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The evolution of New Zealand insects: summary and prospectus for future research

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Complete List of Authors:	Buckley, Thomas; Landcare Research, Krosch, Mathew; The University of Queensland, Centre for Water in the Minerals Industry Leschen, Richard; Landcare Research,
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The evolution of New Zealand insects: summary and prospectus for future research

Thomas R. Buckley[1,2,3,*]

Matt Krosch[4]

Richard A.B. Leschen[1]

[1] *Landcare Research, Private Bag 92170, Auckland, New Zealand*

[2] *School of Biological Sciences, The University of Auckland, Private Bag 92019, Auckland, New Zealand*

[3] *Allan Wilson Centre, Auckland, New Zealand*

[4] *Centre for Water in the Minerals Industry, Sustainable Minerals Institute, The University of Queensland, Brisbane, Queensland 4072, Australia*

*buckleyt@landcareresearch.co.nz

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Abstract

Knowledge on the evolution of the New Zealand insect fauna is reviewed and outstanding questions are highlighted. The New Zealand insect fauna is a composite of old and recent lineages and many spectacular examples of evolutionary processes are evident including; adaptive radiation, hybridisation, and unusual adaptations. We discuss the origins and evolution of four key communities within the insect fauna: terrestrial lowland insects, alpine insects, aquatic insects, and insect communities from offshore islands. Within each of these communities key lineages are discussed and in particular the key adaptations that enable these species to thrive. Glacial history has had a dramatic impact on the New Zealand insects, and the effects on different lineages are discussed. The New Zealand insects are unique, yet many are threatened with extinction and efforts to preserve the fauna are reviewed. Despite the accumulating knowledge, major gaps still exist and these are outlined, as are opportunities to address key questions. The review ends with a synthesis and a discussion of how systematics, new technologies, and integrative approaches have the promise to improve dramatically our understanding of New Zealand insect evolution.

Key words biogeography, adaptation, alpine, freshwater, island

INTRODUCTION

The origins and evolution of the New Zealand biota have been of great interest to biologists ever since Owen (1843) began describing moa bones, and Darwin's (1859) seminal work. Although well known for the relictual lineages within the vertebrate fauna (Tennyson 2010; Allentoft & Rawlence 2012; Mitchell *et al*. 2014; Rheindt *et al*. 2014), the New Zealand insect fauna is equally as interesting (Fig 1). This fauna also contains relictual lineages (Leschen 2006), as well as unusual radiations (Fleming 1975; Marshall *et al*. 2008), uncharacteristically depauperate lineages (Gibbs 1980; Watt 1975), gigantism (Kuschel & Worthy 1996; Leschen & Rhode 2002; Gibbs 1998; Painting *et al*. 2014), and many unusual ecological interactions (Dugdale 1975). In addition to understanding the evolution of particular lineages and taxa that display the above features, the New Zealand insects offer unlimited opportunities for deepening our understanding of fundamental evolutionary processes such as speciation (Marshall *et al*. 2008, 2011; Albre *et al*. 2012), adaptation (Buckley & Simon 2007; McCulloch *et al*. 2009; Dunning *et al*. 2013a, 2014), hybridisation (e.g. Chinn & Gemmell 2004; Morgan-Richards & Wallis 2003; Morgan-Richards *et al*. 2010), and phylogeography (e.g. Marske *et al*. 2012; Goldberg & Trewick 2011). Previously, much research on the evolution of New Zealand insects has focussed on pattern-based questions, such as the enduring vicariance versus dispersal debate (e.g. Craw 1988; Trewick & Wallis 2001). However, many other questions and conundrums have been neglected, which we highlight and discuss here. Biogeographic patterns in the New Zealand insect fauna have been reviewed comprehensively at broad (e.g. Goldberg *et al*. 2008; Trewick *et al.* 2011) and more local scales (e.g. Buckley & Leschen 2013) and we do not attempt to update these reviews here. Our purpose is to cover outstanding questions on the evolution of the New Zealand insect fauna, to summarise current knowledge, and then to outline a prospective research agenda designed to advance the field of the evolutionary biology of New Zealand insects. Although this review is limited to the insects, we mention other terrestrial and aquatic invertebrate taxa where they illustrate a pattern or process that has been poorly studied in the insects, yet likely to be of importance.

We divide this examination of the New Zealand insect fauna into several sections. The first four sections review the origins and evolution of four different components of the insect fauna; terrestrial insects from lowland habitats, alpine insects, freshwater insects, and insect communities on New Zealand offshore islands. The debate on the origins of the fauna has been at the heart of New Zealand insect biogeography for many years and much recent progress has been made with phylogenetic approaches. Nevertheless, large elements of the insect biota, particularly from the cryptic and hyperdiverse soil and saprophagous communities, have barely been examined.

We discuss landscape changes that occurred during the Cenozoic and in particular the reduction in land area during the Late Oligocene, postulated to have caused massive turnover in terrestrial biodiversity (e.g. Cooper & Cooper 1995; Landis *et al*. 2008). Moreover, New Zealand harbours diverse terrestrial ecosystems with numerous fascinating species interactions that are as complex and intricate as on any landmass. We mention several systems and focus in particular on the sooty mould biota, a complex web of interactions between insects, fungi and plants. The freshwater and alpine zone insect faunas are well known for their endemism and unusual adaptations and we discuss the origins of this diversity. We focus particularly on the unusual physiological and biochemical adaptations that have enabled insect lineages to radiate into alpine environments. These adaptations include suites of behavioural, physiological, and biochemical strategies and we are only beginning to the scratch the surface of the underlying evolutionary processes (Sinclair *et al*. 1999; Dunning *et al*. 2014). In a following section, we assess the influence of Pleistocene glaciation and climate change in shaping the diversity and distributions of New Zealand insects. We review the effects these processes have had on the geographic distributions of lineages at both the interspecific and intraspecific levels and discuss evidence for the geographic location and nature of glacial refugia. We also address the insect fauna of New Zealand offshore islands as these areas are a key focus for conservation biologists as refuges for wildlife that has been driven to extinction on the mainland (Towns *et al*. 2012). Furthermore, these islands contain many endemic lineages that are a result of the individual geological histories of each island (e.g. Buckley & Leschen 2013). We summarise the phylogenetic patterns and discuss some unique features of the island insect faunas, relating these to the history of land connections to the New Zealand mainland. We discuss the current conservation threats and requirements of the New Zealand insect fauna that are underway to ensure this unique biodiversity survives for future generations to enjoy. This review concludes with a synthesis and a summary of promising future research directions.

AGE AND ORIGINS OF NEW ZEALAND TERRESTRIAL INSECTS

How old is the terrestrial insect fauna and what are its origins?

The New Zealand terrestrial insect fauna is characterised by its disharmonic nature and mixture of old and young lineages (Watt 1975). Although levels of endemism at the generic and species level are very high (Watt 1975; Gibbs 2006), there are only six insect families that are endemic namely: Mnesarchaeidae moths (Gibbs 1989), Mystacinobiidae bat flies (Holloway 1976), and the four beetle families Agapythidae (Leschen *et al*. 2005), Chalcodryidae (Watt 1974), Metaxinidae (Kolibáč 2004), and Cyclaxyridae (Gimmel *et al*. 2009). Some insect lineages that are highly diverse in neighbouring landmasses are either absent in New Zealand, such as many beetle families, or have relatively low diversity, such as Orthoptera, Neuroptera, Apoidea, Formicidae, and the butterflies (Watt 1975; Gibbs 1980). Other lineages are highly diverse in New Zealand, yet typically have lower relative diversity elsewhere, such as Zopheridae beetles (Lord & Leschen 2014) and Oecophoridae moths (Hoare 2005, 2010). This disharmony may be related to the long-term isolation of the New Zealand landmass and absence of other key groups leading to novel ecological opportunities (Duthie *et al*. 2006) and dramatic environmental changes causing unequal rates of species turn-over among lineages (e.g. Watt 1975). Understanding this disharmony and the composite nature of old and young lineages requires an understanding of the timing and processes by which insect lineages have arrived in New Zealand and subsequently evolved and diversified.

Biogeographic studies to determine the geographic location of sister taxa to New Zealand clades and then infer the process by which these lineages have come to inhabit New Zealand have revealed several patterns. New Caledonia was the Gondwanan landmass to which New Zealand was connected most recently (Herzer *et al*., 1997; Lee *et al*. 2001; Ladiges & Cantrill, 2007; Schellart *et al*., 2009), and not unexpectedly some New Zealand insect lineages have sister taxa in New Caledonia, including cicadas (Arensburger *et al*. 2004), stick insects (Buckley *et al*. 2009a, 2010a), dung beetles (Monaghan *et al*. 2007), and possibly some of the Anostostomatidae weta (Pratt *et al*. 2008). However, many questions remain unanswered about the nature of this biogeographic connection. One significant question is the uncertainty around the timing of the final breaking of land connections between New Zealand, New Caledonia, and Australia, which may not have occurred until 55 million years ago (Schellart *et al*. 2006; Allentoft & Rawlence 2012) or even later (Ladiges & Cantrill 2007). Many authors interpret divergence dates between New Zealand lineages and their sister taxa in Australia or New Caledonia of much less than 80 million years ago as indicating dispersal rather than a vicariant origin. However, if these latter dates for the final rupturing of land connections to the north of New Zealand are correct then some previous conclusions about dispersal need revisiting. The movement of island arcs, especially on the Norfolk, Three Kings and Reinga Ridges in the Cenozoic could have acted to transport biota from New Caledonia to New Zealand (Herzer *et al*. 2007; Buckley *et al*. 2010a). Schellart *et al*. (2009) also argued for an arc of volcanoes between New Caledonia and New Zealand along the Loyalty and Three Kings Ridges during the Cenozoic that could have provided a means for island hopping at least between the two landmasses. Undoubtedly many lineages have arrived by long-distance dispersal (e.g. Arensburger *et al*. 2004). Others studies have inferred sister group relationships between New Zealand and Australia (e.g. Arensburger *et al.* 2004; Allegrucci *et al*. 2010; Kayaalp *et al.* 2013), indicative of a range of processes leading to the assembly of the insect fauna. The geology of the Southwest Pacific is certainly complex, yet more detailed reconstructions of the history of emergent land since the late Cretaceous are required to gain a better understanding of the mechanisms underlying sister taxa relationships between New Zealand and New Caledonia.

The absence of some insect groups in New Zealand, when they are present in neighbouring landmasses, can be attributed either to; 1) the lineage being younger than the rifting date, 2) the lineage being older than the rifting date, yet absent in the New Zealand region of Gondwana prior to rifting, and 3) a post rifting extinction in New Zealand (Craw & Waters 2006; Giribet & Boyer 2010; Sharma & Wheeler 2013). The lack of clarity around the timing of the loss of land connections makes it difficult to determine if absence of a lineage is due to it being younger than the age of rifting. Undoubtedly biotic regionalisation existed across Gondwana (e.g., Scotese 2004; Murienne *et al*. 2014) and this may have influenced the absence of some lineages from modern New Zealand. Post rifting extinction clearly has played a role in the evolution of the flora, with many plant genera present in the fossil record absent in the modern flora (e.g. Lee *et al*. 2001). However, with such a poor fossil insect record (e.g. Kaulfuss *et al*. 2010), extinctions are very difficult to detect in insects. The loss of major plant groups such as *Eucalyptus*, *Acacia*, *Casuarina*, and many Proteaceae species since the Miocene likely would have caused extinctions in the insect fauna among specialised herbivores. Furthermore, host shifts would have occurred as herbivores adapted to new host plants when their older hosts became extinct. For example, Australian congeners of the New Zealand cecidomyiid fly *Eucalyptodiplosis chionochloae* Kolesik, Safarti, Brockerhoff and Kelly form galls exclusively on *Eucalyptus*. Yet in New Zealand *E. chionochloae* feeds on seeds from the tussock grasses *Chionochloa* (Kolesik *et al*. 2007). Possibly this host shift is the result either of extinction of the previous *Eucalyptus* host in New Zealand, or alternatively dispersal from Australia following the extinction for *Eucalyptus* and an immediate host switch to *Chionochloa*. Floral turnovers may have also influenced specialised saproxylic beetles that would have tracked changes in coarse-woody debris. Other species that are polyphagous on their deadwood hosts and/or fungi may have been less strongly effected (Leschen 2006), but further research is required.

