

Assessing the species richness of Afrotropical ichneumonid wasps with randomly placed traps provides ecologically informative data

T. Hopkins^{1*}, H. Roininen², I.E. Sääksjärvi¹

¹*Zoological Museum, Biodiversity Unit, FI-20014 University of Turku, Finland*

²*Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland*

**To whom correspondence should be addressed. E-mail: tapani.e.hopkins@utu.fi*

Keywords: Africa, Kibale National Park, Ichneumonidae, rainforest, species diversity, random trap placement

Abstract

The tropical ichneumonid wasps are poorly sampled, particularly in the Old World, despite their ecological importance and high species richness. Existing inventories also tend to have had a taxonomic focus, with trap placement reflecting the need for maximal sample size rather than rigorous ecological comparisons. Here, we report the results of an intensive sampling effort at Kibale National Park, Uganda, carried out with randomised trap locations.

We sampled ichneumonid faunas for a year (2011-2012) with Malaise traps, in eight successional sites ranging from clearcut exotic plantations to primary rainforest. The traps were situated in ten random locations at each site and were moved between locations once a week. The total sampling effort encompassed 231 trap months (using traps smaller than the standard size), one of the largest we know of from a single Afrotropical location. We sorted the collected ichneumonids into subfamilies and investigated whether their community composition differed between the sites.

Ichneumonid faunas differed between forest and former plantation sites, with both the overall difference and that of four subfamilies significant. Our sample size was unexpectedly small (1212 individuals), but we estimate that the model-based analyses we used could still have given a significant result with a smaller (954 individual) sample.

Overall, randomly placed Malaise traps detected ecological patterns in Afrotropical ichneumonid distributions. Our data also showed that there is a rich and at least partly undescribed ichneumonid fauna still awaiting discovery in the Afrotropical rainforests. Future inventories of this fauna may, however, have to compromise on objective random trap placement in order to get a large sample size.

Introduction

Tropical rainforests host a bewildering diversity of species, many of which remain poorly known or undiscovered. The ichneumonid wasps are no exception. This ecologically important parasitoid family is extremely diverse (probably over 100 000 species worldwide as estimated by Gauld 2002) and is found on all continents with the exception of Antarctica (Yu et al. 2011). Yet its tropical

diversity is still very poorly known. Indeed, until very recently ichneumonids were believed to be so species-poor in the tropics that they became a textbook example of an anomalous latitudinal diversity gradient - and numerous hypotheses have tried to explain why they do not follow the conventional pattern of greatest diversity in the tropics (Owen & Owen 1974, Janzen & Pond 1975, Rathcke & Price 1976, Janzen 1981, Gauld 1987, Gauld et al. 1992). This belief has lost ground after extensive surveys in the Neotropical region, especially in Amazonia (Sääksjärvi et al. 2004, Veijalainen et al. 2012, Veijalainen et al. 2013) revealed countless undiscovered tropical species and very high local species richness, but has yet to be conclusively disproved (Quicke 2012).

Extensive long-term surveys appear to be required to adequately inventory tropical ichneumonid faunas (Sääksjärvi et al. 2004). However, such surveys represent a distinct minority in the tropics, and the few studies carried out to date concentrate mainly on Central America (Gauld 1991 and subsequent publications) and Western Amazonia (Sääksjärvi et al. 2004 and subsequent publications). A number of localities in South Africa have also been extensively sampled, e.g. Hantam Botanical Gardens which was surveyed for a total of 258 trap months, but the data has not yet been analysed (Simon van Noort pers. comm.). Other tropical areas have not been equally extensively surveyed, and the Old World rainforests may well harbour largely unexplored faunas. Townes (1969), for example, estimated that only 15% of the ichneumonid species occurring in the Ethiopian (i.e. Afrotropical) region had been reported in 1969. Currently the described fauna of the Afrotropics includes only 2097 ichneumonid species in 26 subfamilies and 360 genera (Yu et al. 2011, van Noort 2017), a mere fraction of the estimated total of 12100 species (Townes & Townes 1973, van Noort 2017). A limited number of assessments have been conducted in Sierra Leone and Uganda (Owen & Owen 1974), Namibia (van Noort et al. 2000), Gabon (van Noort 2004), the Central African Republic, Tanzania, Uganda and South Africa (van Noort pers. comm.).

