



MINOR REVIEW

Latitudinal patterns in tachinid parasitoid diversity (Diptera: Tachinidae): a review of the evidence

ZELIA L. BURINGTON,¹ DIEGO JAVIER INCLÁN-LUNA,^{2,3} MARC POLLET^{4,5} and JOHN O. STIREMAN III^{1,2}  ¹Department of Biological Sciences, Wright State University, Dayton, OH, USA, ²Instituto Nacional de Biodiversidad, Sección Invertebrados, Quito, Ecuador, ³Facultad de Ciencias Agrícolas, Universidad Central del Ecuador, Quito, Ecuador, ⁴Research Institute for Nature and Forest (INBO), Brussels, Belgium and ⁵Entomology Unit, Royal Belgian Institute of Natural Sciences (RBINS), Brussels, Belgium

Abstract. 1. Insect parasitoids may be an exception to the typical biogeographic pattern of increasing species richness at lower latitudes exhibited by most taxa. Evidence for this ‘anomalous’ latitudinal gradient has been derived from observations of hymenopteran parasitoids and it has been argued that other parasitoid groups should show a similar pattern of diversity. Several mechanisms have been proposed to explain this disparity, most notably the nasty host and resource fragmentation hypotheses.

2. We review and evaluate these hypotheses with respect to tachinid flies (Diptera: Tachinidae), and bring to the argument evidence from eight trapping surveys from temperate and tropical regions in the Americas including the United States, Costa Rica, and Ecuador. We find no evidence that tachinid fly diversity is lower in the tropics than in the temperate region. Our results, along with other lines of evidence, rather suggest that New World Tachinidae likely conform to the same negative relationship between latitude and richness as their largely phytophagous host taxa.

3. We discuss geographic patterns of tachinid diversity in relation to ecological and evolutionary processes, and why they may differ from their hymenopteran parasitoid counterparts. Parasitoid taxa appear to vary strongly in their diversity responses to latitude and we concur with previous researchers that more survey data are necessary to reach strong conclusions about parasitoid latitudinal diversity patterns.

Key words. Flies, insect surveys, latitudinal diversity gradient, nasty host hypothesis, resource fragmentation hypothesis, tropical biodiversity, Hymenoptera, species abundance distribution.

Introduction

One of the most pervasive biogeographic patterns is the increase in species richness towards equatorial regions, regardless of taxon, geographic context, or geologic era (Stehli *et al.*, 1969; Hillebrand, 2004; Crame, 2001; Sax, 2001; Turner & Hawkins, 2004; Lomolino *et al.*, 2010). In a meta-study of analyses of latitudinal diversity gradients – including both animal and plant groups at multiple spatial and taxonomic scales – 71% of 135 studies found that species richness increased towards the tropics, and other patterns (decreases, mid-latitude peaks, and distinct pattern absent; ~10% each) were similarly represented (Willig *et al.*, 2003). This

general latitudinal diversity gradient is evident in many insect groups, including butterflies (Kocher & Willams, 2000), grasshoppers (Davidowitz & Rosenzweig, 1998), ants (Cushman *et al.*, 1993), scarab beetles (Lobo, 2000), leafhoppers (Yuan *et al.*, 2014), thrips (Wang *et al.*, 2014), and plant-feeding Hemiptera (Andrew & Hughes, 2005).

A much smaller number of taxa have been proposed to exhibit ‘anomalous’ or inverse latitudinal patterns of species richness. These groups exhibit a pattern in which species diversity declines towards the equator, often with a mid-latitude peak (Kindlmann *et al.*, 2007). Insect taxa that show such anomalous diversity gradients include aphids (Dixon *et al.*, 1987), sawflies (Kouki *et al.*, 1994), and stream-dwelling leaf shredders (e.g. Trichoptera, Plecoptera; Boyero *et al.*, 2011), among others.

An often cited example of anomalous diversity patterns are ichneumonid wasps, which were reported by Janzen (1981) to

Correspondence: *John O. Stireman III, Department of Biological Sciences, Wright State University, Dayton, Ohio 45435, USA. E-mail: john.stireman@wright.edu

show an apparent New World peak in diversity in the southern United States (42–35° N) and a decline towards Central America (<27° N). This observed departure from typical latitudinal trends has been identified in surveys of Ichneumonidae in other regions as well (Owen & Owen, 1974; Janzen & Pond, 1975; Heinrich, 1977; Skillen *et al.* 2000; Jones *et al.* 2012), and a similar pattern has been reported for North American Braconidae (Quicke & Kruff, 1995). Furthermore, studies of specific parasitoid communities (e.g. fig wasp parasitoids, Hawkins & Compton 1992 and *Leptopilina* (Figitidae) parasitoids of *Drosophila*, Lue *et al.* 2018) have also suggested inverse latitudinal gradients in diversity. It has been suggested that this pattern holds for parasitoids generally (Janzen, 1981; Gauld *et al.*, 1994). Nevertheless, recent studies have shown that some parasitoid taxa, including a number of ichneumonid groups (Sääksjärvi *et al.*, 2004; Veijalainen *et al.*, 2012; Timms *et al.*, 2016), exhibit more typical patterns of high tropical diversity, and it has been argued that our understanding of parasitoid distributions is still too limited to reach conclusions concerning broad latitudinal patterns (Quicke 2012; Gomez *et al.*, 2018).

Two major hypotheses have been forwarded to explain why parasitoids might exhibit anomalous latitudinal diversity patterns: the resource fragmentation hypothesis (Janzen, 1981) – also known as the common host hypothesis (Dixon *et al.*, 1987; Kindlmann, 1988) – and the nasty host hypothesis (Gauld *et al.*, 1992). The resource fragmentation hypothesis proposes that in highly diverse tropical communities, spatial fragmentation of host resources reduces the viability of specialist parasitoid populations. The rarity of individual host species and their patchiness in the landscape (Janzen, 1981), and the declining efficiency of host searching (Kindlmann, 1988), leads to a lower likelihood of parasitoids encountering preferred hosts and a corresponding increase in the likelihood of parasitoid extinction. The resource fragmentation hypothesis predicts that tropical latitudes will exhibit lower numbers of relatively specialised koinobiont species (parasitoids that allow their hosts to continue to feed and grow) and a higher frequency of more generalised idiobiont species (parasitoids that paralyse their hosts) (Kindlmann *et al.*, 2007).

The other primary explanation to explain why parasitoids may not be more diverse at tropical latitudes, the nasty host hypothesis, is related to the hypothesis that tropical plants tend to possess more diverse and higher concentrations of allelopathic secondary compounds than temperate plants (Levin, 1976; Coley & Aide, 1991; though see Marquis *et al.*, 2012). These secondary plant compounds may in turn be used by herbivorous insects for their own defence (Duffey *et al.*, 1986), resulting in chemically ‘nastier’ herbivores. Thus, in the tropics, parasitoids should experience more intense selection for adaptations to overcome or avoid these chemical defences, which should favour host-specialisation. As the resource fragmentation and nasty host hypotheses predict opposite, antagonistic selection pressures upon tropical parasitoids (either favouring or disfavouring greater host-breadth), the result should be a decline in parasitoid richness beyond mid-latitudes (Gauld *et al.*, 1994).

Several additional hypotheses have been forwarded that predict relatively lower diversity of tropical parasitoids, including greater predation on hosts in the tropics (Rathcke & Price,

1976), greater predation on adult parasitoids in the tropics (Gauld, 1987), and, more generally, intense ‘inter-phyletic competition’ in the tropics (i.e. competition with microorganisms and fungi; Eggleton & Gaston, 1990). These hypotheses have received somewhat less attention than the nasty host and resource fragmentation hypotheses (Quicke, 2014); however, parasitoid diversity patterns could potentially be affected by a combination of several or all of these processes.

Although originally formulated to explain patterns of ichneumonid wasp diversity, these hypotheses may apply to parasitoids in general. Thus, we might expect anomalous diversity patterns in other parasitoid lineages within the Hymenoptera, Diptera, and other orders (Janzen, 1981; Gauld *et al.*, 1992), including the parasitoid fly family Tachinidae (Diptera). Tachinids represent the most diverse lineage of insect parasitoids outside of the Hymenoptera (ca. 8500 described species; O’Hara, 2013) and they predominantly attack larvae of phytophagous insects that are likely to meet assumptions of the resource fragmentation and nasty host hypotheses (Stireman *et al.*, 2006). Indeed, it has been suggested that tachinid flies should ‘show an even more extreme pattern of reduced species richness with declining latitude than do the Ichneumonidae’ (Janzen, 1981) due to the high diversity of concealed hosts in the tropics that should be inaccessible to most tachinids, which lack piercing ovipositors to penetrate plant tissues.