The Oligocene Drowning and changing shorelines

Following the rifting from the eastern margin of Gondwana, New Zealand's land area began to erode during the Paleocene and by the late Oligocene had decreased to approximately 15% of its current land area (Fleming 1979; Cooper & Cooper 1995; Landis *et al*. 2008; Scott *et al*. 2014). The "Oligocene Drowning" hypothesis of Cooper and Cooper (1995) predicted that this reduction in land area caused a bottleneck in vertebrate lineages that can be observed in the post-Oligocene radiations of some vertebrate groups (Cooper & Cooper 1995; Bunce *et al*. 2009). However, the effect of the Oligocene Drowning on the insect fauna is still very poorly known. Although the exact area of land during the maximum extent of the drowning has not been determined (Scott *et al*. 2014), Lee *et al*. (2001) argued that the total land area would have exceeded that of modern New Caledonia, which itself harbours a diverse insect fauna (Chazeau 1993). This raises the prospect that the Oligocene Drowning may have had little effect on the diversity of insects, unlike the vertebrate fauna, which could have been more susceptible to a reduction in land area. However, if the total land area was in fact less than that proposed by Cooper and Cooper (1995) and Lee *et al*. (2001) then the impact on the insect fauna may have been more significant. Resolution of this issue will require dated phylogenies for a range of lineages distributed across the New Zealand region with appropriate outgroups, that survived through the Oligocene. Selection of lineages that are younger than the breakup of Gondwana leads to weak tests of vicariance as pointed out by Murienne *et al*. (2014), but application of diversification models (e.g. Rabosky 2006) to these phylogenies will enable robust testing of these hypotheses. If a bottleneck can be observed in New Zealand insect lineages then this begs the question as to what are the intrinsic and extrinsic factors that enabled some lineages to survive with their diversity intact whereas other lineages experienced elevated extinction rates. The application of diversification models with dated phylogenies and species traits will assist in resolving this question.

Recent geological models for the Cenozoic evolution of the New Zealand landmass have shown a 500 km displacement along the alpine fault, most of which has occurred over the past 23 million years (Bunce *et al*. 2009). The associated shoreline reconstructions show a lack of direct land connections between northern and southern New Zealand from the early Miocene until the Pleistocene (Bunce *et al*. 2009; Trewick & Bland 2012). This reconstruction suggests the Cenozoic geological history of New Zealand is defined by a “northern” and a “southern” island or island groups that do not correspond exactly to the modern North and South Islands. These models show a seaway between the “southern” and “northern” islands since the Miocene that has periodically had smaller islands within it. The general geological pattern is that of a southern migration of this seaway. Furthermore, the southern tip of the Wellington region had land connections with the upper South Island throughout the Miocene and Pliocene to as recently as less than 1 million years ago when the modern Cook Strait formed (Bunce *et al*. 2009). This model has significant implications for the interpretation of biogeographic features and phylogenetic patterns across New Zealand (e.g. Stevens & Hogg 2004; Buckley *et al*. 2011; Trewick & Bland 2012). For example, it has long been noted that there is a biogeographic and phylogeographic break across the middle of the North Island (see Taupo Line, below) and this could be explained in part by the Cenozoic “northern” and “southern” islands. Furthermore, many species and lineages are distributed from the South Island across Cook Strait into the lower North Island and this can potentially be explained by the Cenozoic South Island – lower North Island land connection (e.g. Marra *et al*. 2008; Marske *et al*. 2011; Trewick & Bland 2012). The ephemeral islands in the Cenozoic seaway may also be responsible for the number of endemic insect species and lineages found in southern Hawke’s Bay area (e.g. Morgan-Richards & Gibbs 1995; Marshall *et al*. 2011).

Ecological relationships of terrestrial insects

The disharmonic nature of the New Zealand biota includes occupancy by many species of atypical or novel niches (e.g. Duthie *et al*. 2006) and the formation of unusual ecological interactions and cospeciation events (e.g. Dugdale 1975). Host-plant interactions in New Zealand have not been covered broadly, though specific relationships exist in many groups of herbivore lineages, especially weevils (e.g. Kuschel 1971, 1990; May 1993) and Lepidoptera (Dugdale 1975). Also poorly known are insect-host fungal relationships, with an unusual association between many species of beetles and various taxa of polyporoid and corticioid fungi (e.g. Marske *et al*. 2009; Yavorskya *et al*. 2014). In this case, fungal polyphagy is predominant in mycophagous insects, with few associations of monophagy like the very specific host associations of beetles on *Ganoderma* fungi (e.g. Kadowaki *et al*. 2011a,b). This latter interaction also includes one corylophid that has a larva with a weevil-like snout for feeding on spores deeply within the hymenium (i.e. Kadowaki *et al*. 2011b; Yavorskya *et al*. 2014).

A notable fungal relationship is the sooty mould fauna; notable because sooty moulds can form huge masses on several tree species, mainly Nothofagaceae and *Leptospermum*, and accumulate on any stationary surface. Sooty moulds are found worldwide (Chomnunti *et al*. 2014) but are particularly abundant in New Zealand (Hughes 1976). These fungi thrive especially on the exudates of stenorrhynchan Hemiptera and in New Zealand large masses form on the exudates of the scale insect *Ultracoelostoma assimile* (Maskell) (Morales *et al*. 1988). Most extraordinary are their thick masses in beech forests in the South Island, especially in Canterbury and Northwest Nelson. These host many species of insects (Morales *et al*. 1988), especially beetles, and include derodontids, nitidulids, salpingids, anthribids (e.g., Klimaszewski & Watt 1997; Carlton & Leschen 2007) and the endemic families Metaxinidae (Kolibáč 2004; Johnson *et al.* 2008; 1 sp.), Agapythidae (Leschen *et al.* 1995; 1 sp.), and Cyclaxyridae (Gimmel *et al*. 2009; 2 spp.). The exact number of true sooty mould specialists is unknown because detailed surveys have not been conducted throughout New Zealand. Moreover, exact diets of the sooty mould beetles are unclear. Some species may be feeding as parasites on the scale insects (Morales *et al*. 1988) and others feeding on the sooty moulds and/or the exudates as reported in other predators of hemipterans (Leschen 2000).

The unusual number of endemic beetle families associated with sooty moulds indicates an ancient association and this is confirmed by recent molecular evidence that shows

Cyclaxyridae and Agapythidae diverged from their sister taxa in the Cretaceous, Metaxinidae in the Paleogene, while *Nothoderodontus* Crowson (a derodontid genus distributed also in Chile and Australia) is dated to the Jurassic (Duane McKenna, personal communication). If the remaining members of the sooty mould fauna are as old as these examples, future systematics studies of groups that contain a mix of sooty mould and “free-living” species should reveal older sooty mould lineages relative to sister taxa.

Meanwhile, a few specialist groups of which are present in New Zealand, that occur in comparatively higher numbers elsewhere (see freshwater commensal midges below). For example, there are few species of eusocial insects with only eleven species of native ants (Don 2007) and one termite (*Kalotermes brouni* Frogatt), though one extinct species has been recently described from the Miocene (Kaulfuss *et al*. 2010). Ant and termite inquilines are common throughout the world but there is only one species of New Zealand beetle inquiline repeatedly reported in the literature: *Holloceratognathus passaliformis* (Holloway) (Lucanidae) described from nests of *Prolasius advena* (Fr. Smith) (Holloway 2007). The lack of inquilines, however, is due to bias in collecting and lack of detailed studies, as there are several staphylinid beetles associated with three species of native ant (S. Nomura and R.A.B. Leschen, in prep.). The preceding inquiline and sooty mould examples and other community-level phenomena, like the overdominance of white flowers (Heine 1937; Primack 1978, 1993; Swenson & Bremer 1997), indicate that many of New Zealand’s ecological relationships require detailed study, or have yet to be discovered or appreciated in the scientific literature.

ORIGINS AND SPECIATION OF ALPINE INSECTS

Age of the alpine environment and the insect fauna

A dominant geographic feature of New Zealand are the main axial mountain ranges that run the length of South Island and into the southern North Island. They reach their peak in the central region of the Southern Alps where Aoraki / Mount Cook is 3,764 metres in elevation and well above the summer snow line. The rate of uplift of the Southern Alps as well as other ranges such as the Kaikoura Range is particularly rapid by international standards (Tippett & Kamp 1993; Kao 2001; Robinson *et al*. 2004). This, coupled with the relatively soft sedimentary rock of which many mountain ranges are comprised and extensive faulting, has led to a high erosion rate and unstable landscape. The landscape has been further influenced by the erosional effects of recent glaciation. The mountains of North Island are by contrast much lower than the Southern Alps, with the high point being the active volcano Mount Ruapehu at 2,797 metres, below the summer snow line. The other alpine zones of North Island are fewer and much smaller in size, scattered and often separated by large distances in contrast to South Island.

The New Zealand alpine flora is highly endemic at the species level (McGlone *et al*. 2001) and similarly for the insect fauna, although this has yet to be quantified. There are also strong biogeographic patterns with many groups, such as the cicada genus *Maoricicada* Dugdale showing higher species richness in the northern and southern regions of South Island relative to the central South Island and North Island (Dugdale & Fleming 1978). Chinn and Gemmell (2004) demonstrated that cockroaches of the genus *Celatoblatta* Johns share mitochondrial haplotypes in the central region of the Southern Alps, yet were monophyletic at this locus in the northern and southern alpine areas of South Island. This was attributed to secondary contact between species previously isolated to the north and south of the Southern Alps due to the high rate of uplift, erosion and other environmental changes in the central region of South Island. Similar processes are likely occurring in other alpine insect groups such as grasshoppers (Trewick 2007). Some alpine species also show high levels of genetic variation among populations, with little or no sharing of haplotypes (e.g. Trewick *et al*. 2001; O’Neill *et al*. 2009; Dunning *et al*. 2014), indicative of reduced gene flow between alpine populations isolated on “sky islands”. At the species level some species are widespread across large areas (e.g. *Maoricicada* cicadas; Dugdale & Fleming 1978) whereas others are restricted to single mountain ranges (e.g. *Syrphetodes* Pascoe beetles; Leschen & Buckley 2014). Identification of these areas or local endemism, disconnected from surrounding populations, will be critical for species management as geographic distributions shift due to climate change. Although there are clear biogeographic patterns across the New Zealand alpine zone, we lack enough phylogenetic reconstructions from diverse insect groups to identify common driving forces.

A remarkable aspect of the New Zealand alpine habitat is the extraordinary diversity of plants and animals coupled with its young age (Heenan & McGlone 2012). Permanent and widespread high alpine habitats above the tree line became established only <1.5 million years ago (mya), although upland and open habitats have existed since the Miocene. Heenan and McGlone (2012) reviewed the ages of plant lineages that inhabit various parts of the alpine environment. Bog-inhabiting lineages were found to be older than those of open habitat generalists, which in turn were older than the alpine specialists, consistent with alpine specialists having evolved from ancestors inhabiting open habitats. The alpine specialists for which molecular dates are available were all less than 2 million years old, consistent with the first appearance of a permanent alpine zone (< 1.5 mya). Buckley and Simon (2007) reviewed the ages of lineages that contained species found in alpine habitats. These ages ranged from 2.6 mya for the grasshopper genus *Alpinacris* Bigelow (Trewick & Wallis 2001) to 17 million years for the weta genera *Hemideina* Walker and *Deinacrida* White (Trewick & Morgan-Richards 2005). These dates are overestimates for the origin of the alpine species because they are crown diversification ages for clades containing both lowland and alpine species. For example, Buckley and Simon (2007) estimated a crown age for *Maoricicada* from the mid to late Miocene. However, this genus contains low-altitude open habitat species in addition to high alpine specialists. The diversification of the high alpine *Maoricicada* specialists was estimated to have occurred in the Pliocene and Pleistocene, in agreement with Heenan and McGlone's (2012) model. Furthermore, Buckley and Simon (2007) estimated a low elevation habitat for the ancestor of the alpine species using ancestral character state reconstruction, again consistent with Heenan and McGlone (2012). Although this model has been validated for several insect lineages further studies are required for taxa encompassing a broad range of habitats, with well dated nodes at the point that habitat transitions have occurred.

As noted above, alpine insect species richness varies across New Zealand. Although figures have not been compiled for the alpine insects, like they have for vascular plants (e.g. Wardle 1963, 1988), similar patterns have become apparent in some insect groups (e.g. Dugdale & Fleming 1978). Notable patterns include the low levels of endemism on the volcanic uplands of North Island, and high levels of endemism in the vast alpine expanse of Northwest Nelson. More detailed information is required on alpine insect species distributions across New Zealand and this will require intensive and specialised sampling of inaccessible areas such as Fiordland

and Northwest Nelson. Only when such information is available will we be able to reconcile insect and higher vascular plant distribution patterns.

