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1 TITLE: The diet of open-habitat chimpanzees (*Pan troglodytes schweinfurthii*)
2 in the Issa valley, western Tanzania

3

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23 **Abstract**

24 Comparative data on the diets of extant primates inform hypotheses about
25 hominin resource use. Historically, data describing chimpanzee diets stem
26 primarily from forest-dwelling communities, and we lack comparative data
27 from chimpanzees that live in mosaic habitats that more closely resemble
28 those reconstructed for Plio-Pleistocene hominins. We present data on the
29 diet of a partially-habituated community of open habitat chimpanzees (*Pan*
30 *troglodytes schweinfurthii*) from the Issa valley, western Tanzania, collected
31 over a four-year period. Based mostly on macroscopic faecal analysis, Issa
32 chimpanzees consumed a minimum of 69 plant species. There was no
33 relationship between plant consumption and either fruit availability or feeding
34 tree density; the most frequently consumed plant species were found in
35 riverine forests, with woodland species consumed more frequently during the
36 late dry season. We conclude by contextualising these findings with those of
37 other open-habitat chimpanzee sites, and also by discussing how our results
38 contribute towards reconstructions of early hominin exploitation of mosaic
39 landscapes.

40

41 **KEY WORDS:** great ape diet; savanna-woodland mosaic; food availability;
42 hominin; East Africa

43 **Introduction**

44 Of the 14 mid- or long-term studies on wild chimpanzees, 11 are based
45 in tropical forests, whilst only three focus on drier (savanna-woodland mosaic)
46 populations. Thus, our understanding of extant chimpanzees as well as
47 reconstructions of early hominin behaviour (e.g. bipedalism: Hunt, 1994;
48 hunting: Stanford, 1996) have been based mostly on data from studies in
49 tropical forests. However, Plio-Pleistocene hominin environments did not
50 resemble the tropical forests of most contemporary chimpanzee study sites.
51 Instead, there is increasing sedimentological, faunal, and isotopic evidence
52 that especially early Pliocene hominin environments were mosaics comprised
53 of different vegetation types: woodlands, grasslands, and riverine forests
54 (WoldeGabriel et al., 2001; White et al., 2009, 2015; Cerling et al., 2011).
55 Consequently, the density and distribution of chimpanzee dietary plants in
56 similar, contemporary environments provides a paleoecological context for
57 reconstructing early hominin resources. *Australopithecus* diet, for example, is
58 thought to have diverged from great ape diet, with those early hominins
59 probably consuming more seeds, nuts, underground storage organs, and soft
60 fruits (Plummer, 2004; Ungar, 2004). Thus, a better understanding of the
61 abundance, distribution and consumption of contemporary (especially dry-
62 habitat) ape plant foods may help us reconstruct floral paleocommunity-use
63 by hominins.

64 Moreover, it has long been recognized that early hominin evolution
65 occurred at a time of increasing seasonality, and Foley (1993) suggested that
66 responses to this seasonality may have catalysed the evolution of later
67 hominins, especially *Homo*. However, our ability to consider the full

68 implications of seasonal resource variation on hominins is hampered by the
69 relative lack of knowledge about seasonal resource distribution and use in
70 analogous habitats today, especially those of savanna or open-habitat
71 chimpanzees¹, which are more strongly seasonal than forested sites (Moore,
72 1992). Chimpanzee responses to seasonal shortages of preferred foods can
73 result in a reliance on poorer quality, tougher foods than those consumed
74 during fruit-rich periods (e.g., tree bark [Pruetz, 2006]), or else can have
75 consequences for ranging behavior, whereby parties travel greater distances
76 to forage on preferred fruits (Sugiyama and Koman, 1992).

77 Studies using stable isotopes from open-habitat chimpanzees have
78 provided insight into general patterns of resource use (Schoeninger et al.,
79 1999, 2015; Sponheimer et al., 2006). Schoeninger et al.'s (1999) analysis of
80 hairs from Ishasha (Democratic Republic of Congo) and Ugalla (Tanzania)
81 chimpanzees highlighted the importance of woodland resources in their diets,
82 especially for the Tanzanian population. Sponheimer et al. (2006) followed
83 this work by analysing samples from Fongoli (Senegal) chimpanzees,
84 reporting remarkably low C4 values, despite the abundance of C4 grasses in
85 their habitat, in stark contrast to what had been reported for *Australopithecus*.

¹ No chimpanzee population is truly 'savanna', defined ecologically by mixed tree–grass systems immersed in a continuous grass layer with discontinuous tree canopy (Scholes and Archer, 1997; Ratnam et al., 2011; Domínguez-Rodrigo, 2014). Thus henceforth, we use the term 'open-habitat' to refer to chimpanzees living in open, dry habitats compared to forest-dwelling chimpanzees. See Moore (1992) for a review of this issue.

86 Whilst these studies provide information about broad dietary patterns and
87 some (in other apes, e.g., *Gorilla beringei*) revealed seasonal shifts
88 (Blumenthal et al., 2012), limitations are apparent, not least that using
89 isotopes to reconstruct consumption patterns can underrepresent botanical
90 diversity, with numerous foods failing to reveal isotopic signatures (Fontes-
91 Villalba et al., 2013).

92 Chimpanzees are highly frugivorous omnivores (Newton-Fisher, 1999;
93 Basabose, 2002; Watts et al., 2012). Previous research of open-habitat
94 chimpanzees has consistently revealed narrower diets (fewer total species
95 consumed) than those of forest-dwelling populations and, except for Fongoli
96 (Pruetz, 2006), these studies have relied on indirect methods of diet
97 composition (Table 1). We add to this literature by providing data from the
98 Issa valley, western Tanzania, a particularly valuable sample given that most
99 work on open-habitat chimpanzees stems from western Africa, whereas the
100 hominin fossil record is dominated by eastern African deposits. Given the
101 importance of studying diet in extant apes that live in environments similar to
102 those reconstructed for early hominins, we aimed to establish dietary breadth
103 and seasonal consumption, as well as assess the relationship between the
104 distribution of those foods across vegetation types within the habitat. We
105 predicted that (1) Issa chimpanzees would resemble other open-habitat
106 communities and consume fewer total plant species than forest-dwelling
107 chimpanzees. Additionally, given the increased species richness of gallery
108 forests compared to woodlands (Piel and Stewart, unpublished data), we
109 expected that (2) chimpanzees would rely heavily on gallery forests for foods
110 throughout the year. Finally, if open-habitat chimpanzees exhibit 'savanna'

111 adaptations (sensu Moore, 1992) then we predicted that (3) preferred foods at
112 Issa will differ from those of nearby forest-dwelling chimpanzees at Gombe
113 and Mahale. Finally, we discuss what our results might reveal about the
114 relationship between environment, diet, and early hominin exploitation of a
115 mosaic landscape.

116

117 TABLE 1 ABOUT HERE

118 **Materials and methods**

119 *Study site and subjects*

120 We collected data between January 2009 and March 2014 in the Issa valley,
121 western Tanzania (Figure 1). The Issa valley lies >90 km from the nearest
122 national park boundary (Mahale Mountains, along Lake Tanganyika) and ~60
123 km from the nearest village (Uvinza). The landscape consists of broad valleys
124 separated by steep mountains and flat plateaus ranging from 900 to 1800 m
125 above sea level. Vegetation is dominated by miombo woodland— *Brachystegia*
126 and *Julbernardia* (Fabaceae) – although it also includes swamp and
127 grassland (together, we classified all of these habitats as ‘open’ vegetation
128 types), as well as thin strips of riverine and thicket forests (‘closed’ vegetation
129 types, hereafter called just ‘forest’). Forest comprises ~7% of the total study
130 area. There are two distinct seasons: wet (Nov – April) and dry (May –
131 October), with dry months experiencing <60 mm of rainfall (Whitmore, 1975).
132 Rainfall averaged 1220mm per annum (range: 930–1490mm from 2009–
133 2014) and temperatures ranged from 11° C to 38° C (Figure 2).

134 Chimpanzees were first studied in this area from 2001 to 2003
135 (Hernandez-Aguilar, 2006), when researchers based themselves at a
136 temporary camp 9 km north and 400 m lower in elevation than the current
137 camp, from which research has been continuous since 2008. Preliminary
138 genetic identifications suggest the core study area of $\sim 85\text{km}^2$ is used by a
139 single community of at least 67 individuals, although given their low density
140 (0.25 individuals/ km^2 [Piel et al., 2015]), it is likely that the home range of this
141 community is substantially larger (Rudicell et al., 2011). Whilst the majority of
142 the data for the current study come from faecal sieving (see below), we
143 supplemented with direct feeding observations that were made
144 opportunistically during party follows.

