nestedness (temperature), G_q = generality, V_q = vulnerability, G = average generalists, S_P = average specialists, E = entropy.

2.5 Discussion

Here I have demonstrated the potential utility of network analysis for determining the complex changes in food webs that may be observed when ecosystems become degraded. Network analysis is not only useful in showing complex changes in food webs but also how these changes occur, providing insight into mechanisms of change such as trophic cascades. The suppression of nutrient subsidies via rat invasion is likely the major cause of the food web complexity collapse observed in this study. Nutrient subsidies are universally important drivers of ecosystems and the food webs they contain. This research further demonstrates their importance and shows the extent of change that can occur when these subsidies are lost.

These network differences among islands were largely associated with differences in total soil N (Table 2.1), with less soil N on the invaded islands (Appendix S1: Table S2; Fukami et al. 2006). Reduced soil N concentration is related to the suppression of seabird derived nutrient subsidies (Fukami et al. 2006; Wardle et al. 2009; Mulder et al. 2009). In addition, while biogeographical factors (e.g., island size and isolation) explained variation for some variables, soil N concentrations themselves or island status (which was strongly correlated with soil N) significantly explained variation in all but one model. The lower soil N apparent on rat invaded islands could influence litter invertebrate networks either through decreased net primary productivity and plant biomass, or through lower nutrient quality of leaves and leaf litter (Siemann 1998; Nordin et al. 1998). On these same islands, Mulder et al. (2009) demonstrated that primary productivity, leaf mass and vegetation diversity were not significantly lower on the invaded islands compared to the seabird islands. However, both Mulder et al. (2009) and Wardle et al. (2009) found that foliar N concentrations for several plant species were lower on the invaded islands, and Wardle et al. (2009) showed that leaf litter N and the release of N during leaf litter decomposition was also lower for those islands. Based on those results it seems likely that the lower N apparent on the rat invaded islands is influencing the food webs through the lower nutrient quality of both foliar leaves and leaf litter rather than through lower plant productivity or biomass. This conclusion is also supported by Fukami et al. (2006) who showed that introduced predators disrupted seabird nutrient subsidies resulting in decreased forest fertility and wide-ranging cascading effects on below-ground organisms.

These changes in forest fertility brought about by rat suppression of seabirds and their subsidies may result in both bottom-up and top-down trophic cascades (Siemann 1998), which helps explain the changes in the complexity of food webs observed. Siemann (1998) showed that an increase in foliar nutrient content ultimately resulted in greater invertebrate community complexity over time in a grassland ecosystem. One reason suggested for this increased complexity was an interplay between top-down and bottom-up forces, whereby higher foliar nutrients resulted in a greater abundance and nutrient quality of primary consumers, and led to a greater abundance and diversity of secondary and tertiary consumers which then regulated the diversity of the primary consumers. I argue that the inverse may be occurring on invaded islands: lower foliar (and leaf litter) nutrients will lead to lower abundance and nutrient content of primary consumers which in turn leads to the decline of secondary and tertiary consumer diversity. Less diversity amongst these tertiary and secondary consumers can decrease competition within these trophic levels, ultimately decreasing the diversity of prey due to decreased apparent mutualisms (in line with the principle that ‘the predator/competitor of my predator is my friend; Abrams 1987; Abrams and Matsuda 1996; Long et al. 2012). This decrease in prey diversity would finally serve to increase the competition between predators, decreasing the persistence of less competitive predator species (Kratina et al. 2007; Hammill et al. 2015), and further decreasing the number of species the ecosystem can support. These trophic cascades would ultimately result in a simple food web (with low entropy) that is characterised by high competition (i.e., fewer generalists, low generality), and a low number of coexisting species (i.e., low total species). The observed decreases in total species abundance, generalists, generality, and entropy on invaded islands supports this theory.

Previous research has demonstrated that ecosystems with more generalists are less susceptible to random extinction events because if one food source disappears there are many others available (Saint-Béat et al. 2015). Food webs characterised by low generality and vulnerability will have few consumers feeding on fewer resources. The low vulnerability apparent on invaded islands shows that there are less options for consumers, this would mean that resource switching to avoid competition would not occur as much and the benefits gained to those species consumed from high competition between consumers (e.g. apparent mutualisms) would also be less apparent. Network entropy is also a quantitative measure of resistance (Demetrius and Manke 2005), defined as a network's capacity to remain functional in the face of random perturbations (Gauzens et al. 2015). The low generalism and entropy apparent on the invaded islands is therefore an indicator of low ecosystem resistance, demonstrating that rats create not only simpler but also less stable food webs (Demetrius and Manke 2005; Svanbäck et al. 2015; Saint-Béat et al. 2015).

My study has shown that the invertebrate food webs on islands invaded by rats are smaller, less complex and may be less resistant to disturbance than those where seabirds are not suppressed. It also suggests that reduced food web size, complexity and resistance to disturbance are related to the lower soil N concentrations on invaded islands and resultant diminishment of trophic cascades. While these indirect effects of rats via changed nutrient subsidies is likely to be the overarching mechanism through rats' impact on these ecosystems (Fukami et al. 2006; Wardle et al. 2009), other factors such as the direct consumption of predatory invertebrates and lizards may also play a role (Towns et al. 2009). Regardless of the precise mechanism by which rats affect

seabird island food webs, the management implications remain the same: rats must be removed from island ecosystems if their food webs are to recover. However, if rats are removed seabirds will also need to recolonize and re-establish in order to exert their subsidising effects and seabird recovery does not always happen passively (Mulder et al. 2009; Buxton et al. 2014; Borrelle et al. 2015). If seabirds do return to these islands (or are reintroduced), the resulting ecosystems still may not revert to their previous state if key components of island food webs are missing, or if there are species that have become locally extinct and that are incapable of returning unaided. In order to identify whether there are missing species or trophic links, further comparisons will need to include islands undergoing restoration.

2.6 Supplementary material for Chapter two:

Table 2.2 Traits of islands used in Chapter 2.

Island name	Island status	Longitude Latitude	Area (ha)	Elevation (m)	Distance 1 (km)	Distance 2 (km)	Distance 3 (km)	Rat invasion*
Tawhiti Rahi	Rat	174.71°E	158.2	191	21.79	21.79	130, 130	Never
	Free	35.45°S						
Aorangaia	Rat	174.74 °E	5.6	102	21.53	0.20	80, 40	Never
	Free	35.48 °S						
Aorangi	Rat	174.72 °E	107.1	216	20.64	0.36	190, 165	Never
	Free	35.48 °S						
Archway	Rat	174.74 °E	6.3	97	20.84	0.11	30, 30	Never
	Free	35.49°S						
Middle	Rat	175.84 °E	13.5	85	9.30	1.67	80, 80	Never
	Free	36.60°S						
Green	Rat	175.85 °E	2.5	50	7.22	0.84	30, 30	Never
	Free	36.64 °S						
Ohinauiti	Rat	175.88 °E	5.9	40	5.31	0.53	60, 55	Never
	Free	36.71 °S						
Ruamaahuanui	Rat	176.09 °E	32.4	160	19.99	15.70	130, 130	Never
	Free	36.95°S						
Ruamahuaity	Rat	176.06 °E	25.3	180	18.14	1.94	115, 80	Never
	Free	36.97°S						
Aiguilles	Rat	175.39 °E	72.7	120	47.67	0.13	240, 205	<i>R. rattus</i>
	Invaded	36.03 °S						
Goat	Rat	174.8 °E	13.4	60	0.14	0.14	130, 30	<i>R. rattus</i>
	Invaded	36.26 °S						
Motukaramarama	Rat	175.37 °E	10.1	71	3.34	0.46	70, 70	<i>R. norvegicus</i>
	Invaded	36.68 °S						
Motuhoropapa	Rat	174.96 °E	8.6	50	13.64	0.19	80, 70	<i>R. norvegicus</i> †
	Invaded	36.69 °S						
Otata	Rat	174.97 °E	16.8	67	14.90	2.29	70, 65	<i>R. norvegicus</i> †
	Invaded	36.69 °S						
Motuatoruhi	Rat	175.38 °E	58.0	169	2.80	1.52	20, 15	<i>R. norvegicus</i> or <i>R. rattus</i>
	Invaded	36.73 °S						
Motutapere	Rat	175.4 °E	45.6	175	2.51	0.57	80, 70	<i>R. rattus</i>
	Invaded	36.78 °S						
Motueka	Rat	175.8 °E	6.2	46	1.20	1.68	30, 30	<i>R. norvegicus</i> or <i>R. rattus</i>
	Invaded	36.82 °S						
Hauturu	Rat	175.89 °E	10.3	85	0.54	0.54	150, 55	<i>R. norvegicus</i> ‡
	Invaded	37.21 °S						

Distance 1, distance to mainland (North Island of New Zealand). Distance 2, distance to nearest larger island (including North Island). Distance 3, distance from shore of plots. *Rat-invaded islands are likely to have also been invaded by the Pacific rat *R. exulans*. †Exterminated in 1987, 1991, and 2002. ‡The mouse *Mus musculus* is also present.

Table 2.3 Environmental variables on seabird dominated islands compared with non-seabird islands. Mean values \pm SEM are presented for both island types ($n = 9$). P values from Student's t-tests are presented. (ns = not significant, * < 0.05 , ** < 0.01 , *** < 0.001).

	Seabird islands (\pm SEM)	Non-seabird islands (\pm SEM)	<i>t</i>	<i>p</i>
Burrows per 100m ²	36.5 (± 11.3)	1.5 (± 0.8)	6.4	***
Litter dry weight (g 2L ⁻¹)	306.5 (± 37.5)	194.8 (± 16.1)	2.9	**
pH	5.2 (± 0.3)	6.7 (± 0.1)	3.1	**
Total soil C %	11.1 (± 2.0)	5.2 (± 0.4)	3.3	**
Total soil N %	0.9 (± 0.1)	0.4 (± 0.0)	3.5	**
Olsen P	237.0 (± 77.6)	46.2 (± 13.6)	2.7	*
Soil $\delta^{13}\text{C}$	-26.3 (± 0.2)	-25.6 (± 0.3)	2.0	ns
Soil $\delta^{15}\text{N}$	13.7 (± 0.7)	9.2 (± 1.1)	3.0	*
<i>M. ramiflorus</i> Leaf $\delta^{13}\text{C}$	-31.3 (± 0.3)	-32.8 (± 0.4)	2.8	*
<i>M. ramiflorus</i> Leaf $\delta^{15}\text{N}$	10.5 (± 0.7)	6.1 (± 1.0)	3.5	**
Invertebrate $\delta^{15}\text{N}$	15.4 (± 0.6)	7.8 (± 0.8)	7.3	***
Distance to mainland	15.9 (± 2.3)	9.6 (± 5.1)	1.1	ns
Island Size	39.6 (± 18.4)	26.8 (± 8.3)	0.6	ns

Table 2.4 Food web metrics on seabird dominated islands compared with non-seabird islands. All networks are measured on a linear scale except nestedness which is a linear inverse scale of 1 – 100 with 1 = total nestedness and 100 = total randomness. Adjusted mean values \pm SEM are presented for both island types ($n = 9$). In the column marked 'At', *t* and *p* values from Students' t-tests using ANCOVA corrected means (when taking into account the variation in island size and distance to the mainland) are presented. P-value symbols: ns = non-significance, * < 0.05 , ** < 0.001 , *** < 0.0001 .

	Seabird islands (\pm SEM)	Non-seabird islands (\pm SEM)	<i>At</i>
FCL	3.91 (± 0.02)	3.75 (± 0.03)	1.78 _{ns}
Mean species (<i>S_T</i>)	46.11 (± 2.58)	32.88 (± 2.23)	2.43*
Mean links (<i>L</i>)	276.00 (± 28.56)	142.44 (± 16.34)	2.90*
Nestedness (<i>T</i>)	5.89 (± 0.62)	8.52 (± 0.95)	-1.19 _{ns}
Generality (<i>G_q</i>)	5.87 (± 0.35)	4.22 (± 0.28)	2.58*
Vulnerability (<i>V_q</i>)	5.70 (± 0.35)	4.08 (± 0.27)	2.57*
Mean generalists (<i>G</i>)	7.66 (± 0.66)	3.66 (± 0.66)	3.16**
Mean specialists (<i>S_P</i>)	6.66 (± 0.64)	4.77 (± 0.54)	1.28 _{ns}
Entropy (<i>E</i>)	1.80 (± 0.03)	1.62 (± 0.03)	2.18*

**Chapter three: Effects of litter water and nutrient
subsidies on invertebrate food webs in an island
forest ecosystem.**

3.1 Abstract

The movement of nutrients across ecosystem boundaries is a ubiquitous phenomenon in many ecosystems. How these nutrients effect their recipient ecosystems depends on many factors with an important one being water availability. I used artificial nutrient subsidies mimicking those of seabirds to determine their effects on the structure and function of leaf litter invertebrate food webs. The research was carried out during a period of drought and subsequent rainfall which increased water availability in the ecosystem exponentially over time. I therefore used data on water availability and soil nutrients to determine the effects of and interplay between nutrient subsidies and water availability on invertebrate food webs. While I found that the nutrient subsidies added to the ecosystem had no effect on any of the invertebrate food webs or soil nutrient content, there were natural nutrient gradients across the island and through time. I found that the invertebrate food webs were larger and more complex with increases in species diversity, food web entropy, and food chain length as litter water increased and soil C: N slightly decreased. There was increased generalism and omnivory between species as water availability increased, but not soil nutrients, which showed no effect on these variables. A key finding was the resilience of the invertebrate food webs, which shrunk to a fraction of their full potential complexity during arid periods then reconstructed themselves with increased water availability.

3.2 Introduction

The movement of nutrients across ecosystems boundaries (nutrient subsidies) is a ubiquitous phenomenon across many biomes and ecosystems (Ben-David et al. 1998; Hilderbrand et al. 1999; Bouchard and Bjorndal 2000; Farina et al. 2003; Hannan et al. 2007). However, how subsidies affect food webs is varied, with factors such as rainfall, seasonality, relative productivity of connected ecosystems, and the perimeter/area ratio of the recipient ecosystem affecting the degree and importance of resource subsidisation (Polis et al. 1997; Stapp and Polis 2003). Artificial nutrient subsidy experiments may be capable of providing more information on the interplay between abiotic factors and subsidies and how this affects the recipient food webs. Many offshore islands worldwide are dominated by seabirds and the nutrients they supply to these systems (Jones 2010). These nutrient subsidies have been shown to have many effects upon different aspects of these island food webs (Bancroft et al 2005; Fukami et al. 2006; Kolb et al. 2010 and 2011; Ellis 2011; Caut et al. 2012). However, how the effects of these subsidies may change throughout the seasons is less understood. In temperate ecosystems, temperature may play a major role in the way subsidies affect food webs (Basset 1991; Kai and Corlett 2002). Elsewhere, factors such as increases in drought length and severity (Dale et al. 2001; Allen et al. 2010; Carnicer et al. 2011) may play an increasingly large role (Levings and Windsor 1985; Frith and Frith 1990; Pinheiro et al. 2002).

Artificial nutrient subsidy experiments (i.e. fertilisation experiments) have been used in the past largely in the context of farming or forestry. There has been little research focused on replicating the effects of natural subsidies such as those found on seabird islands with high nutrient inputs. In addition, many of the studies

focused on the effects of nutrient subsidies on invertebrate food webs have been contentious, with conflicting results. Haddad et al. (2000) showed that long-term subsidies in a grassland ecosystem decreased overall invertebrate diversity, and herbivore and predator diversity, but increased detritivore diversity and overall insect abundance. These effects were attributed to changes in the plant communities, with decreased species richness and productivity, increased tissue nitrogen and a composition shift from C4 to C3 species (Haddad et al. 2000). Alternately, Siemann (1988) found that while high nutrient input over time resulted in decreasing plant diversity in a grassland ecosystem it did not result in decreasing invertebrate diversity. Invertebrate food webs were more complex with greater species diversity, longer food chains, and more diverse predator and parasite communities. There are many studies that support the results of Haddad et al. (2000): (i.e. Bakelaar and Odum 1978; Huhta et al., 1986; Tilman 1988, 1993, 1996; Theodose and Bowman 1997), and many others that support Siemann (1988): (i.e. Hurd et al. 1971; Hurd and Wolf 1974; Kirchner 1977; Sedlacek et al. 1988), the research is thus unclear as to whether artificial nutrient subsidies have largely positive or negative effects on invertebrate communities. One of the rare studies aimed at simulating the effects of natural subsidies was carried out by Jones (2010) who studied the effects of seabird derived nutrients on a grassland island ecosystem. She found that subsidies can increase arthropod abundance, decomposition rates and GANPP (gross annual net primary productivity), but only with relative high nutrient additions (i.e. high seabird densities). A shortfall of many of these studies is the fact that they were often based only on data for soil and leaf chemistry, but little information about other abiotic influences such as rainfall or temperature.

Natural nutrient subsidies on seabird islands are imported into island ecosystems via guano, with the potential of increasing concentrations of soil N up to 100 times and P by 400 times (Furness 1991). These marine subsidies often result in complex food webs, with increased primary productivity and plant and consumer: nutrient status, size, abundance and diversity (Polis and Hurd, 1995; Anderson and Polis, 1999; Kolb et al. 2010 and 2011; Mulder et al., 2011). However, in areas where seasonality is strong the effects of these subsidies vary according to numerous abiotic factors, with an important and prevalent factor being rainfall. On the arid islands in the Gulf of California, seabird derived nutrient subsidies support only ectoparasites and detritivores until wet years when there is a veritable explosion of life. On these islands, wet years lead to higher primary productivity due to a combination of highly available nutrients and water, resulting in periodic nutrient-rich plant growth (Polis and Hurd 1996; Polis et al. 1997; Anderson and Polis 1999; Sánchez-Piñero and Polis 2000; Anderson et al. 2008). These nutrient rich plants support a high diversity and abundance of herbivorous invertebrates resulting in extremely high densities of orb-web spiders, lizards and mice (Polis and Hurd 1995; Sánchez-Piñero and Polis 2000; Stapp and Polis 2003; Barret et al. 2005).

A common theme to studies of both natural and artificial nutrient subsidies is that they focus on how subsidies affect the structure (i.e. individual species, families or functional groups) of a food web, not on its functional aspects (i.e. the interactions it contains). Changes in interactions within a food web are important to understand in order to appreciate not only why these food webs might change, but also how the webs are effected. Network analysis provides a way of quantifying food webs and the interactions they contain (Forup et al. 2008, Tylianakis et al. 2010). However, as the use of this technique in ecology is relatively new, there are few studies showing

the effects of nutrient subsidies on food web interactions. One such study (Thoresen et al. Chapter 2) indicated that invertebrate food webs were larger and more complex due to seabird derived nutrient subsidies, primarily N availability. The authors showed that complexity shifted partly as a response to changes in the feeding habits of the invertebrates, with species becoming more generalist as nutrient subsidies increased. However, the study focused only on the effects of subsidies on the food web interactions without detailing the individual families or functional groups that made up those food webs. Including changes in both the structural and functional aspects of a food web should provide a clearer understanding of mechanisms of nutrient subsidies and seasonality within an ecosystem.

While artificial nutrient subsidy experiments have led to many conflicting results, studies on natural subsidies like those on seabird islands have consistently pointed to numerous pathways through which subsidies influence food webs. Understanding how nutrient subsidies affect food webs is key to the restoration of such ecosystems, especially as seasonality can alter these effects. As there are numerous abiotic factors that can potentially influence nutrient subsidies and food webs, I focus on water availability or rainfall. Water is an important factor that strongly influences biogeochemistry (Burke et al. 1997) and invertebrate food webs (Levings and Windsor 1985; Frith and Frith 1990; Pinheiro et al. 2002) and as such it is likely to have an effect on the interplay between the two. The effects of seasonal variations in water availability has not been studied for temperate ecosystems driven by seabird nutrient subsidies. Here I aim to understand the importance of, and interplay between, water availability and simulated seabird nutrient subsidies on invertebrate food webs in a forested offshore island ecosystem in New Zealand. I set out to answer this aim using the following hypotheses; 1) artificial nutrient subsidies

will have a positive effect on food web structure and function with larger, more complex food webs in areas of higher subsidies, 2) water availability will increase food web complexity and size across all subsidy treatments but higher complexity will be found in areas of higher nutrient subsidies.

3.3 Methods

3.3.1 Study site

The study was carried out on Motuoropapa Island in the Noises Group, Hauraki Gulf, New Zealand (Mackay et al. 2007). The Noises are made up of 4 main islands: Otata (21.8 ha), Motuoropapa (9.5 ha), Maria (2.0 ha), David Rocks (2.0 ha) and several islets smaller than 1ha; the whole group lies approximately 24km north-east of Auckland (-36.6892, 174.9639). The forest on Motuoropapa is well established due to the vegetation being relatively undisturbed for over a 100 years (Cunningham and Moors 1985; Cameron 1998). Common flora species include; pohutakawa (*Metrosideros excelsa*), kohekohe (*Dysoxylum spectabile*), mapou (*Myrsine australis*), and five finger (*Pseduopanax arboreus*). The island has been free of invasive predators since 2002 (Russell et al. 2005; Clout and Russell 2006) when Norway rats (*Rattus norvegicus*) were eradicated. Small, localised populations of grey-faced petrels (*Pterodroma macroptera gouldi*) coexisted with Norway rats and currently form one small colony (Mackay et al. 2007, James Russell *pers. comm.*).

3.3.2 Experimental set up

Nutrient addition plots were set up on Motuoropapa Island using a GIS randomised block study design, with five treatments of 2m² plots per block. With six

replicate blocks, there were a total of 30 plots. Blocks were placed at least 50m apart to ensure independence. In each block, the five treatments were randomly assigned: (1) control (no fertiliser), (2) low seabird density (1 burrow/m²), (3) medium seabird density (3 burrows/m²), (4) medium-high seabird density (5 burrows/m²), and (5) high seabird density (10 burrows/m²) (Jones 2010a). For each block, the plots were placed at locations with an incline <30°, to prevent excess leaching (Towns et al., 2009) and without seabird burrows. I used a mixture of marine based fertiliser; Verteflow 8.3.6 (a liquid fish-based fertilizer; Fertilizer New Zealand, Nelson, New Zealand) supplemented with uric acid, ammonium nitrate and time-release fertiliser to simulate seabird guano following Jones (2010a), (see Supplementary material Table 3.4 for amounts of fertiliser used). The amount of fertiliser added to each plot calculated by Jones (2010a) was based on data from Mulder and Keall (2001). The fertiliser mixture was applied twice during the austral summer (once in December 2014 and once more in January 2015). Before each treatment was applied, 100g samples of soil (taken from the top 10cm soil layer) and 2 litres of leaf litter (from across the entire 2m² plot) were taken from each plot along with measurements of vegetation diversity and density. Four months after the final application of fertiliser in late April 2015 final soil and leaf litter samples were taken to evaluate ecosystem response to the nutrient addition. Soil samples were dried at 60°C for 48h to determine water content, then homogenised and analysed for total N and C, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a Mass Spectrometer and elemental analyser. These were carried out in order to independently test for a subsidy effect on soil chemistry and in order to test for any potential seabird effects that may occur on the island. Leaf litter samples were weighed and left in Tullgren funnels for seven days to extract the invertebrates. The holding jars beneath the funnel were weighed before and after invertebrate

extraction to estimate the total invertebrate mass. The invertebrate mass was subtracted from the difference in leaf litter weight before and after extraction (seven days of passive drying under the light in the Tullgren funnel) to estimate the water content of the litter. All invertebrates were identified to family level using a dissection microscope and then organised into one of seven functional groups: predators, parasitoids, detritivores, herbivores, fungivores, saprophagivores and phytophagivores.

3.3.3 Food web methods

Food webs were described following the methods of Thoresen et al. (2017; Chapter 2). Taxa were identified to family; however, if larvae differed in their feeding strategies they were defined as a separate group. Trophic links were determined from the literature and through communication with experts (Digel et al. 2014; Gauzens et al. 2015). Where there was little information on feeding habits, I estimated feeding category through taxonomic similarities, i.e. groups from morphologically similar families were assumed to have similar diets, or only slight modifications due to size effects (Gauzens et al. 2015). I used this information to describe 90 food webs, one for each treatment plot across each of the three trips (see Appendix B for a full list of invertebrates and their feeding strategies). I used nine food web metrics in total, two that characterised the entire food web; entropy and nestedness (Ings et al. 2009; Allesina and Pascual 2009; Tylianakis et al. 2010; Thompson et al. 2012; Zeng et al. 2014; Gauzens et al. 2015), and seven general metrics, including; species diversity, link diversity, food chain length, generality, vulnerability, the generalist to specialist ratio and the omnivory index (Dunne et al. 2002; Post 2002; Kondoh and Ninomiya 2009; Tylianakis et al. 2010). For greater understanding of these metrics refer to Thoresen et al. (Chapter 2). I used the

package ‘NetIndices’ (Kones et al. 2009) to calculate all general network metrics. To estimate nestedness I used the Nestedness Temperature calculator in the R (version 3.1.0) package ‘vegan’ (Oksanen et al. 2015). To assess if the values observed were higher than expected by random interaction patterns I tested the nestedness of each network using null models generated using the R package EcoSimR (Gotelli and Ellison 2013). I calculated entropy following the methods of Gauzens et al. (2015).

I verified the effectiveness of my network description approach by comparing my empirical networks to those constructed using the niche model (Williams and Martinez 2000; Dunne et al. 2002; Williams and Martinez, 2008; Williams et al. 2010; Thompson et al. 2012) (see Appendix A for detailed explanation and discussion of niche model construction and analyses used, Table A2). Six of the ten metrics used to compare the networks were no different from the niche model. The other differences may reflect an inaccuracy in my description methods, although the niche model has also been shown to not be fully accurate in predicting realistic food webs (Williams and Martinez, 2008). While the niche model may be inaccurate in some areas, it has been used in the past to draw conclusions on how the structure and function of real-world food webs may change in relation to external stimuli. These comparisons show that my food webs are at least partially accurate when compared to the niche model, which in itself is also partially accurate. In addition, while some of these metrics may be inaccurate due to the methods I used in describing the food webs, they still change in predictable ways. As such, I can use them to predict changes in food webs (at least when they are described in the same way) despite any inaccuracies that may exist when they are compared to full food webs.

3.3.4 Statistical methods

I used ANOVAs on the environmental variables and food web metrics to determine if the treatment level categories had any effect on soil nutrient availability or food web structure and function. Normality and homogeneity of all variables was assessed using Levene's tests and quantile-quantile plots, non-homogenous or normal variables were log transformed to meet test assumptions. I compared the variation in these variables between trips, treatments, blocks and all of the two way interactions between these categories. I then carried out Tukey post-hoc tests to determine the differences within trips, treatments and blocks.

I then used multiple linear models on all of the data collectively, disregarding the categorical variables, to determine if nutrient and water availability had effects on the invertebrate orders, functional groups and food webs. The predictor variables were standardised by subtracting their means from them. I used the model selection algorithm in R; stepAIC to simplify the models to those of the best fit. Finally, I presented the food web graphs of the least and most complex food webs (by entropy) over the three trips in order to visually demonstrate the differences in food web structure between trips. All statistics were carried out in R version 3.1.2 (R Core Team, 2013), I used the open source network analysis program Gephi (Bastian et al. 2009) to visualise the food webs.

3.4 Results

I found significant differences between trips one (before initial fertilisation), two (one month after initial fertilisation) and three (four months after final fertilisation) for all environmental variables (Table 3.1). Soil N, C, C: N and leaf litter water was higher on trip three compared with trips two ($p < 0.001$ for N, C, C:

N and litter water) and one ($p < 0.05$, < 0.01 , < 0.001 for C, C: N, and litter water respectively). Trip two had the lowest C, N, C: N and leaf litter water, although was only consistently significantly lower than trip three. The opposite patterns were apparent for the stable isotope variables $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, where trip three was lower than trip two ($p < 0.001$) or one ($p < 0.001$ and < 0.1 respectively). Despite nutrient addition, there were no significant differences between treatments for C, N, C: N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 3.1, Figure 3.1).

Table 3.1 F-values from multilevel ANOVAs for the environmental variables between trips ($n = 3$), treatments ($n = 5$) and plots ($n = 6$). Where $n = 90$ for each environmental variable. Degrees of freedom = 2 for trip, 4 for treatment, 5 for plot, 8 for trip:treatment, 10 for trip:plot, and 20 for plot:treatment. p symbols are ns = non-significant, * < 0.05 , ** < 0.001 , and *** < 0.0001

	Trip	Treatment	Block	Trip: Treatment	Trip: Block	Block: Treatment
C	23.09***	1.21 <i>ns</i>	11.94***	2.36*	0.97 <i>ns</i>	3.17***
N	14.45***	1.48 <i>ns</i>	16.66***	1.20 <i>ns</i>	1.20 <i>ns</i>	3.40***
$\delta^{13}\text{C}$	39.09***	5.94**	13.82***	1.13 <i>ns</i>	1.80 <i>ns</i>	3.18***
$\delta^{15}\text{N}$	28.09***	3.12*	17.90***	2.53*	0.88 <i>ns</i>	4.89***
Litter water	203.37***	1.41 <i>ns</i>	1.42 <i>ns</i>	0.87 <i>ns</i>	0.97 <i>ns</i>	1.50 <i>ns</i>

In addition, I found no evidence of any marine signatures in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ either from the artificial subsidies or natural sources via seabirds. There were, however, significant differences found between blocks for all variables except leaf litter water (Table 3.1). There was a significant effect found between the interaction between block and treatment and the four nutrient variables (Table 3.1). This means there was an effect the potential differences between blocks had on the treatments

which in turn affected the nutrient variables.

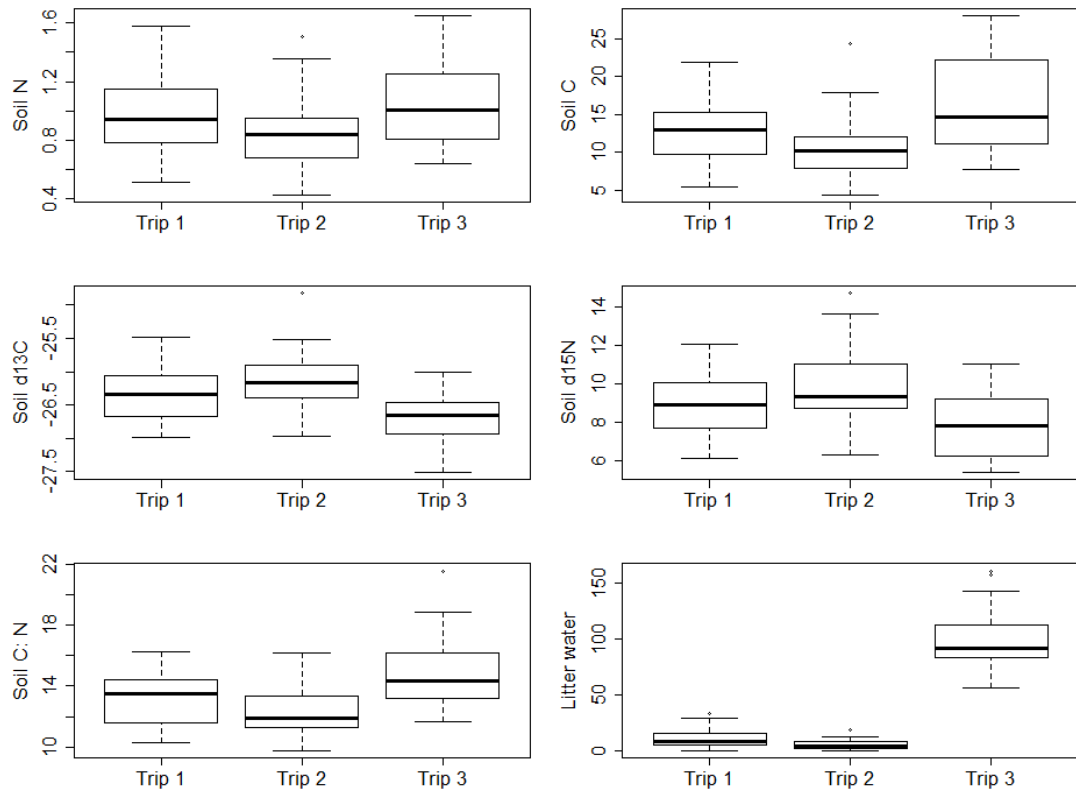


Figure 3.1 Boxplots of environmental variables between the three sampling trips on Motuhoropapa.

Further ANOVAs were completed on the seven major orders of invertebrates (plus the class Acari), and the seven functional groups used in this study (hereafter collectively referred to as ‘groups’. There was consistent highly significant difference found between trips for all of the invertebrate groups excluding parasitoids (Table 3.2). Trip three had greater abundances of every group, excluding parasitoids, compared with trip two ($p < 0.001$) and trip one ($p < 0.001$). Trip one was also significantly higher than trip two for Diplopoda ($p < 0.05$) but no other groups. When the invertebrate groups were compared amongst treatments no significant differences were found (Table 3.2). Likewise, the interactions were largely insignificant with few strong effects of one predictor variable on any other that would cause an effect on the response variables (Table 3.2).

Table 3.2 F-values from multilevel ANOVAs for all invertebrate Orders (plus the Class Acari), functional groups, and network metrics between trips (n = 3), treatments (n = 5) and replicate blocks (n = 6). Where n = 90 for each invertebrate group. Degrees of freedom = 2 for trip, 4 for treatment, 5 for plot, 8 for trip:treatment, 10 for trip:plot, and 20 for plot:treatment. p symbols are ns = non-significant, * < 0.05, ** < 0.001, and *** < 0.0001

Class/Order	Trip	Treatment	Block	Trip: Treatment	Trip: Block	Block: Treatment
Entognatha	60.32***	0.80 <i>ns</i>	0.98 <i>ns</i>	0.87 <i>ns</i>	1.13 <i>ns</i>	1.16 <i>ns</i>
Acari	80.83***	0.52 <i>ns</i>	1.20 <i>ns</i>	0.40 <i>ns</i>	1.20 <i>ns</i>	0.99 <i>ns</i>
Araneae	25.09***	0.49 <i>ns</i>	1.17 <i>ns</i>	0.55 <i>ns</i>	0.74 <i>ns</i>	0.85 <i>ns</i>
Lepidoptera	27.60***	2.22 <i>ns</i>	3.69**	1.34 <i>ns</i>	1.82 <i>ns</i>	1.30 <i>ns</i>
Diptera	59.75***	2.30 <i>ns</i>	0.63 <i>ns</i>	3.07**	2.00 <i>ns</i>	1.14 <i>ns</i>
Diplopoda	41.20***	1.63 <i>ns</i>	3.82**	2.24*	1.95 <i>ns</i>	0.80 <i>ns</i>
Coleoptera	43.16***	0.27 <i>ns</i>	1.37 <i>ns</i>	0.83 <i>ns</i>	1.69 <i>ns</i>	1.19 <i>ns</i>
Chilopoda	170.57***	2.23 <i>ns</i>	5.28***	2.23*	5.28***	1.00 <i>ns</i>
Functional Groups						
Detritivores	64.27***	0.23 <i>ns</i>	0.83 <i>ns</i>	0.42 <i>ns</i>	0.86 <i>ns</i>	0.74 <i>ns</i>
Fungivores	88.32***	0.66 <i>ns</i>	1.39 <i>ns</i>	0.44 <i>ns</i>	1.54 <i>ns</i>	1.04 <i>ns</i>
Saprophagivores	53.56***	0.63 <i>ns</i>	0.72 <i>ns</i>	0.59 <i>ns</i>	0.79 <i>ns</i>	1.01 <i>ns</i>
Herbivores	47.41***	1.20 <i>ns</i>	2.50*	0.77 <i>ns</i>	1.37 <i>ns</i>	1.30 <i>ns</i>
Phytophagivores	40.81***	0.47 <i>ns</i>	4.44**	0.37 <i>ns</i>	4.61***	1.08 <i>ns</i>
Predators	72.10***	1.50 <i>ns</i>	1.95 <i>ns</i>	1.57 <i>ns</i>	0.43 <i>ns</i>	0.89 <i>ns</i>
Parasitoids	2.60 <i>ns</i>	0.82 <i>ns</i>	0.30 <i>ns</i>	1.02 <i>ns</i>	0.84 <i>ns</i>	0.68 <i>ns</i>
Network metrics						
Species diversity	212.25***	1.64 <i>ns</i>	1.47 <i>ns</i>	0.75 <i>ns</i>	3.15**	1.61 <i>ns</i>
Entropy	128.46***	1.82 <i>ns</i>	2.42 <i>ns</i>	0.77 <i>ns</i>	3.56**	1.49 <i>ns</i>
Total links	207.15***	1.06 <i>ns</i>	0.42 <i>ns</i>	0.93 <i>ns</i>	2.62*	1.35 <i>ns</i>
Food Chain Length	24.62***	0.88 <i>ns</i>	0.39 <i>ns</i>	1.23 <i>ns</i>	0.95 <i>ns</i>	1.57 <i>ns</i>
Nestedness	1.64 <i>ns</i>	2.08 <i>ns</i>	2.49*	0.96 <i>ns</i>	1.95 <i>ns</i>	1.75 <i>ns</i>
Generality	128.62***	0.90 <i>ns</i>	0.92 <i>ns</i>	0.84 <i>ns</i>	2.64*	1.16 <i>ns</i>
Vulnerability	134.25***	1.14 <i>ns</i>	0.87 <i>ns</i>	0.88 <i>ns</i>	2.62*	1.18 <i>ns</i>
Generalists: Specialists	91.32***	0.85 <i>ns</i>	0.68 <i>ns</i>	0.83 <i>ns</i>	0.76 <i>ns</i>	1.29 <i>ns</i>
Omnivory index	7.80**	0.29 <i>ns</i>	2.52*	0.34 <i>ns</i>	0.94 <i>ns</i>	1.24 <i>ns</i>

The interaction between trips and treatment had a significant effect on Diptera, Diplopoda, and Chilopoda, but no differences found for the functional groups (Table 3.2). There were also significant differences for the invertebrate

groups between blocks for Lepidoptera, Diplopoda, Chilopoda, herbivores and phytophagivores (Table 3.2). Finally, the interaction between trips and blocks had a significant effect on both Chilopoda and phytophagivores (Table 3.2). The significant interactions between blocks and trip likely show the variation in invertebrate food webs across the island and over time.

For the significant invertebrate groups, I then carried out post-hoc tests between treatments for each trip. I found no significant differences between treatments for Diplopoda for any trip. The difference in Diptera abundance between the high and low treatments during trip three were near significant ($p < 0.1$); no other differences came close to significance for any trip. There were no Chilopoda for either trips one or two and no significant differences between any of the treatments for trip three.

Final ANOVAs were completed on the nine food web metrics. Once again, the only consistent significant differences were found between trips (Table 3.2), with all of the network metrics, excluding nestedness, significantly higher on trip three compared with trip two ($p < 0.001$) and trip one ($p < 0.01$, excluding omnivory index). Trip one also showed higher values for all network metrics, except nestedness and omnivory index compared with trip two ($p < 0.05$). No significant differences were found between treatments or between the interactions between treatments and trips and blocks (Table 3.2). There were differences found between blocks for nestedness and the omnivory index, and between the interactions between blocks and trips for; species diversity, entropy, total links, generality, and vulnerability.

