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THE UNIVERSITY OF AUCKLAND

MASTERS THESIS

**Optimising Capture Methods for
the Evaluation of Parasitoid Wasp
Diversity**

Thomas Edward SAUNDERS

*A thesis submitted in fulfilment of the requirements for the degree of
Master of Science*

School of Biological Sciences

Faculty of Science

November 30, 2016

*Dedicated to all those who have ever contributed to the study of the natural world.
I have stood on the shoulders of giants, and I am truly grateful for the view.*

ABSTRACT

Parasitoid wasps are mega-diverse, ecologically dominant, but poorly studied components of global biodiversity. Despite their intensive application within pest management as biocontrol agents, little is known about native species. To understand their basic biology they must be collected in sampling programs. However, invertebrate surveys are increasingly subject to funding and time constraints that often preclude complete faunal inventories. In order to maximise the efficiency and reduce the cost of their collection, the application of optimal sampling techniques within a Rapid Biodiversity Assessment framework is proposed. Two sites in the Waitakere Ranges were sampled three times over the summer. An intensive sampling effort of 840 Malaise-trap-days over a three month period was used to determine the relationship between sampling effort and observed species richness. Rarefaction techniques and non-parametric estimators were used to predict true species richness and to evaluate the completeness of sampling. Results show that an intensive Malaise-trapping regime over the summer can capture two-thirds of parasitoid wasp species present. Sampling recommendations are provided to guide optimal usage of Malaise traps for both ecological studies and faunal inventories. Modern taxonomic methods are reviewed and a new species of parasitoid wasp is described, representing the first New Zealand species from the genus *Lusius* (Ichneumonidae: Ichneumoninae). Morphological measurements confirm the new species represents a significant range expansion for the genus. Greater collaboration between ecologists and taxonomists is encouraged, in order to make more efficient use of resources, data, and expertise unique to each discipline. This is the first study to investigate the relationship between sampling effort and parasitoid wasp diversity in New Zealand. It shows that very high sampling effort fails to catch all species present. Parasitoid wasps are known to be keystone species that show promise as indicators of environmental quality and as surrogates for the diversity of other taxa. The development of optimal sampling strategies will therefore provide an important foundation for their future study.

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1

Biodiversity Science in an Age of Extinction

Degithina sp.

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1. Introduction

1.1 Global Species Diversity

Biodiversity is "the total variety of living organisms on earth" (Secretariat of the CBD, 1992, pg. 3). Biodiversity can be broken down into a nested hierarchy consisting of three levels: genes, species, and ecosystems (Harper & Hawksworth, 1994). Genetic diversity describes the proportion of polymorphic loci in a genome, the number of alleles at a locus, and the probability of heterozygosity at a particular locus (Templeton, 1994). Species diversity represents the number of species (species richness) and how the abundance of each species relates to the others (species evenness) (Gaston, 1996a). Ecological diversity describes the differences between 'ecological units,' which are usually delimited by their physical characteristics and the communities of species that are typically found within them (e.g. coral reefs, kauri forests) (Groombridge, 1992). Despite the myriad ways of measuring and evaluating biodiversity across these levels, species richness has emerged as an all-encompassing shorthand for biodiversity (Gaston, 1996b). This is largely because species richness is simpler to understand than gene pools or the structuring of ecosystems, especially for non-specialists and policy makers (May, 1994).

Approximately 1.95 million species have been catalogued and described over the last three centuries (ISSE, 2011). While impressive, this number likely represents a fraction of total species diversity (Raven & Wilson, 1992). Estimates of the total diversity of life vary widely as a function of the methodologies that are used to obtain them. For example, Erwin (1982) proposed an upper figure of 30 million species based on his experience measuring arthropod diversity in the tropics. More recent estimates have been considerably lower, with one study estimating a total of only 2 million species based on projected rates of species descriptions (Costello et al., 2011). These figures should be considered as upper and lower bounds. The majority of estimates fall somewhere between 5-10 million species, but this is still an area of active debate (Stork et al., 2015; Wheeler et al., 2012; Gaston, 1991).

What is clear, is that invertebrates dominate every measure of global species diversity (Chapman, 2009). The most recent estimates place their total richness at

7 million species, of which 80% are insects (Stork et al., 2015). However, despite comprising the largest, and perhaps most important component of biodiversity, invertebrates are rarely included within conservation strategies (Kremen et al., 1993). The reasons for this are complex (see New, 1998), but they ultimately stem from three areas: a lack of public and governmental understanding of their importance (social); a lack of biodiversity assessment funding (economic); and a lack of taxonomic capability required for the description and identification of taxa (professional). When these barriers are foregrounded against rapid environmental change and species extinctions, it becomes clear that they represent serious challenges to the study of invertebrates.

1.2 Measuring the Biodiversity Crisis

Species extinctions are an inevitable evolutionary process, but there is overwhelming evidence that the current rate of biodiversity loss is mostly due to anthropic activity (MEA, 2005a; Kim, 1993). Certain human activities, particularly those resulting in habitat destruction, have led to environmental decline with associated impacts on biodiversity (Gaston, 1996b). A growing awareness of the impacts of human modification to natural ecosystems has influenced the discourse surrounding a biological diversity 'crisis' among the scientific community (Wilson, 1985, 1988). The resulting public, academic, and governmental pressure have encouraged international efforts to assess and monitor the potential impacts of further declines on different indices of biodiversity.

The Millennium Ecosystem Assessment was initiated in 2001 to "assess the consequences of ecosystem change for human well-being and the scientific basis for action needed to enhance the conservation and sustainable use of those systems" (MEA, 2011). A number of reports have been released under its auspices to these ends. The MEA 'Biodiversity Synthesis' (2005a) presented a set of case studies that demonstrate how fluctuations in biodiversity that surrounds human settlements can have negative outcomes for human wellbeing and self-determination. It found that species diversity is directly related to an ecosystem's ability to be resilient when under pressure from human activities or climate change. In other words, "biodiversity and human wellbeing are inextricably linked" (p.iii).

The 'Synthesis of Biodiversity and Health' (MEA, 2005b) corroborated these findings by emphasising the practical consequences of biodiversity loss on

human health, which are particularly severe in developing nations. It concluded that the maintenance of biodiversity is essential for the health and wellbeing of the human species. An example of this concept is illustrated by recent experimental work showing that increased levels of biodiversity lead to decreasing pathogen infection rates among amphibians in wetland communities (Johnson et al., 2013). A larger diversity of host assemblages inhibit pathogen transfer to frogs, suggesting that increased levels of biodiversity produce a buffering effect to prevent the spread of disease. This has important implications for pathogen transfer to and within human communities, especially those within developing nations. By maintaining high levels of biodiversity, disease rates may be stabilised or even reduced in these areas, which would result in considerable health and economic benefits for the human inhabitants.

A different approach to understanding the practical importance of biodiversity is the application of economic theory to the valuation of biodiversity. The Economics of Ecosystems and Biodiversity report was commissioned for this reason (TEEB, 2010). Its principal aim was to highlight the economic linkages between ecosystem services, conservation of the natural environment, and human prosperity. The report found that many of the world's key ecosystems have been degraded to the point where their ability to provide essential services is severely reduced. This is concerning, because biodiversity contributes to ecosystem resilience, or the capacity of an ecosystem to continue supplying services during periods of environmental change. The report acknowledged that market forces contribute to the externalising of costs onto the environment in a way which has a disproportionate impact on rural, indigenous, and marginalised peoples who tend to depend more on natural resources for daily survival. In sum, a better understanding of the natural sciences that both underpin, and are impacted by, economic decision-making, is a top priority for sustainable development.

Agriculture is recognised as both a key component of economic development but also one of the leading causes of biodiversity loss (TEEB, 2010). There is mounting evidence that incorporating greater levels of biodiversity into agricultural systems can have a positive effect on the sustainability and economics of food production (Kremen & Miles, 2012). Benefits include: better quality topsoils; more efficient pest, weed, and disease management; and increased pollination services. The maintenance of biodiversity in agroecosystems produces fewer adverse environmental impacts than lower diversity systems, with only a

minor drop in average productivity (Kremen & Miles, 2012). Experimental evidence shows that greater levels of biodiversity supplement natural pest control by providing floral resources for predators and parasitoids (Géneau et al., 2012). Géneau and colleagues showed that greater plant biodiversity in cropping systems led to higher parasitization rates of cabbage moths by their parasitoid wasp *Microplitis mediator* Haliday. The floral resources conferred their benefits selectively, with only the parasitoids enjoying increased longevity from their nectar-feeding (Géneau et al., 2012). This is one of many examples that highlight the economic importance of parasitoid wasps. They belong to one of the most diverse and important orders of insects, the Hymenoptera.

1.3 Hymenoptera: Megadiverse and Understudied

Hymenoptera is one of the most diverse, widespread, and ecologically significant groups of animals on the planet, comprising bees, ants, wasps, and sawflies (Mason & Huber, 1993). Around 145,000 species are currently described (Huber, 2009) with an estimated total richness of around 600,000 species (Gaston, 1991). Representing an estimated 10% of all living species (Sharkey, 2007), Hymenoptera may be the most diverse order in both tropical and temperate regions (Stork, 1991). As a diverse and widespread order, the Hymenoptera exert a considerable influence on human populations.

The Hymenoptera contains a considerable number of important pest species (LaSalle, 1993). Among these, highly invasive 'tramp ants' have exploited trade and commerce pathways to disperse far outside their native range. For example, the Argentine ant, *Linepithema humile* Mayr, is an aggressive species of tramp ant that rapidly invades new areas and displaces native ants through interference competition (Rowles & O'Dowd, 2006). Social wasps can also be highly invasive, damaging, and are difficult to eradicate once established. Vespid wasps (Vespidae) have been shown to compete with native birds and invertebrates in New Zealand beech forests by monopolising the honeydew produced by endemic scale insects (Beggs, 2001). Sawflies and woodwasps can have devastating impacts on crop yields. For example, the wheat stem sawfly (*Cephus cinctus* Norton) is responsible for hundreds of millions of dollars in annual crop losses in North America as a result of destruction caused by the burrowing action of its larvae inside host plants (Beres et al., 2011). Chemical controls and resistant cultivar breeding have proven

ineffective against the sawfly, but two species of parasitoid wasp show promise as biocontrol agents (Beres et al., 2011).

The Hymenoptera contains more species beneficial to humans than any other order (Sharkey, 2007). While some ant species are highly visible and damaging, most make significant contributions to important ecosystem services such as decomposition and nutrient cycling (Holldobler & Wilson, 1990). Perhaps the most well-known beneficial group of species in the world are the bees. Bees are dominant pollinators of the earth's flowering plants including the food, fibre, and forage crops that human societies rely on, and they also produce a variety of useful products such as wax and honey (Michener, 2000). Parasitoid wasps are another important beneficial group, particularly in biocontrol, where many parasitoid species have been used to successfully manage other insect pests in agroecosystems (Huber, 1993). The financial value of naturally occurring pest control (largely down to parasitoid wasps), has been estimated at US\$4.5 billion annually for the United States alone (Losey & Vaughan, 2006). Walker et al. (2010) highlight the important contribution that *Cotesia kazak* Telenga makes to the integrated pest management of *Helicoverpa armigera* Hübner, a significant crop pest in New Zealand and around the world. When infestation levels in tomato fields surpass a predetermined economic damage threshold, spray recommendations are made based on current levels of parasitism (65% of collected host larvae in this study). The use of parasitoids has contributed to a 95% reduction in insecticide application within this cropping system.

1.4 The Importance of Parasitoid Wasps

Askew (1971) provided one of the earliest comprehensive examinations of parasitic insects, describing parasitoids as "insect protelean parasites that eventually kill their hosts." Subsequent definitions refined the term and removed the requirement that a parasitoid be an insect, for example, "an organism which develops on or in another single ('host') organism, extracts nourishment from it, and kills it as a direct or indirect result of that development" (Eggerton & Gaston, 1990). However, the vast majority of parasitoids are wasps, and conversely, over 80% of Hymenoptera are parasitoids. For this reason I refer to 'parasitoid wasps' as parasitoids from now on.

Female parasitoids use their highly developed ovipositor to lay eggs near, on, or inside their hosts, even drilling through wood or plant tissue when necessary (Godfray, 1994). Parasitoids display a variety of reproductive strategies (Quicke, 2015); ecto/endoparasitoids refer to those which lay eggs onto/inside their hosts; while idiobionts/koinobionts are parasitoids that halt/allow the continued development of their hosts. Ectoparasitoids may have as many as fifty different host species (Hawkins & Sheehan, 1994). Endoparasitoids generally have a narrower range of hosts due to the physiological adaptations required to live inside another insect (Gauld, 1984). Hyperparasitoids occupy the fourth trophic level, parasitising the larvae of primary parasitoids, which are themselves feeding on a host organism (Mommott & Godfray, 1994).

Parasitoid species diversity is immense worldwide (Veijalainen et al., 2012). In Costa Rica, Gaston & Gauld (1993) caught 150 species from a single subfamily over a five year period. Similarly high levels of richness have been reported from South American lowland rainforest (Sääksjärvi et al., 2004). Unusually, parasitoid diversity is also very high in temperate regions. For example, Fraser et al. (2007) caught a total of sixty species from four subfamilies across fifteen farm woodland sites in the Vale of York, UK. Over 300 species of Ichneumonidae were caught in a suburban English garden over several years, representing 16% of the described British fauna (Owen & Owen, 1974).

Parasitoids are major contributors to terrestrial foodwebs, and their removal has flow on effects to other organisms (Mills, 2005; LaSalle, 1993; LaSalle & Gauld, 1991). Parasitoids are also highly extinction prone because they are specialised, heavily reliant on the diversity of their host populations, and they occupy upper trophic levels (Shaw & Hochberg, 2001). Many regional faunas contain high rates of endemic species, have many species which are present in naturally low numbers, and contain species which are sensitive to environmental disturbance (LaSalle, 1993). These attributes make them ideal candidates as bioindicators, but despite some promising leads, their use is currently inhibited by "the general difficulty with identifying many to species level" and the fact that "for most areas there are few reliable baseline studies" (Quicke, 2015). These issues are particularly relevant for the New Zealand fauna.

1.5 New Zealand's Parasitoid Fauna

Insects constitute almost half of New Zealand's total recorded biodiversity of 35,000 species (Gordon, 2009; DoC, 2000), and only about 50% of the total number of insects are estimated to have been described (Cranston, 2010). New Zealand's invertebrate fauna reflects a uniquely Gondwanan biogeography, and 90% of its species are found nowhere else in the world (New & Samways, 2014; Watts et al., 2012; McGuinness, 2001). Evolutionarily distinctive higher taxa continue to be discovered in New Zealand, for example, the parasitoid wasp family Maamingidae (Early et al., 2001).

There are currently around 700 recognised species in New Zealand, with a further 900 known to genus, from a total fauna estimated to be in excess of 3,000 species (Landcare Research, 2016). The New Zealand Hymenoptera fauna is unusual when compared to other regions (Berry 2010). For example, fourteen families are represented only by introduced species, including the Vespidae, Apidae and Sphecidae, while woodwasps are naturally species poor (Ward & Edney-Browne, 2016; Valentine, 1970). New Zealand has only 130 aculeate species out of a global fauna of 49,000, and about half of these are exotic (Gordon, 2009). Of the 42 bee species known from New Zealand, 28 are endemic, 5 originated in Australia, 1 from Europe, and the rest were introduced deliberately from the Northern Hemisphere (Donovan, 2016; Donovan, 2007). The ant fauna is unusually depauperate, with only 11 endemic species out of the 37 known to be established (Don, 2007). On the other hand, New Zealand is known to contain over 10% of the world's Myrmecidae (Noyes & Valentine, 1989). Parasitoid wasps clearly dominate the New Zealand Hymenoptera fauna, but paradoxically, they are the least studied group (Ward et al., 2012).

Surprisingly little is known about New Zealand's parasitoid fauna, and present data is patchy at best (Berry, 2007). There are estimated to be around 3,000 species of parasitoid wasp in New Zealand, but only one fifth are currently described (Berry, 2010). The Chalcidoidea is the only parasitoid superfamily known reasonably well in NZ (Berry, 2010; and see 'Fauna of New Zealand' series). In the most comprehensive assessment of New Zealand's biodiversity to date, Berry (2010) highlights the Ichneumonoidea as one of the most economically and ecologically important groups of animals, but considers their unresolved taxonomy and lack of diversity data to be an obstacle to their inclusion in conservation planning and sustainable pest management programs.

In comparison to other NZ invertebrate groups, the history of research into the Hymenoptera fauna has been characterised by a lack of resources and expertise for quite some time (Valentine, 1970; Pilgrim, 1970). The first study was a description of three ichneumonids in 1775 by Fabricius, with specimens collected during the voyage of *Endeavour* in 1769 (Valentine, 1970). Other authors such as W. H. Ashmead, P. Cameron, and F. Smith described the majority of the 100 or so species recorded up until the 20th century.

Most work on parasitoids in New Zealand has related to the importation of biological control agents (Cameron, 1989; Charles, 1998). As public pressure over pesticide use and residues intensified, biological control became established as a key part of New Zealand's Integrated Pest Management strategy (Cameron, 1989). Imported parasitoid wasps have been involved in major programs to control *Sirex noctilio* F. in radiata pine plantations, and *Vespula* wasps. Beggs (2008) showed that the parasitoid introduced to control *Vespula* wasps (*Sphecophaga vesparum vesparum* Curtis) was not having the predicted impact. Further work has shown that the parasitoids were derived from a single female belonging to a genetic strain now known to be outside the range of the ancestral *Vespula* specimens that established in New Zealand (Groenteman, 2016). This means that *Sphecophaga* trials will resume with new breeding stock, and could prove more effective than other methods such as baits, lures, and pheromone traps (Lester et al., 2013). Research on the biological control of this group being conducted in New Zealand has international implications.

Despite many successes, some workers have questioned the environmental safety of biological control introductions. For example, Barratt et al (2000) highlighted the risk of non-target impacts even when control agents have been extensively tested. They showed that *Microctonus aethiopoides* Loan, a parasitoid introduced to control forage pests, attacked ten native beetle species and four other introduced non-target organisms in the field. The risk of non-target impacts raises an important question: could a greater understanding of native parasitoids reveal species that are suitable as biocontrol agents against introduced or native pests? The use of native species would avoid much of the uncertainty, risk, and approval costs inherent in biocontrol programs, and it may create a more sustainable approach to pest management (Dr G. Avila 2016, pers. comm., 2 November). But given the lack of knowledge about parasitoids in New Zealand, this is difficult at present.

Recent research has underscored the complexity of interactions between parasitoids and their greater ecological communities in New Zealand. Schnitzler (2008) examined the impacts of forest fragmentation, urban encroachment, and vegetation diversity on parasitic wasps in the Wellington and Hutt Valley regions. He found that parasitoid community structure responded primarily to plant richness and fragment isolation, but this effect was only observed for smaller bodied species. Peralta et al (2014) constructed host-parasitoid food webs to examine relationships between resource (host) partitioning and parasitism rates. They showed that different parasitoid species employed different host-utilisation strategies, with the net effect being higher levels of parasitism. Frost et al (2015) identified the predators and parasitoids that were moving from forest plantations to adjacent natural habitats. They showed that net spillover was from managed to natural forest, and contrary to most previous findings, specialist parasitoids also had significant spillover. These examples of recent work have established that parasitoids have important roles within ecosystems, and that their conservation deserves more attention.

1.6 Towards Conservation of Parasitoid Wasps

The protection of insects has only entered New Zealand conservation policy recently (Watts et al., 2012). The Department of Conservation has taken a precautionary approach in ascribing threat status to insects, but it has been difficult to stimulate interest or research into non-economic arthropod species and their conservation status (Watts et al., 2012). A recent assessment of 'critical issues facing NZ entomology' concluded that there is a lack of biological spatial data to inform invertebrate conservation in New Zealand (Lester et al., 2014). It may be necessary to select certain groups of highly diverse and ecologically significant invertebrates as priority groups for study, in order to develop conservation strategies that maximise coverage of keystone taxa before they are lost (Oliver & Beattie, 1996). The parasitic Hymenoptera are a good example of such a group (LaSalle & Gauld, 1991). A recent assessment of the conservation status of New Zealand Hymenoptera could only identify a small number of species that are considered to be threatened, but this is largely because of deficient data on the vast majority of species (Ward et al., 2012).

1.7 Study Objectives

The present study aims to contribute towards a greater understanding of parasitoid diversity. This is primarily through the development of better informed sampling methods which can then be used in the planning and execution of future studies on parasitic hymenoptera. Objectives include:

- To quantify trapping effort in relation to parasitoid diversity using a set of standardised sampling protocols.
- To obtain quantitative presence/absence and abundance/occupancy data on parasitoid communities.
- To explore the influences of habitat and seasonal factors on the structuring of parasitoid communities.
- To describe a new species of parasitoid wasp.

1.8 Thesis Structure

This thesis contains two research chapters. Chapter two considers the development of optimal sampling methods to capture parasitoids efficiently, in order to accurately measure their diversity and community structure. Chapter three begins with a discussion of the science of taxonomy, followed by a species description of a parasitoid wasp from a genus new to New Zealand.

I have deliberately chosen to combine ecological methods with a taxonomic component in my thesis. This is primarily to demonstrate the importance and complementarity of each discipline. I want to draw attention to the necessity of cross-disciplinary collaboration between ecologists and taxonomists so that biodiversity may be studied in a more effective way. By recognising and respecting the unique epistemological foundations, methodologies, and contributions made by each discipline, it should be possible to accelerate knowledge production in the life sciences. This benefits us all.

