1  **Ecological and dietary differences between Ugandan chimpanzee communities with**

2  **possible implications on tool use**

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20  SIGNIFICANCE STATEMENT – HIGHLIGHTED STUDENT PAPER

21  *To advance our knowledge of the role of ecological factors in the emergence of tool use in*

22  *chimpanzees, a nuanced understanding of the ecological conditions different chimpanzee*

23  *communities experience is needed. We studied four Ugandan chimpanzee communities in*

24  *two forests. One of these communities, Sonso, in the Budongo Forest, is well-known for its*

25  *restricted range of tool types, including a total absence of stick use. Food diversity and*

26  *abundance were highest, and stick tool use opportunities (abundance of sticks and insect*

27  *nests) were lowest for the core-habitat of the Sonso chimpanzees in contrast to the other*

28  *communities. We argue that ecological factors play a role in their unusual pattern of tool use,*

29  *and make predictions about the expected types of tool use in the other communities based*

30  *on their ecology. Thus, our study provides information that may help advance our*

31  *understanding of how  tool use arises under varied socioecological circumstances.*

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33  **AUTHOR CONTRIBUTIONS**

34  TG and IB formulated the idea. DM and IB conducted the transects. IB did the feeding

35  observations and faecal analyses. MB and IB analysed the data. IB, TG, CH and MB wrote

36  the manuscript.

37

38  **ABSTRACT**

39  Some East African chimpanzee (*Pan troglodytes schweinfurthii*) communities, such as the

40  Sonso chimpanzees, display an unusually limited range of tool-use, but it remains unclear

41  whether this is due to ecological and/or cultural factors. Information on ecological conditions

42  and the diet of the Sonso chimpanzees in relation to neighbouring communities is needed.

43  Here, we studied three adjacent communities in Budongo Forest (Sonso, Waibira, and

44  Kamira), and the presumed core area of an undescribed community (Mwera), in the

45  neighbouring Bugoma Forest. Through line-transects, we investigated (i) whether there were

46  differences in food diversity and abundance between the communities' home ranges; (ii)

47  whether the home ranges differed in abundance of sticks and insect nests; and (iii) whether

48  Sonso and Mwera chimpanzees differed in their diet (using faecal samples). Across

49  communities, Sonso had the richest food availability and the lowest insect nest abundance.

50  However, food availability in Mwera, Bugoma, was richer than Budongo communities that

51  neighbour the Sonso territory, suggesting that there may be variation within Budongo. Data

52  from faecal samples replicated our direct observations of food availability suggesting that

53  Sonso chimpanzees had a broader diet than Mwera chimpanzees. This difference in food

54    availability may partially explain the Sonso chimpanzees' lack of stick-tool-use, and low

55    levels of insectivory. The tool repertoire of the other communities is currently unknown;

56    however, we make predictions based on our ecological data. More detailed knowledge of

57    small-scale variation in ecology within and between forest habitats may be important to

58    advancing our understanding of the drivers of tool-use.

59    **KEYWORDS**

60    Tool use; chimpanzee; food availability; diversity; ecological influence on behaviour

61

62 **INTRODUCTION**

63 In a landmark study, Whiten et al. (1999) showed that 39 behavioural patterns, mainly in the

64 domain of tool use, were customary in some communities, but not in others. While the

65 original article did not discuss ecological explanations in detail, much debate has followed

66 regarding the impact of ecological variation on chimpanzee cultural behaviour, particularly

67 tool use in the context of foraging (Laland and Janik, 2006; Krutzen et al., 2007). The current

68 consensus is that diversity, distribution, and varying abundance of chimpanzee food sources

69 as well as variation in available tool materials are likely to impact the occurrence, innovation,

70 and maintenance of tool use (Möbius et al. 2008; Schöning et al., 2008; Humle and

71 Matsuzawa, 2002; Gruber et al. 2012; Sanz and Morgan 2013; Gruber et al., 2016; Grund et

72 al. 2019). Two hypotheses: the "necessity", and "opportunity" hypotheses, relate ecological

73 factors to the emergence of tool use (Fox, Sitompul and Van Schaik, 1999). The necessity

74 hypothesis predicts the emergence of tool use in response to food scarcity (Fox, Sitompul

75 and Van Schaik, 1999), and the opportunity hypothesis proposes that the likelihood for tool

76 use increases when both tool materials and resources requiring tools for exploitation are

77 frequently encountered (Koops, McGrew and Matsuzawa, 2013). Both hypotheses have

78 received empirical support (Koops, McGrew and Matsuzawa, 2013; Yamakoshi, 1998; Sanz

79 and Morgan, 2013; Spagnoletti et al., 2012), and the two hypotheses are not mutually

80 exclusive; thus, both ecological and cultural factors may influence food-related tool use

81 behaviour (Gruber 2013; Grund et al. 2019; see also Rutz and St Clair, 2012).

82 Ugandan chimpanzees (*Pan troglodytes schweinfurthii*) exhibit a comparatively restricted

83 range of tool use behaviour as compared to other chimpanzee populations and subspecies

84 (McGrew, 2010). For example, the Ngogo and Kanyawara communities in Kibale Forest, and

85 the Sonso community in Budongo Forest (200 km away) respectively show only four, two

86 and one tool use behaviour in relation to food acquisition (Gruber et al., 2012). Nevertheless,

87 the appearance (Hobaiter et al., 2014) and subsequent social spread (Lamon et al., 2017) of

88 the use of a water sponging tool shows that the Sonso chimpanzees are capable of

89  innovation. These observations raise the question of why Ugandan chimpanzees rarely

90  engage in extractive tool use during foraging, despite possessing the cognitive abilities to do

91  so. One possible explanation is that environmental changes have increased food availability

92  (and loss of cyclic food scarcities), causing the Sonso chimpanzees to lose their knowledge

93  of stick-tool manufacture and use in the recent or more distant past (Gruber et al., 2012;

94  Gruber 2013). Humans have played a large role in the forest dynamics and plant species

95  composition of Uganda forests (Reynolds, 2005; Babweteera et al. 2012). For example, four

96  large sawmills were active in Budongo through the 20$^{th}$ century (Synott, 1985), with

97  subsequent logging and species-specific use of arboricides permanently influencing the

98  composition of the forest (Plumptre, 1996), and leading to an increase in the abundance of

99  fruiting trees, such as figs (Tweheyo and Lye, 2003).

100  While communities living in small riverine fragment forests in close proximity to Budongo

101  (e.g. Bulindi, 60 km away) have been documented to use stick tools during foraging

102  (McLennan, 2011), it is unknown whether the chimpanzees that inhabit the closest large

103  forest between Budongo and Kibale, the Bugoma forest, use tools (Figure 1). In this study

104  we compared the ecological conditions four chimpanzee communities are exposed in two

105  forest areas in order to test hypotheses about the impact of small scale variation in forest

106  ecology on chimpanzee tool using. We compared the potential food availability and tool use

107  opportunities of several communities in the long-term Budongo and newly-established

108  Bugoma forest field sites. We divided our research aim into three parts: firstly, we compared

109  potential chimpanzee food availability in the home range of the respective communities. We

110  expected the diversity and abundance of trees that chimpanzees are known to feed on

111  (Known Feeding Trees) to be highest in the Sonso home range, due to the increased

112  presence of fruit-bearing trees as a by-product of the historical timber production that was

113  centred around this community's territory (Reynolds, 2005; Gruber, 2013). Furthermore, we

114  expected that the communities' home ranges differed in Known Feeding Trees species

115  composition.

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116    Secondly, we compared the tool use opportunities in the home ranges of the four

117    communities. We focused on extractive tool use in a foraging context (here the use of sticks

118    to extract insects, as employed by other communities within Uganda, e.g. Watts, 2008).

119    When describing tool use opportunities, we recorded the abundance of termite, *Cubitermes*

120    *ugandensis*, and ant nests, *Dorylus* spp, and the presence of potential extractive tool

121    materials, such as sticks. The insect species compared were chosen based on previous

122    records of abundance and feeding observations in the Budongo Forest (Hedges and

123    McGrew, 2012). We expected to find fewer tool use opportunities in Sonso as compared to

124    other areas because of the use of poison to control termite populations in recent decades

125    (Reynolds 2005).

126    Finally, we compared the diet of one chimpanzee community in each forest, Sonso in

127    Budongo and Mwera in Bugoma, using faecal samples from both groups and direct

128    observation of feeding behaviour in Sonso. We expected to find a greater abundance and a

129    more diverse array of seeds in the samples of the Sonso community, due to the predicted

130    difference in Known Feeding Tree abundance described above. To assess the efficacy of

131    faecal analyses, we compared dietary species composition obtained from feeding

132    observations of the Sonso community, with the species composition of their faecal samples.

