Lincoln University Digital Thesis

All aboard the emergent ark:

Biogeography of the dune insect fauna of

New Zealand and Chatham Island

_____

A thesis

submitted in partial fulfilment

of the requirements for the Degree of

Doctor of Philosophy

at

Lincoln University

by

Nathan Richard Curtis

_____

Lincoln University

2011

Abstract of a thesis submitted in partial fulfilment of the
requirements for the Degree of Doctor of Philosophy.

**All aboard the emergent ark: Biogeography of the dune insect fauna of New
Zealand and Chatham Island**

by

Nathan Richard Curtis

Oceanic islands, and the processes by which they are colonised from mainland source
populations of flora and fauna, have been a major component of biogeographical research for
over half a century. This study addresses the biogeographical relationship between the coastal
dune insect fauna of mainland New Zealand (NZ) and those of Chatham Island (CI), an
outlying oceanic island some 850 km distant across open ocean.

I conducted a comprehensive entomological survey of Coleoptera, Diptera and Hymenoptera
from the coastal dune habitat of the NZ east coast and CI. Over 5000 insect samples were
collected, consisting of over 650 species. Comparison of the NZ and CI insect communities
using the survey data showed that CI has a lower number of insect species per site than NZ.
The degree to which the CI diversity was lower approximately equated with the relative dune
area available in NZ and CI.

Re-sampling techniques were used to create a null hypothesis assuming random immigration
from NZ to CI. The observed number of taxa found on CI was compared to the null
hypothesis. CI was found to have significantly fewer Hymenoptera and significantly more
Diptera than NZ.

The likelihood of a specific taxon immigrating successfully varied considerably between taxa.
The higher proportions of Diptera and lower proportions of Hymenoptera on CI appeared to
be driven by a few very successful or unsuccessful taxonomic groups. There was no clear
effect due to taxonomic order on immigration likelihood.

Factors which were deemed to have a potential effect on immigration success were modelled
using GLM models. Abiotic and biotic effects were modelled against immigration likelihood.
The factor most influencing immigration success were the relative difference in mean

temperature, taxa with an NZ range which included sites of a similar mean temperature to the CI had a higher the probability of successful immigration to CI. Immigration success was also found to be significantly influenced by the number of sites a taxon had been collected from. The more widely distributed taxa were the most successful immigrants.

Genetic analysis of mitochondrial cytochrome oxidase I sequences from six taxon groups showed that genetic divergence has occurred between NZ and CI populations. All but one of the taxon groups have a distinct monophyletic CI population. Two of the CI populations appear to derive from a NZ SI population.

Randomisation was also used to detect whether the barcoding gap between NZ and CI populations varied significantly from that of randomised samples. For all the taxa tested the genetic divergence between NZ and CI populations was significantly different from a randomly determined sample pool.

The results of this project provide valuable information for the ecology and conservation of NZ dune systems and extend the entomological knowledge of these rapidly declining areas of habitat and have given insight into the biogeographical relationship between NZ and CI dune insect populations and the factors which influence immigration between NZ and CI.

Acknowledgements

The assistance and support I have received over the last 5 years has been so much more than the sum of its parts. That said some of the more notable parts are as follows.

My initial thanks go to my supervisor Adrian Paterson, whose quiet confidence and steady guidance has allowed me to take on and complete this project. Also to Rob Cruickshank, my associate supervisor, whose advice and contributions are equally appreciated. Thanks also to my advisors on all things entomological, Rowan Emberson and John Marris, to you all – Kio ora.

For fieldwork assistance on Chatham Island, thanks to Adrian, Myles MacKintosh and Phil Servid.

Lincoln University Ecology department: I don't think I could have enjoyed such a challenging time anywhere else. The support, advice and friendship of staff and students has been invaluable.

To my wife Robyn, for her support, encouragement, empathy and fieldwork assistance, thank you.

Finally, a thank you to the William Machin Trust, whose scholarship provided the means for me to eat and drink during the first three years of the project.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

"...wherever we trace the animals in their present distributions, we find them scattered over the surface of our globe in such a manner, according to such laws, and under such special adaptations, that it would baffle the most fanciful imagination to conceive such an arrangement as the mere result of migrations, or of the influence of physical causes over the dispersion of both animals and plants.."

(Agassiz, 1850)

1.1   Overview

The intricacies of scientific study and application of scientific process can be fraught with difficulty, uncertainty and wrong turns as progress is made towards a deeper understanding of a particular sphere of study. These complicating factors can be especially great for ecologically based subjects where much of the data and theories come from observations and inductive explanations. Biogeography, the study of biotic distribution patterns throughout the world and the processes behind them, is proving to be no different. Bringing together biogeography's eclectic mix of zoology, botany, geology, taxonomy, geography, genetics, ecology, evolution and more, can be especially difficult.

The following chapter introduces the development of biogeography together with its major points of contention and developing theories. The importance of one particular aspect, dispersal, is discussed in more detail. The importance of dispersal in its application to island biogeography is looked at, as well as how arthropods achieve dispersal to islands. Also examined are the factors that potentially have a strong influence on the likelihood of a taxon successfully dispersing. The importance of southern hemisphere biogeography is introduced together with how New Zealand's (NZ) geological past has influenced its biota and biogeography geology. Chatham Island (CI) geology is also put in context relative to NZ and CI biogeography. Finally, the aims and intentions of this project are introduced together with a synopsis of the following chapters.

1.2   Introduction

Over the last 4.6 billion years (Moorbath, 1985) planet Earth has developed from a sphere of molten rock to become a life sustaining habitat of some 510,072,000 km^2 in surface area of which 361,132,000 km^2 (70.8%) consists of ocean and 148,940,000 km^2 (29.2%) of terrestrial environment (Pidwirney, 2006). Contained within these realms there is an enormous variety of environments, habitats and niches. Multicellular life has been utilising these niches and habitats for two billion years (El Albani, et al., 2010) and evolution has since produced a vast array of diverse flora and fauna that now inhabit the Earth. Currently there are some 290,000 plant species and 1.25 million animal species (Baille, et al., 2004) that are named. Habitats range from the overtly benign, such as tropical rain forests, through harsher more demanding habitats, and finally to the incredibly severe, such as deep ocean thermal vents and soda lakes.

The ability of flora and fauna to survive in the more extreme habitats has amazed and fascinated humans, prompting much research into the physiology and chemistry behind such extreme survival. However, the ability to survive in and colonise habitats is really the second half of a complex puzzle. Perhaps a more fundamental question to be asked is about where taxa in a particular habitat come from and through what mechanism or processes they reach their current habitat.

Mankind has long observed and exploited the concept of animal dispersal, although it was not until the 18th century that worldwide exploration allowed scientists to observe the extensive distributions of disparate and similar taxa in both flora and fauna. Naturalists rigorously recorded their finding in logs and journals (Darwin, 1838-1843; Forster, 1777; Hooker, 1844-1860). From these observations and recording came the beginnings of new theories to explain the distributions of the flora and fauna (Darwin, 1859; Wallace, 1855). Scientists were now thinking beyond old ideas that distributions were divinely instigated and all life radiated from a single point (Agassiz, 1850). Scientists of the 19th century produced works on the dispersal and distribution of a huge variety of taxa including birds (Wallace, 1859), marine animals (Dana, 1853), mammals (Murray, 1866) and insects (Wollaston, 1854).

In his 'Origin of the Species' (Darwin, 1859), Darwin declared his support for dispersal as a means of explaining the distributions of taxa. Darwin held the view that the world's continents were fixed and had never been in contact with one another. He concluded that distribution patterns were created as taxa moved away from the 'one spot' where the parent species resided. An alternative to Darwin's centre of origin dispersal hypothesis was proposed by Hooker (Hooker 1860), in which he suggests that the biota of some areas are so similar

that the land they inhabit must have been connected at some time in the past. Hooker's comments were perhaps the first serious thoughts on what was to become vicariance biogeography.

The word 'dispersal' can encompass a number of biological descriptions which will be addressed in a later section (section 1.4). Attempts have been made to qualify its biogeographic meaning either by declaring what dispersal is (Udvardy 1959), or what it is not (Platnick, 1976a). For the purposes of this study dispersal is defined as, the movement of members of a taxon to an area not previously inhabited by that taxon.

An alternative explanation to dispersal for the distribution of organisms throughout the world is vicariance biogeography. Vicariance biogeography was many things to many people as late as the 1950s (Macfadyen, 1954) and was still being defined in the 1970s (Croizat, et al., 1974). The derivation of the term vicariance, from the latin for substitute, gives a clue to its meaning. When an original species population is divided or split so that gene flow can no longer take place between them, each population can develop into a species different from the original species. The two (or more) new species are termed sister species (or vicariants) and have now replaced (or substituted) the original single species. Within the terms of vicariance biogeography the splitting of the original species is due to the creation of a barrier to gene flow by some event or phenomena. The wide range of potential barrier causing events have been summarized as TECO events; **T**ectonic, **E**ustatic (sea level changes) , **C**limatic and **O**ceanographic (Rosen, 1984). The essentials of vicariance biogeography are that allopatric speciation has occurred between fractions of a formerly continuous single population due to the cessation of gene flow between these new populations, brought about by a geographical barrier preventing interbreeding between the new populations (Croizat, et al., 1974).

1.3   Biogeography: birth, growing pains and petulant adolescene

"A reasonable biogeographer is neither a vicarist nor a dispersalist but an eclecticist" (Simpson, 1980)

As befits any area of scientific interest, biogeography has endured a tumultuous progress; initial data collection and exploration; formulation of initial theories that have been ardently attacked and defended; major paradigm shifts; radicalised methodologies; and bitter academic infighting, most of which continues into the 21st century.

In the 19th century most scientists considered the globe to be formed from solid rock and the geography of the land and sea in a permanent, fixed state. Dispersal then took place against this background of permanent landscape. There was, therefore, a major challenge in explaining trans-oceanic distributions. Trans-oceanic distribution patterns were originally accounted for by the presence of ancient tracts of land which had once connected the known continents of the world. These tracts of land formed 'land bridges' over which flora and fauna could travel from one area to another (Metcalf, 1923; Scharff, 1909; Schuchert, 1932; Simpson, 1943, 1946) and were given names such as Archatlantis, Archelenis, Lemuria and Tasmantis (Darlington Jr., 1938b; Ortmann, 1910; Stevens, 1980). The land bridges would have subsequently submerged beneath the oceans leaving separated continents with different biota inhabiting them.

In the early 20th century Alfred Wegener proposed and then improved upon his 'displacement hypothesis' in that the terrestrial land masses were slowly moving around the earth as part of large plates of the earth's crust (Wegener, 1912, 1915). Although he received some support at the time (Du Toit, 1927, 1937; Longwell, 1944), the majority of the geological and geophysical fraternity were dismissive. Throughout the early 20th century work continued apace into all aspects of dispersal(Camp, 1947; Coe, 1946; Elton, 1925; Fraenkel, 1932; Gadow, 1913; Ridley, 1930; Scharff, 1907). By the 1940s more biogeographers were beginning to accept the theory of continental drift and apply it to the problems of faunal distributions (Amadon, 1948; Du Toit, 1944; Longwell, 1944). All this scientific discovery and consideration can be thought to be the beginnings of the subject we now know of modern biogeography. By the late 1960s advances in geophysical methods had enabled the theories of plate tectonics and continental drift, as proposed by Alfred Wegener back in 1912, to move from ridicule to general acceptance.

The major flaw in the land bridge theory was how to explain the disappearance of these vast areas of land. Initial attempts involved whittling down the size of these bridges to allow a minimal amount of land to be explained away. However, these reduced areas or 'isthmian links' were formed from continental crust and its physical and chemical makeup meant it was less dense than the surrounding oceanic crust. Continental crust's lower density deemed it virtually impossible for its disappearance to be explained by it sinking back into the oceanic crust (Stevens, 1980). The refinement in the detection of three major geophysical phenomena in the 1950s and 60s greatly contributed to the acceptance of continental drift as an alternative to land bridges.

The potential for radioactive decay to be used in aging rocks has been known since its formulation by Sir Ernest Rutherford and Frederick Soddy during the early 20th century (Rutherford & Soddy, 1902). By the late 1950s radiometric dating was regularly being used to calculate the age of rock formations (Chapman, et al., 1955; Curtis, et al., 1958; Quinn, et al., 1957). The directional magnetic properties of rock have also been known for centuries.

By the 16th century it was discovered that the earth's magnetism also has inclination, or dip, which varies in angle depending on where on the earth's surface it is measured (Norman, 1581). When rock is created the magnetic elements within it align themselves to the direction and inclination of the local magnetic field. This information is stored within the rock, unchanging unless the rock becomes molten. Geologists can use this paleomagnetic data to ascertain where on the earth's surface rocks were created relative to the poles. Initial study of rocks around the world seemed to indicate that the poles had moved, or 'wandered' over time, as detected in the rock's magnetism. However, it was eventually realised that the continents themselves were moving relative to the poles. Coupled with radiometric dating, paleomagnetism allowed the re-creation of the earth's past continental geography (Irving, 1964). Fossil evidence, radiometric dating and paleomagnetism had all provided evidence that the continents had moved in the past and could still be moving. But the major remaining issue was explaining the mechanism behind this movement.

Research into earthquakes and atomic bomb testing helped in the discovery of the asthenosphere or 'low velocity zone', a viscous region below the crust extending 100-250+ km below the earth's surface (Gutenberg, 1960). The existence of this zone countered the argument that the earth was solid which would make continental movement impossible. Paleomagnetism was again prominent, this time in explaining the concept of sea floor spreading. New oceanic crust is created along a plate margin and the new material pushes the existing crust further apart, so expanding that area of ocean floor (Vine, 1966). By the 1960s geology and geophysics had supplied enough evidence for continental drift to be taken seriously as a theory and its implications for biogeography were being realised (Hallam, 1967; McKenna, 1972).

The late 19th century and first half of the 20th century had been dominated by evolutionary dispersalists such as Darwin, Mathew, Simpson and Darlington (Ball, 1975; Funk, 2004). The application of the theories was very much inductive, based on observations of the current distribution of extant and fossil taxa. The fact that any particular observation could be logically attributed to any number of potential dispersal scenarios led to the accusation that the theories were simply narrative or 'story telling' (Ball, 1975; Eldredge, 1981). To be

regarded as anything more than pseudo-science biogeographical theories needed to contain elements that could be empirically tested and predictions made about similar scenarios (Ball, 1975). Dispersal especially was seen as intuitive, inductively derrived and most importantly, not falsifiable or testable. It was argued that dispersal could be used to explain any possible biogeographic scenario and that predictions could not be made about the dispersal likelihood of one taxon based on observations of another different taxon (Eldredge, 1981; Platnick & Nelson, 1978). Dispersal was seen as rare ad-hoc events that did not correlate with geological processes or genealogical relationships, and therefore was not predictive (Endler, 1982). To counter this lack of testability more quantitative methods of classification were sought and introduced in the 1950s and 1960s.

Phylogenetic systematics was brought to the fore with the English translation of Willi 's 1950 book '*Phylogenetic systematics*' (Hennig, 1966). Although based his methods on a centre of origin, phylogenetic biogeography presented a method of deducing evolutionary succession based on phylogenetic relationships rather than phenetic similarities. To Henning the only meaningful relationship between taxa was a monophyletic one. The taxa contained within a monophyletic group are termed a clade, and so this method of classification was eventually referred to as cladistics. Henning's phylogenetic method was further demonstrated using southern hemisphere chironomid midge distributions (Brundin, 1966). Another quantitative classification method gaining headway in the late 1950s and 1960s was numeric taxonomy, or phonetics, e.g. (Sneath & Sokal, 1963). Phonetics took less notice of phylogentic relationships but based classification on numerical values assigned to weighted character traits. Numerical taxonomy aimed to be "*objective, explicit and repeatable*" (Sneath & Sokal, 1963). The numerical data could then be then subjected to statistical analysis. The 1960s also saw much of the work of the controversial figure of Leon Croizat. His biogeographical method involved mapping the occurrences of a great number of taxa throughout the world. Lines between these occurrences were considered tracks. Where multiple tracks coincided he called these generalized tracks, and where these generalized tracks crossed he called these points nodes. He then extrapolated a taxon's ancestral range from the generalised tracks. He called this method panbiogeography. Although Croizat recognized dispersal could occur it was deemed irrelevant to the distribution of a taxa (Croizat, 1978, 1982). However, Croizat's work was still considered too inductive (Ball, 1975). But not, needless to say, by Croizat himself (Croizat, 1978).

In the 1970s Gareth Nelson saw an opportunity to introduce a more deductive and falsifiable methodology to biogeography. He did this by combining the hypothetico-deductive

philosophy of Karl Popper with the works of Henning, Brundin and Croizat (Funk, 2004). Nelson took the non-phylogenetic but vicariance based methods of Croizat and combined them with the phylogeny based but non-vicariant methods of . He had created what is now arguably (and boy has it been argued over! (Croizat, 1982; Hull, 1988)) known as vicariance biogeography. He quickly gained support for the method with examples from Caribbean taxa (Rosen, 1975) and spiders (Platnick, 1976b). Like Croizat's work, vicariance biogeography did allow for dispersal, but in minor role, especially in regard to being the cause of sympatry (Nelson, 1974; Platnick & Nelson, 1978).

Since the late 1970s an enormous amount of biogeography based research had been carried out on huge range of taxa, from all over the globe (Colinvaux, 1998) and continues today. Many opinions were, and still are, being aired on the definition and validity of the biogeographic methods (Cracraft, 1994; Crisci, 2001; de Queiroz & Gauthier, 1992; Donoghue & Moore, 2003; Grehan, 1994; Heads, 2009; Morrone & Crisci, 1995; Nelson & Platnick, 1980). However, the crux of the disagreement continues to be whether dispersal or vicariance is the main driving process for evolution and distribution. Opponents of dispersal considered it a random happening and that theories were just 'story telling' that was not falsifiable or testable and therefore not properly scientific (Rosen & Buth, 1980). Hope however for dispersalists was to be provided in the advancement of genetic techniques.

Biochemical analysis of proteins and the idea of a 'molecular clock' had been applied to phylogenetic problems since the 1960s (Read, 1975). In 1965 Mayr suggested that "*Perhaps the logical consequence ... is to use the information in the DNA itself*", and that … "*if the method proves successful it may lead to spectacular advances in animal classification*" (Mayr, 1965). The method has proved successful and with the creation of a workable PCR technique in the 1980s a burgeoning new area of science had been created. The interest generated by this nascent subject can be seen with the start-up of two influential new journals, 'Molecular Biology and Evolution' and 'Molecular Ecology', in the early 1980s.

By the mid 1990s genetic sequencing and molecular phylogenetic techniques had progressed greatly (Goodman, 1992). Researchers could process and analyse large numbers of samples enabling the testing of a greater range of biogeographic scenarios. The idea of a 'molecular clock', in that that genetic mutation rates can be used to date the divergence times between taxa was first developed in the early 1960s (Morgan, 1998). Increased understanding of molecular clock techniques has allowed the use of the type of reliable dating techniques that Platnick and Nelson had earlier stated were needed to be able to falsify dispersal theories (Kumar, 2005; Platnick & Nelson, 1978). Ironically, scenarios that were previously seen as

congruent between phylogenies and area cladograms have now been revealed to be pseudo-congruences when a reliable temporal component is introduced (Riddle, 2005) .

Improved accuracy of divergence dates meant that taxa could be shown to have split from sister taxa much more recently than previously thought. Combined with geological data, the more recent divergence times meant that certain groups must have been separated *after* some barrier forming (vicariant) event had happened. The inference can now be made that the taxa were separated by dispersing across the barrier at a later date, rather than being separated by it at an earlier time in their history. By the 21st century dispersal was again considered a viable alternative to viacaiance (de Queiroz, 2005; Didham, 2005; Nathan, 2005; Riddle, 2005) and was often the only option that satisfied the scenarios described by the dates of separation provided by genetic data. Distributions of taxa were now being directly tested against dispersal scenarios (Hurr, et al., 1999; Noonan & Chippindale, 2006; Trewick, 2000; Zhoun, et al., 2006).

Support for all areas of biogeographical methodology continues today. High powered computers and complex software have meant vast amounts of data can be processed much more quickly. Despite this there seems no easy answer to the very complex model of biotic distributions. Different taxa show support for different theories and no theory accounts for all cases.

1.4   Dispersal, colonisation and expansion

"Dispersal, a vital aspect of zoogeography, is of prime importance for the species if it is to succeed."

(Holzapfel & Harrell, 1968)

The simple term dispersal and the underlying mechanisms cover a wide range of scenarios (Dieckmann, et al., 1999). Dispersal is often seen as the initial phase in the whole process of a taxon moving from one area to another. Dispersal may then lead to successful establishment and subsequent expansion of the taxon in the new area (Colautii, et al., 2006; Mack, et al., 2000; Shea & Chesson, 2002; Sol, 2007). Within this project the term immigration is used to encompass the whole process of dispersal, colonisation and expansion.

The initial act of dispersal can vary from a few metres to vast journeys covering thousands of kilometers being passively carried by high altitude jet streams. Dispersal is not, however, movement within a known territory or area (dispersion). Nor does it involve a regular journey

return journey from the new area (migration). As defined earlier, dispersal involves, *'the translocation of members of a taxa to an area not previously inhabited by that taxa'*. Subsequent 'dispersal' to the area by other taxon members would be termed dispersion.

Dispersal can either be active, such as flight or swimming, or passive, such as being carried by the wind and sea currents or even other fauna (Brochet, et al., 2009; Stewart & Schlichting, 1966). Dispersal can also be described as 'range expansion' or 'jump dispersal' (Giller, et al., 2004). Range expansion involves the spread of individuals from their home range into an adjacent area, often instigated by change in conditions, such as habitat or climate. The more dramatic 'jump dispersal' involves the crossing of a geographic barrier, such as a mountain range or an ocean. Although jump dispersal is seen as a rare event, it is considered an important factor in distributions and a necessity for the colonisation of islands.

Dispersal events on shorter temporal and geographic scales can be seen in the study of population genetics (Herzig, 1995; Markow & Castrezana, 2000), biocontrol (Porter, 2010), behavioural research (Antolin & Strong, 1987; Poethke, et al., 2010) and foraging (Jones & Parker, 2000) to mention but a few. However, this project is concerned with dispersal that takes place across great distances and is potentially measured over geological time. These events are known as long distance dispersal (LDD) and often involve dispersal across barriers such as seas, oceans and mountains.

Dispersal can be seen to be random (stochastic), most likely to happen only under rare extreme circumstances, but this would unfairly preclude infrequent but regular occurrences. It would also discount constant dispersal mediums, such as major ocean currents and wind systems. Is dispersal initiated by certain behaviours? Some arthropod taxa take advantage of winds by raising their wings or 'ballooning' using silk as a natural kite. Coconuts and sea bean seeds can float, and appear to have evolved to make use of oceanic currents. So traits and behaviours have evolved to help certain species to disperse, but there seems little control over the direction or distance dispersed. Finally, is there a unidirectional element to the definition of dispersal? Is dispersal in the return direction still dispersal or simply dispersion within the new range? So although the original description of dispersal was quite general it still seems appropriate and covers all options in a description of dispersal.

Dispersing to a new land area is just the start of the process for any taxon. To be effective in creating a new population and potentially a new species, successful dispersal then needs to be followed by successful colonisation. Colonisation can be seen as two distinct processes. First, a taxon must establish a foothold in the new area. This means the taxon must have suitable

conditions and be in sufficient numbers to survive, find a mate and successfully breed. Having established a taxon must then expand to a level of population growth which will allow it to overcome the possibility of short to medium term stochastic extinction (Lockwood, et al., 2005; Sol, 2007). So physical dispersal ability (vagility), establishment and expansion can be seen as three steps in the immigration process (Reaka, 1980).

Immigration research covers a wide gamut with many different taxa being subject to study. Early work included a variety of mammal, birds and insect taxa. More recent work has progressed into the realms of microbes (Marshall & Chalmers, 1997; Parker, et al., 2008) and parasites (Vogwill, et al., 2008). There has also been extensive work on the dispersal of marine organisms throughout the world (Harwell & Orth, 2002; Woodson & McManus, 2007).

For much of the late 20th century, long distance dispersal (LDD) had been dismissed as being just 'noise' and un-testable. However, the 21st century has seen a rejuvenation of the study of LDD. Associated with this wave of renewed interest comes discussion on the varied methods of testing dispersal scenarios (Nathan, 2001). Study of LDD has been playing 'catch-up' and is now spawning new and creative research approaches (McGlone, 2005). The 'raison d'etre' of LDD study may seem to be the elucidation of historical biogeographic patterns but concerns over exotic pests in an agricultural and horticultural economy, such as NZ, bring a potential applied angle to the research (McGlone, 2005).

So what drives the immigration process? A major question in the debate is whether immigration is a stochastic process, in that over time an area will eventually become populated by the random arrival of taxa (Sanmartin & Ronquist, 2004). Alternatively there may be factors, abiotic or biotic which are driving immigration along a particular route. Abiotic factors to be considered here include sea currents and wind patterns and location of the founder population (relative to the dispersal area), whereas biotic factors include taxonomic level, size, and life history of the taxa in question. The ability to disperse can also be seen as an advantageous trait that has evolved, but at detriment to other potentially beneficial traits (Nathan, 2001; Roff, 1977)

Dispersal is seen as one of the two major theories explaining the distribution of taxa throughout the world. Some research suggests vicariance as the prominent process (Allwood, et al., 2010; Boyer & Giribet, 2009; Giribet & Boyer, 2010); some propose a combination of the two (Noonan & Chippindale, 2006; Sanmartin & Ronquist, 2004; Veith, et al., 2003).

There are, however, some places in the world where the only possible method of colonisation is through dispersal, such as on newly created oceanic islands.

1.5   Immigration and islands

Population via dispersal is the only option when habitats are created anew, devoid of both flora and fauna. Although this scenario can occur within a large land area, the classic example of this situation is islands. Volcanism is often the mode from which new islands are created, especially out into an ocean, far from active plate boundaries. Over time these newly created islands become populated by taxa that have managed to disperse to the island and successfully colonise. Observations on island biogeography were ongoing from the late 1770s (Forster, 1777) and much influenced Darwin and Wallace (Whittaker, 2004). Island biogeography is considered important enough to warrant its own sphere of study, at least partly instigated by the studies of Arrhenius, Wilson and others (Arrhenius, 1921; MacArthur & Wilson, 1963; Simberloff & Wilson, 1969a). Not only are islands interesting per se but they provide 'natural laboratories' which can be observed and even manipulated experimentally (Simberloff & Wilson, 1969a).

Islands have two factors which are deemed an important influence on their biotic content. These are the size of the island (area) and its distance from other land (isolation). Low species number on remote islands was originally regarded as a factor of their isolation in that they were more difficult to reach. They would, however, fill up over time as more taxa arrived.

In 1963 McArthur and Wilson challenged the idea that islands continue to build species numbers over time with their 'equilibrium theory of island biogeography' (ETIB) (MacArthur & Wilson, 1963). They proposed that for any particular island the number of species found would be at equilibrium. This equilibrium is a function of island size, island isolation, immigration rates and extinction rates. Immigration (successful colonisation) is negatively affected by isolation in that fewer taxa will reach the island. But immigration is positively affected by size; larger islands will have more niches and less competition, especially early in the colonisation process. New taxa can also be created by speciation of taxa already present. As colonisation is contributing to the species count, extinction is removing taxa. Extinction is also affected by island size; lower total population numbers on smaller islands make taxa more suscepatble to extinction through stochastic events. Other characteristics of the taxa types and the island will fine tune the immigration and extinction rates for each specific situation. Larger islands will generally host more species.

Initial colonisation will be greater with a larger source pool from which to emigrate from. However, colonisation will slow as more species become established, although in some cases the prescence of certain taxa may facilitate the establishment of others (Fukami, et al., 2007; Weiher & Keddy, 1999). Higher species counts will also lead to lower abundance for each taxon and so increase likely extinction rates.

The species turnover rate for an island is then a function of immigration and extinction rates, both of which have numerous influencing factors. The ETIB then set the scene for further research and discussion.

In the1970s Diamond added a successional component to the ETIB. He looked further into the effects of taxa life cycle properties and habitat disturbance on species numbers and abundances (Diamond, 1974). His work culminated in the forming of his 'assembly rules' for islands. The assembly rules were soon disputed and criticised for being predictive of patterns that could be expected by random dispersal (Connor & Simberloff, 1979). Diamond, of course, disputed this criticism (Diamond & Gilpin, 1982; Gilpin & Diamond, 1982).

Like most biogeographical theories the ETIB and assembley rules have been challenged and tested in different island situations (Brown & Dinsmore, 1988; Gaston, et al., 2003; Gilbert, 1980; Morrison, 2010; Spengler, et al., 2011; Susic, 1994). Much of biogeographical research has been applicable to a specific taxon in a specific area, but all contribute to the mix of ideas which progress the island biogeography debate. The importance of island study is that it contains many examples of long distance dispersal, often overlooked in favour of vicariance studies within continental scenarios (Cowie & Holland, 2006).

The flora and fauna of many well known 'oceanic' island archipelagos have now been studied. These include the Galapagos (Andrus, et al., 2009; Benavides, et al., 2009; Peck, 2005), Hawaii (Gruner, et al., 2008; Price & Clague, 2002) and Indonesia (Walton, et al., 1997). A major focus of such studies is explaining how organisms reach islands, their provenance and movements around archipelagos once the first in the chain had been colonised. Occasionally scientists get to experience 'nature as a laboratory'. A prime example of this was the eruption of Krakatoa and the study of the recolonisation of the barren island (Bush & Whittaker, 1991; Whittaker, et al., 1989). The volcanic islands of and Sursey (Fridriksson, 1989) and Motmot (Thornton, 2001)have also been subject to study since their creation in 1963 and 1968 respectivley.

From the variety of study sites, taxa and conclusions emanating from island biogeography it is evident that further research, especially with novel taxa in less researched areas would add significantly to the ocean of knowledge currently being acquired.

1.6   Trans-oceanic dispersal of arthropods

At first thought it may seem unlikely that creatures as small as 0.5 mm can travel across hundreds of kilometres of ocean, to arrive at and colonise new land. The fact that insects do travel these distances has been shown many times. Record of insects found at sea and in the air have been sporadic but constant since the early 20th century (Holzapfel & Harrell, 1968). Sampling surveys of insects from mid-ocean have shown that a wide and varied insect fauna can be found hundreds of kilometres out to sea. Many organisms have been collected from the sea surface (Cheng & Birch, 1978; Cheng & Holdway, 1995; Peck, 1994b). Similar oceanic surveys have also collected many insect taxa directly from the air (Felt, 1925; Hardy & Cheng, 1986; Hardy & Milne, 1938; Holzapfel, et al., 1978; Holzapfel, et al., 1970; Murata, et al., 2007; Peck, 1994a; Yoshimoto & Gressit, 1963). There is also evidence that winds have enabled dispersal between Australia and NZ (Close, et al., 1978; Fox, 1973), and from Australia and NZ out to sub-antarctic islands (Greenslade, et al., 1999).

It is hypothesized that insects can be transported within logs and other plant material (Thiel & Gutow, 2005; Thiel & Haye, 2006). Transportation within wood seems especially likely for the many species that use logs as sites for eggs and larvae. There are often vast amounts of driftwood on beaches ranging in size from a few centimetres to over five metres in length, almost all of which shows the traces of insect burrows, tunnels or galleries (Curtis pers. obs), see Appendix A for CI driftwood summary. Driftwood is often observed to have travelled between land masses (Barber, et al., 1959; Darwin, 1859) and is associated with a range of invertebrate families (Chakona, et al., 2008; Haden, et al., 1999; Wheeler, 1916). Seaweed mats have also been found to contain invertebrates (Cheng & Birch, 1978; Komatsu, et al., 2008; Smith & Simpson, 2002; Vandendriessche, et al., 2007) and can be found at sea in vast numbers (Smith, 2002). Sea ice has also been suggested as a potential for dispersal of flora (Darwin, 1859; Johansen & Hytteborn, 2001). Collembola are known to use their own shed exoskeleton to double as a raft and food source (Hawes, Worland, Bale, et al., 2007). Beetles have also been found alive floating, many kilometres out at sea, without the aid of flotsam (Peter Johns pers. comm).

Surviving the journey does not seem to be difficult for some arthropods. Collembola and mites have remained alive in cold salt water long enough to endure 700 km journeys (Coulson, Hodkinson, Webb, & Harrison, 2002). Collembola from the Antarctic are able to last up to 300 days of rafting and can still produce viable young after 100 days of rafting (Hawes, Worland, Bale, et al., 2007).

1.7 Factors influencing immigration

Dispersal research has considered a number of factors which may influence or enhance dispersal opportunities. Some of these factors, such as sea and air currents, are part of the global ecosystem and are there to used by plants and animals. Taxa may also evolve physical or behavioural traits, such as size, breeding cycles or food preferences, and which allow them to proactively or passively take advantage of dispersal opportunities.

It is has been shown that flora and fauna are transported around the globe by wind and water. But can patterns of marine and air currents, or biotic traits have a bearing on population distributions and genetic structure?

1.7.1 It must be something in the water …

"Even if there is only one chance in a million that any given individual of a species will cross a given water gap, out of any million individuals some may be sure to cross"
(Darlington Jr., 1938a)

The major ocean currents of the world are known to transport material vast distances between land masses. Networks of smaller localised currents connect to these providing idiosyncratic dispersal routes and opportunities.

As discussed above, flora and fauna can travel the world using sea and air currents as a means of dispersal. However, does this simply mean there is random dispersal via these mediums or can currents account for common distribution patterns of taxa? Sea currents have been found to influence the distribtution of plant taxa (Kadereit, et al., 2005; Westberg & Kadereit, 2009). Much of the research on dispersal and fauna consists of the pelagic larval stage of marine organisms which are most affected by currents as the adults stages are often benthic and far less mobile. Studies have shown that properties, such as surface temperature and oceanic currents, can affect the genetic structure of populations (Banks, et al., 2007). Recent work has

also shown the effect of the circumpolar current on crustacean populations (Nikula, et al., 2010; Waters, 2008)

The islands of NZ and the Chathams are surrounded by a large reticulation of sea currents connecting the coastline of NZ with itself and with continents and land masses further afield (Chiswell, 2009). Some of the more direct associations with NZ are those with Australia, across the Tasman Sea. Southern hemisphere lands have been linked via the circumpolar current for over 25 my. Even older currents connect NZ to the Pacific and South-east Asia (Stevens, 1980). The currents between NZ, the Chathams and sub-Antarctic islands have also been shown to influence the structure and variability of populations (Chiswell, 2009; Goldstein, et al., 2009). It seems very likely then that the dispersal of flora and fauna and the structure of populations are influenced by oceanic currents (Banks, et al., 2007; Waters, 2008; Westberg & Kadereit, 2009).

1.7.2 And in the air …

"*Men instinctively underestimate the lifting power of air*"
(Darlington Jr., 1938a)

Major world wind patterns such as the trade winds as well as more localised wind patterns have been shown to carry organisms long distances, depositing them on land hundreds of kilometres later. Wind patterns are often the driving force behind sea currents and can also be responsible for sea current variability (Chiswell, 1996). Wind assisted dispersal is well known in plants, from grasses (Nathan, et al., 2002) to trees (Horn, et al., 2001). The small light seeds of plants are ideal for aerial transport. Amongst arthropods perhaps spiders with their 'ballooning' behaviour are the most familiar example of aerial dispersal (Horner, 1974). As with the ocean currents, it is known that wind currents transport flora and fauna, but do they help structure populations via dispersal?

Some research has alluded to the effects of aerial dispersal in structuring plant (Dos Santos & Da Costa) and animal (Darlington Jr., 1938a) populations. Wind has also been shown to enable the pollination of trees by directly dispersing the insects that perform the pollination (Ahmed, et al., 2009)

There are many observational studies that show arthropods being transported by air currents across sea and land (Coulson, Hodkinson, Webb, Mikkola, et al., 2002; Dantart, et al., 2009;

Drake, et al., 1981; Ducheyne, et al., 2007; Farrow, 1984; Feng, et al., 2007; Hawes, Worland, Convey, et al., 2007; Pathak, et al., 1999; Tronstad, et al., 2007). However, there still seems to be a paucity of genetic based studies directly linking structured arthropod populations with wind assisted long distance dispersal. In many cases plant seed and pollen have evolved to be distributed by wind and so windblown dispersal is not a surprise. What has been shown, though, is that long distance aerial dispersal is responsible for the structure of floral and possibly faunal populations across wide barriers.

Air currents around NZ and the Chathams are less consistent than the sea currents but do show patterns which are usually seasonally variable. Most wind though is in a north westerly direction from Australia to NZ partly driven by the West Wind Drift. Numerous records show that flora and fauna have been carried across the Tasman sea via aerial transport (Close, et al., 1978; Fox, 1973). More detailed studies have found that the easterly air flow has had a great influence on dispersal of plants to NZ from Australia, and other southern hemisphere lands (Heenan, et al., 2010; Wagstaff, et al., 2002; Winkworth, et al., 1999; Winkworth, et al., 2002).

1.7.3 Body size

The influence of body size on the immigration ability of a taxon was addressed early in biogeographical studies (Allen, 1876). Depending on the taxon, size can be a measure of body length, body mass, wing length (Chaput-Bardy, et al., 2010; Wiklund, 1996), and wing span (Lindstrom, et al., 1994).

From the 1920s researchers have also taken an interest in whether body size in insects has an effect on dispersal and subsequent colonisation (Anholt, 1990; Elton, 1925; Gaston & Lawton, 1988; Zimmerman, 1942). Whilst insects are amongst some of the smallest animals, there is still a wide variation in size and mass within insects, enough to potentially affect immigration ability.

Any effect of body size could be due the physical attributes it bestows on organisms, such as strength in flight, or temperature and starvation survivability. Body size could also provide an advantage or disadvantage depending on the particular dispersal vector involved. For instance, it can be argued that a small insect, say 0.5 mm, might quite easily be carried for hundreds of kilometres by prevailing winds (Vagvolgyi, 1975). Larger insects, however, might have the physical toughness and energy reserves to survive a long sea crossing buried within a log or

mass of vegetation. The relative energetic cost of flight is also lower for larger insects (Juliano, 1983). This ties in with the findings of some studies that active dispersers are affected by body size whereas passive ones are not (Jenkins, et al., 2007).

Body size in insects has been linked to dispersal behaviour (Chaput-Bardy, et al., 2010; McCauley, 2010). Flying ability has also found to be affected by body size (Derr, et al., 1981; Dingle, et al., 1980). In shrimps larger body size has led to increased dispersal ability (Reaka, 1980). It has been proposed that for some taxa then, that body size does have a bearing on dispersal ability (Dingle, et al., 1980) but not in others (Juliano, 1983). However, direct links to body size and dispersal based population structure are not evident.

Body size is widely studied and interest in the effects of body size on dispersal ability, abundance and distribution, from many different taxonomic groups are still pertinent in modern research (Gaston & Blackburn, 1996; Jenkins, et al., 2007; Woodward, et al., 2005)

1.7.4 Life history traits

Life history traits of taxa may predispose them to successful immigration. In plants, traits such as life history and life form have influenced dispersal ability (Syphard & Franklin, 2010). Some amphidromous gastropods also show how life history traits affect genetic structure of populations (Crandall, et al., 2010). Many insects, especially beetles, have eggs and larvae contained within wood. Generalist plant feeders may well be able to find sufficient food supplies from a floating vegetative mat, whereas specialist predators may not be so able to find food. The fate of parasitic taxa may depend on whether they disperse as a parasite within a host, or as a free living adult form. It has also been suggested that there is an evolutionary trade off in some taxa between dispersal ability and other potentially advantageous traits (Gibbs & Van Dyck, 2010; Yamane, et al., 2010).

1.7.5 Taxonomic level

Any particular combination of characters may lead to a taxon having an advantageous likelihood of dispersal than another. Whilst this may superficially seem to correlate with life history traits there could well be differences between the dispersal abilities of a small herbivorous weevil, a leaf mining fly and gall forming wasps based on taxonomic level rather than, for example, size or feeding guild. Care must be taken though when comparing traits between species (Harvey, 1996; Harvey, et al., 1995). Phylogeny must be taken into account

as trends and traits within a taxonomic group may be spuriously correlated with abilities of that group and cannot necessarily be extrapolated further to other groups of organisms.

"Because ecologists are interested in the traits or characteristics of species which make them more or less successful under particular ecological circumstances, it is important to take into account the fact that traits are not randomly distributed across species hence the importance of phylogenies" (Harvey, 1996)

1.7.6 Other factors

There are many other factors that could play a role in immigration. The distance that an organism needs to travel to successfully disperse can have a bearing on how many taxa ultimately reach an area. In island biogeography this 'degree of isolation' is one of the fundamental factors delimiting the makeup of the island's ecosystem (MacArthur & Wilson, 1963). Climate (Juliano, 1983), habitat (Crandall, et al., 2010) and population sex ratios (Chaput-Bardy, et al., 2010) may also have a bearing on a taxon's ability or desire to disperse and ultimately affect immigration potential.

1.8   Why has it all gone south?

"*In the southern hemisphere if we compare large tracts of land in Australia, South Africa and western South America ... we shall find parts extremely similar in all their conditions*" …

(Darwin, 1859)

Although interest and application of biogeography is worldwide, the studies of southern hemisphere biota, geography and biogeography have been subjects of intense interest since the mid 1800s (Hooker, 1844-1860; Hutton, 1896; McGlone, 2005; Ortmann, 1901; Sanmartín, et al., 2007). Specific southern hemisphere patterns of biotic distribution have long been acknowledged in both flora and fauna. The closeness of the biogeographic relationship between the South America, the sub-antarctic islands, Antarctica and NZ caused them to be defined by Miklos Udvardy (1975) as a distinct geographical area known as the Antarctic Realm. Within this he described four provinces, Insulantarctica, Neozelandia, Maudelandia and Marielandia (Figure 1-1).
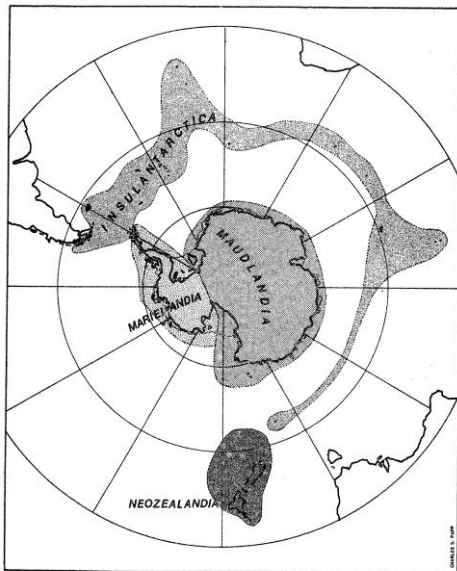
Figure 1-1: Biogeographical Provinces of the Antarctic biogeographical realm, from (Udvardy, 1975)

Most of the land currently in the southern hemisphere was once part of the ancient landmass of Gondwanaland. By the mid to late Jurassic, about 170mya, Gondwanaland had become a vast southern continent, separated from the northern lands of Laurasia by the Thethys ocean. Gondwanaland began to break up again about 160 mya and this separation continued until South America and Antarctica finally parted some 31 mya (Lawver & Gahagan, 2003). As the land broke apart each landmass carried its own collection of flora and fauna. Once separated each biota was subject to a unique selection of evolutionary forces (Scotese, 2002).

Explanations for current southern hemisphere biotic distributions have been covered by the usual biogeographic theories. Land bridges were initially proposed (Hedley, 1893; Schuchert, 1932). The break-up of Gondwanaland through continental drift prompted vicariance explanations to hold sway, dominating biogeographical views up until the 21st century. With the advent of superior molecular techniques some of these distributions have been being re-evaluated in favour of a long distance dispersal scenario (Knapp, et al., 2005).

In the wake of progressive distribution theories concerning Gondwanaland, the use of the term "Gondwanan" concerning NZ biogeography can be used to imply up to three differing scenarios (Goldberg, et al., 2008). First, a taxon can be said to have a Gondwanan distribution if it is now present in land previously part of Gondwana, e.g South American, South African, India, Antarctica, Australia and NZ. No common biogeographical process is implied in the first description. Second, an NZ taxon may also be Gondwanan if it has been present on the Zealandia land mass since it split from Gondwana. Finally, Gondwanan may also imply that

an NZ taxon evolved from ancestors that inhabited Gondwana before Zealandia split off from Gondwana and have since dispersed to NZ.

Climatic and geological processes at work in the southern hemisphere provided ample opportunity for LDD (Givnish & Renner, 2004; Munoz, et al., 2004; Waters, 2008). Wind and sea currents are known vectors for LDD. As Gondwanaland split apart new routes and opportunities were created for dispersal. Perhaps the most well known of these is the circumpolar current driven by the West Wind Drift. This combination of winds and currents circling Antarctica was set in motion 30 mya as the parting of South America and Antarctica created Drake's Passage (Lawver & Gahagan, 2003). This allowed the potential for biota to be carried around the South Pole, connecting with South America, Southern Africa, Australia, Antarctica and NZ.

Research into southern hemisphere biogeography has covered many faunal groups from chironomid midges (Brundin, 1966) and weevils (Morrone, 1998) to current molecular research into Antarctic crustaceans (Gobbeler & Klussmann-Kolb, 2010; Leese, et al., 2010). Biogeographical interest is often further focused on the area of Zealandia and NZ Interest in NZ and its immediate area is partly due to the relative 'simplicity' of the region's geological history, the long history of isolation and the large distance from a source of colonists.

1.9   New Zealand geology and biogeography

"*Geology is one of the pivotal disciplines of historical biogeography*"

(Gibbs, 2008)

Within the sphere of biogeography the subjects of geology and biology are inextricably linked. Understanding the processes and patterns within one subject helps direct and formulate ideas and understanding about the other. Fossil outcrops provide evidence for continental drift (Du Toit, 1927). Conversely the theory of continental drift has been used to explain seemingly disjunct populations. Charcoid fishes, chironomid midges and lichens are amongst many taxa whose present distribution can be accounted for by the action of continental drift (Galloway, 1988; Keast, 1971).

The country we know as NZ consists of 280,000 km^2 of land (Wright & Wood, 2008). The terrestrial portion of NZ is simply the tip of a further 3.5 million km^2 of continental crust known as Zealandia. Zealandia is approximately half the size of Australia and yet only 10% is

currently emerged above the sea (Campbell & Hutching, 2007; Mortimer, 2004). Other emergent areas of Zealandia include New Caledonia, Chatham Islands and the Sub-Antarctic islands of NZ (Wright & Wood, 2008).

Many authors have recognised that NZ's geological history comprises of many of the geological events and scenarios that provide an excellent background to testing theories of dispersal and biogeography (Daugherty, et al., 1994; Diamond, 1984; Gibbs, 2008).

1.9.1 New Zealand's geological history

The rocks that currently make up 60% of the NZ land mass began their journey over 490 mya (Campbell & Hutching, 2007). Millions of years of crustal movement led to the creation of a vast area of land stretching from the equator to beyond the South Pole (Gondwanaland) which consisted of the land that was to become the continents of South America, Africa, India, Australia, Antarctica and Zealandia. From the Ordovician period (490 mya) to the early Cretaceous (140 mya), the granite of eastern Gondwanaland was subject to a steady erosion. The eroded rock was transported into oceanic basins east of Gondwanaland where it formed into greywacke, a sedimentary sandstone, subtlety altered by the forces of heat and pressure (Campbell & Hutching, 2007). This rock remained on the seafloor until the beginning of the Jurassic (200 mya). As the Pacific plate moved towards Gondwanaland it caused a period of crustal collision known as the Rangitata Orogeny. This crustal movement squeezed the greywacke on the sea floor against the eastern edge of Gondwanaland, forcing it upwards. Much of the ancient schist found in NZ today was formed as the heat and pressure of the collision transformed the greywacke. This squeezing and uplift continued for over 100 my finally ending about 105 mya (Coates & Cox, 2002). This era of tectonic activity led to the creation of a large area of new land off the east coast of Gondwanaland destined to become Zealandia. For a period of 20 myr this area was geologically calm. The Rangitata Mountains, created over the previous 150 my, slowly eroded, washing sediments into the sea to form the mudstones and sandstones now found in east NZ. Importantly for NZ, the accumulation of layers of swampy plant material during this period is now mined as coal 90 my later.

150 mya Gondwanaland began breaking apart and the disparate land masses started to move across the globe. Around 90 mya it was Zealandia's turn to begin breaking away (Gaina, et al., 1998). On the east coast of Gondwanaland changes in the earth's crust created a new plate margin pushing between Gondwanaland and Zealandia (Bryan, et al., 1999). Over the next 20

ma this spreading sea floor forced Zealandia away to the east and in doing so created the Tasman Sea. By 60 mya the active margin had subsided (Gaina, et al., 1998).

As Zealandia moved east the crust was stretched and became thinner in depth. The thinning of the crust, combined with the weight of the land caused it to slowly sink. 90-70mya was also a period of low geological activity and subsequently no great forces to raise the land. The combination of the sinking land and 60 million years of erosion with no uplift meant that by the late Oligocene (25 mya) Zealandia had virtually disappeared beneath the sea.

Australia and Antarctica began to part 45 mya, finally separating 32 mya (Lawver & Gahagan, 2003). The sea between them is still widening today. Also around 33 mya further geological activity saw the creation of the South Fiji basin and the parting of New Caledonia from Zealandia (Stevens, 1980).

The beginning of the Miocene (25 mya) saw the beginning of the Kaikoura orogeny, a period of geological activity that still persists today. Pressure in the mantle had initiated the creation of a massive plate margin 45 my previously and by 25 mya these forces increased to a point where they had a major effect on Zealandia. The new plate margin struck through the centre of what would become NZ. In the north of Zealandia the subduction zone where the Pacific oceanic plate was diving below Australian oceanic plate created a string of volcanoes. These volcanoes created land and deposited rock from Northland to the mid and east North Island. In the south the continental crust of Zealandia was split, creating the Alpine fault. Here the Australian plate pushed under the westerly moving Pacific plate, the exact opposite to the northern situation. Unlike in the north both these plates in the south carried blocks of continental crust which did not sink but collided against one another. This collision of the plates forced the land upwards and also sideways, so that the rocks making up the west coast of NZ were progressively shunted northwards as land east of the alpine fault moved south (Coates & Cox, 2002).

The volcanism of the Miocene was not restricted to the North Island. In the south, volcanism around Dunedin and later activity at Banks Peninsula laid the foundations for the harbours of Port Chalmers, Lyttleton and Akaroa. Beyond the shores of 'New Zealand' volcanic eruptions created the sub-antarctic islands of the Auckland and Campbell islands. The late Miocene eruption of the Mangere volcano produced land in the Chatham Island area, but this was eroded away within a few million years of its creation (Campbell & Hutching, 2007).

The last 5 my have seen both the northern volcanics and southern uplift increase rapidly. The volcanoes of the Taupo volcanic zone have been created and are still active. The Southern

Alps are pushing up at a rate of 10 mm year, and were they not being constantly eroded could have been 20 km high by today (Coates & Cox, 2002). The lateral movement is even more pronounced with land west of the Alps moving north at a rate of 20-30 mm per year (Campbell & Hutching, 2007). This uplift and erosion has finally exposed the schists formed from the original Gondwanaland greywacke 300 mya.

The Pleistocene period (1.8 mya -10,000 ya) the was subject to up to 20 cycles of dramatic cooling, collectively known as the 'Ice ages' (Stevens, 1980). During these times glaciers carved mountains and lakes, moving vast amounts of rock as they did so. Sea level fell and continued erosion by glaciers and rivers deposited sediments onto the land and into the receding sea. Much of this river and marine deposited sediment was re-deposited on land by wind action as fine loess sediment.

So what of the future? NZ is currently situated on one of the most geological volatile inhabited areas of the planet (as I found during the course of my PhD). The land is split down the middle and is being rotated and subducted continuously. Volcanism is still active as are other major geological phenomena. Today we see just a snapshot of a continuous geological process stretching back millions of years. Who knows what this process will hold for NZ's biota for the millions of years ahead.

1.9.2 New Zealand's ancient biota

We get some idea of the flora and fauna that inhabited Zealandia in the past 500 my from inspecting the fossil record. Fossils also help identify the climatic and environmental conditions at the time. Much of NZ's oldest rocks were deposited in a marine environment. The oldest NZ fossils date back to the Cambrian (505 mya) and consist of marine trilobites (Campbell & Hutching, 2007). Millions of years of marine life followed, with fossils of condodonts, graptolites and fish appearing in the late Devonion (360 mya). Fossils from the late Permian (255 mya), contribute to the evidence of a Gondwanan history with a variety of marine fossils matching those from Australia. Permian rocks have revealed NZ's earliest plant fossil, *Glossopteris* which was widespread throughout Gondwanaland.

The first indication of land in the NZ area was the discovery of a mid Triassic amphibian. This amphibian fossil together with plant flora, such as *Dicroidium,* again reinforce the Gondwanan link (Holmes & Anderson, 2005). More terrestrial fauna has been discovered from the Jurassic (170 mya), including a small theropod dinosaur, a weta-like locust

(*Notohaglia mauii*) and a whole fossilised forest floor. So far these fossils have confirmed that early NZ was part of Gondwanaland, first as an offshore marine basin and then later as a raised area of land on the east coast

By the late Cretaceous (85 mya) Zealandia had completely separated from Gondwanaland (Gaina, et al., 1998). Late Cretaceous Zealandia contained a large biota; flowering plant families, ferns and trees ferns; Conifers; as well as a rich marine fauna and dinosaurs (Campbell & Hutching, 2007; White, 1999)

Initially, Cretaceous flora and fauna would have been able to cross the embryonic Tasman Sea relatively easily. Dispersing across the sea would become harder as it widened over the next 20 my. By 65 mya Zealandia had reached its current position replete with its own biota which would develop over the next tens of millions of years into a unique Zealandian biota. This unique Zelandian biota was derived from, but not the same as, the Gondwanan biota. As Zealandia was inundated in the Oligocene (25 mya), much, if not all this Zealandian biota was potentially lost as competition for space and resources caused extinctions.

Following the virtual disappearance of NZ during the Oligocene, the Miocene period (24-6 mya) saw the beginning of a slow accumulation of landmass that constitutes the NZ of today (Stevens, 1980; Stevens, 1985). Earth movement associated with the plate margin running through NZ caused the land to rise with volcanoes erupting in the Coramandel, Banks Peninsula and Dunedin areas. By the end of the Miocene (6 mya) a long thin piece of land, stretching from modern day Northland to beyond Stewart Island had been created. Alpine fault activity had created a system of geological faulting, which led to the creation of early mountains around the Wellington and Marlborough regions. Volcancoes were now prevalent in the Coromandel, Taranaki, Lyttleton and the Otago Peninsula.

Importantly for the NZ biota, the Miocene started to create land that could be dispersed to and colonised. Immigration from Australia was also enhanced by an increase in the intensity of the west wind drift (Stevens, 1985). A cross-section of Miocene biota can be seen in sedimentary deposits at Middlemarch maar and St. Bathans, both in Otago. Between them the sites have an excellent record of plants, fish, birds, reptiles, snails and bats (Campbell & Hutching, 2007).

Perhaps the most intriguing find is of some tiny fossils from the St.Bathans site. The fossils are of terrestrial mammalian origin and flew in the face of the long held belief that NZ had never been inhabited by terrestrial mammals Of course this find has raised more questions

than it has answered. Had the group survived the Oligocene drowning? Why did they die out? How many mammal taxa were there? Intriguing indeed!

By the beginning of the Pliocene (6 mya) much of the land associated with modern NZ had been created. Geological activity became more intense, activating all the alpine fault system creating much of the Southern Alps and mountains of the East Cape (Stevens, 1985). Changes to the geography of NZ produced a greater variety of habitats and also climatic zones for potential colonisation. Throughout the Pliocene the NZ climate was cooling and this culminated in the beginning of the ice age in the late Pliocene (2.2 mya). The ice age began with 12 short (40,000 years) periods of cyclical glaciation lasting until the early Pleistocene (0.85 mya). From 0.85 mya to 14,000 ya there were fewer but longer periods of glaciation. With the end of the ice age the climate became warmer and sea levels rose as the ice sheets melted.

The changes to NZ's geography and climate have profoundly affected its flora and fauna. The build up of land since the Miocene has seen a proliferation of biota immigrating to NZ. Over 23 my the climate and geography have moulded the NZ biota. The cycles of glaciations over the last 2 my has caused the extinction of many of NZ's warmer climate biota, such as *Eucalyptus* and *Acacia* (Stevens, 1980), crocodiles (Campbell & Hutching, 2007) ants and termites (Gibbs, 2008) and possibly even the 'miocene' mammals. The glacial periods also promoted the rapid speciation of alpine adapted taxa, such as *Hebes,* cicadas, kaka and gekos, which had evolved from lowland species (Gibbs, 2008; Stevens, 1980). In the period since the end of the ice age, flora and fauna has re-inhabited southern NZ. Expanding forest has been augmented by temperate adapted arrivals carried by the west wind drift. As NZ continues to change geologically and climatically, its biota too will evolve and adapt to new circumstances.

1.9.3 New Zealand's biogeography

NZ is an important part of the southern hemisphere puzzle and is interesting on many levels. It has connections with the whole of former Gondwanaland, historically and currently via oceanic wind and sea currents. NZ has more recent links with landmasses, such as Antarctica, Australia and New Caledonia. It also has its own collection of smaller islands scattered within its waters from the Kermadec Islands in the North to the Chatham Islands in the east and the sub-antarctic islands in the south. The NZ biogeographic relationships with all these areas are worthy of research and have warranted investigation.

Zealandia separated from Gondwanaland 85 mya and the idea of it moving across the Pacific with its own unique biota has spawned such phrases as 'Moa's Ark' (Bellamy, et al., 1990) and 'Gondwanan Life raft' (Briggs, 2003; Sparks & Smith, 2005). For some, the theory of moving continents was enough to explain the majority of biotic distribution throughout the world. The unique Gondwanaland fauna of NZ had remained isolated and unaffected by the rest of the world's biota, allowing us to glimpse life 'as it was' 85 mya. However, this vicariance based explanation is not supported by most recent evidence (Goldberg, et al., 2008). Long distance dispersal (LDD) had also been considered a likely source of NZ biota (Fleming, 1962, 1976).

