



Extrapolations from field studies and known faunas converge on dramatically increased estimates of global microgastrine parasitoid wasp species richness (Hymenoptera: Braconidae)

JOSEPHINE J. RODRIGUEZ,¹ JOSE L. FERNÁNDEZ-TRIANA,^{2,3}
M. ALEX SMITH,² DANIEL H. JANZEN,⁴ WINNIE HALLWACHS,⁴
TERRY L. ERWIN⁵ and JAMES B. WHITFIELD⁶

¹National Center for Ecological Analysis and Synthesis (NCEAS), University of California, Santa Barbara, CA, USA, ²Department of Integrative Biology and The Biodiversity Institute of Ontario, University of Guelph, Guelph, ON, Canada, ³Canadian National Collection of Insects, Ottawa, ON, Canada, ⁴Department of Biology, University of Pennsylvania, Philadelphia, PA, USA, ⁵Department of Entomology, Smithsonian Institution, National Museum of Natural History, Washington, DC, USA and ⁶Department of Entomology, University of Illinois, Urbana, IL, USA

Abstract. 1. We extrapolate a new range of estimates of the species richness of Microgastrinae (Hymenoptera: Braconidae) wasps, a diverse group of small parasitoids that attack caterpillars of Lepidoptera.

2. Our estimates, using an array of focal study faunas to provide reasonable bounds for minimum and maximum values, range from 17 000 to 46 000+ species. These calculations make use of a geographically relatively constant proportion of the total number of local caterpillar species to species of Microgastrinae, and extend what is known from better studied areas to those less thoroughly studied.

3. This new estimate of species richness for Microgastrinae is 8–20 times that of the ~2000 currently described species, and 2–10 times greater than that of previously published estimates.

Key words. Biodiversity, extrapolation, lepidoptera, microgastrinae, parasitism, parasitoid wasps, species richness.

Introduction

Microgastrinae (Braconidae) is a hyperdiverse and globally ubiquitous subfamily of parasitoid wasps, commonly encountered as pupae or prepupae encased in white silk cocoons on or near the dead or dying bodies of their host caterpillars. All Microgastrinae are obligate endoparasitoids of larval Lepidoptera (butterflies and moths), and have a significant long-term physiological interaction with their hosts (koinobionts *sensu* Askew & Shaw, 1986), in part mediated by a symbiotic relationship with braco-

viruses (Strand & Burke, 2012). There is a tendency for species that attack large caterpillars ('macrolepidoptera') to develop in large broods ('gregarious' species), whereas those that attack small, mostly concealed, caterpillars develop one per host ('solitary' species), but there are some exceptions. In terms of diversity, the group is the most important single wasp group of parasitoids of caterpillars. Microgastrine wasps have garnered attention as biological control agents of pest Lepidoptera (Whitfield, 1997) and ecological studies of tropical host-specificity (Smith *et al.*, 2008), and in assessing insect diversity in various ecosystems such as mixed hardwood forests under different management regimes (Lewis & Whitfield, 1999), endangered tallgrass prairies (Whitfield & Lewis, 2001), and subarctic ecosystems undergoing climate change (Fernández-Triana *et al.*, 2011). These studies depend

Correspondence: James B. Whitfield, Department of Entomology, University of Illinois, 320 Morrill Hall, 505 S. Goodwin Ave., Urbana, IL 61801, USA. E-mail: jwhitfie@life.illinois.edu

on accurate species identification. Microgastrine wasps, however, are a taxonomically challenging group, with identification hindered by the difficulties imposed by morphological homogeneity, small body size and exceptional species richness (Smith *et al.*, 2008). There are ~2000 described species (Yu *et al.*, 2005), but as small-bodied parasitoid wasps, the group is likely to be severely under-described, as is the case with many groups of insect parasitoids (Quicke, 2012).

Previous published estimates of the number of species of Microgastrinae range from 4000 to 5500 species (Jones *et al.*, 2009) to ~10 000 (Mason, 1981). Mason (1981) used museum records to extrapolate the existence of 5000–10 000 species based on the ~1500 species then described, reclassified into 51 genera. Dolphin and Quicke (2001) used two methods to extrapolate the species richness of Braconidae (including Microgastrinae), the first using rates of description over time, the second using geographical distributions of species in two well surveyed groups, butterflies and (primarily) mammals. The results from the different sources of comparison differed strongly, but varied from 4178 species (using rates of description) to 3617 (using mammal distribution). More recently, Jones *et al.* (2009) used taxonomic revision data to arrive at their species estimates (arriving at an estimate of 3900–5500 species for Microgastrinae). Their analysis recognised the limitations of taxonomic revision data for projecting absolute species richness, but it has the strength that the data (both in terms of previously and of newly described species) are solid. But, many very recent morphology-based taxonomic revisions, especially those that integrate with molecular data (e.g. DNA barcoding) and/or host rearing data, have revealed extensive numbers of cryptic species (e.g. Smith *et al.*, 2008, 2009; Fernández-Triana, 2010; Fernández-Triana *et al.*, 2011), suggesting that even Mason's projected world total is a severe underestimate.

