

**DRIVERS OF ICHNEUMONID WASP RICHNESS IN A TROPICAL BIODIVERSITY
HOTSPOT**

**Determinantes da Riqueza de Vespas Parasitoides Ichneumonidae (Hymenoptera) em um
Hotspot de Biodiversidade Tropical**

**Universidade Federal do Rio de Janeiro, Brazil
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SUMMARY

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INTRODUCTION

Earth's first-order biodiversity pattern is the latitudinal gradient in species richness (Krug et al. 2009), with species richness generally increasing from the poles to the equator (Gaston & Blackburn 2000). Although this pattern is one of the longest-described in ecology (Von Humboldt 1814), and has been described from a large number of terrestrial and marine taxa (Hillebrand 2004), the underlying drivers are still considerably debated (Rohde 1992, Willig et al. 2003). One line of inquiry which holds considerable potential for understanding latitudinal richness gradients, is to understand what controls variability around this gradient (Hillebrand 2004). A number of groups of insects and other animals have been proposed to exhibit exceptions to the normal gradient including aphids, sawflies, bumblebees, and the hyperdiverse parasitoid wasp family Ichneumonidae (Willig et al. 2003). This project will identify drivers of ichneumonid wasp species richness in a tropical biodiversity hotspot in order to better understand how this sizeable but understudied component of biodiversity is distributed and regulated. Understanding large scale biodiversity patterns is also vital for designing effective conservation strategies (Myers et al. 2000). Thus, this project will also contribute towards global efforts to halt biodiversity loss.

Ichneumonidae (Fig 1) is the most speciose family of parasitoid wasps (Hymenoptera), containing about 24,000 described species (Quicke 2012). Most recent workers think that the total richness of the family exceeds 100,000 species. Parasitoids are insects which develop by feeding in or on the body of another host arthropod host, eventually killing it (Eggleton & Belshaw 1992; Godfray 1994; Quicke 1997). Although several insect groups have parasitoid members, the greatest number is found in the order Hymenoptera, which accounts for nearly 75% of species (Feener & Brown 1997; Belshaw *et al.* 2003). The number of described Hymenoptera species is approximately 115 000 (LaSalle & Gauld 1993), but estimates of their total species richness range from 130 000 to 2.5 million (Brown 1982; Gauld & Bolton 1988; Gaston 1991; LaSalle & Gauld 1991; Stork 1997; Ulrich 1999), indicating that most species are still undescribed. The parasitic Hymenoptera are particularly poorly known: LaSalle and Gauld (1993) estimated that at least 77% of the species have not yet been described, while less than half of the species of one of the largest and better studied parasitic groups, the family Braconidae, have been formally described (Dolphin & Quicke 2001; Jones *et al.* 2009). Furthermore, taxonomic work is biased against the description of tropical and small-bodied species (Gaston 1993; Jones *et al.* 2009). Ichneumonid wasps therefore are an example of a hyperdiverse but under-studied and poorly-known element of biodiversity.

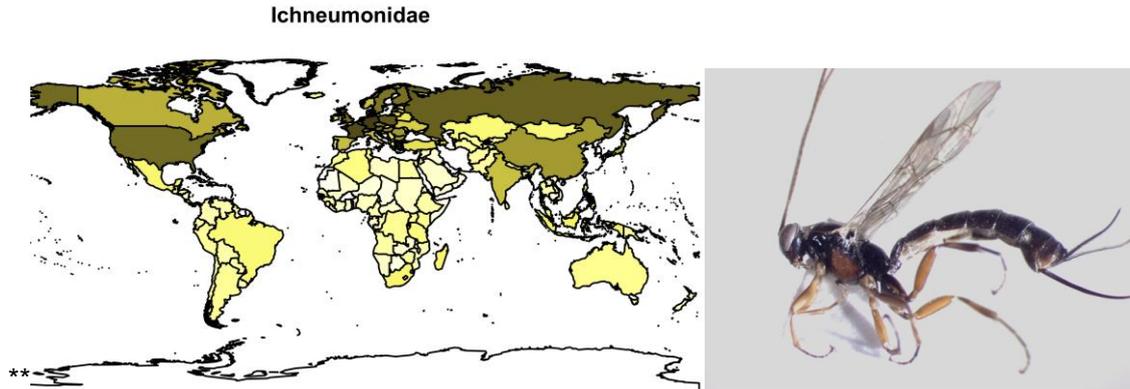


Fig. 1. Distribution (left) of ichneumonid genera by country (Max shading = 518 genera), illustrating the low described richness from tropical regions, from Quicke (2012). Right: a pimpline ichneumonid.