Geological evidence also shows that from 80 mya Zealandia was slowly sinking, culminating in a period of maximum inundation 25-22 mya, the 'Oligocene drowning' (Cooper & Millener, 1993; Landis, et al., 2008). The Oligocene period of Zealandia's history is currently a fervent topic of debate based over what proportion of the the NZ landmass was eventually flooded. If the sea managed to cover the whole of the land, even for a geologically short time, then all terrestrial life would have been wiped out. This means the loss of all the Gondwanaland species on Zealandia and thus the subsequent re-population of NZ from the Miocene onwards will have been by LDD from surrounding areas, although these source populations would also have been of Gondwanan ancestry. It has been argued, quite correctly, that there is no geological proof that there was no land in the NZ region 25 mya. Conversely there is no geological evidence that there was land in the region either (Campbell & Hutching, 2007). What the geology does show is that if there was land in the NZ region then it was very much smaller in area than exists today (Campbell & Hutching, 2007). From what we know of island biogeography and species area relationships, a significant loss of biodiversity would accompany a loss of land area. So even if enough land did remain during the Oligocene for some species to survive, the majority of current NZ lineages have arrived and colonised within the last 25 my. From 25-2 mya was a period of marine regression, increasing NZ's land area. New taxa continued to arrive via dispersal, supplying the continuous cycle of immigration, evolution and extinction in the expanding new land(Stevens, 1980; Stevens, 1985).

Within the last 2 my the cycles of glaciation of the Pleistocene have also had an effect on the biota of NZ. Much of the tropically adapted taxa, survivors from when NZ was a warmer land, died out. NZ's Pleistocene legacy is a wide range of alpine adapted species of both flora and fauna (Gibbs, 2008). There are two main explanations for how the large alpine biota arose. The first is that some species already present on the wide flat grasslands quickly

adapted to the new niches, probably due to some pre-existing advantageous character trait. Another theory is that taxa already adapted to alpine conditions dispersed to NZ via suitable regions of the world (Raven, 1973). The conditions in the ice age created many isolated refugia in which led to a high rate of allopatric speciation. The fact that NZ has high rates of radiation in some taxa, but is also missing some of the world major taxonomic groups was described by Mueller-Dombois as being naturally depauperate, but secondarily rich (Gibbs, 2008).

NZ holds a unique fascination for biogeographers. It is seen in the imagination somewhere between a large island and a small continent (Daugherty, et al., 1994) and has even been described as the nearest thing to an alien biota on earth (Diamond, 1997). NZ's biota has long being viewed as of vicariant origin, relicts from ancient Gondwanaland. However, despite the long standing vicariant view of NZ biogeography the NZ biota has many of the characters expected from a dispersal based island ecosystem (Goldberg, et al., 2008). Consolidating the dispersal based position are the ever growing number of molecular studies which show taxa have dispersed and speciated following NZ's break away from Gondwanaland. Molecular studies also show that NZ biota also has a strong Pacific connection as well as the much vaunted 'Gondwanan' link (Miller 2007).

NZ was once the once the archetypal example of a vicariance which is now being seen in a new light as an example of how effective dispersal and rapid speciation can be in creating a unique ecosystem. The story of NZ is slowly unravelling but is a long way off being completely told. Further molecular studies, an open mind and an eye for new data are urgedto progress this most intriguing biogeographic conundrum (Goldberg, et al., 2008).

1.9.4 The Chatham Islands and the Chatham Rise

NZ has a number of smaller, younger islands surrounding it. The Chatham island archipelago is one of these. It lies 850 km east of Christchurch, NZ at 43° 53′ 0″ S, 176° 31′ 0″ W. It consists of three main islands: Main Chatham (92,000 ha), Pitt (6400 ha) and Rangitira (249 ha) as well as numerous smaller islands and rocky outcrops, including The Sisters and The 44s (Miskelly, 2008). Unlike a typical Pacific volcanic island the Chatham islands are an eclectic mix of ancient rocks, recent sedimentation and volcanics (Campbell, et al., 1994).

The Chatham Islands are a small emergent part of the Chatham Rise; a long ridge of elevated sea floor stretching for over 1000 km eastwards from Banks Peninsula. Like the rest of

Zealandia it is comprised of continental crust and follows a similar geological history to that described for Zealandia. In this respect the Chatham islands are very important as they are a rare opportunity to see the stratigraphic record from Zealandia on land that has not been subject to the deformations of the last 25 my (Campbell & Hutching, 2007).

Since the parting with Gondwanaland, the Chatham Islands have remained in the same position relative to the NZ east coast as they are now. The Chatham Rise was most likely submerged about 90 mya and since this time volcanism has been the main creative force in the Chatham island area. Most of southern Chatham Island is formed from material laid down about 80 mya by a large shield volcano centred in what is now the Pitt Straight (Campbell & Hutching, 2007). Pliocene volcanics 6-2.7 mya created many of the outlying islands and high peaks found on the north of Chatham Island. The Managere volcano 5 mya created land but subsequently eroded away and the Chathams were once again below sea level. A further combination of volcanism and mantle instability 3-5 mya caused the Chathams to re-emerge above the sea, where they still remain (Campbell & Hutching, 2007; Timm, et al., 2010).

The biogeographical history of the Chatham Islands had, until recently, been seen as similar to that of the NZ mainland. It was thought that there had been a terrestrial presence in the Chatham area for at least the last 70 my (Emberson, 1995). Whether the Chatham Islands had been totally isolated during this time or had closer connections to NZ was a point of conjecture. Some saw the Chatham islands as a 'mini moa's ark', containing ancient Gondwanan lineages, whereas others viewed the current biotic composition of the Chatham islands as evidence of some closer connection with NZ since 70 mya (Emberson, 1995).The discovery that the Chatham islands emerged above sea level no more than 5 mya (Campbell, 1998; Campbell, et al., 2006) changed this view of things. This 'recent' emergence means that all flora and fauna currently on the island must have arrived and colonised within the last 3-5 my. Clearly all terrestrial species in the archipelago have had to arrive in the Chatham islands by over water dispersal. This scenario is ideal for the study of dispersal effects and their factors.

The Chatham Rise plays an important role in the potential dispersal of biota to the Chatham Islands. The warm East Cape Current flows southwards down the east coast of NZ where it meets the Chatham Rise (Chiswell, 1998). Flowing up from the south is the colder and less saline Southland current. They meet over the Chatham Rise forming the Subtropical Convergence where they are then directed towards the Chatham Islands (Goldstein, et al., 2009). This sea current corridor must certainly be a force in directing large amounts of vegetative matter from NZ to the Chatham Islands. Simple observation of Chatham Island

beaches shows a far greater amount of driftwood (and plastic bottles) on the western coast than the eastern coast (N. Curtis pers. obs).

1.9.5 NZ / CI biogeographic research

Despite the suitability of the New Zealand / Chatham Islands relationship as a potential study site for island biogeography relatively few biogeographic studies have been performed. As with the NZ scenario, vicariance was an early favourite to account for the biotic distributions of the Chatham Islands (Craw, 1989). More recently molecular data has been used to ascertain the likely mechanisms behind Chatham Island distributions of fauna and flora. In their work on NZ cockroaches, Chin and Gemmell (2004), proposed an eastern south island, dispersal based origin for the CI species *Celatoblatta brunni* (Chinn & Gemmell, 2004; Heenan, et al., 2010; McGaughran, et al., 2006; Trewick, 2000) and flora (Shepherd, et al., 2009; Wagstaff, et al., 2002).

1.10 Summary

From the wide range of topics covered in the introduction it is clear that biogeography is a complex subject. Biogeography is a concept that has intrigued science for centuries but yet has only evolved as a subject with a scientific basis replete with theories and thorough methodologies within the last 150 years. Much of the academic discussion has been over the viability of two major theories of distribution, vicariance and long distance dispersal. Both have had their proponents and both are still held up to be the primary process behind global biotic distribution.

The importance of geological history in biogeography has been shown and the geological history of the NZ region described. This is linked in with the fauna and flora that existed in the NZ region over time and the effect the geological history has on NZ biogeography.

Dispersal is viewed as the most likely method of distribution in the NZ/CI scenario. Dispersal is discussed and described together with examples of dispersal based research. The role of molecular phylogenetics in promulgating the dispersal theory is also shown. Finally, factors that affect dispersal and alter the chances of it being successful are mentioned and described.

1.11 Overview of project aims and goals

Much biogeographic research has concentrated on one geographic area or a specific taxon, often generalising biogeographic theories based on the results. This project will also focus on one particular geographic area and a specific range of taxa within it. The study concentrates on the mechanisms of trans-oceanic dispersal with particular reference to the colonisation of an oceanic island by a mainland insect fauna. The mainland in question is that of NZ and the oceanic island is Chatham Island (CI), the main island in the Chatham Island archipelago.

The study will examine the sandy shore insect fauna of NZ and CI and will test whether particular chosen traits, biotic or abiotic increase a taxon's chance of successfully emigrating to CI from NZ. The study will concentrate on the orders of Coleoptera, Diptera and Hymenoptera.

Selected coastal locations on the NZ mainland and CI were sampled for their insect fauna. The insect fauna collected was identified as accurately as possible (no small feat in itself). Using this data the question of the probability of a taxon dispersing to the CI was addressed. The field work for the study took place over a period of 4 years, 2005-2009. Collection events took place between late November and February, dependent on availibility of site access and transport/accomodation. A re-sampling technique was devised to create a null hypotheis of an expected CI dune community created from random immigration from NZ.

The study will also include genetic analysis of taxa that inhabit the NZ mainland and CI that are currently considered of the same species on both. Genetic divergence will be tested for and commented on.

Throughout the study re-sampling and randomisation techniques will be used to introduce quantitative analysis to the biogeographical scenarios. Metrics created by the re-sampling will be statistically tested against generated null hypotheses to assess the level of significance of the observed data. This quantitative approach will be used in the context of taxon count data as well as molecular data.

1.12   Summary of project aims and goals

1)   Sample from NZ and CI sandy shores habitat to:

    a.   Add to body of knowledge of NZ sandy shore insect biodiversity

    b.   Create a dataset in order to analyse the effect of biotic and abiotic traits on a taxon's likelihood of dispersing to CI from NZ

2)   Addresses the methodology and techniques used to collect and process the insect samples necessary for this project

3)   Examine the differences in insect dune fauan between NZ and CI.

4)   Assess wheter prescribed biotic and abiotic traits influence a taxon's likelihood of dispersing to CI from NZ

5)   Examine the genetic divergence between NZ and CI populations with a view to assessing whether CI populations can be considered separate species.

1.13   Summary of following chapters

1.13.1 Chapter 2

The second chapter addresses the methodology and techniques used to collect and process all the insect samples necessary for this project. General trends in the data are highlighted and the efficacy of the trapping methods is evaluated. The process of identifying the samples and the degree of unidentified taxa and its impact on the project is also examined. The importance of 'natural history' in general is discussed and extended to encompass NZ and especially the study of NZ and world dune insect taxa.

1.13.2 Chapter 3

This chapter analyses the degree of difference in the taxon proportions between NZ and CI. Differences are examined over three main taxonomic levels.

1.13.3 Chapter 4

The effect of factors with the potential to influence immigration success are analysed. Anlysis of immigration success is performed by modelling the likelihood of dispersal against the factors using GLM modelling. Variables used include climatic, geographic and biological factors.

1.13.4 Chapter 5

Many of the insects found on CI are regarded as being the same species as exists on NZ. It is likely, however, that genetic flow between the two populations (NZ & CI) has slowed dramatically or ceased all together. In either case the two population's genetic makeup will be slowly diverging. The level of divergence is looked at by using data gathered from sequencing the COI gene of six species. The genetic distance between the current NZ and CI populations are compared to randomised NZ and CI populations from the same samples. Phylogenies of the six taxa will be used to ascertain whether the CI populations are more likely to have originated from the North or South Islands of NZ.

1.13.5 Chapter 6

Chapter six provides a summary of the complete study. It briefly comments on the major topics addressed in the the project and pertenant results and findings. The approach, methods and techniques used in the study are dicussed in relation to usablity and whether they achieved their purpose. The direction of potential future work is also discussed.

Chapter 2

The insect fauna of New Zealand and Chatham Island sand dune habitats: Sample collection and inventory collation

2.1   Introduction

The study of organisms, their habits, habitats and life histories has often been associated with the age of the amateur gentleman naturalist, enthusiastically collecting and pinning exotic butterflies and beetles for a collection. However, the importance of sound taxonomy, accurate surveys and comprehensive inventories of a region's fauna is now being realised by governments and conservation organisations. Novel use of new technology, such as the internet, has allowed collaboration on a global scale and helped to offset problems, such as the shortage of taxonomic experts and the difficulty in disseminating pertinent information and literature.

The data provided from inventories is used to address many ecological and environmental issues. The disparity between two communities, whether temporal or spatial, can be used to provide insight into the effects of impacts, such as pollution or conservation measures. Gauging the effect of environmental conditions, e.g. climate, altitude or latitude, on community composition is another use for inventory data.

Chapter 1 covers the importance of natural history in the study of biological and ecological phenomena. This importance is further examined in the context of the natural history of New Zealand (NZ) and Chatham Island (CI) insect fauna, especially those of the sandy shore habitat. The specimens for creating an inventory of NZ dune insect species and producing presence/absence matrices were collected from sand dune habitats on the south and east coasts of NZ and around main CI.

2.2   The study of 'Natural history'

"*A biotic inventory is the inaugural step in knowledge generation … It follows that biotic inventories constitute core discovery processes; investigators across all the sciences exploit these discoveries for derived and/or synthetic knowledge*"

(Cotterill & Foissner, 2010)

All scientific subjects, and more especially ecology and biogeography, have their basis in sound data collection and observation. The observing, ordering and describing of nature, or 'natural history', has been an essential factor in attempts to understand the world for thousands of years (Godfray & Knapp, 2004; Herman, 2002; Penev, et al., 2008). The recognition of 'natural history' as a specific area of interest and study developed in the 17th and 18th centuries and covered the areas of zoology, botany and geology or mineralogy (Bartholomew, 1986; Cotterill & Foissner, 2010). From even this loose description it can be seen how the concept of natural history was, and still is, important to the study of biogeography. Biogeography, recording and explaining the distribution of species, has arisen from the detailed records and observations of such enthusiastic and diligent natural historians as Humboldt, Darwin, Wallace, Banks, Solander and Hooker (Herman, 2002; Lomolino, et al., 2004)

Most biogeographic study is based on observing the natural history of an area and recording of the presence (and absence) of taxa. Biogeographic theories can then be extrapolated from these data. Some major pieces of biogeographic study have culminated from large and extensive studies on one particular taxon and from one specific geographic region (Brown, 1971; Brundin, 1966; Diamond, 1974; Wilson, 1959). Taxon distributions may also include the fossilised remains of extinct ancestors. Biogeographic study relies on accurate taxon identification, accurate distribution records and often an understanding of the phylogenetic relationship of the taxon or taxa involved in the study. All these criteria stem from sound taxonomic study, a fundamental aspect of natural history study (Gotelli, 2004a; May, 2004; Wilson, 2004).

The study of natural history is not always seen as 'proper science'. Over the last 150 years science has become more compartmentalised with experts and specialists studying their own narrow fields of study (Bartholomew, 1986; Dayton, 2003). Ecological study is particularly prone to this reductionist approach to science as researchers attempt to understand specific pieces of a vastly complex puzzle (Coreau, et al., 2010; Inchausti, 1994) An increased level of specialisation in ecology has led to a pervasive '*denigration of natural history*' and a loss

of an appreciation for its fundamental importance (Cotterill & Foissner, 2010). However, Cotterill and Foissner (2010) argue that only the unique information gained from focussed, specific observations leads to an understanding of the natural history of organisms allowing more generalised, all encompassing models and laws to be formulated and applied (Cotterill & Foissner, 2010). Rigorous taxonomy and the construction of inventories can be fundamental to gaining the specific knowledge that supports the development of ecological concepts, models and laws.

"Unprecedented advances in knowledge are set to follow on consummate inventories of biodiversity"

(Cotterill & Foissner, 2010)

"…, the need for concrete natural history information—basic data on where species exist, what they need to thrive, and how fast they can move from one place to another—is in greater demand than ever before in human history "

(Network, 2007)

In order to conduct a meaningful survey the ability to accurately identify taxa, often to species level, is crucial (Gotelli, 2004b). Identification is fraught with potential pitfalls. The description and publication of taxonomic keys for a group of insects can be a lifetime's work. Reduced funding for taxonomy has led to fewer accessible taxonomic experts and subsequently fewer newly trained researchers to fill academic positions (Godfray & Knapp, 2004; Network, 2007; Wilson, 2003). The paucity of taxonomists can lead to large gaps in the published works for a geographical (or subject) area, especially where difficult or less prominent taxa are concerned. Despite this, thousands of new species are identified and described each year (May, 2004). The many thousands of taxonomic groups, coupled with evolutionary and phylogenetic factors, mean that establishing a fully accepted, accurate and complete species list for any region is extremely difficult (Isaac, et al., 2004).

Taxonomic descriptions (of Animalia) increased steadily from the mid 16th century to 1914. World wars, reduced funding and resources have seen the number of annual descriptions fall gradually until c.2000 (Sarkar, et al., 2008). However, taxonomy is a vital part of realising the extent of global biodiversity (Padial, et al., 2010; Wheeler, et al., 2004). Since 2000 global initiatives to describe the world's species and make this information widely available (Clark, et al., 2009; Global Biodiversity Information Facility, 2010; Polaszek, 2005; Species 2000, 2010) has seen taxonomic descriptions return to a yearly rate comparable with the early 20th

century (Sarkar, et al., 2008; Zhang, 2008). The increase in annual taxonomic descriptions and information dissemination being is further mediated by the exponential growth in digital and on-line information. Taxonomic information can be digitised, data-based and compiled into formats accessible to many researchers throughout the world (Global Biodiversity Information Facility; Species 2000, 2010; Wilson, 2003). Specific taxonomic journals e.g. ZooKeys and Zootaxa, and especially those with on-line open access (Eysenbach, 2006), encourage and stimulate interest and participation in this important field of science. Taxonomic descriptions of animal life now hovers around 19,000 new species a year with almost 20% of these new descriptions appearing in Zootaxa (Zhang, 2008).

Natural history surveys and inventories are not just important for biogeography. Conservation relies heavily on knowing the distributions of taxa and their levels of abundance (Dayton, 2003; Mace, 2004). The 21st century is seeing a rapid decline of the world's natural ecosystems. A manifestation of this decline is the recording of large numbers of biological extinctions (the 'sixth great extinction') (Barnosky, et al., 2011; McCarter, et al., 2001; Trombulak & Fleischner, 2007). An understanding of natural history and its processes are seen as going someway to ameliorate this ecological trauma (Network, 2007; Trombulak & Fleischner, 2007). Effective conservation of taxa and ecosystems ultimately depends on a thorough knowledge of the organisms under scrutiny (Greene, 2005).

Temporally based comparative studies can aid research into the potentially damaging effects of pollution and climate change. The basic importance of the natural history survey can be seen by the enormous number of surveys carried out by conservation based institutions throughout the world: United Nations (United Nations Environment Programme, 2010); Caribbean (CARMABI, 2010), Vietnam (Hurley, 2002), and Russia (Vinogradov & Kamennova, 2004). Further important spheres of human interest enhanced by an knowledge of an organisms' natural history, include crop protection (Dwomoh, et al., 2008), health (Butler & Friel, 2006) and climate change (Deutch, et al., 2008).

Coastal regions of the world are just one of the many vulnerable types of habitat that are under pressure from human induced pressures. These pressures include habitat destruction, pollution and introduction of invasive alien species (Garmendia, et al., 2010; Putten, et al., 2005; Scapini & Ciampi, 2010) . To gauge the degree of pressure that a coastal area is under it is essential that the composition of the flora and fauna is known. Coastal management, restoration and conservation programs are in effect throughout the world. However, much of this work is concerned with the physical structure of the dune systems, with most conservation and restoration projects concentrating on the floral and vegetative make up of

dune systems (Nordstrom, et al., 2009; Peyrat, et al., 2009; Torres, et al., 2010). Surprisingly, especially in the light of the importance of the natural history of an area and the importance of inventories, there is relatively little research into the insect fauna of dune systems. In fact, Howe comments that apart from one U.K survey (Buglife, 2003)

"… there has been no published attempt to identify all the invertebrate species that are dependent upon or strongly associated with coastal dunes, either in Europe or within the UK"

 (Howe, et al., 2010).

Dune insect inventories would seem to be a conservation priority as arthropods are especially useful in responding relatively rapidly to environmental stresses (Kremen, et al., 1993; Rainio & Niemela, 2003). Dune systems are also known to be rich in thermophilic invertebrate fauna and often contain rare hymenopteran species. Dunes can also provide a refuge for insect fauna affected by destruction of other native habitats (Howe, et al., 2010). Although some inventories have been published (Majka, et al., 2008), most research on dune insects has focused on the effect of the environment or management on specific invertebrate groups (Aloia, et al., 1999; Gheskiere, et al., 2005; Huntzinger, et al., 2008)

2.3   Natural history study in New Zealand

"This morn We took our leave of Poverty bay with not above 40 species of Plants in our boxes, which is not to be wonderd at as we were so little ashore and always upon the same spot; the only time we wanderd about a mile from the boats was upon a swamp where not more than 3 species of Plants were found"

Joseph Banks (Beaglehole, 1962).

With the arrival of Captain James Cook and his crew in October 1769, NZ became subject to the zoological and botanic scrutiny of European science (Beaglehole, 1962). Following on from the original work of Banks and Solander (Duyker, 1998) the last 250 years have seen a wealth of data gathered pertaining to the unique biota of NZ. Much of NZ's biota, however, unlike its land, is still an undiscovered country.

"A thorough knowledge of our biota is the essential basis for environmental and applied biology in New Zealand"

(Watt, 1976).

Both globally and within NZ, insects and other invertebrate groups comprise the vast majority of animal life (Watt, 1975). Insects play vital roles in ecological processes, such as organic decomposition, soil structuring and pollination (Patrick, 1994). Like all areas of the world, NZ contains its own unique biota. NZ's history of geological change and isolation has led to over 90% of NZ insect species being endemic (Patrick, 1994). At genus level endemism is high, although the only endemic insect family in NZ is the forest dwelling Mnesarchaeid moths (Gibbs, 2008; Gibbs, 1979; Watt, 1975).

Current estimates of described NZ insect species range from 10,000 to over 20,000 (McGuiness, 2001; Patrick, 1994; Watt, 1975). Bearing in mind NZ's innumerable islands, wide climatic, altitudinal and latitudinal range and areas of virtually inaccessible native bush, this current species range estimate could be substantially lower than is eventually realised. The need for accurate surveys and inventories leading to the creation of descriptions and keys of NZ insects has long been recognized amongst NZ entomologists (Watt, 1976). Previous studies have set out to record the fauna of a particular area or region (Emberson, 2006b; Hutcheson, 1992; MacFarlane, 1979; Marris, 2000). More specific surveys have been associated with specific restoration projects and pollution monitoring (Jamieson, 2010; Winterbourn, 1998). Since 2000 some inventories of the major insect orders have been produced and published; Coleoptera (Leschen, et al., 2003); Hymenoptera (Landcare Research, 2009); Diptera (MacFarlane, et al., 2000); and Hemiptera (Lariviere, 2005 (and updates)). Realisation of the importance of comprehensive, cohesive inventories has seen NZ involved in programs to formulate regional databases of the world's fauna (Species 2000, 2010). A spin off from the Species2000 program has been the New Zealand Organism Register (NZOR, 2010), a three year project to catalogue the names of all NZ taxa.

Being a long, thin island nation, NZ's 11,000 km of coastline (Hesp, et al., 1999) forms a significant and important part of its natural environment. However, the coastal habitat and its native biota are being destroyed and degraded by human activity, including building projects and introduction of exotic species (Hesp, et al., 1999; Hilton, et al., 2000; Konlechner & Hilton, 2009). It has been estimated that the area of NZ's unstable foredune habitat has fallen by 70% from 129,999ha in the 1900s to around 39,000 by the 1990s, and is almost certainly still declining (Hilton, et al., 2000). If stable rear dunes are factored into the estimate, barely 10% of 305,000ha of dune exists in anywhere near to pristine state. Coastal dune restoration projects are common and seek to ameliorate the effects of coastal damage (Dune Restoration Trust of New Zealand, 2007; Jamieson, 2010). The progress and efficacy of these projects is often recorded by the use of surveys and inventories of both flora and fauna.

In common with many studies around the globe, much research into dune ecosystems in NZ has been concerned with the floral communities and the effects of exotic dune grasses (Jamieson, 2010; Sykes & Wilson, 1991). Even so, there has only been one plant based nationwide assessment of NZ sand dune conservation status (Hilton, et al., 2000): the 1992 sand dune and beach vegetation inventory of NZ (Johnson, 1992; Partridge, 1992). Those surveys which do concern insects are often unpublished and not widely available (McFarlane, 2010). However, some small scale dune specific invertebrate surveys have been carried out. La Cock and Stanley (2007) compared the beetle fauna of the two dune grasses, native spinifex (*Spinifex sericeus*) and exotic marram.(*Ammophila arenaria*) (La Cock & Stanley, 2007). Christchurch City council's report by MacFarlane is one of the more comprehensive dune based surveys from NZ, covering the major insect orders (MacFarlane, 2010). Despite these surveys more widespread and thorough inventories are needed to provide an insight into NZ's dune system fauna and its conservation status (McGuiness, 2001).

"In New Zealand, however, there is relatively little published information on the flora and fauna of dunelands, active or stabilised, the location of dunelands, the conservation status of dunelands or trends in duneland condition"

(Hilton, et al., 2000)

" ... a national biological survey is very desirable. Such a survey would be an inventory of the biota and an account of the main characteristics of the species found here"

(Watt, 1976)

2.4 Collection of samples and collation of inventory

2.4.1 Aims

The major aims of the data collection phase of this study are:

1) To create an inventory of selected insect orders found on sand dune habitat from the south and east coasts of mainland NZ and the beach habitat of CI.

2) To create a physical collection to be deposited in the Lincoln University Entomological Research Museum.

3) To collect data to examine the biogeographical relationship between NZ mainland and CI dune based insect communities (The biogeographical relationship itself will be examined in future chapters).

4) Design and appraise a methodology for collection and processing of insects samples from the dune habitat. Data assessed to include trap efficacy, size range of samples collected and the level at which confident identification of the samples is made.

2.4.2 Study area

Dune habitats were selected from the NZ mainland and CI. CI is situated 850 km east of the NZ South Island at 44' S 176' W (Figure 2-1)
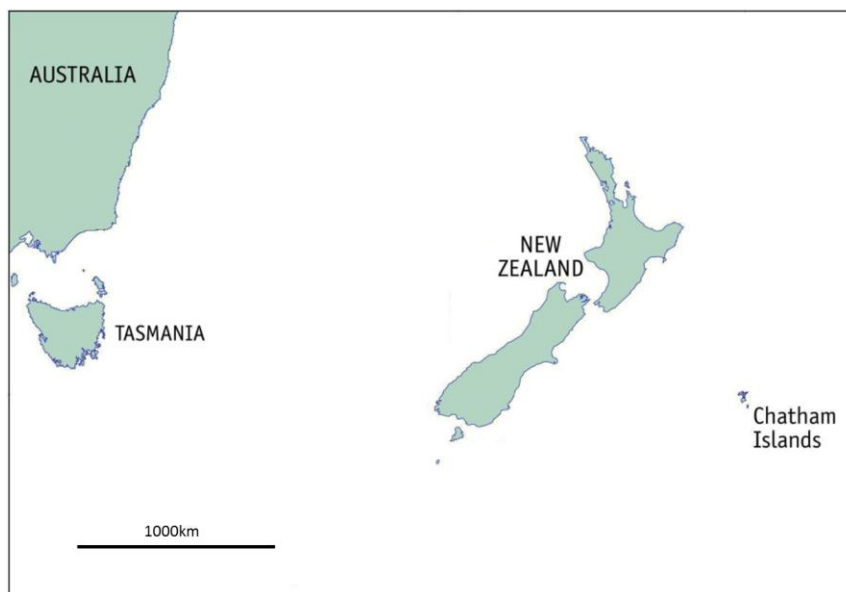
Figure 2-1: Location of CI, relative to NZ and the east coast of Australia.

NZ is ideally located for biogeographic and dispersal based studies, being an isolated landmass, uniquely positioned amongst major tidal and air currents. NZ's position allows it to be both a point of arrival for dispersed fauna, mainly from the west (Australia) and north/north-east (South East Asia and the Pacific islands), and a source of fauna for smaller islands to the south (sub-antarctic islands) east (Chatham islands) and north west (Pacific islands) (Fleming, 1976).

The physical relationship between NZ and CI is ideally suited for testing biogeographic scenarios. The CI shares the same continental crust with NZ and once shared similar Zealandian flora and fauna. However, over the last 60 million years the CI area has been

submerged and emergent several times, most recently emerging above the sea no more than 3-5 mya (Campbell & Hutching, 2007; Coates & Cox, 2002; Stevens, 1980). Therefore, all previous terrestrial life on CI has been lost and the community we see today must have dispersed across 850 km of ocean and successfully colonised CI within the last 6my. The wide stretch of ocean separating the CI from NZ is large enough to potentially create an effective barrier to dispersal and, therefore, provides an opportunity to test whether insect dispersal is affected by such a significant barrier.

2.4.3 Collection sites

A number of criteria were used to select sites for this study. All mainland sites were located in areas where the passing ocean currents followed the coast of NZ towards Banks Peninsula and then out towards CI via the Chatham Rise. The sites were sand dune habitats, with a beach front leading back to grasses and low shrubs and progressing to larger shrubs and trees. All sites needed to be accessible enough to transport collecting equipment and to enable visits throughout the survey period. The sites on CI were chosen to provide a sample of beach habitat from the west, north and east coasts of the northern half of CI (Figures 2-2, 2-3; Table 2-1).
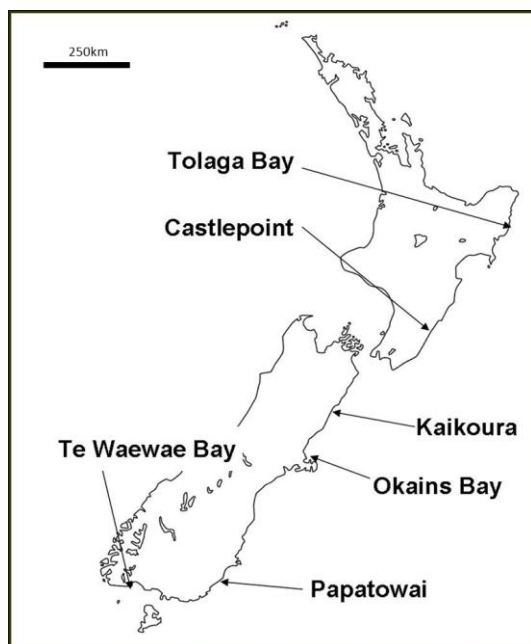
Figure 2-2: Location of New Zealand collection sites
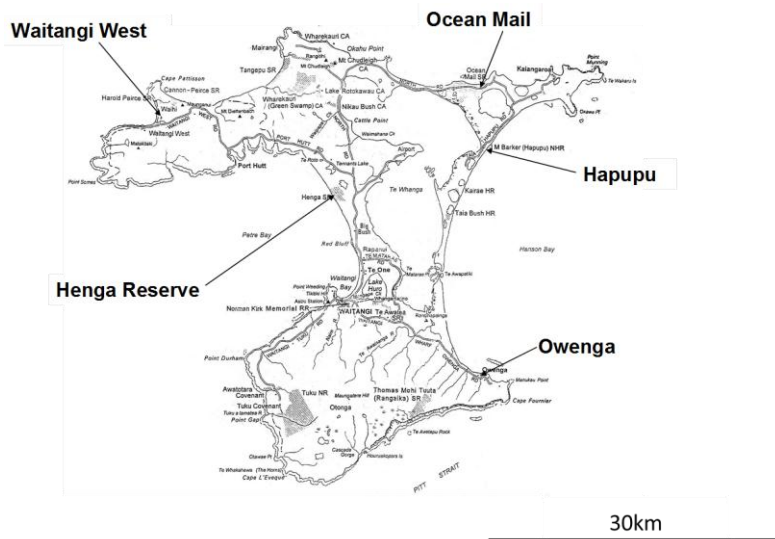
Figure 2-3: Location of Chatham Island collection sites.

Table 2-1: New Zealand and Chatham Island collection sites with geographical and collection information.

Study site	Label	Island	Grid ref		Date collected
Tolaga bay	TB	North Island	38.382589 S	178.317429 E	Jan 2009
Castlepoint	CP	North Island	40.835730 S	176.249921 E	Jan 2009
Kaikoura (Peketa)	KK	South Island	42.433929S	173.589161E	Jan 2007
Okains Bay	OB	South Island	43.696555S	173.063602E	Nov 2006
Papatowai	PT	South Island	46.557158S	169.494958E	Feb 2007
Te Waewae Bay	TW	South Island	46.156701S	167.518446E	Dec 2008
Henga Reserve	HG	Chatham Island	43.856316 S	176.572266 W	Nov / Dec 2005
Waitangi West	WW	Chatham Island	43.78448 S	176.814308 W	Nov / Dec 2005
Ocean Mail reserve	OM	Chatham Island	43.739352 S	176.362152 W	Nov / Dec 2005
Hapupu	HP	Chatham Island	43.807774 S	176.345673 W	Nov / Dec 2005
Owenga	OW	Chatham Island	44.018496 S	176.345673 W	Feb 2007

2.4.4 Collection of specimens

Selected coastal locations on NZ and CI were sampled for their insect fauna. The field work for the study took place over a period of 4 years, 2005-2009. Collection events took place between late November and February, dependent on availibility of site access,transport and accomodation. All samples were transported to the laboratory for sorting, mounting and identification.

The more insect taxa that could be collected during the project the better, allowing analysis to be performed across a wide a range of insect types as possible and with as high number of taxa as possible. Maximizing the number of taxa sampled had to be performed within the confines of the time and budget of the project. Logistically this meant limiting the taxa to be focused on and using trapping methods to maximize sampling of the chosen taxa and at the same time be logistically feasible for one, or occasionally two, people to manage.

Initially, five orders of insects were proposed for sampling, as well as any spider fauna that was collected in the traps. The original five orders were Coleoptera, Hymenoptera, Diptera, Hemiptera and Lepidoptera. These five were chosen as they contain the highest number of recorded species thus providing a wide range of potential samples (Watt, 1975). These orders are also relatively well studied and described in the NZ context.

Following the initial collecting fieldtrip on the CI and the processing of samples it was decided that two of the insect orders (Lepidoptera and Hemiptera) and the spiders were to be dropped from the survey. This was due to low sample numbers for Hemiptera and Lepidoptera as well as the difficulty of providing a consistent seven nights of light trapping for Lepidoptera. For the spiders, sample counts proved satisfactory but the time needed for processing and identification proved to be prohibitive for this study, although see Appendix B for information on new spider records to CI.

The collecting methods used for this study were chosen to maximize the variety of insect fauna sampled. Sampling methods used were, malaise traps, pitfall traps, yellow pan traps and beating. The tent like malaise trap was invented in the 1930s (Malaise, 1937) and is designed to trap phototactic flying insects. The efficacy of

malaise traps can be affected by the weather and positioning (Ozanne, 2005). They are effective at sampling taxa, such as Diptera, Hymenoptera and Lepidoptera (Campbell & Hanula, 2007; Jennings & Hilburn, 1988; Ozanne, 2005). Pitfall traps target epigeal insects and are a good method of comparing the community structure of different areas (Landcare Research, n.d.; Perner & Schueler, 2004). Pitfall traps are particularly useful for sampling ground beetles (Carabidae) and rove beetles (Staphylinidae) (Woodcock, 2005). Moericke yellow traps or yellow pan traps (Mazon & Bordera, 2008; Monsevieius, 2004) catch a wide range of flying insects and are commonly used for insect surveys (Young, 2005). Yellow pan traps are effective for Hymenoptera and Diptera (Campbell & Hanula, 2007; Cane, et al., 2000; Landcare Research, 2009) and flying Coleoptera (Leksono, et al., 2005). The sampling methods mentioned here were all simple to transport, easily set up and could be left for 2-3 days if necessary before emptying. To increase the variety of potential specimens half an hour of hand beating was also carried out in the area that the traps were set up each time the traps were checked.

The time of year in which sampling is carried out does affect the the likely taxa found (Basset, 1988). Ideally all sampling would have taken place in the same month each year. However the logistics of sampling from many sites and with the few resources available, meant that this was not possible.

2.4.5 Sampling methodology

The sampling procedure at each site involved the use of three main trapping techniques, malaise, pitfall and yellow pan traps. Hand collecting and beating were also used. These trapping methods were chosen to enable a large a variety of insect taxa to be sampled within the logistical framework allowed.

The pitfall traps were 15 cm diameter translucent plastic beakers. They were set with 4 cm of water in the beaker together with a teaspoon of sodium benzoate (preservative) and 2-3 drops of detergent (surfactant). Each trap was covered with a tin roof to reduce evaporation and protect from larger foreign objects. The CI methodology also involved placing an object, such as a log, over the tin roof to deter the theft of both beaker and roof by local weka (*Gallirallus australis*). The yellow pan

traps consisted of two litre yellow plastic ice cream containers which were filled with water to 5-6cm with sodium benzoate and detergent added. The malaise traps were standard six foot malaise traps with the collection beakers filled with 95% ethanol. The yellow pan and pitfall traps were checked every other day and, if necessary, samples removed and extra water added. The malaise trap was checked every second day and emptied at the end of the seven day period. Beating was performed for half an hour every second day.

Each site sampled was divided into three areas based on habitat and vegetation. Area 1, was situated a metre or so above the high tide mark. Care was needed with placement in this area as a position too near to high tide meant a high risk of loss of collecting equipment to the sea. Area 2 was 10-30 m wide section of grasses and small shrubs immediately behind area1 and was predominately on older dunes and sandy soil. The final area, area 3, followed on from area 2 and consisted of mature shrubs and trees approximately 20 m from area 2. Every effort was made to select sites that contained as high a proportion of native flora as possible.

Each area was sampled using nine pitfall traps and two yellow pan traps. Malaise traps were only placed in areas 2 and 3. Malaise trapping was not used in area 1 due to excessive exposure to the potentially damaging elements of wind and sea. Sites were sampled for one week.

2.4.6 Identification of samples

"In Europe, good illustrated identification manuals for the most popular groups have been available since the early 1800s … The least known groups are better known that most New Zealand arthropods"

(Watt, 1976)

For the purposes of the faunal survey and to provide good data for the next stages of the project, an accurate identification of the samples was needed. The initial approach to this was to find relevant experts to perform the identifications. However, it soon became evident that for two of the three orders under scrutiny there was no expert able to commit the time needed to complete all the specimens (and that often there were no experts for many of the taxa). For the Diptera and Hymenoptera and some Coleoptera, the onus for sample identification was upon myself, and so a steep

learning curve ensued. Luckily, in the case of the Coleoptera, Dr. Rowan Emberson, an eminent New Zealand coleopterist was available to help process a majority of the specimens after they had been sorted and appropriately mounted. Also available at Lincoln University was the insect research museum curator and coleopterist, John Marris.

An on-going difficulty in the identification of NZ fauna has been the lack of taxonomists and the large range of as yet un-described and un-sorted collected specimens (Watt, 1976). Finding the relevant taxonomic information and access to published keys to can be difficult, even for intensively studied regions, such as Europe and North America. NZ taxonomic data can be patchy and despite many excellent works there are still major gaps in the available information. The Fauna of New Zealand series is particularly informative but only covers a fraction of the insect fauna in NZ. The latest available taxonomic keys for taxa ranged from 1927 for Mycetophilidae (Tonnoir & Edwards, 1927) to a key for NZ bees (Donovan, 2007). One further resource available was Lincoln University's Entomological Research Museum with its extensive collection of NZ insects.

2.5   Other dune survey data

Comparison with other dune surveys was difficult as very few published records exist from sandy dune habitat. Data from two coastal sand dune based inventories that were found are used as a comparison to this survey. The first is of a dune system from New Brighton beach in Christchurch, NZ (MacFarlane, 2010). The second is a list of dune based insects found in the U.K. (Buglife, 2003; Howe, et al., 2010).

2.6   Analysis of data

For post hoc comparison of between two or more proportions the function prop.test is used from the "stats" package within the R programming (R Development Core Team, 2010). If prop.test indicates that one or more of the proportions being compared are significantly different from the others, the Marascuilo procedure then is used. The Marascuilo procedure performs pairwise comparisons of the proportions and compares them to a critical range base on actual and expected proportion. If the

calculated actual critical value for a pair of proportions exceeds the expected critical range for that pair, then the difference between that pair of proportions is deemed significant (NIST/SEMATECH, 2003). The R procedure used for this analysis was written by Sefan Th. Gries, from the University of California (Stefan Th. Gries, pers comm.). All statistical analysis was performed using R software v. 2.1.1.

2.7 The collection, inventory and data trends

2.7.1 Introduction

From the vast number of insects collected in this project, over 5000 specimens were sorted, mounted and identified. A complete inventory of all species collected is presented in Appendix C. Counts were made for all three orders (Coleoptera, Diptera and Hymenoptera) at taxonomic levels and for all sites (see Appendix D).

2.7.2 Taxon numbers

In total, 675 species were collected, which is approximately 1.4x that of the 490 genera and 7x that of the 95 families collected (Figure 2-4). At family and genus level each order represents a satistically equal proportion (approx 33%) of the total for each taxonomic level (Marascuilo test). At species level, only Hymenoptera represent 33% of the total (prop.test p = 0.8219). Diptera and Coleoptera species counts showed to be significantly higher and lower than 33% respectivley (Marascuilo test).
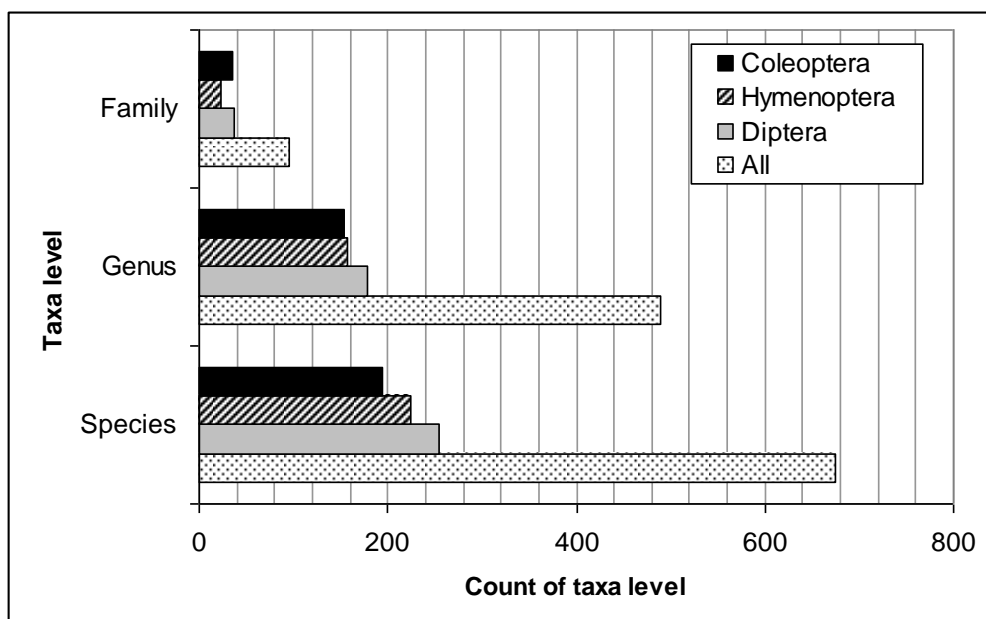
Figure 2-4: Total number of taxa collected. Family, genus and species level counts are shown for each order collected and for the total collection.

2.7.3 Trapping methods

Each of the four trapping methods contributed a different proportion of the final taxon total (Figure 2-5). Malaise trapping collected over 50% of the total species sampled, although not statistically more than the yellow pan traps. Pitfall traps collected the fewest number of species, although not statistically less than beating.
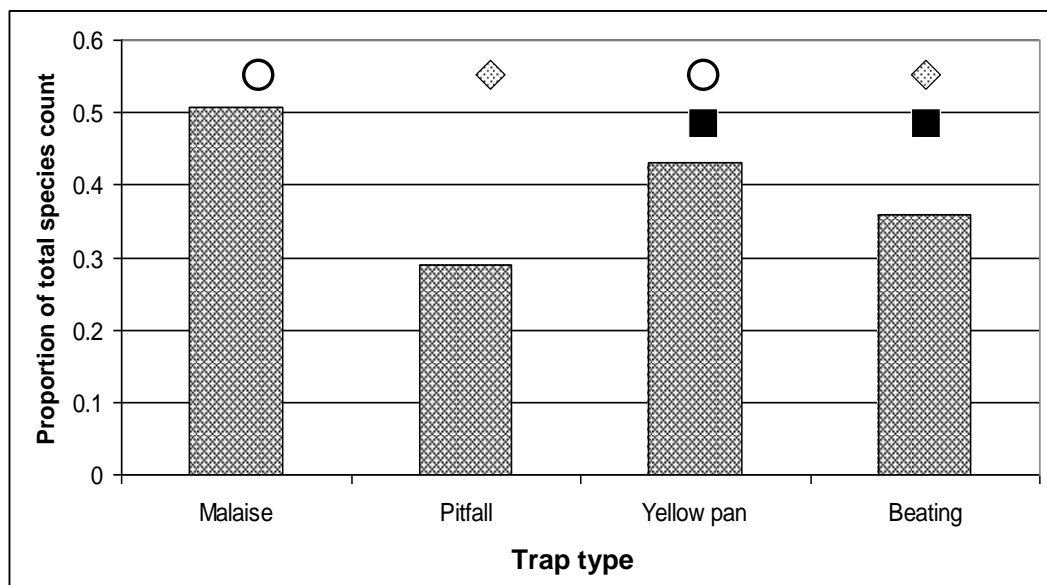
Figure 2-5: Proportion of total taxa collected by each of the four sampling methods. Similar symbols represent a significantly similar proportions (Marascuilo test). Traps are assessed by the using the proportion of the total species count represented in the trap. These do not add up to 1.0 as many species are caught in more than one trap type.

The efficacy of each trapping method changed quite markedly for each of the three orders collected. Malaise trapping caught just over 50% of all species, over 70% of all Diptera, under 50% of all Hymenoptera and just under 30% of all Coleoptera species. All proportions were significantly different. For the three other trapping methods the proportion of total Diptera and Hymenoptera were equivalent. However, catch proportions for Coleoptera varied from around 50% for pitfall and beating to just over 20% for yellow pan traps, all significantly different to the Diptera and Hymenoptera proportions (Figure 2-6). The data in figure 2-6 can also be represented by order to gauge which trap is most effective for each order (see Appendix E).
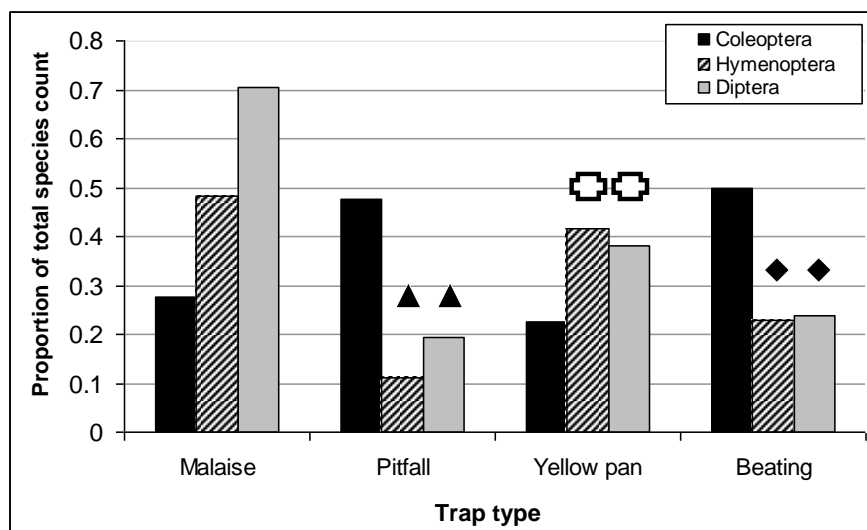
Figure 2-6: Proportion of each order's total count collected in each trap. Statistical significance shown within trap type. Same symbol = statistically equivalent proportion (p<0.05). Traps are assessed by the using the proportion of the total species count represented in the trap. These do not add up to 1.0 as many species are caught in more than one trap type.

2.7.4 Unidentified taxa

All mounted samples were identified to family level. The level of identification at sub-family to species level was dependant on the order (Figure 2-7) and the taxon level being assessed (Figure 2-8).
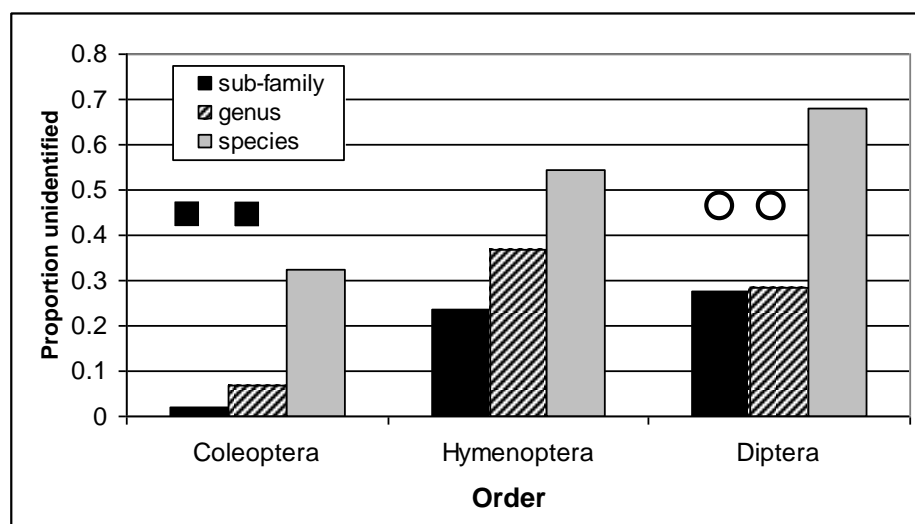
Figure 2-7: The proportion total RTUs unidentified. Statistical significance shown within order. Same symbol = statistically equivalent proportion (p<0.05).
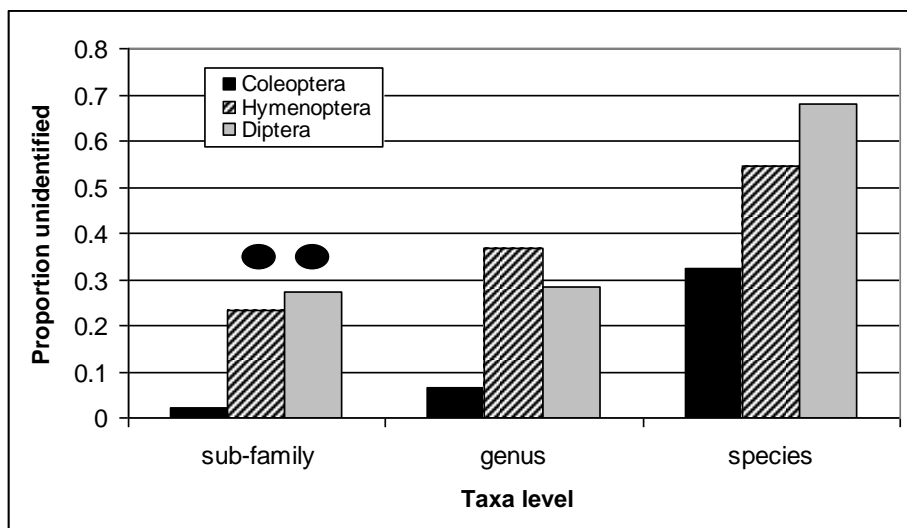
Figure 2-8: The proportion of total RTUs unidentified for three taxonomic levels. Statistical significance shown within taxonomic level. Same symbol = statistically equivalent proportion (p<0.05).

The proportion of the total sample count contributed to by each order varied between different dune system surveys (Figure 2-9).
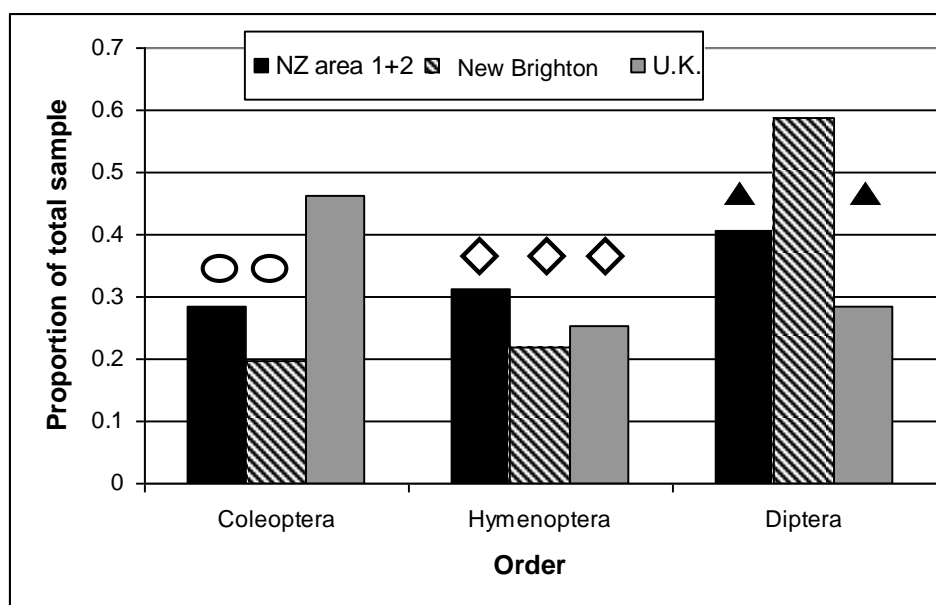
Figure 2-9: Contribution of order to the total sample count. Comparisons are between three different dune system surveys. Same symbol = statistically equivalent proportion (p<0.05).

2.8   Discussion

2.8.1   Coastal dune survey

The coastal dune survey produced for this study is geographically extensive and contains over 5000 mounted specimens. As well as the major objective of comparing the NZ insect dune fauna with that of CI, it has also provided a sample of the NZ insect dune fauna from sites as disparate as the warm wet Pacific east coast of NZ's North Island at Tolaga Bay, to the cold and even wetter south coast of the South Island at Te Waewae Bay (NIWA, 2011). A range of over 1300 km of coastline, 12 degrees of latitude and 11 degrees of longitude.

2.8.2   Comparisons to other surveys

Ideally this discussion would centre on the comparison of this sand dune survey with those from other sites around NZ and the rest of the world. However, as previously noted (Howe, et al., 2010), published inventories of coastal sand dune sand insect fauna are few and far between. Although there are many projects concerning the ecology, behaviour and physiology of dune and beach insects throughout the world, many of these studies concentrate on a specific taxon and do not encompass a wide range of insect fauna.

The community ecology of sphecid wasps (Inoue & Endo, 2006) and bees (Oliveira, et al., 2010) found on dunes has been studied in Japan and Brazil, respectively. Digging wasps are also used to study anthropogenic changes on the France/Belgium coast (Bonte, 2005). Beetles are often studied in monitoring the effects of tourism on the French Mediterranean coast (Comor, et al., 2008) and examining the health of Italian dune systems (Zanella, et al., 2009). Many other insect and arthropods also appear in sand dune research; ants (Boomsma & Loon, 1982); collembolan (Fernandes, et al., 2009), butterflies and grasshoppers (Bonte & Maes, 2008), spiders and grasshopper (Cherrill & Begon, 1989).

Of the two coastal sand dune based inventories that have been found, one is a comprehensive survey of a dune system of New Brighton beach within Christchurch, NZ (MacFarlane, 2010). The second is a list of dune based insects found in the U.K. (Buglife, 2003; Howe, et al., 2010). Whilst comparisons of taxon numbers are

difficult, as surveys will vary in collection methods, duration and site size, we can compare the structure of the relevant orders of the collections. As the New Brighton beach and U.K. surveys are only concerned with the dune area near to the beach, the data used from this project is only that of area 1 and area 2 (high tide and fore dunes).

The proportion of Coleoptera, Hymenoptera and Diptera within the subset of these three orders, for each inventory, illustrates some pertinent points. The proportion of Diptera in the Christchurch inventory was much higher than the other two. When examining the methodology of this survey this does not come as a surprise as the author admits…

"*I wished to use techniques, which favoured insect orders that were unrecorded in previous publications in New Zealand. The limited published information on insects from sand dunes in New Zealand has focused on … moths … and collecting for beetles* "

… and so the survey was biased against moths and beetles. The U.K inventory does not state any variables as to the geographic range or collecting methods employed. It is almost certainly the result of accumulated expert knowledge rather than a systematic research survey of the specific area. In fact the U.K inventory lists a significantly greater proportion of Coleoptera than either of the two NZ based inventories. Hymenoptera, however, occurred in equivalent proportions in all three inventories.

2.8.3 Taxon numbers

The absolute number of taxa collected was a factor of time spent collecting, trapping methods used and identification strategies, and so is unique to this particular project. The number of taxa collected at each taxon level was statistically the same for all three orders at all three taxon levels, except for between Coleoptera and Diptera at species level. The fact that there were more Diptera than Coleoptera at species levels could be attributed to a couple of factors. First, the trapping methods may have biased the collection of Diptera. The two traps that caught the highest percentage of the collection, malaise traps and yellow pan traps were also best the best for trapping Diptera. It could of course be that there were a large number of Diptera to be caught and the malaise and yellow pans happened to be the best traps for doing this.

Coleoptera were mostly caught in pitfall traps and by beating. Pitfalls are most likely sampled from a smaller area than the malaise and yellow pans as they rely on insects reaching the trap from within 'walking distance' and so have a smaller potential pool of taxa to sample from. Having said this, the Hymenoptera catch total at all three taxonomic levels did not differ statistically from either Diptera or Coleoptera and they too were caught predominantly in the malaise and yellow pans.

Second, the level of expertise available for identification could also play a part in increasing the numbers of some orders. Only Coleoptera were able to be identified by an expert in the NZ fauna. Identification by a non expert and an acknowledged lack of keys for NZ taxa (Curtis pers obs, MacFarlane pers comm.) could well have had a bearing on the level of accuracy of species identification. It might also be that there are more Diptera species in the areas sampled.

2.8.4 Trapping methods

The trapping methods showed differing abilities in sampling the different insect orders in this survey. Malaise traps were best at collecting Diptera, with yellow pans good for Diptera and Hymenoptera. Pitfall traps and beating were best for sampling Coleoptera. The malaise trap proved most successful of all the traps with over 50% of total taxa represented in the malaise trap catch. However, nearly 45% of the total taxa were also found in the catch from the yellow pans, which was statistically equivalent to the malaise trapping. Pitfall trapping sampled the lowest proportion of the final count although the difference between the pitfall proportion and beating was not significant.

