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Anthropogenic disturbance and chimpanzee (*Pan troglodytes*) habitat use in the Masito-Ugalla Ecosystem, Tanzania

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The habitat quality of chimpanzee (*Pan troglodytes*), including the availability of plant food and nesting species, is important to ensure the long-term survival of this endangered species. Botanical composition of vegetation is spatially variable and depends on soil characteristics, weather, topography, and numerous other biotic and abiotic factors. There are few data regarding the availability of chimpanzee plant food and nesting species in the Masito-Ugalla Ecosystem (MUE), a vast area that lies outside national park boundaries in Tanzania, and how the availability of these resources varies with human disturbance. We hypothesized that chimpanzee plant food species richness, diversity, and abundance decline with increasing human disturbance. Further, we predicted that chimpanzee abundance and habitat use is influenced negatively by human disturbance. Published literature from Issa Valley, Gombe, and Mahale Mountains National Parks, in Tanzania, was used to document plant species consumed by chimpanzees, and quantify their richness, diversity, and abundance, along 32 transects totaling 63.8 km in length across four sites of varying human disturbance in MUE. We documented 102 chimpanzee plant food species and found a significant differences in their species richness ($H = 55.09$, $P < 0.001$) and diversity ($H = 36.81$, $P < 0.001$) across disturbance levels, with the moderately disturbed site exhibiting the highest species richness and diversity. Chimpanzees built nests in 17 different tree species. The abundance of nesting tree species did not vary across survey sites ($H = 0.279$, $P > 0.964$). The least disturbed site exhibited the highest encounter rate of chimpanzee nests/km, with rates declining toward the highly disturbed sites. Our results show that severe anthropogenic disturbance in MUE is associated with the loss of chimpanzee plant food species and negatively influences chimpanzee habitat use, a relationship that threatens the future of all chimpanzee populations outside national parks.

Key words: anthropogenic disturbance, habitat use, nests, species abundance, species diversity, species richness

Habitat loss and overexploitation of natural resources are major challenges for biodiversity conservation (Rands et al. 2010). These processes are driven mainly by human poverty and increasing human population size, which, when combined, result in overdependence on nature, thus threatening wildlife (Hackel 1999). Increasing human population sizes and encroachment on wildlife habitat are the core incitement of human–wildlife conflicts, habitat fragmentation and loss, and associated biodiversity loss in most areas (Brooks et al. 2002; Fahrig 2003; Hanski 2011). A number of primate species, including chimpanzees (*Pan troglodytes*), inhabit human-impacted landscapes (Hockings et al. 2012, 2015; Bryson-Morrison et al. 2016, 2017), following the continuous contraction of their natural ranges as a result of human encroachment. To understand how chimpanzees will persist in human encroached landscapes, we need to assess the relationship between chimpanzee habitat degradation and the availability of resources used by this species.

The availability and quantity of food resources in chimpanzee habitat is one of the primary factors that drives chimpanzee abundance and distribution (Stevenson 2001; Foerster et al. 2018). Hence, as the density of food resources declines, chimpanzee range tends to increase to compensate for reduced food availability (Baldwin et al. 1982). Alternatively, chimpanzees might instead consume more nutrient-poor foods (Doran 1997; Basabose 2005), which may reduce their fitness and survival. Chimpanzees are omnivorous and feed on fruits, leaves and other plant parts, vertebrates, and invertebrates, as well as on inorganic substances (i.e., termite mound soil and rocks—Goodall 1968; Nishida and Uehara 1983; Newton-Fisher 1999; Nishida 2012; Watts et al. 2012a, 2012b; Itoh and Nakamura 2015; Piel et al. 2017). Notwithstanding, chimpanzees predominantly depend on plant matter, especially ripe fruits, which constitute the majority of their diet (Goodall 1968; Nishida 1968; Nishida and Uehara 1983; Nakamura et al. 2013).

In addition to food resources, the availability of nesting sites is another key factor influencing chimpanzee presence, abundance, and distribution (Carvalho et al. 2015). Nesting is a daily behavior in all great ape species (Goodall 1968; Fruth et al. 2018). All weaned great apes, including chimpanzees, build night nests for sleeping, occasionally build daytime nests for resting, and rarely re-use nests (Goodall 1962; Rothman et al. 2006). Although any woody species is a potential nesting site, chimpanzees nest nonrandomly wherever the behavior has been studied (Basabose and Yamagiwa 2002; Hernandez-Aguilar 2009; Stewart et al. 2011; Last and Muh 2013). Chimpanzee nests, therefore, are a good proxy for chimpanzee presence (Hernandez-Aguilar et al. 2013) and reveal chimpanzee habitat use as well as population density and trends (Kühl et al. 2017). Indeed, most approaches for estimating wild chimpanzee populations rely on nest counts (Plumptre and Reynolds 1997; Bonnin et al. 2018). In some areas, chimpanzees occur at low densities and thus nest counts are impracticable over a large area. Nevertheless, recent work using drones (Bonnin et al. 2018) demonstrates the effectiveness of nest counts for population size estimates in wild chimpanzees.