Parasitoids interact ecologically with many other species, both directly and indirectly, and thus contribute towards the structuring of animal communities and the regulation of populations in the second trophic level (Lewis et al., 2002; Tylianakis et al., 2007; Dyer et al., 2010). In spite of their ecological importance, relatively little is known about large scale diversity gradients in parasitoids. Studies based on data from field surveys initially suggested that, unusually, this family is less species rich in the tropics than in temperate regions (Fig. 1) (Owen & Owen 1974; Janzen & Pond 1975; Janzen 1981; Askew & Shaw 1986; Gauld 1986; Noyes 1989; Askew 1990; Hawkins & Compton 1992; Hawkins 1994; Skillen *et al.* 2000). In particular, the proportion of species that allow their host to continue to develop after parasitization (koinobionts) appears to increase with latitude in several studies (Quicke and Santos 2011). Koinobionts are often associated with high host-specificity, so this observation has been used to infer specific mechanisms which might limit ichneumonid species richness in the tropics (Hawkins 1994). However, there is a distinct possibility that this apparent trend is an artefact of biases in species sampling and description. In particular, tropical ichneumonid communities contain a high fraction of rare species which are often undercollected, especially in short-term field inventories (Sääksjärvi *et al.* 2004), whilst it is probable that small-bodied taxa suffer from taxonomic under-description (Quicke and Santos 2011, Quicke 2012).

More recent studies of tropical Ichneumonidae species richness (i.e. the group most famous for its anomalous diversity), based on intensive Malaise trap sampling (Fig 2), have shown that at least for several studied taxa, tropical species richness exceeds that of well-studied temperate regions (Gaston 1993; Sääksjärvi *et al.* 2004, Veijalainen et al. 2012). However, these studies are still extremely limited both spatially and taxonomically. For example, until 2004 there was not a single set of intensive samples from the whole of tropical

South America (Sääksjärvi *et al.* 2004), where samples still remain confined to parts of Western Amazonia. Most tropical regions, including many biodiversity hotspots, remain completely unsurveyed. Effort has also been limited largely to the subfamily Pimplinae (Fig 2), which largely comprises medium-sized to large species.

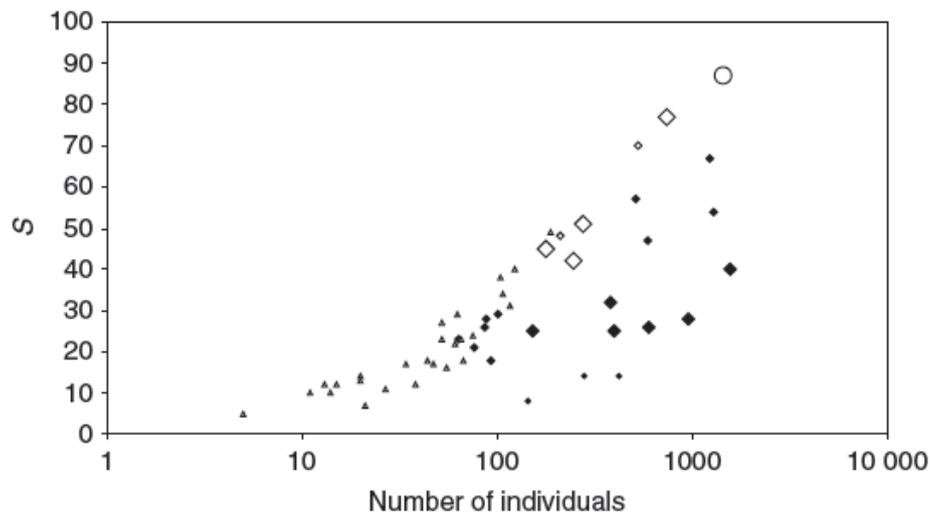


Fig 2. High richness of recent intensive samples of Pimplinae ichneumonids from Western Amazonia (open symbols), showing the increasing richness with increasing sampling intensity. From Sääksjärvi *et al.* (2004)

