TURUN YLIOPISTO

Local species richness of parasitoid wasps (Ichneumonidae: Pimplinae) in Ugandan tropical forest

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Abstract

It has been suggested that the highly species-rich Ichneumonidae family of parasitoid wasps has an anomalous latitudinal diversity gradient, peaking in species richness outside the tropics. Extensive studies of the family in the tropics, especially in the Afrotropics, are scarce. Here, I study the local species richness and biological composition of pimplines (Ichneumonidae: Pimplinae) in the Afrotropics. The samples were collected 9/2014–9/2015 with 32 Malaise traps in four forest types and farmland in Kibale National Park, Uganda. They are a subset of 108.5 trap months of the total sample size of 373.5 trap months. I produced species rarefaction curves of sorted species to model species accumulation rates by habitat type and biological pimpline group. A total of 1,925 pimplines in 112 species were collected. Trapping accumulated species slower in farmland than in forest types. Species accumulation rates differed between all four biological pimpline groups, with the accumulation rates of species of koinobiont ectoparasitoids of spiders differing between forest types. Few rarefaction curves were near stabilizing, suggesting that the local fauna was incompletely sampled. These are the first results of the species richness of pimplines caught with extensive Malaise trapping in the Afrotropics. The biological composition of the local fauna was typical, with most collected species being idiobiont parasitoids of weakly concealed hosts. At a given number of individuals sampled, only a few pimpline collections in the Neotropics surpass the observed species richness. The observed richness lends no support to the purported anomalous latitudinal diversity gradient of the family.

Keywords: biological composition, Hymenoptera, idiobiont parasitoid, Kibale National Park, koinobiont ectoparasitoid, latitudinal diversity gradient, species rarefaction

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1 Introduction

1.1 The species-rich Ichneumonidae

It is well known that tropical areas support more species-rich communities than extratropical areas in both aquatic and terrestrial systems (Hillebrand, 2004; Brown, 2013). This is expressed by a latitudinal diversity gradient (LDG) of increasing species richness from the poles to the equator (Hillebrand, 2004; Mittelbach et al., 2007). Nevertheless, some groups are known to be exceptions to this trend in having greater species numbers in higher latitudes than in the tropics (Cerezer et al., 2022). It has been suggested that the highly species-rich Ichneumonidae family of parasitoid wasps is among these exceptions in exhibiting an "anomalous" LDG that peaks in species richness outside the tropics (Owen & Owen, 1974; Janzen & Pond, 1975; Janzen, 1981). However, this suggestion has been called into question by recent studies revealing unexpectedly species-rich ichneumonid faunas in tropical regions, especially in the Neotropics (e.g. Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Veijalainen et al., 2012; Gómez et al. 2017; Higa & Penteado-Dias, 2020; Camargo et al., 2022; Flinte et al., 2023).

The Ichneumonidae family is a cosmopolitan group of Hymenoptera that is among the most diverse insect groups on this planet. They are parasitoids that feed on arthropods, usually insects, i.e. one or more parasitoid larvae feed on a host's tissues, resulting in the host dying either in the process of the wasp's development or of venom used in oviposition (Quicke, 2015). This way, in addition to some adult ichneumonids killing prey in destructive host-feeding, they have a key role in regulating population densities of many arthropods (Briggs & Hoopes, 2004; Liu & Ueno, 2012). These features of their life cycle have resulted in some ichneumonid species being successfully used in biological control of pest insect populations in agriculture (Sarfraz et al., 2005; Wang et al., 2019). Already half a century ago it was estimated by Townes (1969) that there could be around 60,000 ichneumonid species in the world, with more recent estimates being more than 100,000 species partly due to poorly studied tropical regions housing more species than previously thought (Gauld, 1997). If the latter estimate is close to the actual number of mere extant species, Ichneumonidae might well be the most species-rich animal family on this planet throughout its history.

1.2 Latitudinal diversity gradient

The LDG of the Ichneumonidae family has generated much discussion after Owen and Owen (1974) first suggested it to be anomalous or "inverse" in terms of temperate areas supporting

more species-rich faunas than the tropics (e.g. Janzen & Pond, 1975; Rathcke & Price, 1976; Janzen, 1981; Gauld, 1987, 1991; Gauld et al., 1992; Gauld & Gaston, 1994; Sääksjärvi et al., 2004; Santos & Quicke, 2011; Timms et al., 2015; Gómez et al., 2017). The relatively low diversity (or total absence) of some ichneumonid groups (e.g. Orthopelmatinae and Tryphonine) in the tropics can be explained by a shortage of their primary host groups (Quicke, 2015). Nevertheless, additional explanations are required to explain the suggested anomality of the LDG of the family because many host groups, such as Coleoptera and Lepidoptera, exhibit their highest species richness in the tropics (Kocher & Williams, 2000; Andrew & Hughes, 2004; Pinkert et al., 2022).

Five main hypotheses have been put forward to explain the purported anomalous LDG of parasitoid wasps, particularly Ichneumonidae (Santos & Quicke, 2011): (1) According to the resource fragmentation hypothesis, the high diversity of hosts in the tropics results in hosts being rare, making it difficult for specialist parasitoids (i.e. koinobionts; see description of ichneumonid life strategies below) to maintain viable populations on such rarely encountered and scattered host populations (Janzen & Pond, 1975; Janzen, 1981); (2) The predation hypothesis states that the higher predation pressure on herbivores, likely disproportionately more on parasitized herbivores, in the tropics renders immature stages of their parasitoids vulnerable to higher predation rates than their temperate counterparts (Rathcke & Price, 1976); (3) Another predation type hypothesis in Gauld (1987) postulates that adult parasitoids experience higher predation pressure in the tropics as a result of having to spend additional time exposed searching for scarcer hosts; (4) The interphyletic competition hypothesis suggests that parasitoid diversity is reduced in the tropics due to parasitoids being outcompeted in host usage by other parasitoid groups that are likely more diverse in the tropics (Eggleton & Gaston, 1990); (5) The nasty host hypothesis proposes that tropical herbivores accumulate more chemical toxins from plants than their temperate counterparts, making tropical herbivores generally more unfit as hosts for parasitoids (Gauld et al., 1992; Gauld & Gaston, 1994).

It is important to note that the abovementioned five hypotheses are not mutually exclusive but may serve as explanations of different ecological features affecting the LDG of parasitoids. Additionally, most of these hypotheses predict that the LDG of koinobionts should be more affected by the mentioned difficulties of forming and maintaining species-rich communities in the tropics (Santos & Quicke, 2011). There is some support for the prediction that koinobionts exhibit stronger adherence to an anomalous LDG than idiobionts (e.g. Askew & Shaw, 1986; Gauld, 1986; Askew, 1990). However, the purported anomalous LDG of ichneumonids may at

least partly be a result of vastly incomplete sampling in the tropics and biased taxonomic efforts (Santos et al., 2010; Santos & Quicke, 2011). This is highlighted by relatively recent studies indicating that tropical faunas are highly species-rich for at least some ichneumonid groups (e.g. Gauld, 1991; Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Smith et al., 2008; Veijalainen et al., 2012; Flinte et al., 2023).

1.3 Sampling of ichneumonids

Many attempts at estimating and comparing the species richness of ichneumonids at different sites have been limited by an insufficient sampling effort (Quicke, 2012; Gómez et al., 2017). Several variables need to be considered in establishing sampling parameters for obtaining reliable species richness estimates (Morrison et al., 1979; Quicke, 2015). Firstly, all seasons within at least one year should be sampled to include seasonal variation in the abundance of species. Secondly, the sampling needs to cover variation in local habitat types, considering both small- and large-scale variation. Thirdly, as ichneumonid collections are characterized by high numbers of rarely caught species, the sample sizes will likely need to be quite exhaustive, measured in e.g. trap months (Owen & Owen, 1974; Gauld, 1991; Sääksjärvi et al., 2004). Different trap types would ideally be used to capture species that may be inefficiently sampled by any one trap type, e.g. Malaise traps, flight intercept traps, and pan traps (Quicke, 2015). However, the trap type needs to be the same for comparing trap catches, which means it may be more practical to adopt a widely used and generally efficient trap type (Darling & Packer, 2012). Consequently, Malaise traps are recommended for extensive sampling of ichneumonids for this purpose (see description of Malaise traps below). Failure to consider the abovementioned variables in sampling may result in local species not being collected or in a false impression of the rarity of some species, a result of their suboptimal sampling rather than actual rarity. Additionally, the obtained estimate of species richness may be inaccurate and may not be comparable to that of other locations.

Few tropical sites have been extensively sampled, with Afrotropical sites lagging behind in faunistic research of ichneumonids compared with relatively recent sampling in the Neotropics (e.g. Gauld, 1991; Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Veijalainen et al. 2012, 2014; Flinte et al. 2023). The Afrotropical ichneumonid fauna is poorly known with respect to most subfamilies but has been estimated to be highly species-rich (Meier et al., 2024). Meier et al. (2024) estimated that only 13–22% of the ichneumonid species of the five most extensively studied countries in the Afrotropics are known. They also estimated 9,206–15,577 ichneumonid

species within the Afrotropics, which is manifold compared to the mentioned 2,322 recorded species, although the estimate was still deemed probably too low for various reasons. No studies investigating the species richness of individual subfamilies in the Afrotropics seem to have been conducted with sufficiently large sample sizes for reliable estimates except for Hopkins et al. (2018, 2019a,b, 2024) which focused on the relatively small Rhyssinae subfamily. This leaves considerable gaps in the knowledge of the LDG of the family, even affecting estimates of global animal diversity. Moreover, with accurate up-to-date knowledge of the diversity of parasitoid wasps in Afrotropical sites, trends in their diversity can be monitored and conservation efforts of parasitoids can more effectively be implemented where most needed (Flinte et al., 2023). Serious conservation efforts directed at parasitoid wasps will in any case benefit from first describing the composition of the local fauna to assess its conservation potential.

