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

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Abstract

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

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

Introduction

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

Moreover, it has long been recognized that early hominin evolution occurred at a time of increasing seasonality, and Foley (1993) suggested that responses to this seasonality may have catalysed the evolution of later hominins, especially *Homo.* However, our ability to consider the full implications of seasonal resource variation on hominins is hampered by the relative lack of knowledge about seasonal resource distribution and use in analogous habitats today, especially those of savanna or open-habitat chimpanzees[1], which are more strongly seasonal than forested sites (Moore, 1992). Chimpanzee responses to seasonal shortages of preferred foods can result in a reliance on poorer quality, tougher foods than those consumed during fruit-rich periods (e.g., tree bark [Pruetz, 2006]), or else can have consequences for ranging behavior, whereby parties travel greater distances to forage on preferred fruits (Sugiyama and Koman, 1992).

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

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[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.

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

Chimpanzees are highly frugivorous omnivores (Newton-Fisher, 1999; Basabose, 2002; Watts et al., 2012). Previous research of open-habitat chimpanzees has consistently revealed narrower diets (fewer total species consumed) than those of forest-dwelling populations and, except for Fongoli (Pruetz, 2006), these studies have relied on indirect methods of diet composition (Table 1). We add to this literature by providing data from the Issa valley, western Tanzania, a particularly valuable sample given that most work on open-habitat chimpanzees stems from western Africa, whereas the hominin fossil record is dominated by eastern African deposits. Given the importance of studying diet in extant apes that live in environments similar to those reconstructed for early hominins, we aimed to establish dietary breadth and seasonal consumption, as well as assess the relationship between the distribution of those foods across vegetation types within the habitat. We predicted that (1) Issa chimpanzees would resemble other open-habitat communities and consume fewer total plant species than forest-dwelling chimpanzees. Additionally, given the increased species richness of gallery forests compared to woodlands (Piel and Stewart, unpublished data), we expected that (2) chimpanzees would rely heavily on gallery forests for foods throughout the year. Finally, if open-habitat chimpanzees exhibit ‘savanna’ adaptations (sensu Moore, 1992) then we predicted that (3) preferred foods at Issa will differ from those of nearby forest-dwelling chimpanzees at Gombe and Mahale. Finally, we discuss what our results might reveal about the relationship between environment, diet, and early hominin exploitation of a mosaic landscape.

TABLE 1 ABOUT HERE

Materials and methods

Study site and subjects

We collected data between January 2009 and March 2014 in the Issa valley, western Tanzania (Figure 1). The Issa valley lies >90 km from the nearest national park boundary (Mahale Mountains, along Lake Tanganyika) and ~60 km from the nearest village (Uvinza). The landscape consists of broad valleys separated by steep mountains and flat plateaus ranging from 900 to1800 m above sea level. Vegetation is dominated by miombo woodland– *Brachystegia* and *Julbernardia* (Fabaceae) – although it also includes swamp and grassland (together, we classified all of these habitats as ‘open’ vegetation types), as well as thin strips of riverine and thicket forests (‘closed’ vegetation types, hereafter called just ‘forest’). Forest comprises ~7% of the total study area. There are two distinct seasons: wet (Nov – April) and dry (May – October), with dry months experiencing <60 mm of rainfall (Whitmore, 1975). Rainfall averaged 1220mm per annum (range: 930–1490mm from 2009–2014) and temperatures ranged from 11^{o} C to 38^{o} C (Figure 2).

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

FIGURE 1 & 2 ABOUT HERE

Dietary composition

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

We followed recommendations of macro-specific analytical techniques of primate faecal analysis (McGrew et al., 2009; Phillips and McGrew, 2013) and estimated the proportions of matrix and undigested contents for each sample. We categorized *Ficus* seeds and insect parts into many, some, few, or none, and counted all other seeds as well as other animal matter, whole leaves, and parasitic worms. We described, photographed, and assigned a seed type number to all unidentified seeds, and recorded data on datasheets or Google Nexus 7 tablets using Open Data Kit software (ODK). We then stored a library of seeds for identification in transparent container boxes. We collected data on consumed foods through direct observation of foraging events by following chimpanzee parties. We recorded data on species and plant part consumed.

Phenology

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

Environmental monitoring

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

Botanical surveys and vegetation classification

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

The plot data provided density estimates for most feeding species. However, because many feeding species occurred at extremely low densities, we still did not obtain 10 specimens for each species, so we employed two additional methods that targeted the top 15 plants most frequently identified in faecal samples, to increase our sample size. First, we overlaid a 50 x 50 m grid over a map of the study area, and randomly selected grid cells (Method B). At the center point of each cell, we established a 10x10 m box, within which we identified all trees that met the above criteria, including being a feeding species. We used the point center quadrat method (Walker, 1970; Mitchell, 2010) to measure the distance of each member of the top 15 feeding species to the nearest member of the same species within 100 m in four quadrats (if we observed no species member within 100 m, no value was recorded). The results of these measurements provided additional density estimates as well as data on feeding plant distribution. Finally, we restricted the grid coverage to forests (Method C), and repeated the above steps, eventually adding an additional 111 plots using these last two methods, bringing the total plots to 293 and the total surveyed area to 8.39 hectares.

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

Data analyses

To calculate fruit availability, we followed Chancellor et al. (2012). We used the density and basal area [($^1/_2$(DBH)^2 x Pi] of each tree species and then calculated a monthly fruit availability index (F_m) using the following formula:

$$F_m = \mathbf{\Sigma\, P_{km} \times B_k}$$

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

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

We measured diet breadth in two ways: the mean number of plant species per faecal sample, and the total number of different plant species recorded in all samples collected over the course of a month, controlling for total samples collected (following Pruetz, 2006). For the initial plot surveys (Method A), we calculated plant density by dividing the total number of specimens of a given species by the total number of hectares surveyed in each vegetation type. For the non-transect plots (Methods B and C), we followed Mitchell (2010) to calculate an absolute and relative density of each key feeding species. To calculate the absolute density of a particular species (individuals/hectare), we divided the number of plot quarters with that species by the number of total quarters surveyed, then multiplied this value by the absolute density of all the feeding species.