Chimpanzee populations are declining rapidly (Junker et al. 2012), threatened by habitat loss, poaching, disease, and the pet trade (Leendertz et al. 2006; Hockings et al. 2015; Kühl et al. 2017, 2019). In Tanzania, eastern chimpanzees (*P. t. schweinfurthii*) are distributed across the western region (TAWIRI 2018), with an estimated total population of less than 2,500 individuals (Moyer et al. 2006; Piel and Stewart 2014). More than 75% of the current population lives outside national parks (Piel et al. 2015a). Chimpanzee numbers outside national parks have significantly declined in the 2000's (Yoshikawa et al. 2008; Ogawa et al. 2013) and a significant subpopulation is found in the Masito-Ugalla Ecosystem (MUE; Fig. 1; Moore and Vigilant 2013; Piel et al. 2015a). Surveys across MUE in 2012 revealed a density of 0.1 individuals/km^2 (Piel et al. 2015a), and a total population of about 288 individuals, or > 10% of Tanzania's chimpanzees.

Studies on the relationship between disturbance and primate populations have been conducted on a number of species. Chapman and Chapman (2000) found that anthropogenic disturbance affected the abundance and group size of red colobus and red-tailed guenons in Kibale National Park, Uganda. Cavada et al. (2019) described the relationship between anthropogenic disturbance and the density of arboreal primate species in the Udzungwa Mountains of Tanzania and showed that disturbance negatively affected primate density. Herrera et al. (2011), examining the effects of disturbance on lemurs at Ranomafana National Park, Madagascar, found that anthropogenic disturbance did not always have deleterious effects on primates. The variation in lemur abundance was related to diet (i.e., feeding guilds) rather than disturbance, with frugivorous species more prone to population declines than folivores or insectivores. Moreover, anthropogenic disturbance not only affects primate densities but also their behaviors (Kühl et al. 2019). In most environments where nonhuman primates coexist with people, primates exhibit behavioral flexibility, including dietary adjustments, to survive (McCarthy et al. 2017; McLennan et al. 2017).

There are a number of studies that described chimpanzee diet across western Tanzania (Table 1). However, the only two studies that described chimpanzee diet in MUE were undertaken in the Issa Valley, and at Nguye and Bhukalai sites. Based on chimpanzee diet studies across western Tanzania, Yoshikawa and Ogawa (2015) found a proportion (range: 20–39%) of the identified chimpanzee plant food species to overlap between Nguye, Bhukalai, Gombe, and Mahale Mountains. For example, of 100 plant food species identified in Nguye and Bhukalai, 39% of the plant food species also were consumed by the Mahale chimpanzees, and 33% by the Gombe chimpanzees. Out of 198 plant food species identified in Mahale Mountains National Park, Nguye and Bhukalai chimpanzees consumed 20%, and of 147 plant food species identified in Gombe National Park, Nguye and Bhukalai chimpanzees consumed 22%.

While Balcomb et al. (2000) found a positive relationship between the density of fleshy fruit trees and chimpanzee density measured across six sites in Kibale Forest, Uganda, a similar study on plant food availability and habitat disturbance has yet to be carried out at MUE, where anthropogenic disturbance is high (Plumptre et al. 2010; Wilfred and MacColl 2014). Increasing threats from agricultural expansion, settlements, cattle herding, annual fires, logging, and poaching have been reported in the region and threaten chimpanzee habitat. Given the rate of disturbance across MUE in western Tanzania and the direct result disturbance has on chimpanzees and population-specific cultures (Kühl et al. 2019), a clearer understanding of the relationship between habitat disturbance, resource availability, and chimpanzee abundance is required.

In this study, we compared the availability of chimpanzee plant food and nesting species across four areas within MUE to investigate whether human disturbance levels are associated with chimpanzee plant food species, nesting tree species, and chimpanzee abundance. Following Morgan et al.'s (2018) model of assessing the impact of human activities on great apes and their habitat, we quantified the extent of human disturbance in MUE and related the levels of human disturbance to chimpanzee abundance and resources. We hypothesized first, that chimpanzee plant food species richness, diversity, and abundance, decline