133    Based on Phillips and McGrew (2013) we expected to identify around 80% of the species

134    from which fruit had been eaten, but only around 20% from which leaves had been eaten,

135    and 60% of species overall in the faecal samples, due to the difficulty of identifying non-

136    frugivory dietary parts at species level (Phillips and McGrew, 2013). We expected the

137    proportional abundance of seeds of a species in the faecal samples to increase the longer

138    we observed the chimpanzees to feed on that species. If faecal analysis in Sonso revealed

139    itself to be a good estimator of diet, we could then use the samples collected in Mwera, to

140    describe the diet of the yet unhabituated chimpanzees.

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142    **METHODS**

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143    **a) Study sites**

144       ***i)  Budongo Forest***

145    The Budongo Forest is 435km$^2$ of continuous semideciduous tropical rain forest, located at

146    the top of the Albertine Rift in western Uganda between 1°37'N- 2°03'N and 31°22'-31°46'E

147    with a mean altitude of 1,100m (Plumptre, 1996; Figure 1). Chimpanzee density is estimated

148    to be 1.32 chimpanzees/km$^2$ (Plumptre and Cox, 2006). Plumptre (1996) showed that

149    Budongo exhibits a gradual change of tree species composition from the southwest to the

150    northeast, with the southwest having more species associated with Colonizing and Mixed

151    Forest, and the northeast being predominantly *Cynometra* Forest.

152    ***ii)    Bugoma Forest***

153    Bugoma Forest (01°15'N 30°58'E) covers 400km$^2$ and is situated between 990 and 1,300 m

154    of elevation (Plumptre, 2010). It is separated from Budongo Forest by around 80km and is

155    the closest major forest to Budongo (Figure 1, Reynolds, 2005), located at an intermediate

156    point between the Budongo and Kibale forests. Much less is known about the history and

157    forest composition of Bugoma than Budongo. In 2006, the density of chimpanzees was

158    estimated to be 1.99 chimpanzees/km$^2$ (Plumptre and Cox, 2006).

159    **b) Study communities**

160    ***Sonso community (Budongo Forest)***

161    The Sonso community (around 70 individuals) has become well-known for its comparatively

162    restricted tool repertoire, particularly in a foraging context (Reynolds, 2005; Gruber et al.,

163    2009). In contrast to all other chimpanzee communities that have been studied long-term,

164    Sonso chimpanzees have never been observed to use sticks to extract food (Whiten et al.,

165    1999). Field experiments involving a hole filled with honey drilled in a log showed that Sonso

166    chimpanzees do not make use of sticks even when put directly into the hole (Gruber et al.,

167    2011). However, Sonso chimpanzees can use objects in a goal-directed manner for water

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168    absorption (leaf and moss sponges; Hobaiter et al. 2014; Lamon et al, 2017, 2018), nest

169    building, body care (e.g. leaf-napkin), and social signals (buttress-beat) (Whiten et al., 1999;

170    Gruber et al., 2009; Reynolds, 2005).

### Waibira community (Budongo Forest)

172    The Waibira community ranges North-East of the Sonso core area, with overlapping

173    resource use at times. The Waibira community is estimated to total at least 120 individuals;

174    however, as the habituation process started in 2011 some individuals remain only partially

175    habituated. The Waibira chimpanzees have never been observed to use sticks as tools,

176    thus, suggesting the absence of a stick-tool use culture, similar to Sonso. However, since

177    the Waibira chimpanzees have only recently been habituated it is likely that substantial

178    elements of their behaviour and diet remain unknown. They have been observed on two

179    occasions to use leaf-tools to feed on *Dorylus* 'army-ants' (Mugisha et al. 2016; Hobaiter,

180    2019 pers. observation), a task for which other chimpanzee communities employ stick-tools.

181    Insectivory has been previously reported in Budongo chimpanzees but is rare (Newton-

182    Fisher, 1999; Reynolds, 2005) and the Sonso community have not been observed to feed on

183    this species, or to use leaf-tools during insectivory.

### Kamira community (Budongo Forest)

185    This community is located North-West of the Sonso chimpanzee range. There is no direct

186    observation of the resident community. As for all other chimpanzee communities in

187    Budongo, there is no direct evidence that the Kamira chimpanzees engage in stick-tool use.

### Mwera community (Bugoma Forest)

189    Habituation of the Mwera chimpanzee community in Bugoma began in January 2016. Direct

190    observation of the chimpanzees remains challenging, and their tool repertoire is unknown. A

191    biodiversity survey suggested that Bugoma Forest is ecologically more similar to Kibale than

192    Budongo Forest (Plumptre et al., 2010). In Kibale Forest, the diversity of tree species that

193    produce chimpanzee foods is lower than in Budongo, which has been suggested to impact

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194    the increased levels of insectivory and presence of stick-tool use for extractive foraging

195    (Gruber et al., 2012).

196        **c) <u>Data collection</u>**

197            ***i)        Transects***

198    To compare chimpanzee food availability, we conducted 12 500m-long line-transects in both

199    the Sonso and Mwera home range (May- August 2017), and 11 500m-long line-transects in

200    both the Waibira and Kamira home range (July – December 2015; see Supplementary

201    Material for a detailed transect protocol and locations, Table S1-3, Figure S1-2). We

202    identified trees (wherever possible to species level) and ascertained whether it was a Known

203    Feeding Tree based on previous Budongo feeding records from the Sonso and Waibira

204    communities. As fruit represents the major component of chimpanzee diets (Newton-Fisher,

205    1999), and high fruit abundance has been used to explain the lack of extractive tool use

206    behaviour of the Sonso community (Gruber et al., 2012), we separately compared the

207    abundance and diversity of the subset of Known Feeding Trees from which the fruit is eaten

208    (Known Fruit Trees; Supplementary Material). Occasionally it was not possible to identify the

209    tree; however, this was only ever the case for tree species that chimpanzees were not

210    known to feed on (Non-Feeding Trees). When this occurred, we noted all characteristics as

211    below, but classified the tree as "unidentified".

212    The diameter at breast height (DBH) was recorded for all trees that had a DBH of ≥10cm

213    and where at least 50% of the DBH fell within the transect zone. Within Sonso and Mwera

214    community ranges, DBH measurements were recorded for all trees (Known Feeding Trees

215    and Non-Feeding Trees), whereas for Waibira and Kamira, DBH measurements were only

216    recorded for Known Feeding Trees.

217    When we encountered an insect nest (termite mounds, *Cubitermes ugandensis*, and ant

218    nests, *Dorylus* spp), we took its GPS location, measured its height, determined whether it

219    was active, identified the species (with the help of an experienced field assistant), and

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220 assessed surrounding tool availability. Tool availability was assessed by measuring a 5m

221 radius around the mound, scrutinizing a NW (270-360) 90-degree quadrant (or SW (180-

222 270) if NW was not available), and counting all plants capable of producing termite-fishing

223 probes or dipping sticks (classified as twigs, vines, or terrestrial herbaceous vegetation

224 (THV) (Hedges and McGrew, 2012).

225 ***ii)   Feeding observations***

226 The Sonso community numbered around 70 individuals during this study (May through

227 August 2017); however, we only encountered a subset of individuals. We exclusively

228 followed adult chimpanzees, and we balanced as much as possible the choice of focal

229 individuals according to sex and social rank. We followed 8 male and 5 female chimpanzees

230 between 7:30am and 16:30pm. One to six days of feeding observations, with up to a

231 maximum three consecutive days, were made for each focal individual. The total focal

232 sampling time was 246.57 hours (females: mean = 22.29 ± 11.01 hours; males: mean =

233 15.23 ± 8.93 hours), of which 88.13 hours (females: mean 8.67 ± 5.58 hours; males: mean =

234 6.92 ± 4.44 hours) were spent feeding by a focal individual. During each follow we used a

235 stop-watch to record the date and time from the beginning of the feeding event until the end.

236 We defined a feeding event as "item placed into mouth, remaining there (or parts thereof)

237 and seen to be either chewed or swallowed" (Phillips and McGrew, 2013). We identified the

238 plant species being eaten (Observed Feeding Plant) with the help of an experienced

239 Budongo Conservation Field Station field assistant. We also noted the food item that was

240 eaten, which we categorized for plant material as: ripe fruit, unripe fruit, mature leaves,

241 young leaves, bark, root, flowers, pith, resin, and rotten wood. We made a subcategory of

242 Observed Feeding Plants from which chimpanzees ate fruit (Observed Fruit Plants,

243 Supplementary Material). Non-plant food items included invertebrates, vertebrates, soil, and

244 honeycomb. We noted the time the focal was lost or out of sight to obtain the total number of

245 minutes a focal was observed for.

