Received: 10 June 2025 | Accepted: 22 August 2025

DOI: 10.1111/icad.70017

ORIGINAL ARTICLE

Insect Conservation and Diversity
Royal Entomological Society

Local species richness of parasitoid wasps (Ichneumonidae: Pimplinae) in Afrotropical forest: Conservation perspectives

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Funding information
Svensk-Österbottniska Samfundet; Waldemar von Frenckells Stiftelse; Suomen Kulttuurirahasto; Oskar Öflunds Stiftelse; Alfred Kordelinin Säätiö; The Entomological Society of Finland; Opetus- ja Kulttuuriministeriö; Academy of Finland

Editor: Raphael K. Didham and **Associate Editor:** Gavin Broad

Abstract

1. Effective conservation of biodiversity relies on an understanding of its composition and distribution. Parasitoid wasps are an ecologically important and highly species-rich group of Hymenoptera but are poorly known in the tropics. One strategy for conserving their richness is based on finding out how the richness is distributed in different habitats.
2. Here, we investigate the local species richness and biological composition of parasitoid wasps (Ichneumonidae: Pimplinae) collected with Malaise traps in Ugandan tropical forest. We link the richness of Pimplinae and its four biological groups to habitat types across a successional gradient.
3. We found higher pimpline richness in forest than in nearby farmland, with the highest richness in the group of idiobiont parasitoids of weakly concealed hosts.
4. Our results suggest that protecting primary tropical forest may be particularly important for conserving a high richness of koinobiont ectoparasitoids of spiders and that nearby disturbed forest can have high parasitoid wasp richness after a few decades of regeneration.
5. Trapping in forest collected 5623 individuals of 83 species, which is high compared with pimpline richness at temperate latitudes, supporting a typical latitudinal diversity gradient of at least the Pimplinae subfamily of Ichneumonidae.

KEYWORDS
biodiversity, biodiversity loss, conserving unknown biodiversity, Kibale national park, latitudinal diversity gradient, tropical insect diversity, Uganda malaise trapping 2014–2015

INTRODUCTION

Global biodiversity, both known and unknown, is declining at an alarming rate, posing one of the most significant threats to ecological integrity and human well-being (Díaz et al., 2006; Isbell et al., 2018; Meyer et al., 2016). A recent global assessment on biodiversity and ecosystem services suggests human activity is driving up to 1 million species towards extinction within the coming decades, primarily due to changes in land or sea use, direct exploitation of organisms, climate change, pollution and the introduction of invasive alien species (Brondizio et al., 2019). A major way of conserving Earth's biodiversity has been to designate protected areas (Lovejoy, 2006). However, this relies on a robust understanding of how biodiversity is composed and distributed (Burbano-Girón et al., 2022; Revollo-Cadima & Salazar-Bravo, 2024).

Shortfalls and biases in the knowledge of biodiversity can constitute significant obstacles to effective conservation (Clark & May, 2002; Kim & Byrne, 2006). Knowledge of the species richness and distribution of many taxa is relatively weak in the tropics compared to temperate regions, despite the tropics usually having a higher richness (Brown, 2013; Titley et al., 2017). Conservation research is also heavily biased towards well-known groups such as vertebrates and flowering plants, while invertebrates receive little attention, despite being among the most species-rich groups on Earth (Joppa et al., 2011; Stork, 2018; Titley et al., 2017). Increased knowledge of highly rich, poorly studied taxa can help conservation strategies to better suit biodiversity as a whole, not just well-known, species-poor groups.

Parasitoid wasps, including the family Ichneumonidae, are among the most diverse yet poorly known insect groups on earth. Their larvae feed on the tissues of an arthropod host, killing it. Consequently, they have a key role in regulating population densities of many arthropods (Quicke, 2015; Segoli, 2016; Várkonyi et al., 2002). Some species are also used in the biocontrol of pest insect populations (Sarfraz et al., 2005; Wang et al., 2019). The global richness of Ichneumonidae was initially estimated to be around 60,000 species (Townes, 1969). However, more recent estimates based on more extensive tropical sampling suggest over 100,000 species (Gauld, 1997), of which about 24,000 have been described (Aguiar et al., 2013). If the latter estimate is close to the actual number of species, Ichneumonidae is potentially the richest animal family on Earth.

Parasitoid wasps are barely part of conservation strategies, even though their high trophic level, specialised biology and often unknown status are likely to make them particularly vulnerable to extinction by human activity (Shaw, 2006; Shaw & Hochberg, 2001). It has also been argued that they promote diversity and stability within herbivore insect communities, which then carry over to plant communities (Freeland & Boulton, 1992; LaSalle & Gauld, 1993). Moreover, particularly in the tropics where parasitoids such as the Ichneumonidae are largely unknown, conservation is hampered by challenges relating to unknown biodiversity; that is, most species are undescribed, their hosts and ecology are poorly known, and prior knowledge of the species richness and distribution is scarce. Conservation strategies that consider unknown biodiversity, such as tropical parasitoid wasp communities, will probably benefit most from research on the basic features of the communities, such as their species richness.

However, extremely high species richness and the scarcity of experts often make it impractical to measure parasitoid richness directly. Instead, as Flinte et al. (2023) suggest, parasitoids could be included in conservation strategies if different environments were used as surrogates for their richness. Thus, protecting environments supporting high parasitoid richness should be prioritised to maximise the number of species conserved. On a small scale, this could mean identifying habitat types with high parasitoid richness. Ideally, this would be complemented by an understanding of how human-induced disturbance of parasitoid environments impacts their richness. For example, forest disturbance such as logging and conversion into forestry or agriculture can significantly alter the community composition of organisms on a local scale (Cardelús et al., 2019; Velho & Krishnadas, 2011).