Both research chapters are presented and formatted in such a way as to facilitate submission to academic journals. Little repetition exists across each chapter's abstract, introduction, and discussion. Tables, figures, and references are pooled and compiled at the end of the thesis.

To conclude, a general discussion synthesises the most important concepts discussed throughout the work.

2

Malaise-Trap Protocols for the Rapid Assessment of Parasitoid Wasp Diversity

William Harris Ashmead
(1855 - 1908)

*"It is just as permissible for naturalists, as it is for philosophers, to draw
sometimes upon their imagination in order to interpret nature."*

The Phylogeny of the Hymenoptera
1896

2. Introduction

2.1 Ecological sampling

Biodiversity can only be measured confidently through the development and application of accurate, consistent sampling techniques (Southwood & Henderson, 2000). Sampling a community is a practical necessity when it is impossible to catalogue every individual in a habitat (Leather & Watt, 2005). The development of appropriate sampling regimes considers the target taxa, capture methods, level of taxonomic resolution desired, and the resources available for identification (New, 1996). A sampling regime consists of three major components (Leather & Watt, 2005; Morris, 1960): the sampling unit, or the proportion of habitat from which samples are taken; the sampling technique, or the method to collect information from sampling units; and the sampling regime, or the procedure for applying the sampling technique to take a sample (size, number, frequency and timing of sampling). Care needs to be taken when designing surveys so that methods are standardised, in order to facilitate comparison with future studies (New, 1998). It is useful to have some measure of sample completeness to understand what proportion of taxa have been captured, and sampling effort must be quantified in order to determine what would be gained from further sampling.

Several key decisions need to be made early on for any survey (Magurran, 2004): whether sampling will be individual-based or sample-based; whether sampling effort will be spread equally between sites; whether sampling should be more intense at fewer sites or less intense across a larger number of sites; whether a single or multiple sampling methods should be used; whether data need to be standardised, transformed, or normalised. One major difficulty inherent to biodiversity surveys is that the researcher must make decisions about these parameters without knowing beforehand how large the assemblage of species is, or what the relationship is between the focal taxa and the level of sampling effort required to catch them (Magurran, 2004). It is frequently recommended to consult species inventories that list all taxa at a site when designing a sampling regime (Mills, 2005), but of course, in many cases it is precisely the development of faunal lists which motivates sampling in the first place. This leads to an obvious catch-22, where the researcher is expected to both use and develop optimal methods at the

same time. In other words, researchers need to understand how many species they are likely to capture with a given number of traps, in a given time frame, and how many traps they would need in order to capture every species at a site. This information is more useful when it can be obtained before the start of sampling so that it can be incorporated into the planned sampling regime. These 'optimal sampling' concepts are seldom discussed for terrestrial invertebrate assemblages (New, 1996) although their importance is widely recognized in studies of benthic marine invertebrates (Basualdo, 2011).

2.2 Optimising Sampling Methods

Despite the fact that invertebrates are key drivers of ecological processes in natural and human-modified ecosystems, it is often considered 'too difficult' to monitor and include them within conservation frameworks because of their staggering diversity, and the resources required to capture, sort, identify, and store them (Rohr et al., 2007; Ward & Larivière, 2004; Oliver & Beattie, 1996b). Additionally, the decline of biodiversity research funding, specialist university courses, and expertise within taxonomy and field ecology, is a well-known phenomenon, predicted to have serious implications for research projects that rely on these resources and experiences (Wheeler, 2008b; Oliver & Beattie, 1993; Noss, 1996). A series of approaches and perspectives have emerged that acknowledge these challenges and seek to improve the efficiency of biodiversity surveys by providing cost effective methods for the sampling of mega-diverse invertebrate faunas, and by simplifying the interpretation of complex ecological data (New, 1998). These 'Optimal sampling' and 'Rapid Biodiversity Assessment' (RBA) techniques have the potential to improve the way biodiversity studies are conducted, provided they are used in ways that respect their limitations.

Optimal sampling is an approach to survey design that aims to expedite the collection and analysis of biodiversity data in response to mounting pressures faced by researchers and their stakeholders (New, 1998). Practical considerations often mean that survey design is constrained by the expertise, equipment, time, and increasingly, the funding available to complete them. Accordingly, the development of accurate, standardised, and cost-effective sampling methods have become critically important to ensure the long-term sustainability of field surveying (Bennet et al., 2014; Hammond, 1994). It would of course be wasteful to continue

sampling when few species at a site remain to be captured. But how does an investigator know if this is the case, and how do they know how much additional effort would be required to ensure that it is the case? Optimal approaches identify an appropriate level of sampling effort to match the desired species richness; they make use of extrapolation techniques to judge the completeness of samples; and they may also include methods that fall under the umbrella of RBA, in order to reduce the time and resources required to collect and process samples (Oliver & Beattie, 1996a).

RBA is a set of methods that utilise different forms of 'surrogacy' in order to construct a sampling regime in a way that is likely to produce the most useful data with the fewest resources (Ward & Larivière, 2004). Five broad categories of surrogacy can be distinguished (Barratt et al., 2003; Beattie & Oliver, 1994; Oliver & Beattie, 1996a, 1996b): (i) the use of restricted rather than extensive sampling (sampling surrogacy); (ii) the use of focal taxa rather than all taxa (taxon-focusing); (iii) the use of Recognizable Taxonomic Units rather than formal species (RTUs or 'morphospecies'); (iv) the use of non-specialist biodiversity technicians to sort RTUs (parataxonomists); and (iv) the use of taxonomic ranks other than species (taxonomic minimalism). The adoption of RBA approaches in New Zealand would help to address the challenges of sampling and therefore understanding our highly endemic and poorly known invertebrate fauna, especially since there are few trained taxon specialists in the country (Ward & Larivière, 2004). Uniting the tenets of optimal sampling within an RBA framework would provide a robust foundation for designing the sorts of sampling methods that are currently in demand, although this process must acknowledge the limitations of certain RBA approaches.

Taxonomists and ecologists have expressed valid concerns about some of the suggestions and ideas within RBA, and these will need to be accounted for when designing projects and sampling regimes. It will be important to move away from the notion of taxonomic minimalism described by Beattie & Oliver (1994), because species-level resolution provides the most useful information for ecological studies (Wheeler, 1995). Goldstein (1997, 1999), in his series of replies to Oliver & Beattie (1996a, 1996b), questions the wisdom of reducing taxonomic information as a solution to the neglect of the discipline itself. He argues that valid species names should always be the goal, in order to best reflect biological realities. In addition, maintaining separate voucher collections of morphospecies is viewed as a wasteful duplication of effort that exacerbates work for the taxonomist instead of easing the

impediments under which they currently work (Brower, 1995; de Carvalho et al., 2008). There is a lack of the necessary training resources to shift the cost-benefit ratio in favour of a 'morphospecies' approach, meaning that casual technicians are more likely to make mistakes, and are less invested in the project outcome than properly trained taxon specialists (de Carvalho et al., 2014). "Every specimen added to a collection from this point forward should be done in a way that is part of the solution and not part of the problem" (Wheeler et al., 2012, p.11).

2.3 Towards a Unified Sampling Protocol

Time, money and taxonomic expertise is in short supply, and yet the urgency with which biodiversity surveys must be completed has never been greater (Magurran, 2004). A standardised set of sampling methods used to collect data on a subset of invertebrate taxa from a variety of ecosystems would prove to be an efficient and useful way to monitor ecologically significant species and habitats (Ward & Larivière, 2004). In their report on the value of indicator species for conservation in New Zealand, Hutcheson et al (1999) describe how standardised baseline sampling of different habitats and species offers a way to conserve resources while allowing for more accurate biodiversity comparisons across multiple sites. They note that in order to gain widespread acceptance, these methods would need to sample passively and continuously, be relatively cheap and easy to operate, and be able to compare several sites over the summer months when insect flight activity peaks. They also recommend high resolution taxonomy, to species if possible, to provide ecologically meaningful data that takes functional aspects of the community into account. A pragmatic compromise involving the allocation of difficult or undescribed taxa to RTUs based on morphological characters may be necessary in order to develop standardised methods, although such an approach depends on consistent RTU placement (Oliver & Beattie, 1996b). "In the interim, collaboration between research groups to ensure a standardised approach to methodologies (particularly of insect taxonomy) is absolutely crucial" (Hutcheson et al., 1999, p.62).

The rationale for the recommendations made by Hutcheson et al (1999) rests on earlier work demonstrating that restricted sampling, analysis of subsamples, and the allocation of difficult taxa to RTUs, allows the calculation of the minimum sampling effort needed to accurately represent invertebrate communities across

several sites (Hutcheson, 1990). Weekly trapping conducted in early summer was sufficient to make fine distinctions between the beetle assemblages collected from different habitat types. In a follow up study, Hutcheson & Kimberley (1999) increased the number and area of samples over a longer study period. They again showed that sampling over the summer period was sufficient to obtain samples representative of the entire sampling period, and that habitat variation explained variation in beetle diversity. Hutcheson et al (1999) concluded that the Malaise-trapped beetle regime proposed by Hutcheson (1990) was pragmatic and useful as a method of sampling optimally within an RBA framework, as the samples collected and analysed during the study were representative of the larger beetle community.

Using surrogates or indicators in this way to monitor the biodiversity of larger systems has attracted widespread research interest among ecologists and conservation biologists, who have tried to demonstrate correlations between a chosen surrogate taxon and the wider community (Hammond, 1994). However, in order to properly test these concepts, an accurate baseline or inventory is required to ensure that the abundances or compositions being correlated are actually representative of the community being sampled (Rohr et al., 2007). Quantifying the relationship between sampling effort and species richness or abundance is an important first step, along with assessing sample completeness and identifying the true species richness at a site (Kremen et al., 1993). Before broad-scale relationships between taxa can be reliably established, the sampling methods used to collect the data (that will potentially inform conservation decisions) should be scrutinised and refined.

Surveys are only useful if the level of sampling effort is accounted for in the analysis of species richness data (Gaston, 1996). This is because accounting for sampling effort is required to understand the completeness of diversity samples, or in other words, how many species out of the total number at the site were actually captured (Lewis & Basset, 2007). The only real way to ensure that a biodiversity survey has reached 100% coverage is to observe that all species are represented by at least two individuals or more (Colwell & Coddington, 1994). Because this approach is impractical for megadiverse groups such as arthropods, innovative statistical methods for estimating species richness have been devised.

2.4 Estimating species richness

Estimating species richness is often one of the key drivers behind sampling biodiversity. A growing awareness of the importance of biodiversity has led to the development of powerful statistical techniques to aid in its estimation (Magurran, 2004). Statistical procedures for estimating species richness and the completeness of samples commonly involve the generation of species accumulation curves and the application of non-parametric estimators (Chao & Chiu, 2016). Species Accumulation Curves (SACs) plot the increasing number of species discovered as a function of the sampling effort expended to catch them (Colwell & Coddington, 1994). As more samples are added to the analysis, the steepness of the curve gradually reduces until, in principle, an asymptote is reached, indicating that all species have been collected from the site. A smoothed SAC is generated by randomising the order in which samples are added to the analysis, repeating this many times, and averaging the result (Magurran, 2004). SACs are commonly extrapolated forward in order to estimate the total richness of an assemblage, and therefore the likely sampling effort required to obtain it. Rarefaction curves are similar, but are scaled to the number of individuals on the x axis, and interpolated backward from the maximum observed richness in order to compare two or more assemblages that may have differing abundances (Colwell et al., 2004; Gotelli & Colwell, 2001). Interpolation and extrapolation are therefore two sides of the same coin: they both estimate the underlying relationship between species richness and sampling effort based on the reference sample (Colwell et al., 2012).

A variety of non-parametric estimators of species richness have become increasingly popular for measuring biodiversity over the last two decades (Gotelli & Colwell, 2011). In general, they use the frequency (or ratio) of singletons, doubletons, or rare species in an assemblage of samples to calculate a lower limit of species richness (Gotelli & Colwell, 2001). Once an estimator asymptotes it is considered to have provided an accurate estimate of true species richness. The most effective and popular suite of estimators were derived by Anne Chao and her colleagues, in what is considered to be one of the most important developments within the field of biodiversity measurement for over two decades (Chao & Chiu, 2016; Magurran, 2004). Her abundance-based (Chao1, ACE) and incidence-based estimators (Chao2, ICE) derive minimum species richness by using information about the rare species present in an assemblage (Chao, 1984; Chao et al., 2000).

Jackknife estimators (Jack1, Jack2) have also proven to be a valuable method of richness estimation (Heltshel & Forrester, 1983; Smith & van Belle, 1984), and are included here for comparison with Chao estimators. The combination of rarefaction techniques with non-parametric estimators allows an investigator to: (i) determine the minimum species richness present at the site(s); (ii) extrapolate the total species richness at the site(s); (iii) determine the amount of sampling effort required to obtain the corresponding number of species; and (iv) determine how much extra sampling effort would be required to obtain the total estimated species richness.

2.5 Aims

The aim of this study was to investigate how parasitoid species richness was related to sampling effort. The primary aim was to discover how much sampling effort would be required to capture all parasitoid species at each of the two Kauri forest sites surveyed. A broad definition of sampling effort was taken to include the number of traps used, their spacing, how frequently sampling was undertaken, and how long traps were left out for. The intention was to develop a set of guidelines for Malaise-trapping of parasitoid wasps that could then be used as a first approximation by other investigators planning their own studies. The development of optimal methods to estimate parasitoid richness will allow sampling resources to be spread as thinly as possible while providing the most useful information for the research project in question (Colwell & Coddington, 1994). In the process, the collection of basic presence/absence and abundance/occupancy data on parasitoid assemblages will contribute to a fledgling understanding of how both native and introduced species are distributed and structured.

2.6 Methods

Sites

Two sites within the greater Waitakere Ranges Ecological Area were selected for insect sampling (Thomas & Ogden, 1983). The Waitakere Ranges are situated on volcanic sedimentary rocks which uplifted out of the sea about 16 million years ago to form the Waitakere Volcano (Hayward, 2006). Eleven large

streams drain a catchment dominated by Kauri (*Agathis australis* D. Don) and the understory plants that are in competition with them (Cranwell-Smith, 2006). The Ranges are an ecologically significant area comprising 17,000 hectares of land in close proximity to the Auckland Metropolitan area (ARC, 2010; Cameron & Morton, 1993). A history of the area can be found in Esler (2006, 1983).

Both sites are characterised as Kauri forest in various stages of regeneration. Patches of fragmented habitat near urban settlements can contain large numbers of parasitoid species and are worth investigating for their conservation value (Schnitzler, 2008). Thomas & Ogden (1983) provide an overview of each of the University's reserves. The Huapai reserve is 15 hectares. Rainfall is higher than Auckland City at 2,000mm per annum. Understorey vegetation is dominated by *Cyathea dealbata* (G.Forst.) Sw., *Coprosma arborea* Kirk and *Myrsine australis* (A.Rich.) Allan. Other common species include Nikau palms, supplejack, and cabbage trees. The Oratia site is between 61m and 91m ASL. Rainfall and temperatures are similar to the Huapai site. Vegetation is characterised by a mixture of Kauri, podocarp and broadleaf species, with *Phyllocladus trichomanoides* D. Don and *Dacrydium cupressinum* Sol. ex G.Forst relatively common.

The mean temperature over the study period was 17.7°C (lowest 11.8°C, highest 25.1°C). Total rainfall was 71.2mm. Average windspeed was 3.6km/h.

Focal Taxa

Parasitoid wasps are ideal focal groups for ecological and conservation studies because they represent the diversity of the hosts they attack, as well as their host's food-plants (Sharkey, 2007). Their sensitivity to environmental changes means they should demonstrate the impacts of disturbance at a higher resolution than other groups (LaSalle, 1993). The Superfamily Ichneumonoidea (Hymenoptera) was selected because it is a highly diverse and ecologically important group of parasitoid wasps with a worldwide distribution (Quicke, 2015; Yu et al., 2005). It is the most economically important group of parasitoid wasps as it is widely used in biocontrol programs (Heraty, 2009). Collectively, it encompasses a wide range of parasitism strategies, host preferences, and has intimate ecological links with other taxa (Wahl & Sharkey, 1993). Many of these wasps attack the larvae of moths and butterflies, but almost every group of holometabolous insects are represented as hosts (Askew, 1971). The superfamily

consists of two families: the Braconidae and the Ichneumonidae, together comprising 41,000 described species with many more times that number awaiting discovery (Quicke, 2015).

Sampling Regime

Malaise traps are tent-shaped flight interception traps effective at capturing understorey insects, and are frequently used for the collection of Hymenoptera (Malaise, 1937; Townes, 1972; Van Achterberg, 2009; Ozanne, 2005). Twenty Malaise traps were deployed at each of the two sites in order to maximise within-site replication, while preserving a measure of across-site replication. Traps were of the Townes (1972) style commonly used for insect surveys, predominantly of the 'ez-Malaise trap' commercial variant (<http://bugdorm.megaview.com>). Most traps were spaced 20m along a central transect that ran approximately through the middle of each site. Additional traps were haphazardly placed 20m either side of the central traps. Where possible, traps were positioned across flight paths with the head facing the sun's zenith (Noyes, 1989; Van Achterberg, 2009). Efforts were made to sample as many distinctive microenvironments as possible (New, 1998).

Traps differed in minor details of construction and colouring such that three groups were recognisable. Trap group was included in the analysis to account for any biases in the resulting catch. Traps were set up and dismantled at the start and end of each sampling period. Sampling took place over the 2014-2015 summer, and periods were 1 week long at each site. Huapai was sampled between 24/11-1/12/2014, 7-14/1/2015, and 2-9/2/2015. Oratia was sampled between 2-9/12/2014, 17-24/1/2015, and 10-17/2/2015. This gave a total of 420 Malaise-trap-days for each site. The decision was made to restrict sampling to the summer period because that is when insects are most active in New Zealand (Hutcheson et al., 1999), and because catches of Ichneumonoidea are largely determined by seasonal temperatures (Owen et al., 1981). Collection bottles were filled with a 50/50 mix of ethanol and glycol.

Environmental Data

In order to determine the influence of vegetation and environmental variables on Hymenoptera catches, a set of environmental measurements were taken. At each trap a quadrat of 5m diameter was used to measure the following: (i) proportional measures of five ground cover types: Kauri debris; Nikau debris; coarse woody debris (CWD); other leaf litter; and bare ground; (ii) the total number of pieces of CWD; (with a diameter of at least 7cm); and (iii) the number and species of plants.

Sorting & Identification

Labelled collection bottles had their contents strained, and fresh ethanol was added for the sorting process. Specimens were initially sorted to Hymenoptera and subsequently sorted to family level. Specimens belonging to the superfamily Ichneumonoidea (i.e. Ichneumonidae and Braconidae) were sorted to the lowest level possible. Handling, preparation, and labelling of specimens generally follows that of Walker & Crosby (1988). Specimens were labelled, databased, and deposited into the New Zealand Arthropod Collection (NZAC) to support verification and future work.

All microscope work was conducted using a Leica MZ6 stereomicroscope with a Leica CLS 150X light source, or an Olympus 10-40x stereomicroscope with desk lamp.

A 'morphospecies' or RTU approach was used to sort below the level of genus (New, 1998), particularly for genera with few species described (which is common among the New Zealand parasitoid fauna). While adoption of this approach is often a practical necessity for the initial sort of Hymenoptera (Gauld, 1984), species-level, or at least genus-level identifications were preferred to gain the most useful information possible (Kim, 2009; Ward & Stanley, 2004; Derraik et al., 2010). Males were sorted, but excluded from the analysis due to inconsistency in assigning them to their corresponding female RTUs. Identifications were primarily carried out by comparing specimens to those in the NZAC, and through the use of published keys and literature (Schnitzler & Ward, 2013; Valentine & Walker, 1991; Goulet & Huber, 1993; Gauld, 1984; Berry, 2007; Berry, 1990; Berry & Walker, 2004; Bain, 1970; Wahl, 1991).

RTUs will be referred to as species herein.

Data Analysis

All plots other than MDS were plotted in R (R Core Team, 2015).

Diversity

Species abundances were examined with Whittaker rank-abundance plots (Magurran, 2004), where rank-abundance was generated from the pooled dataset to examine total parasitoid species evenness and rarity. Due to the relatively small range of abundance for each species, the y-axis was scaled to proportion rather than a log format. The eight most abundant species were compared over time to examine fluctuations in their abundance. Simpson's Diversity was selected as a relatively simple and robust way to compare species richness between the two sites. In a recent evaluation of diversity metrics, Morris et al (2014) found that Simpson Diversity was best at discriminating sites based on the underlying species assemblages.

Species Accumulation Curves

A range of species richness indices and estimators were generated from sample-based abundance datasets in EstimateS v9.1.0 (Colwell & Elsensohn, 2014). A total of 1000 randomizations were used for each analysis, and the upper abundance limit for rare or infrequent taxa was left at the default of 10. Six richness estimators were selected on the basis of their accuracy under different conditions (reviewed by Hortal et al 2006): abundance-based estimators (ACE, Chao1), incidence-based estimators (ICE, Chao2) and first and second-order 'jackknife' estimators. The 'classic formula' was used for calculating Chao1 and Chao2 values as recommended in software (Colwell & Elsensohn, 2014).