Most recently, Veijalainen *et al.* (2013) reported the subfamily abundance composition of ichneumonids collected in the lowland rain forests of Ecuador and Peru. Contrary to common assumptions, a number of ichneumonid subfamilies were found to be very abundant and presumably species rich in the western Amazon Basin (Fig 3). However, certain subfamilies (e.g. those whose primary hosts are rare in the tropics: Ctenopelmatinae, Tryphoninae) may still be more diverse in the temperate than in tropical zones. Thus, each ichneumonid subfamily (the taxonomic unit generally employed in these diversity studies) displays unique combinations of behavioural traits that defy attempts to generalise across the whole family (Veijalainen, 2012).

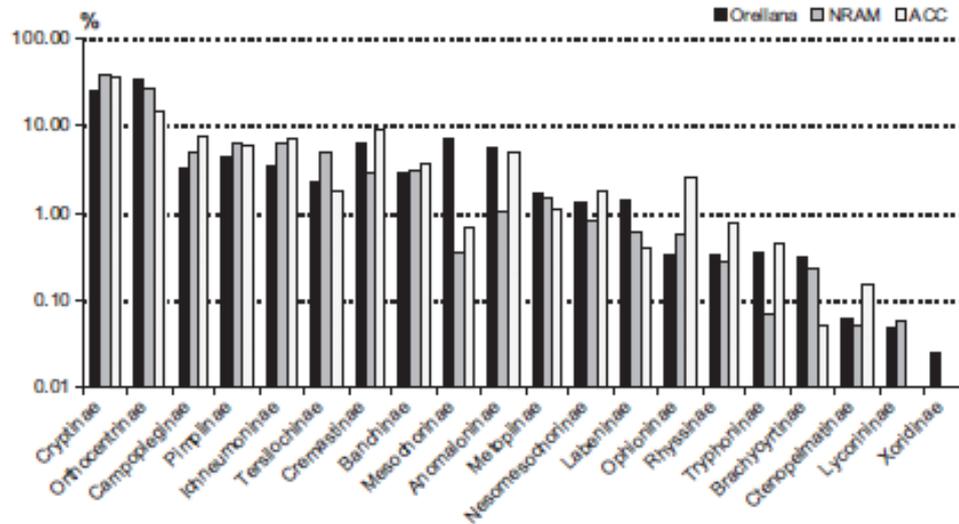


Fig. 3. Proportional subfamily abundance of some recent collections of ichneumonids (Veijalainen et al. 2013) from Western Amazonia (Ecuador and Peru), showing relatively high abundance of some koinobiont subfamilies such as Orthocentrinae, and Banchinae, previously thought to be rare in tropical communities. Ecuador, Orellana (Orellana); Peru, Loreto (NRAM); Peru, Madre de Dios (ACC).

As well as latitude, and its interactions with subfamily biology, researchers have investigated other potential drivers of parasitoid richness over large spatial scales. Altitude (Fig 4) is a variable that, like latitude, is expected to exert a strong influence on species richness. In better known taxa such as birds, regions with high altitudinal ranges contain many more species for their latitude than those with no altitudinal variation (Davies et al. 2007). Since many species have narrow physiological thermal tolerances and they are specialised for living conditions at specific elevations and habitats (Janzen 1967a, Colwell et al. 2008, Deutsch et al. 2008), species in tropical mountainous areas are sensitive to accelerating anthropogenic habitat modifications, including global warming (Chen et al. 2009). Many species in these areas are under a great risk of going extinct before their scientific documentation and study has taken place. The limited studies of tropical ichneumonids conducted to date suggest that those taxa that inhabit high altitudes in tropical regions tend to be more common at high latitudes (Veijalainen, 2012), and this aids an understanding of which subfamilies are likely to be richer in the tropics.