The proportions shown in the results are only part of the story. Even though some traps collect a lower proportion of an order's total count they may in fact be sampling a different set of taxa from that order. Differential catch compositions are recorded from malaise traps and yellow pan traps for Ichneumonidae (Aguiar & Santos, 2010; Mazon & Bordera, 2008). Although not analysed in this project, a comparison of species distribution throughout the traps would be quite feasible with this data.

2.8.5 Identification of samples

The identification of the collected specimens was perhaps the most time consuming aspect to the project. Expert time proved to be an almost impossible resource to harness and consequently the only taxon to be expertly appraised was Coleoptera. This fact is borne out in the greater proportion of Diptera and Hymenoptera that remained unidentified.

2.8.6 New records, new discoveries

The insect fauna of NZ is conservatively estimated to be 20,000 species. Of this 20,000, only 10,000 have been officially described (McGuiness, 2001; Patrick, 1994; Watt, 1975). It comes as no surprise then (and is somewhat reassuring) that of the 675 RTUs collected during this project, 359 (53%) remain unidentified at species level. However, some of these will be succesfully identified with further investigation and expert help. It is also very likely that many will be taxa previously undescribed in NZ records. Of the three orders studied, the Coleoptera were examined by one of NZ's foremost beetle experts, yet some 33% of the Coleoptera from the collection remain unidentified to species level.

Based on published records and expert knowledge some taxa from the survey have been declared as new records. Currently one taxon is a possible new spceies, although further examination of the collection by experts may well reveal more new species amongst the collection (Emberson pers. comm.).

Two confirmed new records were provided for Chatham Island: *Hybolasius crista* (Fabricus, 1775) (Coleoptera : Cerambycidae : Lamiinae) (Kuschel & Emberson, 2008); *Stethorus bifidus* (Kapur,1948) (Coleoptera : Coccinellidae) (Emberson, 2006a). There was one probable new record for Chatham Island:*Parentia sp.* (Hardy) (Diptera : Dolichopodidae) (Bickel, 1991). One new distribution record (already recorded from Chatham Island) of a rare endemic Chatham Island beetle was also noted: *Amychus candezei* (Pascoe 1876) (Coleoptera : Elateridae) (Rowan Emberson, pers comm).

One potential new species of dolichopodidae was collected from Rangatira (N.B. – This taxon was not included in the data analysis for CI taxa as all statistical analysis

pertained to samples collected from the specific colletion sites on CI. But is worthy of a mention none the less.) *Parentia n.sp* (Hardy) (Diptera : Dolichopodidae) (Dan Bickel, pers comm).

2.8.7 Physical collection and inventory

Much of the value of this section of the overall project is in the 70 boxes of 5000 or so mounted insect specimens that will contribute to the Lincoln Entomological Research Museum collection. Once incorporated into the collection they will be available for use by researchers of all levels. Those specimens that have been confidently identified will add to NZ entomological records, help in the teaching and learning of insect identification and allow comparisons with unknown specimens collected elsewhere. The rest of the specimens can be further investigated in order to identify them. It is quite possible that some are in fact new records for NZ or even new species. Possible new species would be available for description and/or a review of the taxa in question. The inventory of taxa collected provides data on the distributions of NZ insect taxa. It is a sound basis for future collecting data to be added too, from more geographical locations and an expansion of the taxa sampled. The information can easily be added to databases, such as used at Lincoln Entomological Research Museum.

2.9 Conclusion

The collection and inventory part of the project has successfully provided a large amount of data from which dispersal and island biogeography based hypotheses can be addressed and tested in future chapters. Diptera were the most commonly collected at all taxonomic levels.

Malaise trapping proved to be the most effective method of collection, with pitfall trapping being the least effective. Trapping methods also varyied in their effectiveness in sampling a particular order of insects e.g. despite being least effective over all, pitfall trapping was the most effective method of collecting beetles.

Identification of samples proved to be a difficult task. Over half of Diptera and Hymenoptera are yet to be identified to species level although they were able to be divided into RTUs. Of Coleoptera, over a third remain unidentified, even with the assistance of a NZ expert in the order. Some of these may yet be recognised as new species and described as such.

An extensive collection and inventory of over 600 species has been made of Coleoptera, Hymenoptera and Diptera from the sandy dune habitat of NZ and CI. Dunes are a wide ranging and important habitat from which the insect fauna has not been widely surveyed. Globally there appears to be a lack of inventory information concerning sand dune insect fauna. The information gained from this survey can be applied to many fields of study including conservation projects, of both sand dune habitats and of the insects themselves, taxonomic reviews and biogeographical research.

Accurate estimates of worldwide dune habitat are highly erratic, very much dependant on a specific country to perform studies and release data (Encora, 2007). The best information for NZ is that there are 39,000 ha of active dunelands, with up to 40,000 ha of backdunes (Hilton, et al., 2000). The dearth of worldwide published entomological inventories for sand dunes habitat shows the need for basic, targeted surveys, such as this one. The project has also highlighted the paucity of available taxonomic expertise within NZ. Hypothesis testing and conclusions gleaned from this data is in some way only as robust as the level of acceptable identification. Accurately identified specimens are the cornerstone of future research and provide to raise the level of taxonomic knowledge, both within NZ and worldwide.

Further research on the many as yet unexplored dune systems of NZ would help to increase the knowledge of this environment.

Chapter 3

Comparison of the New Zealand and the Chatham Islands' faunal composition, based on three orders of insect: Coleoptera, Diptera and Hymenoptera

3.1 Introduction

Islands have held the fascination of natural historians for centuries. They represent "natural laboratories" where specific factors can be studied in isolation within fixed geographic boundaries and then extrapolated into larger continental animal and plant communities (Carlquist, 1966; Whittaker & Fernandez-Palacios, 2007).

The presence or absence of different taxa is important in assessing whether an island's community differs substantially from its nearest mainland neighbour. Differences are found within islands and also between islands and mainland regions. Compositional differences between islands and their nearest mainland may be simply the natural outcome of the unique evolution, selection and extinction in each area. Alternatively it could be the product of the specific properties of the island and its relationship with a particular mainland area.

Differences between islands and their main source of biota are often attributed to filtering effects. Filters are any process or condition that biases the selection of one taxon over another. Factors affecting a taxon's ability to reach an island are based on relative isolation of the island and dispersal traits and include the water gap distance to be crossed and dispersal specific adaptations (active or passive) of the taxon in question (Whittaker & Fernandez-Palacios, 2007). Successful colonisation can be greatly dependent on the climate of an island. Island climates are often less variable, more humid and windier than continents of the equivalent latitude (Williamson, 1981). Climate will thus select against, and so 'filter out' those mainland taxa not able to survive the island's climatic conditions. Climatic filtering can lead to biotic assemblages on islands being 'more polar' than their respective mainland regions (Whittaker & Fernandez-Palacios, 2007; Williamson, 1981).

In this chapter we look for evidence of filters between New Zealand (NZ) and the Chatham Islands (CI) and identify if they vary in their effects on taxa. To find evidence for filtering, the community structure of the insect fauna for the mainland NZ and CI are compared by addressing a number of ecological questions (section 3.3.1).

3.2   Islands

Naturalists have been intrigued by islands and their idiosyncratic biotas for hundreds of years (Wallace, 1881). An entire branch of ecology, 'island biogeography' has arisen in an attempt to account for the presence of species found on an island, their ecology, evolution and conservation. As an ecological description the term 'island' is vague, ranging from a flower head, to a continental landmass (Gillespie & Roderick, 2002; Whittaker & Fernandez-Palacios, 2007). However, this study looks at the relationship between a large oceanic island group of continental origin (NZ) with a much smaller island of continental origin, 850 km distant and most recently emerged above sea level 3-5 mya (CI) (Trewick, et al., 2007).

It has long been known that species numbers on islands are lower than equivalent areas of mainland habitat. Early in the 20th C, studies by Arrhenuis (1921) revealed one of the fundamental tenets of island ecology, that of the species-area relationship. The species-area relationship is an observable relationship but does not attempt to explain the mechanisms by which island biotas arise. An influential attempt to explain the formation of an island community came with the equilibrium theory of island biogeography (MacArthur & Wilson, 1963; MacArthur & Wilson, 1967). Island biogeography has also naturally benefited from the study of wider ecological factors which can then be applied in an island context.

The observation that islands contain fewer taxa compared to a similar area of a mainland was described by Hooker in 1866 (Williamson, 1981), formalized by MacArthur and Wilson (1963) and has been recorded for numerous taxa since (Blondel, et al., 1988; Dapporto & Dennis, 2010; Juan, et al., 2000; Kingston & Waldren, 2003; MacArthur & Wilson, 1963; Martin & Lepart, 1989; Wilder & Felger, 2010). The phenomenon of lower biotic diversity on islands has been variously

termed depauperation (Carlquist, 1970; Preston, 1962b), impoverishment (Williamson, 1981) and 'species poverty' (Whittaker & Fernandez-Palacios, 2007).

Early explanations for impoverishment were based on the fact that islands further from a source pool were less likely to be encountered by long distance dispersers, were physically difficult to get to and took longer to reach. These ideas have been enhanced by the equilibrium theory of island biogeography which introduced the idea that island populations are determined by a continuous regime of immigration, speciation and extinction (Whittaker, 2004). Further theories such as the general dynamic theory have taken this idea further by introducing the life stage of the island itself as a factor influencing colonisation, speciation and extinction rates (Losos & Ricklefs, 2010; Whittaker, 2004; Whittaker, et al., 2008).

Ecological research has produced copious models and predictive formulae to account for the structuring of biotic communities. Following a drive towards a more rigorous quantitative and testable approach to community ecology these predictions and models have been placed (some retrospectively) under the umbrella term of 'assembly rules', a term first coined by Jared Diamond in the mid 1970s (Diamond, 1975; Weiher & Keddy, 1999; Whittaker & Fernandez-Palacios, 2007). The formulation of assembly rules is an attempt to understand and quantify the mechanisms of community structure based on observed assemblage patterns within biotic communities. Assembly rules are pertinent to biogeography as the concepts behind the creation of community patterns can be also be inferred across larger geographical scales (Gotelli, 2004a). Although there is no specific definition of an 'assembly rule', three main themes dominate (Gotelli, 2004a).

- The taxonomic ratio between species/genus may quantify biodiversity patterns and was one of the earliest described use of assembly rules (Elton, 1946; Gotelli, 2004a). Discussion of this concept (and other ratios, such as individuals/species and species/family) centered on whether the low ratios seen in small, local communities were due to competition between phylogenetically similar species from the same genus.

- Nested communities of taxa occur where the species that constitute a smaller community are the subset of a larger community. The degrees of nestedness within archipelagoes and whether nested communities are driven by

immigration and/or extinction processes is an on-going theme in island biogeography (Gotelli, 2004a; Weiher & Keddy, 1999).

- The question of whether communities are a random assortment of taxa or a more structured assemblage of co-evolved taxa is subject to much study and research (Gotelli, 2004a). The presence or absence of a particular species can be seen to encourage or 'forbid' the presence of another species, rendering the final community structure non-random (Cody & Diamond, 1975; Diamond, 1975). Other research, however, set out to show that this was not the case and the structure of communities was no different from a random selection of the local mainland biota (Connor & Simberloff, 1979). Further recent analysis of Diamond's data has shown that communities may in-fact be structured by non-random processes (Gotelli & McCabe, 2002).

Many current fields of ecology have evolved from the works of Darwin, MacArthur and Wilson (Losos & Ricklefs, 2010). Theories espoused in MacArthur and Wilson's *The theory of island biogeography* have inspired approaches to understanding subjects such as habitat destruction, species loss, life history evolution, meta-population biology, landscape ecology and conservation biology (Losos & Ricklefs, 2010). Further areas are also beginning to be researched, such as haphazard long distance dispersal, 'de novo' island speciation and the effects of evolution on biogeographic scenarios (Losos & Ricklefs, 2010). As MacArthur and Wilson said,

"the fundamental processes, namely dispersal, invasion, competition and extinction, are amongst the most difficult in biology to study and understand"
(MacArthur & Wilson, 1967).

One question to be asked is whether, for any individual, the process of dispersal and colonisation is regulated by factors such as distance or body size. Conversely, is the dispersal process random, in that, given enough time, any individual from any taxon could successfully disperse irrespective of taxon related traits, such as its size, life history or feeding guild. Lourens Baas Becking's concept of *"everything is everywhere, but the environment selects"* (Quispel, 1998) has been a central tenet of microbiology since the early 20th century (O'Malley, 2008).

This study examines the biogeography of a unique island/mainland relationship. A survey of sandy shore insect fauna from NZ and CI provides an insight to the

differences and similarities between the two regions, and provides data to form a hypothesis as to the processes driving the insect composition seen on CI. NZ and CI dune insect communities are compared using a set of ecological questions (section1.3.1) applied to the presence/absence data collected during the survey phase of the study.

The questions are designed to understand the compositional differences between the NZ and CI fauna, and are based on standard ecological parameters.

Taxon level ratios e.g. species/genus, genus/family and species/family are much used in biogeography (see below). The ratios are believed to indicate how the the relative degree of competition between taxa leads to the variation in the number of lower level taxa present in any particular habitat (Jarvinen, 1982). Lower ratios are often found on islands (Elton, 1946) and this is attributed to a higher level of inter taxa competition. However Jarvinen (1982) maintains that the ratio is simply a product of sample size and lower raios on islands are due to there being lower numbers of taxa.

In this project three taxonomic ratios are compared. The ratios are compared using the full number of taxa found on NZ and CI, and a second comparison is made using a resampled sub-set of the NZ population consisting of the same number of taxa as in the CI population. Thus removing any sample size bias to the ratios.

Species/Genus – flora, birds (Simberloff, 1970), ants (Andersen, 1995) bivalves (Krug, et al., 2008), Bolivian flora (Larrea-Alcazar & Lopez, 2005), bats (MacFarlane, 1991), rainforest insects (Novotny, et al., 2004).

Species/Family -Scandinavian flora (Grytnes, et al., 2000), marine fauna (Doerries & Van Dover, 2003), North American flora (Bennett, 1996), rainforest insects (Novotny, et al., 2004).

Genus/Family –Fossils (Darroch, 2010; Valentine, 1970), South African flora (Cowling, et al., 1997), marine fauna (Doerries & Van Dover, 2003); global tree flora (Condit, et al., 2005).

One criticism levelled at biogeographical studies is that they lack the application of quantitative measures (Gibbs, 2008). In this study compositional differences between

NZ and CI are compared using a null hypothesis based on assumed random immigration from NZ to CI. The issue of whether island populations are random subsets of mainland source populations was addressed using a re-sampling design. Re-sampling allowed many random subsets of the mainland population to taken from the full NZ dataset. The null hypothesis is tested by using the re-sampled NZ data to generate a CI dune insect composition that would be expected under a regime of random immigration. The expected composition is then compared to the actual composition found on CI. Further details of this re-sampling are found in the analysis section of this chapter (section 1.4).

3.3 Methods

3.3.1 Ecological questions

Using the concept of assembly rules, the following questions are used to address potential differences in the structure and composition of the sand dune insect fauna from NZ, and those of the CI dune systems.

High level questions, such as number and size of taxa, are dealt with first. Further questions look at the structure of the community at different taxonomic levels. Finally, any overall trends between the orders and between taxon levels are assessed.

1) How do the numbers of insect taxa sampled vary between NZ and CI?

2) How does the mean number of taxa per site compare between NZ and CH?

3) How does the structure of the NZ and CI communities compare when based on the relative proportions of Coleoptera/Hymenoptera/Diptera in the two regions?

4) How do the ratios between species/genus, species/family and genus/family compare between NZ and CI?

5) How does the structure of the NZ and CI communities compare when based on presence/absence records?

6) Does the actual composition of taxa on CI differ from that expected, assuming random dispersal?

3.4 Analysis of data

The analysis of the comparisons of proportions uses the same R packages and procedures as detailed in Chapter 2. The current study also uses non-metric multi-dimensional scaling (NMDS) methods to gauge the degree of similarity between NZ and CI communities. The use of multivariate statistics, of which NMDS is part, is commonly used within ecology and especially in comparing community structure between sites and changes in community structure due to treatments or over time (Legendre & Legendre, 2003; McCune & Grace, 2002; Zuur, et al., 2007). Multivariate statistics are used as there are often large numbers of contributing variables involved in comparing communities. In this study the variables used are the taxa found to be present or absent at a site.

A major part of creating NMDS graphs is choosing the relevant similarity co-efficient to use in calculating the degree of association between whichever group of objects (usually sites) or descriptors (taxa levels in this study) are being compared (Legendre & Legendre, 2003). Much of this choice depends on how the data is represented, the ecological question being asked and what future use the similarity matrix produced will be used for.

For this study the Jaccard similarity co-efficient was used as it is able to handle binary (presence/absence) data and is asymmetrical (would treat double zeros, i.e. taxa NOT found at both sites, as a difference and not a similarity) (Legendre & Legendre, 2003).

Another consideration when using NMDS was which dimensions (axes) to use when plotting the data. A higher number of dimensions generally lead to a lower stress value (the lower the stress value the more accurately the data fits the NMDS graph). However, too many dimensions have an adverse effect on the interpretation of the final results (McCune & Grace, 2002). One method of assessing the appropriate dimension is to plot the dimensions against the stress values obtained at those dimensions. The plotted data indicates the optimal balance between strees level and dimensions as a 'kink' or 'elbow' in the curve (McCune & Grace, 2002). With our data the highest dimension from which we still gained information without losing quality was 4 (Figure 3-1).
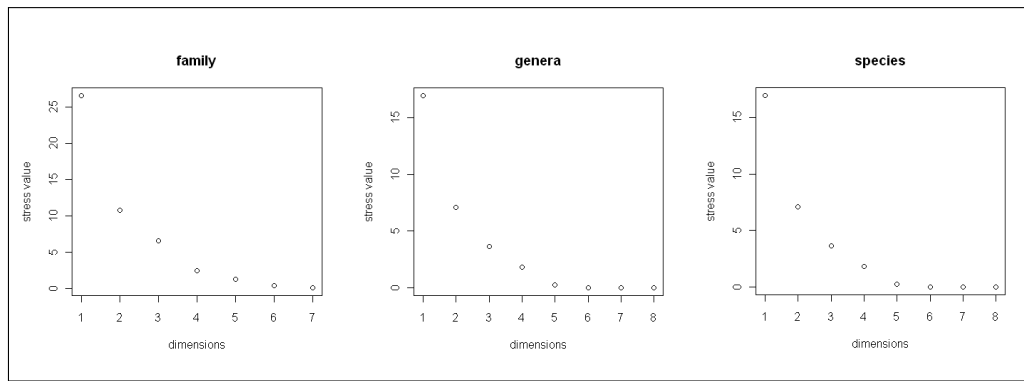
Figure 3-1: Stress levels generated for family, genus and species taxonomic levels. For all three taxa the stress levels do not lessen greatly below the fourth dimension, showing that the fourth dimension will give the best analysis of the insect diversity whilst minimising loss of statistical accuracy.

The difference between the communities on NZ and CI was assessed using analysis of similarity (ANOSIM). A distance matrix was created from the presence/absence data, again using the Jaccard co-efficient. This distance matrix was rearranged 9999 times. The actual arrangement of the presence/absence values of the true data was compared (by the software) to the 9999 random matrices. An R-value was produced between the value of -1 and 1. R-values of -1 are quite rare and should not be of concern here. A value of 0 indicates that data tested is no more different that any of the random samples generated. If taxa within NZ and CI are more similar to each other within each region rather than between regions, then the R-value will be >0. An R-value of over 0.25 indicates that the factors in the tested data have significantly different sets of insect fauna (McCune & Grace, 2002).

Testing of assembly rules often involves the introduction of a null hypothesis against which to examine data for significant deviations from a random pattern. The creation of appropriate null hypotheses for ecological research is the subject of intense and rigorous debate (Gotelli, 2004a).

Testing of assembly rules often involves the development of an a-priori null hypothesis (Weiher & Keddy, 1999). The null hypothesis can be based on previuos studies and / or prior knowledge of the ecology of the taxa concerned. In this study a wide range of insect taxa constituted the population tested.

66

A priori null hypotheses were not used in this study; instead random dispersal was assumed, with every taxon having an equal chance of successfully immigrating to CI from NZ. This strategy was due to the difficulty in finding a satisfactory null hypothesis to account for the whole population. Also by using this approach, any indication that a taxon, or trait, was over or under represented on CI, could then be further tested in the modeling phase of the study.

One important factor not incorporated into this study was time; how long the insect populations had inhabited NZ and CI and how this period of time affects the composition of the populations (Whittaker, et al., 2008).

In this project the null hypothesis was created by multiple re-sampling of the NZ data. Here a sample of 187 species was selected from the NZ species pool. The 187 species sample simulates the effect of random dispersal of a cohort of insects' equivalent to the number of species sampled from the CI. The re-sampling was performed 10,000 times to ensure the results generated were statistically meaningful.

The re-sampling creates a normal distribution of metrics (count or proportion) for the order and taxonomic level being addressed, e.g. the metric could be the count of Coleoptera families selected from when the NZ sample size is 187. These 10,000 counts have a normal distribution. The mean of this metric can then be calculated and is taken to be the value that would be expected to be found on CI under a regime of random dispersal. The null hypothesis assumes no a priori knowledge of dispersal and colonisation abilities. A statistic (e.g. mean of the counts) is generated from the 10,000 NZ samples and a standard deviation of the statistic is calculated (the standard error). This study uses an alpha value of 0.05 to imply significance. Multiplying the standard error by 1.96 provides a value for a 95% confidence interval for the NZ data. To be significantly different from the NZ data the CI count value for taxa will need to fall outside this 95% confidence interval range.

The re-sampled data was also used to ascertain whether statistics obtained from the CI data are more likely to be due to factors affecting dispersal and colonisation, or are more likely to be artifacts of sampling size.

3.5 Results

1) How do the numbers of insect taxa sampled vary between NZ and CI?

The percentage of the total collection present on NZ was significanlty higher than the percentage of the total collection sampled from CI (Figure 3-2).
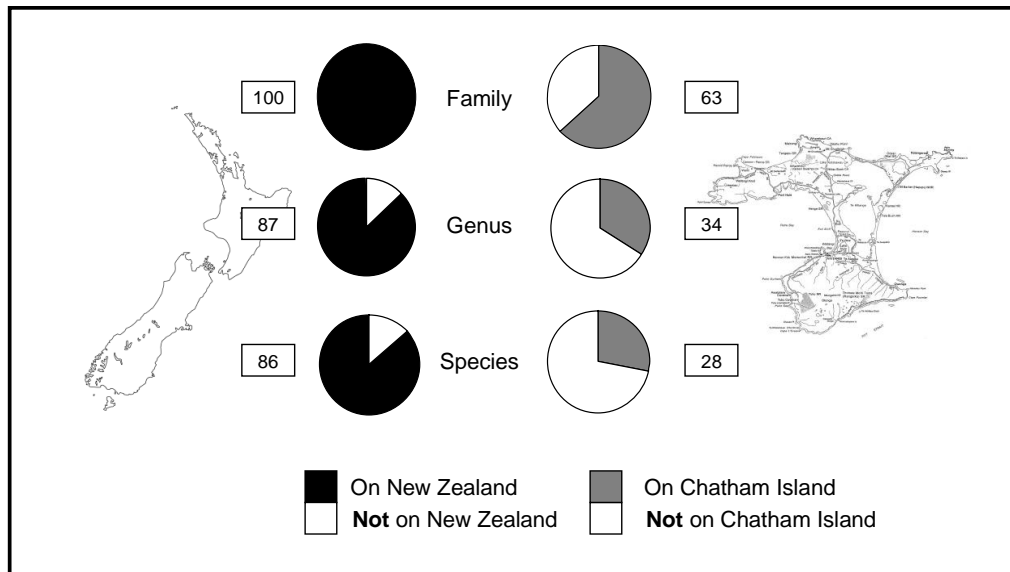
Figure 3-2: Percentage of total collection found on NZ and CI respectively, by taxonomic level.

The ratio of NZ to CI taxa count is included here as an indication of the degree of difference between NZ and CI. Over 85% of the total taxa sampled were found on NZ. At family level all taxa identified were present on the mainland. None of the families collected were unique to CI. For all orders and at all taxonomic levels the proportion of the total taxa was significantly less on CI than on NZ ($p < 0.05$ using prop.test)

2) How does the mean number of taxa per site compare between NZ and CH?

The number of taxa identified from the collection sites was consistently lower for CI sites, for all three orders and at all taxonomic levels ($p < 0.05$ using Wilcoxon test) (Table 3-1).

Table 3-1 Comparison of mean site counts, by taxonomic level and order. Wilcoxon test p-value showing all NZ sites with significantly more taxa than CI. * = p<0.05.

		Mean taxa count per site		Wilcoxon test P-value
		NZ	CI	
Family	All	57	35	0.0043*
	Col	17	12	0.0422*
	Hym	16	6	0.0077*
	Dip	26	18	0.0104*
Genus	All	134	58	0.0080*
	Col	38	18	0.0078*
	Hym	43	12	0.0080*
	Dip	55	29	0.0043*
Species	All	158	60	0.0043*
	Col	39	18	0.0080*
	Hym	50	12	0.0078*
	Dip	69	29	0.0080*

3) How does the structure of the NZ and CI communities compare when based on the relative proportions of Coleoptera/Hymenoptera/Diptera in the two regions?

For all taxon levels the percentage represented on NZ is statistically similar to the

percentage represented on CI (p < 0.05 using prop.test) (Figure 3-4).
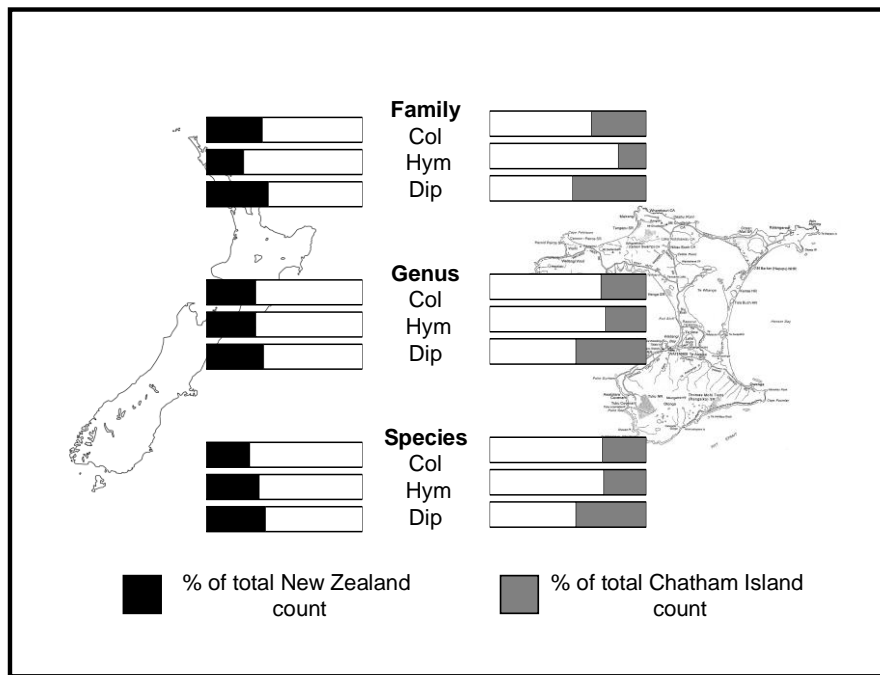
Figure 3-3: Proportion of the total count for each region (NZ and CI). By taxa level and order.

In NZ all the the three orders are equally represented at family and generic level (p>0.05 using prop.test). It is only at species level that there is any difference between the orders. This difference can be seen in the number of Coleoptera species collected being significantley fewer than the number of dipteran species collected (Marascuilo test). Both Coleoptera and Diptera, however, are found on NZ in the statistically similar proportions as Hymenoptera.

On CI there is a definite difference in the orders at a higher taxonomic level (Figure 3-5). Hymenoptera families represent a much lower proportion of the CI fauna than the dipteran families (Marascuilo test). Hymenopteran families are also found to represent a lower proportion of CI families than Coleoptera, although this difference is not statistically significant.
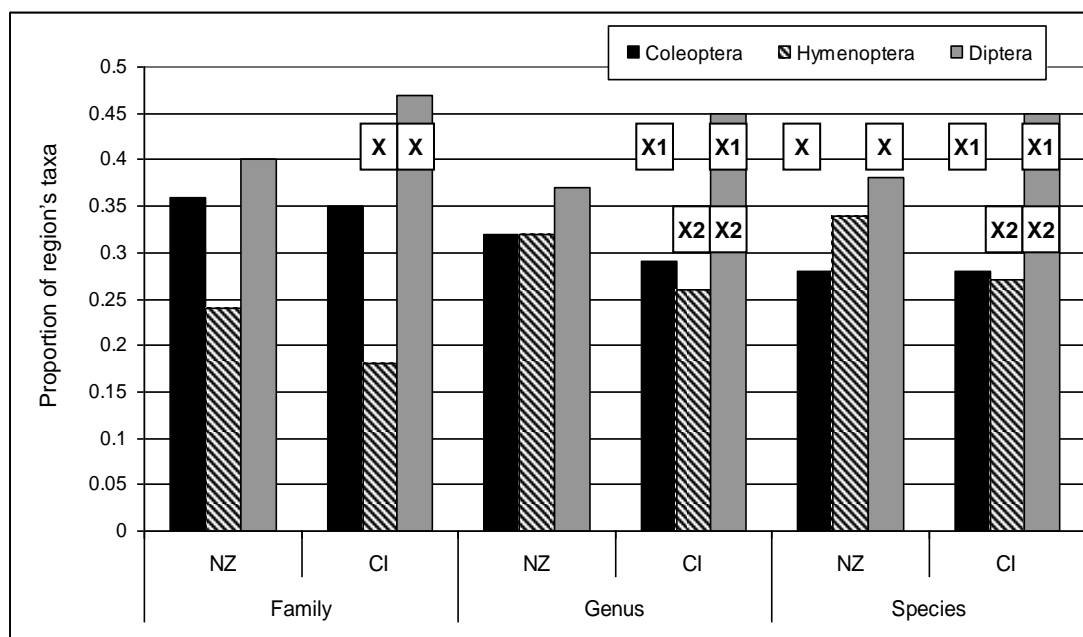
Figure 3-4: The proportion of a region (NZ,CI) represented by each taxonomic level. Proportions are displayed by order. Statistical comparisons are made between orders within the same region, based on the proportion of the taxonomic level represented in that region. Statistical difference = X,X1,X2 (Marascuilo test).

To allow for the effect of sample size, the proportions represented on NZ by the three orders were calcualted by resampling the NZ data as described in the methods and analysis sections (Tab 3-2).

Table 3-2: Actual proportion of the CI taxa represented by each order compared to the expected proportion based on resampling of NZ taxa. The test to see whether the CI proportion is within the 95% confidence interval of the expected value is performed for 3 orders, at family, genus and species level. * = CI value significant as it falls outside the 95% confidence interal of the re-sampled NZ value.

Taxa level	Order	% of total NZ taxa	Re sampled mean taxa count as % of NZ taxa (expected CI value)	95% ci of resampled NZ mean	% of total CI taxa (actual value)
Family	Col	36	33.00	+- 5.85	35
	Hym	24	27.28	+- 4.85	18 *
	Dip	40	39.73	+- 5.82	47 *
Genus	Col	32	29.75	+- 5.38	30
	Hym	32	32.72	+- 5.32	26 *
	Dip	37	37.59	+- 5.63	45 *
Species	Col	28	28.15	+- 5.34	30
	Hym	34	33.96	+- 5.62	26 *
	Dip	38	37.87	+- 5.76	45 *

Clear differences were found between the NZ and CI proportions for two of the three orders used in this comparison. Hymenoptera are under represented on CI at family, genus and species level. Conversly, the Diptera show a greater proportion of the CI total than would be expected from their proportion of the NZ total. Diptera show this over representation on CI at all three taxonomic levels.

4) How do the ratios between species/genus, species/family and genus/family compare between NZ and CI?

When using a full NZ pool of taxa the NZ taxa ratios are consistently higher than the ratios seen on CI (Table 3-2). The ratio calculated from a NZ sample pool equal in size to the CI pool shows no significant difference between the areas.

Table 3-3: Comparison of S/G, S/F and G/F ratios between NZ and CI. Comparisons shown using full NZ sample pool and using a re-sampled NZ sample pool equal in size to that of the CI species pool (n=187).   * =<0.05

Column number		1	2	3	4	5	6
Taxa Ratio being tested	Order	Ratio of NZ using full NZ sample pool X : 1		Prop.test p-value	Mean ratio of re-sampled NZ species pool (n=187)	Equivalent proportion (the ratio in col 4 as a proportion)	Prop test p-val Test between proportions of col 2 & 5
		NZ	CI				
Species/ Genus	Col	1.23	1.06	0.03924*	1.05	0.95	1.0
	Hym	1.43	1.19	0.05575	1.16	0.86	1.0
	Dip	1.38	1.12	0.003212*	1.18	0.85	0.4926
Species/ Family	Col	4.66	2.48	0.01160*	2.48	0.40	1.0
	Hym	8.61	4.63	0.1058	3.22	0.31	0.3926
	Dip	5.92	3.00	0.003037*	3.14	0.32	0.9737
Genus/ Family	Col	3.77	2.33	0.0533	2.30	0.43	1.0
	Hym	6.00	3.91	0.2787	2.78	0.36	0.3763
	Dip	4.30	2.67	0.03707*	2.66	0.37	0.973

The ratios were re-calculated for NZ taxa using sample sizes ranging from 50 to 584 (Figure 3-6). All the NZ ratios become greater as the sample size increased. The predicted ratio values at the CI sample size are very similar to those calculated by the re-sampling procedure (Table 3.2).
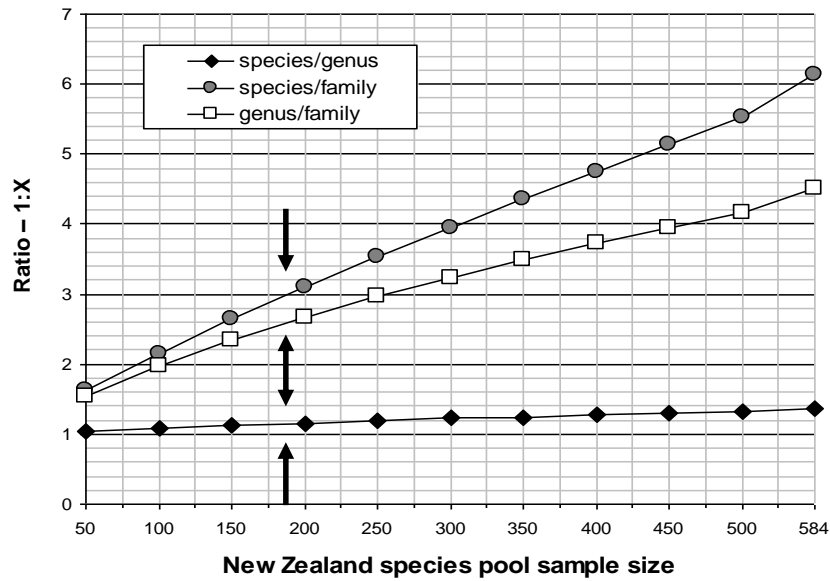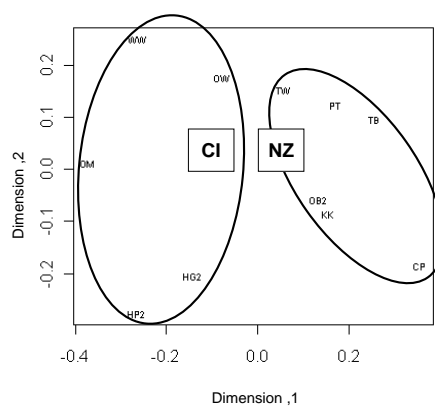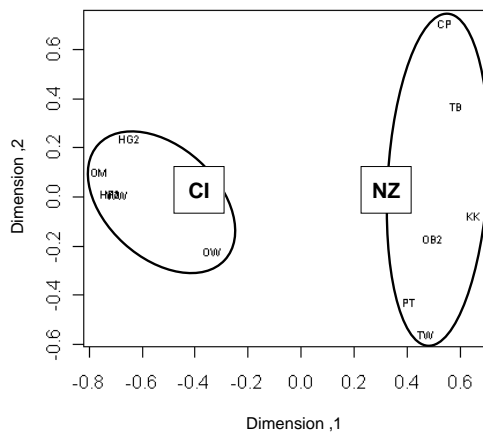
Figure 3-5: Species/genus, species/family and genus/family ratios based on a range of samples sizes from the NZ sample pool. CI sample size (n=187) is highlighted by arrows.

5) How does the structure of the NZ and CI communities compare when based on presence/absence records?
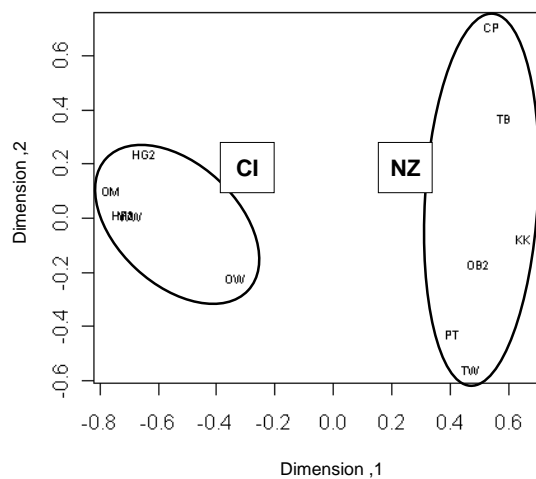
NMDS analysis for the whole collection, at three taxonomic levels, shows a difference between NZ and CI (Figures 3-7a-c).

3-6a:

3-6b:

3-6c:

Figure 3-6: NMDS graph for three taxonomic levels. A: Family, (ANOSIM,R=0.77), B: Genus,(ANOSIM, R=0.88), C: Species,(ANOSIM, R = 0.94). Ovals applied manually to highlight NZ and CI groupings. Sites represented by labels as described in Table 2-1.

A significant degree of difference in the composition of insect taxa between NZ and CI was shown at all three taxonomic levels. NZ and CI were most similar in their composition of families although the lack of many families sampled form CI led to a significant difference in composition (R=0.77). The composition of genera (R=0.88) and species (R=0.94) were even more dissimilar with high levels of difference of composition.

75

A closer look within the orders shows that at family level the Coleoptera and Diptera have NZ compositions closer to CI compositions than does Hymenoptera (Table 3-3). Coleoptera maintains a similar level of difference through genus and species. However, the level of difference at genus and species level increases greatly for Diptera. Hymenoptera maintains a high level of difference between NZ and CI composition at genus and species level.

Table 3-4: R values based on NMDS distance matrices for presence / absence data. * = p<0.05

	Taxa level		
	Family	**Genus**	**Species**
All orders	0.77*	0.88*	0.94*
Coleoptera	0.59*	0.53*	0.6*
Hymenoptera	0.75*	0.79*	0.88*
Diptera	0.53*	0.85*	1.08*

6) Does the actual composition of taxa on CI differ from that expected, assuming random dispersal.

Taxon numbers on CI were compared to an expected taxon count based on a random re-sampling of the NZ species pool (Table 3-4). CI taxon counts for Coleoptera were not significantly different from the expected number at all 3 taxonomic levels. Diptera showed a higher than expected count at species level only. Hymenoptera showed a lower than expected CI count at family and species level.

Table 3-5: Actual numberof the CI taxa represented by each order compared to the expected number based on resampling of NZ taxa. The test to see whether the CI proportion is within the 95% confidence interval (ci) of the expected value is performed for 3 orders, at family, genus and species level. * = CI value significant as it falls outside the 95% confidence interal of the re-sampled NZ value.

Taxa level	Order	Total NZ count	Total CI count (actual count)	Mean NZ resampled count (expected CI count)	95% ci of resampled NZ mean
Family	Col	35	21	20.64	+/- *4.05*
	Hym	23	11*	17.80	+/- 3.33
	Dip	38	28	26.73	+/- 4.13
Genus	Col	132	49	48.10	+/- 9.32
	Hym	138	43*	53.39	+/- 9.41
	Dip	159	75*	60.79	+/- 9.5
Species	Col	163	52	52.23	+/-10.06
	Hym	198	51*	63.46	+/-10.53
	Dip	219	84*	70.45	+/-10.79

Comparisons were also conducted between the expected species count of selected named taxonomic levels, and the actual species count within that taxa seen from CI (see Appendix F for full table). At lower taxonomic levels only those taxa containing sufficient species could be used. Coleoptera showed a consistent patteren throughout all taxonomic levels. Species counts for all Coleoptera taxonomic levels were within the 95% confidence interval of the expected value. Hymenoptera showed, despite an overall pattern of under representaion on CI, that for certain taxa the species counts on CI were found as expected, and in some cases (Ichneumonidae and Mymaridae) greater than expected. Diperan taxa showed trends in both directions. Over representaion as an order was continued through super-family and family to genus level (Hydrellia). However, other dipteran taxa were under-represented, at super-family (Scaroidea) and family (Mycetophilidae and Tachinidae) levels.

3.6 Discussion

3.6.1 Taxon numbers

The results obtained in this survey show whether there is a significant difference between the dune insect communities of NZ and CI. The initial comparisons between NZ and CI are at a high level, using counts and ratios and move into more detailed comparisons using presence/absence and examining specific taxa groups.

The number of taxa sampled from NZ was over three times greater than from CI. This increase is not unexpected as mainland NZ's 268,000 km^2 (Kuschel, 1975) is almost 300x greater than Chatham Island's 920 km^2 (Miskelly, 2008). That said, neither of the two regions were totally covered by the survey, being a dune habitat project. Even so the total coastline encompassed by the NZ survey was 1700 km, 7 times greater than that of the 250 km of Chatham Island coastline surveyed. The disparity in coastline length is mitigated at least somewhat by the wider variety of land use and non dune habitat found on the NZ coast. Areas of intensive farming and human habitation have often reduced, or destroyed former duneland areas and duneland vegetation (Hilton, et al., 2000; Jamieson, 2010). In contrast, the northern half of CI is more or less one large sand dune, with many protected areas of conserved duneland structure and ecology (Curtis pers obs.). If loss of duneland on the 1700 km length of NZ coast is consistent with national NZ figures (Hilton, et al., 2000), then maybe only 170-510 km remains of original duneland habitat. The ratio of actual duneland on the NZ coast compared to CI would then vary between 1.4x and 2.0x.

The lack of suitable dune habitat on the NZ coast help to account for the fact that NZ taxa counts are not 7 times those of CI. Two other factors that contribute to the lower than expected disparity are that each site collected from was approximately the same size, and because species area curves are not linear, species numbers do not rise at the same rate as the rate of increase in area. The increased taxon count from the mainland was also carried through to site level. At this level all sampling factors were consistent between sites (e.g. duration, trap types). On average, NZ sites contained 1.6x more families, 2.3x more genera and 2.6x more species than CI sites, which is very similar to the postulated ratio of NZ to CI duneland.xxx

Although the same degree of sampling was performed at each site the mere fact that NZ sites were geographically more separated means they would share fewer taxa and

so increase the total taxon count. In the results we see how the more distant the sites were from one another, the higher the cumulative taxa count was.

Finding that the NZ mainland has a higher diversity than CI reinforces the common biogeographic concept of impoverishment. Despite its lower diversity how does the structure of the CI population compare to that of NZ?

3.6.2 Community structure

Addressing the structure and composition of island populations in respect to their nearest mainland region introduces another biogeographical concept, that of disharmony. In its simplest definition disharmony describes the fact that island communities do not fully reflect the diversity seen on the mainland. Bearing in mind that islands are smaller than the mainland, they will never be a direct reflection of the mainland community. However, disharmony is not simply a result of having fewer taxa, it also implies a degree of selection or filtering which has influenced which taxa disperse to and colonise the island. It is not, therefore, a random selection from the mainland population (Whittaker & Fernandez-Palacios, 2007). Filtering is thought to work in favour of taxa with a long distance dispersal ability, sometimes referred to as waif taxa (Carlquist, 1970). Attempts have been made to show islands have a higher proportion of waif taxa in their community assemblage. However, showing this is difficult and confounded by numerous factors which can mask the representation of the waif taxa in the population. As well as the waifs, island can be populated by older lineages inherited from a split with a larger landmass (relics), lineages evolved from the original colonisers that are now very different to their waif ancestors, continuing immigration and extinction of old waif lineages. We can see then that island age, isolation, geological history and size will all affect the degree of disharmony seen on an island.

It has been shown in this study that CI dune insect fauna appears to differ from that of NZ in its relative proportions of Diptera and Hymenoptera. The initial results showed that all orders and all taxa levels were statistically similar between NZ and CI. However, analysis of the expected taxon counts showed Diptera having a higher than

expected CI count at species level and Hymenoptera lower than expected CI count at family and species level.

The numerical differences were borne out when looking at the proportions within a region. Within NZ, all but one taxonomic level showed the three orders in equivalent proportions (some difference at species level between Coleoptera and Diptera). On CI differences in proportions between the orders are apparent as high as family level. Diptera are consistently seen in significantly higher proportions than Hymenoptera at all levels and are greater than Coleoptera at genus and species level. Similar results are seen when the site counts are used, although the Diptera/Coleoptera differences do not register as significant.

A taxon's lower than expected presence on an island is often regarded as an indicator of poor dispersal ability (Carlquist, 1970; Williamson, 1981). Hymenoptera counts on CI were lower than expected, Coleoptera were within expected limits and Diptera counts were consistently higher than expected. The lower than expected numbers of Hymenoptera implies that they are somehow disadvantaged in dispersal and/or colonisation compared to Coleoptera and Diptera. Conversely, Diptera seem to have some greater ability to disperse and/or colonise CI. This putative lack of immigration ability in Hymenoptera has also been attributed to the low numbers of the order found on Pacific islands (Watt, 1975)

The effect on immigration seems to have an influence even at family level. Fewer than half of hymenopteran families found on NZ were found on CI, whereas over ¾ of the NZ Diptera families from NZ were represented on CI. Interestingly even though there are fewer hymenopteran families on CI, their mean number of genera/family and species/genera are higher than the dipteran families.

Although other similar studies are limited, there are some that can be compared to the CI fauna. Collections from Niue have found Hymenoptera to be in significantly lower proportions that Coleoptera (Given, 1959). On South Georgia Hymenoptera were found in significantly lower proportions that Coleoptera and Diptera. Significant differences were seen between all three orders from Campbell Island, with Hymenoptera the lowest and Diptera of highest proportions (Gressit & Yoshimoto, 1974). Macquarie Island sampling found Diptera made up more of the fauna than Coleoptera and Hymenoptera (Gressit, 1962). An example from the recently (1960s)

emerged volcanic island of Sursey shows a high number of chironomid midges (Diptera) as some of the first insects to reach the island (Edwards & Thornton, 2001). In fact some 40 years after its creation over half of Motmot's arthropod taxa were Diptera (New, 2008).

In all the previous examples Hymenoptera had the fewest taxa and Diptera the most in all but the Niue collection. What may cause the lower than expected number of Hymenoptera and greater numbers of Diptera? Hymenoptera taxa are ecological specialists often being specifically adapted to a particular habitat (Meyer, 2009b). In fact many hymenopteran habitats are the bodies of other living arthropods. Some 75% of the sub-order Apocrita (ants, bees and wasps) are parasitoids at some stage of their life cycle (Mason & Huber, 1993). This parasitoid lifestyle may limit the opportunities for Hymenoptera to successfully disperse and colonise new areas. They would be reliant on a parasitised host to disperse successfully. Even if a parasitoid managed to develop and emerge it would still have to be in sufficient numbers to reproduce and establish a population. On Anak Krakatau hymenopteran parasitoids of Lepidoptera were found to be more numerous than parasitoids of other insect orders, attributed to the fact that lepidopteran parasitoids are generally less host specific than the parasitoids of the other insect orders (New, 2008). The impediment to colonisation argument for parasitoids also holds for the dipteran Tachinidae family, many members of which are parasitoids, and which is also found in lower than expected numbers on CI.

In contrast to Hymenoptera, Diptera can be far more generalist in their habitat and diet (Meyer, 2009a). Diptera are found in almost all non marine habitats in the world. The extensive distribution of Diptera is almost certainly aided by their excellent flying ability and utilisation of some extreme habitats, enabling them to disperse and colonise successfully.

How do the island taxa counts differ from that of their mainland neighbours? Many of the studies mentioned earlier would need further investigation, especially in regard to the taxon composition of their respective mainlands. Does age of the island have an effect on species composition? In an experiment on re-colonisation of six defaunated islands in the Florida Keys, Simberloff and Wilson found that in the first two years more Hymenoptera were sampled from 5 of the 6 islands than either Diptera or

Coleoptera. In fact Diptera were the least common of the three orders with Diptera only found on 1 of 6, and 1 of 4 islands after 1 and 2 years respectively (Simberloff & Wilson, 1969b, 1970). In the context of these six Florida Keys islands the results are not unexpected as they accurately reflect the faunal composition of the islands before the defaunation took place. These islands are also very different to those previously mentioned. They are very small tropical mangrove islands some 11-18 m in diameter with only a few trees at best and are nested within a complex system of other islands of varying size and shape (Wilson & Simberloff, 1969). Again it would be very interesting to have knowledge of the composition the source pool for the earlier islands examples to gauge the percentage of insects that are dispersing to the islands.

From these disparate sets of data we can see that each island situation can be very different. From the CI, South Georgia and Campbell Island it could be inferred that Diptera are better dispersers and colonizers than Coleoptera and Hymenoptera, and that Hymenoptera are relatively poor dispersers. The insect community on an island can depend on the age and size of the island as well as the proximity to a larger source pool. Perhaps, however, the most important factor is the composition of the source community from which the island community is derived.

Of course a source community is itself a uniquely formed entity. In this project NZ was considered the 'mainland' source pool. However, NZ itself is regularly regarded in research as a large continental Pacific island (Gibbs, 2008; Gillespie & Roderick, 2002; Goldberg, et al., 2008). Being as such, NZ's insect community is often identified with island like attributes, including a low proportion of Hymenoptera (Watt, 1975) and a disharmonic mix of taxa (Carlquist, 1970; Gillespie & Roderick, 2002; Watt, 1975).

The blurring of the distinction between 'island' and 'mainland' raises questions as to whether perceived phenomena such as impoverishment and disharmony can be used as meaningful terms. All areas no matter how large or small, defined as islands or not, will be different from any other. Are these concepts island specific or just an observation of the infinite ecological continuum that is the living world?

3.6.3 Impoverishment and disharmony

The concepts of impoverishment and disharmony have been revealed through many studies of island biota. Although the ideas have been long been recognized, their validity as viable concepts has been challenged (Whittaker & Fernandez-Palacios, 2007). Preston (1962a) discusses whether islands are truly impoverished in that mainland taxon counts are 'samples' of a greater area, whereas island counts are 'isolates' and therefore counts will naturally be smaller. The idea that disharmony is just an acknowledgement that different places and different habitats have differently structured communities, whether they are separated by a stretch of water or not is also argued (Berry, 1992; Whittaker & Fernandez-Palacios, 2007). Disharmony and impoverishment are still acknowledged in biogeography, although within the journals "Biodiversity and Conservation" and "The Journal of Biogeography" only two papers mention impoverishment or disequilibrium (disharmony) in their title in the last five years (and they are by the same author (Dapporto & Dennis, 2010; Dapporto, et al., 2011)). It has been suggested that these terms continue as they still convey to biographers a lower biodiversity or different species composition in a convenient and easily understood terminology (Whittaker & Fernandez-Palacios, 2007).

The concepts that islands have a lower biodiversity than equivalent mainland areas, and that the structure of island communities may be different from neighbouring mainland, have been shown to be valid. Naming these concepts allows discussion and communication on the subjects without resorting to lengthy explanations. Perhaps the problem with the current terms, disharmony and impoverishment, is that they imply that the island community is lacking in some element, or is not quite a 'proper' community. NZ itself is classically described as disharmonic (Gibbs, 2008; Goldberg, et al., 2008; McDowall, 2008), yet it has been evolving and adapting to changing environmental conditions for over 23 my. All ecological communities are valid and have grown to exist under their own unique conditions. Disharmony and impoverishment will undoubtedly remain in use, but the underlying concepts must be understood and applied correctly.

In summary, the proportions of taxa found in this project and their deviation from a randomly generated proportions show that at some degree, disharmony does exist between the taxa of NZ and CI.

3.6.4 NMDS graphs

The proportions at which the three orders co-exist on NZ and CI are known for the project data. Even though the proportions of the orders are the same (or similar), does not mean that actual taxon groups at the lower level show similar degrees of 'similarity'. We can see from the NMDS graphs that the NZ and CI communities are quite different at all three taxon levels at which they were tested.

Difference in the NZ and CI communities becomes more apparent as the level of taxa compared moves from family to species. This community difference is also shown in the R values which get closer to 1.0 as the taxonomic levels become lower, indicating that the NZ and CI communities are more dissimilar. This dissimilarity is reflected in a higher CI endemicity at species level (Emberson, 2006b). The NMDS graphs also show that, within NZ, sites closer geographically to one another are more similar in their species composition (i.e. they are closer to one another on the NMDS graph). The CI sites are less dissimilar to one another because they are all within a smaller geographic area. The greater similarity of taxa between closer sites agrees with the earlier observation that cumulative taxon counts of any two sites increased as the distance between the sites increased.

The large disparity between regions at species level is not surprising as CI has been isolated some 3-5 my, quite long enough for the evolution of new species in either area and the loss of species in NZ. Endemicity in CI beetle species is estimated to be over 25% (Emberson, 2006b). The samples from this project show species endemicity rates of a 6% for Coleoptera, 3.7% for Diptera and 0% for Hymenoptera. The disparity in these percentages can be surmised. Coleoptera appear to be by far the most studied of these three orders on CI (Emberson, 2006b), and so knowledge of the endemic species is far greater, making accurate, effective comparisons more likely. Apart from inclusion in general CI insect surveys (MacFarlane, 1979; MacFarlane, et al., 1991), Diptera and Hymenoptera do not seem to have had dedicated CI inventories, so making comparison with NZ taxa more difficult. It could also be that Coleoptera have actually evolved more endemic species than either Diptera or Hymenoptera. The 0% for Hymenoptera may be due to difficulty in identification of small parasitic wasps and a lack of data sources on endemic CI Hymenoptera.

The 6% Coleoptera endemicity found in this study compared to the 25% of Emberson's study, could be attributable to the far higher family and species counts in the latter (21 verus 47 and 52 verus 329 respectively) and the fact the 25% endemicity in Emberson's study includes all islands and rock outcrops in the Chatham Islands, rather than just concentrating on CI itself. Including small outlying islands would increase likelihood of endemic species being found. Further work may also reveal more endemics amongst the as yet unidentified portion of the collection from this study.

Even though NMDS graphs are not quantitative assessments of inter-community taxon similarity they give a good visual guide to when differences lie and how pronounced these differences are. The next stage of the project lookeds at the taxa which are creating the differences between NZ and CI.

3.6.5 Comparison using specific named taxa

Having ascertained that the three orders differ in their relative proportions on CI, it is interesting to see whether these proportions are reciprocated at specific lower taxonomic levels. For example, despite having lower proportion of the CI taxa overall, are all hymenopteran taxa groups represented by fewer species on CI than NZ? At super-family level Coleoptera numbers show no difference to the expected counts. For Hymenoptera only 1/8 super-families (Proctotrupoidea) is under represented with none over represented. Diptera has 1/17 (Sciaroidea) under represented and 4/17 over represented. So, though Diptera as an order is over represented on CI, one super-family is found in lower than expected numbers.

Within the family level, Coleoptera numbers continues to equal expected counts. Hymenoptera show deviation from the order based data, with only 1/7 family under represented and 2/7 over represented. Diptera still have families that are underrepresented, 2/6, although more are over represented 4/6, running counter to the results of the order level data.

Although expected results were calculated for a few specific genera, there were not sufficient genera with enough species within them to make the results worthwhile. However, it is worth mentioning two dipteran genera over represented on CI,

Hydrellia and *Scatella.* These genera are from the family Epihyridae, shore or brine flies, which has a huge range of species, many of which are scavengers and detritivores. Some can even tolerate the cytotoxins and bio-toxins found in cyanobacteria (Foote, 1995). Inherent in the family is an also an ability to adapt to extreme and hostile habitats, some species living in salt marshes, alkaline lakes, hot and cold springs and crude oil (Foote, 1995). Epihyridae, then, has evolved traits giving its members every chance of successful colonisation of new environments.

General statements concerning the dispersal/colonising abilities calculated from a higher taxon level cannot be extrapolated to lower taxonomic levels. Inferred distribution patterns based on higher taxonomic levels are influenced by strong signals from specific family and genera. Conversely general statements concerning attributes of the orders cannot be made from studying a single genus or family.

It is intriguing then to consider what traits or factors cause specific taxa to be over or under represented. Are the patterns of distribution reflected in other surveys on other islands, or does CI have its own unique pattern of fauna?

3.6.5.1 Taxon ratios

The community structures were also compared using species/genus, species/family and genus/family. Although species/genus (the others less so) is a widely used ratio in ecological studies care must be taken when calculating the relevant ratios (Jarvinen, 1982; Simberloff, 1970). The calculated ratio is dependent on sample size and so accurate comparisons between communities of differing taxon size must be performed with the sample size from the larger pool being the same as that of the smaller pool. To accommodate this issue multiple calculations were performed using different random sample sizes from the NZ pool. The resultant analysis clearly shows the ratios increase as the sample sizes increase. When the NZ ratio was re-calculated using the mean ratio of 10,000 random samples (n=187) the ratios obtained were statistically equivalent to the CI ratios for all orders and taxon levels. This similarity in species ratio is seen in many other studies comparing island populations with their source pool (Elton, 1946; Jarvinen, 1982; Simberloff, 1970; Williams, 1947)

3.6.6 Data and statistics used

The data collected for this survey was recorded by noting the presence or absence of a taxon at a particular site. The overriding reason for using presence/absence (P/A) was a matter of logistics. The collecting, processing and identifying the specimens took a large proportion of the allocated project time. Forming a realistic count (abundance) of every taxon found would have added considerably to the time taken to collate the results. Where feasible however abundance would add another factor to potentially affect immigration probability. Carrying out counts of taxon abundance for this study would have involved a reduction in the number of taxa studied and limited the taxa to those that were readily identifiable. Therefore, taxon counts for this study were not used as the strength of this study was in its use of many different taxa. Not using abundance enabled the use of as a large a cross section of the insect community as possible in the time available.