145

146 FIGURE 1 & 2 ABOUT HERE

147 *Dietary composition*

148 To obtain fresh chimpanzee faecal samples, research teams searched for
149 chimpanzees by listening for calling parties early in the morning, by targeting
150 areas known from motion-triggered cameras and autonomous acoustic
151 recording units to be used by chimpanzees (Kalan et al., 2016), and by
152 conducting reconnaissance walks throughout the study area. We collected all
153 fresh (estimated at <12 hours old) chimpanzee faeces in clean plastic bags
154 and brought them back to camp for sluicing in a 1mm-wide screened sieve.

155 We followed recommendations of macro-specific analytical techniques
156 of primate faecal analysis (McGrew et al., 2009; Phillips and McGrew, 2013)
157 and estimated the proportions of matrix and undigested contents for each
158 sample. We categorized *Ficus* seeds and insect parts into many, some, few,

159 or none, and counted all other seeds as well as other animal matter, whole
160 leaves, and parasitic worms. We described, photographed, and assigned a
161 seed type number to all unidentified seeds, and recorded data on datasheets
162 or Google Nexus 7 tablets using Open Data Kit software (ODK). We then
163 stored a library of seeds for identification in transparent container boxes. We
164 collected data on consumed foods through direct observation of foraging
165 events by following chimpanzee parties. We recorded data on species and
166 plant part consumed.

167 *Phenology*

168 In October 2008, we established two phenology transects to monitor monthly
169 fruiting patterns of 597 individual plants (trees, lianas, and shrubs): 396 in
170 woodland and 201 in riverine forest. Transects were stratified by vegetation
171 type (woodland and forest), with the woodland transect following a randomly
172 chosen compass bearing. The bearing of the forest transect was manually
173 selected to follow forest vegetation, being shifted 50 m at one location to
174 ensure that it continued to follow the forest. We identified all trees over 10 cm
175 diameter at breast height (DBH) and above 2 m tall that lay within 2.5 m of
176 each side of the transect. We attached a metal tag with an identification
177 number to each tree and estimated counts of mature fruit. In July 2011, we
178 added a phenology “trail”, which was used to monitor an additional 423
179 woodland trees that met the above criteria, and that were also known to be
180 chimpanzee feeding species based on a previous study (Hernandez-Aguilar,
181 2006).

182 *Environmental monitoring*

183 In January 2009, we deployed temperature/relative humidity loggers (Onset
184 Corp.) in woodland and forest 1.5 km from the researcher base station.
185 Measurements were recorded at 30-minute intervals. We also deployed an
186 electronic rain gauge (Onset Corp., HOBO, model RH3) at the base station
187 that recorded each 2 mm of rainfall.

188 *Botanical surveys and vegetation classification*

189 To calculate feeding species density in the study area, we set an arbitrary
190 goal of $n=10$ stems/feeding plant species. To accomplish this, we sampled in
191 three ways. First, we placed 182 20x20 m botanical plots every 100 m from
192 the start of six line transects that cross-cut the study area (Method A).
193 However, this method produced only minimal representation of forest species
194 (most forest strips are less than 50 m wide, for example). Therefore, when
195 botanical teams crossed forests, they sampled additional plots at 50 m
196 intervals following forest strips to increase forest species representation. In all
197 plots, we identified all trees over 10 cm DBH to species level when possible
198 and recorded the vegetation type as either open or closed (see above). We
199 conducted surveys in 122 (67%) of these plots, or 4.88 hectares in forest
200 vegetation, versus 60 (33%) plots, or 2.4 hectares, in woodland vegetation.
201 The inequality in survey effort was because forests host more diversity and
202 thus require more sampling than woodland vegetation.

203 The plot data provided density estimates for most feeding species.
204 However, because many feeding species occurred at extremely low densities,
205 we still did not obtain 10 specimens for each species, so we employed two
206 additional methods that targeted the top 15 plants most frequently identified in

207 faecal samples, to increase our sample size. First, we overlaid a 50 x 50 m
208 grid over a map of the study area, and randomly selected grid cells (Method
209 B). At the center point of each cell, we established a 10x10 m box, within
210 which we identified all trees that met the above criteria, including being a
211 feeding species. We used the point center quadrat method (Walker, 1970;
212 Mitchell, 2010) to measure the distance of each member of the top 15 feeding
213 species to the nearest member of the same species within 100 m in four
214 quadrats (if we observed no species member within 100 m, no value was
215 recorded). The results of these measurements provided additional density
216 estimates as well as data on feeding plant distribution. Finally, we restricted
217 the grid coverage to forests (Method C), and repeated the above steps,
218 eventually adding an additional 111 plots using these last two methods,
219 bringing the total plots to 293 and the total surveyed area to 8.39 hectares.

220 To ascribe a vegetation type to each plant species, we divided the
221 number of individual stems recorded in forest plots by the total number of
222 individuals observed overall to obtain a “Vegetation score” from 0 to 1, with 0
223 representing no evidence of the plant in forest and 1 indicating that all
224 occurrences were in forest. We categorized those plants with scores 0–0.25
225 as woodland, 0.26–0.75 as both forest and woodland, and 0.76–1 as forest
226 plants. For those food plants that were absent in botanical survey plots,
227 botanists familiar with the local flora ascribed categorization whenever
228 possible.

229 *Data analyses*

230 To calculate fruit availability, we followed Chancellor et al. (2012). We used
231 the density and basal area [$(1/2)(DBH)^2 \times \pi$] of each tree species and then
232 calculated a monthly fruit availability index (F_m) using the following formula:

233

$$234 \quad F_m = \sum P_{km} \times B_k$$

235

236 where P_{km} denotes the proportion of plants in fruit for species k in month m
237 and B_k represents the total basal area per hectare for species k .

238 To calculate a monthly fruit availability index (FAI – the total availability
239 of fruits in a given month), we used the total area of all transect botanical plots
240 in hectares (ha), to calculate the number of trees/ha of that species. We then
241 calculated a mean DBH for all members of the same species, and
242 subsequently calculated the B_k value. We only used FAI values for species
243 for which we had a minimum of five individuals, to reduce problems
244 associated with small sample sizes.

245 We measured diet breadth in two ways: the mean number of plant
246 species per faecal sample, and the total number of different plant species
247 recorded in all samples collected over the course of a month, controlling for
248 total samples collected (following Pruetz, 2006). For the initial plot surveys
249 (Method A), we calculated plant density by dividing the total number of
250 specimens of a given species by the total number of hectares surveyed in
251 each vegetation type. For the non-transect plots (Methods B and C), we
252 followed Mitchell (2010) to calculate an absolute and relative density of each
253 key feeding species. To calculate the absolute density of a particular species

254 (individuals/hectare), we divided the number of plot quarters with that species
255 by the number of total quarters surveyed, then multiplied this value by the
256 absolute density of all the feeding species.

257 We calculated the relative density of each species by dividing the
258 absolute density of a given species by the absolute density of all stems
259 combined, and then multiplying by 100 to convert into a percentage. Finally,
260 we compared the mean nearest neighbor distance (NN) of the top 15 species.
261 Plant species with lower NN distances were considered more clumped than
262 those with larger NN distances (see Clark and Evans, 1954). We conducted
263 Pearson's correlations on rainfall and FAI, Spearman's rank-order correlations
264 on FAI and dietary breadth (total species consumed/month), and Student's t-
265 tests on seasonal differences in species consumption. All tests were
266 conducted in R (R Development Team, 2017).

267 All research complied with ethical policies, regulation, and guidelines
268 from the Tanzanian Wildlife Research Institute (TAWIRI) and Commission for
269 Science and Technology (COSTECH).

270 **Results**

271 We analysed 810 chimpanzee faecal samples: 348 from the wet season and
272 462 from the dry season (monthly range = 2 to 72). Table 2 lists all identified
273 chimpanzee plant foods, identified to species where possible. Peak seed
274 diversity tended to be at the end of the wet and the beginning of the dry
275 season (April–May).

276

277 TABLE 2 ABOUT HERE

278

279 We identified 51 plant genera consumed by Issa chimpanzees, with
280 another eight individual seeds to which we could not assign even a Family.
281 We identified 54 species, either based on seed morphology or direct
282 observation, but could identify seven additional foods only to the genus, giving
283 a total of at least 61 species. Including the eight unidentified seeds brings this
284 to a minimum of 69 plant species. In addition, termites (probably
285 *Macrotermes*) were consumed largely during the early and late wet season,
286 but also at times during the dry season (Stewart and Piel, 2014). Other
287 invertebrates consumed include driver ants (*Dorylus* sp.) and beetle larvae
288 (Curculionidae). Most surprisingly, we did not find a single example of
289 vertebrate prey in any of the 810 samples.