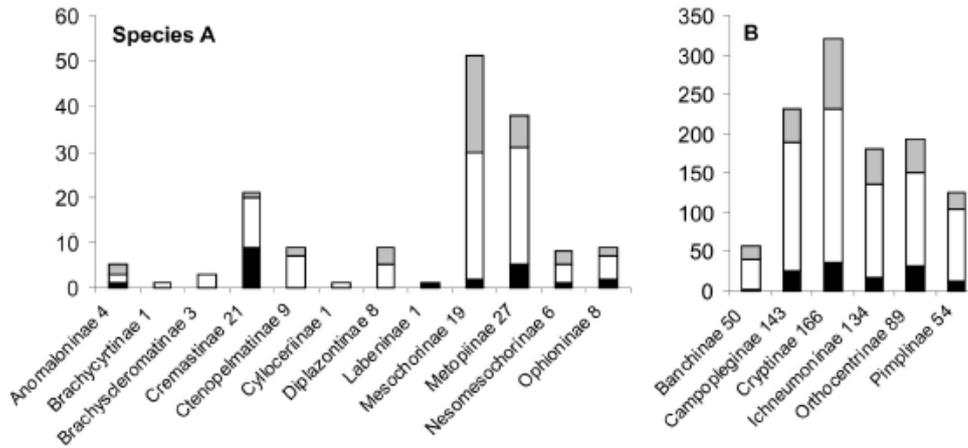


Fig. 4. Ichnumonid subfamily richness at different altitudes in Mesoamerica (grey=high, white = medium, black = low altitudes) from Veijalainen (2012). **A**: relatively rarely observed subfamilies (<80 individuals), **B**: relatively frequently observed subfamilies.

Latitude and altitudinal variation are extremely valuable practical predictors of biodiversity change as they are easily recorded for a given locality. The same can be said of vegetation structure and composition. Relative to other biotic predictors, vegetation is relatively easily surveyed across sites and is widely used in conservation prioritizing. Previous studies have suggested that vegetation holds some power to predict ichneumonid species richness: both Fraser et al. (2007) and Sääksjärvi *et al.* (2006) found an association between plant species richness and richness in the ichneumonid subfamily Pimplinae (Fig 5), although in the former study this was not replicated in the subfamily Diplazontinae. The association likely follows from the higher range of hosts and other resources required by parasitoids in habitats that contain many plant species (Shaw 2006). The lack of such a correlation for Diplazontinae may be because they are parasitoids of predatory insects, hence less directly dependent on the richness of producers. However, these ideas have not been tested more broadly within the subfamily within natural ecosystems.

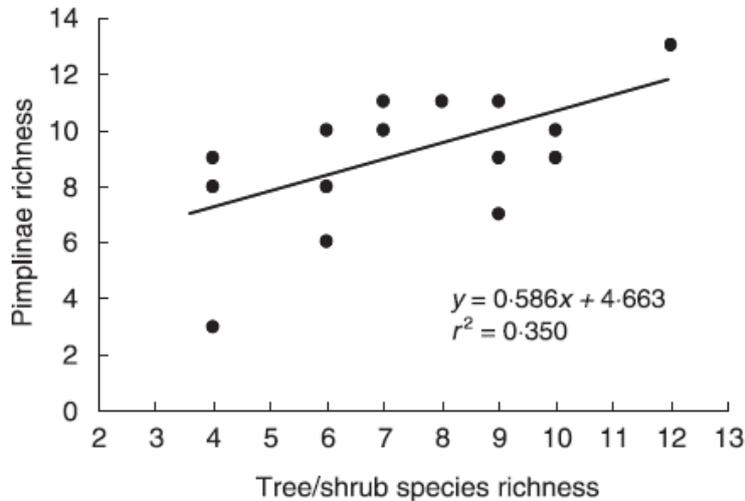


Fig. 5. The increase in Pimplinae richness with tree/shrub richness from Fraser et al. (2007).

