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A comparison of the parasitoid wasp species richness of tropical forest sites in Peru and Uganda – subfamily Rhyssinae (Hymenoptera: Ichneumonidae)

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22 **ABSTRACT**

23 The global distribution of parasitoid wasp species richness is poorly known. Past attempts to
24 compare data from different sites have been hampered by small sample sizes and lack of
25 standardisation. ~~During the past decades,~~ we have carried out long-term Malaise trapping using
26 a standardised approach in the tropical forests of Peru (western Amazonia) and Uganda
27 (eastern Africa). Here, we test how well such data can be used for global comparisons, by
28 comparing the results for the subfamily Rhyssinae (Hymenoptera: Ichneumonidae). We found
29 that more rhyssine species were caught in Peru than in Uganda, despite the Ugandan samples
30 containing many more individuals both in absolute terms and per unit time. The difference in
31 the number of individuals caught may largely be due to more rainfall in Peru, since rain reduces
32 Malaise trap catches. Peruvian traps caught species at a faster rate (per individual caught) than
33 Ugandan traps. We interpret this as a sign that the Peruvian sites have more species than the
34 Ugandan site. Long-term, standardised Malaise trapping showed promise for global
35 comparisons of species richness. Sampling more sites on both continents, and analysing all
36 subfamilies, would give an estimate of which continent has more parasitoid wasp species. We
37 suggest some refinements to the sampling design that would further improve sampling
38 efficiency for future studies.

39

40

41 **Keywords:** biodiversity, idiobiont parasitoids, latitudinal diversity gradient, Malaise trap, Uganda
42 Malaise trapping 2014-2015, Amazon Malaise trapping 2000

43

Introduction

45 Darwin wasps or ichneumonids (parasitoid wasps of the family Ichneumonidae) were once believed to
46 display an "anomalous latitudinal diversity gradient": to be more species rich in mid and high latitudes than
47 in the tropics (Owen & Owen, 1974; Janzen & Pond, 1975; Janzen, 1981), instead of peaking in the tropics as
48 is the case with most groups of organisms (Hawkins, 2001; Willig et al., 2003). Although this belief has lost
49 ground after the discovery of numerous unknown tropical species, especially in Central America and South
50 America (Gauld, 1991; Gaston & Gauld, 1993; Sääksjärvi et al., 2004), we still do not have enough data to
51 draw reliable conclusions on where the species richness of Darwin wasps peaks (Quicke, 2012). We especially
52 do not know how other tropical areas compare to the unexpectedly species-rich South American sites.

53 Long-term Malaise trapping is one potential way of finding out how the species richness of flying insects
54 is distributed on our planet. Malaise traps are tent-like passive traps that collect flying insects, especially
55 Diptera and Hymenoptera, giving large sample sizes with relatively little effort in terms of person-hours (Van
56 Achterberg, 2009; Saunders & Ward, 2018). Since Malaise traps are widely used and are available
57 commercially in standard sizes, the potential for getting comparable samples from different sites is high.
58 However, large sample sizes and several traps may be needed since the catches tend to vary greatly. Malaise
59 traps typically catch quite different numbers of individuals even when placed near each other in the same
60 habitat, depending on how their position relates to popular insect flight routes (Fraser et al., 2008; Saunders
61 & Ward, 2018). Weather also affects catches: traps typically catch less in rainy weather, due to flying insects
62 being less active, which can be hard to disentangle from genuine, seasonal changes in abundance (e.g.
63 Hopkins, Roininen, & Sääksjärvi, 2019b). However, it is possible to estimate by mathematical modelling how
64 large a catch (number of individuals of each species) to expect in given weather conditions and habitat. Such
65 modelling has been done for the Ugandan [site of the present paper](#) (Hopkins, Roininen, & Sääksjärvi, 2019b).

66 Despite the potential of long-term Malaise trapping for faunistic comparisons, few attempts have been
67 made to compare the Malaise trapped Darwin wasp faunas of different sites. Timms et al. (2016) took 38
68 Darwin wasp datasets which had been gathered by Malaise trapping between latitudes 82°N and 25°S.
69 Although they got some interesting results indicating that the latitudinal pattern displayed by Darwin wasps
70 varies between subfamilies, only four of the datasets had been identified to species level, and those sites
71 were so undersampled that the number of species and the number of individuals caught were
72 interchangeable (figure 3 in [the paper](#), although note that the authors [interpreted this differently](#)). Also, it is
73 worth noting that the number of traps used at different sites was not taken into account: the apparently
74 higher abundance in the tropics (e.g. figure 4a in the paper), for example, simply reflects the fact that more
75 traps were used in the tropics than at higher latitudes. Gómez et al. (2017) compared the data of 97 sites on
76 three different continents. Although their results tentatively suggested that the species richness of the
77 subfamilies Pimplinae and Rhyssinae might peak in the tropics, the sample sizes were too small for firm
78 conclusions. There was also a lot of variation in how the Malaise trapping had been conducted: the Kibale
79 site in Uganda, for example, [had been sampled with unusually small Malaise traps](#) (Hopkins et al., 2018). The
80 general picture emerging from these two attempts is that comparing the Darwin wasp species richness of
81 different sites is challenging, due to most Malaise trapping having yielded small sample sizes and not having
82 been conducted in a standard fashion.

83 Recently, we have published the first results of long-term Malaise trapping in Kibale National Park,
84 Uganda (Hopkins, Roininen, Noort, et al., 2019; Hopkins, Roininen, & Sääksjärvi, 2019b). These results are on
85 the relatively rarely caught rhyssine wasps (subfamily Rhyssinae), the only subfamily [currently available for](#)
86 [study in the material](#). Since the methodology is the same as in our earlier long-term sampling in Peru
87 (Sääksjärvi et al., 2004; Gómez et al., 2015), this allows us to compare the species richness of tropical forest
88 sites on two continents, with material that has reasonable sample sizes and has been collected in a standard

89 fashion. In this work, we compare the abundance and species richness of rhyssine wasps in Peruvian and
90 Ugandan Malaise trap samples. Our aim is to show that similar analysis of other (more abundant)
91 subfamilies, and further sampling at more sites, would allow the species richness of African and South
92 American tropical forests to be compared.

93

Methods

94 Study sites

95 The two main study sites were Allpahuayo–Mishana National Reserve in north-eastern Peru (western
96 Amazonia, South America), and Kibale National Park in Uganda (eastern Africa). Both are near the equator
97 and predominantly covered by tropical forest. We also included data from a second western Amazonian site,
98 Los Amigos Conservation Concession in south-eastern Peru.

