# Integrative, next-generation, collaborative vascular plant systematics in New Zealand

**Heidi M. Meudt***
Museum of New Zealand Te Papa Tongarewa, PO Box 467, Cable St, Wellington 6140, New Zealand

Systematics is a synthetic science which focuses on species delimitation, taxonomy, classification, and phylogeny, with an additional aim of understanding underlying evolutionary and biogeographic patterns and processes. Systematic research has many downstream benefits including underpinning conservation management, biosecurity and health. In this short overview article, I will give a brief synopsis of integrative systematics, in which multiple data sets are used to robustly test species limits in a statistical framework, and illustrate why I think we need integrative systematics in New Zealand. I will then discuss examples from my own systematics research, especially on the flowering plant families Plantaginaceae (*Ourisia, Plantago, Veronica*) and Boraginaceae (*Myosotis*), as well as from other vascular plant systematics research being done by colleagues in New Zealand and elsewhere. Through these examples, I will show how using an integrative systematics approach to analysing morphological, molecular, cytological and other data sets can aid species delimitation and new species discovery, and allow inferences into questions regarding such diverse themes as diversification, variability and conservation of threatened species, polyploidy (whole genome duplication) and biogeography of New Zealand vascular plants. I will also argue that the future of systematics should not only be integrative, but also next-generation and collaborative, and that such forward-looking, cooperative research – and the institutional and governmental investment to support it – is essential for New Zealand.

## What is integrative systematics?

Systematics is a synthetic science which focuses on the naming (taxonomy), classification, and phylogeny (evolutionary relationships) of species. The core aspects of systematics research are species discovery and description; testing and defining species limits; determining species relationships; naming and classifying species; and providing the fundamental systematic information, collections and databases that form the essential backbone to studies in all other biological fields. On any given day, systematists might be in the field collecting specimens and samples; in the herbarium measuring morphological characters on voucher specimens or actively contributing new material and data to our substantial institutional collections and databases; in the lab extracting DNA or generating sequences; or in front of the computer writing grant proposals, performing statistical analyses on different data sets, or writing up and submitting results as scientific papers, floras and faunas, or books. Increasingly, systematists are also communicating their latest discoveries with the public, government and other relevant end-users via newsletters, articles, reports, lectures, websites, blogs and social media. Systematics research has the additional benefit of elucidating evolutionary patterns and processes, including understanding the origins and biogeography of our flora and fauna (Stuessy 2009; Schlick-Steiner *et al.* 2014). Systematics research also provides fundamental knowledge for biosecurity, human health, conservation and threatened species management, sustainability, and economics, among others (Royal Society of New Zealand 2015).

The main questions systematists are trying to answer are: How many species are there in a particular group? What distinguishes them? How are they related to one another? Where do they come from? To answer these questions, systematists have historically used information from multiple data sources, including standard and time-tested methods (e.g. morphology) as well as new methods and ideas such as next-generation sequencing. Thus, systematics has always been a synthetic and integrative science, and indeed over the last century, different terms have been used to describe these inherent qualities, such as 'statistical systematics', 'biosystematics,' 'experimental taxonomy', 'new systematics' and 'comparative biology' (Stuessy 2009). 'Integrative taxonomy' came into use mostly in the zoological systematics literature when molecular data were being increasingly incorporated into systematics research, and use of the term was partly a reaction against the idea that DNA barcoding might go beyond aiding species identification to eventually replace (rather than enhance) taxonomy (e.g. Dayrat 2005, Will *et al.* 2005; Pires & Marinoni 2010). At about the same time, a renewed discussion was taking place among systematists about the best way to delimit species while also considering their evolutionary history (e.g. the general lineage concept of de Queiroz (2007)).

*Correspondence: heidim@tepapa.govt.nz

**Heidi Meudt** is an American-New Zealander who completed a BSc in Biology and Spanish in her home state of Wisconsin, a PhD in Botany at the University of Texas at Austin, and a National Science Foundation postdoctoral fellowship at Massey University, Palmerston North. In 2006 she started her current position as Research Scientist (Botany) at Te Papa, where she uses integrative systematics methods to study the taxonomy, phylogeny, classification and species limits of native New Zealand flowering plants. From 2012 to 2014 she was an Alexander von Humboldt Experienced Researcher at the University of Oldenburg, Germany. She is also a Fellow of the Linnean Society.

