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Spatiotemporal Variation in Bonobo (*Pan paniscus*) Habitat Use in a Forest–Savanna Mosaic

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Abstract

Understanding the ecological and behavioral variation of primates is central to improving conservation strategies. Studies of chimpanzees (*Pan troglodytes*) have shown marked behavioral variability across a wide range of habitats. By comparison, bonobos (*Pan paniscus*) occur mainly in continuous forest sites, and socioecological models explaining behavioral differences between the two species are based on the assumption that bonobo habitat is richer and more stable than chimpanzee habitats. The objective of this study was to assess bonobo ecology in a forest–savanna mosaic. We specifically explored 1) bonobo home range size, habitat use, and dietary composition; 2) forest fragmentation in a bonobo community's home range; and 3) seasonality of dietary diversity, habitat use, and spatial distribution. Using 2 years of observational data on location, habitat type, and dietary composition, we found that the bonobo community's home range size, density, and dietary diversity were similar to those observed in continuous forest sites. Bonobos used areas with lower forest fragmentation than the surrounding areas and preferentially spent time in forested habitats. During the dry season, bonobos consumed a lower diversity of fruit species, spent more time in sparse forest with Marantaceae understory, and were closer to the seasonal center of their home range than during the rainy season. Our results contribute to our understanding of behavioral variation in bonobos and suggest that forest–savanna mosaic is valuable to bonobo conservation.

Keywords Democratic Republic of the Congo · Forest fragmentation · Habitat use · Home range · *Pan paniscus* · Spatial analyses

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Introduction

A better understanding of the extent of behavioral variation in threatened species is of critical importance to tailor conservation action to ecological need (Strier 2017). Multiple field studies are therefore needed to understand the ecology of species whose range encompasses diverse environments. This approach is particularly relevant for primates, as most primates are threatened and inhabit various environments (Estrada *et al.* 2017), including mosaic vegetation types (forest–savanna, forest–agriculture mosaic); fragmented and continuous forests; and with variation in the extent of human proximity, density, and practices resulting in diverse levels of anthropogenic pressure.

Field studies of primates have highlighted many intraspecific differences in ecological strategies. Intraspecific differences are particularly evident in home range size, daily path length, diet, and habitat use (e.g., guerezas, *Colobus guereza*: Harris and Chapman 2007; diademed sifakas, *Propithecus diadema*: Irwin 2008; blue monkeys, *Cercopithecus mitis*: Tesfaye *et al.* 2013; crab-eating macaques, *Macaca fascicularis*: Sha and Hanya 2013; northern pig-tailed macaques, *Macaca leonina*: Gazagne *et al.* 2020; chimpanzees, *Pan troglodytes*: Potts *et al.* 2011). Many taxa exhibit seasonal variation in ranging patterns, habitat use, and diet within the same groups (e.g., olive baboons, *Papio anubis*: Barton *et al.* 1992; white-headed langur, *Trachypithecus poliocephalus*: Hendershott *et al.* 2018; northern pig-tailed macaques: Gazagne *et al.* 2020; chimpanzees: Chancellor *et al.* 2012). The spatiotemporal availability of food resources influences feeding strategies and habitat use (Fan and Jiang 2008; Tutin *et al.* 1997; Wallace 2008). Feeding strategies and habitat use are closely related to each other, and during periods of fruit scarcity, a group's home range may be smaller and primates may consume fallback foods. Alternatively, a group may extend its home range to meet resource needs (Hendershott *et al.* 2018; Schoener 1971; van Schaik and Brockman 2005). In fragmented environments, forest patch size can positively influence home range size, but the effect of habitat fragmentation on home range size differs greatly according to the matrix configuration and a species' ability to travel between forest patches (e.g., Bicca-Marques 2003; Boyle *et al.* 2013; Irwin 2008; Onderdonk and Chapman 2000; Tutin 1999). Other factors affecting home range and feeding strategies include intraspecific competition, intergroup dynamics, and interspecific competition (Grant *et al.* 1992; Mitani and Rodman 1979). The lack of comparability between studies, often due to the use of different methods, limits our understanding of factors underlying these different strategies (Boyle *et al.* 2009; Pearce *et al.* 2013).

Chimpanzees are the most widely distributed great apes (Humble *et al.* 2016) and live in a variety of habitats, from open mosaic environments to continuous tropical forest, that differ in vegetation, climate, elevation, topography, and human sociocultural context. Within their range of habitats, studies of chimpanzees in savanna mosaic habitats have been particularly fruitful and relevant to our understanding of their behavioral and ecological variation (Moore 1996; Lindshield *et al.* in prep.). Along the continuum of habitats inhabited by chimpanzees, savanna habitats are particularly dry (annual rainfall <1360 mm/yr) and sparsely forested (forest cover <12.5%) compared to other chimpanzee habitats (van Leeuwen *et al.* 2020). Chimpanzees inhabiting savanna habitats have a larger home range size, a lower density (2–50 times), and a lower dietary diversity than those inhabiting more forested environments, probably because of lower availability and higher spatial dispersion of food resources and water

(Baldwin *et al.* 1982; McGrew *et al.* 1988; Ogawa *et al.* 2007; Piel *et al.* 2017; Pruetz 2006; Pruetz and Bertolani 2009; Skinner and Pruetz 2012; van Leeuwen *et al.* 2020; *cf.* Basabose 2005). Chimpanzees in savanna mosaic environments use forest preferentially relative to its availability but also rely frequently on open woodland habitats, especially for foraging and nesting (Hernandez-Aguilar *et al.* 2013; McGrew *et al.* 1988; Ndiaye *et al.* 2018; Piel *et al.* 2017; Pruetz and Bertolani 2009). The high seasonality of rainfall and water availability, temperature, and food availability in these environments likely influences seasonal variation in chimpanzee habitat use (Baldwin *et al.* 1982; Wessling *et al.* 2018), but seasonal patterns of savanna chimpanzee space use have not yet been directly investigated.