Ichneumonids have an important ecological role in regulating population densities of other insects and spiders (Gauld & Bolton 1988, and e.g. Várkonyi et al. 2002, Morris et al. 2004, Roslin et al. 2013). They are parasitoids of other arthropods, so their numbers and diversity reflect that of their hosts and (indirectly) of other species such as plants that the hosts use (May 1988, Sääksjärvi et al. 2006, Basset et al. 2012). Also, their position high in the food web means they are likely to be sensitive to ecological disturbances; the first organisms to be visibly affected when communities are disturbed. Their main drawback when it comes to ecological research is their relatively low tropical population densities, which makes it difficult to collect large representative samples of the local species pool (Sääksjärvi et al. 2004).

Of the many methods used to collect ichneumonids, Malaise traps are the most efficient for large scale inventories of the local mobile species. These tent-like traps collect flying insects continuously and can be placed in large numbers in the field, often resulting in large catches with relatively little effort. This gives a representative view of which species are present and (to some extent) of their relative abundances.

Conventionally, Malaise traps are placed with some care on the likely flight paths of ichneumonids. This maximises sample sizes since ichneumonids, along with other insects, generally fly along specific paths. It does, however, make the process of placing traps subjective: researchers generally rely on experience to choose a good spot with criteria which are not particularly quantifiable, nor easy to describe objectively. When the focus is faunistic or taxonomical (e.g. listing the species present in an area) such a sampling is not a problem. But if the focus is on an ecological hypothesis (e.g. comparing the fauna of different forest types) a different approach may be preferable. Possible

alternatives include randomising trap locations, situating traps on a regular grid, or some other objective way of deciding beforehand where the traps will be placed.

In this work, we began a long-term project aimed at repeating the Amazonian ichneumonid inventories (Sääksjärvi et al. 2004) in Africa, by carrying out an intensive sampling of Afrotropical ichneumonids with randomly placed Malaise traps. Our aim was to assess the suitability of the resulting material for ecological research. The traps were located in eight ecologically distinct sites in Kibale National Park, Uganda. Specifically, we asked if differences in subfamily composition could be discerned on a successional gradient from clearcut plantations to partially logged forest to undisturbed primary forest (such as have been detected for other taxa; e.g. Nyafwono et al. 2014).

Materials & Methods

Study site

The Malaise traps were placed near the Makerere University Biological Field Station (0°35' N 30°20' E; approximately 1500 m a.s.l.) in Kibale National Park (795 km²), Western Uganda. The park contains medium altitude moist evergreen forests as well as swamps, grasslands, woodland thickets and colonizing shrubs (Struhsaker 1997, Chapman & Lambert 2000) and is surrounded by agricultural land, including tea plantations and small farms. It was formerly closely connected to the forest of the Congo Basin although this connection has deteriorated due to human activity (Chapman & Chapman 1997, Naughton-Treves 1998). There are two wet and two dry seasons each year (Chapman et al. 1999).

In Kibale, the traps were located in eight sites of varying successional status (Fig. 1). Four former conifer plantations were clearcut at different times and left to naturally regenerate into rainforest: R03, R01, R98 and R93 (clearcut between 2002-2004, 2000-2001, 1995-1999 and 1987-1994 respectively). These had regenerated for an average of 9, 11, 14 and 19 years at the time of our study, and have in earlier work been referred to as RAC9, RAC11, RAC14 and RAC19 (Nyafwono et al. 2014). Two forest sites were partially logged in 1968-1969 and had regenerated for 43 years: K13 (50% basal area reduction during logging, also treated with the arboricide Finopal DT) and K15 (40% basal area reduction). The remaining two forest sites are primary forest and have experienced minimal disturbance. Site K30 was minimally logged (2-3 trees / km²) before 1970, and site K31 has confusingly been referred to both as primary untouched forest (e.g. Nyafwono et al. 2014) and as heavily logged forest (Struhsaker 1997). Our traps were located in what we believe to be an unlogged part of K31, with most traps in the southern half of the site (the area called K32 by Olupot 2000).

The above eight sites form a successional gradient from primary forest to recently clearcut plantation (K31, K30, K15, K13, R93, R98, R01, R03). This gradient can be divided into successional classes at many different resolutions; in this work, we primarily grouped the sites into the two successional classes of forest (K31, K30, K15, K13) and former plantation (R93, R98, R01, R03). We chose this grouping due to our relatively small sample size, which did not allow the sites to be analysed separately.

Malaise traps

We used 30 Malaise traps to collect flying insects from the different sites during Sep 2011 - Oct 2012. The traps were of a relatively small size (140 × 55 cm vertical trap surface, covered by a narrow triangular roof) and lacked rain covers over the sample containers, since we wanted to make

them easy to move between sites. Insects were preserved in ethanol. We emptied the traps at one week intervals.

At each forest site, we used ten random locations for the traps. The four former plantation sites had an average of ten random locations per site, but the amount varied between sites. The locations are the same as used by Nyafwono et al. (2014) for collecting fruit-eating butterflies, though the plantation sites have since been renamed.