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Over the last 15 years, 4000 papers using the terms 'integrative taxonomy' or (less frequently) 'integrative systematics' have been published (Google Scholar search performed by the author in October 2016), with increasing numbers of papers each year (see Pante *et al.* 2015). Several thorough reviews provide an excellent summary of the development and current status of integrative systematics (e.g. Dayrat 2005; Valdecasas *et al.* 2008; Padial & De La Riva 2010; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010; Fujita *et al.* 2012).

Integrative systematics can be defined as being a science that incorporates as many available sources of data as possible to develop and test species hypotheses (Dayrat 2005; Will *et al.* 2005; Yeates *et al.* 2011), and includes analyses of multiple types of data including DNA, morphology, habitat, chromosome number, and others. This definition effectively equates analyses of multiple data sets with integrative systematics and is used by many systematists, including myself in this article. An integrative framework allows systematists to treat species boundaries as hypotheses to be tested with different pieces of evidence – simultaneously and/or consecutively – to find agreement and correlation among different data sets. Such an approach is generally more robust for delimiting species than relying on one type of data only, and when data sets do not agree, discrepancies may help bring to light underlying biological or evolutionary processes (Schlick-Steiner *et al.* 2010). Integrative systematics research can include a range of analysis methods and data sets. At its most basic level, integrative systematics can test species concepts based on previous (descriptive) morphological-based taxonomy with phylogenetic analyses of one or few sequenced DNA markers (or DNA fingerprinting), and there are several New Zealand examples of such studies from plants (Tay *et al.* 2010a; Prebble *et al.* 2012; Brownsey & Perrie 2014; Ohlsen *et al.* 2015) and animals (Trewick 2008; Boyer *et al.* 2011). A further step towards increased integration includes using multivariate statistical analyses of morphological data that are analysed in conjunction with those of molecular and other data sets – from the same individuals, when possible – to revise species limits and taxonomy, including some examples from my own research (Meudt 2008; Meudt 2012; Meudt *et al.* 2013; see below for more details). In these and other studies, integrative systematics is often an iterative process of continually testing and retesting species boundary hypotheses with new data sources (Yeates *et al.* 2011).

Some recent reviews have suggested that current integrative systematics methods are rather qualitative, not repeatable, and ad hoc, and suggest that truly integrative systematics should entail quantitative co-analyses of different types of data generated from the same individuals (e.g. Padial *et al.* 2010; Yeates *et al.* 2011). The integrative systematics of the future should include quantitative methods that provide objective assessments of species limits in a statistical framework, both for analyses of morphological or molecular data alone as well as for co-analyses of molecular, morphological and other data sets. For molecular data, many analytical methods currently exist to test species limits for single or multiple molecular markers; for a nice review with a focus on lichens see Leavitt *et al.* (2015). Many advocate the use of the multispecies coalescent model as the standard approach for species tree estimation using sequences from multiple genes, in which hypotheses about species relationships and species limits can be tested by integrating multiple genetic data sets to identify evolutionary lineages (e.g. Knowles & Carstens 2007; Carstens & Dewey 2010; Fujita *et al.* 2012; Jones 2016; Leaché *et al.* 2014; Jones *et al.* 2015; Fujisawa *et al.* 2016). Such approaches are not always possible, because it may not always be feasible to acquire DNA sequences of multiple or even single genes for the individuals under study; or, when available, such data are not sufficiently variable or taxonomically useful; or the necessary models and software to analyse them are not yet fully developed (although much progress has been made over the last decade). But the fact that integrative systematics is moving to incorporate such methodologies, where appropriate and feasible, is encouraging. Even more promising is the recent progress regarding new integrative systematics methods for co-analyses of multiple sources of data (such as genetic, morphological and ecological niche modelling data sets) to test species boundaries by combining multivariate and clustering techniques (Edwards & Knowles 2014) or using a Bayesian framework (Solís-Lemus *et al.* 2015). These and other such methods are the way forward for integrative systematics (e.g. Yeates *et al.* 2011), and further investigation and developments in this area are warranted and welcome (Jones 2016).