290 Following Pruetz (2006), we considered key plant food species those
291 recorded in >50% of samples in any one month. These included nine species,
292 but of these, only *Ficus* sp. and *G. huillensis*, *S. comorensis*, and *G.*
293 *rugosifolia* occurred in >50% of faecal samples in more than two months
294 (Table 2). Fruit availability showed a significant inverse relationship to rainfall
295 ($t = 2.57$, $df = 37$, $p = 0.01$), peaking in the early dry season during each of the
296 three full years where data were available (2009, 2012–2013) and showed a
297 similar pattern in 2014 (Figure 3). The number of species consumed per
298 month ($r_s = -0.06$, $p = 0.72$) was not influenced by monthly fruit availability.
299 Furthermore, no significant difference existed in the mean number of species
300 consumed per month between dry ($M = 3.24$, $SD = 0.73$) and wet ($M = 3.14$,
301 $SD = 1.00$) seasons ($t(35) = 0.33$, $p = 0.74$).

302 For those 12 species most often identified in faecal samples, the monthly
303 proportions of samples that contained seeds were not significantly related to
304 absolute densities ($r_s = 0.06$, $p=0.84$; Figure 4). On the contrary, species with
305 seeds routinely found in faeces existed generally at low densities, whereas
306 abundant species were not consumed as much as their density might predict.

307

308 FIGURES 3 and 4 ABOUT HERE

309 *Food species distribution and density*

310 The most common genus in the all plots was *Julbernardia* (37.5 stems/ha),
311 followed by *Lannea* (6.98 stems/ha), *Vitex* (6.11 stems/ha), and *Brachystegia*
312 (5.68 stems/ha) (Table 3). Considering vegetation plots located only in valleys
313 (versus on plateaus where chimpanzees rarely nest or forage), *Vitex* (7.2%)
314 was the most commonly encountered species, followed by *Parinari* (6.08%),
315 *Strychnos* (2.98%), and *Lannea* (2.98%). Moreover, in those same areas,
316 *Vitex* and *Garcinia* were the most widely spaced, with mean distances
317 between trees of over 30 and 25 m, respectively. *Grewia*, *Keetia* and *Ficus*
318 were the most clumped, with all averaging less than 10 meters between adult
319 trees (Figure 5). Of the twelve most frequently consumed plants, four were
320 observed only in the forests, with all others encountered in open and closed
321 vegetation types (Figure 6).

322

323 FIGURES 5 and 6 ABOUT HERE

324

325 Twelve plant genera appeared at least once a month on average in the
326 chimpanzees' diet over the course of the study. *Ficus* spp. was the most

327 frequently consumed food, with chimpanzees consuming them in 37 of 41
328 months (90.2%) and was the most common seed identified across seasons
329 (present in 83.9% of all samples); *Garcinia* (51.6%), *Saba* (38.2%), and
330 *Grewia* (27.8%) were the next most frequently found, followed by *Cordia*
331 (16.8%), *Flacourtia* (16.6%), *Parinari* (15.6%), *Vitex* (15.3%), *Keetia* (14.5%),
332 and *Strychnos* (10.9%), *Citropsis* (10.0%), and *Lannea* (5.4%). Whilst
333 chimpanzees consumed some plants frequently in both wet and dry seasons
334 (e.g., *Ficus*, *Garcinia*, *Saba*), others were more important during only one
335 season (e.g., *Grewia*, *Parinari* – dry; *Flacourtia* – wet – Figure 7).

336 When we compared the results from Issa to those reported at nearby
337 Gombe (Foerster et al., 2016) and Mahale Mountains (Nishida and Uehara,
338 1983) National Parks, we found considerable overlap in the 12 most important
339 foods (Table 4). Three genera (*Ficus*, *Garcinia*, and *Saba*) are important for
340 all three chimpanzee communities, whilst another five (*Baphia*, *Parinari*,
341 *Pseudospondias*, *Pterocarpus*, *Vitex*) are important for two communities.

342

343 FIGURE 7 ABOUT HERE

344 TABLE 4 ABOUT HERE

345 **Discussion**

346 In the current study, we macroscopically analysed 810 chimpanzee faecal
347 samples from the Issa community that lives in a mosaic woodland
348 environment of western Tanzania. The limitations of this method are well
349 established (McGrew et al., 2009; Phillips and McGrew, 2013), with vegetative
350 foods (pith, leaf, stem) and flowers typically not identifiable and thus not

351 accurately represented in comprehensive food lists (Tutin and Fernandez,
352 1993). Consequently, our results likely underestimate plant diversity.
353 Nonetheless we interpret them here in the context of other studies of savanna
354 chimpanzees where the same methods were used to infer diet. We also
355 compare our results with published results from forest-dwelling chimpanzees
356 in nearby Gombe and Mahale National Parks to draw comparisons on plant
357 species consumption and preference across different habitats.

358 Issa chimpanzees consumed a minimum of 69 plants over a 41-month
359 study period. Combining our dataset with a previous study by Hernandez-
360 Aguilar (2006) from nearly the same area (see Table 2), we reach a total of 77
361 consumed plants. As we predicted, their diet is very narrow relative to forest-
362 dwelling communities, and consistent with other open-habitat chimpanzees. In
363 fact, in a recent analysis of chimpanzee diet across the entire 3300km² Ugalla
364 region (which encompasses Issa), Yoshikawa and Ogawa (2015) listed only
365 100 consumed plants, considerably less than nearly every other study site of
366 chimpanzees (Table 1). McGrew et al. (1988) reported Mt. Assirik (Senegal)
367 chimpanzees to consume 84 species (41 of which were inferred). Even at
368 Fongoli, the lone habituated open-habitat chimpanzee community under
369 study, dietary breadth reaches only 77 different species (Bertolani and Pruetz,
370 2011). Table 1 compares these figures to forest-dwelling chimpanzee
371 communities, which regularly consume between 150 and 200 different
372 species.

373 When we compared the most important plants at Issa, Gombe, and
374 Mahale, we found that three plants overlap at all three sites: *Ficus*, *Garcinia*,
375 and *Saba* (Nishida and Uehara, 1983; Foerster et al., 2016). These species

376 are the three most important plants for the Issa chimpanzees and two of the
377 top three at Mahale. In fact, almost a third (11/36) of the top consumed
378 species at the three sites overlap. With Issa chimpanzees favoring largely the
379 same plants as nearby forest-dwelling communities, despite dramatic
380 differences in the physical environment, e.g., plant diversity and density,
381 seasonality, rainfall (Collins and McGrew, 1988), it is likely that population
382 density, ranging, and grouping patterns (rather than diet) are the most
383 significant and different in open-habitat chimpanzees compared to their forest-
384 dwelling cousins. While population density is known to differ in significant
385 ways (density at Issa = 0.25 individual/km², compared to e.g., Gombe, ~3
386 individual/km²), data are not yet available from Issa on ranging and grouping
387 behaviour.

388

389 *Absence of vertebrate remains in faeces*

390 There was no evidence of vertebrate prey in the current study. Despite the
391 presence of red colobus (*Procolobus tephrosceles*) and galagos (*Otolemur*
392 *crassicaudatus*, *Galago senegalensis*, *Galago moholi*) in the study area, as
393 well as other species confirmed as chimpanzee prey elsewhere (blue duiker,
394 red-tailed monkey [Uehara, 1997]), the only evidence of vertebrate prey
395 consumption at Issa until 2015 consisted of a single antelope hoof (possibly
396 *Oreotragus oreotragus*) recovered in 2008 prior to systematic sampling (Piel
397 and Stewart, pers. obs.) and an unidentified bone reported by Hernandez-
398 Aguilar (2006). The lack of evidence for meat-eating is surprising given not
399 just the propensity for hunting in other open-habitat communities Fongoli
400 (Pruetz et al., 2015) and nearby Gombe (Gilby et al., 2006) and Mahale

401 (Takahata et al., 1984), but also that Issa chimpanzees often encounter
402 potential prey (e.g., bushbuck, klipspringer, and yellow baboons - Piel et al.,
403 unpublished data].

404 This paucity of vertebrate consumption is consistent with other studies
405 that relied on macroscopic analyses of open-habitat chimpanzee faecal
406 specimens (Suzuki, 1966; McGrew, 1983; Pruetz, 2006; Yoshikawa and
407 Ogawa, 2015), but contrasts with recent observations at Issa. A 2015 report of
408 blue duiker consumption at Issa (Ramirez-Amaya et al., 2015) and two
409 additional observations since then (Piel and Stewart, unpublished data)
410 support earlier discussions on the limitations of using indirect methods to
411 reveal chimpanzee meat-eating (Boesch and Boesch, 1989).

412
413 *Vegetation type and spatiotemporal patterns in plant consumption*
414

415 There was no relationship between fruit availability or feeding tree density and
416 consumption. Nonetheless, despite the dry-season reliance of Issa
417 chimpanzees on woodlands, of the 60 food plants to which we were able to
418 assign a dominant vegetation type, a similar proportion was found in each
419 vegetation type (38.3% for forest, $n=23$, and 43.3% - for woodland, $n=26$),
420 while 11 were categorized from both. These proportions parallel results from
421 Mahale (Tanzania), where Nishida and Uehara (1983) reported 41.7% of
422 feeding species to be from forests, versus 38.0% from woodlands, and 5.7%
423 to be from both. Similar to most other communities (Doran, 1997; Newton-
424 Fisher, 1999; Basabose, 2002; Pruetz, 2006; Watts et al., 2012),
425 chimpanzees consumed at least some fruit in every month.