The Pimplinae subfamily is commonly used as a representative clade of Ichneumonidae in diversity gradient studies due to the family being highly diverse both taxonomically and biologically, making it more practical to study its features in parts (e.g. Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Gómez et al., 2017; Flinte et al., 2023). The emerging picture of the LDG of the Pimplinae subfamily indicates that it may be more species-rich in the Neotropics than in temperate regions (Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Gómez et al., 2017). Gómez et al. (2017) found fewer pimpline and rhyssine species in Afrotropical collections than at Peruvian sites. However, of the sites in the Afrotropics, the Ugandan site with the largest sample size consisted of only 50 individuals, which is too small to draw reliable conclusions about species richness. The current number of 174 described pimpline species (in 23 genera) that have been recorded from the Afrotropics is likely only a fraction of the actual number of species occurring in the area (Meier et al., 2024; van Noort, 2024).

1.4 Aims and purpose of thesis

In this thesis, I study the species richness and biological composition of the subfamily Pimplinae of the Ichneumonidae family using specimens collected by an extensive sampling campaign in Ugandan tropical forest. I analyse species richness in different habitat types in the study area, reflecting how richness is distributed spatially, and between biological pimpline groups, indicating how the biological composition of the local fauna is structured. Based on previous research on the subfamily in other tropical sites, I expect to uncover a comparably species-rich pimpline fauna, disclosing parts of the unknown richness of parasitoid wasps in the Afrotropics (Gauld, 1991; Sääksjärvi et al, 2004; Gómez et al. 2017; Flinte et al., 2023).

2 Material and methods

2.1 Study organisms

2.1.1 The Ichneumonidae family

There are currently over 24,000 described species of ichneumonids in about 1,600 genera split into 41 subfamilies (Aguiar et al., 2013; Bennett et al., 2019). Ichneumonid parasitoids can be classified into two categories based on the location of the larvae's development relative to the host: (1) endoparasitoids develop inside the host's body and (2) ectoparasitoids develop on the host's external surface with their mouthparts penetrating the exoskeleton (Quicke, 2015). Furthermore, they can be classified into two additional categories based on regulation of their host's growth: (1) idiobionts kill or permanently paralyse their host at oviposition while (2) koinobionts allow their host to continue developing after oviposition (Askew & Shaw, 1986).

Idiobiont and koinobiont life strategies are known to be associated with many life history traits and are often treated as surrogate concepts for them as direct records of life history traits are frequently lacking (Askew & Shaw, 1986; Shaw, 1994; Jervis et al., 2001; Quicke, 2015). For example, idiobionts typically attack concealed hosts, have long adult life spans after short larval development times, and develop eggs in their ovaries during their adult life, i.e. synovigenesis. Additionally, with many idiobionts being ectoparasitoids, they can avoid most of their host's immune defences, or if they are endoparasitoids they are associated with attacking host stages with reduced defence capability, i.e. eggs and pupae, more so than koinobionts (Hawkins, 1994; Quicke, 2015). Avoidance of host defences is thought to allow idiobionts to develop on a variety of hosts within a single niche type; they are thus considered generalist parasitoids (Askew & Shaw, 1986; Shaw, 1994; Quicke, 2015). Conversely, koinobionts typically attack relatively exposed hosts, have short adult life spans following long larval development times, and have most of their eggs already matured at eclosion, i.e. pro-ovigenesis. Moreover, koinobionts are typically endoparasitoid specialists with narrower host ranges than idiobionts in terms of their hosts being either closer related phylogenetically or more similar ecologically (Askew & Shaw, 1986; Shaw, 1994; Quicke, 2015). The higher degree of specialization in koinobionts is principally explained by koinobionts having to adapt to withstand a prolonged and more intensive interaction with the defences of their active hosts, which facilitates specialization on hosts on which they can develop successfully (Askew & Shaw, 1986; Quicke, 2015).

2.1.2 The Pimplinae subfamily

The Pimplinae subfamily has a cosmopolitan distribution, is sufficiently species-rich, and is one of the most studied subfamilies of Ichneumonidae, all of which make it a suitable group for comparative species richness studies (Quicke, 2015). Pimplinae is a relatively large subfamily with about 1,700 described species in about 79 genera (Broad et al., 2018). However, what sets the Pimplinae subfamily apart is how biologically diverse it is in exhibiting unusually many life strategies for a single subfamily (Gauld, 1991; Broad et al., 2018). Most pimpline species are idiobiont ectoparasitoids of immature stages of holometabolan insects (i.e. insects with complete metamorphism) or idiobiont endoparasitoids of lepidopteran or hymenopteran pupae. Species of the *Polysphincta* genus group are koinobiont ectoparasitoids of spiders, another exceptional feature of the Pimplinae (Gauld & Dubois, 2006).

2.2 Study specimens

2.2.1 Sorting of parasitoid wasp samples

Collected samples were processed by various workers at the Zoological Museum of the University of Turku (ZMUT), where members of Ichneumonoidea (Braconidae and Ichneumonidae) were separated and a random subset of the samples pinned; all samples were deposited at ZMUT. However, a fraction of the smaller Ichneumonoidea specimens were likely left unprocessed, possibly including some small pimplines. I separated all specimens of Pimplinae from a pinned subset consisting of random Ichneumonoidea samples. I then sorted the pimpline specimens into morphospecies (henceforth referred to as species) mostly via systematically sorting them first into tribes, then into genus groups, and then into genera using mainly keys and diagnoses in Gauld (1991) and Townes (1969). Throughout the sorting process, I generally sorted female specimens first due to them having more reliable diagnostic characters. This often allowed me to subsequently connect males to corresponding female species. I was unable to identify the genus of nine male specimens of the tribe Ephialtini and thus excluded them from the samples of this thesis. This should have minimal impact on the results. Species delimitation was based on finding at least one morphological character (or a combination thereof) that was unique to the species. Differences in colouration were of secondary importance and generally supported differing morphological characteristics. I did not treat differences in colouration as sufficient for species delimitation on their own as they are known to vary greatly within tropical ichneumonid species (Gauld, 1991). The species

delimitation was verified by Ilari Sääksjärvi. I did not identify the sorted species into described species as there are currently no identification manuals available for Afrotropical Pimplinae and I suspected that many of the species were undescribed.

2.2.2 Classification of Pimplinae

To study the biological composition of the local pimpline fauna, I classified them into four categories based on life strategies following Gauld (1991) and Sääksjärvi et al. (2004): (1) idiobiont parasitoids of deeply concealed hosts (IDC; females of this group generally have long ovipositors for oviposition into deep substrates such as wood); (2) idiobiont parasitoids of weakly concealed hosts (IWC; females of this group generally have shorter ovipositors than the former group for attacking exposed hosts or hosts hiding in shallow substrates such as leaf rolls); (3) koinobiont ectoparasitoids of spiders (KES; all genera of this group belong to the *Polysphincta* genus group); (4) pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders (Pseudo/IES).

2.3 Study area

Samples were collected near the Makerere University Biological Field Station (0.5625°N, 30.3561°E; about 1500 m above sea level) in Kibale National Park (795 km^2), located slightly north of the equator in Western Uganda (figure 1). Kibale National Park (KNP) is a protected area that contains medium altitude moist evergreen forest in addition to swamps, grasslands, woodland thickets, and colonizing shrubs and is bordered by anthropogenic landscapes, mainly agricultural land, that have cut off its former connection to the forest of the Congo Basin (Struhsaker, 1997; Naughton-Treves, 1998; Chapman & Lambert, 2000). The mean minimum and maximum daily temperatures in the area are about 16 °C and 24 °C, respectively, and the annual rainfall is about 1,700 mm, which is seasonally distributed into two dry seasons (December–February and June–August) and two wet seasons (March–May and September–November; Chapman et al., 1999).

I adopted the ordering of the main habitat types of the study area into successional classes from Hopkins et al. (2019a, 2024), ordered from least to most disturbed: primary forest (including swampy primary forest), disturbed forest, clearcut plantation, and farmland (figure 1). Sampled regions in the primary forest sites (K30, K31) had either likely not been logged at all or had experienced minimal logging more than 54 years before the sampling (Chapman & Lambert, 2000). These minimally disturbed sites were divided into swampy primary forest with

waterlogged ground (e.g. swamp or stream) and primary forest without waterlogged ground. Sites classified as disturbed forest (K14, K15, K13) have been estimated to have lost anywhere from about 25% to 50% of their trees by partial logging and had 46 years to regenerate (Chapman & Lambert, 2000; Duclos et al., 2013; Owiny et al., 2016). Clearcut plantation sites were former conifer plantations that had been clearcut relatively recently and left to regenerate (Nyafwono et al., 2014). These encompassed four sites (R03, R01, R98, R93) that had an average time of 12, 14, 17, and 22 years to regenerate, respectively. The vegetation near traps R93T1 and R93T2 were typical of disturbed and primary forest, respectively, and were classified accordingly despite being located at a clearcut plantation site. The traps were likely in an unlogged or rapidly recovered part of the R93 site. The farmland site was located a bit outside KNP and is considered an extra site alongside the forest sites (figure 1). The study area was described in greater detail in Hopkins et al. (2019a), where it was also noted that many of the successional sites were quite heterogenous, with the disturbed forest sites having been unevenly logged and the primary forest in the area being a varied mosaic of different habitat patches that varied in at least elevation, moisture, soil, and vegetation.