99 Allpahuayo–Mishana National Reserve contains moist tropical forest that is known for its habitat
100 heterogeneity (Whitney & Alonso, 1998; Sääksjärvi et al., 2004). The reserve is about 25 km southwest from
101 the city of Iquitos (3°57 S, 73°26 W, approx. 110–180 m.a.s.l.: Gómez et al., 2015). We broadly classified the
102 non-inundated forest (*tierra firme*) into forest types based on soil characteristics (Sääksjärvi et al., 2006;
103 Hopkins, Gómez, et al., 2023). Mean annual rainfall is approximately 3000 mm and mean annual
104 temperature is 26°C (Sääksjärvi et al., 2006). Weather data, consisting of daily rainfall and daily mean
105 temperatures, were available for Iquitos city from NOAA/NCEI (<https://www.ncdc.noaa.gov>, Menne et al.,
106 2012). In the analyses, we replaced any missing rain data with the 29-day average rainfall (average over the
107 time period from 14 days before to 14 days after the day whose rain datum was missing). The study site is
108 described in greater detail in our earlier papers (Sääksjärvi et al., 2004, 2006; Gómez et al., 2015) and one of
109 the datasets associated with the present paper (Hopkins, Gómez, et al., 2023).

110 Los Amigos Conservation Concession contains moist tropical forest growing on a mosaic of different soils
111 (Gómez et al., 2017). Our study site was near the Los Amigos Biological Station (CICRA, 12°34 S, 70°05 W,
112 approx. 230–270 m.a.s.l.: Gómez et al., 2017). We broadly classified the habitat into inundated (floodplain)
113 and non-inundated (terrace) forest. Mean annual rainfall is approximately 2770 mm and mean annual
114 temperature is 23°C (Gómez et al., 2017). Weather data, including daily rainfall and daily mean
115 temperatures, were available for the field station from the AABP Atrium (AABP Atrium, 2013). The study site
116 is described in greater detail in our earlier paper (Gómez et al., 2017) and one of the datasets associated with
117 the present paper (Hopkins, Gómez, et al., 2023).

118 Kibale National Park, in western Uganda, contains medium altitude moist evergreen forest as well as
119 swamps, grasslands, woodland thickets and colonizing shrubs (Struhsaker, 1997; Chapman & Lambert, 2000),
120 and is nowadays surrounded by agricultural land. Our study site was near the Makerere University Biological
121 Field Station (0°33.750 N, 30°21.370 E; approx. 1500 m.a.s.l.). The area contains a varied mix of different
122 habitats, which we broadly classified into a successional gradient from farmland and clearcut former
123 plantation to primary forest (Hopkins, Roininen, & Sääksjärvi, 2019a; b). Mean annual rainfall is
124 approximately 1700 mm, mean maximum daily temperature 24°C and mean minimum daily temperature
125 16°C (Chapman et al., 1999). Mean average temperatures are not available for the site, but are estimated to
126 be 20°C by the CHELSA climate data set (Karger et al., 2017, 2021). Weather data consisting of daily rainfall
127 and maximum and minimum temperatures were collected by a worker at the field station during the Malaise
128 trapping. The study site is described in greater detail in our earlier paper and its associated dataset (Hopkins,
129 Roininen, & Sääksjärvi, 2019a; b).

130 Malaise trapping

131 We collected insects by Malaise trapping in the same way in both Peru and Uganda. Malaise traps were
132 of a standard size and design: black with a white roof, approximately 170 cm long with two 1.6 m² openings,

133 with identical fabric, mesh sizes and collecting jars, supplied by Marris House Nets (for Peru) or its successor
134 B&S Entomological Services (for Uganda). The traps were placed on the likely flight paths of insects, and they
135 collected flying insects into approximately 80% ethanol. In both Peru and Uganda, traps were used for a
136 whole year to cover all seasons, and large numbers of traps were placed in different habitats. In Peru, three
137 shorter sampling campaigns were also carried out. Traps were emptied at intervals mostly ranging from one
138 to three weeks.

139 The Peruvian Malaise trapping consisted of a full year in 2000 (January 2000 – January 2001), and three
140 shorter sampling campaigns in 1998 (August 1998 – January 1999), 2008 (May – August 2008) and 2011
141 (April – December 2011). In 1998, ten traps were placed in Allpahuayo-Mishana: four in clay soil forest and
142 six in white sand forest. The total sampling effort was 45.8 trap months (c.f. 44 trap months mentioned in
143 Sääksjärvi et al., 2004). In 2000, seventeen traps were placed in Allpahuayo-Mishana: two in clay soil forest,
144 four in loamy soil forest and a total of eleven in three kinds of white sand forest (varying e.g. in canopy
145 height and reflecting the high habitat heterogeneity of the study area). Fourteen of these traps were in place
146 for the whole time period, but one trap (i3) was stolen in June 2000, and two traps (k1, k2) were installed as
147 a replacement in July 2000. The total sampling effort was 151 trap months according to the compiled data
148 (c.f. 141 trap months mentioned in Sääksjärvi et al., 2004). In 2008, nine traps were placed in Los Amigos:
149 four in floodplain forest and five in terrace forest. The total sampling effort was 27.1 trap months. In 2011,
150 fourteen traps were placed in secondary forest in Allpahuayo-Mishana. Only four of them were in place the
151 whole time period: eight others were placed in October, one was stolen before it collected any samples, and
152 one was stolen in August. The total sampling effort was 45.8 trap months (c.f. 45 trap months mentioned in
153 Gómez et al., 2017).

154 Except for the rhyssine wasp data, all the Peruvian data used in the present paper is from the compiled
155 dataset (Hopkins, Gómez, et al., 2023). The 1998 and 2000 sampling campaigns have been described in
156 greater detail by Sääksjärvi et al. (2004, 2006), and the 2008 and 2011 sampling campaigns by Gómez et al.
157 (2017).

158 The Ugandan Malaise trapping consisted of a full year, September 2014 – September 2015. A total of 34
159 traps were placed: sixteen in primary forest, seven in disturbed forest, nine in clearcut former plantations
160 and two outside the natural park in agricultural land. The total sampling effort was 373.5 trap months, with a
161 further 8.9 trap months being unrepresentative of a normal catch for various reasons, e.g. due to the traps
162 and their samples being trampled by elephants. The Ugandan Malaise trapping data used in the present
163 paper is from a previously published dataset (Hopkins, Roininen, & Sääksjärvi, 2019a). The sampling
164 campaign has been described in greater detail by Hopkins et al. (2019b).

165 The original data from the Peruvian sampling campaigns had become partly fragmented over the years,
166 so we recompiled the data from a variety of sources, such as old computer files and the labels on insect
167 specimens and sample jars. The compiled dataset is available online (Hopkins, Gómez, et al., 2023). It
168 includes a complete list of the Peruvian Malaise samples: what samples were collected, when they were
169 collected and what trap they came from. The dataset also provides information on the trap sites (including
170 vegetation near the traps) and on the weather during the Malaise trapping. The source material and files
171 detailing how the data were compiled and inconsistencies resolved are also provided.