426 Twelve of the 15 most often-consumed plants were recorded in forest,
427 and six of the top seven were exclusively from forest (Table 2). This reliance
428 on forest species is striking given that only 7% of the study area is classified
429 as forest, versus over 60% woodland. It also contrasts with how McGrew and
430 colleagues (1988) described chimpanzee feeding species distribution at Mt.
431 Assirik: 59% of consumed foods from woodland species, versus only 29%
432 from forest species. Seasonally, the data suggest that Issa chimpanzees
433 consume forest fruits for much of the year, but increase their foraging in
434 woodlands in the dry season, when forest fruits are less abundant. In that
435 sense, similarly to some chimpanzees increasing travel distance (Sugiyama
436 and Koman, 1992) or eating tougher foods (Pruetz, 2006) in response to food-
437 poor times, Issa chimpanzees may also shift primary use of vegetation types,
438 in line with what occurs with their nesting locations (Hernandez-Aguilar, 2009;
439 Stewart et al., 2011).

440 Relatedly, we observed chimpanzees consume bark 27 times over the
441 study period, and most observations were made from the late wet season, the
442 period of lowest (overall) fruit availability. Multiple studies have reported bark
443 consumption across the Order (e.g., *P. troglodytes* - Nishida, 1976;
444 *Cercopithecus l'hoesti* - Kaplin et al., 2000; *Lemur catta* - Yamashita, 2002;
445 *Alouatta belzebul* - Pinto and Setz, 2004) and wood is known to provide a
446 critical sodium source not just for primates (Rothman et al., 2006), but also
447 herbivorous mammals (Iwata et al., 2015). In Mahale, chimpanzees exhibited
448 two annual peaks of bark consumption, both during fruit-lean times (Nishida,
449 1976). Moreover, whilst they were observed to consume the bark of 21
450 different tree species, one third of observations were of *Brachystegia bussei*

451 bark consumption – similar to at Issa ($8/27 = 29.6\%$). Thus, as at Mahale,
452 chimpanzees at Issa may be compensating for low nutrient consumption
453 during fruit-poor periods by stripping and eating woodland bark. Bark was also
454 likely to have been an important and seasonal component of *Australopithecus*
455 *sediba* diet as well (Henry et al., 2012), but the extent of its importance
456 throughout hominin evolution remains unclear. Our results support the idea of
457 an ape reliance on bark at certain times of the year, at Issa probably to
458 compensate for a scarcity of higher-quality foods.

459 Contemporary eastern African seasonality patterns strongly resemble
460 those predicted for the same area between 3.0 and 2.0 Ma, during a critical
461 time of *Australopithecus* – *Homo* evolution (Reed and Rector, 2007). Such
462 seasonality has been implicated as a primary catalyst for the origins of *Homo*,
463 with a transition away from anatomical and towards technological adaptations
464 to a shifting environment (Foley, 1993). One key element of adapting to new
465 environments involves how animals exploit available foods, from where, and
466 when during the year. As a result, improvements in our comparative data for
467 the diets of extant primates can directly inform our predictions about the diet
468 of extinct hominins (Wood and Schroer, 2012).

469 In her analysis of how hominins would have responded to harsher,
470 drier habitats that offered widely distributed food sources during the Plio-
471 Pleistocene, Copeland (2009) suggested that such conditions may promote
472 consumption of underground storage organs (USOs), expansion of home
473 ranges, and restriction to thin, forest strips. Previous work has inferred
474 chimpanzee consumption of USOs at Issa (Hernandez-Aguilar et al., 2007),
475 and preliminary evidence suggests that day and annual ranging distances are

476 also atypically high for the species (Piel and Stewart, unpublished data). In
477 contrast to Copeland's prediction of forests as a limiting factor, though,
478 chimpanzees at Issa may seasonally expand their foraging niche. Analysis of
479 nesting patterns at Issa suggested that chimpanzees ranged more widely in
480 the dry season (Hernandez-Aguilar, 2009). Here is where habitat
481 reconstructions, and definitions, are important (White et al., 2009a;
482 Domínguez-Rodrigo, 2014). If the savannas that surrounded early paleo-
483 forests comprised treeless 'savannas', then hominins may very well have
484 been confined to forest strips that afforded protection from terrestrial
485 carnivores. However, if something more akin to woodlands surrounded the
486 forests, hominins may have exhibited a chimpanzee model of exploitation of
487 this open vegetation that would have offered, like at Issa, important foods
488 such as *Parinari* and *Keetia*.

489 Morphological, microwear and isotope data are the most common ways
490 of reconstructing hominin diet. Yet a fundamental problem with modeling
491 hominin behavior is that, even within the hominins, there is no single story,
492 and Sponheimer et al. (2013) note the significant variability in, for example,
493 isotope data once hominins regularly began consuming C₄ foods. Despite the
494 Issa chimpanzee reliance on *Ficus* throughout the year, they consume a wide
495 variety of plant foods, which are all C₃ (similar to the pattern at Fongoli
496 [Sponheimer et al., 2006]). Thus, either australopithecines had a dramatically
497 different diet than do extant open-habitat chimpanzees, or the (fossil) isotope
498 data mask variability in dietary composition. Given the importance of fruit to
499 extant chimpanzees, future studies should examine the isotope composition
500 of heavily consumed fruit species and incorporate those figures where

501 possible into models. For example, non-photosynthesizing plant parts are
502 slightly more ^{13}C enriched than leaves, but the leaves form the basis of our
503 understanding of $^{13}\text{C}/^{12}\text{C}$ distribution across landscapes. By doing this, it may
504 be possible to have a more nuanced understanding of dietary components for
505 extant and extinct primates, including the relative importance of C_4 plant
506 consumption in open habitats.

507 Our results here add to a growing body of data revealing how extant
508 chimpanzees live and use a potentially mosaic habitat, one analogous to
509 those reconstructed for early hominins. White and colleagues (2015) have
510 argued that fossils, phytoliths, and soil-based isotopic data all suggest the
511 presence of grass in *Ardipithecus* habitat, but the plentiful colobine and kudu
512 remains, combined with *Ardipithecus* morphology, suggest “woodland-to-
513 forest” adaptations for a species living in a mosaic landscape. However, the
514 temporal and phylogenetic distance between extant chimpanzees and extinct
515 hominins should not be underestimated. The limitations to chimpanzees as
516 analogous models for hominin evolution are well-established (Sayers and
517 Lovejoy, 2008). Added to this, recent work has emphasized how intraspecific
518 ecological differences can result in profound cultural (Kamilar and Marshack
519 2012) and life history variation among chimpanzee communities, which in turn
520 may skew our understanding of the transition to a ‘human-like’ pattern (Wood
521 et al. 2017). Significant variation has been demonstrated even between
522 communities within the same national park, for example, where chimpanzees
523 at Ngogo feed most frequently, and for longest, on *Ficus* species, versus at
524 Kanyawara, where *Ficus* represents a negligible part of the diet (Watts et al.
525 2012). One emergent challenge when using extant primates in models for

526 human evolution is therefore to understand and account for the effects of
527 variation and variability, and how it might alter our perceptions of the shift from
528 a more chimpanzee-like last common ancestor to a more human-like grade.
529 Another, recurring, challenge is for primatologists to identify much more
530 explicitly which hominin species is being modeled when data from extant
531 animals are being applied. The shared characteristics between the mosaic
532 habitat of Issa chimpanzees and reconstructions of *Ardipithecus* habitat
533 (White et al., 2009a), suggest that our data have more bearing for earlier,
534 rather than later (e.g., *Homo*) hominins. This idea is supported by analyses of
535 hominin dental anatomy that suggest a shift in early and especially later *Homo*
536 away from soft, fibrous foods towards tough plant products and likely animal
537 tissues (Ungar, 2012), extremely infrequent foods in Issa chimpanzee diet.
538 Overall, our data contribute to the debate on the behavioral ecology of the
539 earliest hominins (e.g., *Ardipithecus*) and simultaneously highlight major
540 differences between extant open-habitat chimpanzees and early *Homo*.

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542

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- 778

779 **Figure captions**

780

781 **FIGURE 1** – Map of western Tanzania, with the Issa study area (black box) as
782 well as Gombe and Mahale National Parks (green shaded) labeled. Credit: L.
783 Pinteá, The Jane Goodall Institute, USA.

784 **FIGURE 2** – Mean monthly rainfall (shaded) and minimum, mean, and
785 maximum temperatures in the study area.

786 **FIGURE 3** - Mean monthly Fruit Availability Index (FAI).