The other *Pan* species, the bonobo (*Pan paniscus*), ranges only within the Democratic Republic of the Congo (DRC) (Fruth *et al.* 2016). Its geographic range is smaller than that of chimpanzees and has little variation in habitat types across its range compared with chimpanzees (mainly equatorial forest, and forest–savanna mosaic at the southern periphery; Gruber and Clay 2016; Pennec *et al.* 2016; Thompson 2002; White and Wrangham 1988). This apparent ecological stability has led to a hypothesis to explain behavioral differences between the two *Pan* species (Boesch *et al.* 2002; Furuichi 2009), namely that richer and less variable food resource availability (especially fruits and high-quality terrestrial herbs) in bonobo habitats led to more tolerant relationships, more stable diets, and smaller home ranges in bonobos than in chimpanzees (Hohmann *et al.* 2006; Kano 1992; Wrangham *et al.* 1996; *cf.* Georgiev *et al.* 2011).

Understanding intraspecific differences in ecological strategies will further elucidate the boundaries of bonobo behavioral variation, which we can then compare to variation observed in chimpanzees. Information about bonobo ranging patterns and habitat use is available for some forest field sites in DRC. At Lomako, two studies found substantial differences in home range size for the same bonobo communities (2 and 22 km²; Badrian and Badrian 1984; Waller 2011), without clear explanations for these differences. At Wamba, three studies found different home range sizes and densities for the same bonobo communities, and seasonal changes in habitat preference (Hashimoto *et al.* 1998; Hashimoto and Furuichi 2015; Terada *et al.* 2015). This seasonality in habitat use is probably linked to spatiotemporal variability in fruit availability, because fruit is the preferred food of bonobos (Conklin-Brittain *et al.* 2001). For example, when fruits of *Uapaca* sp. are available in swamp forest at Wamba, bonobos spend more time in this forest type (Terada *et al.* 2015). Terrestrial herbaceous vegetation (THV) also plays a major role in the bonobo diet (Badrian and Malenky 1984; Conklin-Brittain *et al.* 2001; Malenky and Stiles 1991) and when fruit availability is lower, bonobos may eat more THV and spend more time in THV-rich forest types (Kano and Mulavwa 1984; Terada *et al.* 2015). However, other studies in bonobos have found no effect of fruit availability on THV consumption (Malenky and Wrangham 1994; White and Wrangham 1988). Finally, bonobos have been described as nesting mostly in mixed *terra firma* forest, also called primary forest or dry forest, with a predominance of mixed forest with Marantaceae understory (Hashimoto *et al.* 1998; Idani *et al.* 1994; Kano 1992; Reinartz *et al.* 2006; Terada *et al.* 2015).

We have a poor understanding of bonobo ecology in a mosaic environment in contrast to forest field sites. Broad-scale models that predict suitable habitats for bonobos have found negative influences of forest fragmentation and human proximity,

except at the west of their range (Hickey *et al.* 2012, 2013), making this region interesting to assess ecological and behavioral variation in bonobos. Moreover, a better understanding of the temporal variation in habitat types used by bonobos is important when developing conservation strategies, especially in landscape mosaics where forest patch composition and forest connectivity can limit migration between communities (Serckx *et al.* 2014; Terada *et al.* 2015).

The Manzano study site is at the southwestern periphery of the bonobos' geographic range (Bolobo Territory, DRC) and consists of a forest–savanna mosaic (Inogwabini *et al.* 2008; Pennec *et al.* 2016). Located at the edge of the Congo Basin, this mosaic probably originates from both natural and anthropogenic influences, including seasonal fires in savannas and slash-and-burn agriculture (Demichelis *et al.* 2020; Namur 1990). In this forest–savanna mosaic environment, bonobo density and dietary diversity falls within the range of the more forested bonobo study sites (Hashimoto *et al.* 1998; Inogwabini *et al.* 2008; Mohneke and Fruth 2008; Narat 2014; Sabater Pi and Veà 1990; Serckx *et al.* 2014, 2015; Uehara 1988; Van Krunkelsven 2001). Additionally, a previous study in the same region found high seasonal variation of fruit availability and, based on a multi-year transect survey, suggested that bonobos adapt their ranging patterns to local fruit availability (Serckx *et al.* 2014). While it appears that dietary diversity and bonobo density in this forest–savanna mosaic do not follow the pattern observed in savanna mosaic chimpanzees (lower density and lower dietary diversity) data are lacking on their home range, habitat use, and the potential seasonality of these parameters.

The objective of this study was to assess aspects of bonobo ecology in a forest–savanna mosaic. We specifically explored 1) bonobo home range size, habitat use, and dietary composition; 2) forest patch fragmentation level in the community home range relative to the broader landscape; and 3) seasonal variation in dietary diversity, habitat use, and spatial distribution. To do this, we analyzed 2 years of observational data on bonobo location, habitat type, and dietary composition to determine bonobo home range and seasonal variations in dietary diversity, habitat use, and spatial distribution. We used satellite images to characterize edge density and determine if bonobos selected areas with relatively lower fragmentation compared with what is available in this region. The bonobo community we studied lives in a forest–savanna mosaic, and the proportion of forest landcover in this area is lower compared with continuous forest sites. We hypothesized that food resources determine home range size. If resources are more dispersed than at sites with more continuous forest cover, as observed for chimpanzees in savanna habitats, we predicted that the bonobos' home range would be larger than in sites with more continuous forest cover (Baldwin *et al.* 1982; McGrew *et al.* 1988; Ogawa *et al.* 2007; Pruetz and Bertolani 2009; Pruetz 2006; Skinner and Pruetz 2012). Second, we hypothesized that the level of fragmentation influences bonobo distribution locally. Because forest fragmentation is a negative predictor of bonobo occurrence at a broad scale (Hickey *et al.* 2013), we predicted that the level of forest fragmentation would be lower in the bonobo home range than in the surrounding area. Finally, although habitats inhabited by bonobos are considered more stable and less seasonal compared to those inhabited by chimpanzees (Oelze *et al.* 2016; White 1998), fruit availability shows high temporal variation in this forest–savanna mosaic (Serckx *et al.* 2015). We hypothesized that this temporal variation in food availability would be linked to variation in the bonobo dietary diversity. Because fruit availability is

lower in the dry season (Malenky and Wrangham 1994; *cf.* van Schaik and Pfannes 2005), we predicted that we would observe lower fruit dietary diversity during the dry season than the wet season. As bonobos consume fallback foods during periods of low preferred food availability (Serckx *et al.* 2015), we predicted that bonobos would shift their habitat use and space use to feed on these fallback foods during the dry season.