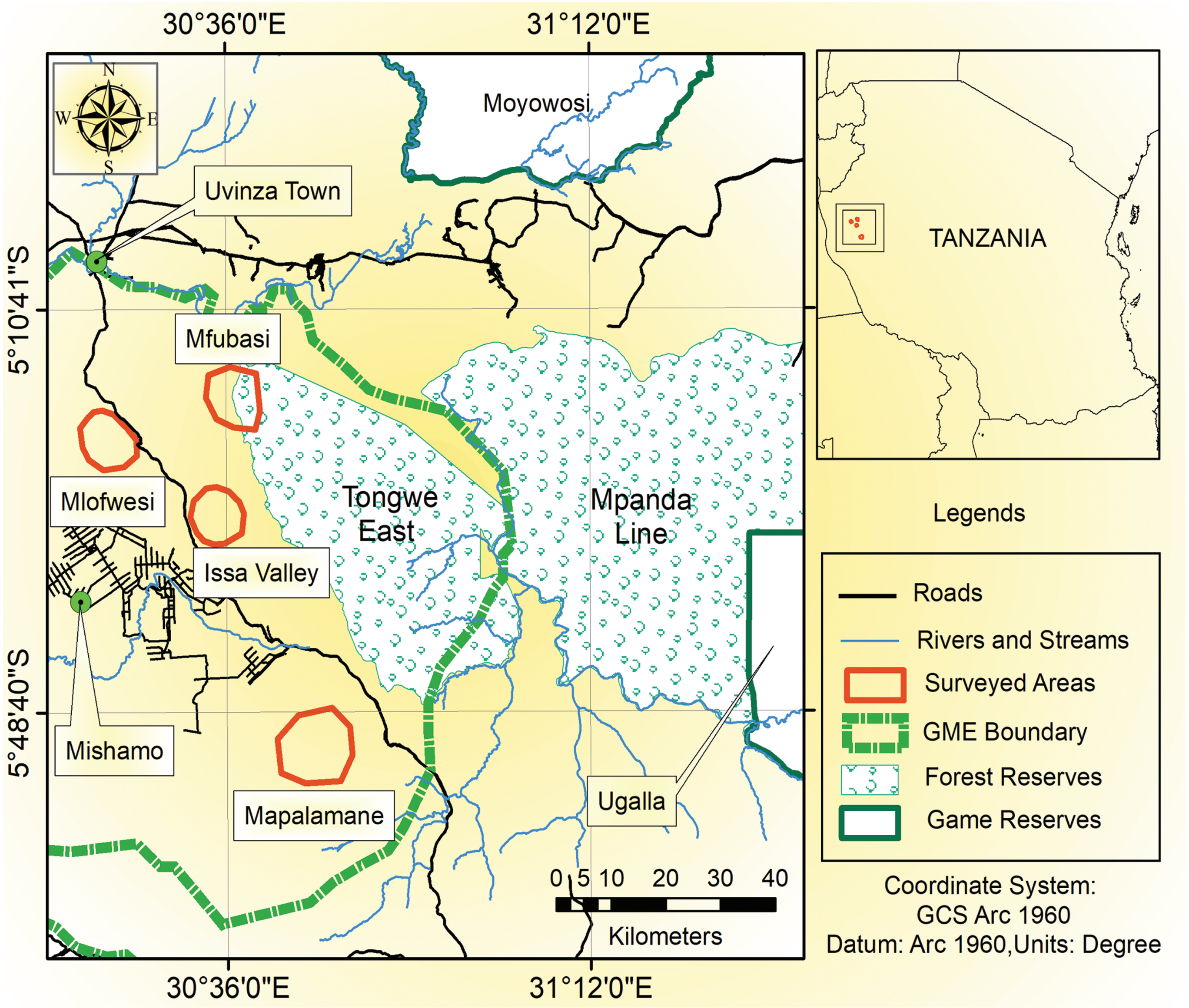

Fig. 1.—Map of the four survey sites located in the Masito-Ugalla Ecosystem, western Tanzania.

Table 1.—Chimpanzee diet data summarized from western Tanzania communities. Indirect and direct refer to observation methods (indirect methods used fecal analyses and food remains; direct methods used observations through focal follows).

Site	Vegetation	Method	# Fecal samples	# Species consumed	Reference
Issa Valley	Open habitat	Indirect	810	69	Piel et al. (2017)
Nguye and Bhukalai	Open habitat	Indirect	465	100	Yoshikawa and Ogawa (2015)
Mahale	Forested	Direct	NA	198	Nishida and Uehara (1983)
Gombe	Forested	Direct	NA	147	Wrangham (1975)

with increasing human disturbance. Second, that chimpanzee abundance—as inferred from nest counts—would be negatively associated with human disturbance: we predicted that nest counts would be high in areas of low or no human disturbance.

Materials and Methods

This study was carried out in the MUE at four sites (Issa Valley, Mfubasi, Mlofwesi, and Mapalamane; Fig. 1) during the wet season from February to May, 2019. MUE is a region located in western Tanzania and forms a part of the Greater Mahale Ecosystem (GME), covering an area of 5,756 km^2 (Piel et al. 2015a). The region is a biodiversity-rich habitat (Moyer et al. 2006) and is protected partly as the Tongwe Forest Reserves (TFRs). Major threats to the region include agriculture, which represents the main economic income source for people (Mwageni et al. 2015), illegal logging, livestock grazing, bush fires, and poaching (Plumptre et al. 2010; Pintea 2012; Wilfred and MacColl 2014). Wilfred and MacColl (2014) reported on the pattern of illegal natural resource exploitation in

Ugalla, western Tanzania, and found poaching, logging, and bushmeat hunting, to be the dominant illegal activities.

Elevation across MUE ranges from 900 to 1,800 masl, with average annual temperatures from 11°C to 35°C (Piel et al. 2015a) and average annual rainfall between 900 and 1,400 mm, mainly falling between November and April (Piel et al. 2015b). The ecosystem is characterized by five different vegetation types: (1) miombo woodland, dominated by *Brachystegia* spp. and *Julbernardia* spp., interspersed with (2) seasonally inundated grasslands, (3) rocky outcrops, as well as (4) evergreen riparian and (5) thicket riverine forests (Piel et al. 2017). Open woodland (i.e., more open miombo woodland) is reported as wooded grassland in this study. Issa Valley, Mfubasi, Mlofwesi, and Mapalamane vary in protection status. Issa Valley and Mfubasi are located in Tongwe East Forest Reserve, Mlofwesi is located in Tongwe West Forest Reserve, and Mapalamane is located in Mishamo Village Forest, a lower level protection status from the TFRs, which are District forest reserves. Despite the difference in protection status, all the sites experience anthropogenic activities. Issa Valley has an established long-term research presence, which has been shown to deter some human activities (Piel et al. 2015b). In contrast, Mfubasi, Mlofwesi, and Mapalamane, all have experienced extensive disturbance over the last 10 years (Piel and Stewart 2014).