I next carried out multiple linear models to determine the major predictor contributing to the consistent differences observed in all invertebrate groups and network metrics (excluding the variables parasitoids and nestedness) between trips. I used a model selection algorithm to determine the model of best fit for each invertebrate group or network metric. Using this algorithm, 13 of 22 models included litter water, the ratio of C: N, and the interaction term between C: N and litter water, the rest of the models only included litter water as a predictor. Leaf litter water was consistently and strongly positively significant in every model (Table 3.3, Figures 3.2 and 3.3). The ratio of C: N in the soil was significant for only around half of the response variables and generally showed a weak negative relationship (Figure 3.2 and 3.3).

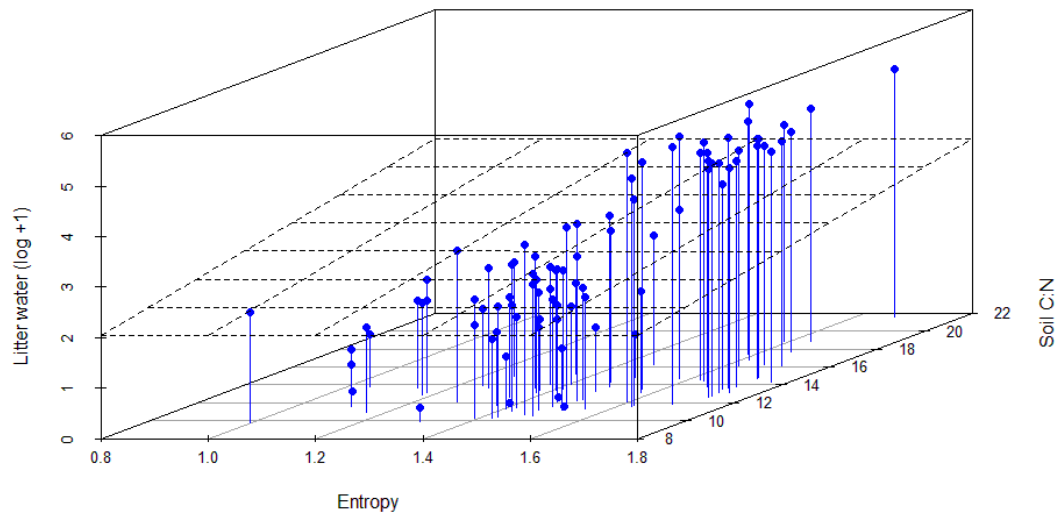


Figure 3.2 Three dimensional regression graph showing the effects of litter water and soil C: N on food web entropy. The dotted plane grid shows the three way regression from Table 3.3 where only litter water and soil C: N have a significant effect on entropy, not the interaction between them.

The significant variables included Entognatha, Diptera, Coleoptera and the overall abundance of all invertebrate groups, the functional groups fungivores, saprophagivores, phytophagivores and predators; and the network metrics species

diversity, entropy, total links, food chain length and the ratio of generalists: specialists (Table 3.3). The interaction term between the ratio of C: N and litter water was significant for Diptera and saprophagivores (Figure 3.3). The full models were all highly significant with adjusted R^2 values ranging from 0.10 for omnivory index to 0.68 for Acari; however, most R^2 of the models were between 0.40 and 0.70 (Table 3.3).

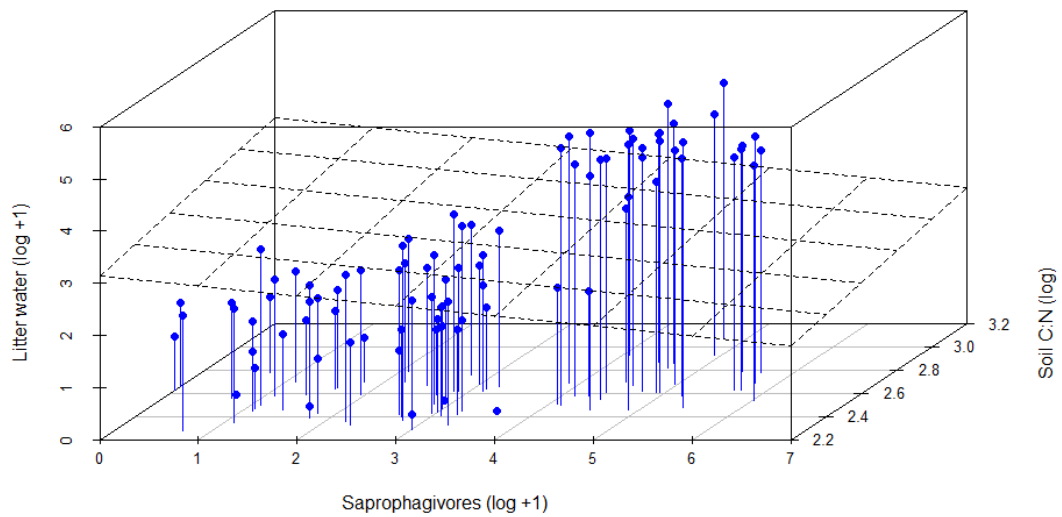


Figure 3.3 Three dimensional regression graph showing the effects of litter water and soil C: N on the abundance of saprophagivores. The dotted plane grid shows the three way regression from Table 3.3 where litter water, soil C:N and their interaction have a significant effect on saprophagivores abundance.

Table 3.3 Multiple linear models of the abundances of invertebrate orders (and the class Acari) and functional groups, and network metrics against soil nitrogen, leaf litter water content and the interaction term between the two. Where n = 90 for each Class/Order, functional group, and network metric, Adj R² = Adjusted R squared, and p symbols are ns = non-significant, * < 0.05, ** < 0.001, and *** < 0.0001, degrees of freedom for each single regression = 1.

	C:N		Litter Water		C:N: Litter Water		Full Model	
Class/Orders	Est	F	Est	F	Est	F	Adj R ²	F
Entognatha	-0.03	31.26***	0.77	132.56***	0.04	2.54 _{ns}	0.64	55.46 _(3,86) ***
Acari			0.95	193.67***			0.68	193.70 _(1,88) ***
Araneae			0.34	64.38***			0.41	64.38 _(1,88) ***
Lepidoptera			0.57	70.56***			0.43	70.56 _(1,88) ***
Diptera	-0.09	5.52*	0.45	63.87***	0.05	4.61*	0.44	24.67 _(3,86) ***
Diplopoda			0.48	70.89***			0.43	70.89 _(1,88) ***
Coleoptera	-0.01	21.42***	0.49	66.91***	0.04	2.91 _{ns}	0.49	30.42 _(3,8) ***
All Class/Orders	-0.03	35.80***	0.74	143.62***	0.05	3.85 _{ns}	0.66	61.10 _(3,88) ***
Functional Groups								
Detritivores			0.55	112.02***			0.55	112.02 _(1,8) ***
Fungivores	-0.03	34.48***	0.83	131.10***	0.06	3.95 _{ns}	0.65	56.51 _(3,86) ***
Saprophagivores	-0.07	25.09***	0.83	114.10***	0.08	5.90*	0.61	48.37 _(3,86) ***
Herbivores			0.51	79.91***			0.46	79.91 _(1,88) ***
Phytophagivores	-0.01	7.90**	0.24	23.24***	0.04	3.46 _{ns}	0.26	11.54 _(3,86) ***
Predators	-0.04	14.54***	0.52	75.67***	0.04	2.37 _{ns}	0.50	30.86 _(3,86) ***
Network metrics								
Species diversity	-0.06	22.93***	5.64	143.84***	0.41	3.75 _{ns}	0.65	56.85 _(3,86) ***
Entropy	-0.00	18.67***	0.10	102.88***	0.00	2.85 _{ns}	0.57	41.47 _(3,86) ***
Total links	-2.20	28.14***	28.26	151.73***	1.60	2.36 _{ns}	0.66	60.75 _(3,86) ***
Food Chain Length	-0.00	7.54**	0.09	25.28***	0.01	2.10 _{ns}	0.26	11.65 _(3,86) ***
Generality			0.39	153.84***			0.63	153.84 _(1,88) ***
Vulnerability			0.37	157.83***			0.63	157.83 _(1,88) ***
Generalists: Specialists	0.01	37.17***	0.24	81.95***	0.02	3.35 _{ns}	0.57	40.83 _(3,86) ***
Omnivory index			0.01	11.72***			0.10	11.73 _(1,88) ***

Finally, I graphed six of the 90 food webs described; the food webs with the lowest and highest entropy for each of the three trips (Figure 3.4). These networks visually show the variation in food web complexity between and within trips. The

differences between trips one and two are not great, although trip two had a slightly less complex food web for the lowest entropy category.

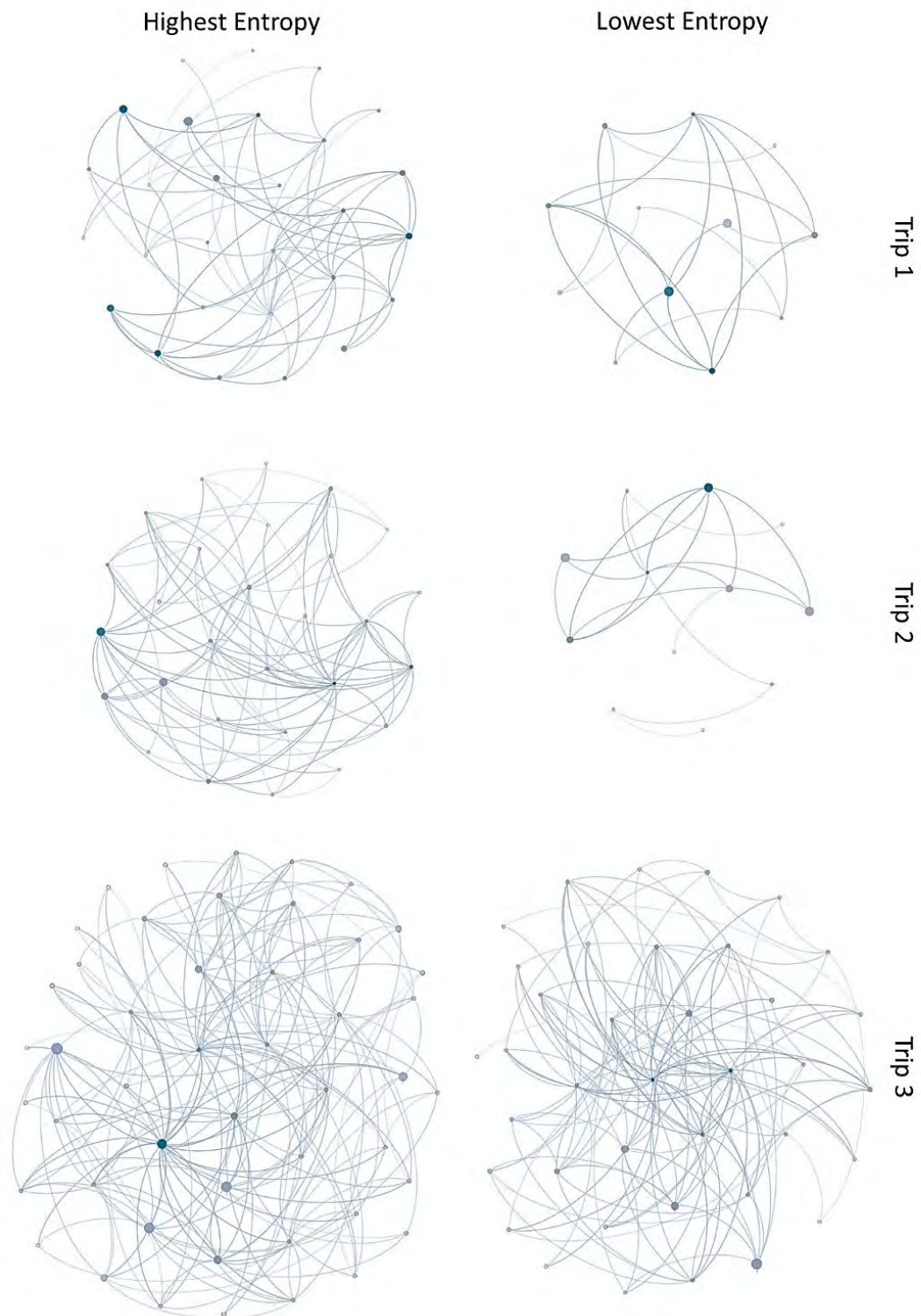


Figure 3.4 Graphs of the highest and lowest entropy food webs for trips 1, 2 and 3 (i.e. before, during and after nutrient subsidy treatment). Colour denotes eigenvector centrality (how connected a node is to every other part of the food web), where dark blue shows high centrality and light blue low. Size of node denotes degree (number of links connected to node) with larger nodes having higher degree. Food webs are arranged to show nestedness

where generalists interact among themselves in a dense core with subsets of lesser and lesser interactions moving outwards with super specialists on the periphery. In addition, the direction of curve shows the feeding interaction, where a curve to the right from a node denotes a consuming interaction and a curve to the left denotes a consumed feeding interaction.

Trip three was much more complex than trips one and two for both the low and high entropy categories. However, the within trip variation for trip three is not overly conspicuous as opposed to the obvious differences in complexity within trips one or two. The least complex food web in trip two, and in fact the least complex of all the 90 food webs over the entire study, is very simple, down to its very basic components.

3.5 Discussion

My results definitively showed no effect of nutrient addition treatment on any of the invertebrate groups or food web metrics. Essentially, the nutrients I added to the ecosystem seemed to disappear quickly, having no effect on the variables I measured. Biogeochemistry is complex and there are a number of possibilities why the nutrients may have quickly disappeared from the system. This may have to do with the aridity of the ecosystem before fertiliser (mixed within water) was added. The addition of short water pulses to dry soils and leaf litter have been shown to cause a fast response in the mineralisation of N and C (Pulleman and Tietema 1999; Austin et al. 2004; Miller et al. 2005; Borken and Metzner 2009), causing N to become useful for vegetation and C to be transformed into CO₂ (Fierer and Schimel 2002; Borken and Metzner 2009). In addition, Cui and Caldwell (1997) showed that plant roots can respond quickly to these water/nutrient pulses, with root ammonium uptake capacity increased significantly within one day of a water and nutrient pulse. However, as the soils become dry again root activity slows down and any excess N is

lost from the system likely due to microbial immobilisation (Vitousek et al. 1982; Wilson and Tilman 1991; Cui and Caldwell 1997).

The uptake of these nutrients from the vegetation would have likely had a bottom-up effect on invertebrates if they were active and present in the ecosystem. However, the results show that during the driest period of the research (trip two) all of the invertebrate groups were significantly reduced in abundance and the food webs simplified. Many studies have shown that invertebrates are seasonal, responding to changes in rainfall and temperature (Frith and Frith 1990; Kai and Corlett 2002; Pinheiro et al. 2002; Cardoso et al. 2007; Silva et al. 2011). Invertebrates in temperate zones like New Zealand, are thought to be more responsive to changes in temperature rather than rainfall (Basset 1991; Kai and Corlett 2002); however, in this study the response of the invertebrate food webs to water availability was particularly strong. In tropical zones, litter invertebrates may have life histories involving dispersal, aestivation, or pupation prior to the dry season, thus declining during periods of drought (Levings and Windsor 1985; Frith and Frith 1990; Lindberg et al. 2002; Pinheiro et al. 2002), a similar mechanism likely occurred during this study. Therefore, the aridity of the ecosystem is likely to have contributed to the loss of nutrients from the soil (via root uptake) and the absence of invertebrates. This combination means that while the vegetation may have benefited from the nutrient subsidies the invertebrates did not, and by the time the food webs built up again these nutrients may have been lost to them.

There may, however, be multiple factors contributing to the results of this study. Most experiments studying the effects of artificial nutrient subsidies on invertebrates have taken place in grassland ecosystems (e.g. Hurd and Wolf 1974; Siemann 1988; Haddad et al. 2000; Jones 2010a). The results of my study may have appeared

inconclusive in comparison to previous research simply due to the differences in how grasslands and forests respond to nutrient subsidies and water. Liu and Greaver (2010) showed in a worldwide meta-analysis that nutrient stimulation increased litter accumulation in grasslands to a much greater extent than in either tropical or temperate forests. As such, artificial nutrient subsidies in grasslands are more likely to have strong effects on leaf litter invertebrates as there is a faster turn over in the detrital layer, rapidly allowing nutrients to become available for detritivorous invertebrates. In addition, the proximity of the nutrient enriched grasses may mean herbivores are quicker to respond to nutrient subsidies compared with forests where leaves can be far away. Finally, it may have simply been that not enough time had passed for the effects of the added nutrients to become visible in the ecosystem.

While my artificial nutrient subsidies failed to affect the food webs, there were natural nutrient gradients across the island and through time. I used these gradients to help answer question two: how water availability (i.e. rainfall) and nutrient subsidies together effect invertebrate food web structure and function. There were more total invertebrates, species, interactions between them, larger food webs (FCL), greater complexity (entropy), and more generalists and specialists with increases in litter water and weak decreases in C: N. Likewise, there were more Entognatha (springtails), Diptera (flies) and Coleoptera (beetles), and more fungivores, saprophagivores, phytophagivores and predators. Many aspects of the food web were only affected by litter water but not C: N. Those affected by litter water included the orders; Acari, Araneae, Lepidoptera, and Diplopoda; the functional groups; detritivores and herbivores, and the food web metrics; generality (prey per predator), vulnerability (predator per prey), and the omnivory index. When controlling for litter water, the effects of C: N were slightly negative. In this study C decreased at a faster

rate to N and this was reflected in the C: N ratio. This difference meant that while there was less food available at lower C: N ratios, the food that was available was of higher quality because of the higher N concentration. This fact may have given rise to the weak negative relationship; while a high C: N ratio is not useful for invertebrates (too much low quality food), a very low one is neither (not enough food), so intermediate measures provide moderate amounts of higher quality food.

The increased contribution by saprophagivores can be explained by the increases in Entognatha and Diptera, both making up the bulk of this functional group. Saprophagivores are small generalist scavengers feeding on everything from carrion, faeces, and fungi to nematodes, bacteria and other small invertebrates. The increase in saprophagivores as well as fungivores likely meant there was an increase in fungal density, which is the case with increased rainfall and soil moisture (Bissett and Parkinson 1979; Bååth and Söderström 1982; Widden 1986). The phytophagivores (nectar and xylem/phloem feeders) were largely made up of Hemiptera and adult Lepidoptera, orders not included separately due to their low abundance. Their increases could have been due to greater vascular transport in plants due to increases in water availability after drought (Sperry 2000; Holbrook and Zwieniecki 2011) or changes in the quality or yield of nectar. The increased proportion of predators is attributable to Araneae, which made up the bulk of the predators but they were only affected by moisture levels, not C: N. Chilopoda, which were not included in the linear models due to their complete absence during trips one and two, also contributed to this result, along with a few predatory families from Coleoptera and Hymenoptera. The increases in predators could have been due to both the indirect effects of the increases in the abundance and diversity of prey and decreases in interspecific competition, and the direct effect of the increase in water availability.

The increases in the food web metrics with litter water and slight decrease with C: N would have largely been due to the increases in overall species abundance and diversity. The metrics that changed: entropy, total links, FCL and generalist: specialists are largely reliant on changes in species diversity as the more species there are the greater the food web complexity will be (entropy) and the more feeding interactions will occur (total links). Increases in species diversity will likely mean there will be more generalists and specialists. Increases in FCL, however, is affected by increases in the abundance or presence of top predators which is the case as can be seen with the increases in both Chilopoda and Araneae. Changes in food web complexity and size was mediated by C: N and litter water; however, changes in the way invertebrates interacted within the food web seemed to have been solely influenced by water availability. The influence of moisture can be seen through the changes in generality, vulnerability and the omnivory index which were only effected by litter water. These results mean that as water availability increases invertebrates become more general in their feeding habits and more omnivorous; feeding more widely from within and between trophic layers. Alternately, as water decreases invertebrates become more specialised. This is likely a response to resource and prey availability and competition. Research has shown how species may expand their niches in response to seasonality, with individuals increasing their diet breadth during wet seasons and decreasing them again in arid periods (Bolnick et al. 2007 Araújo et al. 2009 and 2010). Resource abundance may peak during wet periods (Pinheiro et al. 2002), and niche expansion may be due to seasonal interspecific competition release if competition is high during arid periods when resources are scarce but weaker in wet periods when prey are abundant (Araújo et al. 2010).

In sum, my analyses demonstrate that water availability is of vast importance for invertebrate food webs, with nearly all structural and functional aspects having strong positive relationships with leaf litter water. However, a subtler view of the results also shows that not only is water availability important but C and N are too, and that these variables may interact to influence food web structure. Burke et al. (1997) showed that the relationships between C, N and precipitation are characterised by several interdependencies. The amount of C contained within an ecosystem is largely dependent on annual precipitation (under near steady-state conditions). The amount of C stored within an ecosystem determines the amount of N that can be retained (Burke et al. 1989). N is required for the capture of C, C is required for N retention, and in the absence of disturbance both come into equilibrium with water. In addition, annual net primary productivity (NPP), N use efficiency, and N mineralisation all increase with precipitation. However, while precipitation may have numerous positive effects on C and N, high moisture levels can also cause leaching, depleting nutrients from the soil (Austin and Vitousek 1998). In light of this research and my results, it is likely that the change in water availability between trips two and three caused an increase in the total C and N retained within the ecosystem. However, as C increased faster than N there was a weak negative relationship between C: N and many aspects of the food web as invertebrates may prefer areas with less but higher quality food.

3.6 Conclusion

Artificial nutrient subsidies on a forested island had no discernible effect on any of the food web structural or functional attributes I measured. I therefore was

unable to confirm the initial hypothesis; artificial nutrient subsidies will have a positive effect on food web structure and function with larger, more complex food webs in areas of higher subsidies. Also, this research does not help to clear up the contention, or add to either side of the debate in the literature between the positive and negative effects of subsidies on invertebrate food webs.

The second hypothesis, that water availability will increase food web complexity and size across all subsidy treatments but higher complexity will be found in areas of higher subsidies, was also unable to be confirmed. However, as there was a natural nutrient gradient across the island and between trips I could still identify the effects of soil nutrients in conjunction with water on the food webs. The invertebrate food web structures became larger and more complex with increases in water availability and slight decreases in soil C: N. The functionality of the food web changed via water availability but not soil C: N; there were shifts towards greater generalism and omnivory with increases in litter water.

One finding from my study was the deterioration and reconstruction of invertebrate food webs in response to water availability. This is important to note as it shows the resilience of these food webs and their capability to grow in structure from simple to high complexity; deconstruction followed by reconstruction when conditions are favourable. This resilience also has many implications for food web science; if food webs could be studied in depth across a number of stages of this deterioration and reconstruction trajectory, a great deal of information could be gathered on the resilience of food webs to disturbance and how food webs self-construct.

3.7 Supplementary materials for Chapter three:

Table 3.4 Amounts of nitrogen and phosphorus applied to each seabird density treatment by each fertilizer component (after Jones. 2010).

Nutrient	Seabird density	Time release fertilizer (g)	Urea (g)	Ammonium nitrate (g)	Verteeflow (g)	Total (g)
Phosphorus	<i>Low</i>	1	0	0	1	2
	<i>Medium</i>	2	0	0	4	6
	<i>Medium-High</i>	3	0	0	11	14
	<i>High</i>	4	0	0	34	38
Nitrogen	<i>Low</i>	1.6	5	5	2.4	14
	<i>Medium</i>	3	20.5	20.5	10	54
	<i>Medium-High</i>	4.8	36.1	36.1	29	106
	<i>High</i>	6.4	32.3	32.3	89	160
Total		25.8	93.9	93.9	180.4	394
Total (× 6)		154.8	563.4	563.4	1082.4	2364
Applied twice		309.6	1126.8	1126.8	2164.8	4728

**Chapter four: Network analysis of food webs defines
the restoration status of a seabird island
ecosystem.**

4.1 Abstract

Burrowing seabirds are a major driver of change on islands worldwide but they have been lost from many of their island nesting sites through habitat loss and mammal invasion. Once invasive mammals are eradicated from these islands and seabirds start to return the ecosystems can recover quickly, returning to a predisturbance state within as little as 20 years. However, island ecosystems are complex entities and more research is needed to further the understanding of their recovery. Here I used network analysis of invertebrate food webs across 19 islands off north-eastern New Zealand to determine the state of recovery of Korapuki, a recovering seabird island. I used eight food web metrics, six functional groups and environmental and geochemical data to compare the four island types of recovering (i.e. Korapuki), reference (i.e. Ruamaahuanui), uninvaded (eight uninvaded islands in north-eastern New Zealand) and invaded (nine invaded islands in north-eastern New Zealand). I found that Korapuki supports some areas that are virtually indistinguishable from an uninvaded burrowing seabird island and it demonstrated strong environmental gradients indicative of a recovering island. However, there were still a number of areas with food web attributes similar to an invaded island on Korapuki. I concluded that as seabirds spread across Korapuki these food web gradients will become weaker and these areas similar to invaded islands, fewer as the island starts to fully resemble a burrowing seabird island ecosystem.

4.2 Introduction

Island ecosystems throughout the world have suffered greatly from anthropogenic disturbance, often via the introduction of invasive mammals but also through deforestation and disease (Howald et al. 2007; Bellingham et al. 2010; Towns et al. 2013). Over the last 20-30 years, considerable effort has been devoted to restoration on islands, largely through the eradication of invasive mammals but also through the reintroduction of previously extirpated species (Howald et al. 2007; Rauzon 2007; Bellingham et al. 2010; Keitt et al. 2011; Towns et al. 2013). Historical approaches to ecological restoration involves re-creating a system that does not differ significantly from an undisturbed reference site (e.g. Simberloff 1990). However, defining this reference site can prove confusing, leaving ambiguous restoration targets (Jones et al. 2011). Solutions to this issue have been found using two different methods: historical records of species present before disturbance (e.g. Veitch et al. 2004; Lyver et al. 2016) and contemporaneous reference ecosystems (e.g. Towns et al. 1990). Clear measures of change are also necessary in order to assess the extent a recovering ecosystem differs from reference sites (Atkinson 1988; Ruiz-Jaen & Aide 2005; Suding 2011; Wortley et al. 2013). Such measurements should be based on an understanding of the processes that drive ecosystem function and could include measures of biogeochemistry, vegetation structure, customary harvest index, and the abundance and diversity of plants and animals (Ruiz-Jaen & Aide 2005; Mulder et al. 2009; Jones 2010a, b; Clucas et al. 2012; Orwin et al. 2016).

Many species of procellariiform seabirds are ecosystem engineers; the construction of nest burrows and introduction of marine nutrient subsidies create unique and diverse habitats (Bellingham et al. 2010; Kolb et al. 2011; Mulder et al. 2011). However, invasive mammals are a major threat to these seabirds and the

habitats they create (Fukami et al. 2006; Howald et al. 2007; Croxall et al. 2012). Comparative studies of islands with and without procellariiform seabirds have shown islands lacking seabirds, largely due to the presence of invasive rats (e.g. *Rattus rattus*, *R. norvegicus*), have less C, N, P and $\delta^{15}\text{N}$ in soils, less plants and animals, higher soil pH and more leaf litter (Fukami et al. 2006; Wardle et al. 2007 & 2009; Mulder et al. 2009; Jones 2010a; Towns et al. 2009; Orwin et al. 2016). When invasive mammals are removed, seabirds should recolonise, thus reinstating their engineering effects. Worldwide, there are now more than 300 examples of successful invasive mammal eradications from seabird islands (Rauzon 2007; Keitt et al. 2011) and on many of these islands seabirds have indeed begun to recolonise (Rauzon 2007; Buxton et al. 2014; Borrelle et al. 2015). Chronosequences of recovering seabird islands have shown that $\delta^{15}\text{N}$ and C:N ratios of soils, plants and spiders take two to three decades to recover to seabird influenced levels even after a century of rat infestation (Jones 2010b).

A growing body of research has focused on determining the extent of ecosystem recovery on seabird islands (e.g. Mulder et al. 2009; Jones et al. 2011; Buxton et al. 2014; Orwin et al. 2016; Jones et al. 2016). However, when studying communities this research largely focuses on structural aspects of biodiversity, such as species richness and abundance. An alternative is to emphasize functional aspects such as patterns of interactions between species (Forup et al. 2008) which is achievable through network analysis. Research using networks to determine the extent of ecosystem recovery is rare, presumably due to its novelty. However a small number of studies is available including Thoresen et al. (Chapter 2), who used network analysis to compare the differences in food webs between seabird and non-seabird islands in New Zealand and Forup et al. (2008) who compared pollinator

networks between ancient and restored British heathlands. Both studies found that the networks were significantly more complex in the undisturbed sites, which potentially demonstrates the high resilience of these communities. Network analysis is a method of simplifying the complexity found in food webs. Using this technique, it should be possible to use community dynamics as a measure of ecosystem recovery.

Here I use contemporaneous reference ecosystems to define the restoration status of a seabird island ecosystem in the process of recovery. I do so using the theory that, if ecological processes within reference ecosystems can be assigned empirical measures (in this case geochemistry and food web dynamics), the extent to which ecosystems in recovery converge with these measures should define the systems place on a restoration trajectory. I predict that as seabirds recolonise islands following invasive predator removal, changes in geochemistry will become apparent due to the increasing nutrient subsidies. These changes will flow up through resident food webs, altering food web structure (Thoresen et al. Chapter 2). Finally, as seabirds are usually colonial, their engineering effects are likely to be more heterogeneous on islands where they are recolonising compared to islands with large long-term resident populations. I predict that this heterogeneity will likely cause the effects of seabirds to demonstrate stronger gradients when compared to islands with high and homogenous seabird densities.

Using data from 9 islands invaded by rats and 8 that have never been invaded in north-eastern New Zealand I defined the characteristics of invaded (few seabirds) and uninvaded (numerous seabirds) island types (Fukami et al. 2006; Wardle et al. 2007; Mulder et al. 2009; Towns et al. 2009). The functional traits of these ecosystems were characterised using; 1) functional groups (fungivores,

saprophagivores, herbivores, detritivores, predators and parasitoids), 2) food web topological metrics (entropy, nestedness, generality, vulnerability, food chain length, and species, generalist and specialist diversity), and 3) abiotic variables (seabird burrow density, leaf litter dry weight, soil pH and the ratio of C: N in soil). I then compared the intra-island relationships between seabird activity, geochemistry and food webs on Korapuki Island, (a recovering island) with Ruamaahuanui Island (an undisturbed island). I based my study of food webs on leaf litter macro-invertebrates due to their complex communities and their sensitivity to direct and indirect change in burrowing seabird densities (Towns et al. 2009; Gardner-Gee et al. 2015).

I used food web and environmental data to determine where Korapuki is positioned within the spectrum of invaded and uninvaded islands, whether seabirds are having localised effects on Korapuki, and whether there are differences in the effects of seabirds on environmental gradients between uninvaded and recovering islands based on three key questions: 1) Are the environmental and food web measures from Korapuki typical of invaded or uninvaded islands?; 2) When compared with Ruamaahuanui are any plots on Korapuki typical of an uninvaded island?; and, 3) When comparing Ruamaahuanui with Korapuki are there any differences in the way that environmental and food web metrics interact?

4.3 Methods

4.3.1 Study areas

This research was based on data from a number of previous studies of islands (3-148 ha) in north-eastern New Zealand. These previous studies included, Fukami et al. (2006), Mulder et al. (2009), Towns et al. (2009) and Wardle et al. (2009) which

outlined ecological differences between nine islands invaded by ship rats (*R. rattus*) and/or Norway rats (*R. norvegicus*) and eight uninvaded, seabird dominated, islands. All of these islands were uninhabited and covered in secondary forest with dominant species including *Metrosideros excelsa*, *Kunzea ericoides* and *Melicytus ramiflorus*. This first set of studies was used to set the geochemical and food web parameters typical of seabird and non-seabird islands.

The second set of studies included sites used by Orwin et al. (2016) but were used in my study to compare a recovering island (i.e. all invasive species removed) and a reference island (i.e. never invaded) against the seabird and non-seabird island parameters derived from the first studies (Fukami et al. 2006; Mulder et al. 2009; Towns et al. 2009; and Wardle et al. 2009). The islands in these studies included Ruamaahuanui (36° 95' S, 176°09' E, 32.4 ha, maximum elevation 160 m) as a reference site and Korapuki (36° 39' S, 175° 50' E, 18 ha, maximum elevation 81 m) as the restoration site. These islands were chosen as they are heavily used by seabirds, are close together (less than 25km), share similar climates, parent materials (volcanic) and Maori occupation histories (Orwin et al. 2016). Both islands are also covered in secondary forest of similar age (ca. 70 years) dominated by the trees *Coprosma macrocarpa*, *Melicytus ramiflorus*, *Metrosideros excelsa* and *Pittosporum crassifolium*, however, *M. excelsa* is more widespread on Korapuki. Both islands are now free of all invasive mammals; however, Korapuki was inhabited by Pacific rats (*R. exulans*) and rabbits (*Oryctolagus cuniculus*) until c. 30 years ago (Towns and Atkinson 2004), while Ruamaahuanui has never been invaded (Orwin et al. 2016). Since the eradication of invasive mammals from Korapuki burrowing seabirds (Procellariiformes) have recolonised, attaining localised densities similar to those found in uninvaded islands (Jones 2010a; Buxton et al. 2014).

4.3.2 Field methods

For the first set of studies (used within chapter two), the 18 islands were sampled within a 67-day period between February and April 2004 to minimise potential seasonal effects. On each island, two 10×10 m plots were set up within forested areas and on slopes of $< 30^\circ$ to ensure potential litter accumulation (Towns et al. 2009). The data for the two plots on each island were combined so that each island served as the unit of replication to avoid pseudoreplication. Entrances of seabird burrows were used as a proxy of seabird density (Fukami et al. 2006); within each plot they were counted by systematically walking along predetermined belt transects covering the entire area. A sample of surface mineral soil (depth layers: 0-10cm) was collected from a 0.5×0.5 m subplot within each plot and analysed for %N, %P, %C, Olsen P and pH (data from Fukami et al. 2006 and Mulder et al. 2009). Fukami et al. (2006) have previously tested these environmental variables using ANCOVAs and found no change in the significance of the differences between island types when considering island isolation or size. From each plot a single 2 litre sample of leaf litter was collected to the soil surface level and stored in a cloth bag. Invertebrates from this litter were extracted into ethanol within three days of sampling using Tullgren funnels running for seven days (Towns et al. 2009). After invertebrate extraction the litter was then oven dried (60°C until constant weight) and weighed. The invertebrates were then sorted into taxonomic units and counted (Towns et al. 2009) and in my study were classified to family level using a dissection microscope.

On Korapuki and Ruamaahuanui islands, field work was carried out in March 2011. On each island plots of 10×10 m were randomly assigned using ArcGIS 10 software (ESRI, Redlands, CA, USA). Locations for plots were further refined,

excluding areas of shoreline, steep inaccessible parts of the islands, or areas without forest. Of all the random plots, 15 were selected to represent the range of burrow densities present on each island (Orwin et al. 2016). The distances between the plots ranged from 29-148m on Ruamaahuanui and 15-200m on Korapuki. Within each plot the number of burrow entrances was recorded and soil and litter samples collected. Burrow entrances were counted if the burrow cavity was deeper than 20cm and the centre of the burrow roof was within or overlapped the plot boundary. Burrows were predominantly (97.7%) occupied by grey-faced petrels (*Pterodroma Gouldi*), with other species occupying an average of 2.9% of the burrows (Orwin et al. 2016). Each 10 × 10m plot was divided into four equal 5 × 5m quadrants and a 1 litre soil sample was collected from the centre of each quadrant by digging a 100 × 100 × 100mm pit. All four samples were then bulked and homogenised before being subdivided for further analysis (Orwin et al. 2016). To quantify seabird effects on soil chemistry, soil samples were then analysed for pH (in water 1:2.5), % C and N (by combustion), and total P (wet Kjeldahl oxidation process) (Orwin et al. 2016).

A similar process was carried out for litter, where 4 × 1 litre samples were collected from each quadrant to give 4 litres of leaf litter per plot. Because seabird activity had different effects on litter availability in each plot, the area required to obtain the 1 litre sample was also measured and litter quantities were standardised to g dry weight m⁻² (Towns et al. 2009; Orwin et al. 2016). Invertebrates were extracted from the litter into ethanol using Tullgren funnels run over 7 days. Extracted invertebrates were then sorted, counted (Towns et al. 2009), and subsequently, as a part of this study, identified to Family level using a dissection microscope.

Based on the analysis of environmental variables and food web metrics in the first studies, I selected the environmental variables and food web metrics that were

significantly different between seabird and non-seabird islands as the parameters to define the island types. The environmental variables used included: burrow density, soil pH, leaf litter dry weight and the ratio of C: N in soil (Fukami et al. 2006, Towns et al. 2009). Food web metrics included: species, generalist and specialist diversity, generality, vulnerability, nestedness, food chain length, and entropy.

4.3.3 Food web methods

Food webs were described following the methods of Thoresen et al. (2017; Chapter 2). Taxa were identified to family level; however, if larvae differed in their feeding strategies they were defined as a separate group. Trophic links were determined from the literature and through communication with experts (Digel et al. 2014; Gauzens et al. 2015). Where there was little information on feeding habits, I estimated feeding category through taxonomic similarities, i.e. groups from similar families were assumed to have similar diets, or only slight modifications due to size effects (Gauzens et al. 2015). I used this information to describe 30 food webs from Korapuki and Ruamaahuanui. For comparison, I used 17 food webs from studies previously described in Thoresen et al. (2017; Chapter 2). For consistency, as data from Ruamaahuanui and Korapuki studies excluded any micro-invertebrates, such as mites (*Acari* sp.) all the food webs described here are based on macro-invertebrates.

I verified the effectiveness of my network description methods by comparing my empirical networks to those constructed using the niche model (Williams and Martinez 2000; Dunne et al. 2002; Williams and Martinez, 2008; Williams et al. 2010; Thompson et al. 2012) (see Appendix A for detailed explanation of niche model construction and analyses used, Table A3). Six of the eleven metrics used to compare the networks were no different from the niche model. The other differences

may reflect an inaccuracy in my description methods, although the niche model has also been shown to not be fully accurate in predicting realistic food webs (Williams and Martinez, 2008). While the niche model may be inaccurate in some areas it has been used in the past to draw conclusions on how the structure and function of real-world food webs may change in relation to external stimuli. These comparisons show that my food webs are at least partially accurate when compared to the niche model, which in itself is also partially accurate. In addition, while some of these metrics may be inaccurate due to the methods I used in describing the food webs, they still change in predictable ways. As such, I can use them to predict changes in food webs (at least when they are described in the same way) despite any inaccuracies that may exist when they are compared to full food webs.

I calculated six general food web metrics including: (1) species diversity (i.e. trophic group diversity); (2) generalist diversity (i.e., the number of species where the number of items a species feeds on (i.e. in-degree) is equal to or greater than the maximum in-degree of the least complex network); (3) specialist diversity (i.e., the number of species with an in-degree greater than zero but less than the average first quartile of all empirical networks); (4) the maximum food chain length per network (FCL) (Dunne et al. 2002; Post 2002; Kondoh & Ninomiya 2009; Tylianakis et al. 2010); (5) generality (i.e., the mean number of consumed species per consumer); and, (6) vulnerability (i.e., the mean number of consumers per consumed species). I used the package 'NetIndices' (Kones et al. 2009) to calculate all general network metrics.