Tropical biodiversity is disappearing at an alarming rate owing to human activities (Bass et al., 2010), accentuating the need for accurate assessments of biodiversity. However, conservation assessments almost never take into account parasitoids, which, given their immense richness and potential susceptibility to extinction, calls into question the utility of conservation initiatives which ignore them (Shaw and Hochberg 2001). Given the lack of even basic information on parasitoid richness, distributions and the factors determining them, there is a risk that this large fraction of biodiversity will suffer disproportionately by ignorance or neglect. By providing information on how rich are tropical assemblages, how such richness varies spatially and taxonomically, how it is predicted by altitude, local climate, and vegetation, we will provide information that can permit conservationists to make informed assessments of which locations are likely to have high richness of parasitoid wasps, thus beginning to close the knowledge gap necessary to provide them with effective conservation (Fraser et al 2009).

Our proposal is timely as the distribution and conservation of under-studied biodiversity is a subject of increasing and broad interest given the urgent need to halt tropical biodiversity loss and given the small but growing number of studies attempting to address this. It will reach a broad readership as the drivers of tropical diversity are the subject of perennial interest both with ecologists, conservationists, and the general public worldwide. It has a high potential for novel discoveries as the group we study is very diverse, and our study site is part of a biodiversity hotspot in which ichneumonid distributions have never been systematically surveyed, whilst the total number of surveys of tropical ichneumonid richness remain very small. Our study proposal brings together a range of unique and essential

expertise both local to the study regions and from international colleagues who have excellent track records of publishing related work in high impact international journals.

Goals and objectives

1. To make extensive, replicated, and standardized collections of ichneumonid wasps over a wide range of altitudes, and consequent climatic and vegetation types, at Serra dos Órgãos National Park, Brazil.
2. To identify these specimens as far as taxonomically feasible within the time-frame of the project, and at least to subfamily and morphospecies, and to deposit representative specimens in publically accessible collections for future taxonomic work.
3. To train a PhD student in a range of scientific and transferable skills, and afford them valuable experience related to the project in order to enhance their prospects of a future career in research or elsewhere.
4. To critically analyze the data in (2) to test the following hypotheses and publish the results in high impact international journals.

Hypotheses

1. That the local species richness of ichneumonids is high relative to other comparable studies in tropical and temperate regions (see e.g. Veijalainen 2012, Sääksjärvi et al. 2004).
2. That koinobiont subfamilies (e.g. Anomaloninae, Banchinae, Cremastinae, Orthocentrinae) generally thought to have low richness in the tropics, are amongst the most abundant and species-rich ichneumonid subfamilies collected (e.g. Veijalainen et al. 2012).
3. That ichneumonid species richness is correlated with habitat structural diversity (e.g. Fraser et al. 2007, Saaksjaarvi et al. 2006).
4. That ichneumonid species richness is highest at mid-elevations or high elevations (e.g. Veijalainen et al. 2012), and that assemblages turn over more between locations at different altitudes than between locations of the same altitude.
5. That ichneumonid species richness is highest in warmer and wetter environments along an altitudinal gradient, reflecting species-energy theory.
6. That local plant structural diversity are more important determinants of ichneumonid species richness than local climate or altitude *per se*. It is not clear whether to expect climate, altitude or vegetation to be better local predictors of richness, but our data will enable us to ask this question for the first time.

7. That the relationships described in 1, 3-6 are different for different subtaxa of Ichneumonidae.

MATERIAL AND METHODS

Field work will be carried out at Serra dos Órgãos National Park, in the Atlantic Forest in Rio de Janeiro State, Southeast Brazil (Figure 6). It is one of the oldest National Parks in the country and now covers an area of 20,024 ha with higher elevations nearing 2,200 m. The Park encloses four different phytophysionomies within the domain of the tropical Atlantic Rain Forest which are related to temperatures and rainfall: submontane forest (up to 500 m), montane (500-1500 m), high-montane (1300-1800 m) and high altitude grassland, named *campos de altitude* (starting at 1800 m) (Rizzini 1954; Veloso *et al.* 1991). The climate in the region is tropical mesothermic (Köppen 1936), with a short relatively dry season, mild summers and lower temperature due to the altitude (Figure 7).

In 2009, Flinte *et al.* compared temperature and precipitation data between 980 m and 2,140 m altitudes from December 2007 to August 2008 and found that the mean temperature difference was 7.2°C, representing a decrease of approximately 0.62°C for each 100 m altitude. This matches almost exactly the variation of 0.6°C per 100 m altitude described in the literature (Odgen & Powell 1979). According to Flinte *et al.* (2009) rainfall volume was lower at the higher altitude (total of 311.2 mm difference).