246 ***iii)   Faecal samples***

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247     In Sonso, we collected samples as soon as possible after a defecation event (never after

248     more than 15min) in a ziplock bag, and noted the producer of the sample, the time, and an

249     estimated percentage of deposited faeces obtained. A sample was considered as complete

250     if ≥95% of the content was collected. Incompleteness was due to faeces consistency, rushed

251     collection due to rapid movement of the focal chimpanzee, or the dispersion of the faeces

252     over a large area (particularly from arboreal defecations).

253     For the Mwera community, samples were collected opportunistically when found on the

254     ground (only samples estimated to be ≤ 3 days old were collected). We did not record

255     sample completeness for Mwera, as this was not possible to determine without having

256     observed the defecation event. We obtained 105 samples from the Sonso chimpanzees, and

257     45 from the Mwera chimpanzees. Upon return to the research station, we weighed all

258     samples using a digital scale (Kenex KX digital scale, 400 x 0.1 g), and we added cotton

259     soaked in ethanol into the ziplock bags so that the samples could be stored before

260     processing (up to a maximum of 3-days after collection). All samples were collected between

261     May and August 2017. We processed the faecal samples following McGrew, Marchant and

262     Phillips (2009) in the veterinary laboratory of the Budongo Conservation Field Station (see

263     Supplementary Material for the protocol followed).

264     **d) Data analysis**

265     We conducted all analyses in R Studio version 1.0.153 (RStudio, 2016).

266     *i) Known Feeding Tree abundance*

267     As a considerable proportion of Non-Feeding Trees could not be identified, it was only

268     possible to compare the frequency and diversity of Known Feeding Trees between the

269     ranges of the communities. We compared the abundance of Known Feeding Trees between

270     the communities using Generalized Linear Mixed Models (GLMMs) with forest identity as a

271     random term (random intercept with fixed mean), and chimpanzee community identity and

272     researcher identity as predictor variables.

273   ### ii) Known Feeding Tree sizes

274   We log-transformed the DBH data so that they were normally distributed (Figure S3). We

275   fitted GLMMs with forest identity as the random term (random intercept with fixed mean),

276   chimpanzee community identity and researcher identity as predictor variables, and the log-

277   transformed DBH of Known Feeding Trees as the response variable.

278   ### iii) Overall potential food availability

279   We used the summed DBH of all Known Feeding Trees of each forest sample as a

280   surrogate measure for potential maximum chimpanzee food abundance. The DBH of a tree

281   is considered a reliable measure of the quantity of fruit it may bear (Chapman et al., 1992).

282   Thus, summing this over all the Known Feeding Trees in a sample yields information on the

283   maximum fruit (and foliage) abundance available to chimpanzees.

284   We also summed the DBH of all Non-Feeding Trees for Sonso and Mwera, which allowed us

285   to calculate the ratio of the total DBH of Known Feeding Trees to the total DBH of Non-

286   Feeding Trees.

287   ### iv)    Diversity of Known Feeding Trees

288   We chose the Shannon-Wiener index to calculate $\alpha$ diversity, as it is the only measure that

289   can be separated into meaningful independent $\alpha$ and $\beta$ components when community

290   weights are unequal, and because species are weighted by their relative abundance (Jost,

291   2007; see Supplementary Material for more information). This weighting means that neither

292   very rare nor very abundant species have a disproportionate impact, and that species

293   richness and species evenness are given equal importance (Jost, 2007; Supplementary

294   Material). We chose the Horn index to calculate $\beta$ diversity, since it uses abundance data

295   (rather than presence-absence data), it relates to Shannon entropy, and when the properties

296   of $\beta$-metrices were compared, $\beta_{horn}$ scored highly (Barwell, Isaac and Kunin, 2015;

297   Supplementary Material). All diversity indices are entropies (which gives the uncertainty in

298   the species identity of a sample), not diversities, and to be able to interpret them properly we

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299 converted them to true *α* and *β* diversities respectively through calculating the exponential of

300 the indices (Jost, 2006; Table S4). We then compared the *α* diversity and the *β* diversity of

301 Known Feeding Trees using GLMMs with forest identity as a random term (random intercept

302 with fixed mean), and chimpanzee community identity and researcher identity as predictor

303 variables. We then calculated the *γ* diversity of each community's home range (Table S4).

304 To illustrate our results, we produced a species rank abundance curve and a species

305 accumulation curve using the package "vegan".

### *v)      Known Feeding Tree species composition*

307 We used PRIMER 6 (Clarke and Gorley, 2005) for an Analysis of Similarity (ANOSIM) to

308 determine whether the chimpanzee communities' home ranges differ in Known Feeding Tree

309 species composition. To visualize dissimilarities between communities we constructed Non-

310 Metric Multidimensional Scaling (NMDS) ordination plots using the package "vegan" in R.

311 Using the package "indicspecies" we looked for the indicator species of each community's

312 home range and of combinations of two communities (De Caceres, Legendre and Moretti,

313 2010).

### *vi)      Insect nest abundance*

315 We compared the abundance of two species of termite mounds, *Cubitermes ugandensis*,

316 and ant nests, *Dorylus* spp, per transect between the communities' home ranges using a

317 GLMM with forest identity as the random term (random intercept with fixed mean), and

318 chimpanzee community identity and researcher identity as predictor variables.

### *vii)      Abundance of tool material (THV, twigs, and vines)*

320 We contrasted tool availability (i.e. the abundance of THV, vines, and twigs around an insect

321 nest) using a GLMM with chimpanzee community identity and researcher identity as

322 predictor variables, and forest identity as a random term (random intercept with fixed mean).

### *viii)      Faecal samples as predictors of chimpanzee diet*

324 As we were not able to distinguish different *Ficus* species in the faecal samples, we

325 combined the *Ficus* species we recorded during feeding observations. Firstly, we fitted a

326 linear model to assess whether the number of plant species identified in the faecal samples

327 could be predicted by the number of Observed Feeding Plants, accounting for the number of

328 hours the respective chimpanzee was observed, and the weight of the faecal sample. If the

329 weight and the hours of observation did not have a significant effect, then we excluded them

330 from the full model.

331 Secondly, we arcsine square root transformed the proportion of seeds of a given plant

332 species in the faecal samples to meet the assumption of homogeneity of variance (Figure

333 S4). With this as the response variable, we fitted a GLMM with the proportion of time (out of

334 all the recorded feeding time) a chimpanzee was observed to feed on the respective species

335 as the predictor variable, and individual chimpanzee identity as the random term (random

336 intercept with fixed mean). In the full model, we included the total number of hours a

337 chimpanzee was observed, and the total weight of all faecal samples of the respective

338 chimpanzee as covariates. If the reduced models did not differ significantly from the full

339 model, then we excluded the respective covariate from the final model.

340 ***ix)    Abundance and α, β and γ diversity of seeds in faecal samples***

341 We calculated the $\alpha$, $\beta$ and $\gamma$ diversity of each community from the seeds identified in the

342 faecal samples with the same methods we used when we determined Known Feeding Tree

343 diversity from the transects. However, there were nine samples from Mwera we had to

344 exclude to calculate $\beta$ diversity, because they did not contain any seeds.

345 After assessing whether the weight of a faecal sample was correlated with the respective

346 predictor variable (using Spearman's rank correlation), we compared seed abundance and $\alpha$

347 diversity using Wilcoxon tests, and $\beta$ diversity using a two-sample *t*-test.

348

349 **RESULTS**

350      ***i)***   ***Known Feeding Tree abundance***

351    The communities did not differ in abundance of Known Feeding Trees (GLMM, $\chi^2_{2,6}$ = 2.30, p

352    = 0.32).

353      ***ii)***   ***Known Feeding Tree sizes***

354    The mean DBH of Known Feeding Trees differed between the communities' home ranges

355    (GLMM, $\chi^2_{2,6}$ = 7.86, p < 0.020). Only Sonso differed from all other communities, with a

356    greater mean DBH (Table 1, Table S6).