## Why do we need integrative systematics, particularly in New Zealand?

Although New Zealand is small in size, the country has a rich and diverse biota with high endemism, with an estimated 49,579 total native species, of which over half are endemic (Table 1; Gordon 2013). Endemism is particularly high for certain groups such as gymnosperms (100%) and flowering plant species (84%) (Wilton & Breitwieser 2000; McGlone *et al.* 2001; Wilton *et al.* 2016). Even more astounding is that systematists estimate that over 65,000 species have yet to be discovered or described in New Zealand (Table 1), which means we are not even half way there yet to knowing and documenting our biodiversity! Although the majority of these undiscovered species are animals or fungi, my focus in this overview is constrained largely to vascular plants, since it is the group of organisms that I work on and am most familiar with. Plant systematists estimate that nearly 1200 New Zealand plant species remain undescribed (Table 1), and of these, about 300–400 are angiosperms (flowering plants). Furthermore, the current *Flora of New Zealand* (Allan 1961) was published 55 years ago and is well overdue for a major rewrite, and many of New Zealand's plant genera have not had recent taxonomic revisions. The good news is, this rewrite is now under way. Since 2014, new taxonomic treatments – particularly of ferns and mosses – based on new systematic data are being published in an online New Zealand eFlora (http://www.nzflora.info/), an exciting collaborative development. As our knowledge of the systematics of New Zealand fauna, fungi, non-green algae and other organisms are in a much worse state than vascular plants (Table 1), that the need

**Table 1. New Zealand's rich biota (from Gordon 2013).**

| Kingdom | Total no. species | No. native species (%) | Percent native species that are endemic | No. undiscovered species |
|---|---|---|---|---|
| bacteria | 701 | ?? | ?? | ?? |
| protozoans | 539 | 516 (96%) | 4.7% | 770 |
| Chromista | 4,208 | 3,921 (93%) | 7.2% | 4,695 |
| plants | 7,555 | 4,970 (66%) | 48.2% | 1,175 |
| fungi | 8,395 | 6,402 (76%) | 26.0% | 23,525 |
| animals | 36,017 | 33,770 (94%) | 68.0% | 35,340 |
| TOTAL | 57,415 | 49,579 (86%) | 55.2% | 65,505 |

for sysetmatics research – ideally using integrative systematics methods – is undeniably clear.

New Zealand has a unique combination of both oceanic island features (e.g. small area, long isolation from continental land masses, and topographic and climatic diversity) as well as continental features (including a long fossil record), which have shaped the history of the flora and fauna in myriad ways. New Zealand's flora and fauna have diverse origins, including a mixture of older, Gondwanan elements as well as more recent components (e.g. McGlone *et al.* 2001). For many New Zealand flowering plant lineages, both the fossil record and molecular phylogenetic studies show evidence of dispersal to New Zealand within the last 5–10 million years, which coincides with a period of tectonic activity and glacial-interglacial cycles (Winkworth *et al.* 2005). During this time, plant survival would have depended on the ability to cope with changing environments, and many would have gone extinct. But other plant lineages probably encountered great opportunities for rapid expansion and diversification into new forms and habitats (also likely accompanied by hybridisation) to produce much of the remarkable morphological and ecological diversity of the present day flora (Winkworth *et al.* 2005).

These recent species radiations offer both challenges as well as opportunities for the practising vascular plant systematist. In particular, species limits may be blurred because certain data may not be taxonomically useful or well-resolved in a certain group, different data sets may not agree with one another, and confounding biological and evolutionary processes are also at play. Plants of closely-related species can often interbreed, and this lack of reproductive barriers facilitates hybridisation, which is sometimes also accompanied by whole genome duplication (polyploidy). Hybridisation can obscure species boundaries when hybrids later interbreed with their parental species, but to further complicate matters, it can also lead to the formation of new species. Furthermore, it is important to remember that speciation is an ongoing process, so it may be difficult to delimit species when species are at the beginning or middle stages of that process, especially given that many of our New Zealand plant genera are the result of recent and rapid divergence and have low DNA sequence diversity at standard DNA sequencing markers. However, this recent diversification is the reason why New Zealand is arguably one of the best places in the world to investigate evolutionary processes.