A potential large-scale surrogate of parasitoid richness is the latitude, as most communities display a latitudinal diversity gradient (LDG) of increasing species richness from the poles to the equator (Hillebrand, 2004). This can be significant from a conservation perspective given ongoing rapid deforestation especially in South America and Africa (FAO, 2020). However, the LDG of parasitoid wasps is still unconfirmed. It has even been suggested that Ichneumonidae displays an “anomalous” LDG that peaks in species richness outside the tropics, at temperate latitudes (Janzen & Pond, 1975; Janzen, 1981; Owen & Owen, 1974; Santos et al., 2025), although this may be a result of insufficient sampling in the tropics and biased taxonomic efforts (Quicke, 2012; Santos et al., 2010; Santos & Quicke, 2011). Recent studies indicate that tropical faunas are highly species-rich for at least some ichneumonid groups (e.g. Flinte et al., 2023; Gauld, 1991; Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Smith et al., 2008; Veijalainen et al., 2012), and many host groups such as Coleoptera and Lepidoptera exhibit their highest richness in the tropics (Andrew & Hughes, 2004; Kocher & Williams, 2000; Pinkert et al., 2022).

Few tropical sites have been extensively sampled for parasitoid wasps, and the few that have are largely outside the Afrotropics (c.f. e.g. recent Neotropical sampling: Flinte et al., 2023; Gauld, 1991; Gaston & Gauld, 1993; Sääksjärvi et al., 2004; Veijalainen et al., 2012, 2014). Consequently, the Afrotropical parasitoid wasp fauna is particularly poorly known. Meier et al. (2024) estimated that only 13%–22% of the ichneumonid species of the five most extensively studied countries in the Afrotropics have been described. They estimated that there are 9206 to 15,577 ichneumonid species in the entire Afrotropics, although they considered this to probably be an underestimate. No studies with sufficiently large sample sizes for reliably estimating the richness of ichneumonids at Afrotropical sites have been published, except for Hopkins et al. (2018, 2019a, 2019b, 2024) on the relatively small Rhyssinae subfamily.

The Pimplinae subfamily of Ichneumonidae is commonly used in species richness studies, as the family is highly diverse both taxonomically and biologically, allowing conclusions on the relative richness of different subgroups (e.g., Flinte et al., 2023; Gaston & Gauld, 1993; Gómez et al., 2017; Sääksjärvi et al., 2004). The emerging picture of the LDG of the Pimplinae suggests it may be more species-rich in the Neotropics than in temperate regions (Flinte et al., 2023; Gómez et al., 2017; Sääksjärvi et al., 2004; but see Santos et al., 2025).

In this study, we investigate the species richness and biological composition of the Pimplinae subfamily of Ichneumonidae using specimens collected in an extensive sampling campaign in Ugandan tropical forest. We compare the species richness of different habitat types across a successional gradient, both for pimplines as a whole and for four biological pimpline groups separately. We also compare the observed richness and composition to that of other collections. Our aim is to both investigate how rich a fauna exists at the site and to draw conclusions for conservation. Based on previous research at other tropical sites, we expected to discover a highly species-rich pimpline fauna, revealing some of the unknown richness of parasitoid wasps in the Afrotropics (Flinte et al., 2023; Gauld, 1991; Gómez et al., 2017; Sääksjärvi et al., 2004).

MATERIALS AND METHODS

Study area

The samples are from near the Makerere University Biological Field Station (0.5625° N, 30.3561° E; about 1500 MASL) in Kibale National Park, Western Uganda (Figure 1). The park (795 m^2) is a protected area that contains medium altitude moist evergreen forest, swamps, grasslands, woodland thickets and colonising shrubs (Chapman & Lambert, 2000; Struhsaker, 1997). It has been effectively isolated by the surrounding agricultural land that has cut off its former connection to the forest of the Congo Basin (Hartter, 2007). The mean minimum and maximum daily temperatures in the area are about 16°C and 24°C, respectively, and the annual rainfall is about 1700 mm, which is