Since there were many more locations (80) than available traps (30), we kept traps in the same location for a week then moved them to adjacent locations. The traps were evenly distributed among the eight sites at all times, and each location was sampled several times per season. The total sampling effort was 1006 samples, i.e. roughly 7042 trap days or 19.3 trap years. There were 442 samples which contained ichneumonids. Nine of these samples were excluded from analyses due to their trap location being lost.

The samples were sorted into orders at the Estonian University of Life Sciences under the coordination of Olavi Kurina. We then pinned all the ichneumonid specimens and sorted them into subfamilies. The ichneumonids are deposited at the Zoological Museum of the University of Turku (ZMUT), Finland.

Statistical analyses

To analyse how ichneumonid faunas differ between sites, we used a mix of distance-based and modelling-based approaches. We first visualised differences between sites with non-metric multidimensional scaling. Then, since the results of the visualisation suggested a difference between forest and former plantation sites, we estimated the relative abundance of each subfamily in forest and former plantation with generalised linear models. We also analysed the difference between forest and former plantation separately with distance based methods. Finally, we estimated the minimum sample size needed to detect a significant difference between forest and former plantation.

We visualised differences in community composition between sites with non-metric multidimensional scaling (function ‘metaMDS’ of the R package *vegan*; Oksanen et al. 2016). Since catch sizes differed between sites, we first standardised the data by dividing by each site’s total. Distances between sites were calculated using Bray-Curtis dissimilarities.

We estimated the expected catch size of each subfamily in forest and former plantation by fitting generalised linear models (GLM) to our data (package *mvabund* of the R software; Wang et al. 2016). We assumed negative binomial errors and a log link function, and calculated 95% confidence intervals by bootstrapping the trap sites. To test if the catch differed between forest and former plantation, we calculated likelihood ratios for each subfamily and compared these to a null distribution (acquired by resampling our trap sites 999 times). We tested the significance of the overall difference between forest and former plantation (sum of likelihood ratios) by the same method. To adjust for possible false positive results, we also calculated subfamily significance levels which were corrected for multiple testing (using a step-down resampling procedure; Wang et al. 2016).

We also used distance-based methods to test if the catch differed between forest and former plantation. These are analogous to the GLMs, but use Bray-Curtis distances between trap sites. We tested if the distances between forest and former plantation were significantly greater than within

these two areas with permutational manova (function ‘adonis’ of the R package *vegan*; Oksanen et al. 2016). We also assessed which subfamilies contributed to the difference using a modified form of the *simper* procedure. Conventional *simper* uses average forest-plantation distances to calculate contributions and performs poorly if there is a high variance in taxa abundances (Warton et al. 2012), which we tried to alleviate by using the overall forest-plantation distance instead. The analysis was otherwise identical to conventional *simper*, and was based on the ‘*simper*’ function of the R package *vegan* (Oksanen et al. 2016).

To estimate the minimum sample size needed to get a significant result, we took random subsamples of our data, and checked how large a subsample was needed for the GLMs to consistently identify a significant forest-plantation difference. We resampled the trap sites (with replacement) 400 times for each investigated sample size, and required that at least 95% of the resamplings be identified as significant by the GLMs. To decrease computation time, we used Poisson distributed errors instead of negative binomial - we expect this to have little effect on the overall result.

All analyses were carried out in the R software, version 3.2.1 (R Core Team 2015). The complete analyses and data are available online (Hopkins et al. 2017).

Results

A total of 1212 ichneumonid wasps were caught in 433 samples. These belonged to 17 different subfamilies. Non-metric multidimensional scaling suggested that the ichneumonid community composition differed between forest and former plantation sites (Fig. 2).

The expected catch sizes in forest and former plantation differed (manyglm $p=0.009$; Fig. 3). Four subfamilies had significantly different catch sizes (manyglm $p<0.05$; Fig. 3), but all except Ichneumoninae could potentially be false positives (Ichneumoninae manyglm $p=0.02$ after adjusting for multiple testing).

Permutational manova did not detect a significant difference between forest and former plantation communities ($p=0.059$; $F_{1,78}=1.86$). However, modified *simper* identified three subfamilies that significantly contributed to the (insignificant) difference: Ichneumoninae, Orthocentrinae and Anomaloninae with 20%, 17% and 10% contributions.

Resampling suggested that 63 trap sites (out of 80) would have been sufficient to get a significant overall difference between forest and former plantation (manyglm $p\leq 0.05$ in at least 95% of resamplings).