My own research to date has focused on several New Zealand flowering plant genera: native mountain foxgloves (*Ourisia*), hebes (*Veronica*), plantains (*Plantago*), and forget-me-nots (*Myosotis*). These genera contain multiple, closely-related and mostly endemic species that have diversified within the last few million years. I have used an integrative approach including analyses of comparative morphology, DNA (genotyping and sequencing), pollen, chromosome number, geography and habitat to infer the phylogeny, identify lineages, test species limits, discover and describe new species, and revise the taxonomy of these genera. For example, using a combination of molecular phylogeny (Tay *et al.* 2010a; Tay *et al.* 2010b), genotyping using DNA fingerprinting (Meudt 2011), statistical analyses of morphology (Meudt 2012), and new chromosome counts (Murray *et al.* 2010), my colleagues and I provided evidence for eleven native New Zealand species of *Plantago* in three separate evolutionary lineages. In this case there was a striking congruence among the data sets, and our integrative approach allowed us to also discover and describe a new species, *Plantago udicola* Meudt & Garn.-Jones, which has a unique chromosome number ($2n = 96$), and is ecologically, genetically and morphologically distinct (Meudt 2011). We used a similar approach to confirm the previous descriptive morphology-based taxonomy (Meudt 2006) of the 13 endemic mountain foxgloves (*Ourisia*) from New Zealand and one from Tasmania, and elevate a subspecies to species rank based on the new molecular evidence from DNA fingerprinting (*Ourisia calycina*; Meudt *et al.* 2009); readjust species and subspecies limits and taxonomy in the snow hebes (*Veronica*) of subalpine New Zealand and Australia, including reducing one species into synonymy based on morphology and molecular data (Meudt 2008; Meudt & Bayly 2008); and revise the taxonomy of the *Myosotis petiolata* species complex, including discovery and description of a new subspecies *Myosotis pansa* subsp. *praeceps* Meudt *et al.* based on molecular and morphological analyses (Meudt *et al.* 2013).

In some instances, however, this combination of molecular and morphological approaches has not provided enough variation for phylogenetic reconstruction or species delimitation, and additional methods are being explored. The New Zealand hebes are in the plant genus *Veronica,* which has the most (124) native species in New Zealand (Wilton *et al.* 2016) and is our largest and arguably most loved plant species radiation. Although there has already been much effort and many years of collaborative research on hebes, there are still several systematic issues that need to be resolved in this genus, perhaps in part due to whole genome duplication (polyploidy) and hybridisation which are blurring some species boundaries. Despite several studies (Wagstaff *et al.* 2002; Albach & Meudt 2010; Meudt *et al.* 2015b) we still do not have a fully resolved phylogeny of New Zealand *Veronica.* For our latest *Veronica* research (Mayland-Quellhorst *et al.* 2016, see below), we sequenced 48 new nuclear markers and 48 new microsatellite markers, each in 48 different individuals, to validate the newly-developed sequencing markers. We have only just begun detailed analyses of this data, but some of these markers appear to be quite variable for New Zealand *Veronica,* which will make them extremely useful for improving species delimitation via documented interspecific genetic differences, resolving the phylogeny, and answering questions about the evolution of polyploidy in the genus. We have also recently estimated the genome sizes of a number of New Zealand and Australian *Veronica* species for the first time and analysed these data phylogenetically to show that New Zealand hebes have experienced genome downsizing (DNA loss), which is associated with both polyploid radiation and higher rates of diversification (Meudt *et al.* 2015b). When used alongside chromosome counts, genome size can be very useful in systematic studies of *Veronica*, and perhaps other New Zealand genera, but to date only about 5–8% of New Zealand plant species have known genome sizes (http://data.kew.org/cvalues/), and most of those were published by Brian Murray (University of Auckland, now retired).