To help characterise the entire food webs I used the metrics nestedness (Ings et al. 2009; Tylianakis et al. 2010; Thompson et al. 2012; Zeng et al. 2014) and entropy (Allesina and Pascual 2009; Gauzens et al. 2015). Nestedness, or community

cohesiveness, is a useful metric that characterises the generalist-specialist balance in ecological networks (Araujo et al. 2010). In highly nested networks, generalist species are organised in a dense core of interactions while a large number of specialists coexist with a few super generalists (Araujo et al. 2010; Tylianakis et al. 2010). To estimate nestedness I used the Nestedness Temperature calculator in the R (version 3.1.0) package ‘vegan’ (Oksanen et al. 2015). To assess if the values observed were higher than expected by random interaction patterns I tested the nestedness of each network using null models generated using the R package EcoSimR (Gotelli & Ellison 2013). In order to characterise food-web complexity I used entropy as according to the Kolmogorov-Sinai definition (Billingsley 1965). In network analysis, entropy measures the diversity of pathways of energy flow between species in the trophic network (Gauzens et al. 2015). I followed the methods of Allesina and Pascual (as referenced in Gauzens et al. 2015); to account for the circulation of energy (Allesina and Pascual 2009) a root node is attached to the network with links pointing to all the basal nodes (i.e. primary producers and detritus) and all other nodes are connected to this root node. In this way the root node acts to represent the build-up of detritus that is in turn partially recycled into the food web (Allesina and Pascual 2009). For a binary matrix, entropy is the logarithm of the dominant eigenvalue of the matrix. Entropy increases with species richness and maximal entropy is obtained when all matrix entries equal one.

4.3.4 Statistical methods

Analyses for question one (above) compared invaded and uninvaded islands, in which individual islands served as the units of replication. The invertebrate assemblages from both plots were combined to describe one food web per island. For questions two and three (above) comparing the reference (Ruamaahuanui) and

recovering (Korapuki) islands all data were analysed separately and one food web was described for each of the 15 plots on each island. The variation in seabird burrow density between plots is likely to represent the range in suitable nesting habitat or time since colonisation. Analysis of environmental variables for all questions were previously carried out in Fukami et al (2006), Towns et al. (2009), Wardle et al (2009) and Mulder et al (2009) for question one and Orwin et al. (2016) for questions two and three.

I used box and whisker plots coupled with ANOVAS and post-hoc Tukey tests to compare six invertebrate functional groups and eight food web metrics between all island types for question one. Normality was assessed using multivariate quantile-quantile plots and plots of residuals vs fitted values and leverage. Nine linear discriminant analyses were then carried out using the R package MASS (Venables & Ripley 2002) to assign plots on Korapuki and Ramaahuanui to either 'reference' or 'recovering' based on the food web metrics.

I used regressions in order to determine the differences in gradients of the food web metrics against environmental variables between Korapuki and Ruamaahuanui. Environmental variables were log transformed to meet test assumptions where necessary. As nestedness was consistently significant in the single regressions I carried out multiple linear models for nestedness on Korapuki to discover which of the four variables the more important predictors were. I first carried out a multiple linear model with no interaction terms between predictor variables, with nestedness compared against burrow density, pH, soil C: N, and leaf litter dry weight. I then carried out a model selection algorithm using the R package stepAIC, which simplified this model down to soil C: N and leaf litter dry weight. I used this result to create a multiple linear model with the interaction term soil C: N

vs. leaf litter included. I then carried out the model selection algorithm a final time, which simplified the model to soil C: N and leaf litter. All analyses used R statistical software v. 3.1 (R Core Team, 2013).

4.4 Results

The functional group boxplots showed complex relationships (Figure 4.1), with the significant ANOVA results for fungivores ($F = 19.66_{3,44}$, $p < 0.001$), herbivores ($F = 9.36_{3,43}$, $p < 0.001$), detritivores ($F = 12.64_{3,44}$, $p < 0.001$), predators ($F = 15.41_{3,44}$, $p < 0.001$), and parasitoids ($F = 5.34_{3,44}$, $p < 0.05$). The differences between saprophagivores were insignificant ($F = 2.21_{3,44}$, $p = 0.09$). The most distinct differences were between parasitoids, with less parasitoids on both the invaded and recovering (Korapuki) islands when compared with the reference (Ruamaahuanui) and seabird islands (Figure 4.1). Saprophagivores, herbivores and detritivores showed little consistent differences between island types. Finally, there were less predators on the invaded islands than any other island type.

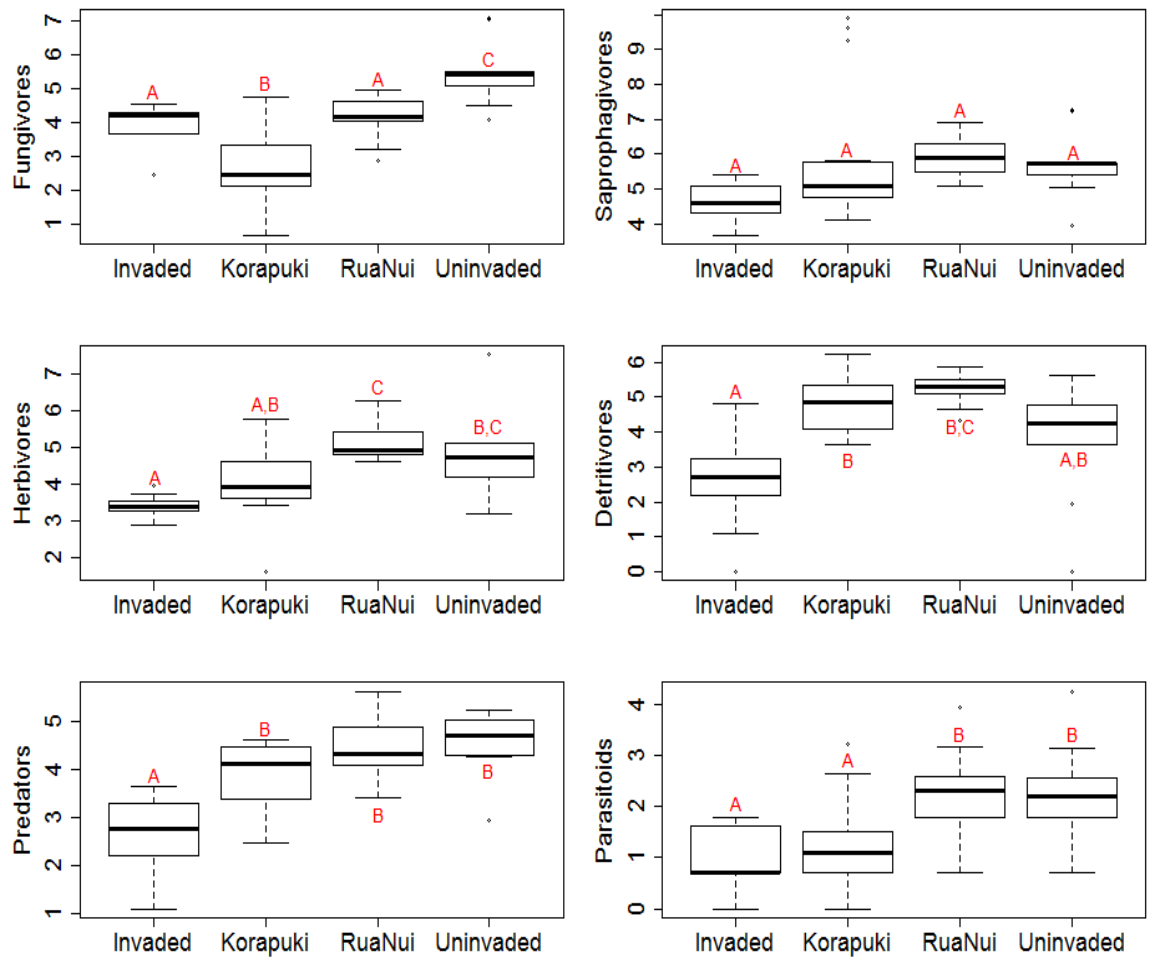


Figure 4.1 Boxplots of invertebrate functional group abundance (log + 1 transformed) comparing invaded and uninvaded islands with Korapuki and Ruamaahuanui islands. Letters above or below the box plots denote the groups that are significantly different ($p < 0.05$) after using ANOVAS with Tukey tests. Where all plots in group A are not significantly different from each other but are different from plots in group B or C. Where there are two letters above a plot this means they are in both groups, i.e. B,C denotes this plot is not significantly different from other plots in both groups B and C but is different from a plot in group A. Where $n = 15$ for both recovering and reference, 8 for uninvaded and 9 for invaded.

The food web boxplots showed complex relationships (Figure 4.2), with the significant ANOVA results for species diversity ($F = 8.62_{3,43}$, $p < 0.001$), generalist diversity ($F = 11.57_{3,43}$, $p < 0.001$), FCL ($F = 11.64_{3,43}$, $p < 0.001$), generality ($F = 7.14_{3,43}$, $p < 0.001$), vulnerability ($F = 7.42_{3,43}$, $p < 0.001$), nestedness ($F = 5.38_{3,43}$, $p = 0.003$) and entropy ($F = 8.32_{3,43}$, $p < 0.001$), while specialist diversity was marginally non-significant ($F = 2.62_{3,43}$, $p = 0.06$). Overall the most significant differences between island types were between Ruamaahuanui and the invaded

islands, and uninverted and invaded islands with five significant differences out of the eight food web metrics for each. Ruamaahuanui and the invaded islands were significantly different for species diversity ($p = 0.0001$), generalist diversity ($p < 0.0001$), FCL ($p < 0.0001$), nestedness ($p = 0.003$) and entropy ($p = 0.0001$). The invaded and uninverted islands were significantly different for species diversity ($p = 0.001$), generalist diversity ($p = 0.02$), generality ($p = 0.0003$), vulnerability ($p = 0.0002$) and entropy ($p = 0.0004$). There were only two significant differences between Korapuki and Ruamaahuanui islands; FCL ($p = 0.004$) and nestedness ($p = 0.02$), and only one significant difference between Korapuki and the invaded islands; generalist diversity ($p = 0.001$). There were three significant differences between both the uninverted and Korapuki islands; generality ($p = 0.004$), vulnerability ($p = 0.02$) and entropy ($p = 0.01$), and the uninverted and Ruamaahuanui islands; FCL ($p = 0.001$), generality ($p = 0.03$) and vulnerability ($p = 0.02$).

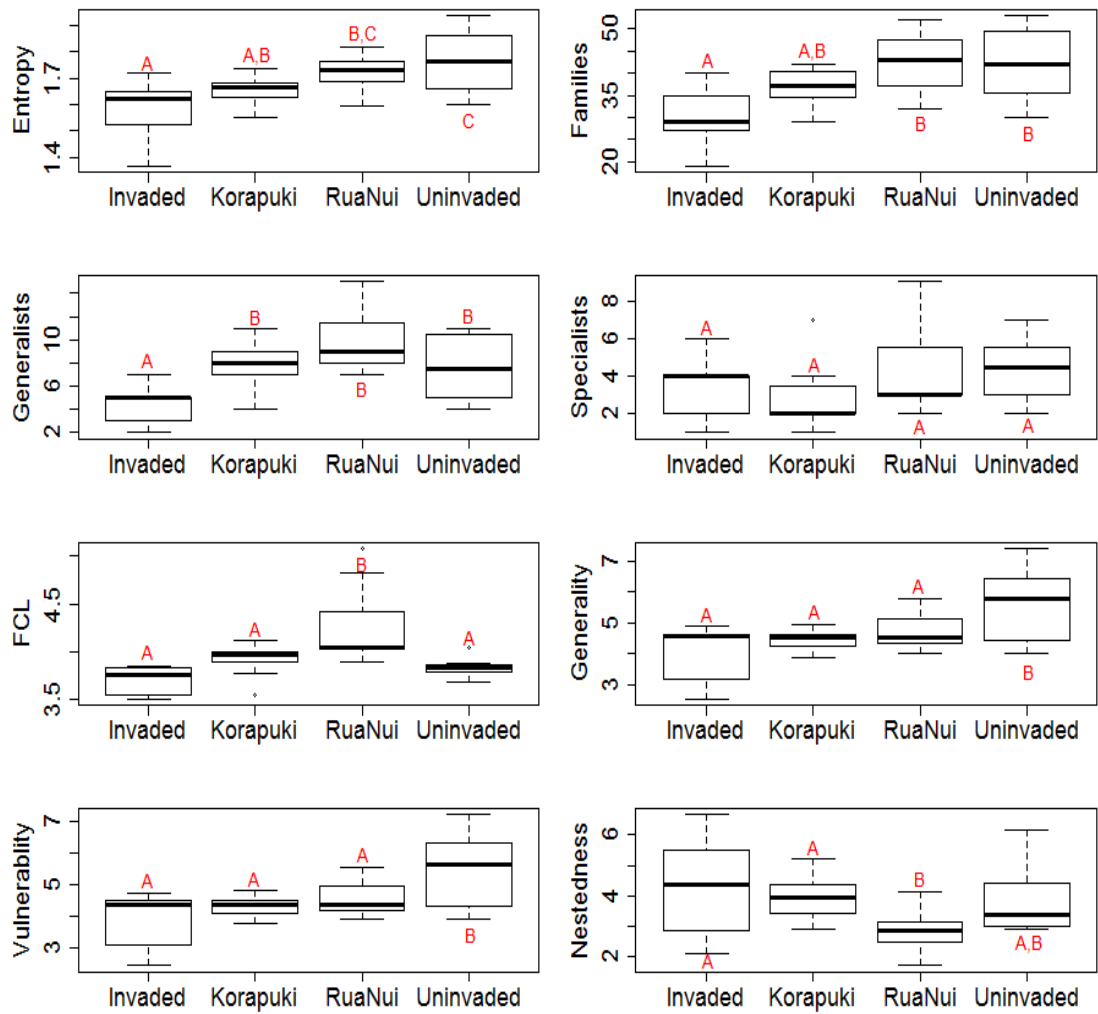


Figure 4.2 Boxplots of all eight food web metrics comparing invaded and uninvaded islands with Korapuki and Ruamaahuanui islands. Letters above or below the box plots denote the groups that are significantly different after using ANOVAS with Tukey tests. Where all plots in group A are not significantly different from each other but are different from plots in group B or C. Where there are two letters above a plot this means they are in both groups, i.e. B,C denotes this plot is not significantly different from other plots in both groups B and C but is different from a plot in group A. Where $n = 15$ for both recovering and reference, 8 for uninvaded and 9 for invaded.

The results of the linear discriminant analysis (Table 4.1) show that Korapuki (recovering) had some plots that overlapped with Ruamaahuanui (reference) for each food web metric; this overlap ranged from 13% for FCL to 46% for vulnerability. On average 28% of the plots on Korapuki were predicted to have come from the reference island (Ruamaahuanui), whereas 44% of the plots on Ruamaahuanui were predicted to have come from the recovering island (Korapuki).

Table 4.1 Linear discriminant function analysis showing the proportion of plots on Korapuki and Ruamaahuanui grouped into either the recovering or reference island type for each network metric

Island type	Korapuki (Recovering)		Ruamaahuanui (Reference)	
Predicted Island type	Recovering	Reference	Recovering	Reference
Species diversity	0.60	0.40	0.33	0.66
Entropy	0.80	0.20	0.26	0.73
FCL	0.86	0.13	0.60	0.40
Specialist diversity	0.73	0.26	0.53	0.46
Generalist diversity	0.80	0.20	0.53	0.46
Generality	0.60	0.40	0.53	0.46
Vulnerability	0.53	0.46	0.53	0.46
Nestedness	0.80	0.20	0.20	0.80
Average	0.72	0.28	0.44	0.55

On Korapuki the metrics entropy, generalist diversity, FCL, and nestedness were the more precise predictors, with at least 80% of plots grouped accurately; that is, they were predicted to have come from the recovering (Korapuki) island (Table 4.1). On average only 55% of the plots on Ruamaahuanui (reference) were predicted accurately, whereas 71% of the plots on Korapuki were predicted accurately (Table 4.1). The metrics entropy and nestedness were the most accurate predictors on Ruamaahuanui with 73% and 80% of plots respectively grouped into the reference island category.

those in the simpler food webs. The trophic levels in the complex food web on Korapuki (recovering) seem to be more distinctly separated than those on Ruamaahuanui (reference). There also seem to be less top-predators and parasitoids on Korapuki which supports the previous findings in figure 4.1.

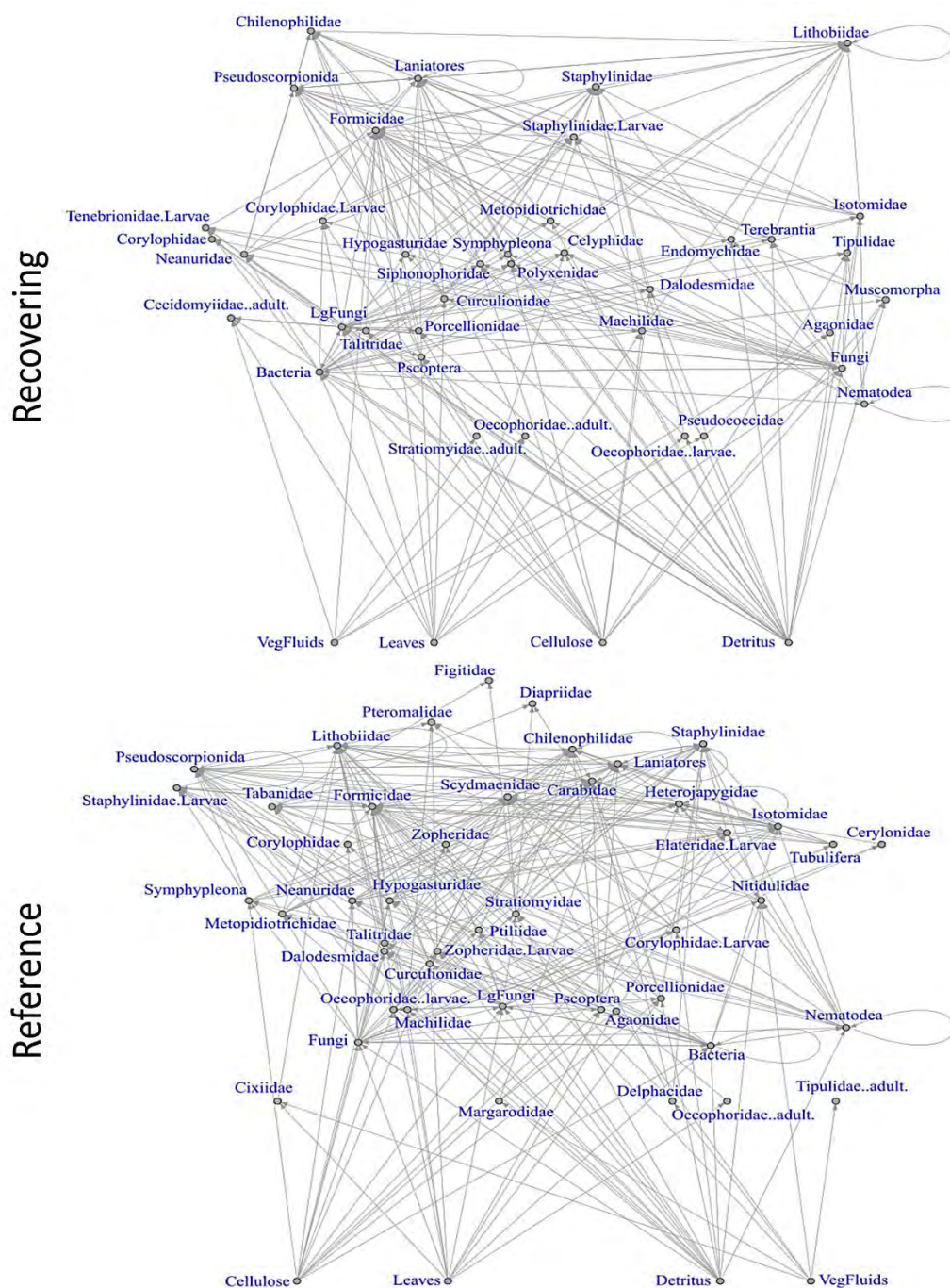


Figure 4.4 Food webs organised by trophic level and labelled by functional group for the most complex (by entropy) food webs on the recovering (Korapuki) and reference (Ruamaahuanui) islands.

Four significant positive regressions were found for Korapuki (recovering) and two were negative; these included; nestedness vs. pH and the ratio of soil C:N (Figure 4.5), species diversity vs. burrow density and leaf litter dry weight (Figure 4.5), and nestedness vs. leaf litter dry weight, and burrow density (Figure 4.5) respectively. The only significant negative regression for Ruamaahuanui (reference) was specialist diversity vs. pH (Figure 4.5). There were consistent differences in the relationships between the recovering and reference islands. All of the significant models for one island failed to reach significance for the other. The reference island showed no gradients between the food web metrics and any environmental variables, other than for specialist diversity vs. pH, where there was a strong negative relationship. There was no relationship for specialist diversity vs. pH on the recovering island. There was one notable relationship when the data for both islands were collated, that of soil C: N and burrow density (Figure 4.5). This relationship was weak but significant, with soil C: N decreasing as burrow density increased.

In order to determine which of the four predictor variables explained most of the variation in food web nestedness on Korapuki, I carried out multiple linear models using the model selection algorithm in R; stepAIC. These results showed that when accounting for the variation of leaf litter dry weight, the ratio of C:N in the soil has a very strong positive relationship with food web nestedness (estimate = 0.30, $F = 35.262$, $p < 0.0001$). In addition, when accounting for the large effect of C:N, leaf litter dry weight has a weak negative effect on food web nestedness (estimate = -0.002, $F = 20.862$, $p < 0.001$). The overall model with both C:N and leaf litter dry weight combined was strongly significant (Adjusted $R^2 = 0.79$, $F = 28.062_{12}$, $p < 0.0001$). It must be noted, however, nestedness is measured on an inverse scale: as

the ratio of C:N increases, nestedness decreases on the recovering island.

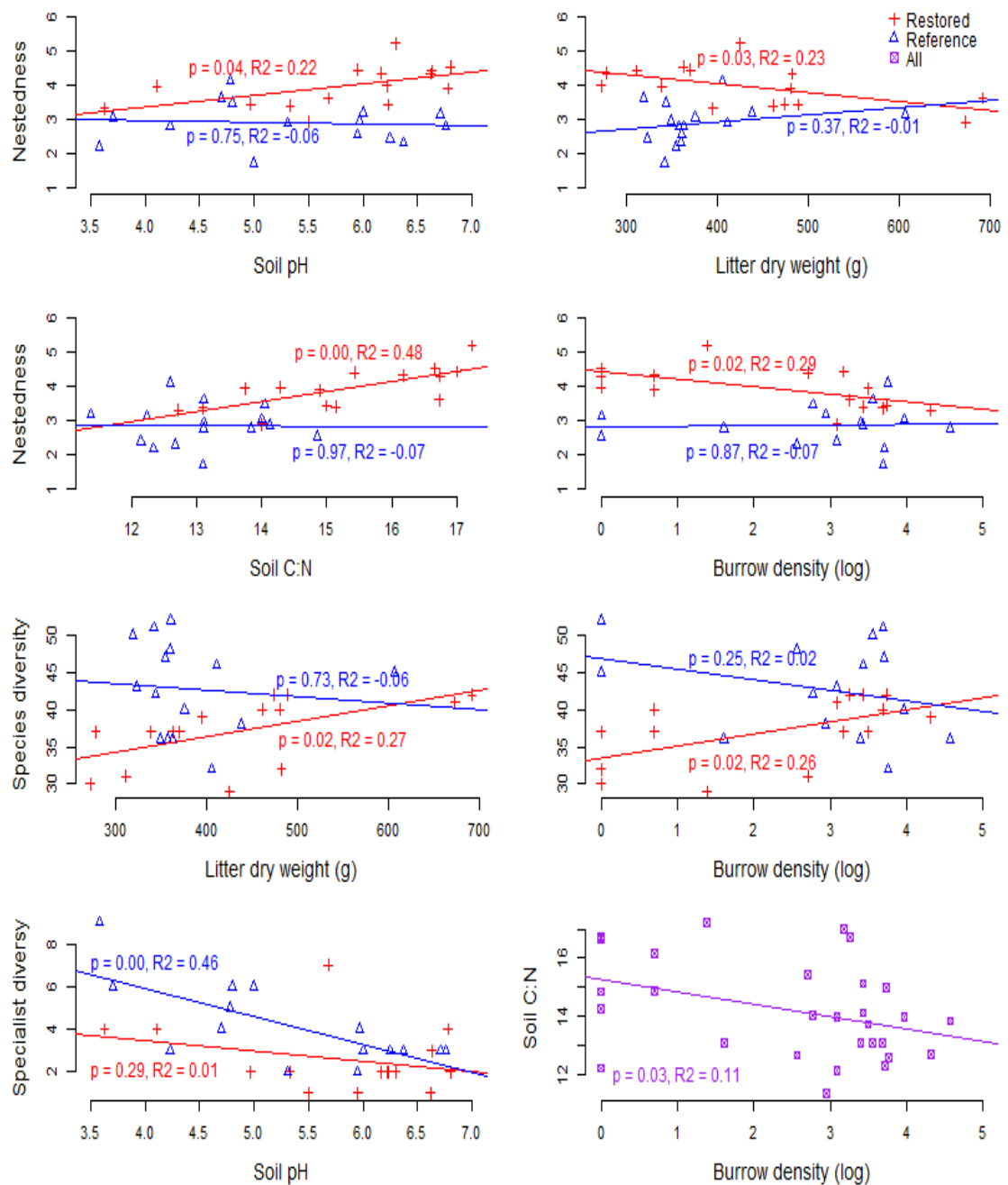


Figure 4.5 Linear models of nestedness, species and specialist diversity, and soil C: N against pH, leaf litter dry weight, soil C:N and burrow density (log transformed). Both the reference (Ruamaahuanui) and recovering (Korapuki) islands are present on each plot with p and R² denoted either above or below the lines of best fit. For the significant models on the recovering island F = 5.06, 5.2, 13.95, and 6.84 for nestedness vs. pH, leaf litter dry weight, C:N, and burrow density respectively. For species diversity vs. leaf litter dry weight F = 6.44 and burrow density F = 6.1. For the significant model on the reference island F = 13.15 for specialist diversity vs. pH. The last plot is a model using collective data from both islands comparing soil C: N and burrow density, for this model F = 4.80. Where n = 15 for each island type and degrees of freedom = 1,13 for all models.

4.5 Discussion

My first questions explored whether the food web measures from Korapuki typical of an invaded or uninvaded island? I found that the food web metrics and functional groups from Korapuki were typical of both invaded and uninvaded islands; Korapuki shared many food web characteristics with both Ruamaahuanui (6 of 8) and the invaded islands (7 of 8) but less so with the uninvaded islands (5 of 8). In addition, while Korapuki may have had similar amounts of predators, detritivores and saprophagivores to Ruamaahuanui, it had less parasitoids, herbivores and fungivores. Korapuki had more predators than the invaded islands but had similar amounts of parasitoids, this result is interesting as it infers an extinction cascade that has affected one of the top trophic tiers (parasitoids) but not the other (predators). This may be due to the sensitive nature of small parasitoid wasps but also to their level of specialism, where highly specialised species are more likely to go extinct first.

The one food web difference between Korapuki and the invaded islands was in generalist diversity, with Korapuki having a greater number of generalist species. Uninvaded islands and Ruamaahuanui had similarly higher generalist diversity than the invaded islands, but were not different from Korapuki. Generalist diversity was the only metric showing this pattern, indicating that Korapuki and other seabird islands can be distinguished from invaded islands using this attribute. Food chain length (FCL) on Ruamaahuanui was higher than all other island types. However, as all the other islands had similarly low FCL, I concluded that this was an unusual result and was unlikely to indicate important differences between the islands. Ruamaahuanui demonstrated much lower nestedness than both Korapuki and the invaded islands and was similar to the other uninvaded islands. Nestedness is

inextricably linked with generalist and specialist diversity and the interactions between the two (Bascompte & Jordano 2006 & 2007; Rezende et al. 2007; Dattilo et al. 2013). If generalist diversity is high nestedness will likely be low (Dattilo et al. 2013) and, as in this case, generalist diversity was high on Ruamaahuanui, nestedness would be expected to be low here too. As I previously concluded that high generalist diversity is indicative of seabird island food webs I also conclude that so too is low nestedness. Entropy is the one metric that showed multiple differences between all the island types. The results showed that the invaded islands were the least complex, followed by Korapuki, with Ruamaahuanui being more complex and the uninvaded islands being the most. Entropy, thus forms a gradient that may indicate a restoration trajectory. If this were the case then the place that Korapuki sits would show its place in this trajectory, i.e. around halfway between an invaded and uninvaded island.

Only nestedness showed a clear difference between Korapuki and the uninvaded food webs. In addition, while there was only one difference; that of generalist diversity, between Korapuki and the invaded food webs, this difference was an important one. Based on these results I can answer question one; most of the food web metrics on Korapuki are not typical of an uninvaded island but there are similarities, so too are the metrics not typical of an invaded island, but again similarities are present. Most, but not all, of the metrics are outside of the bounds generated by the normal dynamic processes of seabird-island ecosystems.

My second question addressed whether any plots on Korapuki were typical of a reference ecosystem when compared with Ruamaahuanui. The results for Korapuki indicated that less than a third of the plots on the island demonstrated food web attributes typical of a seabird driven ecosystem. On Ruamaahuanui, however, the

analysis showed an almost 50/50 overlap, where the food web metrics often showed half of the plots or more were more similar to Korapuki than Ruamaahuanui. This is likely due, however, to four of the food web metrics being homogenous, all showing 53% overlap with Korapuki. Three of the food web metrics (species diversity, entropy and nestedness) were much more accurate, not only for Ruamaahuanui but also on Korapuki. If these metrics are used alone then the average overlap is around a third for both islands which is more consistent with what would be expected. These results show the area on Ruamaahuanui that is not directly affected by seabirds; areas where seabirds cannot burrow due to shallow soils, areas vulnerable to flooding or otherwise unsuitable habitats (Buxton et al. 2016). The three accurate metrics of nestedness, species diversity and entropy show around 70% of the plots on Ruamaahuanui and Korapuki are representative of a seabird island and non-seabird island, respectively. This analysis also highlights the metrics that are more sensitive when demonstrating the differences in food webs between these island types and, perhaps, in general when studying changes in food webs during ecosystem restoration.

Finally, I used regressions and multiple linear regressions to answer question three: when comparing Ruamaahuanui with Korapuki are there any differences in the way that environmental and food web metrics interact? Strong gradients were apparent on Korapuki (recovering) that were not apparent on Ruamaahuanui (reference), the most significant being between food web nestedness and the ratio of C: N in the soil. The nestedness value increased with increasing C: N on Korapuki, as nestedness is measured on an inverse scale this means that the food webs became less nested with increasing C in relation to N. Previous research has found that high C: N ratios are found in the soils of less vital forests (van Straalen et al. 1988); as the

C: N ratio tends to decrease as litter decomposes (Swift et al. 1979) a high ratio is indicative of an overrepresentation of undecomposed material in the litter (van Straalen et al. 1988), which may be related to reduced microorganism activity (Bosatta 1982; Klein et al. 1984). Nestedness, or community cohesiveness, characterises the generalist-specialist balance in ecological networks (Araujo et al. 2010). High nestedness is associated with a greater degree of generalisation within the network, reduced competition within trophic levels, and an increase in the number of coexisting species (Bascompte & Jordano 2006 & 2007; Araujo et al. 2010; Tylianakis et al. 2010 Rezende et al. 2007; Dattilo et al. 2013). Ecosystems that produce organic matter with high C to nutrient ratios are likely to result in inefficient trophic transfer (Mulder & Elser 2009) and herbivores with increased ingestion rates (Urabe & Waki 2009). This inefficient trophic transfer would likely result in reductions in generalism and increases in competition as species focus their limited energy on feeding on one easy food source. This change in feeding strategies could then cause less competitive species to disappear, with most of these being super-specialists. Ultimately a food web would result with fewer coexisting species and less generalisation with less super-specialists and super-generalists. Such a food web would be characterised by low nestedness (i.e. values closer to 100). Alternatively, inefficient trophic transfer could result in greater degrees of generalism as species eat anything that is available in order to counter the low nutritional content of food. However, this would not explain the significant relationship between the C: N ratio and food web nestedness. When measured across both islands the ratio of C: N had a weak but significant negative relationship with seabird burrow density (Figure 4.5). In sum, I predicted that changes in geochemistry would become apparent on Korapuki as seabirds recolonise which my results appear

to support. Increases in burrow density on Korapuki lead to lower C: N ratios and subsequently more vital forests with a greater rate of litter decomposition and food webs characterised by high nestedness (i.e. values closer to 0).

There was one strong gradient on Ruamaahuanui that was not apparent on Korapuki: pH versus specialist diversity, with diversity increasing as pH becomes more acidic. Orwin et al (2016) found that soil pH decreased with increasing seabird burrow density on these islands, which may have played a factor in the observed effects on specialists. However, on islands with dense seabird populations (i.e. Ruamaahuanui) when burrow density increases, so too does disturbance (Bancroft et al. 2004) which might be expected to have a negative impact on specialist diversity. However, such is not the case. The effects of pH on community dynamics are often complicated (van Straalen et al. 1988 and references therein), and increased acidification of soils has been shown to have both positive and negative effects on various invertebrates (Hagvar and Amundsen 1981; Abrahamsen 1983; van Straalen et al. 1988; Driscoll et al. 2003). Why acidification combined with disturbance should have a positive effect on an entire category of invertebrates, i.e. specialists, but nothing else within a food web is unclear. It could be that these specialists are not only dietary but habitat specialists as well, thriving in conditions that would otherwise be adverse for any other species; i.e. extremophiles/acidophiles.

I made the prediction that there would be strong gradients apparent on Korapuki that would not be visible on Ruamaahuanui and this is indeed the case. These results are likely because on islands where seabird populations are increasing, their colonial behaviour will lead to localised aggregations and heterogeneous engineering effects. The fact that there are strong gradients apparent on Korapuki shows the effects of localised dense seabird colonies as opposed to Ruamaahuanui

where the effects of seabird colonies are homogenously spread across the island. The gradients apparent on Korapuki should decrease in strength over time as the island becomes more seabird dominated.

4.6 Conclusion

I stated previously that restoration could be considered successful if I can demonstrate that the structure and function of a recovering ecosystem is functioning within the bounds of a reference system. Using network analysis of food webs, I found that Korapuki supports some areas that are virtually indistinguishable from an uninvaded seabird island. However, parts of Korapuki still show strong gradients, in how the food web metrics interact with environmental metrics. These gradients were not apparent on the uninvaded islands as these islands had more homogenous seabird nest densities. The heterogeneity in nest density on Korapuki that gave rise to strong gradients in the relationships between environmental and food webs metrics demonstrates that Korapuki is not restored fully and the ecosystem is not fully representative of an uninvaded seabird island. Given the presence of areas now indistinguishable from uninvaded islands, I predict that as seabirds spread across Korapuki over the next few decades, gradients will become weaker and a greater proportion of the island will appear uninvaded. I have also identified that complex food webs can be reconstituted when seabirds recolonise and that there is little evidence from my network analysis of lasting effects of seabird suppression.

**Chapter Five: The legacy effects of invasive
predatory mammals on invertebrate families on
recovering seabird islands.**

5.1 Abstract

Seabird islands are vulnerable to the invasion of predatory mammals such as rats, which can have lasting effects even after these pests are eradicated. Islands invaded by rats support fewer species and have less complex invertebrate food webs than those inhabited by seabirds. However, these food webs may be capable of reconstructing over time once invasive mammals are eradicated. In spite of this components of some trophic levels could be lost entirely. I compared two recovering islands with nine invaded and ten uninvaded islands to test the hypothesis that islands where rats had been eradicated will lack more invertebrate family groups than those never invaded. ANCOVAs were used to tease apart the effects of the covariates; samples size, island size and island isolation with the effect of rat invasion or the legacy of invasion. I found that the recovering islands had a similar number of missing families to invaded islands and were missing more family groups than islands that had never been invaded when controlling for covariates. Korapuki Island was missing five families that were common on all other islands and Motuhoropapa was missing three. The family groups missing from Korapuki may have been important and their absence may contribute to a decrease in the redundancy of this ecosystem. However, this may not have been the case of Motuhoropapa and this is possibly due to several differences between the islands such as isolation, forest regeneration, and invasion and disturbance history. I conclude that the absence of these families was due to the suppression of these groups via rats and the legacy of this suppression.

5.2 Introduction

Islands are globally important hotspots of biodiversity, occupying *c*5.5% of the terrestrial surface area but containing more than 15% of terrestrial species. These island ecosystems contain 61% of all recently extinct species and 37% of all critically endangered species on the International Union for the Conservation of Nature (IUCN) red list (Jones et al. 2016). Invasive predatory mammals (hereafter referred to as ‘invasive mammals’) are linked to most of these extinctions and threatened species (Clavero and Garcia-Berthou 2005; Howald et al. 2007; Szabo et al. 2012; Tershy et al. 2015; Jones et al. 2016). In response, eradicating invasive mammals from islands has been at the forefront of island conservation for more than 30 years (Howald et al. 2007; Towns et al. 2013). Many islands worldwide are inhabited by resident populations of seabirds, which through nest building, such as burrowing, and the introduction of marine derived nutrients, have engineering effects on these ecosystems (Polis and Hurd 1996; Sánchez-Piñero and Polis 2000; Stapp and Polis 2003; Barrett et al. 2005; Bancroft et al. 2005; Wright et al. 2010; Ellis et al. 2011; Kolb et al. 2011). Invasive mammals often suppress these seabirds (Jones et al. 2008; Towns et al. 2009) impeding their engineering effects and directly and indirectly, ecosystem structure and function (Fukami et al. 2006; Towns et al. 2009; Wardle et al. 2009; Mulder et al. 2009).

Invasive rodents, rats (*Rattus* spp.) and house mice (*Mus musculus*) are the archetypal island invaders; worldwide they are likely responsible for the greatest number of extinctions and ecosystem changes on islands (Howald et al. 2007; Towns et al. 2006). The direct effects of invasive rodents include the suppression and often localised, if not complete, extinction of invertebrates, reptiles, birds, mammals and plants (Howald et al. 2007; Jones et al. 2016). On seabird islands, these species are

responsible for the suppression and sometimes localised extinction of seabird populations (Jones et al. 2008). Rats have also been shown to disrupt nutrient subsidies brought to these islands via seabirds causing declines in both above and below ground fauna and changes to the nutrient content, form, diversity and density of plants and animals (Fukami et al, 2006; Wardle et al. 2009; Towns et al. 2009; Mulder et al. 2009).

Islands invaded by rats, and with no or few seabirds also have greatly diminished invertebrate food webs when compared with uninvaded islands, retaining dense colonies of seabirds (Thoresen et al. Chapter 2). However, if rats are removed and seabirds recolonise invertebrate food webs will reconstruct over time probably due to reinstituted nutrient subsidy effects (Thoresen et al. Chapter 4). Network analysis indicated that food webs can return to their previous functional state and reach a similar complexity to those islands never invaded by rats (Thoresen et al. Chapter 4). However, while the overall food webs may prove resilient in terms of structure and capable of recovering from invasions, their composition could be permanently effected. My evidence indicates that some individual families or species may be heavily suppressed but still recover after invasions, but others may be lost completely, and incapable of recovering without human intervention. However, the theory of ecosystem redundancy proposes that some species can be lost from an ecosystem without negative effects if they are redundant; that is, they held a common function within the ecosystem shared by other organisms (Walker, 1992). A contrary idea involves the 'popped rivets' notion; that only a small number of redundant species can be lost after which the entire ecosystem fails (i.e. like rivets on the wings of a jet) (Ehrlich and Walker 1998; Kareiva and Levin, 2003). Ecosystem redundancy therefore counters the idea that biodiversity begets stability; that greater

biodiversity will always be more resilient in terms of ecosystem functionality (McCann 2000; Hooper et al. 2005). Naeem (1998) argues that highly redundant ecosystems will be more reliable, likening them to engineered structures where the probability of reliable system performance is closely tied to the level of engineered redundancy in the design. Redundant species should thus be preserved if ecosystems are to function reliably and to provide goods and services (Naeem, 1998). The loss of species or family groups from an island following rat invasion may decrease the ecosystem redundancy and could then subtly change functionality in spite of restoration efforts and food web reconstruction over time.