A perspective on actual species richness can be provided from well studied microgastrines in the context of their host caterpillars. An exceptionally well studied fauna of Microgastrinae is in Area de Conservación Guanacaste (ACG), north-western Costa Rica, where many of the microgastrines known are reared from wild-caught hosts as part of the ACG caterpillar, plant and parasitoid inventory (e.g. Smith *et al.*, 2008; Janzen *et al.*, 2009, 2011; Sharkey *et al.*, 2011). Almost 800 species of Microgastrinae (J. Fernandez-Triana, J. B. Whitfield, M. A. Smith, D. H. Janzen, W. Hallwachs, A. R. Deans and J. J. Rodríguez, unpubl. data) have already been recovered from ACG, where ~5000 species of caterpillars have been reared (Janzen & Hallwachs, 2011) and sampled for parasitisation. The continued rearing of microgastrines from ACG caterpillars further supports the high specialisation of Microgastrinae as reported by Smith *et al.* (2008).

Undoubtedly, more microgastrine wasps are yet to be reared from caterpillars, as there are estimated to be ~15 000 species of caterpillars in ACG (Janzen & Hallwachs, 2011; DHJ and WH, using information from Janzen & Hallwachs, 2012). Given that so many of the ~15 000

ACG caterpillar species remain to be reared for adults and parasitoids, how many species of microgastrine wasps are there? More broadly, given that there are estimated to be upwards of 500 000 species of caterpillars worldwide (Kristensen *et al.*, 2007), how many more species of microgastrine wasp are there?

A key ratio for estimation

Comparing the number of Lepidoptera species to species of Microgastrinae, the L/M ratio, was used by Fernández-Triana (2010) to estimate 550 species of Microgastrinae in Canada and Alaska, more than double the 225 known species. He calculated the L/M ratio for three regions in Canada that had well-known Microgastrinae and Lepidoptera faunas and found the average of the resulting quotients was 12. He interpreted this as, on average, for every 12 species of Lepidoptera there is one microgastrine species. Using 12 as the quotient and 6700 (number of Lepidoptera species in Canada/Alaska) as the dividend, Fernández-Triana solved for the divisor. The divisor, 550, represented the estimated number of microgastrines in Canada/Alaska.

Goals of the present study

The present work extends the use of Fernández-Triana's L/M ratios to provide additional estimates of total diversity using L/M ratios from several well studied and more geographically disparate geographical areas. To facilitate microgastrine species identification, this study also makes use of extensive preliminary genetic sampling using standardised genetic markers (DNA barcodes) (Hajibabaei *et al.*, 2007). Currently there are 20 000+ DNA microgastrine barcodes that is unprecedented for a group of parasitoid wasps (Quicke *et al.*, 2012; M. A. Smith, J. L. Fernández-Triana, E. Eveleigh, J. Gómez, C. Guclu, W. Hallwachs, P. Hebert, J. Hrccek, J. Huber, D. Janzen, P. Mason, S. Miller, D. L. J. Quicke, J. J. Rodríguez, R. Rougerie, M. R. Shaw, G. Varkonyi, D. Ward, J. B. Whitfield, A. Zaldivar-Riveron, unpubl. data). Here we provide what we believe to be – realistic estimates of the total species of Microgastrinae. The main goal is to provide reasonable upper and lower bounds for species richness of Microgastrinae based on extrapolation from extensive field data from multiple sites, rather than to attempt a single estimate based on highly limited data.

Methods

We extrapolate the diversity of Microgastrinae in the context of all possible microgastrine hosts – the world fauna of Lepidoptera – because essentially all recorded hosts of Microgastrinae are Lepidoptera caterpillars. The numbers used to represent species of Lepidoptera are 160 000

described species (Footitt and Adler, 2009), and two estimates of total diversity: 300 000 (Footitt and Adler, 2009) and 500 000 (Kristensen *et al.*, 2007). We suspect that the latter will be found to be closer to reality once the same methods of integrated morphological and molecular study have been applied to Lepidoptera as are being applied to Microgastrinae discussed here. Described species of Lepidoptera and Microgastrinae from eleven particularly well studied areas were extracted, to establish the distribution of the proportion of Lepidoptera to Microgastrinae (L/M) (Table 1).