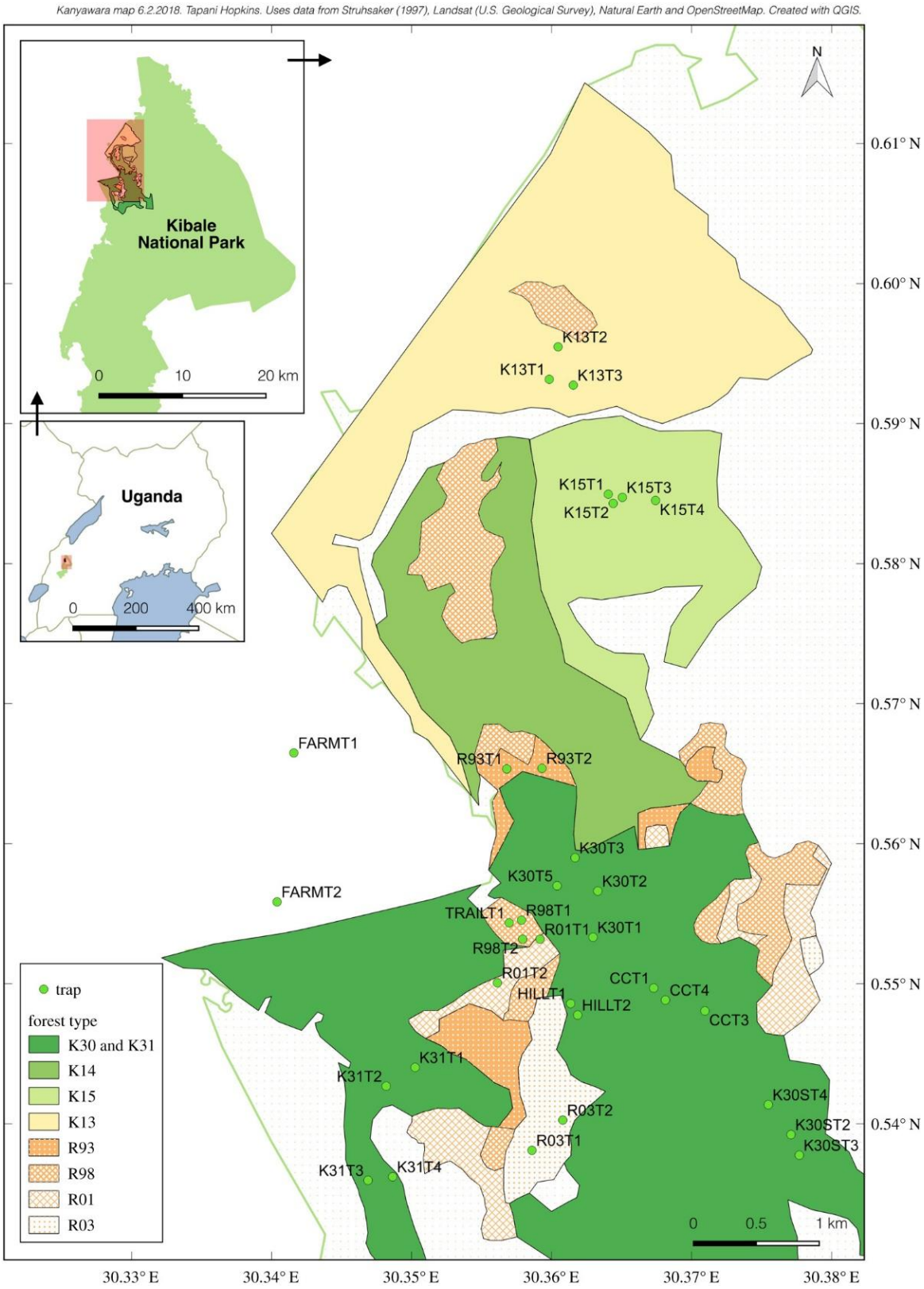

Figure 1. Map of the study area in Kibale National Park, Uganda. The full sampling campaign (9/2014–9/2015) included 34 Malaise traps (32 here) in primary forest (K30, K31, vegetation by trap R93T2), disturbed forest (K14, K15, K13, vegetation by trap R93T1; here no samples from K13T2), clearcut plantation (R93, R98, R01, R03; here no samples from R01T1), and farmland (FARM; just outside the park). From Hopkins et al. (2019a). CC BY 4.0.

2.4 Sampling methods

Samples were collected with Malaise traps for one year (8 September 2014–14 September 2015) to cover all seasons. Malaise traps are tent-like traps that passively collect flying insects, whose flight paths are stopped by the trap's fine mesh netting. Once stopped, the netting guides upward going insects to the highest corner of the trap, from where they fall into a chamber with preservative agent. The agent used here was about 80% ethanol that was emptied along with its samples about every two weeks. The Malaise traps were standard-size traps (about 1.7 m long with two 1.6 m^2 openings) with black netting and a white roof. They were manufactured by B&S Entomological Services (nowadays owned by Watkins & Doncaster, Leominster, Herefordshire, United Kingdom). This trap model has also been used successfully in sampling campaigns in the Neotropics (e.g. Gauld, 1991; Sääksjärvi et al., 2004; Gómez et al. 2017).

The full sampling was performed with 34 traps (samples from 32 traps here) that were in use for most of the sampling year; of these, 17 were placed in primary forest, eight in disturbed forest (samples from seven here), seven in clearcut plantations (samples from six here), and two on outside farmland (figure 1). The traps were placed in various microhabitats within habitat types to capture heterogeneity in terms of variation in, for example, vegetation, elevation, and substrate type. Moreover, to maximize sample size and habitat coverage, traps were placed on likely flying routes of insects, and whenever possible, close to ecologically distinctive microhabitats, such as fallen trees. The full sampling effort was 373.5 trap months (number of traps x number of months sampled), with an additional 8.9 trap months not being representative of a normal catch due to the samples being partially lost or damaged (not included here). About a quarter of the samples (108.5 trap months) were included here. The sampling campaign was carried out by Tapani Hopkins and was described in greater detail in Hopkins et al. (2019a) and the trap sites in Hopkins et al. (2019b).

2.5 Data analysis

I produced species rarefaction curves to model species accumulation rates, which give an idea of total species richness. The curve is an average of resamples and displays an estimate of how the number of collected species is expected to increase as a function of the number of collected individuals. The rarefaction was based on resampling trap samples without replacement 999 times, with each roughly two-week sampling interval constituting a trap sample. Thus, the individuals of each trap sample were kept together in resampling. The number of collected

individuals was displayed on the x-axis of the rarefaction curves instead of the number of trap catches per unit of time for three reasons: (1) the number of species collected is directly constrained by the number of individuals collected, (2) the number of trap samples in the included subset without pimplines was unknown, and (3) the rarefaction curves are generally more comparable with other studies in this format.

I produced separate rarefaction curves for each habitat type and biological pimpline group (these also by habitat), with data from farmland being presented mostly separately. I also produced separate rarefaction curves for dry and wet seasons to check if there was a need to treat the data of different seasons separately. To estimate whether curves differed significantly from each other, I calculated 84% confidence intervals, which overlap when $p \geq 0.05$ (MacGregor-Fors & Payton, 2013). However, since intervals were approximated by resampling, the significances that follow are also approximations and should be viewed critically. I also calculated average trap catches per trap day to measure how abundances were distributed between traps. However, there I did not include measures of dispersion as they are not particularly informative (or even misleading) for this data given that samples without pimplines were not included and that the data was far from normally distributed. I performed all analyses in R version 4.3.3 (R Core Team, 2024) with the R package 'turkuwasps' (Hopkins, 2023).

3 Results

3.1 Pimplinae

A total of 1,717 pimplines were collected from forest sites and sorted into 105 species in 14 genera (table 1). Trapping in farmland collected 208 pimplines, sorted into 18 species (seven species not found in forest) in 11 genera (appendix 1). When the farmland site is included in the study area, a total of 112 species in 14 genera were collected (1,925 individuals).

Pimplines were quite abundant in the study area as they were frequently collected in all habitat types, with traps in primary forest (36.2 Malaise trap months, MTM), swampy primary forest (19.5 MTM), disturbed forest (17.7 MTM), clearcut plantation (25.0 MTM), and farmland (10.0 MTM) having collected on average 0.73, 0.47, 0.48, 0.50, and 0.68 individuals per trap day, respectively. However, average trap catches varied greatly within habitat types (figure 2). Species accumulated at roughly similar rates (per individual caught) in dry and wet seasons in each habitat type (appendix 4).

Table 1. Faunistic composition of pimplines collected by 30 Malaise traps in forest sites of the study area in Kibale National Park, Uganda.

Biological group	Genus	Species	Individuals
idiobiont parasitoids of deeply concealed hosts	*Xanthephialtes*	1	7
	Xanthophenax	10	266
	sum	**11**	**273**
idiobiont parasitoids of weakly concealed hosts	*Acropimpla*	6	28
	Camptotypus	15	127
	Echthromorpha	1	540
	Itoplectis	3	139
	Pimpla	5	28
	Sericopimpla	1	12
	Theronia	5	161
	Xanthopimpla	22	243
	sum	**58**	**1278**
koinobiont ectoparasitoids of spiders	*Eruga*	8	57
	Zatypota	24	50
	sum	**32**	**107**
pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders	*Afroanomalia*	1	12
	Zaglyptus	3	47
	sum	**4**	**59**

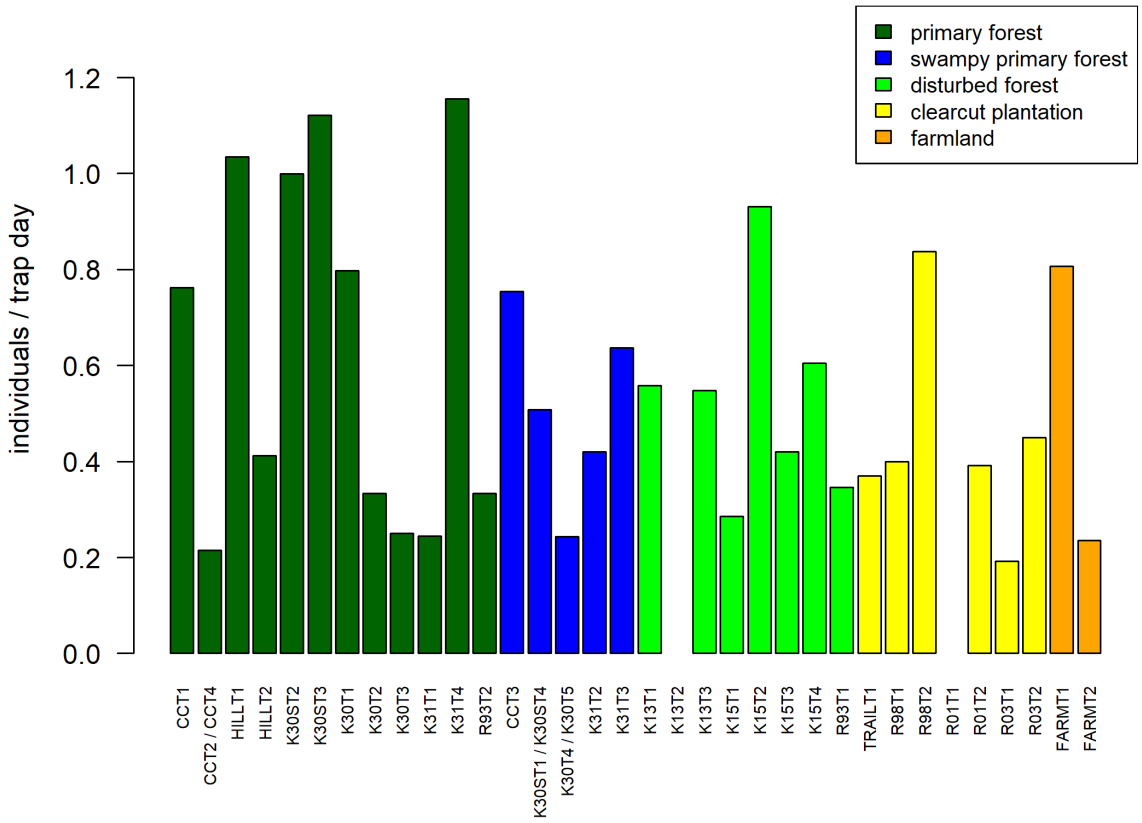

Figure 2. Average number of pimplines collected per trap day for each Malaise trap (n = 32) by habitat type in the study area in Kibale National Park, Uganda. Samples of the traps K13T2 and R01T1 were not included here. Data of other traps were based on a subset of samples (108.5 trap months) that each contained at least one pimpline specimen.