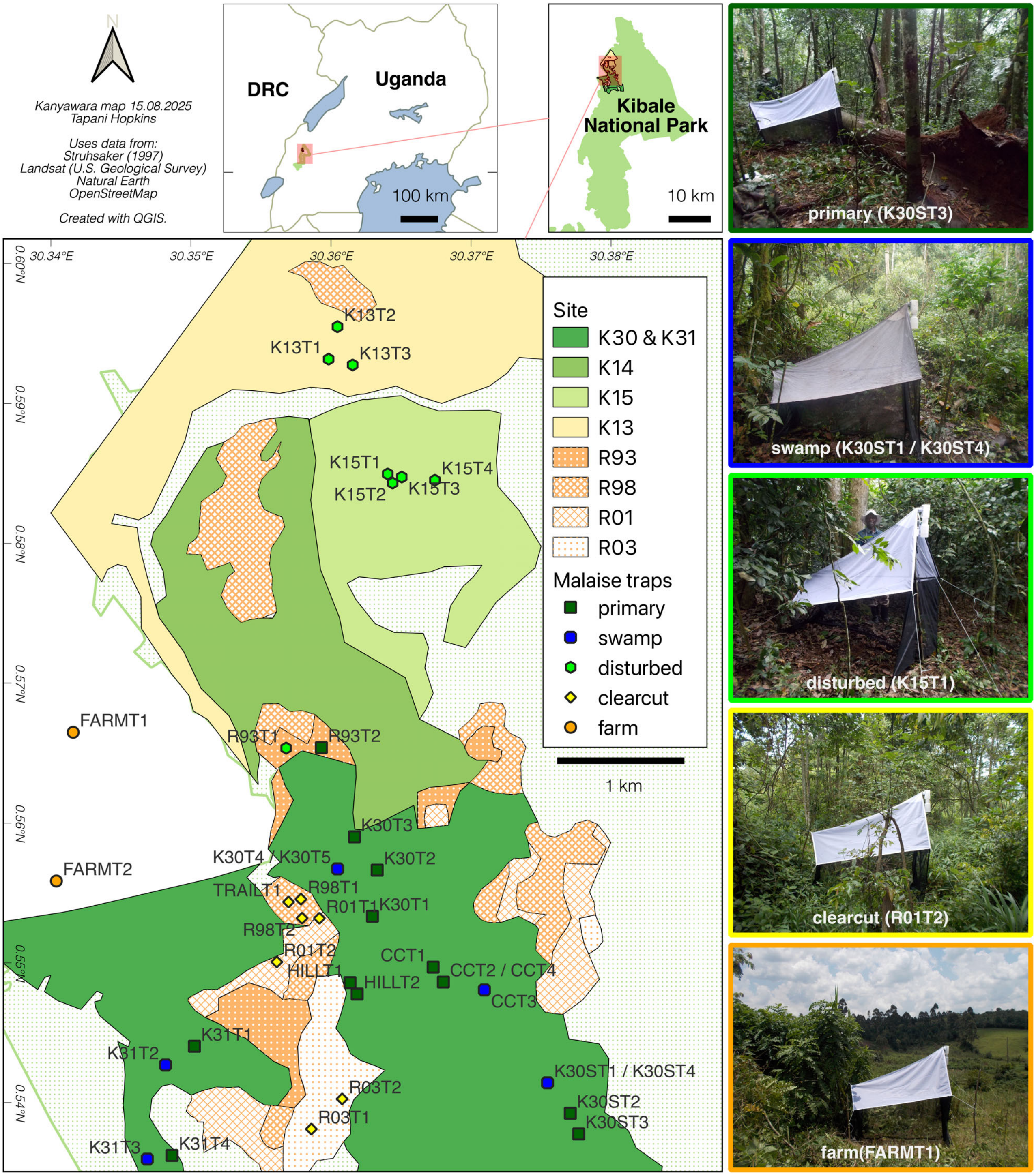

FIGURE 1 Map of the study area, showing the 34 Malaise trap locations, and the sites and habitat types in successional order. Adapted from Hopkins et al. (2019b).

distributed across two dry and two wet seasons (Hopkins et al., 2019b).

We adopted the classification of the main habitat types in the study area, and their ordering into successional classes, from Hopkins et al. (2019a, 2024); ordered from least to most disturbed: primary forest (including swampy primary forest), disturbed forest, former clearcut plantation and farmland (Figure 1). Primary forest sites were either unlogged or minimally logged more than 54 years before the sampling (Chapman & Lambert, 2000). Within these minimally disturbed sites, areas with waterlogged ground (e.g., swamp or stream) are classified as swampy primary forest. Sites classified as disturbed forest have been estimated to have lost about 25%–50% of their trees by partial logging and had 46 years to regenerate (Chapman & Lambert, 2000; Duclos et al., 2013; Owiny et al., 2016). Former clearcut plantation sites were former conifer plantations that had been clearcut on average about 12–22 years before sampling and left to regenerate (Nyafwono et al., 2014). The farmland site was located a little way outside the park and we include it here as an extra site alongside the forest sites. The study area is described in greater detail in Hopkins et al. (2019a, 2019b). It should be emphasised that many of the sites were quite heterogeneous, with 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.

Sampling methods

We collected samples with Malaise traps for 1 year (8 September 2014–14 September 2015) to cover all seasons. Malaise traps are tent-like traps which passively collect flying insects. Insects were guided upwards into a bottle, filled with about 80% ethanol, that was emptied about every 2 weeks. The traps were a standard size (about 1.7 m long with two 1.6 m^2 openings) with black netting and a white roof, manufactured by B&S Entomological Services (nowadays owned by Watkins & Doncaster, Leominster, Herefordshire, UK). This same trap model has also been used in sampling campaigns in the Neotropics (e.g., Gauld, 1991; Gómez et al., 2017; Sääksjärvi et al., 2004).

We used 34 traps that were mostly in use for the entire sampling year. They were placed as follows: 17 in primary forest, eight in disturbed forest, seven in former clearcut plantation and two in farmland (Figure 1). The traps were in various microhabitats within habitat types to capture variation in, for example, vegetation, elevation and substrate type. To maximise both sample size and habitat coverage, we placed traps on likely flying routes of insects, and whenever possible, close to ecologically distinctive microhabitats such as fallen trees.

The sampling effort totalled 876 samples and 382.4 trap months. Of these, 49 samples and 22.6 trap months did not give a full pimpline catch, due to, for example, the sample going missing, being trampled by elephants in Uganda, or rotting before the pimplines were pinned. The sampling campaign is described in greater detail in Hopkins et al. (2019a, 2019b).

Study organisms

There are currently about 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 where the larva develops: *endoparasitoids* develop inside the host's body and *ectoparasitoids* develop on the host's surface. They can also be classified into two categories based on the regulation of the host's growth: *idiobionts* kill or permanently paralyse their host at oviposition, and *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 proxies 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 a brief larval development and develop eggs in their ovaries during their adult life (i.e. synovigenesis). Idiobionts are often also ectoparasitoids and can avoid most of their host's immune defences. If they are endoparasitoids, they typically attack host stages with reduced defences, for example, eggs and pupae, more than koinobionts (Hawkins, 1994). 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). Conversely, koinobionts typically attack relatively exposed hosts, have short adult life spans after a long larval development and have most of their eggs already matured at eclosion (i.e., pro-ovigenesis). Koinobionts are typically endoparasitoid specialists with narrower host ranges than idiobionts, with hosts being either closely related phylogenetically or similar ecologically (Askew & Shaw, 1986; Shaw, 1994). The higher degree of specialisation in koinobionts is largely due to the need to adapt to their active hosts' immune system (Askew & Shaw, 1986; Quicke, 2015).