We then follow two approaches in extrapolating the diversity of Microgastrinae:

- 1 We use the percentage of the world fauna of Lepidoptera that is estimated to occur in three well studied areas (Ottawa, Canada; British Isles; and ACG, north-western Costa Rica. It is then assumed that Microgastrinae in those areas represent similar percentages of the world fauna, within similar relative bounds of vari-

ation. Although the L/M ratio does (as expected) vary geographically, the variation in this value is surprisingly limited from site to site, (with an average and standard deviation of 16.4 ± 7.6), so that the microgastrine species richness values calculated by extrapolation from them are not likely to be wildly off, especially when the variation is taken into account.

- 2 We use the proportion of Lepidoptera/Microgastrinae species (L/M) from several areas of the world where both groups are reasonably well known (Table 1) to calculate the expected total of Microgastrinae species based on the number of currently described Lepidoptera species and the two estimates of total Lepidoptera species richness (as above).

Results

The estimated species richness of Microgastrinae, as calculated by extrapolation from Lepidoptera species numbers (Table 2), obviously depends upon the species richness of Lepidoptera. There is obviously also an element of under-description of Microgastrinae relative to Lepidoptera (even in well studied regions) that might also show a geographical pattern, but this cannot be accurately estimated without knowing the full diversity of Microgastrinae (which we are estimating). We have to assume that such a possible pattern of underdescription does not bias our estimates in any strong systematic fashion.

On the basis of the number of currently described Lepidoptera species, we estimate that 11 540–13 650 species of wasps exist. Using the proportion of Lepidoptera/Microgastrinae species (Table 3), the estimated total species richness of Microgastrinae was 10 060, using only the 160 000 described Lepidoptera species.

On the basis of the estimated numbers of Lepidoptera species, we obtain a value between 21 430 and 46 400 species of wasps. Again, using the proportion of Lepidoptera/Microgastrinae species (Table 3), we obtained a total of between 18 870 and 31 450 species. There were a few outliers from the values calculated using different geographical areas as a basis for extrapolation. The outliers at both extremes seemed to be from Arctic and subarctic regions, where we expect that more than one species of wasp are using a single caterpillar species (the reverse of tropical data).

Discussion

Both approaches rendered similar results when estimating the species richness of Microgastrinae, although the first method (21 430–46 400 spp.) demonstrated higher variability as well as higher estimates than the second (18 870–31 450). The second approach seems to us to be more accurate, and it suggests a rather similar ratio of Lepidoptera/Microgastrinae (mostly ranging from 10 to 20/1) regardless

Table 1. Proportion of Lepidoptera and Microgastrinae in several geographical areas. The highest and lowest values of L/M are in bold. For Lepidoptera, the numbers of estimated total (not estimated described) species are taken from Danks (1981) for the Canadian Arctic Archipelago; personal communication from CNC lepidopterists for Churchill (unpubl. data based on ongoing studies); Lafontaine and Wood (1997) for Ottawa; Lafontaine and Wood (1997) for the Yukon Territory; Fauna Europaea (2010) for British Isles, Germany, Hungary, Russia and Sweden; D. Janzen & W. Hallwachs (unpubl. data based on ongoing studies) for Area de Conservacion Guanacaste, north-western Costa Rica; Dugdale (1988) for New Zealand. For Microgastrinae, the numbers are taken from Fernández-Triana (2010) and Fernández-Triana *et al.* (2011) for all Canadian regions and localities; Yu *et al.* (2005) for Palaearctic countries; Janzen *et al.*, 2009, D. Janzen & W. Hallwachs (unpubl. data based on ongoing inventory for Area de Conservación Guanacaste, north-western Costa Rica; J. Fernández-Triana & D. Ward for New Zealand (unpubl. data based on ongoing studies).

	Lepidoptera spp. (L)	Microgastrinae spp. (M)	L/M
Canadian Arctic Archipelago	136	20	6.8
Churchill, Canada	500	79	6.3
Ottawa, Canada	2070	150	13.8
Yukon Territory, Canada	2000	100	20.0
British Isles	2700	232	11.6
Germany	3532	248	14.2
Hungary	3580	316	11.3
Russia	8879	291	30.5
Sweden	2855	117	24.4
ACG, Costa Rica	15 000	800	18.75
New Zealand	1761	80	22.3
Average \pm Standard deviation	–	–	16.4 ± 7.6

Table 2. Calculations of Microgastrinae species richness based on data from Lepidoptera species. Highest and lowest values are in bold. In the case of Ottawa and the British Isles, the numbers for Lepidoptera and Microgastrinae are based on the known (described) species; although in the case of ACG, most of the species do not have a formal name yet – but have been recognised using DNA barcoding and biology data and have received interim names pending further taxonomic reviews.