I here aim to answer the question: is there a legacy of indirect rat suppression on invertebrate food web composition? I do so via the sub-questions: 1) Are family groups missing and is this due to invasion status or covariates? 2) What family groups are missing from recovering islands but common on uninvaded islands and what are their functional roles? 3) Are there differences in the proportions of each functional group on all of the islands reflective of the differences in missing or total family groups? And 4) if more samples were taken might these missing families have eventually been found? i.e. how close to an asymptote of family richness was reached for each island and their respective sample sizes? I studied the indirect effects of invasive mammals by comparing family richness and presence of families of litter invertebrates across 20 islands in north-eastern New Zealand with different invasion histories. Nine of these islands were invaded by rodents and had low densities of seabirds; nine were never invaded by rats and were characterised by high densities of seabirds; two were invaded but subsequently all pests were eradicated; seabirds had started to recolonise. By using these varied island types, I tested the

hypothesis that islands where rats had been eradicated will lack specific invertebrate family groups when compared to uninvaded islands.

5.3 Methods

5.3.1 Study sites

Data from 21 islands in north-eastern New Zealand were collated from previous research by Fukami et al. (2006), Wardle et al. (2009), Towns et al. (2009), Mulder et al. (2009) and Orwin et al. (2016). These studies can be organised into three groups based on the data used from them; studies comparing eighteen invaded and uninvaded islands (Fukami et al. 2006; Wardle et al. 2009; Towns et al. 2009 and Mulder et al. 2009), a study comparing one recovering with one uninvaded island (Orwin et al. 2016) and one studying a single recovering island in depth (Chapter 3). Field work methodologies for these studies were thoroughly described in all previous research, so I only briefly summarise them here. Of the islands used in this study, nine had been invaded by the rats *Rattus rattus* and *R. norvegicus* introduced by Europeans 50 to 150 years ago and support few or no seabirds. Nine others had never been invaded (supporting high seabird densities) and two were invaded but have subsequently had all invasive mammals eradicated from them (one supporting mid to high seabird densities (i.e. Korapuki) and one supporting low densities (Motuhoropapa)). The islands Ruamaahuanui and Motuhoropapa appear in this dataset twice, Ruamaahuanui is included as one island out of the nine uninvaded islands but also included as a stand-alone example of an uninvaded island, while Motuhoropapa is included in the nine invaded islands but also as a stand-alone recovering island. Ruamaahuanui was sampled twice during two separate studies that

have been used in this paper. The island was sampled once using two plots in 2004 and a second time using 15 plots in 2011. I believe that the different sampling methods and extended time period between the two studies represent independent samples, so both studies are included here. Motuhoropapa was also sampled twice, once in 2004 and again in 2015. The time period between the two means that in 2004 this island was still occupied by rodents, and so was included in the invaded island category, but by 2015 the island had had all pests removed and so was then included in the recovering island category. In addition, the sampling methods were dramatically different; in 2004 there were two samples taken from the island and in 2015 an exhaustive survey of the island was undertaken using 90 samples.

Only uninhabited islands were used that contained coastal forest and lacked farm stock. The islands were constrained in geographical range ($35^{\circ}25'S$ to $37^{\circ}12'S$) to avoid variation in the species pool of native plants and seabirds (Mulder et al. 2009; Towns et al. 2009). Since portions of these islands were burned by humans from about 800 to 50 years ago, the sampling was confined to well-developed multi-tree species secondary forest to maximize comparability across islands (Fukami et al. 2006). The soil types across the 18 islands varied, with the majority being of volcanic origin. It was assumed that seabird effects on soil would override variations in soil properties, with previous studies throughout New Zealand supporting this assumption (Atkinson, 1964; Hawke et al. 1999; Mulder and Keall, 2001; Markwell and Daugherty, 2003).

The research in this chapter uses data from three different studies stretching back thirteen years. Each of these studies are separated not only by time but also by methodology. The statistics used were designed to overcome some of these issues (i.e. differences in sample size) but could not account for all the differences between

studies. As such, these limitations must be taken into account when interpreting the results.

5.3.2 *Field methods*

For the first set of studies, the 18 islands were sampled within a 67-day period between February and April 2004 to minimise potential seasonal effects. On each island, two 10×10 m plots were set up within forested areas and on slopes of $< 30^\circ$ to ensure potential litter accumulation (Towns et al. 2009). The data for the two plots on each island were combined so that each island served as the unit of replication to avoid pseudoreplication. Entrances of seabird burrows were used as a proxy of seabird density (Fukami et al. 2006); within each plot they were counted by systematically walking along predetermined belt transects covering the entire area. A sample of surface mineral soil (depth layers: 0-10cm) was collected from a 0.5×0.5 m subplot within each plot and analysed for %N, %P, %C, Olsen P and pH (data from Fukami et al. 2006 and Mulder et al. 2009). Fukami et al. (2006) have previously tested these environmental variables using ANCOVAs and found no change in the significance of the differences between island types when considering island isolation or size. From each plot a single 2 litre sample of leaf litter was collected to the soil surface level and stored in a cloth bag. Invertebrates from this litter were extracted into ethanol within three days of sampling using Tullgren funnels running for seven days (Towns et al. 2009). After invertebrate extraction the litter was then oven dried (60°C until constant weight) and weighed. The invertebrates were then sorted, counted (Towns et al. 2009) and for this study, classified to family level using a dissection microscope.

For the studies using Korapuki and Ruamaahuanui, plots of 10 by 10m were randomly assigned using ArcGIS 10 software (ESRI, Redlands, CA, USA), and field work was carried out in March 2011. Steep inaccessible parts of the islands, or areas without forest were excluded. A total of 15 plots (between 15 and 200m apart) for each island was used, which were considered representative of the range of seabird burrow densities present (Orwin et al. 2016). Within each plot the number of burrow entrances was recorded and soil and litter samples collected. A total of four litter samples per plot were collected and subsequently bulked into one following the methods described by Orwin et al. (2016). For all samples invertebrates were extracted using Tullgren funnels run over seven days. Invertebrates were then sorted, counted and classified to family using a dissection microscope. Litter was then oven dried at 60°C until a consistent weight was reached (Townes et al. 2009).

The final study used Motuhoropapa Island in the Noises Group, Hauraki Gulf, New Zealand (Mackay et al. 2007). Nutrient addition plots were set up on Motuhoropapa Island using a GIS randomised block study design, with five treatments of 2m² plots per block. Six replicate blocks provided a total of 30 plots. Blocks were placed at least 50m apart to ensure independence. In each block, the five treatments were randomly assigned: (1) control (no fertiliser), (2) low seabird density (1 burrow/m²), (3) medium seabird density (3 burrows/m²), (4) medium-high seabird density (5 burrows/m²), and (5) high seabird density (10 burrows/m²) (Jones 2010a). Before each treatment was applied, 100g samples of soil (taken from the top 10cm soil layer) and 2 litres of leaf litter (from across the entire 2m² plot) were taken from each plot. Four months after the final application of fertiliser in late April 2015 final soil and leaf litter samples were taken to evaluate ecosystem response to the nutrient addition. Soil samples were dried at 60°C for 48h to determine water content, then

homogenised and analysed for total N and C, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a Mass Spectrometer and elemental analyser.

For all studies, invertebrates were extracted from litter using Tullgren funnels run over seven days, then sorted, counted and classified to family using a dissection microscope.

5.3.3 *Statistical methods*

ANCOVAs were used to compare the average family richness and the prevalence of missing families (hereafter called ‘missing families’) which were characterised as total families absent from any one island that are present on any other specific island across the collective island categories: invaded, uninvaded and recovering. The mean family richness and missing families were corrected for the variance in sample size, island size and the distance to the mainland for each island. Post-hoc Tukey tests were carried out on these corrected means to determine if there remained any differences between these island types after controlling for covariates. The functional groups present on each island were plotted using the proportion of each group for the two island categories of invaded and uninvaded, the two recovering islands and the one stand-alone undisturbed island. The common missing family groups from the two recovering islands were counted, and identified. These were different from the total missing families used in the ANCOVAs in that only missing family groups that were common on the majority of other islands were identified. This different count of missing species was done to correct for the potential in identification error for small, cryptic and rare invertebrate families. I then plotted species accumulation curves using the R package ‘Vegan’ (Oksanen et al. 2015) to estimate the total family richness given the asymptote of the sampling effort

on each of the five island types. I used the Chao2 non-parametric asymptotic species richness estimator (Chao et al. 2009) to further reinforce these accumulation curves. I compared the uninvaded and invaded island types with Korapuki (recovering), Ruamaahuanui (uninvaded) and Motuhoropapa (recovering). On Motuhoropapa I used each of the three sampling months and then once with all sampling times combined to better predict the estimated species (in my case, family) richness and to compare this with the predictions of family richness from the other island types. This also estimates the probability of finding new family groups given one extra sample and the extra number of plots or samples needed to reach an asymptote of family richness.

5.4 Results

After controlling for variations in sample size, island size and isolation the adjusted means of the missing common family groups (Figure 5.1) still showed significant differences between the uninvaded, invaded ($t = -2.62$, $p < 0.05$) and recovering islands ($t = -3.32$, $p < 0.05$). The recovering islands were not significantly different from the invaded islands although the results were near significant ($t = 2.19$, $p < 0.10$). When comparing the family richness (Figure 5.1) and controlling for the same covariates, the adjusted means were less different than for the missing families. The only significant difference found was between the uninvaded and invaded islands ($t = 2.55$, $p < 0.05$). The invaded and recovering islands were not found to be

different ($t = 1.68$, $p > 0.1$) and neither were the uninvasive and recovering islands ($t = -0.77$, $p > 0.5$).

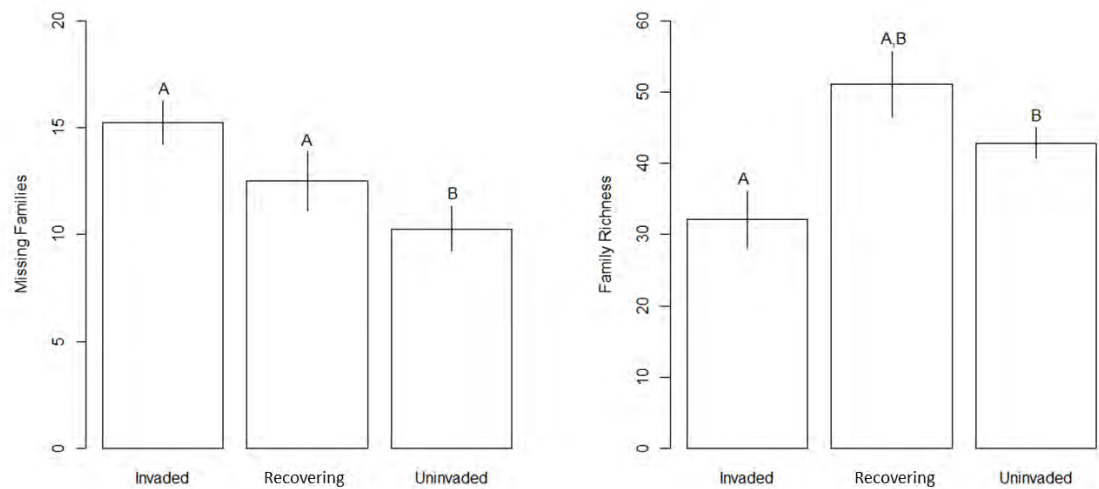


Figure 5.1 Adjusted mean families and missing families (\pm standard error) from the invaded, recovering and uninvasive islands after controlling for the variance in sample size, island size, and the distance to the mainland using ANCOVAs. Island types sharing a letter are not significantly different, where $p > 0.05$.

Families missing from Korapuki that were common on all other islands were Elateridae, Carabidae, Cerambycidae (Coleoptera), Lygaeidae (Hemiptera), and Myrmecidae (Hymenoptera). Of these families, three were phytophagous/herbivorous (Elateridae adult, Cerambycidae and Lygaeidae), two predatory (Carabidae and Elateridae larvae), and one a parasitoid (Myrmecidae) (Klimaszewski, 1950; Linsley, 1959; Sweet, 1960; Jackson, 1961; Huber, 1986; Lövei and Sunderland, 1996; Rainio and Niemelä, 2003). Common family groups missing from Motuhoropapa were Symphypleona (Collembola), Nematocera (Diptera), and Aphididae (Homoptera). Of these two are saprophagous (Symphypleona and Nematocera larvae), one haematophagous (Nematocera adult), and one phytophagous (Aphididae) (Moran, 1986; Buckley, 1987; McLellan, 1988; Chahartaghi et al. 2005; Hishi et al. 2007). When the proportion of invertebrates in each of seven functional groups is compared

for each of the island types (Figure 5.2), Ruamaahuanui, Motuhoropapa and the invaded and uninvaded islands all have similar proportions of invertebrates in each functional group, although Motuhoropapa had less parasitoids than the other islands (Figure 5.2). Korapuki was skewed towards saprophagivores, with the majority of all invertebrates on the island found in this functional group. This was due to an overrepresentation of Collembola in all of the samples with over 40,000 collembolans recorded on this island (Thoresen *pers. obs.*), vastly outnumbering any of the records for any other island type. In addition, although not identified on the graph, there were invertebrates present in both the phytophagivore and parasitoid functional groups; however, these groups were too small to show up meaningfully on the proportional graph.

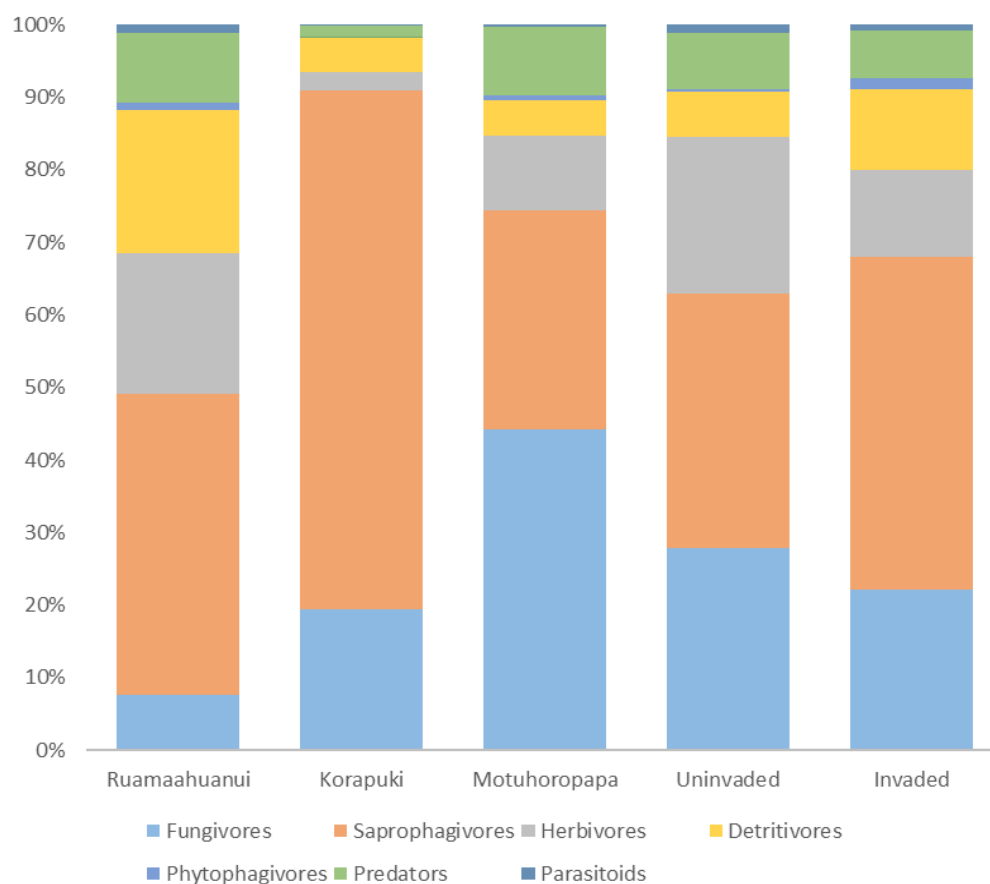


Figure 5.2 Proportion of invertebrates in each functional group on each of the three islands Korapuki, Motuhoropapa, and Ruamaahuanui, and the collective invaded and uninvaded islands.

The results of the species accumulation curves (Figure 5.3) showed that Korapuki, Ruamaahuanui and Motuhoropapa all reached close to an asymptote with the sample sizes used for these islands. Neither the invaded nor uninvaded island types showed asymptotic curves, although if a sample size similar to the other islands was used they would likely have demonstrated one. If a greater sample size was used for these island types the invaded island would still likely be lower than any other island type while the uninvaded islands would be the highest.

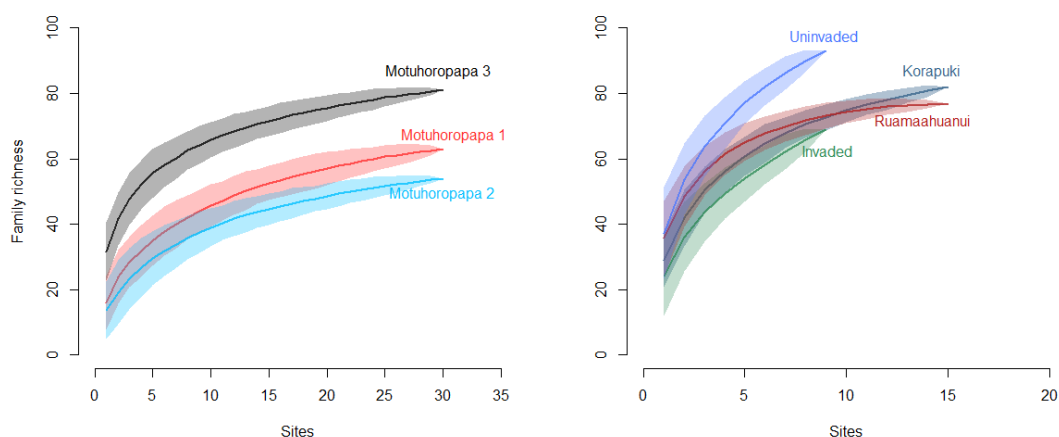


Figure 5.3 Family accumulation curves for each of the three sampling efforts on Motuhoropapa (left graph) and comparing Korapuki and Ruamaahuanui with the collective invaded and uninvaded islands.

The Chao2 species richness estimator predicted that the uninvaded islands would reach an asymptote at the highest family richness compared with all other island types (Table 5.1). The uninvaded island type also showed the highest probability of finding new family groups if further samples were taken and had one of the lowest further samples needed to reach the predicted asymptote. The comparisons of each of the three accumulation curves for each sampling trip on Motuhoropapa with the overall accumulation curve showed the accuracy of this method of predicting family richness.

Table 5.1 Estimated sampling effort required to acquire representative samples of all invertebrate families on each Island and Island type. Abbreviations are: **n**, number of samples collected; **S_{obs}**, observed species (family) richness; **S_{est}**, estimated asymptotic species (family) richness, based on the Chao2 estimator (Chao et al. 2009); **Q₁**, the number of species represented by exactly one sample (“uniques”); **Q₂**, the number of species represented by exactly two samples (“duplicates”); **q_o**, the probability that the next observed sample contains a species new to the sample. The entries in each “g” column represent the number of additional samples needed to reach 100% (**g** = 1), 95% (**g** = 0.95), and 90% (**g** = 0.90), respectively of the species estimate (**S_{est}**). Where entry is N/A **g** must be greater than 0.93 because of the restriction of **gS_{est} > S_{obs}**.

	n	S_{obs}	S_{est}	Q₁	Q₂	q_o	g = 1	g = 0.95	g = 0.90
Invaded	9	68	75.29	20	24	0.02	19.24	2.24	0.03
Uninvaded	8	92	107.84	47	61	0.04	21.63	3.41	1.22
Korapuki	15	84	92.71	28	42	0.02	28.89	3.24	0.05
Ruamaahuanui	15	78	88.99	35	52	0.03	30.61	4.69	1.15
Motuhoropapa 1	30	65	72.83	18	20	0.01	66.80	10.36	0.98
Motuhoropapa 2	30	54	57.48	12	20	0.01	38.89	1.75	N/A
Motuhoropapa 3	30	82	91.03	27	39	0.02	55.60	7.21	0.02
Motuhoropapa All	90	92	100.01	18	20	0.01	138.32	4.88	N/A

When each of the trips were plotted (i.e. with sample sizes of 30 each) they all showed predicted asymptotic richness values lower than the overall accumulation curve using all trips/plots (90 samples); however, the final trip (Motuhoropapa 3) did show a similar value, 91 predicted families compared with the 92 observed families for all trips. This result indicates that this method of predicting family richness will only be accurate if sampling at an optimal time with optimal conditions, as trip 3 occurred after rainfall and a period of drought (Chapter three). Finally, in order to reach 95% of the predicted asymptote few extra samples would have been needed for any of the islands suggesting that the observed family richness for each island type was relatively close to the number of families actually present.

5.5 Discussion

Both the recovering islands Korapuki and Motuhoropapa, lacked invertebrate families that were common on uninvaded islands, and had significantly more missing family groups when compared with the uninvaded islands. However, there were no significant differences when the recovering islands were compared with invaded

islands. These comparisons remained significant even when controlling for sample size and island isolation. My data may indicate these family groups were missing on invaded islands due to the effects of rats, and on recovering islands as a legacy effect of rat invasion.

The Chao2 estimator and species accumulation curves showed that Motuhoropapa, Korapuki and Ruamaahuanui all reached close to their predicted asymptotes for family richness given the sample sizes used on these islands. The results for the collective invaded and uninvaded islands, however, did not appear to be approaching their predicted asymptote. Despite this, if further samples were taken on the invaded islands they still would not have reached the family richness of either the uninvaded islands or the recovering islands. Conversely, if further samples were taken on the uninvaded islands they would only have further increased family richness from an already high richness. The probability of finding new families given one more sample was highest on the collective uninvaded islands and Ruamaahuanui. The invaded islands plus Korapuki and Motuhoropapa showed similarly low probabilities of finding new families. In addition, the number of samples needed to reach 95% of the predicted asymptote were relatively low for all islands. In sum, if more samples were taken from these islands it is unlikely many missing family groups would be found. Finally, if missing groups were found they would most likely be rare families, whereas families that are generally common such as the Carabidae, Cerambycidae and Elateridae, but missing from Korapuki, would be very unlikely to have been missed due to the effects of sample size.

The family groups missing from Korapuki but common on all other islands included three beetles, one true bug and a parasitoid wasp. Their trophic roles included one family that was herbivorous, one a generalist predator, one a parasitoid

of Lepidoptera and Hemiptera, and two that were phytophagous. On Motuhoropapa, missing families included one springtail, a fly and a true bug. Of these, two were saprophagous, one haematophagous and one phytophagous. The functional groups of which the missing families are part, were still intact on both islands so the loss of one or two families from these groups probably did not cause measurable changes to trophic structure. There were differences in the proportion of functional groups between each island but these differences were not large. Of the two recovering islands, Korapuki showed the greatest difference from the other islands due to an overrepresentation of saprophagivores, this was due to an extremely large amount of collembolans found in these samples. Each island type had family groups present in each of the seven functional groups described; there were no groups absent altogether despite the differences in family richness and missing families between the islands.

Simply noting the absences of family groups does not tell us what effect these groups might have on these ecosystems or each group's level of ecological redundancy. Beetles missing from Korapuki such as Elateridae (herbivore/phytophagivore as an adult, larval stage are predatory/saprophagous) and Cerambycidae (phytophagivore/herbivore), are usually abundant lower trophic level families in any ecosystems they inhabit (Klimaszewski, 1950; Linsley, 1959). Likewise, the missing fly from Motuhoropapa; Nematocera is an abundant saprophagivore while a larvae and a common blood-feeding adult (McLellan, 1988). The fact that Nematocera was missing from Motuhoropapa may be because there are few large animals resident on the island on which the adult can feed and potentially due to the drought that occurred during the sampling period meaning there would be few areas of standing water for larvae to inhabit (McLellan, 1988). The missing

Carabidae predator from Korapuki is also a widespread family group which can grow relatively large (Lövei and Sunderland, 1996; Rainio and Niemelä, 2003) and so is likely to have strong top down effects upon any food web it inhabits. The parasitoid family missing from Korapuki, Mymaridae, is a parasitoid of Coleoptera, Lepidoptera, Hemiptera and Psocoptera (Jackson, 1961; Huber, 1986) and the absence of this family could lead to a release in the concentrated top-down pressure this group would assert upon the family groups it would normally parasitize. The missing Homoptera/Hemiptera from both islands, Lygaeidae from Korapuki and Aphididae from Motuhoropapa, are potentially due to the nature of these families, in that they generally inhabit canopy or sub-canopy areas, and the samples were taken from the leaf-litter. However, aphids are generally very common and the fact that none were found on Motuhoropapa despite 90 samples taken suggests they are absent. The absence of aphids may have bottom-up effects on those species that would normally predate on this common prey family. Finally, the missing Collembola from Motuhoropapa, Symphypleona, was saprophagous and is from a relatively rare family when compared to the other collembolans present. As saprophagivores are an abundant functional group the absence of one family from it is unlikely to have a large effect other than enabling other saprophagivores to become more abundant. Most of these families should be capable of recolonising; all of these families, excluding Symphypleona, contain species that are capable of flight in at least one life stage. However, small sensitive families such as Mymaridae and Aphididae may not be capable of flight, or surviving flight, over the relatively long distances from source populations on the mainland or nearby large islands.

Any missing families from higher up a food chain (i.e. predators and parasitoids) will reduce the redundancy of the ecosystem even if they do not have

any effects on its functionality. The loss of any family from these top tier functional groups should be viewed with great concern, as these groups are small but have the potential to have large top-down effects upon all the functional groups below them. The absence of the family groups in these top tiers on Korapuki (i.e. Carabidae, Elateridae larvae, and Mymaridae) may have contributed to the overrepresentation of Collembola and the saprophagous functional group found on this island. In addition, the absence of these groups, especially the high tier predators or parasitoids such as Carabidae and Mymaridae may show evidence of a bottom-up extinction cascade; where the loss of prey families triggers further extinctions of predators and parasitoids (Fowler, 2010; Sanders et al. 2013 and 2015). Parasitoids were much less abundant on the invaded and recovering islands when compared with uninvaded islands (Chapter 4). This may be due to a ‘horizontal’ extinction cascade where the loss of one parasitoid leads to competitive exclusion at the prey trophic level, leading to extinctions of further parasitoid families (Sanders et al. 2013 and 2015). The absence of family groups near the bottom of a food chain (i.e. herbivores, saprophagivores, fungivores and detritivores) will be less likely to effect the overall redundancy of an ecosystem. If a family is missing that would otherwise have been abundant, however, (like Elateridae or Cerambycidae) this is likely to have an effect on other families within its functional group, due to decreased competition, and those higher up due to potential weakening in bottom-up effects. The absence of any family may have large effects on an ecosystem that could only be evident once they were returned to where they were lost.

It is arguable that at least three of the family groups missing from Korapuki (Elateridae, Cerambycidae, and Carabidae) are important families and their absence may reduce the redundancy of the ecosystem. If they were returned large-scale

changes would likely occur, at least on the scale of leaf-litter invertebrates and likely higher up, effecting the insectivorous reptiles and birds common on the island. Motuhoropapa, however did not seem to be missing any families that might have large effects if they were returned. These two islands were roughly the same size; however, Korapuki is much more isolated than Motuhoropapa. In addition, Korapuki was recently modified from fire and due to this there was very little forest cover as recently as the 1940s, and the forest cover that remains now is predominantly young seral scrub (Towns and Atkinson 2004). Motuhoropapa has also had a history of fire but not as recent; the island has a well-developed vegetation cover as it has remained relatively undisturbed for over a hundred years (Cunningham and Moors 1985; Cameron 1998; MacKay et al. 2007). The invasion histories of both islands differ as well, Korapuki was invaded by both kioie (*Rattus exulans*) and rabbits (*Oryctolagus cuniculus*) until the mid-1980s (Towns and Atkinson 2004), whereas Motuhoropapa was invaded by Norway rats (*R. norvegicus*) until 2002 (MacKay et al. 2007). The fact that it will be harder for new families to colonise Korapuki in conjunction with other factors such as the recentness of a near total burn off and the island's invasion history may be why there are important families missing from Korapuki that are not absent from Motuhoropapa.

5.6 Conclusion

I concluded that there were more family groups missing from both the recovering and invaded islands compared with the uninvaded islands and that this was likely due to the suppression of these groups via rats and the legacy of this suppression. However, it may have also been due to the differences between the

islands in isolation, forest cover, and disturbance and invasion history. If more samples were taken further family groups would have been found but it is very unlikely the absent family groups that would have otherwise been common (i.e. Elateridae, Cerambycidae and Carabidae on Korapuki) would have been found. Finally, the family groups missing from Korapuki were likely important and their absence contributed to a decrease in the redundancy of this ecosystem.

It is possible that the differences found in invertebrate assemblages between islands will have simply been due to the differences in methodologies and times between the three different studies used in this chapter. However, while these differences may have given rise to randomness and false positives it is unlikely to be the case for the missing common family groups such as elateridae or caribidae. As these groups are usually very common their absence is unlikely to have occurred by chance.

Chapter six: Discussion

6.1 Introduction

Litter invertebrates on seabird islands can form complex communities that are reflective of geochemical conditions in the soil (Kolb et al. 2011). However, until now no research has shown how the complexity itself might arise and change as seabirds return to, or are suppressed from their island ecosystems. I found that, as a result of the engineering effects of burrowing seabirds, invertebrate food webs become larger and more complex, in part due to nutrient subsidies of nitrogen (Chapters 2 and 4; Figure 6.1). However, interactions between nutrient subsidies and moisture may influence the way seabirds effect invertebrate food webs (Chapter 3). Rats prey on seabirds resulting in suppression of their nutrient subsidies and engineering effects and the decline in the size and complexity of invertebrate food webs (Chapters 2 and 4; Figure 6.1). When rats are eradicated in order to restore island ecosystems, the food webs become more complex, but only in areas where seabirds have returned in high densities, and their subsidy effects are reinstituted (Chapter 4; Figure 6.1). However, some invertebrate family groups were still missing from these recovering islands even almost 30 years after rat removal, resulting in direct and indirect legacy effects of these invasive mammals (Chapter 5; Figure 6.1).

How do seabirds, rat invasion, and ecosystem restoration effect the food webs of invertebrates on offshore islands?

Question 1, Chapter 2
Are food webs on invaded islands different from uninvaded islands?

Conclusions:

- 1) On invaded islands invertebrate food webs were smaller, less complex, and had traits of less resistant food webs.
- 2) The suppression of nutrient subsidies by rats is likely the major cause of these changes.

Yes, so then...

Question 3, Chapter 4
Do restored island food webs differ from invaded or uninvaded islands?

Conclusions:

- 1) The food webs metrics from Korapuki Island (restored) were typical of both uninvaded and invaded islands.
- 2) Korapuki supports some areas that are virtually indistinguishable from an uninvaded seabird island.
- 3) Parts of Korapuki still show strong gradients and attributes of food webs reflective of invaded ecosystems.

Kind of, but...

Yes, but...

Question 2, Chapter 3
How do nutrient subsidies and water availability effect food web structure?

Conclusions:

- 1) Artificial nutrient subsidies on a forested island had no discernible effect on any of the food web structural or functional attributes we measured.
- 2) The invertebrate food web structures became larger and more complex with increases in water availability and slight decreases in soil C:N.
- 3) Food webs collapsed and reconstructed themselves in response to water availability.

Question 4, Chapter 5
Is there a legacy of indirect rat suppression on invertebrate food web composition on restored islands?

Conclusions:

- 1) More family groups were missing from the restored and invaded islands due to rat suppression and the legacy of this suppression.
- 2) Family groups were missing from both restored islands which are common on uninvaded islands.
- 3) If more samples were taken on the restored islands some missing family groups would have been found, but not the missing groups that would have otherwise been common.

Figure 6.2 A summary of the findings of each chapter of this thesis.

6.2 The effects of seabirds and rats

When compared with seabird islands, the networks within invertebrate communities on rat-dominated islands were smaller, less complex, had a decreased number of generalist, specialist and overall species, and had almost half as many links among species (Chapter 2). These results indicate that while seabirds promote diversity and complexity in invertebrate communities, rats impede them (Figure 6.2). The results also show promotion (seabirds) and suppression (rats) of diversity and complexity at every level of a trophic network. In addition, these differences in network complexity between invaded and seabird islands were largely due to differences in total soil nitrogen (N), which was a result of the seabird derived nutrient subsidies and their suppression via rats (Fukami et al. 2006; Wardle et al. 2009; Mulder et al. 2009). These changes in soil N could influence litter invertebrate networks through changes in net primary productivity and plant biomass, or nutrient quality of leaves and leaf litter (Siemann 1998; Nordin et al. 1998). On these same islands, Mulder et al. (2009) demonstrated that primary productivity, leaf mass and vegetation diversity were not significantly lower on the invaded islands compared to the seabird islands. However, both Mulder et al. (2009) and Wardle et al. (2009) found that foliar N concentrations for several plant species were lower on the invaded islands, and Wardle et al. (2009) showed that leaf litter N and the release of N during leaf litter decomposition was also lower for those islands. In addition, Fukami et al. (2006) revealed that introduced predators disrupted seabird nutrient subsidies resulting in decreased forest fertility and wide-ranging cascading effects on below-ground organisms (Figure 6.2). The differences in N between these island types therefore influences food webs through the associated changes in nutrient quality of both foliar leaves and leaf litter rather than through lower plant

productivity or biomass. The fact that there were changes in complexity at every level of the trophic structure of these food webs then infers the existence of trophic cascades.

To explain the differences in food web complexity observed, I theorised the existence of successive bi-directional trophic cascades (as explained in (Siemann, 1998)) when rats invaded and suppressed seabirds and their associated nutrient subsidies. Rats suppress subsidies leading to lower foliar and leaf litter nutrients on invaded islands which leads to lower abundance and nutrient content of primary consumers which in turn leads to the decline of secondary and tertiary consumer diversity (i.e. a bottom-up trophic cascade; cascade 1, Figure 6.2). Low diversity amongst tertiary and secondary consumers can decrease inter-trophic competition, thus decreasing the diversity of prey as apparent mutualisms, supporting prey diversity, decline (top-down trophic cascade; cascade 2) (Abrams 1987; Abrams and Matsuda 1996; Long et al. 2012). Reduced prey diversity would next increase competition between predators, causing less competitive predators to potentially be lost (Kratina et al. 2007; Hammill et al. 2015), further reducing the species the ecosystem can support (bottom-up cascade; cascade 3). Finally, low prey diversity means there are less options for consumers, so resource switching to avoid competition would be infrequent and the benefits gained to those species consumed from high competition between consumers (i.e. apparent mutualisms) would be less apparent. Such a successive bi-directional trophic cascade would ultimately result in a simple food web (with low entropy) with few coexisting species (i.e., low total species) that is characterised by high competition (i.e., fewer generalists, low generality) but few benefits of this competition to those species consumed (i.e. low vulnerability). The observed decreases in total species abundance, generalists,

generality, vulnerability, and entropy on invaded islands supports this theory (Figure 6.2).

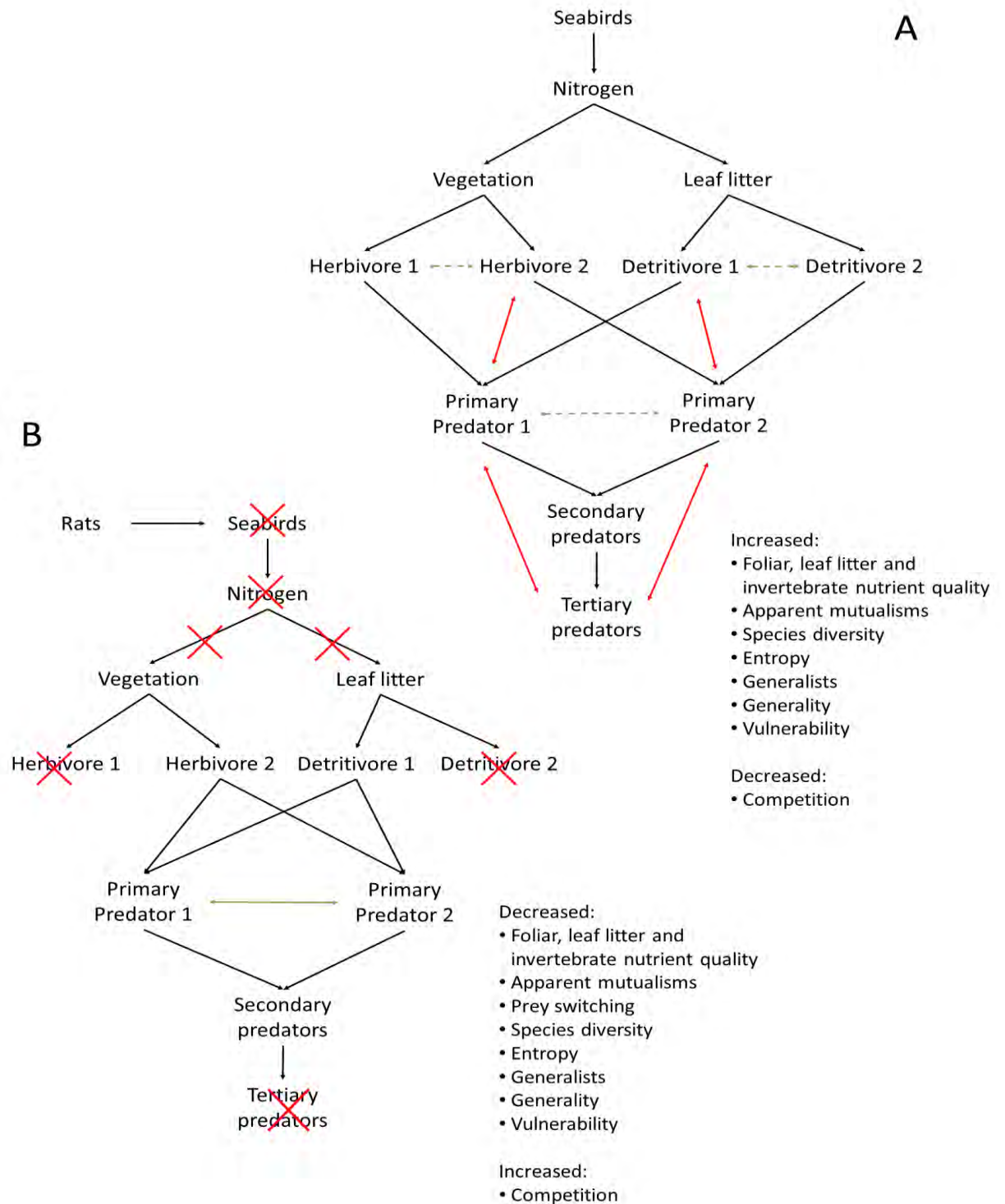


Figure 6.3 A simplified conceptual diagram of the effects of seabirds and rats on invertebrate food webs. Black arrows represent nutrient flow (i.e. as in a food web), red arrows represent apparent mutualisms and green

competition. Red crosses in diagram B show the loss of nutrient flow and species. Solid arrows show strong interactions and dashed lines weak interaction (i.e. in A, the dashed green lines signify weak competition, whereas the solid line in B denotes strong competition). Two types of apparent mutualisms are represented; predator and competitor mutualisms. For example, in diagram A, the presence of primary predator 1 benefits herbivore 2 as it predate on herbivore 1; herbivore 2s competitor (competitor apparent mutualism). Also in diagram A, primary predators 1 and 2 benefit from the presence of tertiary predators as they predate on the secondary predators that predate on primary predators 1 and 2 (predator apparent mutualism).