P/A recording also removes any major sampling bias created by uneven sampling. There was potential for a seasonal bias in the sampling as the times of collection ranged from late November to late February. In many insect taxa population numbers can fluctuate throughout the year (Basset, 1988). Potentially two sites that both contain a taxon will be seen as having quite different communities based on the time of the survey and thus the number of specimens caught. Although there is certainly that taxa will have been missed from the sampling, the use of count data will not have overcome this problem.

The achievement of this part of the study was the simple but effective use of re-sampling to create a null hypothesis for dune insect community structure on CI. Re-sampling allowed the creation of a normally distributed set of mean counts from the NZ dataset. The CI data values could then be compared to the re-sampled NZ dataset and any similarities or differences would be statistically sound.

Not only was this approach easy to use, but it is also flexible. Taxon numbers sampled and the total number of re-sampling events can by easily altered. For this study the null hypothesis for testing was deemed to be a completely random immigration scenario. However, null hypotheses can be generated with an a-priori knowledge of likely proportions of taxa and those allowed for in the re-sampling technique. Results from the re-sampling not only stand on their own merit but can also be combined with

the post-hoc methods of comparison (ie Marascuilo procedure) to create further hypothesis for future research.

3.7   Conclusion

This project has shown that the CI dune insect biota concurs with many other analyses of island biota from around the world. An extra dimension has been added to this project by collecting and using the data from the mainland source so that mainland and island biota can be compared using a variety of ecological methods. This comparison is especially interesting as it is NZ itself that is usually regarded as the island and deemed to have an island like fauna.

The composition of an island fauna can vary from island to island and be determined by a number of factors. One major factor influencing the island population is of course the species pool available from the mainland. It seems paramount then that before the dispersal and colonisation abilities of taxa are inferred from island population, a knowledge of the 'mainland' source is needed.

The re-sampling technique devised during this study successfully obtained information on the structure of the mainland insect fauna. Importantly re-sampling NZ sub-sets that were equal in size to the CI population meant that variation in taxon count was not attributable to sample size and could be tested with statistical rigour. Through re-sampling disharmony was detectable at order level, although it is probable that the disharmony is being driven by specific lower level taxonomic groups.

Generalising then about the expected representation of taxon groups on islands based on higher level taxon grouping is not reliable as there seems to be no relationship between the expected results for a lower taxon group based on its higher taxon levels.

Chapter 4

Modelling factors that may influence insect immigration to Chatham Island from New Zealand

4.1   Introduction

Biogeographers have long recognised that the ability of a taxon to disperse to, establish in, and populate a new area is dependent on numerous factors. In this study the successful accomplishment of all three of the above stages is often discussed as one process, namely immigration. Both immigration and emigration are used to describe the process of dispersing from a home range to successfully arrive at and populate a novel area (Hoberg & Brooks, 2008; Lomolino, et al., 2004). However, immigration emphasises the arrival and colonisation of Chatham Island (CI) in particular, rather than simply to ability to leave the New Zealand (NZ).

Factors deemed to affect immigration probability range from inherent biological traits of the organism, for example, size, breeding strategy, behaviour to climatic conditions, such as mean temperature and lowest temperature at the point of dispersal and area of arrival (Drake, et al., 1989; Sol, 2007). Such factors create conditions that enhance the chances of immigration for some taxa and decrease chances for others. The fact that some factors reduce the chances of a taxon from successfully immigrating has resulted to them sometimes being referred to as 'filters' (Colautii, et al., 2006; Simpson, 1943; Whittaker & Fernandez-Palacios, 2007; Williamson, 1981).

We have seen from Chapter 3 that this study supports the idea of a level of disharmony between the insect dune community of NZ and that of CI. The concept of disharmony is strongly linked to the idea of filters, the disharmony being created by the action of filters on taxa.

The effect of filters can be seen in the zones of biological demarcation, such as Wallace's, Huxley's, Webber's and Lydekker's lines (de Lang & Vogel, 2006; Esselstyn, et al., 2010). These zones are attributed to the influence of many different filters exerting greater or lesser influence upon the local flora and fauna (Esselstyn, et al., 2010). Filters can also be more or less effective depending on the direction of

attempted dispersal. Archipelagos situated between mainland areas have shown that filters can act in more than one direction, with islands becoming progressively less speciose as they increase in distance from their respective mainland source (Williamson, 1981).

There is more than one phase (or barrier to overcome) to complete a successful immigration (Colautii, et al., 2006; Mack, et al., 2000; Shea & Chesson, 2002; Sol, 2007). The first phase is dispersal to a new area (dispersal phase). Dispersal simply involves a member of a species managing to physically arrive in the new area. Dispersal may be passive (via water and air currents, attached to animals, plants or other substrates) or active (flying, swimming, or walking). In the second phase (establishment), a taxon must create a foothold or viable population in the new area. The taxon must have suitable conditions to survive, and be in sufficient numbers to find mates and successfully breed. In the third phase, having successfully established, a species must then expand to a level of population growth which will allow it to overcome the possibility of short to medium-term stochastic extinction (expansion phase), (Lockwood, et al., 2005; Sol, 2007). Within this study all taxa found on CI are presumed to have established on the island.

The range of filters in a specific situation will have differing degrees of influence at each phase of the immigration process, some aiding dispersal, others only being of benefit once dispersal has been achieved by the taxon. Filters will also vary in their effect depending on the length of time an area has been available for immigration. The ability to compete for resources and evade enemies becomes more important as the new area becomes more heavily populated by immigrants and, over time, with new species evolving from earlier founder taxon populations. Filters can be grouped into those mostly affecting the dispersal phase (isolation or dispersal filters) and those having most effect on the establishment and expansion chances of the taxa (colonisation filters) (Whittaker & Fernandez-Palacios, 2007). They may well be filters that affect the ability of a taxon to expand within an island scenario, for example, available habitat and competition with other taxa (expansion filters).

Much of the research and experimentation on immigration has involved the study of insects when used as part of a biological control program, as well as analysis of the progress of deliberately introduced vertebrate taxa (Simberloff, 1989; Sol, 2007).

Data for biocontrol and introductions is often more detailed and well understood than observations based on natural immigration/invasion. Even so, problems still arise due to lack of information about failed biocontrol introductions. Biocontrol experiments have highlighted a number of potential factors influencing the chances of a successful insect introduction; similarity of climate between source and target areas (Simberloff, 1989; Wilson, 1960); similarity of vegetation (Lattin & Oman, 1983); body size (Lawton & Brown, 1986); generality of habitat use (Simberloff, 1989; Sol, 2007); and number and population size of introductions (Lockwood, et al., 2005; Williamson, 1989).

Statistical analysis of ecological data is a huge and often intricate subject. A balance needs to be met between describing the ecological situation as accurately as possible, but still being comprehensible and practical to use. Biology, and especially invasion biology, often relies on data collected at different places and different times. The statistical analysis of immigration success has a number of features that can be addressed using generalised liner mixed models (GLMM) and generalised linear models (GLM) (Sol, 2007).

The binomial nature of an immigration response (success or failure) can be accounted for in GLMM/GLMs thus allowing probabilities of success to be attributed to variables even though for any one taxon the actual data will simply show success or failure. The immigration process is unlikely to be influenced by only one major factor (although this possibility should not be completely rejected). Using GLMs will reduce the filter options to those that appear to be having a significant effect on the likelihood of successful immigration. When using multi species data, all the species will have features in common with others from the same taxonomic group, e.g. genus, family. These confounding factors of evolutionary similarity can greatly bias any analysis that assumes that all the data points (species in this case) are independent (Blackburn & Gaston, 1998; Nieminen, et al., 1999). Using GLMs can account for confounding factors of taxonomic similarity by entering them into the model as random factors (Blackburn & Duncan, 2001).

As is the case with many ecological questions, the use of models cannot give a definite answer, especially in such a complicated subject as invasion biology and biogeography. However, combined with sound biological knowledge and considered

choice of filter factors GLMM/GLM modelling can give direction to future hypothesis and research scenarios.

4.2 Filters used in the study

The choice of filters that could exert an influence on the immigration process is almost infinite (Colautii, et al., 2006). However, judicious use of available data and the findings of previous studies have identified the following filters from which to model the probability of immigration success from to CI from NZ.

4.2.1 Climatic filters

Island usually have cooler, windier but more stable climates than the equivalent latitude on mainland areas (Whittaker, 2004; Whittaker & Fernandez-Palacios, 2007). The cooler, windier climates may remove taxa that are not able to survive the island's harsher climate (Whittaker & Fernandez-Palacios, 2007).

A number of potentially influential climatic variables are modeled against CI presence to find out whether similarity of climate is an advantage to colonisation. This allows us to ask the following questions:

Does a difference in climate between NZ and CI affect immigration (especially colonisation) likelihood? And if so, which climatic difference has the greatest effect?

The climatic variables used as filter factors in the modeling are annual figures for mean temperature (°C), maximum temperature (°C), minimum temperature (°C), rainfall (mm), sunshine (hours), and frost days. All climatic data was provided by the National Institute of Water and Atmospheric Research (NIWA) and covers a recording period of 1971-2000 (NIWA, 2008).

Climatic variables were entered into models as the difference between NZ values and CI values.

4.2.2 Immigration filters

4.2.2.1 *Physical position*

Habitat count

For the purposes of the survey the dune habitat was divided into three areas. The areas selected represented a change in habitat available to the insect taxa: near high tide, fore dune (grasses and low shrubs) and rear dune (larger shrubs and trees). Taxa were given a value of 1, 2 or 3 signifying how many of these areas they were sampled from. The number of areas a taxon was found in gives an indication as to the specificity of habitat, or "niche breadth" (Simberloff, 1989; Sol, 2007), for which a particular taxon can tolerate.

Does a wide range of potential habitats increase immigration opportunities?

Site count

A narrow species range may limit a taxon's access to islands. Site count measures how many NZ sites taxa were sampled from which gives an indication of range size.

Does having a greater geographical spread, and so more launching points, as well as likely higher tolerance for habitat and climate, increase the chances of a successful immigration event?

Distance

Isolation is seen as a strong factor in limiting taxon access to islands (MacArthur & Wilson, 1967; Whittaker & Fernandez-Palacios, 2007). The distance used in this project is the coastal distance from the sample site to Banks Peninsula. Not including the distance over water to CI, emphasises the distance needed to disperse within NZ, and assumes each taxon has an equal chance of crossing the 850 km ocean between NZ and CI.

Does distance needed to disperse have an effect on likelihood of successful colonisation?

4.2.2.2 Effects of wind and sea currents

The existence of seemingly beneficial wind and sea currents may have an effect on the likelihood of a taxon dispersing to CI. The following variables were modelled against taxon presence on CI.

North and south of the Chatham Rise

The Chatham Rise is an area of sea floor with an average depth of 400-600 m and extending for some 1000 km from Banks Peninsula to beyond the Chatham Islands (Cook, et al., 1989). In fact, the Chatham Islands themselves are simply an emergent portion of this part of the continental crust.

Major ocean currents flow around NZ from Antarctica, Australia and the Pacific region. Parts of Antarctic and Australian currents merge to create the Southland current. The Southland current flows around the south and east coasts of South Island before eventually being deflected east to the CI by the Chatham Rise. From the north, the East Cape Current flows south along the east coast to be eventually directed towards the CI by the Chatham Rise.

It is known that insects can be carried for long distances and survive for substantial periods of time whilst rafting in vegetation in the ocean (Smith, 2002; Vandendriessche, et al., 2006). Live insects have also been sampled from the water surface far out to sea (Cheng & Birch, 1978; Peck, 1994b).

Do the currents contribute significantly to the immigration process by transporting insects and insect covered flotsam to Chatham Island? And is if so, is one direction of flow more effective than the other?

Wind based factors

The wind currents from NZ are more seasonally variable than the sea currents and are greatly influenced by local geography (NZ Meteorological Service, 2011; Tomlinson, 1973). However, the prevailing wind direction in NZ is westerly providing the

conditions for wind assisted dispersal across the 850 km of sea from NZ to CI (Coulter, 1975). Many insects have been sampled from the air many hundreds of kilometers from land showing that wind-assisted movement is ever present and may be an effective means of dispersal (Murata, et al., 2007; Peck, 1994a). Wind direction and strength is certainly a factor in the number of insect taxa that disperse in a westerly direction from Australia to NZ (Close, et al., 1978; Fox, 1973; Tomlinson, 1973).

Mean wind speed gives an indication of the overall windiness of a site. A windier site could give rise to more opportunities for westerly wind dispersal. However, wind may only become a significant factor once it reaches a particular intensity. Gale days (days with gusts over 63 k/hr) may be a better indication of how much 'effective' wind occurs at a site.

Does prevailing wind direction or wind speed have a bearing on the likelihood of successful immigration to CI?

4.2.2.3 Biological filters
Taxonomic rank

From the work in chapter 3 it seems that there could be filters having an effect at order level. Taxon rank needs to be addressed in the modelling to account for any effect of phylogenetic relationships. Taxonomic rank can be seen as a confounding effect as taxa within the same rank, by definition, share many of the same traits. The variation in the model due to the effects of taxonomic similarity must be shown to be spread evenly across the taxonomic ranks, so that the effects of the variable/s being modelled can be ascertained without being masked by any taxonomic rank effect.

Does taxonomic rank have an effect on the likelihood of successful immigration to CI?

Larval food

The feeding habits and preferences across the taxa sampled are extremely varied. Larval food preferences are chosen as many adult insects feed on pollen or not at all, living just long enough to reproduce. Larval stages, however, have a wide variety of

food preferences and this phase can be the majority an insect's life. Food types range from feeding on a single plant species, fungi, parasitism on other insects, to active hunting and omnivory.

For the modelling process species were divided into herbivore (including fungivore, saprophage and detritivore), predator and parasite. The grouping was performed so as to keep ecologically similar taxa together whilst having few enough variables to provide a sound statistical outcome (reducing the number of degrees of freedom).

Do the feeding habits of the larval stages of taxa sampled have an effect on the likelihood of successful immigration to CI?

Insect body size

Body size is often associated with immigration probability in organisms ranging from mammals and birds, to invertebrates (Simberloff, 1989; Sol, 2007). The effect of body size on immigration in insects has been examined across taxa and within species. Body size has been found to have both positive and negative effects on insect immigration (Pimm, 1989). Smaller bodies are more likely to be carried by air currents, whereas larger bodies may be more likely to survive the rigours of a journey across water, possibly lasting several weeks.

Does body size affect immigration chances in this project?

4.3   Methods

4.3.1 Modelling approach

The initial modeling approach addresses each factor individually in order to assess whether the factor modeled has any degree of influence on successful immigration even before being entered into a maximal model. The individual GLM models use the model formula of *binary response variable ~ single factor.* The following values are obtained from the individual model output.

χ^2 **p-value:** P-value based on the χ^2 distribution of the null and residual deviances, indicating whether the deviances are significantly different from one another (a=0.05).

Coefficients: an indication of the direction and degree of influence the factor has on the binary response. Coefficients are only displayed if the χ^2 p-value is significant.

Following the individual modeling, the factors were placed into groups of similar type and maximal models (MM) created for groups of factors. Separating the factors into different models removes the possibility of a more significant factor overriding others from another group which may be also be significant but not quite to the same extent. If a significant factor overrides one from its own group, at least it can be seen that that type of factor is important. The groupings used were, biological traits, wind/sea currents, geographical factors and climatic factors.

To find the final minimum adequate model (MAM), GLMs were used using backward deletion. In this method the factors with lowest influence were progressively dropped from the MM until a MAM is created. The final MAM contains only significant factors.

Before creating maximal models, continuous explanatory variables that could be included in the same model are checked against one another for correlation. Assessing for correlation removes variables that have similar trends in their data values and so would elicit a similar pattern in the response variable. Including correlated variables in backward deletion of a maximal model can confound the results by emphasizing certain factors or hiding the significance of others.

Variables highly correlated with other variables (>0.05) can be removed from consideration in the maximal model (Table 4.1). Some correlates are environmentally obvious, such as maximum temperature with sunshine, or minimum temperature with frost days. Others, such as habitat count and occurrence, correlate due to the factors being calculated in a similar manner.

Table 4-1: Main variables for use in maximal models with correlated variables with a correlation value of >0.5.

Main variable	Correlated variable	Correlation Value
Mean temperature	Rainfall	0.5655
Maximum temperature	Sunshine	0.5927
Minimum temperature	Frost days Rainfall	0.9592 0.6903
Site count	Habitat count	0.6256
Gale days	Wind speed	0.5135

Using knowledge of the biological systems and robustness of the factors, the following variables were selected for the maximal models: climate (mean temperature, maximum temperature and minimum temperature), geography (site count and distance), wind/sea currents (gale days, north/south of Chatham Rise).

The following values are obtained from the MAM output:

Factors in MM: All the factors in the initial maximal model

Factor/s in MAM: The significant factors that remain in the minimum adequate model

χ^2 **p-value**: P-value based on the χ^2 distribution of the null and residual deviances, indicating whether they are significantly different from one another (a=0.05).

Factor levels + Coefficients: An indication of the direction and degree of influence the factor has on the binary response. Factor levels are only displayed if the variable is categorical. Coefficients are only displayed if χ^2 p-value is significant.

4.3.2 Analysis of data

To ascertain which factors (if any) have a significant effect on the number of taxa reaching CI, generalized linear mixed effect modeling (GLMM) and generalized linear modeling (GLM) techniques were used. GLMs are useful when the variance of the data is not constant and/or the errors are not normally distributed (Crawley, 2008). The modeling approach in this chapter uses a binary response variable in which these two data situations are very likely. The explanatory variables (filter factors) are fitted into a model which, when complete, gives an indication of how well the data provided fits the model created.

In this project the response variable used is a binomial indicator of successful immigration to CI. Species found on NZ AND on CI are assumed to have successfully immigrated to CI. Those found on NZ and NOT on CI are assumed not to have immigrated to CI (or are not currently on CI). Due to the binary response variable (success or not) the type of GLM used is based on logistic regression and uses the Logit link function. Using Logit allows probabilities of success to be calculated for variables even though the data for each taxon has only a binomial success or failure of immigration.

Phylogenetic effects are accounted for by introducing the taxonomic factors into the model as random factors. Models were created using only the taxonomic variables against the binary response variable (CI presence or absence) (Blackburn & Duncan, 2001). Three models were created with the following nestedness of taxonomic factors as the explanatory variables: order, order+family, order+family+genus. Using ANOVA, the variation attributed to each model was compared to the variation of the other two models to ascertain whether any combination of taxonomic levels had a greater effect on the model variation than either of the other two models (Blackburn & Duncan, 2001). To further test the effect of taxonomic order the MAMs were run against data sets specific to each order and the three sets of results compared to gauge any difference of outcome when analyzing the separate orders. All modeling was performed using the R statistical package (R Development Core Team, 2010).

4.4 Results

4.4.1 Individual GLM models

Running GLM models for individual factors against CI presence/absence revealed that 10 of the 15 variables chosen showed a significant effect on immigration success (Table 4-2). Climatic variables, such as mean temperature, rainfall and frost days, had a more positive effect on immigration the less the NZ values deviated from CI values. Maximum NZ temperature and sunshine hours had no effect on immigration success. Increased area and site counts both had a positive influence on immigration. Being closer to Banks Peninsula (distance) also improved immigration success. A taxon's chances of immigration increased if they were found both north and south of the Chatham Rise. Taxa found only south of the Rise were slightly less likely to successfully disperse than those found only north of the Rise. Neither wind speed nor gale days affected immigration likelihood. Of the three orders, Diptera were most likely to immigrate to CI from NZ, with Hymenoptera least likely. Across all orders, a predatory larval stage increased immigration chances, although parasitism decreased chances of immigration. Body size did not affect the likelihood of successful immigration to CI from NZ.

Table 4-2: Output values from modelling individual factors against the binary response variable of CI presence or absence. * = χ^2 p-value <0.05. For a explanation of each factor see the text. Coefficient of categorical factors are relative to the intercept and show the relative effect the factor has on immigration likelihood.

Factor modelled	LRT	X^2 p-value	Coefficients (if significant)
Mean temperature	15.467	8.396e-05 *	-0.7743
Maximum temperature	0.29767	0.5853	Ns
Minimum temperature	7.8028	0.0052 *	-0.1823
Sunshine	0.94205	0.3318	Ns
Rainfall	10.133	0.0015 *	-0.0041
Frost days	7.9914	0.0047 *	-0.01436
Habitat count	103.44	2.2e-16 *	+1.6361
Site count	31.104	2.445e-08 *	+0.5695
Distance	21.802	3.023e-06 *	-0.001972
Chatham Rise	16.8	0.0002 *	Intercept (North) South -0.5949 both +0.7590
Wind speed	0.44825	0.5032	Ns
Gale days	2.0938	0.1479	Ns
Order	9.4639	0.00881 *	Intercept (Col) dip 0.6420 hym -0.110
Body Size	2.1738	0.1404	Ns
Larval food	3.1317	0.02536 *	Intercept (Herbivore) Host -0.6135 Predator 0.1763

Following individual modelling, the use of minimum adequate models showed which variables had most influence on immigration from within a group of similarly themed variables (Table 4-2). Variables with a significant effect within these models show that they affect immigration despite the effects of other, possibly more significant

variables in the same model. If variables were found to be correlated (Table 4-3), only one of the correlated variables was included in the MM.

Mean temperature and minimum temperature still maintained their significant effect on immigration. Both mean and minimum temperatures were more influential to immigration success the more the NZ value differed from that of CI. Site count had more of an effect on immigration success than distance, but both were significant. As in the individual modelling, taxa found north and south of the Chatham Rise had a greater chance of immigration and those south of the Rise had less likelihood of immigration. Gale days had no influence of immigration likelihood. Of the biological traits, only taxonomic order had a significant effect on immigration, increasing likelihood for Diptera, decreasing immigration likelihood for Hymenoptera. When included in the model with order, larval food type and size were not significant.

Table 4-3: Values derived from the minimum adequate models (MAM) of immigration likelihood created from backward deletion of maximal models (MM). * $= \chi^2$ p-value<0.05. Coefficient of categorical factors are relative to the intercept and show the relative influence of the factors within each model, on immigration likelihood.

Factors in MM	Factor/s in MAM	χ^2 p-val	Factor levels + Coefficient
Mean temperature Maximum temperature Minimum temperature	Mean temperature Minimum temperature	0.00012 * 0.00740 *	-0.75014 -0.17605
Site count Distance	Site count / Distance	0.00017 * 0.02533 *	+0.4334811 -0.0011314
Chatham Rise Gale days	Chatham Rise	0.00022 *	Intercept (North) na South -0.5949 both +0.7590
Body size Larval Food Order	Order	0.02474 *	Intercept (Col) na Diptera +0.6420 Hymenoptera -0.1110

In the case of continuous variables, the predicted probability of immigration success can be plotted against a range of possible values for the continuous variable. The immigration likelihood decreases as mean and minimum difference in temperature

increases, and distance to Banks Peninsula increases (Figures 4-1, 4-2,4-4). A greater site count increases immigration likelihood (Figure 4-3).
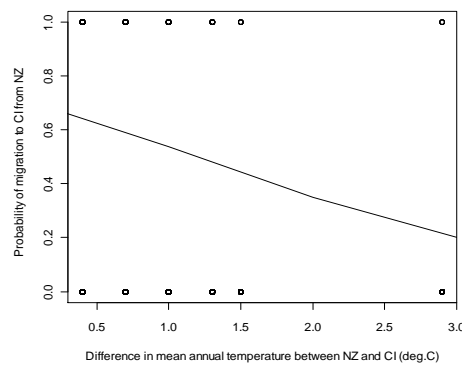
Figure 4-1: Probability of a taxon migrating to CI, against mean temperature difference. Showing a decreasing probability from >0.6 for a mean temperature difference of 0^OC, to a probability of 0.2 for a mean temperature difference of 3^OC.
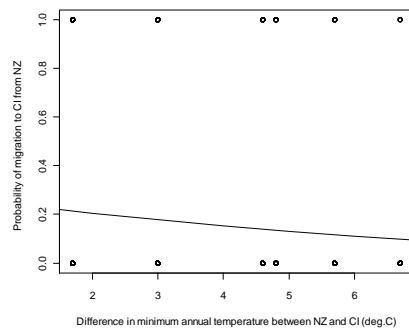
Figure 4-2: Probability of a taxon migrating to CI, against minimum temperature difference. Showing a decreasing probability from >0.2 for a minimum temperature difference of 0^OC, to a probability of 0.1 for a minimum temperature difference of 7^OC.
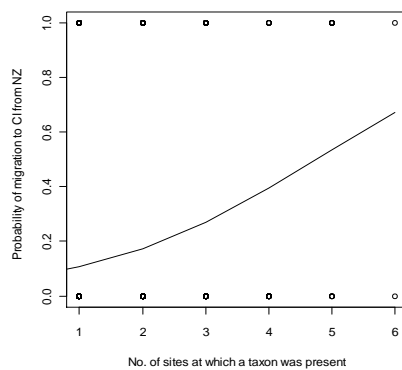
Figure 4-3: Probability of a taxon migrating to CI, against site count. Showing a increasing probability from 0.1 for a site count of 1, to a probability of 0.55 for a site count of 6.
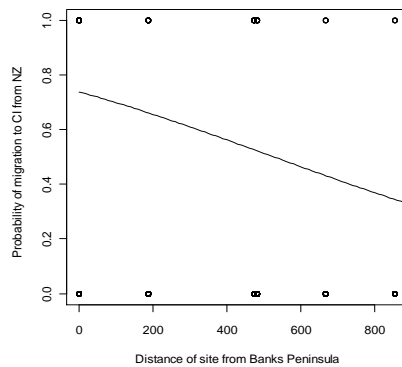
Figure 4-4: Probability of a taxon migrating to CI, against distance of site from Banks Peninsula. Showing a decreasing probability of immigration from >0.7 for a distance of 0km (on Banks Peninsula), to a probability of <0.4 for a distance of 700km.

The potential effects of phylogenetic relatedness were addressed by creating a model using just the taxonomic variables represented as random factors. The different variance in the models due to the effect of the random variables were compared between the models using ANOVA and subjected to a CHISQ test. There was no significant difference in the variance due to random factors between any of the models (alpha=0.05) (Table 4-4)

Table 4-4: Output from GLM models using only taxonomic variables and representing the taxonomic variables as random factors.

Model name (Mx)	Random factors included in model	χ^2 p-value from ANOVA of Model Mx against …		
		M1	M2	M3
M1	Order		0.2985	0.4399
M2	Order/Family	0.2985		0.4536
M3	Order/Family/Genus	0.4399	0.4536	

The effect on phylogeny was also assessed by running the MAMs against data sets containing only one particular taxonomic order and comparing any change in the significance of the results. No change in χ^2 p-value was seen between taxonomic variables for any of the MAM models (Table 4-5).

Table 4-5: Output from Minimal Adequate Models run against all orders and each order individually.

MAM Factors	X^2 p-values for all orders and individual orders tested separately			
	All	Coleoptera	Hymenoptera	Diptera
Chatham Rise	0.0002244	0.0002244	0.0002244	0.0002244
Mean temperature	0.0001172	0.0001172	0.0001172	0.0001172
Min temperature	0.0074033	0.0074033	0.0074033	0.0074033
Site count distance	0.000153 0.024880	0.000153 0.024880	0.000153 0.024880	0.000153 0.024880

4.5   Discussion

Modeling individual factors

Individual factors were modeled to examine their affect on a taxon's chances of dispersing to Chatham Island. Of the two biological factors modeled, body size and larval food type, only larval food type appeared to have a bearing on probability of a taxon reaching CI.

The effect of larval feeding guild appears to never have been addressed. The factors levels assigned in this project indicate that predators are relatively more successful colonizers than both herbivores and parasites, albeit not that much better than herbivores. However, those taxa whose larvae rely on a parasitic lifestyle may be disadvantaged. Adult parasites could quite possibly successfully disperse to CI but lack the colonizing opportunity due to a lack of a suitable host on the island. Larvae developing within hosts would have to rely on the host to disperse and in sufficient numbers to provide more adult parasites and a food source for future parasitic larvae. Food type is potentially interesting but also difficult to assign to many less well-known taxa. Adult and larval feeding habitats can also be very different. However, feeding habits might explain the relatively lower proportions of Hymenoptera found on CI as many of the hymenopteran taxa are parasitoids of other arthropod taxa. For preferred food types, comparison with biocontrol introductions is difficult as the nature of the biocontrol projects is to specifically target pest species with minimal damage to native flora or fauna.

Body size might have been expected to have more of an influence. Size certainly seems to play a part of promoting immigration where the taxa are passively dispersed by air currents. Snail taxa on Pacific islands have been found to be significantly smaller than continental snails (Vagvolgyi, 1975). However, size does not directly influence range size for passively dispersed seed types (Edwards & Westoby, 1996). Where dispersal is active there a tendency for larger taxa to be more inclined to dispersal behaviour; such as in insects (Dingle, et al., 1980; Gutierrez & Menendez, 1997; Roff, 1977) and crustaceans (Reaka, 1980). Larger body size is thought to convey immigration advantages such as greater energy, more economic flight and greater reproductive ability on arrival (Dingle, et al., 1980; Juliano, 1983; Roff, 1977). Body size has also been linked to reproductive strategy, with smaller taxa reproducing

more quickly, creating another factor from which immigration probability can be affected (Saether, 1988; Simberloff, 1989). Conversely, smaller insects have shorter life spans and are more vulnerable to fluctuations in climate (Pimm, 1989, 1991). So at certain scales and within specific taxa, size can have a role to play in immigration ability. However, at this stage in the biological history of CI, any patterns of composition that may have previously existed due to body size effects have most probably been masked by other factors. Despite the large distance (850 km) between NZ and CI, the length of time available for immigration (3-5my) has allowed even poor dispersers a chance to eventually immigrate to CI. The water gap is a significant barrier even for strong fliers to negotiate without an opportunity to rest and refuel, and so strong fliers may not have much of an advantage. Following on from this, the model specifically testing the influence of taxonomic levels reinforces the finding from previous chapters. Taxonomic order does appear to have some effect, with Diptera somehow advantaged in immigration chances compared to Coleoptera and Hymenoptera. As seen before, Hymenoptera are less likely to successfully migrate than either Coleoptera or Diptera. However, as alluded to in chapter 3, the effect of taxonomic levels needs to be addressed further. It is quite possible that the taxonomic order effects are being driven by one or two influential taxa of a lower taxonomic level (e.g. family, genera).

Other research has shown that closely related bird species can vary considerably in their ability to invade new areas (Ehrlich, 1989) and in general close relatives to invasive species are not themselves invasive (Mack, et al., 2000). Such statements add weight to the argument that perhaps higher taxonomic levels have less effect on invasion success than do the specific traits of lower level taxa. However, being closely related to a good invader does not always predict poor invasive capabilities. There are some examples of closely related grass and bird taxa both being successful invaders (Daehler & Strong Jr, 1993; Mack, et al., 2000).

Within the factors based on geographic position and range there is a general theme. Taxa that have higher values for factors which imply a wide geographic range (site count), wide habitat range (habitat count) or a combination of both (occurrence), all show an increased likelihood of being represented on CI. Conversely, and not surprisingly, the distance factor shows a negative effect on CI presence.

High numbers of individuals, an extensive geographic range or a wide habitat tolerance are often seen as factors in successful immigration (Drake & Lodge, 2006; Sol, 2007; Weese, et al., 2011). Introduced avian taxa (Duncan, et al., 2003) and insects (Williamson, 1989) are known to have increased colonisation success where introduction effort is high. Greater numbers of a taxon found in NZ ties in with the idea of propagule pressure as an important factor in immigration (Colautii, et al., 2006; Copp, et al., 2010; Duncan, et al., 2003; Johnston, et al., 2009). The more members a taxon has, the more attempts that a taxon can make to disperse and the more likely it is to ultimately achieve successful immigration (Drake & Lodge, 2006). Another argument that can be put forward is that successfully immigrating taxa may already have a wide range on the mainland before immigration to CI becomes an option. Those able to survive in a wider range of habitats will also be pre-disposed to successful colonisation. Taxa that are generalists in habitat and diet are often found to be successful invaders as they are more likely to find a habitat and food source from which they can survive (Simberloff, 1989).

Climatic factors too displayed trends. Sunshine hours and maximum temperature show little effect on immigration success. The factor having the strongest influence was mean temperature difference. The higher the mean temperature difference the lower was a taxon's probability of successfully emigrating to CI. The influence of having a similar climate to the target area certainly appears to make sense. The more similar the CI climate is to the original mainland climate the more likely are the survival chances. At this stage of the modeling, minimum temperature, frost days and rainfall also have a small degree of influence. The effect of these last three factors is also negative; supporting the trend that difference in climatic conditions is detrimental, or at least neutral, to colonisation success, even when moving from a cooler environment to a warmer one. Similarity of climate between the source and target area has been found to be a positive factor in immigration success for insects (Williamson, 1989; Wilson, 1960), mammals (Forsyth, et al., 2004), vertebrates (Ehrlich, 1989) and birds (Blackburn & Duncan, 2001).

Wind speed and gale days have a logical potential influence on immigration chances by transporting taxa in air currents. Wind may also be a factor in maintaining a supply of new recruits from NZ, thus maintaining genetic variability and possibly preventing extinction by 'topping up' dwindling populations (the 'rescue effect'(Brown &

Kodric-Brown, 1977; Weese, et al., 2011)). However, neither wind speed nor gale days had a significant effect on immigration probability when modeled individually. The lack of effect seen for wind speed and gale days is intriguing as many insects are known to be transported great distances by wind. Further investigation as to direction and intensity may reveal interesting results. It could of course be that in the wind borne taxa have a greater effect in the early stages of island immigration with non wind borne taxa colonising after a longer period. It must also be noted that even though strong wind conditions would logically seem to predict immigration success, many insects shelter from strong winds and a reluctant to fly in these conditions (Baker, et al., 1942; Moreton, 1945).

The individual model of the relative location to the Chatham Rise shows a significantly increased likelihood of success where the taxon occurs north and south of the Chatham Rise. The increased likelihood for taxa from north and south of the Chatham Rise again highlights that taxa with a wider range have more opportunity to disperse. Even though there is a slight decrease in success rate amongst those taxa that only occur south of the Chatham Rise it is not significantly greater than the taxa only occurring north of the Chatham Rise.

The lack of significance in wind and current based factors does not mean, however, that wind and ocean currents do not have a bearing on immigration success. As previously mentioned many species of insect can be found many kilometres out to sea, both on the sea surface and in the air (Peck, 1994a, 1994b). Oceanic currents are also known to aid dispersal of the larvae of marine crustaceans (Adams & Flierl, 2010). The likelihood is that the major currents driving eastwards are no doubt aiding dispersal of taxa from north of the Chatham Rise just as much as from south.

Studies of newly created volcanic islands have shown some interesting immigration trends. Wind is a major dispersal mechanism for very early colonists (New, 2008) with many arthropods colonising islands even before vegetation has established (Edwards & Thornton, 2001). Initial colonists often include chironomid midges and damselflies which can breed in pools of water. Spiders, too, appear early and prey upon other arthropods such as the midges and damselflies (Edwards & Thornton, 2001; Thornton, 1984). Other early arrivals are often scavengers or carrion feeders, such as the *Heleomyza borealis* (Diptera) the larvae of which feed upon carcasses of

fish and seabirds (New, 2008). Coincidently the larvae of *Heleomyza borealis* are extremely cold tolerant, having been known on to survive temperatures of -60 $^{\circ}$C (Worland, et al., 2000), almost certainly enhancing its survival chances. Initial colonisation then appears limited to those taxa that can survive without the need for resources provided by vegetation.

Early colonisation does not mean future success. High species turnover rates and competition from species accompanying vegetation and vertebrate immigration often mean species found in the early years of an island's life may be extinct within years of their initial arrival (New, 2008; Simberloff & Wilson, 1970).

Minimal Adequate Models

Even though factors appear significant when modeled individually, some factors may be exerting a greater influence than others. The maximal models of grouped factors can be pared down to the minimum adequate model (MAM). Once again neither body size or larval food type are significant factors. The insect taxonomic level had a more significant effect on emigration success than did body size or larval food type. Of the geographical factors, the MAM consisted of site count and distance. From this result it can be hypothesized that wide ranging taxa have an advantage when it comes to immigration success. As mentioned earlier are these taxa wide ranging because they are good dispersers or because of some other reason? The habitat count factor correlated well with the site count (so was not put in the MM), implying that the wide ranging taxa are also found in a wide variety of habitats, reinforcing the fact that generality of lifestyle is important at aiding establishment after successful dispersal. Distance was shown to be a significant factor in the geographic model, although less so than site count. Sites further away from Banks Peninsula had a lower probability of being found on CI.

The MAM for the climate factors included the mean temperature and minimum temperature differences. Similar to the individual modeling the difference in mean temperature is showing a strong influence on the likelihood of colonisation. The climate MAM also highlights the importance of minimum temperature. Taxa adapted to cooler conditions might be disadvantaged in areas where frosts are fewer

(minimum temperature correlated with frost days) and the minimum temperatures not so low. The competitive advantage of cold tolerance will have been removed to some degree leaving cold tolerant species to compete for a foothold based on traits that are stronger in other less cold adapted taxa.

Taxonomic level does not seem to influence the likelihood of successful immigration. None of the three models using taxonomic level as random variables showed any significant difference from one another. In all three cases where the MAM was tested against the taxonomic order data sets the significance of the result remained the same. The consistency of the statistical significance implies that any factors tested in this research are having an effect irrespective of the taxonomic level of the species being affected. As previously seen, some taxa are predisposed to successful immigration despite having close relatives that are not.

Invasion biology has been well studied for at least the last 80 years (Cook, 1931; Di Castri, 1989; Elton, 1958; Kolar & Lodge, 2001; Prider, et al., 2011; Vervoort, et al., 2011). Emphasis has ranged from identifying the many traits that could contribute to a species being a good invader, to why some areas are prone, or resistant to, invasion by alien species (Drake, et al., 1989). Many of the factors examined in this research have also been subject to experimentation and analysis with many differing taxa and ecological scenarios (Drake, et al., 1989; Sol, 2007).

Much effort has been exerted in finding the traits which enable a species to be a good invader/disperser/coloniser and whether certain species are pre-adapted to be good colonisers (Sax & Brown, 2000). However, despite many findings that promote certain traits in a particular taxa, there is also a widely held opinion that traits cannot be universally used to predict the success or failure of introductions or colonisation attempts (Simberloff, 1989). This lack of predictability is partly due to the high degree of stochasticity involved in determining which trait will be important at any one time and place (Simberloff, 1989) as well as the complexity of interaction between invading taxa its target area (Shea & Chesson, 2002; Sol, 2007).

Of course it must be realised that nearly all mainland/island situations are physically and temporally unique. Each situation has its own combination of positive and negative filter factors interacting with one another and influencing the fate of potential migrants. Even so, although no island's unique situation can be replicated, islands do

share many characteristics that can be measured and compared to other islands. These characteristics include many of the factors tested in this project. All islands have distance from the nearest mainland, climate, species count and composition, prevailing wind and sea currents as influencing factors. With most of these factors differing for each island scenario, the results from each can contribute to the ever growing pool of data for island immigration. So enabling further understanding of the intricate and complicated ecological processes involved in immigration of islands (Gillespie & Roderick, 2002).

Immigration to CI from NZ (and possibly vice versa) has been on-going for 3-5 my. This huge amount of time will have consequences for the degree of influence the different filters have on immigration success. With time comes an increased probability that the taxa less able to disperse will eventually reach CI and successfully colonise. Factors, such as resource competition and enemy evasion, will also become more important the longer an island is available for colonisation. The large over-water distance involved in NZ to CI immigration may reduce the advantage of strong fliers that might have easily actively dispersed over 50, 100 or 200 km of ocean. CI does, however, have strong currents propelling biota toward it from NZ that may help mitigate the effect of distance and increase immigration rates.

It would seem that perhaps factors affecting establishment, and especially expansion, may be more important at the current time for CI taxa. However, it must not be forgotten that strong immigration factors will continue to provide new individuals to be both competition and succour for incumbent CI populations. So not only do the factors themselves have bearings on immigration success or failure but so does the phase of immigration on which they are acting, as well as the age and history of the area being emigrated to.

The filter factors used in this study served two main purposes. First, they were used to distinguish the driving forces behind successful immigration in the NZ/CI scenario. The differing filters modelled did indeed having differential effects on immigration likelihood. Now, with a more sound knowledge of the most influential filters, further hypothesis can be generated and put forward to be tested. Secondly the filter factors can be used to compare and contrast other island scenarios. The filters were chosen due to their putative effect on immigration potential, which has also seen them used in

other research to explain island immigration scenarios (Gillespie & Roderick, 2002). The dominant filters from different island situations can be compared and contrasted using similar filter factors.

4.6   Conclusion

The GLM modelling of the NZ/CI data has provided some interesting trends from which further hypothesis and continued investigation can be performed.

The biological characteristics of the taxa do not have a great influence on the likelihood of successful immigration from NZ to CI. The strongest of these is taxonomic order which reinforces the idea of disharmony discussed in the previous chapter. This significance of the taxonomic order however is most likely being driven by a few influential species. The strongest indicators of immigration potential are the number of sites that a taxon has been sampled from, the number of areas a taxon was sampled from and a similarity in the mean temperature of the mainland site to that of CI.

Even though deliberate introductions are artificially created, and the majority of the analyses are from projects concerned with birds and mammals, many of the finding from these projects show similar trends to those of propagule pressure, climate and habitat found in this research.

Unfortunately scenarios such as a recently emerged CI, one without strong feeder currents, or even one from 5 my in the future, from which to compare and contrast with the current NZ/CI situation can only be imagined. However, the results from this research, across a wide range of insect taxa will provide a basis for further enquiry and research.

Chapter 5

Genetic variation between New Zealand and Chatham Island populations

5.1 Overview

This chapter introduces the major biological themes of genetic variation and speciation to the study. Genetic data were collected from New Zealand (NZ) and Chatham Island (CI) samples to assess the levels of genetic variation between six groups of conspecific taxa from NZ and CI.

5.2 Introduction

Genetic change can come about through different processes. The genetic complement of a population can change naturally through a process described as genetic drift. Genetic drift has a stronger effect in small populations and occurs as alleles within a population are effectively randomly sampled by the formation of gametes, resulting in stochastic change in allele frequencies in different generations (Avise, 2004; Lowe, et al., 2004). Over time, the changes brought about by genetic drift can become fixed in the population. Other genetic changes can be actively selected, either positively or negatively, directly or indirectly (Coyne & Orr, 1994). The ability to survive extreme cold could become more prominent in lower latitude populations, or a prominent colour pattern lost due to ease of predation. One important biological process which may be influenced by genetic change is reproduction. Small changes over time may cause physical or behavioural incompatibility between two populations. These changes mean that if the populations regain contact they may no longer be able to reproduce (Lowe, et al., 2004). Reproductive incompatibility between populations is sometimes seen as indication that the two, formerly conspecific taxa, are now separate species (De Queiroz, 2007; Mallet, 2010)

Island populations are often less genetically diverse than mainland populations (Browne, 1977; Cardoso, et al., 2009; Frankham, 1997; Knopp, et al., 2007; Seddon & Baverstock, 1999). The founder population itself is likely to have been only a small

sample of the total genetic variation of the mainland population. They may already possess characteristics that allowed them to successfully disperse and colonise, and so could be further differentiated from the mainland population. A restricted gene pool, and potentially harsh selection pressures, could also drive island populations to be reproductively incompatible with the mainland population. Conversely, immigration from multiple sources has been shown to produce a more varied genetic diversity on islands than is found for the equivalent mainland area (Algar & Losos, 2011).

The classification of living organisms relies on grouping together those that share similar traits. Shared traits in higher taxonomic groups are quite general, becoming more specific for lower taxonomic groups. Within the taxonomic classification of life, the species level grouping has been seen as the fundamental unit of biology (Lowe, et al., 2004), and crucial to the measurement of biodiversity (Butlin, et al., 2009; De Queiroz, 2007). However, argument over what constitutes a species and how to define the disjunction between sub-species and species, or species and genera is an enduring theme in biology.

The introduction of molecular sequencing techniques as another classification tool has added a further level of complexity to the species debate. Almost no individual shares an identical genome with another, and so the question for taxonomists is not so much about whether there is genetic variation between groups of organisms, but how much variation there is.

Molecular techniques can also be used to create phylogenies for taxa.

"*Evolutionary biologists and ecologists are increasingly turning to molecular phylogenetics for studying oceanic plants and animal communities*"
(Emerson, 2002)

"*Phylogenies are increasingly being used to attempt to answer biogeographical questions*"
(Cook & Crisp, 2005)

Using phylogenies, genetic variation can be used to trace the evolutionary history of a taxon and used to highlight where a specific group of genetically similar individuals may have separated from the main population (Cook & Crisp, 2005; Emerson, 2002) . More advanced molecular techniques can introduce a temporal element to taxonomic

relationships and help ascertain the timing of separation of populations. Inferences can then be made as to the possible causes behind the separation, such as geological, dispersal or environmental events (Emerson, 2002; Liggins, et al., 2008; Marshall, et al., 2008).

5.2.1 Detecting genetic variation

Genetic variation between two populations can be calculated using data from DNA sequencing (Avise, 2004; Lowe, et al., 2004). DNA-based data can be used to address many biological issues, including DNA taxonomy, in which molecular data are used to investigate genetic variation between populations (Alexander, et al., 2009; Brown, et al., 1999; Wiemers & Fiedler, 2007). Genetic variation can be used to help delimit taxonomic boundaries, and to decide whether superficially similar populations should be regarded as distinct taxonomic groups. DNA taxonomy can use different gene and gene segments depending on the taxon used and the specific taxonomic questions being asked. Another widely implemented use of molecular data is DNA 'barcoding'(Hebert, et al., 2003). Whereas DNA taxonomy aids in the delimitation of species, DNA barcoding is used to identify which species a particular specimen belongs to (specimen identification).

Barcoding was developed from genetic sequencing and is a methodology designed to identify taxa to species level based on a 648 bp segment of the COI gene. The COI segment is seen as a character unique to a species. DNA barcoding has several advantages over morphology based taxonomy, being a relatively quick and easy identification process that that uses small tissue samples and is available for a non-expert on the taxon. Since its conception in the early 21st century (Hebert, et al., 2003) barcoding has become a major component of fields such as bio-control, conservation, and biodiversity studies. In 2010 a major international project was instigated to database the barcode sequences of thousands of different animal and plant species (Jinbo, et al., 2011).

The relative ease of processing COI has seen it widely used in species identification and taxonomy (Cook, et al., 2010). So far in 2011, some of the many barcoding projects have addressed Canadian bug identification (Park, et al., 2011). Persian gulf

fish biodiversity (Asgharian, et al., 2011), snake smuggling in India (Dubey, et al., 2011), African antelope conservation (Bitanyi, et al., 2011), the biodiversity of deep Antarctic waters (Grant, et al., 2011), looper moths (Dewaard, et al., 2011) and plum trees (Quan & Zhou, 2011).

DNA taxonomy studies have included, lobsters (Cabezas, et al., 2011), sea urchins (Hart, et al., 2011), wood boring beetles (Jordal, et al., 2011), Mantophasmatodea (Eberhard, et al., 2011), rotifers (Fontaneto & Jondelius, 2011), blowflies (Singh, et al., 2011), fungus gnats (Martinsson, et al., 2011), teleost fish (Heras & Roldán, 2011) and nutmeg shells (Modica, et al., 2011).
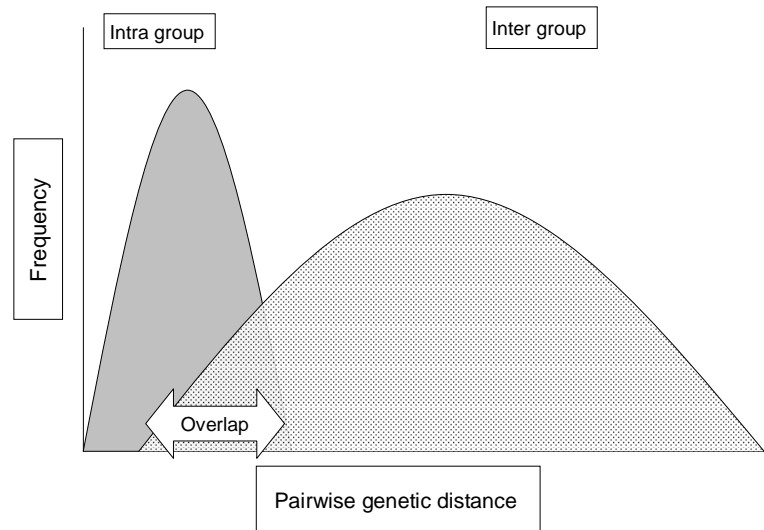
5.2.2 Using genetic variation

The detection and application of genetic variation data has many and varied uses. One use is to detect whether two populations are diverging genetically and, if so, how different they have become. Associated with genetic variation between populations are methods used to infer taxonomic relationships based on their degree of genetic divergence.
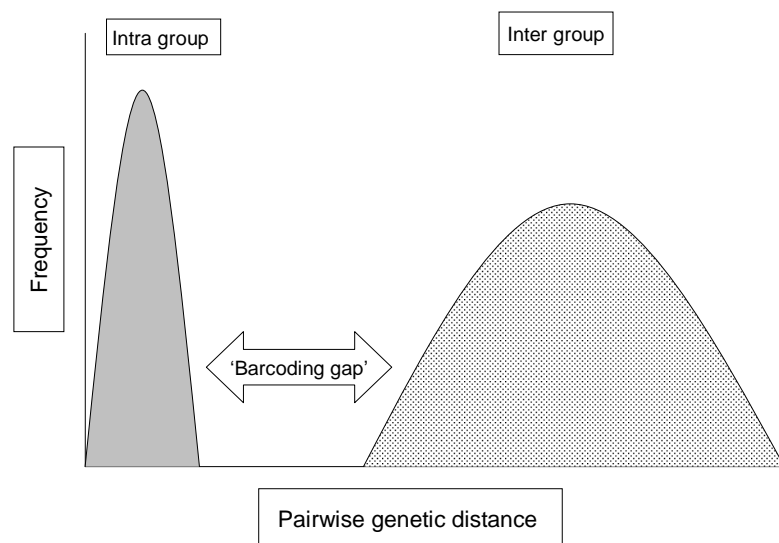
Methods used to assess levels of genetic divergence between populations often use the concept of intra and inter group genetic distances. DNA sequences can be used to calculate intra-group genetic variation and inter-group genetic variation of the sequenced populations (Hajibabaei, et al., 2006; Wiemers & Fiedler, 2007). The genetic variation within a species is the intra-specific variation; the variation between species is the inter-specific variation. The fact that populations can have a degree of genetic divergence between them naturally leads to the question; at what point are two populations no longer deemed to be the same species? At least four approaches have been suggested as a guide to whether two populations could be different species.

One simple assessment of population difference is to calculate the degree of genetic divergence between two populations and compare this to a particular threshold value. The amount of divergence used to suggest separate species varies between gene regions and species. However, a general rule for insects, using the COI gene, is that a divergence of over 2% implies a potentially different species (Cognato, 2006; Hung, et al., 1999).

Two other indicators involve the concept of a 'barcoding gap'. One maintains that a clear gap between the intra-specific pairwise distances and the inter-specific pairwise distances could imply that the population being tested is significantly different from the other (Figure 5-1a) (Meyer & Paulay, 2005).

A:

B:

Figure 5-1: Hypothetical intra-specific and inter-specific genetic distances plotted on the same axis. A: showing a clear barcoding gap between intra and inter-specific distances. B: with no barcoding gap and an overlap of values between intra and inter-specific distances. (adapted from Meyer and Paulay 2005).

The second indicator of potential speciation is that the barcoding gap is at least 10x that of the intra-specific distance (Hebert, et al., 2004; Wiemers & Fiedler, 2007). Care must be taken when assessing a barcoding gap, as too small a sample size can indicate a barcoding gap in the sampled population where none actually exists in the true population. Situations do also occur where no clear gap is evident and distances overlap (Figure 5-2b). Situations where overlap occurs need to undergo further scrutiny and the application of ecological and biological knowledge of the taxon.

The previous three species delimitation methods all involve the application of a fixed value to genetic distance data, and use that value to assess the likelihood of a population being a separate species.

A fourth method of species delimitation has been developed from the understanding that evolution and speciation do not produce such definite demarcations of genetic distance between taxonomic levels. The general mixed yule coalescent model (GMYC) (Monaghan, et al., 2009; Pons, et al., 2006) uses the genetic data from the group in question to determine species groups. GMYC relies on detecting a change of branching rate in the group phylogeny and ascertaining the transition point; the point at which the branching rate changes from one due to within species coalescence to branching rates representing a speciation event (Monaghan, et al., 2009; Pons, et al., 2006). The point at which speciation is determined is then reliant on the data obtained from the group itself, and will therefore vary depending on the taxon being analysed.

5.2.3 New Zealand and Chatham Island

"*most indigenous taxa of the Chatham Islands have clear affinities with New Zealand* (Shepherd, et al., 2009)

The scenario presented in this project involves the immigration of individuals to an isolated island (CI) from a mainland, (NZ) population. Those individuals that successfully immigrate from NZ to CI will, to some degree depending on the taxon and its dispersal ability, be reproductively isolated from the NZ population. Gene flow between the two populations will slow or cease and the populations will become more genetically differentiated.

In the 3-5 million years since CI emerged above sea level and became available for colonisation, a variety of taxa present on CI have evolved to become CI endemic species. Endemic CI insects species constitute 20-25% of the 800 or so found on CI (Dugdale & Emberson, 2008). Of the Coleoptera, 93 of 329 species (28%) are endemic, with 4 of 218 (1.8%) coleopteran genera endemic (Emberson, 2006b). Within CI plant species, 35 from 414 (7%) are deemed endemic (Heenan, et al., 2010), of which 19 of 40 (47.5%) are woody shrubs and trees (Shepherd, et al., 2009). However, the majority of species on CI are similar enough in appearance to be classified as conspecific with NZ populations (Emberson, 2006b; Heenan, et al., 2010). A major study of the genetic relationships between NZ and CI flora (Heenan, et al., 2010), has shown that most CI endemic species are most closely related to common and widespread NZ species within the same genus.

It has been shown that at least some CI biota show a degree of genetic divergence from the nearest relative (Heenan, et al., 2010; Liggins, et al., 2008; Smissen & Heenan, 2010; Trewick, 2000). However, many of the taxa analysed were known to be separate species within the same genus. What is also of interest is the degree to which current NZ and CI conspecific taxa differ genetically, if at all.

NZ is a relatively large archipelago, heterogeneous in habitat, over 250,000 km^2, and stretching 1700 km north to south. NZ comprises two large islands separated by a by a rough and windy stretch of water, the Cook Straight. So far in this study the overall likelihood of a taxon migrating to CI from NZ in the presence of certain factors has been examined. However, given the disparity of habitat and conditions within NZ as a whole, it could be that 'successful' immigrants to CI are in fact only emigrating from one area of NZ.

5.3   Aims and approach

The first aim of this chapter is to identify whether NZ and CI populations of taxa, currently described as the same species, have begun to show any genetic divergence, and if so, by how much. The degree of genetic divergence between the NZ and CI populations will be measured between the two populations. Whether any actual

divergence found is statistically significant will be assessed using a null hypothesis based on random permutations of the NZ and CI data (see methods).

Assessment of genetic divergence between populations assumes genotypic clustering (Mallet, 1995). In genotypic clustering, populations are considered to be different species if they show a bimodal distribution of genotype frequencies and that there are gaps between these groups of genotypes (Jiggins & Mallet, 2000). Although this concept is in some ways similar to Darwin's morphological species concept (Mallet, 2011), the genotypic species concept can separate groups where other concepts may continue to place them as the same species.

The randomisation method used to detect significant genetic variation will be compared to three methods of species determination described in section 1.2.2, to ascertain whether these different methods generate similar conclusions. GMYC will not be addressed in this study as a wider taxonomic range of sequence data will need to be collected to make this approach feasible. The likelihood of the taxa examined containing more than one species will be assessed.

The second aim of this chapter is to assess whether the North (NI) or South Island (SI) of NZ is more likely to be the source of the CI population for six selected taxon groups. Phylogenies based on likelihood methods will be used to trace character history. The 'character' in this study is the region from which the sample was collected (NI, SI or CI). Tracing character history will show the likely points of divergence for populations and give an indication of the chronological order in which populations split of from their putative sister taxa.

The two approaches described above will be used to examine the data, and any trends or patterns will be commented on. Proposals for new hypotheses and further work to improve the current dataset and to progress the investigation in a number of directions will be made.

5.4 Methods

5.4.1 Taxa chosen

Six taxa were chosen for genetic comparison (Table 5.1). These six taxa were chosen due to their geographical distribution, ease of sequencing, occurrence in sufficient numbers and were from one of the three orders used in the study.

Table 5.1: Taxa sequenced and primers used to sequence the COI gene region.

Order	Family	Species	Primers	COI sequence length obtained (max)
Coleoptera	Curculionidae	*Cecyropa tychioides*	MLepF1, LepR1	330bp
	Phycosecidae	*Phycosecis limbatus*	MLepF1, LepR1	330bp
Hymenoptera	Crabronidae	*Tachysphex nigerrimus*	LCO, HCO	720bp
	Ichneumonidae	*Aucklandella* sp.	LCO, HCO	720bp
Diptera	Ephydridae	*Hydrella enderbii*	LCO, HCO	720bp
	Agromyzidae	*Cerodontha angustipennis*	MLepF1, LepR1	330bp

5.4.2 DNA extraction and sequencing of COI gene region

The DNA extraction method used varied slightly depending on the taxon being sampled. Small beetles and flies (1-2 mm) were pierced on the ventral side of the thorax and abdomen using a minuten pin. Larger insects had either a whole or part of a leg removed which was then cut into 4-5 pieces using a clean scalpel blade. The removed tissue was placed in solution from the Qiagen DNeAsy Tissue kit (Qiagen Inc.) and incubated overnight as per the manufacturer's instructions.