New Zealand forget-me-nots (*Myosotis,* Boraginaceae) are another group with very low levels of genetic variation for standard sequencing markers, which have frustratingly told us very little about species identities and relationships (Winkworth *et al.* 2002; Meudt *et al.* 2015a). Although species in the *M. petiolata* complex were able to be distinguished using DNA fingerprinting, this molecular method was not useful for other species in the genus (Meudt *et al.* 2015a). The majority of the

40+ New Zealand native forget-me-not species are threatened or at risk, with many exhibiting very restricted geographical ranges and/or occupying very specific habitats (de Lange *et al.* 2013; Meudt *et al.* 2015a). About two dozen putative new species have been given informal tag names (Druce 1993) and need to be studied in detail. All of this means *Myosotis* is a very high priority for systematics and conservation research, and is the focus of most of my current research (http://collections.tepapa.govt.nz/topic/3714). In addition to adding to morphological data sets, generating additional data sets will be critical for revising the taxonomy of this group. Recently I have shown that pollen morphology is useful for delimiting forget-me-not species groups and in some cases individual species (Meudt 2016). Jessie Prebble's recently completed PhD thesis on pygmy forget-me-nots is also a significant milestone, as it bridges systematics, population genetics and conservation, and is integrative in nature (Prebble, unpubl. thesis, defended November 2016). A novel aspect of this research is that morphological data from both herbarium specimens and live plants were compared. In addition to developing novel microsatellite DNA markers from next-generation sequencing data (Prebble *et al.* 2015), over 500 pygmy forget-me-nots were genotyped, and this data was analysed alone and in parallel with morphological and ecological niche modelling data using integrative statistical methods (Edwards & Knowles 2014). In the last chapter of the thesis, a taxonomic revision is proposed based on all available data. These chapters are currently being prepared for submission to scientific journals for publication. The data have already been used to make a submission to the New Zealand Threat Classification panel (J.M. Prebble, pers. comm.), which will ultimately help the Department of Conservation (DOC) undertake conservation management of these species to help protect them. Overall, Jessie Prebble's PhD thesis is a great example of New Zealand vascular plant integrative systematics, and it also exemplifies both next-generation and collaborative systematics, which are explored in more detail in the following two sections.

## What is the role of next-generation sequencing in systematics?

'Next generation' is a fashionable phrase of the moment in biological research, and is being used to describe recent developments in diverse fields from crop breeding and biogeography to medicine and cancer. Often the phrase refers to next-generation sequencing (NGS), which over the past decade has caused a genomic revolution in all fields of biological research, including systematics (Harrison & Kidner 2011; Straub *et al.* 2012; Soltis *et al.* 2013; Barrett *et al.* 2016). In 2012, an entire issue of the *American Journal of Botany* was dedicated to 'Methods and Applications of Next-Generation Sequencing in Botany' (http://www.amjbot.org/content/99/2.toc). NGS allows systematists to generate and analyse unprecedented amounts of molecular sequence data which may allow whole genome phylogenetics and population genetics analyses, species delimitation via quantitative methods, better interpretation and comparisons of data sets, and perhaps even the detection of the genetic basis of interspecific differences. Although systematists should (and increasingly do) incorporate NGS data sets into their integrative taxonomic research, just as the integrative taxonomists warned a decade ago, we should be wary of equating next-generation sequencing (on its own) with next-generation systematics.

NGS methods and analyses also require significant resources (high performance computing, Unix/Linux operating systems), constant upskilling, and multidisciplinary collaboration, and are currently hindered by a substantial bioinformatics bottleneck. For many NGS methods, the bioinformatics bottleneck refers to a lack of access to essential computing resources (in some cases, the appropriate resources may not yet exist) and key skills to analyse the data. Although collaboration with colleagues who have bioinformatics skills is one option, upskilling is equally important (Barrett *et al.* 2016): 'It is very important for students to acquire adequate training in using Unix/Linux operating systems and at least one high-level programming language like Perl, Python, or Shell... Perhaps one of the most important things students can do at this point of time is to complement the obvious requirement of competence in taxonomy/systematics with expertise in genomics, informatics, and computational biology…' (Soltis *et al.* 2013, p. 895). When reading 'students', we should read 'all systematists'! It is difficult, however, to stay up-to-date, as NGS technologies are rapidly changing: 'Systematists are now faced with what may seem a bewildering array of next-generation sequencing (NGS) options… Most will be outdated or upgraded in the next several years, but the power of these current instruments is astonishing… [T]he field is moving so quickly that current techniques and applications will be rapidly superseded by upcoming advances…' (Soltis *et al.* 2013, p. 886–887).