6.3 The interplay between nutrient subsidies and water

In order to further tease apart the effects of nutrient subsidies on invertebrate food webs, I then conducted a fertilisation experiment where nutrients were added to plots on a forested island largely devoid of seabirds and rats (Motuoropapa), mimicking the nutrient subsidies of seabirds (Chapter 3). The results for this experiment definitively showed no effect of the nutrient addition treatment on any of the invertebrate functional groups or food web metrics as well as the nutrient content of the soils in any plot. Essentially, the nutrients I added to the ecosystem quickly disappeared, having no effect on the variables I measured, possibly due to the aridity of the ecosystem before fertiliser (mixed within water) was added. Short water pulses introduced to arid soil create a rapid response in the mineralisation of N and C (Pulleman and Tietema 1999; Austin et al. 2004; Miller et al. 2005; Borken and Metzner 2009). This mineralisation causes N uptake from vegetation and C to be lost to the atmosphere (Fierer and Schimel 2002; Borken and Metzner 2009). Plant roots also respond rapidly to water and nutrient pulses. Root ammonium uptake capacity increases significantly within one day of a water and nutrient pulse (Cui and Caldwell 1997). As wetted soils then re-dry, root activity decreases and any excess N is lost, likely due to microbial immobilisation (Vitousek et al. 1982; Wilson and Tilman 1991; Cui and Caldwell 1997). If any invertebrates were present in this system a bottom-up effect would likely have occurred, but the aridity likely contributed to the fact that there were very few invertebrates present at this time and

so, they did not (at least measurably) benefit from these nutrient pulses (Frith and Frith 1990; Kai and Corlett 2002; Pinheiro et al. 2002; Cardoso et al. 2007; Silva et al. 2011). This result was also contrary to the result of Jones (2010a) who used the same methodology but on a grassland island. These differing results may also show the differences between the way grasslands and forests respond to brief nutrient subsidies.

The artificial nutrient subsidies had no discernible effect on the invertebrate food webs even in the very high amounts, equivalent to the subsidies of densely packed seabird colonies. This may show that in order for seabirds to effect these food webs through nutrient subsidies they must be active and present on these islands for long periods of time and successive breeding years. The cumulative effect of seabird nutrient subsidies over many years will eventually lead to the saturation of nutrients such as N within soils and vegetation on these islands, which will then lead to the differences in food web complexity observed in Chapter 2.

While the artificial nutrient subsidy experiment produced no measurable response, there were natural nutrient and water gradients across the island and through time, which were used to help answer how leaf litter and soil moisture and nutrient subsidies together effect invertebrate food web structure and function (Chapter 3). The invertebrate food webs were strongly affected by water availability (leaf litter water content) and weakly affected by the ratio of C: N in the soil. The food webs were larger and more complex with more abundant total invertebrates, generalists and specialists with increases in water and weak decreases in C: N. There were also increases in the orders Entognatha (springtails), Diptera (flies) and Coleoptera (beetles) and the functional groups fungivores, saprophagivores, phytophagivores and predators. Other aspects of the food webs were only affected by

water availability, these included the behavioural aspects of the food web: generality (prey per predator), vulnerability (predator per prey), and the omnivory index, the orders Acari (mites), Araneae (spiders), Lepidoptera (moths and butterflies), and Diplopoda (millipedes), and the detritivore and herbivore functional groups.

The weak negative response of the food webs to the ratio of C: N may have been due to the rate at which C and N changed in relation to each other in the soil. C decreased at a faster rate to N which meant that while there was less food at lower C: N ratios, the available food was of higher quality, with high N concentrations. While a high C: N ratio provides too much low quality food, a very low one doesn't provide enough food, and so intermediate measures provide moderate amounts of high quality food. Changes in food web complexity and size was mediated by C: N and litter water; however, changes in the how invertebrates interacted within the food web seemed to have been solely influenced by water availability. As water availability increases invertebrates become more general in their feeding habits and more omnivorous; feeding from more trophic layers. Alternately, as water decreases invertebrates become more specialised, which is likely a response to resource and prey availability and competition. Seasonality may cause species to expand their niche. Individuals may increase their range of food items during favourable conditions (e.g. during wet periods) and decrease them again as conditions decline (e.g. due to drought) (Bolnick et al. 2007 Araújo et al. 2009 and 2010). These changes in conditions are likely to affect resource availability which generally peaks during favourable environmental conditions (Pinheiro et al. 2002). Niche expansion may also be due to seasonal competition release as inter- and intra-specific competition is likely high during unfavourable conditions when resources are scarce (Araújo et al. 2010).

Water availability is of vast importance for invertebrate food webs, but C and N are important too; furthermore, these variables interact in complex ways. The relationships between C, N and precipitation are characterised by several interdependencies (Burke et al. 1997). The amount of C contained within an ecosystem is largely dependent on annual precipitation (under near steady-state conditions). The amount of C stored within an ecosystem determines the amount of N that can be retained (Burke et al. 1989). N is required for the capture of C, C is required for N retention, and in the absence of disturbance both come into equilibrium with water. In addition annual net primary productivity (NPP), N use efficiency, and N mineralisation all increase with precipitation, but so too do the effects of leaching (Austin and Vitousek 1998).

This research highlights the way rainfall and seasonality may influence the way seabird derived subsidies affect the invertebrate food webs. In times of aridity the lack of water will override the effects of high nutrient concentrations and so invertebrate food webs will become less complex. This is very much the case on arid islands such as those extensively studied in the Gulf of California where seabird derived nutrient subsidies support few species until wet years where a veritable explosion of life occurs (Polis and Hurd 1995; Sánchez-Piñero and Polis 2000; Stapp and Polis 2003; Barret et al. 2005). However, while these islands go through arid and wet periods over decades, depending on the effects of the El Niño Southern Oscillation (Polis and Hurd 1995), the islands in New Zealand may do so over a single year. This means that the food webs on these islands are capable of responding to rainfall and recovering from the disturbance of aridity very quickly; reconstructing themselves into complex systems after being disturbed into simplicity. If this is the

case for the disturbance of aridity, then this reconstruction may also occur as seabirds return to previously invaded islands reinstituting their nutrient subsidies.

6.4 The effects of restoration

In order to determine the effects of restoration on the potential for reconstruction of food webs (Chapter 4), I compared the invertebrate food webs of a recovering island: Korapuki, to a reference island: Ruamaahuanui, and the nine invaded and eight uninvaded islands used in the second chapter. I determined that the food webs and environmental measures on Korapuki were typical of both invaded and uninvaded islands, with some key differences. There were also areas on Korapuki where the food webs were indistinguishable from those found on the reference island Ruamaahuanui. Finally, nutrient and disturbance gradients were apparent on Korapuki that had effects on the invertebrate food webs. These gradients were not apparent on Ruamaahuanui and were indicative of an island where seabirds had not reached high enough densities to fully influence the entire ecosystem.

There was one key difference in the food webs between Korapuki and the invaded islands: generalist diversity, with Korapuki having a greater number of generalist species. The uninvaded islands and Ruamaahuanui had similarly high generalist diversity when compared with Korapuki, and all were significantly higher than the invaded islands. Generalist diversity was the only metric showing this pattern, indicating that Korapuki and the seabird islands can be distinguished from the invaded islands using this attribute. Nestedness was a key attribute that distinguished the seabird islands from Korapuki and the invaded islands. Ruamaahuanui demonstrated much lower nestedness than both Korapuki and the

invaded islands and was similar to the other seabird islands. This metric is inextricably linked with generalist and specialist diversity and the interactions between the two (Bascompte & Jordano 2006 & 2007; Rezende et al. 2007; Dattilo et al. 2013). If generalist diversity is high nestedness will likely be low (Dattilo et al. 2013) and, as in this case, generalist diversity was high on Ruamaahuanui, nestedness would be expected to be low here too. As I previously concluded that high generalist diversity is indicative of seabird island food webs I conclude that so too is low nestedness. Entropy is the only metric that showed multiple differences between all the island types. The invaded islands had the lowest entropy (complexity), followed by Korapuki, with Ruamaahuanui being more complex and the uninvaded islands being the most. Entropy thus forms a gradient that may indicate a restoration trajectory. If this were the case then the place that Korapuki sits would show its place in this trajectory, i.e. around halfway between an invaded and uninvaded island. Only nestedness showed a clear difference between Korapuki and the uninvaded food webs. In addition, while there was only one difference between Korapuki and the invaded food webs; that of generalist diversity, this difference was an important one. I thus concluded that Korapuki has food webs with attributes similar to, but not the same as both invaded and uninvaded islands.

The comparison of the food webs within each plot on Korapuki with those on Ruamaahuanui gave similar results. Less than a third of the plots on Korapuki demonstrated food web attributes typical of a seabird driven ecosystem. When the less accurate metrics were excluded from the analysis I found that around 70% of the plots on Ruamaahuanui and Korapuki were representative of a seabird island and non-seabird island, respectively. This shows that Ruamaahuanui is largely a seabird island, and that Korapuki mostly still appears invaded, but contains some areas that

are similar to Ruamaahuanui. The 30% of plots on Ruamaahuanui that were not indicative of a seabird island were likely the few areas on the island that were not directly affected by seabirds; areas where seabirds cannot burrow due to shallow soils, areas vulnerable to flooding or otherwise unsuitable habitats (Buxton et al. 2016).

Finally, I compared how the food web and environmental metrics interacted between Korapuki and Ruamaahuanui. As seabirds are usually colonial, their engineering effects are likely to be more heterogeneous on islands where they are recolonising compared to islands with large long-term resident populations. The effects of seabirds are therefore likely to demonstrate stronger gradients on recovering islands when compared to islands with high and homogenous seabird densities. This was indeed the case: strong gradients were apparent on Korapuki that were not apparent on Ruamaahuanui, the most significant being between food web nestedness and the ratio of C: N in the soil; the food webs became less nested with increasing C in relation to N. Low nestedness is associated with a lower degree of generalisation within the network, increased competition within trophic levels, and an decrease in the number of coexisting species (Bascompte & Jordano 2006 & 2007; Araujo et al. 2010; Tylianakis et al. 2010 Rezende et al. 2007; Dattilo et al. 2013). Ecosystems that produce organic matter with high C to nutrient (C: N and C: P) ratios are likely to result in inefficient trophic transfer, as less nutrients are passed between trophic levels (Mulder & Elser 2009) and herbivores with increased ingestion rates, to offset the low nutrient quality of abundant food (Urabe & Waki 2009). This inefficient trophic transfer would likely result in reductions in generalisation and increases in competition as species focus their limited energy on feeding on one easy food source. This change in feeding strategies could then cause

less competitive species to disappear, with most of these being super-specialists. Ultimately a food web would result with fewer coexisting species and less generalisation with less super-specialists and super-generalists, i.e. a food web would be characterised by low nestedness. When compared across both islands, the ratio of C: N had a weak but significant negative relationship with seabird burrow density. Increases in burrow density on Korapuki led to lower C: N ratios and subsequently more vital forests (van Straalen et al. 1988) with a greater rate of litter decomposition (Swift et al. 1979) and food webs characterised by high nestedness. This is also supported by the fact that the uninvaded islands all had significantly higher nestedness than both the invaded and recovering islands.

Food webs on Korapuki have reconstructed and increased in complexity following restoration, but only in localised areas that are heavily influenced by the recolonising seabirds. In addition, these food webs have not become as complex as those found on islands that have never been disturbed. Gradients were apparent on Korapuki between the food webs metrics and the environmental variables that were typical of an island with seabird populations recolonising but not yet entrenched. These gradients further support the conclusion previously made: the cumulative effect of seabird nutrient subsidies over many years will eventually lead to the saturation of nutrients such as N within soils and vegetation on these islands, which will then lead to the differences in food web complexity observed in Chapter 2. The fact that the food webs on Korapuki seemed to be reconstructing but were not as complex as those on undisturbed islands leads on to the questions: will they be as complex if given the time? Are there absences in the invertebrate communities on these islands, due to the legacy effects of rat invasion and disturbance, which could

prevent the full reconstruction of these food webs, thus creating less redundant ecosystems?

6.5 The legacy effects of rats

In order to answer these questions, I then compared the invertebrate communities on all the islands used in this thesis to determine if there were legacy effects of rat invasion on the two islands that were recovering: Korapuki and Motuhoropapa (Chapter 5). Using species accumulation curves and a true species richness estimator I showed that Motuhoropapa, Korapuki and Ruamaahuanui all reached close to their predicted asymptotes for family richness given the sample sizes used on these islands. The probability of finding new families given one more sample was highest on the collective uninvaded islands and Ruamaahuanui. The invaded islands plus Korapuki and Motuhoropapa showed similarly low probabilities of finding new families. It is therefore unlikely more family groups would have been found on either the invaded or recovering islands if more samples were taken.

Both Korapuki and Motuhoropapa as recovering islands, lacked invertebrate families that were common on uninvaded islands, and had significantly more missing family groups when compared with the uninvaded islands. However, there were no significant differences when recovering islands were compared with invaded islands. These comparisons remained significant even when controlling for sample size and island isolation. These results indicate that some family groups were missing on invaded islands due to the effects of rats, and remained absent on recovering islands as a legacy effect of rat invasion. The common family groups missing from Korapuki included three beetles (Carabidae, Cerambycidae, and Elateridae), one true bug

(Lygaeidae) and a parasitoid wasp (Mymaridae). Their trophic roles included one family that was herbivorous, one a generalist predator, one a parasitoid of Lepidoptera and Hemiptera, and two that were phytophagous. On Motuoropapa, missing families included one springtail (Symphypleona), a fly (Nematocera) and a true bug (Aphididae). Of these, two were saprophagous, one haematophagous and one phytophagous.

It is arguable that at least three of the family groups missing from Korapuki (Elateridae, Cerambycidae, and Carabidae) are ecologically important. If they were returned, large-scale changes would be likely, at least on the scale of leaf-litter invertebrates and possibly higher up, effecting the insectivorous reptiles and birds common on the island. For example, the absence of the family groups in the top trophic tiers on Korapuki (i.e. Carabidae, Elateridae larvae, and Mymaridae) may have contributed to the overrepresentation of Collembola found on the island. In addition, the absence of these predator and parasitoid families may show evidence of a bottom-up extinction cascade; where the loss of prey families triggers further extinctions of predators and parasitoids (Fowler, 2010; Sanders et al. 2013 and 2015).

Motuoropapa, however, did not seem to be missing any families that might have large effects if they were returned (excluding perhaps, Aphididae). These two islands were roughly the same size; however, Korapuki is much more isolated than Motuoropapa. In addition, Korapuki was recently modified from fire and due to this there was very little forest cover as recently as the 1940s, and the forest cover that remains now is predominantly young seral scrub (Towns and Atkinson 2004). Motuoropapa has also had a history of fire but not as recent; the island has a well-developed vegetation cover as it has remained relatively undisturbed for over a

hundred years (Cunningham and Moors 1985; Cameron 1998; MacKay et al. 2007). The invasion histories of both islands differ as well, Korapuki was invaded by both kiore (*Rattus exulans*) and rabbits (*Oryctolagus cuniculus*) until the mid-1980s (Towns and Atkinson 2004), whereas Motuhoropapa was invaded by Norway rats (*R. norvegicus*) until 2002 (MacKay et al. 2007). The fact that it will be harder for new families to colonise Korapuki in conjunction with other factors such as the recentness of a near total burn off and the islands invasion history may be why there are families missing from Korapuki that are not absent from Motuhoropapa.

Many of the absent families should be capable of recolonising; all of these families, excluding Symphypleona, contain species that are capable of flight in at least one life stage. However, the parasitoid wasp family Mymaridae contains many species that have vestigial wings and are incapable of flight (Noyes and Valentine 1989). In addition, small sensitive families such as Aphididae may not be capable of flight, or surviving flight, over the relatively long distances from source populations on the mainland or nearby large islands. Therefore, absences due to the legacy effects of rat invasion could potentially prevent the full reconstruction of the invertebrate food webs, at least in terms of those few invertebrates unable or unlikely to naturally recolonise.

6.6 Conclusion

New Zealand conservationists pride themselves on being leaders in island ecosystem restoration; however, the way in which we go about restoring these ecosystems is arguably, superficial. We are masters at pest eradication (Towns et al. 2013), but usually once this is carried out these islands are left to recover passively

with little further restoration effort taken (Borrelle et al. 2015; Buxton et al. 2016). In the few cases where further effort is put into restoring these ecosystems, this effort is focused on afforestation and the reintroduction of large or charismatic species. While afforestation and species reintroductions are important aspects of ecosystem restoration, little to no effort has so far been devoted to restoring the more complex aspects of an ecosystem such as the invertebrate communities or nutrient cycling. This is, perhaps due to the idea that if reforestation is carried out then these more complex aspects will sort themselves out.

The two recovering islands used in this thesis demonstrate the two predominant methods of island ecosystem restoration. Korapuki has been actively managed since invasive mammals were eradicated in the mid-1980s and Motuhoropapa has been left to passively recover (Cunningham and Moors 1985; Cameron 1998; Towns and Atkinson 2004; MacKay et al. 2007). There are many differences between these two islands, with the key ones being the differences in herpetofauna and avifauna. Motuhoropapa has few resident bird species and possibly no resident reptiles, likely due to the fact that no effort had been carried out to encourage their recovery or reintroduce species (Cunningham and Moors 1985; MacKay et al. 2007). Korapuki on the other hand has diverse and highly dense populations of reptiles and many birds, including recovering populations of seabirds; largely grey faced petrels (*Pterodroma gouldi*) (Towns and Atkinson 2004; Towns et al. 2016). However, when I compared these islands I found that the invertebrate communities on Motuhoropapa seemed to be more intact than those on Korapuki. There were important family groups missing from Korapuki that were not missing from any other recovering or uninvaded island. This is evidence of what may occur

when invertebrate communities are largely ignored in the restoration process; important deficiencies can persist.

Returning the missing families might have unforeseen adverse effects, with the potential for these families failing to survive, in an environment of abundant insectivorous reptiles and birds. Conversely, not returning these families may be lead to adverse effects to the ecosystem. There were hugely abundant populations of collembolans on Korapuki, which could be evidence of a release in predation pressure. The common predators on Korapuki i.e. birds and reptiles are likely too large to directly predate on collembolans; however, some of the missing families i.e. Carabidae and Elateridae are not. Collembolans are saprophagivores, meaning they feed on fungi, bacteria, detritus and other smaller invertebrates (Petersen 2002; Ferlian et al. 2015). Huge populations of invertebrates within this functional group could be reducing leaf litter decomposition rates due to overgrazing of fungi and bacteria that break down leaves and potentially high predation of small detritivorous invertebrates. If this were true, then these abundant collembolans could be contributing to the gradients in the C: N ratio observed in the soils on Korapuki disturbing the greater food web via its effect on nestedness. Collembolans can influence nutrient cycles, especially in high densities where they have been shown to reduce fungal growth, increasing the leaching of ammonium nitrate and calcium due to overgrazing (Ineson et al. 1982; Petersen 2002). It is thus possible that the extremely high abundance of collembolans on Korapuki is due to a release in predation pressure which has contributed to the way the nutrient subsidies effect the invertebrate food webs.

6.7 Management recommendations

Before any actions are taken to restore an ecosystem it is important to understand the ecosystem that restoration efforts aim to achieve (e.g. a reference ecosystem) but also the current ecosystem (i.e. before restoration efforts begin) in order to determine if the changes made will lead to the aims set. If certain aspects of food web structure are ignored, or overlooked, ecosystems can revert to alternate stable states and not the ecosystem intended (e.g. Mulder et al. 2009). This thesis highlights that it is possible to obtain deep understanding of the consequences of invasive species on invertebrate food webs.

There needs to be more research carried out on the effects of ecosystem restoration on invertebrates. For example, a research priority should be to discover if invertebrates recolonise or reappear after being relict or functionally extinct from an ecosystem. Before-after-control-impact (BACI) experiments should be carried out, along with long-term monitoring during recovery to determine how the invertebrate communities respond to restoration efforts. In addition, methods that are more comprehensive are needed. To date many restoration programs only use pit-fall traps to census invertebrates, which are lacking in their scope, especially when compared to invertebrates extracted from leaf litter or soil using Tullgren funnels. The effects of restoration will also change from ecosystem to ecosystem, so even if these questions are answered in one area they may not apply in another. It is therefore important for every restoration effort to incorporate invertebrate communities into their management plans. In this way, any important absences in the make-up of the communities can be identified. Further management may then be taken such as reintroductions. Reintroducing entire invertebrate communities to an area if needed

could be a relatively simple prospect; it is possible that all that would be needed is a few buckets of leaf litter. Again, this is an avenue for future research.

When building a skyscraper engineers will always start from the ground up, initially laying strong foundations and then starting on the greater structure. Why should this be no different to constructing an ecosystem which is orders of magnitude more complex than a building? The invertebrate communities in most ecosystems are arguably the foundations; influencing nutrient cycles, vegetation, pollination, fungi and bacteria as well as providing food for large insectivorous vertebrates. When restoring an ecosystem, we should first start at this level (after reforestation, if needed); fully understanding the invertebrate communities present and reintroducing any species incapable of recolonising in the short timeframe of restoration. Only once the invertebrate communities are well established should further reintroductions take place.

References

- Abrahamsen, G. 1983. Effects of lime and artificial acid rain on the Enchytraeid (Oligochaeta) fauna in coniferous forest. *Holarctic Ecology*, 6, 247-254.
- Abrams, P. A. 1987. Indirect interactions between species that share a predator: varieties of indirect effects. In: Kerfoot, C. W. and A. Sih. (Eds.), *Predation: direct and indirect impacts on aquatic communities*. London: University Press of New England. ISBN 0-87451-376-6.
- Abrams, P. A., and H. Matsuda. 1996. Positive indirect effects between prey species that share predators. *Ecology*, 77, 610-616.
- Aizen, M. A., Sabatino, M., and Tylianakis, J. M. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science*, 335, 1486-1489.
- Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... and Gonzalez, P. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, 259, 660-684.
- Allesina, S., & Pascual, M. 2009. Googling food webs: can an eigenvector measure species' importance for coextinctions. *PLoS Computational Biology*, 5, e1000494.
- Anderson, W. B., and Polis, G. A. 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. *Oecologia*, 118, 324-332.
- Anderson, W. B., Wait, D. A., and Stapp, P. 2008. Resources from another place and time: responses to pulses in a spatially subsidized system. *Ecology*, 89, 660-670.
- Araujo, A. I., de Almeida, A. M., Cardoso, M. Z., and Corso, G. 2010. Abundance and nestedness in interaction networks. *Ecological Complexity*, 7, 494-499.

- Araújo, M. S., Bolnick, D. I., Martinelli, L. A., Giaretta, A. A., and Dos Reis, S. F. 2009. Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology*, 78, 848-856.
- Araújo, M. S., Martins, E. G., Cruz, L. D., Fernandes, F. R., Linhares, A. X., Dos Reis, S. F., and Guimarães, P. R. 2010. Nested diets: a novel pattern of individual-level resource use. *Oikos*, 119, 81-88.
- Atkinson, I. A. E. 2004. Successional processes induced by fires on the northern offshore islands of New Zealand. *New Zealand Journal of Ecology*, 28, 181-193.
- Atkinson, I. A. E. 1964. The flora, vegetation, and soils of Middle and Green Islands, Mercury Islands Group. *New Zealand Journal of Botany*, 2, 385-402.
- Atkinson, I. A. E. 1988. Presidential address: opportunities for ecological restoration. *New Zealand journal of ecology*, 1-12.
- Austin, A. T., and Vitousek, P. M. 1998. Nutrient dynamics on a precipitation gradient in Hawai'i. *Oecologia*, 113, 519-529.
- Austin, A. T., Yahdjian, L., Stark, J. M., Belnap, J., Porporato, A., Norton, U., ... and Schaeffer, S. M. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, 141, 221-235.
- Bååth, E., and Söderström, B. 1982. Seasonal and spatial variation in fungal biomass in a forest soil. *Soil Biology and Biochemistry*, 14, 353-358.
- Bakelaar, R. G., and Odum, E. P. 1978. Community and Population Level Responses to Fertilization in an Old-Field Ecosystem. *Ecology*, 59, 660-665.
- Bancroft, W. J. 2004. Environmental response to burrowing seabird colonies: a study in ecosystem engineering (Doctoral dissertation, University of Western Australia).

- Bancroft, W. J., Garkaklis, M. J., and Dale Roberts, J. 2005a. Burrow building in seabird colonies: a soil-forming process in island ecosystems. *Pedobiologia*, 49, 149-165.
- Bancroft, W. J., Hill, D., and Roberts, J. D. 2004. A new method for calculating volume of excavated burrows: the geomorphic impact of Wedge-Tailed Shearwater burrows on Rottne Island. *Functional Ecology*, 18, 752-759.
- Bancroft, W. J., Roberts, J. D., and Garkaklis, M. J. 2005b. Burrowing seabirds drive decreased diversity and structural complexity, and increased productivity in insular-vegetation communities. *Australian Journal of Botany*, 53, 231-241.
- Barrett, K., Anderson, W. B., Wait, D. A., Grismer, L. L., Polis, G. A., and Rose, M. D. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations. *Oikos*, 109, 145-153.
- Bascompte, J. and P. Jordano. 2006. The structure of plant–animal mutualistic networks. In: Pascual, M. and Dunne, J. (Eds.), *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, pp. 143–159.
- Bascompte, J. and P. Jordano. 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 38, 567-593.
- Bascompte, J., Jordano, P., and Olesen, J. M. 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science*, 312, 431-433.
- Bascompte, J., Melián, C. J., and Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences*, 102, 5443-5447.
- Basset, Y. 1991. The seasonality of arboreal arthropods foraging within an Australian rainforest tree. *Ecological Entomology*, 16, 265-278.

- Bastian M., Heymann S. and M. Jacomy 2009. Gephi: an open source software for exploring and manipulating networks. International AAAI Conference on Weblogs and Social Media.
- Bellingham, P. J., Towns, D. R., Cameron, E. K., Davis, J. J., Wardle, D. A., Wilmshurst, J. M., & Mulder, C. P. 2010. New Zealand island restoration: seabirds, predators, and the importance of history. *New Zealand Journal of Ecology*, 34, 115.
- Ben-David, M., Hanley, T. A., and Schell, D. M. 1998. Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos*, 1, 47-55.
- Bersier, L. F., Banašek-Richter, C., and Cattin, M. F. 2002. Quantitative descriptors of food-web matrices. *Ecology*, 83, 2394-2407.
- Bildstein, K. L., Blood, E., and Frederick, P. 1992. The relative importance of biotic and abiotic vectors in nutrient transport. *Estuaries*, 15, 147-157.
- Billingsley, P. 1965. *Ergodic theory and information*. ISBN 0124366406
- Bissett, J. and Parkinson, D. 1979. Functional relationships between soil fungi and environment in alpine tundra. *Canadian Journal of Botany*, 51, 1642–1659.
- Bolnick, D. I., Svanbäck, R., Araújo, M. S., and Persson, L. 2007. Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proceedings of the National Academy of Sciences*, 104, 10075-10079.
- Borken, W., and Matzner, E. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Global Change Biology*, 15, 808-824.

- Borrelle, S. B., Buxton, R. T., Jones, H. P., and Towns, D. R. 2015. A GIS-based decision-making approach for prioritizing seabird management following predator eradication. *Restoration Ecology*, 23, 580-587.
- Borrelli, J. J., and Ginzburg, L. R. 2014. Why there are so few trophic levels: selection against instability explains the pattern. *Food Webs*, 1, 10-17.
- Bosatta, E. 1982. Acidification and release of nutrients from organic matter – A model analysis. *Oecologia*, 55, 30-33.
- Bosman, A. L., and Hockey, P. A. R. 1988. The influence of seabird guano on the biological structure of rocky intertidal communities on islands off the west coast of southern Africa. *South African Journal of Marine Science*, 7, 61-68.
- Bosman, A. L., Du Toit, J. T., Hockey, P. A. R., and Branch, G. M. 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Estuarine, Coastal and Shelf Science*, 23, 283-294.
- Bouchard, S. S., and Bjorndal, K. A. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology*, 81, 2305-2313.
- Brooke, M. D. 2004. *Albatrosses and Petrels Across the World* (Bird Families of the World). Oxford University Press, Oxford.
- Buckley, R. C. 1987. Interactions involving plants, Homoptera, and ants. *Annual review of Ecology and Systematics*, 18, 111-135.
- Burke, I. C., Lauenroth, W. K., and Parton, W. J. 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. *Ecology*, 78, 1330-1340.

- Burke, I. C., Yonker, C. M., Parton, W. J., Cole, C. V., Schimel, D. S., and Flach, K. 1989. Texture, climate, and cultivation effects on soil organic matter content in US grassland soils. *Soil science society of America journal*, 53, 800-805.
- Buxton, R. T., Jones, C. J., Lyver, P. O. B., Towns, D. R., & Borrelle, S. B. 2016. Deciding when to lend a helping hand: a decision-making framework for seabird island restoration. *Biodiversity and Conservation*, 25, 467-484.
- Buxton, R. T., Jones, C., Moller, H., and Towns, D. R. 2014. Drivers of seabird population recovery on New Zealand islands after predator eradication. *Conservation biology*, 28, 333-344.
- Cameron, E. K. 1990. Flora and vegetation of Middle Island, Mercury Islands Group, eastern Coromandel, northern New Zealand. *Journal of the Royal Society of New Zealand*, 20, 273-285.
- Cameron, E. K. 1998. Botanical Society trips to the Noises (Hauraki Gulf) and an updated species list. *Auckland Botanical Society Journal*, 53, 25-35.
- Cardoso, P., Silva, I., De Oliveira, N. G., and Serrano, A. R. 2007. Seasonality of spiders (Araneae) in Mediterranean ecosystems and its implications in the optimum sampling period. *Ecological Entomology*, 32, 516-526.
- Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sánchez, G., and Peñuelas, J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences*, 108, 1474-1478.
- Caut, S., Angulo, E., Pisanu, B., Ruffino, L., Faulquier, L., Lorvelec, O., ... and Courchamp, F. 2012. Seabird modulations of isotopic nitrogen on islands. *Plos One*, 7, e39125.

- Chahartaghi, M., Langel, R., Scheu, S., and Ruess, L. 2005. Feeding guilds in Collembola based on nitrogen stable isotope ratios. *Soil Biology and Biochemistry*, 37, 1718-1725.
- Chao, A., Colwell, R. K., Lin, C. W., and Gotelli, N. J. 2009. Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, 90, 1125-1133.
- Clavero Pineda, M., and García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, 20, 110.
- Clout, M.N. and Russell, J.C. 2006. The eradication of introduced mammals from New Zealand Islands pp. 127-141 In: Iwatsuki, K.; Urano, K. (ed.) *Proceedings of the international conference on assessment and control of biological invasion risks*. Gland, IUCN.
- Clucas, R., Moller, H., Bragg, C., Lyver, P.O'B., and Fletcher, D. 2012. Hunting diaries for monitoring sustainability of muttonbirding in New Zealand. *New Zealand Journal of Zoology*, 39: 155–177
- Craig, J., Anderson, S., Clout, M., Creese, B., Mitchell, N., Ogden, J., Roberts, M., and Ussher, G. 2000. Conservation Issues in New Zealand. *Annual Review of Ecology and Systematics*. 31, 61-78.
- Croll, D. A., Maron, J. L., Estes, J. A., Danner, E. M., and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science*, 307, 1959-1961.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, 97, 153-166.

- Croxall, J. P., Butchart, S. H., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., and P. Taylor. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, 22, 1-34.
- Cui, M., and Caldwell, M. M. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil*, 191, 291-299.
- Cunningham, D.M., and Moors, P.J. 1985. The birds of the Noises Islands, Hauraki Gulf. *Notornis* 32: 221-243.
- Dale, V. H., Joyce, L. A., McNulty, S., Neilson, R. P., Ayres, M. P., Flannigan, M. D., ... and Simberloff, D. 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience*, 51, 723-734.
- Dattilo, W., Rico-Gray, V., Rodrigues, D. J., and T. J. Izzo. 2013. Soil and vegetation features determine the nested pattern of ant–plant networks in a tropical rainforest. *Ecological Entomology*, 38, 374-380.
- Demetrius, L., and T. Manke. 2005. Robustness and network evolution—an entropic principle. *Physica A: Statistical Mechanics and its Applications*, 346, 682-696.
- Digel, C., Curtsdotter, A., Riede, J., Klarner, B., and U. Brose. 2014. Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. *Oikos*, 123, 1157-1172.
- Drake, D. C., Smith, J. V., and Naiman, R. J. 2005. Salmon Decay-Nutrient Contributions to Riparian Forest Soils. *Northwest science*, 79, 61.

- Driscoll, C. T., Driscoll, K. M., Mitchell, M. J. and D. J. Raynal. 2003. Effects of acidic deposition on forest and aquatic ecosystems in New York State. *Environmental Pollution*. 123, 327-336.
- Dunne, J. A., Williams, R. J., and N. D. Martinez. 2002. Food web structure and network theory: the role of connectance and size. *PNAS*, 20, 12917-12922.
- Durrett, M. S., Wardle, D. A., Mulder, C. P., and Barry, R. P. 2014. Seabirds as agents of spatial heterogeneity on New Zealand's offshore islands. *Plant and Soil*, 383, 139-153.
- Ehrlich, P., and Walker, B. 1998. Rivets and redundancy. *BioScience*, 48, 387-388.
- Ellis, J. C. 2005. Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecology*, 181, 227-241.
- Ellis, J. C., Fariña, J. M., and Witman, J. D. 2006. Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. *Journal of Animal Ecology*, 75, 565-574.
- Ellis, J.C., Bellingham, P.J., Cameron, E.K., Croll, D.A., Kolb, G.S., Kueffer, C., Mittelhauser, G. H., Schmidt, S., Vidal, E., and Wait, D.A. 2011. Effects of seabirds on plant communities; Chapter six in *Seabird islands: ecology, invasion, and restoration*. Oxford University Press: New York. ISBN 978-0-19-973569-3.
- Erksine, P. D., Bergstrom, D. M., Schmidt, S., Stewart, G. R., Tweedie, C. E., and Shaw, J. D. 1998. Subantarctic Macquarie Island a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. *Oecologia*, 117, 187-193.

- Fariña, J. M., Salazar, S., Wallem, K. P., Witman, J. D., and Ellis, J. C. 2003. Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galapagos sea lion *Zalophus wollebaecki*. *Journal of Animal Ecology*, 72, 873-887.
- Fariña, J. M., Sepulveda, M., Reyna, M. V., Wallem, K. P., and Ossa-Zazzali, P. G. 2008. Geographical variation in the use of intertidal rocky shores by the lizard *Microlophus atacamensis* in relation to changes in terrestrial productivity along the Atacama Desert coast. *Journal of Animal Ecology*, 77, 458-468.
- Ferlian, O., Klarner, B., Langeneckert, A. E., and Scheu, S. 2015. Trophic niche differentiation and utilisation of food resources in collembolans based on complementary analyses of fatty acids and stable isotopes. *Soil Biology and Biochemistry*, 82, 28-35.
- Fierer, N., and Schimel, J. P. 2002. Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology and Biochemistry*, 34, 777-787.
- Forup, M. L., Henson, K. S., Craze, P. G., & Memmott, J. 2008. The restoration of ecological interactions: plant–pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology*, 45, 742-752.
- Fowler, M. S. 2010. Extinction cascades and the distribution of species interactions. *Oikos*, 119, 864-873.
- Frith, D., and Frith, C. 1990. Seasonality of litter invertebrate populations in an Australian upland tropical rain forest. *Biotropica*, 22, 181-190.
- Fukami, T., Wardle, D. A., Bellingham, P. J., Mulder, C. P., Towns, D. R., Yeates, G. W., ... & Williamson, W. M. 2006. Above-and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecology Letters*, 9, 1299-1307.

- Furness, R. W. 1991. The occurrence of burrow-nesting among birds and its influence on soil fertility and stability. In: Meadows P. S. and A Meadows (Eds.). The environmental impact of burrowing animals and animal burrows. Oxford University Press, Oxford, 53-65.
- Gardner-Gee, R., M.C. Stanley, and J.R. Beggs. 2015. Reforestation restores native dominance in an island beetle fauna. *Restoration Ecology* 23: 268–276.
- Gauzens, B., Legendre, S., Lazzaro, X. and G. Lacroix. 2015. Intermediate predation pressure leads to maximal complexity in food webs. *Oikos*, 125, 595-603. Doi: 10.1111/oik.02627.
- Gende, S. M., Edwards, R. T., Willson, M. F., and Wipfli, M. S. 2002. Pacific Salmon in Aquatic and Terrestrial Ecosystems. *BioScience*, 52, 917-928.
- Gillham, M. E. 1956. Ecology of the Pembrokeshire Islands: IV. Effects of treading and burrowing by birds and mammals. *The Journal of Ecology*, 44, 51-82.
- Gotelli, N.J. and A.M. Ellison. 2013. EcoSimR 1.00.
<http://www.uvm.edu/~ngotelli/EcoSim/EcoSim.html>
- Grant-Hoffman, M. N., Mulder, C. P., and Bellingham, P. J. 2010a. Effects of invasive rats and burrowing seabirds on seeds and seedlings on New Zealand islands. *Oecologia*, 162, 1005-1016.
- Grant-Hoffman, M. N., Mulder, C. P., and Bellingham, P. J. 2010b. Invasive rats alter woody seedling composition on seabird-dominated islands in New Zealand. *Oecologia*, 163, 449-460.
- Green, C. J. 2002. Restoration of tree weta (Orthoptera: Anostomatidae) to a modified island. In *Turning the tide: the eradication of invasive species. Proceedings of the*

international conference on eradication of island invasives. Occasional Paper of the ICUN Species Survival Commission (No. 27, p. 407).

Grime, J. P. 2002: Plant Strategies, Vegetation Processes and Ecosystem Processes. John Wiley & Sons. New York, NY, USA. ISBN: 978-0-470-85040-4.

Haddad, N. M., Haarstad, J., and Tilman, D. 2000. The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, 124, 73-84.

Hagvar, S. and T. Amundsen. 1981. Effects of liming and artificial acid rain on the mite (Acari) fauna in coniferous forest. *Oikos*. 37, 7-20.

Hammill, E., Kratina, P., Vos, M., Petchey, O. L., and B. R. Anholt. 2015. Food web persistence is enhanced by non-trophic interactions. *Oecologia*, 178, 549-556.

Hannan, L. B., Roth, J. D., Ehrhart, L. M., and Weishampel, J. F. 2007. Dune vegetation fertilization by nesting sea turtles. *Ecology*, 88, 1053-1058.

Harding, J. S., Hawke, D. J., Holdaway, R. N., and Winterbourn, M. J. 2004. Incorporation of marine-derived nutrients from petrel breeding colonies into stream food webs. *Freshwater Biology*, 49, 576-586.

Hawke, D. J., and J. Newman. 2004. Inventories and elemental accumulation in peat soils of forested seabird breeding islands, southern New Zealand. *Soil Research*, 42, 45-48.