Trapping in forest sites accumulated pimpline species significantly faster (per individual caught) than trapping in farmland after about 50 individuals caught (figure 3). Species accumulation rates were roughly similar between forest types, with the accumulation rate of trapping in clearcut plantation possibly having exceeded that of primary forest after about 350 individuals caught and of swampy primary forest after about 250 individuals caught (figure 3). Moreover, trapping in disturbed forest might have accumulated species faster than in swampy primary forest after about 250 individuals caught (figure 3).

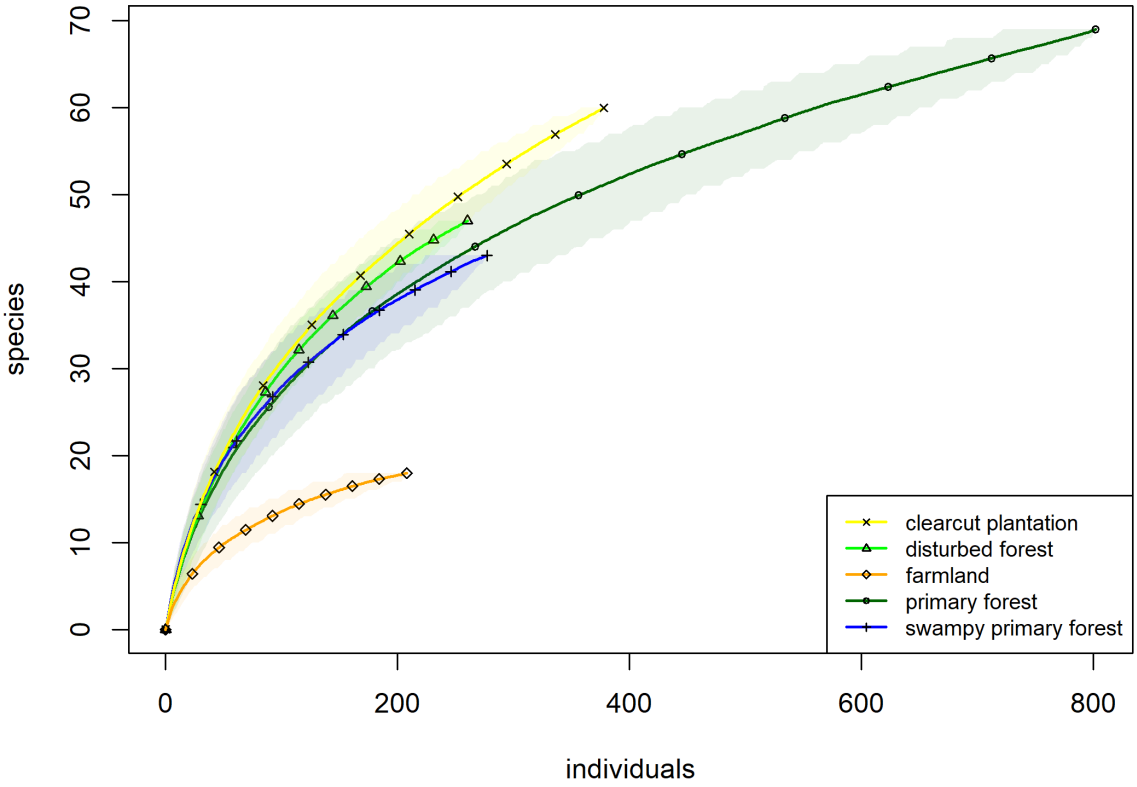

Figure 3. Species rarefaction curves of pimplines by habitat type caught in 32 Malaise traps in the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

3.2 Biological pimpline groups

Sampling in the forest sites of the study area accumulated species of all four biological pimpline groups (per individual caught) at rates that differed significantly from each other after about 20–60 individuals caught, ordered from slowest to fastest accumulation: Pseudo/IES < IDC < IWC < KES (figure 4). The accumulation rates between habitat types within groups Pseudo/IES and IDC did not differ significantly at current sample sizes (appendix 3), but differences were present within groups IWC and KES (figures 5–6).

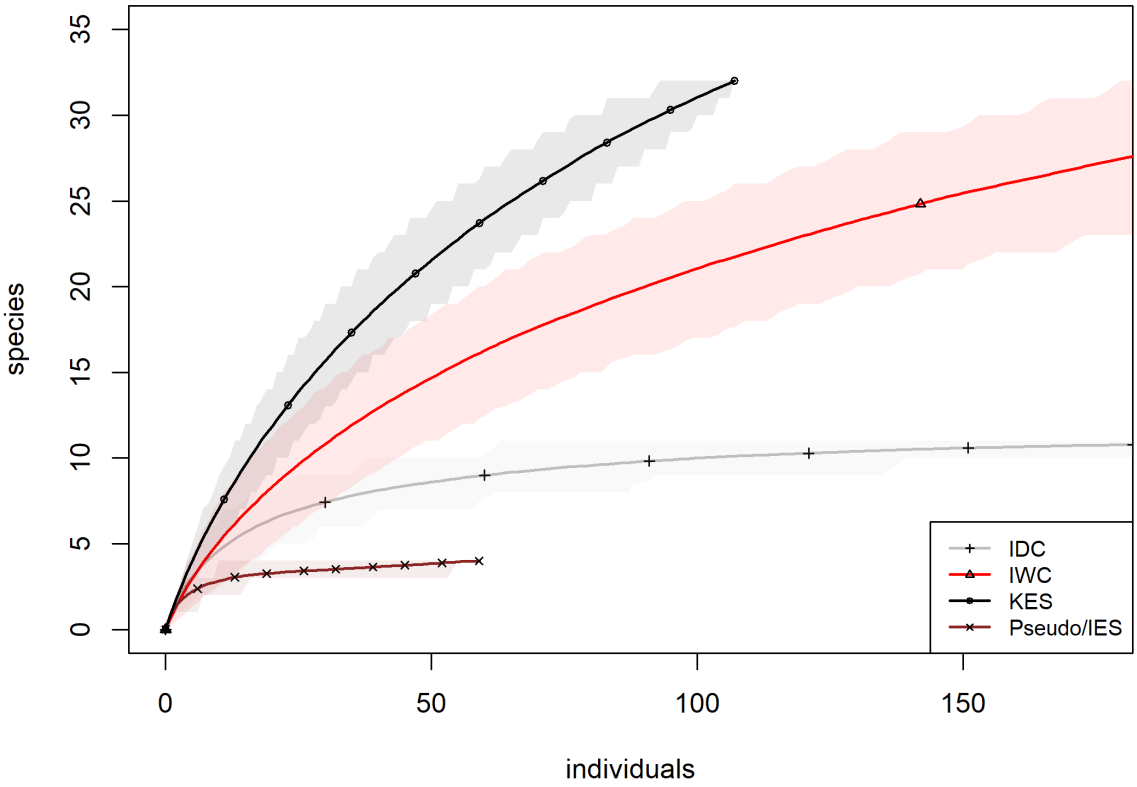

Figure 4. Species rarefaction curves of biological pimpline groups caught in 30 Malaise traps in the forests (samples from farmland excluded) of the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals. Groups: IDC = idiobiont parasitoids of deeply concealed hosts; IWC = idiobiont parasitoids of weakly concealed hosts; KES = koinobiont ectoparasitoids of spiders; Pseudo/IES = pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders.

Unlike for other biological pimpline groups, trapping in forest sites accumulated species of idiobiont parasitoids of weakly concealed hosts significantly faster (per individual caught) than trapping in farmland after about 40 individuals caught (figure 5). Species accumulation rates were roughly similar between forest types, with the accumulation rate of trapping in clearcut plantation possibly having surpassed that of primary forest after about 250 individuals caught and of swampy primary forest after about 175 individuals caught (figure 5).