787 **FIGURE 4** – The density of the twelve most frequently observed plants in
788 faeces and the mean monthly proportion of faecal samples that contained
789 each plant. Plants are ordered from left to right in order of consumption rank.

790 **FIGURE 5** – Mean distance to the nearest neighbor of the same species, with
791 plants ordered from most commonly occurring (i.e., *Ficus*) to the least (i.e.,
792 *Canthium*).

793 **FIGURE 6** – Eleven of the 12 most frequently observed plant seeds observed
794 in faeces and the vegetation types in which they were categorized. The
795 individual plant consumption rank is in parentheses next to the name. We did
796 not encounter the fourth most consumed plant, *Grewia rugosifolia*, in botanical
797 plots.

798 **FIGURE 7** – Proportion of faeces with the seeds of the top 12 consumed
799 plants, separated between wet and dry seasons. Plants are ordered from left
800 to right in order of consumption rank

Table 1 Environmental metrics, isotope values, mammalian fauna diversity, and chimpanzee feeding data from medium and long-term study sites.^a

Dominant vegetation	Site (Country)	Annual rainfall	Dry season (months)	Annual temp	Temp Monthly LOW	Temp Monthly HIGH	Vegetation score	Isotope data (13C value)	Sympatric medium-large mammalian fauna species	Diet sample size	Plants consumed	Method
	Bossou (Guinea, Conakry)	- 1489	-	-	-	-	-	-	-	NA	200	D
Forested	Budongo (Uganda)	+ 196.6	3	20-38	-	-	0.0%	-	15	2641	58	D
	Bwindi (Uganda)	1100- 2400	-		-	-	0.0%	-	29	187	32	I/D
	Gishwati (Rwanda)	-	-	-	-	-	-	-	-	1381	23	I
	Gombe	1430-	6		19*	28*	34.0%	-	25	807	147	D

(Tanzania)	2542											
Goualougo												
(Rep. of												
Congo)	-	-	-	-	-	-	-	19	NA	116	D	
Ituri (Dem.												
Rep.												
Congo)	-	-	-	-	-	NA	-16%	-	-	-	-	
Kahuzi												
Biega												
(Dem.												
Rep.												
Congo)	-	-	-	-	-	-	-	-	7212	110	I/D	
Kibale												
(Uganda)	1536	5	19.2	12.3	26.6	0.0%	-14.5	37	1059	102	D	
Liberia	-	-	20.1	16	26.1	26.6%	-21.5	23	-	-	-	
Lope												
(Gabon)	-	6	25.2	26	28	NA	-	25	1854	132	I	
Mahale	1762	5-6	20.2	12	27	82.5%	-	30	-	198	D	

	(Tanzania)	+ - 125										
	Tai (Ivory Coast)	1803						-				
		+ - 66	3	26.2	21.7	30.1	0.0%	24.7/25%	25	-	-	D
<hr/>												
	Fongoli											
	(Senegal)	900	7	28.4	17.1	38.9	97.6%	-22.20%	22	1320	77	I/D
	Ishasha											
	(Dem. Congo)	-	-	-	-	-	-	-23.10%	-	-	-	-
Open-habitat		1094										
	Issa valley	(827-										
	(Tanzania)	1395)	6	23.9	11.7	38.7	93.0%	-22.12%	36	812	77	I
	Kasakati											
	(Tanzania)	962	6	22.1	16.5*	26*	90.1%	-	37*	7	78	I
	Mt. Assirik	954+-										
	(Senegal)	182	7	29	23.1	34.9	95.5%	-	27	60	43	I
	Nguye,	-	-	-	-	-	-	-	-	465	100	I

Bhukalai												
(Tanzania)												
Semliki	1389											
(Uganda)	+ - 41	5	24.06&	20^	34^	87.8%	-	26	72	36		

^a “Indirect” evidence includes faecal analysis and feeding remains, whilst “Direct” refers to observations. Table modified from Moore (1992) and Morgan and Sanz (2006).

1

2 Table 2 A list of all consumed plant species at Issa, recorded from our faecal analysis and direct observations and those of
 3 Hernandez-Aguilar (2006), the dominant vegetation type in which they were found, and when and to how often seeds were
 4 recorded in >50% of faecal samples in any one month for nine important species (in bold).

5

<i>Genus</i>	<i>Species</i>	Family	Identified from faeces (F), our direct observation (O), or recorded by Hernandez- Aguilar, 2006 (H- A)	Number of individuals recorded in plots	Calculated vegetation score	Predominant vegetation type	Months observed >50% of samples (<i>n</i> =41 months)	Months consumed	Season
<i>Aframomum</i>	<i>angustifolium</i>	Zingiberaceae	F	10	0.7	Both			
<i>Allophylus</i>	<i>congolanus</i>	Sapindaceae	F	20	0.95	Forest			
<i>Ampelocissus</i>	<i>spp.</i>	Vitaceae	F,O			Woodland			
<i>Anisophyllea</i>	<i>boehmii</i>	Anisophylleaceae	F,O	28	0.179	Woodland			
<i>Annona</i>	<i>senegalensis</i>	Annonaceae	F	6	0.167	Woodland			
<i>Antidesma</i>	<i>venosum</i>	Euphorbiaceae	F			Woodland			
<i>Aspila</i>	<i>pluriseta</i>	Asteraceae	F	1	0	Woodland			

<i>Bauhinia</i>	<i>thonningii</i>	Fabaceae	H-A						
	<i>boehmii</i>		O	40	0.325	Both			
	<i>bussei</i>		O	35	0.029	Woodland			
<i>Brachystegia</i>	<i>microphylla</i>	Fabaceae	O	56	0.321	Both			
	<i>spiciformis</i>		O	9	0.222	Woodland			
	sp.		O	161	0.124	Woodland			
<i>Canthium</i>	spp.		F	13	1	Forest			
<i>Carpolobia</i>	<i>goetzei</i>	Polygalaceae	F			Forest			
<i>Carissa</i>	<i>spinarium</i>	Apocynaceae	H-A						
<i>Cissus</i>	spp.	Vitaceae	F			Both			
Citropsis	articulata	Rutaceae	F,O	24	1	Forest	2	July-Aug	Dry
<i>Combretum</i>	sp.	Combretaceae	O	40	0.525	Both			
Cordia	sp.	Boraginaceae	F,O	13	1	Forest	2	May	Dry
<i>Costus</i>	<i>macranthus</i>	Zingiberaceae	F			Woodland			
<i>Dalbergia</i>	<i>Mochisia</i>	Fabaceae	H-A						
<i>Diplorhynchus</i>	<i>condylocarpon</i>	Apocynaceae	O			Woodland			
<i>Fadogia</i>	<i>triphylla</i>	Rubiaceae	F			Woodland			
	exasperata		O	12	1	Forest	14	Jan-Sept	Both
Ficus	ottoniifolia	Moraceae	O						
	variifolia		O						
<i>Flacourtia</i>	<i>indica</i>	Flacourtiaceae	F	4	1	Forest			
Garcinia	huillensis	Guttiferae	F,O	33	0.97	Forest	8	Jan, Oct-	Wet

							Dec		
Grewia	rugosifolia	Tiliaceae	F,O			Both	4	August	Dry
<i>Guizotia</i>	<i>scabra</i>	Asteraceae	F						
<i>Hexalobus</i>	<i>monopetalus</i>	Annonaceae	F	1	0	Woodland			
<i>Isoberlinia</i>	<i>tomentosa</i>	Fabaceae	O	16	0	Woodland			
<i>Julbernardia</i>	<i>unijugata</i>	Fabaceae	O	163	1	Forest			
<i>Julbernardia</i>	<i>globiflora</i>	Fabaceae	O	67	0.164	Woodland			
Keetia	gueinzii	Rubiaceae	F	5	1	Forest	2	Sept	Dry
<i>Landolphia</i>	<i>owariensis</i>	Apocynaceae	F,O	2	1	Forest			
<i>Lannea</i>	<i>spp.</i>	Anacardiaceae	F	38	0.868	Forest			
<i>Manilkara</i>	<i>mochisia</i>	Sapotaceae	H-A						
<i>Monanthotaxis</i>	<i>poggei</i>	Annonaceae	F	3	1	Forest			
<i>Opilia</i>	<i>amentacea</i>	Opiliaceae	F	1	1	Forest			
<i>Oxyanthus</i>	<i>speciosus</i>	Rubiaceae	F	2	1	Forest			
Parinari	curatellifolia	Chrysobalanaceae	F,O	18	0.167	Woodland	2	Aug	Dry
<i>Piliostigma</i>	<i>thonningii</i>	Fabaceae	F,O	2	1	Woodland*			
<i>Pleurostyli</i>	<i>africana</i>	Celastraceae	F			Woodland			
<i>Pseudolachnostyli</i>	<i>maprouneifolia</i>	Euphorbiaceae	H-A						
<i>s</i>									
<i>Psychotria</i>	<i>spp.</i>	Rubiaceae	F			Both			
<i>Pterocarpus</i>	<i>tinctorius</i>	Fabaceae	O	45	0.133	Woodland			
<i>Pyrostria</i>	<i>lobulata</i>	Rubiaceae	H-A						