On the other hand, there are several reasons why tachinid flies may not exhibit an anomalous latitudinal diversity pattern. The Neotropical region currently harbors the greatest diversity of described tachinid species (3088) of any biogeographic region, even the much larger Palaearctic (2112 spp.; O’Hara *et al.* 2020), and taxonomists have long considered there to be a great undescribed diversity of tropical (especially Neotropical) tachinid flies (Guimarães, 1971; O’Hara, 1989; Wood & Zumbado, 2010). Furthermore, it is not clear that tachinids should respond in the same way to resource fragmentation and “nasty hosts” as expected for parasitoid wasps. As parasitoids, tachinids fundamentally differ from Hymenoptera in multiple aspects of their life history (Feener & Brown, 1997; Stireman, 2016). For example, they tend to be more polyphagous than their koinobiont wasp counterparts and thus may suffer less from resource fragmentation. They may also be less sensitive to host physiological defences (Eggleton & Gaston, 1992; Stireman *et al.*, 2006), potentially relaxing constraints posed by chemically defended hosts. Finally, it may be that conclusions about anomalous diversity patterns in parasitoids generally have been premature. Growing evidence that a number of hymenopteran parasitoid taxa exhibit high tropical richness (Veijalainen *et al.*, 2013; Timms *et al.*, 2016) suggests that hypothesised constraints on diversity may be overcome. Based upon these considerations, we predict that tachinid flies should exhibit greater richness at tropical latitudes than in temperate areas and this should be evident at the level of local communities (i.e. alpha diversity).

Here, we evaluate this prediction of high tropical diversity by opportunistically using data from insect surveys to compare tachinid richness and diversity between sites in North America (Maryland, Ohio, Arizona), Central America (Costa Rica), and South America (Ecuador). We further examine evidence from the literature for anomalous diversity patterns in other parasitoid

taxa, evaluate the hypotheses forwarded to explain diversity patterns in the face of recent ecological theory and findings, and assess how proposed constraints on tropical parasitoid diversity may or may not apply to understanding diversity patterns in Tachinidae. Finally, we consider the limitations of available data to address questions concerning geographic patterns of parasitoid diversity.

Materials and methods

Study sites

We compiled data on tachinids from surveys at eight sites: Middle Patuxent Environmental Area, Howard Co., Maryland (Maryland: MD); Huffman Metropark, Dayton, Ohio (Ohio-1: OH1); Wright State University Woods, Dayton, Ohio (Ohio-2: OH2); Empire Gulch, Greaterville, Arizona (Arizona); **Zurquí de Moravia, San Jose, Costa Rica (Costa Rica: CR)**; Yanayacu Biological Station (Ecuador-1: EC1) and the Cynthia Trail (Ecuador-2: EC2) near YBS, Napo Province, Ecuador; and Podocarpus-El Condor Biosphere Reserve, southern Ecuador (Ecuador 3: EC3) (Table 1). These surveys were not designed as a cohesive experiment to examine geographic patterns of diversity, rather each was conducted independently and for different objectives. For example the Maryland, Costa Rica, and Ecuador-3 data were derived from general Diptera surveys, not focused on Tachinidae. As such, they employed different methods and were conducted for different durations (Table 1). To allow effective comparison among sites, we limited our analyses to sites in which at least 200 tachinid specimens were collected.

The Middle Patuxent Environmental Area (MD) is a 1021 acre (4.1 km²) natural area at the southern edge of the Eastern Coastal Forest Ecoregion in Howard Co. (MD, USA). The protected area, established in 1993, is primarily closed canopy deciduous forest with some open meadows and is managed for previous effects of soil runoff and invasive species such as autumn olive (*Elaeagnus umbellata*). The site includes both drier upland areas and lowland areas along the Middle Patuxent River.

Arizona (AZ) was a site located on U.S. Bureau of Land Management lands in the foothills of the Santa Rita Mountains in

Southern Arizona. The habitat was oak-mesquite grassland savanna, with woody plants (e.g. *Quercus*, *Prosopis*, *Acacia*, and *Juniperus* spp.), perennial grasses (*Muhlenbergia* and *Bouteloua* species), and diverse forbs. Traps were placed along a dry shallow drainage about 100 m from an unpaved road (see below).

The Wright State University Woods (OH1) is an 80 ha (0.8 km²) mixed primary and secondary growth Eastern Nearctic deciduous forest located on the Wright State University campus (290 m) in Dayton (OH, USA). The forest canopy is composed largely of hardwood species such as *Acer saccharum* and *Quercus rubrum*, with native understory trees including *Asimina triloba* and *Lindera benzoin*. Invasive honeysuckle (*Lonicera maackii*) and garlic mustard (*Aliaria petiolata*) are common around the edges. An intermittent stream runs through the eastern portion.

The Huffman Metropark (OH2) is part of the Dayton Regional Metropark system. The trap was placed in a powerline right-of-way amidst prairie/old-field forbs (e.g. *Solidago* spp., *Symphoricarpon*, spp.) and grasses (e.g. *Sorghastrum nutans*). This right of way was surrounded by second growth Eastern U.S. deciduous forest (e.g. *Acer* spp., *Fraxinus* spp., *Carya* spp., *Quercus* spp. and invasive *Lonicera maackii*).

The Yanayacu Biological Station (EC1) is located at 2100 m elevation on the eastern slope of the Andes in North-central Ecuador. The habitat surrounding the station is largely intact tropical montane forest, with a smaller area (20%) composed of abandoned pasture. The reserve is adjacent to two national preserves and is mostly contiguous forest (Stireman *et al.*, 2009). Tree diversity is high (55 spp. per hectare), and the understory is dominated by palms and ferns (Valencia, 1995) with large patches of *Chusquea* bamboo on steep slopes and along streams (Greeney *et al.*, 2011). The Cynthia trail site (EC2) was located on a steep hillside of mixed pasture and early secondary forest (ca. 2200 m) about 0.5 km away from the field station where the main sampling took place.

Zurquí de Moravia (CR) is a 5-acre patch of tropical montane forest at 1585 m adjacent to Braulio Carrillo Parque Nacional and located near Cerro Zurquí of the Cordillera Central in Moravia canton, San José, Costa Rica. It was recently the focus of a large-scale biodiversity inventory of all Diptera species, the Zurquí All-Diptera Biotic Inventory, or ZADBI project (Borkent &

Table 1. Site and sampling information for survey localities. The schedule of sampling for Costa Rica varied with sampling method. See text for details.

Locality	Coordinates	AAP	Elev.	Duration	Method	Schedule	MTMs
Maryland (MD)	39.21, -76.91 39.22, -76.91	1035	111 89	4	Mal.	Weekly/biweekly	1
Ohio-1 (OH1)	39.81, -84.09	1040	251	12.5	Mal.	Bimonthly	~12.5
Ohio-2 (OH2)	39.79, -84.06	1040	269	7	Mal.	Weekly	14
Arizona (AZ)	31.71, -110.78	360	1575	8	pan	Monthly	0*
Costa Rica (CR)	10.05, -84.01	~3500	1600	12	Various	Various	24*
Ecuador-1 (EC1)	-0.60, -77.88	~2600	2100	24	Mal., pan	Monthly	8*
Ecuador-2 (EC2)	-0.60, -77.89	~2600	2173	6	Mal.	Weekly	6
Ecuador-2 (EC3)	-4.09, -79.13	~3000	3000	2	Mal., pan	Various	~1*

*All or some proportion of samples at these sites were not from Malaise traps.

AAP is approximate annual precipitation in mm. Elev. is the elevation in metres, Duration indicates the number of months over which sampling took place, Method refers to Malaise (Mal.) and or pan traps, schedule gives the frequency of sample collections, and MTMs indicates Malaise trap months.

Brown, 2015; Brown *et al.*, 2018; Borkent *et al.*, 2018). The site was targeted for the survey as the insect diversity of the area was previously known to be high. Initial identifications revealed 73 families of Diptera and an estimate of over 4300 species, including 286 of Tachinidae (Brown *et al.*, 2018).

Podocarpus-El Condor Biosphere Reserve (EC3) is a large, ~1400 km² national park in the Andes of southern Ecuador. It is well known for its high animal and plant diversity and wide elevational gradient (900–3700 m). It was chosen as a target for a ~1 month survey of Dolichopodidae along a latitudinal gradient at three sites (Pollet, 2009), including one in the nearby San Francisco Reserve (provinces Loja and Zamora Chinchipe). The survey at Cajanuma, an upper montane forest site at 3000 m, collected an appreciable number of Tachinidae in addition to the target taxon. The other two sites (Bombuscaro and San Francisco Reserve) are not analysed here due to low numbers (<200 individuals) of Tachinidae collected.

Sampling protocols

Samples from Maryland were obtained using two Townes-style Malaise traps: one was located in a small meadow clearing surrounded by deciduous forest and one along a forested trail adjacent to the Middle Patuxent River. The traps were run wet (95% ethanol) from May until the end of August 2012, with trap samples being collected weekly (occasionally biweekly). Samples from both traps were combined for analysis.

Sampling methods at Ohio-1 (Wright State University) consisted of two Malaise traps operational from March through September 2010. One was placed adjacent to a stream in the older growth area; the other was placed in a clearing within the newer growth. Trap samples were exchanged with fresh 80% ethanol weekly. At Ohio-2 (Huffman Metropark), a single dry-head Malaise trap was operated June to November 2008 and March to November 2009, being emptied once or twice per week (Inclán & Stireman, 2011).

At the Arizona site, 24 white rectangular pan traps (39 × 15 × 5 cm) were placed in the field during September 1998 (twice) and monthly March to September 1999 (Stireman, 2008) for 48 h. Eight of the traps were placed on the ground in the open, eight were placed under the canopy of trees and eight were suspended ~2 m high in trees.

Sampling at Yanayacu Biological Station (Ecuador-1) consisted of a single wet (70% ethanol) Malaise trap and several yellow and white pan traps filled with soapy water placed adjacent to the main buildings on site (numbers of pan traps were not recorded). Traps were set out for about 1 week each month and checked either daily (pan traps) or weekly (Malaise trap). Samples of the pan traps and the Malaise trap were pooled semi-monthly. The survey was conducted between January 2007 and December 2008. Sampling at the neighbouring Ecuador-2 site (Cynthia Trail) was conducted similarly with a single Malaise trap with 95% ethanol, serviced weekly, between December 2012 and June 2013.