Methods

Study Site

We conducted our study in Manzano forest near Embirima Village (2°34'S 16°22'E), Bolobo Territory, DRC (Fig. 1). Located in the southwestern part of the Congo Basin, the local climate features tropical characteristics with an alternation of dry and rainy

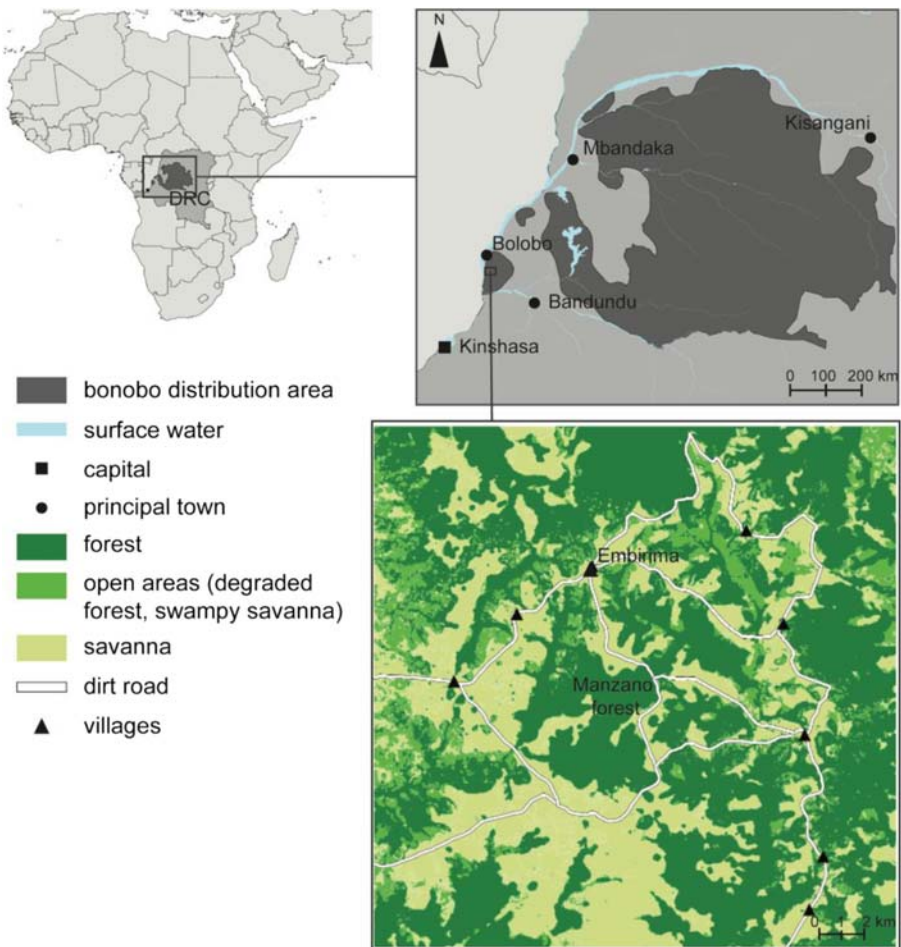


Fig. 1 Location of Manzano forest within the Democratic Republic of the Congo (DRC).

seasons and the mean annual rainfall is 1625 mm. The vegetation is 58% forest and 42% savanna with an elevation of 332–557 m (Pennec *et al.* 2016). Thus, this area is less forested than the other bonobo study sites in forest–savanna mosaic (e.g., Lukuru: 80% forest, 20% savanna, Thompson 1997). Although it can be characterized as a mosaic habitat, this study site is not comparable to the most extreme savanna habitats inhabited by chimpanzees, typically characterized as <12.5% forest cover and <1360 mm of annual rainfall (van Leeuwen *et al.* 2020). Forest patches are mainly composed of *terra firma* forest and seasonally inundated forests. Two main types of savannas are present: seasonally inundated herbaceous savannas and shrub savannas. The two most frequently encountered primate species are bonobos and red-tailed monkeys (*Cercopithecus ascanius*). The human population of the nearby Embirima village is *ca.* 800 people and the land managed by the village occupies an area of 135 km², resulting in a human density of 6 inhabitants/km² (Mbou-Mon-Tour NGO, *unpubl. data*). Local people, the Bateke, respect a taboo against eating bonobos and use the forest daily for activities such as slash and burn agriculture, hunting, fishing, and gathering (Narat *et al.* 2015a). The local people participate in a community-based conservation project (Forest Concession of Local Communities of the Mbali River) led by the Congolese NGO Mbou-Mon-Tour and initiated in 2001 in the Bolobo Territory and in 2006 for this village (Narat *et al.* 2015a). As part of this project, villagers have designated areas dedicated to conservation and rules of use in these areas. Among the 82.6 km² of forest managed by this village, 35.9 km² are community conservation forests for bonobos and monkeys where some activities are forbidden (hunting, fishing with poison, agriculture), whereas others are permitted (e.g., caterpillar, fruit and leaf gathering, and fishing). This conservation strategy aims to maintain spatial overlap between humans and primates. Habituation of the Manzano bonobo community began in 2012, and long-term protocols have been established to study bonobo ecology, sociality, and health since 2015 (Narat *et al.* 2015b).

Data Collection

From February 2016 to January 2018, we followed the Manzano bonobo community for 205 days and conducted 469 h of direct observation (days per month with bonobo observations: mean = 8.5 ± SD 3.7, range = 1–17). The community was composed of 22–24 individuals (3 adult males and 6 or 7 adult females) at time of this study. We collected data using *ad libitum* sampling (Altmann 1974). When we were with bonobos, we recorded geographical coordinates (using a Garmin GPSMAP 64) every 50 m, and recorded the following data for each set of geographical coordinates (defining an observation point): start and end time; habitat type; and feeding events, defined as the consumption of one item of one species at this observation point. We also recorded fresh (estimated to <1 h) food remains of bonobos, even if we did not directly observe its consumption, as supplemental data to improve the description of diet at each observation point.