To survey chimpanzee plant food species, we laid out eight 2-km-long transects radially around a center point established in each study site. We walked approximately 1 km away from the center point before starting transects, covering different vegetation types. In some cases, we walked for more than 1 km until a particular vegetation type was reached. That is, the start point of transects depended on the availability of a particular vegetation type and the direction followed the extension of such vegetation type. Because riparian forests rarely are sited along cardinal directions, we followed these forests regardless of the cardinal direction. Along each transect, we established 10 vegetation plots of 25 m × 25 m each, with 200 m between plots, summing up to 199,375 m^2 (0.199 km^2) of the total sampled vegetation plot area across survey sites. We did not conduct vegetation plots in cultivated areas. Since most of MUE is miombo woodland with few strips of riparian forest and very few patches of wooded grassland, we used stratified sampling to have sufficient representation of chimpanzee plant food species. The vegetation plots covered wooded grassland, riparian forest, and miombo woodland. A total of 6 (2%) vegetation plots were sampled in wooded grassland, 137 (43%) in riparian forest, and 176 (55%) in miombo woodland. Published literature (Goodall 1968; Wrangham 1975; Nishida and Uehara 1983; Nakamura et al. 2015; Piel et al. 2017) was used to document chimpanzee plant food species (Supplementary Data SD1). In each plot, we documented and counted all known chimpanzee plant food species and determined their growth form and diameter at breast height (DBH).

We inferred chimpanzee abundance from chimpanzee nest presence (Plumptre and Reynolds 1997; Kouakou et al. 2009; Bonnin et al. 2018) and identified nesting tree species. Chimpanzee nests visible along and from transects were counted and recorded, and we established a 10-m radius around any nest to document nearby nests. Chimpanzee nest number served as a proxy for chimpanzee abundance as our sample size did not warrant further analyses using DISTANCE to calculate population density (Buckland et al. 2001). Using nest counts as a proxy measure for population density has known limitations. For instance, nest age and nest production rate (both of which influence density calculations) can vary by region and season. However, previous work in Tai Forest, Cote d'Ivoire, that tested the reliability of nest counts with known population sizes demonstrated nest counts as an effective method to document wild chimpanzee population sizes and confirmed that the method produced reasonable density estimates (Kouakou et al. 2009).

To quantify anthropogenic disturbance, we documented human activities that interrupted the natural state of chimpanzee habitat. We recorded different human activities based on visible signs along transects and in vegetation plots (Table 2). All signs, e.g., cattle bomas, houses, farms, etc., within 50 m of transects and plots were documented. We used the presence of houses and people to count households. Agricultural activity was determined based on the presence of cultivated fields and areas cleared for cultivation, and the number of different farms based on farm demarcations; visible cattle herds and bomas represented livestock grazing. When more than one sign of different human activities was observed in a single location, e.g., logging on farms, beekeeping on farms, etc., we recorded only the major activities that were presumed to cause the greatest impact on chimpanzee habitat, regardless of the others. In general, we recorded type, frequency, and location, of each event of illegal human activity and assumed that each recorded activity had a different impact on chimpanzee habitat. Based on the presumed impact, we assigned impact scores following Morgan et al. (2018) between 1 (lowest impact) and 5

Table 2.—Human activities recorded across Masito-Ugalla Ecosystem (MUE) with respective weight of destructive impacts (impact score) on chimpanzee habitat. Impact scores of a particular human activity were based on the extent of disturbance the activity is likely to pose on chimpanzee habitat.

Human activities	Signs for identification	Impact score
Agriculture	Cultivated fields	5
	Cleared areas for farming	5
Beekeeping	Commercial beehives	1
	Illegal beehives	2
	Debarking tree for beehives	2
Harvesting medicinal plants	Peeling of tree barks	1
	Digging for tree roots	1
Livestock grazing	Cattle herds	3
	Cattle bomas	4
Logging	Logging sites	4
	Cut logs	2
	Logging stumps	2
Poaching	Snares	1
	Encountered poachers	2
Settlement	Households	4
Small fires	Burnt vegetation	3

(highest impact) to all types of human activities observed across MUE (Table 2).

We computed the frequency of anthropogenic evidence by using encounter rates of the signs per kilometer walked. Following Morgan et al. (2018), we multiplied the weighted impact scores by the frequency of encounters of each sign and then summed an overall measure of severity of disturbance per site. Based on the disturbance measure, we placed survey sites into four categories, i.e., least disturbed, mildly disturbed, moderately disturbed, and highly disturbed sites (Table 3).