Sampling of the Cajanuma area of Podocarpus Biosphere Reserve (Ecuador-3) occurred from 13 February to 5 March 2009 and consisted of a primary and two supplementary

sampling sites. Primary sites consisted of one wet Malaise trap, and four units of 10 pan traps of four different colours (yellow, white, blue, and red). At each supplementary site, 10 yellow pan traps were in operation. All traps were placed at soil surface level along extant forest trails or within the forest itself. Pan traps were emptied every 5–7 days, the Malaise trap only once (Pollet, 2009).

Sampling in Costa Rica (Zurqui) consisted of a diverse set of methods, including Malaise traps, emergence traps, pan traps, sugar water baiting, light traps, and hand collecting. The multi-member intensive effort was conducted throughout the whole year during 2013 (Borkent *et al.*, 2018; Brown *et al.*, 2018). The project also included a single Malaise trap operated at two other sites in central and southern Costa Rica, but due to low numbers of Tachinidae collected (<200), these are not included here.

Specimen identification

Specimens from Ohio sites 1 and 2 and Maryland were identified to genus using Wood (1987) and to morphospecies or species level as available literature and/or reference to identified specimens in collections at Wright State University, the U.S. National Museum, and the Canadian National Collection permitted. Specimens from Ecuador sites 1–3 and Costa Rica were identified to genus level to the extent possible using Wood and Zumbado (2010), then separated into morphospecies based on external features. In most cases, we did not attempt to match morphospecies across sites and therefore were generally unable to assess the degree of taxon overlap or turnover among sites. Although species identities could not be established for most tropical specimens (and a number of temperate ones), for simplicity, we refer to our recognised morphospecies as species. All specimens are currently housed in the collection of J.O. Stireman at Wright State University (JOSC). Costa Rica specimens will be deposited at INBio in Costa Rica and representative specimens from Ecuador 1, 2 and Ecuador 3 will be deposited at the Museo Nacional de Quito and the Instituto de Ecología, Universidad Técnica Particular de Loja (UTPL), respectively, in Ecuador.

Analysis

The number of specimens per species was enumerated for each data set. Individual-based rarefaction, estimates of total community diversity (Chao 1; Chao, 1987), and diversity indices were estimated for each data set using EstimateS 9.1.0 with 500 randomisations (Colwell, 2013). Rarefaction curves were generated and visualised in R 3.5.1 (R Core Team, 2018). To compare shapes of species abundance distributions (SADs), we fit Pareto distributions to the data and calculated the α shape parameter using the R script of Forister *et al.* (2015). The α parameter is a useful summary statistic that gives a sense of the concavity of the SAD distribution, where higher values indicate a more strongly peaked distribution with many rare species and lower values a more even distribution of abundances (see Forister *et al.*, 2015). We statistically compared mean species richness and Pareto α parameters of tropical (Ecuador, Costa Rica)

and temperate (Ohio, Maryland, Arizona) data sets at the lowest comparable sampling of individuals ($n = 241$) using non-parametric Wilcoxon rank-sum tests in R. We chose this test due to the low sample sizes and skewed distributions of the data, but traditional t-tests produced similar results.

Results

A total of 7354 individuals comprising 1155 morphospecies identifications were obtained from the eight localities (Table 2). Total survey sizes ranged from 241 individuals (EC3) to 2969 individuals (EC1), with a mean survey size of ~1000 individuals. Species richness at sites ranged from 75 (EC3) to 290 (CR), with a mean species richness of ~140 species. Of these, 495 species were singletons (collected once) and 207 species were doubletons (only two specimens collected). Extrapolated Chao 1 estimates of total species richness per site ranged from 104 to 440, with site order mirroring that of observed richness (Table 3).

Individual-based rarefaction curves (Fig. 1) are non-asymptotic for each of the survey sites, indicating very incomplete sampling at all sites. The curve of the AZ locality exhibits the lowest and that of the CR locality (Costa Rica) the highest slope. Comparisons of rarefied species richness estimates among sites at a sample size of $N = 241$ individuals (i.e. the lowest yield of all surveys) reveals no indication that tachinid richness increases with latitude (Table 3; Fig. 2). Indeed, all tropical sites exhibit greater richness and greater diversity (e^H , Simpson) than any of the temperate sites (Tables 2 and 3). Richness estimates at this common sample size match the order for total species richness, which suggests that the rarefaction curves do not substantially change character with greater sample sizes. These results support the view that tropical tachinid communities are more species rich than temperate communities (Wilcoxon rank-sum $P = 0.0286$; Table 3), and that their SADs are more concave, suggesting a greater proportion of rare species (Pareto α , Wilcoxon rank-sum $P = 0.0286$; Table 3). Welch two sample t-tests revealed similar results despite low sample size and skewed distributions (richness: $t = -3.12$, $df = 3.3$, $P = 0.047$; α : $t = -4.24$, $df = 3.96$, $P = 0.013$). The overall percentage of rare species (the proportion of singletons and doubletons) was high, varying

from 68.3% (CR) to 52.6% (EC1), with a mean of ~60% (Table 1; Fig. 3).

Discussion

Our results indicate that tropical communities of Tachinidae in Ecuador and Costa Rica are likely more diverse than tachinid communities in Ohio and Maryland, which lie within the Nearctic latitudes of purported peak ichneumonid species richness (Janzen, 1981). Each of the tropical sites exhibits greater richness than any of the temperate sites at rarified minimum sample size, and three of the four exhibit greater total species richness and Chao-1 expected richness than any temperate site. Even the high elevation Podocarpus site is on par with the temperate sites in total richness, despite limited sampling effort. This finding of relatively high Neotropical diversity of tachinids must be interpreted cautiously, as it is based on a small number of sites with limited geographic area scope. It represents but a first step in evaluating patterns of tachinid diversity using quantitative sampling. However, our conclusions are consistent with several other lines of evidence including numbers of described species from different regions, surveys of adult tachinids from other temperate areas, and caterpillar rearing programmes. In addition, we argue that several of the hypotheses put forward to explain anomalous diversity in other parasitoid taxa may not apply to tachinids. We discuss these other lines of evidence below.

Other sources of evidence

Overall, the described Nearctic (North of Mexico) species diversity (~1305 spp.) is less than one-half that of the Neotropical region (~3088 spp.) (O'Hara *et al.*, 2020), despite the Neotropical Region being smaller in area and much less well studied. Although the Neotropical Region also includes southern temperate biomes, the vast majority of the region is tropical whereas the Nearctic Region lies entirely outside the tropics (i.e. North of the Tropic of Cancer, $23^{\circ}26'$). On the other hand, the fauna of the Palaearctic region (2112 spp.) dwarfs that of the Afrotropical (1130 spp.) or Oriental (1222 spp.), but the Palaearctic region is also much larger and much better studied.

Table 2. Summary information for Tachinidae data sets.

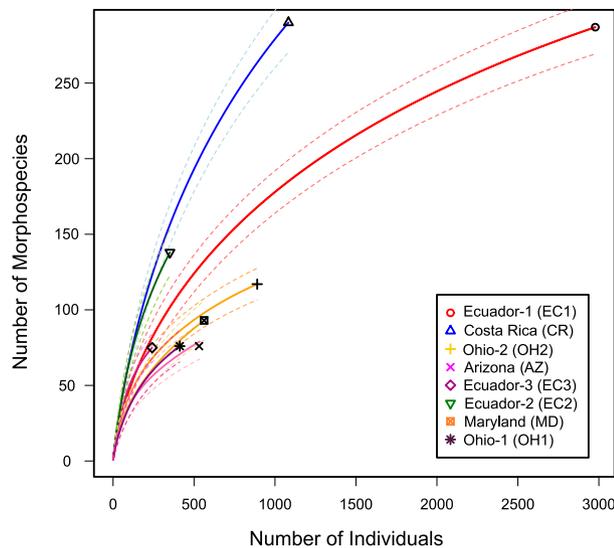
Locality	Latitude	Individuals	Species	Mean inds./sp.	Singlets	Doublets	% Singlets and doublets
Maryland	39°	562	93	6.04	46	12	62.4
Ohio-1	39°	890	117	7.61	42	23	55.6
Ohio-2	39°	412	76	6.33	33	12	59.2
Arizona	32°	534	79	6.76	31	9	52.6
Costa Rica	10°	1083	290	3.73	137	61	68.3
Ecuador-1	0°	2978	287	10.37	109	52	56.1
Ecuador-2	0°	654	138	2.54	67	24	65.9
Ecuador-3	-4°	241	75	3.21	30	14	58.7

'Individuals' is the total number of individuals, 'species' is the total number of species, 'Mean inds./sp.' is the average number of individuals per species, 'singlets' and 'doubletons' are the number of species with only one or two individuals collected, and '% singlets and doublets' is the percentage of singlet and doublet species.

Table 3. Community estimates of richness (Chao I), diversity (e^H = exponent of Shannon diversity), and shape of the species abundance distribution (α shape parameter of the fitted Pareto distribution, see text). R_{241} indicates estimated richness at 241 individuals (our lowest sample size).