We recorded all signs of human presence when searching for or following bonobos to describe human activities (hunting, fishing, gathering, agriculture, moving, fire, other) in areas used by bonobos. However, because of the strong bias in these data, which we collected only when searching for or following bonobos, we did not analyze these data as factors that could influence bonobo presence.

At each observation point, we recorded the main habitat types based on descriptions by Pennec *et al.* (2016). Mixed forest with open understory (MFO) had a high density of trees (426 trees/ha) and lianas (136 lianas/ha) among *terra firma* forests, with *Pentaclethra eetveldeana*, *Plagiostyles africana*, *Anonidium manii*, and *Staudtia kamerunensis* as the most important species, as determined by the Importance Value Index (Curtis 1959) calculated for each species. The understory had abundant woody regeneration with low herbaceous plant density. Mixed forest with Marantaceae understory (MFM) had a similar structure to MFO, with *Plagiostyles africana*, *Sorindeia juglandifolia*, *Chaetocarpus africanus*, and *Piptadeniastrum africanum* as the important tree species. The understory had a low density of woody regeneration but high Marantaceae density (*Sarcophrynium schweinfurthianum* dominating *Haumania liebrechtsiana*). Sparse forest with Marantaceae understory (SFM) had the highest diversity index and tree composition was similar to MFM. However, the structure was different with lower density of trees, an underrepresentation of trees with diameter at breast height (DBH) < 30 cm, and with important large tree species including *Celtis tessmannii*, *Klainedoxa gabonensis*, and *Millettia laurentii*. *Pentaclethra eetveldeana* was the most frequently represented species in SFM. The understory had the poorest woody regeneration but high Marantaceae density (*H. liebrechtsiana* dominating *S. schweinfurthianum*). Seasonally inundated forest (SIF) had high tree and liana densities (343 trees/ha and 235 lianas/ha) and 80% of trees with DBH \leq 30 cm. The understory was seasonally inundated with a moderate density of woody regeneration and Marantaceae species dominated by other herbaceous species. *Hymenocardia acida*, *Maprounea africana*, and *Annona senegalensis* generally dominated shrub savannas, but some savannas were herbaceous and swampy. Other habitat types were field and fallow (resulting from slash and burn agriculture technique maintaining a canopy cover dense enough to consider these vegetation types as forested), edge, and road (dirt).

We collected daily rainfall with a rain gauge from 2012 to 2018 and calculated the mean monthly rainfall over this period. We defined dry and rainy seasons using a threshold of 100 mm/month (Dupain *et al.* 2002; Hunt and McGrew 2002) (Fig. 2). According to this definition, the dry season lasts from June to September and the rainy season from October to May (Fig. 2). The bonobo observation time was distributed between seasons as follows: 87 days (221 h) during the dry season and 118 days (248 h) during the rainy season.

Data Analyses

Home Range Size, Habitat Use, and Dietary Composition

We determined home range using three complementary methods: minimum convex polygons (MCPs), grid cell adjustment, and kernel density estimation. First, we determined bonobo home range size with MCPs (Mohr 1947; Southwood 1978) of all observation points collected during the study period. This method overestimates the home range size but the data are easily comparable with those of previous studies (e.g., Terada *et al.* 2015; Waller 2011) (see Table II). To assess the robustness of our dataset, we used the following resampling strategy: for each number of data points (N) in increments of 10, we randomly selected N observation points from our full data set ($N =$

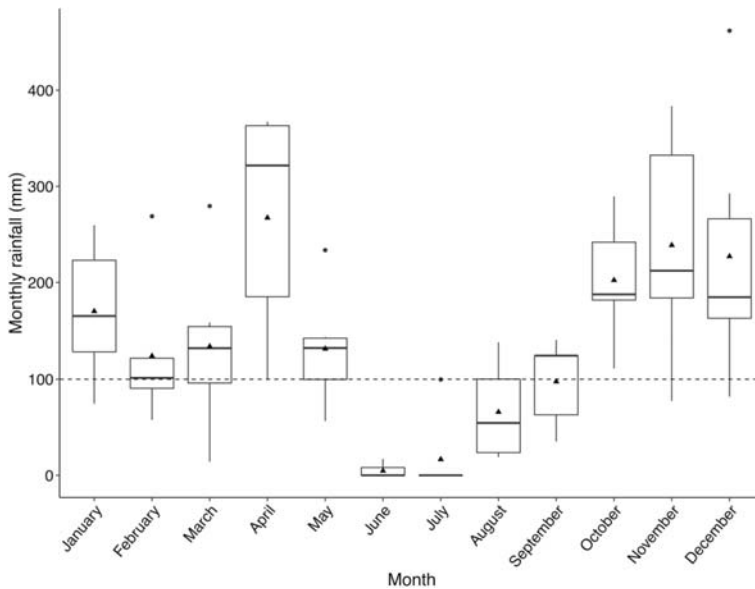


Fig. 2 Boxplot of monthly rainfall recorded near Manzano forest from 2012 to 2018. Triangles represent the mean, black bars the median, and white boxes the interquartile range (25th–75th percentile). The lower limits of the vertical lines represent the smallest value within 1.5 times the interquartile range below the 25th percentile, and the upper limits represent the largest value within 1.5 times the interquartile range above the 75th percentile for that month. Black dots are values outside of these limits. The horizontal dashed line shows the threshold between dry and rainy seasons.

794) with replacement 1000 times, and computed the MCP home range estimate for each iteration. Second, to exclude the areas from the polygon where bonobos were never observed, we adjusted the polygon by superimposing a 500-m grid and clipping out cells that were never visited (Grueter *et al.* 2009; Hashimoto *et al.* 1998; Vieira *et al.* 2019). We also used this grid cell method to facilitate comparisons with some existing data on bonobo home range size (Hashimoto *et al.* 1998). Third, we weighted each location observation by the time spent at each point and employed the QGIS HEATMAP plugin to generate a kernel density map (radius = 200 m, pixel size = 25 m, quartic kernel shape) (Ferreguetti *et al.* 2018; Katsis *et al.* 2018; Kshetry *et al.* 2017). This analysis generates a map of intensity of use and allows identification of the areas of highest use by bonobos within their home range. Based on this layer, we defined hotspots as those pixels with the highest 10% of values from the map of intensity of use (kernel analyses with a threshold of 10%). To describe habitat use, we determined the percentage of time spent in each habitat type based on the data collected at each observation point. We included all species consumed by bonobos (from direct observation or fresh food remains) at least once during the study period in the dietary composition.