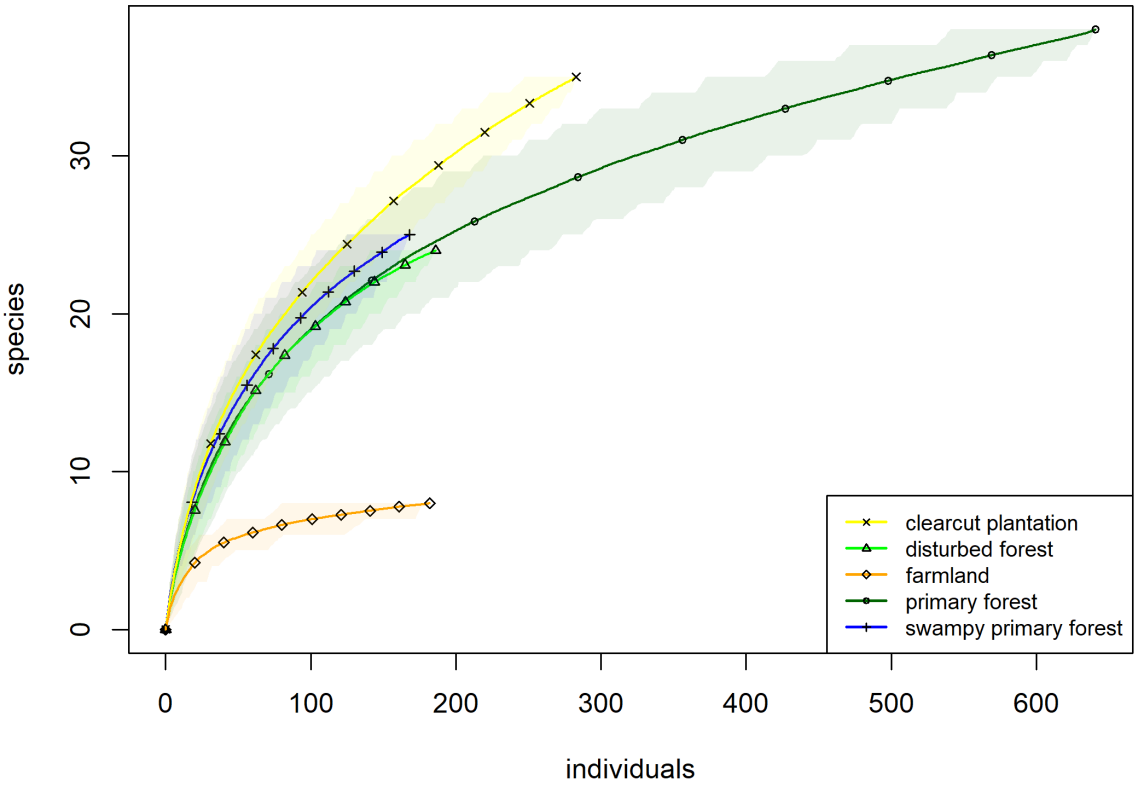

Figure 5. Species rarefaction curves of pimpline group IWC (idiobiont parasitoids of weakly concealed hosts) by habitat type caught in 32 Malaise traps in the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

For koinobiont ectoparasitoids of spiders, trapping in primary forest and disturbed forest accumulated species significantly faster (per individual caught) than in clearcut plantation after about 20 and 10 individuals caught, respectively (figure 6). The accumulation rates of trapping in swampy primary forest and farmland did not differ from that of other habitat types at current sample sizes (figure 6).

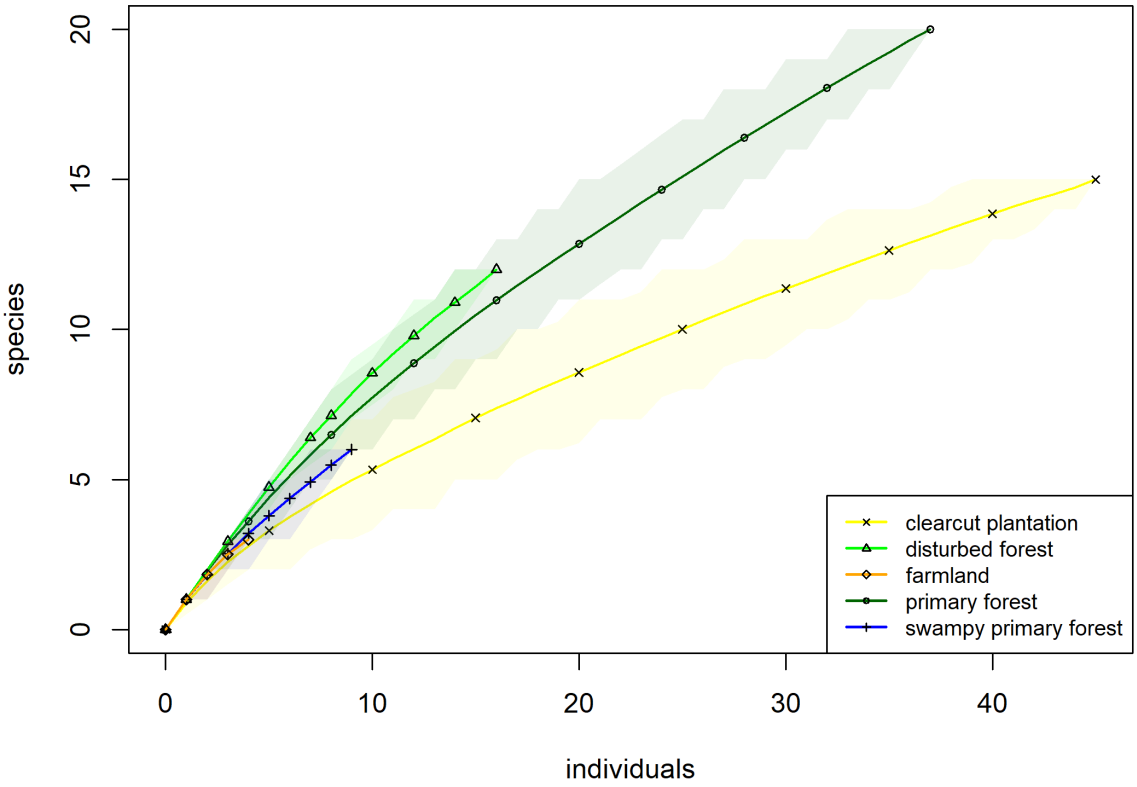

Figure 6. Species rarefaction curves of pimpline group KES (koinobiont ectoparasitoids of spiders) by habitat type caught in 32 Malaise traps in the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

4 Discussion

4.1 Observed species richness

4.1.1 Pimplinae

This thesis shows for the first time that extensive Malaise trapping in tropical forest in Africa can uncover highly species-rich pimpline faunas. Species richness of this magnitude is contrary to what the limited sampling of Gómez et al. (2017) suggested for Kibale but in line with estimates in Meier et al. (2024) of high pimpline richness in the Equatorial Afrotropics. With the present samples containing 105 pimpline species (112 including farmland), Kibale National Park may well be among the sites with the most species-rich pimpline faunas of the world. However, even this species number can be taken to represent the minimum number of species in the samples as any cryptic species were, like in most similar studies, not considered.

Rarefaction curves by habitat type for Pimplinae are generally far from stabilizing, suggesting that more species would have been collected with larger sample sizes from each habitat (figure 3). Larger sample sizes would likely yield least new species per habitat type in farmland as the curve is closest to stabilizing (figure 3).

Although trapping in farmland accumulated fewer pimpline species than trapping in other habitat types, traps in farmland collected second most individuals per trap day (figure 2–3). Interestingly, traps in farmland (10.0 MTM) collected unusually many individuals of three species of the genus *Pimpla*, few of which were collected in other traps (98.5 MTM). Traps in farmland collected 28/28, 92/96, and 37/37 of the individuals of *Pimpla* sp. 1, 6, and 7, respectively. This, coupled with seven out of the 18 species of pimplines collected by traps in farmland being unique to that habitat type, suggests that there is a distinctive, but comparably species-poor, pimpline fauna at the farmland site (appendix 1). This pattern may be explained by trapping in farmland having collected abundant pimpline species that are parasitoids of agricultural pest insects occurring of the farm. This further suggests that the farm likely houses a relatively species-poor but abundant host fauna of Lepidoptera, as they are thought to be the main hosts of species of *Pimpla* (van Noort, 2024). However, it is not known if ichneumonids have been used as biological control in the region.

4.1.2 Biological pimpline groups

All species accumulation curves of biological pimpline groups differed significantly from each other, with curves of idiobiont parasitoids of weakly concealed hosts and koinobiont ectoparasitoids of spiders being far from stabilizing (appendix 2). However, curves of idiobiont parasitoids of deeply concealed hosts and pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders seem to be near stabilizing at 11 and four individuals collected, respectively (figure 4). This suggests that the two latter groups are less species-rich in the study area than the two former groups. Sample sizes were likely too low for the rarefaction to reveal possible differences between habitat types in species accumulation rates within groups IDC and Pseudo/IES (appendix 3).

The shapes of the rarefaction curves for idiobiont parasitoids of weakly concealed hosts generally resemble those for all Pimplinae as this pimpline group dominated in numbers of individuals and thus had the strongest influence on overall pimpline rarefactions (figures 3 and 5). Only the curve for farmland was near stabilizing at eight species for the IWC group (figure 5). As was noted earlier, it is possible that pimpline species of this group accumulated faster into traps in clearcut plantation than in primary and disturbed forest (figure 5). This could be due to the relatively small clearcut sites generally being surrounded by relatively large primary forest sites, resulting in traps in clearcut sites capturing species of the fauna of primary forest in addition to their own fauna as especially this group of pimplines contains large species that are strong flyers, plausibly with large ranges (figure 1).

Species of koinobiont ectoparasitoids of spiders accumulated faster in primary and disturbed forest than in clearcut plantation (figure 6). This could be due to the two former habitat types having more diverse flora, supporting more host species and individuals (of spiders). However, this pattern may be only evident for smaller species such as members of this biological group that are likely weaker flyers with smaller ranges, and thus more restricted to their habitat.

The species number of the genus *Zatypota* (of the KES group) seems unusually high with respect to the number of individuals collected (table 1). It is possible that some actual species may have been split into morphological variants as species delimitation of the specimens of this genus was most challenging. However, in the taxonomic revision of spider ectoparasitoids of Gauld & Dubois (2006), it is suggested that "*Zatypota* probably includes as many species as there are in all other genera in the *Polysphincta* genus-group combined." Practically no work has been done on the species richness of *Zatypota* in the Afrotropics prior to this thesis. It

remains to be seen whether similar species richness patterns of *Zatypota* can be independently replicated from Afrotropical collections.