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

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

Results

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

TABLE 2 ABOUT HERE

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

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

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

FIGURES 3 and 4 ABOUT HERE

Food species distribution and density

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

FIGURES 5 and 6 ABOUT HERE

Twelve plant genera appeared at least once a month on average in the chimpanzees' diet over the course of the study. *Ficus* spp. was the most frequently consumed food, with chimpanzees consuming them in 37 of 41 months (90.2%) and was the most common seed identified across seasons (present in 83.9% of all samples); *Garcinia* (51.6%)*, Saba* (38.2%)*,* and *Grewia* (27.8%) were the next most frequently found, followed by *Cordia* (16.8%), *Flacourtia* (16.6%), *Parinari* (15.6%), *Vitex* (15.3%)*, Keetia* (14.5%)*,* and *Strychnos* (10.9%), *Citropsis* (10.0%), and *Lannea* (5.4%)*.* Whilst chimpanzees consumed some plants frequently in both wet and dry seasons (e.g., *Ficus, Garcinia, Saba*), others were more important during only one season (e.g., *Grewia*, *Parinari* – dry; *Flacourtia* – wet – Figure 7).

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

FIGURE 7 ABOUT HERE

TABLE 4 ABOUT HERE

Discussion

In the current study, we macroscopically analysed 810 chimpanzee faecal samples from the Issa community that lives in a mosaic woodland environment of western Tanzania. The limitations of this method are well established (McGrew et al., 2009; Phillips and McGrew, 2013), with vegetative foods (pith, leaf, stem) and flowers typically not identifiable and thus not accurately represented in comprehensive food lists (Tutin and Fernandez, 1993). Consequently, our results likely underestimate plant diversity. Nonetheless we interpret them here in the context of other studies of savanna chimpanzees where the same methods were used to infer diet. We also compare our results with published results from forest-dwelling chimpanzees in nearby Gombe and Mahale National Parks to draw comparisons on plant species consumption and preference across different habitats.

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

When we compared the most important plants at Issa, Gombe, and Mahale, we found that three plants overlap at all three sites: *Ficus, Garcinia, and Saba* (Nishida and Uehara, 1983; Foerster et al., 2016). These species are the three most important plants for the Issa chimpanzees and two of the top three at Mahale. In fact, almost a third (11/36) of the top consumed species at the three sites overlap. With Issa chimpanzees favoring largely the same plants as nearby forest-dwelling communities, despite dramatic differences in the physical environment, e.g., plant diversity and density, seasonality, rainfall (Collins and McGrew, 1988), it is likely that population density, ranging, and grouping patterns (rather than diet) are the most significant and different in open-habitat chimpanzees compared to their forest-dwelling cousins. While population density is known to differ in significant ways (density at Issa = 0.25 individual/km^2, compared to e.g., Gombe, ~3 individual/km^2), data are not yet available from Issa on ranging and grouping behaviour.

Absence of vertebrate remains in faeces

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

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

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

Vegetation type and spatiotemporal patterns in plant consumption

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

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

Relatedly, we observed chimpanzees consume bark 27 times over the study period, and most observations were made from the late wet season, the period of lowest (overall) fruit availability. Multiple studies have reported bark consumption across the Order (e.g., *P. troglodytes* - Nishida, 1976; *Cercopithecus l'hoesti* - Kaplin et al., 2000; *Lemur catta* - Yamashita, 2002; *Alouatta belzebul* - Pinto and Setz, 2004) and wood is known to provide a critical sodium source not just for primates (Rothman et al., 2006), but also herbivorous mammals (Iwata et al., 2015). In Mahale, chimpanzees exhibited two annual peaks of bark consumption, both during fruit-lean times (Nishida, 1976). Moreover, whilst they were observed to consume the bark of 21 different tree species, one third of observations were of *Brachystegia bussei* bark consumption – similar to at Issa (8/27 = 29.6%). Thus, as at Mahale, chimpanzees at Issa may be compensating for low nutrient consumption during fruit-poor periods by stripping and eating woodland bark. Bark was also likely to have been an important and seasonal component of *Australopithecus sediba* diet as well (Henry et al., 2012), but the extent of its importance throughout hominin evolution remains unclear. Our results support the idea of an ape reliance on bark at certain times of the year, at Issa probably to compensate for a scarcity of higher-quality foods.

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

In her analysis of how hominins would have responded to harsher, drier habitats that offered widely distributed food sources during the Plio-Pleistocene, Copeland (2009) suggested that such conditions may promote consumption of underground storage organs (USOs), expansion of home ranges, and restriction to thin, forest strips. Previous work has inferred chimpanzee consumption of USOs at Issa (Hernandez-Aguilar et al., 2007), and preliminary evidence suggests that day and annual ranging distances are also atypically high for the species (Piel and Stewart, unpublished data). In contrast to Copeland's prediction of forests as a limiting factor, though, chimpanzees at Issa may seasonally expand their foraging niche. Analysis of nesting patterns at Issa suggested that chimpanzees ranged more widely in the dry season (Hernandez-Aguilar, 2009). Here is where habitat reconstructions, and definitions, are important (White et al., 2009a; Domínguez-Rodrigo, 2014). If the savannas that surrounded early paleo-forests comprised treeless 'savannas', then hominins may very well have been confined to forest strips that afforded protection from terrestrial carnivores. However, if something more akin to woodlands surrounded the forests, hominins may have exhibited a chimpanzee model of exploitation of this open vegetation that would have offered, like at Issa, important foods such as *Parinari* and *Keetia*.