Forest Fragmentation and Edge Density

To evaluate forest fragmentation, we performed an unsupervised classification (Landsat 8, August 14, 2016) using ENVI 4.5 (K-means method, 10 iterations, four classes) to determine both the forest cover and edge. We used the normalized difference vegetation index (NDVI) obtained from the red and near infrared bands of the Landsat 8 image to

calculate the mean NDVI of the four spectral classes (NDVI value increases with photosynthetic activity, Myneni *et al.* 1995). Then, based on these values and our knowledge of the area, we assigned vegetation types to the spectral classes: continuous canopy forest (mean NDVI = $0.27 \pm \text{SD } 0.02$), open areas (degraded forests and swampy savanna, mean = $0.21 \pm \text{SD } 0.03$), savanna type 1 (mean = $0.14 \pm \text{SD } 0.02$), and savanna type 2 (mean = $0.10 \pm \text{SD } 0.03$). We used the continuous canopy forest class to determine the forest cover, and its contour to determine the edge. To estimate forest fragmentation, we calculated the edge density (m/ha) of the home range (Hickey *et al.* 2012) for the MCP and grid adjustment (a single value for each home range assessment method) as follows:

$ED = D \div A$, where ED is the edge density, D is the linear distance of edge (meters) in the area considered and A is the area (ha).

To assess if bonobos home ranges have lower edge density than the surrounding area, we also determined the edge density in two larger circles. For the immediate vicinity of the home range, we determined the radius of a circle using the maximum distance between the weighted home range center—defined as the average geographic coordinates weighted by the duration at each point—and the limit of the MCP. We then defined a circle with three times this radius, excluding the first circle, to characterize the edge density of the surrounding region.

Seasonal Variation in Dietary Diversity, Habitat Use, and Spatial Distribution

To analyze seasonal patterns in space use, we performed the same analysis as with the full dataset (kernel density maps: radius = 200 m, pixel size = 25 m, quartic kernel shape) on points collected during the dry season and those collected during the rainy season, weighted by the time spent at each point. We defined seasonal hotspots as the highest 10% of values.

To explore seasonal differences in plant dietary diversity, we first calculated an index of plant taxa diversity consumed in seasonal hotspots, accounting for hotspot size and time spent in hotspots, as follows:

$Dt_i = Nt_i / A_i * T_i$ where Dt_i is the diversity of taxa consumed in hotspot i , Nt_i is the number of taxa consumed in hotspot i , A_i is the area of hotspot i (ha), and T_i is the time spent in hotspot i (hours). Then, we used a Wilcoxon test to compare the diversity index in hotspots between seasons (both for all plant items and only for fruits).

To assess seasonal differences in habitat use, we calculated the percentage of time spent in each habitat type for all points recorded during the dry season and the rainy season, and for those located only in seasonal hotspots. Then, we compared these percentages between the dry and rainy seasons, both for all points and for those located in seasonal hotspots with a chi-squared test. To simplify the analyses to conform to a chi-squared test structure, we grouped all habitats with a percentage value lower than 5% as “other.”

To examine seasonal variation in the spatial distribution of bonobos, we calculated the average geographic coordinates weighted by the duration at each point for each season to represent the seasonal weighted home range center. Then, we used a Wilcoxon test to compare the mean distance of observation points to the seasonal weighted home range center between seasons.

We used QGIS software (version 3.4.1-Madeira, QGIS Development Team 2018) for all spatial analyses. We used R (version 3.5.1, R Core Team 2018) for statistical analyses.

Ethical Note

Our study adhered to all research requirements of the DRC. We obtained research authorization through our local collaborator, the NGO Mbou-Mon-Tour. The authors have no conflict of interest or competing financial interests to declare.

Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Results

Home Range Size, Habitat Use, and Dietary Diversity

Using the MCP method, the bonobo home range was 20.3 km² during the study period ($N=794$ points; 365 for the dry season and 429 for the rainy season) and included 72% forest cover (Fig. 3). The maximum distance between the weighted home range center and the limit of the MCP was 4 km. When we resampled observation points with

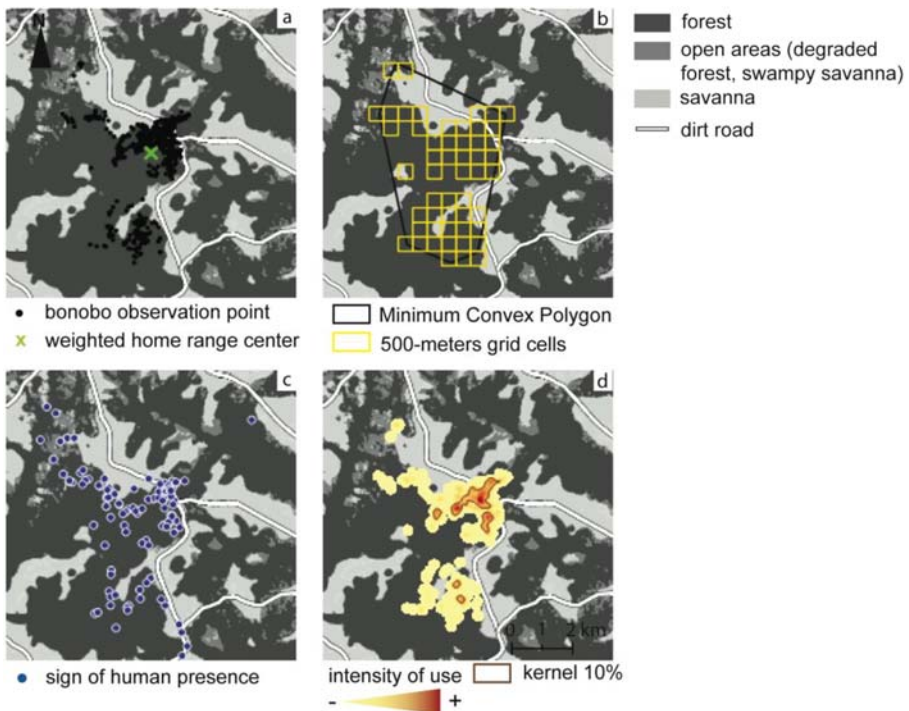


Fig. 3 (a) Spatial distribution of bonobo observation points in Manzano forest, DRC, from February 2016 to January 2018. (b) Home range estimated by the minimum convex polygon and 500-m grid cell methods. (c) Signs of human presence. (d) Intensity of space use by bonobos (kernel 100% and hotspots based on kernel 10%).