Sample-based rarefaction curves were generated from EstimateS output for each period at each site, by plotting estimated richness (S_{est}) against the number of samples. S_{est} combines several mathematical approaches and allows integration between interpolated rarefaction curves and extrapolated accumulation curves in order to produce a unified accumulation curve (Colwell et al., 2012). S_{est} is calculated differently for rarefaction and extrapolation (Colwell, 2013).

Additionally, individual-based rarefaction was plotted to provide a more valid comparison of species richness between the two sites using pooled data from both. Even when sampling effort is standardised within and between sites, species richness can only be compared between sites when replotted against the number of individuals collected rather than the number of samples (Gotelli & Colwell, 2001). The x-axis was restricted to 1240 individuals for readability (to avoid a very long tail), resulting in a cut-off of only one species for each site. Confidence intervals were generated and inspected for all accumulation and rarefaction curves. However, they were omitted from plots in favour of visual clarity.

Community Composition

Similarity-based, multivariate analyses were conducted in PRIMER-E v.6 (Clarke & Gorley, 2006), following the procedures and rationale outlined in Clarke & Warwick (2001). Data did not require standardising as identical sampling procedures and effort were maintained over the course of the study. Parasitoid abundance data were square root transformed. Plant species (sampled as presence-absence data) were left untransformed. Environmental data were normalised by subtracting the mean and dividing by the standard deviation within each variable. Site (Oratia or Huapai); trap type (one of three Townes-style designs used); sample month (Dec, Jan, Feb); and trap distance group (based on distance from first trap) were added as factors.

Resemblance matrices were constructed by applying the appropriate similarity coefficient (Clarke & Gorley, 2006): a zero-adjusted Bray-Curtis coefficient to parasitoid abundance, the Sorenson coefficient to plant species, and Euclidean distance to environmental data. A zero-adjusted Bray-Curtis coefficient addresses the 'double zero' problem and helps to correct the erratic behaviour of the coefficient when samples become sparse (Clarke et al., 2006). In PRIMER-E, zero-adjusting the coefficient is accomplished by adding a 'dummy variable' with values of 1 for each sample (Clarke & Gorley, 2006). This method was justified because sample sizes were sufficiently large and were taken close enough together in space to assume that samples would be denuded for the same reason.

Hierarchical agglomerative-clustering using the 'group average' method was undertaken to identify any natural groupings of samples between sites and sampling periods. A SIMPROF test was used to evaluate the statistical significance of the

structure of any resulting clusters. The relative similarity of samples was further explored through the use of Non-metric Multi-Dimensional Scaling (MDS) ordination. MDS is an appropriate statistical technique to visualise the similarity of groups of samples and is widely used in ecological studies (Clarke & Gorley, 2006). MDS was selected over PCA because it's more flexible and makes fewer assumptions (Clarke & Warwick, 2001). Fifty restarts with a minimum stress value of 0.01 were used for each analysis. Clusters were overlaid on the MDS plots at 30% similarity. Taken together, clustering and MDS act in synergy to aid identification of natural groupings of samples (Clarke & Warwick, 2001).

ANOSIM tests were carried out to determine if any differences in parasitoid assemblages could be explained by vegetation, site, sampling period, or trap spacing (Clarke & Gorley, 2006). A two-way crossed layout ANOSIM tested the null hypothesis that wasp assemblages cannot be explained by sampling month or site differences. A one-way ANOSIM was used to test the null hypothesis that wasp assemblages cannot be explained by the plant species found around the traps at each site, and that trap spacing cannot explain parasitoid composition. BEST and RELATE tests were used to establish whether there was a relationship between the among-sample patterns in the parasitoid assemblage, and any combination of environmental variables. BEST attempts to find a combination of environmental variables that 'best' explain the patterns of species abundance, while RELATE is a non-parametric Mantel test between two similarity matrices testing agreement between a species assemblage and the whole suite of environmental variables common to both sites (Clarke & Gorley, 2006).

2.7 Results

Parasitoid Diversity

A total sampling effort of 840 Malaise-trap-days over a period of 3 months resulted in the capture of 87 species, from 946 individuals (348 females and 598 males). The lowest level of identification varied: species (16; 18%); genus (58; 67%); subfamily (9; 10%); and family (4; 5%). Fifty four species are classified as endemic, 1 as native, 1 as introduced, 1 as a biocontrol agent, and the remaining 30 are of unknown biostatus, but are likely to be endemic (Landcare Research, 2009).

Forty one species were found only at the Huapai site (47.1%), 17 were exclusive to Oratia (19.5%), and 29 were found at both localities (33.3%). Ichneumonidae accounted for 56 species and 583 individuals (198 females, 425 males), making them more diverse than Braconidae with 31 species and 322 individuals (150 females, 172 males). The pooled assemblage contained 37 singletons and 18 doubletons.

The Whittaker Rank-Abundance plot shows that the combined parasitoid assemblage from both sites is highly uneven (Fig. 1). 63% of the species captured during the study are known from only one or two individuals (37 singletons and 18 doubletons). On the other hand, only 8 species contributed 10 or more individuals. Of these 8 species, the top 3 most abundant were only captured in two months out of the three (Fig. 2), while the rest of the top species were captured in all 3 months (with the exception of *Aucklandella* sp.13 (Ichneumonidae: Ichneumoninae)). *Campoplex* sp.6 (Ichneumonidae: Campopleginae) was by far the most abundant species.

Species Accumulation Curves

Despite an intensive sampling effort of 420 Malaise-trap-days per site over a 3 month period, observed richness failed to reach an asymptote, which means that true species richness was underestimated (Fig. 3).

Table 1 summarises the biodiversity measures and richness estimators calculated in EstimateS. Observed species richness peaked in January at Huapai, and in February at Oratia. Twice as many individuals, and one and a half times the number of species were recorded from Huapai. The Oratia site was characterised by a greater proportion of singletons than Huapai. The non-parametric richness estimators were generally in agreement with each other. However, very high Chao estimator values (Chao1, Chao2, ACE, ICE) were obtained for the December period at Huapai. The first and second-order Jackknife estimators (Jack1 and Jack2) consistently offered the lowest estimates of total species richness for each sampling period.

Figures 4 & 5 show the relationship between observed and estimated species richness for each sampling period at Huapai and Oratia, respectively. Figure 6 shows the same with pooled data from Huapai (A), Oratia (B), and the total dataset (C). Several estimators for the December period at Huapai (Fig. 4A) are cut off for

readability and to maintain comparisons with the other periods, because they are likely to be erroneous (see discussion). The non-parametric richness estimators appear to stabilise for the last two periods sampled at Huapai (Figs. 4B and 4C), and for the first period sampled at Oratia (Fig. 5A). Although the pooled estimates for each site do not appear to asymptote (Fig. 6A and 6B), the total assemblage estimators are closer to reaching a plateau (Fig. 6C). Table 2 shows that all measures of sampling efficiency were highest for the Huapai site in the January period. For Oratia, the most efficient single sampling period was December, but a higher proportion of the total species richness was captured in February.

The Oratia site collected one third of the individuals of the Huapai site. Because abundances clearly differed, curves were replotted and scaled to individuals in order to control for the effect that greater abundance has on species richness (i.e. as a larger number of individuals are collected, a larger number of species are observed) (Colwell et al., 2012). Despite a noticeable difference in species richness shown by the sample-based accumulation curves (Fig. 3), when species richness was scaled to individuals, it became clear that the sites did not differ in species richness (Fig. 7; comparing both sites with pooled data). Additionally, a two-sample t-test assuming equal variances showed that there is no significant difference in Simpson Diversity between the sites ($p = 0.46$).

Community Composition

Non-metric MDS plots showed that the composition of parasitoids at each site was more similar at the beginning of the study than at the end (Fig. 8). Hierarchical agglomerative clustering and SIMPROF analyses showed that all pictured clusters were non-randomly structured, except the two smaller clusters in January. By February, a distinction between sites can be observed (Fig. 8C). Visualising each sampling period in this way produced stress values that indicate a "good" to "potentially useful" representation (Clarke & Warwick, 2001, p.5-6), however, the combined dataset was not represented in a useful way in two dimensions (Stress = 0.27). A two-way ANOSIM test showed that parasitoid diversity was only weakly affected by site ($R = 0.161$) and month ($R = 0.109$). Because of a lack of evidence for site and seasonal differences in parasitoid assemblage, SIMPER analyses were not performed. A one-way ANOSIM showed that trap type had a weak effect on parasitoid diversity ($R = 0.239$, $p = 0.001$).

Environment

A total of 71 plant species were found within the trap location quadrats from both sites. Of these, 19 were found only at Huapai, 29 only from Oratia, and 23 species were shared between both sites. Hierarchical clustering showed that each site has a distinctive vegetation community. This was confirmed by a SIMPROF test which showed very little overlap in vegetation profile between sites at the level of 5% significance (Fig. 9A). The corresponding MDS plot provides further visual confirmation of this separation (Fig. 9B). A one-way ANOSIM test showed moderately strong separation between the vegetation assemblage at the two sites ($R = 0.673$, $p = 0.001$). However, plant diversity only had a weak effect on parasitoid composition (RELATE, $Rho = 0.126$). Similarly, a BEST analysis showed that there was no optimal combination of environmental factors to explain patterns of parasitoid composition ($Rho = 0.18$). A one-way ANOSIM showed that trap catches could not be explained as a function of their relative position when classified into 20 meter 'bands' of increasing distance from the first trap.

2.8 Discussion

The aims of this study were to quantify trapping effort of parasitoid diversity, to obtain basic diversity data, and to explore potential factors that structure parasitoid assemblages. Despite an intensive Malaise-trapping regime of 840 Malaise trap days over a 3 month summer period, only 70% of the parasitoid wasp species were captured at the two forest sites surveyed. The total assemblage was highly uneven, with 63% of species recorded from 1 or 2 individuals, and only 9% known from 10 or more individuals. Despite revealing distinctive vegetation assemblages at each site, there were no correlations between parasitoid diversity and the environmental variables measured.

Parasitoid diversity

Species richness and abundance peaked in January and February at Huapai and Oratia, respectively. Ichneumonidae were more numerous, accounted for a

greater number of species, and were composed of a higher proportion of males than the Braconidae. Sex ratio was biased towards males overall at a ratio just under 2:1 (348 females, 598 males). This is unusual, as studies conducted overseas frequently find either a female bias or a relatively even sex ratio (e.g. Mazon & Bordera, 2008). In New Zealand, the opposite seems to be the norm (Kendall & Ward, 2016).

Approximately half of the species were unique to Huapai, one fifth were unique to Oratia, and one third were caught from both sites. As well as containing higher species diversity, the Huapai site also contributed about two thirds of the parasitoid abundance to the study. The Huapai site is a relatively small fragment of native bush situated 8km north of the Waitakere Ranges, linked by a corridor of fragmented patches of vegetation (Thomas & Ogden, 1983). It seems surprising that lower species richness, and fewer individuals would be recorded from the Oratia site, which is directly connected to the eastern Waitakere Ranges. One explanation for this disparity could be that the more isolated Huapai site is acting as a refuge for parasitoids from the surrounding landscape (Gaigher et al., 2015; Fraser et al., 2007). It may be concentrating a community of parasitoids that use it as a centralised 'hub' in order to access the outlying areas for foraging, mate location, or oviposition.

The total parasitoid assemblage was characterised by unevenness and low abundance: over half of the species were represented by only one or two individuals; only 8 species were represented by 10 or more individuals; and these top 8 species accounted for 41% of the total abundance. Catches of parasitoid wasps are frequently characterised by high unevenness and a large proportion of rare species (Fraser et al., 2008; Sääksjärvi et al., 2004). Owen et al (1981) reported 455 species of Ichneumonidae from 6,455 individuals caught over a two year period in a suburban English garden. Of these species, 31% were known from only a single individual, while the most abundant 7% of species accounted for over half of the individuals collected. These relative abundances are similar to what were found in the present study. Parasitoid structure is known to be both highly scale and taxon-dependent (Fraser et al., 2008). However, in order to make valid inferences about parasitoid assemblage structure and rarity, we must assume that the assemblage observed in this study (and others) actually reflect real parasitoid assemblages.

Because parasitoid wasps are known to be both highly diverse and poorly described, it was anticipated that many observed 'species' would either be undescribed or difficult to identify. This was indeed the case, as identification to

species was only possible in 18% of RTUs collected, and males had to be excluded entirely due to difficulties in identifying them or matching them to female RTUs. However, the classification to species-level in 18% of RTUs presented here is comparable with the 19% of Kendall & Ward (2016), and the 13% of Schnitzler (2008).

Plant Diversity & Environment

A weak association was found between plant diversity and parasitoid diversity within the sites and times sampled. Additionally, no single environmental variable, or combination thereof, was able to adequately explain parasitoid diversity. Plant diversity and habitat complexity are thought to play important roles in structuring parasitoid wasp communities (Sääksjärvi et al., 2004; Fraser et al., 2007), and other invertebrate communities are known to be structured by plant diversity in New Zealand forests (Crisp et al., 1998). However, previous work has only ever demonstrated weak, statistically insignificant, taxon-specific effects between parasitoid wasps and plant diversity in New Zealand (Kendall & Ward, 2016; Schnitzler, 2008). Results from New Zealand conflict with those generated overseas, where parasitoid diversity is more likely to be strongly associated with plant diversity and habitat structure (Arnan et al., 2011; Fraser et al., 2007; Fraser et al., 2007). This may be because sampling area is greater, many more sites are surveyed, and spatial autocorrelation is better factored in to experimental designs (Horak, 2013). Total volume of CWD or dead wood is often positively correlated with invertebrate abundance (Evans et al., 2003). This effect was not observed in the present study, probably due to the fact that environmental measurements were restricted to areas closer to traps than previous work.

Another reason for why studies typically show a correlation between parasitoid species richness and environmental variables may be their failure to account for differing parasitoid abundances between sites. In the present study, when species richness was plotted against number of samples, the site with a lower parasitoid abundance showed a corresponding drop in species richness relative to the other site. It was only by replotting the data on individual-based rarefaction curves that no difference in parasitoid richness between sites was revealed. This is a common pitfall in the use of accumulation curves and rarefaction techniques to estimate species diversity between sites (Gotelli & Colwell, 2001).

Of course, the environmental variables used for studying the structure of parasitoid assemblages are really proxies for the distributions of the parasitoids hosts. Investigations of parasitoid wasp ecology must rely on such proxies in the absence of host records for the majority of taxa in New Zealand (Berry, 2010). Parasitoid wasps are intimately linked with the distributions of their hosts, which they regulate through 'top-down' processes (Shaw, 2006). Host populations will therefore exert a strong influence on parasitoid structure, in terms of how many host species are present, in what numbers, and how evenly they are spread. In New Zealand, hosts are predominantly lepidopterans, of which there are around 1,800 species currently described, 90% of which are endemic (Dugdale, 1988). Mass rearing has been suggested as a method to obtain accurate and properly documented host records (Quicke, 2015), although the logistical difficulties associated with mass rearing programs generally exclude them from being undertaken on large scales.

Rarefaction & Extrapolation

Despite the relatively high number of species collected (87), the lack of an asymptotic relationship between observed species richness and sampling effort meant that there were many taxa still to be collected. Results indicate that additional sampling will invariably result in the capture of more species of parasitoid wasps at these sites. Singletons and doubletons accounted for 42.5% and 20.7% of the species found, respectively. High proportions of singletons and doubletons are frequently observed in studies of parasitoid wasps, even for locally intensive surveys conducted over a period of several years (Owen et al., 1981). The high proportion of singletons can be interpreted in several ways as representing: resident species that are naturally rare or uncommon within the habitat; resident species that are not captured in proportion to their abundance due to biases in trapping methods; or 'tourist' species that are moving from one patch to another (Mohamad et al., 2015; Shaw, 2006). No trapping method can define which category a given species falls into, but repeated sampling over longer time periods will eventually show which species are non-resident.

The non-parametric estimators summarised in Table 1 show a reasonably narrow range and good agreement. However, their interpretation requires a proper understanding of how they work (from Magurran, 2004). Chao1 is sensitive to the

ratio of singletons to doubletons, and will increase steeply when singletons are favoured in that ratio. This relates to the concept whereby at least two individuals for every species would need to be observed before a complete inventory can be declared (Colwell & Coddington, 1994). As the inventory approaches completion, the Chao1 estimate drops closer and closer to the observed richness. Thus for Chao1, if a large number of singletons are observed relative to doubletons, the resulting estimate will be very large. Chao2 takes a similar approach but instead uses the number of species found in either of one or two samples, and is intended for use with presence/absence data. ACE is a coverage-based estimator that draws inferences from how many species there are in a sample set with 10 individuals or less. ICE is similar to ACE, but instead focuses on the number of species found in 10 or more samples. The jackknife estimators work in a similar way to their respective Chao estimator, but tend to give a more conservative estimate.

Despite representing a breakthrough in estimating species richness, these statistics have some important limitations which must be considered when selecting the most informative among them (Magurran, 2004). Chao1 and ACE will fail when there are more uniques than singletons, which happens when levels of rarity are very high. Using a single sampling technique is known to exaggerate levels of rarity, which can then inflate estimators (Longino et al., 2002). Another important limitation is that these estimators may be unreliable when extrapolating past a tripling of the observed sample sizes (Gotelli & Colwell, 2011). An examination of the variance produced for the extrapolated dataset in the present study suggests that extrapolating beyond this limit does not substantially increase the standard deviation of the estimate (S_{est}), but that the 95% confidence intervals do expand by a greater margin.

Few comparisons of these estimators are able to unequivocally recommend a single estimator that will always provide the most accurate total species richness (Gotelli & Colwell, 2011; Hortal et al., 2006; Colwell & Coddington, 1996). This is because all of the Chao-derived and jackknife estimators generally perform well (Hortal et al., 2006). However, out of the six best performing estimators included here, Chao1 has been shown to result in reliable estimates when richness is relatively high, and it is not affected by sample size (Basualdo, 2011). For these reasons, Chao1 has been selected as a representative value on which to base further interpretations. When taking Chao1 as the most reliable estimator, the sampling efficiency (the proportion of taxa caught from the estimated number) is 68.5% for

Huapai and 47.7% for Oratia. The overall sampling efficiency was therefore 70% (87 species caught from an estimated pool of 124). This is similar to Kendall & Ward (2016), who captured 136 species out of an estimated total of 186, for a reported sampling efficiency of 72.7%. This means an intensive sampling effort at just two sites in the present study, resulted in the capture of two thirds of the total richness that Kendall & Ward (2016) extrapolated from their ten sites (186 species). Overall, the richness estimators did not convincingly asymptote for any sampling periods in this study, although most periods came close. True minimum species richness of the parasitoid assemblage has probably been underestimated at both sites (Sääksjärvi et al., 2004). In that case, the estimated species richness would be higher and sampling efficiency would be lower.

The combination of sample-based Species Accumulation Curves with non-parametric estimators is frequently recommended to estimate and compare species richness within and between assemblages (Colwell et al., 2012; Rohr et al., 2007; Hortal et al., 2006). However, rarefaction techniques assume several conditions: sufficient, standardised, independent sampling; taxonomic similarity between assemblages; and relatively closed communities (Gotelli & Colwell, 2011). The anomalous estimator values provided for the December sampling period at Huapai illustrate some of the limitations. It is likely that the very high ratio of singletons to doubletons was a chance collection event rather than indicating that the total species richness during this period was over 300 species. This situation underscores the need to capture a reasonable number of individuals so that the ratio between singletons and doubletons are more likely to reflect real biological patterns rather than one-off sampling events.

Sampling Effort

An intensive sampling effort of 840 Malaise-trap days over a period of 3 months produced only 946 specimens in total. On average, only 1.1 specimens were caught during each Malaise-trap-day (only 0.4 female specimens). The design of the current study is broadly comparable to Kendall & Ward (2016). They sampled a greater number of sites with less effort per site, but also captured just over 1 female specimen per Malaise-trap-day. Fraser et al (2007, 2008) sampled four parasitoid subfamilies in UK farm woodlands using different configurations of traps and sites, each standardised to the same number of Malaise-trap-days as the current

study (840). The former (2007) caught 1543 individuals from 60 species across 15 sites, with two traps at each site. The latter (2008) caught slightly fewer individuals (1323) and species (55) across two sites, with 15 traps at each site. The obvious result of comparing these four studies is that more intensive sampling at fewer sites produces a far more thorough inventory of those sites than what is produced from spreading sampling effort thinly over many sites. Even in the tropics there is considerable variability in trap catches, for example, catches can be as low as 0.26 individuals per Malaise-trap-day for the Pimplinae/Rhyssinae (Sääksjärvi et al., 2004), while they can be six times higher for Orthocentrinae (Veijalainen et al., 2012). Parasitoid assemblages are characterised by a high proportion of taxa represented by only one or two individuals, so by definition they require extra sampling effort compared to more even groups (Magurran, 2004).