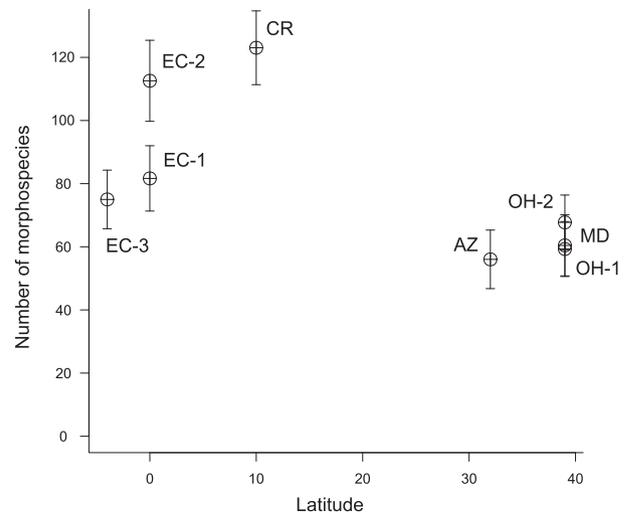
Locality	Chao 1 95% CI			Diversity metrics			
	Mean	Lower	Upper	R_{241}^*	e^H^*	Simpson [*]	Pareto α^*
Maryland	172.5	129.4	266.7	60.6	33.2	18.3	0.437
Ohio-1	152.8	133.6	194.2	67.7	44.1	21	0.580
Ohio-2	116.6	92.9	173.2	59.3	23.7	9.9	0.531
Arizona	135.0	102.0	215.4	56.0	32.3	18.2	0.542
Costa Rica	440.1	386.6	523.3	123.0	133.7	57.1	1.016
Ecuador-1	398.0	355.0	468.3	81.7	60.9	22.1	0.667
Ecuador-2	240.0	193.0	327.2	112.6	95.6	68.2	0.933
Ecuador-3	103.9	86.7	146.0	75.0	49.8	33.4	0.843

All metrics with asterisks differ significantly between the tropical and temperate samples based on Wilcoxon sum-rank tests.

**Fig. 1.** Individual-based rarefaction curves of Tachinidae species sampled from eight sites in the New World. Dashed lines indicate 95% confidence intervals (see Table 1 for site information)

Sampling surveys of adult tachinids in England and Italy are roughly consistent with our temperate North American sites with lower richness than our tropical sites, given sampling effort (Table 4).

Caterpillar rearing surveys in Central and South America (Janzen & Hallwachs, 2006; Stireman *et al.*, 2009, 2017), North America (McGugan, 1958; Stireman & Singer, 2003), and Papua New Guinea (Hrcek *et al.*, 2013) can also provide evidence concerning latitudinal patterns of diversity (Table 4). Unfortunately, these data sets are difficult to compare, as methods and objectives vary widely in terms of survey effort and target number of reared Lepidoptera, and are not readily comparable with trapping data sets. Yet, if 60% of tachinids use lepidopteran hosts (Cerretti, 2010), then the extrapolated estimate of total tachinid diversity at Yanayacu Biological Station (EC1) and surrounding areas would be about two-thirds the tachinid diversity of all of North America (Stireman *et al.*, 2017). Results from the passive trapping data set from EC1 used here suggest a more

**Fig. 2.** Rarefied numbers of tachinid species for each survey estimated at $N = 241$ individuals, the smallest sample size. Vertical bars indicate 95% confidence limits.

conservative estimate of ~30% of the species richness of North America – although this represents but a single location. For the largest rearing database of Tachinidae, with over 27 000 records from an ongoing survey of the Lepidoptera from the Area de Conservación Guanacaste, Costa Rica (Janzen & Hallwachs, 2006), an estimated ~1100 species of Tachinidae have been reared from ~5000 species of Lepidoptera (D. Janzen, pers. comm.). This figure, for mostly caterpillar-attacking species from an area half the size of West Virginia or Wales (~12 000 km²), is comparable to the entire described North American tachinid fauna. As a whole these surveys hint at a vast diversity of tropical Tachinidae far exceeding that of the temperate region in the New World.

Hypothesised constraints on parasitoid diversity

The resource fragmentation hypothesis provides an organised ecological framework for explaining anomalous diversity

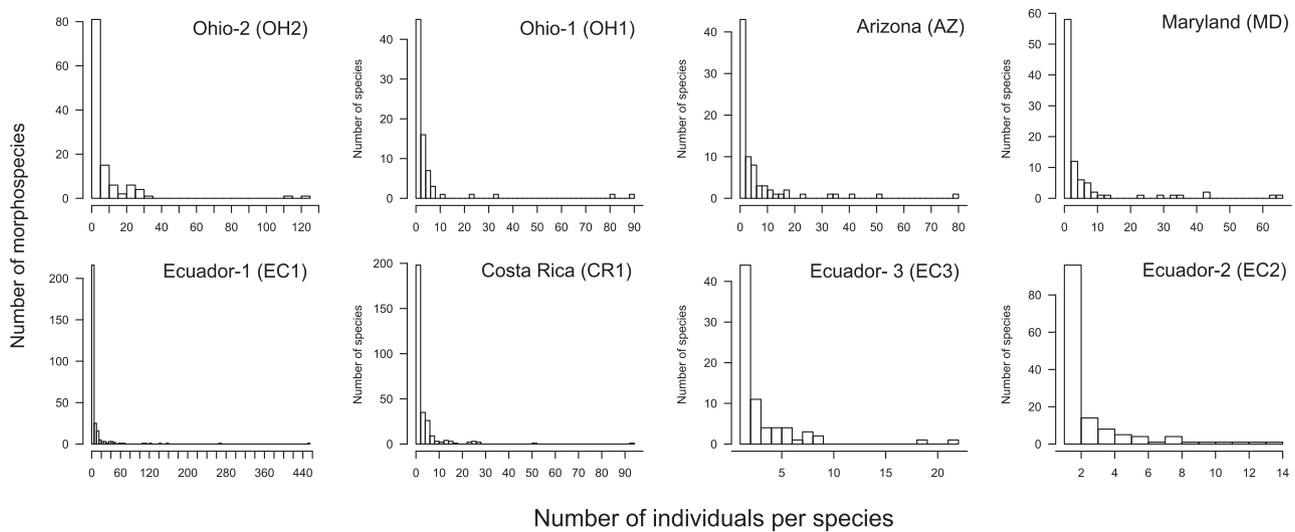


Fig. 3. Species abundance distributions for each survey, illustrating the ‘hollow curve’ of large numbers of rare species.

Table 4. Summary information of tachinid species richness estimates from surveys of adults in Europe and from caterpillar rearing studies.

Locality	Lat.	Species	<i>N</i>	References
<i>Adult surveys</i>				
Southern England	51°	84	3055	Belshaw (1992)
Central Italy (canopy)	45°	47	798	Stireman <i>et al.</i> (2012)
Central Italy	43°	129	1528	Inclán <i>et al.</i> (2014)
<i>Caterpillar rearing programmes</i>				
Southern Arizona	32°	64	327	Stireman and Singer (2003)
Costa Rica (ACG)	11°	~1100	~27 000	Janzen and Hallwachs (2006); D. Janzen per. Comm.
Ecuador (EC1)	0°	279	1350	Stireman <i>et al.</i> (2017)
Papua New Guinea	−5°	75	241	Hrcek <i>et al.</i> (2013)

Latitudes (Lat.) are approximate. *N* = total number individuals for adult surveys and number of records for rearing, with possibly multiple individual tachinds per record.

patterns in many taxa. Yet, it is not likely to apply well to Tachinidae as they lack key attributes required by the hypothesis. First, tachinid flies vary considerably in host range, and polyphagous species are distributed across the phylogenetic breadth of the family (Stireman, 2005). This is in contrast to koinobiont Hymenoptera in which most lineages are relatively specialised on a narrow range of hosts. If tachinid flies have a tendency towards polyphagy, their potential host habitat may be more abundant and less fragmented than those of more specialised Hymenopteran parasitoids. Indeed, at least some lineages of idiobiont Hymenoptera (e.g. Ichneumonidae subfamilies Pimplinae and Rhyssinae) appear to exhibit greater diversity at tropical latitudes (Gauld 1986, 1987; Quicke 2012; Gomez *et al.*, 2018). Second, calyptate flies, including tachinids, are highly vagile and are strong fliers relative to many of the smaller bodied parasitic Hymenoptera. These flying abilities have been exaggerated at times (Townsend, 1927), but more modest flight ranges upwards of 5 km in 2 h have been recorded for morphologically similar horn flies (Muscidae) (Sheppard, 1994), and tachinid flights of several kilometres have been documented (Elkinton *et al.*,

2006). In combination, these characteristics of broader host ranges and strong directed dispersal ability suggest that tachinid flies should not be as greatly affected by low host density in tropical ecosystems as some parasitoid taxa may be. Indeed, it has been suggested that tachinids often persist at low densities themselves, which would explain the tendency towards landmark mating systems commonly seen in this family (Alcock & Kemp, 2006).