172 **Rhyssine wasps**

173 In this paper, we compare the Peruvian and Ugandan Darwin wasps of the subfamily Rhyssinae, which
174 are idiobiont ectoparasitoids of holometabolous insects. The subfamily is cosmopolitan in distribution and
175 moderately small in terms of species richness. The species of the subfamily are mostly large and vividly
176 coloured. The female rhyssines possess a long ovipositor that is used for ovipositing into hosts living deeply
177 concealed in decaying wood (e.g. Siricoidea wasps and wood-boring beetles).

178 The rhyssines and other ichneumonoid wasps (families Ichneumonidae and Braconidae) were separated
179 from the Malaise samples, and are currently at the Zoological Museum of the University of Turku (ZMUT),
180 Finland. All Peruvian wasps have been pinned and sorted to subfamilies. Ugandan wasps are still being
181 processed, but all rhyssines have been pinned.

182 The Peruvian rhyssines had not been databased before this study. We databased a total of 94 individuals:
183 87 individuals found at the museum, and a further seven individuals that were mentioned in an earlier paper
184 (Gómez et al., 2015). Four of these were left out of analyses due to it being unclear which sample they came
185 from. We expect the effect of any rhyssines being missed during databasing to be small, since other potential
186 sources of error (e.g. wasps lost during the processing of samples) are much greater. Other sources give the
187 total as 96 rhyssines (Gómez et al., 2017) or 93 rhyssines (file 2 in folder "1 Raw Data" of Hopkins, Gómez, et
188 al., 2023). Sääksjärvi et al. (2006, Appendix 1) reported 945 rhyssine+pimpline individuals caught in 2000,
189 which is 8% more than in our data (874 rhyssines+pimplines in file 2 in folder "1 Raw Data" of Hopkins,
190 Gómez, et al., 2023).

191 The rhyssine wasps were sorted into species at ZMUT. Peruvian rhyssines were identified to species
192 mainly by Ilari Sääksjärvi and Isrrael Gómez, and the species delimitation was later verified by Tapani
193 Hopkins. Ugandan rhyssines were identified to species mainly by Tapani Hopkins, and the species
194 delimitation was verified by Ilari Sääksjärvi. Species delimitation was based on finding at least one
195 morphological character (or combination of characters) unique to the species, backed up by differences in
196 colouration. Colour was mostly not used as a morphological character, since in our experience it varies within
197 wasp species. However, the colour of the hind wing was assumed to be species-specific for the Peruvian
198 rhyssines, due to other distinguishing characters being unclear or otherwise hard to use for identifying
199 specimens. The Peruvian species have been taxonomically reviewed by Gómez et al. (2015) and the Ugandan
200 species by Hopkins, Roininen, Noort et al. (2019).

201 To check if differences in how Peruvian and Ugandan species were delimited could have affected the
202 results by inflating the number of Peruvian species, we created two additional Peruvian species delimitations.
203 In the "semi-conservative" delimitation, *Epirhyssa zaphyma* Porter (Porter, 1978) and *E. lutea* Gómez &
204 Sääksjärvi (Gómez et al., 2015) were treated as the same species. These species would likely not have been
205 treated as different species if they had been caught in Uganda instead of Peru, since they are very similar and
206 the two main characters that separate them (clypeus, tergite 1) varied greatly within Ugandan species. In the
207 "conservative" species delimitation, the colour of the hind wing was also discounted as a character, and
208 species were merged if they were not clearly separated by some additional character that was at least as
209 clear as the characters used to separate Ugandan rhyssine species. This delimitation is overly conservative in
210 Peru and merges obviously valid species, which makes it useful in giving an absolute lower bound to the
211 Peruvian species count, irrespective of how species are delimited. In particular, it ignores subtle
212 distinguishing characters (such as e.g. the proportions of wing vein lengths), many of which were too
213 inconvenient for everyday species identification to be included in Gómez et al. 2015. In this conservative
214 delimitation, the following species pairs were treated as if they were one species: *Epirhyssa zaphyma* and *E.*
215 *lutea*; *E. diatropis* Porter (Porter, 1978) and *E. ignisalata* Gómez & Sääksjärvi (Gómez et al., 2015);
216 *E. braconoides* Porter (Porter, 1978) and *E. cochabambae* Porter (Porter, 1978); and *E. pertenuis* Porter
217 (Porter, 1978) and *E. iiapensis* Gómez & Sääksjärvi (Gómez et al., 2015) (this last pair turned out not to affect
218 our results, as no *E. pertenuis* were found in our samples).

219 The data on all the rhyssine wasps used in the present paper is available in the supplementary dataset
220 (Hopkins, Tuomisto, et al., 2023). This contains the full specimen data of all the rhyssines caught by Malaise
221 trapping during the four Peruvian sampling campaigns and the Ugandan sampling campaign, and includes the
222 place of deposition of each specimen.

223 Analyses

224 We compared the Peruvian and Ugandan rhyssines using two counts: the number of individuals caught,
225 and the number of species caught.

226 To examine how the number of rhyssine *individuals* caught in Peru and Uganda differed, we calculated
227 the number of individuals caught during each sampling campaign per trap day (average number of
228 individuals caught by one trap in one day) or trap month (30.5 trap days). This adjusts for the different
229 sampling efforts.

230 Since rainfall often decreases Malaise trap catches, and it rained more in Peru than in Uganda, we
231 estimated if observed differences in the number of individuals caught could be due to differences in rainfall.
232 We estimated how many rhyssines would have been caught in Uganda if it had rained as much as it did
233 during the main Peruvian sampling campaign in 2000. We did this by transferring Peruvian daily rainfall to
234 the Ugandan data, then scaling down Ugandan catches based on how much the rainfall increased. We
235 calculated the decrease in catches using the model in Hopkins et al. 2019 (Hopkins, Roininen, & Sääksjärvi,
236 2019b). This model is based on comparing the Ugandan rhyssine catches to weather data, and gives a
237 separate estimate of the effect of rainfall for each species. This provides only a rough estimate, since we are
238 extrapolating beyond the Ugandan data which the model is based on, but is sufficient for our purpose of
239 checking if rainfall could plausibly be the cause of observed differences in Malaise sample abundances.

240 To compare the rate at which *species* were caught in Peru and Uganda, and thereby obtain an idea of
241 overall species richness, we created species rarefaction curves. These show an estimate of how the number
242 of observed species is expected to increase as a function of the number of individuals caught. Because the
243 number of species observed is directly constrained by the number of individuals observed, and traps differed
244 in how many individuals they captured per day, we used the observed number of individuals on the x axis of
245 the rarefaction curves instead of the number of trap days (Gotelli & Colwell, 2011; Gómez et al., 2017).
246 Nevertheless, the curves are sample-based rarefaction curves, where each sampling interval of roughly two
247 weeks each was considered a sample, and these were resampled without replacement 100 times. We
248 produced separate species accumulation curves for each sampling campaign and forest type. For the
249 Ugandan samples, we also produced separate species accumulation curves for the wet season and the dry
250 season.