<i>Rothmannia</i>	<i>fischeri</i>	Rubiaceae	F	21	0.952	Forest			
Saba	comorensis	Apocynaceae	F,O	3	1	Forest	6	Jan;	Both
								Sept,	
								Oct, Dec	
<i>Sclerocarya</i>	<i>birrea</i>	Anacardiaceae	F,O			Woodland			
	<i>cocculoides</i>		F,O	31	0.903	Forest			
<i>Strychnos</i>	<i>innocua</i>	Loganiaceae	F,O						
	<i>pungens</i>		F						
<i>Syzygium</i>	<i>guineense</i>	Myrtaceae	F	38	0.974	Forest			
<i>Tacca</i>	<i>leontopetaloides</i>	Taccaceae	F			Woodland			
<i>Thespesia</i>	<i>garckeana</i>	Malvaceae	F,O			Both			
<i>Tricalysia</i>	<i>coriacea</i>	Rubiaceae	F	3	1	Forest			
<i>Trichodesma</i>	<i>Zeylanicum</i>	Boraginaceae	H-A						
<i>Uapaca</i>	<i>kirkiana</i>	Phyllanthaceae	F,O	8	0.125	Woodland			
<i>Uapaca</i>	<i>nitida</i>	Phyllanthaceae	F						
<i>Uvaria</i>	<i>angolensis</i>	Annonaceae	F			Forest			
<i>Vangueria</i>	<i>Volkensii</i>	Rubiaceae	H-A						
<i>Vigna</i>	<i>monophylla</i>	Fabaceae	F			Both			
Vitex	doniana	Verbenaceae	F,O	38	0.421	Both	2	May	Dry
Vitex	mombassae	Verbenaceae	F,O						
<i>Ximenia</i>	<i>caffra</i>	Olacaceae	F,O			Both			
<i>Zanha</i>	<i>africana</i>	Sapindaceae	F,O	2	0	Woodland			

Ziziphus

abyssinica

Rhamnaceae

F

Woodland

6

7 * Indicates the species was found only once in botanical plots, and in forest, but is a well-established woodland species, and so has been labelled accordingly

1 TABLE 3 Density, basal area (per hectare [ha]), mean distance to their nearest neighbor of the same species, % of faecal samples
 2 containing seeds of the top-25 consumed plant species and their corresponding frequency rank.^a

3

Plants	Life form ^b	Density	Mean distance to nearest neighbor	Basal area (B _k)	% faeces with seeds	Rank
		(stems/ha)	(m)	(cm/ha)		
<i>Aframomum angustifolium</i>	Herb	1.62			0.86	25
<i>Anisophyllea boehmii</i>	Tree	4.55		1767.37	3.69	16
<i>Annona senegalensis</i>	Tree	0.97		129.68	1.97	21
<i>Canthium burttii</i>	Shrub	2.60	10.1	141.21	3.94	14
<i>Cissus quarrei</i>	Herb	0			2.95	19
<i>Citropsis articulata</i>	Tree	3.90	6.7	242.93	6.15	10
<i>Cordia</i> (all species)	Tree	2.11	13.2	2352.89	6.27	9
<i>Ficus</i> (all species)	Tree	2.11	7.7	2199.73	33.91	1
<i>Flacourtia indica</i>	Tree	0.65		381.49	5.41	11

<i>Garcinia huillensis</i>	Tree	5.36	26.7	848.40	30.14	2
<i>Grewia rugosifolia</i>	Liana	0	3.3		13.78	4
<i>Keetia guenzii</i>	Tree	0.81	6.5	141.15	9.10	7
<i>Lannea schimperii</i>	Tree	6.98	12.5	3298.92	4.55	12
<i>Opilia celtidifolia</i>	Liana	0.16			3.57	17
<i>Parinari curatellifolia</i>	Tree	2.92	23.7	1160.81	12.18	5
<i>Psychotria</i> (all species)	Tree	1.30		98.76	4.06	13
<i>Saba comorensis</i>	Liana	1.12	8.1		21.89	3
<i>Strychnos</i> (all species)	Tree	5.03	13.0	902.40	9.84	6
<i>Thespesia garckena</i>	Tree	0.16		8.78	1.23	24
<i>Uapaca kirkiana</i>	Tree	0		0	1.84	22
<i>Uapaca nitida</i>	Tree	1.30		278.71	1.60	23
<i>Uvaria angolensis</i>	Shrub	0			3.69	15
<i>Vitex</i> (all species)	Tree	6.11	30.3	2709.0	7.63	8
<i>Ximenia americana</i>	Shrub	0.32		50.77	1.97	20

<i>Zanha africana</i>	Tree	0.32	106.64	3.20	18
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4 ^a Plants with missing values were not observed in botanical plots. The top twelve most consumed plants are in bold.

5 ^b From <http://specimens.kew.org/herbarium/>

6

1

2 Table 4 The top 12 feeding plants and their respective ranking for chimpanzees in western Tanzania: Issa, Gombe National Park

3 (Kasekela) and Mahale Mountains National Park (M-group).

4

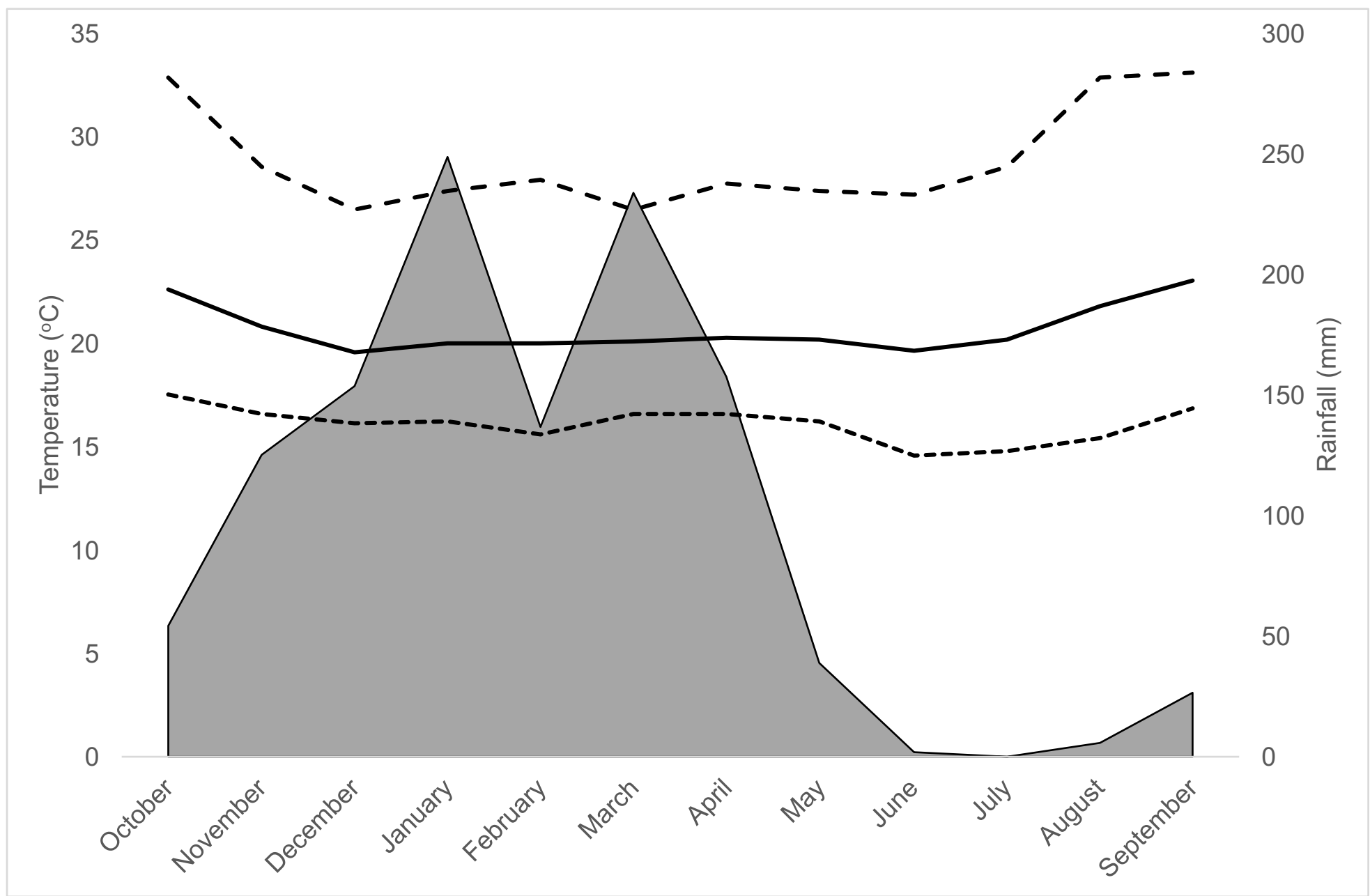
<i>Genus</i>	<i>Species</i>	<i>Family</i>	<i>Site rank</i>		
			<i>Issa</i>	<i>Gombe</i>	<i>Mahale</i>
<i>Aframomum</i>	sp.	Zingiberaceae			7
<i>Baphia</i>	<i>cappariifolia</i>	Fabaceae		11	4
<i>Brachystegia</i>	<i>bussei</i>	Fabaceae			12
<i>Citropsis</i>	<i>articulata</i>	Rutaceae	11		
<i>Cordia</i>	sp.	Boraginaceae	5		
<i>Diplorhynchus</i>	<i>condylocarpon</i>	Apocynaceae			9
<i>Elaeis</i>	<i>guineensis</i>	Rubiaceae		5	
<i>Ficus</i>	sp.	Moraceae	1	6	1