4.2 Species richness patterns

The rarefaction curves for Pimplinae (figure 3) suggest that species richness in the study area is high compared with other pimpline collections using Malaise trapping (see supporting information in Gómez et al. (2017) for a summary of collections). It seems that of published pimpline collections with over 100 individuals, only four collections in the Neotropics have species richnesses that are in the vicinity of those attained here for a given number of individuals sampled (Gómez et al. 2017; Higa & Penteado-Dias, 2020; Flinte et al., 2023). Two of these collections (from SE Peru and SE Brazil) have species richnesses that slightly exceed those seen here and two (NE Peru and SE Brazil) fall slightly short for a given number of individuals (figure 7). However, a major concern with simple comparisons like this is that habitat heterogeneity and elevation range are not accounted for, e.g. in both collections in SE Brazil sampling was done along an elevation gradient, which could lead to higher species richness as taxonomic composition of pimplines has been shown to generally change with elevation (Hall et al., 2014; Veijalainen et al., 2014; Higa & Penteado-Dias, 2020; Flinte et al., 2023).

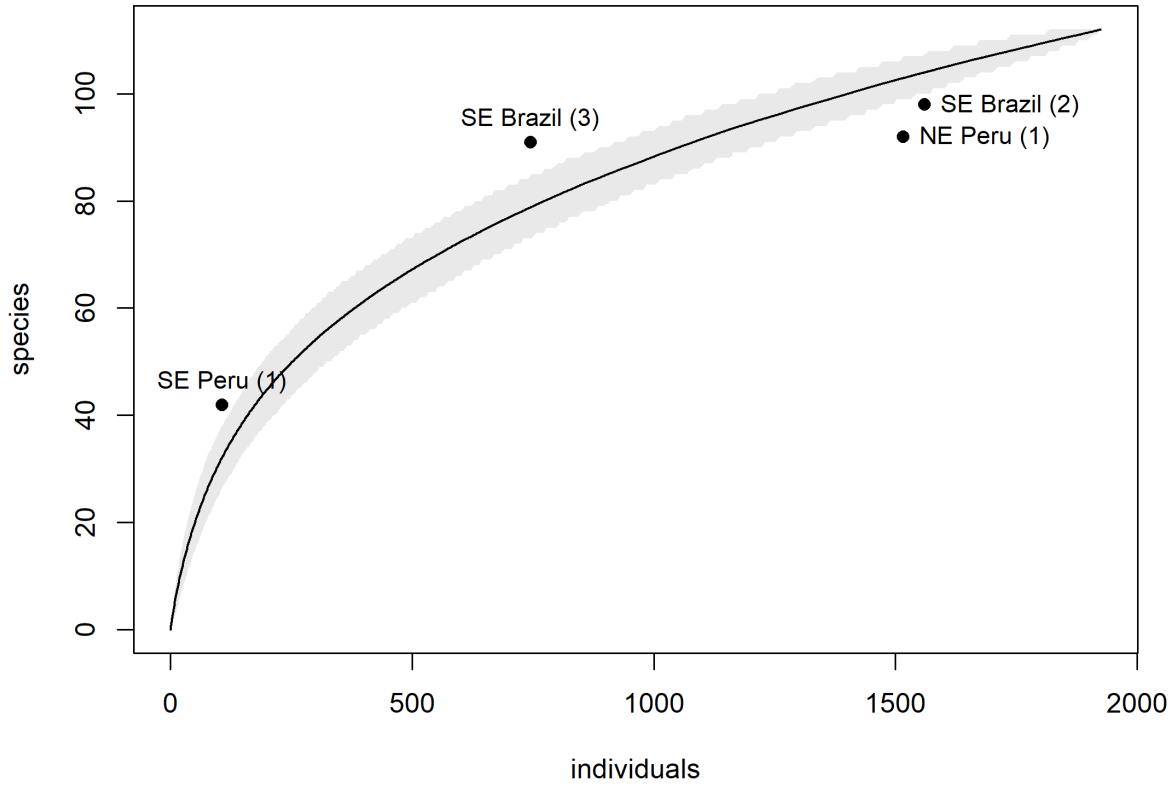

Figure 7. Species rarefaction curve of pimplines caught in 30 Malaise traps in the forests (samples from farmland excluded) of the study area in Kibale National Park (Uganda), with pimpline species numbers plotted against the number of collected individuals from the most species-rich sites published in the literature. The curve is sample-based and shows the accumulation rate of species per individual caught, with an 84% confidence interval. Plotted collections were caught with Malaise traps in the Neotropics: (1) Gómez et al. (2017); (2) Flinte et al. (2023); (3) Higa & Penteado-Dias (2020).

Overall, the case for the anomalous latitudinal diversity gradient of ichneumonids is not supported by the high species richness of pimplines seen here. It is possible that tropical ichneumonid faunas simply require more sampling intensity to present an accurate picture of their species richness as abundance distributions of tropical species are generally flatter (Brown, 2013). This, coupled with previously insufficient ichneumonid sampling in the tropics, may explain parts of why the LDG of ichneumonids was thought to be anomalous, but may in reality not be. However, what the present species richness reveals of the family's richness in the area will depend on how well the richness of pimplines represents that of ichneumonids. Based on present results, I expect sampling campaigns in the tropics to reveal more species-rich faunas of at least other generalist subfamilies closely related to pimplines than at temperate locations, provided sufficient sampling intensities. This is also suggested by the comparison of pimpline and rhyssine species richnesses from 97 sites on three continents in Gómez et al. (2017).

4.3 Biological composition

The biological composition of collected pimplines follows what can be regarded as the typical pattern of group IWC having the highest species numbers of all four groups when simply comparing the number of collected species without controlling for abundance (table 1, appendix 1). In Sääksjärvi et al. (2004), the biological composition of Pimplinae *sensu lato* (includes relatively small subfamilies Rhyssinae and Poemeniinae) collections of seven sites were compared like this. There, despite rhyssines and poemeniins being included (which are all of group IDC), group IWC had the highest species number in all four tropical sites [three in Costa Rica (Gauld, 1991) and one in Peru (Sääksjärvi et al., 2004), with 39–88 species each]. The remaining three sites were in temperate areas [one in Finland (Jussila, 1984), one in England (Owen et al., 1981), and one in Poland (Sawoniewicz, 1986)] and had collections with overall species numbers of 18–28 species of Pimplinae *s.l.* per site, likely based on sample sizes too low for reliably comparing group-specific species numbers. Nevertheless, group IWC had either the highest or second highest species number (being second by at most one species). However, since none of these collections likely included all species of the local fauna, a more reliable comparison of group-specific species numbers will have to be done at equal numbers of total individuals, considering the accumulation rate of species.

It seems that the only published Malaise trap collections of pimplines (or Pimplinae *s.l.*) that have been classified into corresponding four biological groups are those included in Sääksjärvi et al. (2004) and Gómez et al. (2017). When rhyssines are excluded from the A-M (Allpahuayo-Mishana, NE Peru) and LA (Los Amigos, SE Peru) collections included in Gómez et al. (2017), they consist of 92 and 42 pimpline species, respectively (species delimitation verified by Ilari Sääksjärvi like here). It is notable that the order of species numbers of the biological groups is the same as here (for forest), from smallest to largest: Pseudo/IES < IDC < KES < IWC (table 2).

Interestingly, species numbers of the more species-rich pimpline groups IWC and KES of the A-M and LA collections in Gómez et al. (2017) are roughly similar to the present ones for a given number of individuals sampled, except that the present collection reaches the species number of group KES of the A-M collection at a much smaller sample size (figure 8). However, the difference regarding group KES should be viewed critically as the species number of the genus *Zatypota* (of group KES) may be somewhat excessive here. As for the less species-rich groups IDC and Pseudo/IES, the species numbers of the A-M and LA collections are roughly

similar to the ones here at a given number of individuals, except for group IDC in A-M, which contained somewhat fewer species than here at equal numbers of individuals (figure 9). The collection in LA is less comparable as the sample size was much smaller than for the A-M and present collections. Overall, these similarities suggest that the biological composition of pimpline faunas in Afrotropic and Neotropic forest may be quite similar. By contrast, the taxonomic composition of local pimpline faunas differed markedly, with the A-M and LA collections combined having only three out of 16 genera in common with the 14 genera of the present collection: *Pimpla*, *Zatypota*, and *Xanthopimpla*.

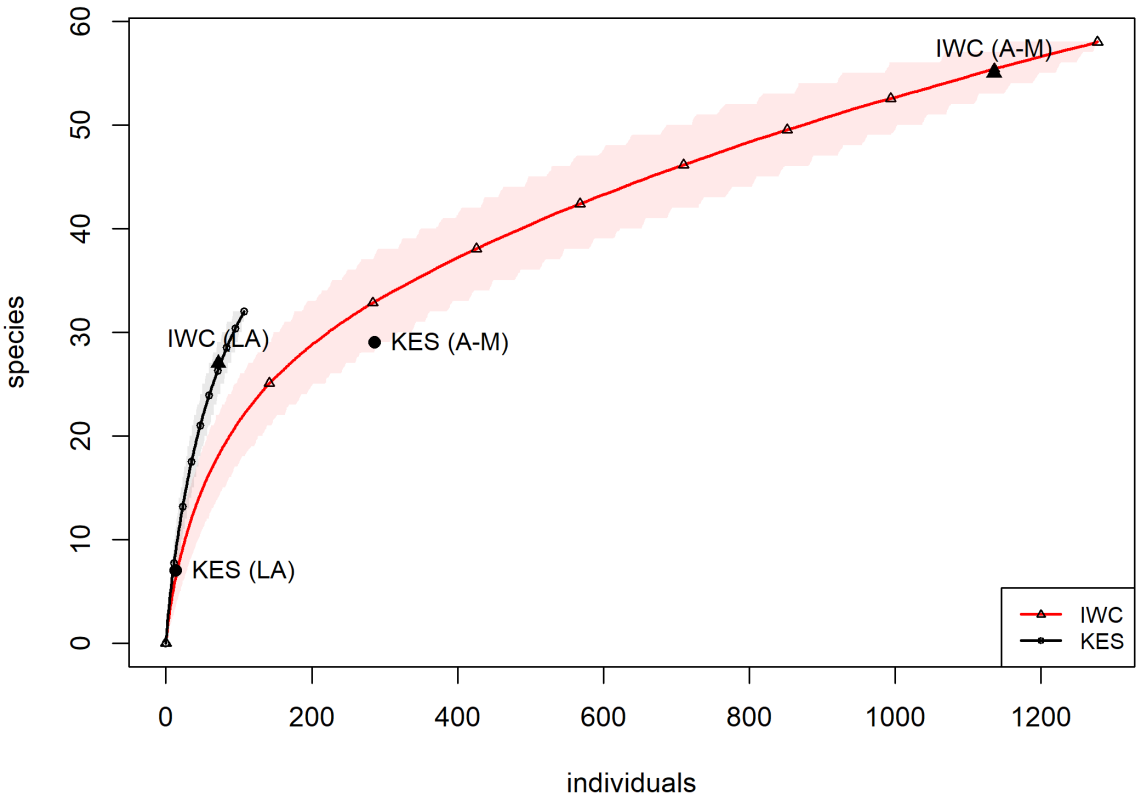

Figure 8. Species rarefaction curves of pimpline groups IWC (idiobiont parasitoids of weakly concealed hosts) and KES (koinobiont ectoparasitoids of spiders) caught in 30 Malaise traps in the forests (samples from farmland excluded) of the study area in Kibale National Park (Uganda), with corresponding species numbers of the A-M (Allpahuayo-Mishana, NE Peru) and LA (Los Amigos, SE Peru) collections included in Gómez et al. (2017) plotted against the number of individuals sampled. The curves are sample-based and show the accumulation rate of species per individual caught, with 84% confidence intervals.