Morphological, microwear and isotope data are the most common ways of reconstructing hominin diet. Yet a fundamental problem with modeling hominin behavior is that, even within the hominins, there is no single story, and Sponheimer et al. (2013) note the significant variability in, for example, isotope data once hominins regularly began consuming C_4 foods. Despite the Issa chimpanzee reliance on *Ficus* throughout the year, they consume a wide variety of plant foods, which are all C_3 (similar to the pattern at Fongoli [Sponheimer et al., 2006]). Thus, either australopithecines had a dramatically different diet than do extant open-habitat chimpanzees, or the (fossil) isotope data mask variability in dietary composition. Given the importance of fruit to extant chimpanzees, future studies should examine the isotope composition of heavily consumed fruit species and incorporate those figures where possible into models. For example, non-photosynthesizing plant parts are slightly more ^{13}C enriched than leaves, but the leaves form the basis of our understanding of $^{13}C/^{12}C$ distribution across landscapes. By doing this, it may be possible to have a more nuanced understanding of dietary components for extant and extinct primates, including the relative importance of C_4 plant consumption in open habitats.

Our results here add to a growing body of data revealing how extant chimpanzees live and use a potentially mosaic habitat, one analogous to those reconstructed for early hominins. White and colleagues (2015) have argued that fossils, phytoliths, and soil-based isotopic data all suggest the presence of grass in *Ardipithecus* habitat, but the plentiful colobine and kudu remains, combined with *Ardipithecus* morphology, suggest “woodland-to-forest” adaptations for a species living in a mosaic landscape. However, the temporal and phylogenetic distance between extant chimpanzees and extinct hominins should not be underestimated. The limitations to chimpanzees as analogous models for hominin evolution are well-established (Sayers and Lovejoy, 2008). Added to this, recent work has emphasized how intraspecific ecological differences can result in profound cultural (Kamilar and Marshack 2012) and life history variation among chimpanzee communities, which in turn may skew our understanding of the transition to a ‘human-like’ pattern (Wood et al. 2017). Significant variation has been demonstrated even between communities within the same national park, for example, where chimpanzees at Ngogo feed most frequently, and for longest, on *Ficus* species, versus at Kanyawara, where Ficus reoresents a negligible part of the diet (Watts et al. 2012). One emergent challenge when using extant primates in models for human evolution is therefore to understand and account for the effects of variation and variability, and how it might alter our perceptions of the shift from a more chimpanzee-like last common ancestor to a more human-like grade. Another, recurring, challenge is for primatologists to identify much more explicitly which hominin species is being modeled when data from extant animals are being applied. The shared characteristics between the mosaic habitat of Issa chimpanzees and reconstructions of *Ardipithecus* habitat (White et al., 2009a), suggest that our data have more bearing for earlier, rather than later (e.g., *Homo*) hominins. This idea is supported by analyses of hominin dental anatomy that suggest a shift in early and especially later *Homo* away from soft, fibrous foods towards tough plant products and likely animal tissues (Ungar, 2012), extremely infrequent foods in Issa chimpanzee diet. Overall, our data contribute to the debate on the behavioral ecology of the earliest hominins (e.g., *Ardipithecus*) and simultaneously highlight major differences between extant open-habitat chimpanzees and early *Homo*.

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Figure captions

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

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

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

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

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

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

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

Table

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
Forested	Bossou (Guinea, Conakry)	-	-	-	-	-	-	-	-	NA	200	D
	Budongo (Uganda)	1489 +- 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
Open-habitat	Fongoli (Senegal)	900	7	28.4	17.1	38.9	97.6%	-22.20%	22	1320	77	I/D
	Ishasha (Dem. Rep. Congo)	-	-	-	-	-	-	-23.10%	-	-	-	-
	Issa valley (Tanzania)	1094 (827-1395)	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 (Senegal)	954+-182	7	29	23.1	34.9	95.5%	-	27	60	43	I
	Nguye,	-	-	-	-	-	-	-	-	465	100	I

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

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[a] "Indirect" evidence includes faec**al** analysis and feeding remains, whilst "Direct" refers to observations. Table modified from Moore (1992) and Morgan and Sanz (2006).

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

Genus	***Species***	**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 (*n*=41 months)**	**Months consumed**	**Season**
Aframomum	*angustifolium*	Zingiberaceae	F	10	0.7	Both			
Allophylus	*congolanus*	Sapindaceae	F	20	0.95	Forest			
Ampelocissus	*spp.*	Vitaceae	F,O			Woodland			
Anisophyllea	*boehmii*	Anisophylleaceae	F,O	28	0.179	Woodland			
Annona	*senegalensis*	Annonaceae	F	6	0.167	Woodland			
Antidesma	*venosum*	Euphorbiaceae	F			Woodland			
Aspila	*pluriseta*	Asteraceae	F	1	0	Woodland			