The Pimplinae subfamily of Ichneumonidae has a cosmopolitan distribution, is reasonably species-rich and is one of the most studied subfamilies of Ichneumonidae (Quicke, 2015). These make it a suitable group for species richness studies of parasitoids. Pimplinae is a relatively large subfamily with about 1700 described species in about 79 genera (Broad et al., 2018). However, what sets this 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 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, and some closely related genera are idiobiont ectoparasitoids of spiders or pseudoparasitoids of their eggs (Gauld & Dubois, 2006).

Pimplinae specimens

Members of Ichneumonoidea (Braconidae and Ichneumonidae) were separated from the collected samples and deposited at the Zoological

Museum of the University of Turku (ZMUT), Finland. We separated pimplines from these ichneumonoid samples, pinned them and sorted them into genera mainly using the keys and diagnoses in Gauld (1991) and Townes (1969). We are confident that the overwhelming majority of pimplines have been pinned; small spider parasitoids in, for example, genus *Zatypota* are the most likely to have been missed due to their small size and similar appearance to other subfamilies.

We further sorted the genera into morphospecies (henceforth referred to as species). We sorted female specimens first due to the fact that they have more reliable diagnostic characters. Subsequently, this often allowed males to be connected to corresponding female species. Species delimitation was based on finding at least one morphological character (or a combination thereof) that was unique to the species. We did not treat differences in coloration alone to be sufficient for species delimitation as they are known to vary greatly within tropical ichneumonid species (Gauld, 1991; Hopkins et al., 2024). The species were delimited by Emil Österman and the delimitation was verified by Ilari Sääksjärvi. Morphological variation indicates that some of the sorted species may represent cryptic species complexes. Although the use of morphospecies may cause some species to be split or lumped together, they are broadly used as surrogates for species in studies of arthropods, making the observed richness more comparable to that of other studies (Derraik et al., 2002, 2010; Oliver & Beattie, 1996). We did not identify most specimens to described species for this work, as there are currently no identification keys available for Afrotropical Pimplinae. Nonetheless, we identified the specimens of mainly smaller, representative genera to described species to obtain a preliminary understanding of the proportions of undescribed species in the collection.

To study the biological composition of the local pimpline fauna, we classified them into four categories based on life strategies. For ease of comparison with other studies, we followed the classification adopted by Gauld (1991), Sääksjärvi et al. (2004) and Gómez et al. (2017):

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 IDC 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).

The IDC classification is slightly uncertain. We classified genera as IDC based on containing species with very long ovipositors, as host records were not available. However, many smaller species have quite short ovipositors, and there may be variation in host use within the genera. For the time being, in the absence of better information, they are kept in the IDC group.

Data analysis

We modelled species accumulation rates with rarefaction curves. These provide an idea of the total species richness, whether or not all species have been sampled, and which sites likely have more species (since species generally accumulate faster where there are more species in total). Each curve is an average of resamples and estimates 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 the roughly two-week samples without replacement 400 times. Thus, the individuals of each sample were kept together in resampling. We produced separate rarefaction curves for each habitat type and biological pimpline group. We also checked if there was a need to treat dry and wet seasons separately by producing curves for the different seasons.

To estimate whether curves differed significantly from each other, we calculated approximate 84% confidence intervals. These do not overlap when $p < 0.05$ (MacGregor-Fors & Payton, 2013, though c.f. Colwell et al., 2012 for a discussion of 84% vs. 95%). For estimating if point values differed significantly from curves, we used 95% confidence intervals on the curves. However, the confidence intervals should be viewed as rough approximations. We estimated confidence intervals by resampling the samples with replacement and calculating the standard error of this bootstrapped distribution. This underestimates the variance since we are only resampling from the set of samples we collected instead of all possible samples. The bias should, however, be small for samples such as ours which have a good coverage (i.e., have collected all the common species).

To see if differences in the abundances of pimpline species could have affected the rarefaction curves, we estimated the evenness of the abundances of each curve. Rarefaction curves, by their nature, accumulate species faster both when there are more species present and also when the abundances of the species are more even. Since we are only interested in the former, we roughly controlled for this effect by calculating an evenness index based on the abundances of the collected species. There are a bewildering variety of evenness indices (Tuomisto, 2012), of which we arbitrarily chose the one referred to by Tuomisto (2012) as ^2E. The index ranges from near zero (very uneven abundances, species accumulation is slower) to one (all species have the same abundance, species accumulation is rapid).

We performed all analyses in R version 4.4.3 (R Core Team, 2025) with the R package 'turkuwasps' (Hopkins, 2025; https://doi.org/10.5281/zenodo.16790133). The analyses are available online (Hopkins et al., 2025; https://doi.org/10.5281/zenodo.16882929).

RESULTS

Pimplinae

We collected a total of 5892 pimpline individuals, which we sorted into 86 species in 14 genera. Of these, forest sites had a total of 5623

TABLE 1 Faunistic composition of pimplines collected by 32 Malaise traps in forest sites in Kibale National Park, Uganda.

Biological group	Genus	Species	Individuals
Idiobiont parasitoids of deeply concealed hosts	*Xanthephialtes*	2	70
	Xanthophenax	13	876
	Sum	**15**	**946**
Idiobiont parasitoids of weakly concealed hosts	*Acropimpla*	3	113
	Camptotypus	12	328
	Echthromorpha	1	1550
	Itoplectis	4	474
	Pimpla	6	140
	Sericopimpla	2	48
	Theronia	2	488
	Xanthopimpla	18	740
	Sum	**48**	**3881**
Koinobiont ectoparasitoids of spiders	*Eruga*	3	251
	Zatypota	13	251
	Sum	**16**	**502**
Pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders	*Afroanomalia*	1	66
	Zaglyptus	3	228
	Sum	**4**	**294**

Note: The bold values sum the species and individual numbers of each biological group.

pimplines of 83 species and 14 genera (Table 1). Farmland had 269 pimplines of 20 species and 10 genera (Table S1). Species accumulated at roughly similar rates (per individual caught) in dry and wet seasons in each habitat type (Figure S1). The evenness of species abundances varied (Figures S2–S4), but only the difference between the curves for swampy primary forest and primary forest, for the KES biological group, could have been affected by this. No other difference in evenness could plausibly have affected the significance of a difference between curves.