replacement and recomputed home range area, increasing sample size reduced estimate variance and estimates converged toward the value obtained in our complete dataset (Fig. 4). Bonobos occurred in 13.0 km² with a 500-m grid superimposed on the MCP (83% forest cover), and 9.4 km² with the map of intensity of use (86% forest cover; Fig. 3). Based on the Manzano community composition during the study period (10 adults, 5 subadults, and 9 juveniles), we calculated densities of 0.5 mature individuals/km² and 1.2 individuals/km² with the MCP method, and 0.8 mature individuals/km² and 1.8 individuals/km² with the 500-m grid cell method.

Three hotspots were located in the northeastern part of the home range (67 ha, 16 ha, 6 ha) and represented 58.3% of the total observation time. Two smaller hotspots were in the southern part of the home range (5 ha, 4 ha) and represented 4.7% of the total observation time. Bonobo space use outside these hotspots accounted for the remaining 37.0% of total observation time.

We described habitats for more than 85% of the observation points over the study period. Observation points without habitat description are due to omission during data collection. We observed bonobos in forested habitat types 97% of observation time (37% in SFM, 28% in MFO, 24% in MFM, 5% in fallow, 2% in SIF, and 1% in field) and in savannas (1%), edge (1%), and road (1%). We observed the same general pattern in the percentage of habitat types in the hotspots during the overall study period: bonobos occurred principally in SFM (44%), MFO (24%), and MFM (21%).

We recorded 919 plant consumption events. Bonobos consumed 83 plant taxa (55 identified to the species level, 17 to the genus level, 2 to the family level, and 9 with

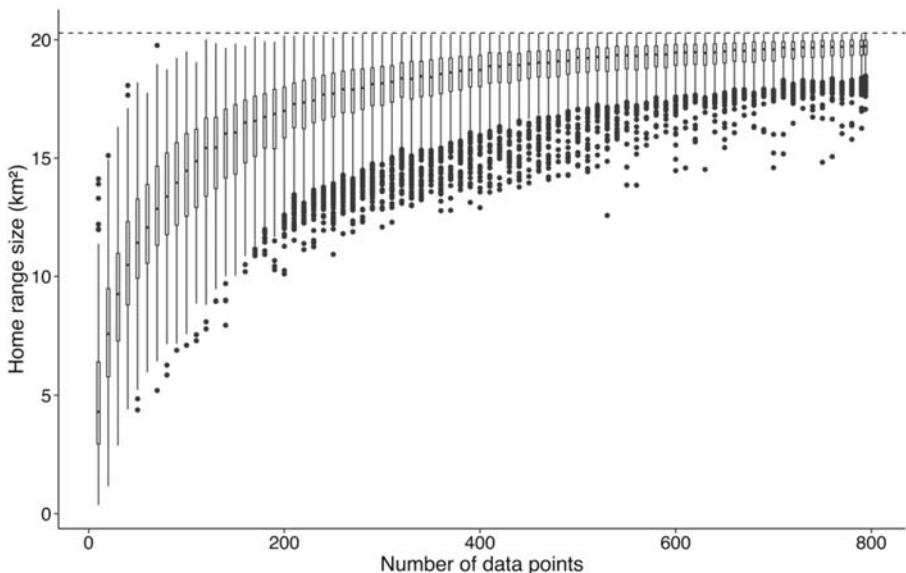


Fig. 4 Estimates of home range area for bonobos in Manzano forest, DRC, between February 2016 and January 2018 for 1000 resamples with replacement per sample size. Horizontal dashed line represents the home range estimate in our complete dataset. Black bars represent the median, and white boxes the interquartile range (25th–75th percentile). The lower limits of the vertical lines represent the smallest value within 1.5 times the interquartile range below the 25th percentile, and the upper limits represent the largest value within 1.5 times the interquartile range above the 75th percentile for that month. Black dots are values outside of these limits. $N = 794$ data points for the full data set.

only vernacular identification), including consumption of fruit from 69 taxa (Electronic Supplementary Material [ESM] Table SI).

Edge Density

We estimated an edge density of 16.7 m/ha using the MCP home range, 19.5 m/ha using the 500-m grid cell home range, and 19.9 m/ha using the kernel 100% home range. Edge density was higher in the immediate vicinity of the home range (24.9 m/ha) than in the home range, and even higher in the larger surrounding neighborhood (38.6 m/ha) (Table I).

Seasonal Variation in Dietary Diversity, Habitat Use, and Spatial Distribution

Bonobos consumed lower fruit diversity/ha/h in dry season hotspots than in rainy season hotspots ($N_{\text{hotspots dry season}} = 4$, $N_{\text{hotspots rainy season}} = 14$, Wilcoxon test, $W = 7$, $P = 0.04$) (ESM Fig. S1), but we found no significant seasonal difference when comparing the taxonomic diversity of all items (/ha/h) consumed in hotspots (Wilcoxon test, $W = 11$, $P = 0.13$).

Bonobos spent a higher percentage of time in SFM during the dry season and in MFO and MFM during the rainy season (224 h of observation with habitat description during the rainy season and 180 h during the dry season, chi-squared test: $\chi^2 = 13.4$, $df = 3$, $P = 0.004$; the “other” category includes SIF, fallow, field, savanna, edge and road; Fig. 5a). Seasonal hotspots showed the same difference in habitat use (147 h of observation with habitat description during the rainy season and 105 h during the dry season, chi-squared test: $\chi^2 = 29.0$, $df = 3$, $P < 0.001$; Fig. 5b).