357      ***iii)***   ***Potential food availability in each community's home range***

358    The summed DBH of Known Feeding Trees was highest for Sonso, which was almost twice

359    as high as the summed DBH of the other two Budongo Forest communities: Waibira and

360    Kamira. Mwera in Bugoma Forest had the second highest summed-DBH value. For Sonso,

361    the summed DBH of Known Feeding Trees was over twice as high as the summed DBH of

362    Non-Feeding Trees; the ratio was roughly 1:1 for Mwera (Table 1).

364      ***iv)***   ***Diversity of Known Feeding Trees***

365    The *α* diversity of Known Feeding Trees differed between the communities' home ranges

366    (GLMM, $\chi^2_{2,6}$ = 11.97, p < 0.001), where the *α* diversity of Sonso was roughly 2.5 times

367    greater than the *α* diversity of any other community (Table 2, Figure 2). Sonso was the only

368    community that had a greater *α* diversity of Known Feeding Trees than any other community

369    (Table S7). The *β* diversity of Known Feeding Trees differed between the communities'

370    home ranges (GLMM, $\chi^2_{2,6}$ = 8.55, p = 0.014), where Kamira had a lower diversity than any

371    other community, albeit not strongly (Table S7). The *γ* diversity of Known Feeding Trees in

372    Sonso was roughly 2.60 times greater than in any other community (Table 2, Figure 2).

374    The abundance of species, represented by Known Feeding Tree species richness and

375    species evenness, were greatest for the Sonso community's range (Figure 3a). The species

376    accumulation curves are in line with the results from the diversity analyses since the number

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377    of Known Feeding Tree species recorded was highest for Sonso for a given number of

378    transects (Figure 3b).

### v)    Known Feeding Tree species composition

380    The Known Feeding Tree species composition differed between the community home

381    ranges (ANOSIM, R= 0.41, p= 0.001). The home ranges of Waibira and Kamira had a similar

382    species composition and relative abundance of Known Feeding Trees, whereas Sonso and

383    Mwera differed in this respect (Figure 4).

384    We only found indicator Known Feeding Tree species for the home ranges of Sonso and

385    Mwera, implying that Kamira and Waibira home ranges are populated by species that are

386    commonly found at the other communities' home ranges (Table S8). We found ten indicator

387    species for Sonso (all indigenous rather than introduced species), where *Trichilia rubescens,*

388    *Teclea nobilis,* and *Croton sylvaticus* had the highest indicator values, meaning that they are

389    the most characteristic species. Mwera was characterized by three species: *Morus lactea,*

390    *Chrysophyllum muerense,* and *Sterculia dawei* (also indigenous species). We found three

391    community combinations with indicator species, all of which included Sonso. Thus, the home

392    range of Sonso appears to contain many Known Feeding Tree species that are absent or

393    rare at other home ranges.

### vi)    Insect nest abundance

395    The abundance of termite and ant nests differed between the forests (GLMM, $χ^2_{2,6}$ = 7.18, p

396    = 0.028), where Kamira had a greater abundance than Mwera and Sonso, and Waibira a

397    greater abundance than Sonso (Figure 5,Table S10).

### vii)    Abundance of tool material (THV, twigs, and vines)

399    The abundance of THV, twigs and vines did not differ between the communities' home

400    ranges (GLMM, $χ_{2,6}^2$ = 4.88, p = 0.087).

### viii)    Faecal samples' predictive power

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402    Around half (48.73%) of the Observed Plant Species in Sonso were found in the faecal

403    samples. Fig species accounted for 79.53% of the seeds, followed by *Broussonetia*

404    *papyrifera* (11.24%) and *Psidium guajava* (8.76%; Table 3). From the feeding observations,

405    figs were most heavily fed on, accounting for 30.82% of the feeding time. Similar to the

406    faecal samples, *Broussonetia papyrifera* was an important feeding species (17.10%; Table

407    3), but *Psidium guajava* only accounted for 2.59% of the feeding time. In contrast, we

408    observed the Sonso chimpanzees to feed on *Cordia millenii* 17.92% of the time (Table 3),

409    but just 0.039% of the seeds found in faecal samples were of that species (Table 3). Overall,

410    species richness and evenness appear to be lower for the faecal samples.

412    The number of plant species found in the faecal samples was not affected by the number of

413    Observed Feeding Plants (lm, $F_{1,11} = 2.03$, p = 0.18), when the weight of the faecal samples,

414    and the duration of observation were excluded due to their non-significance (lm, $F_{1,10} = 0.73$,

415    p = 0.42; lm, $F_{1,10} = 4.85$, p = 0.055; Figure S5).

416    The total weight of the faecal samples for a given chimpanzee did not affect the proportion of

417    a particular species in the faecal samples (GLMM, $\chi^2_{1,6} = 0.040$, p = 0.84) and was thus

418    excluded from the model, as were the hours a chimpanzee was observed for (GLMM, $\chi^2_{1,6} =$

419    0.028, p = 0.87). The greater the proportion of time a chimpanzee fed on a plant species, the

420    higher the proportion of its seeds in the faecal samples (GLMM, $\chi^2_{1,4} = 161.9$, p < 0.0005,

421    coefficient = 0.83; Figure S6).

422        ***ix)    Abundance and α, β and γ diversity of seeds in faecal samples***

423    Seed abundance positively correlated with the weight of the sample (Spearman's rank

424    correlation, $S_{151} = 426640$, p = 0.0029). However, the average weight of a sample did not

425    differ between the Sonso and Mwera communities (two sample *t*-test, $t_{149} = 1.032$, p = 0.30),

426    meaning that we were able to exclude weight from subsequent analyses. The mean

427    abundance of seeds per faecal sample was greater for the Sonso community (2060.82 ±

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428    366.99 s.e.) than the Mwera community (839.46 ± 441.28 s.e.; Wilcoxon, $W_{151}$ = 1052, p <

429    0.001; Figure S7).

430    Given that the data of the $α$ diversity of seeds of faecal samples did not exhibit homogeneity

431    of variance, we were unable to perform an ANCOVA. However, the weight of a faecal

432    sample did not correlate with the $α$ diversity of that sample (Spearman's rank correlation,

433    $S_{151}$ = 571800, p = 0.97), and was thus excluded from the model. The $α$ diversity of seeds in

434    faecal samples was 1.5 times greater for the Sonso community (Wilcoxon, $W_{151}$ = 518, p <

435    0.001; Table 4; Figure S8).

436    Due to the nature of how $β_{horn}$ is calculated, it was not possible to assess whether the weight

437    of the sample had an effect. However, as shown above, weight did not appear to differ

438    between the two communities. The $β$ diversity was 1.09 times greater for the Mwera

439    community (two sample $t$-test, $t_{5949}$= -5.34, p < 0.001; Table 4;Figure S8), but γ diversity was

440    1.38X greater for the Sonso community (Table 4).

442    The species rank abundance curve of the species identified from seeds in the faecal

443    samples suggests a lower species evenness and species richness in the diet of the Mwera

444    chimpanzees (Figure 6a). The species accumulation curve suggests a greater species

445    richness in the diet of the Sonso chimpanzees (since for a given number of faecal samples,

446    the number of species recorded is greater for Sonso), although there is considerable overlap

447    of the 95% confidence intervals (Figure 6b).

448

449    **DISCUSSION**

450    We analysed a range of ecological indicators that might influence the likelihood of wild

451    chimpanzees engaging in extractive tool use in two Ugandan forests. We found that, while

452    most groups' territories did not differ substantially in these factors, the Sonso community's

453    home range in the Budongo forest had both a higher diversity and biomass of chimpanzee

454    feeding species. In addition, Sonso chimpanzees had the greatest number of Known

455    Feeding Tree species unique to their range, and the lowest termite and ant nest abundance.

456    The abundance of potential tool materials did not differ between any of the communities'

457    home ranges. Faecal samples underestimate food species richness, under-representing

458    some species, and over-representing others. However, they nevertheless provided valuable

459    insight into chimpanzee diets and remain a useful tool for describing unhabituated

460    chimpanzee feeding behaviour. The greater abundance and diversity of seeds we found in

461    the Sonso chimpanzees' faecal samples is likely to reflect a genuine difference in diet

462    between the Sonso and Mwera chimpanzees, which may have consequences for their tool

463    use behaviour.

464    ***Potential food availability differs between chimpanzee communities' home ranges***

465    While the abundance of chimpanzee feeding trees did not differ between the communities'

466    home ranges (either within or between forests); there was a small difference in biomass – a

467    measure of the potential fruit abundance – suggesting, that the Sonso community benefits

468    from particularly high food availability. Systematic managed logging occurred across the

469    Ugandan National Forest Reserves; however, within them some areas were designated

470    'Nature Reserves' with no legal logging taking place. Only the Kamira chimpanzee's home

471    range overlapped with one of these reserve areas, making it hard to draw meaningful

472    inferences about the impact of managed logging. However, the presence of widespread

473    illegal logging may better explain the observed pattern of variation in biomass. Illegal loggers

474    particularly target large mature trees. While illegal logging occurs across all four

475    communities' home ranges, the presence of an active research station in the Sonso

476    community's range for almost 30-years appears to have conferred significant protection

477    (Babweteera et al., 2012), allowing a greater proportion of trees to mature.