There are numerous NGS platforms that systematists use, and these have been compared and discussed at length elsewhere in the literature (e.g. Glenn 2011). Irrespective of the platform, there are essentially two main methodological NGS approaches currently in use, i.e. restriction-enzyme-based methods and targeted methods. For both approaches, the central aim is to generate markers from a reduced representation of the genome, as we are not yet at the stage where we can sequence an entire (nuclear) genome. Examples of restriction-enzyme based methods (Davey *et al.* 2011) are restriction-site associated DNA sequencing (RAD-Seq; Baird *et al.* 2008; Peterson *et al.* 2012) and genotyping by sequencing (GBS; Elshire *et al.* 2011). Targeted methods include genome skimming, whole chloroplast DNA sequencing, high-throughput *de novo* transcriptome sequencing (RNA-Seq; Mortazavi *et al.* 2008), sequence/exon capture, Hyb-Seq (Weitemier *et al.* 2014), and anchored phylogenomics (Lemmon *et al.* 2012). Although these methods show great promise (e.g. Uribe-Convers & Tank 2016), I find few published examples of their use in New Zealand systematics to date (e.g. RAD-Seq in plants: Roda *et al.* 2013; and animals: Herrera & Shank 2016; note some studies using these methods are in progress and as yet unpublished, and GBS has been used in New Zealand in some horticultural and agricultural applications). RNA-Seq has been used to understand evolutionary questions in crops (e.g. cotton and soybean) as well as natural systems, including New Zealand plants (*Pachycladon,* Voelckel *et al.* 2012) and animals (stick insects, Morgan-Richards *et al.* 2016). My colleagues and I have recently used RNA-Seq to develop novel sequencing markers in New Zealand and European *Veronica* (Mayland-Quellhorst *et al.* 2016) that may provide additional data sets to improve the phylogeny and resolve problematic species limits when used in an integrative context. Finally, many plant microsatellite markers have also been developed recently for New Zealand plants using NGS genomic data (e.g. McLay *et al.* 2012; Van Etten *et al.* 2013, 2014; Prebble *et al.* 2015; Pilkington & Symonds 2016; Breitweiser *et al.* 2015), but whether these and/or RNA-

Seq data and markers developed from them are effective for integrative systematics remains to be seen.

## How can we foster collaborative systematics in New Zealand and beyond?

During an Olympic year, I once heard a botanist at a conference say that if systematics were an Olympic sport, it would be decathlon. Just as one decathlete is expected to excel in ten different disciplines, so systematists use a wide array of methods in their research. And just as the decathlon evolved from sports with fewer events such as the pentathlon and heptathlon, so systematists continue to add new data, methods and skills to their systematic toolkits. Thus, superficially, this analogy does seem to speak to both the nature and breadth of the work integrative systematists do. But upon further thought, the decathlon may not be the best model. First of all, only men can compete in the Olympic decathlon! (NB: Taxonomists in New Zealand as a group are a 'male-dominated, aging workforce'; Royal Society of New Zealand 2015.) Secondly, although systematists do a lot of their own research, they also collaborate. Although mixed-gender medley relay races do exist at some swimming or track and field competitions (not yet including the Olympics), probably no current sport can truly embody all aspects of integrative systematics as practised today.

Collaboration is important in systematics when using both standard methods as well as new techniques, and it is probably essential for research involving NGS and bioinformatics. It is likely that all systematists (and indeed all scientists) have all had both positive and negative experiences when collaborating. When it works well, collaborative systematics has very important benefits for systematists individually and collectively, and of course for the organisms under study. There are many benefits of practising collaborative systematics, including contributing additional data sets to an integrative research framework, filling knowledge/skill gaps for a particular project, facilitating upskilling, enabling the sharing and passing on of knowledge and experience, and creating synergy which allows more systematics research to get done together than when working alone.