The nasty host hypothesis proposes that the prevalence of allelochemically defended hosts in the tropics limits the viability of polyphagous or oligophagous parasitoids. Nevertheless, evidence for increased chemical ‘nastiness’ of tropical hosts is mixed (Levin & York, 1978; Coley & Aide, 1991; Moles *et al.*, 2011b; Marquis *et al.*, 2012). For example, a meta-analysis of 56 comparative studies found that less than 20% reported evidence of increased defences in tropical plants relative to temperate ones (Moles *et al.*, 2011a). Furthermore, there is evidence that plant secondary chemicals can interfere with host immune defences potentially making them more vulnerable to parasitoids (Smilanich *et al.*, 2009). Some evidence indicates that tachinid

flies can be susceptible to indirect effects of plant chemical defences (Singer *et al.*, 2009; Ichiki *et al.*, 2014), but it has been suggested that, in general, this susceptibility is lower than that of parasitoid Hymenoptera (Eggleton & Gaston, 1992). Finally, even if tropical hosts are generally better defended chemically, these hosts could act as enemy-free-space (Jeffries & Lawton, 1984) for parasitoids, allowing parasitoid larvae to escape predation (Murphy *et al.*, 2014; Gentry & Dyer, 2002). If predation rates on hosts are higher in the tropics, then tachinid flies may benefit from using heavily defended hosts, even if this incurs physiological costs.

A third hypothesis to explain anomalous diversity gradients of parasitoids is that intense predation on adults, especially by birds, limits tropical parasitoid diversity (Gauld, 1987). Yet, predation on adults appears unlikely to be a strong constraint on dipteran diversity in the tropics. Insectivorous birds appear to eat relatively few flies and of these most seem to be slow flying ‘Nematocera’ and small acalyptates; the birds’ primary arthropod food sources tend to be Hymenoptera and Coleoptera (Hespenheide, 1971, 1973; Poulin & Lefebvre, 1997). As noted previously, tachinid flies and their relatives are fast flying insects and are likely difficult for birds to capture (Hespenheide, 1973). They may also be defended in other ways, as many species, particularly larger bodied ones, appear to display aposematic coloration and often possess heavy spines on their bodies that may deter predators. Overall, there appears to be little reason to believe that predation on adult tachinid flies strongly constrains their local diversity.

Finally, it has been suggested that tachinid richness should decline towards the tropics due to greater proportions of vegetation-concealed hosts that are inaccessible for tachinid oviposition (Janzen, 1981). While this is not an entirely convincing argument as tachinids may deposit eggs on the concealing vegetation itself, species that must oviposit directly on or within their hosts are at a disadvantage in attacking concealed hosts (Wood, 1987). Conversely, tachinids that indirectly oviposit planidia-form larvae or possess long ovipositors are unlikely to be deterred by leaf rolls (Wiman & Jones, 2013) and may possibly gain a parasitoid version of enemy-free space from the association (Murphy *et al.*, 2014). Abundant rearing records of tachinids from caterpillars of the families Crambidae and Tortricidae suggests that leaf-rollers and leaf-tiers are not particularly protected from attack by tachinid flies (Arnaud, 1978; Janzen & Hallwachs, 2006). Therefore, vegetation-concealing tactics should not overall cause hosts to be inaccessible to tachinid flies generally.

Limitations of available data

Assessing differences in species richness of tachinids between tropical and temperate areas using trapping data sets is plagued by a number of difficulties and there are several caveats associated with our interpretations. Local habitat can strongly affect the richness and composition of parasitoid communities (Belshaw, 1992; László & Tóthmérész, 2013). This heterogeneity of habitats means that the particular habitat or location of the trap may not be representative of regional tachinid diversity or

represent a tachinid rich biotope. For example, our Arizona data set from a semi-arid oak savanna in a dry year exhibited among the lowest species richness of our sites and does not appear to reflect the diverse tachinid fauna of the larger Southwest U.S. (O’Hara, 2012). A more accurate accounting of diversity in this region would likely result in a more linear increase in richness towards the tropics. Similarly, the relatively low diversity at Podocarpus, at 3000 m, likely reflects a decline in tachinid diversity at high elevations, potentially obscuring larger patterns of diversity. The EC1 and EC2 sites were quite close together, differing primarily in habitat, and it may be that the EC2 trap collected a relatively wider diversity of taxa due to movement of flies up the slope relatively to the EC1 site on the valley floor; again illustrating the influence of local habitat on patterns of tachinid diversity.

Variation in species turnover among habitats within sites or regions may also obscure patterns of diversity. The three sites of the Ecuadorian Podocarpus Diptera survey [Cajanuma (used here), Bombuscaro and San Francisco Reserve] exhibited very low apparent overlap in species despite their relative proximity (Jaccard similarity indices of 0.003–0.028), whereas Maryland and Ohio-2 (Huffman) sites had higher species overlap (Jaccard: 0.25) despite substantial distance (> 600 km). These observations, as well as the low overlap in tachinid species among Malaise trap samples from the ZADBI project (Jaccard similarities ranging from 0.000 to 0.076 among sites and 0.006 to 0.125 within sites; see Borkent *et al.*, 2018), suggest that tachinid beta diversity in the tropics may be quite high relative to temperate communities.

Another consideration is that many species in the Neotropical data sets may be overlooked due to poor taxonomic resolution and a large number of cryptic species, leading to underestimates of tropical diversity. Taxonomic documentation of Tachinidae in the Nearctic region is relatively well-resolved (Wood, 1987; O’Hara & Wood, 2004), while the fauna of the Neotropical region is exceedingly difficult taxonomically even for tachinid specialists (O’Hara, 2013), with no modern key to genera outside Central America (Wood & Zumbado, 2010). Here, we separated Neotropical morphospecies using external characteristics without examination of genitalia or genetic data. Yet, mitochondrial DNA studies of reared tachinids in Costa Rica have found pervasive evidence of genetically distinct but morphologically cryptic species, with some apparently polyphagous taxa consisting of as many as a dozen closely related species (Smith *et al.*, 2006, 2007). Recent DNA sequencing studies of temperate tachinids have also revealed cryptic species, but at an apparently lower frequency (Pohjoismäki *et al.*, 2016). Interestingly, a recent DNA barcode-based analysis of latitudinal patterns of diversity in Hymenopteran parasitoids failed to find evidence for greater hymenopteran parasitoid richness in the tropics (Eagalle and Smith, 2017).

Finally, methods and durations of sampling varied considerably between localities. Most surveys used only one or two passive trapping methods, while the ZADBI survey used a myriad of methods, both passive and active (Borkent *et al.*, 2018). The high slope of the CR locality in comparison with the milder slope – despite the relatively large sample size – from EC1 may be due, at least in part, to this disparity in collection method

diversity. More diverse sampling at EC1, including active methods, would likely reveal a trajectory of species richness more comparable to that of **Costa Rica**. In addition, sampling from Podocarpus and Arizona was far more limited than the other sites and consisted mostly or wholly of pan traps, which may have contributed to lower observed diversity (although most EC1 samples were also from pan traps).

Comparisons of species richness across sites must also consider the distribution of species abundances. Greater species richness tends to decrease overall evenness (Willig *et al.*, 2003) suggesting that much longer sampling regimes across many localities are needed to accurately predict richness of diverse communities (Morrison *et al.*, 1979). Particularly notable in our results is the high proportion (>50%) of singletons and doubletons found across datasets. Singletons and doubletons may reflect the species rarity when sampling is comprehensive, but high temporal variability and inadequate sampling can mask the left side of species-abundance distributions and skew interpretations of rarity (Preston, 1948). Surveys of tropical arthropod communities tend to record singleton frequencies of 30% or higher and very intensive survey efforts are necessary to reduce these frequencies below 20% (Coddington *et al.*, 2009). Rarefaction curves and species abundance distributions of the survey sites reported here clearly indicate that much greater sampling effort is needed for accurate richness estimates of Tachinidae in all of these communities.

Although our analysis supports high tropical richness of tachinid parasitoids, clearly the sampling intensity, distribution, and number of these existing data sets by themselves remain insufficient to draw strong conclusions about latitudinal patterns of diversity for this group. Several researchers have argued that data on parasitoid diversity in general is too limited to draw conclusions about latitudinal patterns (Quicke, 2012; Veijalainen *et al.*, 2012; Gomez *et al.*, 2018), let alone the underlying factors that influence them. In particular, sampling of tropical parasitoid communities has been inadequate to understand their diversity with most surveys occurring at a single site for a single season (Hespenheide, 1979, Morrison *et al.*, 1979). More intensive sampling in tropical regions has in some cases revealed parasitoid richnesses comparable to the richnesses of their hosts, including those hosts thought to disfavour parasitoids in the tropics (Veijalainen *et al.*, 2013).

Recent studies based on intensive sampling suggest that a more nuanced perspective concerning parasitoid diversity patterns is necessary as phylogenetic and functional groups vary in their diversity responses to latitude. Indeed, Timms *et al.* (2016) point out that the ichneumonid subfamilies on which Janzen (1981) based his original conclusion of a mid-latitude peak failed to include several whose species richness peaks at low latitudes (Ophioninae; Gaston & Gauld 1993) and high ones (e.g. Tryphoninae). In the case of Tachinidae, all four recognised subfamilies exhibit similarly greater Neotropical than Nearctic diversity (ranging from 2.0 to 2.57 fold) based on described species, although no such differences in described species are apparent for Old World taxa (O'Hara *et al.*, 2020).