Adaptation to the alpine environment

The alpine zone is inhabited by all insect orders present elsewhere in New Zealand and these lineages have acquired the adaptations required for alpine survival in a remarkably short time. Insect species that colonise these environments contend with a variety of challenges including; lower temperatures with a higher frequency of freezing events than lower altitudes, cold-associated desiccation, diet shifts due to highly modified host plants, and shortened seasons for juvenile growth and adult reproduction (Sinclair *et al*. 2003b; Wharton 2011; Dennis *et al*. 2014). Many New Zealand insect lineages evidently have adapted to these challenges through modification of their behavioural, morphological, physiological, and biochemical phenotypes (Wharton 2011).

Some of the more notable alpine lineages include the beetle genus *Syrphetodes*, a member of the Ulodidae found across Australia, New Caledonia, and South America that always inhabits forest habitats where the larvae feed on dead wood. However, alpine species in New Zealand are often found far above the tree line in habitats devoid of woody vegetation; clearly there has been a unique and dramatic habitat and host shift (Leschen & Buckley 2014). Many alpine insects are notable for their dark colour relative to lowland sister taxa, and this phenomenon has been observed in the cicada genus *Maoricicada* (Fleming 1975; Buckley & Simon 2007), the terrestrial stonefly *Holcoperla* McLellan (McLellan 2006; McCulloch *et al*. 2010), *Syrphetodes* beetles (Leschen & Buckley 2014), *Percnodaimon* Butler butterflies (Gibbs 1980) and the alpine grasshopper *Brachaspis robustus* Bigelow (Trewick 2001). Many of these same insects demonstrate behavioural adaptations such as basking (e.g., Gibbs 1980). One notable adaptation that appears to be rare in the insect fauna as a whole is diapause, which is common in Northern Hemisphere insects (Roberts 1978; Morris 1989). Instead, many insects show quiescence rather than full diapause during winter months in cooler areas, which has been attributed to the milder climate regime in New Zealand relative to the continental Northern Hemisphere (Dumbleton 1967; Morris 1989).

Although little is known about these behavioural adaptations, even less is known about the physiological, metabolic, and biochemical adaptations that have allowed these alpine insects to radiate into the alpine environment (Sinclair *et al*. 1999). Alpine taxa in some insect clades form monophyletic groups to the exclusion of lowland species (i.e. the alpine *Syrphetodes* clade); however, in other insect lineages that include multiple alpine species these alpine taxa do not form monophyletic groups (e.g. Emerson & Wallis 1995; Morgan-Richards & Gibbs 2001; Dunning *et al*. 2013a). These phylogenetic patterns raise the possibility of multiple, independent colonizations of the alpine zone. We do not know if different, yet closely related lineages that have radiated independently into the alpine zone use similar physiological and biochemical strategies to survive this harsh environment (Wharton 2011). A recent study on the variation of gene expression among populations and species of the stick insect genus *Micrarchus* Carl (Dunning *et al*. 2014) showed large differences in gene expression among lowland and alpine species and among populations of a single alpine species, unrelated to shared ancestry. This suggests different stick insect species are using different strategies to survive in the alpine environment.

Wharton (2011) recently reviewed current knowledge on the biochemical and physiological basis of cold tolerance in New Zealand insects. Cold tolerance typically falls into two categories: freeze tolerance and freeze avoidance. The former category is when the animal can survive the formation of internal ice, and often controls where in the body and at what rate ice forms. The latter is when the animal avoids the formation of internal ice through various biochemical processes. In the Southern Hemisphere, freeze tolerance strategies seem to be more common than freeze avoidance strategies, the reverse of the pattern observed in the Northern Hemisphere (Sinclair *et al*. 2003a). This has been attributed to the milder yet variable climates of the Southern Hemisphere (Sinclair *et al*. 2003b), though Holarctic lineages are more widespread and may have undergone more frequent interchanges than Gondwanan groups (Sanmartín *et al*. 2001). Studies of the alpine weta *Hemideina maori* (Pictet & Saussure) (Ramløv 1992; Sinclair *et al*. 1999) and the alpine cockroach *Celatoblatta quinquemaculata* Johns (Sinclair 1997) show these are freeze tolerant, utilising ice nucleators, which control the temperature and location at which ice forms within the body. The gene expression response of one species of alpine stick insect, *Micrarchus* sp. nov. 2, has been investigated using messenger RNA sequencing and real time PCR (Dunning *et al*. 2013b; 2014). These studies showed that genes associated with the cuticle tended to be expressed differentially relative to a lowland species, and thus modification of the stick insect cuticle may protect this species against ice formation across the cuticle or increasing desiccation resistance.

Both the weta and the cockroach are in clades that contain other alpine and lowland species. With the exception of some data on super-cooling points and ice formation in haemolymph in two other *Hemideina* species, in both cases very little is known about the cold-tolerance processes in related alpine and lowland species. Although we have information on the basis of adaptation to the alpine environment in these species, what is required are detailed studies on the comparative physiology, biochemistry and molecular genetics of cold tolerance within radiations of species restricted to both the lowlands and alpine environments. Lineages such as the cicadas (Buckley & Simon 2007), cockroaches (Chinn & Gemmell 2004), weta (Morgan-Richards & Gibbs 2001; Trewick & Morgan-Richards 2005), stick insects (Buckley *et al*. 2010a; Dunning *et al*. 2013a) and various beetle groups (e.g., Leschen & Buckley 2014) with well-developed or emerging phylogenetic frameworks are ideal for advancing this goal.

THE EVOLUTION OF NEW ZEALAND FRESHWATER INSECTS

Whence (and when) did the freshwater fauna come?

The origins of New Zealand's freshwater insects, like the terrestrial fauna, have long been a contentious issue. Many workers have suggested that a large proportion of New Zealand's freshwater insect fauna are members of austral clades, with relatives in southeastern Australia and South America, which represent Gondwanan relics (e.g. Brundin 1966; Winterbourn 1980; Gibbs 2006; Craig *et al*. 2012). One significant question is the availability of freshwater habitats during the Oligocene drowning (Cooper & Cooper 1995). Recently characterised fossil deposits from the Eocene through Miocene suggest the presence of alluvial floodplain and lacustrine habitats at various locations on the main islands (Ferguson *et al.* 2010; Lee *et al.* 2012). Furthermore, late Oligocene-early Miocene amber from sites on South Island has revealed adults of numerous freshwater taxa (Kaulfuss *et al.* 2013), while compression fossils and their depositional characteristics also imply the enduring presence of freshwater habitat from at least the late Oligocene (Feldman & Pole 1994; McDowall & Pole 1997; Worthy *et al.* 2008; Lindqvist & Lee 2009), and quite possibly much earlier (Feldman 1984). This suggests that not only was there freshwater habitat present during this time, but also that it was inhabited by a recognisable insect fauna.

Gibbs (2006) suggested that extant New Zealand freshwater taxa are most likely to represent Gondwanan relics because of the obvious restrictions on their successful dispersal across lethal salt-water barriers and a general affinity for cold, pristine, lotic ecosystems. Recent molecular phylogenetic studies of some freshwater insect groups also provide evidence for a long history in New Zealand. For example, many groups within the New Zealand non-biting midges (Diptera: Chironomidae) appear to have undergone crown diversification in the mid-Eocene and follow expected area relationships for an austral ancestry (Cranston *et al.* 2010; Krosch *et al.* 2011; Cranston *et al*. 2012; Krosch & Cranston 2013). New Zealand Plecoptera diversification events range from the late Eocene to early Miocene and also largely follow an austral pattern of relationships (McCulloch 2011). Moreover, it has been suggested that many elements of the New Zealand freshwater fauna represent early-branching lineages, thus inferred (sometimes incorrectly) to be 'primitive' types reflective of a retained ancient fauna (Daugherty *et al*. 1993; Collier 1993). For example, the petal-tailed dragonflies (Family Petaluridae) were long considered to be one such group, based on morphological characters, a supposition that has recently been supported by molecular evidence (Ware *et al*. 2014). Taken together, it appears very likely that there has been available freshwater habitat across the New Zealand landmass, however much reduced during the Oligocene, since at least the Eocene and possibly even since the initiation of rifting from Gondwana in the Cretaceous (~80 mya).

Colonisation of remnant or emergent habitats by newly arriving freshwater organisms is likely to have been more complicated than for terrestrial taxa. For taxa that are restricted to freshwater habitats for their entire life history, clearly their dispersal capabilities across saltwater barriers would have limited their colonisation of New Zealand. For taxa with an adult flight stage, availability of appropriate habitat (lotic vs. lentic), adult stage duration, life cycle seasonality, existing food resources and dominant resident taxa will also have had an impact on the success of a colonising individual (Mackay 1992). Furthermore, dispersal in many flighted freshwater insect taxa often is limited to the gravid female seeking an oviposition site. Thus, successful colonisation of new habitats by such taxa requires the female to also find a suitable site to lay her eggs and sufficient survival of the offspring to found a population. Immature stages of most freshwater insects require large amounts of energy for growth and development, and in some taxa such as the Chironomidae this is the major feeding life stage. Most other insect groups also feed as adults to fuel dispersal and mating activity and although there is significant variation in life stage duration across the orders, immature stages are generally shorter than the adult stage. At all life stages there is thus pressure on colonising individuals to locate food resources and this may potentially favour generalist taxa as the most likely to successfully establish in a new habitat.

Of those freshwater taxa inferred to have arrived in New Zealand after Gondwanan fragmentation, many have putative sister groups in Australia or elsewhere in the south Pacific region. Before the formation of the Antarctic Circumpolar Current and the West Wind Drift phenomenon, aerial dispersal of freshwater insects may have been facilitated or at least aided by other major meteorological events such as cyclone fronts. An alternative pathway, which may also have aided fully aquatic taxa, may have been via a series of island chains along the Lord Howe/Norfolk Island Rises that maintained connectivity between New Zealand and the surrounding area during the Palaeogene (Veevers 2012; Krosch & Cranston 2013). Following inception of West Wind Drift around 30 mya (Cook & Crisp 2005), asymmetric dispersal from Australia to New Zealand would have been significantly more probable. Indeed, in more recent times, a so-called ‘rain’ of invertebrates has been recorded dispersing from Australia to New Zealand on wind currents (Tomlinson 1973; Close *et al*. 1978), including many freshwater taxa. These abiotic phenomena, combined with intrinsic life history traits, clearly have influenced which taxa have colonised New Zealand freshwater systems successfully.

Patterns of diversity in the freshwater taxa

Modern day New Zealand freshwater habitats range from lentic bogs and marshes, including high-altitude tarns, to fast-flowing seasonal glacier-fed rivers, volcanic maar lakes to groundwater-fed springs. There are heavily denuded, exposed stream channels, and those hidden deep in prehistoric forest. Braided glacial rivers meander through steep-sided valleys, forest streams trickle down hillsides and waterfalls cascade from mountainsides. The wide ecological breadth of New Zealand's freshwater systems reflects a dynamic landmass in which widespread volcanism, stochastic climatic patterns, glaciation and tectonic uplift all have played a role in diversification of freshwater habitat in New Zealand. In concert, these processes have been central to the development and maintenance of a freshwater fauna very different to that found in other temperate regions of the world, both at the community and species levels (Winterbourn *et al*. 1981; Collier 1993). The dynamic nature of New Zealand's climate and geology apparently drove selection of taxa with wide environmental tolerances, life history flexibility and high vagility (Winterbourn 1997). Many groups do not exhibit seasonal life history traits, such as winter dormancy or diapause (see below), that are typical of taxa from temperate northern hemisphere ecosystems (Dumbleton 1967; Winterbourn *et al*. 1981). This has been attributed to both the presence of evergreen rather than deciduous trees that provide a year-round organic energy source, and potentially that historical cold periods had little evolutionary influence on New Zealand's freshwater insects with regard to traits for cold avoidance (Dumbleton 1967). Moreover, some functional groups (e.g. large particle detritivores) are under-represented compared with northern hemisphere temperate ecosystems (Winterbourn *et al*. 1981), mirroring the 'naturally depauperate' patterns of the terrestrial fauna (Gibbs 2006). The lucky few groups of taxa that either remained on the rifting landmass or arrived as new colonisers have since diversified to fill niches occupied by other insect groups in temperate ecosystems elsewhere. A result of this lowered diversity in many groups of New Zealand freshwater insects is that many aquatic systems comprise similar suites of widespread taxa that are stable over time and despite various forms of impact (Winterbourn 1997). Nevertheless, some freshwater insect groups do exhibit significant species-level diversity and extreme endemism. Taken together, the New Zealand freshwater fauna is enigmatic, with patterns of diversity and endemism variable across many insect orders and taxonomic levels.