The gene region used for amplification and sequencing was the mitochondrial gene cytochrome oxidase subunit I (COI). Genomic amplification for all taxa was initially attempted using the standard HCO2198 :
5'-TAAACTTCAGGGTGACCAAAAATCA-3' and LCO1490: 5'-GGTCAACAAATCATAAAGATATTGG-3' primers (Folmer, et al., 1994). In cases

where the HCO/LCO combination failed to amplify the desired 720 bp region the lepidopteran primer combination of LepR1 : 5-'TAAACTTCTGGATGTCCAAAAAATCA-3' and MLepF1 : 5'-GCTTTCCCACGAATAAATAATA-3' was used instead. These produced well amplified DNA, although for a shorter segment length of DNA.

Polymerase chain reactions (PCR) were performed using the following volumes of reagents: 0.2 µL i*taq* polymerase (5µ/µL), 2.5 µL of x 10 buffer, 0.2 µL of each dNTP, 1.0 µL of each primer from a 10µM stock (all from Invitrogen), 2.5 µL of DNA extraction and 15.3 µL of water.

PCR was carried out in a PCR MasterCycler (Eppendorf) with PCR stages set to the following: Initialisation, at 94ºC for 2 mins, 33 cycles of (denaturation at 94ºC for 40s, annealing at 45ºC for 40s and extension at 72ºC for 90s), a final extension of 72ºC for 5 mins. When complete the PCR product in the PCR MasterCycler was placed on hold at 10 ºC. All PCR runs included a positive and negative control sample. The PCR products were checked by running a 1.5% SYBRSafe (Invitrogen) agarose electrophoresis gel using 5 µL of PCR product mixed with 1 µL of dye. The gel was run for 30 minutes at 80V. The gel was examined for DNA bands using a gel-doc running GenSnap (Syngene, Synoptics Ltd).

PCR products producing clearly visible bands were prepared for sequencing using the following reagents: 0.5 µL of BigDye Terminator (version 3.1), 2 µL of x5 sequencing buffer (both from ABI Prism Cycle Sequencing Kit), 0.8 µL of primer (from a 10 µM stock), 1.0 µL of PCR product and 7.2 µL of water. The sequencing PCR was set to 96°C for 1 min, followed by 25 cycles of 96°C for 10s, 50°C for 5s and 60°C for 4 min. Following the sequencing PCR run the products were processed in an ABI Prism 3130xl Genetic Analyser with a 16 capillary 50cm array installed and using Performance Optimized Polymer 7 (POP7). The program BioEdit (Hall, 1999) was used to manually align the sequences.

5.4.3 Randomisation test of the barcoding gap

Sequence data were saved as Phylip 4.0 files using BioEdit software. Randomisation was performed by randomly selecting n samples (where n= the actual number of

samples from NZ for the species) from the file of all samples sequenced for the species. The set of randomly selected samples was then regarded as the NZ population. The remaining samples were deemed to have come from CI. Intra-group distance matrices, using the Kimura two parameter model (K2P) (Kimura, 1980), were created for the randomly created NZ and CI groups, and an inter-group genetic distance calculated from these NZ and CI populations. The randomisation and associated intra and inter genetic distance calculations were performed 1000 times for each species analysed. The randomisation procedure, distance matrix creation and distance calculation was performed using R software (R Development Core Team, 2010).

From the randomised dataset, the standard deviation, standard error and upper 95% confidence intervals (one tail test) of the mean barcoding gap for each species was calculated. The randomised barcoding gap was calculated as the difference between the mean inter-group distance and the mean intra-group distance. The actual barcoding gap, calculated from the samples collected was compared with the mean randomised barcoding gap values. If the actual barcoding gap fell outside the upper 95% confidence interval of the mean randomised barcoding gap then this was taken to indicate that the actual barcoding gap was significantly greater than the one calculated from a set of random samples.

5.4.4 Inferring immigration history

Maximum likelihood trees, using the Jukes-Cantor 69 model, with bootstrap values were produced using Seaview software (Gouy, et al., 2010). The Jukes-Cantor 69 was found to be the most appropriate model to use after the dataset was analysed using the Modeltest function from the PhyML software (Guindon & Gascuel, 2003) To trace the history of immigration between regions, these maximum likelihood trees were imported into Mesquite (Maddison & Maddison, 2001) and ancestral locations were inferred using parsimony based on the present distribution of extant species.

Outgroup taxa were used in the creation of the trees. However in order to show the detail of the pertinent branches the outgroup branches have been removed from the final figures displayed in the results section.
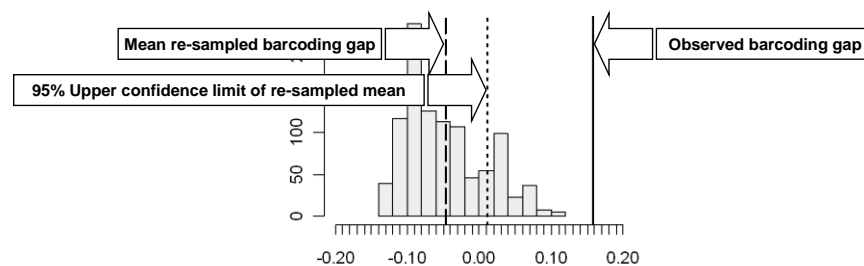
5.5   Results

5.5.1   Randomisation test of the barcoding gap
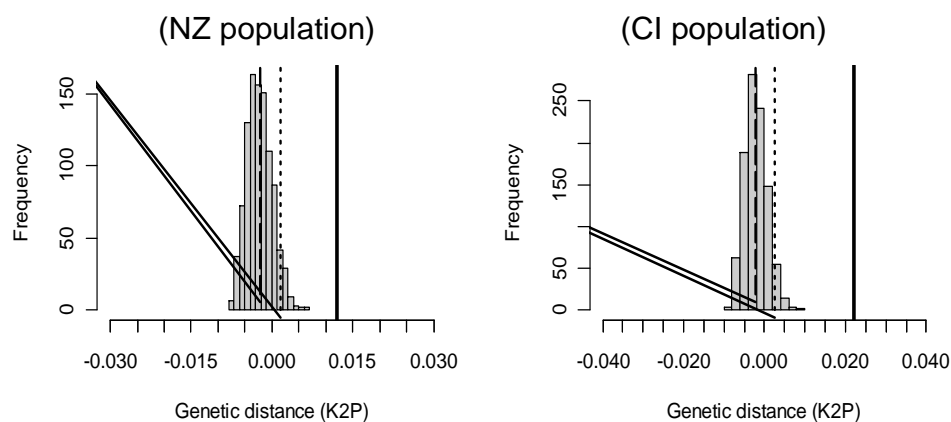
In four of the six taxa analysed, the barcoding gap calculated using the NZ population was significantly greater than the barcoding gap generated by randomisation (Figures 5-2a, 5-2b, 5-2c, 5-2d, 5-2e, 5-2f). In two of the taxa, *Cerodontha angustipennis* (Diptera), and *Cecyropa tychioides* (Coleoptera), the actual barcoding gap calculated was not significantly different from the randomly generated barcoding gap.

When the barcoding gap was calculated using the CI population, all six of the taxa showed barcoding gaps that were significantly greater than the barcoding gap generated by randomisation (Figures 5.2a, 5.2b, 5.2c, 5.2d, 5.2e, 5.2f).

Legend for figures 5.2a-5.2f:
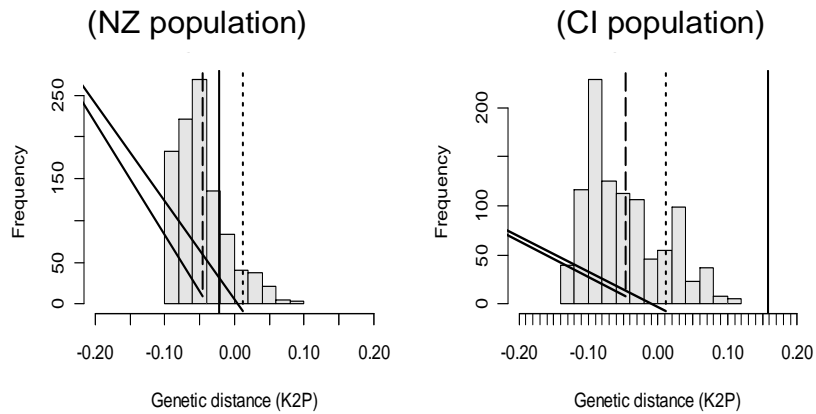
Hydrellia enderbii (Diptera)
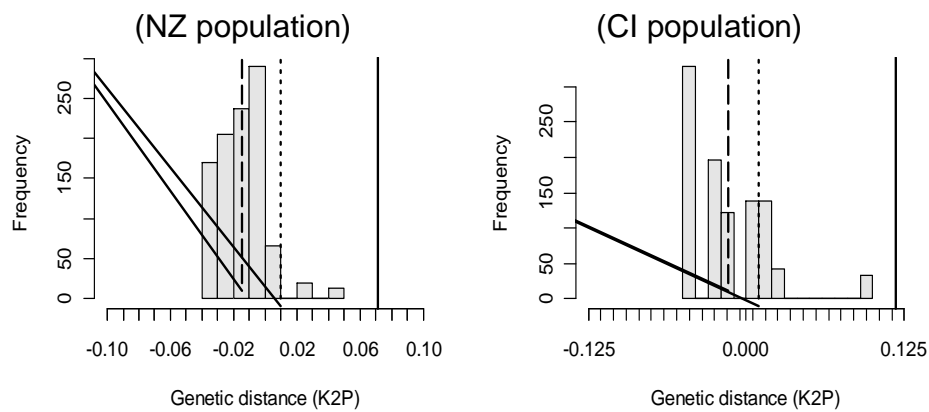
5.2a
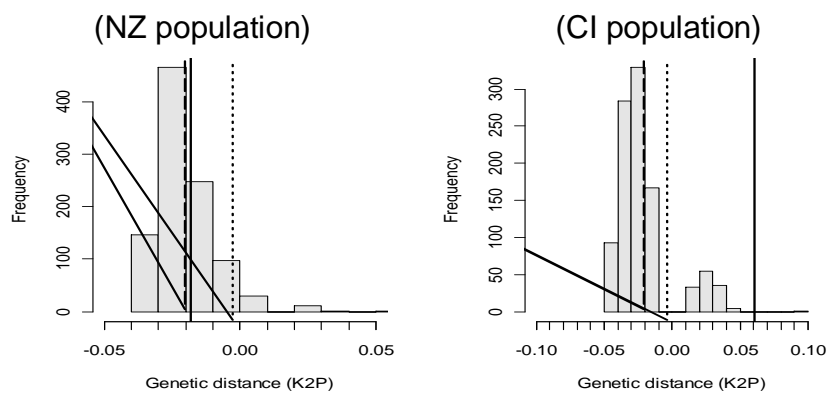
125

Cerodontha angustipennis (Diptera)

(NZ population)

Frequency

Genetic distance (K2P)

(CI population)

Frequency

Genetic distance (K2P)

5.2b

Phycosecis limbata (Coleoptera)

(NZ population)

Frequency

Genetic distance (K2P)

(CI population)

Frequency

Genetic distance (K2P)

5.2c

Cecyropa tychioides (Coleoptera)

(NZ population)

Frequency

Genetic distance (K2P)

(CI population)

Frequency

Genetic distance (K2P)

5.2d

126
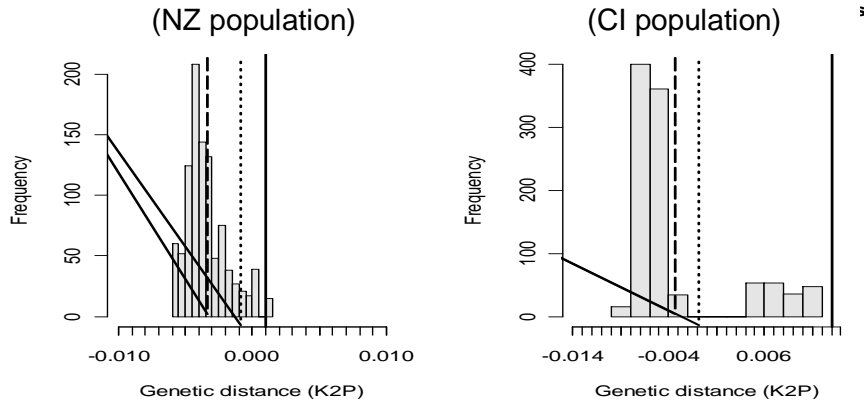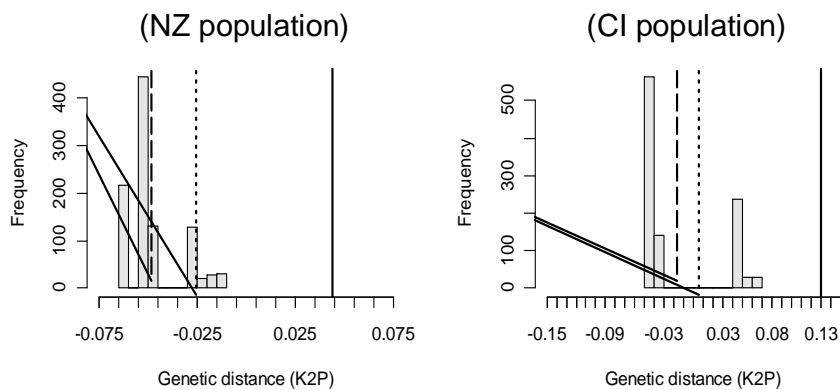
Tachysphex nigerrimus (Hymenoptera)

5.2e

Aucklandella sp. (Hymenoptera)

5.2f

Figure 5-2: Distribution of the randomised barcoding gap with mean re-sampled value (dashed line), upper 95% confidence limit of randomised data (dotted line) and mean actual barcoding gap (black line). 5.2a *Hydrellia enderbii*(Diptera), 5.2b *Cerodontha angustipennis* (Diptera)*,* 5.2c *Physecis limbata*(Coleoptera), 5.2d *Cecyropa tychioides* (Coleoptera), 5.2e *Tachysphex nigerrimus* (Hymenoptera), 5.2f *Aucklandella* sp.(Hymenoptera).

5.5.2 Comparison of the randomisation test to other assessments of genetic divergence

In all taxa, the mean inter-group genetic distance was greater than 2% (Figure 5-3), (see Appendix G for full data). For CI populations, five of the six taxa displayed a clear barcoding gap between the CI intra specific distance and the inter-specific

distance (Figure 5-3). Amongst the NZ populations, only one taxon, *P. limbata* (Coleoptera), had a clear barcoding gap between the NZ intra-group distance and the inter-specific distance.

The actual mean barcoding gap for the CI population ranged from 3.1× to 140× that of the mean intra-group genetic distance for the CI population (see Appendix G). In five of the six taxa, the mean barcoding gap was over 10× that of the mean CI intra-group distance. The actual mean barcoding gap for the NZ population for the six taxa, ranged from -0.18× to1.3× that of the mean intra-group genetic distance for the NZ population. Negative values are due to the intra-group distance being greater than the inter-group distance for the taxon tested.
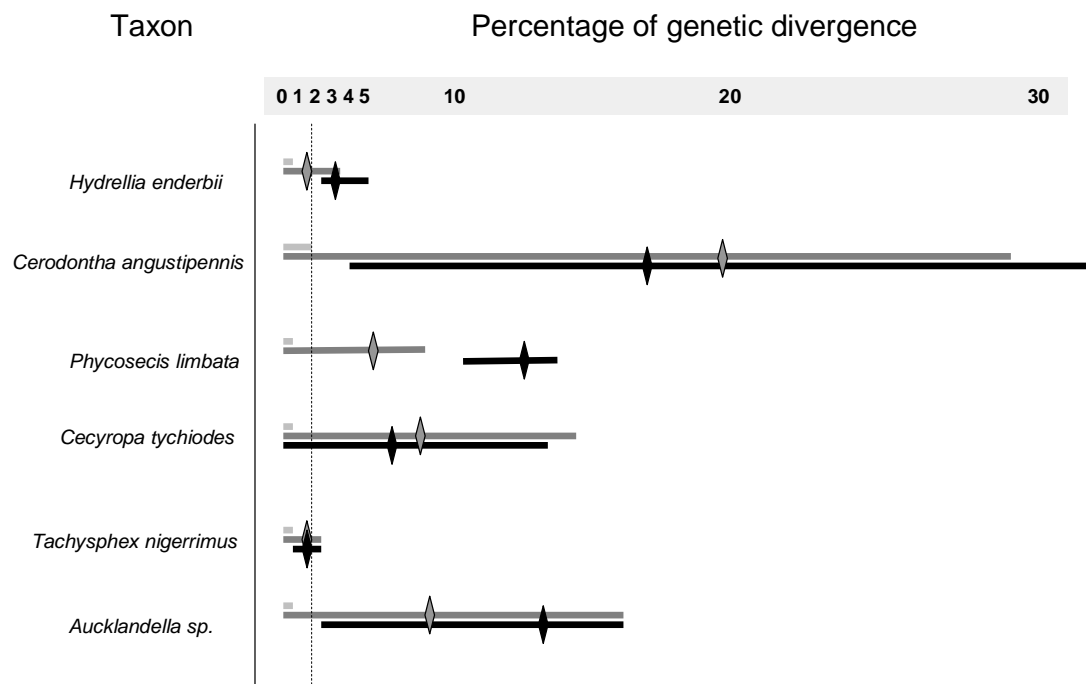
Figure 5-3: Genetic variation of COI for inter-group and intra-group distances. Vertical dashed line= 2% divergence. Light grey=CI intra, Dark grey=NZ intra, Black=Inter. Black diamond=mean Inter group distance, Grey diamond=mean intra NZ distance. N.B Mean CI intra-group not shown.

For both NZ and CI populations, the randomisation assessment of genetic variation gave the same potential species as the 2% threshold (Table 5.2).

For all the CI populations, the randomisation assessment of genetic variation gave the same conclusion of potential species status as the comparison of mean barcoding gap to the mean intra-group genetic distance. For NZ populations, two taxa showed agreement between the randomisation result and the comparison of mean barcoding gap to the mean intra-group genetic distance. For the CI populations, the randomisation data agreed with the test for a clear gap between intra-group distances and inter-group distances in five taxa. For the NZ populations the comparison of the randomised data agreed with the clear gap test in three taxa.

Table 5-1: Taxa sequenced showing the categories under which they would qualify to be judged as separate species. The randomised assessment of genetic divergence (col=Randomisation test) is compared to the tests of genetic variation based on: inter-group genetic divergence (col=Inter group), a clear barcoding gap between the intra-group range and the inter-group range (col=Clear gap) and the ratio between the mean intra-group divergence and the barcoding gap (col=Ratio test). Y= test indicates a potential species level degree of genetic divergence. NZ and CI populations tested separately.

Taxon	Inter group	NZ population			CI population		
		Clear gap	Ratio test	Randomisation test	Clear gap	Ratio test	Randomisation test
Cecyropa tychioides	Y	N	N	N	N	Y	Y
Phycosecis limbata	Y	Y	N	Y	Y	Y	Y
Hydrellia enderbii	Y	N	N	Y	Y	Y	Y
Cerodontha angustipennis	Y	N	N	N	Y	Y	Y
Auklandella sp.	Y	N	N	Y	Y	Y	Y
Tachysphex nigerrimus	Y	N	N	Y	Y	Y	Y

5.5.3 Inferring immigration history

Hydrellia enderbii (Diptera)

The CI *Hydrellia enderbii* (Ephydridae) population consists of a separate clade to the NZ samples, with bootstrap support of 99%. Two separate NZ clades are supported; both with 76% bootstrap support (Figure 5-4a).

The character history trace (Figure 5.4b) suggests an initial split between the SI and CI populations. The direction of the SI / CI split cannot be determind from these data.

Cerodontha angustipennis (Diptera)

The CI *Cerodontha angustipennis* (Agromyzidae) population is separated into a monophyletic clade, with bootstrap support of 100%. The CI clade is nested within a clade consisting of SI and NI samples which has a 94% bootstrap support. A second SI clade is clearly defined which has 100% bootstrap support (Figure 5-5a).

The character history trace (Figure 5-5b) suggests an initial split between SI and NI populations. The direction of the SI / NI split cannot be determind from these data. Colonisation of CI from the SI is supported.

Cecyropa tychioides (Coleoptera)

Two clades containing CI *Cecyropa tychioides* (Curculionidae) are present (Figure 5-6a), both of which are associated with SI samples. The two CI/SI clades have 90% and 75% bootstrap support respectively. One clade of NI samples is nested within a larger clade consisting of SI and CI samples and includes the two previous CI/SI clades. A second well defined SI clade is also present with 100% bootstrap support.

The character history trace (Figure 5-5b) suggests an initial split between two SI populations, or a NI / SI split.

Phycosecis limbata (Coleoptera)

Three distinct *Phycosecis limbata* (Phycosecidae) clades are represented, one for each of NI, SI and CI. Bootstrap support for all three clades is strong, NI=97%, SI=100%, CI=100% (Figure 5-7a).

The character history trace (Figure 5-7b) is ambiguous as to the origins of the CI population for *P. limbata*

Tachysphex nigerrimus (Hymenoptera)

Three distinct *Tachysphex nigerrimus* (Crabronidae) clades are represented, one for each of NI, SI and CI. Bootstrap support for the SI clade strong, 100% (Figure 5-8a). The NI and CI clades have bootstrap support of 49% for each.
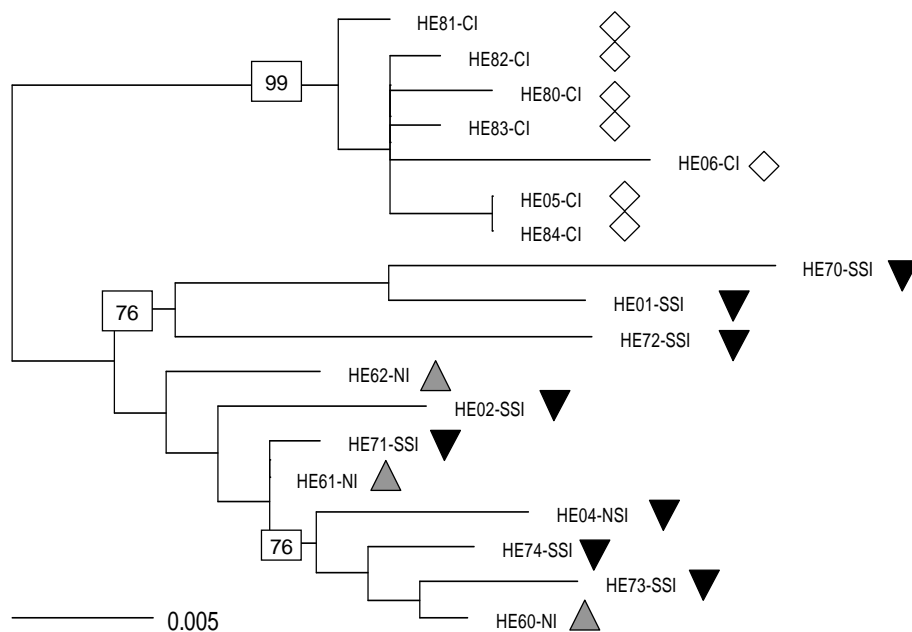
The character history trace (Figure 5-8b) is ambiguous as to the origins of the CI population for *T. nigerrimus.*

Aucklandella sp. (Hymenoptera)
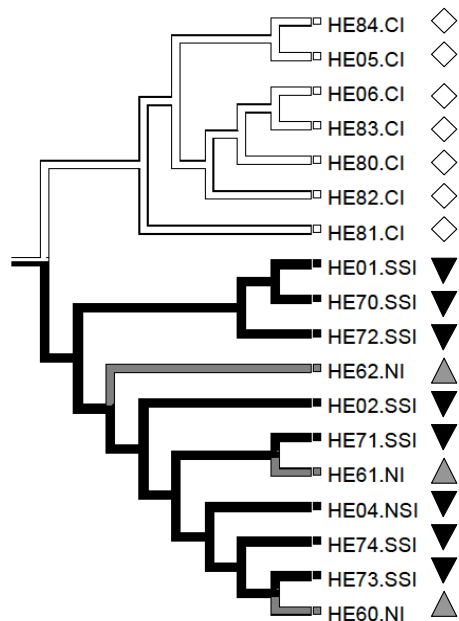
The CI *Aucklandella sp.* (Ichneumonidae) samples form a distinct clade with 95% bootstrap support (Figure 5-9a). The CI clade is itself part of a clade containing SI and CI samples that has a 99% bootstrap support. Two other clades are evident, one containing NI and SI samples, with 99% bootstrap support and another of only SI samples, with 88% bootstrap support.

The character history trace (Figure 5-9b) suggests an initial split between two SI populations. Colonisation of CI from the SI is supported.
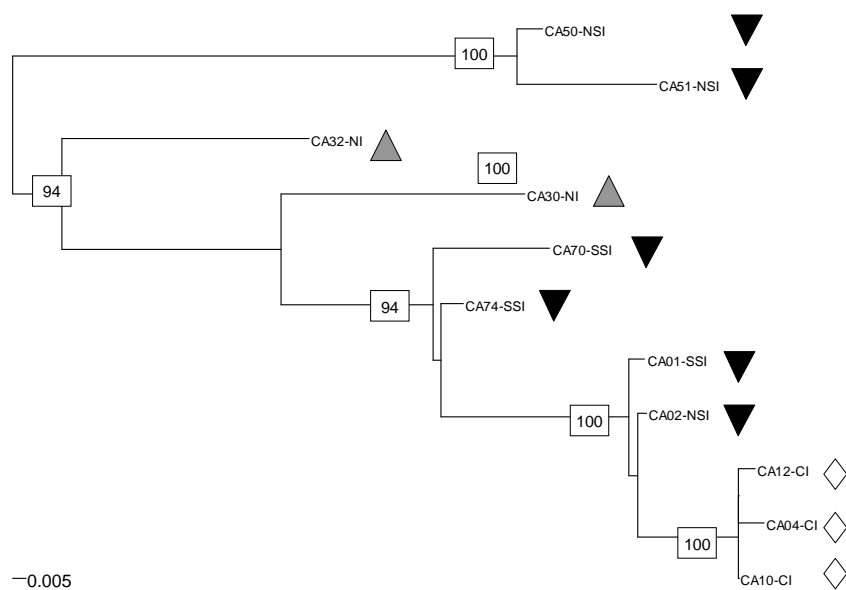
5.4a
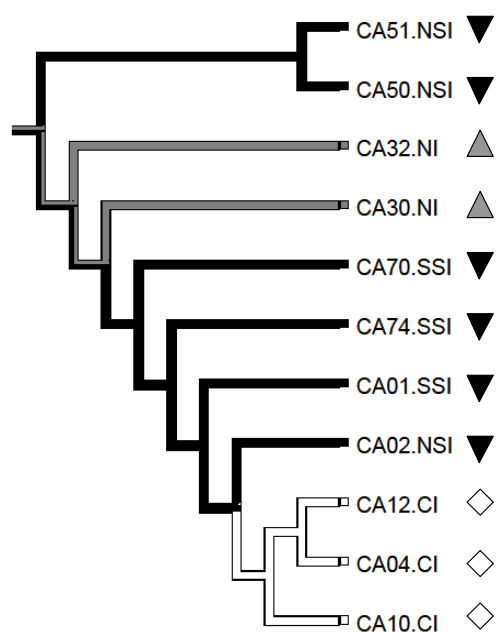
5.4b

Figure 5-4: Maximum likelihood phylogenetic tree for *Hydrellia enderbii* (Diptera).
5-4a: Tree shown with relative branch lengths and with bootstrap values for major
clades. 5-4b: Possible ancestral distributions are shown.

5.5a

5.5b

Figure 5-5: Maximum likelihood phylogenetic tree for *Cerondontha angustipennis* (Diptera). 5-4a: Tree shown with relative branch lengths and with bootstrap values for major clades. 5.4b Possible ancestral distributions are shown.

5.6a

5.6b

Figure 5-6: Maximum likelihood phylogenetic tree for *Cecyropa tychioides* (Coleoptera). 5-6a: Tree shown with relative branch lengths and with bootstrap values for major clades. 5-6b: Possible ancestral distributions are shown.

5.7a

5.7b
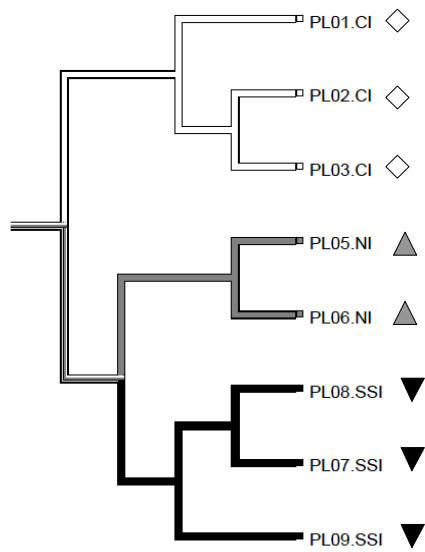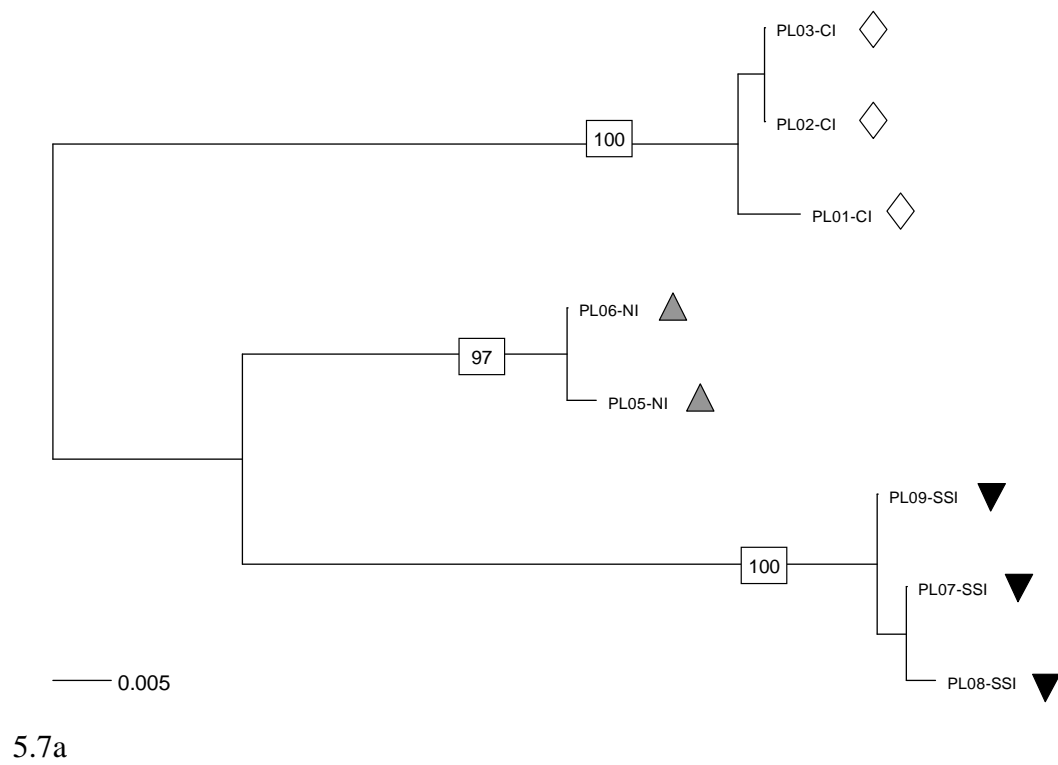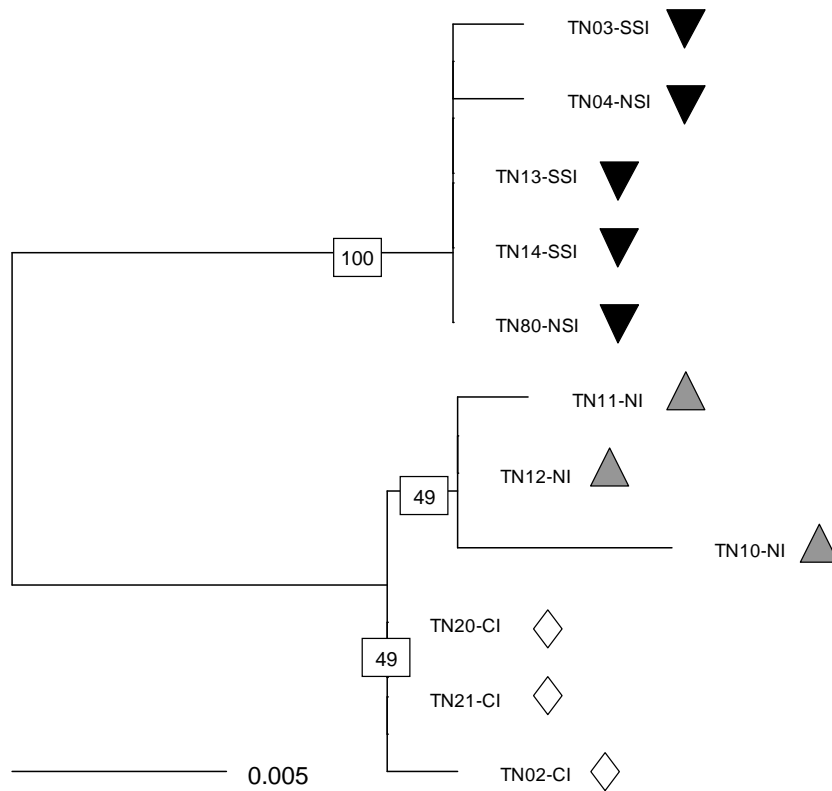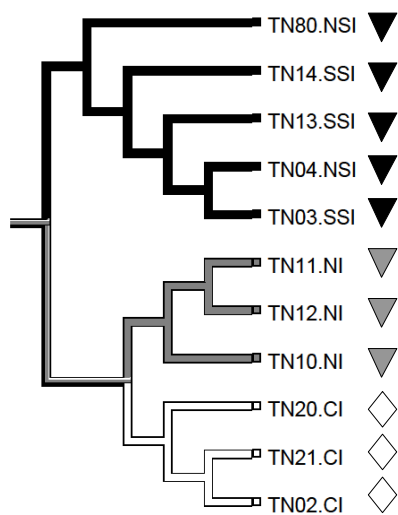
Figure 5-7: Figure 5.7: Maximum likelihood phylogenetic tree for *Phycosecis limbata* (Coleoptera). 5-7a: Tree shown with relative branch lengths and with bootstrap values for major clades. 5-7b: Possible ancestral distributions are shown.

136

5.8a

5.8b

Figure 5-8: Maximum likelihood phylogenetic tree for *Tachyspex nigerrimus* (Hymenoptera). 5-8a: Tree shown with relative branch lengths and with bootstrap values for major clades. 5-8b: Possible ancestral distributions are shown.

5.9a

5.9b
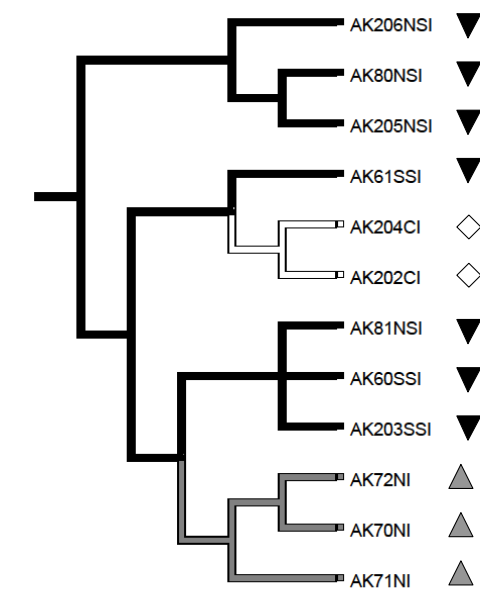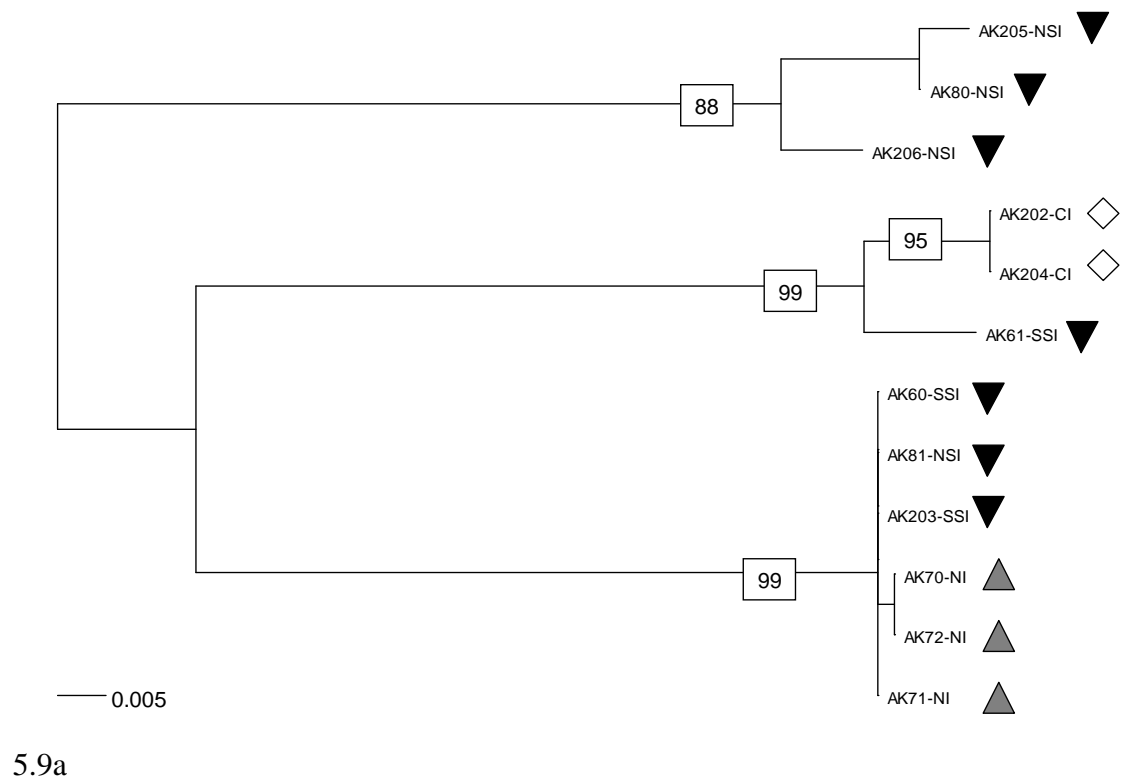
Figure 5-9: Maximum likelihood phylogenetic tree for *Aucklandella sp.* (Hymenoptera). 5-9a: Tree shown with relative branch lengths and with bootstrap values for major clades. 5-9b: Possible ancestral distributions are shown.

5.6 Discussion

5.6.1 Genetic variance

Taxa on the CI are differentiating genetically from the NZ taxa. All CI taxa have a barcoding gap significantly different from a barcoding gap calculated from random g sampling.Even if a CI population is not yet a new species, the data suggest that the speciation process is well underway. Current genetic divergence assessments can determine the degree of divergence within a population. However, the randomisation technique used here has enabled a determination of whether the divergence is significantly different from that of randomly selected specimens.

5.6.2 Comparison to other assessments of genetic variation

In all cases the mean inter-specific distance was greater than 2%, with only two taxa having any values below 2%. In many cases, this degree of genetic variation is taken to imply that the two populations may be separate species (Cognato & Usda, 2007; Hung, et al., 1999). However, this cut-off point is far from universal; many insect species have an COI intra-specific genetic variation of greater than 2% (Cognato, 2006; Cognato & Usda, 2007; Trewick, 2000)

In all CI populations, except *C. tychioides,* there is a clear barcoding gap between the CI intra-group distance and the inter-group distance. In *C. tychioides* there is no clear gap between the CI intra-group distance and the inter-group distance as both have a minimum value of zero. For NZ populations, only *P. limbata* has a clearly defined barcoding gap between the NZ intra-group distance and the inter-group distance. A clear gap between the intra-group distance and the inter-group distance has been used to hypothesise that a population is different enough to be regarded as a new species (Hajibabaei, et al., 2006).

The third test of genetic variance was the ratio between the intra-group distance and the barcoding gap. In the CI populations all the taxa tested had a intra-group distance less than 10× that of the barcoding gap. In the NZ population none of the taxa had a intra-group distance less than 10× that of the barcoding gap.

Many studies using the concept of a barcoding gap test the outcome of the species delimitation tests against known species and comment on the effectiveness or otherwise of the test under scrutiny (Hajibabaei, et al., 2006; Meyer & Paulay, 2005). However, very few of these studies compare the genetic variation found between the tested groups against the expected genetic variation if the samples were randomly distributed. By using randomisation this study can state whether genetic variation in a group is significantly different from randomly distributed samples and thus infer the presence of a barrier affecting gene flow between the tested groups.

The randomisation test of genetic variance appeared to work well. It did not purport to ascribe a particular taxonomic status on the populations being tested, but simply tested whether the two populations were more genetically divergent than a random sampling of the same pool of data.

Where the intra-group distance varied considerably from the inter-group distances, such as in the CI populations, the randomisation test produced a similar level of information as the three other assessments of genetic divergence. However, in the case of the NZ populations, the intra-group genetic distance was not substantially different to the inter-group divergence. In four of the NZ populations, the randomisation test suggested that there was clear divergence between the populations, even though the divergence was not large enough to register an effect using other tests of genetic divergence. Randomisation is also pertinent in situations where other barcoding gap techniques may not distinguish genetically close species, or populations in the process of speciation (Alexander, et al., 2009; Meier, et al., 2006).

5.6.3 Detection of likely source population area

In five of the six taxa analysed, the character state reconstruction implies that the CI population is derived from immigration of members of a SI population. Only *P.limbata* has a likely NI source for the CI population. Studies of CI Coleoptera (Emberson, 2006b) and cockroaches (Chinn & Gemmell, 2004), have shown that some CI populations do have an affinity with SI fauna. Some flora from CI also show a strong relationship with the south of the SI (Heenan, et al., 2010). However, species of CI cicada show an affinity with NI congenerics (Marshall, et al., 2008). Earlier in

this study (Chapter 4) modelling immigration likelihood based on presence or absence on either NI or SI showed no significant difference between NI and SI. It is quite possible though that a NI or SI population has emigrated both to CI and to the other mainland island, and so the source of the CI population would not be easily discernable.

Only *C.tychioides* shows any indication that there has been more than one immigration event to CI from NZ. For *C.tychioides*, one CI clade is genetically very close to some SI samples. This genetic similarity could be an indication of a very recent immigration from NZ to CI (Trewick, et al., 2005). The implication of the observation of predominantly single immigration events is that dispersal and subsequent colonisation is a difficult to achieve for insect taxa, even for those readily placed for dispersal across the ocean. A low rate of immigration would also be more likely to produce the low level CI intra-group divergence seen in the NZ/CI scenarios tested in this study as new genetic input would be a very rare occurrence. None of the character histories suggested any immigration from CI to NZ.

It must be noted here that as COI (mitochondrial DNA) is maternally inherited (Bouille, et al., 2011; Moore, 1995), the phylogenies can only represent the biogeography of female individuals. Although some phylogenetic studies have based conclusions on solely COI phylogenies (Kamgang, et al., 2011; Kolbe, et al., 2008), others have found discrepancies between phylogenies produced using mitochondrial DNA and those using nuclear DNA (Bouille, et al., 2011; Shaw, 2002). The addition of nuclear DNA information would add information from the male individuals enhancing the likelihood of valid conclusions as to the likely source of the CI population.

Many of the phylogenies in this study contained zero length branches, which preclude the use of maximum likelihood reconstruction of ancestral states. Maximum parsimony reconstruction of the ancestral character states was feasible for trees with the some zero length branches but maximum parsimony only allows each node to contain a single character state. Using maximum likelihood based phylogenies would allow nodes to represent the probabilities of a number of possible character states being true at the node (Cook & Crisp, 2005)

The character state analysis performed gives an area cladogram based the assumption of an equal likelihood of immigration between any of the designated regions. However, further study should take into account the probable differing likelihoods of immigration occurring in one direction over another, or the directional asymmetry of dispersal and colonisation (Cook & Crisp, 2005)

Differing probabilities for character state changes could be incorporated in a step matrix for parsimony based analysis, or entered as parameters in a model for maximum likelihood based analysis. The transformation weights and likelihood values used could alter the inferred ancestral character states from those seen in the original analysis of equal probabilities.

In this project, the weighting given could be derived from the results of previous chapters. For example more weight/likelihood could be given to immigration between regions of similar climate. Other factors of influence may be revealed by further research and they too could be incorporated into a more detailed character state anaylsis.

5.6.4 One, or more, species?

The intra-group NZ divergences in this study vary from 0-32%. All but one taxon, *Hydrellia enderbii,* had a mean NZ intra-group divergence of >2%.

Wide NZ intra-group specific variation could point to a number of scenarios. It could be that the taxon is simply very variable. Many species of insect have intra-specific variation of over 2% (Cognato, 2006; Dewaard, et al., 2011). Some species of Coleoptera and lice are purported to have over 15% intra-specific genetic variation (Cognato, 2006). It could also be that there is more than one species within a complex of morphologically similar but genetically divergent, 'cryptic' species, as has been shown in tropical butterflies (Hajibabaei, et al., 2006) and tachinid flies (Smith, et al., 2006).

Three taxa, *C. angustipennis*, *C. tychioides* and *T. nigerrimus* have an NZ intra-group distance means greater than, or equal to the inter-group mean. This wide range in intra-group variation implies that within NZ there are populations more different from one another than the NZ population is from the CI population. These NZ populations

(and the CI population) could all be different species, morphologically very similar, yet genetically different.

5.6.5 Future work

Following on from work already undertaken there are two main avenues of investigation. First, more genetic sampling needs to be carried out. New areas for genetic sampling also need to be targeted. Sampling from other Chatham group islands, such as Pitt Island and Rangitira, would highlight any differentiation with the CI group. Likewise new areas from NZ, such as the west coast, of NI and SI as well as Northland would further emphasise similarities and differences between NZ regions and with CI. The structure of the current phylogenies may be used to help direct the sampling.

The genetic data would also gain immensely from the addition of another gene region, most likely nuclear. Using the COI gene has only allowed inferences based on the biogeographic history of female individuals. It is quite possible that males have different biogeographic influences than females. Use of a nuclear gene would allow data from the male side of the biogeographic equation to be included, effectively increasing the virtual population size (Moore, 1995), and adding a new dimension to the phylogeny and evolutionary history of the taxa concerned.

The sampling of a wider range of taxa would also give a deeper insight into the likely spatial structure of the genetic variation within any species analysed. To this end, additional taxa should be sampled to extend the taxonomic diversity, together with taxa seen as good dispersers and those less likely to disperse. Another interesting approach would be to sample more taxa from within specific families or genera, to build up a more detailed phylogeny of a particular taxon of interest.

There should also be a thorough morphological analysis of the samples collected so far and of any new ones acquired. Some taxa could be part of a cryptic species complex and so morphologically very similar. However, it appears very likely that many of the taxa, from both CI and NZ have not been expertly examined. Further targeted, expert diagnosis may reveal morphological features hitherto unnoticed from

cursory examination. Care must be taken though, as island populations can be morphologically different to their mainland conspecifics (Knopp, et al., 2007).

The acquisition of further genetic data would enable the use of the GMYC method of species delimitation. As mentioned earlier, GMYC relies on data generated by the taxon in question and does not depend on finite genetic distance cut-off points. The GYMC approach would accommodate the genetic variability within each taxon as a product of its own evolutionary and speciation process, rather than being related to processes defining other taxa. Although relatively new, GMYC has now been used in a number of phylogenetic studies (Gattolliat & Monaghan, 2010; Papadopoulou, et al., 2008; Pons, et al., 2006; Pons, et al., 2011; Vuataz, et al., 2011) and would provide an important insight into the evolution and speciation process of the NZ and CI insect populations.

5.7 Conclusion

The data collected shows a definite genetic disparity between conspecific NZ and CI populations. It appears that in some cases, the CI populations are genetically different enough to be considered separate species or are certainly well on their way to becoming so. It is also likely that within NZ there are species complexes that are currently regarded as single species.

The randomisation test used is a good indicator of genetic divergence, especially where divergence is too low for the taxa to be considered separate species. It can also be used to highlight significant genetic divergence that has not yet reached the level of potential speciation.

Further genetic and morphological study is required to fully explore many of the questions raised in this chapter.

Chapter 6
General summary

6.1 Introduction

The question of how and why the flora and fauna of the world are distributed as they are has perplexed and intrigued human beings for thousands of years. Early ideas based on myths, legends and religion have evolved and been enhanced by scientific exploration, accumulation of data and the growth of novel theories (Mayr, 2001). The observations and theories of natural historians have culminated in the melding of a disparate array of sciences, including biology, geology, genetics and mathematics into the subject now known as biogeography.

The issue of biotic distribution was popularized by Darwin and his contemporaries in the late 19th century, with Darwin supporting the idea of oceanic dispersal. Arguments between biogeographers over whether dispersal, or geographically based events, vicariance, are the driving force behind biotic distributions continue to the present day.

Since the days of Darwin, biogeography and biogeographical research has grown, struggled and evolved to become an established scientific discipline. Worldwide scientific interest and application is seen through the many current scientific journals based on biogeographical principles e.g Diversity and Distributions, Ecography, Global Ecology and Biogeography, Journal of Biogeography.

One area of particular interest has been that of island biogeography. The process of species immigration to a newly created island and the subsequent speciation and evolution has led to the specialized subject of island biogeography (Berry, 1992; Gillespie & Roderick, 2002).

Despite a great deal of scientific endeavour, a major criticism of biogeographical theories, and especially dispersal, was that it was not testable or predictive and therefore scientifically redundant. Methodologies introducing more scientific rigor to biogeography have included cladistics, phylogenetics, modeling, improved sampling and more recently molecular based techniques.

The discovery and development of molecular analysis have added a new dimension to biogeographic study. Evolutionary histories, phylogenies, species delimitation and identification can be assessed and analysed using a variety of molecular markers. Concepts such as the 'molecular clock' and the genetic variation between taxa can help to estimate the dates and chronological sequence for divergence of taxa as well as assess the degree of relatedness between taxonomic groups. Inferred divergence dates and sequences are used by biogeographers to relate geological events to biotic distributions and to estimate the relative likelihoods of conflicting biogeographic scenarios.

6.2 This study

Conceptually this study follows in the footsteps of some of the world's greatest biologists and scientists. The study examines the biogeographical relationship between a continental mainland, New Zealand (NZ), and an outlying island, Chatham Island (CI). The NZ/CI scenario is situated within the biogeographically important southern hemisphere and associated with many southern land masses through its ancient Gondwanan heritage.

The study introduces new biogeographical data from the dune habitats of NZ and CI. Also introduced are new methods of re-sampling to ascertain whether trends seen within the collected data are significantly different from random assemblages. Re-sampling techniques were also used to assess whether the NZ and CI populations are genetically disparate enough to be considered separate species.

6.2.1 Collection and dune survey

Reliable and extensive biological surveys and inventories are seen as a fundamental part of study and research into the biodiversity of a region. The data collected through the dune habitat survey of the east coast of NZ and northern CI produced the first comprehensive entomological surveys of dune habitat systems for NZ and possibly the world (Howe, et al., 2010). The collection consists of three orders, Coleoptera, Diptera and Hymenoptera with over 5000 specimens comprising over 650 species.

These specimens will be deposited in the Lincoln University Entomology Research Museum for the further use of researchers, staff and students alike. The collective also provided the raw data for the following sections of the study.

6.2.2 New Zealand and Chatham Island

A disparity in the flora and fauna of islands and their mainland neighbours has long been a theme of island biogeography. Biotic disparity is commonly held to exist at two levels, that of species richness (number of species) and the taxonomic composition of the organisms on the island. The NZ/CI scenario proved to exhibit both these traits in respect to their biogeographic relationship. NZ had approximately 2-6x more species at each site than did CI. This degree of difference also corresponded well with the estimated amount of dune habitat available in each study area. CI was found to have disproportionately fewer Hymenoptera than NZ but more Diptera.

6.2.3 Assessing levels of difference between New Zealand and Chatham Island

The study has shown that at higher taxonomic levels NZ and CI differ. The use of re-sampling techniques to create null hypothesis of expected CI taxa numbers showed that this disparity was not generally reciprocated within the lower taxonomic groups of the three orders. Some hymenoptera families had greater than expected species numbers on CI whereas some coleopteran and dipteran families had fewer. The disparity was also seen at generic level. It appears that trends within taxonomic levels are being driven by particularly successful or unsuccessful lower level taxa. Not only were taxonomic proportions different between NZ and CI, but the composition of the taxa were also different shown by multivariate analysis and MDS graphs.

6.2.4 Modelling filter factors

Another enduring question in biogeography is whether immigration is a random process or if the likelihood of successful immigration can be enhanced or decreased

by the presence or absence of particular factor. Factors can be anything that is considered to possibly affect immigration probability, and can range from biotic (body size, taxonomic group, feeding guild, population abundance) to abiotic (prevailing wind and currents, climate, geographic isolation, geographic size). Factors are seen to 'filter out' taxa that cannot overcome or make use of the particular biogeographic scenario and so can be referred to as filters or filter factors.

Within the parameters of this project the filter factors that had most influence on the immigration success were similarity in climate between NZ and CI, and the initial distribution of a taxon on NZ (the wider the distribution the higher the likelihood of successful immigration).

6.2.5 Genetic variation and potential source population areas

A major issue in biology is that of speciation and the delimitation of species. Populations reaching distant islands are very likely to become reproductively isolated from their mainland conspecifics. Consequently over time changes to the genetic complement of both populations will not be reconciled by gene flow between them. There will come a point where the populations will exhibit difference in appearance and behaviour, and will become reproductively incompatible. One or all of these states of change would justify regarding the two populations as separate species. In this project analysis of molecular data from six taxa lent weight to the argument that the two populations were genetically divergent. In all cases the CI population could possibly be seen to be a new species. The NZ populations themselves could be a complex of one or more species, some sympatric and some split on geographic lines. Initial character state analysis indicated that more CI populations seemed to originate from South Island populations than from North Island populations.

6.3   How did it go?... and future work

The data collective phase of the project proved very successful. The NZ east coast was sampled from Tolaga Bay on the north east coast, to Te Waewae Bay on the south west coast covering 1700 km of coast. On CI, 250 km of duneland was surveyed

from the north of CI (the predominant region with dunes on CI). No previous survey, whether NZ, CI or international, has targeted dune insects in this detail. Three major orders were collected, producing over 5000 mounted specimens and over 650 species or RTUs. A minimum of three new CI records were realised and at least five new species from NZ and CI, including one from outside the study area, on South East Island in the Chatham Island group of islands. The collection methodology was simple and repeatable and well within the capability of a single researcher.

Future work on the collection will include further investigation of as yet unidentified specimens and the description of putative new species. For the purposes of this project RTUs provided adequate information, but insight into potential new species and the ability to add to the ever growing list of NZ insect taxa (Gordon, 2011) will be a significant contribution to NZ entomology, ecology and conservation. To this end collection from NZ areas not collected from in this study, such as the west coast, of North and South Islands, would be worthwhile.

Perhaps the most difficult part of the collection process was finding a suitable site in the first place. As previously mentioned much of NZ duneland is now degraded or lost and is continuing to decline. Finding a suitable site with at least limited vehicular access before arriving in an area was almost impossible. To this end a two day, 1900k reconoiter of the South Island pre-empted the official collecting trips. Another surprisingly useful tool for assessing potential sites was the internet site Google Maps New Zealand, and its street view facility (Google Maps, 2011)

The second part of the project used the data collected from the survey to compare the insect fauna of NZ and CI duneland with view to assessing the biogeographical relationship between the NZ and CI. The use of re-sampling worked well in allowing statistically sound comparisons to be made against a null hypothesis of random immigration. The re-sampling routine, written in R, is flexible enough to change the re-sampled size and the number of re-sampling repeats. It also incorporates the ability to weight the probability of particular groups, if necessary, in future work.

Future work could be taken in two directions. One direction would entail the collection of a wider range of taxa, with more orders and more sites. Alternatively some specific taxa such as a family or genus, could be investigated in more depth, with more samples and more sites. And possibly, time and resources permitting

extend the area of collection to biogeographically pertinent islands, such as New Caledonia and Pacific islands.

Inclusion of filter factors in GLM modelling showed the influence of climate similarity and propagule pressure in the successfully immigrating to CI. The natural progression for the filter modelling would be to include more, carefully chosen, factors into the modelling. Such filter factors could include an estimate of abundance, or the number of species within a taxonomic group.

The COI gene molecular work of the final chapter has shown statistically that the genetic composition of NZ and CI populations are diverging. Depending on the criteria used the NZ and CI taxa could be considered separate species. This assessment of speciation though definitely needs more research before such an assertion can be confirmed. Further research must include more sampling, both in numbers of samples and possibly in sites around NZ and CI. Another gene region, preferably a nuclear gene should also be used to add a different perspective on the evolutionary history of the taxa. Increasing sample number and introducing a new gene will also greatly enhance the data collected so far in assessing which NZ area (if any) is the most likely to contain the ancestral source NZ population from which the CI population has derived.

The re-sampling and randomisation techniques used in this project can be applied to datasets from other projects. They can also be re-applied to the data set from this project when enhanced by the sequencing of more samples. It will be interesting to compare the results of the techniques when applied to datasets from other ecological scenarios. There is also a possibility that the techniques can be incorporated into an R based software package for wider use in the ecological community.

6.4   Conclusion

This PhD project has addressed three major elements of biogeographical research: collection and identification, statistical comparison of mainland and island fauna, genetic divergence and relationship between taxa, and combined them to provide and interesting and meaningful addition to biogeography in NZ and especially that of duneland habitat. Like many biogeographical projects it has raised as many questions

as it has answered and has provided a potential lifetime of work in many and varied directions.

References

Adams, D. K., & Flierl, G. R. (2010). Modeled interactions of mesoscale eddies with the East Pacific Rise: implications for larval dispersal. *Deep-Sea Research Part I-Oceanographic Research Papers, 57*(10), 1163-1176.

Agassiz, L. (1850). Geographical distribution of animals. *Christian Examiner and Religious Miscellany, 48*(2), 181-204.

Aguiar, A. P., & Santos, B. F. (2010). Discovery of potent, unsuspected sampling disparities for Malaise and Moricke traps, as shown for neotropical Cryptini (Hymenoptera, Ichneumonidae). *Journal of Insect Conservation, 14*(2), 199-206.

Ahmed, S., Compton, S. G., Butlin, R. K., & Gilmartin, P. M. (2009). Wind-borne insects mediate directional pollen transfer between desert fig trees 160 kilometers apart. *Proceedings of the National Academy of Sciences of the United States of America, 106*(48), 20342-20347. doi:10.1073/pnas.0902213106

Alexander, L. C., Delion, M., Hawthorne, D. J., Lamp, W. O., & Funk, D. H. (2009). Mitochondrial lineages and DNA barcoding of closely related species in the mayfly genus *Ephemerella* (Ephemeroptera:Ephemerellidae). *Journal of the North American Benthological Society, 28*(3), 584-595.