478    The $\alpha$ diversity of Known Feeding Trees was greatest for Sonso, roughly 2.5X greater than

479    any other community. This difference means that at the local scale (i.e. per transect) Sonso

480    had the greatest diversity. The $\beta$ diversity of Known Feeding Trees was lowest for Kamira,

481    possibly because its location near a nature reserve may mean that the area is relatively

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482     uniform (i.e. a low compositional turnover between transects) in climax species. However,

483     the difference in diversity between areas was quite small. As predicted, the total diversity

484     seemed to be greatest for Sonso (supported by the highest γ diversity). The results are in

485     line with previous studies which found that, when compared to chimpanzees in Kibale, the

486     Sonso chimpanzees diet contains a higher diversity of food items which may limit any

487     negative effect of seasonal food shortages and reduce the necessity to use tools to extract

488     alternative food resources (Reynolds 2005; Gruber et al. 2012). Nevertheless, a cross-

489     seasonal survey of actual chimpanzee food availability is needed to strengthen these

490     arguments.

491     Many indicator species were found for Sonso (alone or in combination with another

492     community's home range). Thus, the Sonso chimpanzees' home range has many species

493     that are absent or rare in other communities' home ranges. This diversity further highlights

494     the range of feeding options available to Sonso chimpanzees, again potentially reducing the

495     impact of cyclic food scarcities in more widely available feeding species.

496     Does the higher potential food availability in Sonso sustain greater chimpanzee and other

497     potential competitor species densities (such as other frugivorous primates and birds)? A

498     similar density of small mammals and birds in Budongo and Bugoma suggests that this is

499     not the case (Owiunji, 2000; Plumptre et al., 2010), and the density of chimpanzees is

500     slightly lower for Budongo, suggesting similar levels of intraspecific and interspecific

501     competition across the forest areas (Plumptre and Cox, 2006).

502     ***Dietary differences between Sonso and Mwera***

503     Based on previous studies of chimpanzee faecal samples (Phillips and McGrew, 2013) we

504     expected to identify around 60% of the species that we had observed the Sonso

505     chimpanzees feeding on in their faecal samples, but we were only able to identify around

506     half. Faecal samples appear to represent the frugivorous component of the Sonso

507    chimpanzees' diet relatively well, but not the folivorous component and we were unable to

508    identify any species from the leaf fragments found in the faecal samples.

509    A comparison of the most common species in the faecal samples to the most frequently

510    recorded Observed Feeding Plants, indicated that, whilst there is considerable overlap, fruits

511    that produce many small seeds (such as *Broussonetia papyrifera, Ficus* spp., and *Psidium*

512    *guajava*) are overrepresented in the faecal samples. In contrast, fruit that produce large

513    seeds, from which the chimpanzees scrape off the flesh with their teeth but then rarely

514    swallow the seeds, are underrepresented. This bias likely explains our observations for

515    *Cordia millenii,* the species we recorded as the one chimpanzees spent the most time

516    feeding on, but which was rarely found in their faecal samples. However, as predicted, the

517    greater the proportion of time chimpanzees fed on a species, the higher the proportion of its

518    seeds were found in the faecal samples. Within this model we aimed to go beyond the

519    discriptive results of previous studies (e.g. Phillips and McGrew, 2013), but it proved

520    challenging due to zero-inflation. The zero-inflation was probably due to us being unable to

521    identify plant species in the faecal samples from which only leaves had been eaten, and

522    chimpanzees feeding on fruits whose large seeds were not regularly swallowed. The zero-

523    inflation of the model is problematic, but it will be difficult to avoid in future studies, even with

524    a larger sample size, given the number of feeding species that are not well represented by or

525    easily identified in faecal samples.

526    As predicted, the abundance and $\alpha$ diversity of seeds were greater for Sonso chimpanzees'

527    faecal samples as compared to the Mwera samples, suggesting that chimpanzees in the

528    Sonso community have a more diverse diet than the latter. The $\beta$ diversity of seeds was

529    slightly greater for the Mwera chimpanzees' samples, however, we were unable to control for

530    individual identity in sample collection (and may have collected disproportion numbers of

531    samples from some individuals, particularly large mature males who are easier to find and

532    approach in less well habituated groups). Furthermore, the sample size for Mwera was

533    roughly half that of Sonso, and to calculate $\beta$ diversity we had to exclude samples from

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534 which we did not record any seeds (which only occurred in Mwera samples). Both factors

535 may have artificially increased the estimate of $\beta$ diversity for Mwera samples and thus the

536 estimates are not sufficiently reliable to warrant interpretation.

537 Nevertheless, across measures, faecal samples provided a relatively good insight into the

538 identity of the most important feeding species, and remain an important tool in the

539 description of chimpanzee feeding behaviour, particularly for comparison of dietary

540 differences between communities.

541

542 ***Variation in extractive tool use opportunities between Budongo and Bugoma Forests***

543 Insectivory is rare in Budongo as well as in Kibale forest chimpanzees (Watts et al., 2012;

544 but see Mugisha et al. 2016), but common in other mid-western areas of Uganda (Semliki:

545 Webster et al., 2014; Bulindi: McLennan, 2014; Kalinzu: Koops et al., 2015). Across the four

546 communities and two forests in our sample, Kamira had the greatest abundance of termite

547 mounds, *Cubitermes ugandensis*, and ant nests, *Dorylus* spp, and Sonso the lowest, both in

548 Budongo. The presence of the research station at the centre of the Sonso community

549 territory likely afforded significant protection from illegal logging of mature trees over the past

550 30-years. However, Sonso also experienced the highest levels of active forest management

551 during the decades of timber production. This management appears to have changed the

552 composition of tree species (as seen in the diversity of species available for chimpanzee

553 feeding) and included the active use of tree-species pesticides and termite mound poisoning

554 (Reynolds 2005). In contrast, the Kamira chimpanzees' territory overlaps an area designated

555 as a Nature Reserve during timber production, and likely received the least invasive use of

556 management practice. The variation in insect nests may reflect the variation in the pattern of

557 human impact, with active management for timber production a possible factor in explaining

558 the low abundance of insect nests even decades after production stopped.

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559    While this suggests that the Sonso chimpanzees have the lowest opportunity to feed on

560    termites and ants within our sample, opportunity is unlikely to fully explain the absence of

561    extractive tool use during foraging in Sonso chimpanzees (Grund et al. 2019). The

562    abundance of tool materials did not differ between the communities' home ranges, and,

563    while low, the abundance of termite and ant nests in Sonso was previously found to be

564    within the range of the densities at sites were tools are used to extract insects (Hedges and

565    McGrew, 2012).

566

567    ***Potential implications of the measured ecological variables on tool use***

568    Our study suggests that a high diversity and biomass of Known Feeding Trees in Sonso

569    underscores the Sonso chimpanzees' comparatively diverse and fruit-rich diet, and supports

570    previous work suggesting that the Sonso chimpanzees have the most diverse food

571    availability out of five Ugandan forest locations (Gruber et al., 2012). In previous work the

572    Kanyawara chimpanzees in Kibale forest were suggested to live in the least favourable

573    environment in terms of food diversity and quality but did not exhibit more extensive tool use

574    than other Uganda chimpanzee communities. As a result, the authors concluded that

575    ecological conditions could not completely explain observed differences in extractive tool use

576    for foraging (Gruber et al., 2012). In this study, we again find differences in food diversity and

577    quality across communities, even those with adjacent territories within the same forest area.

578    However, it is not known whether Kamira and Mwera chimpanzees engage in extractive tool

579    use behaviour (beyond sponging for water), and it appears that Waibira chimpanzees, like

580    Sonso chimpanzees, do not use stick tools (Mugisha et al., 2016), albeit after only a more

581    limited number of years of observation (currently 8 yrs). Nevertheless, the observations

582    available suggest that chimpanzees in Waibira have developed additional strategies relying

583    on tool use to acquire valuable proteins (using leaf tools to feed on *Dorylus* ants, Mugisha et

584    al., 2016) compared to the Sonso chimpanzees, where this behaviour has never been

585    observed in 25 years of continuous study. Once the four communities' tool repertoire is

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586     known, it can be mapped together with our understanding of current and historic socio-

587     ecological conditions.