Many freshwater insect orders, typically diverse elsewhere are not so in New Zealand and yet exhibit high endemicity like the terrestrial fauna already mentioned. The Ephemeroptera are represented by ~30 species (of ~220 in the Australasian region), all of which are endemic to New Zealand, including two monospecific families (McLellan 1975; Barber-James *et al*. 2008). There is a strong pattern of austral relationships among the New Zealand mayfly taxa, which supports a potential Gondwanan origin (Barber-James *et al*. 2008). Odonata is only represented by 17 species (10 endemic to New Zealand), but this includes members of the family Petaluridae which are supported as an 'ancient' group that predates New Zealand's separation from Gondwana (Rowe & Corbet 1987; Daugherty *et al*. 1993; Kalkman *et al*. 2008; Ware *et al*. 2014). Only six freshwater Coleopteran families occur in New Zealand of ~25 known worldwide (Winterbourn & Gregson 1981), including one endemic subfamily of Hydraenidae (Klimaszewski & Watt 1997). At least two species from the family Dytiscidae are known to inhabit cave freshwater systems (Ordish 1976), ecosystems that are poorly characterised in New Zealand. Both Megaloptera and Mecoptera are represented in New Zealand by only single species (Winterbourn & Gregson 1981). The dobsonfly *Archichauliodes diversus* (Walker) is one of New Zealand's largest freshwater insects and inhabits clear, fast-flowing streams on both main islands (Quinn & Hickey 1990). The species can be quite abundant within streams and exhibits significant genetic structure among populations (Hogg *et al*. 2002). The scorpionfly *Microchorista philpotti* (Tillyard) has a highly restricted distribution and the poorly sclerotised larva occurs only in protected slow-moving waters in streams in South Island. The taxon is thought to be closely related to other austral members of the Nannochoristidae, potentially reflecting an ancient Gondwanan heritage (Ferrington 2008). Only six families of aquatic/semi-aquatic Hemiptera are known, compared with 17 for the Australasian region (Winterbourn & Gregson 1981; Polhemus & Polhemus 2008). Without taxonomically well-sampled, dated phylogenies it is difficult to infer the origins and ancestry of many of these species-poor New Zealand insect lineages, particularly those that show affinities to taxa that inhabit similar ecosystems in other austral regions.

By contrast, the Trichoptera are perhaps the best example of a group in which the New Zealand fauna has diversified significantly *in situ* over at least the last ~23mya. The earliest record of a caddisfly is a fossilised larval case from the Foulden Maar deposit, Otago, dated to the earliest Miocene (U. Kaulfuss, unpub. data). Moreover, some groups currently restricted to the austral regions (e.g. Helicophidae and psyllobetine Hydrobiosidae) are known from Eocene Baltic amber (Botosaneanu & Wichard 1981), which suggests these groups may have been retained after succumbing to extinction in the northern hemisphere (de Moor & Ivanov 2008). The New Zealand fauna shows moderate endemicity at the genus level, but the order is highly endemic at the species level. Some New Zealand taxa have developed high salinity tolerance and indeed members of the endemic Chathamiidae family of marine caddisflies inhabit intertidal zones throughout the New Zealand region. Within the trans-Tasman family Conoesucidae, six genera are endemic to New Zealand and their phylogenetic relationships suggest multiple colonisation events (Johanson *et al*. 2009); however, no estimates of divergence dates currently exist. The radiation of caddisfly taxa in New Zealand is thought by some to have been facilitated by their holometabolous life history and diversity of available habitat for colonisation (Winterbourn *et al*. 1981); however, this fails to explain the lack of diversification in insect orders with similar life histories.

New Zealand Plecoptera have been particularly well characterised for species diversity, with some 104 species known, 99 of which are from a single family (McLellan 2006). Taxa included in McCulloch's (2011) molecular phylogeny all exhibited connections with either Australia or South America. Although New Zealand's stoneflies generally prefer cool, flowing freshwater systems (a trait generally associated with Gondwanan relic taxa), most New Zealand stonefly groups are younger than Gondwanan age. Interestingly, it is thought that dispersal is limited in stoneflies due to the ecological requirements of the nymphs and poor flight ability in adults (Fochetti & de Figueroa 2008). It would seem unlikely, therefore, that these taxa would have dispersed across wide ocean gaps to New Zealand, and so perhaps stepping-stone island connections were important for the movement of stoneflies also (McCulloch 2011). Furthermore, numerous New Zealand genera have evolved to be brachypterous (reduced wings) or apterous (wingless) as adults, often in combination with terrestrial nymphs (McLellan 2006). Wingless New Zealand stoneflies generally are restricted to either the alpine zone of the major islands or isolated habitats on some smaller offshore islands (McLellan 2006). Both life history states are unusual for holometabolous freshwater taxa in an environmentally variable region like New Zealand (Roff 1990). Typically, aptery is associated with relaxed selective pressures for dispersal driven by environmental stability, as well as in specific habitats in which a flight stage may be unnecessary. One possible explanation may thus be that the highly exposed and climatically variable nature of these ecosystems instead selected against dispersal in these taxa. In other words, the evolutionary costs associated with flight in such environments (e.g. being blown off course, high energy requirement) may have outweighed the benefits (e.g. increased gene flow among populations), such that individuals that did not disperse possessed an evolutionary advantage.

The Diptera are also considered to be diverse in New Zealand; however, there appears to be marked variation in diversity across families. The Chironomidae are quite diverse with over 60 species known from five subfamilies (McLellen 1975), many of which represent austral elements closely related to groups in Australia and South America, but with several other taxa that represent more recent colonisations by cosmopolitan groups. The ecological breadth of this group is similar to that found elsewhere, with species having radiated to inhabit most niches from rapid glacial rivers to high altitude tarn pools to sea-level lakes. The species *Chironomus zealandicus* Hudsonis perhaps the best-known New Zealand chironomid as it is a pest of sewage treatment works that can undergo such population explosion as to physically block pipeworks (Forsyth 1971). At least three freshwater chironomids (*Tonnoirocladius commensalis* Cranston, *Xenochironomus canterburyensis* Forsyth and *Eukiefferiella* indet.) are commensals of Blepheraceridae larvae, freshwater mussels and mayfly nymphs, respectively (Forsyth 1979; Winterbourn 2004; Cranston 2007). Although commensalism is globally widespread in the Chironomidae, this life history trait is rare among New Zealand freshwater insects as a whole. Commensalism is thought to be an evolutionary strategy for maximising feeding opportunity, mobility, and protection from disturbance while also reducing predation risk (Tokeshi 1993). Certainly some environmental characteristics of New Zealand freshwater systems may indeed have contributed to a selective advantage for commensalism in these taxa. Interestingly, *T. commensalis* was placed phylogenetically within the cold-adapted New Zealand genus *Naonella* Boothroyd (Krosch *et al*. 2011), suggesting *T. commensalis* should be more accurately designated as a species of *Naonella* and acts to highlight the lack of understanding surrounding the development of such an unusual life history trait in these taxa. Another unusual chironomid, the ‘ice-worm’ midge *Zelandochlus latipalpis* Brundin, inhabits the Fox and Franz Josef Glaciers on the west coast of South Island (Boothroyd & Cranston 1999). The larvae inhabit meltwater pools and ice caves within the glacier and exhibit strong photophobia. Adult males inhabit the glacier surface and are apterous, a trait that potentially developed under the same selection pressures as argued for stoneflies above. A recent phylogenetic analysis suggests this taxon diverged from its sister in the Oligocene (Cranston *et al*. 2010). Thus, the apparently high species diversity and ecological breadth observed within the Chironomidae relative to other Dipteran families may reflect a longer history in New Zealand and thus more time to radiate into different niches.

Most of the remaining New Zealand Dipteran families do not possess such high species-level diversity and there is a mix of species endemic to New Zealand and those that are shared with other landmasses in the south Pacific or more widely. Many of these groups are also postulated to have an ancient vicariant origin on New Zealand (Tipulidae – de Jong *et al*. 2008; Blepharaceridae – Wagner *et al*. 2008), although most have not been explicitly tested to date. New Zealand also possesses a single representative of the Keroplatidae, the endemic glow-worm species *Arachnocampa luminosa* (Skuse), which inhabits caves and moist forest environments on both main islands (Pugsley 1984). *Arachnocampa* occurs also in Australia, with *A. luminosa* sister to a clade comprising all eight Australian species (Baker *et al*. 2008). The disjunct austral distribution of the genus, along with the requirement for moist environments, poor adult dispersal and extreme sensitivity to desiccation of these taxa raises questions concerning their origin in New Zealand that have yet to be addressed adequately.

Overall, the New Zealand freshwater insect fauna comprises several groups of taxa that are members of early-branching lineages apparently retained from pre-Gondwanan break-up (e.g., petalurid dragonflies); a select few orders that presumably arrived after New Zealand separated from Gondwana and have had a long history on the landmass, including surviving the Oligocene inundation, such that they have diversified significantly *in situ* (e.g. stoneflies and chironomids); and many groups that are species poor and either represent recently arrived poor dispersers or ancient Gondwanan relic lineages that have been pruned by extinction. Thus, there remain many unanswered questions concerning the evolution of New Zealand's freshwater insects, a conundrum that faces freshwater insects worldwide (Dijkstra et al. 2014). A substantial proportion of New Zealand's freshwater fauna are yet to be studied in a phylogenetic context and determining the phylogenetic placement of New Zealand taxa amongst their austral relatives and ages of diversification will contribute greatly to our understanding of the origins of these groups. Even for studied taxa (e.g. the podonomine chironomids), knowledge gaps exist concerning the affinities of certain taxa amongst the broader New Zealand fauna. The search for fossil evidence of freshwater insects will complement phylogenetic studies and if recent discoveries discussed above are an indication, there could be a wealth of information yet to be revealed by the fossil record. Moreover, incorporating ecological, physiological, and life history information in the interpretation of resulting phylogenies will help to bring resolution to hypotheses about their origins, as well as their diversification in New Zealand.

EVOLUTION OF INSECTS ON OFFSHORE ISLANDS

The New Zealand offshore islands

The geopolitical boundaries of New Zealand, extending from 34° north to 52° south latitudes, encompass subtropical islands to Subantarctic Islands (Fig. 3). The Kermadec Islands, outside this range, are absolutely tropical, and while they share many species in common with the mainland, they also have a Pacific element (e.g. Brown *et al*. 2012). The distance from the New Zealand mainland to these offshore islands varies, but in terms of diversity and conservation value they are biological gems. The most-protected near-shore islands (like Hauturu-o-Toi, Kapiti Island, Takapourewa, and Codfish Island) are utilised by nesting pelagic birds and contain species, mainly larger charismatic species of weevils and weta, that no longer exist on the mainland due to introduced predators or loss of habitat. These islands also have endemic biota whose ancestry provides insights into New Zealand's dynamic biogeological history. There are about 200 off-shore islands, many under the stewardship of the Department of Conservation, including the Subantarctic Islands which have World Heritage status. Only a handful of islands have been intensely studied and typically not completely surveyed, and the most poorly studied are those islands located in the complex network of fjords in Fiordland. We highlight the best known of the off-shore islands that are home to endemic invertebrates, have been moderately to well surveyed, and are central for understanding the evolution of the New Zealand insect fauna.

The Northern Islands

The Three Kings Islands lie 50 km off the northern tip of North Island and can be easily seen on a clear day. The largest island of the archipelago is Great Island or Manawatawhi (407 ha), which is mostly cliff-bound, the rest are mostly rock stacks and are all difficult to access. The Three Kings Islands are an exposed part of the Three Kings Ridge, which is mostly submerged and connected northward to the Norfolk Ridge, which is in turn joined to New Caledonia. The fauna, in some respects, shows this connection (e.g. snails; Ponder *et al*. 2003), but absences, like the erotylid beetle *Kuschelengis* Skelley and Leschen, known from the mainland and New Caledonia, could be attributed to post-rift extinction (see above). What is lacking, however, are phylogenetic hypotheses for older groups present on the Three Kings, New Caledonia, New Zealand, and elsewhere in the Pacific. Though visited several times by invertebrate researchers, a full account of the species has not been published, but, based on unpublished work, 35% of the beetle fauna may be endemic, including several endemic beetle genera (J. Marris, unpubl. data). The great disparity between the mainland and the Three Kings also includes the range limits of Pacific groups (snails), an Austral-Neotropical beetle genus (*Platisus* Erichson), and other groups lacking immediate ancestors in New Zealand. Otherwise, the fauna is related to mainland New Zealand, and in particular, to adjacent areas in Northland, while dated phylogenies represent a range of divergences, with the oldest from the Miocene (Buckley & Leschen 2013).