Malaise Traps

Because certain groups of insects are captured more efficiently by certain techniques, it is necessary to consider how sampling techniques may lead to biases in catch data (Kim, 2009). Malaise traps collect large numbers of specimens with relatively little effort, minimise collection bias by relying on insect phototropism rather than attractants, and their catches can be easily compared (Leather & Watt, 2005; New, 1998). In isolation, Malaise traps have been shown to provide a good approximation of Hymenoptera species diversity at a site, with the exception of microhymenoptera (Darling & Packer, 1988). Noyes (1989) showed that Malaise traps caught the highest number of individuals and species of Ichneumonoidea in a test of five collecting methods. To capture a reference sample of Ichneumonoidea, yellow pan traps required ten times the effort, and regular flight intercept traps required double. Mazon & Bordera (2008) caught 88% of their ichneumonid specimens in Malaise traps, and only a few species were unique to pan traps. In a similar study, Malaise traps consistently provided higher species richness and a more even catch compared to yellow pan traps or regular flight intercept traps (Wells & Decker, 2006). However, the performance of Malaise traps compared to pan traps is likely to be region-specific, as some of the highest records of Hymenoptera diversity have been obtained using pan traps alone (Arnan et al., 2011).

Catches still depend on a number of other factors, including insect abundance, flight behaviour, activity levels, trap design, and the propensity of a given species to be captured (Gaasch et al., 1998). Experienced hymenopterists have predicted that only 20% of the parasitoid wasps that enter the Malaise trap space will end up being captured by it (Owen et al., 1981). Only a particular subcommunity of individuals and species will be available to biodiversity studies because of methodological, spatial, and temporal biases or limitations, and their likelihood of capture may have no relationship with their abundance (Longino et al., 2002). For these reasons, multiple sampling techniques are often recommended (Rohr et al., 2007; Longino et al., 2002; New, 1998), with the expectation that they will lead to a more accurate representation of the community being sampled (provided the methods are tailored to the focal taxa).

Although the three distinct trap 'types' used in this study had only a weak effect on parasitoid catches, they explained more variation in parasitoid composition than any environmental factors. This may be due to the different colours of the traps: the majority were black, and the two other groups were white. Tao et al (2012) showed that adult ichneumonids responded differently to trap colours among three different field sites in China. Black traps caught by far the fewest specimens overall, while white traps caught only a moderate number. They found that yellow and green traps consistently caught more specimens than the other colours they tested.

Sampling Recommendations

This study was designed to test how capture of the greatest number of parasitoid species could be achieved with the least effort and cost. The intention was to provide a practical set of sampling guidelines to achieve these ends. This study has provided further evidence that a reasonable compromise between sampling effort and catch completeness can be achieved with the exclusive use of Malaise traps for sampling parasitoid wasps within a Rapid Biodiversity Assessment framework (Fraser et al., 2008b; Ward & Larivière, 2004). It is possible to census over two thirds of the parasitoid species available by intensively sampling with Malaise traps over a summer period. The thoroughness of sampling provides confidence that the assumptions of rarefaction and non-parametric estimators have been adequately accounted for, so that results are accurate and comparable with

other sites. However, recommendations will of course differ if the aim is an exhaustive inventory of mega-diverse groups such as parasitoid wasps. This is because no study attempting to compromise between sampling effort, time, or cost, will be able to provide a complete species inventory of parasitoid wasps (or many other arthropod groups) (Mazon & Bordera, 2008; Longino et al., 2002; Noyes, 1989).

Recommendations of sampling effort are easiest to implement when they are specified in relation to sampling units, in this case Malaise traps. It is obvious that many traps are required to obtain the highest number of species to maximise sampling efficiency. Even ecological studies comparing relative numbers and diversity of sites would be well advised to incorporate more traps than the conventional usage of just one or two (Quicke, 2015). Recent work suggests that two traps will vastly underestimate diversity in comparative faunal studies of Ichneumonoidea (Mazon & Bordera, 2008; Fraser et al., 2008). Quicke (2015) recommends at least 10 Malaise traps, and this represents a reasonable minimum number in light of the results obtained here and overseas (Kendall & Ward, 2016; Fraser et al., 2007, 2008b).

One of the greatest challenges in measuring parasitoid richness is obtaining a sufficient number of individuals and species to satisfy the assumptions of the statistical techniques that extrapolate diversity (Chao & Chiu, 2016; Longino et al., 2002; Mazón, 2015). Attempting to extrapolate diversity with few individuals or species leads to inaccuracy due to large variances. This study reinforces the concept that comparing species richness across multiple sites is best achieved by scaling to individuals rather than number of traps. Observed species richness is strongly influenced by sample size and impossible to compare across sites or times without standardising for sampling effort, when effort differs, or individuals, when abundance differs (Clarke & Warwick, 2001). Comparisons between sites must take these effects into account. This is because sparser sites may appear to have fewer species, when in actual fact, species richness is similar. The pooled data showed that it would be necessary to capture a total of 1,400 individuals, in order to reach an asymptotic richness of 121 species (107 species at Huapai and 91 species at Oratia). For this reason, using traps as a proxy for sampling effort may not be enough. It may instead depend on ensuring that a sufficient number of individuals are captured in order to provide a desired level of accuracy in subsequent analyses.

Sampling efficiency is the proportion of Chao1-estimated species richness that was captured during a certain sampling period. Results differed for each site, and showed that different measures of sampling efficiency highlighted different aspects of the data (Table 2). The 'period' result measured the proportion of estimated species for that site and period that were observed. The 'site' result measured the proportion of estimated species for the entire site that were captured in that specific period. And the 'total' result measured the proportion of the total number of species estimated for both sites and across all periods, that were observed in that particular period.

An analysis of sampling efficiency showed that the Huapai site is most productive to sample in January for all three measures. At Oratia, a higher proportion of the available species richness in each period was caught in December, but a higher proportion of species available at the site overall were captured in February. This effect can be explained by the way in which the Chao1 estimators change with sampling period. If indicating a real seasonal effect, the results show that changes in species richness and abundance can occur within relatively short time frames. However the statistical analyses revealed that the differences in richness of parasitoid assemblages were not statistically significant, so these results should be interpreted in that light.

The differing sampling efficiencies can be used to make different recommendations based on the type of question being asked. For projects that are concerned with relative ecological characterisations of multiple sites, the results show that it may be best to sample in December and January. This is because sampling efficiency was highest relative to the proportion of species that were caught out of the total number available in those periods. This is important for ecological studies because typically, they aim to represent as much variation in the community as they can in order to obtain the most accurate ecological overview of taxa. On the other hand, for an exhaustive inventory that is seeking the largest number of species overall, it would be better to conduct sampling in January and February. This is because sampling efficiency and observed richness peaked during these periods for both sites. This would result in the highest number of species, but it may not properly characterise site or seasonal differences between multiple sites. These are typically not the aim of exhaustive inventories in any case.

The quantification of sampling effort represented by the accumulation curves show that the conventional usage of only two Malaise traps in invertebrate

surveys would have severely underestimated the parasitoid assemblage. For Huapai, this would have resulted in the capture of around 10 species (provided traps were left out for three one-week sampling periods). This amounts to only 14% of the number of species observed when 20 traps are used, and only 6.8% of the total estimated richness. At Oratia, where parasitoid abundances were even sparser, it would have resulted in even fewer species. This is largely due to the fact that abundance is the limiting factor for obtaining species of highly uneven and naturally uncommon groups like parasitoids. The extrapolated sample-based curves showed that a tripling of effort for Huapai, and perhaps a quintupling of effort for Oratia, would have resulted in capture of the vast majority of species present at the sites. Again, this is largely because the parasitoid faunas are relatively low in abundance as well as being highly diverse, which means they require more sampling effort to characterise.

The season and duration of sample dates is an important consideration for any sampling regime. Although longer and more frequent sampling periods are ideal, a balance needs to be maintained between the completeness of surveying, and the time and resources required to process large numbers of specimens (Oliver & Beattie, 1996). Optimal methods compromise by restricting sampling to the season when insect activity and abundances peak. This study has demonstrated that sampling periods of one week produce a very high proportion of singletons, indicating that shorter sampling periods are inadequate for gaining an accurate picture of parasitoid diversity. These corroborate results obtained from studies in the UK that demonstrate the need for sampling periods that extend for at least two consecutive weeks in order to account for temporal variation (Fraser et al., 2007, 2008b).

The issue of trap distance is complex. The optimal distance between traps is far enough so that traps are sufficiently different in catch, but not so far that catches are entirely dissimilar so that characteristic species may be missed (Colwell & Coddington, 1994). The present study showed that 20 meters may be too close together, because trap catches did not differ between adjoining 'bands' of traps. Increasing the distance to at least 30-40m may ensure a better balance between trap similarity and obtaining more characteristic species (Fraser et al., 2008).

Summary of Recommendations

Based on the results from this study, a set of recommendations are proposed for designing optimal sampling strategies to maximise the capture of parasitoid wasp species. These recommendations are applicable only to a restricted sampling season over the summer period using Malaise-traps.

For obtaining reliable data for ecological studies that attempt to compare multiple sites:

- (i) A minimum number of ten traps per site should be used so that around half of the species present are caught.
- (ii) Sampling should be undertaken in December and January, when it is possible to characterise the sites most thoroughly.
- (iii) Traps should be left out for 2-week sampling periods in each month at each site, in order to capture enough individuals.

For obtaining an exhaustive inventory of a single site:

- (i) A minimum number of twenty traps per site should be used to maximise observed species richness.
- (ii) Sampling should be undertaken in January and February, when it is possible to capture the greatest number of species overall.
- (iii) Traps should be left out to sample as much of the two months as possible, ideally the whole period, in order to maximise capture of individuals (and therefore species).

For both scenarios:

- (i) This study provides a visual comparison of the affect that different amounts of sampling effort will have on observed species richness, allowing the planning of a customised program based either on a desired sampling effort or a desired level of observed richness.
- (ii) Traps should be spaced at least 30 meters apart, and some effort should be made to sample a variety of microhabitats.
- (iii) Collection bottles should be changed every one to two weeks in order to maintain specimen integrity.
- (iv) Molecular methods should be used to match the sexes, to identify the presence of cryptic taxa, and to confirm morphological analyses between similar species.

3

Description of a New Species of Parasitoid Wasp from New Zealand

Dr. Jules Tosquinet

(1824-1902)

"Tosquinet always occupied himself with Natural History; it was a passion that gripped him from his youth and never abandoned him."

"His friendship was energetic and firm, and he knew how to defend his friends and his beloved Entomological Society with a great energy."

G. Severin

1903

3. Introduction

3.1 Taxonomy: The Foundation of Biology

With the publishing of *Systema Naturae* in 1735, the Swedish botanist and physician Carl Linnaeus developed formal methods of naming, describing, and classifying living organisms, including the system of binomial nomenclature (Patterson, 2010). He would go on to earn his epithet as "the father of modern taxonomy" by publishing and revising many important works that established the modern understanding of the living world. The foundations he laid still embody the heart of modern systematics: the study of biological history, as told through phylogenetic techniques that piece together the relationships between living organisms (Wheeler, 2008b).

Taxonomy is an analytical subdiscipline of systematics in which hypotheses regarding biological classification are tested by comparing the characters of known and unknown taxa (Sluys, 2013). Taxonomy is primarily focused on identification, classification, and the assigning of unambiguous, standardised names to taxa, so that biological information is universally accessible (Winston, 1999). By analysing the biological information that has accumulated within taxa during the course of their evolution, taxonomists can organise biodiversity into hierarchical groupings that reflect their common descent (Zhang, 2010). Ultimately, the 'goal' of taxonomy is to describe and understand the evolutionary relationships between every species on earth, through the analysis of their complex characters (Wheeler, 2008a, 2010).

Two hundred and fifty years on from the achievements of Linnaeus, we live in an age characterised by environmental flux and extinction, so the need for descriptive taxonomy has never been greater (Zhang, 2010). Modern taxonomy is an information science involving the coding of a diverse range of morphological, molecular, and behavioural characters within both fossil and living species (Zhang, 2010; Wheeler, 2007). Systematists have developed and incorporated a variety of technologies into their methods to enable more efficient analyses and communication of results. These include high-tech imaging systems, statistical software packages, and high-throughput DNA sequencing (Goldstein & DeSalle, 2011). The generation and communication of biological data through modern

taxonomic techniques is relied upon for the conservation, economic, and social uses of biodiversity.

Character analysis forms the backbone of taxonomy and provides the raw material upon which species descriptions and phylogenetic classifications are based (Wheeler, 2009a). As a comparative, hypothesis-driven science, taxonomy involves the continual revision of biological classifications in order to reflect new data produced through updated analytical methods (de Carvalho et al., 2014; Sluys, 2013). Revisions reflect the fact that organisms are not classified in a vacuum, but rather that their descriptions are in fact "highly selective account[s] of features that are found to be significant in comparison with related things" (Grimaldi & Engel, 2007, p.646). This means that biological classification will never be 'complete' but will instead change to accommodate the analyses of an ever-increasing number of individuals, analysed through an ever-evolving set of methods.

Because the distribution of organisms is unbounded by lines on a map, taxonomic inquiry must also transcend geopolitical demarcations to become a truly collaborative enterprise (Wheeler, 2009b). Approximately 18,000 new species are described each year worldwide, and about three quarters of these are invertebrates (Chapman, 2009). In order to standardise and oversee the naming of animal species across the globe, the International Commission on Zoological Nomenclature was founded in 1895 (ICZN, 1999). The commission aims to facilitate consistency and universality in the naming of species, while respecting the taxonomic judgement of scientists. It receives no governmental or international funding, relying instead on donations and journal subscriptions (Polaszek et al., 2008). It fulfils an important role in dispute mediation when issues arise in the naming and classification of taxa.

3.2 The Importance of Taxonomy

Only systematics can attempt to define the primary unit of biodiversity: the species. A central assumption of defining species is that unique, diagnosable living entities actually exist in nature, and they are discoverable (Nixon & Wheeler, 1990). Part of the difficulty in defining species is the fact that the biological entities humans classify in this way are only representative of a small subset of characters, drawn from a small sample of individuals, observed over a relatively short period of time (Patterson, 2010). These difficulties are yet to be resolved, and the definition of species continues to be an area of debate (see Wilkins, 2009), although some

definitions have proven to be more valuable than others. Several conceptions of species have gained prominence and remain influential today (Wilkins, 2009).

Linnaeus considered species to be the lowest 'kinds' of organisms recognisable as distinct groups (Claridge et al., 1997). The idea that species were true-breeding units gained significance in the late nineteenth century, before the evolutionary synthesis drew together the concepts of Mendelian inheritance and natural selection (Claridge, 2009). Ernst Mayr's 'biological species concept' was central to the formulation of the modern synthesis, and defines species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr, 1942, p. 120). An evolutionary species concept was proposed by de Queiroz & Donoghue (1990) in which species are defined as "a series of entities forming a single line of ancestry and descent" (p. 50). Finally, the phylogenetic species concept (PSC) defines species as the level of biological classification below which cladistic methods are not applicable (Hennig, 1966).

The phylogenetic species concept proposed by Willi Hennig shortly after the Second World War was republished in English in the 1960's. Since then, it has been widely accepted by systematists, who up until then were unsatisfied with the limitations of the biological species concept exposed by phenetic and cladistic methods (Claridge et al., 1997). Hennig's method centred on the branching patterns of phylogenetic trees, although he firmly believed that all available information should be used to understand a species' genealogy (Wheeler et al., 2013). The goal of the PSC is to expose the smallest recognisable units that can be investigated with cladistical methods. Recent revisions of the concept have therefore defined species as "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals" (Nixon & Wheeler, 1990, p. 211). Species are viewed as irreversible packages of characters that are the result of evolutionary processes (Wheeler, 2007).

Systematists often juggle many important responsibilities: they are custodians of biological knowledge accumulated over centuries; they are curators of vast collections holding three billion specimens worldwide and representing millions of human-hours in effort; they are cataloguers of biodiversity who are racing the clock against extinctions; and increasingly, they are seen as service providers of species identifications and datasets (Patterson, 2010; Goldstein & DeSalle, 2011; Wheeler, 2010). Most biologists depend on accurate species

identifications, meaningful schemes of biological classification, and informative scientific names that allow the storage and communication of information about an organism: all are products of careful taxonomic study (Wheeler, 2009b). Reliable species names are strong evolutionary hypotheses that underpin many conservation and biosecurity decisions and form the basis of our understanding of biodiversity and evolution (Sluys, 2013; de Carvalho et al., 2007). Far from arbitrary pigeonholing, modern taxonomic outputs allow accurate predictions to be made about taxa before anything else is known about them (Gauld, 1984).

The neglect of taxonomy has flow-on effects to other areas such as ecology, where work is hampered by a lack of identification resources, amplifying the 'biodiversity crisis' (de Carvalho et al., 2007; Wilson, 1985). Comprehensive biodiversity inventories with appropriate taxonomic resolution are the only way to answer questions relating to the maintenance of ecological processes fundamental to sustaining life on the planet, regardless of the rate or causes of species extinctions (Wheeler, 1995). Taxonomy is the crucial link between our understanding of evolutionary processes, the complexity and diversity of organisms, and the ability to monitor and conserve species and habitats (Wheeler, 2009b). Of course, it is impossible to have any sort of relationship with biodiversity at all if we do not know that it exists (Wheeler, 2008b). Although taxonomic data repositories and collections offer a wealth of information and provide powerful weapons in the fight to halt declining biodiversity, taxonomists continue to face challenges that range from academic marginalisation to a lack of funding (New, 1996).

3.3 State of the Field

Challenges

The sustained, gradual decline of funding, expertise, and academic prestige associated with taxonomy is widely documented, and causing serious concern amongst international agencies and biodiversity scientists (Ebach et al., 2011; Agnarsson & Kuntner, 2007; de Carvalho et al., 2014; Wheeler, 2008b; Kim & Byrne, 2006). The secretariat for the Convention on Biological Diversity (CBD) (2008) stated that although taxonomic information underpins an awareness of

biodiversity and drives policy decisions relating to its management, decades of decline have severely weakened taxonomic capability around the world.

A House of Lords (2008) inquiry into systematic biology in the UK resulted in several important conclusions: systematics underpins all study of the natural world; taxonomic expertise is essential to meet international obligations for monitoring biodiversity; and the vast majority of professional taxonomists surveyed were of the opinion that the decline in both funding and capability is reaching crisis point. The inquiry recommended the commissioning of a study by the Natural Environment Research Council to ascertain taxonomic capability in the UK. This follow-up study found that out of the approximately 1,000 taxonomists working in the UK, only 400 were taxon specialists active in revisionary or descriptive work (Natural History Museum Review Team, 2011). It also showed that the majority were over 40, and that 75% of respondents described their taxonomic area as being in an "unhealthy" state, largely due to the lack of new taxonomists in training.

The epistemological and theoretical foundations of taxonomy are frequently misunderstood by those in academia and government. For instance, the claim that "taxonomy provides opinions on species boundaries" is common (Godfray, 2007, p. 259), and so is the belief that taxonomists' primary duty is to provide species identification services to end-users (de Carvalho et al., 2014). The magnitude of prejudices led Wheeler (2009b) to issue a 'taxonomic declaration of independence', to defend the epistemological basis of taxonomy, and to demand recognition of its value to society. A lack of understanding leads to a decline in prestige and the funding prioritisations that come with it, even in major institutions (de Carvalho et al., 2008; Grimaldi & Engel, 2007). Decision-makers are already biased towards research and methodologies that are perceived to be more 'glamorous' such as molecular techniques (Zhang, 2010; New, 2000). Although taxonomists willingly incorporate molecular methods and collaborate with researchers from other disciplines, many are forced to do so because of administrative and financial pressures stemming from ignorance about what taxonomy actually is, and how it provides value for other areas of the life sciences (de Carvalho et al., 2014).

Opportunities

Despite the challenges, there are exciting opportunities that taxonomists are uniquely positioned to exploit. Relatively small investments in time and funding

can have a disproportionate impact on the expansion and improvement of specimen collections; on the rate of species descriptions (especially in biodiversity hotspots); and on the production of high-quality resources and outputs for end-users such as faunal lists, identification keys, and conservation policy submissions (Wheeler, 2008, 2010; Oliver & Beattie, 1997). Investing in taxonomy can lead to more resilient economies through the discovery and commercialisation of biological resources for food, fuel, fibre, and medicine (Wheeler et al., 2012). Conversely, not investing can have many unforeseen consequences, for example the extinction of a commercially important fish species due to inconsistent identification (Iglesias et al., 2010). Developments in communications and information technologies mean that it is much easier for taxonomists nearing retirement to pass on their knowledge before they leave the field, conserving valuable experience developed over decades (Wheeler, 1995).

DNA Barcoding: At the Crossroads

Hebert et al (2003) emphasised the perceived advantages of DNA barcoding over morphological approaches for species identification. In their highly cited paper, they advocate for DNA barcoding as a solution to most of the challenges facing taxonomy. Their method consists of comparing short sections of mitochondrial DNA. At the same time, Tautz et al (2003) advocated for a paradigm shift away from morphology-based analysis, towards 'DNA taxonomy' in which species are described (and even 'discovered') primarily through molecular means. These related approaches challenge the epistemological basis of taxonomy by proposing that morphological analysis is outdated, and that exclusive reliance on DNA is somehow a more 'objective' means of both identifying known species and discovering new ones (Hebert et al., 2003; Tautz et al., 2003).

Such proposals have inevitably drawn criticism from taxonomists and others who are concerned at the empirical and theoretical flaws characterising 'DNA taxonomy' as it is currently practised (Taylor & Harris, 2012; Goldstein & DeSalle, 2011; Lipscomb et al., 2003; Seberg et al., 2003). DNA proponents argue that "DNA sequence information is digital and is not influenced by subjective assessments" (Tautz et al., 2003, p. 71). However, a review of species-level paraphyly and polyphyly challenged the assumption that alleles within a lineage are always monophyletic, by showing that in fact, the opposite condition is widespread

(Funk & Omland, 2003). The implication is that short segments of DNA may not be able to reveal common descent with as much accuracy and objectivity as DNA proponents claim. Other criticisms characterise 'DNA taxonomy' as a return to single-character approaches (Sluys, 2013); as lacking context and being too subjective (Wheeler et al., 2013); and as siphoning resources away from more fruitful applications (Will et al., 2005). As for species discovery, the idea that species can be described solely through gene sequences is "a pseudoscience based on quantitative manipulations of questionable phenetic data" (Wheeler, 2008a, p. 2).