Hawke, D. J., Holdaway, R. N., Causer, J. E., and S. Ogden. 1999. Soil indicators of pre-European seabird breeding in New Zealand at sites identified by predator deposits. *Australian Journal of Soil Research*. 37, 103-113.

Hilderbrand, G. V., Hanley, T. A., Robbins, C. T., and Schwartz, C. C. 1999. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia*, 121, 546-550.

- Hishi, T., Hyodo, F., Saitoh, S., and Takeda, H. 2007. The feeding habits of collembola along decomposition gradients using stable carbon and nitrogen isotope analyses. *Soil Biology and Biochemistry*, 39, 1820-1823.
- Holbrook, N. M., and Zwieniecki, M. A. (Eds.). 2011. *Vascular transport in plants*. Elsevier Academic Press.
- Holdaway, R. N., Worthy, T. H. and Tennyson, A. J. D. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology*. 28, 119-187.
- Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., ... and Schmid, B. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, 75, 3-35.
- Howald, G., Donlan, C., Galván, J. P., Russell, J. C., Parkes, J., Samaniego, A., ... and Saunders, A. 2007. Invasive rodent eradication on islands. *Conservation biology*, 21, 1258-1268.
- Huber, J.T. 1986. Systematics, biology, and hosts of the Mymaridae and Mymarommatidae (Insecta: Hymenoptera): 1758-1984. *Entomography* 4:185-243.
- Huhta, V., Hyvönen, R., Koskenniemi, A., Vilkamaa, P., Kaasalainen, P., and Sulander, M. 1986. Response of soil fauna to fertilization and manipulation of pH in coniferous forests. *Acta Forestalia Fennica* 195, 1-30.
- Hurd, L. E., and Wolf, L. L. 1974. Stability in Relation to Nutrient Enrichment in Arthropod Consumers of Old-Field Successional Ecosystems. *Ecological Monographs*, 44, 465-482.

- Hurd, L. E., Mellinger, M. V., Wolf, L. L., and McNaughton, S. J. 1971. Stability and diversity at three trophic levels in terrestrial successional ecosystems. *Science*, 173, 1134-1136.
- Iason, G. R., Duck, C. D., and Clutton-Brock, T. H. 1986. Grazing and reproductive success of red deer: the effect of local enrichment by gull colonies. *The Journal of Animal Ecology*, 55, 507-515.
- Ineson, P., Leonard, M. A., and Anderson, J. M. 1982. Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. *Soil Biology and Biochemistry*, 14, 601-605.
- Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F. ... and W. Woodward. 2009. Ecological networks – beyond food webs. *Journal of Animal Ecology*, 78, 253-269.
- Izaguirre, I., Vinocur, A., Mataloni, G., and Pose, M. 1998. Phytoplankton communities in relation to trophic status in lakes from Hope Bay (Antarctic Peninsula). *Hydrobiologia*, 369, 73-87.
- Jackson, D.J. 1961. Observations on the biology of *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a parasitoid of the eggs of *Dytiscidae* (Coleoptera). 2. Immature stages and seasonal history with a review of mymarid larvae. *Parasitology* 51:269-294.
- Jones, C. G., Lawton, J. H., and Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos*, 69, 373-386.

- Jones, C.J., Lyver, P.O'B., Macleod, C.J., Whitehead, A.L. and Forrester, G.J. 2015. Variation in grey-faced petrel (*Pterodroma macroptera gouldi*) productivity with local burrow density and breeding island. *Emu - Austral Ornithology*, 115, 20-28.
- Jones, H. P. 2010a. Prognosis for ecosystem recovery following rodent eradication and seabird restoration in an island archipelago. *Ecological Applications*, 20, 1204-1216.
- Jones, H. P. 2010b. Seabird islands take mere decades to recover following rat eradication. *Ecological Applications*, 20, 2075-2080.
- Jones, H. P., Holmes, N. D., Butchart, S. H., Tershy, B. R., Kappes, P. J., Corkery, I., ... and D. A. Croll. 2016. Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences*, 113, 4033-4038. Doi: 10.1073/pnas.1521179113.
- Jones, H. P., Tershy, B. R., Zavaleta, E. S., Croll, D. A., Keitt, B. S., Finkelstein, M. E., and Howald, G. R. 2008. Severity of the effects of invasive rats on seabirds: a global review. *Conservation Biology*, 22, 16-26.
- Jones, H. P., Towns, D. R., Bodey, T., Miskelly, C. M., Ellis, J. C., Rauzon, M. J., ... and M. McKown. 2011. Recovery and restoration on seabird islands. Chapter eleven in Mulder, C. H., Anderson, W. B., Towns, D. R. and P. J. Bellingham (Eds.). *Seabird islands: ecology, invasion, and restoration*. Oxford University Press: New York. ISBN 978-0-19-973569-3.
- Kai, K. H., and Corlett, R. T. 2002. Seasonality of forest invertebrates in Hong Kong, South China. *Journal of tropical Ecology*, 18, 637-644.

- Kappes, P. J., and H. P. Jones. 2014. Integrating seabird restoration and mammal eradication programs on islands to maximize conservation gains. *Biodiversity and conservation*, 23, 503-509.
- Kareiva, P. M., and Levin, S. A. 2003. *The importance of species: perspectives on expendability and triage*. Princeton University Press.
- Keatley, B. E., Douglas, M. S., Blais, J. M., Mallory, M. L., and Smol, J. P. 2009. Impacts of seabird-derived nutrients on water quality and diatom assemblages from Cape Vera, Devon Island, Canadian High Arctic. *Hydrobiologia*, 621, 191-205.
- Keitt, B., K. Campbell, A. Saunders, M. Clout, Y.W. Wang, and B. Tershy. 2011. The global islands invasive vertebrate eradication database: a tool to improve and facilitate restoration of island ecosystems. Pages 74–77 in C.R. Veitch, M.N. Clout, and D.R. Towns, editors. *Island invasives: Eradication and Management*. IUCN, Gland, Switzerland.
- Kirchner, T. B. 1977. The effects of resource enrichment on the diversity of plants and arthropods in a shortgrass prairie. *Ecology*, 58, 1334-1344.
- Klein, T. M., Novick, N. J., Kreitinger, J. P., and M. Alexander. 1984. Simultaneous inhibition of carbon and nitrogen mineralisation in a forest soil by stimulated acid precipitation. *Bulletin for Environmental Contamination Toxicology*. 32, 698-703.
- Klimaszewski, J. 1950. *Coleoptera: family-group review and keys to identification*. J. Klimaszewski and J.C. Watt with illustrations by D.W. Helmore. Lincoln, Canterbury, N.Z. Manaaki Whenua Press, 1997. *Fauna of New Zealand*, ISSN 0111-5383; no. 37. ISBN 0-478-09312-8.

- Kolb, G. S., Jerling, L., and Hambäck, P. A. 2010. The impact of cormorants on plant–arthropod food webs on their nesting islands. *Ecosystems*, 13, 353-366.
- Kolb, G.S., Young, H.S. and W. B. Anderson. 2011. Effects of seabirds on island consumers. Chapter seven in Mulder, C. H., Anderson, W. B., Towns, D. R. and P. J. Bellingham (Eds.). *Seabird islands: ecology, invasion, and restoration*. Oxford University Press: New York. ISBN 978-0-19-973569-3.
- Kondoh, M., and K. Ninomiya. 2009. Food-chain length and adaptive foraging. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3114-3121.
- Kones, J. K., Soetaert, K., van Oevelen, D. and J. Owino 2009. Are network indices robust indicators of food web functioning? a Monte Carlo approach. *Ecological Modelling*, 220, 370-382.
- Kratina, P., Vos, M. and B. R. Anholt. 2007. Species diversity modulates predation. *Ecology*, 88, 1917-1923.
- Levings, S. C., and Windsor, D. M. 1985. Litter arthropod populations in a tropical deciduous forest: relationships between years and arthropod groups. *The Journal of Animal Ecology*, 54, 61-69.
- Lindberg, N., Engtsson, J. B., and Persson, T. 2002. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of Applied Ecology*, 39, 924-936.
- Linsley, E. G. 1959. Ecology of Cerambycidae. *Annual review of entomology*, 4, 99-138.
- Liu, L., and Greaver, T. L. 2010. A global perspective on belowground carbon dynamics under nitrogen enrichment. *Ecology Letters*, 13, 819-828.

- Long, W. C., Gamelin, E. F., Johnson, E. G., and A. H. Hines. 2012. Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. *Marine Ecology Progress Series*, 456, 139-148.
- Lövei, G. L., and Sunderland, K. D. 1996. Ecology and behaviour of ground beetles (Coleoptera: Carabidae). *Annual review of entomology*, 41, 231-256.
- Lyver, P.O'B., Wilmshurst, J.M., Wood, J.R., Jones, C.J., Fromont, M. Bellingham, P.J., Towns, D.R., Stone, C., Sheehan, M. and Moller, H. 2016. Looking Back for the Future: Local Knowledge and Paleoecology Inform Biocultural Restoration of New Zealand Coastal Ecosystems. *Human Ecology*, 43: 681–695.
- Mackay, S.W.B., Russell, J.C. and Anderson, S.H. 2007. Birds of Motuhoropapa I, Noises Group, Hauraki Gulf, North Is, New Zealand. *Notornis* 54: 197-200.
- Marcogliese, D. J., and D. K. Cone. 1997. Food webs: a plea for parasites. *Trends in Ecology and Evolution*, 12, 320-325.
- Marczak, L. B., Thompson, R. M., and Richardson, J. S. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology*, 88, 140-148.
- Marion, L., Clergeau, P., Brient, L., and Bertru, G. 1994. The importance of avian-contributed nitrogen (N) and phosphorus (P) to Lake Grand-Lieu, France. *Hydrobiologia*, 279, 133-147.
- Markwell, T. J., and C. H. Daugherty. 2002. Invertebrate and lizard abundance is greater on seabird-inhabited islands than on seabird-free islands in the Marlborough Sounds, New Zealand. *Ecoscience*, 9, 293-299.

- Markwell, T. J., and Daugherty, C. H. 2003. Variability in $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and Kjeldahl nitrogen of soils from islands with and without seabirds in the Marlborough Sounds, New Zealand. *New Zealand Journal of Ecology*, 27, 25-30.
- McCann, K. S. 2000. The diversity–stability debate. *Nature*, 405, 228-233.
- McKechie, S. 2006. Biopedturbation by an island ecosystem engineer: burrowing volumes and litter deposition by sooty shearwaters (*Puffinus griseus*). *New Zealand Journal of Zoology*, 33, 259-265.
- McLellan, I. D. 1988. A revision of New Zealand Thaumaleidae (Diptera: Nematocera) with descriptions of new species and a new genus. *New Zealand journal of zoology*, 15, 563-575.
- Mellbrand, K. 2009. The spider and the sea: effects of marine subsidies on the role of spiders in terrestrial food webs (Doctoral dissertation, Linköping).
- Miller, A. E., Schimel, J. P., Meixner, T., Sickman, J. O., and Melack, J. M. 2005. Episodic rewetting enhances carbon and nitrogen release from chaparral soils. *Soil Biology and Biochemistry*, 37, 2195-2204.
- Miller, S., Bencini, R., Mills, H., and Moro, D. 2004. Food availability for the dibbler (*Parantechinus apicalis*) on Boullanger and Whitlock Islands, Western Australia. *Wildlife Research*, 30, 649-654.
- Moran, N. A. 1986. Morphological adaptation to host plants in *Uroleucon* (Homoptera: Aphididae). *Evolution*, 40, 1044-1050.
- Morbey, Y. E. 1996. The abundance and effects of ticks (*Ixodes uriae*) on nestling Cassin's Auklets (*Ptychoramphus aleuticus*) at Triangle Island, British Columbia. *Canadian journal of zoology*, 74, 1585-1589.

- Mulder, C. and Elser, J. J. 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology*, 15, 2730-2738.
- Mulder, C. H., Anderson, W. B., Towns, D. R. and P. J. Bellingham. (Eds.) (2011b). *Seabird islands: ecology, invasion, and restoration*. Oxford University Press: New York. ISBN 978-0-19-973569-3.
- Mulder, C. P., and Keall, S. N. 2001. Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. *Oecologia*, 127, 350-360.
- Mulder, C. P., Grant-Hoffman, M. N., Towns, D. R., Bellingham, P. J., Wardle, D. A., Durrett, M. S., ... and K. I. Bonner. 2009. Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of New Zealand seabird islands? *Biological Invasions*, 11, 1671-1688.
- Mulder, C.P.H., Jones H.P., Kameda, K., Palmborg, C., Schmidt,... and Vidal, E. (2011a) The impacts of seabirds on plant and soil properties; Chapter five in *Seabird Islands: ecology, invasion, and restoration*. Oxford University Press: New York. ISBN 978-0-19-973569-3.
- Myrcha, A., and A. Tatur. 1991. Ecological role of the current and abandoned penguin rookeries in the land environment of the maritime Antarctic. *Polish Polar Research*, 12, 3-24.
- Naeem, S. 1998. Species redundancy and ecosystem reliability. *Conservation biology*, 12, 39-45.
- Nakano, S., Miyasaka, H., and Kuhara, N. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology*, 80, 2435-2441.

- Nordin, A., Näsholm, T., and L. Ericson. 1998. Effects of simulated N deposition on understorey vegetation of a boreal coniferous forest. *Functional Ecology*, 12, 691-699.
- Noyes, J. S. and Valentine, E. W. 1989. Mymaridae (Insecta: Hymenoptera) – introduction, and review of genera. *Fauna of New Zealand*, 17.
- Oksanen, J., Blanchet, G. F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., and Wagner, H. 2015. *Vegan: Community Ecology package*. R package version 2.2-1. <http://CRAN.R-project.org/package=vegan>
- Orwin, K., Wardle, D., Towns, D., St John, M., Bellingham, P., Jones, C., Fitzgerald, B., Parrish, R., and P. Lyver. 2016. Burrowing seabird effects on invertebrate communities in soil and litter are dominated by ecosystem engineering rather than nutrient addition. *Oecologia*, 180, 217-230. Doi: 10.1007/s00442-015-3437-9.
- Petersen, H. 2002. General aspects of collembolan ecology at the turn of the millennium: Proceedings of the Xth international Colloquium on Apterygota, České Budějovice 2000: Apterygota at the Beginning of the Third Millennium. *Pedobiologia*, 46, 246-260.
- Pinheiro, F., Diniz, I. R., Coelho, D., and Bandeira, M. P. S. 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. *Austral Ecology*, 27, 132-136.
- Polis, G. A., and Hurd, S. D. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences*, 92, 4382-4386.

- Polis, G. A., and Hurd, S. D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American naturalist*, 147, 396-423.
- Polis, G. A., Anderson, W. B., and Holt, R. D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual review of ecology and systematics*, 28, 289-316.
- Post, D. M. 2002. The long and short of food-chain length. *Trends in Ecology & Evolution*, 17, 269-277.
- Pulleman, M., and Tietema, A. 1999. Microbial C and N transformations during drying and rewetting of coniferous forest floor material. *Soil Biology and Biochemistry*, 31, 275-285.
- Rainio, J., and Niemelä, J. 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity & Conservation*, 12, 487-506.
- Rauzon, M. J. 2007. Island restoration: exploring the past, anticipating the future. *Marine Ornithology*, 35, 97-107.
- Rezende, E. L., Jordano, P., and J. Bascompte. 2007. Effects of phenotypic complementarity and phylogeny on the nested structure of mutualistic networks. *Oikos*, 116, 1919-1929.
- Ripley, E., and Rowland, B. 1995. *Plants of the Perth coast and islands*. Nedlands, WA: University of Western Australia Press xii, 292p.-illus., col. illus.. ISBN, 1875560467.
- Ruiz-Jaen, M. C., & Mitchell Aide, T. 2005. Restoration success: how is it being measured? *Restoration Ecology*, 13, 569-577.

- Russell, J.C., Towns, D.R., Clout, M.N. and Anderson, S.H. 2005. Intercepting the first rat ashore. *Nature* 437: 1107-1107.
- Saint-Béat, B., Baird, D., Asmus, H., Asmus, R., Bacher, C., Pacella, S. R., ... and N. Niquil. 2015. Trophic networks: How do theories link ecosystem structure and functioning to stability properties? A review. *Ecological Indicators*, 52, 458-471.
- Sánchez-Piñero, F., and G. A. Polis. 2000. Bottom-up dynamics of allochthonous input: direct and indirect effects of seabirds on islands. *Ecology*, 81, 3117-3132.
- Sanders, D., Kehoe, R., and van Veen, F. F. 2015. Experimental evidence for the population-dynamic mechanisms underlying extinction cascades of carnivores. *Current Biology*, 25, 3106-3109.
- Sanders, D., Sutter, L., and Veen, F. J. 2013. The loss of indirect interactions leads to cascading extinctions of carnivores. *Ecology letters*, 16, 664-669.
- Sedlacek, J. D., Barrett, G. W., and Shaw, D. R. 1988. Effects of nutrient enrichment on the Auchenorrhyncha (Homoptera) in contrasting grassland communities. *Journal of Applied Ecology*, 25, 537-550.
- Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, 76, 2057-2070.
- Silva, N. A. P. D., Frizzas, M. R., and Oliveira, C. M. D. 2011. Seasonality in insect abundance in the "Cerrado" of Goiás State, Brazil. *Revista Brasileira de Entomologia*, 55, 79-87.
- Simberloff, D. 1990. Reconstructing the ambiguous: Can island ecosystems be restored? Pages 37-51 in D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson, editors.

- Ecological restoration of New Zealand Islands. Department of Conservation, Wellington, New Zealand.
- Sperry, J. S. 2000. Hydraulic constraints on plant gas exchange. *Agricultural and forest meteorology*, 104, 13-23.
- Spiller, D. A., Piovia-Scott, J., Wright, A. N., Yang, L. H., Takimoto, G., Schoener, T. W., and Iwata, T. 2010. Marine subsidies have multiple effects on coastal food webs. *Ecology*, 91, 1424-1434.
- Sprules, W. G., and Bowerman, J. E. 1988. Omnivory and food chain length in zooplankton food webs. *Ecology*, 69, 418-426.
- Stapp, P., and Polis, G. A. 2003a. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia*, 134, 496-504.
- Stapp, P., and Polis, G. A. 2003b. Influence of pulsed resources and marine subsidies on insular rodent populations. *Oikos*, 102, 111-123.
- Suding, K. N.(2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics*, 42, 465.
- Svanbäck, R., Quevedo, M., Olsson, J., and P. Eklöv. 2015. Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. *Oecologia*, 178, 103-114. Doi: 10.1007/s00442-014-3203-4.
- Sweet, M. H. 1960. The seed bugs: a contribution to the feeding habits of the Lygaeidae (Hemiptera: Heteroptera). *Annals of the Entomological Society of America*, 53, 317-321.

- Swift, M. J., Heal, O. W., and J. M. Anderson. 1979. Decomposition in terrestrial ecosystems. Blackwell, Oxford.
- Szabo, J. K., Khwaja, N., Garnett, S. T., and Butchart, S. H. 2012. Global patterns and drivers of avian extinctions at the species and subspecies level. *PloS one*, 7, e47080.
- Tershy, B. R., Shen, K. W., Newton, K. M., Holmes, N. D., and Croll, D. A. 2015. The importance of islands for the protection of biological and linguistic diversity. *BioScience*, 65, 592-597.
- Theodose, T. A., and Bowman, W. D. 1997. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology*, 78, 1861-1872.
- Thompson, R. M., Brose, U., Dunne, J. A., Hall Jr, R. O., Hladyz, S., Kitching, R. L., ... and Tylianakis, J. M. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in ecology & evolution*, 27, 689-697.
- Thompson, R. M., Hemberg, M., Starzomski, B. M., and Shurin, J. B. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, 88, 612-617.
- Thoresen, J. J., Towns, D., Leuzinger, S., Durrett, M., Mulder, C. P. H. and Wardle, D. A. 2017. Invasive rodents have multiple indirect effects on seabird island invertebrate food web structure. *Ecological Applications*. doi:10.1002/eap.1513
- Tilman, D. 1996. Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350-363.
- Towns, D. R., Atkinson, I. A., and Daugherty, C. H. 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological invasions*, 8, 863-891.

- Towns, D. R., Borrelle, S. B., Thoresen, J., Buxton, R. T., & Evans, A. 2016. Mercury Islands and their role in understanding seabird island restoration. *New Zealand Journal of Ecology*, 40, 235.
- Towns, D. R., Simberloff, D., and Atkinson, I. A. 1997. Restoration of New Zealand islands: redressing the effects of introduced species. *Pacific Conservation Biology*, 3, 99-124.
- Towns, D. R., Wardle, D. A., Mulder, C. P., Yeates, G. W., Fitzgerald, B. M., Richard Parrish, G., ... and K. I. Bonner. 2009. Predation of seabirds by invasive rats: multiple indirect consequences for invertebrate communities. *Oikos*, 118, 420-430.
- Towns, D. R., West, C. J., and Broome, K. G. 2013. Purposes, outcomes and challenges of eradicating invasive mammals from New Zealand islands: an historical perspective. *Wildlife Research*, 40, 94-107.
- Towns, D.R., and I.A.E. Atkinson. 2004. Restoration plan for Korapuki Island (Mercury Islands), New Zealand. Wellington, Department of Conservation.
- Towns, D.R., Atkinson, I.A.E, and Daugherty C.H. 1990. The potential for ecological restoration in the Mercury Islands. Pages 91-108 in D.R. Towns, C.H. Daugherty, and I.A.E. Atkinson, editors. *Ecological restoration of New Zealand Islands*. Department of Conservation, Wellington, New Zealand.
- Tylianakis, J. M., Laliberté, E., Nielsen, A., and J. Bascompte. 2010. Conservation of species interaction networks. *Biological conservation*, 143, 2270-2279.
- Urabe, J., and N. Waki. 2009. Mitigation of adverse effects of rising CO₂ on a planktonic herbivore by mixed algal diets. *Global Change Biology*. 15, 523-531.

- Van Straalen, N. M., Kraak, M. H., and C. A. Denneman. 1988. Soil microarthropods as indicators of soil acidification and forest decline in the Veluwe are, the Netherlands. *Pedobiologia*. 32, 47-55.
- Veitch, C. R., Miskelly, C. M., Harper, G. A., Taylor, G. A., & Tennyson, A. J. 2004. Birds of the Kermadec Islands, south-west Pacific. *Notornis*. 51, 61-90.
- Venables, W. N. & Ripley, B. D. 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer. New York. ISBN 0-387-95457-0
- Villegas-Amtmann, S., Costa, D. P., Tremblay, Y., Salazar, S., and Auriolles-Gamboa, D. 2008. Multiple foraging strategies in a marine apex predator, the Galapagos sea lion *Zalophus wollebaeki*. *Marine Ecology Progress Series*, 363, 299-309.
- Vitousek, P. M., Gosz, J. R., Grier, C. C., Melillo, J. M., and Reiners, W. A. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. *Ecological monographs*, 52, 155-177.
- Wainright, S. C., Haney, J. C., Kerr, C., Golovkin, A. N., and Flint, M. V. 1998. Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. *Marine Biology*, 131, 63-71.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation biology*, 6, 18-23.
- Wardle, D. A., Bellingham P.J., Fukami T., and Mulder C.P.H. 2007. Promotion of ecosystem carbon sequestration by invasive predators. *Biology Letters* 3: 479–482.
- Wardle, D. A., Bellingham, P. J., Bonner, K. I., and Mulder, C. P. 2009. Indirect effects of invasive predators on litter decomposition and nutrient resorption on seabird-dominated islands. *Ecology*, 90, 452-464.

- Widden, P. 1986 Functional relationships between Quebec forest soil microfungi and their environment. *Canadian Journal of Botany*, 64, 1424–1432.
- Williams R. J., Anandanadesan A., and Purves D. 2010. The Probabilistic Niche Model Reveals the Niche Structure and Role of Body Size in a Complex Food Web. *PLoS ONE*, 5: e1209 doi:10.1371/journal.pone.0012092
- Williams, R. J., and Martinez, N. D. 2000. Simple rules yield complex food webs. *Nature*, 404, 180-183.
- Williams, R. J., and Martinez, N. D. 2004. Limits to trophic levels and omnivory in complex food webs: theory and data. *The American Naturalist*, 163, 458-468.
- Williams, R. J., and Martinez, N. D. 2008. Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, 77, 512-519.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature*, 404, 180-183.
- Wilson, S. D., and Tilman, D. 1991. Component of plant competition along an experimental gradient of nitrogen availability. *Ecology*, 72, 1050-1065.
- Wolfe, K. M., Mills, H. R., Garkaklis, M. J., and Bencini, R. 2004. Post-mating survival in a small marsupial is associated with nutrient inputs from seabirds. *Ecology*, 85, 1740-1746.
- Wortley, L. J.-M. Hero, and M. Howes. 2013. Evaluating ecological restoration success: a review of the literature. *Restoration Ecology* 21: 537–543.
- Wright, A. C. S. 1961. Soils. - In: Hamilton, W. M. (comp.), *Little Barrier Island (Hauturu)*. N. Z. Dept Sci. Ind. Res. Bull. 137, pp. 57-76.

Wright, D. G., van der Wal, R., Wanless, S., and R. D. Bardgett. 2010. The influence of seabird nutrient enrichment and grazing on the structure and function of island soil food webs. *Soil Biology and Biochemistry*, 42, 592-600.

Zeng, Z. G., Bi, J. H., Li, S. R., Chen, S. Y., Pike, D. A., Gao, Y., and W. G. Du. 2014. Effects of habitat alteration on lizard community and food web structure in a desert steppe ecosystem. *Biological Conservation*, 179, 86-92.

Appendix A: The Niche Model

The niche model uses species number and connectance to develop networks based on simple parameters. Each ‘species’ is assigned a randomly drawn niche value from the interval of 0 – 1. The species are then constrained to consume all prey species within one range of values whose randomly chosen centre is less than the consumer’s niche value (Williams and Martinez, 2000). In this way a model can be created which accurately predicts many network metrics (Dunne et al. 2002; Williams and Martinez, 2008; Williams et al. 2010; Thompson et al. 2012). I used the total species and network connectance values for each of the eighteen food webs used in Chapter 2 (Table A1), 30 randomly chosen food webs from Chapter 3 (Table A2), and each of the 30 food webs in Chapter 4 (Table A3) to create the same number of niche models of the same size. The metrics used included average species, links, generalists, specialists, food chain length, nestedness, generality, vulnerability, omnivory index, and link density (Dunne et al. 2002; Post 2002; Kondoh and Ninomiya 2009; Ings et al. 2009; Araujo et al. 2010; Tylianakis et al. 2010; Aizen et al. 2012; Thompson et al. 2012; Zeng et al. 2014).

For the food webs in Chapter 2 I found that total links, link density, nestedness, generality, and vulnerability did not differ significantly (Table A1) between the empirical and modelled networks (using Student’s t-tests), suggesting that the empirical models are accurate representations of ecological networks. When FCL and the number of generalists and specialists were compared, the niche modelled webs demonstrated significantly longer food chains ($P < 0.001$) with more generalists ($P = 0.003$) and specialists ($P < 0.001$).

Table A1 Comparison of the empirical food webs to those constructed using the niche model for Chapter 2. Results show the mean \pm SE, the t-value and significance of the t-test. No t-tests were carried out for species diversity as these values were used to construct the niche model in order to constrain their size. Where $n = 30$ for both model types. P-value symbols: ns = non-significance, * < 0.05, ** < 0.001, *** < 0.0001.

	Empirical (\pm SEM)	Niche Model (\pm SEM)	T	P
Connectance	0.13 (\pm 0.00)	0.13 (\pm 0.00)	0.00	1.00
Total Species	39.5 (\pm 2.30)	39.5 (\pm 2.30)	0.00	1.00
Food chain length	3.83 (\pm 0.03)	7.87 (\pm 0.73)	5.48	0.00
Total Links	209.2 (\pm 22.70)	205.1 (\pm 25.30)	0.12	0.90
Link Density	5.05 (\pm 0.28)	4.9 (\pm 0.37)	0.30	0.75
Nestedness	7.21 (\pm 0.64)	7.47 (\pm 0.68)	0.28	0.77
Generality	5.05 (\pm 0.29)	5.27 (\pm 0.39)	0.45	0.65
Vulnerability	4.89 (\pm 0.29)	5.19 (\pm 0.39)	0.53	0.59
Generalists	5.66 (\pm 0.39)	10.83 (\pm 1.42)	3.28	0.00
Specialists	5.72 (\pm 0.47)	9.16 (\pm 0.80)	3.70	0.00

When the food webs in Chapters 3 and 4 were compared, I found that total links, connectance, generality, vulnerability, degree, and generalist diversity did not differ significantly from the niche models. But FCL, the omnivory index, specialist diversity and nestedness did.

Table A2 Comparison of the empirical food webs to those constructed using the niche model for Chapter 3. Results show the mean \pm SE, the t-value and significance of the t-test. No t-tests were carried out for species diversity as these values were used to construct the niche model in order to constrain their size. Where $n = 30$ for both model types. P-value symbols: ns = non-significance, * < 0.05, ** < 0.001, *** < 0.0001.

	Empirical	Niche model	t
Connectance	0.10 (\pm 0.01)	0.11 (\pm 0.01)	-0.95 ns
Links	84.66 (\pm 8.91)	90.80 (\pm 10.80)	-0.43 ns
Food chain length	4.00 (\pm 0.05)	5.55 (\pm 0.27)	-4.07**
Nestedness	3.25 (\pm 0.12)	4.13 (\pm 0.34)	-2.38*
Generality	2.77 (\pm 0.13)	2.95 (\pm 0.18)	-0.80 ns
Vulnerability	2.63 (\pm 0.12)	2.95 (\pm 0.18)	-1.48 ns
Degree	5.41 (\pm 0.25)	5.91 (\pm 0.26)	-1.14 ns
Generalists	3.86 (\pm 0.73)	4.83 (\pm 0.40)	-1.14 ns
Specialists	6.73 (\pm 0.49)	3.43 (\pm 0.59)	4.27***
Omnivory index	0.33 (\pm 0.01)	1.09 (\pm 0.19)	-3.93**

The consistent differences found between the models for FCL are likely due to an inaccuracy of the niche model at predicting this metric (Williams and Martinez, 2008). Food chains in nature are rarely longer than five trophic levels (Borrelli and Ginzburg 2014). The maximum trophic level within the empirical networks was

4.08, reflecting this natural shortness; however, using the Niche Model the maximum trophic level was 15.44, which is far too high than is likely in nature.

Table A3 Comparison of the empirical food webs to those constructed using the niche model for Chapter 4. Results show the mean \pm SE, the t-value and significance of the t-test. No t-tests were carried out for species diversity as these values were used to construct the niche model in order to constrain their size. Where $n = 30$ for both model types. P-value symbols: ns = non-significance, * < 0.05 , ** < 0.001 , *** < 0.0001 .

	Empirical (\pm SEM)	Niche model (\pm SEM)	t
Links	183.86 (\pm 8.17)	177.06 (\pm 9.42)	0.54 <i>ns</i>
Connectance	0.11 (\pm 0.01)	0.11 (\pm 0.01)	1.21 <i>ns</i>
Food chain length	4.08 (\pm 0.05)	7.56 (\pm 0.65)	-5.29***
Omnivory index	0.31 (\pm 0.01)	2.54 (\pm 0.67)	-3.29**
Generality	4.59 (\pm 0.08)	4.36 (\pm 0.15)	1.26 <i>ns</i>
Vulnerability	4.42 (\pm 0.07)	4.36 (\pm 0.15)	0.32 <i>ns</i>
Degree	9.01 (\pm 0.15)	8.73 (\pm 0.31)	0.79 <i>ns</i>
Specialists (S)	3.36 (\pm 0.36)	5.83 (\pm 0.34)	-4.91***
Generalists (G)	9.06 (\pm 0.44)	8.26 (\pm 0.60)	1.07 <i>ns</i>
Nestedness	3.41 (\pm 0.14)	5.29 (\pm 0.49)	-3.61**

For the differences observed between the omnivory index, specialist diversity and nestedness, these may reflect inaccuracies in my food web description methods or inaccuracies in the niche model. Omnivory in natural food webs may be quite limited (Williams and Martinez 2004), although Thompson et al. (2007) argues that it is not. Omnivory, however, is variable between ecosystems (Sprules and Bowerman 1988; Thompson et al. 2007) and so the niche model itself may be unrealistic in that its constraints mean it is unable to reflect this natural variation. This does not eliminate the fact that omnivory in these food webs was low; this may be reflective of natural variation or the effect of identifying invertebrates to family and not species level. The fact that specialist diversity was higher in the niche models may be due to the ‘lumping’ that was carried out in my empirical networks. As the invertebrates were only identified to family level this could necessitate lower specialism as there may be differing degrees of specialism for species within a family.

While the niche model may be inaccurate in some areas, it has been used in the past to draw conclusions on how the structure and function of real-world food webs may change in relation to external stimuli. The results show that the empirical food webs are accurate to an extent when compared to the niche model, which as a model, is not fully accurate itself. The methods I used in describing the food webs may have caused some metrics to be inaccurate but they still change in predictable ways; as such, I was confident in using them to predict changes in the food webs.

References

- Aizen, M. A., Sabatino, M., and Tylianakis, J. M. 2012. Specialization and rarity predict nonrandom loss of interactions from mutualist networks. *Science*, 335, 1486-1489.
- Araujo, A. I., de Almeida, A. M., Cardoso, M. Z., and Corso, G. 2010. Abundance and nestedness in interaction networks. *Ecological Complexity*, 7, 494-499.
- Borrelli, J. J., and Ginzburg, L. R. 2014. Why there are so few trophic levels: selection against instability explains the pattern. *Food Webs*, 1, 10-17.
- Borrelli, J. J., and Ginzburg, L. R. 2014. Why there are so few trophic levels: selection against instability explains the pattern. *Food Webs*, 1, 10-17.
- Dunne, J. A., Williams, R. J., and Martinez, N. D. 2002. Food web structure and network theory: the role of connectance and size. *PNAS*, 20, 12917-12922.
- Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., ... and Woodward, W. 2009. Ecological networks – beyond food webs. *Journal of Animal Ecology*, 78, 253-269.

- Kondoh, M., and Ninomiya, K. 2009. Food-chain length and adaptive foraging. *Proceedings of the Royal Society B: Biological Sciences*, 276, 3114-3121.
- Post, D. M. 2002. The long and short of food-chain length. *Trends in Ecology & Evolution*, 17, 269-277.
- Sprules, W. G., and Bowerman, J. E. 1988. Omnivory and food chain length in zooplankton food webs. *Ecology*, 69, 418-426.
- Thompson, R. M., Brose, U., Dunne, J. A., Hall Jr, R. O., Hladyz, S., Kitching, R. L., ... and Tylianakis, J. M. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in ecology & evolution*, 27, 689-697.
- Thompson, R. M., Hemberg, M., Starzomski, B. M., and Shurin, J. B. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. *Ecology*, 88, 612-617.
- Tylianakis, J. M., Laliberté, E., Nielsen, A., and Bascompte, J. 2010. Conservation of species interaction networks. *Biological conservation*, 143, 2270-2279.
- Williams R. J., Anandanadesan A., and Purves D. 2010. The Probabilistic Niche Model Reveals the Niche Structure and Role of Body Size in a Complex Food Web. *PLoS ONE*, 5: e1209 doi:10.1371/journal.pone.0012092
- Williams, R. J., and Martinez, N. D. 2000. Simple rules yield complex food webs. *Nature*, 404, 180-183.
- Williams, R. J., and Martinez, N. D. 2004. Limits to trophic levels and omnivory in complex food webs: theory and data. *The American Naturalist*, 163, 458-468.
- Williams, R. J., and Martinez, N. D. 2008. Success and its limits among structural models of complex food webs. *Journal of Animal Ecology*, 77, 512-519.

Zeng, Z. G., Bi, J. H., Li, S. R., Chen, S. Y., Pike, D. A., Gao, Y., and Du, W. G.

2014. Effects of habitat alteration on lizard community and food web

structure in a desert steppe ecosystem. *Biological Conservation*, 179, 86-92.

Appendix B: Invertebrate identification

Table B1 Feeding strategies of all identified family groups.