Algar, A. C., & Losos, J. B. (2011). Evolutionary assembly of island faunas reverses the classic island-mainland richness difference in Anolis lizards [ ]. *Journal of Biogeography, 38*(6), 1125-1137. doi:10.1111/j.1365-2699.2010.02466.x

Allen, J. A. (1876). Geographical variation among North American mammals, especially in respect to size. *Bulletin of the United States Geological and Geographical Survey of the Territories, 2*(4), 309-344.

Allwood, J., Gleeson, D., Mayer, G., Daniels, S., Beggs, J. R., & Buckley, T. R. (2010). Support for vicariant origins of the New Zealand Onychophora. *Journal of Biogeography, 37*(4), 669-681.

Aloia, A., Colombini, I., Fallaci, M., & Chelazzi, L. (1999). Behavioural adaptations to zonal maintenance of five species of tenebrionids living along a Tyrrhenian sandy shore. *Marine Biology, 133*, 473-487.

Amadon, D. (1948). Continental drift and bird migration. *Science, 108*(2817), 705-707.

Andersen, A. N. (1995). Measuring more of biodiversity: genus richness as a surrogate for species richness in Australian ant faunas. *Biological Conservation, 73*(1), 39-43.

Andrus, N., Tye, A., Nesom, G., Bogler, D., Lewis, C., Noyes, R., et al. (2009). Phylogenetics of *Darwiniothamnus* (Asteraceae: Astereae) - molecular evidence for multiple origins in the endemic flora of the Galapagos Islands. *Journal of Biogeography, 36*(6), 1055-1069.

Anholt, B. R. (1990). Size-biased dispersal prior to breeding in a damselfly. *Oecologia, 83*(3), 385-387.

Antolin, M. F., & Strong, D. R. (1987). Long-distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host. *Oecologia, 73*(2), 288-292.

Arrhenius, O. (1921). Species and area. *Journal of Ecology, 9*(1), 95-99.

Asgharian, H., Sahafi, H. H., Ardalan, A. A., Shekarriz, S., & Elahi, E. (2011). Cytochrome c oxidase subunit 1 barcode data of fish of the Nayband National Park in the Persian Gulf and analysis using meta-data flag several cryptic species [Article]. *Molecular Ecology Resources, 11*(3), 461-472. doi:10.1111/j.1755-0998.2011.02989.x

Avise, J. C. (2004). *Molecular Markers, Natural History, and Evolution* Sunderland: Sinauer Associates.

Baille, J. E. M., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2004). *2004 IUCN Red List of Threatened Species. A Global Species Assessment*. Gland: IUCN.

Baker, F. T., Ketteringham, I. E., Bray, S. P. V., & White, J. H. (1942). Observations on the biology of the carrot fly (*Psila rosae* Fab.) : Assembling and oviposition. *Annals of Applied Biology, 29*(2), 115-125.

Ball, I. R. (1975). Nature and formulation of biogeographical hypotheses. *Systematic Zoology, 24*(4), 407-430.

Banks, S. C., Piggott, M. P., Williamson, J. E., Bove, U., Holbrook, N. J., & Beheregaray, L. B. (2007). Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. *Ecology, 88*(12), 3055-3064.

Barber, N. H., Herbert, E., Dadswell, & Ingle, H. D. (1959). Transport of driftwood from South America to Tasmania and Macquarie Island. *Nature, 184*(4681), 203-202-204.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature, 471*(7336), 51-57. doi:10.1038/nature09678

Bartholomew, G. A. (1986). The role of natural history in contemporary biology. *Bioscience, 36*(5), 324-329.

Basset, Y. (1988). A composite interception trap for sampling arthropods in tree canopies. *Journal of the Australian Entomological Society, 27*, 213-219.

Beaglehole, J. C. (Ed.). (1962). *The Endeavour Journal of Joseph banks 1768-1771* (Vol. 1). Sydney: Angus and Robertson Ltd.

Bellamy, D., Springett, B., & Hayden, P. (1990). *Moa's Ark, the voyage of New Zealand*. New York: NY: Viking

Benavides, E., Baum, R., Snell, H. M., Snell, H. L., & Sites Jr, J. W. (2009). Island biogeography of Galapogos lava lizards (Tropiduridae: *Microlophus*): Species diversity and colonization of the archipelago. *Evolution, 63*(6), 1606-1626.

Bennett, J. P. (1996). Floristic summary of 'Manual of Vascular Plants of Northeastern United States and Adjacent Canada,' second edition. *The Botanical Review, 62*(2), p203(204).

Berry, R. J. (1992). The significance of island biotas. *Biological Journal of the Linnean Society, 46*(1-2), 3-12.

Bickel, D. J. (1991). *Fauna of New Zealand Number 23 Sciapodinae, Medeterinae (Insecta: Diptera) with a generic review of the Dolichopdidae*. Auckland: New Zealand: DSIR Plant Protection.

Bitanyi, S., Bjornstad, G., Ernest, E. M., Nesje, M., Kusiluka, L. J., Keyyu, J. D., et al. (2011). Species identification of Tanzanian antelopes using DNA barcoding [ ]. *Molecular Ecology Resources, 11*(3), 442-449. doi:10.1111/j.1755-0998.2011.02980.x

Blackburn, T. M., & Duncan, R. P. (2001). Determinants of establishment success in introduced birds. *Nature, 414*(6860), 195-197.

Blackburn, T. M., & Gaston, K. J. (1998). Some methodological issues in macroecology. *American Naturalist, 151*(1), 68-83.

Blondel, J., Chessel, D., & Frochot, B. (1988). Bird species impoverishment, niche expansion, and density inflation in mediterranean island habitats. *Ecology, 69*(6), 1899-1917.

Bonte, D. (2005). Anthropogenic induced changes in nesting densities of the dune-specialised digger wasp *Bembix rostrata* (Hymenoptera : Sphecidae). *European Journal of Entomology, 102*(4), 809-812.

Bonte, D., & Maes, D. (2008). Trampling affects the distribution of specialised coastal dune arthropods. *Basic and Applied Ecology, 9*(6), 726-734. doi:10.1016/j.baae.2007.09.008

Boomsma, J. J., & Loon, A. J. V. (1982). Structure and diversity of ant communities in successive coastal dune valleys. *Journal of Animal Ecology, 51*(3), 957-974.

Bouille, M., Senneville, S., & Bousquet, J. (2011). Discordant mtDNA and cpDNA phylogenies indicate geographic speciation and reticulation as driving factors for the diversification of the genus *Picea*. *Tree Genetics & Genomes, 7*(3), 469-484.

Boyer, S. L., & Giribet, G. (2009). Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography, 36*, 1084-1099.

Briggs, J. C. (2003). Fishes and birds: Gondwana life rafts reconsidered. *Systematic Biology, 52*(4), 548-553.

Brochet, A., Guillemain, M., Fritz, H., Gauthier-Clerc, M., & Green, A. J. (2009). The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. *Ecography, 32*(6), 919-928.

Brown, B., Emberson, R. M., & Paterson, A. M. (1999). Phylogeny of "*Oxycanus*" lineages of Hepialid moths from New Zealand inferred from sequence variation in the mtDNA COI and II gene regions. *Molecular Phylogenetics and Evolution, 13*(3), 463-473.

Brown, J. H. (1971). Mammals on Mountaintops: Nonequilibrium Insular Biogeography. *The American Naturalist, 105*(945), 467-478.

Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography:effect of immigration on extinction. *Ecology, 58*, 445-449.

Brown, M., & Dinsmore, J. J. (1988). Habitat islands and the equilibirum theory of island biogeography - testing some predications [ ]. *Oecologia, 75*(3), 426-429.

Browne, R. A. (1977). Genetic variation in island and mainland populations of *Peromyscus Leucopus*. *American Midland Naturalist, 97*(1), 1-9.

Brundin, L. (1966). Transantarctic relationships and their significance as evidenced by midges. *Kungliga Svenska Vetenskapsakademiens Handlinger, 4*(11), 1-472.

Bryan, C. S., Philip, T. L., Stephen, D. W., Robert, J. P., & et al. (1999). Mantle plumes and Antarctica-New Zealand rifting: Evidence from mid-Cretaceous mafic dykes. *Journal of the Geological Society, 156*, 659.

Buglife. (2003). *Notable invertebrates associated with coastal sand dunes*. Retrieved 30/11/2010, from http://www.buglife.org.uk/Resources/Buglife/Migrated%20Resources/Documents/0820Notable20invertebrates20associated20with20coastal20sand20dunes.pdf

Bush, M. B., & Whittaker, R. J. (1991). Krakatau: Colonization patterns and hierarchies. *Journal of Biogeography, 18*(3), 341-356.

Butler, C. D., & Friel, S. (2006). Time to regenerate: Ecosystems and health promotion. *PLoS Med, 3*(10), e394.

Butlin, R., Bridle, J., & Schluter, D. (2009). Speciation and patterns of diveristy In R. Butlin, J. Bridle & D. Schluter (Eds.), *Speciation and Patterns of Diveristy* Cambridge: Cambridge University Press.

Cabezas, P., Macpherson, E., & Machordom, A. (2011). *Allogalathea* (Decapoda: Galatheidae): a monospecific genus of squat lobster? [ ]. *Zoological Journal of the Linnean Society, 162*(2), 245-270. doi:10.1111/j.1096-3642.2010.00681.x

Camp, W. H. (1947). Distribution patterns in modern plants and the problems of ancient dispersals. *Ecological Monographs, 17*(2), 159-183.

Campbell, H., & Hutching, G. (2007). *In search of ancient New Zealand*. North Shore: New Zealand: Penguin Books.

Campbell, H. J. (1998). Fauna and flora of the Chatham Islands: less than 4MY old? (Eds S.A. Trewick & M. J. Phillips). *Geological Society of New Zealand. Miscellaneous Publication, 97*, 15-16.

Campbell, H. J., Andrews, P. B., Beu, A. G., Maxwell, P. A., Edwards, A. R., Laird, M. G., et al. (1994). *Cretaceous-Cenozoic geology and biostratigraphy of the Chatham Islands, New Zealand*: Institute of Geological and Nuclear Science Mongraph 2.

Campbell, H. J., Begg, J. G., Beu, A. G., Carter, R. M., Davies, G., Holt, K., et al. (2006). On the turn of a scallop (Eds S.A Trewick & M.J Phillips). *Geological Society of New Zealand, Miscellaneous Publication, 121*, 9.

Campbell, J. W., & Hanula, J. L. (2007). Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems [ ]. *Journal of Insect Conservation, 11*(4), 399-408. doi:10.1007/s10841-006-9055-4

Cane, J. H., Minckley, R. L., & Kervin, L. J. (2000). Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal of the Kansas Entomological Society, 73*(4), 225-231.

Cardoso, M. J., Eldridge, M. D. B., Oakwood, M., Rankmore, B., Sherwin, W. B., & Firestone, K. B. (2009). Effects of founder events on the genetic variation of translocated island populations: implications for conservation management of the northern quoll. *Conservation Genetics, 10*(6), 1719-1733.

Carlquist, S. (1966). The biota of long-distance dispersal. I. Principles of dispersal and evolution. *The Quarterly Review of Biology, 41*(3), 247-270.

Carlquist, S. (1970). *Island biology*. New York: Natural History Press.

CARMABI. (2010). *Biological inventories and determination of conservation priorities. *. Retrieved 14/09/2010, from http://www.carmabi.org/consultancy/biological-inventories

Chakona, A., Phiri, C., Magadza, C., & Brendonck, L. (2008). The influence of habitat structure and flow permanence on macroinvertebrate assemblages in temporary rivers in northwestern Zimbabwe. *Hydrobiologia, 607*(1), 199-209.

Chapman, R. W., Gottfried, D., & Waring, C. L. (1955). Age determination on some rocks from the boulder batholithand other batholiths of western Montana. *Geological Society of America Bulletin, 66*, 607-610.

Chaput-Bardy, A., Gregoire, A., Baguette, M., Pagano, A., & Secondi, J. (2010). Condition and phenotype-dependent dispersal in a Damselfly, *Calopteryx splendens*. *Plos One, 5*(5). doi:10.1371/journal.pone.0010694

Cheng, L., & Birch, M. C. (1978). Insect flotsam: an unstudied marine resource. *Ecological Entomology, 3*(2), 87-97.

Cheng, L., & Holdway, P. (1995). Populations of *Halobates* (Hemiptera, Gerridae) across 2 oceans. *Raffles Bulletin of Zoology, 43*(2), 313-327.

Cherrill, A. J., & Begon, M. (1989). Predation on grassghopper by spiders in sand dune grasslands [ ]. *Entomologia Experimentalis Et Applicata, 50*(3), 225-231.

Chinn, W. G., & Gemmell, N. J. (2004). Adaptive radiation within New Zealand endemic species of the cockroach genus *Celatoblatta* Johns (Blattidae): a response to Plio-Pleistocene mountain building and climate change. *Molecular Ecology, 13*(6), 1507-1518. doi:10.1111/j.1365-294X.2004.02160.x

Chiswell, S. M. (1996). Variability in the Southland Current, New Zealand. *New Zealand Journal of Marine and Freshwater research, 30*, 1-18.

Chiswell, S. M. (1998). The East Cape Current and two eddies: a mechanism for larval retention? *New Zealand Jouranl of Marine and Freshwater Research, 32*, 385-397.

Chiswell, S. M. (2009). Colonisation and connectivity by intertidal limpets among New Zealand, Chatham and Sub-Antarctic Islands. II. Oceanographic connections. *Marine Ecology Progress Series, 388*, 121-135.

Clark, B. R., Godfray, H. C. J., Kitching, I. J., Mayo, S. J., & Scoble, M. J. (2009). Taxonomy as an eScience [Proceedings Paper]. *Philosophical Transactions of the Royal Society a-Mathematical Physical and Engineering Sciences, 367*(1890), 953-966. doi:10.1098/rsta.2008.0190

Close, R. C., Moar, N. T., Tomlinson, A. I., & Lowe, A. D. (1978). Aerial dispersal of biological material from Australia to New Zealand. *International Journal of Biometeorology, 22*(1), 1-19.

Coates, G., & Cox, G. (2002). *The Rise and Fall of the Southern Alps*. Christchurch: New Zealand Canterbury University press.

Cody, M. L., & Diamond, J. M. (Eds.). (1975). *Ecology and Evolution of Communities*. Cambridge Harvard University Press.

Coe, W. R. (1946). The means of dispersal of bathypelagic animals in the North and South Atlantic Oceans. *American Naturalist, 80*(793), 453-469.

Cognato, A. I. (2006). Standard percent DNA sequence difference for insects does not predict species boundaries [Review]. *Journal of Economic Entomology, 99*(4), 1037-1045.

Cognato, A. I., & Usda. (2007). A standard DNA taxonomy for insects? In *Proceedings from the Third Workshop on Genetics of Bark Beetles and Associated Microorganisms* (pp. 11-12). Ft Collins: Us Dept Agr, Forest Serv Rocky Mt Forest & Range Exptl Stn. Retrieved from <Go to ISI>://000254163200002

Colautii, R. I., Grigorovitch, I. A., & MacIsaac, H. (2006). Propagule pressure: a null model for biological invasions. *Biological Invasions, 8*, 1023-1037.

Colinvaux, P. A. (1998). A new vicariance model for Amazonian endemics. *Global Ecology and Biogeography Letters, 7*(2), 95-96.

Comor, V., Orgeas, J., Ponel, P., Rolando, C., & Delettre, Y. R. (2008). Impact of anthropogenic disturbances on beetle communities of French Mediterranean coastal dunes. *Biodiversity and Conservation, 17*(8), 1837-1852. doi:10.1007/s10531-007-9290-3

Condit, R., Ashton, P., Balslev, H., Brokaw, N., Bunyavejchewin, S., Chuyong, G., et al. (2005). Tropical tree a-diversity: Results from a worldwide network of large plots. In I. Friis & H. Balslev (Eds.), *Plant diversity and complexity patterns: local, regional, and global dimensions : proceedings of an international symposium held at the Royal Danish Academy of Sciences and Letters in Copenhagen, Denmark, 25-28 May, 2003*

Connor, E. F., & Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology, 60*(6), 1132-1140.

Cook, L. G., & Crisp, M. D. (2005). Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *Journal of Biogeography (J. Biogeogr.), 32*, 741-754.

Cook, L. G., Edwards, R. D., Crisp, M. D., & Hardy, N. B. (2010). Need morphology always be required for new species descriptions? [ ]. *Invertebrate systematics, 24*(3), 322-326. doi:10.1071/is10011

Cook, R. A., Wood, R. A., & Campbell, H. J. (1989). The Chatham Rise: An exploration frontier*New Zealand Geological Survey*. Symposium conducted at the meeting of the New Zealand petroleum conference

Cook, W. C. (1931). Notes on predicting the probable future distribution of introduced insects. *Ecology, 12*(2), 245-247.

Cooper, R. A., & Millener, P. R. (1993). The New Zealand biota - Historical background and new research [Review]. *Trends in Ecology & Evolution, 8*(12), 429-433.

Copp, G. H., Vilizzi, L., & Gozlan, R. E. (2010). The demography of introduction pathways, propagule pressure and occurrences of non-native freshwater fish in England [ ]. *Aquatic Conservation-Marine and Freshwater Ecosystems, 20*(5), 595-601. doi:10.1002/aqc.1129

Coreau, A., Treyer, S., Cheptou, P. O., Thompson, J. D., & Mermet, L. (2010). Exploring the difficulties of studying futures in ecology: what do ecological scientists think? *Oikos, 119*(8), 1364-1376. doi:10.1111/j.1600-0706.2010.18195.x

Cotterill, F. P. D., & Foissner, W. (2010). A pervasive denigration of natural history misconstrues how biodiversity inventories and taxonomy underpin scientific knowledge. *Biodiversity and Conservation, 19*, 291-303.

Coulson, S. J., Hodkinson, I. D., Webb, N. R., & Harrison, J. A. (2002). Survival of terrestrial soil-dwelling arthropods on and in seawater: implications for trans-oceanic dispersal. *Functional Ecology, 16*(3), 353-356.

Coulson, S. J., Hodkinson, I. D., Webb, N. R., Mikkola, K., Harrison, J. A., & Pedgley, D. E. (2002). Aerial colonization of high Arctic islands by invertebrates: the diamondback moth *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species. *Diversity and Distributions, 8*(6), 327-334.

Coulter, J. D. (1975). The Climate. In G. Kuschel (Ed.), *Biogeography and Ecology in New Zealand* (pp. 87-138). The Hague: Dr. W. Junk. b.v.

Cowie, R. H., & Holland, B. S. (2006). Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *Journal of Biogeography, 32*(2), 193-198.

Cowling, R. M., Richardson, D. M., & Pierce, S. M. (Eds.). (1997). *The Vegetation of Southern Africa*. Cambridge: Cambridge University press.

Coyne, J. A., & Orr, H. A. (1994). *Speciation*. Sunderland: Sinauer Associates.

Cracraft, J. (1994). Species Diversity, Biogeography and the Evolution of Biotas. *American Zoologist, 34*(1), 33-47.

Crandall, E. D., Taffel, J. R., & Barber, P. H. (2010). High gene flow due to pelagic larval dispersal among South Pacific archipelagos in two amphidromous gastropods (Neritomorpha: Neritidae). *Heredity, 104*(6), 563-572. doi:10.1038/hdy.2009.138

Craw, R. (1989). New-Zealand Biogeography - a Panbiogeographic Approach. *New Zealand Journal of Zoology, 16*(4), 527-547.

Crawley, M., J. (2008). *Statistics : an introduction using R*. Chichester: John Wiley and Sons Ltd.

Crisci, J. V. (2001). The voice of historical biogeography. *Journal of Biogeography, 28*(2), 157-168.

Croizat, L. (1978). Deduction, induction, and biogeography. *Systematic Zoology, 27*(2), 209-213.

Croizat, L. (1982). Vicariance / vicariism, panbiogeography, "vicariance biogeography," etc... : A clarification. *Systematic Zoology, 31*(3), 291-304.

Croizat, L., Nelson, G., & Rosen, D. E. (1974). Centers of origin and related concepts. *Systematic Zoology, 23*(2), 265-287.

Curtis, G. H., Evernden, J. F., & Lipson, J. (1958). *Age determination of some granitic rocks in California by the Potassium-Argon method*: California Dept. Natur. Resources, Div. Mines

Daehler, C. C., & Strong Jr, D. R. (1993). Prediction and biological Invasions. *Trends in Ecology & Evolution, 8*(10), 380.

Dana, J. D. (1853). On an isothermal oceanic chart, illustrating the geographical distribution of marine animals. *American Journal of Science and Arts, 16*(2), 153-167,314-327.

Dantart, J., Stefanescu, C., Avila, A., & Alarcon, M. (2009). Long-distance wind-borne dispersal of the moth *Cornifrons ulceratalis* (Lepidoptera: Crambidae: Evergestinae) into the northern Mediterranean. *European Journal of Entomology, 106*(2), 225-229.

Dapporto, L., & Dennis, R. L. H. (2010). Skipper impoverishment on large West Mediterranean islands (Lepidoptera Hesperioidea): deterministic, historical and stochastic factors. *Biodiversity and Conservation, 19*(9), 2637-2649. doi:10.1007/s10531-010-9863-4

Dapporto, L., Schmitt, T., Vila, R., Scalercio, S., Biermann, H., Dincă, V., et al. (2011). Phylogenetic island disequilibrium: evidence for ongoing long-term population dynamics in two Mediterranean butterflies. *Journal of Biogeography*. doi:10.1111/j.1365-2699.2010.02452.x

Darlington Jr., P. J. (1938a). The Origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. *The Quarterly Review of Biology, 13*(3), 274-300.

Darlington Jr., P. J. (1938b). Was there an Archatlantis? *American Naturalist, 72*(743), 521-533.

Darroch, S. A. F. (2010). A new method for visualizing the evolution of beta-diveristy on continental scales, using cenozoic mammals *Geological Society of America.* Symposium conducted at the meeting of the GSA Denver Annual Meeting, Denver, Colorado.

Darwin, C. (1838-1843). *The zoology of the voyage of H.M.S. Beagle. Edited and superintended by Charles Darwin* London: Henry Colburn.

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or, The Preservation of Favoured Races in the Struggle for Life.* London: John Murray.

Daugherty, C. H., Gibbs, G. W., & Hitchmough, R. A. (1994). Mega-island or micro-continent - New-Zealand and its fauna (Vol 8, Pg 437, 1993). *Trends in Ecology & Evolution, 9*(1), 6-6.

Dayton, P. K. (2003). The Importance of the Natural Sciences to Conservation. (An American Society of Naturalists Symposium Paper). *The American Naturalist, 162*(1), 1-13.

de Lang, R., & Vogel, G. (2006). The snakes of Sulawesi. In M. Vences, L. Kohler, T. Ziegler & W. Bohme (Chair), Symposium conducted at the meeting of the Herpetologia Bonnensis II

de Queiroz, A. (2005). The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology & Evolution, 20*(2), 68-73. doi:10.1016/j.tree.2004.11.006

De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology, 56*(6), 879-886. doi:10.1080/10635150701701083

de Queiroz, K., & Gauthier, J. (1992). Phylogenetic taxonomy *Annual Review of Ecology and Systematics, 23*, 449-480.

Derr, J. A., Alden, B., & Dingle, H. (1981). Insect life histories in relation to migration, body size, and host plant array: a comparative study of *Dysdercus*. *Journal of Animal Ecology, 50*(1), 181-193.

Deutch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Cameron, K. G., Haak, D. C., et al. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 6669-6672.

Dewaard, J. R., Hebert, P. D. N., & Humble, L. M. (2011). A comprehensive DNA barcode library for the looper moths (Lepidoptera: Geometridae) of British Columbia, Canada. *Plos One, 6*(3), 6.

Di Castri, F. (1989). History of biological invasions with special emphisis on the Old World. In J. M. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson (Eds.), *Biolgical Invasions: A Global Perspective*. New York: John Wiley & Sons.

Diamond, J. M. (1974). Colonisation of exploded islands by birds. *Science, 184*, 803-806.

Diamond, J. M. (1975). Assembly of species Communities. In M. L. Cody & J. M. Diamond (Eds.), *Ecology and Evolution of Communities* (pp. 342-344). Cambridge, MA: Havard University Press.

Diamond, J. M. (1984). Distributions of New Zealand birds on real and virtual islands. *New Zealand Journal of Ecology, 7*, 37-55.

Diamond, J. M. (1997). *Guns, germs and Steel: the fates of human societies*. London: UK: Random House.

Diamond, J. M., & Gilpin, M. E. (1982). Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. *Oecologia, 52*(1), 64-74.

Didham, R. (2005). New Zealand: 'Fly-paper of the Pacific?'. *The Weta, 29*, 1-5.

Dieckmann, U., O'Hara, B., & Weisser, W. (1999). The evolutionary ecology of dispersal. *Trends in Ecology & Evolution, 14*(3), 88-90.

Dingle, H., Blakley, N. R., & Miller, E. R. (1980). Variation in body size and flight performance in milkweed bugs (*Oncopeltus*). *Evolution, 34*(2), 371-385.

Doerries, M. B., & Van Dover, C. L. (2003). Higher-taxon richness as a surrogate for species richness in chemosynthetic communities [ ]. *Deep-Sea Research Part I-Oceanographic Research Papers, 50*(6), 749-755. doi:10.1016/s0967-0637(03)00052-9

Donoghue, M. J., & Moore, B. R. (2003). Toward an integrative historical biogeography. *Integrative and Comparative Biology, 43*(2), 261-270.

Donovan, B. (2007). *Fauna of New Zealand Number 57 Apoidea (Insecta : Hymenoptera)*: Manaakai Whenua Press.

Dos Santos, N. D., & Da Costa, D. P. Phytogeography of the liverwort flora of the Atlantic Forest of south-eastern Brazil. *Journal of Bryology, 32*, 9-22. doi:10.1179/037366810x12578498135634

Drake, J. M., & Lodge, D. M. (2006). Allee effects, propagule pressure and the probability of establishment: Risk analysis for biological invasions [ ]. *Biological Invasions, 8*(2), 365-375. doi:10.1007/s10530-004-8122-6

Drake, J. M., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M., et al. (1989). *Biological Invasions: A Global Perspective*. New York: John Wiley & Sons.

Drake, V. A., Helm, K. F., Readshaw, J. L., & Reid, D. G. (1981). Insect migration across Bass Strait during Spring - a radar study. *Bulletin of Entomological Research, 71*(3), 449-466.

Du Toit, A. L. (1927). *A geological comparison of South America with South Africa.* Washington D.C.: Carnegie Institution of Washington.

Du Toit, A. L. (1937). *Our wandering continents; an hypothesis of continental drifting*. Edinburgh & London: Oliver & Boyd.

Du Toit, A. L. (1944). Tertiary mammals and continental drift; a rejoinder to George G. Simpson. *American Journal of Science and Arts, 242*(3), 145-163.

Dubey, B., Meganathan, P. R., & Haque, I. (2011). DNA mini-barcoding: an approach for forensic identification of some endangered Indian snake species [ ]. *Forensic Science International-Genetics, 5*(3), 181-184. doi:10.1016/j.fsigen.2010.03.001

Ducheyne, E., De Deken, R., Becu, S., Codina, B., Nomikou, K., Mangana-Vougiaki, O., et al. (2007). Quantifying the wind dispersal of Culicoides species in Greece and Bulgaria. *Geospatial Health, 1*(2), 177-189.

Dugdale, J. S., & Emberson, R. M. (2008). Terrestrial invertebrates. In C. Miskelly (Ed.), *Chatham Islands: Heritage and Conservation* (2 ed., pp. 116-124). Christchurch: Canterbury University Press.

Duncan, R. P., Blackburn, T. M., & Sol, D. (2003). The ecology of bird introductions [Review]. *Annual Review of Ecology Evolution and Systematics, 34*, 71-98. doi:10.1146/annurev.ecolsys.34.011802.132353

Dune Restoration Trust of New Zealand. (2007). Retrieved 24/08/2010, from http://www.dunestrust.org.nz/research.html

Duyker, E. (1998). *Nature's argonaut*. Melbourne: The Miegunyah Press.

Dwomoh, E. A., Ackonor, J. B., & Afun, J. V. K. (2008). Survey of insect species associated with cashew (*Anacardium occidentale* Linn.) and their distribution in Ghana. *African Journal of Agricultural Research, 3*(3).

Eberhard, M. J. B., Picker, M. D., & Klass, K. D. (2011). Sympatry in Mantophasmatodea, with the description of a new species and phylogenetic considerations. *Organisms Diversity & Evolution, 11*(1), 43-59.

Edwards, J. S., & Thornton, I. W. B. (2001). Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VI. The pioneer arthropod community of Motmot. *Journal of Biogeography, 28*(11-12), 1379-1388.

Edwards, W., & Westoby, M. (1996). Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. *Journal of Biogeography, 23*(3), 329-338.

Ehrlich, P. R. (1989). Attributes of invaders and the invading process: vertebrates. In J. M. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson (Eds.), *Invasion Biology: A Global Perspective* New York: John Wiley & Sons Ltd.

El Albani, A., Bengtson, S., Canfield, D. E., Bekker, A., Macchiarelli, R., Mazurier, A., et al. (2010). Large colonial organisms with coordinated growth in oxygenated environments 2.1 Gyr ago [ ]. *Nature, 466*(7302), 100-104. doi:10.1038/nature09166

Eldredge, N. (1981). The Riddle of Dispersal: Discussion. In G. Nelson & D. Rosen, E (Eds.), *Vicariance Biogeography: A Critique* New York: Columbia University Press.

Elton, C. S. (1925). The dispersal of insects to Spitsbergen. *Transactions of the Entomological Society of London 1925, 73*, 289-299.

Elton, C. S. (1946). Competition and the structure of ecological communities. *Journal of Animal Ecology, 15*(1), 54-68.

Elton, C. S. (1958). *The ecology of invasions by animals and plants*. London: Meuthen.

Emberson, R. M. (1995). The Chatham Islands beetle fauna and the age of separation of the Chatham Islands from New Zealand. *New Zealand Entomologist, 21*, 25-64.

Emberson, R. M. (2006a). The beetle (Coleoptera) fauna of the Chatham Islands. *New Zealand Entomologist, 21*, 25-64.

Emberson, R. M. (2006b). *The beetle fauna (Coleoptera) of the Chatham Islands*.

Emerson, B. C. (2002). Evolution on oceanic islands: molecular phylogenetic approaches to understanding pattern and process [Review]. *Molecular Ecology, 11*(6), 951-966.

Encora. (2007). *Coastal and marine areas and locations*. Retrieved 3/7/2010, from http://www.coastalwiki.org/coastalwiki/Category:Coastal_and_marine_areas_and_locations

Endler, J. A. (1982). Review: Puberty Rites of Biogeography. *Evolution, 36*(1), 207-209.

Esselstyn, J. A., Oliveros, C. H., Moyle, R. G., Peterson, A. T., McGuire, J. A., & Brown, R. M. (2010). Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line [Review]. *Journal of Biogeography, 37*(11), 2054-2066. doi:10.1111/j.1365-2699.2010.02378.x

Eysenbach, G. (2006). Citation advantage of open access articles. *Plos Biology, 4*(5), 692-698. doi:10.1371/journal.pbio.0040157

Farrow, R. A. (1984). Detection of trans-oceanic migration of insects to a remote island in the coral sea, Willis Island. *Australian Journal of Ecology, 9*(3), 253-272.

Felt, E. P. (1925). The dissemination of insects by air currents. *Journal of Economic Entomology, 18*(1), 152-158.

Feng, H. Q., Zhang, Y. H., Wu, K. M., Cheng, D. F., & Guo, Y. Y. (2007). Nocturnal windborne migration of ground beetles, particularly *Pseudoophonus griseus* (Coleoptera : Carabidae), in China. *Agricultural and Forest Entomology, 9*(2), 103-113.

Fernandes, L. H., Nessimian, J. L., & Mendonca, M. C. d. (2009). Structure of Poduromorpha (Collembola) communities in "restinga" environments in Brazil [ ]. *Pesquisa Agropecuaria Brasileira, 44*(8), 1033-1039. doi:10.1590/s0100-204x2009000800036

Fleming, C. A. (1962). New Zealand biogeography: a paleontologist's approach. *Tuatara, 10*(2), 53-108.

Fleming, C. A. (1976). New Zealand as a minor source of terrestrial plants and animals in the Pacific *Tuatara, 22*(1), 30-37.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology, 3*(5), 294-299.

Fontaneto, D., & Jondelius, U. (2011). Broad taxonomic sampling of mitochondrial cytochrome c oxidase subunit I does not solve the relationships between Rotifera and Acanthocephala. *Zoologischer Anzeiger - A Journal of Comparative Zoology, 250*(1), 80-85.

Foote, B. A. (1995). Biology of shore flies [Review]. *Annual Review of Entomology, 40*, 417-442.

Forster, G. (1777). *A Voyage Round the World, in His Britannic Majesty's Sloop, Resolution, Commanded by Capt. James Cook, During the Years 1772, 3, 4, and 5.* : B. White, J. Robson, P. Elmsly, & G. Robinson

Forsyth, D. M., Duncan, R. P., Bomford, M., & Moore, G. (2004). Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia [Review]. *Conservation Biology, 18*(2), 557-569.

Fox, K. J. (1973). Trans-oceanic dispersal of insects to New Zealand. *New Zealand Entomologist, 5*(3), 240-243.

Fraenkel, G. S. (1932). Die Wanderungen der Insekten. *Ergebnisse der Biologie, 0*, 1-238.

Frankham, R. (1997). Do island populations have less genetic variation than mainland populations? *Heredity, 78*, 311-327.

Fridriksson, S. (1989). The volcanic island of surtsey, iceland, a quarter-century after it rose from the sea [ ]. *Environmental Conservation, 16*(2), 157-162.

Fukami, T., Beaumont, H. J. E., Zhang, X. X., & Rainey, P. B. (2007). Immigration history controls diversification in experimental adaptive radiation [ ]. *Nature, 446*(7134), 436-439. doi:10.1038/nature05629

Funk, V. A. (2004). Revolutions in historical biogeography In M. V. Lomolino, D. F. Sax & J. H. Brown (Eds.), *Foundations of biogeography: classic papers with commentaries* (pp. 1291). Chicago: University of Chicago Press.

Gadow, H. F. (1913). *The Wanderings of Animals*. Cambridge, UK: Cambridge Univ. Press.

Gaina, C., Muller, R. D., Roest, W. R., & Symonds, P. (1998). The opening of the tasman Sea: a gravity anomaly animation. *Earth Interactions, 2*(4), 1-23.

Galloway, D. J. (1988). Plate-tectonics and the distribution of cool temperate southern-hemisphere macrolichens. *Botanical Journal of the Linnean Society, 96*(1), 45-55.

Garmendia, E., Gamboa, G., Franco, J., Garmendia, J. M., Liria, P., & Olazabal, M. (2010). Social multi-criteria evaluation as a decision support tool for integrated coastal zone management. *Ocean & Coastal Management, 53*(7), 385-403. doi:10.1016/j.ocecoaman.2010.05.001

Gaston, K. J., & Blackburn, T. M. (1996). Global Scale Macroecology: Interactions between Population Size, Geographic Range Size and Body Size in the Anseriformes. *Journal of Animal Ecology, 65*(6), 701-714.

Gaston, K. J., Jones, A. G., & Hanel, C. (2003). Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London series B-Biological sciences, 270*, 1091-1098.

Gaston, K. J., & Lawton, J. H. (1988). Patterns in body size, population dynamics, and regional distribution of bracken herbivores. *The American Naturalist, 132*(5), 662-680.

Gattolliat, J.-L., & Monaghan, M. T. (2010). DNA-based association of adults and larvae in Baetidae (Ephemeroptera) with the description of a new genus *Adnoptilum* in Madagascar. *Journal of the North American Benthological Society, 29*(3), 1042-1057.

Gheskiere, T., Vincx, M., Weslawski, J. M., Scapini, F., & Degraer, S. (2005). Meiofauna as descriptor of tourism-induced changes at sandy beaches. *Marine Environmental Research, 60*(2), 245-265.

Gibbs, G. (2008). *Ghosts of Gondwana*. Nelson: Craig Potton.

Gibbs, G. W. (1979). Some notes on the biology and status of the Mnesarchaeidae (Lepidoptera). *New Zealand Entomologist, 7*(1), 2-9.

Gibbs, M., & Van Dyck, H. (2010). Butterfly flight activity affects reproductive performance and longevity relative to landscape structure. *Oecologia, 163*(2), 341-350. doi:10.1007/s00442-010-1613-5

Gilbert, F. S. (1980). The Equilibrium Theory of Island Biogeography: Fact or Fiction? *Journal of Biogeography, 7*(3), 209-235.

Giller, P. S., Myers, A. A., & Riddle, B. R. (2004). Earth history, vicariance and dispersal. In M. V. Lomolino, D. F. Sax & J. H. Brown (Eds.), *Foundations of Biogeography: Classic Papers with Commentaries* (pp. 1291). Chicago: University of Chicago Press.

Gillespie, R. G., & Roderick, G. K. (2002). Arthropods on islands: colonization, speciation, and conservation. *Annual Review of Entomology, 47*, 595-632.

Gilpin, M. E., & Diamond, J. M. (1982). Factors contributing to non-randomness in species co-occurrences on islands. *Oecologia, 52*(1), 75-84.

Giribet, G., & Boyer, S. L. (2010). 'Moa's Ark' or 'Goodbye Gondwana': is the origin of New Zealand's terrestrial invertebrate fauna ancient,recent, or both? *Invertebrate systematics, 24*(1), 1-8.

Given, B. B. (1959). [List of Insects collected on Niue Island during February and March 1959].

Givnish, T. J., & Renner, S. S. (2004). Tropical intercontinental disjunctions: Gondwana breakup, immigration from the boreotropics, and transoceanic dispersal. *International Journal of Plant Sciences, 165*(4), S1-S6.

Global Biodiversity Information Facility. (2010, 14/09/2010). *Global Biodiversity Information Facility*. Retrieved from http://www.gbif.org/

Gobbeler, K., & Klussmann-Kolb, A. (2010). Out of Antarctica? - New insights into the phylogeny and biogeography of the Pleurobranchomorpha (Mollusca, Gastropoda). *Molecular Phylogenetics and Evolution, 55*(3), 996-1007. doi:10.1016/j.ympev.2009.11.027

Godfray, H. C. J., & Knapp, S. (2004). Introduction. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359*(1444), 559-569. doi:10.1098/rstb.2003.1457

Goldberg, J., Trewick, S. A., & Paterson, A. M. (2008). Evolution of New Zealand's terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society B-Biological Sciences, 363*(1508), 3319-3334. doi:10.1098/rstb.2008.0114

Goldstein, S. J., Gemmell, N. J., & Schiel, D. (2009). Colonisation and connectivity by intertidal limpets among New Zealand, Chatham and Sub-Antarctic Islands. I. Genetic connections. *Marine Ecology Progress Series, 388*, 111-119.

Goodman, M. (1992). Editorial. *Molecular Phylogenetics and Evolution, 1*(1), 1-2.

Google Maps. (2011). *Google Maps New Zealand*. Retrieved 3/5/2011, from http://maps.google.co.nz/

Gordon, D. (Ed.). (2011). *New Zealand Inventory of Biodiversity: Volume Two : Kingdom Animalia - Chaetognatha, Ecdysozoa, Ichnofossils*. Christchurch: Canterbury University Press.

Gotelli, N. J. (2004a). Assembly Rules. In M. V. Lomolino, D. F. Sax & B. Brown (Eds.), *Foundations of Biogeography: Classic Papers with Commentaries* (pp. 1027-1035). Chicago: University of Chicago press.

Gotelli, N. J. (2004b). A taxonomic wish list for community ecology. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359*(1444), 585-597. doi:10.1098/rstb.2003.1443

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of J. M. Diamond's assembly rules model. *Ecology, 83*(8), 2091-2096.

Gouy, M., Guidon, S., & Gasdcuel, O. (2010). SeaView version 4 : a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular Biology and Evolution 27*(2), 221-224

Grant, R. A., Griffiths, H. J., Steinke, D., Wadley, V., & Linse, K. (2011). Antarctic DNA barcoding; a drop in the ocean? [ ]. *Polar Biology, 34*(5), 775-780.

Greene, H. W. (2005). Organisms in nature as a central focus for biology. *Trends in Ecology & Evolution, 20*(1), 23-27.

Greenslade, P., Farrow, R. A., & Smith, J. M. B. (1999). Long distance migration of insects to a subantarctic island. *Journal of Biogeography, 26*(6), 1161-1167.

Grehan, J. R. (1994). Guest Editorial: The beginning and end of dispersal: the representation of `panbiogeography'. *Journal of Biogeography, 21*(5), 451-462.

Gressit, J. L. (1962). Insects of Macquarie Island introduction. *Pacific Insects, 4*(4), 905-915.

Gressit, J. L., & Yoshimoto, C. M. (1974). Insect dispersal studies in northern Alaska *Pacific Insects, 16*(1), 11-30.

Gruner, D. S., Gotelli, N. J., Price, J. P., & Cowie, R. H. (2008). Does species richness drive speciation? A reassessment with the Hawaiian biota. *Ecography, 31*(2), 279-285.

Grytnes, J. A., Birks, H. J. B., Heegaard, E., & Peglar, S. M. (2000). Geographical trends in the species-to-family ratio of vascular plants in Fennoscandia. *Norsk Geografisk Tidsskrift - Norwegian Journal of Geography, 54*(2), 60 - 64.

Guindon, S., & Gascuel, O. (2003). A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood [ ]. *Systematic Biology, 52*(5), 696-704. doi:10.1080/10635150390235520

Gutenberg, B. (1960). Low-Velocity Layers in the earth, ocean, and atmosphere. *Science, 131*(3405), 959-965. doi:10.1126/science.131.3405.959

Gutierrez, D., & Menendez, R. (1997). Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. *Journal of Biogeography, 24*(6), 903-914.

Haden, G. A., Blinn, D. W., Shannon, P., & Wilson, K. P. (1999). Driftwood: an alternative habitat for macroinvertebrates in a large desert river. *Hydrobiologia, 397*, 179-186.

Hajibabaei, M., Janzen, D. H., Burns, J. M., Hallwachs, W., & Hebert, P. D. N. (2006). DNA barcodes distinguish species of tropical Lepidoptera [ ]. *Proceedings of the National Academy of Sciences of the United States of America, 103*(4), 968-971.

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series, 41*, 95-98.

Hallam, A. (1967). The bearing of certain paleozoogeographic data on continental drift. In *Foundations of biogeography: classic papers with commentaries* (pp. 1291). Chicago: University of Chicago Press.

Hardy, A. C., & Cheng, L. (1986). Studies in the distribution of insects by aerial currents. III. Insect drift over the sea. *Ecological Entomology, 11*(3), 283-290.

Hardy, A. C., & Milne, P. S. (1938). Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites. *Journal of Animal Ecology, 7*(2), 199-229.

Hart, M. W., Abt, C. H. J., & Emlet, R. B. (2011). Molecular phylogeny of echinometrid sea urchins: more species of Heliocidaris with derived modes of reproduction. *Invertebrate Biology, 130*(2), 175-185.

Harvey, P. H. (1996). Phylogenies for ecologists. *Journal of Animal Ecology, 65*(3), 255-263.

Harvey, P. H., Read, A. F., & Nee, S. (1995). Why ecologists need to be phylogenetically challenged. *Journal of Ecology, 83*(3), 535-536.

Harwell, M. C., & Orth, R. J. (2002). Long-distance dispersal potential in a marine macrophyte. *Ecology, 83*(12), 3319-3330.

Hawes, T. C., Worland, M. R., Bale, J. S., & Convey, P. (2007). Rafting in Antarctic collembola. *Journal of Zoology*, 1-7.

Hawes, T. C., Worland, M. R., Convey, P., & Bale, J. S. (2007). Aerial dispersal of springtails on the Antarctic peninsula: implications for local distribution and demography. *Antarctic Science, 19*(01), 3-10. doi:doi:10.1017/S0954102007000028

Heads, M. (2009). Darwin's changing views on evolution: from centres of origin and telology to vicariance and incomplete lineage sorting *Journal of Biogeography, 36*(6), 1018-1026.

Hebert, P. D. N., Cywinska, A., Ball, S. L., & DeWaard, J. R. (2003). Biological identifications through DNA barcodes [ ]. *Proceedings of the Royal Society of London series B-Biological sciences, 270*(1512), 313-321.

Hebert, P. D. N., Stoeckle, M. Y., Zemlak, T. S., & Francis, C. M. (2004). Identification of birds through DNA barcodes. *Plos Biology, 2*(10), 1657-1663.

Hedley, C. (1893). The paleogeographical relations of Antarctica. *Proceedings of the Linnean Society of London, 124*, 80-90.

Heenan, P. B., Mitchell, A. D., de Lange, P. J., Keeling, J., & Paterson, A. M. (2010). Late-Cenozoic origin and diversification of Chatham Islands endemic plant species revealed by analyses of DNA sequence data. *New Zealand Journal of Botany, 48*(2), 83-136.

Hennig, W. (1966). *Phylogentic systematics*. Urbana: University of Illinois Press.

Heras, S., & Roldán, M. I. (2011). Phylogenetic inference in *Odontesthes* and *Atherina* (Teleostei: Atheriniformes) with insights into ecological adaptation. *Comptes Rendus Biologies, 334*(4), 273-281.

Herman, S. G. (2002). Wildlife biology and natural history: time for a reunion. *The Journal of Wildlife Management, 66*(4), 933-946.

Herzig, A. L. (1995). Effects of Population Density on Long-Distance Dispersal in the Goldenrod Beetle *Trirhabda virgata*. *Ecology, 76*(7), 2044-2054.

Hesp, P. A., Shepherd, M. J., & Parnell, K. (1999). Coastal geomorphology in New Zealand, 1989-99. *Progress in Physical Geography, 23*(4), 501-524.

Hilton, M., Macauley, U., & Henderson, R. (2000). *Inventory of New Zealand's active sand dunes.* (157). Wellington: Department of Conservation.

Hoberg, E. P., & Brooks, D. R. (2008). A macroevolutionary mosaic: episodic host-switching, geographical colonization and diversification in complex host–parasite systems. *Journal of Biogeography, 35*(9), 1533-1550. doi:10.1111/j.1365-2699.2008.01951.x

Holmes, W. B. K., & Anderson, H. M. (2005). The middle triassic megafossil flora of the Basin Creek formation, nymboida coal measures, New South Wales, Australia. Part 4. Umkomasiaceae, Dicroidium and affiliated fructificationse. *Proceedings of the Linnean Society of New South Wales, 126*, 1-37.

Holzapfel, E. P., Clagg, H. B., & Goff, M. L. (1978). Trapping of air-borne insects on ships on the Pacific, Part 9 [ ]. *Pacific Insects, 19*(1/2), 65-90.

Holzapfel, E. P., & Harrell, J. C. (1968). Transoceanic dispersal studies of insects. *Pacific Insects, 10*(1), 115-153.

Holzapfel, E. P., Tsuda, D. M., & Harrell, J. C. (1970). Trapping of air-borne insects in the Antarctic area (Part 3). *Pacific Insects, 12*(1), 133-156.

Hooker, J. D. (1844-1860). *The Botany of the Antarctic Voyage of HMS Discovery Ships "Erebus" and "Terror" in the Years 1839-1843, Under the Command of Captain Sir James Clark Ross*. London: Reeve Brothers.

Horn, H. S., Nathan, R., & Kaplan, S. R. (2001). Long-distance dispersal of tree seeds by wind. *Ecological Research, 16*(5), 877-885.

Horner, N. V. (1974). Annual Aerial Dispersal of Jumping Spiders in Oklahoma (Araneae, Salticidae). *Journal of Arachnology, 2*(2), 101-105.

Howe, M. A., Knight, G. T., & Clee, C. (2010). The importance of coastal sand dunes for terrestrial invertebrates in Wales and the UK, with particular reference to aculeate Hymenoptera (bees, wasps & ants). *Journal of Coastal Conservation, 14*, 91-102.

Hull, D. L. (1988). *Science as a process*. Chicago: University of Chicago Press.

Hung, G. C., Chilton, N. B., Beveridge, I., Zhu, X. Q., Lichtenfels, J. R., & Gasser, R. B. (1999). Molecular evidence for cryptic species within *Cylicostephanus minutus* (Nematoda : Strongylidae). *International Journal for Parasitology, 29*(2), 285-291.

Huntzinger, M., Karban, R., & Cushman, H. (2008). Negative effects of vertebrate herbivores on invertebrates in a coastal dune community. *Ecology, 89*(7), 1972-1980.

Hurley, M. (2002). *Multi-taxa biotic inventories of three unprotected forested ecosystems in Vietnam* Retrieved from http://cbc.amnh.org/vietnamresearch/viet_main.html

Hurr, K. A., Lockhart, P. J., Heenan, P. B., & Penny, D. (1999). Evidence for the Recent Dispersal of Sophora (Leguminosae) around the Southern Oceans: Molecular Data. *Journal of Biogeography, 26*(3), 565-577.

Hutcheson, J. (1992). Observations on the effects of volcanic activity on insects and their habitat on White Island. *New Zealand Entomologist, 15*, 72-76.

Hutton, F. W. (1896). Theoretical explanations of the distribution of Southern faunas *Proceedings of the Linnean Society of New South Wales, 21*(1), 36-47.

Inchausti, P. (1994). Reductionist Approaches in Community Ecology. *The American Naturalist, 143*(2), 201-221.

Inoue, M., & Endo, T. (2006). Spatiotemporal distribution and resource use of scoliid wasps (Hymenoptera) in coastal sand dunes [ ]. *Entomological Science, 9*(4), 359-371.

Irving, E. (1964). *Paleomagnetism and its application to geological and geophysical problems*. New York: John Wiley and Sons.

Isaac, N. J. B., Mallet, J., & Mace, G. M. (2004). Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology & Evolution, 19*(9), 464-469.

Jamieson, S. (2010). *Sand dune restoration in New Zealand: Methods, Motives, and Monitoring* (A thesis submitted for the partial fulfilment for the degree of Master of Science in Ecological Restoration). Victoria University of Wellington. School of Biological Sciences.

Jarvinen, O. (1982). Species-to-genus ratios in biogeography: a historical note. *Journal of Biogeography, 9*(4), 363-370.

Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., et al. (2007). Does size matter for dispersal distance? *Global Ecology and Biogeography, 16*(4), 415-425.

Jennings, D. T., & Hilburn, D. J. (1988). Spiders (Araneae) Captured in Malaise Traps in Spruce-Fir Forests of West-Central Maine. *Journal of Arachnology, 16*(1), 85-94.

Jiggins, C. D., & Mallet, J. (2000). Bimodal hybrid zones and speciation [ ]. *Trends in Ecology & Evolution, 15*(6), 250-255.

Jinbo, U., Kato, T., & Ito, M. (2011). Current progress in DNA barcoding and future implications for entomology [Review]. *Entomological Science, 14*(2), 107-124. doi:10.1111/j.1479-8298.2011.00449.x

Johansen, S., & Hytteborn, H. (2001). A contribution to the discussion of biota dispersal with drift ice and driftwood in the North Atlantic. *Journal of Biogeography, 28*(1), 105-115.

Johnson, N. (1992). *The Sand Dune and Beach Vegetation Inventory of New Zealand. II. South Island and Stewart Island* Christchurch: DSIR Land Resources.

Johnston, E. L., Piola, R. F., & Clark, G. F. (2009). The role of propoagule pressure in invasion success In G. Rilov & J. A. Crooks (Eds.), *Biological Invasions in marine ecosystems* (pp. 133-151). Berlin: Springer-Verlag.

Jones, T. C., & Parker, P. G. (2000). Costs and benefits of foraging associated with delayed dispersal in the spider *Anelosimus studiosus* (Araneae, Theridiidae). *Journal of Arachnology, 28*(1), 61-69.

Jordal, B. H., Sequeira, A. S., & Cognato, A. I. (2011). The age and phylogeny of wood boring weevils and the origin of subsociality. *Molecular Phylogenetics and Evolution, 59*(3), 708-724.

Juan, C., Emerson, B. C., Oromi, P., & Hewitt, G. M. (2000). Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands [Review]. *Trends in Ecology & Evolution, 15*(3), 104-109.

Juliano, S. A. (1983). Body size, dispersal ability, and range size in North American species of *Brachinus* (Coleoptera: Carabidae). *The Coleopterists Bulletin, 37*(3), 232-238.

Kadereit, J. W., Arafeh, R., Somogyi, G., & Westberg, E. (2005). Terrestrial growth and marine dispersal? Comparative phylogeography of five coastal plant species at a european scale. *Taxon, 54*(4), 861-876.

Kamgang, B., Brengues, C., Fontenille, D., Njiokou, F., Simard, F., & Paupy, C. (2011). Genetic structure of the tiger mosquito, *Aedes albopictus*, in Cameroon (Central Africa) [ ]. *Plos One, 6*(5), 10.

Keast, A. (1971). Continental drift and the evolution of the biota on southern continents. *The Quarterly Review of Biology, 46*(4), 335-378.

Kimura, M. (1980). A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences *Journal of Molecular Evolution, 16*(2), 111-120.

Kingston, N., & Waldren, S. (2003). The plant communities and environmental gradients of Pitcairn Island: the significance of invasive species and the need for conservation management. *Annals of Botany, 92*(1), 31-40. doi:10.1093/aob/mcg106

Knapp, M., Stockler, K., Havell, D., Delsuc, F., Sebastiani, F., & Lockhart, P. J. (2005). Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *Plos Biology, 3*(1), 38-43.

Knopp, T., Cano, J. M., Crochet, P. A., & Merila, J. (2007). Contrasting levels of variation in neutral and quantitative genetic loci on island populations of moor frogs (Rana arvalis). *Conservation Genetics, 8*, 45-56. doi:10.1007/s10592-006-9147-4

Kolar, C. S., & Lodge, D. M. (2001). Progress in invasion biology: predicting invaders [Review]. *Trends in Ecology & Evolution, 16*(4), 199-204.

Kolbe, J. J., Larson, A., Losos, J. B., & de Queiroz, K. (2008). Admixture determines genetic diversity and population differentiation in the biological invasion of a lizard species. *Biology Letters, 4*(4), 434-437.

Komatsu, T., Matsunaga, D., Mikami, A., Sagawa, T., Boisnier, E., Tatsukawa, K., et al. (2008). Abundance of drifting seaweeds in eastern East China Sea. *Journal of Applied Phycology, 20*(5), 801-809.

Konlechner, T. M., & Hilton, M. J. (2009). The potential for marine dispersal of *Ammophila arenaria* (Marram Grass) rhizome in New Zealand. *Journal of Coastal Research*, 434-437.

Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R. F., & Sanjayan, M. A. (1993). Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology, 7*(4), 796-808. doi:10.1046/j.1523-1739.1993.740796.x

Krug, A. Z., Jablonski, D., & Valentine, J. W. (2008). Species-genus ratios reflect a global history of diversification and range expansion in marine bivalves [ ]. *Proceedings of the Royal Society B-Biological Sciences, 275*(1639), 1117-1123. doi:10.1098/rspb.2007.1729

Kumar, S. (2005). Molecular clocks: four decades of evolution [Review]. *Nature Reviews Genetics, 6*(8), 654-662. doi:10.1038/nrg1659

Kuschel, G. (1975). Introduction. In G. Kuschel (Ed.), *Biogeography and Ecology in New Zealand* (pp. 507-535). The Hague: Dr. W. Junk.

Kuschel, G., & Emberson, R. M. (2008). Notes on *Hybolasius trigonellaris* Hutton from the Chatham Islands (Coleoptera: Cerambycidae: Lamiinae). *New Zealand Entomologist, 31*, 89-92.

La Cock, A., & Stanley, M. (2007). Beetles in sand dunes - spinifex or maram grass? . *Weta, 32*(1), 19-22.

Landcare Research. (2009). *Checklist of New Zealand Hymenoptera v7.0.* Retrieved 10/10/2010, from http://www.landcareresearch.co.nz/research/biosystematics/invertebrates/hymenoptera/2009/checklist_index_2009.asp

Landcare Research. (n.d.). *Pitfall traps*. Retrieved 17/10/2010, from http://www.landcareresearch.co.nz/research/biocons/invertebrates/idsurveillance/pitfall.asp

Landis, C. A., Campbell, H. J., Begg, J. G., Mildenhall, D. C., Paterson, A. M., & Trewick, S. A. (2008). The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora [Review]. *Geological Magazine, 145*(2), 173-197. doi:10.1017/s0016756807004268

Lariviere, M.-C. (2005 (and updates)). *Checklist of New Zealand Hemiptera (excluding Sternorrhyncha)* Retrieved from http://hemiptera.landcareresearch.co.nz/

Larrea-Alcazar, D., & Lopez, R. P. (2005). An estimation of the floristic richness of Bolivia's Andean dry valleys [ ]. *Biodiversity and Conservation, 14*(8), 1923-1927. doi:10.1007/s10531-004-2122-9

Lattin, J. D., & Oman, P. (1983). Where are the exotic insect threats? . In C. Graham & C. Wilson (Eds.), *Exotic PLant Pests and North American Agriculture* (pp. 93-137). New York: Academic Press.

Lawton, J. H., & Brown, K. C. (1986). The population and community ecology of invading insects. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 314*(1167), 607-617.

Lawver, L. A., & Gahagan, L. M. (2003). Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeography Palaeoclimatology Palaeoecology, 198*(1-2), 11-37. doi:10.1016/s0031-0182(03)00392-4

Leese, F., Agrawal, S., & Held, C. (2010). Long-distance island hopping without dispersal stages: transportation across major zoogeographic barriers in a Southern Ocean isopod. *Naturwissenschaften, 97*(6), 583-594. doi:10.1007/s00114-010-0674-y

Legendre, P., & Legendre, L. (2003). *Numerical Ecology*. Amsterdam: Elsevier Science B.V.

Leksono, A. S., Takada, K., Koji, S., Nakagoshi, N., Anggraeni, T., & Nakamura, K. (2005). Vertical and seasonal distribution of flying beetles in a suburban temperate deciduous forest collected by water pan trap. *Insect Science, 12*(3), 199-206. doi:10.1111/j.1005-295X.2005.00025.x

Leschen, R., Lawrence, J. F., Kuschel, G., Thorpe, S., & Wang, Q. (2003). Coleoptera genera of New Zealand. *New Zealand Entomologist, 26*, 15-18.