Towards an Integrated Taxonomy

Just as the careless application of molecular tools can harm the taxonomic cause, the nuanced application of these methods can also support its goals and aspirations by providing another data stream. Introducing DNA barcoding into studies of parasitoid wasps can provide a supplementary evidence pool to reinforce species delimitation among cryptic or sexually dimorphic species (Alex Smith et al., 2013). Smith et al., (2012) released a dataset generated from DNA sequences extracted from over 20,000 specimens of microgastrine wasps (Hymenoptera: Braconidae), sequenced over the course of 8 years. They recognise that "for groups where traditional taxonomic knowledge exists, the DNA barcode may be used in ... the identification process, but not necessarily to replace it". Similarly, Janzen et al (2009) described how DNA barcoding was used within parasitoid wasp inventories in Costa Rica to improve the depth of the inventory by revealing cryptic species that can then, for the most part, be identified and clarified by morphological traits previously ascribed to variation within a species.

These types of approaches illustrate 'integrative taxonomy', that is, the use of a diverse set of methods to generate multiple sources of relevant data to answer taxonomic questions and pose new ones (Wheeler et al., 2012; Will et al., 2005). Despite some scepticism (e.g. Sluys, 2013), cybertaxonomy is gaining traction as an emerging method to support the traditional goals of taxonomy by embracing the technological capabilities provided by online collections, extremely large datasets, improved imaging systems, and the integration of disparate sources of information into a single place (Patterson, 2010; Wheeler, 2007). A wealth of opportunities exist for increased automation of the taxonomic workflow including the capture, analysis

and automatic extraction of relevant characters from images that can then be stored in databases (Clark et al., 2009; de Carvalho et al., 2007; La Salle et al., 2009). Innovative mega-journals allow the rapid publishing of descriptive work with few restrictions on content or length of manuscripts (Zhang, 2008). For example, *Zootaxa* contributed 14% of all new descriptions of taxa indexed by Zoological Record in 2007, and continues to experience exponential growth. Finally, citing primary taxonomic literature has the potential to add back the credit, prestige, and citation metrics that are used to judge academic performance at many institutions (Agnarsson & Kuntner, 2007).

3.4 Insect Taxonomy

The sheer abundance and diversity of insects amplifies all of the taxonomic challenges, and opportunities, associated with studying other groups (Wheeler, 2009a). With over 1 million species currently described and many times that number undocumented, insects present unique challenges due to their incredible diversity and a lack of trained insect taxonomists (Adler & Footit, 2009; Wheeler, 2009a; Wilson, 1988). The extra demands of insect taxonomy have necessitated the training of 'parataxonomists' who act as a first filter through which large volumes of specimens are passed before reaching the specialist (Kim, 2009). A lack of job prospects, and an increasing emphasis on molecular methods and 'keyboard biology' (Noss, 1996), means that students training to be taxonomists either become distracted from alpha taxonomy or are unable to pursue it due to administrative pressure to engage in 'more glamorous' areas rather than what is commonly perceived to be 'Victorian natural history' (de Carvalho et al., 2014; New, 2000). These attitudes make it difficult to compete for funding and prestige, despite the clear knowledge gaps that can only be filled by modern taxonomists who pursue an integrated approach to their work (Kim, 2009).

These problems also exist in New Zealand. A recent Royal Society of New Zealand report assessing national taxonomic collections found that taxonomy is under-resourced and lacks a coordinated focus (Nelson et al., 2015). The report drew attention to the linkages between taxonomy and primary production, biosecurity, international obligations, biodiversity monitoring, resource management, human health, and research quality. The loss of expertise in invertebrate taxonomy is a major issue likely to negatively impact New Zealand's

primary industries, of which insects are both major pests and beneficial organisms (Lester et al., 2014). Lester and colleagues identified weak investment in taxonomy, a shortage of employed personnel, and a lack of diagnostic capability as posing threats to New Zealand's long-term production and trade.

In terms of Hymenoptera diversity, there has been a narrow focus on imported species, and less effort has been directed towards the native Hymenoptera in New Zealand; meaning that the diagnosis and classification of New Zealand's parasitoid wasp diversity presents a serious challenge (Ward et al., 2012). This is concerning considering the fundamental economic and ecological importance, and the large diversity of parasitic Hymenoptera in both natural and modified ecosystems (Gauld, 1984). Due to their ecological dominance and species diversity, neglecting the taxonomic treatment of parasitoid wasps and failing to include them in conservation planning undermines those initiatives and makes them difficult to justify (Shaw & Hochberg, 2001). All of these challenges contribute to an enormous taxonomic impediment, and mean that for parasitic Hymenoptera, perhaps only 10% of the world fauna is currently described (Huber, 2009).

3.5 The genus *Lusius*

Lusius Tosquinet (Hymenoptera: Ichneumonidae: Ichneumoninae) is a genus of parasitoid wasp that has been found all over the world, but appears to be naturally uncommon, with few specimens collected from any single location (Rousse et al., 2013). Tosquinet (1903) collected specimens from Indonesia in 1890 on which to base the description of the genus. Currently, there are seven described species (*L. aborensis*, *L. anguinus*, *L. apollo*, *L. flummo*, *L. gracilis*, *L. macilentus*, and *L. tenuissimus*). The earliest published record is *Mesoleptus anguina* described as part of the Mexican fauna in Cresson (1873), and later revised to *Lusius anguinus*. The two species described from India (*Oedematopsis apollo* and *O. aborensis*) by Morley (1913, 1914) were subsequently transferred to *Lusius* by Cushman (1937), who included extra material from Taiwan and the Philippines. A new species, *L. gracilis*, and a redescription of *L. apollo*, were provided by Kusigemati (1986) from material collected in Taiwan. More recently, Rousse et al. (2013) described *Lusius flummo* from Uganda, and redescribed *L. tenuissimus*.

Here I present a description of a new species of parasitoid wasp from the genus *Lusius*, the first species of this genus to be described from New Zealand.

Lusius is one of the very few genera of Ichneumoninae in New Zealand (Ward & Schnitzler, 2013), and its widespread distribution makes it of interest for further study.

3.6 Methods

Microscopy

All microscope work was conducted using a Leica MZ6 stereomicroscope fitted with a micrometer-calibrated ocular scale bar, and a Leica CLS 150X light source. Images were taken using a Leica M205A stereomicroscope fitted with a Nikon Digital Sight DS-R1i camera. A series of TIFF images were captured from different focal planes in NIS Elements F v4.00.00 and then 'stacked' together in Zerene Stacker 1.04 using the Pmax function. The stacked image was then adjusted in Adobe Lightroom 6 and exported to JPEG format.

Conventions

Anatomical nomenclature follows Rouse et al., (2013) who have recently revised the Afrotropical Phaeogenini (Ichneumonidae: Ichneumoninae) including a new species of *Lusius*. Wing venation follows Gauld (1984). Fore and hind wings were dissected from a single specimen and slide-mounted in Canada balsam before being imaged. New Zealand Region codes follow Crosby et al (1998). Material examined from: **NZAC**: New Zealand Arthropod Collection; **LUNZ**: Entomology Research Collection, Lincoln University.

Specimens were first compared against diagnostic characters for the genus to check if they conformed. Comparisons with other described species of *Lusius* are based on data and descriptions in Cresson (1874), Morley (1913, 1914), Kusigemati (1986) and Rouse et al (2013).

Measurements

Measurements from twenty three individuals were made. The last two measurements (**Ti** and **Rsi**) are not used in Rousse et al., (2013) but are used in previous species descriptions for *Lusius*, and are included here for comparison.

Body length (mm): Measured from toruli to metasomal apex.

Forewing length (mm): Measured from tegula to wing apex.

HdWi (head dorsal width index): maximal width / central length of head in dorsal view.

HfWi (head frontal width index): maximal width / central height of head in frontal view.

Mi (malar line index): malar line / basal mandibular width.

IOi (inter-ocellar index): shortest distance between posterior ocelli / ocellus diameter.

OOi (oculo-ocellar index): shortest distance between eye and posterior ocellus / ocellus diameter.

Fli_n (length index of flagellomere n): length / width of flagellomere n.

OTi (ovipositor sheath-tibia index): length of ovipositor sheath / length of hind tibia.

Ti (tergite index): length tergite 1 / length tergite 2.

Rsi (Rs/1m-cu index): length Rs vein / length 1m-cu vein in forewing.

3.7 Results

3.8 *Lusius malfoyi*: A New Parasitoid Wasp from New Zealand

FAMILY ICHNEUMONIDAE LATREILLE, 1802

GENUS *LUSIUS* TOSQUINET, 1903

Diagnostic features of the genus include: unidentate mandibles; hemispherical head; males with elongate gonoforceps; open areolet; and missing 3Rs-m vein.

Lusius malfoyi Saunders & Ward, **sp. nov.**

Material Examined

Holotype

Female (NZAC). NZ, AK, Birkenhead, 1/01/1981, J. F. Longworth, Malaise trap in second growth bush (NZAC04054629).

Paratypes. NZAC.

4 Females (NZAC). NZ, AK, Birkenhead, 1/01/1981, J. F. Longworth, Malaise trap in second growth bush (NZAC04054216, NZAC04053831, NZAC04054418, NZAC04054398).

Female (NZAC). NZ, AK, Birkenhead, 1/03/1981, J. F. Longworth, Malaise trap in second growth bush (NZAC04054123).

Female (NZAC). NZ, AK, Birkenhead, 1/02/1981, J. F. Longworth, Malaise trap in second growth bush (NZAC04053912).

Female (NZAC). NZ, AK, Birkenhead, 1/12/1980, J. F. Longworth, Malaise trap in second growth bush (NZAC04054523).

Female (NZAC). NZ, AK, Lynfield, 21/09/1980, G. Kuschel, Malaise trap (NZAC04054497).

Female (NZAC). NZ, AK, Lynfield, 19/10/1980, G. Kuschel, Malaise trap (NZAC04053893).

Female (NZAC). NZ, HB, Puketitiri, Little Bush, 20/12/1998, T. H. Davies, Cyanide, Malaise trap (NZAC04054066).

2 Females (NZAC). NZ, NN, Cobb Reservoir, 1/01/1981, A. R. Curtis, Malaise trap on edge of Nothofagus forest (NZAC04053926, NZAC04054499).

Female (NZAC). NZ, NN, Cobb Reservoir, 1/02/1981, A. R. Curtis, Malaise trap on edge of Nothofagus forest (NZAC04054539).

Female (NZAC). NZ, DN, #422 Pinehill Rd, Dunedin, 6-20/12/2011, D. Ward, Malaise trap in resident garden (NZAC04044699).

Male (NZAC). NZ, AK, Birkenhead, 01/11/1980, J. F. Longworth, Malaise trap in second growth bush. (NZAC04054534).

Male (NZAC). NZ, CO, Kawarau Gorge, 1600m, 20/03/1975, J. C. Watt, Malaise trap. (NZAC04053849).

Male (NZAC). NZ, NN, Cobb Reservoir, 01/01/1981, A. R. Curtis, Malaise trap on edge of Nothofagus forest. (NZAC04053851).

Paratypes. LUNZ.

LUNZ01: Female (LUNZ). NZ, TK, Mt. Egmont E Side, 850m, 16.xii.1983, J. W. Early, sweeping in kamahi forest.

LUNZ02: Female (LUNZ). NZ, TK, Mt Egmont, 610m, East side, Stratford Mtn rd, 16.xii.1983, sweeping in mixed kamahi podocarpus forest, J. W. Early.

LUNZ03: Female (LUNZ). NZ, FD, Fiordland NP, Deep Cove, 3-ii-83, S. Warner, sweeping ferns in forest.

LUNZ04: Female (LUNZ). NZ, BR, Lewis Pass Scenic Res nr Marble Hill, 5.1v.1983, J.W. Early, sweeping ground cover in nothofagus forest.

LUNZ05: Female (LUNZ). NZ, BR, Cobb V., 820m, Trilobite Hut, 8-11.ii.1985, J.W. Early, Malaise trap at Nothofagus forest edge.

Diagnosis

Lusius malfoyi sp. nov. can be distinguished from the other species of *Lusius* by the following characters. The light-brown to light-orange body colouration of *Lusius malfoyi* sp. nov., is distinct from the predominantly black colouration of *L. aborensis*, or the pale white colouration of *L. anguinus*. The antennae of *L. malfoyi* are light-brown, with no white band, distinguishing it from *L. gracilis*, *L. macilentus*, *L. tenuissimus*, and *L. apollo*s. Finally, the evenly rounded clypeal margins seen in *L. malfoyi* are distinct from *L. flummox*, where they are strongly pointed apico-laterally.

Description

Female. **Body length** 4.7-7.8mm; **Forewing length** 4.1-5.3mm, **Rsi** 0.8-1.2. (Figures 10-14)

Colour

Head cream yellow or light brown with cream patches; vertex, occiput, interocellar space, scape, pedicel and flagella light orange infusate; face beige, sometimes with light orange infusate markings extending from toruli to margin of clypeus, frons sometimes brown. Mesosoma cream or beige, always with dark

brown band that extends from upper mesopleuron or lower pronotum, to metapleuron; mesoscutal lobes light orange infusate to brown; propodeum light orange infusate, sometimes dark brown; wings hyaline with infusate venation. Fore, mid coxae, and trochanter pale yellow; hind coxae pale yellow, sometimes light orange infusate; rest of the legs light orange, tarsi brown. Tergite 1, 2, and gastrocoelus light orange infusate to brown.

Head

Face quadrate, punctate, head wider than long (**HdWi** 1.6-2.8, **HfWi** 1.0-1.5); clypeus apical margin transverse, with evenly rounded lateral margins, punctate with few hairs; malar line long (**MI** 1.5-1.8); deep subocular sulcus; palpi elongate, maxillary palpus reaching almost to epicnemium; frons smooth and carinae absent; vertex hardly sculptured, ocellar triangle wider than long (**IOi** 1.3-2.3, **OOi** 1.3-2.3); temple mostly smooth, swollen behind eyes; antenna very long and slender, scape reduced, flagella rectangular, 30-34 flagellomeres; **Fli**₁ 3.6-7.0; **Fli**₂ 3.4-6.7; **Fli**₃ 2.8-6.3; **Fli**₁₅ 1.2-2.

Mesosoma

Polished; pleurae densely punctate to punctate-reticulate; pronotum with epomia weak to moderate; sternaulus weak, extending one fifth length of mesopleuron; epicnemial carina long, reaching midpoint of mesopleuron to propleuron; notaulus moderately deep, wrinkled; mesoscutum smooth and polished with few apical striations; scutellum strongly convex, mostly smooth, some lateral striations; propodeum weakly rugose with transverse striations, apical and posterior transverse carinae absent; hind tibia narrowed basally.

Metasoma

Tergite 1 slender and smooth, its posterior third slightly swollen dorsally; tergite 2 finely and densely reticulate, tergite 1 and tergite 2 approximately the same length (**Ti** 0.87-1.07); gastrocoelus long but very shallow, within anterior quarter of tergite; ovipositor straight and short, **OTi** 0.12-0.25.

Male.

Follows description for female, except anterior transverse carina on propodeum present but variable in strength, faint to moderately strong.

3.9 Discussion

Etymology

Noun in the genitive case. This species is named after Lucius Malfoy, a character in J. K. Rowling's *Harry Potter* stories, for two reasons. First, the study of parasitoid wasps is an enjoyable and 'magical' experience. Second, the fictional namesake and his family have a sinister reputation in the *Harry Potter* stories, but in the end their love for each other separates them from the evil forces with which they were once aligned. This parallels the way in which many people view wasps in a negative way, even though only a small proportion of wasp species cause damage or harm. It is my hope that the reputation of wasps can be restored through a better understanding of their ecology and behaviour.

Distribution

Widespread on the New Zealand mainland (Fig. 16). Found in the North Island (AK, BP, HB, TK) and South Island (NN, MB, CO, OL, WD, FD). Has not been collected from offshore islands. Absence is likely to represent a lack of sampling effort in those areas rather than true absence. Collection records date from 1926 to 2012.

Comments

Host records for *L. malfoyi* are unknown. A single collection record notes that the specimen was "Bred x pupa of moth x native tree motueka" (NZAC04054002). Based on this record and knowledge of the genus, a lepidopteran host is likely. All *L. malfoyi* specimens were collected during September to March (spring to late summer), from a range of different habitats including second-growth bush, *Nothofagus* forest edges, and residential gardens. It is a naturally uncommon species, as few specimens have been collected from any one area. For example, two months of Malaise trapping at four sites in the Dunedin City area captured only five specimens, all from one site.

Lusius has a widespread global distribution (Fig. 16). Its biogeographic range includes Mexico, Brazil and Argentina (*L. anguinus*, *L. ferrugineus* from only Brazil); India (*L. aborensis* and *L. apollo*); Kenya, Madagascar, and Tanzania (*L. tenuissimus*); Uganda (*L. flummox*); China, Taiwan, and the Philippines (*L. apollo*, *L. gracilis* from China and Taiwan, *L. macilentus* from the Philippines). Records of undescribed species have been reported from Brazil (Graf, 2000); Argentina (Reguilón, 2014); and Mexico (Ruíz-Cancino, 2015). The genus is not currently known from Australia (Gauld, 1984). The origins of the genus in New Zealand are unclear. Its range outside New Zealand shows a typical Gondwanan distribution, as it is found in South America and Madagascar. It could therefore be descended from an ancient Gondwanan lineage, or it could be a more recent dispersal. Future work could investigate this question through comparative morphological and molecular means.

4. General Discussion

4.1 Parasitoid Wasp Diversity & Conservation

The distribution and composition of biodiversity has profound impacts on the processes that support life on this planet, and therefore these factors exert a considerable influence on the ways in which human beings live (MEA, 2011; Secretariat of the CBD, 1992). A wider recognition of this fact has prompted individuals, organisations, and governments to take a greater interest in how best to measure and monitor the species and environments in both human-modified, and natural systems (TEEB, 2010). Parasitoid wasps are dominant species that act as top-down regulators of hosts in natural systems, and economically important biocontrol agents in modified systems (LaSalle & Gauld, 1993). Despite these facts, parasitoids are rarely considered in conservation strategies because so little is known about their diversity. Although 150 species of Hymenoptera are found on the IUCN red list, none of these are parasitoids (Baillie & Groombridge, 1996). Conserving parasitoids in their native ranges is seen as important not just for their ecological roles within natural systems, but to provide a reservoir of potential natural enemies that could be applied against introduced (or native) pests in the future (Heraty, 2009). This is particularly important for nations whose economies are based on their primary production and environment, such as New Zealand.

As a signatory to the UN Convention on Biological Diversity, the New Zealand government has committed itself to developing the scientific and institutional capacities necessary to implement measures to halt biodiversity declines (Secretariat of the CBD, 1992, Article 7). Specifically, this means that the nation will "identify components of biological diversity important for its conservation" and "monitor, through sampling and other techniques, the components of biological diversity identified... paying particular attention to those requiring urgent conservation measures." Priority for identification and monitoring is to be given to species and communities which are threatened; are of economic or agricultural importance; are important for conservation research as indicator species; or are highly endemic or unique. Unfortunately, a lack of distribution and abundance data means that we know very little about the threat status and ecological requirements of our unique endemic taxa, particularly invertebrates (Watts et al.,

2012; Myers et al., 2000). Even with our present understanding, the New Zealand parasitoid fauna clearly encapsulates most of the criteria that characterise groups with high research and conservation value (Ward et al., 2012; Berry, 2010).

4.2 Optimising Sampling Methods

A lack of accurate, standardised, cost-efficient sampling methods is widely recognised to be one of the most important barriers to understanding and managing biodiversity (Stork et al., 2015; Southwood & Henderson, 2000; New, 1998). Unfortunately, the development of such methods are more difficult for hyper-diverse taxa such as parasitoid wasps, where even modest efforts capture large numbers of species almost anywhere in the world (Veijalainen et al., 2012; Owen et al., 1981). The present study has demonstrated that it is possible to census two thirds of the parasitoid wasp diversity characterising local sites by employing an intensive Malaise-trapping regime over the summer. Key sampling recommendations include the need for a minimum number of 10 traps that are placed to maximise site coverage, and that at least two 2-week sampling periods should be completed at different times depending on the nature of the study.

A baseline representation or estimate of biodiversity is a prerequisite to the development of monitoring strategies to document spatial and temporal changes in abundance and composition of target taxa. No study has ever attempted to quantify sampling effort in relation to parasitoid species richness in New Zealand. This is unfortunate, because the establishment of accurate and reliable sampling protocols depends on a good understanding of how species richness is affected by the sampling methodology employed. Therefore, the development of accurate, cost-effective, restricted sampling methods is a top priority for the accurate measurement and monitoring of parasitoid wasps: mega-diverse, ecologically dominant, and economically important taxa. Quantifying sampling effort in relation to species richness is the first step in developing sampling protocols that can be used confidently in taxonomic and ecological studies to measure completeness of inventories and compare richness across sites. Therefore, this study provides an important foundation for future work because it allows researchers to plan and make use of limited resources more effectively when studying parasitoid biodiversity.