We estimated between 26% and 63% of collected species to be undescribed, based on estimations of eight mostly small genera (Table 2).

Trapping in forest sites accumulated species of Pimplinae significantly faster (per individual caught) than trapping in farmland after about 50 individuals caught (Figure 2). Species accumulation rates were roughly similar between forest types.

Biological groups

Trapping in forest sites accumulated species of each biological pimpline group (per individual caught) at rates that differed significantly from each other after about 100 individuals were caught; ordered from slowest to fastest accumulation: Pseudo/IES < IDC < KES < IWC (Figure 3).

TABLE 2 Estimated number of undescribed species of the number of collected species in eight mostly small pimpline genera.

Genus	Undescribed species	Total species
Acropimpla	0–2	3
Afroanomalia	0	1
Camptotypus	2–8	12
Echthromorpha	0	1
Sericopimpla	1	2
Theronia	0–1	2
Xanthephialtes	1	2
Zaglyptus	3–4	4
Total	7–17	27

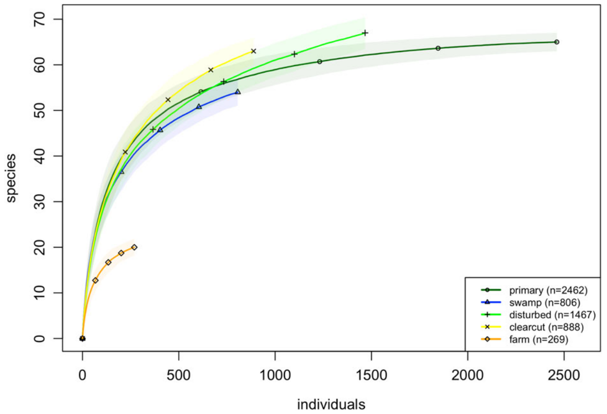

FIGURE 2 Species rarefaction curves of pimplines by habitat type caught in 34 Malaise traps in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

Trapping in former clearcut plantation accumulated species of IDC significantly faster (per individual caught) than in primary and disturbed forest after about 80 individuals were caught (Figure 4). Species accumulation rates between habitat types were otherwise roughly similar, although the sample size of farmland was low.

Trapping in forest sites accumulated species of IWC significantly faster (per individual caught) than trapping in farmland after only about 30 individuals were caught (Figure 5). Species accumulation rates were roughly similar between forest types, with the exception of disturbed forest whose accumulation exceeded that of primary forest after about 900 individuals were caught (Figure 5).

Trapping in primary forest accumulated species of KES significantly faster (per individual caught) than in swampy primary forest after about 40 individuals were caught (Figure 6). However, swampy primary forest also had a less even species abundance, which may explain part or all of the difference (Figure S3). Species accumulation rates between habitat types were otherwise roughly similar, although the sample size of farmland was low.

Species of Pseudo/IES accumulated at roughly similar rates between habitat types (Figure 7). Sample sizes were low for all habitats except primary forest and disturbed forest, where the number of species stabilised at three.

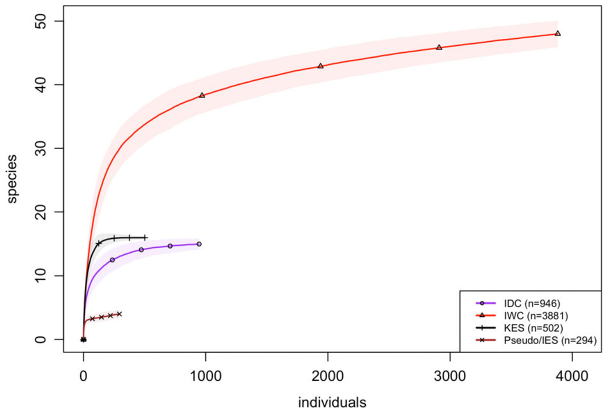

FIGURE 3 Species rarefaction curves of biological pimpline groups caught in 32 Malaise traps in forest sites in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals. IDC = idiobiont parasitoids of deeply 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.

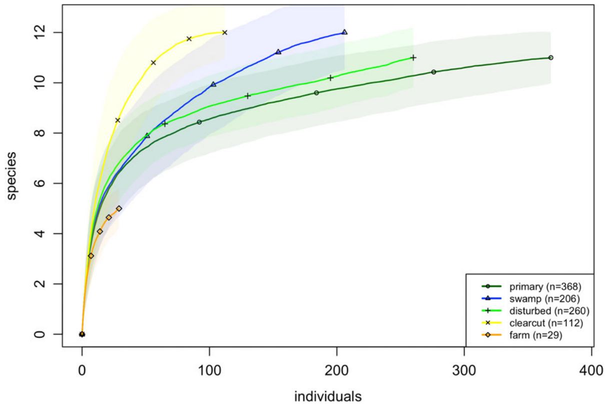

FIGURE 4 Species rarefaction curves of pimpline group IDC (idiobiont parasitoids of deeply concealed hosts) by habitat type, caught in 34 Malaise traps in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