We calculated chimpanzee plant food species richness by counting the total number of plant food species in each vegetation plot and then determined Shannon–Wiener diversity indices. We defined chimpanzee plant food abundance as the total number of individual plant species with DBH > 10 cm per site. Based on the hypothesis that chimpanzee plant food species richness, diversity, and abundance, decline with increasing human disturbance, we averaged the values and compared the intersite values across disturbance categories.

To determine if the data were normally distributed, we carried out a Shapiro–Wilk test followed by a Levene's test for homogeneity of variances (Shapiro and Wilk 1965). We used a Kruskal–Wallis test with Dunn's post hoc test to compare the variation of chimpanzee plant food species richness, diversity, and abundance, among and within sites as the data sets were non-normal. We also compared chimpanzee plant food species richness, diversity, and abundance across vegetation types. We converted chimpanzee nest number into nests/km walked in each survey site and related these proportions to disturbance categories. We carried out all statistical analyses in Paleontological Statistics software (PAST Version 3.20—Hammer et al. 2001) and for all statistical tests, statistical significance was set at $P = 0.05$.

Table 3.—Encounter rates of human activities per km walked in each survey site and the severity of disturbance calculated by multiplying the weighted impact scores and the frequency of encounters of each human activity and then summed as an overall measure of severity of human disturbance. The values indicate the rate of encounter of a particular human activity per km walked in different survey sites. Last row on the bottom show severity of disturbance (=Severity).

Severity	Issa Valley	Mfubasi	Mlofwesi	Mapalamane
Cultivated fields	0.00	0.00	0.00	2.00
Cleared areas for farming	0.00	0.00	0.00	0.31
Commercial beehives	0.00	0.00	2.06	0.00
Illegal beehives	0.06	0.81	3.56	0.44
Debarking tree for beehives	0.00	0.06	0.75	0.00
Peeling of tree barks	0.06	0.00	0.06	0.00
Digging for tree roots	0.00	0.00	0.00	0.13
Cattle herds	0.00	0.31	0.13	0.63
Cattle bomas	0.00	0.13	0.06	0.50
Logging sites	0.13	0.31	0.81	0.19
Cut logs	0.00	0.44	0.69	0.00
Logging stumps	0.00	0.25	1.13	0.19
Snares	0.19	0.00	0.38	0.00
Encountered poachers	0.00	0.13	0.00	0.00
Households	0.00	0.00	0.00	2.88
Burnt vegetation	0.31	0.00	0.13	0.00
Severity of disturbance	29	77	294	465
Disturbance category	Least disturbed	Mildly disturbed	Moderately disturbed	Highly disturbed

Results

The types and frequency of anthropogenic activities differed across survey sites and disturbance categories (Table 3). At Issa Valley (the least disturbed site), anthropogenic signs were old and we observed no active signs during the survey. In Mfubasi (the mildly disturbed site), we documented recent signs of livestock activities, beekeeping, poaching, and logging. At Mlofwesi (the moderately disturbed site) we found evidence of active logging, poaching signs, livestock grazing, illegal beekeeping, and commercial beekeeping. In Mapalamane (the highly disturbed site), we observed predominantly active agricultural activities, numerous settlements, and livestock activities. Mapalamane was inhabited with people in established settlements and contained cleared land for cultivation of corn (*Zea mays*), cassava (*Manihot esculenta*), tobacco (*Nicotiana tabacum*), cotton (*Gossypium* sp.), sunflower (*Helianthus* sp.), beans (*Phaseolus vulgaris*), and other crops.

Logging and illegal beekeeping were present across all four survey sites in MUE. Logging threatened *Pterocarpus angolensis* and *P. tinctorius* tree species. The latter species is an important food source for chimpanzees (Piel et al. 2017). We observed cut logs of both species in Mfubasi and Mlofwesi sites. We recorded seven locations of already cut logs (range: 1–4 logs) in Mfubasi and 11 locations (range: 1–6 logs) in Mlofwesi. Mlofwesi had a slightly but not significantly higher mean of cut logs 3.1 (3.1, $SE = 0.5$) than Mfubasi 2.1 (2.1, $SE = 0.4$; $t = 1.049$, $P = 2.119$). Illegal beekeeping threatened *J. globiflora* and *B. speciformis* because local people debark these tree species to make local beehives. These two tree species provide chimpanzees with food (Piel et al. 2017) and are important tree species used in nesting.

We documented a total of 102 potential chimpanzee plant food species that occurred within MUE (Supplementary Data SD1). Of these plant species, most were trees (62%), followed by herbs (12%), shrubs (9%), lianas (8%), climbers (7%), and grasses and palm trees (1% each). Chimpanzee plant food species richness differed significantly among sites with different disturbance levels ($H = 55.09$, $P < 0.001$; Fig. 2), with Mlofwesi and Mapalamane exhibiting the highest richness values. These two sites also exhibited higher chimpanzee plant food diversity compared to the other two ($H = 36.81$, $P < 0.001$; Fig. 3). Chimpanzee plant food abundance (i.e., trees, shrubs, and liana species with DBH > 10 cm) did not differ significantly across sites ($H = 2.477$, $P = 0.478$). Riparian forest exhibited chimpanzee plant food species richness that was nearly twice that of wooded grassland ($H = 33.58$, $P < 0.001$; Fig. 4). Chimpanzee plant food diversity did not differ significantly across vegetation types ($H = 1.334$, $P = 0.513$); however, chimpanzee plant food abundance (i.e., trees, shrubs, and liana, species with DBH > 10 cm)