Summary and conclusions

Latitudinal surveys and theoretical predictions have suggested that some parasitoids exhibit anomalous diversity gradients, with peaks in diversity at higher latitudes. Anecdotal evidence from the taxonomic literature has long suggested a great and largely unknown diversity of tachinid flies in the Neotropics, contrasting with a much smaller Nearctic richness. Measures of community species richness in temperate and tropical sites in the Americas presented here provide evidence supporting greater tropical diversity of Tachinidae rather than an anomalous diversity gradient extrapolated from studies of particular hymenopteran parasitoids (Janzen, 1981; Gauld *et al.*, 1994). Results from other surveys and insect rearing programmes support this conclusion; however, more data are needed to draw strong conclusions about broad patterns in tachinid diversity. Given their frequent polyphagy, relative insensitivity to variation in host physiology and allelochemicals, and strong directed dispersal abilities, tachinids should not be particularly constrained by processes hypothesised to limit koinobiont wasp diversity in the tropics.

The lack of intensive, long-term survey data from multiple regions is the biggest impediment to understanding large-scale geographic patterns in parasitoid diversity and their underlying causes. Future research evaluating such patterns for tachinids and other parasitoid taxa would benefit from both more surveys and more standardised sampling methods. These standards will allow estimates of time and scale of sampling regimes necessary for accurate detection of species richness and abundances. Finally, broader studies of tachinid ecology and natural history are needed. It is yet unclear if breadth of host use and spatial-temporal turnover of Tachinidae communities differ between tropical and temperate ecosystems. Systematic rearing surveys and measures of beta diversity between neighbouring localities could shed light on these issues.

Acknowledgements

Thanks go to Sonja J. Scheffer and Mathew L. Lewis for specimens from Maryland, and to Brian V. Brown and Art Borkent for specimens from the ZADBI project. We thank Wilmer Simbaña, Jose Simbaña, and Harold F. Greeney for collection of the Yanayacu Biological Station material and Karen Pedersen for collection of the Cynthia Trail material. The participation of MP to the Podocarpus Parque Nacional survey in 2009 was supported by the European Distributed Institute of Taxonomy (EDIT), the Flemish Fund for Scientific Research (FWO-Vlaanderen, Belgium) and the Leopold III Fund for Nature Research and Nature Conservation (L III, Belgium). MP is also greatly indebted to Jörg Zielinger and Dr Felix Matt, the coordinators of the San Francisco Estación Biológica, for their continuous and kind assistance during this expedition. Many thanks are also due to the Ecuadorian crew of this biological station (e.g. car drivers, cooks), and the Belgian expedition team led by Dr Maurice Laponce (RBINS). We also thank Isaac Winkler for initial sorting of the Podocarpus tachinids, Monty Wood for initial sorting and determination of the ZADBI material, and **Daniel Janzen** for information on species richness at Area de Conservación

Guanacaste. Finally, we thank Ilari E. Sääksjärvi and an anonymous reviewer for their helpful criticisms and comments. This work was supported by National Science Foundation grants DEB 1020571, 1146269, and 1442134 to JOS. The ZADBI project was supported by NSF grant DEB 1145890 to B. V. Brown and A. Borkent.

Conflict of Interest

All authors have declared that there is no conflict of interest.

References

- Alcock, J. & Kemp, D.J. (2006) The hilltopping mating system of *Leschenaultia adusta* (Loew) (Diptera: Tachinidae). *Journal of Insect Behavior*, **19**, 645–656.
- Andrew, N.R. & Hughes, L. (2005) Diversity and assemblage structure of phytophagous Hemiptera along a latitudinal gradient: predicting the potential impacts of climate change. *Global Ecology and Biogeography*, **14**, 249–262.
- Arnaud, P.H. (1978) *A Host-Parasite Catalog of North American Tachinidae (Diptera)*, Vol. **1319**, pp. p. 1–860. United States Department of Agriculture, Washington, D.C.
- Belshaw, R. (1992) Tachinidae (Diptera) assemblages in habitats of a secondary succession in southern Britain. *Entomologist*, **111**, 151–161.
- Boyero, L., Pearson, R.G., Dudgeon, D., Graca, M.A.S., Gessner, M.O., Albarino, R.J., Ferreira, V., Yule, C.M., Boulton, A.J., Arunachalam, M., Callisto, M., Chauvet, E., Ramirez, A., Chara, J., Moretti, M.S., Goncalves, J.F., Jr., Helson, J.E., Chara-Serna, A.M., Encalada, A.C., Davies, J.N., Lamothe, S., Cornejo, A., Li, A.O.Y., Buria, L.M., Villanueva, V.D., Zuniga, M.C. & Pringle, C.M. (2011) Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. *Ecology*, **92**, 1839–1848.
- Borkent, A. & Brown, B.V. (2015) How to inventory tropical flies (Diptera) - One of the megadiverse orders of insects. *Zootaxa*, **3949**, 301–322.
- Borkent, A., Brown, B., V., Adler, P.H., Amorim, D.D.S., Barber, K., Bickel, D., Boucher, S., Brooks, S.E., Burger, J., Burington, Z.L., Capellari, R.S., Costa, D.N.R., Cumming, J.M., Curler, G., Dick, C. W., Epler, J.H., Fisher, E., Gaimari, S.D., Gelhaus, J., Grimaldi, D. A., Hash, J., Hauser, M., Hippha, H., Ibanez-Bernal, S., Jaschhof, M., Kameneva, E.P., Kerr, P.H., Korneyev, V., Korytkowski, C.A., Kung, G., Kvitte, G.M., Lonsdale, O., Marshall, S.A., Mathis, W.N., Michelsen, V., Naglis, S., Norrbom, A.L., Paiero, S., Pape, T., Pereira-Colavite, A., Pollet, M., Rochefort, S., Rung, A., Runyon, J. B., Savage, J., Silva, V.C., Sinclair, B.J., Skevington, J.H., Stireman, J.O.I.I.I., Swann, J., Vilkamaa, P., Wheeler, T., Whitworth, T., Wong, M., Wood, D.M., Woodley, N., Yau, T., Zavortink, T.J. & Zumbado, M.A. (2018) Remarkable fly (diptera) diversity in a patch of **costa rican** cloud forest: why inventory is a vital science. *Zootaxa*, **4402**, 53–90.
- Brown, B.V., Borkent, A., Adler, P.H., Amorim, D.d.S., Barber, K., Bickel, D., Boucher, S., Brooks, S.E., Burger, J., Burington, Z.L., Capellari, R.S., Costa, D.N.R., Cumming, J.M., Curler, G., Dick, C. W., Epler, J.H., Fisher, E., Gaimari, S.D., Gelhaus, J., Grimaldi, D. A., Hash, J., Hauser, M., Hippha, H., Ibanez-Bernal, S., Jaschhof, M., Kameneva, E.P., Kerr, P.H., Korneyev, V., Korytkowski, C.A., Kung, G., Kvitte, G.M., Lonsdale, O., Marshall, S.A., Mathis, W., Michelsen, V., Naglis, S., Norrbom, A.L., Paiero, S., Pape, T., Pereira-Colavite, A., Pollet, M., Rochefort, S., Rung, A., Runyon, J. B., Savage, J., Silva, V.C., Sinclair, B.J., Skevington, J.H., Stireman, J.O.I.I.I., Swann, J., Vilkamaa, P., Wheeler, T., Whitworth, T., Wong, M., Wood, D.M., Woodley, N., Yau, T., Zavortink, T.J. & Zumbado, M.A. (2018) Comprehensive inventory of true flies (diptera) at a tropical site. *Communications Biology*, **1**, 21.
- Cerretti, P. (2010) *I tachinidi della fauna italiana (Diptera Tachinidae), con chiave interattiva dei generi ovest-paleartici*, Vol. **I**. Centro Nazionale Biodiversità Forestale – Verona, Cierre Edizioni, Verona, Italy.
- Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M. & Hormiga, G. (2009) Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*, **78**, 573–584.
- Coley, P.D. & Aide, T.M. (1991) Comparison of herbivory and plant defences in temperate and tropical broad-leaved forests. *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (ed. by P.W. Price, T.M. Lewinsohn, G. W. Fernandes and W.W. Benson), pp. p. 25–49. Wiley-Interscience, Hoboken, NJ.
- Colwell, R.K. (2013) *EstimateS: Statistical estimate of species richness and shared species from samples*. <<http://purl.oclc.org/estimates>>.
- Crame, J.A. (2001) Taxonomic diversity gradients through geologic time. *Diversity and Distributions*, **7**, 175–189.
- Cushman, J., Lawton, J. & Manly, B. (1993) Latitudinal patterns in European ant assemblages - variation in species richness and body-size. *Oecologia*, **95**, 30–37.
- Davidowitz, G. & Rosenzweig, M. (1998) The latitudinal gradient of species diversity among North American grasshoppers (Acrididae) within a single habitat: a test of the spatial heterogeneity hypothesis. *Journal of Biogeography*, **25**, 553–560.
- Dixon, A., Kindlmann, P., Leps, J. & Holman, J. (1987) Why there are so few species of aphids, especially in the tropics. *American Naturalist*, **129**, 580–592.
- Duffey, S.S., Bloem, K.A. & Campbell, B.C. (1986) Consequences of sequestration of plant natural products in plant-insect-parasitoid interactions. *Interactions of Plant Resistance and Parasitoids and Predators of Insects* (ed. by D.J. Boethel and R.D. Eikenbary), pp. p. 31–60. Ellis Horwood, Chichester.
- Eagale, T. & Smith, M.A. (2017) Diversity of parasitoid and parasitic wasps across a latitudinal gradient: using public DNA records to work within a taxonomic impediment. *Facets*, **2**, 937–954.
- Eggleton, P. & Gaston, K.J. (1990) Parasitoid species and assemblages convenient definitions or misleading compromises. *Oikos*, **59**, 417–421.
- Eggleton, P. & Gaston, K.J. (1992) Tachinid host ranges: a reappraisal (Diptera: Tachinidae). *Entomologist's Gazette*, **43**, 139–143.
- Elkinton, J.S., Parry, D. & Boettner, G.H. (2006) Implicating an introduced generalist parasitoid in the invasive browntail moth's enigmatic demise. *Ecology*, **87**, 2664–2672.
- Feener, D.H. & Brown, B.V. (1997) Diptera as parasitoids. *Annual Review of Entomology*, **42**, 73–97.
- Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y., Butterill, P.T., Cizek, L., Coley, P.D., Dem, F., Diniz, I.R., Drozd, P., Fox, M., Glassmire, A.E., Hazen, R., Hrcek, J., Jahner, J. P., Kaman, O., Kozubowski, T.J., Kursar, T.A., Lewis, O.T., Lill, J., Marquis, R.J., Miller, S.E., Morais, H.C., Murakami, M., Nickel, H., Pardikes, N.A., Ricklefs, R.E., Singer, M.S., Smilanich, A.M., Stireman, J.O., Villamarin-Cortez, S., Vodka, S., Volf, M., Wagner, D.L., Walla, T., Weiblen, G.D. & Dyer, L.A. (2015) The global distribution of diet breadth in insect herbivores. *Proceedings*