588     The study of chimpanzees in forest areas that lie intermediate between Budongo where

589     stick-tool use appears absent, and forest areas with communities that do employ stick-tool

590     use (for example in Kibale) is of significant interest. The Bulindi chimpanzee community lives

591     in a small riverine fragment less than 60km from Budongo, and has been shown to employ

592     stick-tool use to obtain honey (McLennan, 2014). The Budongo and Bulindi communities

593     show dramatic differences in habitat, particularly in respect to chimpanzee feeding tree

594     species, which may underlie their variation in diet and tool use (McLennan, 2014). But it

595     remains unknown whether or not the Bulindi chimpanzees a) re-innovated tool use in

596     response to the degradation of their fragmenting habitat, b) differed from other Budongo

597     communities before their forest areas diverged, or c) retained extractive stick tool use while

598     other Budongo communities lost it. The difficulty that chimpanzees experience in re-

599     innovating tool use (e.g. Gruber et al., 2011) suggests that option a) is either unlikely, or

600     requires substantial pressure. Once more information on the tool repertoires of the four

601     communities we studied becomes known, the ecological data we collected will help answer

602     these questions.

603     Nevertheless, based on our ecological findings, we predict that the Mwera community

604     engages in extractive tool use behaviour in a foraging context. Potential food availability and

605     tool use opportunities were comparatively low within the Mwera chimpanzee range, they

606     appear to have a less diverse diet than the Sonso chimpanzees, and are geographically

607     closer to the chimpanzee communities in both Kibale and Bulindi that use stick-tools. As

608     habituation improves, direct observations will allow us to test this prediction.

609     Future work exploring tool use, and variation in tool-using across chimpanzee communities

610     in the Budongo and Bugoma forests will be of particular interest to explanations for its

611     unusual absence in the Sonso chimpanzees. The information obtained can then be paired

612     with the ecological and dietary insights we gained in this study and contribute to our wider

613    understanding of the interactions between ecological and cognitive aspects of chimpanzee

614    tool use.

615

621    **CONFLICT OF INTEREST**

622    None of the authors experienced any conflict of interest.

623    **ETHNICAL APPROVAL**

624    All applicable international, national, and/or institutional guidelines for the care and use of

625    animals were followed.

626    **INFORMED CONSTENT**

627    The research did not involve human participants. Research on wild chimpanzees was in

628    accordance with international guidelines and that of the research station.

629    **DATA AVAILABILITY**

630    All data was collected by the authors. If any raw data and/or analyses (incl. R-code) are

631    wanted the corresponding author, Iris Berger, can provide them.

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765

**Figure captions**

**Figure 1.** Map of the two study sites: Budongo and Bugoma forest. (Inset map copyright Matthew McLennan; reproduced here with permission)

**Figure 2.** Boxplot illustrating the median and the upper and lower quartiles of the (a) alpha and (b) beta diversity of Known Feeding Trees of the home ranges of the four communities. The communities from Budongo forest are shaded in yellow, and the Mwera community (Bugoma forest) is shaded in blue.

**Figure 3.** (a) Species rank abundance curve of Known Feeding Tree species recorded during the transects for each community's home range. Species richness is illustrated by the length of the line (i.e. the number of species) and species evenness is indicated by the steepness of the line (i.e. the abundance of a species in relation to the other species in the forest), which are both highest for Sonso. (b) Species accumulation curve for Known Feeding Trees depicting how the number of recorded Known Feeding Tree species increases the more transects we conducted. For any given number of transects, the number of recorded species was highest for Sonso, followed by Mwera. The areas shaded in show the 95% confidence intervals.

**Figure 4.** Non-Metric Multidimensional Scaling ordination plot of dissimilarities between the Known Feeding Tree community of the home ranges of the different chimpanzee communities. Each point represents a different transect and the closer the points are the more similar the transects are to each other. Thus, points of a given community are clustered together. Kaimira and Waibira are very similar to each other, whereas Sonso and Mwera differ, with more pronounced variation between the transects within Mwera.

**Figure 5.** Boxplot illustrating the median and the upper and lower quartiles of the number of termite mounds and ant nests per transect for each community's home range. The communities that are found in Budongo forest are shaded in yellow.