Collaboration is particularly important in New Zealand, where the small systematics community is physically isolated from colleagues in other countries, capability and funds are declining, and contestable research grants for systematics and other collection-based research are non-existent (Royal Society of New Zealand 2015). Furthermore, systematists at universities, museums and Crown Research Institutes are all under pressure to conduct systematics research in addition to teaching, working on exhibitions, and completing contracts. Because of limitations in resources and available expertise, coordinated, cross-institutional prioritisation at the national level regarding what systematics research should be done, on which organisms, to what degree, and by whom, is crucial, but does not yet occur (Royal Society of New Zealand 2015). Given these circumstances, it can sometimes be difficult for systematists to collaborate even though collaboration may help them achieve more fruitful results in their research projects. Nevertheless, it is clear that collaborative plant systematics is happening in New Zealand; that is, systematists routinely collaborate with other systematists and with non-systematists on integrative systematics research. Below I will mention some examples of this, but I will also argue that more can be done to foster increased collaboration at the local, national, regional and international levels by systematists themselves, their institutions, other organisations, and the government.

Some examples of synergy and collaboration from my own work are: recent collaboration on *Veronica* with New Zealand, German and Spanish colleagues (Meudt *et al.* 2015b; Mayland-Quellhorst *et al.* 2016); co-supervision of students Mei Lin Tay (MSc) and Gustavo Hassemer (PhD) on *Plantago* involving collaboration with scientists from Victoria University and Auckland University, and the University of Copenhagen and Museum of Natural History Denmark, respectively (Murray *et al.* 2010; Tay *et al.* 2010a; Tay *et al.* 2010b; Hassemer *et al.* 2015); and systematics research on *Myosotis*, including co-supervision of PhD student Jessie Prebble, collaboration with scientists from Te Papa, Massey University, DOC, city councils, among others (Meudt *et al.* 2013; Meudt *et al.* 2015a; Prebble *et al.* 2015). Recent collaboration on New Zealand *Veronica* systematics is a subset of other current and past complementary collaborations, many of which have had Northern + Southern Hemisphere and trans-Tasman components (e.g. Wagstaff *et al.* 2002; Bayly & Kellow 2006; Garnock-Jones *et al.* 2007). New Zealand fern systematics is another good example of collaboration between New Zealand and Australia (e.g. Perrie *et al.* 2014) and within New Zealand (e.g. Te Papa and DOC; Brownsey *et al.* 2013). Research on the New Zealand everlasting daisies (tribe Gnaphalieae) is an early and still ongoing example of integrative, collaborative systematic research by staff at Landcare Research and colleagues on a group of flowering plants. In their PhD theses, both Ward (1981) and Breitwieser (1990) argued that the taxonomic confusion in this group – especially in terms of generic boundaries – would require using as many and varied characters as possible, and, to this end, morphology, anatomy, isozymes, flavonoid chemistry, pollen, chromosome counts, molecular phylogeny, and microsatellites have so far been employed (e.g. Haase *et al.* 1993; Ward 1993; Breitwieser & Sampson 1997; Ward & Breitwieser 1998; Breitwieser *et al.* 1999; Dawson & Ward 1999; McKenzie *et al.* 2004; Breitwieser *et al.* 2015).

Postgraduate student co-supervision is a great way to collaborate, particularly between institutions (Royal Society of New Zealand 2015), and can be hugely beneficial for all involved. Systematists at Te Papa, for example, have successfully co-supervised a number of postgraduate plant systematics students to completion of their Honours, MSc and PhD degrees in collaboration with New Zealand and overseas universities. Plant systematists must also continue to build upon regional professional networks, e.g. Australasian Systematic Botany Society (ASBS; http://www.asbs.org.au/) and Council of Heads of Australasian Herbaria (CHAH; http://www.chah.gov.au/). At the regular meetings for these organisations, formal and informal hands-on workshops are critical for transfer of knowledge and skills among colleagues. Attending other specialised annual meetings in New Zealand can also foster upskilling in the latest molecular analysis techniques as well as collaboration with the wider evolutionary biology community (e.g. Annual New Zealand Phylogenomics Meeting http://www.math.canterbury.ac.nz/bio/events/; New Zealand Molecular Ecology Conference http://www.nzmolecol.org/). Unfortunately the Systematics Association of New Zealand (SYSTANZ; http://www.math.canterbury.ac.nz/bio/pages/SYSTANZ/) has not been active for some time, and the informal New Zealand Plant Radiation Network (NZPRN; https://nzprn.otago.ac.nz/NZPRN) does

not meet regularly; these organisations hold great promise for collaboration among systematists, but it seems that lack of time and resources in a small community, rather than a lack of interest, is what is currently holding them back from doing more.