Discussion

Sampling the Afrotropical ichneumonid fauna with randomly placed Malaise traps resulted in ecologically informative data, even with a catch containing relatively low numbers of individuals. We detected differences in ichneumonid community composition between the two ecologically distinct habitats of forest and clearcut former plantation (with model-based if not distance-based statistical methods). We were also able to quantify how the individual subfamilies were distributed between these two habitats, and identify at least one subfamily (Ichneumoninae) which was significantly more abundant in one habitat than in the other. Analysing the distributions at a finer resolution than forest versus former plantation would require a larger data set, but we note that our

data also suggests the existence of finer scale patterns: a possible separation between successional older and younger former plantation sites (Figure 2).

Randomising trap locations provided statistically robust and ecologically informative data, but at the possible cost of an extremely small sample size. We caught an average of 1.2 ichneumonids per one-week sample. Typical catches for our Amazonian inventories are about 30 ichneumonids per trap week (e.g. Veijalainen et al. 2013), and have been even larger in our later, currently unpublished Afrotropical sampling at the same site. Our choice of sampling design may have contributed to this low sample size: we optimised the design for ecological comparisons by selecting a large number of randomly located trap sites, and regularly moving traps between them. This means that we did not place the traps near perceived insect flight paths as is conventional in Malaise trapping. Furthermore, the need to regularly move traps led to our using relatively small, simple traps that lacked rain covers. Thus, our low sample size suggests there may be a trade-off between objective trap placement (i.e. random trap locations, multiple sites per trap) and sample size.

It is clear that further ichneumonid taxa remain to be discovered at the site. Of the seventeen subfamilies we found, two (Lycorininae and Sisyrustolinae) were represented by a single individual. There were also no specimens of the subfamily Rhyssinae in the material, despite our having caught several species of this subfamily in later (currently unpublished) samplings. At the species level, it should be noted that the material contains a large number of undescribed species: three new species of Tersilochinae have already been described from this material (Khalaim et al. 2014).

Of the two statistical approaches we used, generalised linear models (GLM) performed distinctly better than distance-based methods for our data. The better statistical power of GLMs (c.f. Warton et al. 2012) proved especially important for our relatively small dataset: indeed, if we had relied on distance-based methods alone we would have detected no significant difference between forest and former plantation communities. In contrast, resampling our data suggested that a smaller sampling of 63 trap sites (79% of our data, ca. 954 ichneumonids) would still have given a significant result with GLMs. Both approaches, however, gave qualitatively similar results. The subfamily Ichneumoninae, for example, was highlighted by both analyses as being especially unevenly distributed between the two habitats.

Overall, we have demonstrated that Afrotropical ichneumonid communities can successfully be inventoried with randomly placed Malaise traps. Even very small samples ($n < 1000$ individuals) can reflect ecological gradients at the study site, especially if analysed with model-based rather than distance-based methods. There also appears to be a rich and at least partly undescribed ichneumonid fauna awaiting discovery in the Afrotropical rainforests. Future inventories, however, may have to compromise on objective trap placement if large sample sizes are desired.

Acknowledgements

This study was partly funded by the Finnish Cultural Foundation, Oskar Öflunds Stiftelse and the Helsinki Entomology Society (grants to TEH), and by the Finnish Academy (HR, Grant No. 138899). Isaiah Mwesige, John Koojo and Richard Sabiiti maintained the Malaise traps and ably carried out a whole range of other field work. Olavi Kurina (Estonian University of Life Sciences, Estonia) organised the sorting of the samples into higher taxonomic groups. Our field research was supported by the staff of the Makerere University Biological Field Station. Members of the University of Turku Amazon Research Team (UTU-ART) gave helpful comments on the statistical

methods, and two anonymous reviewers on the manuscript as a whole. These contributions are gratefully acknowledged.

The required research permits were issued by the Uganda National Council of Science and Technology and the Uganda Wildlife Authority.