**Figure 6.** (a) Species rank abundance curves for the seeds identified in the faecal samples for the Sonso and Mwera chimpanzee communities. Species richness is illustrated by the length of the line (i.e. the number of species) and species evenness is indicated by the steepness of the line (i.e. the abundance of a species in relation to the other species in the forest): both are higher for the Sonso chimpanzees. (b) Species accumulation curve, illustrating how the number of species identified from seeds increases with the number of faecal samples analysed for both chimpanzee communities, which is higher for Sonso. The areas shaded in represent the 95% confidence intervals, which overlap.
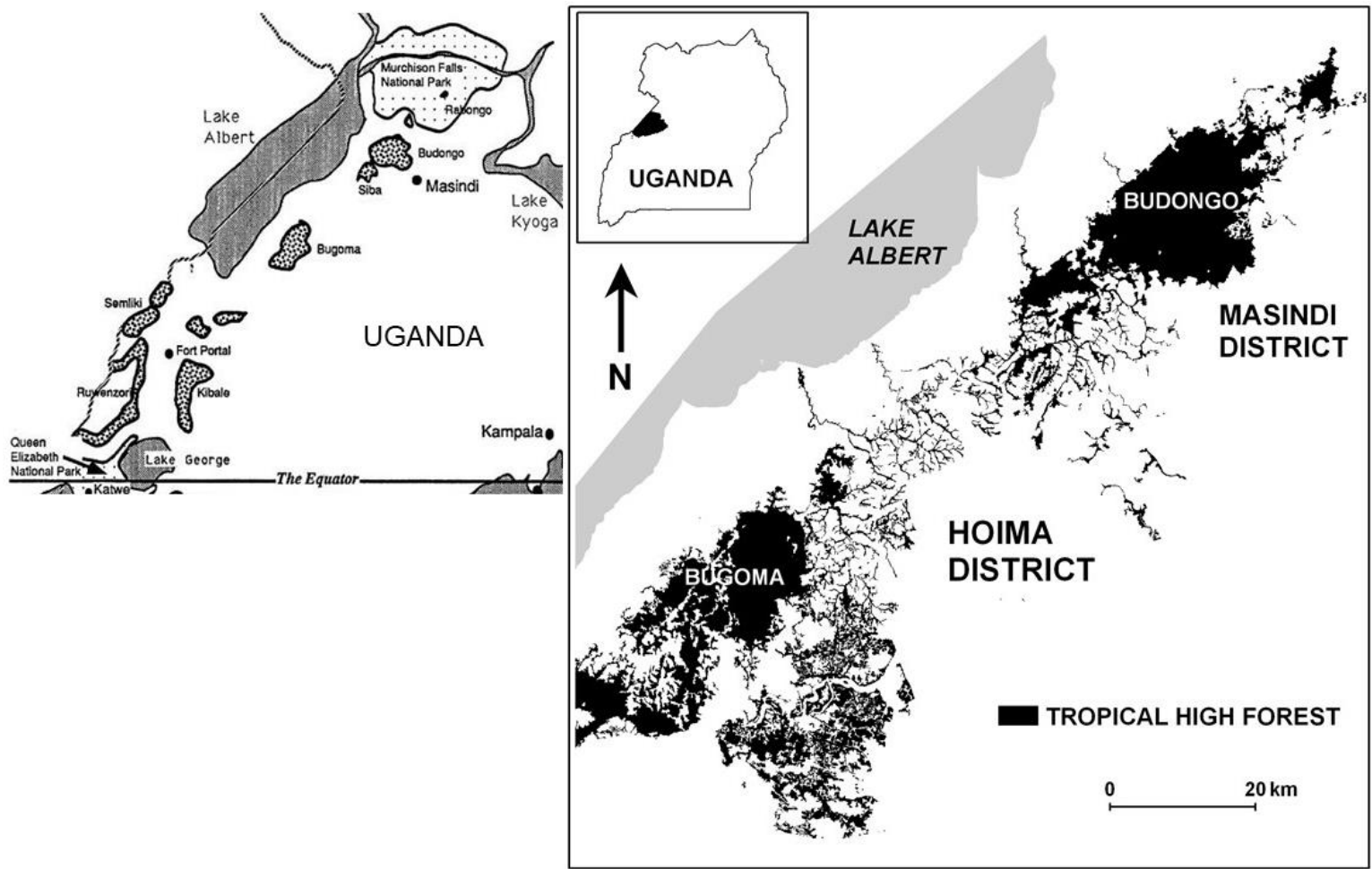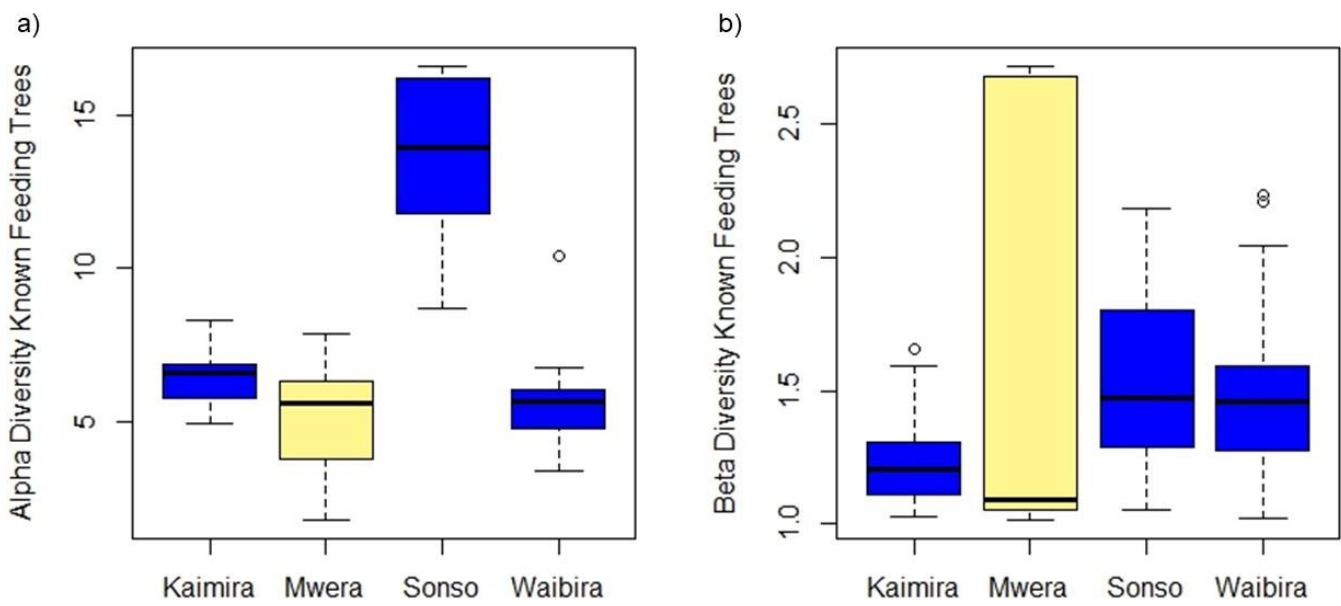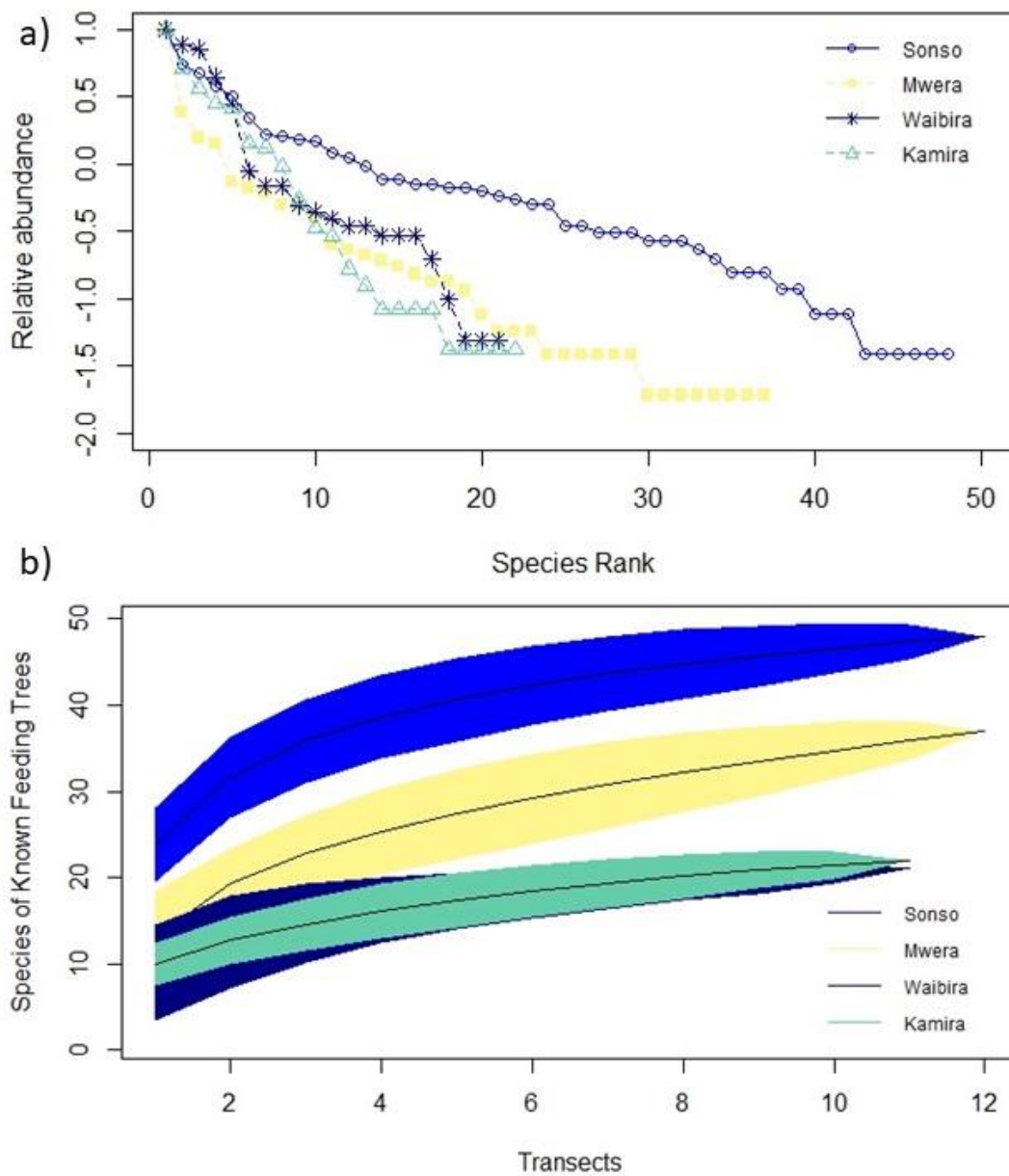
## **Figures**
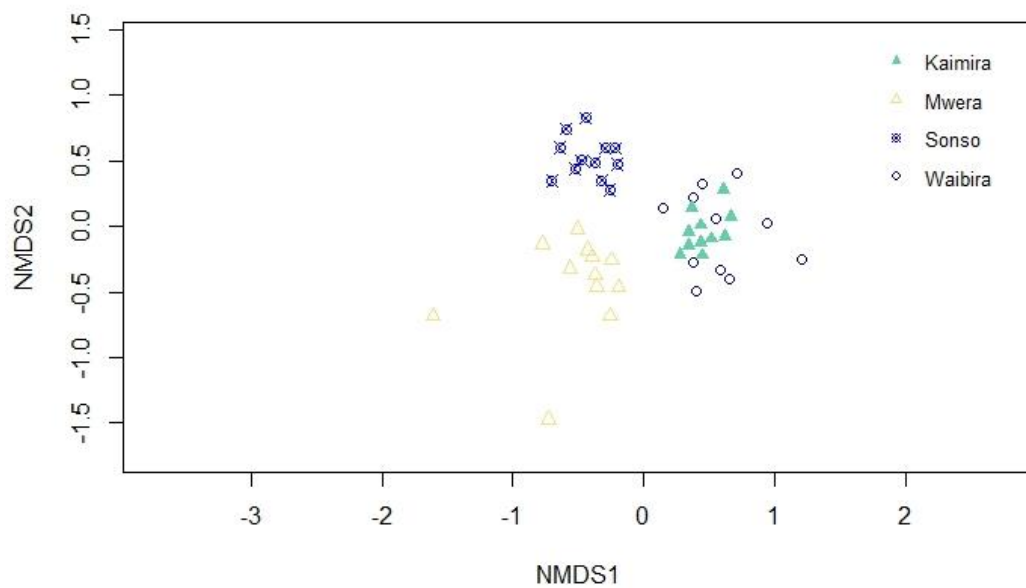