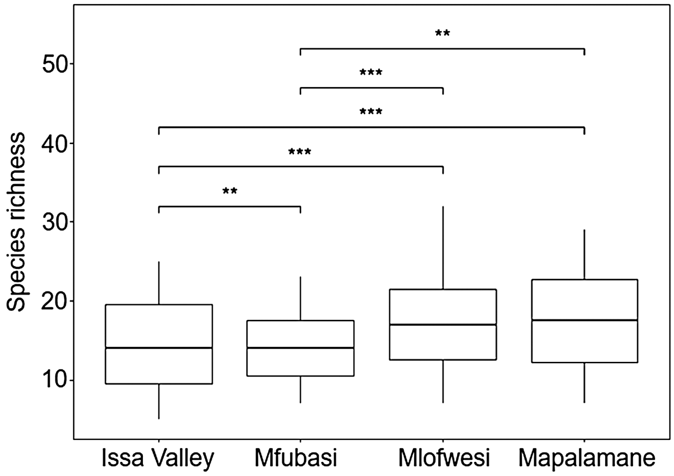

Fig. 2.—Variation in average chimpanzee plant food species richness across the four sites of different disturbance levels in the Masito-Ugalla Ecosystem (MUE). The averages were calculated from vegetation plots (*n* = 80 in Issa Valley, 80 in Mfubasi, 79 in Mlofwesi, and 80 in Mapalamane). Issa Valley = least disturbed site, Mfubasi = mildly disturbed site, Mlofwesi = moderately disturbed site, and Mapalamane = highly disturbed site. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. ***P* < 0.01, and ****P* < 0.001, based on a Kruskal–Wallis test.

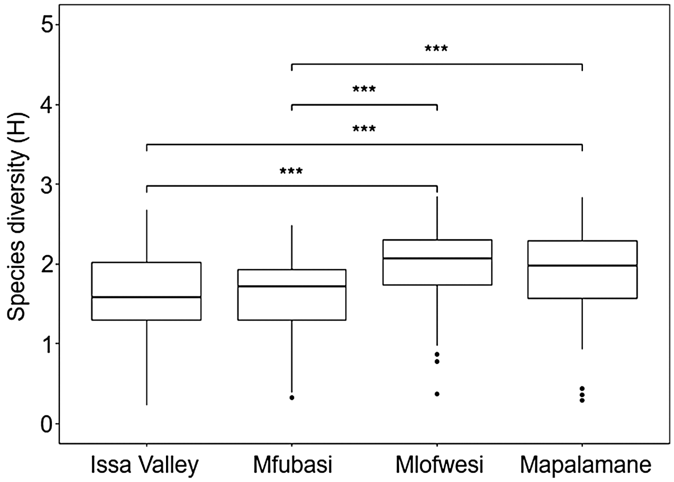

Fig. 3.—Variation in average chimpanzee plant food diversity across the four sites of different disturbance levels in the Masito-Ugalla Ecosystem (MUE). The averages were calculated from vegetation plots (*n* = 80 in Issa Valley, 80 in Mfubasi, 79 in Mlofwesi, and 80 in Mapalamane). Issa Valley = least disturbed site, Mfubasi = mildly disturbed site, Mlofwesi = moderately disturbed site, and Mapalamane = highly disturbed site. The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. ****P* < 0.001 based on a Kruskal–Wallis test.

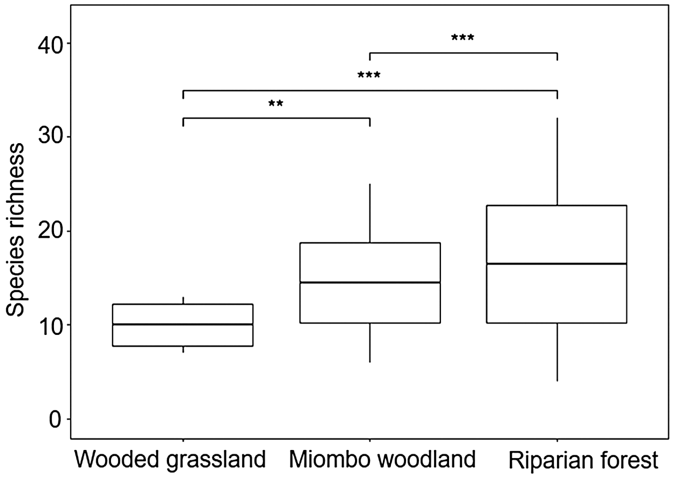

Fig. 4.—Variation in average chimpanzee plant food species richness across vegetation types. The averages were calculated from vegetation plots (*n* = 6 in wooded grassland, 176 in miombo woodland, and 137 in riparian forest). The line in the box represents the median and the box the upper and lower quartile, each representing 25% of data scores. Whiskers are variability of data scores outside the upper and lower quartiles, and points represent outliers. ***P* < 0.01, and ****P* < 0.001 based on a Kruskal–Wallis test.

was higher in miombo woodland compared to riparian forest and wooded grassland ($H = 9.163$, $P < 0.01$).