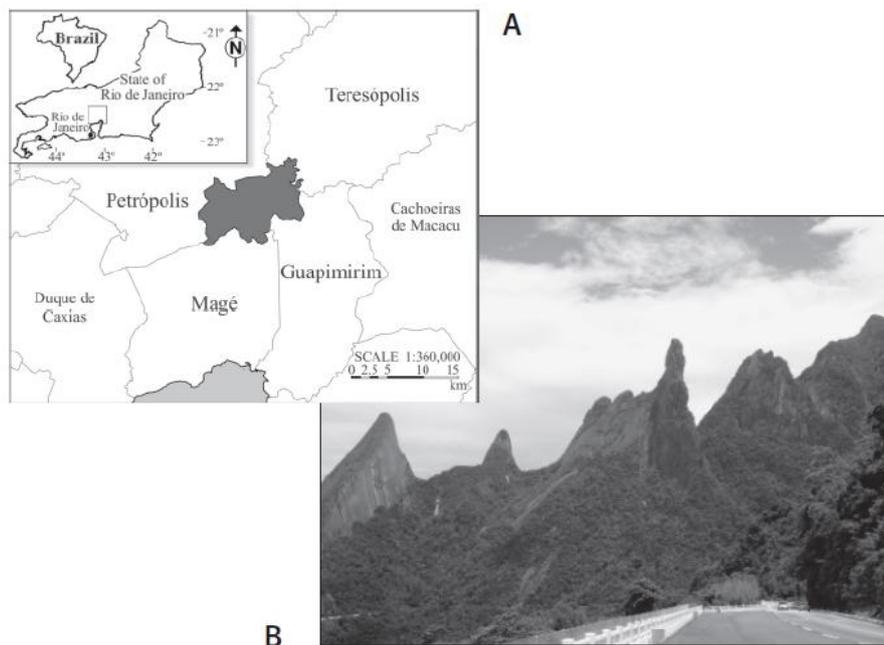


Fig 6.. Location of the Serra dos Órgãos National Park in the State of Rio de Janeiro (A) and picture of the mountain summits, including the nationally famous *Dedo de Deus* ("God's Finger") at the center (B). From Flinte *et al.* (2009).

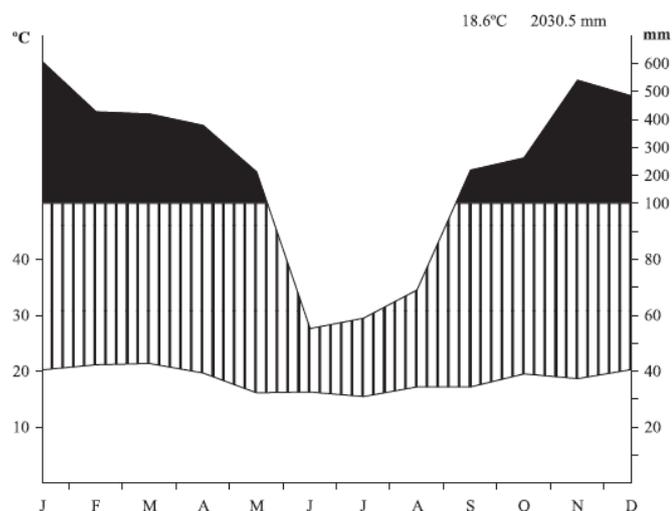


Fig. 7. Climatic diagram of the Serra dos Órgãos National Park (meteorological station at 980 m altitude, from the National Institute of Meteorology), compiled for the period of January 2007 to November 2008. Striped area= humid period; Black area= superhumid period. From Flinte et al. (2009).