Bauhinia	*thonningii*	Fabaceae	H-A						
	boehmii		O	40	0.325	Both			
	bussei		O	35	0.029	Woodland			
Brachystegia	*microphylla*	Fabaceae	O	56	0.321	Both			
	spiciformis		O	9	0.222	Woodland			
	sp.		O	161	0.124	Woodland			
Canthium	spp.		F	13	1	Forest			
Carpolobia	*goetzei*	Polygalaceae	F			Forest			
Carissa	*spinarium*	Apocynaceae	H-A						
Cissus	*spp.*	Vitaceae	F			Both			
Citropsis	***articulata***	**Rutaceae**	**F,O**	**24**	**1**	**Forest**	**2**	**July-Aug**	**Dry**
Combretum	sp.	Combretaceae	O	40	0.525	Both			
Cordia	**sp.**	**Boraginaceae**	**F,O**	**13**	**1**	**Forest**	**2**	**May**	**Dry**
Costus	*macranthus*	Zingiberaceae	F			Woodland			
Dalbergia	*Mochisia*	Fabaceae	H-A						
Diplorhynchus	*condylocarpon*	Apocynaceae	O			Woodland			
Fadogia	*triphylla*	Rubiaceae	F			Woodland			
	exasperata		**O**	**12**	**1**	**Forest**	**14**	**Jan-Sept**	**Both**
Ficus	***ottoniifolia***	**Moraceae**	**O**						
	variifolia		**O**						
Flacourtia	*indica*	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**
Guizotia	*scabra*	Asteraceae	F						
Hexalobus	*monopetalus*	Annonaceae	F	1	0	Woodland			
Isoberlinia	*tomentosa*	Fabaceae	O	16	0	Woodland			
Julbernardia	*unijugata*	Fabaceae	O	163	1	Forest			
Julbernardia	*globiflora*	Fabaceae	O	67	0.164	Woodland			
Keetia	***gueinzii***	**Rubiaceae**	**F**	**5**	**1**	**Forest**	**2**	**Sept**	**Dry**
Landolphia	*owariensis*	Apocynaceae	F,O	2	1	Forest			
Lannea	*spp.*	Anacardiaceae	F	38	0.868	Forest			
Manilkara	*mochisia*	Sabotaceae	H-A						
Monanthotaxis	*poggei*	Annonaceae	F	3	1	Forest			
Opilia	*amentacea*	Opiliaceae	F	1	1	Forest			
Oxyanthus	*speciosus*	Rubiaceae	F	2	1	Forest			
Parinari	***curatellifolia***	**Chrysobalanaceae**	**F,O**	**18**	**0.167**	**Woodland**	**2**	**Aug**	**Dry**
Piliostigma	*thonningii*	Fabaceae	F,O	2	1	Woodland*			
Pleurostylia	*africana*	Celastraceae	F			Woodland			
Pseudolachnostylis	*maprouneifolia*	Euphorbiaceae	H-A						
Psychotria	*spp.*	Rubiaceae	F			Both			
Pterocarpus	*tinctorius*	Fabaceae	O	45	0.133	Woodland			
Pyrostria	*lobulata*	Rubiaceae	H-A						

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

Ziziphus	*abyssinica*	Rhamnaceae	F	Woodland

* 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

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

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

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

Zanha africana	Tree	0.32			106.64	3.20	18

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[a] Plants with missing values were not observed in botanical plots. The top twelve most consumed plants are in bold.

[b] From http://specimens.kew.org/herbarium/

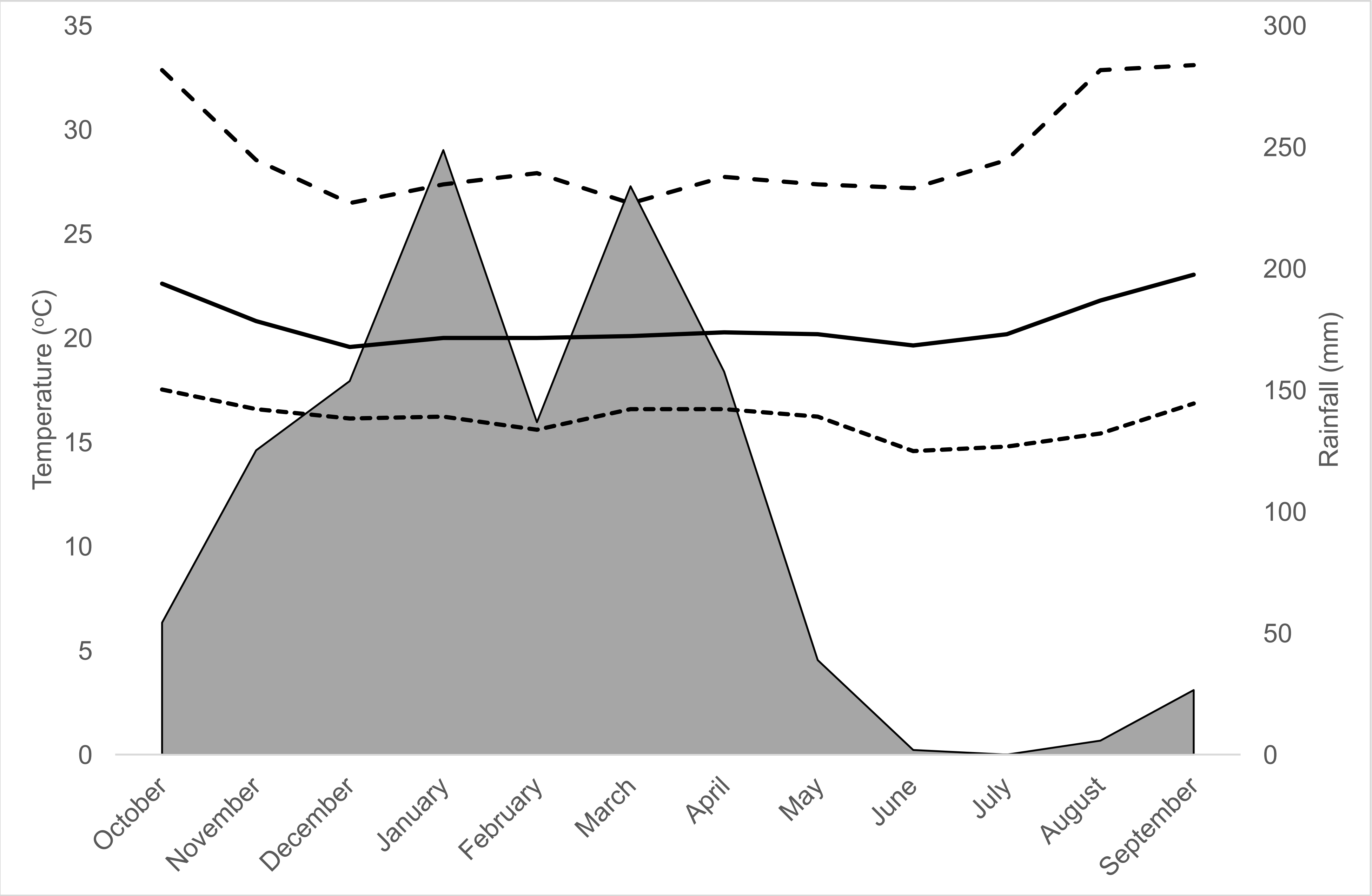
Table 4 The top 12 feeding plants and their respective ranking for chimpanzees in western Tanzania: Issa, Gombe National Park (Kasekela) and Mahale Mountains National Park (M-group).