Short-cuts and cost-effective invertebrate monitoring programs are frequently recommended, for example "once a thorough community

characterization has been conducted, these data can be used to identify surrogates of biodiversity" (Rohr et al., 2007, p.424). However, sampling invertebrates is inherently difficult because of "the multitude of methods that can be used for their sampling, and the paltry funds available for their inventory and monitoring" (p.424). Herein lies the paradox: thorough, expensive, time-consuming community inventories are required for the development of restricted, cost-effective, and rapid sampling approaches. This leads to a circular argument in which the objective of developing optimal methods is in fact mooted by the requirements of developing those same methods. A potential solution is an initial investment to undertake local inventories. The results can then be extrapolated to other areas, and incorporated into optimal sampling strategies. These strategies can then form the backbone of rapid, cost-effective monitoring strategies in the long term. Developing efficient sampling methods by using preliminary methods that are themselves suboptimal, uncalibrated, and non-standardised, are likely to lead to failure to capture the most important information about an ecosystem on which decisions regarding conservation may depend. The success of optimal sampling methods therefore depends on the thorough testing of methods with real world data.

There is growing evidence demonstrating the potential of Hymenoptera as indicator taxa for environmental assessments, or as surrogates for extrapolating the diversity of other taxa (Mazón, 2015; Anderson et al., 2011; Rohr et al., 2007). Parasitoid wasps have been recommended as "a simple and practicable monitoring tool for tracking change in wider arthropod diversity in agroecosystems" (Anderson et al., 2011, p. 382). However, for these concepts to be tested properly, it is essential that the sampling methods used to obtain data on species abundances and distributions are robust and take into account some of the pitfalls of estimating species richness (Gotelli & Colwell, 2002). For these procedures to gain widespread acceptance they must incorporate sampling regimes that are not only accurate, but cost effective and simple to compare with other surveys (Ward & Larivière, 2004). A restricted sampling regime using Malaise-trapped parasitoid wasps over the summer period, of the sort described here, could be a fruitful avenue to explore in relation to these types of research questions.

4.3 Integrating Taxonomy & Ecology

Two important themes emerged during the planning and execution of this study. The first was that undertaking any ecological study on highly diverse invertebrate assemblages immediately reveals the pressing need for descriptive taxonomy in these groups. Second, and conversely, the taxonomic treatment of the species described here revealed a lack of understanding about its ecology and behaviour. It seems self-evident that the most fruitful approach to both types of work, ecological and taxonomic, would result from increasing collaboration between these two important disciplines. Indeed this sort of collaboration has been encouraged for many years (Halme et al., 2015; New, 2000), and there are examples where it has been implemented successfully (Janzen et al., 2009). However, a more widespread and far-reaching adjustment in attitude is required by all of those working to study the natural world, to overcome the preconceptions and habits that hold one back from incorporating different methods or collaborating with those outside their immediate discipline.

In the absence of a large bee, ant, or aculeate wasp fauna, parasitoid wasps dominate the New Zealand Hymenoptera (Ward et al., 2012). However, only about a quarter of New Zealand's estimated 3,000 species of Hymenoptera have been described (Berry, 2010). Unsurprisingly, few studies are able to identify the bulk of their parasitoid wasps to species level. Taxonomists and ecologists could seize this opportunity to increase the scope and impact of their research by collaborating on the planning of research, and by pooling their resources and expertise. Exhaustive inventories not only provide taxonomists with updated species lists, but when carried out in a standardised way they also provide a wealth of data relevant to the goals of ecologists. Ecologists are uniquely positioned to provide input into survey design and trapping methods to ensure the greatest possible catch, while taxonomists are uniquely positioned to offer experience in the identification of taxa. Taxonomists also have a good knowledge of where sampling effort should be applied to get the highest return on expanding the coverage of undersampled areas.

4.4 Future Directions

Several practical measures would help to inform a general understanding of parasitoids and provide information pertinent to their conservation, for example Fraser et al (2008b) listed several: (i) preliminary species inventories; (ii) an investigation of the relationship between parasitoids and plant communities; and

(iii) the development of techniques to monitor parasitoid communities over time. The short term development, as well as the long term accuracy, uptake, and success of these measures, requires an understanding of how sampling can be optimised in order to catch the greatest number of parasitoid species with the least amount of effort and cost. A better understanding of parasitoid distributions, host preferences and life cycles, and how these change over space and time, would greatly inform the development of optimal sampling techniques (Shaw, 2006). Therefore, it is clear that improvements in sampling techniques and a wider appreciation of parasitoid ecology will need to evolve in synergy. Research that investigates both sampling techniques and ecology would be most appropriate for this reason.

The impact of trap construction and colouration on parasitoid catches is an important area for future work. If colouration has a significant impact on catches (*sensu* Tao et al., 2012), then the manufacture and selection of traps requires more careful consideration than previously thought. Sampling strategies that rely on a single collection method need to ensure that the method of capture is accurate, reliable, and catching a sufficient number of individuals to generate useful data. If certain trap characteristics mean that traps are underperforming in their collection of parasitoids then these should be investigated further. Tao et al (2012) have shown that yellow Malaise-traps catch higher numbers of parasitoid individuals. While this may help to improve the number of individuals caught per trap-day, it is important to consider whether this improved catch may in fact be biased towards certain groups and distort the composition of the captured assemblage due to the attractant effect of colour. Perhaps more neutral colours would be better suited for the construction of malaise traps. These ideas could be easily tested through colour-choice experiments in a range of parasitoid taxa.

Reliable data from studies that test the eligibility of surrogate or indicator taxa is desperately needed. It may be that Hymenoptera (or another group) offer a useful shortcut in the monitoring of environments or other taxa (Oliver & Beattie, 1996). Or it may be that when more rigorous sampling methods are applied in the search for such groups, the relationships or correlations disappear (Brower, 1995). The only way to know for sure is through the development and widespread application of optimal sampling strategies to studies that are evaluating these relationships.

Perhaps most important for future research involving parasitoid wasps is the need for a large body of taxonomic work on the group. Species descriptions,

revisions, monographs, sound classifications, faunal lists, and accessible identification keys form the foundation upon which all other biological work rests. It is clear that parasitoid taxonomy in New Zealand is still in a stage of infancy, but it needs to grow up quickly if the advantages of improved sampling methods are to be realised. What is desperately needed are the funds, facilities, training, jobs, and understanding to support existing taxonomists, and to produce more to fill the ranks of an aging workforce.

Appendix A: Tables

Table 1: Summary of biodiversity statistics and richness estimators for each sampling period, and a pooled dataset, for each site: number of individual specimens (I), number of species (i.e. observed richness) (S_{obs}), number of singletons (species with 1 individual, S_1), number of doubletons (species with 2 individuals, S_2); Species richness estimators: Chao1 (S_{Chao1}), ACE (S_{ACE}), Jackknife1 (S_{Jack1}), Chao2 (S_{Chao2}), ICE (S_{ICE}), Jackknife2 (S_{Jack2}).

SITE	Period	I	S_{obs}	S_1	S_2	S_{Chao1}	SD_{Chao1}	S_{ACE}	S_{Jack1}	SD_{Jack1}	S_{Chao2}	SD_{Chao2}	S_{ICE}	S_{Jack2}
Huapai	Dec	61	32	25	1	339.38	331.52	145.19	55.75	5.49	180.44	121.21	136.85	76.54
	Jan	100	42	22	8	71.95	17.47	69.53	63.85	3.97	69.92	15.81	78.74	76.88
	Feb	92	37	21	7	68.16	18.83	64.45	57.9	4.95	69.84	19.57	78.27	71.73
	All	253	70	30	14	102.02	15.55	106.29	100.4	7.35	107.42	17.89	113.06	118.12
Oratia	Dec	26	18	13	4	38.31	15.82	50.32	30.35	4.42	38.07	15.64	45.87	38.64
	Jan	33	18	13	2	58.97	37.37	64.96	30.35	3.17	44.76	22.04	50.58	39.49
	Feb	36	24	18	3	76.5	39.8	72.34	41.1	5.14	75.3	38.9	71.06	54.74
	All	95	46	27	7	96.52	28.71	96.32	71.6	6.52	91.55	25.04	95.58	89.98
Pooled	Total	348	87	37	18	124.91	16.52	133.76	123.1	7.28	121.29	14.72	136.6	140.24

Table 2: Sampling efficiency for each period based on the observed species richness during that period as a proportion of the Chao1 estimated total richness of the assemblage for each period, site, and the combined assemblage. Also shown is the average (E_{Avg}), minimum (E_{Min}), maximum (E_{Max}), and range (E_{Range}) among the non-parametric estimators featured in Table 1.

		Period	Site	Total	E_{Avg}	E_{Min}	E_{Max}	E_{Range}
Huapai	Dec	9.43%	31.37%	25.62%	155.69	55.75	339.38	283.63
	Jan	58.37%	41.17%	33.62%	71.81	63.85	78.74	14.89
	Feb	54.28%	36.27%	29.62%	68.39	57.90	78.27	20.37
	All		68.61%	56.04%	107.89	100.40	118.12	17.72
Oratia	Dec	46.99%	18.65%	14.41%	40.26	30.35	50.32	19.97
	Jan	30.52%	18.65%	14.41%	48.19	30.35	64.96	34.61
	Feb	31.37%	24.87%	19.21%	65.17	41.10	76.50	35.40
	All		47.66%	36.83%	90.26	71.60	96.52	24.92

Appendix B: Figures

Figure 1: Whittaker rank-abundance curve showing the proportional abundance of each species rank for the combined assemblage.

Figure 2: Number of individuals over time for the top 8 species (those with more than 10 individuals counted during the study).

Figure 3: Species accumulation curves comparing observed species richness (solid line) and extrapolated richness (dashed line) as a function of the number of samples for December (blue), January (green), and February (red). A. Huapai. B. Oratia.

Figure 4: Species accumulation curves for each sampling period at Huapai, comparing observed species richness with a suite of non-parametric estimators of total species richness. A. December. B. January. C. February.

Figure 5: Species accumulation curves for each sampling period at Oratia, comparing observed species richness with a suite of non-parametric estimators of total species richness. A. December. B. January. C. February.

Figure 6: Species accumulation curves comparing observed species richness with a suite of non-parametric estimators of total species richness. Data pooled. A. Huapai. B. Oratia. C. Total assemblage.

Figure 7: Individual-based rarefaction curves. Observed richness data (solid lines) extended with extrapolated accumulation curves (dotted lines) for both sites. Extrapolation stopped at 1240 individuals.

Figure 8: MDS plots showing similarity of parasitoid assemblages across site and time. Clusters plotted at 30% similarity using hierarchical agglomerative-clustering. Huapai (red squares) and Oratia (blue circles). A. December. B. January. C. February. D. Combined dataset.

Figure 9: A. Hierarchical agglomerative cluster analysis of vegetation assemblages characterising trap locations at Huapai (red squares) and Oratia (blue circles). Red lines indicate clusters characterised as non-randomly structured by SIMPROF test. B. MDS plot of vegetation assemblages overlaid with clusters at 30% similarity.

Figure 10: *Lusius malfoyi* sp. nov. **Top.** Habitus view. **Bottom.** Habitus dorsal view. Scale bar is 2mm.

Figure 11: *Lusius malfoyi* sp. nov. **Top.** Mesosoma, lateral view. **Bottom.** Head, anterior view. Scale bar is 0.5mm.

Figure 12: *Lusius malfoyi* sp. nov. **Top.** Propodeum, dorsal view. **Bottom.** Tergites, dorsal view. Scale bar is 0.5mm.

Figure 13: *Lusius malfoyi* sp. nov. **Top.** Ovipositor. **Bottom.** Hind tibia. Scale bar is 0.4mm.

Figure 14: *Lusius malfoyi* sp. nov. **Top.** Forewing. **Bottom.** Hindwing. Scale bar is 1mm.

Figure 15: Distribution map of *Lusius malfoyi* sp. nov. collection records in NZ.

Figure 16: World distribution of *Lusius* records.

References

- Adler, P. H., & Foottit, R. G. (2009). Introduction. In R. G. Foottit & P. H. Adler (Eds.), *Insect Biodiversity: Science & Society* (pp. 1–6). Wiley-Blackwell. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch1/summary>
- Agnarsson, I., & Kuntner, M. (2007). Taxonomy in a changing world: Seeking solutions for a science in crisis. *Systematic Biology*, 56(3), 531–539. <https://doi.org/10.1080/10635150701424546>
- Alex Smith, M., Fernández-Triana, J. L., Eveleigh, E., Gómez, J., Guclu, C., Hallwachs, W., ... Zaldívar-Riverón, A. (2013). DNA barcoding and the taxonomy of Microgastrinae wasps (Hymenoptera: Braconidae): Impacts after 8 years and nearly 20,000 sequences. *Molecular Ecology Resources*, 13(2), 168–176. <https://doi.org/10.1111/1755-0998.12038>
- Anderson, A., McCormack, S., Helden, A., Sheridan, H., Kinsella, A., & Purvis, G. (2011). The potential of parasitoid Hymenoptera as bioindicators of arthropod diversity in agricultural grasslands. *Journal of Applied Ecology*, 48(2), 382–390. <https://doi.org/10.1111/j.1365-2664.2010.01937.x>
- ARC. (2010). *Regional parks management plan* (p. 511). Auckland, NZ: Auckland Regional Council. Retrieved from <http://www.aucklandcouncil.govt.nz/EN/planspoliciesprojects/plansstrategies/Documents/Regional%20Parks%20Management%20Plan%202010/regionalparksmanagementplan2010.pdf>
- Arnan, X., Bosch, J., Comas, L., Gracia, M., & Retana, J. (2011). Habitat determinants of abundance, structure and composition of flying Hymenoptera communities in mountain old-growth forests. *Insect Conservation and Diversity*, 4(3), 200–211. <https://doi.org/10.1111/j.1752-4598.2010.00123.x>
- Askew, R. R. (1971). *Parasitic insects*. London, UK: Heinemann Educational Books.
- Baillie, J., & Groombridge, B. (Eds.). (1996). *The 1996 IUCN red list of threatened animals*. Gland: IUCN.
- Bain, J. (1970). New Zealand species of Lissonota (Hymenoptera: Ichneumonidae). *New Zealand Entomologist*, 4(4), 80–87.

- Barratt, B. I., Ferguson, C. M., Goldson, S. L., Phillips, C. M., & Hannah, D. J. (2000). Predicting the risk from biological control agent introductions: A New Zealand approach. In *Nontarget effects of biological control* (pp. 59–75). Springer. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4615-4577-4_5
- Barratt, B. I. P., Derraik, J. G. B., Rufaut, C. G., Goodman, A. J., & Dickinson, K. J. M. (2003). Morphospecies as a substitute for Coleoptera species identification, and the value of experience in improving accuracy. *Journal of the Royal Society of New Zealand*, 33(2), 583–590. <https://doi.org/10.1080/03014223.2003.9517746>
- Basualdo, C. V. (2011). Choosing the best non-parametric richness estimator for benthic macroinvertebrates databases. *Revista de La Sociedad Entomológica Argentina*, 70.
- Beattie, A. J., & Oliver, I. (1994). Taxonomic minimalism. *Trends in Ecology & Evolution*, 9(12), 488–490. [https://doi.org/10.1016/0169-5347\(94\)90320-4](https://doi.org/10.1016/0169-5347(94)90320-4)
- Beggs, J. (2001). The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. *Biological Conservation*, 99(1), 17–28. [https://doi.org/10.1016/S0006-3207\(00\)00185-3](https://doi.org/10.1016/S0006-3207(00)00185-3)
- Beggs, J. R., Rees, J. S., Toft, R. J., Dennis, T. E., & Barlow, N. D. (2008). Evaluating the impact of a biological control parasitoid on invasive *Vespula* wasps in a natural forest ecosystem. *Biological Control*, 44(3), 399–407. <https://doi.org/10.1016/j.biocontrol.2007.10.016>
- Beres, B. I., Dossall, L. M., Weaver, D. K., Cárcamo, H. A., & Spaner, D. M. (2011). Biology and integrated management of wheat stem sawfly and the need for continuing research. *The Canadian Entomologist*, 143(02), 105–125. <https://doi.org/10.4039/n10-056>
- Berry, J. A. (1990). The New Zealand species of the subfamily Metopiinae (Hymenoptera: Ichneumonidae). *New Zealand Journal of Zoology*, 17(4), 607–614. <https://doi.org/10.1080/03014223.1990.10422958>
- Berry, J. A. (2007). *Alysiinae (Insecta: Hymenoptera: Braconidae)*. Lincoln, NZ: Manaaki Whenua Press.
- Berry, J. A. (2010). Order Hymenoptera: Sawflies, wasps, ants, and bees. In D. Gordon (Ed.), *New Zealand Inventory of Biodiversity, Vol. 2: Kingdom Animalia. Chaetognatha, Ecdysozoa, Ichnofossils*. Christchurch, NZ: Canterbury University Press.
- Berry, J. A., & Walker, G. P. (2004). *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae: Euphorinae): An exotic polyphagous parasitoid in New Zealand. *New*

- Zealand Journal of Zoology*, 31(1), 33–44.
<https://doi.org/10.1080/03014223.2004.9518357>
- Brower, A. V. Z. (1995). Taxonomic minimalism. *Trends in Ecology & Evolution*, 10(5), 203.
- Cameron, E., & Morton, J. (1993). Rain forest and scrub. In J. Morton (Ed.), *A Natural History of Auckland* (pp. 25–40). Auckland, New Zealand: David Bateman Ltd.
- Cameron, P. J. (1989). *A review of biological control of invertebrate pests and weeds in New Zealand 1874 to 1987*. Wallingford England: CAB International Institute of Biological Control & DSIR Entomology Division.
- Chao, A. (1984). Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11(4), 265–270.
- Chao, A., & Chiu, C.-H. (2016). Nonparametric estimation and comparison of species richness. In *eLS* (pp. 1–11). Chichester, UK: John Wiley & Sons, Ltd. Retrieved from <http://doi.wiley.com/10.1002/9780470015902.a0026329>
- Chao, A., Hwang, W.-H., Chen, Y. C., & Kuo, C. Y. (2000). Estimating the number of shared species in two communities. *Statistica Sinica*, 227–246.
- Chapman, A. D. (2009). *Numbers of living species in Australia and the world*. Canberra: Australian Biological Resources Study. Retrieved from <https://www.environment.gov.au/system/files/pages/2ee3f4a1-f130-465b-9c7a-79373680a067/files/nlsaw-2nd-complete.pdf>
- Charles, J. G. (Horticulture and F. R. I. of N. Z. L. (1998). The settlement of fruit crop arthropod pests and their natural enemies in New Zealand: An historical guide to the future. *Biocontrol*, 19(2), 47N–57N.
- Claridge, M. F. (2009). Insect species: Concepts and practice. In R. G. Foottit & P. H. Adler (Eds.), *Insect Biodiversity: Science & Society* (pp. 381–395). Wiley-Blackwell. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch15/summary>
- Claridge, M. F., Dawah, H. A., & Wilson, M. R. (1997). Practical approaches to species concepts for living organisms. In M. F. Claridge, H. A. Dawah, & M. R. Wilson (Eds.), *Species: The Units of Biodiversity* (p. 439). London, UK: Chapman & Hall.
- Clark, B. R., Godfray, H. C. J., Kitching, I. J., Mayo, S. J., & Scoble, M. J. (2009). Taxonomy as an eScience. *Philosophical Transactions of the Royal Society of London A: Mathematical, Physical and Engineering Sciences*, 367(1890), 953–966.
<https://doi.org/10.1098/rsta.2008.0190>

- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, 18(1), 117–143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>
- Clarke, K. R., & Gorley, R. N. (2006). *PRIMER v6: User manual/tutorial*. (p. 192pp). Plymouth: PRIMER-E.
- Clarke, K. R., Somerfield, P. J., & Chapman, M. G. (2006). On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology*, 330(1), 55–80. <https://doi.org/10.1016/j.jembe.2005.12.017>
- Clarke, K. R., & Warwick, R. M. (2001). *Change in marine communities: An approach to statistical analysis and interpretation* (2nd ed.). Plymouth: PRIMER-E.
- Collins, R. A., & Cruickshank, R. H. (2013). The seven deadly sins of DNA barcoding. *Molecular Ecology Resources*, 13(6), 969–975. <https://doi.org/10.1111/1755-0998.12046>
- Colwell, R. K. (2009). Biodiversity: Concepts, patterns, and measurement. In S. A. Levin, S. R. Carpenter, H. C. J. Godfray, A. P. Kinzig, M. Loreau, J. B. Losos, ... D. S. Wilcove (Eds.), *Princeton Guide to Ecology*. Retrieved from http://www.newbooks-services.de/MediaFiles/Texts/9/9780691128399_Excerpt_014.pdf
- Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. – User’s Guide and application at <http://purl.oclc.org/estimateS>.
- Colwell, R. K., Chao, A., Gotelli, N. J., Lin, S.-Y., Mao, C. X., Chazdon, R. L., & Longino, J. T. (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, 5(1), 3–21. <https://doi.org/10.1093/jpe/rtr044>
- Colwell, R. K., & Coddington, J. A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 345(1311), 101–118. <https://doi.org/10.1098/rstb.1994.0091>
- Colwell, R. K., & Elsensohn, J. E. (2014). EstimateS turns 20: Statistical estimation of species richness and shared species from samples, with non-parametric extrapolation. *Ecography*, 37(6), 609–613. <https://doi.org/10.1111/ecog.00814>