	Ottawa	British Isles	ACG
Latitudinal gradient (area km ²)	45°N (8000)	49–59°N (245 000)	11°N (16)
Species of Lepidoptera in the area	2070	2700	15 000
Species of Microgastrinae in the area	150	232	800
(1)% of the world species of Lepidoptera as currently known (Footitt and Adler, 2009)	1.3	1.7	9.4
(2)% of the world spp. of total Lepidoptera estimated by Footitt and Adler (2009)	0.7	0.9	5.0
(3)% of the world spp. of total Lepidoptera estimated by Kristensen <i>et al.</i> (2007)	0.4	0.5	3.0
(4) # of expected world spp. of Microgastrinae	11 540	13 650	8510
(5) # of expected world spp. of Microgastrinae	21 430	25 780	16 000
(6) # of expected world spp. of Microgastrinae	37 500	46 400	26 670

(1), (2), (3) – The number of world Lepidoptera spp. was: (1) – 160 000 currently known species (Footitt and Adler, 2009), (2) – 300 000 estimate (Footitt and Adler, 2009), and (3) – 500 000 estimate (Kristensen *et al.*, 2007). Values were calculated as: # of Lepidoptera in a particular area/# of World Lepidoptera × 100% [e.g. for row (1) and Ottawa area the calculation would be 2070 species/160 000 species × 100% = 1.3%]. (4), (5), (6) – Values calculated as: # of known Microgastrinae spp. in a particular area/% of world spp. of Lepidoptera in the particular area × 100%. [e.g. for row (1) and Ottawa area]. The percentages of the global species of Lepidoptera in a particular area were taken from rows (1), (2) and (3).

Table 3. Estimated species of Microgastrinae based on L/M values from Table 1 and three values of Lepidoptera species richness. Highest and lowest values are in bold. The currently known number of Lepidoptera species and Estimate 1 were taken from Footitt and Adler (2009). Estimate 2 was taken from Kristensen *et al.* (2007).

	Lep. known (160 000 spp.)	Estimate 1 (300 000 spp.)	Estimate 2 (500 000 spp.)
Lowest L/M (6.3)	25 400	47 620	79 360
Highest L/M (30.5)	5250	9840	16 390
Average L/M (16.4)	9760	18 290	30 490

of the geographical area of the two groups. It will be instructive to determine whether similar ratios are the norm globally. If so, that could allow prediction of the sizes of local faunas of Microgastrinae based on (much better known) Lepidoptera, and might have significant implications for discussion of latitudinal species richness trends in herbivorous insects (Novotny *et al.*, 2006; Dyer *et al.*, 2007) and their parasitoids (e.g. Janzen & Pond, 1975; Gauld *et al.*, 1992; Quicke *et al.*, 2012). A remaining issue is the extent to which the described diversity of Lepidoptera is representative of the total diversity, in ecological terms.

From the extrapolations made here, the richness of Microgastrinae seems to be 8–20 times greater than the total currently described in the literature of ~2000 species

(Yu *et al.*, 2005). Our results are 2–10 times higher than those of the Jones *et al.* (2009) estimates of 3900–5500 species and the Mason (1981) estimates of 5000–10 000 species. Although our estimates might seem extreme relative to these earlier species richness estimates, they are more in line with the relatively non-asymptotic species accumulation curves from recent field studies (e.g. from the ACG Inventory in north-western Costa Rica (Smith *et al.*, 2008) and D. Janzen & W. Hallwachs unpubl. data; and from Churchill, Manitoba, Canada (Smith *et al.*, 2009; Fernández-Triana *et al.*, 2011).

Why are our results so different from those of Jones *et al.* (2009)? At first glance, it may appear obvious that extrapolations based on different sources of data can easily arrive at markedly different totals. The answer as to exactly why this is so, appears to lie in what the two studies were attempting to estimate.

Jones *et al.* (2009) compared species richness in genera before and after recent comprehensive revisions and asked the question (paraphrased from their study): if all braconid genera were to be revised in the same manner as previous revisions, what would be the resulting total number of species? (they went on to pose further questions about regional and body size patterns in ‘underdescription’, including the impact of small body size). The answer to their main question can be taken to be an estimate of total braconid species richness *if* it is possible to assume that (a) comprehensive morphology-based taxonomic revisions produce relatively complete species richness data, and, as a partial corollary, (b) the morphospecies that are recognised in revisionary work thoroughly capture the species richness of a group. In addition, it assumes that

Microgastrinae have been relatively well collected. There are several reasons to believe that both assumptions (a) and (b) can be seriously violated in species-rich groups of relatively tiny organisms, in ways that will be familiar to most if not all revisionary taxonomists (as indeed it was to Jones *et al.*, 2009) and as are portrayed unambiguously in Smith *et al.* (2007, 2008).