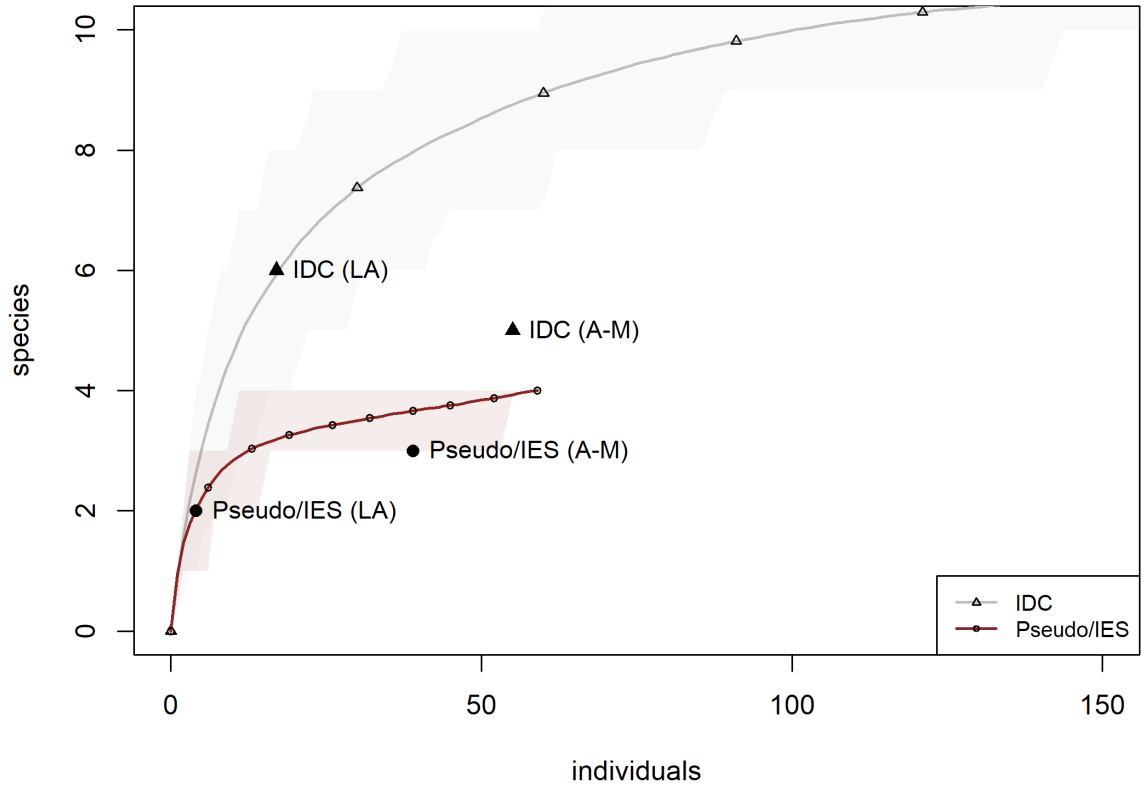

Figure 9. Species rarefaction curves of pimpline groups IDC (idiobiont parasitoids of deeply concealed hosts) and Pseudo/IES (pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders) caught in 30 Malaise traps in the forests (samples from farmland excluded) of the study area in Kibale National Park (Uganda), with corresponding species numbers of the A-M (Allpahuayo-Mishana, NE Peru) and LA (Los Amigos, SE Peru) collections included in Gómez et al. (2017) plotted against the number of individuals sampled. The curves are sample-based and show the accumulation rate of species per individual caught, with 84% confidence intervals.

4.4 Sampling completeness

Species rarefaction curves of the whole subfamily suggest that the pimpline community was incompletely sampled with respect to sample size, and possibly also trap type and locations (figure 3). More samples would naturally help in including rare species. However, as was noted earlier, locally rare or uncollected species may be more abundant in different habitats nearby, or even further away as ichneumonids are generally strong flyers with good dispersal ability. In such cases, placing traps in unsampled nearby habitats, such as in papyrus swamp in Kibale, to improve habitat coverage may be more important than simply including more samples from used traps in collecting a larger portion of the regional species pool. However, this is further complicated in Kibale by the fact that the vegetation there is known to vary along a north-south gradient (Chapman & Lambert, 2000). Especially in cases of sampling in areas with high habitat

heterogeneity or gradients, the sampling programme may benefit from additional sampling methods to check if Malaise trapping is systematically biased, as was done in Gómez et al. (2017).

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Appendices

Appendix 1. Faunistic composition of pimplines in farmland

Table 1.1. The faunistic composition of pimpline specimens collected by two Malaise traps in farmland near the study area in Kibale National Park, Uganda. Parentheses show the number of species unique to farmland.

Biological group	Genus	Species	Individuals
idiobiont parasitoids of deeply concealed hosts	*Xanthophenax*	6	21
	sum	**6**	**21**
idiobiont parasitoids of weakly concealed hosts	*Camptotypus*	1	2
	Echthromorpha	1	14
	Itoplectis	1 (1)	4
	Pimpla	3 (2)	157
	Theronia	1	4
	Xanthopimpla	1 (1)	1
	sum	**8 (4)**	**182**
koinobiont ectoparasitoids of spiders	*Eruga*	1	1
	Zatypota	2 (2)	3
	sum	**3 (2)**	**4**
pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders	*Zaglyptus*	1 (1)	1
	sum	**1 (1)**	**1**

Appendix 2. Full-size rarefaction curves of biological pimpline groups

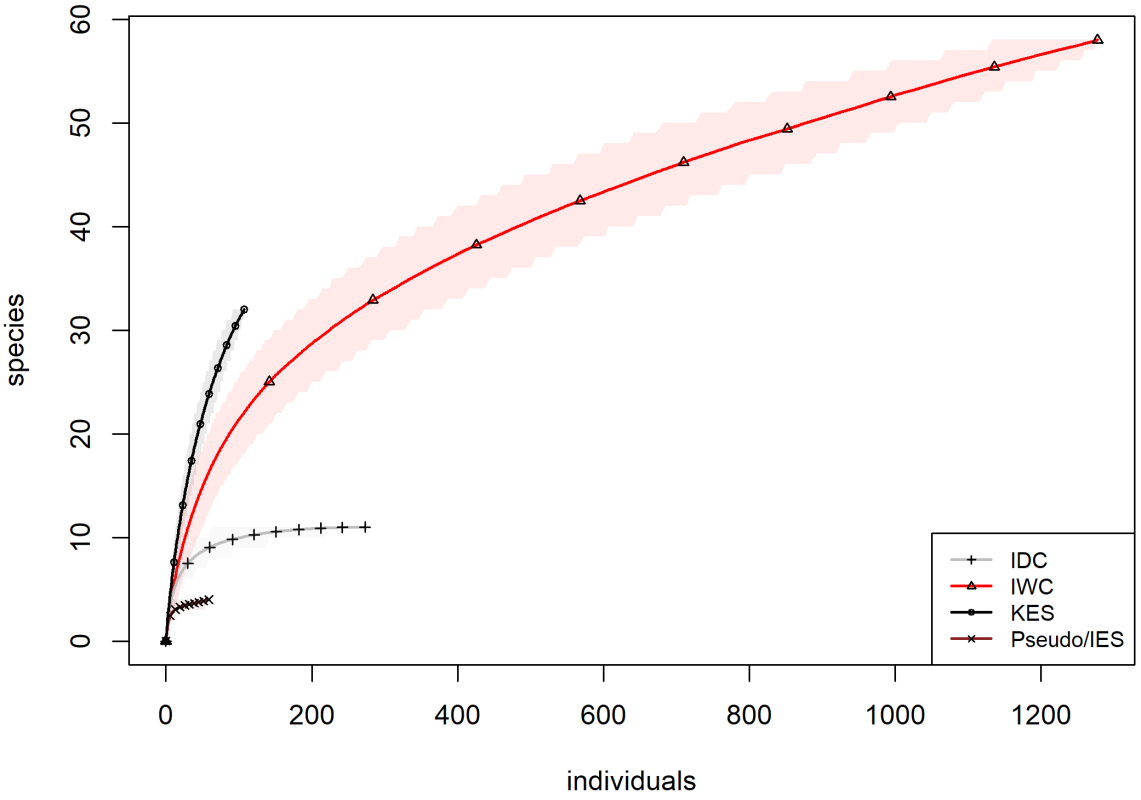

Figure 2.1. Full-size species rarefaction curves of biological pimpline groups caught in 30 Malaise traps in the forests (samples from farmland excluded) of the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals. Groups: IDC = idiobiont parasitoids of deeply concealed hosts; IWC = idiobiont parasitoids of weakly concealed hosts; KES = koinobiont ectoparasitoids of spiders; Pseudo/IES = pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders.