- Colwell, R. K., Mao, C. X., & Chang, J. (2004). Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology*, 85(10), 2717–2727.
- Costello, M. J., Wilson, S., & Houlding, B. (2011). Predicting total global species richness using rates of species description and estimates of taxonomic effort. *Systematic Biology*, syr080. <https://doi.org/10.1093/sysbio/syr080>
- Cracraft, J. (1983). Species concepts and speciation analysis. In R. F. Johnston (Ed.), *Current ornithology* (pp. 159–187). Springer.
- Cranston, P. S. (2010). Insect biodiversity and conservation in Australasia. *Annual Review of Entomology*, 55, 55–75. <https://doi.org/10.1146/annurev-ento-112408-085348>
- Cranwell-Smith, L. (2006). Rain forests of the Waitakeres. In B. Harvey & T. Harvey (Eds.), *Waitakere Ranges: Ranges of Inspiration* (pp. 49–66). Waitakere City, NZ: Waitakere Ranges Protection Society.
- Cresson, E. T. (1874). Descriptions of Mexican Ichneumonidae. *Proceedings of the Academy of Natural Sciences of Philadelphia, 1873*, 104–176.
- Crisp, P. N., Dickinson, K. J. M., & Gibbs, G. W. (1998). Does native invertebrate diversity reflect native plant diversity? A case study from New Zealand and implications for conservation. *Biological Conservation*, 83(2), 209–220. [https://doi.org/10.1016/S0006-3207\(97\)00053-0](https://doi.org/10.1016/S0006-3207(97)00053-0)
- Crosby, T. K., Dugdale, J. S., & Watt, J. C. (1998). Area codes for recording specimen localities in the New Zealand subregion. *New Zealand Journal of Zoology*, 25(2), 175–183.
- Cushman, R. A. (1937). H. Sauter's Formosa collection: Ichneumonidae. *Arbeiten Uber Morphologische Und Taxonomische Entomologie Aus Berlin-Dahlem*, 4(4), 283–311.
- Darling, D. C., & Packer, L. (1988). Effectiveness of Malaise traps in collecting Hymenoptera: The influence of trap design, mesh size, and location. *The Canadian Entomologist*, 120(8–9), 787–796. <https://doi.org/10.4039/Ent120787-8>
- de Carvalho, M. R., Bockmann, F. A., Amorim, D. S., & Brandão, C. R. F. (2008). Systematics must embrace comparative biology and evolution, not speed and automation. *Evolutionary Biology*, 35(2), 150–157. <https://doi.org/10.1007/s11692-008-9018-7>

- de Carvalho, M. R., Bockmann, F. A., Amorim, D. S., Brandão, C. R. F., Vivo, M. de, Figueiredo, J. L. de, ... Nelson, G. J. (2007). Taxonomic impediment or impediment to taxonomy? A commentary on systematics and the cybertaxonomic-automation paradigm. *Evolutionary Biology*, 34(3–4), 140–143. <https://doi.org/10.1007/s11692-007-9011-6>
- de Carvalho, M. R., Ebach, M. C., Williams, D. M., Nihei, S. S., Trefaut Rodrigues, M., Grant, T., ... Nelson, G. (2014). Does counting species count as taxonomy? On misrepresenting systematics, yet again. *Cladistics*, 30(3), 322–329. <https://doi.org/10.1111/cla.12045>
- de Queiroz, K., & Donoghue, M. J. (1990). Phylogenetic systematics and species revisited. *Cladistics*, 6(1), 83–90. <https://doi.org/10.1111/j.1096-0031.1990.tb00527.x>
- Derraik, J. G. B., Closs, G. P., Dickinson, K. J. M., Sirvid, P., Barratt, B. I. P., & Patrick, B. H. (2002). Arthropod morphospecies versus taxonomic species: A case study with Araneae, Coleoptera, and Lepidoptera. *Conservation Biology*, 16(4), 1015–1023. <https://doi.org/10.1046/j.1523-1739.2002.00358.x>
- Derraik, J. G. B., Early, J. W., Closs, G. P., & Dickinson, K. J. M. (2010). Morphospecies and taxonomic species comparison for Hymenoptera. *Journal of Insect Science*, 10(1), 108. <https://doi.org/10.1673/031.010.10801>
- Disney, H. (1998). Rescue plan needed for taxonomy. *Nature*, 394(6689), 120–120. <https://doi.org/10.1038/28027>
- DoC. (2000). *New Zealand biodiversity strategy*. Wellington, NZ.
- Don, W. (2007). *Ants of New Zealand*. Dunedin, N.Z: Otago University Press.
- Donovan, B. J. (2007). *Apoidea: (Insecta: Hymenoptera)*. Lincoln, NZ: Manaaki Whenua Press.
- Donovan, B. J. (2016). Description of *Leioproctus* (*leioproctus*) *hukarere* new species (Hymenoptera: Apoidea: Colletidae), a new native bee from the Mackenzie Country, New Zealand. *New Zealand Entomologist*, 0(0), 1–15. <https://doi.org/10.1080/00779962.2016.1152871>
- Early, J. W., Masner, L., Naumann, I. D., & Austin, A. D. (2001). Maamingidae, a new family of proctotrupoid wasp (Insecta: Hymenoptera) from New Zealand. *Invertebrate Systematics*, 15(3), 341–352.

- Ebach, M. C., Valdecasas, A. G., & Wheeler, Q. D. (2011). Impediments to taxonomy and users of taxonomy: Accessibility and impact evaluation. *Cladistics*, 27(5), 550–557. <https://doi.org/10.1111/j.1096-0031.2011.00348.x>
- Eggleton, P., & Gaston, K. J. (1990). “Parasitoid” species and assemblages: Convenient definitions or misleading compromises? *Oikos*, 59(3), 417–421. <https://doi.org/10.2307/3545155>
- Erwin, T. L. (1982). Tropical forests: Their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin*, 36(1), 74–75.
- Esler, A. (2006). Forest zones. In B. Harvey & T. Harvey (Eds.), *Waitakere Ranges: Ranges of Inspiration* (pp. 67–73). Waitakere City, NZ: Waitakere Ranges Protection Society.
- Esler, A. E. (1983). Forest and scrubland zones of the Waitakere Range, Auckland. *Tane*, 29, 109–117.
- Evans, A. M., Clinton, P. W., Allen, R. B., & Frampton, C. M. (2003). The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. *Forest Ecology and Management*, 184(1–3), 251–262. [https://doi.org/10.1016/S0378-1127\(03\)00158-0](https://doi.org/10.1016/S0378-1127(03)00158-0)
- Fraser, S. E. M., Dytham, C., & Mayhew, P. J. (2007). Determinants of parasitoid abundance and diversity in woodland habitats. *Journal of Applied Ecology*, 44(2), 352–361. <https://doi.org/10.1111/j.1365-2664.2006.01266.x>
- Fraser, S. E. M., Dytham, C., & Mayhew, P. J. (2008). The effectiveness and optimal use of Malaise traps for monitoring parasitoid wasps. *Insect Conservation and Diversity*, 1(1), 22–31. <https://doi.org/10.1111/j.1752-4598.2007.00003.x>
- Frost, C. M., Didham, R. K., Rand, T. A., Peralta, G., & Tylianakis, J. M. (2015). Community-level net spillover of natural enemies from managed to natural forest. *Ecology*, 96(1), 193–202. <https://doi.org/10.1890/14-0696.1>
- Funk, D. J., & Omland, K. E. (2003). Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 397–423. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132421>
- Gaasch, C. M., Pickering, J., & Moore, C. T. (1998). Flight phenology of parasitic wasps (Hymenoptera: Ichneumonidae) in Georgia’s Piedmont. *Environmental Entomology*, 27(3), 606–614. <https://doi.org/10.1093/ee/27.3.606>

- Gaigher, R., Pryke, J. S., & Samways, M. J. (2015). High parasitoid diversity in remnant natural vegetation, but limited spillover into the agricultural matrix in South African vineyard agroecosystems. *Biological Conservation*, 186, 69–74. <https://doi.org/10.1016/j.biocon.2015.03.003>
- Gaston, K. J. (1991). The magnitude of global insect species richness. *Conservation Biology*, 5(3), 283–296.
- Gaston, K. J. (1996a). Species richness: Measure and measurement. In K. J. Gaston (Ed.), *Biodiversity: A Biology of Numbers and Difference* (pp. 77–113). Cambridge, MA: Blackwell Science.
- Gaston, K. J. (1996b). What is biodiversity? In K. J. Gaston (Ed.), *Biodiversity: A Biology of Numbers and Difference* (pp. 1–12). Cambridge, MA: Blackwell Science.
- Gaston, K. J., & Gauld, I. D. (1993). How many species of pimelines (Hymenoptera: Ichneumonidae) are there in Costa Rica? *Journal of Tropical Ecology*, 9(04), 491. <https://doi.org/10.1017/S0266467400007550>
- Géneau, C. E., Wäckers, F. L., Luka, H., Daniel, C., & Balmer, O. (2012). Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic and Applied Ecology*, 13(1), 85–93. <https://doi.org/10.1016/j.baae.2011.10.005>
- Godfray, H. C. J. (1994). *Parasitoids: Behavioral and evolutionary ecology*. Princeton, New Jersey: Princeton University Press.
- Godfray, H. C. J. (2007). Linnaeus in the information age. *Nature*, 446(7133), 259–260. <https://doi.org/10.1038/446259a>
- Goldstein, P. Z. (1997). How many things are there? A reply to Oliver and Beattie, Beattie and Oliver, Oliver and Beattie, and Oliver and Beattie. *Conservation Biology*, 11(2), 571–574. <https://doi.org/10.1046/j.1523-1739.1997.96119.x>
- Goldstein, P. Z. (1999). Functional ecosystems and biodiversity buzzwords. *Conservation Biology*, 13(2), 247–255. <https://doi.org/10.1046/j.1523-1739.1999.013002247.x>
- Goldstein, P. Z., & DeSalle, R. (2011). Integrating DNA barcode data and taxonomic practice: Determination, discovery, and description. *BioEssays*, 33(2), 135–147. <https://doi.org/10.1002/bies.201000036>
- Gordon, D. (Ed.). (2009). *New Zealand inventory of biodiversity: Kingdom Animalia* (Vol. 2). Christchurch, NZ: Canterbury University Press 2009-.

- Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4(4), 379–391.
- Gotelli, N. J., & Colwell, R. K. (2011). Estimating species richness. In *Biological diversity: frontiers in measurement and assessment* (pp. 39–54). Oxford University Press. Retrieved from <http://www.uvm.edu/~ngotelli/manuscriptpdfs/Chapter%204.pdf>
- Goulet, H., & Huber, J. T. (Eds.). (1993). *Hymenoptera of the world: An identification guide to families*. Ottawa, Canada: Centre for Land and Biological Resources Research.
- Graf, V. (2000). O gênero *Lusius* Tosquinet, 1903 (Hymenoptera, Ichneumoninae, Heterischnini) na América do Sul. *Acta Biológica Paranaense*, 29, 169–176.
- Grimaldi, D. A., & Engel, M. S. (2007). Why descriptive science still matters. *BioScience*, 57(8), 646–647. <https://doi.org/10.1641/B570802>
- Groenteman, R. (2016). Wasp biocontrol update 7. Retrieved October 17, 2016, from <http://www.landcareresearch.co.nz/about/news/snippets/wasp-biocontrol-update-7>
- Groombridge, B. (Ed.). (1992). *Global biodiversity*. Dordrecht: Springer Netherlands. Retrieved from <http://link.springer.com/10.1007/978-94-011-2282-5>
- Halme, P., Kuusela, S., & Juslén, A. (2015). Why taxonomists and ecologists are not, but should be, carpooling? *Biodiversity and Conservation*, 24(7), 1831–1836. <https://doi.org/10.1007/s10531-015-0899-3>
- Hammond, P. M. (1994). Practical approaches to the estimation of the extent of biodiversity in speciose groups. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 345(1311), 119–136. <https://doi.org/10.1098/rstb.1994.0092>
- Harper, J. L., & Hawksworth, D. L. (1994). Biodiversity: Measurement and estimation. *Philosophical Transactions of the Royal Society of London*, 345, 5–12.
- Hawkins, B. A., & Sheehan, W. (1994). Introduction. In B. A. Hawkins & W. Sheehan (Eds.), *Parasitoid Community Ecology* (pp. 1–18). New York: Oxford University Press.
- Hayward, B. (2006). The structure of the land. In B. Harvey & T. Harvey (Eds.), *Waitakere Ranges: Ranges of Inspiration* (pp. 36–40). Waitakere City, NZ: Waitakere Ranges Protection Society.

- Hebert, P. D. N., Cywinska, A., Ball, S. L., & deWaard, J. R. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B: Biological Sciences*, 270(1512), 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Heltsh, J. F., & Forrester, N. E. (1983). Estimating species richness using the jackknife procedure. *Biometrics*, 39(1), 1–11. <https://doi.org/10.2307/2530802>
- Hennig, W. (1966). *Phylogenetic systematics*. Urbana: University of Illinois Press.
- Heraty, J. (2009). Parasitoid biodiversity and insect pest management. In R. G. Foottit & P. H. Adler (Eds.), *Insect Biodiversity: Science & Society* (pp. 445–462). Wiley-Blackwell. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch19/summary>
- Holldobler, B., & Wilson, E. O. (1990). *The ants* (1st edition). Cambridge, MA: Belknap Press.
- Holwell, G. I., & Andrew, N. I. (2014). Protecting the small majority: Insect conservation in Australia and New Zealand. In A. Stow, N. Maclean, & G. I. Holwell (Eds.), *Austral Ark: The State of Wildlife in Australia and New Zealand*. Cambridge: Cambridge University Press. Retrieved from <http://ebooks.cambridge.org/ref/id/CBO9781139519960>
- Horak, J. (2013). Effect of site level environmental variables, spatial autocorrelation and sampling intensity on arthropod communities in an ancient temperate lowland woodland area. *PLOS ONE*, 8(12), e81541. <https://doi.org/10.1371/journal.pone.0081541>
- Hortal, J., Borges, P. a. V., & Gaspar, C. (2006). Evaluating the performance of species richness estimators: Sensitivity to sample grain size. *Journal of Animal Ecology*, 75(1), 274–287. <https://doi.org/10.1111/j.1365-2656.2006.01048.x>
- House of Lords, Science and Technology Committee. (2008). *Systematics and taxonomy: Follow-up* (5th Report of Session 2007–08 No. HL 162) (p. 386). London, UK. Retrieved from <http://dera.ioe.ac.uk/17738/>
- Huber, J. T. (1993). Introduction. In H. Goulet & J. T. Huber (Eds.), *Hymenoptera of the world: An identification guide to families* (pp. 1–3). Ottawa, Ontario: Centre for Land and Biological Resources Research.
- Huber, J. T. (2009). Biodiversity of Hymenoptera. In R. G. Foottit & P. H. Adler (Eds.), *Insect Biodiversity: Science & Society* (pp. 303–323). Wiley-Blackwell. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch12/summary>

- Hutcheson, J. (1990). Characterization of terrestrial insect communities using quantified, Malaise-trapped Coleoptera. *Ecological Entomology*, 15(2), 143–151. <https://doi.org/10.1111/j.1365-2311.1990.tb00795.x>
- Hutcheson, J. A., & Kimberley, M. O. (1999). A pragmatic approach to characterising insect communities in New Zealand: Malaise trapped beetles. *New Zealand Journal of Ecology*, 69–79.
- Hutcheson, J., Walsh, P., & Given, D. R. (1999). *Potential value of indicator species for conservation and management of New Zealand terrestrial communities* (Science for Conservation No. 109) (p. 90). Wellington, N.Z.: Department of Conservation.
- ICZN. (1999). *International code of zoological nomenclature*. (W. D. L. Ride, H. G. Cogger, C. Dupuis, O. Kraus, A. Minelli, F. C. Thompson, & P. K. Tubbs, Eds.) (4th ed.). London, UK: International Trust for Zoological Nomenclature.
- Iglésias, S. P., Toulhoat, L., & Sellos, D. Y. (2010). Taxonomic confusion and market mislabelling of threatened skates: Important consequences for their conservation status. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 20(3), 319–333. <https://doi.org/10.1002/aqc.1083>
- ISSE. (2011). *State of observed species: A report card on our knowledge of earth's species* (p. 18). Tempe, Arizona: International Institute for Species Exploration. Retrieved from <http://species.asu.edu/SOS>
- Janzen, D. H., Hallwachs, W., Blandin, P., Burns, J. M., Cadiou, J.-M., Chacon, I., ... Lafontaine, D. (2009). Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Molecular Ecology Resources*, 9, 1–26. <https://doi.org/10.1111/j.1755-0998.2009.02628.x>
- Johnson, P. T. J., Preston, D. L., Hoverman, J. T., & Richgels, K. L. D. (2013). Biodiversity decreases disease through predictable changes in host community competence. *Nature*, 494(7436), 230–233. <https://doi.org/10.1038/nature11883>
- Kendall, L. K., & Ward, D. F. (2016). Habitat determinants of the taxonomic and functional diversity of parasitoid wasps. *Biodiversity and Conservation*, 25(10), 1955–1972. <https://doi.org/10.1007/s10531-016-1174-y>
- Kim, K. C. (1993). Biodiversity, conservation and inventory: Why insects matter. *Biodiversity & Conservation*, 2(3), 191–214. <https://doi.org/10.1007/BF00056668>
- Kim, K. C. (2009). Taxonomy and management of insect biodiversity. In R. G. Foottit & P. H. Adler (Eds.), *Insect Biodiversity: Science & Society* (pp. 561–574). Wiley-

- Blackwell. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch24/summary>
- Kim, K. C., & Byrne, L. B. (2006). Biodiversity loss and the taxonomic bottleneck: Emerging biodiversity science. *Ecological Research*, 21(6), 794–810. <https://doi.org/10.1007/s11284-006-0035-7>
- Kremen, C., Colwell, R. K., Erwin, T. L., Murphy, D. D., Noss, R. F., & Sanjayan, M. A. (1993). Terrestrial arthropod assemblages: Their use in conservation planning. *Conservation Biology*, 7(4), 796–808.
- Kremen, C., & Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. *Ecology and Society*, 17(4). <https://doi.org/10.5751/ES-05035-170440>
- Kusigemati, K. (1986). On the Formosan species of the genus *Lusius* Tosquinet, with description of a new species (Hymenoptera: Ichneumonidae). *Memoirs of the Kagoshima University Research Center for the South Pacific*, 7(1), 22–27.
- Landcare Research. (2009). Checklist of New Zealand Hymenoptera V7.0. Retrieved May 12, 2016, from <http://www.landcareresearch.co.nz/resources/collections/nzac/holdings/primary-type-specimens-hymenoptera/checklist-hymenoptera>
- Landcare Research. (2016). Ichneumonidae of New Zealand. Retrieved September 28, 2014, from <http://www.landcareresearch.co.nz/science/plants-animals-fungi/animals/invertebrates/systematics/hymenoptera/ichneumonidae>
- LaSalle, J. (1993). Parasitic Hymenoptera, biological control and biodiversity. In J. LaSalle & I. D. Gauld (Eds.), *Hymenoptera and Biodiversity* (pp. 197–216). Wallingford: CABI.
- LaSalle, J., & Gauld, I. D. (1991). Parasitic Hymenoptera and the biodiversity crisis. *Redia*, 74(3, Appendix), 315–334.
- LaSalle, J., & Gauld, I. D. (1993). Hymenoptera: their diversity, and their impact on the diversity of other organisms. In J. LaSalle & I. D. Gauld (Eds.), *Hymenoptera and Biodiversity* (pp. 1–26). Wallingford: CABI.
- Leather, S. R., & Watt, A. D. (2005). Sampling theory and practice. In S. R. Leather (Ed.), *Insect Sampling in Forest Ecosystems* (pp. 1–15). Malden, MA: Blackwell Publishing.
- Lester, P. J., Beggs, J. R., Brown, R. L., Edwards, E. D., Groenteman, R., Toft, R. J., ... Ward, D. F. (2013). The outlook for control of New Zealand's most abundant,