In addition to professional organisations and annual conferences, New Zealand systematists can also come together in smaller groups to continue or start new collaborative projects, or to visit each other's institutions to learn and share expertise, or run a hands on workshop; this could also be expanded to include the greater Australasian/Pacific region. Although this does occur to some degree, currently there is a lack of investment, coordination and funding for taxonomic collections and research at the national and regional levels – as well as significant time and financial pressures at some institutions – preventing more of this type of collaboration from happening (Royal Society of New Zealand 2015). To this end, establishing a 'systematics collaborative mobility fund' to specifically fund New Zealand systematists to undertake such collaborative professional development and travel would be a step in the right direction. There is a precedent for such funding schemes for European systematists, e.g. the Biotechnology and Biological Sciences Research Council's (BBSRC) now defunct 'Systematics Initiatives' Collaborative Scheme for Systematics Research (Co-Syst) and Systematics and Taxonomy (SynTax), or the current EC-funded SYNTHESYS project (http://www.synthesys.info/). In New Zealand, the establishment of such a scheme could be a small but important part of the recommended creation of a nationally coordinated and financially supported 'whole-of-systems approach' to address investment, coordination, protection, stewardship, and training in New Zealand's biological collections and systematics research (Royal Society of New Zealand 2015).

As to international collaboration opportunities, there is very limited funding available to New Zealand systematists (e.g. in New Zealand: http://www.royalsociety.org.nz/programmes/funds/international/, and elsewhere: https://www.humboldt-foundation.de/web/home.html). And even when external funding is available, it may be difficult for many systematists to take advantage of such opportunities due to other institutional and work commitments. Instead, it is perhaps more common that international colleagues come to New Zealand for meetings, training, upskilling, field work, sabbaticals and other collaborative activities, and this should continue to be encouraged and supported by New Zealand systematists and their institutions. Nevertheless, there are examples of New Zealand systematists going overseas for upskilling. For example, I received an Experienced Researcher Fellowship from the Alexander von Humboldt Foundation in 2012 to work in Dirk Albach's lab at the University of Oldenburg, Germany for 18 months. I was fortunate that I had the support of my family, colleagues and employer to take on what was a highly rewarding experience and collaboration which still continues today. I recently pieced together travel funding from several sources to return to Europe on a short trip to reconnect with my European colleagues and attended two international conferences, which provided some much needed and highly productive face-to-face meetings (http://blog.tepapa.govt.nz/2016/10/12/botany-travels/). Prior to that, in 2004, receiving funding for two years through the United States National Science Foundation International Postdoctoral Research Fellowship (https://www.nsf.gov/od/oise/iprffapp.jsp) was vital in helping me establish my systematics career and collaborative networks in New Zealand. No doubt there are many other examples of New Zealand systematists and their institutions benefitting from such international exchanges, and in general they are taking advantage of such opportunities as best they can, given current funding and capability constraints. Critically, institutions and government must support and invest in new resources and programmes to create more possibilities for current and future systematists (Royal Society of New Zealand 2015).

## Conclusions

Systematics is an exciting, challenging, dynamic, and important science, which combines new and traditional methods to discover and delimit species, and address relevant evolutionary questions. Integrative systematics uses comparative analyses of multiple data sets to robustly test species limits in a statistical framework. Ideally such a framework would include quantitative co-analyses of genetic data together with data from morphology, geographical distribution, chromosomes, anatomy, microscopy, and other data sets. Systematists are increasingly incorporating new methods into their integrative research toolkit, including next-generation sequencing, which require significant computer resources, training and upskilling for bioinformatics and data analysis. Collaboration is also critical for integrative and next-generation systematics research, and systematists, institutions, professional societies and government can and should foster more exchanges within New Zealand as well as with Pacific and Australasian nations and beyond. I argue that the current and future way forward for systematists to effectively and confidently resolve taxonomically challenging groups is by using integrative, next-generation and collaborative systematics, and that such an approach is critical in New Zealand.

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