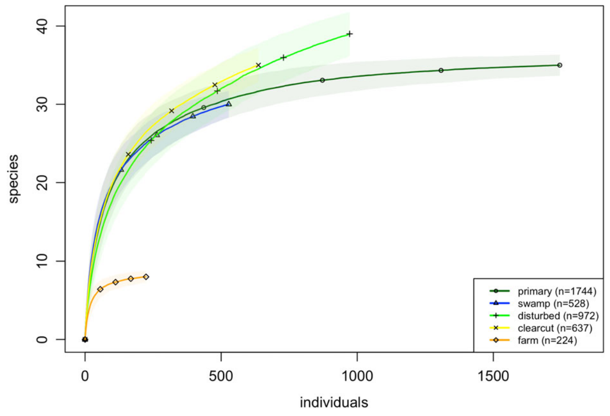

FIGURE 5 Species rarefaction curves of pimpline group IWC (idiobiont parasitoids of weakly concealed hosts) by habitat type, caught in 34 Malaise traps in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

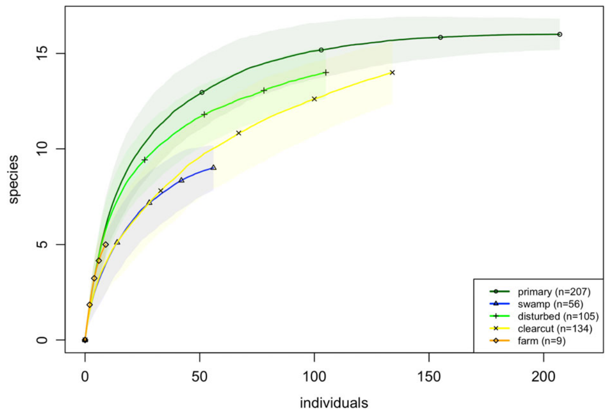

FIGURE 6 Species rarefaction curves of pimpline group KES (koinobiont ectoparasitoids of spiders) by habitat type, caught in 34 Malaise traps in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

DISCUSSION

Richness of Pimplinae

This study shows for the first time that extensive Malaise trapping in Afrotropical forest can uncover a highly species-rich pimpline fauna. This is in line with estimates in Meier et al. (2024) of high pimpline richness in the Afrotropics, and in the Equatorial Afrotropics in particular, where the study area is located. The collected 86 morphospecies should be taken to represent the minimum number of species in the samples, as any cryptic species were, like in most other studies, not considered. Rarefaction curves of Pimplinae in most habitat types were not near stabilising, suggesting more species could still be collected at the same trap sites (Figure 2). However, the majority of species at these trap sites have likely been caught (e.g., the chao1 estimator estimates that 17 species remain; Colwell et al., 2012), and the primary forest curve, with the largest sample size ($n = 2462$), is near stabilising at 65 species. Further undiscovered species likely exist in habitats not covered by our 34 traps. Species that are mainly found in papyrus swamp or the canopy, in particular, will have been caught as isolated stragglers, if at all (Basset et al., 2015; de Souza Amorim et al., 2022).

Many, if not most, of the collected pimpline species are undescribed. Our estimate of the proportion of undescribed species in eight mostly small genera (26%–63% in Table 2) is probably an underestimate for the whole subfamily, as small genera are often better studied than large genera.

From a conservation perspective, the superiority of protected forest sites over farmland in supporting much higher pimpline richness is

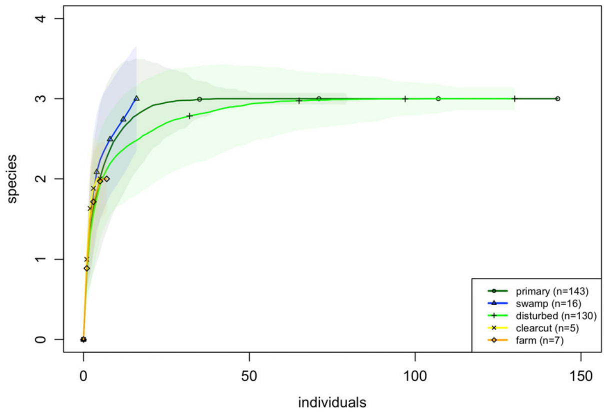

FIGURE 7 Species rarefaction curves of pimpline group Pseudo/IES (pseudoparasitoids of spider egg sacs or idiobiont ectoparasitoids of spiders) by habitat type, caught in 34 Malaise traps in Kibale National Park, Uganda. The curves are sample-based and show the accumulation rates of species per individual caught, with 84% confidence intervals.

evident (Figure 2). Inside the protected forest, there was a surprisingly high pimpline richness in disturbed forest and former clearcut plantation sites, rivalling or sometimes even surpassing that of primary forest. To some extent, this is likely because of primary forest species flying in nearby disturbed or clearcut patches and being trapped there. It is noticeable that the koinobiont spider parasitoids (KES group), which are relatively small and likely do not fly far, had their highest curve in primary forest, and the lowest (though not necessarily significantly lower) forest curves in swamp and clearcut plantation (Figure 6). However, our results at the very least suggest that even strongly disturbed forest can maintain diverse pimpline faunas when there is primary forest nearby.

Richness of biological groups

Species accumulation curves of biological pimpline groups in forest clearly suggest the highest richness is in IWC (48 species caught), followed by a roughly similar richness in KES (16 species caught) and IDC (15 species caught), and the lowest richness in Pseudo/IES (4 species caught) (Figure 3). All curves are near stabilising except for IWC, suggesting more IWC species could be collected in the forest sites (Figure 3).