- widespread and damaging invertebrate pests: Social wasps. *New Zealand Science Review*, 70(4), 54–60.
- Lester, P. J., Brown, S. D. J., Edwards, E. D., Holwell, G. I., Pawson, S. M., Ward, D. F., & Watts, C. H. (2014). Critical issues facing New Zealand entomology. *New Zealand Entomologist*, 37(1), 1–13. <https://doi.org/10.1080/00779962.2014.861789>
- Lewis, O. T., & Basset, Y. (2007). Insect conservation in tropical forests. In A. J. A. Stewart, T. R. New, & O. T. Lewis (Eds.), *Insect Conservation Biology* (pp. 34–56). UK: CABI.
- Lipscomb, D., Platnick, N., & Wheeler, Q. (2003). The intellectual content of taxonomy: A comment on DNA taxonomy. *Trends in Ecology & Evolution*, 18(2), 65–66. [https://doi.org/10.1016/S0169-5347\(02\)00060-5](https://doi.org/10.1016/S0169-5347(02)00060-5)
- Longino, J. T., Coddington, J., & Colwell, R. K. (2002). The ant fauna of a tropical rain forest: Estimating species richness three different ways. *Ecology*, 83(3), 689–702.
- Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, 56(4), 311–323. [https://doi.org/10.1641/0006-3568\(2006\)56\[311:TEVOES\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2)
- Magurran, A. E. (2004). *Measuring biological diversity*. US: Wiley-Blackwell.
- Malaise, R. (1937). A new insect-trap. *Entomologisk Tidskrift*, 58, 148–160.
- Mason, R. M., & Huber, J. T. (1993). Order Hymenoptera. In H. Goulet & J. T. Huber (Eds.), *Hymenoptera of the world: An identification guide to families* (pp. 4–12). Ottawa, Ontario: Centre for Land and Biological Resources Research.
- May, R. M. (1994). Conceptual aspects of the quantification of the extent of biological diversity. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 345(1311), 13–20. <https://doi.org/10.1098/rstb.1994.0082>
- Mayr, E. (1942). *Systematics and the origin of species, from the viewpoint of a zoologist*. Harvard University Press.
- Mazón, M. (2015). Taking shortcuts to measure species diversity: Parasitoid Hymenoptera subfamilies as surrogates of species richness. *Biodiversity and Conservation*, 25(1), 67–76. <https://doi.org/10.1007/s10531-015-1029-y>
- Mazon, M., & Bordera, S. (2008). Effectiveness of two sampling methods used for collecting Ichneumonidae (Hymenoptera) in the Cabaneros National Park (Spain). *European Journal of Entomology*, 105(5), 879–888. <https://doi.org/10.14411/eje.2008.116>

- McGuinness, C. A. (2001). *The conservation requirements of New Zealand's nationally threatened invertebrates* (Threatened Species Occasional Publication No. 20) (p. 44). Wellington, N.Z: Department of Conservation.
- MEA. (2005a). *Ecosystems and human well-being: Biodiversity synthesis* (p. 100). Washington, D.C.: World Resources Institute. Retrieved from <http://www.millenniumassessment.org/documents/document.354.aspx.pdf>
- MEA. (2005b). *Ecosystems and human well-being: Health synthesis* (Millennium Ecosystem Assessment) (p. 64). Geneva, Switzerland: WHO.
- MEA. (2011). Overview of the Millennium Ecosystem Assessment. Retrieved May 28, 2016, from <http://www.millenniumassessment.org/en/About.html>
- Meier, R. (2008). DNA sequences in taxonomy. In *The New Taxonomy* (pp. 95–127). Boca Raton: CRC Press.
- Memmott, J., & Godfray, H. J. C. (1994). The use and construction of parasitoid webs. In B. A. Hawkins & W. Sheehan (Eds.), *Parasitoid Community Ecology* (pp. 300–318). New York: Oxford University Press.
- Michener, C. D. (2007). *The bees of the world* (2nd edition). Baltimore: Johns Hopkins University Press.
- Mills, N. (2005). Parasitoids and predators. In S. R. Leather (Ed.), *Insect Sampling in Forest Ecosystems* (pp. 254–278). Malden, MA: Blackwell Publishing.
- Mohamad, R., Wajnberg, E., Monge, J.-P., & Goubault, M. (2015). The effect of direct interspecific competition on patch exploitation strategies in parasitoid wasps. *Oecologia*, 177(1), 305–315. <https://doi.org/10.1007/s00442-014-3124-2>
- Morley, C. (1913). *The fauna of British India including Ceylon and Burma, Hymenoptera, Vol.3. Ichneumonidae* (Vol. 3). London: Taylor & Francis.
- Morley, C. (1914). XXIII. Hymenoptera, IV: Ichneumonidae. *Records Indian Museum*, 8, 323–328.
- Morris, E. K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. S., ... Rillig, M. C. (2014). Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, 4(18), 3514–3524. <https://doi.org/10.1002/ece3.1155>
- Morris, R. F. (1960). Sampling insect populations. *Annual Review of Entomology*, 5(1), 243–264. <https://doi.org/10.1146/annurev.en.05.010160.001331>

- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>
- Natural History Museum Review Team. (2011). *UK taxonomy & systematics review: Results of survey undertaken by the review team at the natural history museum serving as contractors to the Natural Environment Research Council (NERC)* (p. 37). London, UK: Natural Environment Research Council.
- Nelson, W., Breitwieser, I., Fordyce, E., Bradford-Grieve, J., Penman, D., Roskrige, N., ... Webb, C. (2015). *National taxonomic collections in New Zealand* (p. 68). The Royal Society of New Zealand. Retrieved from <http://www.royalsociety.org.nz/media/2015/12/Report-National-Taxonomic-Collections-in-New-Zealand-2015.pdf>
- New, T. R. (1996). Taxonomic focus and quality control in insect surveys for biodiversity conservation. *Australian Journal of Entomology*, 35(2), 97–106. <https://doi.org/10.1111/j.1440-6055.1996.tb01369.x>
- New, T. R. (1998). *Invertebrate surveys for conservation*. Oxford, NY: Oxford University Press.
- New, T. R. (2000). The conservation of a discipline: Traditional taxonomic skills in insect conservation. *Journal of Insect Conservation*, 4, 211–213.
- New, T. R. (2012). *Hymenoptera and conservation*. Hoboken, NJ: Wiley-Blackwell.
- New, T. R., & Samways, M. J. (2014). Insect conservation in the southern temperate zones: An overview. *Austral Entomology*, 53(1), 26–31. <https://doi.org/10.1111/aen.12071>
- Nixon, K. C., & Wheeler, Q. D. (1990). An amplification of the phylogenetic species concept. *Cladistics*, 6(3), 211–223. <https://doi.org/10.1111/j.1096-0031.1990.tb00541.x>
- Noss, R. F. (1996). The naturalists are dying off. *Conservation Biology*, 10(1), 1–3. <https://doi.org/10.1046/j.1523-1739.1996.10010001.x>
- Noyes, J. S. (1989). A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History*, 23(2), 285–298. <https://doi.org/10.1080/00222938900770181>
- Noyes, J. S., & Valentine, E. W. (1989). *Mymaridae*. Wellington, N.Z.: Manaaki Whenua Press.

- Oliver, I., & Beattie, A. J. (1993). A possible method for the rapid assessment of biodiversity. *Conservation Biology*, 7(3), 562–568.
- Oliver, I., & Beattie, A. J. (1996a). Designing a cost-effective invertebrate survey: A test of methods for rapid assessment of biodiversity. *Ecological Applications*, 6(2), 594–607. <https://doi.org/10.2307/2269394>
- Oliver, I., & Beattie, A. J. (1996b). Invertebrate morphospecies as surrogates for species: A case study. *Conservation Biology*, 10(1), 99–109.
- Owen, D. F., & Owen, J. (1974). Species diversity in temperate and tropical Ichneumonidae. *Nature*, 249(5457), 583–584. <https://doi.org/10.1038/249583a0>
- Owen, J., Townes, H., & Townes, M. (1981). Species diversity of Ochnemonidae and Serphidae (Hymenoptera) in an English suburban garden. *Biological Journal of the Linnean Society*, 16(4), 315–336. <https://doi.org/10.1111/j.1095-8312.1981.tb01656.x>
- Ozanne, C. M. P. (2005). Sampling methods for forest understorey vegetation. In S. R. Leather (Ed.), *Insect Sampling in Forest Ecosystems* (pp. 58–76). Malden, MA: Blackwell Publishing.
- Patterson, D. J. (2010). Future taxonomy. In A. Polaszek (Ed.), *Systema Naturae 250-The Linnaean Ark* (pp. 117–126). Boca Raton: CRC Press.
- Peralta, G., Frost, C. M., Rand, T. A., Didham, R. K., & Tylianakis, J. M. (2014). Complementarity and redundancy of interactions enhance attack rates and spatial stability in host–parasitoid food webs. *Ecology*, 95(7), 1888–1896. <https://doi.org/10.1890/13-1569.1>
- Pilgrim, R. L. C. (1970). An outline of work being done in New Zealand institutions. *New Zealand Entomologist*, 4(3), 25–29. <https://doi.org/10.1080/00779962.1970.9722910>
- Platnick, N. I. (1979). Philosophy and the transformation of cladistics. *Systematic Biology*, 28(4), 537–546. <https://doi.org/10.2307/sysbio/28.4.537>
- Polaszek, A., Pyle, R., & Yanega, D. (2008). Animal names for all: ICZN, Zoobank and the new taxonomy. In *The New Taxonomy* (pp. 129–141). Boca Raton: CRC Press.
- Quicke, D. L. J. (2015). *The braconid and ichneumonid parasitoid wasps: Biology, systematics, evolution and ecology*. Hoboken, NJ: John Wiley & Sons, Ltd.
- R Core Team. (2015). *R: A language and environment for statistical computing*. CRAN. Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.207.1436>

- Raven, P. H., & Wilson, E. O. (1992). A fifty-year plan for biodiversity surveys. *Science*, 258(5085), 1099–1100. <https://doi.org/10.1126/science.258.5085.1099>
- Reguilón, C. (2014). Nuevo registro de parasitoides asociados a Chrysopidae (Neuroptera) en citrus aurantium en tucumán, Argentina. *Acta Zoológica Lilloana*, 57(2), 100.
- Rohr, J. R., Mahan, C. G., & Kim, K. C. (2007). Developing a monitoring program for invertebrates: Guidelines and a case study. *Conservation Biology*, 21(2), 422–433. <https://doi.org/10.1111/j.1523-1739.2006.00578.x>
- Rousse, P., van Noort, S., & Diller, J. (2013). Revision of the Afrotropical Phaeogenini (Ichneumonidae, Ichneumoninae), with description of a new genus and twelve new species. *ZooKeys*, 354, 1–85. <https://doi.org/10.3897/zookeys.354.5968>
- Rowles, A. D., & O'Dowd, D. J. (2006). Interference competition by Argentine ants displaces native ants: implications for biotic resistance to invasion. *Biological Invasions*, 9(1), 73–85. <https://doi.org/10.1007/s10530-006-9009-5>
- RSNZ. (2016). *Climate change implications for New Zealand* (p. 72). Wellington: The Royal Society of New Zealand.
- Ruíz-Cancino, E. (2015). La familia Ichneumonidae (Hymenoptera) en México. *Entomología Mexicana*, 2, 1–13.
- Sääksjärvi, I. E., Haataja, S., Neuvonen, S., Gauld, I. D., Jussila, R., Salo, J., & Burgos, A. M. (2004). High local species richness of parasitic wasps (Hymenoptera: Ichneumonidae: Pimplinae and Rhyssinae) from the lowland rainforests of Peruvian Amazonia. *Ecological Entomology*, 29(6), 735–743. <https://doi.org/10.1111/j.0307-6946.2004.00656.x>
- Schnitzler, F.-R. (2008). *Hymenopteran parasitoid diversity & tri-trophic interactions: The effects of habitat fragmentation in Wellington, New Zealand*. Victoria University, Wellington, NZ. Retrieved from <http://researcharchive.vuw.ac.nz/handle/10063/536>
- Seberg, O., Humphries, C. J., Knapp, S., Stevenson, D. W., Petersen, G., Scharff, N., & Andersen, N. M. (2003). Shortcuts in systematics? A commentary on DNA-based taxonomy. *Trends in Ecology & Evolution*, 18(2), 63–65. [https://doi.org/10.1016/S0169-5347\(02\)00059-9](https://doi.org/10.1016/S0169-5347(02)00059-9)
- Secretariat for the CBD. (1992). *Convention on biological diversity*. Montreal, Canada: UN. Retrieved from <http://www.cbd.int/doc/legal/cbd-en.pdf>

- Secretariat for the CBD. (2008). *Guide to the global taxonomy initiative* (CBD Technical Series no. 30) (p. 105). Retrieved from <https://www.cbd.int/doc/publications/cbd-ts-30.pdf>
- Sharkey, M. J. (2007). Phylogeny and classification of Hymenoptera. *Zootaxa*, 1668, 521–548.
- Shaw, M. R. (2006). Habitat Considerations for Parasitic Wasps (Hymenoptera). *Journal of Insect Conservation*, 10(2), 117–127. <https://doi.org/10.1007/s10841-006-6288-1>
- Shaw, M. R., & Hochberg, M. E. (2001). The neglect of parasitic Hymenoptera in insect conservation strategies: The British fauna as a prime example. *Journal of Insect Conservation*, 5(4), 253–263. <https://doi.org/10.1023/A:1013393229923>
- Sluys, R. (2013). The unappreciated, fundamentally analytical nature of taxonomy and the implications for the inventory of biodiversity. *Biodiversity and Conservation*, 22(4), 1095–1105. <https://doi.org/10.1007/s10531-013-0472-x>
- Smith, E. P., & van Belle, G. (1984). Nonparametric estimation of species richness. *Biometrics*, 40(1), 119–129. <https://doi.org/10.2307/2530750>
- Southwood, R., & Henderson, P. A. (2000). *Ecological methods* (3rd ed.). Malden, MA: Blackwell Science.
- Stork, N. E., McBroom, J., Gely, C., & Hamilton, A. J. (2015). New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. *Proceedings of the National Academy of Sciences*, 112(24), 7519–7523. <https://doi.org/10.1073/pnas.1502408112>
- Tao, L., Mao-Ling, S., Shu-Ping, S., Guo-Fa, C., & Zhi-Hong, G. (2012). Effect of the trap color on the capture of ichneumonids wasps (Hymenoptera). *Revista Colombiana de Entomología*, 38(2), 338–342.
- Tautz, D., Arctander, P., Minelli, A., Thomas, R. H., & Vogler, A. P. (2003). A plea for DNA taxonomy. *Trends in Ecology & Evolution*, 18(2), 70–74. [https://doi.org/10.1016/S0169-5347\(02\)00041-1](https://doi.org/10.1016/S0169-5347(02)00041-1)
- Taylor, H. R., & Harris, W. E. (2012). An emergent science on the brink of irrelevance: A review of the past 8 years of DNA barcoding. *Molecular Ecology Resources*, 12(3), 377–388. <https://doi.org/10.1111/j.1755-0998.2012.03119.x>
- TEEB. (2010). *Mainstreaming the economics of nature: A synthesis of the approach, conclusions and recommendations of TEEB*. Geneva: UNEP.

- Templeton, A. R. (1994). Biodiversity at the molecular genetic level: Experiences from disparate macroorganisms. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 345(1311), 59–64. <https://doi.org/10.1098/rstb.1994.0086>
- Thomas, G. M., & Ogden, J. (1983). The scientific reserves of Auckland University. i. General introduction to their history, vegetation, climate and soils. *Tane*, 29, 143–162.
- Tosquinet, J. (1903). Ichneumonides nouveaux (travail posthume). *Mémoires de La Société Entomologique de Belgique*, 10, 1–434.
- Townes, H. (1972). A light-weight Malaise trap. *Entomological News*, 83, 239–247.
- Valentine, E. W. (1970). Hymenoptera. *New Zealand Entomologist*, 4(3), 47–50.
- Valentine, E. W., & Walker, A. K. (1991). *Annotated catalogue of New Zealand Hymenoptera*. Auckland, NZ: DSIR Plant Protection.
- Van Achterberg, C. (2009). Can Townes type Malaise traps be improved? Some recent developments. *Entomologische Berichten*, 69, 129–135.
- Veijalainen, A., Wahlberg, N., Broad, G. R., Erwin, T. L., Longino, J. T., & Sääksjärvi, I. E. (2012). Unprecedented ichneumonid parasitoid wasp diversity in tropical forests. *Proceedings of the Royal Society of London B: Biological Sciences*, 279(1748), 4694–4698. <https://doi.org/10.1098/rspb.2012.1664>
- Wahl, D. B. (1991). A new species of *Dusona* from New Zealand, and the application of *Dusona* vs. *delopia* (Hymenoptera: Ichneumonidae, Campopleginae). *Proceedings of the Entomological Society of Washington*, 93, 946–950.
- Wahl, D. B., & Sharkey, M. J. (1993). Superfamily Ichneumonoidea. In H. Goulet & J. T. Huber (Eds.), *Hymenoptera of the world: An identification guide to families* (pp. 358–509). Ottawa, Ontario: Centre for Land and Biological Resources Research.
- Walker, A. K., & Crosby, T. K. (1988). *The preparation and curation of insects* (Revised Ed.). Wellington: Science Information Publishing Centre, DSIR.
- Walker, G. P., Herman, T. J. B., Kale, A. J., & Wallace, A. R. (2010). An adjustable action threshold using larval parasitism of *Helicoverpa armigera* (Lepidoptera: Noctuidae) in IPM for processing tomatoes. *Biological Control*, 52(1), 30–36. <https://doi.org/10.1016/j.biocontrol.2009.09.003>
- Ward, D., & Edney-Browne, E. (2015). Poles apart: Comparing trends of alien Hymenoptera in New Zealand with Europe (DAISIE). *PLOS ONE*, 10(7), e0132264. <https://doi.org/10.1371/journal.pone.0132264>

- Ward, D. F., Early, J. W., Schnitzler, F.-R., Hitchmough, R. A., & Stringer, I. A. N. (2012). The conservation status of New Zealand Hymenoptera. *New Zealand Entomologist*, 35(2), 116–119. <https://doi.org/10.1080/00779962.2012.686315>
- Ward, D. F., & Larivière, M.-C. (2004). Terrestrial invertebrate surveys and rapid biodiversity assessment in New Zealand: lessons from Australia. *New Zealand Journal of Ecology*, 28(1), 151–159.
- Ward, D. F., & Stanley, M. C. (2004). The value of RTUs and parataxonomy versus taxonomic species. *New Zealand Entomologist*, 27(1), 3–9. <https://doi.org/10.1080/00779962.2004.9722118>
- Watts, C., Stringer, I., & Gibbs, G. (2012). Insect conservation in New Zealand: An historical perspective. In T. R. New (Ed.), *Insect Conservation: Past, Present and Prospects*. Dordrecht, Netherlands: Springer. Retrieved from <http://link.springer.com/10.1007/978-94-007-2963-6>
- Wells, W., & Decker, T. (2006). A comparison of three types of insect traps for collecting non-Formicidae Hymenoptera on the island of Dominica. *Southwestern Entomologist*, 31(1), 59.
- Wheeler, Q. (2010). What would NASA do? Mission-critical infrastructure for species exploration. *Systematics and Biodiversity*, 8(1), 11–15. <https://doi.org/10.1080/14772001003628075>
- Wheeler, Q., Assis, L., & Rieppel, O. (2013). Phylogenetics: Heed the father of cladistics. *Nature*, 496(7445), 295–296. <https://doi.org/10.1038/496295a>
- Wheeler, Q. D. (1995). Systematics, the scientific basis for inventories of biodiversity. *Biodiversity & Conservation*, 4(5), 476–489. <https://doi.org/10.1007/BF00056338>
- Wheeler, Q. D. (2005). Losing the plot: DNA “barcodes” and taxonomy. *Cladistics*, 21(4), 405–407. <https://doi.org/10.1111/j.1096-0031.2005.00075.x>
- Wheeler, Q. D. (2007). Invertebrate systematics or spineless taxonomy? *Zootaxa*, 1668, 11–18.
- Wheeler, Q. D. (2008a). Introductory: Toward the New Taxonomy. In *The New Taxonomy* (pp. 1–17). Boca Raton: CRC Press.
- Wheeler, Q. D. (Ed.). (2008b). *The new taxonomy*. Boca Raton: CRC Press.
- Wheeler, Q. D. (2009a). Revolutionary thoughts on taxonomy: Declarations of independence and interdependence. *Zoologia (Curitiba)*, 26(1), 1–4. <https://doi.org/10.1590/S1984-46702009000100001>

- Wheeler, Q. D. (2009b). The science of insect taxonomy: Prospects and needs. In R. G. Foottit & P. H. Adler (Eds.), *Insect Biodiversity: Science & Society* (pp. 357–380). Wiley-Blackwell. Retrieved from <http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch14/summary>
- Wheeler, Q. D., Knapp, S., Stevenson, D. W., Stevenson, J., Blum, S. D., Boom, B. M., ... Woolley, J. B. (2012). Mapping the biosphere: exploring species to understand the origin, organization and sustainability of biodiversity. *Systematics and Biodiversity*, 10(1), 1–20. <https://doi.org/10.1080/14772000.2012.665095>
- Wilkins, J. S. (2009). *Defining species: A sourcebook from antiquity to today*. NY: Peter Lang.
- Will, K. W., Mishler, B. D., & Wheeler, Q. D. (2005). The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology*, 54(5), 844–851. <https://doi.org/10.1080/10635150500354878>
- Wilson, E. O. (1985). The biological diversity crisis. *BioScience*, 35(11), 700–706. <https://doi.org/10.2307/1310051>
- Wilson, E. O. (1988). The current state of biological diversity. In E. O. Wilson (Ed.), *Biodiversity* (pp. 19–76). Washington, D.C.: National Academies Press. Retrieved from <http://www.nap.edu/catalog/989>
- Winston, J. E. (1999). *Describing species: Practical taxonomic procedure for biologists*. New York: Columbia University Press.
- Yu, D. S., Van Achterberg, C., & Horstmann, K. (2012). World Ichneumonoidea 2011: Taxonomy, biology, morphology and distribution.
- Zhang, Z.-Q. (2008). Contributing to the progress of descriptive taxonomy. *Zootaxa*, 1968, 65–68.
- Zhang, Z.-Q. (2010). Reviving descriptive taxonomy after 250 years. In A. Polaszek (Ed.), *Systema Naturae 250: The Linnaean Ark* (pp. 95–108). Boca Raton: CRC Press.