251 We compared four of the rarefaction curves in greater detail: the clay and loam soil curves of the main
252 Peruvian sampling campaign in 2000, and the wet and dry season primary forest curves of the Ugandan
253 sampling campaign. These sampling campaigns and forest types gave the largest sample sizes and were the
254 most relevant to compare (e.g. the Peruvian white sand forest has no clear equivalent in Uganda). To roughly
255 estimate whether the Peruvian and Ugandan curves significantly differed from each other, we calculated
256 approximate 84% confidence intervals (see chapter 4.2.6 of Gotelli & Colwell, 2011 for a rationale for
257 choosing 84%). This should, however, be treated as rough guide only, since we are calculating the intervals
258 approximately (by resampling) instead of using unconditional variance as in Gotelli and Colwell (2011). To
259 assess the possibility that the differences between rarefaction curves reflected differences in the evenness of
260 species abundances rather than in species richness (Gotelli & Colwell, 2011), we calculated evenness qE at
261 $q=1$ and $q=2$ (${}^qE = {}^qD/R$, where qD is diversity of order q and R is species richness) (Tuomisto, 2012). The value
262 of this index ranges from $1/R$ to one, with higher values for more even abundances.

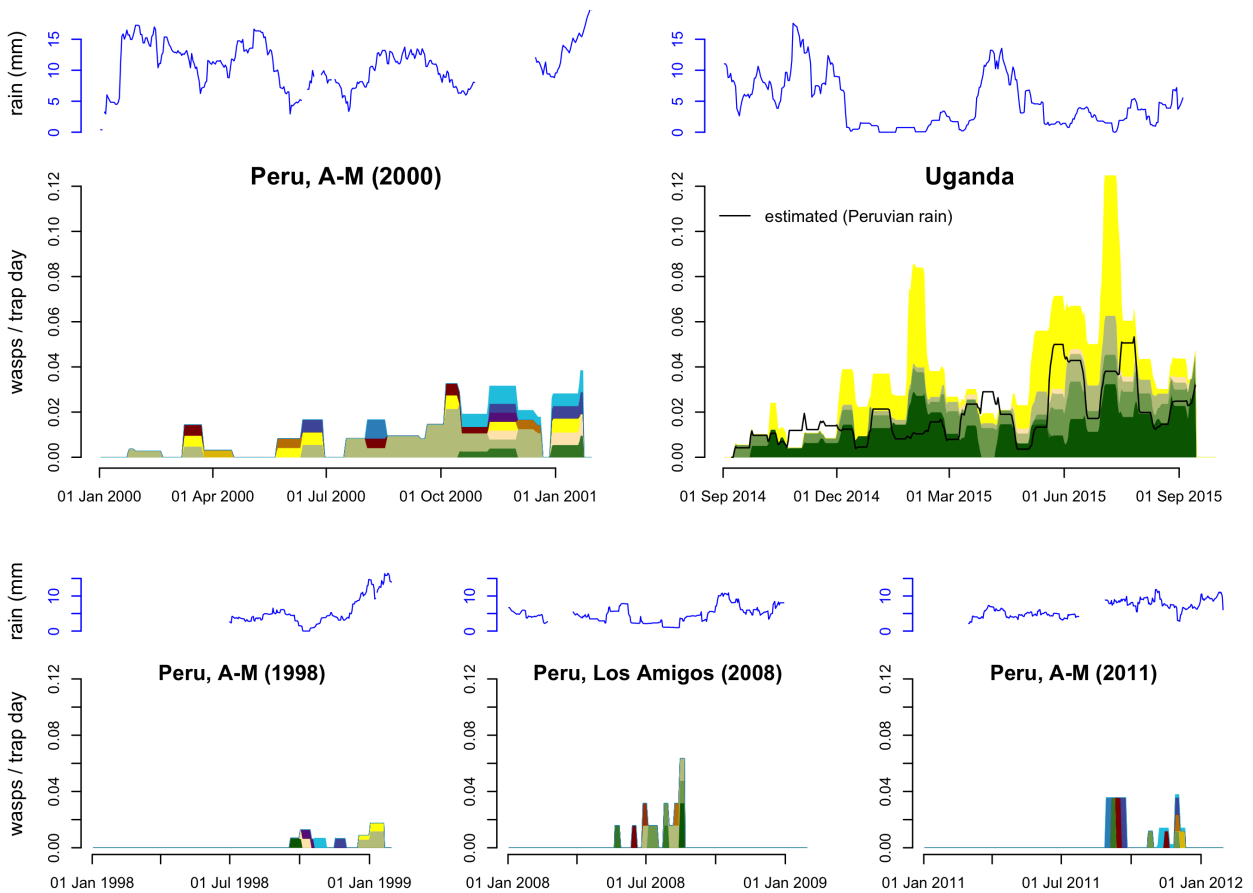
263 All analyses were carried out in the R software, v. 4.2.1 (R Core Team, 2017). The R code and data are
264 available online (Hopkins, Tuomisto, et al., 2023).