- of the National Academy of Sciences of the United States of America, **112**, 442–447.
- Gaston, K.J. & Gauld, I.D. (1993) How many species of pimplines (Hymenoptera: Ichneumonidae) are There in Costa Rica? *Journal of Tropical Ecology*, **9**, 491–499.
- Gauld, I.D. (1986) Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology*, **11**, 155–161.
- Gauld, I.D. (1987) Some factors affecting the composition of tropical ichneumonid faunas. *Biological Journal of the Linnean Society*, **30**, 299–312.
- Gauld, I.D., Gaston, K.J. & Janzen, D.H. (1994) The taste of enemy free space: parasitoids and nasty hosts. *Parasitoid Community Ecology* (ed. by B.A. Hawkins and W. Sheehan), pp. p. 279–299. Oxford University Press, Oxford, UK.
- Gauld, I.D. & Gaston, K.J. & Janzen, D.H. (1992) Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos*, **65**, 353–357.
- Gentry, G. & Dyer, L. (2002) On the conditional, nature of Neotropical caterpillar defenses against their natural enemies. *Ecology*, **83**, 3108–3119.
- Gomez, I.C., Saaksjarvi, I.E., Mayhew, P.J., Pollet, M., Rey del Castillo, C., Nieves-Aldrey, J., Broad, G.R., Roininen, H. & Tuomisto, H. (2018) Variation in the species richness of parasitoid wasps (Ichneumonidae: Pimplinae and Rhyssinae) across sites on different continents. *Insect Conservation and Diversity*, **11**, 305–316.
- Greeney, H.F., Whitfield, J.B., Stireman, J.O., III, Penz, C.M. & Dyer, L. A. (2011) Natural history of *Eryphanis greeneyi* (Lepidoptera: Nymphalidae) and its enemies, with a description of a new species of braconid parasitoid and notes on its tachinid parasitoid. *Annals of the Entomological Society of America*, **104**, 1078–1090.
- Guimarães, J.H. (1971) Family Tachinidae (Larvaevoridae). *A Catalog of the Diptera of the Diptera of the Americas South of the United States. Museu de Zoologia, Universidade de Sãlfo Paulo*, **104**, 1–333.
- Hawkins, B.A. & Compton, S.G. (1992) African fig wasp communities - undersaturation and latitudinal gradients in species richness. *Journal of Animal Ecology*, **61**, 361–372.
- Heinrich, G.H. (1977) *Ichneumonidae of Florida and Neighboring States*. Gainesville, FL, Florida Department of Agriculture and Consumer Services.
- Hespenheide, H.A. (1971) Food preference and the extent of overlap in some insectivorous birds with special reference to the Tyrannidae. *IBIS*, **113**, 59–72.
- Hespenheide, H.A. (1973) Novel mimicry complex - beetles and flies. *Journal of Entomology Series A-Physiology & Behaviour*, **48**, 49–56.
- Hespenheide, H.A. (1979) Are there fewer parasitoids in the tropics? *American Naturalist*, **113**, 766–769.
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 192–211.
- Hreck, J., Miller, S.E., Whitfield, J.B., Shima, H. & Novotny, V. (2013) Parasitism rate, parasitoid community composition and host specificity on exposed and semi-concealed caterpillars from a tropical rainforest. *Oecologia*, **173**, 521–532.
- Ichiki, R.T., Tabata, J., Nakahara, Y., Kainoh, Y. & Nakamura, S. (2014) Effects of food plants of host herbivores on development of a midgut-resident tachinid parasitoid, *Compsilura concinnata* (Diptera: Tachinidae), and two hemocoel-resident parasitoids. *Annals of the Entomological Society of America*, **107**, 461–467.
- Inclan, D.J. & Stireman, J.O., III (2011) Tachinid (Diptera: Tachinidae) parasitoid diversity and temporal abundance at a single site in the northeastern United States. *Annals of the Entomological Society of America*, **104**, 287–296.
- Janzen, D.H. (1981) The peak in North American ichneumonid species richness lies between 38-degrees and 42-degrees-N. *Ecology*, **62**, 532–537.
- Janzen D.H. & Hallwachs, W. (2006) *Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica*. <http://janzen.sas.upenn.edu> (14th February 2017).
- 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.
- Jeffries, M.J. & Lawton, J.H. (1984) Enemy-free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.
- Jones, O.R., Purvis, A. & Quicke, D.L.J. (2012) Latitudinal gradients in taxonomic overdescription rate affect macroecological inferences using species list data. *Ecography*, **35**, 333–340.
- Kindlmann, P. (1988) Extraordinary latitudinal gradients in species richness - one explanation. *Mathematical Ecology* (ed. by T.G. Hallam, L. J. Gross and S.A. Levin), pp. p. 149–157. Springer, Berlin.
- Kindlmann, P., Schodelbauerova, I. & Dixon, A.F.G. (2007) Inverse latitudinal gradients in species diversity. *Scaling Biodiversity* (ed. by D. Storch, P.A. Marquet and J.H. Brown), pp. p. 246–257. Cambridge University Press, Cambridge, UK.
- Kocher, S.D. & Williams, E.H. (2000) The diversity and abundance of north American butterflies vary with habitat disturbance and geography. *Journal of Biogeography*, **27**, 785–794.
- Kouki, J., Niemela, P. & Viitasari, M. (1994) Reversed latitudinal gradient in species richness of sawflies (Hymenoptera, Symphyta). *Annales Zoologici Fennici*, **31**, 83–88.
- László, Z. & Tóthmérész, B. (2013) Landscape and local effects on multiparasitoid coexistence. *Insect Conservation and Diversity*, **6**, 354–364.
- Levin, D.A. (1976) Chemical defenses of plants to pathogens and herbivores. *Annual Review of Ecology and Systematics*, **7**, 121–159.
- Levin, D.A. & York, B.M. (1978) Toxicity of plant alkaloids - ecogeographic perspective. *Biochemical Systematics and Ecology*, **6**, 61–76.
- Lobo, J.M. (2000) Species diversity and composition of dung beetle (Coleoptera: Scarabaeoidea) assemblages in North America. *Canadian Entomologist*, **132**, 307–321.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) *Biogeography*, Vol. , 4th Edn. Sinauer Associates, Sunderland, MA.
- Lue, C., Borowy, D., Buffington, M.L. & Leips, J. (2018) Diversity and Community Composition of Frugivorous *Drosophila* (Diptera: Drosophilidae) and their *Leptopilina* (Hymenoptera: Figitidae) Parasitoids. *Environmental Entomology*, **47**, 1096–1106.
- Marquis, R.J., Ricklefs, R.E. & Abdala-Roberts, L. (2012) Testing the low latitude/high defense hypothesis for broad-leaved tree species. *Oecologia*, **169**, 811–820.
- McGugan, B.M. (1958) The Canadian Forest Insect Survey. Proceedings of the 10th International Congress of Entomology 4, 219–232.
- Moles, A.T., Bonser, S.P., Poore, A.G.B., Wallis, I.R. & Foley, W.J. (2011a) Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*, **25**, 380–388.
- Moles, A.T., Wallis, I.R., Foley, W.J., Warton, D.I., Stegen, J.C., Bisigato, A. J., Cella-Pizarro, L., Clark, C.J., Cohen, P.S., Cornwell, W.K., Edwards, W., Ejmaes, R., Gonzales-Ojeda, T., Graae, B.J., Hay, G., Lumbwe, F.C., Magana-Rodriguez, B., Moore, B.D., Peri, P.L., Poulsen, J.R., Veldtman, R., von Zeipel, H., Andrew, N.R., Boulter, S. L., Borer, E.T., Fernandez Campon, F., Coll, M., Farji-Brener, A.G., De Gabriel, J., Jurado, E., Kyhn, L.A., Low, B., Mulder, C.P.H., Reardon-Smith, K., Rodriguez-Velazquez, J., Seabloom, E.W., Vesik, P.A., van Cauter, A., Waldram, M.S., Zheng, Z., Blendinger, P.G., Enquist, B.J.,