First, the material assembled in museum collections, and therefore the base from which museum taxonomists work, does not (yet) represent the world's full species richness, especially in megadiverse regions. To take Microgastrinae as an example, the number of available specimens in museums numbers in the many hundreds of thousands. These specimens surely represent a significant slice of the world diversity in the group, but given that a disproportionate number of the specimens have come from more well studied (and often less species rich) faunas, and are collected by classical methods that sample only a limited portion of the biodiversity in a place (such as Malaise traps), it is clear that a major proportion of the thousands of existing species will still not have been examined, even if all world collections are studied. For example, Erwin *et al.* (2005) reported an estimate of 100 000+ species of insects and their relatives in a single hectare of equatorial rainforest in the western Amazon Basin. Given that the Amazon Basin is poorly known, and that it encompasses 17 billion hectares, the number of microgastrines to be discovered there will presumably be enormous.

Second, revisionary taxonomists reasonably do not attempt to describe and name new species from single, seemingly 'different', specimens (so-called 'singletons') unless the latter are accompanied by additional data that can be used to justify the recognition of a new species, or unless the differences are 'extreme'. Taxonomic revisions of species-rich genera, especially in previously understudied regions, routinely leave out a significant number of apparent additional species due to paucity of the sample, or poor quality of seemingly conspecific specimens. Thus, even a comprehensive recent revision may reflect only the better understood, or better sampled species. In hyperdiverse taxonomic groups, field samples, characteristically obtained by short-term collecting trips, tend to be extremely rich in singleton species, only some of which will be recovered again in other samples. For example, a recent update on the Microgastrinae from Canada and Alaska (Fernández-Triana, 2010) increased the known number of species by 50%, yet still left as many as 50% or more of the species unregistered until they are better understood.

Third, most large species-rich genera contain taxonomically difficult complexes of 'cryptic' species that classical taxonomic studies do not easily resolve without including genetic or natural history data. As an example, Smith *et al.* (2008) were able to combine DNA sequence data (mostly COI and in difficult cases supplemented with ITS and 28S data), host caterpillar and food plant data, and morphospecies assignments provided by specialists on the groups, to arrive at a total number of species (313) in only six genera of Microgastrinae found in the rearing

inventory of the ACG in Costa Rica (e.g. Janzen *et al.*, 2009). They found that 74% of the 171 morphospecies delineations corresponded exactly to species that were recognised after consideration of the combined data, but the remainder comprised complexes of what appear to be morphologically similar, yet genetically and biologically distinct species. Although we suspect that further detailed examination would often encounter diagnostic morphological characters for these apparently 'cryptic' species, it is clear that standard revisionary work will often fail to distinguish all of the species in a sample. This is a simple reflection of the fact that morphology alone may not always be adequate to discriminate species.

According to Jones *et al.* (2009), the estimated number of microgastrines would be about twice of that currently described (row # 1 of Table 4); that is the final figure would represent an increase of 1.9-fold compared to the present values. If those calculations are reasonable, then a similar increase could be expected from studies integrating morphological and molecular approaches (rows # 2–6 of Table 4), but this is not the case. Table 4 displays much greater increases in the number of species than those predicted if the assumption of Jones *et al.* (2009) would hold true. The values ranged between a 1.7 and 12.1-fold increase. The figure is at the low end in the only temperate area shown (1.7-fold for Canada/Alaska), yet for tropical areas the increase is much higher, averaging almost seven times more than the species currently known there.

The final numbers of species will likely be even higher, because in all cases we took the lowest of the values of potential increase. For example, when calculating the figures for the Arabian Peninsula, the updated values came

Table 4. Species of Microgastrinae currently known (described species) and updated total diversity, as shown by published and/or ongoing studies combining morphology and molecular approaches. Current numbers of species are from Yu *et al.* (2005); except for Costa Rica where we follow Whitfield's (1995) estimate of 200 species (based on examination of 2500 specimens). Updated figures are from: (1) – Jones *et al.* (2009); (2) – J. Fernández-Triana & H. Goulet (unpubl. data based on ongoing studies); (3) – Fernández-Triana (2010); (4) – Smith *et al.*, 2008; J. J. Rodríguez & D. H. Janzen, unpubl. data; (5) – J. Fernández-Triana & D. Ward (unpubl. data based on ongoing studies); (6) – Barcoding of Life Data systems (www.boldsystems.org/). The Arabian Peninsula is regarded here as all countries south of 30°N (i.e. including Israel and Jordan).