During the dry season bonobos used areas significantly closer to the seasonal weighted home range center than in the rainy season ($N_{\text{dry}} = 365$, $N_{\text{rainy}} = 429$, Wilcoxon test: $W = 126,540$, $P < 0.001$). Based on kernel analyses, dry season hotspots were more aggregated and less numerous than those in the rainy season, but did not differ in size (dry season: $N = 4$, mean area = 14.1 ha \pm SD 12.6, range: 2.4–29.8; rainy season: $N = 14$, mean area = 6.3 ha \pm SD 10.4, range: 0.1–40.6; Wilcoxon test: $W = 15$, $P = 0.19$; Fig. 6).

Table I Comparison of edge density in the bonobo home range in Manzano forest, DRC, based on observation points collected from February 2016 to January 2018 (using MCP, 500-m grid cell and kernel 100% methods) and the vicinity of their home range

	Length of edge (m)	Area (ha)	Edge density (m/ha)
Home range measured by MCP	33,906	2028	16.7
Home range measured by 500-m grid cell	25,356	1300	19.5
Home range measured by kernel 100%	18,612	937	19.9
Immediate vicinity circle radius = 4 km	124,473	5001	24.9
Larger area circle radius = 12 km excluding the 4 km radius circle	1,545,524	40,008	38.6

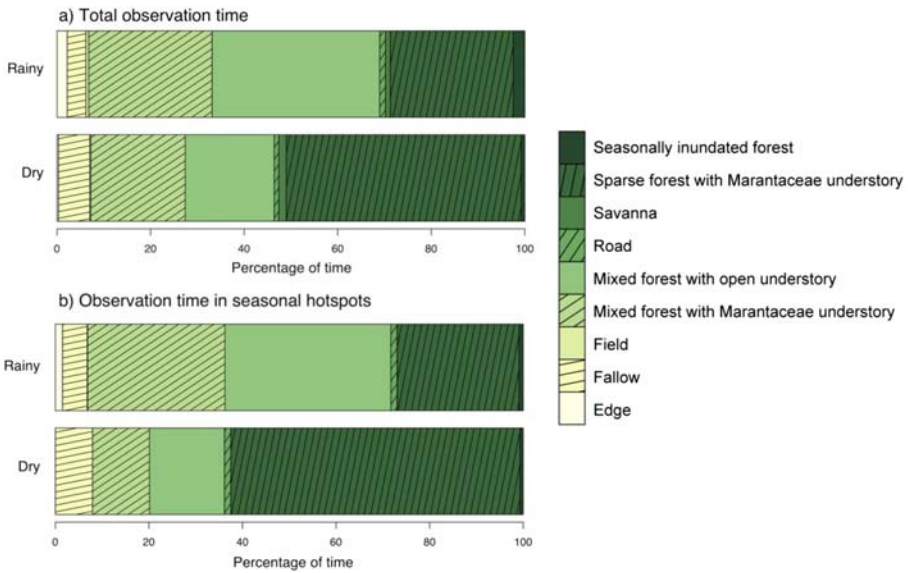


Fig. 5 Percentage of time bonobos spent in different habitat types in Manzano forest, DRC, in each season, **(a)** based on total observation time from February 2016 to January 2018 and **(b)** in seasonal hotspots.

Discussion

In this forest–savanna mosaic, bonobos predominantly used forested habitat and rarely used savannas in their home range. Furthermore, we found that the forest in their home range was substantially less fragmented than the surrounding area. We also identified seasonal differences in diet and space use: in the dry season bonobos consumed a lower diversity of fruit species, spent more time in sparse forest with Marantaceae understorey, and had a more aggregated spatial distribution than in the rainy season.

Home Range Size, Habitat Use, and Dietary Diversity

The home range of the Manzano bonobo community encompassed 20 km² based on the MCP method, 13 km² using the 500-m grid cell method and 9.4 km² based on

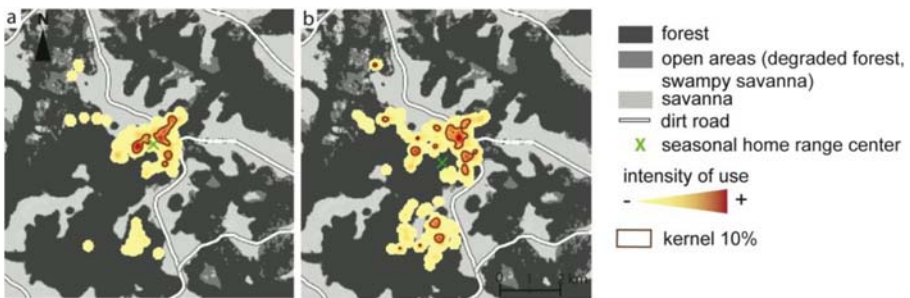


Fig. 6 Intensity of space use by bonobos in Manzano forest, DRC in **(a)** the dry season (kernel 10% representing 63% of observation time) and **(b)** the rainy season (kernel 10% representing 65% of observation time), based on data collected from February 2016 to January 2018.

Table II Comparison of home range size, community size, densities, and dietary diversity across bonobo study sites

Study site	Vegetation type	Home range size (km ²)	Community size	Density (ind./km ²)	Density mature individuals (ind./km ²)	Dietary diversity (nb of plant species)	References
Kokolopori	continuous forest	35 (kernel 95%)–47.36 (kernel 100%)	13	0.3–0.4 ^a	—	61	Lucchesi et al., 2020; Samuni et al., n.d. preprint
Lilungu	Continuous forest	—	—	—	—	—	—
Lomako	Continuous forest	40 (kernel 95%)–55.92 (kernel 100%)	45	0.8–1.1 ^a	—	61	—
		22 (method unknown)	~50	2	—	123	Sabater Pi and Veà 1994
		40 (method unknown)	8–41	8–13 ^a	—	81	Badrian and Badrian 1984; Badrian and Malenky 1984
Lui Kotale	Continuous forest	2–3.6 (MCP) 0.9–4.8 (kernel 95%)	33–35 mature individuals	—	0.7–0.9	133	Waller 2011
Lukuru	Forest–savanna mosaic	—	—	0.8–1	—	38	Beaune et al. 2013; Mohneke and Fruth 2008
Malebo (same area as Manzano)	Forest–savanna mosaic	—	—	0.5 (based on nest census)	—	61 (based on fecal analysis and food remains)	Thompson 1997
		—	—	2.2 (based on nest census)	—	—	Serexx et al. 2014, 2015
Manzano	Forest–savanna mosaic	20 (MCP) 13.8 (500-m grid cell) 9.3 (kernel 100%)	22–24	1.2–2.4	0.5–1	83	Inogwabini et al. 2008
Salonga National Park	Continuous forest	—	—	—	0.7 (based on nest census)	—	This study
		—	—	—	—	—	Reinartz et al. 2006