Six altitudes (300m, 650m, 1000m, 1350m, 1700m, 2050m) will be sampled for the Ichneumonidae by Malaise traps, a form of flight-interception trap widely recognized for being effective at collecting flying Hymenoptera. Two traps will be set at each altitude, 50m apart from each other set along each of two altitudinal transects. These traps will be set for two consecutive months in the wet and in the dry seasons and the trap bottle will be changed after 15 days making four samples per Malaise and 16 per altitude during the “dry” (July and August) and 16 more during the wet (January and February) seasons in 2014 and 2015. Thus, the total number of trap months will be 192, which compares favourably with the most extensive samples in previous studies, and will allow us the best chance of accurately estimating asymptotic richness in the local sampled community.

The specimens collected will be identified to subfamilies first of all, and then further to subtribes and/or genera, and finally to morphospecies (i.e., hypothetical groups of species based on their external characteristics without formally assigning the specimens to species). Use of morphospecies is necessary since it is likely that a very high proportion of the species collected will be undescribed. Confidence in our identifications will be provided by the involvement of Dr Ilari Sääksjärvi (Turku, Finland) who is a world authority on Neotropical Ichneumonidae. Example specimens will be deposited with important ichneumonid collections in museums (e.g. Natural History Museum London, Zoological Museum, Turku, Museu de Zoologia de São Paulo, Brazil) to enable future taxonomic study.

To complement the Ichneumonidae data we will take vegetation and climatic data local to each trap. Climatic data (temperature and rainfall or relative humidity) will be taken during the Malaise sampling periods by means of automatic dataloggers which will be rotated around the trap sites over a series of days. Data for individual trap locations will be provided by interpolation across the whole data series. Habitat characteristics will, following Fraser et al. (2007), include a survey of a 20m quadrat surrounding each trap location, sampled both during the wet and dry collection period. It will include tree/shrub density; ground cover, canopy cover, plant architectural diversity and plant height diversity, following sampling design of Fraser et al. (2007).

Data Analyses

Asymptotic species richness (i.e. total richness taking into account estimated unsampled species) across all traps and samples will be estimated using non-parametric methods (e.g. ACE, Chao1 and Jack2) and compared with similar studies from other tropical studies. Comparable raw datasets to which we have access through our collaborators include Western Amazonia (Sääksjärvi et al 2004, 2006), as well as ongoing studies in Uganda and French Guiana, (along with published summary statistics from all other relevant previous studies). It is likely that joint publication of these datasets will increase the profile of the publications. These analyses will form the basis of statements about the extent of local ichneumonid richness relative to that at other tropical and temperate localities (Hypothesis 1).

Comparing sampled and estimated asymptotic richness across all samples for the different subfamilies, comparable with other species lists (e.g. Yu et al. 2005) will allow us to test whether koinobiont families are especially rich in our samples compared to other faunas more generally (Hypothesis 2).

For Hypotheses 3-7, there will be several analytical stages (see Fraser et al. 2007). Preliminary analyses will investigate pairwise associations, controlling for multiple comparisons, between ichneumonid richness estimates, diversity indices, and community measures (such as the 1st axis scores of a Principal Components Analysis) and explanatory variables at a trap level. However, it is possible that a) interactions between explanatory variables exist b) that the significance of variables depends on which other variables are entered, and c) that traps are not fully independent of each other due, for example to spatial autocorrelation. To account for these issues we will conduct a series of analyses of greater complexity, including stepwise multiple regressions, and general linear mixed-effect models in which trap is nested as a random factor within altitudinal location, and 15-day period is nested within season and year. Spatial turnover across traps (Hypothesis 4) will be investigated by Mantel tests of association between matrices of pairwise spatial distances and of

community similarity scores (see Fraser et al. 2008), as well as ANOVA of the effect of trap location on pairwise community similarity scores (see Fraser et al. 2008).

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TIMETABLE (trimestral)

	2014				2015				2016			
	1	2	3	4	1	2	3	4	1	2	3	4
Material organization	X											
Visits to the study site to define the points to set up the traps	X	X										
Peter Mayhew visit to Brazil for one month			X				X				X	
Setting up the traps and collection			X		X		X		X			
Vegetation and weather surveying			X		X		X		X			
Additional visits to the area				X		X		X		X		
Insect sorting			X	X	X	X	X	X	X	X		
Insect identification				X	X	X	X	X	X	X		
Data analyses				X	X	X	X	X	X	X	X	
Writing papers					X	X	X	X	X	X	X	X