Rarefaction curves for IWC resemble those for Pimplinae as a whole, as this group dominated in the number of individuals and thus had the strongest influence on Pimplinae curves (Figures 2 and 5). Only the farmland and primary forest curves are near stabilising at eight and 35 species, respectively (Figure 5). Interestingly, species accumulation was faster in disturbed forest than in primary forest after about 900 individuals caught, with the curve reaching 39 species and still rising. One possible explanation of this is that the intermediate disturbance and gap dynamics of partial logging created a diverse vegetation and hence diverse herbivore fauna as hosts for the wasps. This produces ecotones between habitats, which are known to harbour higher diversity (Kark, 2013), and can cause canopy insects to descend to the level of the traps in areas with less canopy coverage (Davis & Sutton, 1998; Gossner, 2009). There is some support for the richness of IWC being positively associated with floristic richness (Sääksjärvi et al., 2006), though not necessarily the richness of the other biological groups that attack either spiders or deeply concealed hosts. This explanation is weakened, however, by Nyafwono et al. (2014) finding lower adult butterfly abundance and richness at disturbed forest sites than at primary forest sites; immature Lepidoptera are important hosts for many species of IWC. Another possibility is that the traps also caught stragglers from primary forest or farmland, although most disturbed forest traps were a considerable distance from both (Figure 1). This is supported by the one trap that was near other habitat types (R93T1) accumulating species quickly: omitting it from the analyses results in a disturbed forest curve that is still higher than primary forest, but not significantly so (Figure S5).

None of the rarefaction curves for IDC are particularly near stabilising, suggesting more species could be sampled from each habitat (Figure 4). Counterintuitively, former clearcut plantation accumulated species faster than disturbed and primary forest (after about 80 individuals caught). Though stragglers from nearby primary forest could partly explain this, the reason remains unclear. The ecology of the genera that belong to IDC, *Xanthephialtes* and *Xanthophenax*, is unclear and may vary within the genera. Preliminary (unpublished) results, for example, suggest that some of the species are associated with dead wood (which is less abundant in clearcut plantation) while others are not.

Rarefaction curves for KES are not close to stabilising except possibly for the primary forest curve, which is near stabilising at 16 species (Figure 6). The lower species accumulation rate in swampy primary forest compared to disturbed or primary forest (after about 40 individuals caught), if genuine, can plausibly be explained by the traits of the species themselves and the ecology of their spider hosts. These wasps are relatively small and are probably weak flyers: the presence of even a small area of open water is likely a major deterrent to them and could plausibly keep entire species away. Waterlogged ground is also not ideal for epigeal spiders, and the structural complexity is comparably low in swampy primary forest, providing few web-building sites. This suggests primary forest is most important in conserving the richness of koinobiont spider parasitoids, particularly since all species were collected there.

Little can be said of Pseudo/IES, except that very few were caught outside primary and disturbed forest (Figure 7). The low sample sizes show no differences in species accumulation rates between habitat types, and the curves of primary and disturbed forest stabilised at three species.

Large-scale species richness patterns

The rarefaction curves for Pimplinae (Figure 2) suggest species richness in the study area is high compared with other Malaise trap

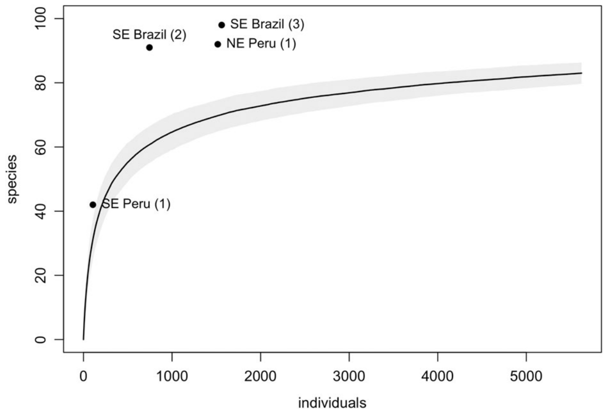

FIGURE 8 Species rarefaction curve of pimplines caught in 32 Malaise traps in forest sites in Kibale National Park (Uganda), with pimpline species numbers plotted against the number of collected individuals from the most species-rich sites published in the literature. The curve is sample-based and shows the accumulation rate of species per individual caught, with a 95% confidence interval. Plotted collections were caught with Malaise traps in the Neotropics: (1) Gómez et al. (2017); (2) Higa and Penteado-Dias (2020); (3) Flinte et al. (2023).

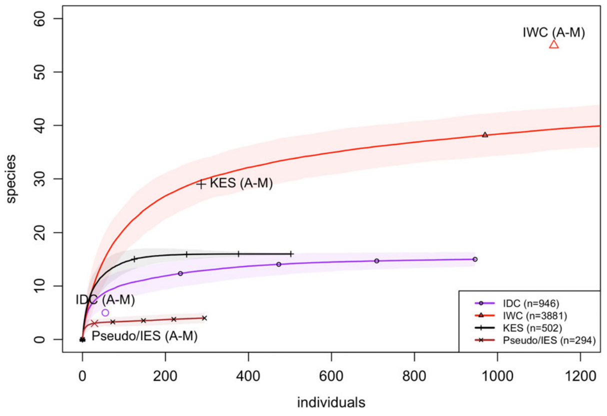

FIGURE 9 Species rarefaction curves of pimpline groups caught in 32 Malaise traps in forest sites in Kibale National Park (Uganda), with corresponding species numbers of the A-M (Allpahuayo-Mishana, NE Peru) collection in Gómez et al. (2017) plotted against the number of individuals sampled. The curves are sample-based and show the accumulation rate of species per individual caught, with 95% confidence intervals (for comparisons to the A-M points). 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.

collections (see Data S1 in Gómez et al. (2017) for a summary of 97 collections of pimplines and rhyssines). Three large (two in SE Brazil and one in NE Peru) and one small (SE Peru) Neotropical collections, which report pimplines separately, surpass the observed species richness when controlling for abundance (Figure 8). This suggests pimpline richness is higher in the Neotropics than at our Ugandan site. It is likely that Neotropical pimpline richness is higher than in the Afrotropics as a whole, not just Uganda, given that our site is expected to be among the more diverse areas in the Afrotropics (Meier et al., 2024). However, a concern with simple comparisons like this is that habitat heterogeneity and elevation range are not considered; for example, sampling was done along an elevation gradient in both collections in SE Brazil, leading to higher species richness, as the taxonomic composition of pimplines typically changes along elevation gradients (Flinte et al., 2023; Hall et al., 2015; Higa & Penteado-Dias, 2020; Veijalainen et al., 2014).