<i>Flacourtia</i>	<i>indica</i>	Flacourtiaceae	6		
<i>Garcinia</i>	sp.	Guttiferae	2	12	5
<i>Glycine</i>	sp.	Fabaceae			11
<i>Grewia</i>	<i>rugosifolia</i>	Tiliaceae	4		
<i>Keetia</i>	<i>gueinzii</i>	Rubiaceae	9		
<i>Landolphia</i>	<i>lucida</i>	Apocynaceae		3	
<i>Lannea</i>	sp.	Anacardiaceae	12		
<i>Monanthes</i>	<i>poggei</i>	Annonaceae		4	
<i>Parinari</i>	<i>curatellifolia</i>	Chrysobalanaceae	7	1	
<i>Pseudospondias</i>	<i>microcarpa</i>	Anacardiaceae		8	8
<i>Pterocarpus</i>	sp.	Fabaceae		9	2
<i>Pyrenanthes</i>	<i>angloensis</i>	Rubiaceae			6
<i>Saba</i>	<i>comorensis</i>	Apocynaceae	3	2	3
<i>Sterculia</i>	<i>Tragacantha</i>	Malvaceae			10
<i>Vitex</i>	sp.	Verbenaceae	8	10	

Figure
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Figure



Figure

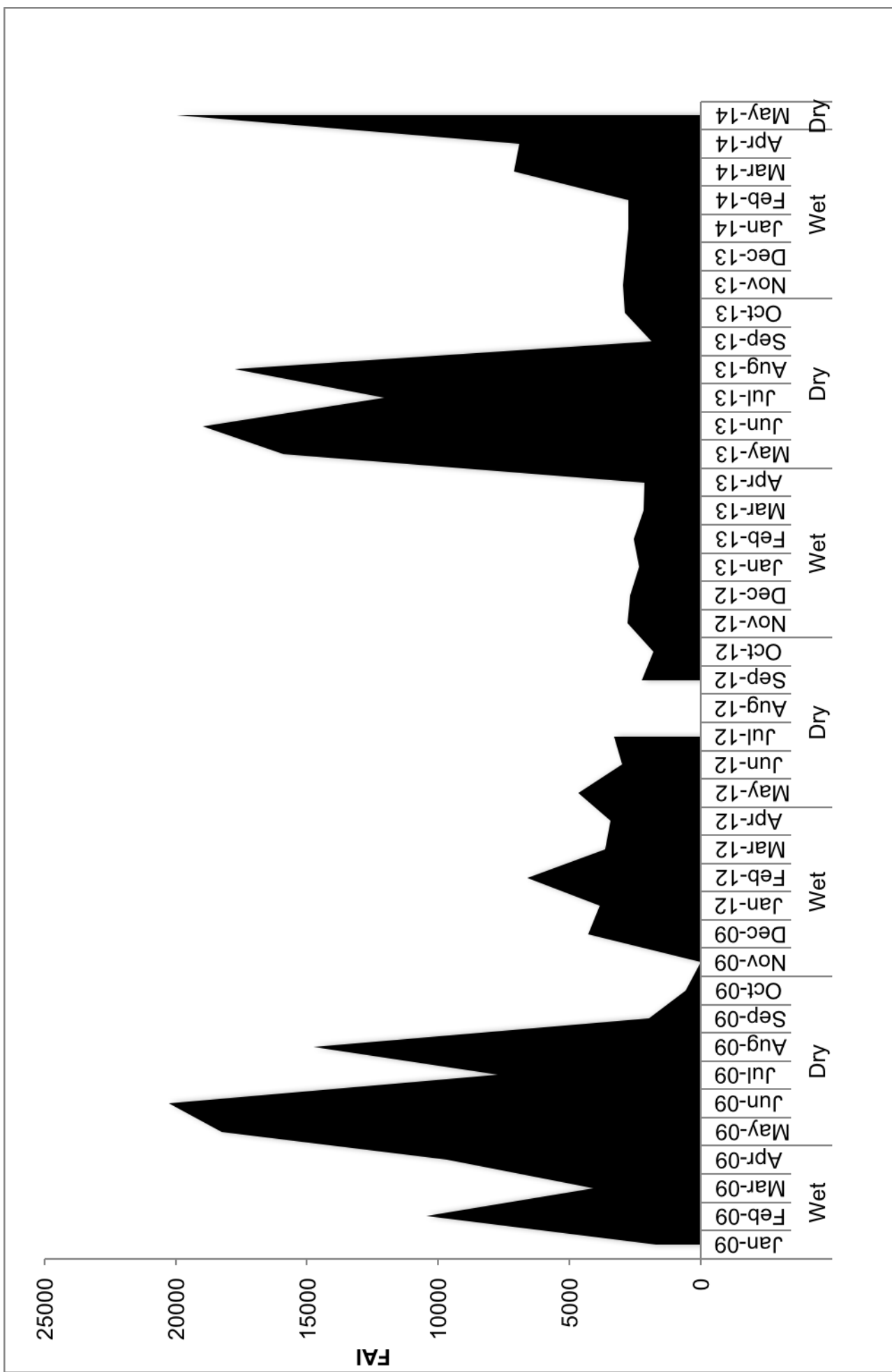
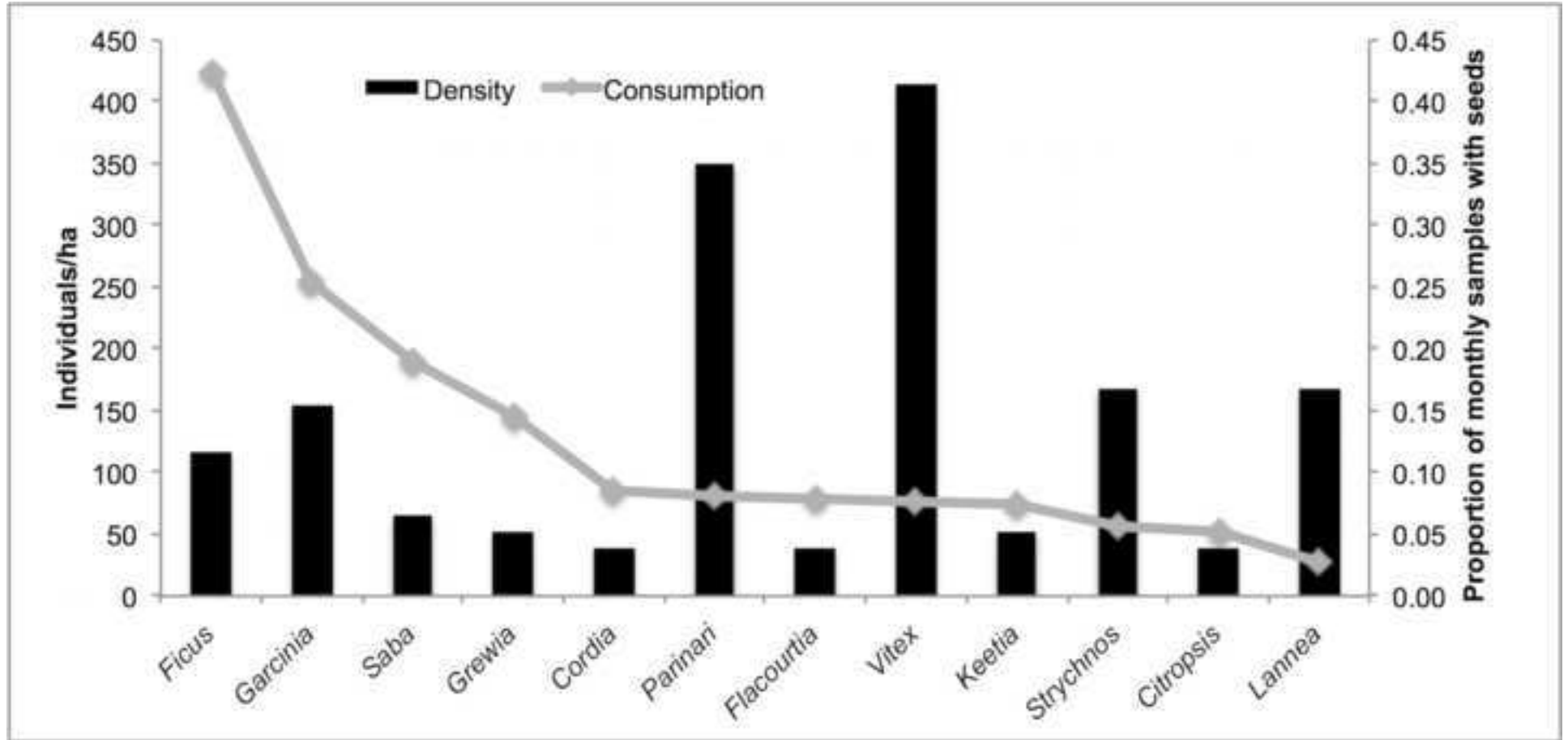
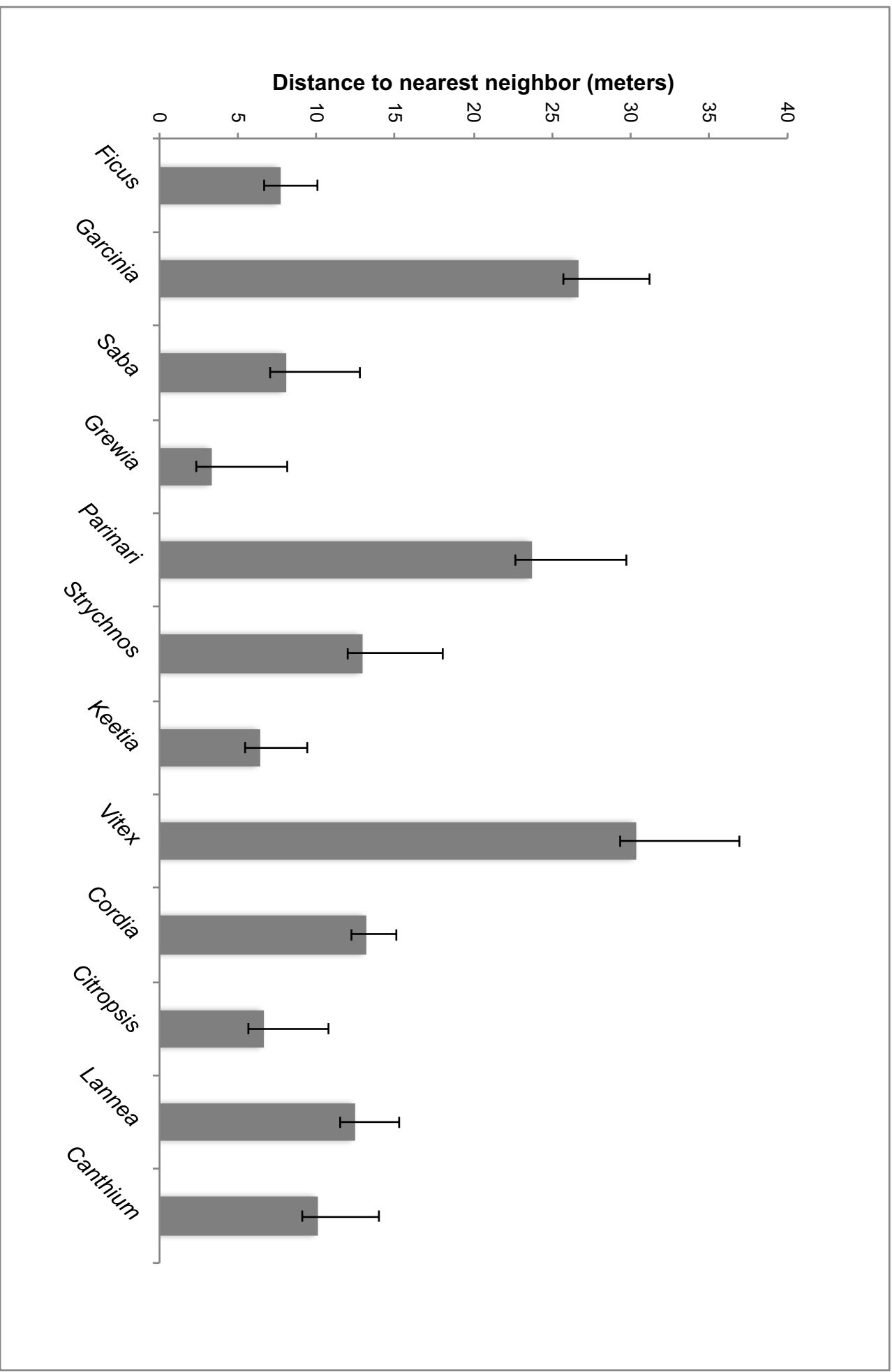