Closer in-shore to the Northland mainland at 22 km are the Poor Knights Islands, which consist of Tawhiti Rahi (151.5 ha) and Aorangi (101 ha), a remnant that may have been separated from the mainland at least during the Last Glacial Maximum (Hayward, 1991). Unlike the Three Kings, there are no endemic plant species (the Poor Knights Lilly, *Xeronema callistemon*, is found elsewhere [de Lange & Cameron 1999]), but it has been estimated that 16% of the invertebrate fauna is endemic, with many species showing close relationships with species found in Northland (Buckley & Leschen 2013), and in one case with the Three Kings Islands (Seldon & Leschen 2011). Phylogenetic studies suggest regional endemism in the Northland islands results from old diversifications associated with isolated islands that were ocean-bound during periods of higher sea levels (e.g. Morgan-Richards *et al.* 2001; Buckley *et al*. 2010b; Leschen & Buckley 2014). Careful and dense regional sampling for phylogenetic studies will help distinguish divergence dates and determine if the ages of the island faunas relate to allopatry following post-glacial sea level rises (Buckley & Leschen 2013) or to preceding periods of land reduction (Bunce *et al*. 2009). Also, the off-shore islands, because of their range of distances from the mainland, differences of island age, and area, represent an opportunity to test questions of island biogeography. For example, we may be able to determine the differences between palaeo and neo-endemic species and the reason why mainland and islands populations tend to express different phenotypes. For example, populations of the trogossitid beetle *Phanodesta brounii* (Pascoe) on the Poor Knights Islands have aberrant elytral features (Leschen & Lackner 2013).

The Chatham Islands

The Chatham Islands group is located on the Chatham Rise, is separated from the mainland by about 680 km and is quite large (90,650 ha). Like the Three Kings Islands the Chathams Islands has a high rate of beetle endemism of about 27%, with at least four endemic beetle genera (Emberson 1998). This includes *Thotmus halli* Broun, collected from Pitt Island, known only from the type specimen (Leschen *et al*. 2012) and thought to be extinct (Stringer & Hitchmough 2012). The Chatham Islands has a permanent residency of over 600 people, though there are forest reserves and smaller islands that have intact faunas, and the smaller Pitt Island (6203), which also supports a small population of people, has slightly more species (Emberson 1998). Recent research (e.g., Trewick 2000) indicates that the biota has dispersed overwater since 2 mya when it was presumably first exposed, despite dates much older for some taxa (Marske *et al.* 2012; Buckley & Leschen 2013), which may indicate potential sunken islands or continual land elsewhere in the archipelago (Heenan *et al*. 2013).

Though questions regarding the source of the fauna remain unclear for some invertebrates (Skelley & Leschen 2007), based on plant patterns, it is likely that sister groups are widespread mainland taxa (Heenan *et al*. 2013). Dispersals and/or sharing ancestors from more distant areas, like the scarab species *Tesarius sulcipennis* (Lea) described from Tasmania may seem unusual (Stebnicka 2001) but not unheard of in other groups distributed in the southern hemisphere. The purported case of long-distance transoceanic dispersal of the monotypic plant *Myosotidium hortensium*, with a sister group occurring in the Mediterranean (with divergences between 3.64 and 22.45 Ma), may seem like a relictual quirk, but relationships among all the species that are not shared with the mainland require intensive phylogenetic study.

The Deep South: the Subantarctic Islands

One of the best taxonomically documented group of the off-shore islands are, surprisingly, the Subantarctic Islands located on the Campbell Plateau, a large microcontinental fragment that may have been a separate geological entity from the remaining northern portions of the mainland New Zealand (Michaux & Leschen 2005). The New Zealand Subantarctic islands have attracted the attention of biologists for well over a century, due to their isolation and importance for sea life. There are five islands or archipelagos (Campbell, Auckland, Snares, Bounty, and Antipodes Islands); this excludes Macquarie Island, which is located on the Macquarie Ridge which, though its fauna is related to those of the Campbell Plateau, has few endemic species (Greenslade 1990). The islands are scattered along the plateau, and range in size from the 135-ha Bounty Islands to the 61,120-ha Auckland Islands, with all but the Bounty and Snares Islands being volcanic remnants. Resting on Palaeozoic rocks, the oldest volcanic extrusions are 12–25 my (Adams 1981). Many of the islands are windswept, with Auckland Islands and Snares supporting forests of *Metrosideros* and *Olearia*, respectively. There are up to 80% levels of endemism for some groups of terrestrial invertebrates. While major surveys occurred in the 1960s, only a few have been sporadically carried out since (see Gressit 1964; Gressit & Wise 1971). Some groups require additional work (soil-dwelling insects, especially staphylinid beetles); and the fauna of the Snares Islands has not been fully and formally documented.

Despite the thorough faunistic and taxonomic works of the 1960s and 1970s, biogeography and evolution of the Subantarctic fauna, however, is surprisingly limited. Most studies have argued that the Subantarctic faunas share relatives with mainland New Zealand, and this includes taxa found also on the Chatham Islands (Kuschel 1971; Craw 1988; Michaux & Leschen 2005; Ward *et al*. 2004; McGaughran *et al*. 2006; 2010; Leschen *et al*. 2011). Distant connections include taxa that have relatives in the northern Pacific (*Baeostethus chiltoni* Broun; Leschen *et al*. 2002; Ahn *et al*. 2010), but Gondwanan relationships predominate (Liebherr *et al*. 2011) with connections to the Patagonian regions of South America (Kuschel 1971) and to Tasmania (Priasilphidae; Leschen & Michaux 2005). The internal biogeographic relationships of the island invertebrates are poorly known. A phylogeny (Leschen *et al*. 2011) of the Subantarctic beetle genus, *Pseudhelops* Guérin Méneville (Tenebrionidae), shows a lineage that has colonised by western drifting, from the main group in the west to the Bounty Platform, which is composed of relatively younger islands (Adams 1981).The evolutionary history among the Campbell Plateau insects remain poorly studied, however, and much work is required to fully appreciate the relationships of the insect fauna to other regions of the world, the relationships among the islands, and especially their natural history.

GLACIAL REFUGIA IN NEW ZEALAND

History of glaciation in New Zealand

New Zealand's history of repeated glaciations throughout the late-Pliocene and Pleistocene has been particularly well characterised (e.g. Mercer 1983; Suggate 1990; Vandergoes & Fitzsimons 2003; Suggate & Almond 2005). Onset of cooling occurred in the Late Pliocene and intensified throughout the Pleistocene, often rendering vast areas of the landmass as tundra. Repeating cycles of glacial cooling and interglacial warm periods occurred during this period, driving expansion and retreat of glaciers and significant sea level fluctuation (Suggate 1990). Indeed, the Last Glacial Maximum (LGM), between 34 and 18 kya, saw extensive glaciation spanning almost the entire Southern Alps, in concert with an approximately 120-m reduction in sea level (Newnham *et al.* 2012). These dramatic changes to New Zealand's climate clearly drove similarly marked transformations in terrestrial habitats across the landmass. Fossil data suggest quite clearly that widespread, contiguous wet forests were fragmented by drier, open grassland and tussock habitats and falls in sea levels exposed new land for colonisation, while simultaneously converting previously coastal habitats into more inland zones (e.g. McGlone 1985; Newnham *et al.* 2012). It could be reasonably expected that many freshwater habitats would have been assimilated by expanding glaciers or dried out completely and perhaps that previously drier regions may have experienced increases in rainfall due to local changes in climate. Although Plio-Pleistocene glaciation was extensive and changes to floral communities significant, it is generally held that the landmass possessed a mosaic of vegetation types, rather than complete conversion of broad regions and extirpation of core species (McGlone *et al.* 2010). Nevertheless, this dramatic and dynamic fluctuation and conversion of habitat types also influenced distributions and population connectivity in many resident insect groups. This section details regions of the New Zealand landmass supported as refugia for insect taxa during past glacial periods.

What makes a refugium?

Glacial refugia are recognised globally as land areas that represent formerly widespread habitats that retracted in range during historical periods of glacial advance (Ferris *et al*. 1999). Typically, though not the rule, terrestrial habitats that retracted into small refugia during glacial periods comprised wet, closed canopy forest taxa that were driven locally extinct elsewhere by the cooling and aridification that characterises glaciation. As a general result, refugial areas often retained greater diversity and endemism than glaciated regions (Hewitt 2000; Byrne 2008); although zones of overlap between refugia where divergent lineages recontact can harbour higher diversity than individual refugia alone (Byrne 2008; Provan & Bennett 2008; Bryant & Fuller 2014). This trend holds for New Zealand, where a previously widespread closed forest flora was fragmented into a mosaic of small isolated refugial areas. Despite New Zealand glaciation occurring in mountainous areas instead of vast lowland ice shields (Suggate 1990), such refugia were often (although not exclusively) located in upland areas or in valleys and gorges resistant to the aridification of lowland areas. The dramatic transitions in floral communities across New Zealand during glacial periods are well-documented in the pollen record, particularly for the late Pleistocene. In some areas this appears to have involved turnover in species composition as changing local climates drove conversion from one habitat type to another (e.g. *Nothofagus*-dominated forest to open grassland), whereas in other areas floral communities appear to have been extirpated by glacial advance (Wardle 1963; McGlone 1985). In contrast, subfossil beetle remains from across New Zealand appear to imply that habitat conversion was not as dramatic as inferred from the pollen record, with many Pleistocene-age fossil deposits suggesting persistence of a mosaic of small forest patches (reviewed by Marra 2008; Marra & Thackray 2010). A further confounding factor for interpreting glacial age signals in New Zealand is that reductions in sea level may have provided opportunities for lowland taxa to establish refugia in areas currently inundated.

North Island – a line in the land

The extensive pollen record for the New Zealand North Island suggests the major centres of floristic richness during Plio-Pleistocene glacial periods were in Northland, Waikato (especially Coromandel Peninsula), and the very south-eastern tip of the island around the Tararua Ranges (Wardle 1963, 1988). Indeed, in a recent meta-analysis of fossil data, Northland and Waikato are the only regions in New Zealand supported as retaining significant tall podocarp forest during the LGM (McGlone *et al.* 2010). Moreover, much of the southern half of the North Island below around 39°S possesses markedly lower diversity and endemism than the northern half. This dividing line has been termed the 'Taupo Line' after the settlement and lake which it intersects in the central North Island. It is a zone of much contention among New Zealand biogeographers, and no consensus for its development exists. Hypotheses include long-term marine transgression (Suggate *et al.* 1978; Bunce *et al*. 2009), widespread tectonic activity (Pulford & Stern 2004) and/or volcanism (Alloway *et al*. 2007). A glacial explanation has also been provided for the Taupo Line that invokes retraction of taxa from southern areas to northern refugia (Wardle 1963). Whatever the case, the pattern suggests there has been little colonisation of much of southern North Island since the LGM, implying that even if the drivers of the boundary are old, it is being maintained by more modern processes.

Insects of the North Island largely reflect the floral data in showing higher levels of diversity (both intra- and interspecific) in northern zones, along with a small area in the southeast, compared with the low diversity zone below the Taupo line. Ecological niche modelling (ENM) of the generalist parthenogenetic stick insect, *Argosarchus horridus* (White), suggests this taxon survived Pleistocene glaciations in refugia along coastal North Island, including the southeast, and northeast North Island (Buckley et al. 2009). Mitochondrial DNA data showed one common widespread clade distributed across South Island and southern North Island, and several rarer clades mostly restricted to northern North Island. Furthermore, most

South Island populations were female-only, while North Island populations had almost equal sex ratios – interpreted as resulting from southward colonisation of habitat during interglacials and a selective advantage for parthenogenesis at the invasion front. This pattern is virtually mirrored in another generalist parthenogenetic stick insect, *Clitarchus hookeri* (White), for which ENMs and mtDNA data also suggest refugia in northern North Island and eastern South Island (Buckley *et al.* 2010). Like *A. horridus*, northern populations of *C. hookeri* are sexual and genetically diverse, whereas southern populations are parthenogenetic and of low diversity (Buckley *et al.* 2010; Morgan-Richards *et al*. 2010). The forest edge cicada species, *Kikihia subalpina* (Hudson), showed a split across the Cook Strait for mitochondrial DNA (Marshall *et al.* 2009), with North Island populations most diverse in the southeast and a single lineage distributed north of the Taupo Line. Refugial areas for two further taxa, the fungus beetle species *Epistranus lawsoni* and *Pristoderus bakewelli*¸ were supported by ENMs for northern and southeastern North Island, including significant land areas in the north that are now below sea level (Marske *et al.* 2011). Although little is known of refugial areas for North Island aquatic taxa during glacial periods, some population genetic studies suggest their persistence in central and northern North Island refugia as a driver of population divergence (Smith *et al.* 2006a,b). Taken together, insect data for North Island match closely the interpretation provided for the pollen record and observed in other terrestrial fauna: the northern portion of the island above the Taupo Line and the southeastern tip were clearly major refugial areas for many taxa during Pleistocene glaciation.