Class	Order	Family	Functional group	Feeding links
Arachnidae	Pseudoscorpionida	Pseudoscorpionidae	Predator	Mites, nematodes, collembolans, pscoptera
		Acardidae	Saprophagous	Micro-fungi, algae decomposing matter
	Astigmata	Cryptostigmata	Fungivorous	Micro-fungi, algae, detritus
		Mesostigmata	Predator	Mites, nematodes, collembolans, pscoptera
	Prostigmata	Raphignathoidea	Predator	Mites, nematodes
	Araneae	Salticidae	Predator	Diptera, formicidae, aranea (web spiders), nectar, orthopterans, coleoptera
		Anapidae	Predator	Collembolans, pscoptera, hemipterans
		Clubionidae	Predator	Formicidae, aranae (inc. cannib.), diptera, blattodea, coleoptera
		Theridiidae	Predator	Aranae (inc. cannib.), diptera, lepidoptera, coleoptera, blattodae
		Thomisidae	Predator	Lepidoptera, diptera, coleoptera, formicidae
		Linyphiidae	Predator	Homoptera (coccoids, aphids), Aranae, collembola, diptera
		Palpatores	Predator	Collembolans, pscoptera, hemipterans, diptera
		Laniatores	Predator	Collembolans, pscoptera, hemipterans, diptera
Entognatha	Collembola	Hypogastruridae	Saprophagous	Micro-fungi, algae detritus, micro-organisms, carrion
		Isotomidae	Saprophagous	Algae, micro-fungi, detritus, micro-organisms, carrion
		Naenuridae	Saprophagous	Algae, micro-fungi, detritus, micro-organisms, carrion
Diplopoda	Diplura	Heterojapygidae	Predator	Collembola, isopoda, fungi, mites, detritus, small myriapods, cannib.
	Julida	Blaniulidae	Detritus	Detritus, micro-fungi, roots
	Siphonophorida	Siphonophoridae	Detritivorous	Detritus, micro-fungi, algae
	Chordeumatida	Metopidiotrichidae	Detritivorous	Detritus, algae, woody material
	Polyxenida	Polyxenidae	Detritivorous	Detritus, algae, macro-fungi
	Polydesmida	Dalodesmidae	Detritivorous	Detritus, algae, woody material, macro-fungi
		Paradoxosomatidae	Detritivorous	Detritus, roots, stems, woody material
Paupopoda	Tetamerocerata	Eurypaurpodidae	Detritivorous	Detritus, micro-fungi, algae
Chilopoda	Lithobiomorpha	Lithobiidae	Predator	Beetles, pscoptera, centipedes, hemipterans, pseudoscorpions
	Geophilomorpha	Chilenophilidae	Predator	Mites, pscoptera, collembolans, pseudoscorpions
	Scolopendromorpha	Scolopendridae	Predator	Centipedes, beetles, hemipterans, blattodea, porcellionidae
Nematoda			Detritivore	Algae, micro fungi, detritus, bacteria, vegetation fluids, nematodes
Malacostraca	Isopoda	Porcellionidae	Detritivorous	Detritus, woody material, macro-fungi, leaves
	Amphipoda	Talitridae	Detritivorous	Detritus, macro-fungi, algae
Insecta	Blattodea		Detritivorous	Detritus, algae, leaves, woody material, macro-fungi

Orthoptera	Anostomatidae	Generalist	Diptera, fruit, seeds, fungi, detritus, pscoptera
Archaeognatha	Machilidae	Herbivore	Leaves, detritus, macro-fungi
Psocoptera		Herbivore	Leaves, detritus, micro-fungi, algae
Thysanoptera	Terebrantia	Generalist	Veg fluids, fungi,
	Thripidae	Generalist	Veg fluids, collembolans, fungi
	Tubulifera	Fungivorous	Macro-fungi
Lepidoptera	Oecophoridae adult	Herbivore	Leaves, detritus
	Lepidoptera Larvae	Herbivore	Leaves, detritus
Diptera	Tipulidae	Nectivorous	Nectar, honeydew
	Tipulidae larvae	Detritus	Algae, bacteria, detritus, leaves
	Tabanidae larvae	Predator	Cannibal, oligochaete, coleoptera, collembola, detritus
	Stratiomyidae	Nectivorous	Nectar, honeydew
	Stratiomyidae larvae	Generalist	Algae, bacteria, detritus, collembolans, fungi, pscoptera
	Cecidomyiidae	Herbivore	Leaves, vegetation fluids
	Calliphoridae larvae	Detritivorous	Detritus, carrion
	Australimyza adult	Saprophagous	Algae, fungi, bacteria
Hemiptera	Enicocephalidae	Phytophagous	Vegetation fluids
	Reduviidae	Predator	Blattodea, coleoptera, homoptera, diplopoda
	Cixiidae	Phytophagous	Vegetation fluids
	Miridae	Phytophagous	Vegetation fluids
	Margarodidae	Phytophagous	Vegetation fluids
	Myerslopiidae	Phytophagous (generalist)	Roots, vegetation fluids, detritus
	Ryparochromidae	Phytophagous	Vegetation fluids
	Coccidae	Phytophagous	Vegetation fluids
	Lygaeidae	Phytophagous	Vegetation fluids
	Pentatomidae	Phytophagous	Vegetation fluids
	Delphacidae	Phytophagous	Vegetation fluids
Hymenoptera	Alysiinae	Parasitoid	Diptera
	Aphelinidae	Parasitoid	Hemiptera (Aleyrodidae specialist)
	Diapriidae	Parasitoid	Diptera
	Figitidae	Parasitoid	Diptera, hymenoptera, neuroptera
	Formicidae	Predator	Generalist predator/scavenger
	Platygastridae	Parasitoid	Diptera, lepidoptera, hemiptera
	Pteromalidae	Parasitoid	Lepidoptera and coleoptera

Coleoptera	Mymaridae	Parasitoid	Lepidoptera and hemiptera
	Anthribidae	Fungivorous	Macro-fungi
	Carabidae	Predator	Lepidoptera, elateridae, diptera, hemiptera, formicidae, seeds, collembola
	Carabidae larvae	Predator	Diptera, coleoptera
	Cerambycidae	Herbivore	Leaves, vegetation fluids
	Cerambycidae larvae	Herbivore	Woody material
	Cerylonidae	Fungivorous	Micro-fungi, macro-fungi
	Coccinellidae larvae	Predator (adult)	Homoptera (coccoids, aphids)
	Curculionidae	Herbivore	Leaves, macro-fungi, wood, roots, seeds, fruits
	Curculionidae larvae	Herbivore/Detritivore	Wood, leaves
	Elateridae	Herbivore	Leaves, vegetation fluids
	Elateridae larvae	Saprophagous	Detritus, lepidoptera larvae, coleoptera larvae
	Holoparamecinae (Endomychidae)	Fungivorous	Micro-fungi, macro-fungi
	Holoparamecinae (Endomychidae) larvae	Fungivorous	Micro-fungi, macro-fungi
	Corylophidae	Fungivorous	Micro-fungi
	Corylophidae Larvae	Fungivorous	Micro-fungi
	Ciidae	Fungivorous	Macro-fungi
	Chrysomelidae	Herbivorous	Leaves
	Latridiidae	Fungivorous	Macro-fungi, algae, detritus
	Latridiidae larvae	Fungivorous	Macro-fungi, algae, detritus
	Mycetophaginae	Fungivorous	Macro-fungi
	Melandryidae	Fungivorous	Macro-fungi, detritus
	Salpingidae	Saprophagous	Mites, vegetation fluids, wood
	Staphylinidae	Predator	Diptera, mites, nematodes, coleoptera
	Staphylinidae Larvae	Predator	Detritus, coleoptera larvae, diptera larvae
	Zopheridae larvae	Fungivorous	Macro-fungi
	Zopheridae	Fungivorous	Fungi

Appendix C: Mercury Islands and their role in understanding seabird island restoration

Mercury Islands and their role in understanding seabird island restoration

David R. Towns^{1,2,*}, Stephanie B. Borrelle², Joshua Thoresen², Rachel T. Buxton³ and Annette Evans⁴

¹Science and Policy Group, Department of Conservation, Private Bag 68 908, Newton, Auckland 1145, New Zealand

²Institute for Applied Ecology, Auckland University of Technology, Auckland 1142, New Zealand

³Department of Zoology and Centre for Sustainability: Agriculture, Food, Energy, Environment, University of Otago, Dunedin 9054, New Zealand

⁴School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand

*Author for correspondence (Email:dtowns@doc.govt.nz)

Published online: 12 January 2016

Abstract: The progressive removal of invasive mammals from the Mercury Islands has led to over 25 years of field study designed to test the processes of restoration and natural recovery of these seabird-driven island ecosystems. Resulting from this work, four key restoration questions can now be identified as fundamental to designing island restoration programmes. The questions are: what is the regional context of the island (biogeography); how does each island ecosystem operate (ecosystem function); how have invasive species changed the ecosystem (response effects); and how can progress towards a restoration goal be defined (outcome measures)? Examples of how these questions influenced restoration in the Mercury Islands are provided with Korapuki Island as a case study. However, unpredicted and subtle responses can eventuate. In the Mercury Islands these included a hitherto unknown honeydew parasite-bird-gecko food web and subtle effects of rats on plant regeneration. Promising outcome measures of restoration progress are now being developed, including indices of marine influence using stable isotopes of nitrogen and the use of network analysis to analyse the composition of invertebrate food webs.

Keywords: biogeography; species area; colonisation; ecosystem function; eradication; reference sites; Korapuki Island; unknown consequences; New Zealand

Introduction

Islands are not only repositories of disproportionately high numbers of endemic species (e.g. Keitt et al. 2011; Tershy et al. 2015), they have frequently become refugia against the spread of invasive species and habitat loss (Daugherty et al. 1990). For example, although New Zealand has the world's largest number of endemic species of seabirds, the country also has the largest number of threatened seabirds, with most species now confined to offshore islands following the spread of invasive species (Croxall et al. 2012). Only 20 years ago, Duffy (1994) lamented that island ecosystems were becoming so modified, most were unrecognisable. Selected invasive mammals have periodically been eradicated from islands for about 100 years (Bellingham et al. 2010a). However, the eradication of the most pervasive group, introduced rodents (Atkinson 1985; Towns et al. 2011), only became effective and widely applied at the time Duffy was despairing for the future. Today, rodent eradications have been attempted globally on at least 500 islands (Russell & Holmes 2015), with the largest number for a single country conducted in New Zealand (Howald et al. 2007; Keitt et al. 2011). The frequency of eradications in New Zealand began to rapidly increase between 1980 and 1990 (Towns et al. 2013), meaning that the potential to learn from the responses of island ecosystems to comprehensive pest removal covers only 30 years. Attempts to restore islands following eradications of rodents have an even shorter history. Here we review 28 years of restoration activity in the Mercury Islands off northeastern New Zealand. Work in the Mercury Islands developed out of two questions posed in the mid-1980s: can rats be eradicated systematically

from islands (Towns 1988), and if they can, is it possible to restore entire ecosystems previously modified by introduced mammals (e.g. Towns et al. 1990; Towns & Atkinson 1991; Towns et al. 1997)?

The developmental history of eradication technology in the context of the Mercury Islands (Towns & Broome 2003) and a summary of achievements that have stemmed from these activities have already been reviewed (Bellingham et al. 2010a; Towns et al. 2013). Instead, we focus on the question of whether entire ecosystems can be restored, since this is often the goal of invasive species eradications (Towns et al. 1990); a goal that may be particularly challenging for island ecosystems penetrated by invasive species (Norton 2009). The first of the Mercury Islands to be cleared of all invasive mammals was Korapuki (Towns & Broome 2003) and an ecological restoration plan for the island was completed 10 years ago (Towns & Atkinson 2004). Here we examine how implementing the Korapuki plan has contributed to the conceptual understanding of island restoration. We aim in particular to address a problem for seabird island ecosystems raised by Duffy (1994): "We cannot put the Humpty Dumpty of an ecosystem back together because we don't know what the original Humpty looked like, nor do we have all the pieces."

This review aims to address the technical issues raised through Duffy's "Humpty Dumpty" problem by using restoration of seabird island ecosystems in the Mercury Islands as a working example. We focus on four key subsidiary questions that are fundamental to understanding the composition and function of island ecosystems: 1) what is the regional context of the island (biogeography); 2) how does each island ecosystem operate (ecosystem function);

3) how did invasive species change the ecosystem and what effects will their eradication have (response effects); and 4) how can progress towards a restoration goal be defined (outcome measures)? The first two questions help to provide the context within which restoration targets can be set, whereas the second two address the progression of an island towards a target and are more site-based. We demonstrate the relevance of context and site-based approaches by using Korapuki Island as a case study.

Biogeography

Study area

The seven Mercury Islands (36.62S; 175.86E) form the largest of four archipelagos from which mammals have been eradicated in their namesake Mercury Islands Ecological District (MIED). The MIED is a biogeographic grouping based on shared geological and biological characteristics (McEwen 1987) and extends from Cuvier Island (36.43S; 175.77E) in the north through to the Aldermen Islands (36.97S; 176.08E) in the south. Cuvier, all Mercury Islands except Great Mercury and the Aldermen are classed as Nature Reserves under the Reserves Act 1977. These are the most highly protected reserves under New Zealand legislation, with access by permit only. Across the MIED, the range of invasive mammals present has included (Atkinson & Taylor 1992): goats (*Capra hircus*), cats (*Felis catus*), ship rats (*Rattus rattus*) and kiore (*R. exulans*) on Great Mercury; goats, cats and kiore on Cuvier; rabbits (*Oryctolagus cuniculus*), kiore and mice (*Mus musculus*) on Ohinau; rabbits and kiore on Stanley and Korapuki; and kiore alone on Double, Red Mercury, and Middle Chain (Supplementary Data). Like most offshore islands, all of the islands in MIED have at some time been modified through burning (Atkinson 2004; Bellingham et al. 2010a).

Two biogeographic concepts discussed below assist with understanding how history influences the way we view restoration of the islands in this district.

Vicariance

The biotic composition of islands in the MIED is largely a function of island origin (e.g. Towns 1994, 2002b; Towns et al. 1997), notably isolation due to sea level rise following the last glaciations (e.g. Hayward 1986). Oceanic islands far from the main islands of New Zealand, such as the Kermadecs (30.37S; 178.48W), were never connected to larger land masses and are colonised by chance, resulting in genetic drift and high levels of endemism of those species that survive (e.g. Carlquist 1965).

In contrast, islands such as those in MIED are within 20 km of the coast (i.e. on the continental shelf) of New Zealand and were part of the mainland during the last glaciation. As sea levels rose, the newly formed islands contained gradually constrained subsets of mainland terrestrial communities. Populations in these subsets were derived from genetically diverse gene pools, so drift was much less likely and thus endemism is relatively uncommon. Furthermore, these islands support many terrestrial species unable to disperse over water, including a great diversity of flightless invertebrates as well as terrestrial reptiles (Daugherty et al. 1990). Bathymetric analyses within MIED indicate that by about 8 000 years ago, Cuvier and the Aldermen had already been separated from the mainland for at least 4 000 years, but the Mercury and Ohinau Islands had only recently lost their dry land connection to the peninsula (Figure 1). At that point, the Mercury archipelago had not formed, but was an extended "Great Mercury super-island". The concept of vicariance applies here: present disjunctive distributions reflecting the fragmentation of contiguous populations by rising sea levels as a geographic barrier (Wiley 1988). Thus, species today confined to individual islands likely once inhabited the whole Great Mercury super-island.

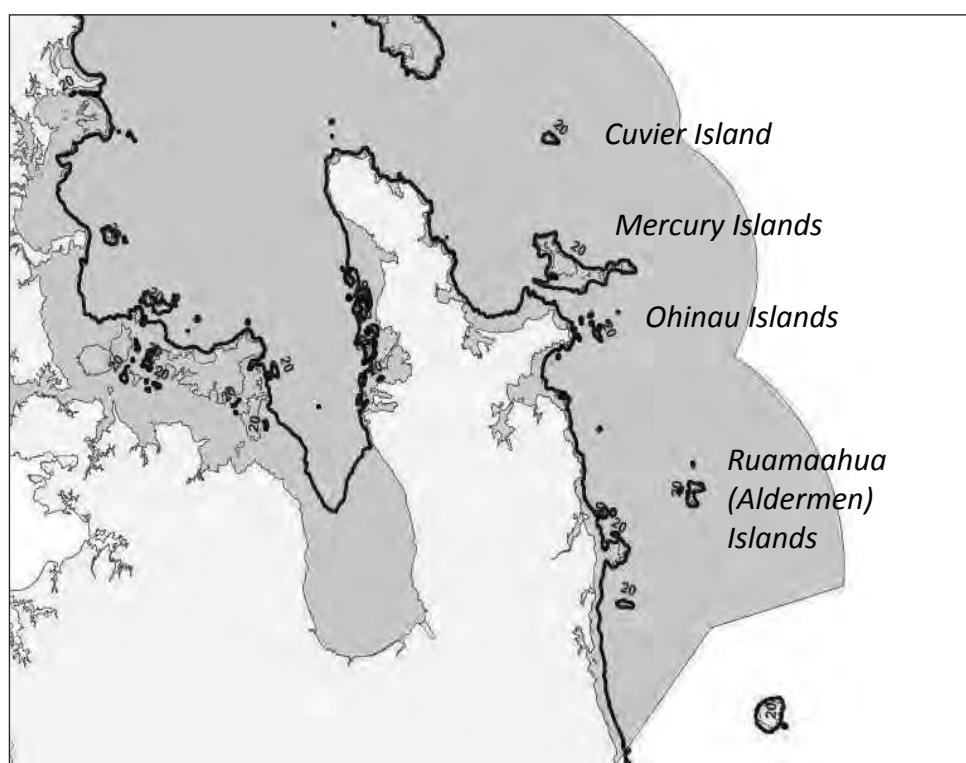


Figure 1. Coastlines around the Coromandel Peninsula at about 8 000 years ago based on the 20 m isobaths (shaded areas are sites within Hauraki Gulf Marine Park) showing four main archipelagos in Mercury Islands Ecological District.

Past connections to the mainland and inclusion within the same ecological district might imply wide application of a variance model. However, the relationship between biota of the Mercury archipelago and others in MIED is not particularly clear. For example, two species of skinks, *Oligosoma whitakeri* and *O. alani*, are present on mammal-free islands in the Mercury Islands but absent from mammal-free islands in the Aldermen. However, a related species, *O. oliveri* is present in both archipelagos (Pickard & Towns 1988). Likewise, the tusked wēta (*Motuweta isolata*), although present in the Mercury Islands, is absent from mammal-free islands in the Aldermen. Subtle differences such as these may reflect differences in isolation history. These differences suggest that for poorly dispersed groups such as flightless invertebrates and reptiles, there has been less unity of distribution than is implied by the vicariance model. Consequently, if high ecological integrity is the restoration goal (see below), the most defensible approach may be to focus within archipelagos; acknowledging that the greatest risk of errors for assumptions about community composition would likely arise from extrapolations between them.

Species-area relationships

A fundamental principle of island biogeography is that, aside from some exceptions, the number of species usually increases in proportion to area (McArthur & Wilson 1967). For example, Whitaker (1978) used this relationship to predict the expected species diversity of reptiles on islands with and without introduced rodents. Although the species-area relationship holds for islands without invasive mammals (e.g. Borrelle et al. 2015), the reverse can develop on islands with invasive vertebrates. As a result, the smallest Mercury Islands, which have not been invaded by mammals, now have more reptile species than larger ones invaded by kiore and rabbits. A similar relationship in response to predation pressure is likely to hold for the large flightless invertebrates.

Species-area relationships are useful because they provide an empirical measure of the proportional reduction of assemblages in the presence of introduced mammals, as well as a basis for predicting the composition of restored assemblages. For example, islands with invasive mammals in the MIED had a 50% reduction in reptile fauna and 75% reduction in wēta fauna (e.g. Towns et al. 1997), which thereby suggests the level of species restoration required for each group.

Ecosystem function

Without detailed understanding of how island ecosystems function when invasive species are absent, it may be difficult to determine how restoration efforts should proceed on islands where invasive species have been present. This understanding can be greatly assisted through the use of reference sites (White & Walker 1997), which are model sites or islands used in order to predict the trajectory or endpoint of an impaired ecosystem after restoration interventions (e.g. Balaguer et al. 2014). Although such sites help with understanding ecosystem function, they do not necessarily indicate the capacity for natural dispersal into previously modified sites. As we discuss below, dispersal ability of some species (particularly plants) often relies on a vertebrate dispersal agent.

Reference sites

Within the MIED, six small islands (3–30 ha) that have never been invaded by introduced mammals can be used as reference sites for restoration of the eight islands (18–1872 ha) from which invasive species have been or are being removed. Five of these reference islands have high seabird abundance and extreme surface fragility due to burrowing by birds. On the larger reference islands (>2 ha), in addition to seabirds, there are dense and diverse reptile populations and numerous species of flightless invertebrates, including wēta, gastropods and spiders (Towns et al. 2009; Bellingham et al. 2010a). These sites indicate the structure and function of seabird driven island ecosystems of different sizes before mammalian predator invasion in the MIED.

Additional reference information can be obtained from invaded islands larger than the uninvaded reference sites. Given their greater area, such islands can have a higher species diversity of plants, which is helpful in identifying species particularly sensitive to browsing (see below). Such sites may only provide fragmentary information, but they extend information available about the composition of local communities as part of an “ecological memory” (*sensu* Balaguer et al. 2014).

Recolonisation potential

When introduced species are removed, many species can return and recover unaided. This recovery is particularly likely for most species of plants, as long as dispersal mechanisms are available and/or local populations remain. For many plants, dispersal is through birds such as kererū or fruit pigeons (*Hemiphaga novaeseelandiae*), which on these islands are the only species capable of long distance seed dispersal of plants with large fruit including kohekohe (*Dysoxylum spectabile*), taraire (*Beilschmedia tarairi*) and tawāpou (*Pouteria costata*; Table 1). Other forms of distribution are less conventional. For example, the seed pods of *Pisonia* are extremely adhesive, potentially as a means of spread between locations by relatively large seabirds, which would explain the wide distribution of the genus throughout the Pacific (e.g. Burger 2005). Given that most islands in the MIED are now free of introduced mammals, it may be possible for natural dispersal through wind and birds to facilitate dispersal of plants.

Despite impressive flight mobility, seabirds still face some barriers to natural dispersal. Studies of seabird colonies have often indicated high philopatry, with birds behaviourally tied to their original birthplace (Warham 1996). A review of colonisation ability of seabirds around New Zealand found more capacity to colonise new islands than had previously been assumed (Buxton et al. 2014). However, frequency of colonisation declined rapidly with distance from source islands, and natural colonisation by most species became unlikely when source populations were >25 km away. Ellipses based on the 25 km radius around uninvaded, densely populated islands in MIED indicate that Mercury, Ohinau and Aldermen archipelagos are all within a 20 km radius (Figure 2). However, Cuvier is between 20 and 25 km from the nearest large uninvaded islands, and still has only been recolonised naturally by three species of Procellariiformes: grey-faced petrel (*Pterodroma macoptera*), flutteringshearwater (*Puffinus gavia*) and diving petrel (*Pelecanoides urinatrix*) (Borrelle et al. 2015).

Table 1. Native species of plants suppressed by kiore as determined from responses of resident species to rodent eradications (from Atkinson 1964; Towns et al. 1997; Campbell & Atkinson 1999, 2002), with canopy species marked*

Species	Study site (s)	Status on reference sites
Kohekohe <i>Dysoxylum spectabile</i> *	Double, Cuvier, Red Mercury	Locally dominant canopy species on larger islands, rare on Middle, unknown from Green
Parapara <i>Pisonia brunoniana</i>	Cuvier, Double, Middle Chain	Subcanopy species capable of forming dense thickets but absent from Middle and Green
Karo <i>Pittosporum crassifolium</i>	Double, Red Mercury, Middle Chain	Widespread and common small tree in coastal areas on Middle and Green
Tawapou <i>Pouteria costata</i> *	Double, Red Mercury, Middle Chain	Often scattered on larger islands but rare on smaller seabird islands such as Middle
Karamu <i>Coprosma macrocarpa</i>	Double, Red Mercury	Widespread and common small tree; now widespread on most islands
Taupata <i>C. repens</i>	Red Mercury	Coastal shrub now common in coastal areas on all islands
Coastal maire <i>Nestigis apetala</i> *	Cuvier	Coastal tree absent from Mercury Islands
Nikau <i>Rhopalostylus sapida</i>	Cuvier	Palm, which can be locally abundant but absent from Mercury Islands
Houpara <i>Pseudopanax lessonii</i>	Double, Cuvier, Middle Chain	Shrub or small tree widespread on Mercury Islands
Milktree <i>Streblus banksii</i> *	Middle Chain	Small tree with extensive areas as canopy on Middle Island and spreading on Stanley
Hymenanthera <i>Melicytus novae-zelandiae</i>	Red Mercury	Shrub widespread in coastal areas on Middle

**Figure 2.** Potential seabird recolonisation ellipses based on 25 km ranges from unininvaded source islands within the Mercury Islands Ecological District.

Effects of invasive species on ecosystem function

Occasionally the effects of invasion are so extreme they are even visible to offshore observers. Examples include extensive vegetation modification and soil loss following decades of browsing by goats (*Capra hircus*) or rabbits (e.g. Merton 1987; Bellingham et al. 2010b). More often the effects are subtle, but even when the invasive species are rodents (e.g. Towns et al. 2006) or ants (e.g. O'Dowd et al. 2003), they can still produce catastrophic changes to ecosystem function.

Studies in New Zealand of the distribution of tuatara (*Sphenodon punctatus*), lizards, invertebrates and plants compared with kiore over a large sample of islands indicate that some species populations are either heavily suppressed by these rats or incompatible with them (Whitaker 1978; Watt 1986; Atkinson 1986; Campbell & Atkinson 1999). A similar comparative approach was used to determine the effects of suppressed seabird populations on island ecosystem function. Nine islands in northern New Zealand (including four in the MIED) with large populations of burrowing seabirds were compared with nine where seabirds were suppressed by introduced rats. On islands with few seabirds, soils had 47% less total C, 45% less total N, 53% less total P and 23% lower marine-derived $\delta^{15}\text{N}$ than on uninvaded islands (Fukami et al. 2006). Furthermore, on islands with few seabirds, 11 orders of leaf-litter and soil-inhabiting invertebrates were less abundant, foliar and litter N concentrations in several plant species were lower, and litter decomposition rates were slower than on uninvaded islands with large seabird colonies (Towns et al. 2009; Wardle et al. 2009). These studies demonstrate the diverse and subtle effects of seabirds on island ecosystems, and conversely, the extent to which the systems can change when mammalian predators invade. Such studies do not demonstrate cause and effect between mammal invasion and shifts in ecosystem function. They do however, provide a powerful basis for developing hypotheses and conceptual models, which can then be tested experimentally (Veltman 1996; Towns et al. 2009).

Three inferences relevant to islands restoration stem from the above observations. First, introduced species likely have direct negative effects on resident species assemblages. Decades after eradication, the legacy of some invasive mammals, such as kiore, remain on islands, as has been demonstrated by the absence of selected species of seabirds, plants, invertebrates and lizards (Townsend 2009). Second, through activities such as burrowing and defecation, seabirds are likely to be one of the most powerful biotic drivers of islands ecosystems around New Zealand (Mulder & Keall 2001) and elsewhere (Mulder et al. 2011). Finally, when invasive species suppress seabird abundance, ecosystem functions engineered by seabirds are suppressed, resulting in a wide range of indirect effects (e.g. Townsend & Atkinson 2004; Russell 2011).

Effects of eradicating invasive species

Four sources of information can help us predict the response of native species and ecosystems to the removal of invasive species from islands: 1) studies of the responses of plants and animals after eradication; 2) the use of reference sites that lack invasive species as defined above; 3) using chronosequences of islands from which invasive species have been removed (e.g. Buxton et al. 2016); and 4) paleoecological studies of plant and animal remains in middens, caves, sand-dunes and wetlands (e.g. Townsend & Ballantine 1993; Wilmshurst et al. 2014). Direct response studies are most valuable on those islands where a single invasive species was introduced then removed, which avoids complications caused by interactions between invasive species (Townsend 2011). An example is provided by tuatara, a species which managed to co-exist with kiore on several islands. In MIED, tuatara were reduced to such low numbers (<20) on kiore invaded islands, their responses to eradication were un-measurable over short timeframes. However, larger numbers of tuatara survived in the presence of kiore in the Marotere Islands, where despite variation between islands, comparisons of recruitment rates of juvenile tuatara before and after kiore eradication demonstrated significant demographic shifts in tuatara populations. Potential competitive effects between kiore and adult tuatara were also revealed by changes in body condition (Townsend et al. 2007). Similar comparisons between islands in MIED, using uninvaded islands and those still with kiore, indicated that kiore suppressed 11 of the 17 species of plants studied (Table 1) and that forest composition on the invaded islands had likely been significantly altered (Campbell & Atkinson 2002).

Some apparently extirpated species have reappeared many years after eradications on islands were completed. For example, five populations of geckos and four populations of skinks have reappeared on islands around New Zealand cleared of invasive mammals. One species of gecko, *Dactylocnemis pacificus*, reappeared on at least two the Marotere Islands less than 10 years after the removal of kiore, but the same species has still not been found on any of the Mercury Island Nature Reserves previously inhabited by invasive mammals despite >20 years of monitoring (D. Townsend unpublished data).

Restoration goals

All restoration projects require a goal or target (Atkinson 1988). This in itself can be problematic if there is little clarity about what the system previously looked like (Duffy 1994) and since

reference sites usually change with time (Simberloff 1990). There are two approaches to defining restoration goals: time or function. A goal could be based on a previous time, such as before the arrival of invasive species, which requires the identification of historic benchmarks (e.g. Atkinson 1988). An alternative is to use ecosystem function as a goal, which does not require the historic reference point, but does require understanding of how key components of ecosystems interact. Such an approach is also greatly assisted if reference sites are available. Now that there is considerable evidence about the engineering role of seabirds (e.g. Mulder et al. 2011), seabird driven island ecosystems as a goal would be a logical option for many islands. This then raises the question of whether intervention is needed.

If the goal is to restore seabird-driven ecosystems, three pieces of evidence suggest that no further manipulation may be required after eradication at many locations (Buxton 2014). First, Jones (2010) analysed marine-derived nitrogen ($\delta^{15}\text{N}$) in soils, plants and spiders (as predatory invertebrates) across islands at different stages of recovery after eradication of mammals. She found increasing evidence of a marine seabird-derived signature with time since mammal eradication and predicted that ecosystems with seabird-driven attributes can recover in a few decades. Second, Buxton et al. (2014) found that the rate of seabird recovery on some islands is higher than might be predicted from the breeding success of residents. They found evidence that existing burrowing seabird colonies attract immigrants, which can be conspecifics, but may also be other species. Finally, where suitable habitat is available, and the density of potential source colonies is sufficient, sites can be identified where natural recovery is most likely (Buxton 2014). In MIED, natural seabird recolonisation potential is high in all archipelagos except Cuvier (Figure 2) (Borrelle et al. 2015).

Given that introduced mammals can extirpate a range of species from within these systems (Table 2), a second option is to extend the functional goal of seabird driven ecosystems to include reintroducing species unable to naturally recolonise. For example, since the above biogeographic analyses support an argument for vicariance within the Mercury islands, restoration could aim to restore seabird-driven ecosystems with community composition typical of the Mercury Islands archipelago. The case study outlined below acknowledges the capacity for natural recovery of seabird populations but also the inability of some species of reptile and invertebrate to re-colonize. For other species, such as the tree wētā (*Hemideina thoracica*) and some species of plants, an overlay of data from reference sites combined with knowledge of the effects of invasive species within the archipelago informed the extended restoration goal.

When is the restoration process complete?

The question of when a restoration project has reached a predefined target is of particular interest to conservation managers. The range of unpredictable outcomes and uncertainties involved with island restoration are so numerous that predicting an endpoint for such an exercise is complex and could involve timescales beyond the life span of a researcher. For example, the time to reach carrying capacity for Whitaker's skinks (*Oligosoma whitakeri*) reintroduced to Korapuki Island was estimated as at least 140 years (Miller 2009). On other islands in the archipelago, such as Red Mercury Island, which is over ten times larger than Korapuki, the recovery of reintroduced populations of the same species will inevitably take even longer.

The criteria for successful restoration through

Table 2. Status of species of flightless invertebrates and reptiles present on mammal-free Mercury islands but absent from Korapuki Island before removal of introduced mammals and identified as candidates for reintroduction by Towns & Atkinson (2004)

Name	Ecological role	Reintroduction status	Tolerance of invasive predators
Gastropoda <i>Rhytida greenwoodi</i>	Predator of gastropods and earthworms	Still to be reintroduced; known only from Green Island	Does not co-exist with kiore on any Mercury Islands, but occasionally does so elsewhere
Arachnida <i>Cambridgea mercurialis</i>	Nocturnal predator	Still to be reintroduced; common in seabird burrows on Middle and Green Islands	No data; does not seem to balloon so may have limited dispersal capabilities (M Fitzgerald pers. comm.)
Orthoptera (Stenopelmatidae) <i>Hemideina thoracica</i>	Folivore	52 from Double Island (1997) now widespread and abundant (Green 2005)	Co-exists with kiore on some Mercury Islands but not others
<i>Hemiandrus pallitarsus</i>	Predator of invertebrates	Still to be reintroduced; present on Middle and Red Mercury	Co-exists with kiore on some Mercury Islands but not others
<i>Motuweta isolata</i>	Predator of invertebrates	100 captive reared originally from Middle Island (2007) now locally abundant (unpublished report, Department of Conservation)	Does not co-exist with kiore
Coleoptera (Tenebrionidae) <i>Mimopeus opaculus</i>	Algal/fungal grazer	100 from Middle Island (2000-2002) now locally abundant (C. Green pers. comm.)	Rarely co-exists with kiore; absent from other Mercury Islands invaded by kiore
Reptilia (Sphenodontidae) <i>Sphenodon punctatus</i>	Apex terrestrial predator of invertebrates, lizards and small seabirds	Still to be reintroduced; dense populations on Middle and Green, relict on Stanley and Red	Coexists with kiore on some other Mercury Islands, but with consistent recruitment failure
(Gekkonidae) <i>Dactylocnemis pacificus</i>	Omnivore, nectar, fruit and invertebrates	Still to be reintroduced; common in forested areas on Middle	Does not co-exist with kiore in Mercury Islands but does in other archipelagos
(Scincidae) <i>Oligosoma alani</i>	Predator of invertebrates and smaller lizards	14 reintroduced (1992-93) from Green; widely dispersed and locally abundant	Does not co-exist with kiore on any islands
<i>Oligosoma oliveri</i>	Predator of invertebrates	25 reintroduced (1992-93) from Green; breeding	Does not co-exist with kiore on any islands
<i>Oligosoma suteri</i>	Intertidal predator of invertebrates	30 reintroduced 1992 from Green; locally abundant	Can co-exist with kiore on islands with appropriate boulder refuges
<i>Oligosoma whitakeri</i>	Predator of invertebrates	28 reintroduced 1988 from Middle; expanding range and locally abundant	Does not co-exist with any mammalian predators on islands

reintroductions are relatively clear (e.g. Towns & Ferreira 2001), and include complete replacement of the release propagule with locally born offspring (Wolf et al. 1996). For some invertebrates, high reproductive output and rapid turnover means that such criteria may be achieved in <10 years. However, for species such as tuatara, adult life spans of up to 100 years mean that monitoring population replacement will require generations of biologists. In contrast to intervention through reintroductions, passive recovery is undirected and process driven. Nonetheless, passive recovery requires monitoring to assess whether hypotheses about ecosystem development are being met. If success is based on changes in ecosystem function, rather than assemblage composition, progress can be estimated in relatively short time scales (Tables 3 and 4). Measures of the recovery of seabird driven ecosystems can include simple measures of burrow density coupled with additional measures of seabird effects. The study of uninvaded islands and those

with seabirds suppressed by invasive mammals (e.g. Fukami et al. 2006; Towns et al. 2009) indicated that soil pH strongly reflects seabird activity. Similarly the measures of C:N and $\delta^{15}\text{N}$ used by Jones (2010) indicate the rate at which seabird effects can be measured. Analyses of food webs on islands with and without procellariiform seabirds indicate the likely responses of ecosystem processes to predator removal if these seabirds recover (Figure 4). Present indications from work on Korapuki Island are that islands within the colonisation range of seabirds could demonstrate many of the functional attributes typical of uninvaded seabird islands within 50 years. More sophisticated investigations of invertebrate community and food web structure should contribute to methods for verifying these functional changes (e.g. Orwin et al. in press).

Restoration case study: Korapuki Island

Korapuki was the first island in the Mercury archipelago from which all introduced mammals were removed (kiore in 1986, rabbits in 1987), has been the site where the conceptual and practical impediments to restoration have been tested, and is also the only island in the group with a comprehensive restoration plan (Towns & Atkinson 2004). The restoration target initially proposed for Korapuki Island by Towns et al. (1990) was for a seabird-reptile-invertebrate-plant system similar to that of Middle and Green Islands. The subsequent restoration plan expanded on this target by emphasizing features of the Middle and Green reference sites, including coexistence of very dense populations of small seabirds (particularly diving petrels) with a high diversity of reptiles and many invertebrate species (Towns & Atkinson 2004). For extirpated species such as tuatara, five species of lizards and many species of flightless invertebrates, natural recovery is unlikely (Towns 2002b). The restoration plan thus recommends re-introduction of those species likely to have been lost through the action of habitat modification (fire) combined with the previous presence of kiore and rabbits (Table 3). For the purposes of this review, we focus on changes to the biota of Korapuki Island since the removal of mammals in 1986-87 (Tables 2 and 4), restoration

activities implemented (Table 3), predicted and unpredicted outcomes, and the many remaining uncertainties in the recovery trajectory of the island (Table 4).

Predicted outcomes

In order to develop hypotheses for the recovery of Korapuki Island after the removal of kiore and rabbits, Towns & Atkinson (2004) constructed conceptual interaction webs. The webs were based on structure of the reference ecosystems of Green and Middle Islands and responses elsewhere in the archipelago to mammal eradications. However, it was not possible at that time to define when various predicted interactions would eventuate, nor were criteria identified as measures of success. Central to the 2004 model was an increasing influence from seabirds adding nutrients to the island’s soils, and an increasing density of seabird burrows, which are used as habitat by tuatara and some species of lizards. The speed at which burrow-nesting seabird populations recover was assumed to rest on three aspects of the biology of Procellariiformes: extreme philopatry; low annual reproductive output; and slow development to reproductive maturity (e.g. Warham 1996). In combination with slow population growth by introduced species of reptiles (e.g. Towns 1994), reactivation of the proposed interaction web was assumed to involve timescales of decades or perhaps centuries.

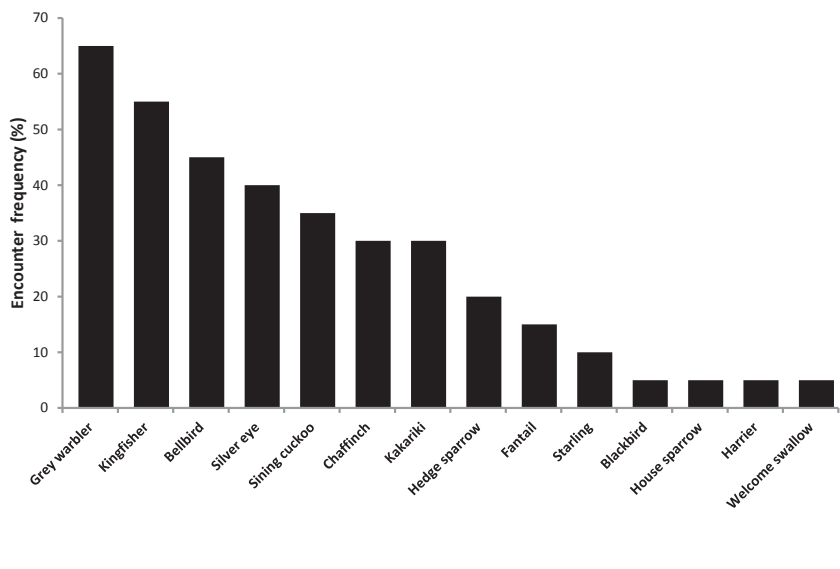


Figure 3. Frequency of forest bird encounters (presence/absence of calls and sightings) at 20 five-minute observation points at 50 m intervals along axial ridges on Korapuki Island in December 2007.

Figure 4. Relative abundance of litter invertebrates from different trophic levels on nine northeastern New Zealand islands invaded by rats and with few seabirds compared with nine islands in the same geographic area never invaded by introduced mammals (for methods and study sites see Towns et al. 2009); Mann-Whitney U Tests were used to compare means with p values identified as * p<0.05, ** p<0.005, *** p<0.0005.

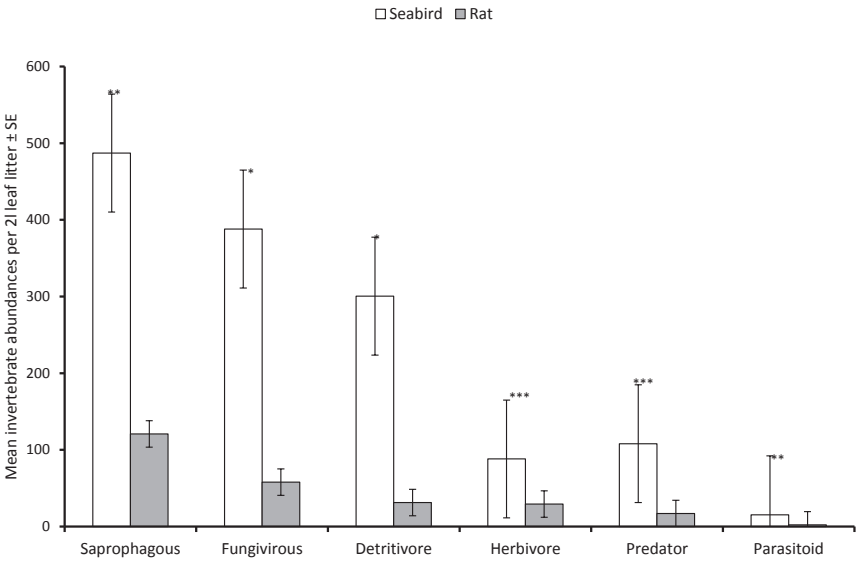


Table 3. Changes to biota of Korapuki Island following the removal of kiore and rabbits.