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Results

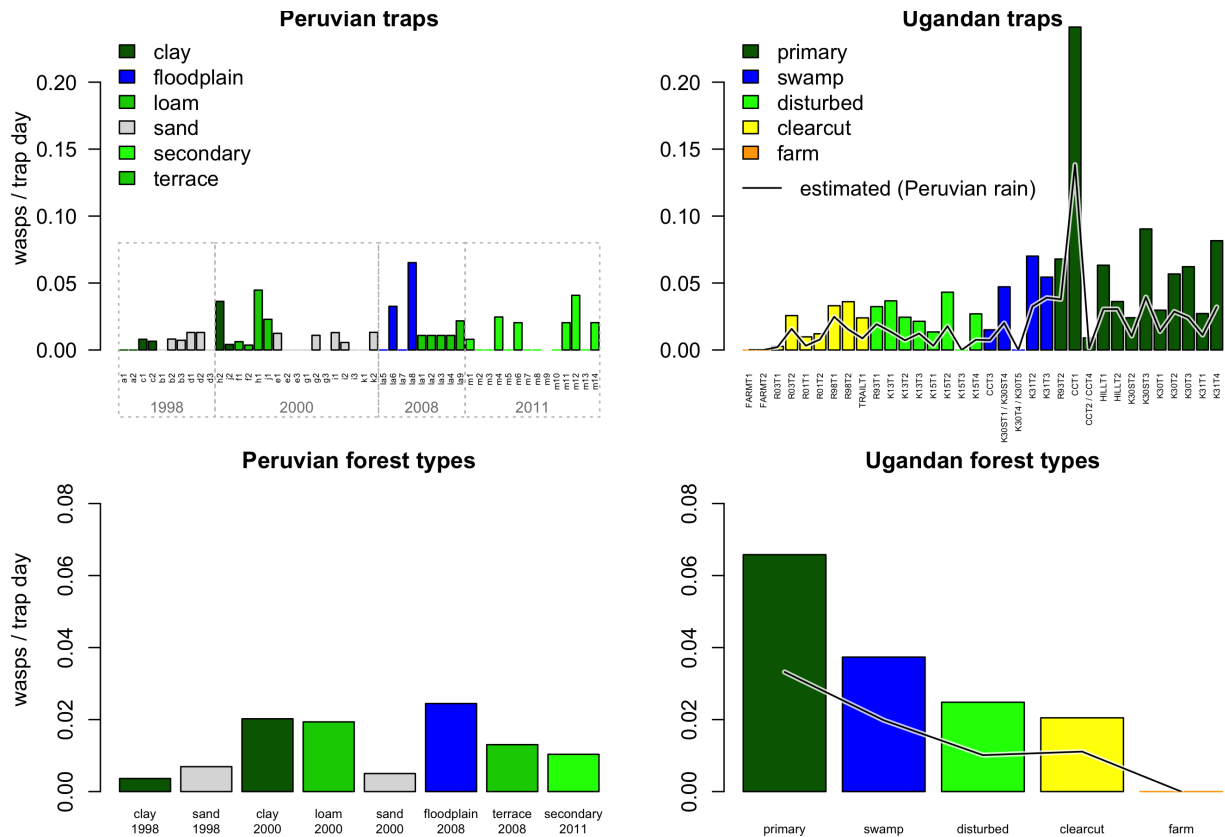
266 Peruvian traps caught a total of 90 rhyssine individuals, which is only a fifth of the 444 individuals caught
267 by Ugandan traps (Figures 1-2). The difference was partly due to a larger total sampling effort in Uganda (374
268 trap months) than in the four Peruvian sampling campaigns (a total of 270 trap months), but there was also a
269 clear difference in the catch per unit time. The Peruvian traps caught 0.2, 0.4, 0.6 and 0.3 rhyssine individuals
270 per trap month during the 1998, 2000, 2008 and 2011 sampling campaigns, respectively. None of these came
271 even close to the average of 1.2 rhyssines per trap month caught in Uganda.

272 The difference between Peruvian and Ugandan rhyssine catch sizes was largely explainable by differences
273 in rainfall (Figures 1-2). Using a regression model based on the Ugandan data, we estimate that a total of 220
274 Ugandan rhyssine individuals (0.6 per trap month) would have been caught if it had rained as much in
275 Uganda as it did during the main Peruvian sampling campaign (2000). This is only half of what the Ugandan
276 traps actually caught, but close to what the Peruvian traps caught.



277

278 **Figure 1** - Rate of rhyssine captures in Malaise traps (individuals / trap day) operated in Peru and
279 Uganda, with the amount of precipitation during the sampling period (29 day rainfall averages for Peru,
280 15 day averages for Uganda). The Peruvian sampling campaign 2000 in Allpahuayo-Mishana (A-M)
281 provided most of the Peruvian data, the three shorter sampling campaigns provided additional data. Far
282 fewer rhyssines were caught in Peru than in Uganda. However, when we estimated how many Ugandan
283 rhyssines would have been caught if it had rained as much as during the Peruvian sampling campaign
284 2000 (black line), the difference was much smaller. The proportions of different species in the catches of
285 each sample (which were accumulated over a time period of 1-3 weeks each) are visualised by colour
286 differences (these are species-specific within but not among panels).



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Figure 2 - Number of rhyssines caught in 50 Peruvian and 34 Ugandan traps. The top panels show the catch (individuals per trap per day) for each trap, and the bottom panels the average catch for each forest type. Far fewer rhyssines were caught in Peru than in Uganda. However, when we estimated how many Ugandan rhyssines would have been caught if it had rained as much as during the Peruvian 2000 sampling campaign (black line), the difference was much smaller.

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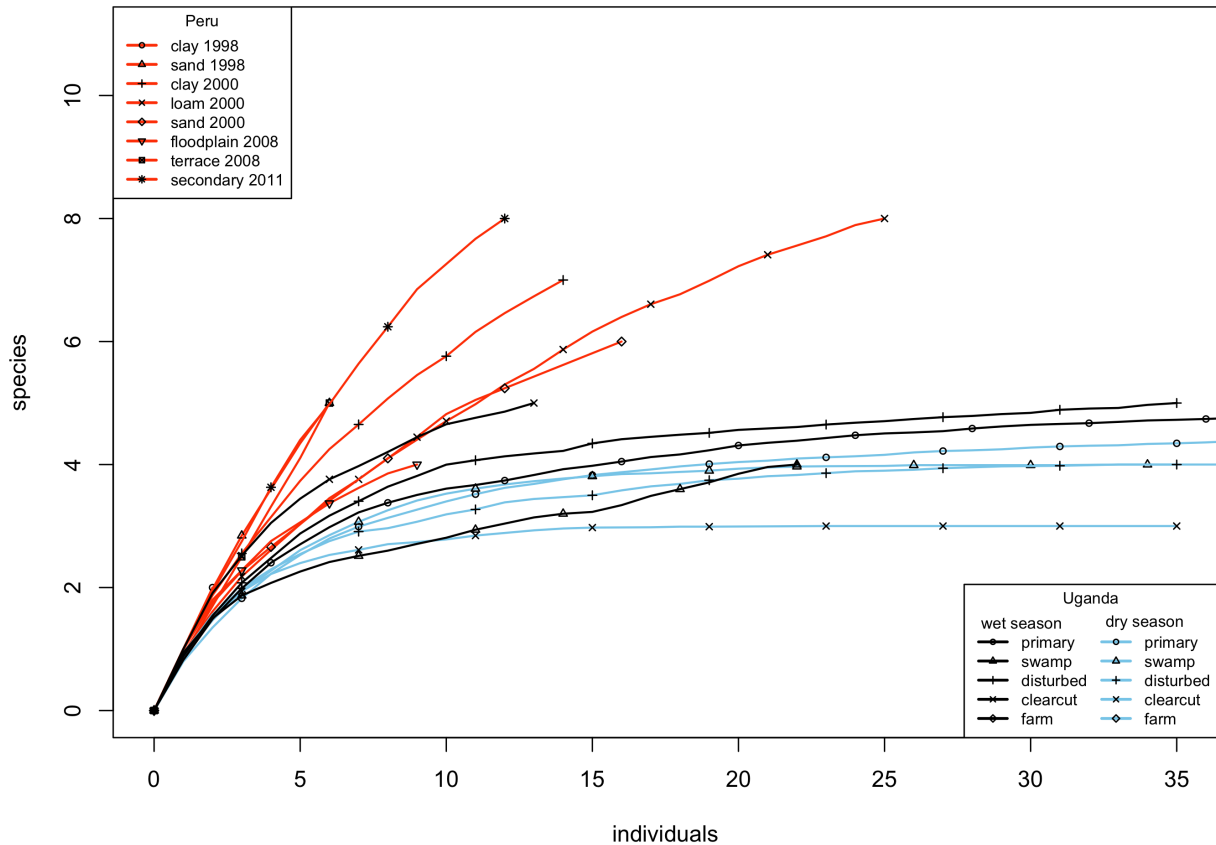
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The Peruvian Malaise trapping caught a total of 14 rhyssine species: 7, 11, 7 and 8 species for the 1998, 2000, 2008 and 2011 sampling campaigns, respectively. The Ugandan Malaise trapping caught only 6 species, despite a larger collecting effort in terms of trap months and a much larger number of individuals caught. The difference was not caused by differences in how species were delimited: the Peruvian species counts for the four sampling campaigns were 7, 10, 7 and 7 species for a semi-conservative species delimitation (with a total of 13 species), and 6, 9, 6 and 6 species for an extremely conservative species delimitation (with a total of 11 species).