South Island – montane mosaic

The topographically diverse South Island experienced major periods of glaciation several times since the Pliocene. Glacial advance was mostly confined to the Southern Alps mountain range; however, significant glaciation of lowland areas, particularly to the west, also occurred, while much of central and eastern South Island supported mostly open grassland and tussock (McGlone *et al.* 2010). Indeed, some fossil evidence suggests only northern South Island (Nelson-Marlborough-Kaikoura), Westland, and a few small isolated areas of Fiordland supported any significant tall forest during the LGM (McGlone *et al.* 2010). Nevertheless, other evidence suggests Otago may have retained refugial areas during glaciations (Wardle 1963; Burrows 1965), as may have areas of Canterbury (Marra *et al.* 2006). Contemporary patterns of floral communities have also informed inferences of the effect of Plio-Pleistocene glacial events and, like the Taupo Line in North Island, areas of biotic disjunction has been recorded throughout New Zealand, especially in the South Island. Much of the central South Island has lower levels of species richness and endemism than adjacent northern and southern areas (Willet 1950; Wardle 1963). This "Biotic Gap" is likely the result of several ecological and historical processes (e.g. Heads 1998; Trewick & Wallis 2001; Haase *et al*. 2006). Of particular note is the "Westland beech gap", a 150 km long region on the West Coast of South Island that lacks beech trees (e.g., Cockayne 1926; Wardle 1963; McGlone *et al*. 1996) and a number of insect taxa (e.g., Leschen *et al*. 2008).

Refugial areas inferred for South Island insects based on molecular phylogeographic studies largely follow predictions made from fossil data. The widely distributed fungus beetles, *Brachynopus scutellaris* (Redtenbacher) and *Hisparonia hystrix* (Sharp), show high intraspecific genetic diversity with divergent lineages distributed across the well-demarcated Westland Beech Gap, but with substructuring of lineages somewhat correlated with geography (Leschen *et al* 2008). Patterns in both species are inferred to have resulted from a complex history of population fragmentation and re-expansion associated with glacial cycling. The stick insect *Niveaphasma annulata* (Hutton) comprises three Pleistocene-age lineages restricted to putative refugial areas in Canterbury, Otago, and Fiordland-Southland (O'Neill *et al.* 2009). Distributions of several species of South Island tiger beetles (*Neocicindela* Rivalier) appear centred around historical refugial areas, especially Nelson-Marlborough, Canterbury, Otago, and the Southern Alps (Pons *et al*. 2011). Many *Neocicindela* species that are distributed across the Biotic Gap also show deep divergence between northern and southern populations and genetic signals suggest the Biotic Gap was recolonised by these taxa during interglacial periods. A study of the forest fungus beetle, *Argyrtodes labralis* (Broun), that incorporated ENMs with traditional molecular phylogeography suggested Pleistocene refugia for this taxon would have been located in northern South Island and the west coast, along with a very restricted zone in Fiordland (Marske *et al.* 2009). The molecular data supported this in showing several highly localised lineages in Kaikoura, Nelson, and Marlborough, with some others more widespread in Otago-Southland and the west coast. Southern regions evidently were not completely extirpated during glaciations, with populations surviving in small zones of suitable habitat, and that west coast refugia were the source populations for eastern and southeastern populations, with very little movement out of

Nelson refugia (Marske *et al.* 2009). The cicada *K. subalpina*, mentioned above, showed significant substructuring among South Island populations, with greatest diversity in the northern refugial regions and little diversity in southern areas (Marshall *et al.* 2009). Both *K. subalpina* and *A. labralis* also inhabit Stewart Island and the surveys described above suggest Stewart Island is likely to have been colonised only since the LGM by populations in southern South Island (Marshall *et al.* 2009; Marske *et al.* 2009).

Some freshwater insects in South Island also show distinct histories of isolation in refugia during glacial cycles. All six co-distributed species of stonefly assessed by McCulloch *et al.* (2010) were concordant in showing deep genetic divergences across the Biotic Gap, with few genetic lineages distributed across the Gap, and centres of diversity correlated with putative refugial areas. Some of the studied species currently inhabit the Biotic Gap and the authors suggest dispersal ability (as determined in this case by aptery vs macroptery) as the crucial factor in facilitating recolonisation of glaciated areas (McCulloch *et al.* 2010). Populations of the non-biting midge, *Naonella forsythi* Boothroyd, in the Upper Buller catchment appear to have experienced significant subdivision, divergence and subsequent re-expansion (Krosch *et al.* 2012), possibly due to glaciation in the region (Suggate 1990). The waterboatman species, *Sigara potamius* Young, also exhibits marked genetic divergence in northern South Island, with some lineages restricted to locations on the west coast and others sympatric in Canterbury (Buckley & Young 2008). Diversification in this species was inferred to have initiated in the Pliocene and it is likely that refugia in northern South Island were important for persistence during the Pleistocene.

In contrast to the evidence above, some taxa are supported as having survived through the Pleistocene glaciations in refugia within the Biotic Gap. The cicada, *Maoricicada campbelli* (Fleming), is suggested to have persisted in the Biotic Gap and diversified in Pleistocene refugia in southern North Island, Marlborough, the Southern Alps, Waitaki, and Central Otago (Buckley *et al.* 2001a; Hill *et al.* 2009).

Confounding interpretations of glacial-age population impacts is the finding that even ecologically similar taxa may respond differently to glaciation, having inhabited different refugial areas, used different recolonisation paths and diversified at different tempos (see Marske *et al.* 2012). Furthermore, many taxa that may have inhabited refugia in the Pleistocene may have lost any genetic signal over the intervening time due to other processes (both intrinsic and extrinsic) and many different geophysical processes may produce the same phylogeographical patterns (Trewick *et al.* 2011). Despite this, and the fact that many taxa apparently were not at all affected by Pleistocene glaciations (Trewick *et al.* 2011) and several insects are endemic to the Westland Beech Gap (e.g. Leschen & Michaux 2005; Seago & Leschen 2011), there remains a clear signal in the evolution of numerous New Zealand insect species of significant impact on populations due to glacial advance. Questions still remain concerning the influence of glaciations in many insect groups and ongoing research is needed to elucidate these effects. Understanding the impact of past climatic fluctuations will facilitate effective prediction and management of future change.

CONSERVATION OF NEW ZEALAND INSECTS

New Zealand insects under threat

The remarkable diversity, endemism and evolutionary histories of New Zealand's insect fauna pose many conservation problems in a changing human-influenced landscape. New Zealand is considered a biodiversity hotspot for conservation and possesses a community of species unique in the world (Myers *et al.* 2000). The often-devastating trident of exotic species, habitat loss/modification (particularly in the lowlands), and climate change represent increasing challenges for the survival of many insect species in New Zealand. Current estimates suggest that of 3,838 terrestrial invertebrate species assessed (26% of the New Zealand total), 193 were considered 'Threatened' (including 106 that were 'Critical'), and a further 1,055 were 'At Risk' (Stringer & Hitchmough 2012). Moreover, 912 species 'At Risk' of extinction were considered 'Naturally Uncommon', an important contributor to their conservation status and meaning that otherwise minor impacts could have a dramatic influence on these taxa. Around 114 species of New Zealand Lepidoptera are considered of conservation significance (Patrick & Dugdale 2000), and many of the large, ground dwelling weta are known to be vulnerable to predation (Gibbs 1998). Already seven insect species are believed recently extinct and others exist now only on smaller islands (Samways 1993; Gibbs 2009). Furthermore, many more species remain undescribed and with unknown conservation status, and thus the true extent of the threat may be greater than currently thought (McGuiness 2001; Stringer & Hitchmough 2012).All is not lost, however; this section will explore some important conservation issues for terrestrial and aquatic taxa, threats, solutions, success stories and the future prospects for New Zealand's insects.

Standing on solid ground

Exotic species have had and will continue to have an enormous impact on native terrestrial insect populations across New Zealand. Several well-known mammalian invaders directly predate on insects, including rodents, possums, mustelids, pigs, and hedgehogs (McGuiness 2001; Gibbs 2009). Several weevil and beetle species, including the largest known ulodid beetle (*Waitomophylax worthyi* [Leschen & Rhode]), are thought to have been driven to extinction from the mainland or altogether due to rat predation (Kuschel & Worthy 1996; Leschen & Rhode 2002; Gibbs 2009; Leschen *et al.* 2012). Throughout the New Zealand archipelago rats have also been a significant causative agent in the decline of many weta species, especially those large taxa that spend much time on the ground and have inadequate defensive strategies (Gibbs 1998, 2009). So effective have rats and other mammalian predators been in reducing mainland populations of such insects, that a number of these insects have been deliberately translocated to mammal-free islands to prevent further decline (Watts *et al.* 2008). Among the translocated species is the Mercury Islands tusked weta, *Motuweta isolata* Johns; the entire extant population of which is descended from three individuals. Since then, individuals from a captive breeding programme were released successfully onto two islands in the Mercury group (Double and Red Mercury Islands) to reduce the potential for accidental extinction on the only island they were known from originally (Middle Island) and from which they have not been recorded for several years (since January 2001) (Stringer & Chappell 2008). Of the other mammal and avian invaders that predate on native insects, little appears to be known of the extent of their impact on populations and it could be assumed that it may be minimal compared with the impact of rats.

Some introduced insects also predate on native taxa, the most well known are the social wasps of the genus *Vespula* Thomson. Two species of this genus, *V. vulgaris* (Linnaeus) and *V. germanica* (Fabricius), have established in New Zealand and both are known to predate on native Diptera, Lepidoptera, and Aranae (Beggs & Rees 1999). Wasp populations have been shown to reach incredible sizes in native forest and can cause dramatic population declines and sometimes local extinctions of native spiders (Toft & Rees 1998) and butterflies (Beggs & Rees 1999).

Wasps also utilise the abundant carbohydrate resources from native scale insect exudate or honeydew (up to 70% of standing honeydew production). This contributes to competition with other honeydew users, including birds and other insects. *Vespula* wasps can dramatically re-structure forest communities during peak wasp season (January-April) as prey species that normally occur are extirpated. Taken together, social wasps represent one of the chief conservation issues concerning exotic invaders for native New Zealand insects.

Some other introduced invertebrates influence native insects through competition, parasitism and predation. For example, the Southern African mantis (*Miomantis caffra* Saussure) has been spreading from Auckland, where it was recorded first in 1978, and displacing the native mantis, *Orthodera novaezealandiae* (Colenso) (see Brockerhoff *et al.* 2010). A few predacious beetles, parasitoid social insects, and ants are established in New Zealand but are rare in native forest and their impact on native insects is thought to be minimal. Likewise, some biocontrol agents have been recorded to exhibit non-specific attack (parasitoid wasps supposed to attack crop and pasture pests also attack native Lepidoptera, weevils); however, their impact on native taxa may yet be minimal – in contrast to many other areas of the world (Brockerhoff *et al.* 2010). Surprisingly little is known of the impact of invasive plants on native insect populations; although there is some evidence that the invasive herb *Tradescantia fluminensis* reduces abundance of epigaeic invertebrates (Standish 2004), but has no impact on beetles or fungus gnats (these instead correlated with vascular plant richness and diversity regardless of presence of exotic flora – Crisp *et al.* 1998; Toft *et al.* 2001).