The encounter rates of the number of chimpanzee nests (i.e., nests/km) differed significantly between sites with different disturbance levels. The least disturbed site had the highest encounter rate of chimpanzee nests (8.5 nests/km); encounter rates declined considerably toward the highly disturbed site (1.5 nests/km). Seventeen different plant species comprised the trees in which all nests were built (Table 4). The abundance of the identified nesting plant species did not vary significantly across sites ($H = 0.279$, $P > 0.964$). *Brachystegia boehmii* and *J. unijugata* were the most frequently used nesting species.

Discussion

In this study, we compared four sites in the MUE area of western Tanzania to investigate the relationship between anthropogenic disturbance and chimpanzee abundance as well as the availability of chimpanzee plant food species (i.e., species richness, diversity, and abundance) and nesting tree species in each of the sites. In contrast to our hypothesis that chimpanzee plant food species richness, diversity, and abundance decline with increasing human disturbance, our results indicate that chimpanzee plant food species richness and diversity increased with increasing human disturbance, while abundance did not.

Table 4.—Average, minimum, maximum, and the sum as well as relative proportions of number of nests observed per plant species that chimpanzees selected for nesting across all survey sites within Masito-Ugalla Ecosystem.

Nesting plant species	Min	Mean	Max	Sum	%
Albizia adianthifolia	3	3	3	3	1.5
Albizia glaberrima	1	1	1	1	0.5
Brachystegia boehmii	1	7.4	16	67	33
Brachystegia bussei	1	2.3	3	7	3.4
Brachystegia microphylla	1	2	3	6	3
Brachystegia sp.	2	2	2	4	2
Brachystegia speciformis	1	3.7	8	11	5.4
Combretum molle	2	2.7	4	8	3.9
Julbernadia globiflora	1	1.7	2	5	2.5
Julbernadia unijugata	1	2.6	7	49	24
Markhamia obtusifolia	2	2.5	3	5	2.5
Parinari curatellifolia	1	1	1	1	0.5
Pericopsis angolensis	2	2	2	2	1
Psydrax parviflora	2	2	2	2	1
Pterocarpus tinctorius	2	3	4	6	3
Syzygium guineense	1	2.3	3	14	6.9
Uapaca guineensis	1	2	4	12	5.9

However, at the site with the highest level of human disturbance both species richness and diversity declined slightly.

Our results are consistent with the intermediate disturbance theory, which suggests that species richness and diversity may increase with disturbance in a particular habitat (Connell 1978; Wilkinson 1999; Catford et al. 2012), provided that the extent of disturbance is neither too low nor too severe. Moderate disturbance in a particular habitat creates unstable environments of low competitive exclusion between co-occurring species and, therefore, supports high species richness and diversity (Willig and Presley 2018). In contrast, high disturbance interrupts and eliminates many species in plant communities, resulting in plant communities dominated by few tolerant species, a situation that may result in taxonomic homogenization (Lôbo et al. 2011). The intermediate disturbance theory might explain why Mlofwesi, with moderate disturbance, exhibited higher values of chimpanzee plant food species richness and diversity compared to sites of relatively low disturbance such as Issa Valley and Mfubasi. Mfubasi, Mlofwesi, and Mapalamane have all experienced extensive disturbance over the last 10 years (Piel and Stewart 2014) and the latter had the highest occurrence of human activities of severe negative influence (e.g., agriculture and settlement) on chimpanzee habitat, which might have influenced the decline of plant food species richness and diversity. Our results suggest that more individual plant species are lost in areas of severe human disturbance than in areas of low human disturbance. This is in agreement with Köster et al. (2013), who reported that environmental conditions in disturbed habitats do not support a variety of tree species because few tree species have the capacity to establish in these habitats.

Moreover, our results show that human disturbance has not yet had an influence on the abundance of chimpanzee plant food and nesting tree species. This is in contrast to Fuller et al. (1998), who found that human disturbance resulted in changes to forest composition and plant species abundance in New England, United States, which granted was carried out in New England–Acadian forest habitat, rather than Tropical forest. In the present study, we did not set up vegetation plots in cultivated fields and in areas cleared for farming, as these activities only were observed in one of the four survey sites. However, we observed signs of selective logging, livestock grazing, and unsustainable beekeeping practices in all survey sites. Since livestock grazing has no immediate effect on the abundance of woody plant species (with the exception of cattle bomas, which also were not sampled for vegetation plots), selective logging and debarking of trees for making beehives, resulting in the death of the affected woody plant species, has potentially the largest influence on chimpanzee plant food and nesting tree abundance. Selective logging threatened *P. angolensis* and *P. tinctorius*. Illegal beekeeping threatened *J. globiflora* and *B. speciformis* because local people around MUE debark these tree species to make local beehives using the bark. However, all these activities often are selective toward certain preferred woody species, and initially do not impact abundance of plant species (Brown and Gurevitch 2004). The selective nature of these activities may explain why the abundance of chimpanzee plant food and nesting tree species did not differ across survey sites with different human disturbance levels.