The Peruvian Malaise trapping accumulated rhyssine species faster (per individual caught) than did Ugandan Malaise trapping, irrespective of forest type (Figure 3). Although there was some variation in how quickly species accumulated, Peruvian and Ugandan rarefaction curves clearly fell outside each other's confidence intervals once a sufficient number of individuals were included (Figure 4). However, Peruvian sample sizes were relatively small (Figures 4–5) and most Peruvian traps only caught a few individuals. The relative abundances of the species followed a similar distribution in Peruvian and Ugandan forest types, with the Peruvian species of some forest types less evenly distributed (Figure 5). Different forest types generally contained the same rhyssine species in Uganda, whereas there was more differentiation between forest types in Peru (Figure 5). No Peruvian trap caught more than seven of the 11–14 species, and no Ugandan trap more than five of the six species.



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311 **Figure 3** - Sample-based species rarefaction curves showing how quickly Malaise traps caught species in
312 Peru and Uganda. Each sample consists of a sample jar representing a sampling interval of mostly
313 between 1 and 3 weeks. Peruvian curves were constructed separately for each forest type and sampling
314 campaign (2008 sampling was at the Los Amigos site, others at Allpahuayo-Mishana). Ugandan curves
315 were constructed separately for each forest type and season.

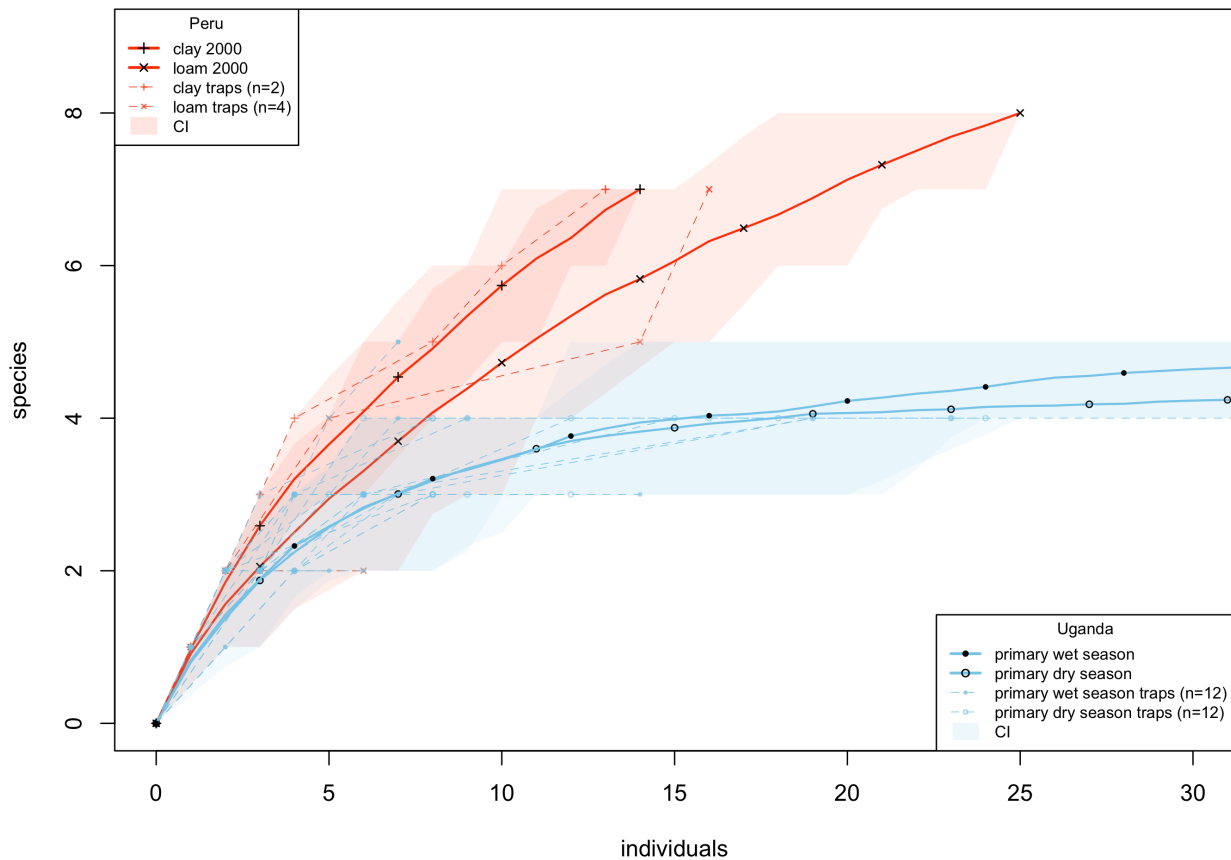
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Discussion

317 **More species but fewer individuals in Peru**

318 We observed two main differences between the Peruvian and Ugandan Malaise trapping results:
319 Ugandan traps caught many more rhyssine individuals per unit time, but Peruvian traps caught more species.