Aside from introduced species, perhaps the greatest threat to native terrestrial insect populations and communities remains habitat loss and modification through human impact, with some groups confined to small areas (Cromwell Chafer, *Prodontria lewisi* Broun, Watt 1979) or forest fragments, like Radar Bush in Northland (Buckley & Bradler 2010). This can be through either wholesale change to a particular parcel of land (e.g. through land clearing) or more minor changes that have ripple effects through the ecosystem (e.g. erosion, trampling, and grazing of native vegetation by livestock). Formerly, subsidies were provided by the New Zealand government and access to cheap loans given to individuals to clear forest to expand agricultural enterprises and for the wood-chipping industry (Howarth & Ramsay 1991). Thankfully, the removal of these incentives has significantly slowed the decline and loss of habitat. Nevertheless, threats from these processes remain and native habitats continue to be disturbed by human practices (be they agriculture, forestry, mining or urban development). It remains unclear whether New Zealand's insect fauna is suitably protected to cope with these ongoing threats; however, recent work suggests the endangered ground beetle, *Holcaspis brevicula* Butcher, whose native range has been fragmented by human practices, has expanded out into forestry plantations that inadvertently provide suitable habitat for it and other beetles (Brockerhoff *et al.* 2005; Pawson *et al*. 2008). Clearly some of New Zealand's insects can adapt to ongoing human influence, but we expect this phenomenon to be the exception.

The life aquatic

The conservation status of many New Zealand freshwater insects is poorly known, and despite a review of this theme in the 1990s (Collier 1993), little new information on this topic has come to light in the years since. Collier (1993) recognised 154 species of insects inhabiting surface waters that possess restricted distributions, as well as 20 species from underground systems and 36 isolated on offshore islands. Localised distributions clearly put taxa at risk of extinction due to habitat change and more data are needed to appropriately assess risks to these taxa. Of those threats to freshwater taxa that have been established, it is abundantly clear that habitat loss and modification is the greatest cause for concern. Loss and modification of freshwater ecosystems can take many forms and include: degradation and loss of riparian zones, channel environments and catchment properties, changes to flow regimes, declines in water quality (increased sediment load, decreased pH, increased nutrient load, altered thermal regimes), and increases in pollution (Collier 1993). Often compounding effects of such impacts is the dendritic nature of river networks that means upstream impacts are cumulative on downstream sections. There are several driving factors behind the modification of aquatic environments, not least of which are urbanisation, mining, forestry, and agriculture. Moreover, grazing of livestock has also been shown to have a dramatic effect on bank damage, riparian degradation, and associated increased sediment load – all of which have a marked effect on insect communities (Quinn *et al.* 1992).

New Zealand's freshwater taxa have also been dramatically affected by exotic invaders, especially fish (most notably brown trout, *Salmo trutta* L.), snails, and macrophytes. The introduction in the mid–late 1800s of brown trout and other salmonids to New Zealand waterways for the angling community is thought to have increased predation pressure on some larger native aquatic invertebrates, including mayfly and stonefly nymphs (Collier 1993). The invasive snail, *Physa acuta* (Draparnaud), has displaced a native species in many areas (Winterbourn 1973). Exotic aquatic flora cause changes to water quality, contribute to habitat degradation, and alter flow regimes by clogging waterways. Invasive macrophytes have also been shown to significantly alter species composition in the littoral zone of lakes and increase the total density, richness, and diversity of insect inhabitants (Kelly & Hawes 2005). In contrast, clogging of waterways by some aquatic weeds can sometimes support an increase in abundance in native snails, Trichoptera and Diptera, possibly by providing an additional food resource, but also perhaps because the weeds exclude predators and provide secluded areas for larval development.

Future prospects and the spectre of changing climate

New Zealand, paradoxically, is well-placed to deal successfully with conservation issues concerning its insect fauna (New & Samways 2013). The public, over many years, has embraced conservation principles and become enamoured with many of New Zealand's iconic insect species such as glow-worms and weta (Cranston 2010). Furthermore, the Department of Conservation (DOC) has been instrumental in managing many of the risks discussed above. For example, although a significant portion of New Zealand's native habitats are privately owned and of uncertain conservation status, protected areas now constitute around 30% of the landmass, including a growing number of 'mainland islands', managed by DOC (Saunders & Norton 2001), local government, trusts, and various citizens groups. This is a remarkable achievement and serves to highlight the importance placed on maintaining significant blocks of continuous habitat. Likewise, urban reserves (smaller patches of native forest in an urbanised landscape) have been shown to be a significant potential refuge for insect diversity in an increasingly modified landscape, thus highlighting the importance of green areas in the urban mosaic (Watts & Lariviere 2004). Of course, passive protection is often insufficient to combat the decline of native species (Clout 2001) and even within protected areas exotic species roam freely.

Mammal invaders are trapped and baited throughout the mainland to control numbers and eradication programmes have been successful on many offshore islands and within the mainland islands (Saunders & Norton 2001; Clout & Russell 2006). For example, removal of rats and weka from the Chetwode Islands in Pelorus Sound resulted in increases in the proportion of active adult weta in a given habitat and the proportion of adults in the population, along with changes to population dynamics and habitat use associated with lowered predation (Rufaut & Gibbs 2003). Several methods of control have been implemented for *Vespula* wasps, including biocontrol using parasitoid wasps (Beggs & Rees 1999) and poison sprays (Beggs *et al.* 1998, Toft & Rees 1998); however, none has succeeded on broad spatial scales (Beggs 2001). Control methods for many invasive plants currently are often long-term and laborious, involving mechanical removal, spraying of often potent herbicides, monitoring, and sometimes grazing with livestock to prevent re-emergence (Ogle *et al.* 2000; Hofstra *et al* 2001). In contrast, biocontrol measures for invasive plants are considered to be quite effective in New Zealand (Fowler *et al.* 2000).

Arguably the most pressing concern for New Zealand's insect fauna, and particularly the alpine taxa, is the influence of climate change. Already, evidence for the influence of changing climate is abundant in New Zealand, with dramatic reductions in many glaciers (Chinn 1996) and rising timberlines (Wardle & Coleman 1992). Unfortunately, there has been little work conducted to identify directly the likely impacts on native insects from future climate change; however, lessons can be learned from historical patterns outlined in previous sections. If future climate change drives higher temperatures and reduced rainfall across New Zealand as appears to be the case (Plummer *et al.* 1999), it is anticipated that susceptible habitats will respond as in the past. That is: closed, wet forest will retract into isolated refugia; dry grassland will expand across the lowlands; cold-adapted taxa will be limited to mountain-tops; and, in the extreme case, taxa that cannot shift distribution will be driven to extinction (Wardle & Coleman 1992). Moreover, climate change may also indirectly impact on freshwater habitats via increased temperatures and more frequent droughts that increase sediment loads and reduce flows. It has been suggested that, depending on the degree of temperature rise, several hundred alpine vascular plant taxa could be lost, along with a substantial proportion of existing alpine 'islands' (Halloy & Mark 2003). Taken together, this clearly presents a significant risk not just to the alpine insect fauna but to that of New Zealand as a whole. There exists a growing need for fundamental research into the potential impacts of climate change on New Zealand insects and whether there are any suitable mitigation strategies that could be put in place. The incredible endemism of New Zealand's insect fauna is worth protecting and concerted effort should be put into ensuring their survival into the future.

PROSPECTUS

We have reviewed some of the major historical processes that have shaped the diversity and special features of the New Zealand insect fauna. While great strides have been made in understanding the origins, diversification, and adaptive evolution of the insect fauna over recent years, there are still significant gaps in our knowledge. Importantly, these gaps impede our ability to manage and protect the insect fauna for future generations. However, there are also great opportunities, not only for increasing knowledge and understanding of individual lineages, but also for using New Zealand insects as model systems to test more generally outstanding hypotheses from the field of evolutionary biology.

One of the most critical knowledge gaps is taxonomic: the insect fauna remains too poorly known (Leschen *et al*. 2009; Lester *et al*. 2014). Even in the 21st Century, large insects from the usually better known terrestrial macrofauna, such as large orthopteroids (e.g. Jewell 2007; Buckley & Bradler 2010; Taylor Smith *et al*. 2013), are being discovered and described. The taxonomic knowledge gaps in the hyperdiverse microfauna are orders of magnitude greater. Furthermore, there are also significant gaps in our understanding of the distributions of species and patterns of species richness at local and national scales. This can only be remedied with specialised collecting techniques, which are required for most insect groups (e.g. Seldon & Beggs 2010), systematics research, and dramatically increasing the degree of curation and data accessibility in collections (e.g. Ward 2012). Targeted surveys of poorly known areas, including the alpine zone, are required urgently and our own collecting on offshore islands, often considered “well collected”, frequently yields new species and even genera (e.g. Théry & Leschen 2013). Family group records that are new to New Zealand are made regularly (e.g. Grebennikov & Newton 2008; Ruta *et al*. 2011). Only by building the taxonomic framework along with comprehensive information on geographic distributions will we be in a position to construct and test detailed hypotheses on the evolution of large elements of the insect fauna.

There are essentially endless opportunities for advancing taxonomic knowledge on the New Zealand insects.

A robust phylogenetic framework is a prerequisite for any evolutionary study (e.g. Felsenstein 1985), and numerous phylogenies have emerged from studies on New Zealand insects that are discussed and cited in this review. However, there is a clear bias in these studies towards the insect macrofauna, such as weta, stick insects, cicadas, and the larger beetles. Clearly neglected are hyperdiverse groups, especially those associated with dead wood, leaf litter, and soil microhabitats, including Oecophoridae moths, Microgastrinae wasps, a number of Diptera families, and many Coleoptera groups, especially Staphylinidae, Curculionidae, Tenebrionidae, and Zopheridae (see Watt 1975; Klimaszewski *et al*. 1996; Lord & Leschen 2014). Even among less diverse invertebrate groups (e.g. Leschen 2006; Boyer & Giribet 2010) from the soil, leaf litter, and dead wood habitat, only a few groups have been examined phylogenetically with absolute or relative divergence time estimation and comprehensive sampling of relevant lineages from other land masses to determine their biogeographic origins, including Cyphophthalmi mite harvestment (Boyer & Giribet 2009), Onychophora (Murienne *et al*. 2014), and earthworms (Buckley *et al*. 2011). None of these groups are from the Insecta, despite the hyperdiversity of insects from soil and saproxylic habitats in New Zealand (e.g. Hoare 2005, 2010; Leschen 2006; Lord & Leschen 2014). We believe that such groups will contain a greater number of archaic lineages relative to more arboreal, winged insects from the macrofauna, many of which show more recent ancestry (e.g. Brown *et al*. 1999; Arensburger *et al*. 2004). Given that the microfauna contain the bulk of New Zealand's insect diversity, it is premature to infer general patterns about the origin and evolution of the insect fauna, until well-supported phylogenetic reconstructions from these groups are obtained.

Extensive progress can also be made through exploiting the information held across the existing, multiple phylogenies. Model-based biogeographic methods exist that are able to draw general patterns from simultaneous analysis of multiple phylogenies that include taxa distributed across common areas (e.g. Sanmartín & Ronquist 2004; Ree & Sanmartín 2009). Comparative biogeographic methods used by Sanmartín and Ronquist (2004) to infer different biogeographic histories across sets of taxa from the Southern Hemisphere are exemplary. Meta-analyses examining dozens of phylogenies for New Zealand insects and other organisms will allow detection of what organismal characteristics, such as taxonomic group, dispersal ability, and ecological trophic level have most strongly influenced insect biogeographic history.

A major technical challenge for gaining greater insight into the ages of different insect lineages in New Zealand is obtaining accurate divergence times. The problematic nature of this has been well covered elsewhere, but includes problems with uncertainty and error in branch length estimation (Buckley *et al*. 2001b), selection and testing of an appropriate relaxed clock model (e.g. Baele *et al*. 2013), and the confounding effects of extinction (e.g. Waters & Craw 1996; Sharma & Wheeler 2013). However, it is widely acknowledged that the greatest potential source of error in molecular dating studies is the reliability of calibrations (Parham *et al*. 2012). Because the New Zealand fossil insect fauna is relatively poor, largely restricted to Quaternary deposits (e.g. Marra 2008) but with a growing number of records from the late Oligocene and early Miocene (Kaulfuss *et al*. 2010), there are few opportunities to internally calibrate phylogenies. One potential solution to this problem is to integrate New Zealand and relevant outgroup lineages into global phylogenies of higher level taxa that are often calibrated with a larger number of fossils. This is because it is easier to assign fossils to a higher level taxon than a lower level taxon such as a genus. This approach was taken by Perrie and Brownsey (2007) to establish the ages of a range of New Zealand fern lineages. The growing number of large phylogenomic data sets with multiple fossil calibrations offers an opportunity to achieve this for New Zealand insect groups. A related approach in the absence of internal fossil taxa is to use an estimated date for the age of a higher level taxon from a multi-calibration phylogenomic study to constrain the age of that lineage in a molecular dating study of New Zealand lineages. This approach was used by Murienne *et al*. (2014) to date the age of lineages of Onychophora, including those from New Zealand. The rapidly growing number of well-calibrated, phylogenomic studies offer great potential to gain increased knowledge of the absolute ages of New Zealand lineages and then relate these ages to various ecological and historical processes.