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

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

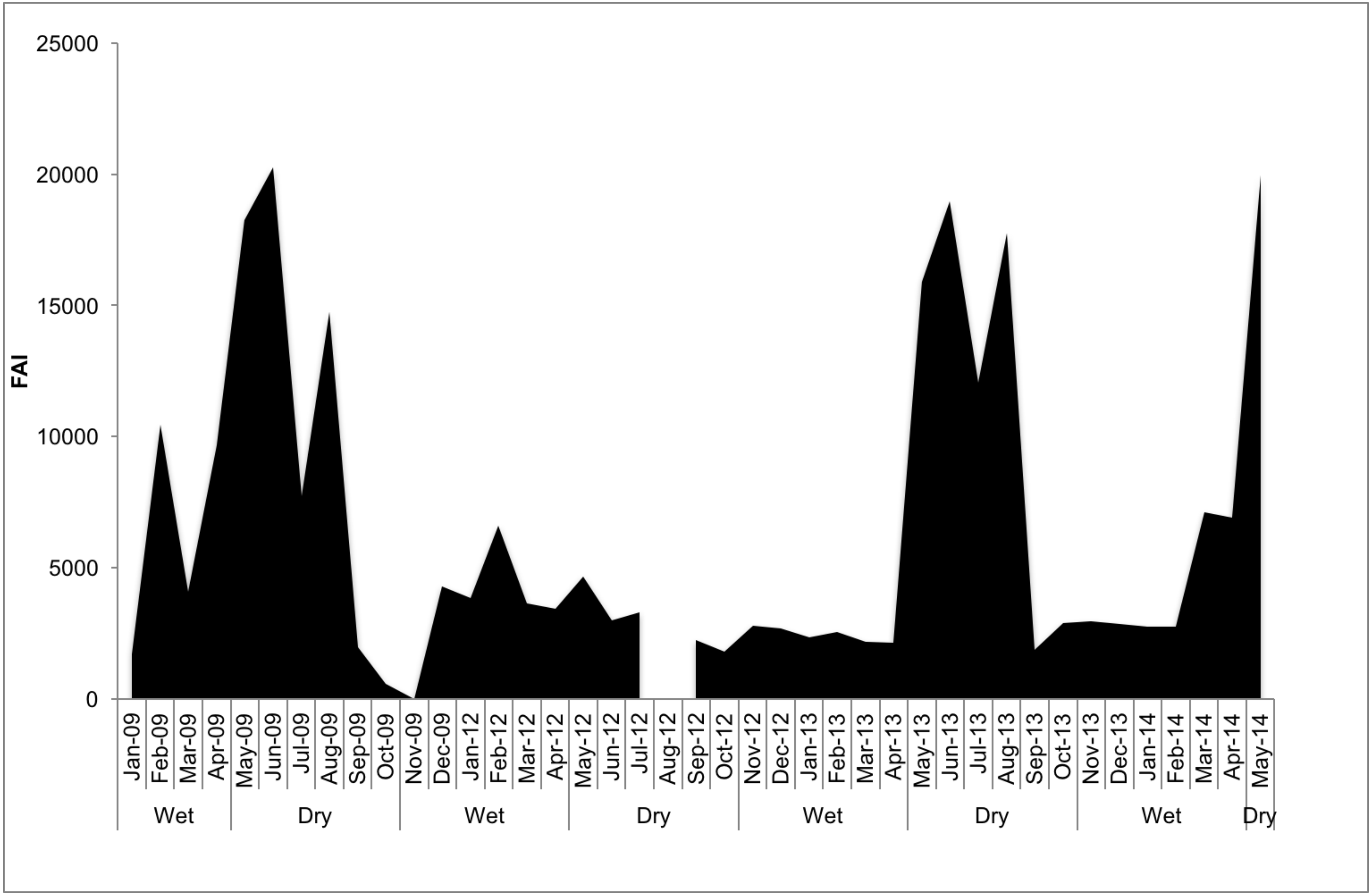

GOMBE–MASITO–UGALLA AND GREATER MAHALE ECOSYSTEM
29.6
29.8
30
30.2
30.4
30.6
30.8
31
31.2
31.4
-4.6
-4.8
-5
-5.2
-5.4
-5.6
-5.8
-6
-6.2
-6.4
-6.6
Tanzania
Gombe National Park
Kigoma
Lugufu
Ilunde
Uvinza
Uvinza
Malagarasi
Lake Tanganyika
Issa Valley
Tongwe East
Mpanda Line
Mpar
Lane11
Mishamo Refugee Settlement
Kungwe Bay
Mahale Mountains National Park
Mpanda
Mpanda
Msaginia
Katavi National Park
● Villages
■ Urban
Major roads
Forest Reserve
State Forest Reserve
Game Reserve
National Park
0
10
20
40 Km