Species of microgastrines	Currently known	Updated figures	Increase
1. World	2067	4025 (1)	1.9
2. Arabian Peninsula	39	98 (2)	2.5
3. Canada and Alaska	135	225 (3)	1.7
4. Costa Rica	200	800 (4)	4.0
5. New Zealand	18	85 (5)	4.5
6. Thailand	17	205 (6)	12.1

only from a very reduced area (Oman, Yemen and UAE), yet still were compared with the total known species from all countries south of 30°N within the peninsula (i.e. a very expanded Arabian Peninsula that even included Israel and Jordan). This means that the calculated proportional increase is lower than the likely true increase. Likewise, for Costa Rica, we show updated figures from only 2% of the country (Area de Conservación Guanacaste contains 1250 km² of terrestrial habitat. The whole country probably has 20 000+ species of Lepidoptera and is 50 000 km²). As for the updated figures, these are also far from complete for Thailand, New Zealand and Canada/Alaska. Taxonomic studies currently underway are expected to significantly increase the final richness estimates for those regions (already the available data have exceeded a 1.9× increase in richness).

A recent article by Mora *et al.* (2011) estimates the total number of species on Earth and discusses the limitations of using ratios between taxa, as we have done, to estimate global numbers of species. The two main limitations they highlight are (i) locally estimated ratios among taxa may not be consistent at a global scale and (ii) at least one of the taxa should be well known at the global scale. Although we cannot totally eliminate either of these limitations for our study, we are confident that our figures are at least reasonably accurate because (i) we have a variety of locally estimated ratios that actually *are* rather consistent with one another despite ranging from tropical through temperate to arctic habitats, and (ii) the Lepidoptera are about as well known as can be obtained for an insect order at a global scale. Unlike Mora *et al.* (2011) and most previous estimation studies, we do not 'scale up' from our focus on microgastrine parasitoid wasps to the entire global parasitoid fauna and/or flora (see Erwin, 2004).

Comparison of the totals estimated by Jones *et al.* (2009) with those calculated by us highlights the kinds of uncertainties we face in obtaining an accurate species richness total for Microgastrinae. Use of taxonomic revision data allowed for greater precision and control over the estimation methods, but at the expense of using taxonomically undersampled data as a basis for extrapolation. Our approach allows us to estimate the actual global species richness totals from more representative samples, but at the expense of having to use cruder methods and data for extrapolation.

The sheer diversity remaining to be described is a sober reminder for parasitoid wasp taxonomists. But, in terms of advancing our comparative knowledge of parasitoid wasp biology and ecology, it is likely that a focus on describing the species (using both molecular and morphological approaches when possible) currently with some associated natural history knowledge (this still includes many hundreds of undescribed species) is a better use of the limited resources available than attempting to find and describe all species present in the environment. The latter approach would require field sampling (mass collecting) at least an order of magnitude more comprehensive than that attempted to date.

Acknowledgements

JJR was supported by the National Center for Ecological Analysis and Synthesis, a Center funded by U.S. N.S.F. (Grant #EF-0553768), the University of California, Santa Barbara, and the State of California and NSF Doctoral Dissertation Enhancement Program award OISE-0809175. JBW was supported by U.S. N.S.F. grants DEB 1020510 and U.S. Department of Agriculture grant 2009-35302-05250. JFT and laboratory analyses on sequences generated since 2009 were funded by the Government of Canada through Genome Canada and the Ontario Genomics Institute (2008-0GI-ICI-03). MAS was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant. DHJ and WH were supported by U.S. N.S.F. grants BSR 9024770 and DEB 9306296, 9400829, 9705072, 0072730, and 0515699, and grants from the Wege Foundation, International Conservation Fund of Canada, Jessie B. Cox Charitable Trust, Blue Moon Fund, Guanacaste Dry Forest Conservation Fund, Area de Conservación Guanacaste, and University of Pennsylvania.