Furthermore, we found that riparian forests had significantly higher chimpanzee plant food species richness compared to miombo woodlands and wooded grasslands. Sabo et al. (2005) revealed that riparian habitats do not harbor higher number of species, but rather support significantly different species from neighboring upland habitats (i.e., habitats along the sides of a river that are slightly higher in elevation and do not contain surface water). In the case of this study, upland habitats were denoted by miombo woodlands and wooded grasslands. High plant species richness in riparian forests has been considered an indication of high levels of biodiversity (Naiman et al. 1993). An array of plants comprising herbs, grasses, lianas, vines, shrubs, and trees, grow in riparian forests, as was observed in this study. Therefore, riparian forests are of major conservation concern due to the support these habitats provide for a large number of species (Sabo et al. 2005). In addition, these habitats can act as corridors between isolated habitats and play important roles in facilitating movement and migration of animals, providing shelter and maintaining biodiversity (Naiman et al. 1993). Despite the importance and ecological relevance of riparian forests, human encroachment through agricultural activities is an important threat to these habitats in MUE. During this study, we observed people establishing farms along the riverbanks in the highly disturbed survey site (Mapalamane), thereby encroaching and diminishing the quality of these habitats. In this study we were not able to quantify the extent to which these habitats have been reduced or even disappeared; however, future studies that integrate remote sensing easily could calculate reliable estimates (see Hansen et al. 2013). While riparian forests are more threatened by farming activities, miombo woodlands and wooded grasslands are threatened by logging, debarking of trees for local beehives, and livestock activities.

We also hypothesized that chimpanzee abundance is influenced negatively by human disturbance and predicted that nest counts would be high in areas of low or no human disturbance. Our results indicate that as human disturbance levels increase, there is a decrease in chimpanzee abundance despite resources being plentiful and more diverse in moderately disturbed sites. Based on our results, we argue that resource availability is not the only factor driving chimpanzee population size in moderately disturbed sites. Our results can be explained in the context of the deterring effect from human presence and activities. This argument is supported by Garriga et al. (2019), who revealed that in the Moyamba district in southwestern Sierra Leone, the presence and the proximity of humans through roads available in chimpanzee habitats negatively influenced chimpanzee relative abundance and their distribution due to the risks associated with the likelihood of encountering people. Our results also are consistent with those of Bryson-Morrison et al. (2017), who showed that chimpanzees in a human-dominated landscape of Bossou, Guinea, preferred habitat types both with low human presence and abundant food availability. As reported by Bryson-Morrison et al. (2017), Bossou chimpanzees preferred to travel, rest, and socialize in areas with low human-induced pressure. Our results suggest that human disturbance in chimpanzee habitat may affect chimpanzee spatial and temporal distribution, regardless of resource availability, i.e., feeding tree species in our case. However, not all human activities increase chimpanzee vulnerability to anthropogenic disturbance. Some studies suggest that chimpanzees can tolerate human disturbance such as agriculture, settlements, and low levels of hunting (Rist et al. 2009; Brncic et al. 2015). This argument is similar to that of Garriga et al. (2019), who found that at larger spatial scales, settlements and human presence did not influence chimpanzee relative abundance. Yet, at a temporal level, they found that chimpanzees tended to reduce their activity at midday when human activity was more prevalent, indicating a certain degree of temporal divergence.

Although we were not able to assess chimpanzee behavior in relation to human disturbance, we acknowledge that chimpanzees may adjust behaviorally to disturbance. Kühl et al. (2019) argued that human disturbance in chimpanzee habitat not only influences critical resources for chimpanzee survival, but also erodes behavioral diversity. Some anthropogenic features are likely to influence chimpanzee behavioral activities (e.g., feeding, nesting, grouping, etc.) in response to human encounters and pressures exerted in their habitats (Brncic et al. 2015; Bryson-Morrison et al. 2016; McLennan et al. 2017). In support of this argument, Yuh et al. (2019) found that chimpanzees avoid nesting in frequently disturbed areas, similar to what may be occurring in MUE. Although chimpanzees are behaviorally flexible and are able to exploit human-influenced habitats (Hockings et al. 2012, 2015; Bryson-Morrison et al. 2016, 2017), anthropogenic activities, especially those that affect habitat integrity, threaten their survival.

Based on our findings, we encourage conservation planners and researchers to conduct extensive regular surveys to examine changes in chimpanzee critical resources over time in relation to levels of anthropogenic disturbance. Researchers should set up gradient studies of proximity to large settlements to examine thresholds for change in wildlife densities. Furthermore, additional effort should be employed to survey large areas and collect sufficient data that will allow for DISTANCE sampling rather than just nest counts. This will enable conservation planners to understand the causative relationships (i.e., effects of anthropogenic activities on chimpanzee resources and abundance), and opt for appropriate conservation actions to conserve the MUE, an important habitat for chimpanzees living outside national parks in western Tanzania.

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Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—A list of chimpanzee plant food species documented in the Masito-Ugalla Ecosystem based on direct observations and the compiled diet lists from Issa Valley, Gombe, and Mahale Mountains National Parks (Goodall 1968; Wrangham 1975; Nishida and Uehara 1983; Nakamura et al. 2015; Piel et al. 2017).

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