Liggins, L., Chapple, D. G., Daugherty, C. H., & Ritchie, P. A. (2008). Origin and post-colonization evolution of the Chatham Islands skink (*Oligosoma nigriplantare nigriplantare*). *Molecular Ecology, 17*(14), 3290-3305. doi:10.1111/j.1365-294X.2008.03832.x

Lindstrom, J., Kaila, L., & Niemela, P. (1994). Polyphagy and adult body size in geometrid moths. *Oecologia, 98*(2), 130-132.

Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2005). The role of propagule pressure in explaining species invasions *Trends in Ecology & Evolution, 20*(5), 223-228.

Lomolino, M. V., Sax, D. F., & Brown, J. H. (Eds.). (2004). *Foundations of Biogeography*. Chicago: University of Chicago Press.

Longwell, C. R. (1944). Some thoughts on the evidence for continental drift. *American Journal of Science and Arts, 242*(4), 218-231.

Losos, J. B., & Ricklefs, R. E. (2010). *The theory of island biogeography revisited*. Princeton: Princeton University press.

Lowe, A., Harris, S., & Ashton, P. (2004). *Ecological Genetics: Design, Analysis and Application*. Oxford: Blackwell Publishing Company.

MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution, 17*(4), 373-387.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogegraphy* Princeton: Princeton University Press.

Mace, G. M. (2004). The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359*(1444), 711-719.

Macfadyen, A. (1954). The Invertebrate Fauna of Jan Mayen Island (East Greenland). *Journal of Animal Ecology, 23*(2), 261-297.

MacFarlane, D. A. (1991). The species-genus relationship in Antillean bat communities. *Mammalia, 55*(3), 363-370. doi:10.1515/mamm.1991.55.3.363

MacFarlane, R. P. (1979). Notes on Insects of the Chatham Islands. *New Zealand Entomologist, 7*(1), 64-69.

MacFarlane, R. P. (2010). [Brighton sand dune summary update].

MacFarlane, R. P., Andrew, I. G., Sinclair, B. J., Harrison, R. A., Dugdale, J. S., Boothroyd, I. K. G., et al. (2000). *Checklist of New Zealand Diptera* Retrieved 20/09/2010, from http://www.ento.org.nz/diptera_checklist.htm

MacFarlane, R. P., Morales, C. F., & Craw, R. C. (1991). *Chatham Island Insect Survey* DSIR Plant protection.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: causes, epidemiology, global consequences, and control [Review]. *Ecological Applications, 10*(3), 689-710.

Maddison, W. P., & Maddison, D. R. (2001). *Mesquite: a modular system for evolutionary analysis. version 2.74.* Retrieved from http://mesquiteproject.org

Majka, C. G., Klimaszewski, J., & Lauff, R. F. (2008). The coastal rove beetles (Coleoptera, Staphylinidae) of Atlantic Canada: a survey and new records. *ZooKeys, 2*, 115-150

Malaise, R. (1937). A new insect-trap. *Entomologisk Tidskrift, 58*, 148-160.

Mallet, J. (1995). A species definition for the modern synthesis. *Trends in Ecology & Evolution, 10*(7), 294-299.

Mallet, J. (2010). Group selection and the development of the biological species concept. *Philosophical Transactions of the Royal Society B-Biological Sciences, 365*(1547), 1853-1863.

Mallet, J. (2011). *Species, species concepts and related topics*. Retrieved 14/6/2011, from http://www.ucl.ac.uk/taxome/jim/Sp/speconc.html

Markow, T. A., & Castrezana, S. (2000). Dispersal in cactophilic Drosophila. *Oikos, 89*(2), 378-386.

Marris, J. W. M. (2000). The beetle (Coleoptera) fauna of the Antipodes Islands, with comments on the impact of mice; and an annotated checklist of the insect and arachnid fauna. *Journal of the Royal Society of New Zealand, 30*(2), 169-195.

Marshall, D. C., Slon, K., Cooley, J. R., Hill, K. B. R., & Simon, C. (2008). Steady Plio-Pleistocene diversification and a 2-million-year sympatry threshold in a New Zealand cicada radiation [ ]. *Molecular Phylogenetics and Evolution, 48*(3), 1054-1066. doi:10.1016/j.ympev.2008.05.007

Marshall, W. A., & Chalmers, M. O. (1997). Airborne dispersal of antarctic terrestrial algae and cyanobacteria. *Ecography, 20*, 585-594.

Martin, J.-L., & Lepart, J. (1989). Impoverishment in the bird community of a Finnish archipelago: the role of island size, isolation and vegetation structure. *Journal of Biogeography, 16*(2), 159-172.

Martinsson, S., Kjærandsen, J., & Sundberg, P. (2011). Towards a molecular phylogeny of the fungus gnat genus *Boletina* (Diptera: Mycetophilidae). *Zoologica Scripta, 40*(3), 272-281. doi:10.1111/j.1463-6409.2011.00474.x

Mason, R. M., & Huber, J. T. (1993). Order Hymenoptera. In H. Goulet & J. T. Huber (Eds.), *Hymenoptera of the world: an identification guide to families.* (pp. vii + 668). Ottawa Canada: Research Branch, Agriculture Canada. Retrieved from <Go to ISI>://CABI:19950201323

May, R. M. (2004). Tomorrow's taxonomy: collecting new species in the field will remain the rate-limiting step. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359*(1444), 733-734.

Mayr, E. (1965). Classification and Phylogeny. *American Zoologist, 5*(1), 165-174.

Mayr, E. (2001). *What Evolution Is*. New York: Basic Books.

Mazon, M., & Bordera, S. (2008). Effectiveness of two sampling methods used for collecting Ichneumonidae (Hymenoptera) in the Cabañeros National Park (Spain). *European Journal of Entomology, 105*, 879-888.

McCarter, J., Boge, G., & Darlow, G. (2001). Essays on science and society: Safeguarding the world's natural treasures. *Science, 294*(5549), 2099-2101.

McCauley, S. J. (2010). Body size and social dominance influence breeding dispersal in male Pachydiplax longipennis (Odonata). *Ecological Entomology, 35*(3), 377-385. doi:10.1111/j.1365-2311.2010.01191.x

McCune, B., & Grace, J. B. (2002). *Analysis of ecological communities*. Glenden Beach: MjM Software Design.

McDowall, R. M. (2008). Process and Pattern in the Biogeography of New Zealand: A Global Microcosm? *Journal of Biogeography, 35*(2), 197-212.

McGaughran, A., Hogg, I. D., Stevens, M. I., Chadderton, W. L., & Winterbourn, M. J. (2006). Genetic divergence of three freshwater isopod species from southern New Zealand. *Journal of Biogeography, 33*, 23-30.

McGlone, M. S. (2005). Goodbye Gondwana. *Journal of Biogeography, 32*(5), 739-740.

McGuiness, C. A. (2001). *The Conservation Requirements of New Zealand's Nationally Threatened Invertebrates*. Wellington: Biodiversity Recovery Unit, Department of Conservation.

McKenna, M. C. (1972). Possible biological consequences of plate tectonics. *Bioscience, 22*(9), 519-525.

Meier, R., Shiyang, K., Vaidya, G., & Ng, P. K. L. (2006). DNA barcoding and taxonomy in diptera: A tale of high intraspecific variability and low identification success [ ]. *Systematic Biology, 55*(5), 715-728. doi:10.1080/10635150600969864

Metcalf, W. D. (1923). The dispersal of land animals. *Scientia (Bologna), 48*, 33-42.

Meyer, C. P., & Paulay, G. (2005). DNA barcoding: Error rates based on comprehensive sampling [ ]. *Plos Biology, 3*(12), 2229-2238. doi:e422 10.1371/journal.pbio.0030422

Meyer, J. R. (2009a). *Diptera*. Retrieved 24/4/2011, from http://www.cals.ncsu.edu/course/ent425/library/compendium/diptera.html

Meyer, J. R. (2009b). *Hymenoptera*. Retrieved 24/4/2011, from http://www.cals.ncsu.edu/course/ent425/library/compendium/hymenoptera.html

Miskelly, C. (2008). *Chatham Islands: heritage and conservation*. Christchurch, New Zealand: Canterbury University Press.

Modica, M. V., Bouchet, P., Cruaud, C., Utge, J., & Oliverio, M. (2011). Molecular phylogeny of the nutmeg shells (Neogastropoda, Cancellariidae). *Molecular Phylogenetics and Evolution, 59*(3), 685-697.

Monaghan, M. T., Wild, R., Elliot, M., Fujisawa, T., Balke, M., Inward, D. J., et al. (2009). Accelerated species inventory on Madagascar using coalescent-based models of species delineation. *Systematic Biology, 58*(3), 298-311. doi:10.1093/sysbio/syp027

Monsevieius, V. (2004). Comparison of three methods of sampling wild bees (Hymenoptera, Apoidea) in Èepkeliai Nature Reserve (South Lithuania). *Ekologija, 4*, 32-39.

Moorbath, S. (1985). The age of the Earth and the oldest rocks. *Geology Today, 1*(3), 75-79.

Moore, W. S. (1995). Inferring phylogenies from mtdna variation - mitochondrial-gene trees versus nuclear-gene trees. *Evolution, 49*(4), 718-726.

Moreton, B. D. (1945). On the migration of flea beetles (*Phyllotreta* spp.) (Col., Chrysomelide) attacking Brassica Crops. *Entomologist's Monthly Magazine, 81*(970), 59-60.

Morgan, G. J. (1998). Emile Zuckerkandl, Linus Pauling, and the molecular evolutionary clock, 1959-1965 [Proceedings Paper]. *Journal of the History of Biology, 31*(2), 155-178.

Morrison, L. W. (2010). Disequilibrial island turnover dynamics: a 17-year record of Bahamian ants [ ]. *Journal of Biogeography, 37*(11), 2148-2157. doi:10.1111/j.1365-2699.2010.02365.x

Morrone, J. J. (1998). On Udvardy's Insulantarctica province: a test from the weevils (Coleoptera: Curculionoidea). *Journal of Biogeography, 25*, 947-955.

Morrone, J. J., & Crisci, J. V. (1995). Biogeography: introduction to Methods. *Annual Review of Ecology and Systematics, 26*, 373-401.

Mortimer, N. (2004). New Zealand's geological foundations [Proceedings Paper]. *Gondwana Research, 7*(1), 261-272.

Munoz, J., Felicisimo, A. M., Cabezas, F., Burgaz, A. R., & Martinez, I. (2004). Wind as a long-distance dispersal vehicle in the Southern Hemisphere [ ]. *Science, 304*(5674), 1144-1147.

Murata, K., Tsuchiya, M., & Hiroaki, M. (2007). Study on airborne insects and insect fauna of Pacific Islands - Possibility of insect dispersal or migration in the Pacific Ocean. *Japanese journal of entomology: (New Series), 10*(4), 75-87.

Murray, A. (1866). *The Geographical Distribution of Mammals*. London: Day & Son.

Nathan, R. (2001). The challenges of studying dispersal. *Trends in Ecology & Evolution, 16*(9), 481-483.

Nathan, R. (2005). Long-distance dispersal research: building a network of yellow brick roads. *Diversity and Distributions, 11*(2), 125-130.

Nathan, R., Katul, G. G., Horn, H. S., Thomas, S. M., Oren, R., Avissar, R., et al. (2002). Mechanisms of long-distance dispersal of seeds by wind. *Nature, 418*(6896), 409-413. doi:10.1038/nature00844

Nelson, G. (1974). Historical biogeography: an alternative formalization. *Systematic Zoology, 23*(4), 555-558.

Nelson, G., & Platnick, N. I. (1980). A vicariance approach to historical biogeography. *Bioscience, 30*(5), 339-343.

Network, N. H. (2007, 13/09/2010). *The Natural History Initiative: From Decline to Rebirth*. Retrieved from www.naturalhistorynetwork.org/articles/esa2010.pdf

New, T. R. (2008). Insect conservation in early succession on islands: lessons from Surtsey, Iceland, and the Krakatau Archipelago, Indonesia. *Journal of Insect Conservation, 12*(3-4), 307-312. doi:10.1007/s10841-008-9155-4

Nieminen, M., Rita, H., & Uuvana, P. (1999). Body size and migration rate in moths. *Ecography, 22*(6), 697-707.

Nikula, R., Fraser, C. I., Spencer, H. G., & Waters, J. M. (2010). Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. *Marine Ecology-Progress Series, 405*, 221-230. doi:10.3354/meps08523

NIST/SEMATECH. (2003). *e-Handbook of Statistical Methods*. Retrieved from http://www.itl.nist.gov/div898/handbook/prc/section4/prc474.htm

NIWA. (2008). *Climate Data and Activities*. Retrieved from http://www.niwa.co.nz/education-and-training/schools/resources/climate

NIWA. (2011). *Mean Monthly Wet Days*. Retrieved from http://www.niwa.co.nz/education-and-training/schools/resources/climate/wetdays

Noonan, B. P., & Chippindale, P. T. (2006). Dispersal and vicariance: The complex evolutionary history of boid snakes *Molecular Phylogenetics and Evolution, 40*, 347-358.

Nordstrom, K. F., Gamper, U., Fontolan, G., Bezzi, A., & Jackson, N. L. (2009). Characteristics of coastal dune topography and vegetation in environments recently modified using beach fill and vegetation plantings, Veneto, Italy. *Environmental Management, 44*(6), 1121-1135.

Norman, R. (1581). *The Newe Attractive*. London

Novotny, V., Basset, Y., Miller, S. E., Kitching, R. L., Laidlaw, M., Drozd, P., et al. (2004). Local Species Richness of Leaf-Chewing Insects Feeding on Woody Plants from One Hectare of a Lowland Rainforest. *Conservation Biology, 18*(1), 227-237.

NZ Meteorological Service. (2011). Retrieved from http://www.metservice.com/learning/nz-climate

NZOR. (2010). *New Zealand Organism Register*. Retrieved from http://www.nzor.org.nz/Home

O'Malley, M. A. (2008). 'Everything is everywhere: but the environment selects': ubiquitous distribution and ecological determinism in microbial biogeography. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences, 39*(3), 314-325.

Oliveira, F. S., Mendonca, M. W. A., Vidigal, M. C. S., Rego, M. M. C., & Albuquerque, P. M. C. (2010). Community of bees (Hymenoptera, Apoidea) in the coastal sand dunes at Panaquatira beach, Sao Jose de Ribamar, Maranhao, Brazil [ ]. *Revista Brasileira De Entomologia, 54*(1), 82-90.

Ortmann, A. E. (1901). The theories of the origin of the Antarctic faunas and floras. *The American Naturalist, 35*(410), 139-142.

Ortmann, A. E. (1910). Tertiary Archhelenis. *The American Naturalist, 44*(520), 237-242.

Ozanne, C. M. P. (2005). Sampling methods for forest understorey vegetation In S. R. Leather (Ed.), *Insect Sampling in Forest Ecosystems* (pp. 58-76). Malden: Mass: Blackwell Publishing.

Padial, J. M., Miralles, A., De la Riva, I., & Vences, M. (2010). The integrative future of taxonomy [ ]. *Frontiers in Zoology, 7*, 14.

Papadopoulou, A., Bergsten, J., Fujisawa, T., Monaghan, M. T., Barraclough, T. G., & Vogler, A. P. (2008). Speciation and DNA barcodes: testing the effects of dispersal on the formation of discrete sequence clusters [ ]. *Philosophical Transactions of the Royal Society B-Biological Sciences, 363*(1506), 2987-2996. doi:10.1098/rstb.2008.0066

Park, D. S., Foottit, R., Maw, E., & Hebert, P. D. N. (2011). Barcoding bugs: DNA-based identification of the true bugs (Insecta: Hemiptera: Heteroptera) [ ]. *Plos One, 6*(4), 9.

Parker, P. E., Bock, C. H., Cook, A. Z., & Gottwald, T. R. (2008). Dispersal of *Xanthomonas citri* subsp *citri* bacteria downwind from harvested, infected fruit. *Phytopathology, 98*(6), S121-S121.

Partridge, T. R. (1992). The sand dune and beach vegetation inventory of New Zealand. I. North Island

Pathak, S. C., Kulshrestha, V., Choubey, A. K., & Parulekar, A. H. (1999). Insect drift over the northern Arabian sea in early summer [ ]. *Journal of Biosciences, 24*(2), 233-240.

Patrick, B. H. (1994). *The importance of invertebrate biodiversity: an Otago conservancy review* (53). Wellington: Department of Conservation

Peck, S. B. (1994a). Aerial dispersal of insects between and to islands in the Galapagos archipelago, Ecuador. *Annals of the Entomological Society of America, 87*, 218-224.

Peck, S. B. (1994b). Sea-surface (pleuston) transport of insects between islands in the Galapagos archipelago, Ecuador. *Annals of the Entomological Society of America, 87*, 576-582.

Peck, S. B. (2005). *The beetles of the Galapagos Archipelago, Ecuador; evolution, ecology, and diversity (Insecta: Coleoptera).* Ottawa, Canada: National Research Council Press.

Penev, L., Erwin, T., Thompson, F. C., Sues, H.-D., Engel, M. S., Agosti, D., et al. (2008). ZooKeys, unlocking earth's incredible biodiversity and building a sustainable bridge into the public domain: From "print-based" to "web-based" taxonomy, systematics, and natural history. . *ZooKeys, 1*(1-7).

Perner, J., & Schueler, S. (2004). Estimating the density of ground-dwelling arthropods with pitfall traps using a nested-cross array. *Journal of Animal Ecology, 73*(3), 469-477.

Peyrat, J., Braun, M., Dolnik, C., Isermann, M., & Roweck, H. (2009). Vegetation dynamics on the eba bar - Poland: a comparison of the vegetation in 1932 and 2006 with special regard to endangered habitats. *Journal of Coastal Conservation, 13*(4), 235-246.

Pidwirney, M. (2006). *"Introduction to the Oceans". Fundimentals of Physical Geography, 2nd Edition*. Retrieved from http://www.physicalgeography.net/fundamentals/8o.html

Pimm, S. L. (1989). Theories of predicting success and impact of introduced species. In J. M. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson (Eds.), *Biological Invasions: A Global Perspective*. New York: John Wiley & Sons Ltd.

Pimm, S. L. (1991). *The Balance of Nature? Ecological issues in the conseravtion and of species and communities*. Chicago: University of Chicago Press.

Platnick, N. I. (1976a). Concepts of dispersal in historical biogeography. *Systematic Zoology, 25*(3), 294-295.

Platnick, N. I. (1976b). Drifting spiders or continents?: vicariance biogeography of the spider subfamily Laroniinae (Araneae: Gnaphosidae). *Systematic Zoology, 25*(2), 101-109.

Platnick, N. I., & Nelson, G. (1978). A method of analysis for historical biogeography. *Systematic Zoology, 27*(1), 1-16.

Poethke, H. J., Weisser, W. W., & Hovestadt, T. (2010). Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. *American Naturalist, 175*(5), 577-586. doi:10.1086/651595

Polaszek, A. (2005). A universal register for animal names. *Nature, 437*, 477.

Pons, J., Barraclough, T. G., Gomez-Zurita, J., Cardoso, A., Duran, D. P., Hazell, S., et al. (2006). Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Systematic Biology, 55*(4), 595-609.

Pons, J., Fujisawa, T., Claridge, E. M., Savill, R. A., Barraclough, T. G., & Vogler, A. P. (2011). Deep mtDNA subdivision within Linnean species in an endemic radiation of tiger beetles from New Zealand (genus Neocicindela) [ ]. *Molecular Phylogenetics and Evolution, 59*(2), 251-262. doi:10.1016/j.ympev.2011.02.013

Porter, S. D. (2010). Distribution of the Formosa strain of the fire ant decapitating fly *Pseudacteon Curvatus* (Diptera: Phoridae) three and a half years after releases in North Florida. *Florida Entomologist, 93*(1), 107-112.

Preston, F. W. (1962a). The canonical distribution of commonness and rarity: Part I. *Ecology, 43*(2), 185-215.

Preston, F. W. (1962b). The canonical distribution of commonness and rarity: Part II. *Ecology, 43*(3), 410-432.

Price, J., & Clague, D. A. (2002). How old is the Hawaiian biota? Geology and phylogeny suggest divergence. *Proceedings of the Royal Society of London series B-Biological sciences, 269*(1508), 2429-2435.

Prider, J. N., Facelli, J. M., & Watling, J. R. (2011). Multispecies interactions among a plant parasite, a pollinator and a seed predator affect the reproductive output of an invasive plant, Cytisus scoparius. *Austral Ecology, 36*(2), 167-175.

Putten, W. H. v. d., Yeates, G. W., Duyts, H., Reis, C. S., & Karssen, G. (2005). Invasive plants and their escape from root herbivory: a worldwide comparison of the root-feeding nematode communities of the dune grass Ammophila arenaria in natural and introduced ranges. *Biological Invasions, 7*(4), 733-746. doi:10.1007/s10530-004-1196-3

Quan, X., & Zhou, S. L. (2011). Molecular identification of species in *Prunus* sect. Persica (Rosaceae), with emphasis on evaluation of candidate barcodes for plants. *Journal of Systematics and Evolution, 49*(2), 138-145.

Quinn, A. W., Jaffe, H. W., Smith, W. L., & Waring, C. L. (1957). Lead-alpha ages of Rhode Island granitic rocks compared to their geologic ages *American Journal of Science, 255*, 547-560.

Quispel, A. (1998). Lourens G. M. Baas Becking (1895–1963), Inspiraton for many (micro)biologists. *International Microbiology, 1*, 69-72.

R Development Core Team. (2010). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from URL http://www.R-project.org.

Rainio, J., & Niemela, J. (2003). Ground beetles (Coleoptera : Carabidae) as bioindicators. *Biodiversity and Conservation, 12*(3), 487-506.

Raven, P. H. (1973). Evolution of the subalpine and alpine plant groups in New Zealand *New Zealand Journal of Botany, 11*, 177-200.

Read, D. W. (1975). Primate phylogeny, neutral mutations, and "molecular clocks". *Systematic Zoology, 24*(2), 209-221.

Reaka, M. L. (1980). Geographic range, life history patterns, and body size in a guild of coral-dwelling mantis shrimps. *Evolution, 34*(5), 1019-1030.

Riddle, B. R. (2005). Is biogeography emerging from its identity crisis? *Journal of Biogeography, 32*(2), 185-186.

Ridley, H. N. (1930). *The Dispersal of Plants Throughout the World*. London: Day & Son.

Roff, D. (1977). Dispersal in Dipterans: Its Costs and Consequences. *Journal of Animal Ecology, 46*(2), 443-456.

Rosen, B. R. (1984). Reef coral biogeography and climate through the late cenozoic: just islands in the sun or a critical pattern of islands? In P. J. Brenchley (Ed.), *Fossils and Climate*. Chichester: John Wiley & Sons.

Rosen, D. E. (1975). A vicariance model of caribbean biogeography. *Systematic Zoology, 24*(4), 431-464.

Rosen, E., & Buth, G. (1980). Empirical Evolutionary Research Versus Neo-Darwinian Speculation. *Systematic Zoology, 29*(3), 300-308.

Rutherford, E., & Soddy, F. (1902). The cause and nature of radioactivity. *Philosophical Magazine, 4*, 370-396.

Saether, B. E. (1988). Pattern of covariation between life-history traits of european birds. *Nature, 331*(6157), 616-617.

Sanmartin, I., & Ronquist, F. (2004). Southern Hemisphere biogeography inferred by event-based models: Plant versus animal patterns. *Systematic Biology, 53*(2), 216-243. doi:10.1080/10635150490423430

Sanmartín, I., Wanntorp, L., & Winkworth, R. C. (2007). West Wind Drift revisited: testing for directional dispersal in the Southern Hemisphere using event-based tree fitting. *Journal of Biogeography, 34*(3), 398-416.

Sarkar, I., Schenk, R., & Norton, C. (2008). Exploring historical trends using taxonomic name metadata. *BMC Evolutionary Biology, 8*(1), 144.

Sax, D. F., & Brown, J. H. (2000). The paradox of invasion [ ]. *Global Ecology and Biogeography, 9*(5), 363-371.

Scapini, F., & Ciampi, G. (Eds.). (2010). *Mediterranean Coastal Areas at Risk Between Conservation and Development*. Dordrecht: Springer Netherlands. doi:10.1007/978-90-481-8854-3_1

Scharff, R. F. (1907). *European Animals: Their Geological History and Geographical Distribution.* London: Archibald Constable & Co. .

Scharff, R. F. (1909). On the evidence of a former land-bridge between northern Europe and North America. *Royal Irish Academy. Proceedings, Section B, 28*(No 1), 28.

Schuchert, C. (1932). Gondwana land bridges. *Bulletin of the Geological Society of America, 43*(4), 875-915.

Scotese, C. R. (2002). *PALEOMAP Project*. Retrieved 21/5/2010, from http://www.scotese.com/earth.htm

Seddon, J. M., & Baverstock, P. R. (1999). Variation on islands: major histocompatibility complex (Mhc) polymorphism in populations of the Australian bush rat. *Molecular Ecology, 8*(12), 2071-2079.

Shaw, K. L. (2002). Conflict between nuclear and mitochondrial DNA phylogenies of a recent species radiation: What mtDNA reveals and conceals about modes of speciation in Hawaiian crickets. *Proceedings of the National Academy of Sciences of the United States of America, 99*(25), 16122-16127.

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions [Editorial Material]. *Trends in Ecology & Evolution, 17*(4), 170-176.

Shepherd, L. D., de Lange, P. J., & Perrie, L. R. (2009). Multiple colonizations of a remote oceanic archipelago by one species: how common is long-distance dispersal? *Journal of Biogeography, 36*(10), 1972-1977. doi:10.1111/j.1365-2699.2009.02120.x

Simberloff, D. S. (1970). Taxonomic diversity of island biotas. *Evolution, 24*(1), 23-47.

Simberloff, D. S. (1989). Which insects introductions succeed and which fail? In J. M. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson (Eds.), *Biological Invasions: A Global perspective*. New York: John Wiley & Sons.

Simberloff, D. S., & Wilson, E. O. (1969a). Experimental zoogeography of islands: The colonization of empty islands *Ecology, 50*(2), 278-296.

Simberloff, D. S., & Wilson, E. O. (1969b). Experimental Zoogeography of Islands: The Colonization of Empty Islands. *Ecology, 50*(2), 278-296.

Simberloff, D. S., & Wilson, E. O. (1970). Experimental zoogeography of islands. a two-year record of colonization. *Ecology, 51*(5), 934-937.

Simpson, G. G. (1943). Mammals and land bridges. *Journal of the Washington Academy of Sciences, 30*(4), 137-163.

Simpson, G. G. (1946). Tertiary land bridges. *Transactions of the New York Academy of Sciences, 8*(8), 255-258.

Simpson, G. G. (1980). *Splendid isolation-the curious history of South American mammals* New Haven: Yale University Press.

Singh, B., Kurahashi, H., & Wells, J. D. (2011). Molecular phylogeny of the blowfly genus *Chrysomya*. *Medical and Veterinary Entomology, 25*(2), 126-134.

Smissen, R. D., & Heenan, P. B. (2010). A taxonomic appraisal of the Chatham Islands flax (*Phormium tenax*) using morphological and DNA fingerprint data. *Australian Systematic Botany, 23*(5), 371-380.

Smith, M. A., Woodley, N. E., Janzen, D. H., Hallwachs, W., & Hebert, P. D. N. (2006). DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera : Tachinidae). *Proceedings of the National Academy of Sciences of the United States of America, 103*(10), 3657-3662.

Smith, S. D. A. (2002). Kelp rafts in the Southern Ocean. *Global Ecology and Biogeography, 11*(1), 67-69.

Smith, S. D. A., & Simpson, R. D. (2002). Spatial variation in the community structure of intertidal habitats at Macquarie Island (sub-Antarctic). *Antarctic Science, 14*(04), 374-384. doi:doi:10.1017/S0954102002000160

Sneath, P. H., & Sokal, R. R. (1963). *Numerical taxonomy: the principles and practise of numerical classification*. San Francisco: Freeman.

Sol, D. (2007). Do successful invaders exist? Pre-adaptions to novel environments in terestrial vertebrates In W. Nentwig (Ed.), *Biological Invasions*. Berlin: Springer-Verlag.

Sparks, J. S., & Smith, W. L. (2005). Freshwater fishes, dispersal ability, and nonevidence: "Gondwana life rafts" to the rescue. *Systematic Biology, 54*(1), 158-165.

Species 2000. (2010). *Species 2000*. Retrieved from http://www.sp2000.org/index.php

Spengler, A., Hartmann, P., Buchori, D., & Schulze, C. H. (2011). How island size and isolation affect bee and wasp ensembles on small tropical islands: a case study from Kepulauan Seribu, Indonesia [ ]. *Journal of Biogeography, 38*(2), 247-258. doi:10.1111/j.1365-2699.2010.02395.x

Stevens, G. (1980). *New Zealand adrift: The theory of continental drift in a New Zealand setting*. Wellington: A.H & A.W Reed Ltd.

Stevens, G. (1985). *Lands in Collision: Discovering New Zealand's Past Geography*. Wellington: Science Information Publishing Centre.

Stewart, K. W., & Schlichting, H. E., Jr. (1966). Dispersal of algae and protozoa by selected aquatic insects. *Journal of Ecology, 54*(3), 551-562.

Susic, G. (1994). Scientific island research - based on the theory of biogeography *Drustvena Istrazivanja, 3*(4-5), 369-379.

Sykes, M. T., & Wilson, J. B. (1991). Vegetation of a Coastal Sand Dune System in Southern New Zealand. *Journal of Vegetation Science, 2*(4), 531-538.

Syphard, A. D., & Franklin, J. (2010). Species traits affect the performance of species distribution models for plants in southern California. *Journal of Vegetation Science, 21*(1), 177-189.

Thiel, M., & Gutow, L. (2005). The ecology of rafting in the marine environment - I - The floating substrata. In *Oceanography and Marine Biology: An Annual Review* (Vol. 42, pp. 181-263). Boca Raton: Crc Press-Taylor & Francis Group.

Thiel, M., & Haye, P. A. (2006). The ecology of rafting in the marine environment. III. Biogeographical and evolutionary consequences. In *Oceanography and Marine Biology - an Annual Review* (Vol. 44, pp. 323-429). Boca Raton: Crc Press-Taylor & Francis Group.

Thornton, I. W. B. (1984). Krakatau - the development and repair of a tropical ecosystem. *Ambio, 13*(4), 217-225.

Thornton, I. W. B. (2001). Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. I. General introduction. *Journal of Biogeography, 28*(11-12), 1299-1310.

Timm, C., Hoernle, K., Werner, R., Folkmar, H., van den Bogaard, P., White, J., et al. (2010). Temporal and geochemical evolution of the Cenozoic intraplate volcanism of Zealandia. *Earth Science Reviews, 98*(1), 38-64.

Tomlinson, A. I. (1973). Metorological aspects of trans-tasman insect dispersal. *New Zealand Entomologist, 5*(3), 253-268.

Tonnoir, A. L., & Edwards, F. W. (1927). New Zealand fungus gnats (Diptera: Mycetophilidae). *Transactions and Proceedings of the New Zealand Institute, 57*, 747-878.

Torres, W., Mendez, M., Dorantes, A., & Duran, R. (2010). Structure, composition and diversity of coastal sand dune scrub of Yucatan. *Boletin De La Sociedad Botanica De Mexico, 86*, 37-51.

Trewick, S. A. (2000). Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *Journal of Biogeography, 27*(5), 1189-1200.

Trewick, S. A., Goldberg, J., & Morgan-Richards, M. (2005). Fewer species of *Argosarchus* and *Clitarchus* stick insects (Phasmida, Phasmatinae): evidence from nuclear and mitochondrial DNA sequence data. *Zoologica Scripta, 34*(5), 483-491.

Trewick, S. A., Paterson, A. M., & Campbell, H. J. (2007). Hello New Zealand. *Journal of Biogeography, 34*(1), 1-6.

Trombulak, S. C., & Fleischner, T. L. (2007). Natural history renaissance. *Journal of Natural History Education, 1*(1), 1-4.

Tronstad, L. M., Tronstad, B. P., & Benke, A. C. (2007). Aerial colonization and growth: rapid invertebrate responses to temporary aquatic habitats in a river floodplain. *Journal of the North American Benthological Society, 26*(3), 460-471.

Udvardy, M. D. F. (1975). *A classification of the biogeographical provinces of the world* (18). Morges: Switzerland: IUCN.

United Nations Environment Programme. (2010). *Conservation of Biological Diversity*. Retrieved 21/3/2011, from http://www.unep.org/documents.multilingual/default.asp?DocumentID=52&ArticleID=63&l=en

Vagvolgyi, J. (1975). Body size, aerial dispersal, and origin of the Pacific land snail fauna. *Systematic Zoology, 24*(4), 465-488.

Valentine, J. W. (1970). How many marine invertebrate fossil species? A new approximation. *Journal of Paleontology, 44*(3), 410-415.

Vandendriessche, S., De Keersmaecker, G., Vincx, M., & Degraer, S. (2006). Food and habitat choice in floating seaweed clumps: the obligate opportunistic nature of the associated macrofauna. *Marine Biology, 149*(6), 1499-1507. doi:10.1007/s00227-006-0292-6

Vandendriessche, S., Vincx, M., & Degraer, S. (2007). Floating seaweed and the influences of temperature, grazing and clump size on raft longevity - A microcosm study. *Journal of Experimental Marine Biology and Ecology, 343*(1), 64-73.

Veith, M., Schmidtler, F., Kosuch, J., & Sietz, A. (2003). Palaeoclimatic changes explain Anatolian mountain frog evolution: a test for alternating vicariance and dispersal events. *Molecular Ecology, 12*, 185-199.

Vervoort, A., Cawoy, V., & Jacquemart, A. L. (2011). Comparative reproductive biology in co-occurring invasive and native Impatiens species. *International Journal of Plant Sciences, 172*(3), 366-377.

Vine, F. J. (1966). Spreading of the ocean floor: new evidence. *Science, 154*(3755), 1405-1415. doi:10.1126/science.154.3755.1405

Vinogradov, V. G., & Kamennova, I. E. (2004). Wetland inventory activities in Russia - a review and required action*Wetlands International.* Symposium conducted at the meeting of the 5th European Regional Meeting on the implementation and effectiveness of the Ramsar Convention, Yerevan, Armenia.

Vogwill, T., Fenton, A., & Brockhurst, M. A. (2008). The impact of parasite dispersal on antagonistic host-parasite coevolution. *Journal of Evolutionary Biology, 21*(5), 1252-1258. doi:10.1111/j.1420-9101.2008.01574.x

Vuataz, L., Sartori, M., Wagner, A., & Monaghan, M. T. (2011). Toward a DNA taxonomy of Alpine Rhithrogena (Ephemeroptera: Heptageniidae) using a Mixed Yule-Coalescent analysis of mitochondrial and nuclear DNA. *Plos One, 6*(5). doi:10.1371/journal.pone.0019728

Wagstaff, S. J., Bayly, M. J., Garnock-Jones, P. J., & Albach, D. C. (2002). Classification, origin, and diversification of the New Zealand hebes (Scrophulariaceae). *Annals of the Missouri Botanical Garden, 89*(1), 38-63.

Wallace, A. R. (1855). On the law which has regulated the introduction of new species. *Annals and Magazine of Natural History, 16*(2), 184-196.

Wallace, A. R. (1859). Letter from Mr. Wallace concerning the geographical distribution of birds. *Ibis, 4*(1), 449-454.

Wallace, A. R. (1881). *Island Life*. New York: Harper and Brothers.

Walton, C., Butlin, R. K., & Monk, K. A. (1997). A phylogeny for grasshoppers of the genus *Chitaura* (Orthoptera: Acrididae) from Sulawesi, Indonesia, based on mitochondrial DNA sequence data. *Biological Journal of the Linnean Society, 62*(3), 365-382.

Waters, J. M. (2008). Driven by the West Wind Drift? A synthesis of southern temperate marine biogeography, with new directions for dispersalism. *Journal of Biogeography, 35*(3), 417-427.

Watt, J. C. (1975). The terrestrial insects. In G. Kuschel (Ed.), *Biogeography and Ecology in New Zealand* (pp. 507-535). The Hague: Dr. W. Junk.

Watt, J. C. (1976). A biological survey in New Zealand? *The New Zealand Entomologist, 6*(2), 143.

Weese, D. J., Schwartz, A. K., Bentzen, P., Hendry, A. P., & Kinnison, M. T. (2011). Eco-evolutionary effects on population recovery following catastrophic disturbance. *Evolutionary Applications, 4*(2), 354-366.

Wegener, A. (1912). "Die Entstehung der Kontinente" (in German). *International Journal of Earth Science, 3*(4), 276.

Wegener, A. (1915). *Die Entstehung der Kontinente und Ozeane*. London: Metheun & Co.

Weiher, E., & Keddy, P. (1999). *Ecological Assembley Rules: Perspectives, Advances, Retreats.* Cambridge: Cambridge University Press.

Westberg, E., & Kadereit, J. W. (2009). The influence of sea currents, past disruption of gene flow and species biology on the phylogeographical structure of coastal flowering plants. *Journal of Biogeography, 36*(7), 1398-1410.

Wheeler, Q. D., Raven, P. H., & Wilson, E. O. (2004). Taxonomy: Impediment or expedient? *Science, 303*(5656), 285-285.

Wheeler, W. M. (1916). Ants carried in a floating log from the Brazilian mainland to San Sebastian island. *Psyche, 23*(6), 180-183.

White, M. E. (1999). *Reading the Rocks*. East Roseville: Kangaroo Press.

Whittaker, R. J. (2004). The Importance of Islands. In M. V. Lomolino, D. F. Sax & J. H. Brown (Eds.), *Foundations of biogeography: classic papers with commentaries* (pp. 1291). Chicago: University of Chicago Press.

Whittaker, R. J., Bush, M. B., & Richards, K. (1989). Plant Recolonization and Vegetation Succession on the Krakatau Islands, Indonesia. *Ecological Monographs, 59*(2), 59-123.

Whittaker, R. J., & Fernandez-Palacios, J. M. (2007). *Island Biogeography* (2nd ed.). New York: Oxford University Press.

Whittaker, R. J., Triantis, K. A., & Ladle, R. J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography, 35*, 977-994.

Wiemers, M., & Fiedler, K. (2007). Does the DNA barcoding gap exist? - a case study in blue butterflies (Lepidoptera: Lycaenidae). *Frontiers in Zoology, 4*, 8.

Wiklund, C. G. (1996). Body length and wing length provide univariate estimates of overall body size in the merlin. *The Condor, 98*(3), 581-588.

Wilder, B. T., & Felger, R. S. (2010). Dwarf giants, guano, and isolation: vegetation and floristic diversity of San Pedro Mártir Island, Gulf of California, Mexico. *Prodeedings of the San Diego Society of Natural History, 42*, 24.

Williams, C. B. (1947). The generic relations of species in small ecological communities. *Journal of Animal Ecology, 16*(1), 11-18.

Williamson, M. (1981). *Island Populations* Oxford: Oxford University Press.

Williamson, M. (1989). Mathematical model of invasion. In J. M. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek & M. Williamson (Eds.), *Biological Invasions: A global perspective*. New York: John Wiley & Sons.

Wilson, E. O. (1959). Adaptive Shift and Dispersal in a Tropical Ant Fauna. *Evolution, 13*(1), 122-144.

Wilson, E. O. (2003). The encyclopedia of life. *Trends in Ecology & Evolution, 18*(2), 77-80.

Wilson, E. O. (2004). Taxonomy as a fundamental discipline. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359*(1444), 739. doi:10.1098/rstb.2003.1440

Wilson, E. O., & Simberloff, D. S. (1969). Experimental Zoogeography of Islands: Defaunation and Monitoring Techniques. *Ecology, 50*(2), 267-278.

Wilson, F. (1960). *A Review of the Biological Control of Insects and Weeds in Australia and Australian New Guinea*: Commonwealth Agricultural Bureaux, Farnham Royal.

Winkworth, R. C., Robertson, A. W., Ehrendorfer, F., & Lockhart, P. J. (1999). The importance of dispersal and recent speciation in the flora of New Zealand. *Journal of Biogeography, 26*(6), 1323-1325.

Winkworth, R. C., Wagstaff, S. J., Glenny, D., & Lockhart, P. J. (2002). Plant dispersal N.E.W.S from New Zealand. *Trends in Ecology & Evolution, 17*(11), 514-520.

Winterbourn, M. J. (1998). Insect faunas of acidic coal mine drainages in Westland, New Zealand. *New Zealand Entomologist, 21*, 65-72.

Wollaston, T. V. (1854). *Insecta Maderensia; being an account of the insects of the islands of the Madeiran group*. London: J. Van Voorst.

Woodcock, B. A. (2005). Pitfall trapping in ecological studies. In S. R. Leather (Ed.), *Insect sampling in forest ecosystems* (pp. 37-57). Malden, Mass.: Blackwell Publishing

Woodson, C. B., & McManus, M. A. (2007). Foraging behavior can influence dispersal of marine organisms. *Limnology and Oceanography, 52*(6), 2701-2709.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., et al. (2005). Body size in ecological networks. *Trends in Ecology & Evolution, 20*(7), 402-409.

Worland, M. R., Block, W., & Grubor-Lajsic, G. (2000). Survival of Heleomyza borealis (Diptera, Heleomyzidae) larvae down to -60 degrees C. *Physiological Entomology, 25*(1), 1-5.

Wright, I., & Wood, R. A. (2008). Undersea Continent In I. J. Graham (Ed.), *A continent on the move: New Zealand geoscience into the 21st century* (pp. 38-41). Wellington: Geological Society of New Zealand

Yamane, T., Okada, K., Nakayama, S., & Miyatake, T. (2010). Dispersal and ejaculatory strategies associated with exaggeration of weapon in an armed beetle. *Proceedings of the Royal Society B-Biological Sciences, 277*(1688), 1705-1710.

Yoshimoto, C. M., & Gressit, J. L. (1963). Trapping of air-borne insects in the Pacific-Antarctic area, 2. *Pacific Insects, 5*(4), 873-883.

Young, M. (2005). Insects in Flight. In S. R. Leather (Ed.), *Insect Sampling in Forest Ecosystems* (pp. 116-145). Malden, Mass.: Blackwell Publishing.

Zanella, L., Uliana, M., Scarton, F., Barbieri, F., & Ratti, E. (2009). Environmental evaluation of some Venetian beach-dune ecosystems by means of the specialised beetle fauna (Insecta, Coleoptera) [Valutazione ambientale di alcuni arenili Veneti con formazioni a dune mediante lo studio della coleotterofauna specializzata (Insecta, Coleoptera).]. *Bollettino del Museo Civico di Storia Naturale di Venezia, 60*, 41-88.

Zhang, Z. (2008). Contributing to the progress of descriptive taxonomy. *Zootaxa, 1968*, 65-68.

Zhoun, Z., Yang, X., & Yang, Q. (2006). Land bridge and long-distance dispersal - Old views, new evidence. *Chinese Science Bulletin, 51*(9), 1030-1038.

Zimmerman, E. C. (1942). Distribution and origin of some eastern oceanic insects. *American Naturalist, 76*(764), 280-307.

Zuur, A. F., Elana, N. I., & Smith, G. M. (2007). *Analysing Ecological Data*. New York: Springer.

Appendix A: Driftwood on CI beaches

Mean counts of 500m surveys (n=2) to count driftwood along the beaches adjacent to four of the duneland areas surveyed.

Driftwood size (cm)	Area and position on CI			
	Henga (west)	Waitangi West (west)	Ocean Mail (north)	Hapupu (east)
100cm – 300cm	37	19	22	11
300 +	14	4	8	1

Examples of insect activity from driftwood found on CI beaches.

Appendix B : Summary of new spider records for CI, from November 2005.

Family	Species	Sites collected from				NZ mainland endemic	Notes
		WW	HG	OM	HP		
Amphinectidae	*Maniho vulgaris*	n	Y	Y	Y	Y	Previously known from central NZ. A new record
Gnaphosidae	*Anzacia gemmea*	n	Y	Y	Y	Y	Widespread throughout NZ, but this appears to be the first time it's been recorded from the Chathams.
Gnaphosidae	*Scotophaeus pretiosus*	Y	n	Y	n	Y	
Tetragnathidae	*Tetragnatha flavida*	Y	Y	Y	Y	Y	Berland (1925) recorded the cosmopolitan Tetragnatha nitens from the Chathams, but not this species.
Theridiidae	*Archaearanea blattea*	n	Y	n	n	N	Widespread throughout NZ, but this appears to be the first time it's been recorded from the Chathams.
Theridiidae	*Archaearanea verculata*	Y	n	Y	n	Y	While first described from NZ, this species has since been recorded from elsewhere (Europe and Australia). It may prove to be exotic, but at this stage is still regarded as a New Zealand spider that has managed to colonize other areas, most likely via anthropogenic dispersal.
Theridiidae	*Moneta conifera*	Y	n	Y	n	Y	Widespread throughout NZ, but this appears to be the first time it's been recorded from the Chathams.

Spiders identified and information provided by Phil Servid, Museum of New Zealand,Te Papa, Tongarewa.

Appendix C: Full list of insect taxa collected from NZ and CI dune habitats

Coleoptera

Order	Super-family	Family	Genus	Species	Region collected	
Col	Bostrichoidea	Dermestidae	Trogoderma	?antennale	NZ	
Col	Byrrhoidea	Byrrhidae	Microchaetes	sp01	NZ	
Col	Caraboidea	Carabidae	Allocinopus	latitarsis		CI
Col	Caraboidea	Carabidae	Anomotarsus	sp01	NZ	CI
Col	Caraboidea	Carabidae	Cicindela	parryi	NZ	
Col	Caraboidea	Carabidae	Cicindela	tuberculata	NZ	
Col	Caraboidea	Carabidae	Clivina	vagans	NZ	
Col	Caraboidea	Carabidae	Ctenognathus	sp01	NZ	
Col	Caraboidea	Carabidae	Haplanister	crypticus		CI
Col	Caraboidea	Carabidae	Harpalus	affinis	NZ	
Col	Caraboidea	Carabidae	Holcaspis	impigra	NZ	
Col	Caraboidea	Carabidae	Hypharpax	australis	NZ	CI
Col	Caraboidea	Carabidae	Laemostenus	complanatus	NZ	CI
Col	Caraboidea	Carabidae	Mecodema	bullatus	NZ	
Col	Caraboidea	Carabidae	Mecodema	infimate-spGroup	NZ	
Col	Caraboidea	Carabidae	Mecodema	sculpturatum	NZ	
Col	Caraboidea	Carabidae	Mecyclothorax	rotundicollis	NZ	
Col	Caraboidea	Carabidae	Megadromus	?sandageri	NZ	
Col	Caraboidea	Carabidae	Megadromus	australasiae group	NZ	
Col	Caraboidea	Carabidae	Notagonum	feredayi	NZ	
Col	Caraboidea	Carabidae	Oopertus	sp01	NZ	
Col	Caraboidea	Carabidae	Selenochilus	syntheticus	NZ	
Col	Caraboidea	Carabidae	Triplosarus	novaezelandiae	NZ	
Col	Cerylonidae	Cerylonidae	Hypodacnella	rubripes	NZ	CI
Col	Chrysomeloidea	Cerambycidae	Arhopalus	ferus	NZ	
Col	Chrysomeloidea	Cerambycidae	Bethelium	signiferum	NZ	
Col	Chrysomeloidea	Cerambycidae	Gastrosarus	nigricollis	NZ	
Col	Chrysomeloidea	Cerambycidae	Hybolasius	crista		CI
Col	Chrysomeloidea	Cerambycidae	Psilocnaeia	asteliae	NZ	CI
Col	Chrysomeloidea	Cerambycidae	Ptinosoma	sp01	NZ	
Col	Chrysomeloidea	Cerambycidae	Somatidia	antarctica	NZ	
Col	Chrysomeloidea	Cerambycidae	Spilotrogia	nrpulchella		CI
Col	Chrysomeloidea	Cerambycidae	Stenellipsis	fragilis	NZ	
Col	Chrysomeloidea	Cerambycidae	Stenellipsis	sp01	NZ	
Col	Chrysomeloidea	Cerambycidae	Xyloteles	griseus	NZ	
Col	Chrysomeloidea	Cerambycidae	Xyloteles	laetus	NZ	
Col	Chrysomeloidea	Cerambycidae	Xyloteles	traversi	NZ	
Col	Chrysomeloidea	Cerambycidae	Zorion	guttigerum	NZ	
Col	Chrysomeloidea	Cerambycidae	Zorion	opacum		CI
Col	Chrysomeloidea	Chrysomelidae	Eucolaspis	afs-brunnea	NZ	

Col	Chrysomeloidea	Chrysomelidae	Eucolaspis	brunnea	NZ	
Col	Chrysomeloidea	Chrysomelidae	Eucolaspis	jucunda	NZ	
Col	Chrysomeloidea	Chrysomelidae	Eucolaspis	puncticollis	NZ	
Col	Cleroidea	Cleridae	Phymatophaea	nsp01		CI
Col	Cleroidea	Cleridae	Phymatophaea	nsp02		CI
Col	Cleroidea	Cleridae	Phymatophaea	sp03	NZ	
Col	Cleroidea	Cleridae	Phymatophaea	sp04	NZ	
Col	Cleroidea	Melyridae	Dasytes'	pittensis		CI
Col	Cleroidea	Melyridae	Dasytes'	sp01	NZ	
Col	Cleroidea	Phycosecidae	Phycosecis	limbata	NZ	CI
Col	Cucujoidea	Coccinellidae	Adalia	bipunctata	NZ	
Col	Cucujoidea	Coccinellidae	Coccinella	leonina	NZ	
Col	Cucujoidea	Coccinellidae	Coccinella	undecimpunctata	NZ	CI
Col	Cucujoidea	Coccinellidae	Rhyzobius	forestieri	NZ	
Col	Cucujoidea	Coccinellidae	Rodolia	cardinalis	NZ	
Col	Cucujoidea	Coccinellidae	Stethorus	bifidus		CI
Col	Cucujoidea	Coccinellidae	Stethorus	griseus	NZ	
Col	Cucujoidea	Coccinellidae	Veronicobius	nr-macrostichus	NZ	CI
Col	Cucujoidea	Coccinellidae	Veronicobius	sp02	NZ	CI
Col	Cucujoidea	Coccinellidae	Veronicobius	spc	NZ	
Col	Cucujoidea	Coccinellidae	Veronicobius	spd	NZ	
Col	Cucujoidea	Corylophidae	Arthrolips	nsp1		CI
Col	Cucujoidea	Corylophidae	Holopsis	sp01	NZ	
Col	Cucujoidea	Corylophidae	Sericoderus	sp01	NZ	
Col	Cucujoidea	Cryptophagidae	Micrambina'	sp01	NZ	
Col	Cucujoidea	Erotylidae	Loberus	nitens	NZ	
Col	Cucujoidea	Lathridiidae	Aridius	bifasciatus	NZ	CI
Col	Cucujoidea	Lathridiidae	Aridius	nodifer	NZ	
Col	Cucujoidea	Lathridiidae	Aridius	sp01		CI
Col	Cucujoidea	Lathridiidae	Bicava	sp01		CI
Col	Cucujoidea	Lathridiidae	Corticaria	formicaephila?	NZ	
Col	Cucujoidea	Lathridiidae	Cortinicara	hirtalis	NZ	CI
Col	Cucujoidea	Lathridiidae	Enicmus	nr-foveatus	NZ	
Col	Cucujoidea	Nitidulidae	Hisparonia	hystrix	NZ	
Col	Cucujoidea	Silvanidae	Cryptamorpha	desjardinsi	NZ	
Col	Curculionoidea	Anthribidae	Dysnocryptus	maculiter	NZ	
Col	Curculionoidea	Anthribidae	Dysnocryptus	pallidus	NZ	
Col	Curculionoidea	Anthribidae	Euciodes	suturalis	NZ	
Col	Curculionoidea	Anthribidae	Nothochoragus	thoracius	NZ	
Col	Curculionoidea	Anthribidae	Phymatus	phymatodes	NZ	CI
Col	Curculionoidea	Anthribidae	Sharpius	sandageri	NZ	
Col	Curculionoidea	Brentidae	Exapion	ulicis	NZ	
Col	Curculionoidea	Curculionidae	(entim01)	sp01	NZ	
Col	Curculionoidea	Curculionidae	(entim02)	sp02	NZ	
Col	Curculionoidea	Curculionidae	(entim03)	sp03	NZ	
Col	Curculionoidea	Curculionidae	(entim05)	sp05	NZ	
Col	Curculionoidea	Curculionidae	(entim06)	sp06		CI
Col	Curculionoidea	Curculionidae	(entim07)	sp07	NZ	
Col	Curculionoidea	Curculionidae	(entim08)	sp08		CI
Col	Curculionoidea	Curculionidae	(entim09)	sp09	NZ	
Col	Curculionoidea	Curculionidae	(entim10)	sp10	NZ	
Col	Curculionoidea	Curculionidae	(entim11)	sp11	NZ	
Col	Curculionoidea	Curculionidae	(eugno01)	sp01	NZ	
Col	Curculionoidea	Curculionidae	Adstantes	nsp01		CI

Col	Curculionoidea	Curculionidae	Aneuma	rubricale	NZ	
Col	Curculionoidea	Curculionidae	Catoptes?	sp01	NZ	
Col	Curculionoidea	Curculionidae	Cecyropa	discors	NZ	
Col	Curculionoidea	Curculionidae	Cecyropa	tychioides	NZ	CI
Col	Curculionoidea	Curculionidae	Crisius	lineirostris		CI
Col	Curculionoidea	Curculionidae	Cryptorhynchini	sp01	NZ	
Col	Curculionoidea	Curculionidae	Gymnetron	pascuorum	NZ	
Col	Curculionoidea	Curculionidae	Hoplocnema	sp01	NZ	
Col	Curculionoidea	Curculionidae	Irenimus	nr(nsp(of-Craw)/'rocklands'	NZ	
Col	Curculionoidea	Curculionidae	Listronotus	bonariensis	NZ	
Col	Curculionoidea	Curculionidae	Macrorhyncolus	littoralis	NZ	CI
Col	Curculionoidea	Curculionidae	Microcryptorhynchus	nrsimilis	NZ	
Col	Curculionoidea	Curculionidae	Microtribus	huttoni	NZ	CI
Col	Curculionoidea	Curculionidae	Naupactus	leucoloma	NZ	
Col	Curculionoidea	Curculionidae	Oreocalus	sp01	NZ	
Col	Curculionoidea	Curculionidae	Otiorhynchus	ovatus	NZ	
Col	Curculionoidea	Curculionidae	Pactola	sp01	NZ	
Col	Curculionoidea	Curculionidae	Pentarthrini	sp01	NZ	
Col	Curculionoidea	Curculionidae	Pentarthrum	auripilum		CI
Col	Curculionoidea	Curculionidae	Peristoreus	sp01	NZ	
Col	Curculionoidea	Curculionidae	Phrynixus	asper		CI
Col	Curculionoidea	Curculionidae	Praeolepra	squamosa		CI
Col	Curculionoidea	Curculionidae	Psepholax	crassicornis	NZ	
Col	Curculionoidea	Curculionidae	Rhinorhynchus	rufulus	NZ	
Col	Curculionoidea	Curculionidae	Rhopalomerus	maculosus	NZ	
Col	Curculionoidea	Curculionidae	Saccolaemus	narinus	NZ	
Col	Curculionoidea	Curculionidae	Scelodolichus	nsp1		CI
Col	Curculionoidea	Curculionidae	Sitona	lepidus	NZ	
Col	Curculionoidea	Curculionidae	Stephanorynchus	curvipes	NZ	
Col	Curculionoidea	Curculionidae	Steriphus	diversipes-lineata		CI
Col	Curculionoidea	Curculionidae	Strongylopterus	hylobiodes	NZ	
Col	Elateroidea	Elateridae	Amychus	candezei		CI
Col	Elateroidea	Elateridae	Conoderus	exsul	NZ	CI
Col	Elateroidea	Elateridae	Ctenicera'	sp01	NZ	
Col	Elateroidea	Elateridae	Metablax	acutipennis	NZ	
Col	Elateroidea	Elateridae	Ochosternus	zealandicus	NZ	
Col	Histeroidea	Histeridae	Parepierus	sp01	NZ	
Col	Histeroidea	Histeridae	Saprinus	nsp01		CI
Col	Scarabaeoidea	Lucanidae	Geodorcus	helmsi	NZ	
Col	Scarabaeoidea	Lucanidae	Mitophyllus	irroratus	NZ	
Col	Scarabaeoidea	Lucanidae	Mitophyllus	parianus	NZ	
Col	Scarabaeoidea	Melandryidae	Hylobia	bulla	NZ	
Col	Scarabaeoidea	Scarabaeidae	Acrossidius	tasmaniae	NZ	
Col	Scarabaeoidea	Scarabaeidae	Costelytra	zealandica	NZ	CI
Col	Scarabaeoidea	Scarabaeidae	Heteronychus	arator	NZ	
Col	Scarabaeoidea	Scarabaeidae	Odontria	aurantia	NZ	
Col	Scarabaeoidea	Scarabaeidae	Odontria	piciceps	NZ	
Col	Scarabaeoidea	Scarabaeidae	Odontria	striata	NZ	
Col	Scarabaeoidea	Scarabaeidae	Odontria	sylvatica	NZ	
Col	Scarabaeoidea	Scarabaeidae	Odontria	varicolorata		CI
Col	Scarabaeoidea	Scarabaeidae	Pericoptus	punctatus	NZ	
Col	Scarabaeoidea	Scarabaeidae	Prodontria	praelatella	NZ	
Col	Scarabaeoidea	Scarabaeidae	Pyronota	festiva	NZ	