Figure 1



Figure 2

*Figure 3*
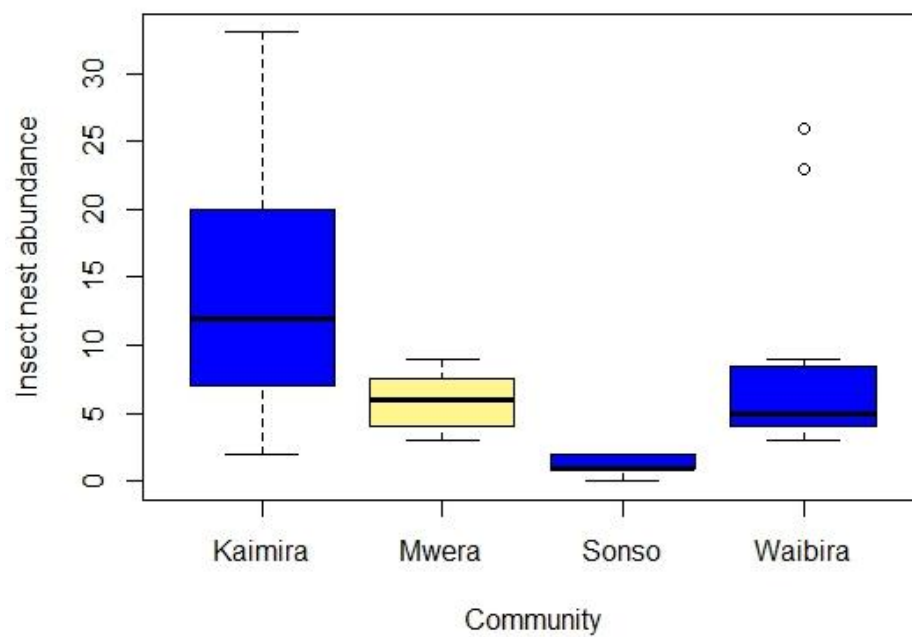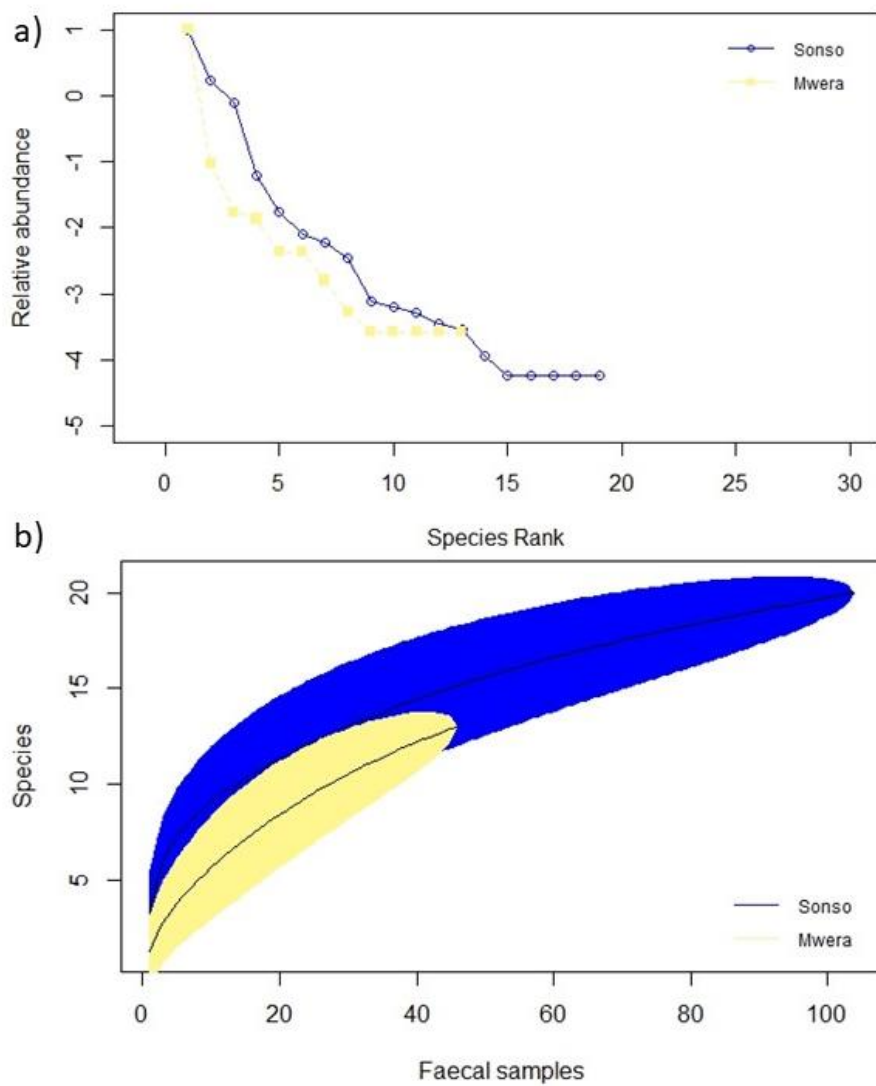
Figure 4



Figure 5

*Figure 6*

**Table captions:**

**Table 1.** The mean DBH and total DBH of all trees encountered during the transects (for Known Feeding Trees and Non-Feeding Trees) for each community. The communities from the Budongo forest are shaded grey.

**Table 2.** Diversity indices and Alpha, Beta and Gamma diversity of Known Feeding Trees for each community's range. The communities from the Budongo forest are shaded grey.

**Table 3.** Preferred Sonso chimpanzee feeding trees described by the percentage of time spent feeding. The species shaded in grey are non-native species introduced to the forest.

**Table 4.** Diversity indices, and Alpha, Beta and Gamma diversity of the seeds found in the faecal samples of the two communities.

**Tables:**

*Table 1*

| Community | | Mean DBH (cm±S.D.) | Summed DBH (cm±S.D.) |
|---|---|---|---|
| Mwera | Known Feeding Trees | 25.1 ± 18.6 | 27215.2 |
| | Non-Feeding Trees | 22.2± 17.5 | 25933.2 |
| Sonso | Known Feeding Trees | 29.7 ± 28.0 | 38483.7 |
| | Non-Feeding Trees | 20.9± 14.7 | 17905.6 |
| Waibira | Known Feeding Trees | 27.4 ± 20.6 | 20384.0 |
| Kaimira | Known Feeding Trees | 27.9 ± 29.9 | 21000.0 |

*Table 2*

| | Known Feeding Trees | | | | |
|---|---|---|---|---|---|
| | Shannon-Wiener | Horn | α | β | Γ |

| | | | | | |
|---|---|---|---|---|---|
| Mwera | 1.56 | 0.35 | 5.15 | 1.57 | 8.17 |
| Sonso | 2.59 | 0.42 | 13.59 | 1.55 | 21.23 |
| Waibira | 1.70 | 0.38 | 5.70 | 1.49 | 8.49 |
| Kaimira | 1.86 | 0.21 | 6.40 | 1.24 | 7.94 |

*Table 3*

| Feeding observations | | Faecal samples | |
|---|---|---|---|
| **Species** | **Percentage** | **Species** | **Percentage** |
| *Cordia millenii* | 17.92 | *Ficus* spp | 79.53 |
| *Broussonetia papyrifera* | 17.10 | *Broussonetia papyrifera* | 11.24 |
| *Ficus mucuso* | 14.89 | *Psidium guajava* | 8.76 |
| *Ficus variifolia* | 8.87 | *Myrianthus holstii* | 0.067 |
| *Ficus exasperate* | 5.47 | *Cordia millenii* | 0.039 |
| *Desplatsia dewevrei* | 4.35 | *Maesopsis eminii* | 0.0081 |
| *Treculia Africana* | 3.84 | *Mildbraediodendron excelsum* | 0.0065 |
| *Cola gigantea* | 3.69 | *Desplatsia dewevrei* | 0.0057 |
| *Khaya anthoteca* | 3.47 | *Pseudospondias microcarpa* | 0.0024 |
| *Syzygium guinense* | 3.10 | *Chrysophyllum gorungosanum* | 0.0016 |

*Table 4*

| Sonso | Mwera |
|---|---|
| | |

| Shannon-Wiener | Horn | α | β | γ | Shannon-Wiener | Horn | α | β | γ |
|---|---|---|---|---|---|---|---|---|---|
| 0.43 | 0.46 | 1.61 | 1.70 | 2.42 | 0.054 | 0.50 | 1.07 | 1.85 | 1.75 |

| Shannon-Wiener | Horn | α | β | γ | Shannon-Wiener | Horn | α | β | γ |
|---|---|---|---|---|---|---|---|---|---|