Appendix 3. Rarefaction curves of pimpline groups IDC and Pseudo/IES

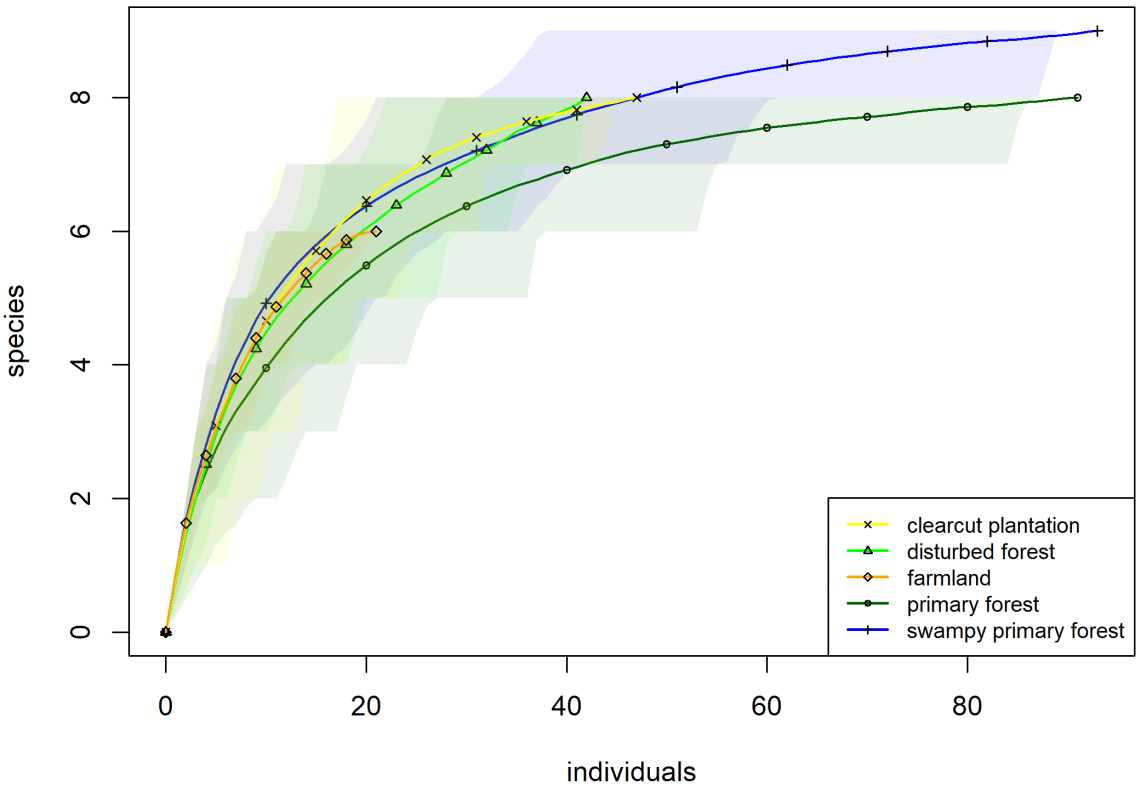

Figure 3.1. Species rarefaction curves of pimpline group IDC (idiobiont parasitoids of deeply concealed hosts) by habitat type caught in 32 Malaise traps in the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

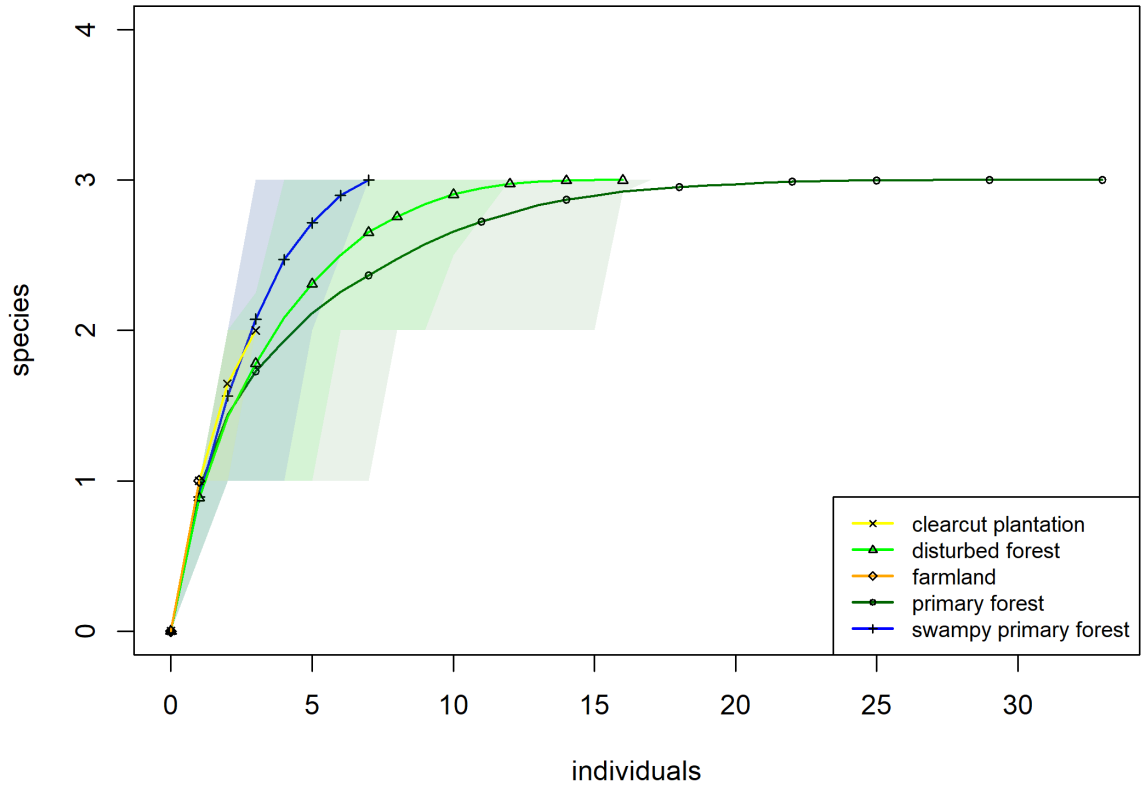

Figure 3.2. Species rarefaction curves of pimpline group Pseudo/IES (pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders) by habitat type caught in 32 Malaise traps in the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

Appendix 4. Pimpline rarefaction curves by season

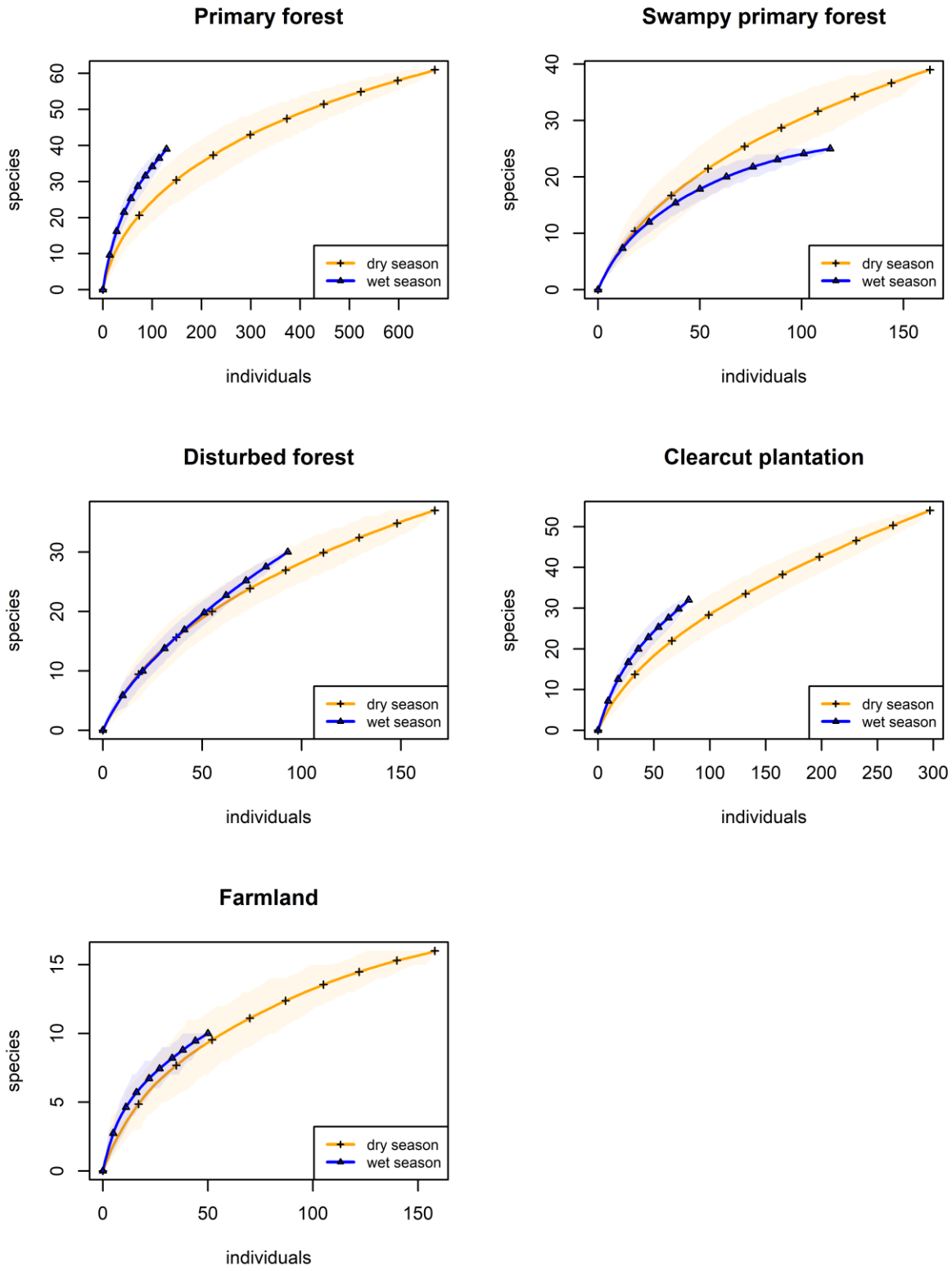

Figure 4.1. Species rarefaction curves of pimplines by dry (December–February and June–August) and wet (March–May and September–November) seasons caught in 32 Malaise traps in the study area in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.