References

- BASSET Y, CIZEK L, CUÉNOUD P, DIDHAM RK, GUILHAUMON F, MISSA O, NOVOTNY V, ØDEGAARD F, ROSLIN T, SCHMIDL J, TISHECHKIN AK, WINCHESTER NN, ROUBIK DW, ABERLENC H, BAIL J, BARRIOS H, BRIDLE JR, CASTAÑO-MENESES G, CORBARA B, CURLETTI G, DUARTE DA ROCHA W, DE BAKKER D, DELABIE JHC, DEJEAN A, FAGAN LL, FLOREN A, KITCHING RL, MEDIANERO E, MILLER SE, GAMA DE OLIVEIRA E, ORIVEL J, POLLET M, RAPP M, RIBEIRO SP, ROISIN Y, SCHMIDT JB, SØRENSEN L & LEPONCE M 2012. Arthropod Diversity in a Tropical Forest. *Science* **338**: 1481–1484.
- CHAPMAN CA & CHAPMAN LJ 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* **29**: 396–412.
- CHAPMAN CA & LAMBERT JE 2000. Habitat alteration and the conservation of African primates: A case study of Kibale National Park, Uganda. *American Journal of Primatology* **50**: 169–185.
- CHAPMAN CA, WRANGHAM RW, CHAPMAN LJ, KENNARD DK & ZANNE AE 1999. Fruit and flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology* **15**: 189–211.
- GAULD ID 1987. Some factors affecting the composition of tropical ichneumonid faunas. *Biological Journal of the Linnean Society* **30**: 299–312.
- GAULD ID 1991. The Ichneumonidae of Costa Rica, 1. *Memoirs of the American Entomological Institute* **47**: 1–589.
- GAULD ID 2002. The Ichneumonidae of Costa Rica, 4. *Memoirs of the American Entomological Institute* **66**: 1–768.
- GAULD ID, GASTON KJ & JANZEN DH 1992. Plant allelochemicals, tritrophic interactions and the anomalous diversity of tropical parasitoids: the "nasty" host hypothesis. *Oikos* **65**: 353–357.
- GAULD I & BOLTON B 1988. *The Hymenoptera*. Oxford University Press & British Museum (Natural History), London.
- HOPKINS T, ROININEN H & SÄÄKSJÄRVI I 2017. *Kibale National Park Malaise trapping 2011-2012 data and analyses*. <https://dx.doi.org/10.6084/m9.figshare.3172780>.
- JANZEN DH 1981. The peak in North American ichneumonid species richness lies between 38 degrees and 42 degrees N. *Ecology* : 532–537.
- JANZEN DH & POND CM 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.
- KHALAIM AI, SÄÄKSJÄRVI IE & ROININEN H 2014. Three new Afrotropical species of Tersilochinae (Hymenoptera: Ichneumonidae) from the Kibale National Park, Uganda. *Zootaxa* **3794**: 536–544.
- MAY R 1988. How many species are there on earth? *Science* **241**: 1441–1449.
- MORRIS RJ, LEWIS OT & GODFRAY HCJ 2004. Experimental evidence for apparent competition in a tropical forest food web. *Nature* **428**: 310–313.
- NAUGHTON-TREVES L 1998. Predicting patterns of crop damage by wildlife around Kibale National Park, Uganda. *Conservation Biology* **12**: 156–168.
- NYAFWONO M, VALTONEN A, NYEKO P & ROININEN H 2014. Butterfly Community Composition Across a Successional Gradient in a Human-disturbed Afro-tropical Rain Forest. *Biotropica* **46**: 210–218.
- OKSANEN J, BLANCHET FG, FRIENDLY M, KINDT R, LEGENDRE P, MCGLINN D, MINCHIN PR, O'HARA RB, SIMPSON GL, SOLYMOS P, STEVENS MHH, SZOECS E & WAGNER H 2016. *vegan: Community Ecology Package*. R package version 2.4-0. <http://CRAN.R-project.org/package=vegan>.
- OLUPOT W 2000. Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology* **14**: 833–843.
- OWEN D & OWEN J 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* **249**: 583–584.
- QUICKE DLJ 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.
- R CORE TEAM 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- RATHCKE BJ & PRICE PW 1976. Anomalous Diversity of Tropical Ichneumonid Parasitoids: A Predation Hypothesis. *The American Naturalist* **110**: 889–893.
- ROSLIN T, WIRTA H, HOPKINS T, HARDWICK B & VÁRKONYI G 2013. Indirect interactions in the high arctic. *PLoS One* **8**: e67367.
- SÄÄKSJÄRVI IE, HAATAJA S, NEUVONEN S, GAULD ID, JUSSILA R, SALO J & BURGOS AM 2004. High local species richness of parasitic wasps (Hymenoptera: Ichneumonidae; Pimplinae and Rhyssinae) from the lowland rainforests of Peruvian Amazonia. *Ecological Entomology* **29**: 735–743.
- SÄÄKSJÄRVI IE, RUOKOLAINEN K, TUOMISTO H, HAATAJA S, FINE PV, CÁRDENAS G, MESONES I & VARGAS V 2006. Comparing composition and diversity of parasitoid wasps and plants in an Amazonian rain-forest mosaic. *Journal of Tropical Ecology* **22**: 167–176.