Species or taxonomic group	Before mammal removal	At least 20 years after mammal removal
Plants	Flora of 96 species (Hicks et al. 1975), with 74% native	Flora of 115 species with 79% native immediately after kiore and rabbit removal (1988); 128 species with 81% native by 2002 (Towns & Atkinson 2004)
Selected woody plants sensitive to kiore	Restricted to <10 known individuals or previously listed as uncommon (a few at one or two locations): <i>Coprosma repens</i> ; <i>Corynocarpus laevigatus</i> ; <i>Melycitus novaezealandiae</i> ; <i>Myoporum laetum</i> ; <i>Pouteria costata</i> ; <i>Streblus banksii</i> (Hicks et al. 1975)	All species except <i>C. laevigatus</i> (spreading but <10 individuals) now present throughout island; <i>P. costata</i> with > 80 young plants in some areas (Towns et al. 1997; Towns & Atkinson 2004)
Invertebrates	Few large invertebrates (beetles and millipedes) > 10 mm seen; no other data (Hicks et al. 1975)	Reappearance of three species of native cockroaches, small wētā <i>Neonetes</i> ? sp. large centipede <i>Cormocephalus rubriceps</i> (Towns et al. 1997) and honeydew scale <i>Coelostomidium zealandica</i> (Towns 2002b); identification of 24 species of terrestria molluscs (includes one exotic species of slug) and 70 species of spiders (Towns & Atkinson 2004)
Reptiles	Five species of lizards recorded but only four of these seen by Hicks et al. (1975): <i>Oligosoma aenea</i> , not seen; <i>Woodworthia maculata</i> and <i>Hoplodactylus duvaucelii</i> <10 seen; <i>O. smithi</i> and <i>O. moco</i> , regarded as common	<i>O. aenea</i> trapped in all forest habitats by 1999 (D Towns unpublished data); demographic shifts and habitat changes recorded for <i>O. smithi</i> (Towns 1991) and <i>H. duvaucelii</i> (Towns 1996); increased capture frequencies of all five species (Monks et al. 2014) sighting frequencies of <i>W. maculata</i> on coast exceeded Middle Island within 15 years of mammal eradication (Towns 2002b)
Seabirds	Eight species listed, seven of which recorded by Hicks et al. (1975): <i>Eudyptula minor</i> , throughout; <i>Puffinus carneipes</i> , few seen; <i>P. griseus</i> , four seen; <i>P. gavia</i> , second-most abundant, <19/ha; <i>P. assimilis</i> , scattered burrows <6.8/ha; <i>Pterodroma macroptera</i> , most common species <36/ha, 600-700 pairs total; <i>Pelecanoides urinatrix</i> , scattered, one site ca 30/ha	<i>Phalacrocorax varius</i> observed by Hicks et al. (1975) in coastal waters, but now breeding in pōhutukawa on SW coast
Native land birds	Eleven species of native birds and four exotic species recorded by Hicks et al. (1975), with native species classed as abundant: <i>Cyanoramphus novaeseelandiae</i> , <i>Rhipidura fuliginosa</i> , <i>Gerygone igata</i> and <i>Zosterops lateralis</i> . Classed as frequent: <i>Circus approximans</i> . Classed as uncommon: <i>Ninox novaeseelandiae</i> , <i>Halcyon sancta</i> , <i>Anthornis melanura</i> and <i>Prosthemadera novaeseelandiae</i>	<i>Hirudo tahitica</i> not recorded by Hicks et al. (1975), but now seen around the entire coastline (Towns & Atkinson 2004); three species classed as uncommon are now widespread and abundant throughout the island but <i>P. novaeseelandiae</i> only reported by A Evans (Unpublished data)

Unpredicted outcomes

Avian predators

Many responses to invasive mammal removals from Korapuki were unpredicted, including the resurgence and recolonisation of two avian predators: the kingfisher (*Todiramphus sanctus*) and the native owl (morepork; *Ninox novaeseelandiae*). Both species were regarded as uncommon by Hicks et al. (1975) and only a single pair of kingfishers was recorded by a survey in 1985 (D. Towns unpublished data). However, in 2007 kingfishers were encountered in over half of the survey sites used (Figure 3).

Moreporks were only occasionally sighted during biennial visits between 1985 and 2009, most likely as visitors from neighbouring islands, as there were no observed territorial calls. By 2009 territorial calls were heard, and in March 2011 moreporks calls were heard across the entire island (D. Towns unpublished data). Moreporks and kingfishers feed on lizards,

large invertebrates and small birds (Robertson 1985). Recovery and recolonisation by these two avian predators could thus be an indirect measure of the increased abundance of their prey, one item of which for moreporks is tree wētā reintroduced to Korapuki in 1997 (Table 2).

Insect parasites

Honeydew scale insects are parasites of many forest plant species in New Zealand (Morales 1991). Their role in providing a high energy carbohydrate resource for birds and lizards on islands was unknown until the appearance of coastal forest plants infested by scale insects *Coelostomidia zealandica* on Korapuki (Towns 2002a). As these parasites have gradually spread, the importance of honeydew and other sources of sugar to geckos on these islands has also become apparent. Common geckos (*Woodworthia maculata*) are now common around fl x (*Phormium tenax*), where they feed from inflorescences and sap.

Table 4. Chronological measures of progress and success for restoration of communities within a seabird-driven ecosystem of Korapuki Island; with projected measures >25 years.

Years since eradication of invasive mammals	Measure	Comment
10	Dispersal to/within island of key canopy plant species	Dominant species of communities on Middle Island as reference site spreading via bird dispersal (Towns & Atkinson 2004) but likely additional species (e.g. kohekohe) yet to establish (Atkinson 2004)
20	Establishment of selected missing invertebrates and reptiles	Five years for establishment of some invertebrates (e.g. Green 2005) and >8 years for some lizards (Towns & Ferreira 2001)
20–25	Recolonisation of top resident avian predator	Moreporks resident (based on territorial calls), but likely contingent on establishment of large invertebrates including tree wētā
50	Marine signature via seabirds within range of uninvaded islands	C:N and $\delta^{15}\text{N}$ concentrations in soils and plants equivalent to islands with unsuppressed seabird populations (extrapolated from Jones 2010); high density seabird colonies present but localised (Buxton et al. 2016)
50–100	Complete infestation of potential hosts for honey dew scale; time required to define success for reintroductions of tuatara	About 20% of island with honeydew infested karo or ngaio plants (Evans et al. 2015); successful reintroductions with each population composed of F1 or greater (D. Towns unpublished data)
150	Carrying capacity reached for reintroduced reptiles with low annual reproductive output	Modelled time to carrying capacity for Whitaker’s skink (Miller 2009) and likely minimum time for tuatara; density of both species linked to seabird burrow density
>300	Replacement of continuous pōhutukawa canopy by diverse coastal species	Likely gradual change from pōhutukawa to karaka (<i>Corynocarpus laevigatus</i>) and kohekohe, but may depend on effects of seabirds

Duvaucel’s geckos (*Hoplodactylus duvaucelii*) and common geckos are also found on the host trees for honeydew scale, although Duvaucel’s geckos are the more abundant at such sites (Evans et al. 2015). Furthermore, bellbirds (*Anthornis melanura*) are often now seen feeding on the honeydew and vocally defending productive scale-infested karo (*Pittosporum crassifolium*) trees (D. Towns unpublished data).

Seabird recovery and recolonisation

The speed at which seabirds have recolonised and influenced restored island ecosystems in New Zealand has confounded assumptions based on philopatry and low immigration rates (Croxall et al. 2012; Kappes & Jones 2014). Through studies of C:N ratios and the concentration of $\delta^{15}\text{N}$ in soils, foliage and spiders, Jones (2010) concluded that ecosystem recovery on northeastern New Zealand islands may be achieved in decades. These conclusions were supported by Buxton et al. (2014), who found that on islands <25 km from other dense seabird colonies, intra- and interspecific social attraction can stimulate immigration to previously depleted colonies or establish new ones. These findings were particularly relevant to Korapuki Island, which at the longest time since eradication of mammals (then 22 years) had the highest soil and plant $\delta^{15}\text{N}$ and lowest C:N of the islands sampled (Jones 2010). In contrast to the scattered low density colonies recorded 10 years before mammal eradication (Hicks et al. 1975), seabird colonies now extend over 70% of surveyed areas on the island (Buxton et al. 2016).

Mysterious declines and disappearances

Surprisingly, we found changes in the abundance and distribution of resident species initially thought to be resistant to the effects of kiore and rabbits. For example, the diurnal shore skink (*Oligosoma smithi*) was regarded as abundant in the presence of kiore and rabbits (Hicks et al. 1975).

However, surveys revealed changes in distribution, increases in mean body size, and increased capture frequency soon after mammals were eradicated (Towns 1991, 1996; Monks et al. 2014). Conversely, recent samples indicate declines in the capture rates of shore skinks, while captures of other species of resident and translocated lizards continue to increase at the same sites (D. Towns unpublished data). Whether the current declines of shore skink captures is related to competition or predation from other species of lizards or the increased density of kingfishers as predators remains unclear.

In their early surveys of Korapuki Island, Hicks et al. (1975) observed few large day-flying insects and noted that the only species observed were cicadas and wasps. We assume that the latter were introduced *Vespula* wasps, since these were still present during our visits 10 years later (C. Green pers. comm.). In New Zealand, these wasps compete with birds for honeydew, can kill nestling birds, and prey heavily on spiders and caterpillars, resulting in modified invertebrate community structure (Beggs 2011). Within five years of the mammal eradication these wasps disappeared and have not been seen since (Bellingham et al. 2010a). Similar disappearances have now been observed on other islands after eradication of rats, including very large islands where *Vespula* wasps were once extremely abundant (T. Lovegrove pers. comm.).

Failed colonisations and unknown consequences

Numerous uncertainties remain about the composition and dynamics of communities on Korapuki Island. For example, seed dispersal will inevitably shape forest composition, which for some species requires kererū visiting from neighbouring islands (Towns & Atkinson 2004). The presence of tawāpou and taraire provides evidence of kererū visitation to Korapuki. However, not all species imported by kererū survive. In 1986, three taraire plants appeared to be thriving on the southwestern part of Korapuki; however, all plants succumbed after a drought

in the early 1990s and none have been seen since. Other species that are dispersed to the island may germinate only to be destroyed by drought, trampling or clipping by seabirds.

The relatively rapid increase in seabird activity brings additional uncertainties for longer term successional processes. In some areas of Korapuki, seabird burrow density is high under a canopy of 100-year old pōhutukawa (*Metrosideros excelsa*) that developed as a result of burning and the activities of rabbits (Atkinson 2004). Long term, this canopy would likely be replaced by a variety of coastal species, but the intense seabird activity could suppress seedling growth and arrest succession. Because Korapuki has a wide range of habitats and soil depths (Towns & Atkinson 2004) such effects are likely to be localised.

Finally, the recovery trajectory of Korapuki will likely be affected by external influences (Towns 2002b), such as climate change, ocean pollution, and other conservation actions. The latter could include success with mammal eradications on other islands in the archipelago. If the eradication of invasive mammals from Great Mercury in 2014 proves to be successful (Supplementary Data), all Mercury Islands will be free of introduced mammals. It is likely that kererū numbers will correspondingly increase, which in turn will increase the frequency of their movements between islands. The resulting seed dispersal could include species currently absent from islands such as Korapuki, with outcomes that at present are unknown. Another conservation action that may elicit indirect consequences on the recovery trajectory of Korapuki is the protection of New Zealand fur seals (*Arctocephalus forsteri*) following heavy exploitation in the 19th century (Harcourt 2005). The species is now reclaiming its former range, which includes sightings in 2012 of male fur seals ashore on Korapuki Island (A. Evans unpublished data). Rookeries may be established on Korapuki Island at some stage, which could significantly modify coastal vegetation, as well as contribute nutrient subsidies to the ecosystem. How fur seals might influence the function of these warm temperate ecosystems remains unclear.

Discussion

Invasive mammals have been eradicated from seven of the islands in the MIED. These eradications included some of the earliest campaigns against rodents, beginning with kiore (and rabbits) on Korapuki Island in 1986, and eventually leading to cats and rats on the eighth and largest of the islands (Great Mercury; 1872 ha), which began in 2014. With almost 30 years free of introduced mammals, Korapuki Island has been invaluable for testing concepts associated with island restoration as well as methods for species reintroductions. For example, a restoration target to “extend the area of unique seabird-reptile-invertebrate-plant communities” typical of the Mercury Islands was proposed soon after eradications were completed on Korapuki (Towns et al. 1990), but was not developed into a completed restoration plan until much later (Towns & Atkinson 2004). Empirical support for the pivotal role of seabirds, as implied in the restoration target, is even more recent (e.g. Fukami et al. 2006; Mulder et al. 2011). The evolution of ideas and collection of supporting data for restoration of these islands was built around four components: biogeography; ecosystem function; the effects of invasive species; and outcome measures (Figure 5). For example, through testing biogeographic theory, our work suggests that

assemblage structure may be most easily predicted on islands previously part of the mainland, but especially those once interconnected.

We have also found that ecosystem function can be determined from two sources: the way resident species respond when invasive species are removed and the use of comparative data from reference sites never occupied by invasive mammals. Reference models are likely to be most instructive when on islands of similar size to the site being restored. As island size increases, reference sites uninvaded by introduced mammals become increasingly rare and for islands >1000 ha do not exist (Parkes & Murphy 2003). However, on some of the larger islands, past assemblage composition can be revealed from the bone fragments, pollen and ancient DNA used for archaeological and palaeoecological studies (Bellingham et al. 2010a; Wilmshurst et al. 2014).

Regardless of the availability of reference sites, the amount of restoration effort required is determined by recolonisation ability; this may vary for seabirds according to the distance from source populations but is consistently poor for reptiles and some terrestrial invertebrates. Finally, restoration endpoints can be defined by combining biogeographic origin, post eradication responses and ecosystem function. For example, a restored seabird-driven ecosystem on Korapuki Island with high ecological integrity typical of the archipelago acknowledges historic vicariance, high rates of natural recolonisation by plants and seabirds, but the extirpation of key reptiles and large flightless invertebrates. However, despite the three decades of reintroductions and recovery on the island, measures of progress towards the restoration endpoints are still in development.

In sum, ecological restoration in the Mercury Islands indicates that the “Humpty Dumpty” problem raised by Duffy (1994) and others who have examined the ambiguity of island restoration (Simberloff 1990) can be addressed within a defensible framework. However, our studies have also revealed many unexpected responses to invasive mammal removal. There are also unpredictable consequences of the previous presence of mammals, responses of species such as kererū to conservation actions elsewhere and the effects of recolonisation of the islands by fur seals. Conversely, there is developing clarity about how these seabird driven systems vary under different climatic and biogeographic regimes and the extent to which they can be modified by introduced animals. Insights have come from comprehensive studies of the general relationships between seabird activity, nutrient subsidy, and vegetation composition beginning in the 1950s (e.g. Gillham 1956a, b), complemented locally by analyses of seabird-soil-plant relationships on Middle Island in the Mercury Group (Atkinson 1964), and extended by studies across islands in northern New Zealand (Fukami et al. 2006) and globally (Mulder et al. 2011). The studies by Jones (2010) and ourselves in the Mercury Islands indicate that removal of predatory mammals can lead to reactivation of the seabird influence on island ecosystems, as long as the birds can recolonise. Furthermore, Buxton et al. (2014) show that there is frequently natural recolonisation of islands <25 km from other large seabird colonies. Collectively, these recent studies indicate that seabird-driven ecosystems in some locations can recover rapidly, but they have also identified markers that can be used to measure the extent of that recovery.

Given that the seabird-driven ecosystem on Korapuki appears to be recovering naturally (Jones 2010; Buxton et al. 2016), is restoration based on pre-determined assemblage composition justified? For example, the ecosystem on Korapuki

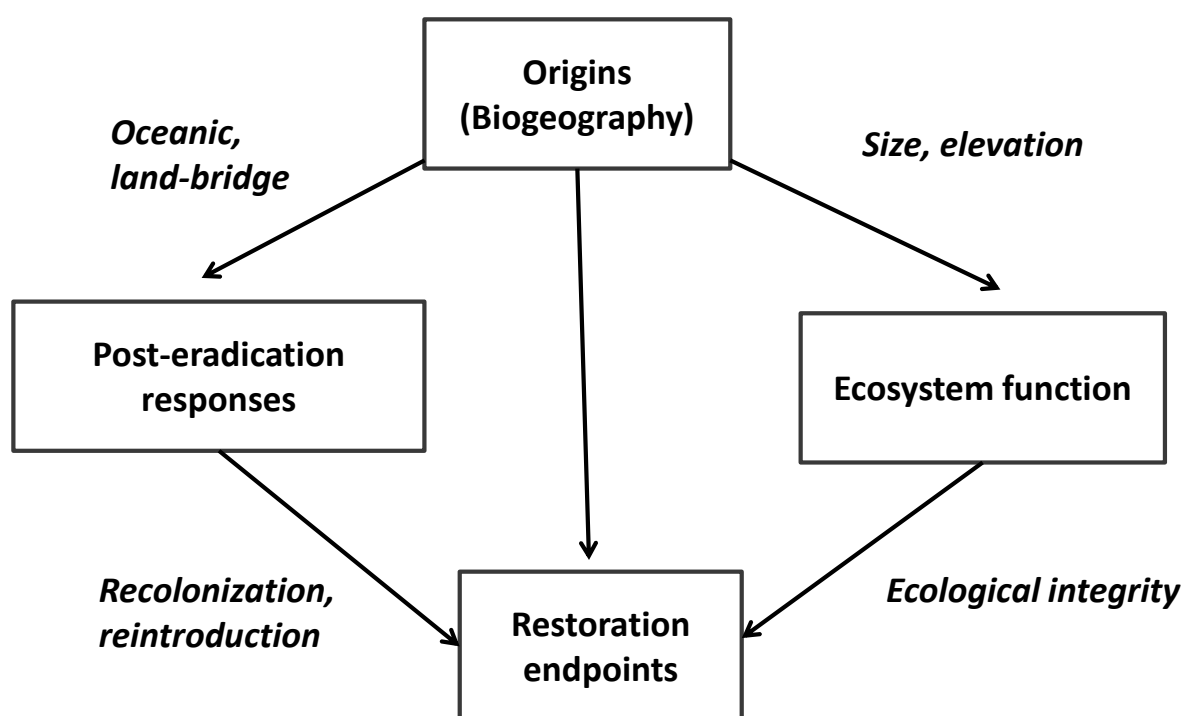


Figure 5. Summary of the relationship between four key components of island restoration.

will not cease to function in the absence of tuatara, which will simply be replaced by Duvaucel's geckos as top reptile predator (Towns 2002b). Furthermore, should we be concerned if ecosystems on islands beyond the natural colonisation range of seabirds enter alternative stable states unlike those with invasive mammals but no longer driven by the engineering effects of seabirds (e.g. Mulder et al. 2009)? Such questions lead us into the realm of value judgements. By phrasing his problem in the context of a children's nursery rhyme, Duffy (1994) implies a social component to restoration, as there is with all conservation biology (e.g. Lawton 1997). One social dimension applied to our study at the outset: a legal framework (i.e. a statutory expression of values) within which to conduct the eradications and attempt ecosystem restoration. Work in the Mercury Islands began on sites administered as Nature Reserves, which mandates the removal of all exotic species where possible (Reserves Act 1977). We therefore assumed that the implicit goal of the reserves is protecting or promoting the highest possible ecological integrity (*sensu* Lee et al. 2005), which on Korapuki includes reintroduction of invertebrates and reptiles (Towns & Atkinson 2004). Nonetheless, even with a legal mandate, when multiple stakeholders are involved there can still be heated debate when invasive species eradications are proposed, as was the case before the removal of kiore from Hauturu (Little Barrier) Island Nature Reserve (Towns et al. 2006). Accordingly, our summary of the essential elements to be considered when undertaking restoration of islands (Figure 5) is a simplified view that excludes the complex regional social issues that may be involved.

Having acknowledged uncertainties about the successional consequences of natural recovery supplemented by reintroductions, our approach on Korapuki has been to allow the ecosystem to develop at its own speed. By facilitating the return of only those components unable to recolonise unaided, we assume that the system will eventually follow a trajectory

typical of other regional islands of equivalent size (Simberloff 1990; Towns 2002b). What still remains unclear from the Korapuki study is whether the strong ecosystem engineering effects of seabirds apply on larger islands, or whether such locations develop into more heterogeneous environments than are found on our small reference islands, such as Middle. Consequently, a great deal is still to be learned from the processes of recovery on other Mercury Islands such as Red Mercury, which is over 20 times larger than their available reference sites within the archipelago.

Acknowledgements

We wish to thank James Russell for inviting our contribution to the workshop on rodent eradications. The ideas presented here have benefited from extensive discussions on Korapuki, especially with Ian Atkinson, Chris Green and Mike Fitzgerald. Infrastructural support for work on the island has frequently been provided by Rob Chappell from the Department of Conservation, for which we express our sincere thanks. We also thank Chris Green, Cheryl Krull, James Russell and two anonymous reviewers for their useful comments on drafts of the manuscript.

References

- Atkinson IAE 1964. The flora, vegetation, and soils of Middle and Green Island, Mercury Islands group. *New Zealand Journal of Botany* 2: 385–402.
- Atkinson IAE 1985. The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifauna. In: Moors PJ ed *Conservation of island birds*. Cambridge, UK, ICBP. Pp. 35–81.
- Atkinson IAE 1986. Rodents on New Zealand's northern

- offshore islands: distribution, effects and precautions against further spread. In: Wright AE, Beever RE eds The offshore islands of northern New Zealand. Department of Lands and Survey Information Series No. 16. Pp. 13–40.
- Atkinson IAE 1988. Presidential address: opportunities for ecological restoration. New Zealand Journal of Ecology 11: 1–12.
- Atkinson IAE 2004. Successional processes induced by fires on the northern offshore islands of New Zealand. New Zealand Journal of Ecology 28: 181–193.
- Balaguer L, Escudero A, Martín-Dubuque JF, Mola I, Aronson J 2014. The historical reference in restoration ecology: re-defining a cornerstone concept. Biological Conservation 176: 12–20.
- Beggs J 2011. Wasps. In: Simberloff D, Rejmánek M eds Encyclopedia of biological invasions. Berkeley, University of California Press. Pp. 685–689.
- Bellingham P, Towns DR, Cameron EK, Davis JJ, Wardle DA, Wilmschurst JM, Mulder C 2010a. New Zealand island restoration: seabirds, predators, and the importance of history. New Zealand Journal of Ecology 34: 115–136.
- Bellingham PJ, Wiser SK, Wright AE, Cameron EK, Forester LJ 2010b. Disperser communities and legacies of goat grazing determine forest succession on the remote Three Kings Islands, New Zealand. Biological Conservation 143: 926–938.
- Borrelle SB, Buxton RT, Jones HP, Towns DR 2015. A GIS-based decision making approach for prioritizing seabird management following predator eradication. Restoration Ecology 23: 580–587.
- Burger AE 2005. Dispersal and germination of seeds of *Pisonia grandis*, an Indo-Pacific tropical tree associated with insular seabird colonies. Journal of Tropical Ecology 21: 263–271.
- Buxton RT 2014. Ecological drivers of seabird recovery after the eradication of introduced predators. PhD Thesis. Dunedin, University of Otago. 209 p.
- Buxton RT, Jones CJ, Moller H, Towns DR 2014. Drivers of seabird population recovery on New Zealand islands after predator eradication. Conservation Biology 28: 333–344.
- Buxton RT, Taylor G, Jones C, Lyver PO'B, Moller H, Cree A, Towns DR 2016. Spatio-temporal changes in density and distribution of burrow-nesting seabird colonies after rat eradication. New Zealand Journal of Ecology 40: 88–99.
- Campbell DJ, Atkinson IAE 1999. Effects of kiore (*Rattus exulans* Peale) on recruitment of indigenous coastal trees on northern offshore islands of New Zealand. Journal of the Royal Society of New Zealand 29: 265–290.
- Campbell DJ, Atkinson IAE 2002. Depression of tree recruitment by the Pacific rat (*Rattus exulans* Peale) on New Zealand's northern offshore islands. Biological Conservation 107: 19–35.
- Carlquist S 1965. Island Life. Garden City, New York, Natural History Press. 451 p.
- Croxall JP, Butchart SHM, Lascelles B, Sattersfield AJ, Sullivan B, Symes A, Taylor P 2012. Seabird conservation status, threats and priority actions: a global assessment. Bird Conservation International 22: 1–34.
- Daugherty CH, Towns DR, Atkinson IAE, Gibbs GW 1990. The significance of the biological resources of New Zealand islands for ecological restoration. In: Towns DR, Daugherty CH, Atkinson IAE eds Ecological restoration of New Zealand islands. Wellington, Department of Conservation. Pp. 9–21.
- Duffy DC 1994. Afterwards: an agenda for managing seabirds and islands. In: Nettleship DN, Burger J, Gochfeld M eds Seabirds on islands: threats, case studies and action plans, Vol 1. Birdlife Conservation Series. 318 p.
- Evans AE, Towns DR, Beggs JR 2015. The relative importance of sugar resources to endemic gecko populations in an isolated island ecosystem. New Zealand Journal of Ecology 39: 262–272.
- Fukami T, Wardle DA, Bellingham PJ, Mulder CPH, Towns DR, Yeates GW, Bonner KI, Durrett MS, Grant-Hoffman MN, Williamson WM 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. Ecology Letters 9: 1299–1307.
- Gillham ME 1956a. Ecology of the Pembroke Islands. IV. Effects of treading and burrowing by birds and mammals. Journal of Ecology 44: 51–82.
- Gillham ME 1956b. Ecology of the Pembroke Islands. V. Manuring by the colonial seabirds and mammals, with a note on seed distribution by gulls. Journal of Ecology 44: 429–454.
- Green C 2005. Using artificial refuges to translocate and establish Auckland tree weta *Hemideina thoracica* on Korapuki Island, New Zealand. Conservation Evidence 2: 94–95.
- Harcourt R 2005. New Zealand fur seal. In: King CM ed The handbook of New Zealand mammals. Melbourne, Oxford University Press. Pp. 225–235.
- Hayward BW 1986. Origin of the offshore islands of northern New Zealand and their landform development. In: Wright AE, Beever RE eds The offshore islands of northern New Zealand. Department of Lands and Survey Information Series No. 16. Pp. 129–138.
- Hicks GRF, McColl HP, Meads MJ, Hardy GS, Roser RJ 1975. An ecological reconnaissance of Korapuki Island, Mercury Islands. Notornis 22: 195–220.
- Howald G, Donlan CJ, Galván JP, Russell JC, Parkes J, Samaniego A, Wang Y, Veitch D, Genovesi P, Pascal M, Saunders A, Tershy B 2007. Invasive rodent eradication on islands. Conservation Biology 21: 1258–1268.
- Jones HP 2010. Seabird islands take mere decades to recover following rat eradication. Ecological Applications 20: 2075–2080.
- Kappes P, Jones H 2014. Integrating seabird restoration and mammal eradication programs on islands to maximize conservation gains. Biodiversity and Conservation 23: 503–509.
- Keitt B, Campbell K, Saunders A, Clout M, Wang YW, Tershy B 2011. The global islands invasive vertebrate eradication database: a tool to improve and facilitate restoration of island ecosystems. In: Veitch CR, Clout MN, Towns DR eds Island invasives: eradication and management. Gland, Switzerland and Auckland, New Zealand, IUCN. Pp. 74–77.
- Lawton JH 1997. The science and non-science of conservation biology. New Zealand Journal of Ecology 21: 117–120.
- Lee W, McGlone M, Wright E 2005. Biodiversity inventory and monitoring: a review of national and international systems and a proposed framework for future biodiversity monitoring by the Department of Conservation. Landcare Research Contract Report LC0405/122. 213 p.
- McArthur RH, Wilson EO 1967. The theory of island biogeography. Princeton, Princeton University Press. 203 p.
- McEwen WM 1987. Ecological regions and districts of New

- Zealand. Wellington, Department of Conservation. 63 p.
- Merton D 1987. Eradication of rabbits from Round Island, Mauritius: a conservation success story. *Dodo* 24: 19–43.
- Miller KA 2009. Founding events and the maintenance of genetic diversity in reintroduced populations. PhD Thesis. Wellington, Victoria University of Wellington. 125 p.
- Monks JM, Monks A, Towns DR 2014. Correlated recovery of five lizard populations following eradication of invasive mammals. *Biological Invasions* 16: 167–175.
- Morales CF 1991. Margarodidae (Insecta: Hemiptera). *Fauna of New Zealand* 21: 124 p.
- Mulder CPH, Keall SN 2001. Burrowing seabirds and reptiles: impacts on seeds, seedlings and soils in an island forest in New Zealand. *Oecologia* 127: 350–360.
- Mulder CPH, Grant-Hoffman MN, Towns DR, Bellingham PJ, Wardle DA, Durrett MS, Fukami T, Bonner KI 2009. Direct and indirect effects of rats: does rat eradication restore ecosystem functioning of New Zealand islands? *Biological Invasions* 11: 1671–1688.
- Mulder CPH, Anderson WB, Towns DR, Bellingham PJ 2011. Seabird islands: ecology, invasion and restoration. New York, Oxford University Press. 512 p.
- Norton DA 2009. Species invasions and limits to restoration: learning from the New Zealand experience. *Science* 325: 569–571.
- O'Dowd DJ, Green PT, Lake PS 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6: 812–817.
- Orwin KH, Wardle DA, Towns DR, St. John MG, Bellingham PJ, Jones C, Fitzgerald BM, Parrish RG, Lyver PO'B in press. Burrowing seabird effects on invertebrate communities in soil and litter are dominated by ecosystem engineering rather than nutrient addition. *Oecologia*.
- Parkes J, Murphy E 2003. Management of introduced mammals in New Zealand. *New Zealand Journal of Zoology* 30: 335–359.
- Pickard CR, Towns DR 1988. Atlas of the amphibians and reptiles of New Zealand. Conservation Sciences Publication No 1. Wellington, Department of Conservation. 59 p.
- Robertson CJR 1985. Readers Digest complete book of New Zealand birds. Sydney, Readers Digest. 319 p.
- Russell JC 2011. Indirect effects of introduced predators on seabird islands. In: Mulder CPH, Anderson WB, Towns DR, Bellingham PJ eds Seabird islands: ecology, invasion, and restoration. New York, Oxford University Press. Pp. 261–279.
- Russell JC, Holmes ND 2015. Tropical island conservation: rat eradication for species recovery. *Biological Conservation* 185: 1–7.
- Simberloff D 1990. Reconstructing the ambiguous: can island ecosystems be restored? In: Towns DR, Daugherty CH, Atkinson IAE eds Ecological restoration of New Zealand islands. Wellington, Department of Conservation. Pp. 37–51.
- Tershy BR, Shen K-W, Newton KM, Holmes ND, Croll DA 2015. The importance of islands for the protection of biological and linguistic diversity. *BioScience* 65: 592–597.
- Towns DR 1988. Rodent eradication from islands - the conservation potential. *Forest and Bird* 19: 32–33.
- Towns DR 1991. Response of lizard assemblages in the Mercury Islands, New Zealand, to removal of an introduced rodent: the kiore (*Rattus exulans*). *Journal of the Royal Society of New Zealand* 21: 119–36.
- Towns DR 1994. The role of ecological restoration in the conservation of Whitaker's skink (*Cyclodina whitakeri*), a rare New Zealand lizard (Lacertilia: Scincidae). *New Zealand Journal of Zoology* 21: 457–471.
- Towns DR 1996. Changes in habitat use by lizards on a New Zealand island following removal of the introduced Pacific rat *Rattus exulans*. *Pacific Conservation Biology* 2: 286–92.
- Towns DR 2002a. Interactions between geckos, honeydew scale insects and host plants revealed on islands in northern New Zealand, following eradication of introduced rats and rabbits. In: Veitch CR, Clout MN eds Turning the tide: the eradication of invasive species. Gland, Switzerland and Cambridge UK, IUCN. Pp. 329–335.
- Towns DR 2002b. Korapuki Island as a case study for restoration of insular ecosystems in New Zealand. *Journal of Biogeography* 29: 593–608.
- Towns DR 2009. Eradications as reverse invasions: lessons from Pacific rat (*Rattus exulans*) removals from New Zealand islands. *Biological Invasions* 11: 1719–1733.
- Towns DR 2011. Eradication of vertebrate pests from islands around New Zealand: what have we delivered and what have we learned? In: Veitch CR, Clout M, Towns DR eds Island invasives: eradication and management. Gland, Switzerland and Auckland, New Zealand, IUCN. Pp. 364–371.
- Towns DR, Atkinson IAE 1991. New Zealand's restoration ecology. *New Scientist* 1765: 36–39.
- Towns DR, Atkinson IAE 2004. Restoration plan for Korapuki Island (Mercury Islands), New Zealand. Wellington, Department of Conservation. 52 p.
- Towns DR, Ballantine WJ 1993. Conservation and restoration of New Zealand island ecosystems. *Trends in Ecology and Evolution* 8: 452–457.
- Towns DR, Broome KG 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. *New Zealand Journal of Zoology* 30: 377–398.
- Towns DR, Ferreira SM 2001. Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. *Biological Conservation* 98: 211–222.
- Towns DR, Atkinson IAE, Daugherty CH 1990. The potential for ecological restoration in the Mercury Islands. In: Towns DR, Daugherty CH, Atkinson IAE eds Ecological restoration of New Zealand islands. Conservation Sciences Publication No. 2. Wellington, New Zealand, Department of Conservation. Pp. 91–108.
- Towns DR, Atkinson IAE, Daugherty CH 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biological Invasions* 8: 863–891.
- Towns DR, Byrd GV, Jones HP, Rauzon MJ, Russell JC, Wilcox C 2011. Impacts of introduced predators on seabirds. In: Mulder CPH, Anderson WB, Towns DR, Bellingham PJ eds Seabird islands: ecology, invasion, and restoration. New York, Oxford University Press. Pp. 56–90.
- Towns DR, Parrish GR, Tyrrell CL, Ussher GT, Cree A, Newman DG, Whitaker AH, Westbrooke I 2007. Responses of tuatara (*Sphenodon punctatus*) to removal of Pacific rats from islands. *Conservation Biology* 21: 1021–1031.
- Towns DR, Simberloff D, Atkinson IAE 1997. Restoration of New Zealand islands: redressing the effects of introduced species. *Pacific Conservation Biology* 3: 99–124.
- Towns DR, Wardle DA, Mulder CPH, Yeates GW, Fitzgerald BM, Parrish GR, Bellingham PJ, Bonner KI 2009. Predation of seabirds by invasive rats: multiple indirect

- consequences for invertebrate communities. *Oikos* 118: 420–430.
- Towns DR, West CK, Broome KG 2013. Purposes, outcomes and challenges of eradicating invasive mammals from New Zealand islands: an historical perspective. *Wildlife Research* 40: 94–107.
- Veltman CJ 1996. Investigating causes of population decline in New Zealand plants and animals: introduction to a symposium. *New Zeal Journal of Ecology* 20: 1–5.
- Wardle DA, Bellingham PJ, Boot KI, Mulder CPH 2009. Indirect effects of invasive predators on plant litter quality, decomposition and nutrient resorption on seabird-dominated islands. *Ecology* 90: 452–464.
- Warham J 1996. The behaviour, population biology and physiology of petrels. London, Academic Press. 616 p.
- Watt JC 1986. Beetles (Coleoptera) of the offshore islands of northern New Zealand. In: Wright AE, Beever RE eds *The offshore islands of northern New Zealand*. Department of Lands and Survey Information Series No. 16. Pp. 221–228.
- Whitaker AH 1978. The effects of rodents on reptiles and amphibians. In: Dingwall PR, Atkinson IAE, Hay C eds *The ecology and control of rodents in New Zealand nature reserves*. Information Series 4. Wellington, Department of Lands and Survey. Pp. 75–86.
- Wilmshurst JM, Moon NT, Wood JR, Bellingham PJ, Findlater AM, Robinson JJ, Stone C 2014. Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. *Conservation Biology* 28: 202–212.
- White PS, Walker JL 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecology* 5: 338–349.
- Wiley EO 1988. Vicariance biogeography. *Annual Review of Ecology and Systematics* 1988: 513–542.
- Wolf GM, Griffith B, Reed C, Temple SA 1996. Avian and mammalian translocations: an update and reanalysis of 1987 survey data. *Conservation Biology* 10: 1142–1154.

Supplementary Data. Rodents and associated species eradicated from Islands in Mercury Islands Ecological District (McEwen 1987) in chronological sequence updated from Towns & Broome (2003).

Location	Area (ha)	Status	Date	Rodent	Other eradications	Method used against rodents	References
Korapuki	18	Wildlife Sanctuary (Nature Reserve)	1986	Kiore	Rabbits	Ground-based: kibbled maize in silos; prefeed followed by maize dosed with bromodialone (0.005% by wt)	McFadden & Towns (1991)
Double	8 (West) +19 (East)	Nature Reserve	1989	Kiore	None	Ground-based: kibbled maize in silos; prefeed with aniseed added followed by maize dosed with bromodialone (0.005% by wt) on West Double. Hand broadcast 4 g pellets of STORM containing flocoumafen (0.005% by wt) at 18.5 kg/ha on East Double	McFadden (1992)
Stanley	100	Nature Reserve	1991	Kiore	Rabbits	Aerial spread by helicopter using modified monsoon bucket; 0.8 g cereal pellets of TALON 20 P containing brodifacoum at 20 ppm with follow-up hand spread of TALON 50WB (wax blocks) containing brodifacoum at 50 ppm; total of 17 kg/ha	Towns et al. (1993)
Red Mercury	225	Nature Reserve	1992	Kiore	None	Aerial spread by helicopter using modified monsoon bucket; TALON 20 P with follow-up hand spread of TALON 50WB; 15 kg/ha	Towns et al. (1994)
Middle Chain	23	Nature Reserve	1992	Kiore	None	Aerial spread of TALON 20 P by helicopter using modified monsoon bucket; 15 kg/ha	
Cuvier	170	Nature Reserve	1993	Kiore	None	Aerial spread of TALON 20 P by helicopter using bait spreader; 15 kg/ha	Towns et al. (1995)
Ohinau	43	Iwi (Ngati Hei)	2005	Kiore, mice	Rabbits	Aerial spread of PESTOFF 20R containing brodifacoum in two operations by helicopter using bait spreader; 8+8 kg/ha	R Chappell (pers. comm.)
Great Mercury	1872	Private	2014	Kiore, ship rats	Goats, cats	Aerial spread of PESTOFF 20R containing brodifacoum in two operations by helicopter using bait spreader; 8.8+13.2 kg/ha	P Corson (pers. comm.)

References

- McEwen WM 1987. Ecological regions and districts of New Zealand. Wellington, Department of Conservation. 63 p.
- McFadden I 1992. Eradication of kiore (*Rattus exulans*) from Double Island, Mercury Group in Northern New Zealand. Science and Research Internal Report No. 130. Wellington, Department of Conservation. 12 p.
- McFadden I, Towns D 1991. Eradication campaigns against kiore (*Rattus exulans*) on Rurima Rocks and Korapuki Island, northern New Zealand. Science and Research Internal Report No. 97. Wellington, Department of Conservation. 18 p.
- Towns DR, Broome KG 2003. From small Maria to massive Campbell: forty years of rat eradications from New Zealand islands. New Zealand Journal of Zoology 30: 377–398.
- Towns D, McFadden I, Lovegrove T 1993. Offshore islands co-operative conservation project with ICI Crop Care Division: Phase One (Stanley Island). Science and Research Internal Report No. 138. Wellington, Department of Conservation. 24 p.
- Towns D, McFadden I, Thomson P, Robertson H, Colbourne R 1994. Offshore islands co-operative conservation project with ICI Crop Care Division: Phase Two (Red Mercury Island). Science and Research Internal Report No. 142. Wellington, Department of Conservation. 12 p.
- Towns D, McFadden I, Thomson P 1995. Offshore islands co-operative conservation project with ICI Crop Care Division: Phase Three (Cuvier Island). Science and Research Internal Report No. 150. Wellington, Department of Conservation. 13 p.