A further promising avenue of research is to explore the characteristics of lineages that have enabled them to speciate. This requires detailed understanding of the adaptations allowing species to survive in their environments in addition to the characters that maintain species integrity. Two study systems that have provided deep insights into basis of New Zealand insect speciation are the cicada genus *Kikihia* Dugdale and the native tortricid moth genera *Planotortrix*

Dugdale and *Ctenopseustis* Meyrick. Like all other cicadas, *Kikihia* species have species specific songs (e.g. Fleming & Dugdale 1984; Marshall *et al*. 2008). Molecular phylogenetic studies have shown that these songs can evolve rapidly in isolated populations (Marshall *et al*. 2011). Although song differences correlate well with genetic lineages, in many cases these do not appear to have completely isolated species, with hybrid zones characterised by introgression of mitochondrial DNA and intermediate song phenotypes being observed (Marshall *et al*. 2008, 2011). Similarly, species within the moth genera *Planotortrix* and *Ctenopseustis* can be defined on the basis of unique pheromone blends (Newcomb & Gleeson 1998), yet the species are very closely related (Langhoff *et al*. 2009). Genomic studies have shown that these differences are the result of differential expression of desaturase genes involved in pheromone biosynthesis in females (Albre *et al*. 2012). On the male side of this interaction, accelerated evolutionary rates of odorant receptors in different lineages are likely responsible for tracking the evolution of the female pheromone signal (Carraher *et al*. 2012). By examining the genetic basis of character systems in other insect lineages, and placing this in a phylogenetic context, we will gain greater insight into the processes that have generated the diversity of New Zealand insects.

Determining the most important organismal characteristics to have influenced biogeography requires extensive knowledge on the biology and ecology of individual insect species, natural history information that is often contained in systematics treatments and in supplementary information in community ecology studies. Specific studies into the underlying biology of various insect groups are underway, including diet and feeding ecology (e.g. Kadowaki *et al*. 2011b; Larsen & Burns 2012; Wehi *et al*. 2013), cold tolerance physiology and genetics (e.g. Sinclair *et al*. 1999; Dunning *et al*. 2014; Minards *et al*. 20014), symbiotic relationships (e.g. Dhami *et al*. 2013), behavioural ecology (e.g. Kelly 2008; Painting & Holwell 2014), herbivory (e.g. Kelly *et al*. 1992), comparative phenology (e.g. Gibbs 2014) and functional morphology (e.g. Painting *et al*. 2014; Yavorskaya *et al.* 2014). Detailed studies of individual taxa lead to great insights, but contrasting traits among related species in a phylogenetic framework will lead to the greatest advances in understanding the evolution of the insect fauna. Such studies will enable us to answer questions concerning how often convergent evolution occurs in species radiations, whether single character state (or key innovations) transformations or combinations of characters have triggered adaptive radiations, and why some lineages have radiated extensively compared with others that are depauperate (e.g. Losos 2010).

The massive increase in the output of DNA sequencing technologies in the past 10 years has been striking. This has significantly impacted all fields of biology, and evolutionary biology is no exception (Ekblom & Galindo 2011; McCormack *et al*. 2013). High throughput DNA sequencing allows a much greater number and range of markers to be applied to a given organism through species-specific marker development (e.g. Abdelkrim *et al*. 2009) or more direct methods such as 'Genotyping by Sequencing' (Elshire *et al*. 2011; Narum *et al*. 2013) and sequence capture (e.g. Faircloth *et al*. 2012; Lemmon *et al*. 2012). The large-scale data sets that result from these technologies offer vastly improved estimates of phylogeny, divergence times, genetic diversity, and gene flow within and among species, and they are already being applied to the New Zealand insect fauna (e.g. Hale *et al*. 2010; Dunning *et al*. 2013b, 2014). A particularly promising research avenue that these methods open up is determining the genetic basis of phenotypic traits and therefore improved understanding of their evolution (e.g. Storz & Wheat 2010; Dalziel *et al*. 2009). Methods such as RNA sequencing allow gene expression to be measured in an organism under different treatment regimes, allowing inference of the genetic basis to the response to specific environmental conditions (e.g. Dunning *et al*. 2014). Other methods, such as RNA interference and *in vivo* expression in cell lines, allow the function of specific genes to be directly determined (e.g. Albre *et al*. 2012), so the genetic basis of function can be examined phylogenetically. The expansion of functional genomics to further elements of the New Zealand insect fauna will facilitate significant advances in our understanding of the evolution of adaptation and how insect species have evolved into unique New Zealand environments.

In summary, no single method or avenue of research is a panacea for understanding the origin and evolution of the New Zealand insect fauna, and a synthesis of systematics, ecological, phenotypic and genomic research is required. The New Zealand fauna is an important part of the global fauna, in age, diversity, and uniqueness. The well-circumscribed geography and improved understanding of geological history means New Zealand is well-suited as a model ecosystem and continues to attract a wide variety of scientists, locally and globally. New Zealand is also a naturally inspiring place with a beautiful range of habitats across a rather small and accessible land area, vast in its rich diversity and offering unlimited evolutionary questions.

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Figure Captions

Fig. 1. Habitus illustrations of four notable New Zealand insects. (a) *Deinacrida rugosa* Buller, a giant weta and one of the largest orthopterans in the world. This species was formerly widespread on the mainland of North Island, but is now restricted to a few predator free offshore island. (b) *Chalcodrya variegata* Redtenbacher a species from the endemic beetle family Chalcodryidae. This species is associated with the sooty mould fauna. (c) *Micrarchus*nov. sp. 2, an undescribed species from northwest Nelson and Westland that is restricted to high alpine areas. Genomic studies are revealing unique adaptations to these harsh conditions. (d) *Zelandochlus latipalpis* Brundin, the 'Ice Worm', a flightless non-biting midge species known from New Zealand's glacier fields. This taxon is thought to have diverged from its sister in the Oligocene. Illustrations (a, (b), and (c) by Des Helmore (© Landcare Research). Illustration (d) reproduced from Brundin (1966).

Fig. 2. Habitats containing notable New Zealand insect species. (a) The fast-flowing Cleddau River slices a path through Nothofagaceae forest in Fiordland. This river is typical of many New Zealand freshwater ecosystems and is inhabited by many endemic aquatic insect groups. (b) Chancellor Shelf, Fox Glacier, home to a wide variety of alpine lineages, many showing unique adaptations to survive in the alpine zone. (c) Carnley Harbour, as seen from Adams Island in the subantarctic Auckland Islands. (d) Kanuka-Broadleaf forest, Karikari Peninsula, Northland. Many of these volcanic uplands in Northland were once islands and still harbour endemic species, witnessing their allopatric past. Photo credits: (a) M. Krosch, (b–d) R. A. B. Leschen.

Fig. 3. Map of New Zealand with place names mentioned in the text marked. The inset map shows the New Zealand region including offshore islands.

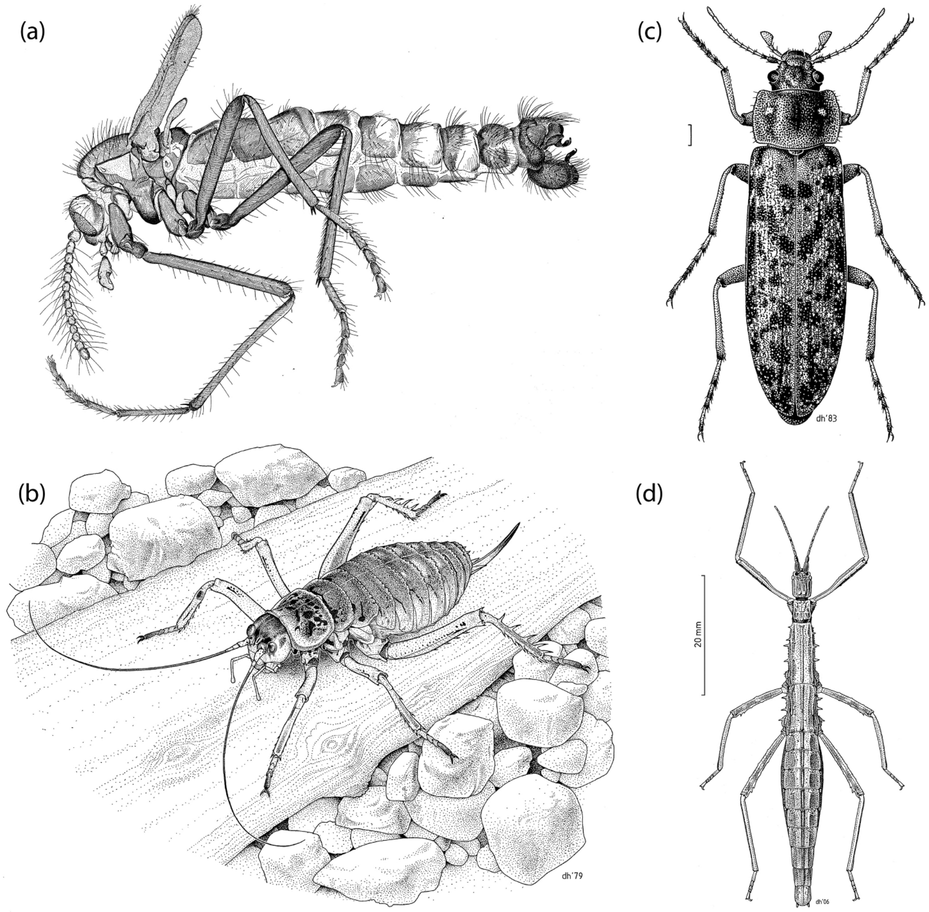

Figure 1
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Figure 2
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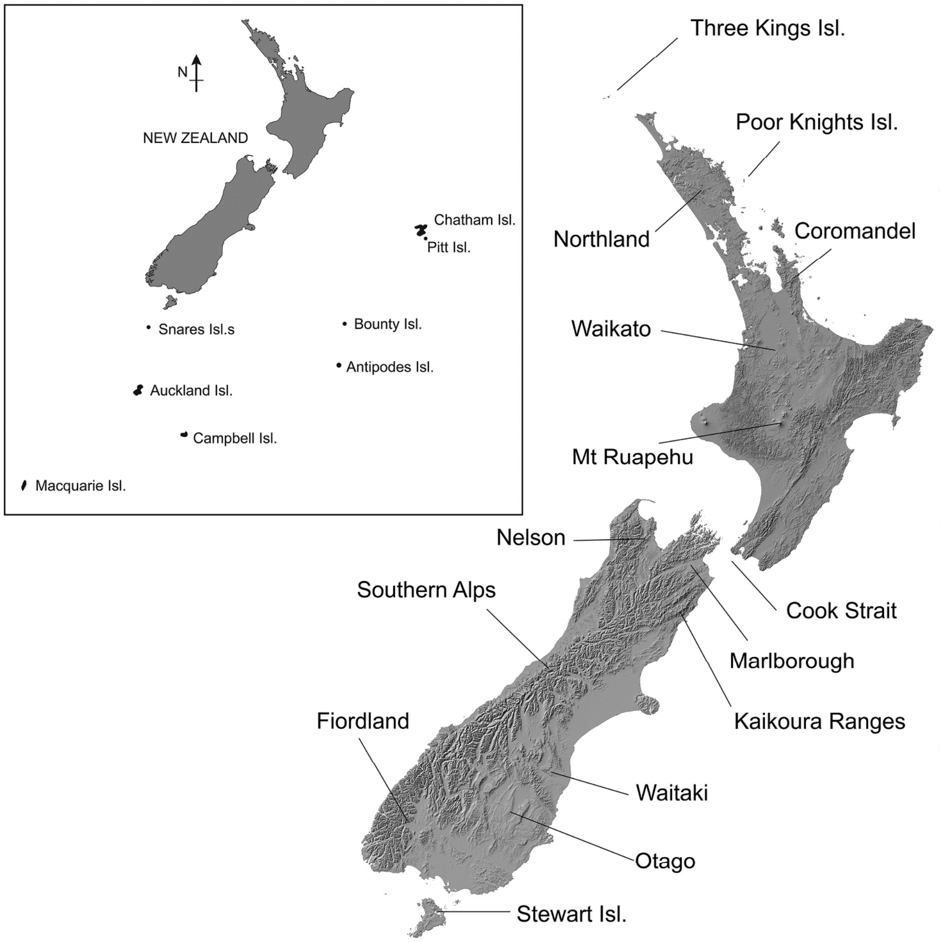

Figure 3
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