- STRUHSAKER TT 1997. *Ecology of an African rain forest: logging in Kibale and the conflict between conservation and exploitation*. University Press of Florida, Gainesville, Florida, USA.
- TOWNES H 1969. The Genera of Ichneumonidae, part 1. (Hymenoptera: Ichneumonidae). *Memoirs of the American Entomological Institute* **11**: 1–300.
- TOWNES H & TOWNES M 1973. A catalogue and reclassification of the Ethiopian Ichneumonidae. *Memoirs of the American Entomological Institute* **19**: 1–416.
- VAN NOORT S 2004. Ichneumonid (Hymenoptera: Ichneumonoidea) diversity across an elevational gradient on Monts Doudou in Southwestern Gabon. *California Academy of Sciences Memoir* **28**: 187–216.
- van Noort S 2017. *Waspweb - Ichneumonidae of the Afrotropical Region*. <http://www.waspweb.org/Ichneumonoidea/Ichneumonidae/>. 29.9.2017.
- VAN NOORT S, PRINSLOO GL & COMPTON SG 2000. Hymenoptera, excluding Apoidea (Apiformes) & Formicidae (Insecta). *Cimbebasia Memoir* **9**: 289–364.
- VÁRKONYI G, HANSKI I, ROST M & ITÄMIES J 2002. Host-parasitoid dynamics in periodic boreal moths. *Oikos* **98**: 421–430.
- VEIJALAINEN A, SÄÄKSJÄRVI IE, ERWIN TL, GÓMEZ IC & LONGINO JT 2013. Subfamily composition of Ichneumonidae (Hymenoptera) from western Amazonia: Insights into diversity of tropical parasitoid wasps. *Insect Conservation and Diversity* **6**: 28–37.
- VEIJALAINEN A, WAHLBERG N, BROAD GR, ERWIN TL, LONGINO JT & SÄÄKSJÄRVI IE 2012. Unprecedented ichneumonid parasitoid wasp diversity in tropical forests. *Proc Biol Sci* **279**: 4694–8.
- WANG Y, NAUMANN U, WRIGHT S, EDELBUETTEL D & WARTON D 2016. *mvabund: Statistical Methods for Analysing Multivariate Abundance Data*. R package version 3.11.9. <http://CRAN.R-project.org/package=mvabund>.
- WARTON DI, WRIGHT ST & WANG Y 2012. Distance-based multivariate analyses confound location and dispersion effects: Mean-variance confounding in multivariate analysis. *Methods in Ecology and Evolution* **3**: 89–101.
- Yu D, van Achterberg C & Horstmann K 2011. *Taxapad database, Ichneumonidae 2011*. <http://www.ichneumonoidea.name/taxapadmain.php>. 18.5.2017.