Figure



35
30
25
20
15
10
5
0
Temperature (ºC)
300
250
200
150
100
50
0
Rainfall (mm)
October
November
December
January
February
March
April
May
June
July
August
September

Figure


25000
20000
15000
10000
5000
0
FAI
Jan-09
Feb-09
Mar-09
Apr-09
May-09
Jun-09
Jul-09
Aug-09
Sep-09
Oct-09
Nov-09
Dec-09
Jan-12
Feb-12
Mar-12
Apr-12
May-12
Jun-12
Jul-12
Aug-12
Sep-12
Oct-12
Nov-12
Dec-12
Jan-13
Feb-13
Mar-13
Apr-13
May-13
Jun-13
Jul-13
Aug-13
Sep-13
Oct-13
Nov-13
Dec-13
Jan-14
Feb-14
Mar-14
Apr-14
May-14
Wet
Dry
Wet
Dry
Wet
Dry
Wet
Dry

Figure
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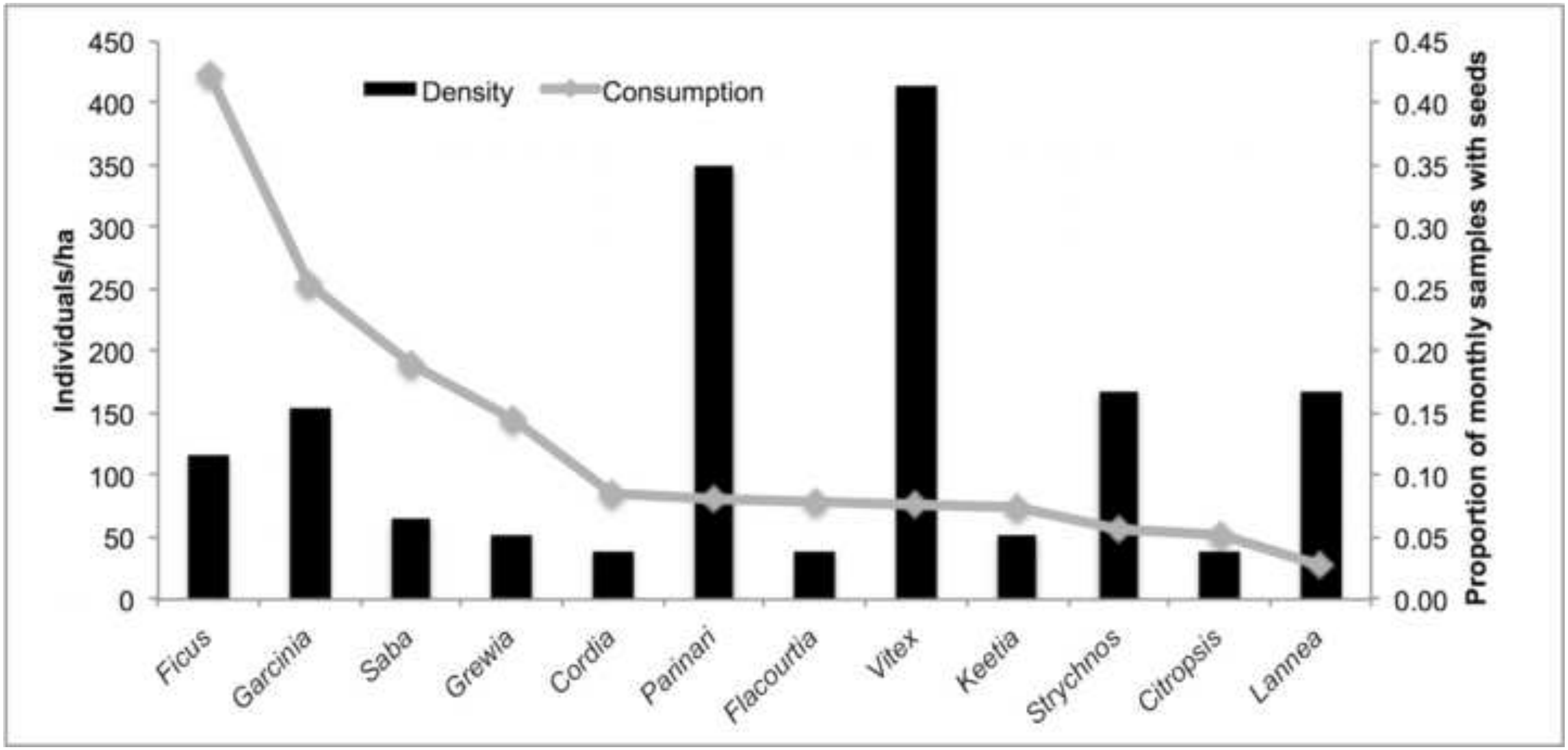
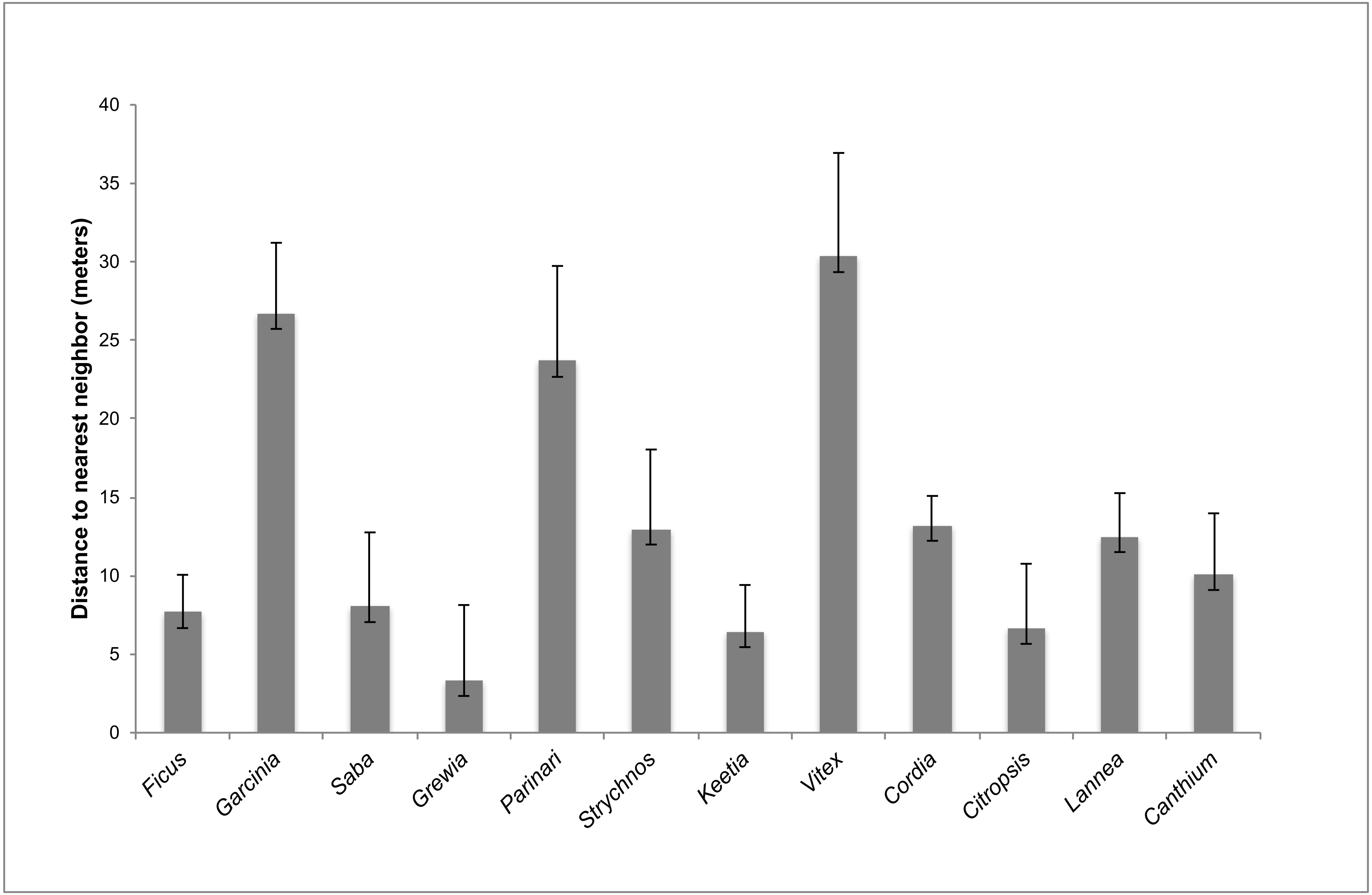
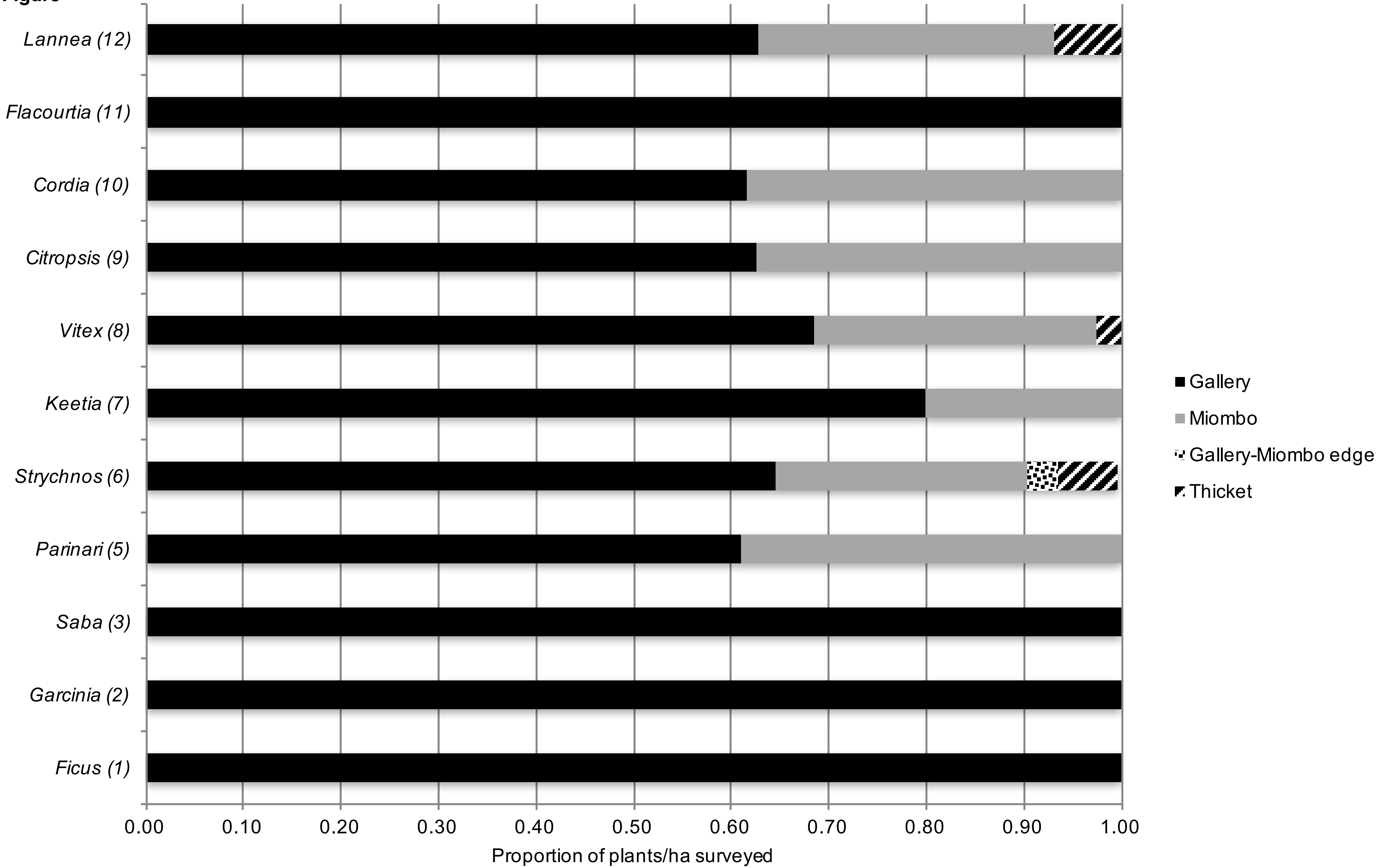