References

- Askew, R.R. & Shaw, M.R. (1986) Parasitoid communities: their size, structure and development. *Insect Parasitoids* (ed. by G. Waage and D. Greathead), pp. 225–263. Academic Press, London, UK.
- Danks, H.V. (1981) *Arctic Arthropods: A Review of Systematics and Ecology with Particular Reference to the North American Fauna*. Entomological Society of Canada, Ottawa, Ontario.
- Dolphin, K. & Quicke, D.L.J. (2001) Estimating the global species richness of an incompletely described taxon: an example using parasitoid wasps (Hymenoptera: Braconidae). *Biological Journal of the Linnean Society*, **73**, 279–286.
- Dugdale, J.S. (1988) Lepidoptera – annotated catalogue and keys to family group taxa. *Fauna of New Zealand*, **14**, 264.
- Dyer, L.A., Singer, M.S., Lill, J.T., Stireman, J.O., Gentry, G.L., Marquis, R.J., Ricklefs, R.E., Greeney, H.F., Wagner, D.L., Morais, H.C., Diniz, I.R., Kursar, T.A. & Coley, P.D. (2007) Host specificity of Lepidoptera in tropical and temperate forests. *Nature*, **448**, 696–700.
- Erwin, T.L. (2004) The biodiversity question: how many species of terrestrial arthropods are there? *Forest Canopies* (ed. by M. D. Lowman and H. Bruce Rinker), 2nd edn., pp. 259–269. Elsevier Academic Press, San Diego, California.
- Erwin, T.L., Pimienta, M.C., Murillo, O.E. & Aschero, V. (2005) Mapping patterns of β -diversity for beetles across the western Amazon Basin: a preliminary case for improving conservation strategies. *Proceedings of the California Academy of Sciences*, Ser. 4, **56** (Suppl. I), 72–85.
- Fauna Europaea (2010) *Fauna Europaea Version 2.4*. <<http://www.faunaeur.org>> 7th November 2010.
- Fernández-Triana, J. (2010) Eight new species and an annotated checklist of Microgastrinae (Hymenoptera: Braconidae) from Canada and Alaska. *Zookeys*, **63**, 1–53.
- Fernández-Triana, J., Smith, M.A., Boudreault, C., Goulet, H., Hebert, P., Smith, A.C. & Roughley, R. (2011) A poorly known high-latitude parasitoid wasp community: unexpected