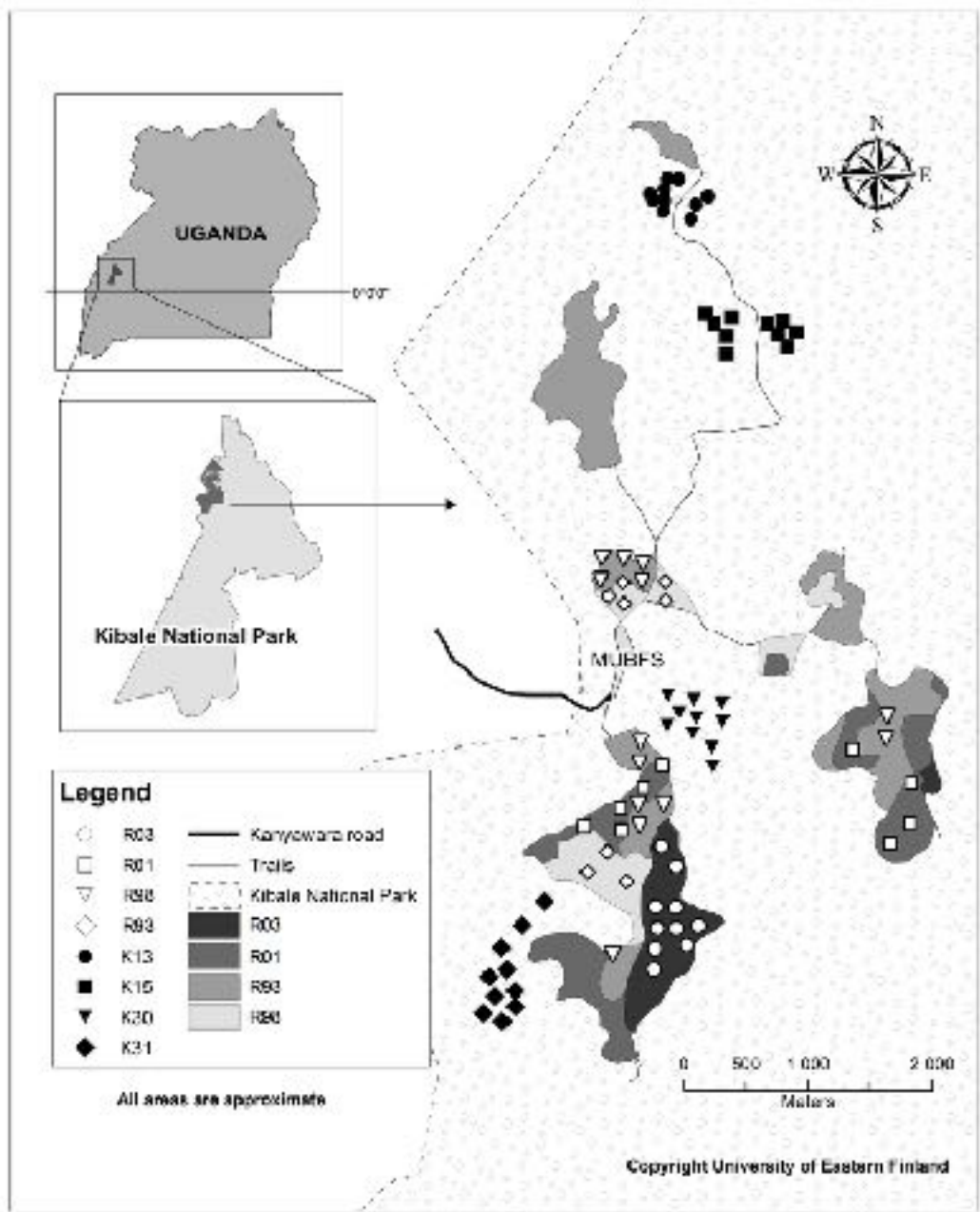


Figure 1. The study site, Kibale National Park in south-western Uganda. Malaise traps were located in clearcut former plantation of varying ages (R93 to R03), partially logged forest (K13 & K15), and primary forest (K30 & K31).