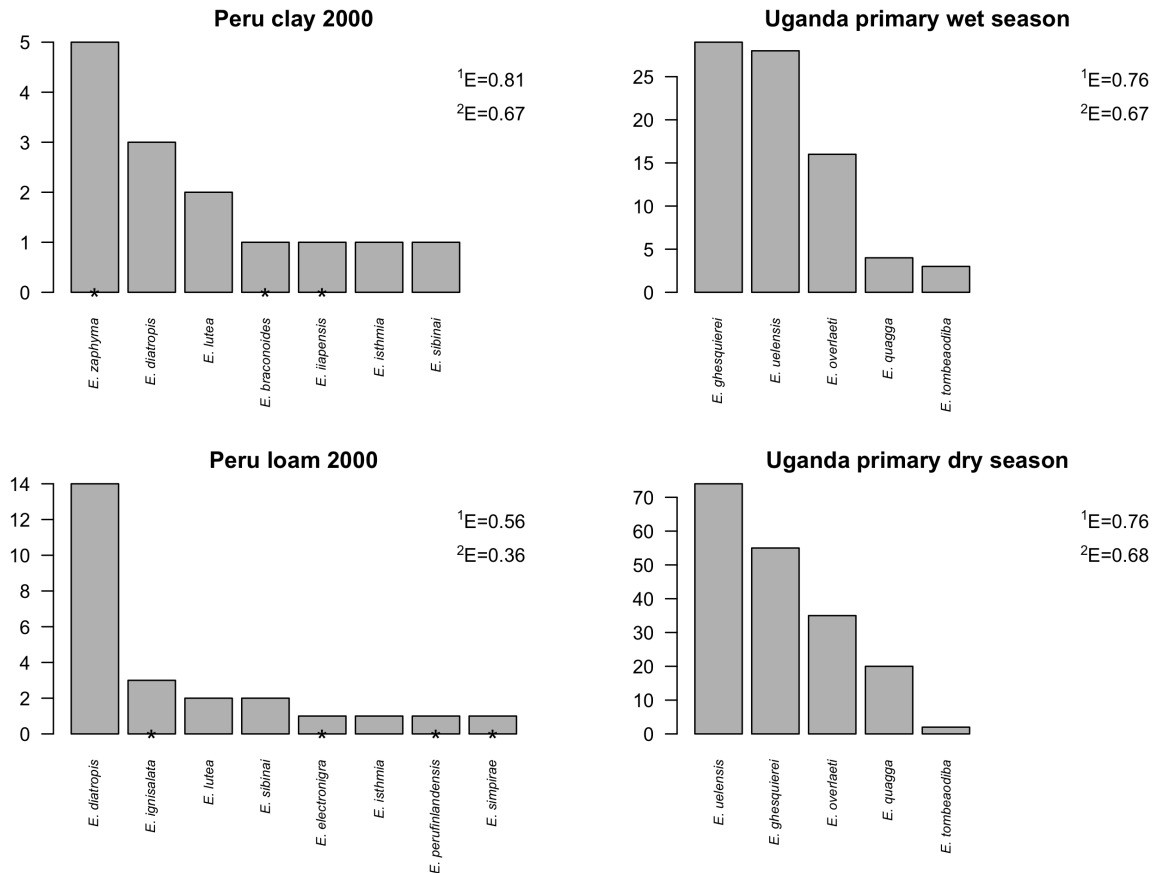
320 The observed difference in the number of rhyssine individuals caught reflects differences in rainfall. Peru
321 had more rain than Uganda, and rainfall has been observed to decrease the number of rhyssines caught by
322 Malaise traps, mostly by decreasing the rhyssines' flight activity (although there are signs that abundances
323 may also be affected: Hopkins, Roininen, & Sääksjärvi, 2019b). We estimated that if it had rained as much in
324 Uganda as in Peru, Ugandan catches would have been halved and would have been much more similar to the
325 Peruvian catches (Figures 1-2). The limitations of this estimate must be born in mind, however: it is a rough
326 estimate based on extrapolating beyond our Ugandan data. Nevertheless, the role of rain is supported by
327 two other observations. First, other taxa also seem to have been affected. Peruvian Malaise samples
328 generally seem to be about a half or one third of the volume of Ugandan samples (based on observing how
329 full the sample containers are after similar lengths of trap operation), which suggests that they contain fewer
330 insects overall. Second, even within Peru, the drier site Los Amigos captured more individuals per trap month
331 than the wetter Allpahuayo-Mishana did (0.6 versus 0.2-0.4 individuals per trap month, respectively). It thus
332 seems plausible that rainfall, rather than some other ecological factor, is the main reason why Amazonian
333 traps catch fewer individuals than Ugandan traps.



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335 **Figure 4** - Selected species rarefaction curves showing how quickly Malaise traps caught species in
336 Ugandan non-inundated primary forest, and in the closest equivalent to this forest type in Peru (main
337 sampling campaign 2000). Shaded areas are confidence intervals that show how much variation there
338 was in a curve (84% of a curve's resamples fell inside its shaded area). The shaded areas of Peruvian and
339 Ugandan curves do not overlap after 16 individuals, which suggests that the difference between them is
340 significant. The accumulation curves of individual traps are also shown: Peruvian sample sizes were
341 relatively low, with only two of the Peruvian traps in this figure catching more than six individuals.

342 We speculate that there could be interesting ecological consequences of rain decreasing the flight
343 activity, and possibly also abundance, of rhyssines: this could favour wood-boring insect larvae (which are
344 the likely hosts of tropical rhyssines) in rainy areas as compared to drier ones. If Malaise traps encounter
345 fewer rhyssines due to rain, wood-boring larvae probably do so too, and thereby face less predation
346 pressure. Although there are other taxa that potentially compete with rhyssines for hosts, and could
347 compensate for the lower predation pressure, many of them are likely also affected by rain. These include
348 e.g. *Apechoneura* (Labeninae), *Dolichomitus* (Pimplinae), *Anastelgis* (Pimplinae) and woodpeckers (Picidae).
349 This hypothesis could be easily tested by measuring the densities of wood-boring larvae in Peruvian and
350 Ugandan decaying wood. For our study sites, we would expect the highest densities of wood-boring larvae in
351 Allpahuayo-Mishana, followed by the somewhat drier Los Amigos, and much lower densities at our Ugandan
352 site. It is, however, possible that some other factor (such as the humidity of the wood) also affects wood-
353 boring larvae densities, so further tests would also be needed to conclusively prove our hypothesis.



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Figure 5 - Number of individuals of each species caught in non-inundated primary forest in Uganda, and in the closest equivalents to this forest type in Peru (main sampling campaign 2000). Species that were only found in one of the forest types are marked with *. The species abundance distributions were approximately equally even in the Peruvian clay soil sites and the Ugandan sites, but the Peruvian loam soil sites showed a smaller evenness value, indicating a higher degree of dominance (evenness values shown to the right of each panel).

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Our species rarefaction curves strongly suggest that Allpahuayo-Mishana in Peruvian Amazonia has more rhyssine species than Kibale National Park in Uganda. In general, the observed number of species increases more rapidly in species-rich communities than in species-poor ones, and the increase was clearly faster in Allpahuayo-Mishana than in Kibale. Marked differences in how even the population densities of the co-occurring species are can also affect the rate of species accumulation, as higher evenness generally increases the rate of species accumulation as compared to having the same number of species with uneven abundances. The relative abundances of different species in our samples (Figure 5) suggest that evenness does not explain the differences we observed. Species accumulated slower in Uganda despite the evenness being roughly the same as for Peruvian clay soil habitat, and greater than for Peruvian loam soil habitat.