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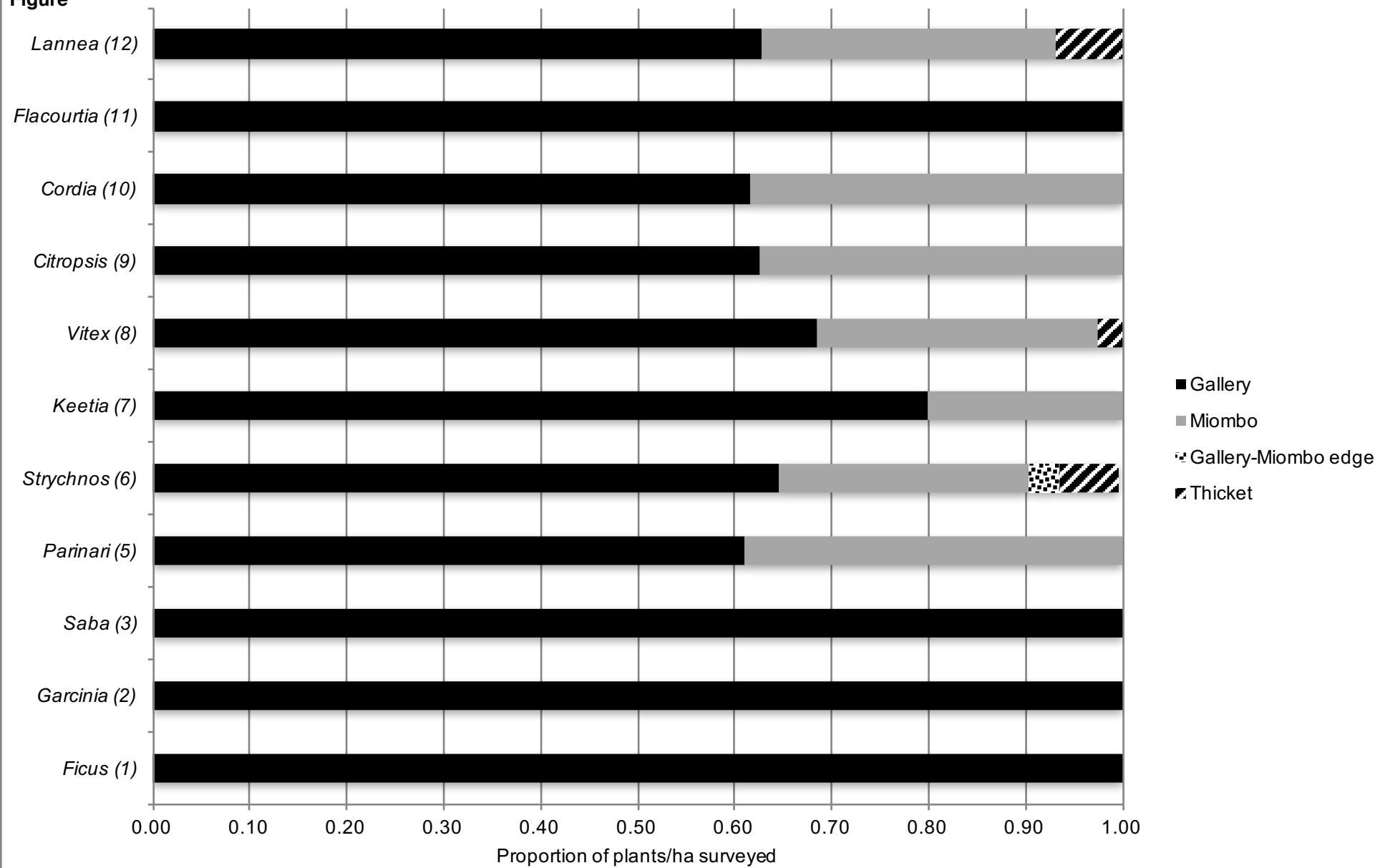
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