Overall, the case for the anomalous LDG of ichneumonids is not supported, to the extent that Pimplinae can represent Ichneumonidae, by the observed high richness of Pimplinae. Although there is far too little global data for firm conclusions, the four temperate collections with over 1000 individuals, from France, Italy and the United Kingdom in Gómez et al. (2017) caught clearly fewer species (25–41 species for 1836–3945 individuals), despite combining Pimplinae and Rhyssinae. However, this is only a rough comparison that does not consider habitat heterogeneity, which was likely much higher in the Ugandan sampling. The Ugandan data are in line with the patterns proposed in Meier et al. (2024), of higher species richness towards the equator, highest Afrotropical richness in Equatorial Africa and Madagascar, and even higher richness in the Neotropics. It is not, however, consistent with the anomalous latitudinal gradient in Malaise samples of Ichneumonidae as a whole found by Santos et al. (2025), for reasons which are currently unclear. The present results suggest that protecting tropical forest conserves more species of at least the Pimplinae subfamily than what an anomalous LDG might indicate, elevating the importance of tropical forest in attempts to protect areas with high parasitoid wasp richness.

Biological composition

The biological composition of collected pimplines follows what appears to be a typical pattern of IWC being the most species-rich group, followed by KES, IDC and Pseudo/IES, both when abundance is controlled for (Figure 9) and when it is not (Table 1). This pattern (uncorrected for abundance) is also found in the NE Peruvian collection (Figure 9) and the SE Peruvian collection in Gómez et al. (2017). Other collections in Gómez et al. (2017) also have IWC as the most species-rich group, except for one where IWC is second most species-rich by one species, although abundance was not controlled for: i.e., three collections in Costa Rica (Gauld, 1991), one in Finland (Jussila, 1984), one in England (Owen et al., 1981) and one in Poland (Sawoniewicz, 1986). This may be a general pattern in at least the tropics. It does not, however, mean that the taxa would be the same: the NE and SE Peruvian collections combined have only three out of 16 genera in common with the 14 genera of the present collection: *Pimpla*, *Zatypota* and *Xanthopimpla*. Nor are the relative richnesses of the biological groups identical: the NE Peruvian collection's higher pimpline richness seems primarily to be due to higher richness of IWC and KES (Figure 9). We are preparing taxonomic works in which the morphospecies of this study are described and identified into described species. If changes to the present species delimitation were to occur in these works, we see it as more likely to increase than to decrease the present number of species.

CONCLUSIONS: IMPLICATIONS FOR CONSERVATION

- The observed high species richness of Pimplinae at such a low latitude emphasises the importance of conserving tropical forest as environments that can support high parasitoid wasp richness, particularly as parasitoid wasps may be especially vulnerable to extinction by anthropogenic disturbances.
- Converting primary forest into agricultural land crashes the local richness of pimplines and likely also many other parasitoids.
- Protecting primary tropical forest from disturbance may be particularly important in conserving a high richness of koinobiont ectoparasitoids of spiders.
- Even heavily disturbed tropical forest sites can display high parasitoid richness (at least of pimplines) after a few decades of regeneration when undisturbed primary forest is nearby.

AUTHOR CONTRIBUTIONS

Emil M. Österman: Conceptualization; writing – original draft; investigation; project administration; writing – review and editing; formal analysis; visualization. **Tapani Hopkins:** Formal analysis; software; writing – review and editing; writing – original draft; resources; methodology; data curation; visualization. **Ilari E. Sääksjärvi:** Supervision; conceptualization; writing – review and editing; resources; investigation; funding acquisition.

ACKNOWLEDGEMENTS

The collecting in Uganda was supported by Heikki Roininen, Isaiah Mwesige and the staff of the Makerere University Biological Field Station. Countless people helped process the Ugandan samples, including the staff of the Zoological Museum of the University of Turku, students of the university and school pupils from the Turku region. These contributions are gratefully acknowledged. The required research and export permits were issued by the Uganda National Council of Science and Technology (NS 504) and the Uganda Wildlife Authority. This research is derived from the first author's master's thesis in biology at the University of Turku. Open access publishing facilitated by Turun yliopisto, as part of the Wiley - FinELib agreement.

FUNDING INFORMATION

This article is part of Emil Österman's doctoral research, which is funded by the Ministry of Education and Culture (Finland) and the Research Council of Finland through the Sustainability Transformations Doctoral Education Pilot. Collection of the material and its processing was supported by the Alfred Kordelin Foundation, The Entomological Society of Finland, the Finnish Cultural Foundation, Oskar Öflunds Stiftelse, Svensk-Österbottniska Samfundet and Waldemar von Frenckells stiftelse (grants to Tapani Hopkins).

CONFLICT OF INTEREST STATEMENT

The authors declare there are no competing interests.

DATA AVAILABILITY STATEMENT

The data, the R code used to analyse it, and supplementary tables and figures are available in the Zenodo repository (Hopkins et al., 2025; https://doi.org/10.5281/zenodo.16882929). The R code uses our general code for analysing tropical wasp data, which we have packaged as R package 'turkuwasps' (Hopkins, 2025; https://doi.org/10.5281/zenodo.16790133).

ETHICS STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the Journal's author guidelines page, have been adhered to.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

How to cite this article: Österman, E.M., Hopkins, T. & Sääksjärvi, I.E. (2026) Local species richness of parasitoid wasps (Ichneumonidae: Pimplinae) in Afrotropical forest: Conservation perspectives. *Insect Conservation and Diversity*, 19(1), 198–210. Available from: https://doi.org/10.1111/icad.70017