- Facelli, J.M., Knight, T., Majer, J.D., Martínez-Ramos, M., McQuillan, P. & Prior, L.D. (2011b) Putting plant resistance traits on the map: a test of the idea that plants are better defended at lower latitudes. *New Phytologist*, **191**, 777–788.
- Morrison, G., Auerbach, M. & McCoy, E.D. (1979) Anomalous diversity of tropical parasitoids - general phenomenon. *American Naturalist*, **114**, 303–307.
- Murphy, S.M., Lill, J.T., Bowers, M.D. & Singer, M.S. (2014) Enemy-free space for parasitoids. *Environmental Entomology*, **43**, 1465–1474.
- O'Hara, J.E. (1989) Systematics of the genus group taxa of the Siphonini (Diptera: Tachinidae). *Quaestiones Entomologicae*, **25**, 1–229.
- O'Hara, J.E. (2012) Review of tachinid fly diversity in the Gila National Forest, New Mexico (Proceedings of the third natural history of the Gila symposium). *The New Mexico Botanist, Special Issue*, **3**, 32–41.
- O'Hara, J.E. (2013) History of tachinid classification (Diptera, Tachinidae). *Zookeys*, **34**, 1–34.
- O'Hara, J.E., Henderson, S.J. & Wood, D.M. (2020) *Preliminary checklist of the Tachinidae of the world. Version 2.1. PDF document*, 1039 pages. <<http://www.nadsdiptera.org/Tach/WorldTachs/Checklist/Worldchecklist.htm>> March 2020.
- O'Hara, J.E. & Wood, D.M. (2004) Catalogue of the Tachinidae (Diptera) of America north of Mexico. *Memoirs on Entomology, International*, **18**, 1–410.
- Owen, D.F. & Owen, J. (1974) Species-diversity in temperate and tropical Ichneumonidae. *Nature*, **249**, 583–584.
- Pohjoismäki, J.L.O., Kahanpää, J. & Mutanen, M. (2016) DNA barcodes for the Northern European tachinid flies (Diptera: Tachinidae). *PLoS One*, **11**, e0164933.
- Pollet, M. (2009) In search for dolichopodid flies in southern Ecuador: the true story. *Fly Times*, **42**, 36–51.
- Poulin, B. & Lefebvre, G. (1997) Estimation of arthropods available to birds: effect of trapping technique, prey distribution, and bird diet. *Journal of Field Ornithology*, **68**, 426–442.
- Preston, F.W. (1948) The commonness, and rarity, of species. *Ecology*, **29**, 254–283.
- Quicke, D.L.J. & Kruff, R.A. (1995) Latitudinal gradients in North American braconid wasp species richness and biology. *Journal of Hymenoptera Research*, **4**, 194–203.
- 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. (2014) *The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics*. Evolution and Ecology, Wiley-Blackwell, Oxford, UK.
- Core Team, R. (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed September 2019.
- Rathcke, B.J. & Price, P.W. (1976) Anomalous diversity of tropical ichneumonid parasitoids - predation hypothesis. *American Naturalist*, **110**, 889–893.
- Sääksjärvi, I.E., Haataja, S., Neuvonen, S., Gauld, I.D., Jussila, R., Salo, J. & Marmol Burgos, A. (2004) High local species richness of parasitic wasps (Hymenoptera: Ichneumonidae; Pimplinae and Rhysinae) from the lowland rain forests of Peruvian Amazonia. *Ecological Entomology*, **29**, 735–743.
- Sax, D.F. (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography*, **28**, 139–150.
- Sheppard, D.C. (1994) Dispersal of wild-captured, marked horn flies (Diptera, Muscidae). *Environmental Entomology*, **23**, 29–34.
- Singer, M.S., Mace, K.C. & Bernays, E.A. (2009) Self-medication as adaptive plasticity: increased ingestion of plant toxins by parasitized caterpillars. *PLoS One*, **4**, e4796.
- Skillen, E.L., Pickering, J. & Sharkey, M.J. (2000) Species richness of the Campopleginae and Ichneumoninae (Hymenoptera: Ichneumonidae) along a latitudinal gradient in Eastern North American old-growth forests. *Environmental Entomology*, **29**, 460–466.
- Smilanich, A.M., Dyer, L.A., Chambers, J.Q. & Bowers, M.D. (2009) Immunological cost of chemical defence and the evolution of herbivore diet breadth. *Ecology Letters*, **12**, 612–621.
- Smith, M.A., Woodley, N.E., Janzen, D.H., Hallwachs, W. & Hebert, P.D.N. (2006) DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera: Tachinidae). *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 3657–3662.
- 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 United States of America*, **104**, 4967–4972.
- 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 United States of America*, **105**, 12359–12364.
- Stehli, F.G., Douglas, R.G. & Newell, N.D. (1969) Generation and maintenance of gradients in taxonomic diversity. *Science*, **164**, 947–949.
- Stireman, J.O., III (2005) The evolution of generalization? parasitoid flies and the perils of inferring host range evolution from phylogenies. *Journal of Evolutionary Biology*, **18**, 325–336.
- Stireman, J.O., III (2008) α and β diversity of a tachinid parasitoid community over space and time. *Annals of the Entomological Society of America*, **101**, 362–370.
- Stireman, J.O., III (2016) Community ecology of the 'other' parasitoids. *Current Opinion in Insect Science*, **14**, 87–93.
- Stireman, J.O., III, Cerretti, P., Whitmore, D., Hardersen, S. & Gianelle, D. (2012) Composition and stratification of a tachinid (Diptera: Tachinidae) parasitoid community in a European temperate plain forest. *Insect Conservation and Diversity*, **5**, 346–357.
- Stireman, J.O., III, Dyer, L.A. & Greeney, H.F. (2017) Specialised generalists? Food web structure of a tropical tachinid-caterpillar community. *Insect Conservation and Diversity*, **10**, 367–384.
- Stireman, J.O., III, Greeney, H.F. & Dyer, L.A. (2009) Species richness and host associations of Lepidoptera-attacking Tachinidae in the northeast Ecuadorian Andes. *Journal of Insect Science*, **9**, 1–19.
- Stireman, J.O., III, O'Hara, J.E. & Wood, D.M. (2006) Tachinidae: evolution, behavior, and ecology. *Annual Review of Entomology*, **51**, 525–555.
- Stireman, J.O., III & Singer, M.S. (2003) Determinants of parasitoid-host associations: insights from a natural tachinid-lepidopteran community. *Ecology*, **84**, 296–310.
- Timms, L., Schwarzfeld, M. & Sääksjärvi, I.E. (2016) Extending understanding of latitudinal patterns in parasitoid wasp diversity. *Insect Conservation and Diversity*, **9**(1), 74–86.
- Townsend, C.H.T. (1927) On the *Cephenemyia* mechanism and the daylight-day circuit of the Earth by flight. *Journal of the New York Entomological Society*, **35**, 245–252.
- Turner, J.R.G. & Hawkins, B.A. (2004) The global diversity gradient. *Frontiers of Biogeography: New Directions in the Geography of Nature* (ed. by M.V. Lomolino and L.R. Hearn), pp. 171–190. Sinauer, Sunderland, MA.

- Valencia, R.R. (1995) Composition and structure of an Andean forest fragment in Eastern Ecuador. *Biodiversity and Conservation of Neotropical Montane Forests* (ed. by S. P. Churchill, H. Balslev, E. Forero and J.L. Luteyn), pp. p. 239–249. Aarhus Universitet, Afdeling for Systematisk Botanik, Denmark.
- Veijalainen, A., Wahlberg, N., Broad, G., Erwin, T., Longino, J. & Sääksjärvi, I.E. (2012) Unprecedented ichneumonid parasitoid wasp diversity in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4694–4698.
- Veijalainen, A., Sääksjärvi, I.E., Erwin, T.L., Gomez, I.C. & Longino, J.T. (2013) Subfamily composition of Ichneumonidae (Hymenoptera) from western Amazonia: insights into diversity of tropical parasitoid wasps. *Insect Conservation and Diversity*, **6**, 28–37.
- Wang, J., Tong, X. & Wu, D. (2014) The effect of latitudinal gradient on the species diversity of Chinese litter-dwelling thrips. *Zookeys*, **417**, 9–20.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics*, **34**, 273–309.
- Wiman, N.G. & Jones, V.P. (2013) Attack biology and egg maturation strategy of two tachinid parasitoids of leafroller (Lepidoptera: Tortricidae) pests in tree fruit. *Annals of the Entomological Society of America*, **106**, 485–490.
- Wood, D.M. (1987) Chapter 110 Tachinidae. *Manual of Nearctic Diptera. Volume 2. Agriculture Canada Monograph 28* (ed. by J. F. McAlpine, B.V. Peterson, G.E. Shewell, H.J. Teskey, J. R. Vockeroth and D.M. Wood), pp. p. 1193–1269. Canadian Government Publishing Centre, Hull, Canada.
- Wood, D.M. & Zumbado, M.A. (2010) Tachinidae (Tachinid flies, parasitic flies). *Manual of Central American Diptera* (ed. by B. V. Brown, A. Borkent, J.M. Cumming, D.M. Wood, N. E. Woodley and M.A. Zumbado), Vol. 2. NRC Research Press, Ottawa, Canada.
- Yuan, S., Huang, M., Wang, X., Ji, L. & Zhang, Y. (2014) Centers of endemism and diversity patterns for typhlocybina leafhoppers (Hemiptera: Cicadellidae: Typhlocybinae) in China. *Insect Science*, **21**, 523–536.

Accepted 23 March 2020