Our second Peruvian site, Los Amigos, may also have more species than Kibale in Uganda. However, the evidence is insufficient since only 15 rhyssine individuals were caught in Los Amigos. It is noticeable that the species did not accumulate as quickly in Los Amigos as in Allpahuayo-Mishana (Figure 3), which could indicate that the total species richness in Los Amigos may be somewhat smaller.

One potential factor affecting the number of species observed at different sites is the geography of the sites and how that geography has been covered. We sampled a very restricted area in Allpahuayo-Mishana (approx. 4 km x 4 km in year 2000, in other years no larger), Los-Amigos (approx 3 km x 3 km), and Kibale, Uganda (approx 4 km x 7 km). This will undoubtedly have restricted the pool of species we were able to discover. In Kibale, for example, the vegetation is known to vary greatly along a north-south gradient

379 (Chapman & Lambert, 2000). Had we placed our traps nine kilometres further north at Sebitoli, or seven
380 kilometres further south near Ngogo, they would have been in noticeably different forest, with even the
381 dominant tree species partly differing, and potentially with different rhyssine species. More importantly, we
382 also know that within our sites, not all habitats were sampled. Allpahuayo-Mishana in particular is known to
383 have a large number of geologically and floristically distinct habitats in a relatively small area (Whitney &
384 Alonso, 1998; Sääksjärvi et al., 2004), and we know of habitats such as papyrus swamp in Kibale which were
385 not covered by our Malaise trapping. To what extent this affects the number of species caught depends on
386 how strongly rhyssines are restricted to specific habitats. It is noticeable that in our Peruvian Malaise
387 trapping, traps in different forest types caught partly different species (e.g. Figure 5), whereas our Ugandan
388 traps largely sampled the same set of species. This may, however, be caused by the relatively small number
389 of rhyssines caught in Peru. Overall, the relatively high diversity of different habitats at Allpahuayo-Mishana
390 could be one factor explaining the larger number of species observed there.

391 If the apparent greater rhyssine species richness of Allpahuayo-Mishana is genuine, and reflects the
392 situation of the rest of lowland Peru, it would match what little is known for other taxa. In general,
393 Neotropical forests are believed to have more species rich floras than Afrotropical forests (Gentry, 1982),
394 and the global species richness of many taxa seems to peak in western Amazonia: reptiles in Allpahuayo-
395 Mishana (Gentry, 1988; reptiles listed in Dixon & Soini, 1975, 1977), trees in A-M (Vásquez Martínez &
396 Phillips, 2000), birds (Pearson, 1977), butterflies in Tambopata, near Los Amigos (Gentry, 1988; butterflies
397 listed in Lamas, 1984). It should also be noted that our Ugandan site is at a higher altitude than our Peruvian
398 site, and species richness is generally thought to decrease with increasing altitude as well as latitude (Wolda,
399 1987; Fernandes & Price, 1988); although some taxa may peak at mid altitudes instead, at least where mid-
400 altitudes have higher humidity and rainfall (Brehm et al., 2007; but see Molina-Martínez et al., 2013).

401 **Future Malaise trapping**

402 Long-term, standardised Malaise trapping showed promise for global comparisons of species richness.
403 Our current results are by no means spectacular in themselves, involving as they do only one (relatively rare)
404 subfamily and just a few sites. However, the fact that we could get reasonable results demonstrates the
405 potential of our method for drawing more far-reaching conclusions. Sampling more sites in both tropical
406 Africa and Amazonia, for example, and analysing all (or at least the most abundant) subfamilies, would give
407 an estimate of which continent has more parasitoid wasp species. It would also detect differences in the
408 relative abundance and species richness of different subfamilies. Such sampling could especially focus on low
409 altitude equatorial sites (e.g. the Democratic Republic of the Congo in Africa).

410 Although our sampling design with standardised Malaise trapping succeeded in getting comparable data,
411 further improvements could be made for future Malaise trapping. These include greater focus on covering all
412 habitats at a site and using modelling approaches to generate easy-to-compare data.

413 Our trap placement was unbalanced between habitat types: if we had placed more Peruvian traps in
414 loam or clay forest, for example, we would have obtained a better coverage of what appear to be highly
415 variable habitats. These habitats were also the ones with a clearest equivalent in Uganda. As it was, we only
416 had six such traps in our main Peruvian sampling campaign. This does not give a good coverage of the kind of
417 varied habitat that could well be subdivided into more than six habitat types (how habitat is classified into
418 habitat types is to some extent a matter of preference). Ideally, since Malaise traps typically give very
419 variable catches even in the same habitat (Fraser et al., 2008; Saunders & Ward, 2011), every habitat type
420 should be covered by several traps. In practice, this requires too many traps to be feasible. We do not have a
421 full solution to this problem, but suggest that future inventories devote effort to obtaining as good a habitat
422 classification as possible at an early stage. Teaming up with a botanist when planning where to place traps,
423 for example, would allow the available traps to be placed optimally (see e.g. Sääksjärvi et al., 2006). Many
424 plant taxa such as ferns have been found to be good indicators of tropical forest habitat types (Salovaara et

425 al., 2004; Pomara et al., 2012; Zuquim et al., 2014). Even the simple expedient of photographing ferns at trap
426 sites, then showing the photographs to a specialist, could help classify the sites into habitat types (Suominen
427 et al., 2015).

428 Having enough traps in each habitat, together with getting a sufficient sample size and coverage of all
429 seasons, allows modelling the expected catches of traps (i.e. how many individuals to expect for a given
430 habitat and weather). This could potentially be a great advantage when comparing two different sites:
431 without a model, we are comparing Malaise samples which stem from a varying mix of different habitats,
432 have been collected during varying weather, and are otherwise hard to treat statistically. In this work, we
433 used a model of how Ugandan rhyssines react to rainfall to account for the effect of different rainfall in Peru
434 and Uganda. Unfortunately, the Peruvian sample sizes (total of 90 rhyssine individuals, split among 14
435 species) were too low to allow modelling of the Peruvian rhyssines. Other subfamilies have mostly not yet
436 been fully processed (except for Peruvian Pimplinae: Sääksjärvi et al., 2004; Gómez et al., 2014), but many
437 should have much larger sample sizes than Rhyssinae and would be modellable. Wherever possible, we
438 suggest building a model of how many individuals to expect in a given habitat and weather, then comparing
439 the models of different sites instead of the raw data (Malaise samples) from which the models have been
440 interpolated.

441

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454

Data, scripts, code, and supplementary information availability

455 The analyses and data are available online in two datasets. The first of these contains the code and data
456 used in the statistical analyses: <https://doi.org/10.5281/zenodo.8208661> (Hopkins, Tuomisto, et al., 2023).
457 The second contains the data on the Peruvian Malaise trapping, and a description of how it was compiled:
458 <https://doi.org/10.5281/zenodo.8208660> (Hopkins, Gómez, et al., 2023).

459

Conflict of interest disclosure

460 The authors declare that they comply with the PCI rule of having no financial conflicts of interest in
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462

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468

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