Col	Scarabaeoidea	Scarabaeidae	Saprosites	communis	NZ	
Col	Staphylinoidea	Leiodidae	Chelagyrtodes	sp01	NZ	CI
Col	Staphylinoidea	Leiodidae	Inocatops	sp01	NZ	
Col	Staphylinoidea	Leiodidae	Mesocolon	nsp01		CI
Col	Staphylinoidea	Staphylinidae	(aleo01)	sp01	NZ	
Col	Staphylinoidea	Staphylinidae	(aleo02)	sp02	NZ	
Col	Staphylinoidea	Staphylinidae	Anotylus	sp01	NZ	
Col	Staphylinoidea	Staphylinidae	Anotylus	sp02	NZ	
Col	Staphylinoidea	Staphylinidae	Baeocera	sp01	NZ	
Col	Staphylinoidea	Staphylinidae	Cafius	quadriimpressus		CI
Col	Staphylinoidea	Staphylinidae	Carpelimus-or-Teropalpus	sp01	NZ	
Col	Staphylinoidea	Staphylinidae	Creophilus	oculatus	NZ	
Col	Staphylinoidea	Staphylinidae	(Omal01)	sp01	NZ	
Col	Staphylinoidea	Staphylinidae	Omaliomimus	robustus		CI
Col	Staphylinoidea	Staphylinidae	Omaliomimus	sp01	NZ	
Col	Staphylinoidea	Staphylinidae	Omaliomimus	sp02	NZ	
Col	Staphylinoidea	Staphylinidae	Xantholini	sp01	NZ	
Col	Tenebrioniodea	Anobiidae	Microsternomorphus	oblongus	NZ	
Col	Tenebrioniodea	Anobiidae	Xenocera	sp01	NZ	
Col	Tenebrioniodea	Anthicidae	Anthicus	kreusleri	NZ	
Col	Tenebrioniodea	Anthicidae	Anthicus	minor	NZ	
Col	Tenebrioniodea	Anthicidae	Lagrioida	brouni	NZ	CI
Col	Tenebrioniodea	Anthicidae	Sapintus	obscuricornis	NZ	
Col	Tenebrioniodea	Anthicidae	Sapintus	pellucidipes	NZ	CI
Col	Tenebrioniodea	Anthicidae	Trichananca	fulgida	NZ	
Col	Tenebrioniodea	Anthicidae	Trichananca	sp01	NZ	
Col	Tenebrioniodea	Mordellidae	Mordella	detracta	NZ	
Col	Tenebrioniodea	Mordellidae	Mordella	jacunda	NZ	CI
Col	Tenebrioniodea	Mordellidae	Stenomordellaria	neglecta	NZ	
Col	Tenebrioniodea	Mycetophagidae	Triphyllus'	hispidellus	NZ	
Col	Tenebrioniodea	Mycetophagidae	Triphyllus'	sp01	NZ	
Col	Tenebrioniodea	Oedemeridae	Baculipalpus	strigipennis	NZ	
Col	Tenebrioniodea	Oedemeridae	Parisopalpus	nigronotatus	NZ	
Col	Tenebrioniodea	Oedemeridae	Thelyphassa	brouni		CI
Col	Tenebrioniodea	Oedemeridae	Thelyphassa	diaphana	NZ	
Col	Tenebrioniodea	Oedemeridae	Thelyphassa	lineata	NZ	
Col	Tenebrioniodea	Oedemeridae	Thelyphassa	nemoralis	NZ	
Col	Tenebrioniodea	Salpingidae	Salpingus	sp01	NZ	
Col	Tenebrioniodea	Scraptiidae	Nothotelus	sp01	NZ	
Col	Tenebrioniodea	Tenebrionidae	Actizita	albata	NZ	
Col	Tenebrioniodea	Tenebrionidae	Artystona	rugiceps	NZ	
Col	Tenebrioniodea	Tenebrionidae	Chaerodes	trachyscelides	NZ	
Col	Tenebrioniodea	Tenebrionidae	Mimopeus	elongatus	NZ	
Col	Tenebrioniodea	Tenebrionidae	Mimopeus	subcostatus		CI
Col	Tenebrioniodea	Tenebrionidae	Omedes	substriatus		CI
Col	Tenebrioniodea	Zopheridae	Notocoxcelus	nsp02		CI
Col	Tenebrioniodea	Zopheridae	Pristoderus	bakewelli	NZ	
Col	Tenebrioniodea	Zopheridae	Pycnomerus	sp01	NZ	

Diptera

Order	Super-family	Family	Genus	Species	Region collected	
Dip	Asiloidea	Apsilocephaldiae	(apsil01)	sp01	NZ	
Dip	Asiloidea	Asilidae	Saropogon	chathamensis	NZ	
Dip	Asiloidea	Therevidae	(there01)	sp01	NZ	
Dip	Asiloidea	Therevidae	(there02)	sp03	NZ	
Dip	Biobionoidea	Bibionidae	Dilophus	nigrostigma	NZ	CI
Dip	Biobionoidea	Bibionidae	Dilophus	tuthilli	NZ	
Dip	Carnoidea	Chloropidae	Aphantotrigonum	huttoni	NZ	
Dip	Carnoidea	Chloropidae	Caviceps	huttoni	NZ	
Dip	Carnoidea	Chloropidae	Caviceps	sp02		CI
Dip	Carnoidea	Chloropidae	Chlorops	sp01		CI
Dip	Carnoidea	Chloropidae	Diplotaxa	gemina	NZ	
Dip	Carnoidea	Chloropidae	Diplotaxa	orbitalis	NZ	
Dip	Carnoidea	Chloropidae	Diplotaxa	sp02	NZ	
Dip	Carnoidea	Chloropidae	Lasiopleura	tonnori	NZ	
Dip	Carnoidea	Chloropidae	Lioscinella	flaviceps	NZ	
Dip	Carnoidea	Chloropidae	Lioscinella	zelandica	NZ	
Dip	Carnoidea	Chloropidae	Tricimba	hippelates	NZ	
Dip	Carnoidea	Chloropidae	Tricimba	watti	NZ	
Dip	Carnoidea	Tethinidae	Tethinosoma	fulvifrons	NZ	CI
Dip	Chironomoidea	Ceratopogonidae	(cerat01)	sp01		CI
Dip	Chironomoidea	Ceratopogonidae	(cerat04)	sp04	NZ	
Dip	Chironomoidea	Ceratopogonidae	(cerat05)	sp05	NZ	
Dip	Chironomoidea	Chironomidae	(chiron01)	sp01	NZ	
Dip	Chironomoidea	Chironomidae	(chiron02)	sp02	NZ	
Dip	Chironomoidea	Chironomidae	(ortho01)	sp01	NZ	
Dip	Chironomoidea	Chironomidae	(ortho02)	sp02	NZ	
Dip	Chironomoidea	Chironomidae	(ortho03)	sp03	NZ	
Dip	Chironomoidea	Chironomidae	Chironomus	zealandicus	NZ	CI
Dip	Chironomoidea	Chironomidae	Gressittius	antarcticus	NZ	CI
Dip	Chironomoidea	Chironomidae	Gymnometriocnemis?	Lobifer	NZ	
Dip	Chironomoidea	Chironomidae	Orthocladius	sp01	NZ	CI
Dip	Chironomoidea	Simulidae	Austrosimulium	sp01	NZ	
Dip	Culicoidea	Culicidae	Maorigoeldia	argyropus	NZ	
Dip	Culicoidea	Culicidae	Ochlerotatus	antipodeus	NZ	CI
Dip	Empidoidea	Dolichopodidae	(doli01)	sp01	NZ	
Dip	Empidoidea	Dolichopodidae	Chrysotimus	sp01	NZ	CI
Dip	Empidoidea	Dolichopodidae	Crysotus	sp01	NZ	
Dip	Empidoidea	Dolichopodidae	Crysotus	sp02	NZ	CI
Dip	Empidoidea	Dolichopodidae	(doli01)	sp01	NZ	
Dip	Empidoidea	Dolichopodidae	Helichochaetus	discifer	NZ	
Dip	Empidoidea	Dolichopodidae	Hercostomus	argentifacis	NZ	
Dip	Empidoidea	Dolichopodidae	Hercostomus	philpotti		CI
Dip	Empidoidea	Dolichopodidae	Hercostomus	sp01	NZ	
Dip	Empidoidea	Dolichopodidae	Ischiochaetus	sp01	NZ	CI
Dip	Empidoidea	Dolichopodidae	Naufraga	sp01	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	calignosa	NZ	

Dip	Empidoidea	Dolichopodidae	Parentia	chathamensis		CI
Dip	Empidoidea	Dolichopodidae	Parentia	defecta	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	dl	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	fuscata	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	fuscata group	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	gemmata	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	milleri	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	milleri/schlingeri?	NZ	
Dip	Empidoidea	Dolichopodidae	Parentia	mobile	NZ	
Dip	Empidoidea	Dolichopodidae	Tetrachaetus	bipunctatus	NZ	CI
Dip	Empidoidea	Empididae	(empid01)	sp01	NZ	
Dip	Empidoidea	Empididae	(empid02)	sp02	NZ	
Dip	Empidoidea	Empididae	(empid03)	sp03	NZ	CI
Dip	Empidoidea	Empididae	Chelipoda	consignata	NZ	
Dip	Empidoidea	Empididae	Chelipoda	modica	NZ	
Dip	Empidoidea	Empididae	(heme01)	sp01		CI
Dip	Empidoidea	Empididae	(heme02)	sp01	NZ	CI
Dip	Empidoidea	Empididae	Hilara	sp01	NZ	
Dip	Empidoidea	Empididae	Hilara	Urophylla	NZ	
Dip	Empidoidea	Empididae	Hilarempis	subdita	NZ	
Dip	Empidoidea	Empididae	Isodrapetis	sp01	NZ	CI
Dip	Empidoidea	Empididae	Oropezella	sp01	NZ	
Dip	Empidoidea	Empididae	Oropezella	sp02	NZ	
Dip	Empidoidea	Empididae	Oropezella	sp03	NZ	
Dip	Empidoidea	Empididae	Phylldromia	sp01	NZ	CI
Dip	Empidoidea	Empididae	Phylldromia	sp02	NZ	
Dip	Empidoidea	Empididae	Platypalpus	sp01	NZ	
Dip	Empidoidea	Empididae	Pseudoscelolabes	fluvescens	NZ	
Dip	Empidoidea	Empididae	Tachydromia	sp01	NZ	
Dip	Empidoidea	Empididae	Thinempis	otakouensis		CI
Dip	Ephroidea	Drosophilidae	Drosophila	hydei	NZ	
Dip	Ephroidea	Drosophilidae	Drosophila	sp10	NZ	
Dip	Ephroidea	Drosophilidae	Scaptomyza	fuscitarsis	NZ	
Dip	Ephroidea	Drosophilidae	Scaptomyza	nsp'Chathams'		CI
Dip	Ephroidea	Ephydridae	Ephydrella	assimilis		CI
Dip	Ephroidea	Ephydridae	Hecamede	granifera	NZ	CI
Dip	Ephroidea	Ephydridae	Hydrella	enderbii	NZ	CI
Dip	Ephroidea	Ephydridae	Hydrella	tritici	NZ	CI
Dip	Ephroidea	Ephydridae	Hydrella	velutinifrons	NZ	
Dip	Ephroidea	Ephydridae	Parahyadina	lacustris	NZ	CI
Dip	Ephroidea	Ephydridae	Psilopa	metalica	NZ	
Dip	Ephroidea	Ephydridae	Scatella	nubeculosa	NZ	CI
Dip	Ephroidea	Ephydridae	Scatella	vitithorax	NZ	CI
Dip	Lauxanoidea	Lauxaniidae	(laux01)	sp01	NZ	
Dip	Lauxanoidea	Lauxaniidae	Poecilohetaerella	bilineata	NZ	CI
Dip	Lauxanoidea	Lauxaniidae	Sapromyza	simillima	NZ	
Dip	Lauxanoidea	Lauxaniidae	Sapromyza	sp01	NZ	
Dip	Lauxanoidea	Lauxaniidae	Sapromyza	sp02	NZ	
Dip	Muscoidea	Anthomyidae	Anthomyia	punctipennis	NZ	
Dip	Muscoidea	Anthomyidae	Delia	sp01	NZ	
Dip	Muscoidea	Muscidae	(musc04)	sp04	NZ	
Dip	Muscoidea	Muscidae	(musc05)	sp05	NZ	
Dip	Muscoidea	Muscidae	(musc07)	sp07	NZ	
Dip	Muscoidea	Muscidae	(musc08)	sp08		CI

Dip	Muscoidea	Muscidae	(musc11)	sp11	NZ	CI
Dip	Muscoidea	Muscidae	(musc13)	sp13	NZ	
Dip	Muscoidea	Muscidae	(musc17)	sp17	NZ	CI
Dip	Muscoidea	Muscidae	(musc31)	sp31		CI
Dip	Muscoidea	Muscidae	(musc32)	sp32	NZ	
Dip	Muscoidea	Muscidae	(musc33)	sp33		CI
Dip	Muscoidea	Muscidae	(musc34)	sp34	NZ	
Dip	Muscoidea	Muscidae	Calliphoroides	antennatis		CI
Dip	Muscoidea	Muscidae	Limnohelina	sp01		CI
Dip	Muscoidea	Muscidae	Limnohelina	sp02	NZ	
Dip	Muscoidea	Muscidae	Limnohelina	sp03	NZ	CI
Dip	Muscoidea	Muscidae	(musc35)	sp01	NZ	CI
Dip	Oestroidea	Calliphoridae	Calliphora	hilli	NZ	
Dip	Oestroidea	Calliphoridae	Calliphora	quadrimaculata		CI
Dip	Oestroidea	Calliphoridae	Calliphora	stygia	NZ	CI
Dip	Oestroidea	Calliphoridae	Pollonia	nrfumosa	NZ	
Dip	Oestroidea	Calliphoridae	Pollonia	nrrudis	NZ	
Dip	Oestroidea	Calliphoridae	Pollonia	sp01	NZ	
Dip	Oestroidea	Calliphoridae	Pollonia	sp02	NZ	
Dip	Oestroidea	Calliphoridae	Ptilonesia	auronotata		CI
Dip	Oestroidea	Calliphoridae	Xenocalliphora	hortona	NZ	CI
Dip	Oestroidea	Sarcophagidae	Oxysarcodexia	varia	NZ	CI
Dip	Oestroidea	Tachindae	(tach02)	sp02	NZ	
Dip	Oestroidea	Tachindae	(tach02)	sp03	NZ	
Dip	Oestroidea	Tachindae	(tach07)	sp07	NZ	
Dip	Oestroidea	Tachindae	(tach08)	sp08	NZ	
Dip	Oestroidea	Tachindae	(tach09)	sp09	NZ	
Dip	Oestroidea	Tachindae	(tach10)	sp10	NZ	
Dip	Oestroidea	Tachindae	(tach14)	sp14	NZ	
Dip	Oestroidea	Tachindae	(tach17)	sp17	NZ	
Dip	Oestroidea	Tachindae	(tach19)	sp19	NZ	CI
Dip	Oestroidea	Tachindae	(tach21)	sp21	NZ	
Dip	Oestroidea	Tachindae	(tach30)	sp30	NZ	
Dip	Oestroidea	Tachindae	(tach34)	sp34	NZ	CI
Dip	Oestroidea	Tachindae	(tach36)	sp36	NZ	
Dip	Oestroidea	Tachindae	(tach37)	sp37	NZ	
Dip	Oestroidea	Tachindae	Avibrissina	sp01	NZ	
Dip	Oestroidea	Tachindae	Heteria	sp01		CI
Dip	Oestroidea	Tachindae	Huttonobasseria	verecunda	NZ	
Dip	Oestroidea	Tachindae	Pales	usitata	NZ	
Dip	Oestroidea	Tachindae	Protohystricia	orientalis	NZ	
Dip	Oestroidea	Tachindae	(tach11)	sp11	NZ	
Dip	Oestroidea	Tachindae	(tach15)	sp01	NZ	
Dip	Oestroidea	Tachindae	(tach31)	sp01	NZ	
Dip	Oestroidea	Tachindae	(tach35)	sp01	NZ	
Dip	Oestroidea	Tachindae	Trigonospila	brevifacies	NZ	
Dip	Oestroidea	Tachindae	Zealandotachina	nigrifemorata	NZ	
Dip	Opomyzoidea	Agromyzidae	Cerodontha	angustipennis	NZ	CI
Dip	Opomyzoidea	Agromyzidae	Cerodontha	australis	NZ	CI
Dip	Opomyzoidea	Agromyzidae	Liriomyza	chenopodii	NZ	
Dip	Opomyzoidea	Agromyzidae	Liriomyza	citreifemorata		CI
Dip	Opomyzoidea	Agromyzidae	Phytomyza	improvisa	NZ	
Dip	Opomyzoidea	Agromyzidae	Phytomyza	phytoliroma	NZ	
Dip	Opomyzoidea	Agromyzidae	Phytomyza	syngenesiae		CI

Dip	Platypezoidea	Lonchopteridae	Lonchoptera	bifurcata	NZ	
Dip	Platypezoidea	Phoridae	(meta03)	sp03	NZ	
Dip	Platypezoidea	Phoridae	(meta04)	sp04	NZ	
Dip	Platypezoidea	Phoridae	(meta05)	sp05	NZ	CI
Dip	Platypezoidea	Phoridae	(meta06)	sp06		CI
Dip	Platypezoidea	Phoridae	(meta07)	sp07	NZ	
Dip	Platypezoidea	Phoridae	(meta12)	sp12	NZ	CI
Dip	Platypezoidea	Phoridae	(phor08)	sp08	NZ	
Dip	Platypezoidea	Phoridae	(phor09)	sp09	NZ	
Dip	Platypezoidea	Phoridae	(phor10)	sp10	NZ	
Dip	Platypezoidea	Phoridae	(phor13)	sp13	NZ	
Dip	Platypezoidea	Phoridae	Abaristophora	sp01	NZ	CI
Dip	Platypezoidea	Phoridae	Abaristophora	sp02		CI
Dip	Platypezoidea	Phoridae	Diploneura	cordata	NZ	
Dip	Psychodomorpha	Anisopodidae	Sylvicola	neozealandicus	NZ	
Dip	Psychodomorpha	Anisopodidae	Sylvicola	notatus	NZ	
Dip	Psychodomorpha	Scatopsidae	(scat01)	sp01	NZ	
Dip	Psychodomorpha	Scatopsidae	(scat02)	sp02	NZ	
Dip	Psychodomorpha	Scatopsidae	(scat03)	sp03		CI
Dip	Sciaroidea	Ditomyiidae	Australosymmerus	trivittata	NZ	
Dip	Sciaroidea	Ditomyiidae	Nervijuncta	nigrescens	NZ	
Dip	Sciaroidea	Ditomyiidae	Nervijuncta	wakefieldii	NZ	
Dip	Sciaroidea	Keroplatidae	Cerotelion	dendyi	NZ	
Dip	Sciaroidea	Keroplatidae	Cerotelion	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	Isoneuromyia	harrisi	NZ	
Dip	Sciaroidea	Keroplatidae	Isoneuromyia	novaezelandiae	NZ	CI
Dip	Sciaroidea	Keroplatidae	(Kero01)	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	(Kero02)	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	(Kero03)	sp01		CI
Dip	Sciaroidea	Keroplatidae	(Kero04)	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	(Kero05)	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	(Kero06)	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	(Kero07)	sp01	NZ	
Dip	Sciaroidea	Keroplatidae	Macrocera	milligani	NZ	
Dip	Sciaroidea	Keroplatidae	Macrocera	scoparia	NZ	
Dip	Sciaroidea	Mycetophilidae	Allocotocera	crassipalpis		CI
Dip	Sciaroidea	Mycetophilidae	Allocotocera	dilatata	NZ	
Dip	Sciaroidea	Mycetophilidae	Allocotocera	sp01	NZ	
Dip	Sciaroidea	Mycetophilidae	Allodia	maculata	NZ	
Dip	Sciaroidea	Mycetophilidae	Anomaloyia	guttata	NZ	CI
Dip	Sciaroidea	Mycetophilidae	Epicypta	dilatata	NZ	
Dip	Sciaroidea	Mycetophilidae	Epicypta	emmaculata	NZ	
Dip	Sciaroidea	Mycetophilidae	Exechia	hiemalis?	NZ	CI
Dip	Sciaroidea	Mycetophilidae	Mycetophila	colorata	NZ	CI
Dip	Sciaroidea	Mycetophilidae	Mycetophila	fagi	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycetophila	impunctata	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycetophila	nitens	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycetophila	solitaria	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycetophila	sp01	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycetophila	subspinigera	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycetophila	sylvatica	NZ	
Dip	Sciaroidea	Mycetophilidae	Mycomyia	flavilatera	NZ	
Dip	Sciaroidea	Mycetophilidae	Neoaphelomera	skusei	NZ	
Dip	Sciaroidea	Mycetophilidae	Parvicellula	ruficoxa	NZ	

Dip	Sciaroidea	Mycetophilidae	Taxicnemis	hirta-varbivitata	NZ	
Dip	Sciaroidea	Mycetophilidae	Tetragoneura	nigra	NZ	
Dip	Sciaroidea	Mycetophilidae	Tetragoneura	obliqua	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	aculta	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	bifascatia	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	costata	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	penicillata	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	ruticolis	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	rutithorax	NZ	
Dip	Sciaroidea	Mycetophilidae	Zygomyia	tritasciata	NZ	
Dip	Sciaroidea	Sciaridae	Scaria	annulata	NZ	CI
Dip	Sciaroidea	Sciaridae	Scaria	philpotti	NZ	
Dip	Sciaroidea	Sciaridae	Scaria	sp02		CI
Dip	Sciaroidea	Sciaridae	Scaria	sp03	NZ	
Dip	Sciaroidea	Sciaridae	Scaria	zealandica	NZ	
Dip	Sciaroidea	Sciaridae	Zygoneura	constrictans	NZ	
Dip	Sciomyzoidea	Coelopidae	Baeopterus	philpotti		CI
Dip	Sciomyzoidea	Coelopidae	(coel03)	sp01	NZ	CI
Dip	Sciomyzoidea	Coelopidae	Coelopella	curvipes		CI
Dip	Sciomyzoidea	Coelopidae	Icaridion	sp01	NZ	CI
Dip	Sciomyzoidea	Coelopidae	Icaridion	sp02	NZ	
Dip	Sciomyzoidea	Coelopidae	Protocoelopa	philpotti		CI
Dip	Sciomyzoidea	Coelopidae	Protocoelopa	sp01	NZ	
Dip	Sciomyzoidea	Sciomyzidae	Neolimnia	striata	NZ	CI
Dip	Sphaeroceroidea	Heleomyzidae	Allophylopsis	chathamensi		CI
Dip	Sphaeroceroidea	Heleomyzidae	Allophylopsis	sp01	NZ	
Dip	Sphaeroceroidea	Heleomyzidae	Fenwickia	sp01	NZ	
Dip	Sphaeroceroidea	Heleomyzidae	Prosopantrum	flavifrons		CI
Dip	Sphaeroceroidea	Sphaeroceridae	Phthitia	empirica		CI
Dip	Sphaeroceroidea	Sphaeroceridae	Phthitia	lobocerus	NZ	
Dip	Sphaeroceroidea	Sphaeroceridae	Phthitia	thomasi	NZ	CI
Dip	Sphaeroceroidea	Sphaeroceridae	Thoracochaeta	sp01		CI
Dip	Stratiomyoidea	Stratiomyidae	Benhamyia	sp01	NZ	
Dip	Stratiomyoidea	Stratiomyidae	Dysbiota	sp01	NZ	
Dip	Stratiomyoidea	Stratiomyidae	Neactina	sp01	NZ	
Dip	Stratiomyoidea	Stratiomyidae	Odontomyia	chathamensis		CI
Dip	Stratiomyoidea	Stratiomyidae	Zealandoberis	sp01	NZ	CI
Dip	Syrphoidea	Pipunculidae	Pipucunculus	sp01	NZ	
Dip	Syrphoidea	Syrphidae	Allograpta	sp01	NZ	
Dip	Syrphoidea	Syrphidae	Helophilus	chathamensis		CI
Dip	Syrphoidea	Syrphidae	Helophilus	Antipodus group sp01	NZ	
Dip	Syrphoidea	Syrphidae	Melangyna	novaezealandia	NZ	CI
Dip	Syrphoidea	Syrphidae	Melanostoma	fasciatum	NZ	CI
Dip	Syrphoidea	Syrphidae	Platycheirus	sp01	NZ	
Dip	Syrphoidea	Syrphidae	(syph32)	sp01		CI
Dip	Tephritoidea	Pallopteridae	Maorina	apicalis	NZ	CI
Dip	Tephritoidea	Pallopteridae	Maorina	sp02		CI

Hymenoptera

Order	Super-family	Family	Genus	Species	Region collected	
Hym	Apoidea	Colletidae	Euryglossina	proctotrypoides	NZ	
Hym	Apoidea	Colletidae	Hylaeus	asperithorax	NZ	CI
Hym	Apoidea	Colletidae	Hylaeus	relegatus	NZ	
Hym	Apoidea	Colletidae	Leioproctus	fulvescens	NZ	
Hym	Apoidea	Colletidae	Leioproctus	metallicus	NZ	
Hym	Apoidea	Colletidae	Leioproctus	paahaumau	NZ	
Hym	Apoidea	Crabronidae	Pison	morosum	NZ	
Hym	Apoidea	Crabronidae	Pison	spinolae	NZ	
Hym	Apoidea	Crabronidae	Podagritus	albipes	NZ	
Hym	Apoidea	Crabronidae	Podagritus	carbonicolor	NZ	
Hym	Apoidea	Crabronidae	Podagritus	chambersi	NZ	
Hym	Apoidea	Crabronidae	Tachysphex	nigerrimus	NZ	
Hym	Apoidea	Halictidae	Lasioglossum	cognatum	NZ	
Hym	Apoidea	Halictidae	Lasioglossum	mataroa	NZ	
Hym	Apoidea	Halictidae	Lasioglossum	sordidum	NZ	CI
Hym	Ceraphronoidea	Ceraphronidae	(ceraph01)	sp01	NZ	
Hym	Ceraphronoidea	Megaspilidae	(megaspil01)	sp02	NZ	
Hym	Ceraphronoidea	Megaspilidae	(megaspil02)	sp03	NZ	
Hym	Ceraphronoidea	Megaspilidae	Dendrocerus	sp01	NZ	
Hym	Chalcidoidea	Agaonidae	(agaon01)	sp01	NZ	
Hym	Chalcidoidea	Aphelinidae	Aphelinus	sp01	NZ	
Hym	Chalcidoidea	Encyrtidae	(encyr01)	sp01	NZ	
Hym	Chalcidoidea	Encyrtidae	(encyr02)	sp02	NZ	
Hym	Chalcidoidea	Encyrtidae	(encyr03)	sp03	NZ	
Hym	Chalcidoidea	Encyrtidae	Adelencyrtoides	sp01	NZ	
Hym	Chalcidoidea	Encyrtidae	Microterys	nietneri	NZ	
Hym	Chalcidoidea	Encyrtidae	Odiaglyptus	biformis	NZ	
Hym	Chalcidoidea	Encyrtidae	Psyllaephagus	sp01	NZ	
Hym	Chalcidoidea	Encyrtidae	Tachinaephagus	zelandicus	NZ	
Hym	Chalcidoidea	Eulophidae	(euloph01)	sp01	NZ	
Hym	Chalcidoidea	Eulophidae	(euloph02)	sp02	NZ	
Hym	Chalcidoidea	Eulophidae	(euloph03)	sp02	NZ	
Hym	Chalcidoidea	Eulophidae	(euloph04)	sp03	NZ	
Hym	Chalcidoidea	Eulophidae	(euloph05)	sp04	NZ	
Hym	Chalcidoidea	Eulophidae	(euloph06)	sp05		CI
Hym	Chalcidoidea	Eulophidae	(euloph07)	sp06	NZ	
Hym	Chalcidoidea	Eulophidae	(tetras01)	sp01	NZ	
Hym	Chalcidoidea	Eulophidae	(tetras03)	sp03	NZ	
Hym	Chalcidoidea	Eulophidae	Closterocerus	sp01	NZ	
Hym	Chalcidoidea	Eulophidae	Closterocerus	sp02	NZ	CI
Hym	Chalcidoidea	Eulophidae	Closterocerus	sp03	NZ	CI
Hym	Chalcidoidea	Eulophidae	Closterocerus	sp04	NZ	
Hym	Chalcidoidea	Eulophidae	Elasmus	sp01	NZ	
Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp01		CI
Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp02	NZ	
Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp03	NZ	

Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp04		CI
Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp05	NZ	
Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp06	NZ	
Hym	Chalcidoidea	Eulophidae	Hemiptarsenus	sp07	NZ	
Hym	Chalcidoidea	Eulophidae	Pediobius	epigonus	NZ	
Hym	Chalcidoidea	Eulophidae	Tetracnemoidea	brevicornis	NZ	
Hym	Chalcidoidea	Eulophidae	Zealachertus	conjunctus	NZ	
Hym	Chalcidoidea	Eulophidae	Zealachertus	nr-nephelion	NZ	CI
Hym	Chalcidoidea	Eupelmidae	Eupelmus	sp01	NZ	
Hym	Chalcidoidea	Mymaridae	(mymar01)	sp01	NZ	
Hym	Chalcidoidea	Mymaridae	(mymar02)	sp02		CI
Hym	Chalcidoidea	Mymaridae	Anagroidea	sp01	NZ	
Hym	Chalcidoidea	Mymaridae	Anagroidea	sp02	NZ	CI
Hym	Chalcidoidea	Mymaridae	Australomymar	sp01	NZ	
Hym	Chalcidoidea	Mymaridae	Ischiodasys	sp01	NZ	CI
Hym	Chalcidoidea	Mymaridae	Ooctonus	sp01		CI
Hym	Chalcidoidea	Pteromalidae	(ptero01)	sp01	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero02)	sp02	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero03)	sp03	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero04)	sp04	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero05)	sp05	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero06)	sp06	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero07)	sp08	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero08)	sp09	NZ	
Hym	Chalcidoidea	Pteromalidae	(ptero09)	sp10	NZ	
Hym	Chalcidoidea	Pteromalidae	Parepistenia	sp01	NZ	
Hym	Chalcidoidea	Pteromalidae	Zeala	sp01	NZ	
Hym	Cynipoidea	Cynipidae	Phanacis	hypochoeridis	NZ	
Hym	Cynipoidea	Figitidae	(Figit01)	sp01	NZ	
Hym	Cynipoidea	Figitidae	Anacharis	zealandica	NZ	CI
Hym	Cynipoidea	Figitidae	Hexacola	sp01	NZ	CI
Hym	Cynipoidea	Figitidae	Kleidotoma	subantarcticana	NZ	CI
Hym	Ichneumonoidea	Braconidae	(aphid01)	sp01	NZ	CI
Hym	Ichneumonoidea	Braconidae	(aphid02)	sp02	NZ	
Hym	Ichneumonoidea	Braconidae	(aphid03)	sp03	NZ	
Hym	Ichneumonoidea	Braconidae	(aphid04)	sp04	NZ	
Hym	Ichneumonoidea	Braconidae	(brach02)	sp02	NZ	
Hym	Ichneumonoidea	Braconidae	(brach03)	sp03	NZ	
Hym	Ichneumonoidea	Braconidae	(brach04)	sp04	NZ	
Hym	Ichneumonoidea	Braconidae	(dory01)	sp01	NZ	
Hym	Ichneumonoidea	Braconidae	(dory02)	sp02	NZ	
Hym	Ichneumonoidea	Braconidae	(micro02)	sp02	NZ	
Hym	Ichneumonoidea	Braconidae	(micro03)	sp03		CI
Hym	Ichneumonoidea	Braconidae	(micro04)	sp04	NZ	
Hym	Ichneumonoidea	Braconidae	(micro05)	sp05		CI
Hym	Ichneumonoidea	Braconidae	(micro06)	sp06	NZ	
Hym	Ichneumonoidea	Braconidae	(micro07)	sp07	NZ	
Hym	Ichneumonoidea	Braconidae	(micro08)	sp08	NZ	
Hym	Ichneumonoidea	Braconidae	(opiiin05)	sp05	NZ	
Hym	Ichneumonoidea	Braconidae	(opiin01)	sp01		CI
Hym	Ichneumonoidea	Braconidae	(opiin02)	sp02	NZ	
Hym	Ichneumonoidea	Braconidae	(opiin03)	sp03	NZ	
Hym	Ichneumonoidea	Braconidae	(opiin04)	sp04	NZ	
Hym	Ichneumonoidea	Braconidae	Aleoides	spb	NZ	CI

Hym	Ichneumonoidea	Braconidae	Aphaereta	aotea	NZ	
Hym	Ichneumonoidea	Braconidae	Ascogaster	iti	NZ	
Hym	Ichneumonoidea	Braconidae	Asobara	ajbelli	NZ	
Hym	Ichneumonoidea	Braconidae	Asobara	antipoda	NZ	
Hym	Ichneumonoidea	Braconidae	Aspilota	sp01	NZ	
Hym	Ichneumonoidea	Braconidae	brach04	sp01	NZ	
Hym	Ichneumonoidea	Braconidae	brach05	sp01	NZ	
Hym	Ichneumonoidea	Braconidae	Choerbus	sp01	NZ	
Hym	Ichneumonoidea	Braconidae	Daenusa	areolaris		CI
Hym	Ichneumonoidea	Braconidae	Dinocampus	coccinellae		CI
Hym	Ichneumonoidea	Braconidae	Dinotrema	longworthii		CI
Hym	Ichneumonoidea	Braconidae	Macrocentrus	sp01	NZ	CI
Hym	Ichneumonoidea	Braconidae	meteorus	cespitator	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(camp01)	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(camp02)	sp02		CI
Hym	Ichneumonoidea	Ichneumonidae	(camp03)	sp03	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(camp05)	sp05	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(crem01)	sp01		CI
Hym	Ichneumonoidea	Ichneumonidae	(crem02)	sp02		CI
Hym	Ichneumonoidea	Ichneumonidae	(ichneu01)	sp01		CI
Hym	Ichneumonoidea	Ichneumonidae	(ichneu02)	sp02	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(ichneu04)	sp04	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(ichneu06)	sp06		CI
Hym	Ichneumonoidea	Ichneumonidae	(ichneu07)	sp07	NZ	
Hym	Ichneumonoidea	Ichneumonidae	(ortho01)	sp01	NZ	CI
Hym	Ichneumonoidea	Ichneumonidae	Anacis	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Anacis	sp02	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp02	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp03	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp04	NZ	CI
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp05	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp06		CI
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp07	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp08	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp09	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp10		CI
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp11		CI
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp12	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp13	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp17	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp18	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Aucklandella	sp19	NZ	CI
Hym	Ichneumonoidea	Ichneumonidae	Camploletis	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Camploletis	sp02		CI
Hym	Ichneumonoidea	Ichneumonidae	Camploletis	sp04	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Camploletis	sp05	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Campoplex	sp01		CI
Hym	Ichneumonoidea	Ichneumonidae	Campoplex	sp02	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Casinaria	sp01		CI
Hym	Ichneumonoidea	Ichneumonidae	Casinaria	sp02	NZ	CI
Hym	Ichneumonoidea	Ichneumonidae	Casinaria	sp03	NZ	CI
Hym	Ichneumonoidea	Ichneumonidae	Casinaria	sp04	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Casinaria	sp05	NZ	

Hym	Ichneumonoidea	Ichneumonidae	Degithina	sp01	NZ	CI
Hym	Ichneumonoidea	Ichneumonidae	Diadromus	collaris		CI
Hym	Ichneumonoidea	Ichneumonidae	Diplazon	laetatorius	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Dusona	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Eutanyacra	licitatoria		CI
Hym	Ichneumonoidea	Ichneumonidae	Glabridorsum	stokesii	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Lissonota	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Megastylus	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Megastylus	sp02	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Mesochorus	sp01	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Netelia	ephippiata	NZ	
Hym	Ichneumonoidea	Ichneumonidae	Xanthocryptus	novozealandicus	NZ	
Hym	Platygastroidea	Platygastridae	(platy01)	sp01	NZ	
Hym	Platygastroidea	Platygastridae	(platy02)	sp02	NZ	
Hym	Platygastroidea	Platygastridae	(platy03)	sp03	NZ	
Hym	Platygastroidea	Platygastridae	Ceratacis	sp01	NZ	
Hym	Platygastroidea	Platygastridae	Platygaster	sp01	NZ	
Hym	Platygastroidea	Platygastridae	Platygaster	sp02	NZ	
Hym	Platygastroidea	Platygastridae	Platygaster	sp05	NZ	
Hym	Platygastroidea	Platygastridae	Platygaster	sp06	NZ	
Hym	Platygastroidea	Platygastridae	Synopeas	sp01	NZ	CI
Hym	Platygastroidea	Scelionidae	(scelion01)	sp01	NZ	
Hym	Platygastroidea	Scelionidae	(scelion02)	sp02	NZ	
Hym	Platygastroidea	Scelionidae	(scelion03)	sp03	NZ	
Hym	Platygastroidea	Scelionidae	(scelion05)	sp05	NZ	
Hym	Platygastroidea	Scelionidae	(scelion06)	sp06	NZ	CI
Hym	Platygastroidea	Scelionidae	(scelion07)	sp07	NZ	
Hym	Platygastroidea	Scelionidae	Probaryconus	sp01	NZ	
Hym	Platygastroidea	Scelionidae	Telenomus	sp01	NZ	
Hym	Platygastroidea	Scelionidae	Trimorus	sp01	NZ	
Hym	Proctotrupoidea	Diapriidae	(bely01)	sp01	NZ	
Hym	Proctotrupoidea	Diapriidae	(bely01)	sp02	NZ	
Hym	Proctotrupoidea	Diapriidae	(bely01)	sp03	NZ	
Hym	Proctotrupoidea	Diapriidae	(bely01)	sp04	NZ	
Hym	Proctotrupoidea	Diapriidae	(diap01)	sp01	NZ	
Hym	Proctotrupoidea	Diapriidae	(diap03)	sp03	NZ	
Hym	Proctotrupoidea	Diapriidae	(diap04)	sp04	NZ	
Hym	Proctotrupoidea	Diapriidae	(diap05)	sp05	NZ	
Hym	Proctotrupoidea	Diapriidae	(diap06)	sp06	NZ	
Hym	Proctotrupoidea	Diapriidae	(diap07)	sp07		CI
Hym	Proctotrupoidea	Diapriidae	(diap08)	sp08	NZ	
Hym	Proctotrupoidea	Diapriidae	Antarctopria	coelopae		CI
Hym	Proctotrupoidea	Diapriidae	Basalys	sp01	NZ	
Hym	Proctotrupoidea	Diapriidae	Basalys	sp02	NZ	
Hym	Proctotrupoidea	Diapriidae	Basalys	sp03	NZ	
Hym	Proctotrupoidea	Diapriidae	Basalys	sp06	NZ	CI
Hym	Proctotrupoidea	Diapriidae	Diphoropria	fulva	NZ	
Hym	Proctotrupoidea	Diapriidae	Diphoropria	kuscheli	NZ	
Hym	Proctotrupoidea	Diapriidae	Diphoropria	sinuosa	NZ	
Hym	Proctotrupoidea	Diapriidae	Hemilexomyia	spinosa		CI
Hym	Proctotrupoidea	Diapriidae	Spilomicrus	carolae	NZ	
Hym	Proctotrupoidea	Diapriidae	Spilomicrus	sp01	NZ	
Hym	Proctotrupoidea	Diapriidae	Spilomicrus	sp02	NZ	
Hym	Proctotrupoidea	Diapriidae	Spilomicrus	sp03	NZ	

Hym	Proctotrupoidea	Diapriidae	Trichopria	sp01	NZ	
Hym	Proctotrupoidea	Diapriidae	Trichopria	sp02	NZ	
Hym	Proctotrupoidea	Diapriidae	Trichopria	sp03	NZ	
Hym	Proctotrupoidea	Diapriidae	Trichopria	sp04	NZ	CI
Hym	Proctotrupoidea	Proctotrupidae	Oxyserphus	sp01	NZ	
Hym	Proctotrupoidea	Proctotrupidae	Oxyserphus	sp02	NZ	
Hym	Proctotrupoidea	Proctotrupidae	Oxyserphus	sp03	NZ	
Hym	Proctotrupoidea	Proctotrupidae	Oxyserphus	sp04	NZ	
Hym	Proctotrupoidea	Serphidae	Fustiserphus	intrudens	NZ	
Hym	Proctotrupoidea	Serphidae	Fustiserphus	sp01	NZ	
Hym	Proctotrupoidea	Serphidae	Fustiserphus	sp02	NZ	
Hym	Vespoidea	Pompilidae	Epipompilus	insularis		CI
Hym	Vespoidea	Pompilidae	Priocnemis	nitidiventris	NZ	
Hym	Vespoidea	Pompilidae	Sphictostethus	nitidus	NZ	
Hym	Vespoidea	Vespidae	Ancistrocerus	gazella	NZ	
Hym	Vespoidea	Vespidae	Polistes	chinensis	NZ	
Hym	Vespoidea	Vespidae	Vespula	germanica	NZ	
Hym	Vespoidea	Vespidae	Vespula	vulgaris	NZ	

Taxa collected outside the assigned collecting days (and so not used in the final analysis)

Order	Super-family	Family	Genus	Species	Region collected	
Col	*Bostrichoidea*	*Dermestidae*	*Trogoderma*	*spa*		CI
Col	*Cucujoidea*	*Coccinellidae*	*Veronicobius*	*spgp*	NZ	
Col	*Cucujoidea*	*Corylophidae*	*Arthrolips*	*spgp*	NZ	
Col	*Cucujoidea*	*Lathridiidae*	*Bicava*	*spgp*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Peristoreus*	*discoideus*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Phrynixus*	*spgp*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Praeolepra*	*infusca*		CI
Col	*Curculionoidea*	*Curculionidae*	*Rhopalomerus*	*sp1*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Rhopalomerus*	*sp2*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Rhopalomerus*	*spgp*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Scelodolichus*	*spgp*	NZ	CI
Col	*Elateroidea*	*Elateridae*	*Agrypnus*	*variabilis*		CI
Col	*Scarabaeoidea*	*Scarabaeidae*	*Ataenius*	*brouni*		CI
Col	*Scarabaeoidea*	*Scarabaeidae*	*Odontria*	*nitidula*		CI
Col	*Scarabaeoidea*	*Scarabaeidae*	*Odontria*	*spgp*	NZ	
Col	*Scirtoidea*	*Scirtidae*	*Cyphon*	*spgp*	NZ	
Col	*Staphylinoidea*	*Staphylinidae*	*Tachyporus*	*nitidulus*	NZ	
Col	*Tenebrioniodea*	*Chalcodryidae*	*Chalcodrya*	*hilaris*	NZ	
Col	*Tenebrioniodea*	*Oedemeridae*	*Selenopalpus*	*aciphyllae*		CI
Dip	*Asiloidea*	*Asilidae*	*Neoitamus*	*bulbus*	NZ	
Dip	*Asiloidea*	*Asilidae*	*Saropogon*	*nrdiscus*	NZ	
Dip	*Bibionomorpha*	*Mycetophilidae*	*Aneura*	*boletinoides*	NZ	
Dip	*Bibionomorpha*	*Mycetophilidae*	*Cycloneura*	*flava*	NZ	
Dip	*Bibionomorpha*	*Mycetophilidae*	*Manota*	*maorica*	NZ	
Dip	*Bibionomorpha*	*Sciaridae*	*Scaria*	*spgp*	NZ	
Dip	*Carnoidea*	*Chloropidae*	*Apotropina*	*tonnoiri*		CI
Dip	*Empidoidea*	*Dolichopodidae*	*?*	*sp01*		
Dip	*Empidoidea*	*Dolichopodidae*	*Hercostomus*	*sp02*	NZ	
Dip	*Empidoidea*	*Empididae*	*Chelipoda*	*audita*	NZ	
Dip	*Empidoidea*	*Empididae*	*Chelipoda*	*cycloseta*	NZ	
Dip	*Empidoidea*	*Empididae*	*Hilarempis*	*diversimana*	NZ	
Dip	*Empidoidea*	*Empididae*	*Thinempis*	*spgp*	NZ	
Dip	*Ephroidea*	*Ephydridae*	*Hecamede*	*spgp*	NZ	CI
Dip	*Nemestrinoidea*	*Acroceridae*	*(acro01)*	*sp01*	NZ	
Dip	*Oestroidea*	*Tachindae*	*(tach18)*	*sp18*	NZ	
Dip	*Oestroidea*	*Tachindae*	*Pales*	*spgp*	NZ	
Dip	*Syrphoidea*	*Syrphidae*	*Helophilus*	*gAntipodus-sp02*	NZ	

Dip	*Syrphoidea*	*Syrphidae*	*Meredon*	*equestris*		CI
Hym	*Apoidea*	*Colletidae*	*Hylaeus*	*agalis*	NZ	
Hym	*Apoidea*	*Colletidae*	*Hylaeus*	*capitosus*	NZ	
Hym	*Apoidea*	*Colletidae*	*Leioproctus*	*vestitus*	NZ	
Hym	*Chalcidoidea*	*Eulophidae*	*(tetras02)*	*sp02*		CI
Hym	*Chalcidoidea*	*Eulophidae*	*Zealachertus*	*sp01*		
Hym	*Ichneumonoidea*	*Ichneumonidae*	*Aucklandella*	*sp20*	NZ	
Hym	*Ichneumonoidea*	*Ichneumonidae*	*Campoplex*	*sp04*	NZ	
Hym	*Platygastroidea*	*Platygastridae*	*Platygaster*	*sp03*	NZ	
Hym	*Proctotrupoidea*	*Diapriidae*	*(diap02)*	*sp02*	NZ	CI
Hym	*Proctotrupoidea*	*Diapriidae*	*Basalys*	*sp04*	NZ	
Hym	*Proctotrupoidea*	*Diapriidae*	*Basalys*	*sp05*	NZ	
Hym	*Proctotrupoidea*	*Serphidae*	*Fustiserphus*	*sp03*	NZ	
Hym	*Proctotrupoidea*	*Serphidae*	*Fustiserphus*	*sp04*	NZ	
Hym	*Vespoidea*	*Pompilidae*	*Priocnemis*	*conformis*	NZ	CI
Hym	*Vespoidea*	*Pompilidae*	*Priocnemis*	*spgp*	NZ	
Hym	*Vespoidea*	*Pompilidae*	*Sphictostethus*	*fugax*		CI
Col	*Caraboidea*	*Carabidae*	*Mecodema*	*spgp*	NZ	
Col	*Chrysomeloidea*	*Cerambycidae*	*Psilocnaeia*	*spgp*		CI
Col	*Chrysomeloidea*	*Cerambycidae*	*Xyloteles*	*spgp*	NZ	
Col	*Cucujoidea*	*Coccinellidae*	*Adoxellus*	*picinus*	NZ	
Col	*Cucujoidea*	*Lathridiidae*	*Cortinicara*	*not-hirt*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Aneuma*	*sp01*	NZ	
Col	*Curculionoidea*	*Curculionidae*	*Crisius*	*spgp*		CI
Col	*Curculionoidea*	*Curculionidae*	*Hylastes*	*ater*	NZ	
Col	*Elateroidea*	*Elateridae*	*Ochosternus*	*spgp*	NZ	
Col	*Scarabaeoidea*	*Scarabaeidae*	*Phycocus*	*graniceps*		CI
Col	*Staphylinoidea*	*Xantholini*	*(xanth)*	*spgp*	NZ	
Col	*Staphylinoidea*	*Leiodidae*	*(leiod)*	*sp01*		
Col	*Staphylinoidea*	*Ptiliidae*	*Acrotrichis*	*insularis*		CI
Col	*Staphylinoidea*	*Staphylinidae*	*Bledius*	*spgp*		CI
Col	*Tenebrioniodea*	*Tenebrionidae*	*Artystona*	*obscura*	NZ	
Col	*Tenebrioniodea*	*Tenebrionidae*	*Cerodolus*	*sp01*	NZ	

Appendix D: Taxa level counts for the total survey, NZ, CI and all collection sites.

New Zealand mainland=NZ, Tolaga Bay=TB, Castlepoint=CP, Kaikoura =KK, Okains Bay=OB, Papatowai=PT, Te Waewae Bay= TW. Chatham Island=CI, Henga=HG, Waitangi West=WW, Ocean Mail=OM, Hapupu=HP, Owenga=OW
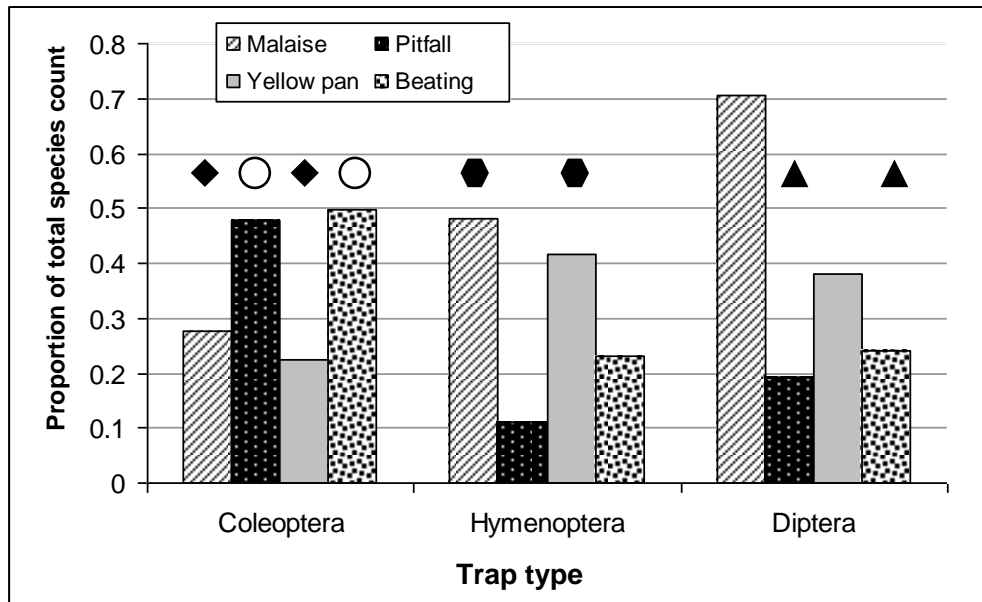
Order / Site	Taxonomic level				
	Super Family	Family	Sub-Family	Genus	Species / RTU
Full Survey	**39**	**95**	**167**	**490**	**675**
All NZ	**39**	**95**	**159**	**428**	**580**
All CI	**35**	**60**	**93**	**167**	**187**
All TB	32	60	82	143	173
All CP	32	65	80	142	163
All KK	36	57	70	130	153
All OB	34	53	70	120	142
All PT	33	56	73	120	144
All TW	30	54	77	147	170
All HG	29	42	57	75	81
All WW	26	35	38	50	52
All OM	20	29	34	43	43
All HP	26	36	48	62	63
All OW	23	34	41	61	62
Coleoptera					
Coleoptera All sites	13	35	74	154	194
Coleoptera NZ	13	35	70	132	163
Coleoptera CI	11	21	31	49	52
Coleoptera TB	9	20	34	48	57
Coleoptera CP	9	20	31	45	48
Coleoptera KK	11	17	20	28	30
Coleoptera OB	9	13	15	22	22
Coleoptera PT	8	14	21	26	30

Coleoptera TW	10	20	30	41	45
Coleoptera HG	8	11	15	16	16
Coleoptera WW	10	15	18	20	21
Coleoptera OM	8	13	17	20	20
Coleoptera HP	9	12	16	18	18
Coleoptera OW	7	10	11	16	17
Hymenoptera					
Hymenoptera All sites	8	23	43	158	226
Hymenoptera NZ	8	23	42	138	198
Hymenoptera CI	7	11	22	43	51
Hymenoptera TB	8	17	24	52	61
Hymenoptera CP	7	17	21	45	52
Hymenoptera KK	8	16	28	49	61
Hymenoptera OB	7	15	22	36	44
Hymenoptera PT	8	16	23	35	38
Hymenoptera TW	6	12	22	41	46
Hymenoptera HG	7	9	16	21	25
Hymenoptera WW	**5**	**6**	**6**	**7**	**7**
Hymenoptera OM	**3**	**4**	**5**	**6**	**6**
Hymenoptera HP	**3**	**3**	**5**	**7**	**7**
Hymenoptera OW	**4**	**6**	**11**	**17**	**17**
Diptera					
Diptera All sites	**18**	**37**	**50**	**178**	**255**
Diptera NZ	**18**	**37**	**49**	**159**	**219**
Diptera CI	**17**	**28**	**41**	**75**	**84**
Diptera TB	**15**	**23**	**25**	**43**	**55**
Diptera CP	**16**	**28**	**29**	**52**	**63**
Diptera KK	**17**	**24**	**23**	**53**	**62**
Diptera OB	**18**	**26**	**34**	**62**	**76**
Diptera PT	**17**	**26**	**31**	**59**	**76**
Diptera TW	**14**	**22**	**27**	**66**	**79**

Diptera HG	15	22	27	38	40
Diptera WW	11	14	15	23	24
Diptera OM	9	12	13	17	17
Diptera HP	14	21	27	38	38
Diptera OW	12	18	20	28	28

Appendix E:

The proportion of each order's total count in caught in each trap. Statistical significance shown within order. Same symbol = statistically equivalent proportion.

Appendix F:

Actual number of CI species within named taxonomic levels, compared to the
expected number based on resampling of NZ taxa. * = CI value significant as it falls
outside the 95% confidence interal of the re-sampled NZ value.

Taxon tested	Order	No. of NZ species	Mean for Resampled NZ pool	95% ci of re-sampled NZ mean	CI count	Over / Under represented on CI
Order						
Coleoptera	Col	163	52.23	+/-10.06	52	
Hymenoptera	Hym	198	63.46	+/-10.53	51 *	Under
Diptera	Dip	219	70.45	+/-10.79	84 *	Over
Superfamily						
Ichneumonoidea	Hym	69	22.25	+/-7.16	28	
Proctotrupoidea	Hym	32	10.32	+/-5.05	5 *	Under
Apoidea	Hym	15	4.84	+/- 3.50	2	
Chalcidoidea	Hym	49	15.71	+/-6.10	10	
Cynipodea	Hym	5	2.04	+/-1.61	3	
Playgastroidea	Hym	18	5.78	+/-3.83	2	
Vespoidea	Hym	6	1.90	+/-2.21	1	
Ceraphronoidea	Hym	4	1.26	+/-1.82	0	
Sciaroidea	Dip	48	15.40	+/-6.07	8 *	Under
Oestroidea	Dip	33	10.59	+/-5.12	8	
Chironomoidea	Dip	12	3.83	+/-3.11	4	
Empidoidea	Dip	38	12.20	+/-5.47	12	
Ephroidea	Dip	11	3.53	+/-3.01	8 *	Over
Lauxanoidea	Dip	5	1.60	+/-2.03	1	
Carnoidea	Dip	11	3.51	+/-3.01	3	

Asiloidea	Dip	4	1.28	+/-1.81	0	
Bibionoidea	Dip	2	0.64	+/-1.30	1	
Muscoidea	Dip	13	4.15	+/-3.25	9 *	Over
Culicoidea	Dip	2	0.63	+/-1.28	1	
Opomyzoidea	Dip	5	1.61	+/-2.05	4 *	Over
Sciomyzoidea	Dip	5	1.6	+/-2.03	6 *	
Sphaeroceroidea	Dip	4	1.27	+/-1.84	5 *	Over
Syrphoidea	Dip	6	1.92	+/-2.11	4	
Stratiomyoidea	Dip	4	1.29	+/-1.83	2	
Platypezoidea	Dip	12	3.83	+/-3.07	5	
Chrysomeloidea	Col	16	5.12	+/-3.61	4	
Caraboidea	Col	19	6.13	+/-3.86	5	
Curcujoidea	Col	21	6.72	+/-4.12	9	
Curclionoidea	Col	41	13.10	+/-5.68	13	
Scaraboidea	Col	15	4.81	+/-3.47	2	
Staphyliniodea	Col	13	4.17	+/-3.28	4	
Tenebrionoidea	Col	27	8.66	+/-4.61	7	
Family						
Cerambycidae	Col	12	3.83	+/-3.18	4	
Coccinellidae	Col	10	3.23	+/-2.90	4	
Oedemeridae	Col	5	1.62	+/-2.06	1	
Braconidae	Hym	29	9.32	+/-4.74	9	
Ichneumonidae	Hym	40	12.90	+/-5.68	19 *	Over
Eulophidae	Hym	22	7.09	+/-4.24	6	
Encyrtidae	Hym	8	2.59	+/-2.57	0 *	Under
Mymaridae	Hym	5	1.61	+/-2.05	4 *	Over

Figitidae	Hym	4	1.29	+/-1.83	3	
Scelionidae	Hym	9	2.88	+/-2.74	1	
Mycetophildae	Dip	28	8.98	+/-4.76	4 *	Under
Keroplatidae	Dip	12	3.86	+/-3.16	2	
Tachinidae	Dip	24	7.74	+/-4.43	3 *	Under
Calliphoridae	Dip	7	2.27	+/-2.41	4	
Ephydridae	Dip	8	2.563	+/-2.57	7 *	Over
Drosphilidae	Dip	3	0.94	+/-1.58	1	
Lauxaniidae	Dip	5	1.44	+/-2.11	1	
Muscidae	Dip	11	3.45	+/-2.93	9 *	Over
Empididae	Dip	18	5.47	+/-3.41	6	
Chloropidae	Dip	10	3.42	+/-2.79	2	
Coelopidae	Dip	4	1.26	+/-1.9	5 *	Over
Agromyzidae	Dip	5	1.73	+/-2.14	4 *	Over
Phoridae	Dip	11	3.48	+/-3.19	5	
Genus						
Veronicobius	Col	4	1.26	+/-1.82	2	
Thelyphassa	Col	3	0.97	+/-1.59	1	
Hydrellia	Dip	3	0.98	+/-1.60	2	
Scatella	Dip	2	0.64	+/-1.3	2 *	
Abaristophora	Dip	1	0.31	+/-0.90	2 *	
Lassioglossum	Hym	3	0.96	+/-1.59	1	

Appendix G:

Relative distance of the barcoding gap to the intra-group distance (column figures in BOLD). Shown for NZ and CI populations. A barcoding gap of >= 10x the intra-group distance implies a potential species level difference.

| Taxon | NZ population | | | | | CI population | | | |
	Mean Inter distance	Mean Intra-NZ distance	Barcoding gap	Barcoding gap: intra NZ distance	Sig dif from random	Mean Intra-CI distance	Barcoding gap	Barcoding gap: intra CI distance	Sig dif from random
Hydrellia enderbii	0.029	0.017	0.012	0.7x	Y	0.007	0.022	3.1x	Y
Cerodontha angustipennis	0.169	0.191	-0.022	Na	N	0.011	0.158	14.3	Y
Cecyropa tychioides	0.064	0.082	-0.18	Na	N	0.003	0.061	20.3x	Y
Phycosecis limbata	0.123	0.052	0.071	1.3x	Y	0.005	0.118	23.6x	Y
Tachysphex nigerrimus	0.014	0.013	0.001	0.008x	Y	0.001	0.14	140x	Y
Auklandella sp.	0.13	0.086	0.044	0.51x	Y	0	0.13	Na	Y