- diversity and dramatic changes through time. *PLoS ONE*, **6**, e23719.
- Footitt, R.G. & Adler, P.H. (eds.) (2009) *Insect Biodiversity: Science and Society*. Wiley – Blackwell, Hoboken, New Jersey.
- Gauld, I., Gaston, K. & Janzen, D. (1992) Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the 'nasty' host hypothesis. *Oikos*, **65**, 353–357.
- Hajibabaei, M., Singer, G.A.C., Hebert, P.D.N. & Hickey, D.A. (2007) DNA barcoding: how it complements taxonomy, molecular phylogenetics and population genetics. *Trends in Genetics*, **23**, 167–172.
- Janzen, D.H. & Hallwachs, W. (2011) Joining inventory by parataxonomists with DNA barcoding of a large complex tropical conserved wildland in Northwestern Costa Rica. *PLoS ONE*, **6**, e18123.
- Janzen, D.H. & Hallwachs, W. (2012) *Event-based database of caterpillars, their food plants, and their parasitoids in Area de Conservación Guanacaste, northwestern Costa Rica*. <<http://janzen.sas.upenn.edu>> 31st May 2012.
- Janzen, D.H., Hallwachs, W., Blandin, P., Burns, J.M., Cadiou, J.-M., Chacon, I., Dapkey, T., Deans, A.R., Epstein, M.E., Espinoza, B., Franclemont, J.G., Haber, W.A., Hajibabaei, M., Hall, J.P.W., Hebert, P.D.N., Gauld, I.D., Harvey, D.J., Hausmann, A., Kitching, I.J., LaFontaine, D., Landry, J.-F., Lemaire, C., Miller, J.Y., Miller, J.S., Miller, L., Miller, S.E., Montero, J., Munroe, E., Green, S.R., Ratnasingham, S., Rawlins, J.E., Robbins, R.K., Rodriguez, J.J., Rougerie, R., Sharkey, M.J., Smith, M.A., Solis, M.A., Sullivan, J.B., Thiaccourt, P., Wahl, D.B., Weller, S.E., Whitfield, J.B., Willmott, K.M., Wood, D.M., Woodley, N.E. & Wilson, J.J. (2009) Integration of DNA barcoding into an ongoing inventory of tropical complex biodiversity. *Molecular Ecology Resources*, **9** (Suppl. 1), 1–26.
- Janzen, D.H., Hallwachs, W., Burns, J.M., Hajibabaei, M., Bertrand, C. & Hebert, P.D.N. (2011) Reading the complex skipper fauna of one tropical place. *PLoS ONE*, **6**, e19874.
- Janzen, D.H. & Pond, C.M. (1975) A comparison by sweep sampling of the arthropod fauna of secondary vegetation in Michigan, England, and Costa Rica. *Transactions of the Royal Entomological Society of London*, **127**, 33–50.
- Jones, O.R., Purvis, A., Baumgart, E. & Quicke, D.L.J. (2009) Using taxonomic revision data to estimate the geographic and taxonomic distribution of undescribed species richness in the Braconidae (Hymenoptera: Ichneumonoidea). *Insect Conservation and Diversity*, **2**, 204–212.
- Kristensen, N.P., Scoble, M.P. & Karsholt, O. (2007) Lepidoptera phylogeny and systematics: the state of inventorying moth and butterfly diversity. *Zootaxa*, **1668**, 699–747.
- Lafontaine, J.D. & Wood, D.M. (1997) Butterflies and moths (Lepidoptera) of the Yukon. *Insects of the Yukon* (ed. by H.V. Danks and J.A. Downes), pp. 723–785. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Ontario.
- Lewis, C.N. & Whitfield, J.B. (1999) Braconid wasp (Hymenoptera: Braconidae) diversity in forest plots under different silvicultural methods. *Environmental Entomology*, **28**, 986–997.
- Mason, W.R.M. (1981) The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): a phylogeny and reclassification of Microgastrinae. *Memoirs of the Entomological Society of Canada*, **155**, 1–147.
- Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G.B. & Worm, B. (2011) How many species are there on Earth and in the ocean? *PLoS Biology*, **9**, 1–8.
- Novotny, V., Drozd, P., Miller, S.E., Kulfan, M., Janda, M., Basset, Y. & Weiblen, G.D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science*, **313**, 1115–1118.
- Quicke, D.L.J. (2012) We know too little about parasitoid wasp distributions to draw any conclusions about latitudinal trends in species richness, body size and biology. *PLoS ONE*, **7**, e32101.
- Quicke, D.L.J., Smith, M.A., Janzen, D.H., Hallwachs, W., Fernandez-Triana, J., Laurene, N.M., Zaldivar-Riveron, A., Shaw, M.R., Broad, G.R., Klopstein, S., Shaw, S.R., Hreck, J., Hebert, P.D.N., Miller, S.E., Rodriguez, J.J., Whitfield, J.B., Sharkey, M.J., Sharanowski, B.J., Jussila, R., Gauld, I.D. (deceased), Chesters, D. & Vogler, A. (2012) Utility of the DNA barcoding gene fragment for parasitic wasp phylogeny (Hymenoptera: Ichneumonoidea): data release and new measure of taxonomic congruence. *Molecular Ecology Resources*, **12**, 676–685.
- Sharkey, M.J., Clutts, S., Tucker, E.M., Janzen, D.H., Hallwachs, W., Dapkey, T. & Smith, M.A. (2011) *Lytopylus* Forster (Hymenoptera, Braconidae, Agathidinae) species from Costa Rica, with an emphasis on specimens reared from caterpillars in Area de Conservación Guanacaste. *Advances in the Systematics of Fossil and Modern Insects: Honouring Alexandr Rasnitsyn* (ed. by D.E. Shcherbakov, M.S. Engel and M.J. Sharkey), *ZooKeys*, **130**, 379–419.
- Smith, M.A., Fernández-Triana, J., Roughley, R. & Hebert, P.D.N. (2009) DNA barcode accumulation curves for understudied taxa and areas. *Molecular Ecology Resources*, **9** (Suppl. 1), 208–216.
- Smith, M.A., Rodriguez, J.J., Whitfield, J.B., Deans, A.R., Janzen, D.H., Hallwachs, W. & Hebert, P.D.N. (2008) Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proceedings of the National Academy of Sciences of the USA*, **105**, 12359–12364.
- Smith, M.A., Wood, D.M., Janzen, D.H., Hallwachs, W. & Hebert, P.D.N. (2007) DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists. *Proceedings of the National Academy of Sciences of the USA*, **104**, 4967–4972.
- Strand, M.R. & Burke, G.R. (2012) Polydnviruses as symbionts and gene delivery systems. *PLoS Pathogens*, **8**, 1–4.
- Whitfield, J.B. (1997) Subfamily Microgastrinae. *Manual of the New World Genera of the Family Braconidae (Hymenoptera)* (ed. by R.A. Wharton, P.M. Marsh and M.J. Sharkey), *Special Publication of the International Society of Hymenopterists*, **1**, 333–364.
- Whitfield, J.B. (1995) Checklist of the Microgastrinae (Hymenoptera: Braconidae) in America north of Mexico. *Journal of the Kansas Entomological Society*, **68**, 245–262.
- Whitfield, J.B. & Lewis, C.N. (2001) Analytical survey of the braconid wasp fauna (Hymenoptera: Braconidae) on six mid-western U. S. tallgrass prairies. *Annals of the Entomological Society of America*, **94**, 230–238.
- Yu, D., van Achterberg, K. & Horstmann, K. (2005) *World Ichneumonoidea. Taxonomy, Biology, Morphology and Distribution. CD/DVD*. Taxapad, Vancouver, Columbia.

Accepted 21 September 2012

Editor: Simon R. Leather
Associate editor: Donald Quicke