Figure

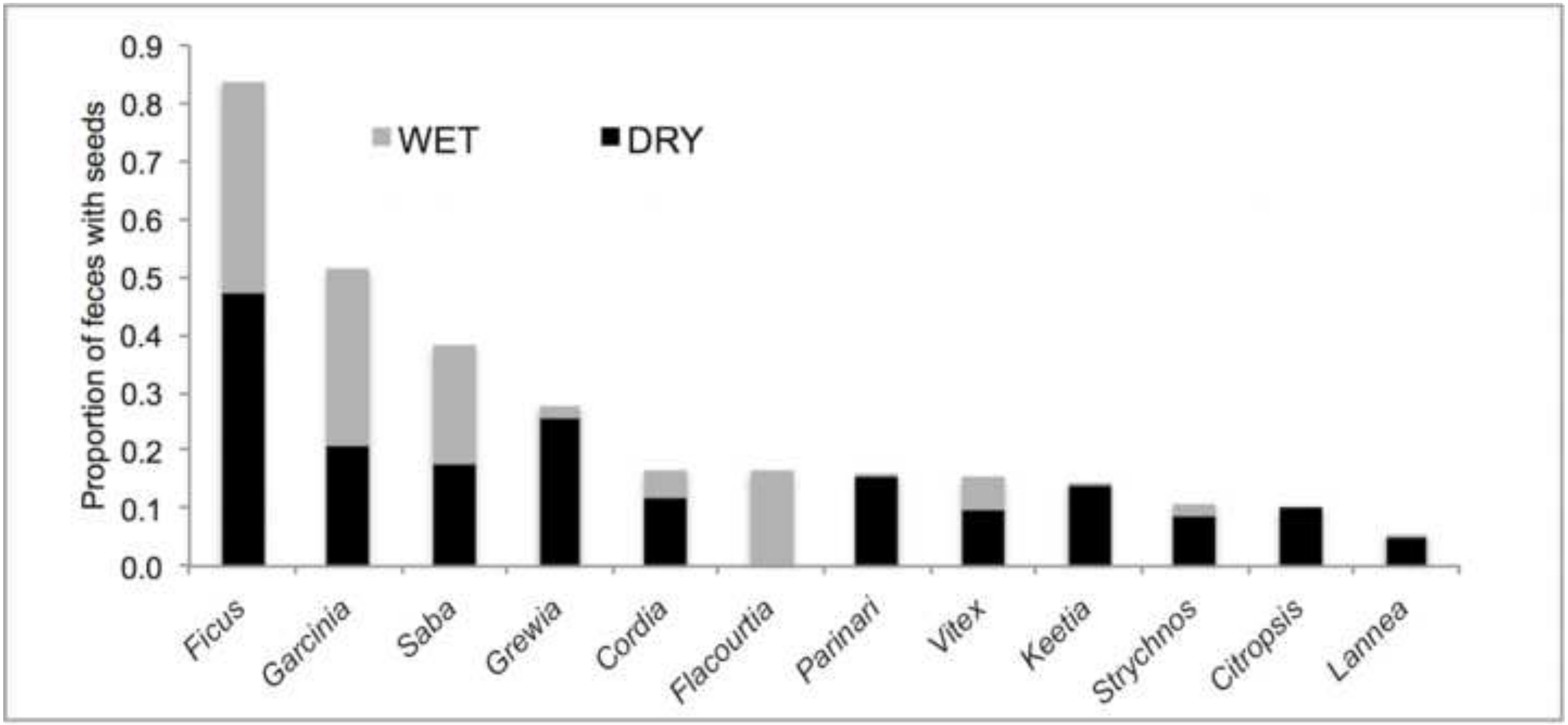

Distance to nearest neighbor (meters)
0
5
10
15
20
25
30
35
40
Ficus
Garcinia
Saba
Grewia
Parinari
Strychnos
Keetia
Vitex
Cordia
Citropsis
Lannea
Canthium

Figure



Lannea (12)
Flacourtia (11)
Cordia (10)
Citropsis (9)
Vitex (8)
Keetia (7)
Strychnos (6)
Parinari (5)
Saba (3)
Garcinia (2)
Ficus (1)
0.00
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
1.00
Proportion of plants/ha surveyed
Gallery
Miombo
Gallery-Miombo edge
Thicket

Figure


Proportion of feces with seeds
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
WET
DRY
Ficus
Garcinia
Saba
Grewia
Cordia
Flacourtia
Parinari
Vitex
Keetia
Strychnos
Citropsis
Lannea