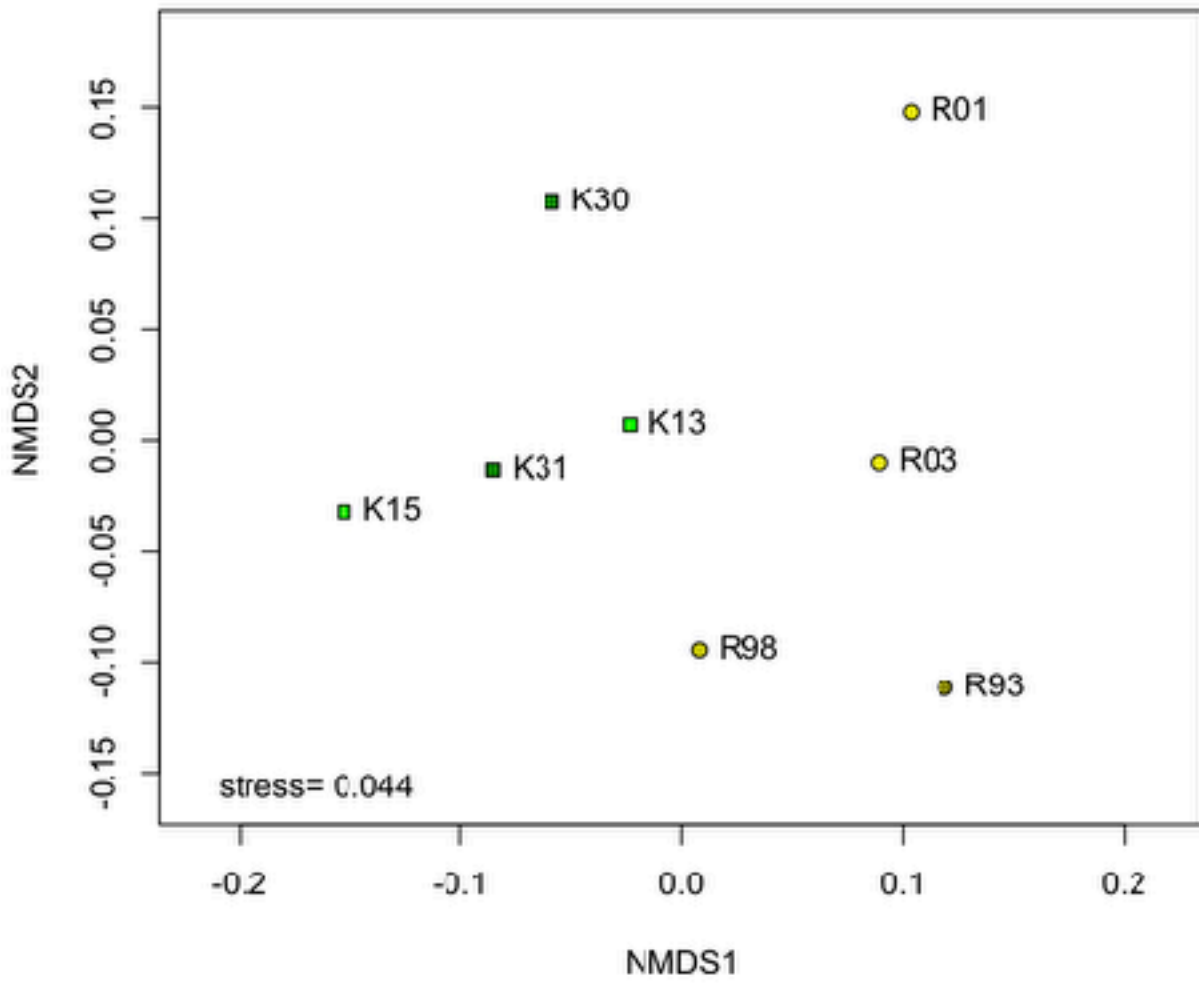


Figure 2. Visualisation of the Bray-Curtis distances between sites (non-metric multidimensional scaling). The forest sites (K31, K30, K15, K13) differed from former plantation sites (R93, R98, R01, R03).

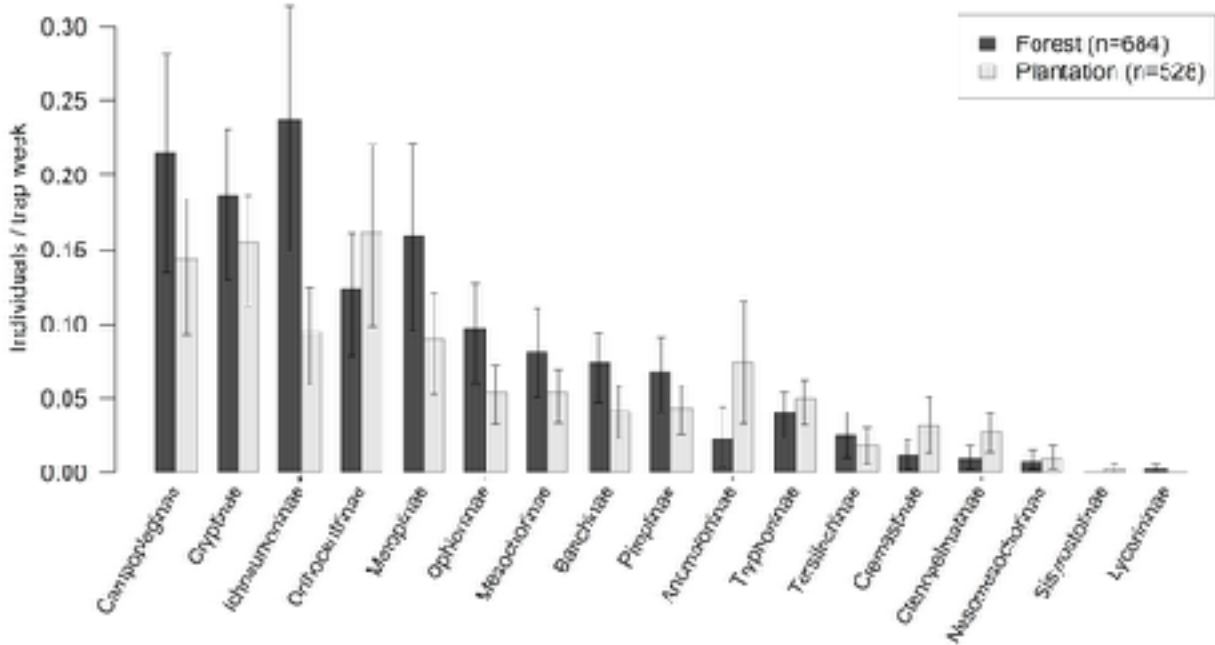


Figure 3. Expected catch sizes for each ichneumonid subfamily in forest and former plantation, as individuals per one week sample. Generalised linear models identified four subfamilies (marked with either a dot or *) as differing significantly between forest and former plantation. Of these, all except Ichneumoninae (marked with a *) could potentially be false positives. Error bars display 95% confidence intervals calculated by bootstrapping the original data. Subfamilies are in order of abundance, with Campopleginae the most common and Lycorinae represented by only one individual.