Table II (continued)

Study site	Vegetation type	Home range size (km ²)	Community size	Density (ind./km ²)	Density mature individuals (ind./km ²)	Dietary diversity (nb of plant species)	References
TL2	Continuous forest	—	—	—	0.4 (based on nest census)	—	IUCN and ICCN 2012
Wamba	Continuous forest	12.3–31.5 (500-m grid cell) 84 (MCP)	25–52 23–24	1.4–2.5 0.3 ^a	—	—	Hashimoto <i>et al.</i> 1998 Terada <i>et al.</i> 2015 Idani <i>et al.</i> 1994

^a Calculated from home range size and community size.

kernel density analyses. The variability of home range size estimates decreased and estimates converged toward the estimated size obtained using our complete data set (Fig. 4). These results indicate that the inferred home range size was not underestimated despite our limited survey effort due to financial constraints. Contrary to our prediction, the Manzano bonobos did not have a larger home range than bonobos living in continuous forest sites, where estimated home range sizes range 2–84 km² (Table II). The Manzano bonobos spent most of their time in forested habitats (97%), of which the composition is typical of Congo Basin forests (Pennec *et al.* 2016). A recent study on another bonobo community living 15 km from our study site found the same pattern with only 0.5% of observation points in savanna (Onishi *et al.* 2020).

Bonobos consumed 83 plant taxa during our study. This estimate is lower than the dietary diversity estimated in a previous study on the same bonobo community (107 plant taxa consumed; Narat 2014), probably due to differences in survey effort (two times more people dedicated to data collection in 2014) and interannual variation. Nonetheless, the dietary diversity is comparable with other more forested bonobo study sites (Table II) and more than double the dietary diversity reported at Lukuru, another bonobo study site described as a forest–savanna mosaic (38 plant taxa; Thompson 1997). This difference could be due to the habituation level of bonobos, the duration of the study, or to specific ecological characteristics of the study sites.

Although several primate species show intraspecific variation in home range size, habitat use, and dietary diversity according to the environment (Gazagne *et al.* 2020; Harris and Chapman 2007; Irwin 2008; Sha and Hanya 2013; Tesfaye *et al.* 2013), our results suggest that bonobos do not vary greatly in these parameters, even in the most fragmented environment known for bonobos. Chimpanzees living in savanna mosaic have larger home range (up to 10 times), lower densities (2–50 times), and a lower dietary diversity than those living in forested habitats (Baldwin *et al.* 1982; McGrew *et al.* 1988; Ogawa *et al.* 2007; Piel *et al.* 2017; Pruetz 2006; Pruetz and Bertolani 2009; Skinner and Pruetz 2012; van Leeuwen *et al.* 2020; *cf.* Basabose 2005). Moreover, although chimpanzees preferentially use forest patches in mosaic habitats, they also frequently use open habitats for foraging and nesting, unlike bonobos we studied (Hernandez-Aguilar *et al.* 2013; McGrew *et al.* 1988; Ndiaye *et al.* 2018; Piel *et al.* 2017; Pruetz and Bertolani 2009). As the main hypothesis to explain the pattern observed in chimpanzees is the high spatial dispersal of food resources, our results suggest that this forest–savanna mosaic has comparable food availability compared to continuous forest inhabited by bonobos. However, further comparisons of spatiotemporal variation in food availability and bonobo diet across study sites are necessary to further examine differences in food availability.

Edge Density and Forest Fragmentation

Because of differences in methodologies used to define the edge and calculate edge density, we cannot directly compare the edge density calculated for this single site to previous studies evaluating edge density at broader scales. However, the edge density within the bonobo home range at Manzano was higher than those previously described for a much larger area at Maringa–Lopori–Wamba (Hickey *et al.* 2012). As predicted, edge density within the Manzano bonobo home range was less than

half of the edge density of the larger surrounding area around their home range (20× the home range size), showing that bonobos tend to use less fragmented areas in this landscape. The effect of fragmented habitat on primates varies with the species' plasticity and with the matrix configuration (Bicca-Marques 2003; Boyle *et al.* 2013; Irwin 2008; Onderdonk and Chapman 2000; Tutin 1999). To explore the complex effect of fragmented landscape on bonobo ecology further, we should consider different scales and include parameters describing both the landscape (e.g., forest cover, number of patches, edge density) and the patches (e.g., size, shape, isolation), as highlighted previously for primates and other large terrestrial mammal species (Galan-Acedo *et al.* 2019; Garmendia *et al.* 2013). As we have observed another bonobo community (unhabituated but identifiable due to physical abnormalities) in the southwestern part of the same forest patch at least three times since 2012, we cannot exclude the presence of bonobos in more fragmented areas surrounding the habituated bonobo community. A regional investigation of bonobo presence would help to define which forest patches shelter bonobo communities and identify potential corridors and potential fragmentation thresholds that limit bonobo migration. As we found that bonobos rarely use savannas and we never observed nests in savannas, they may hinder bonobo migration. It is critical to assess migration patterns in such a fragmented forest region to complement previous genetic data, which indicated that the population in the western portion of the bonobo range is isolated from the population at the center of their range (Kawamoto *et al.* 2013).

Forest fragmentation is often due to human proximity, which increases human access to forest (Wade *et al.* 2003). In future studies, we need to independently assess human activities in this region to evaluate the direct influence of human proximity on bonobo spatial distribution at this site on the periphery of the bonobo home range. Previous studies demonstrate clear negative relationships between human presence and bonobo presence (Hickey *et al.* 2013; Reinartz *et al.* 2006). However, relatively high bonobo densities occur near villages for which eating bonobos is a taboo (Thompson *et al.* 2008), showing the need to consider the sociocultural context to assess the influence of humans on bonobo distribution, as shown for other primate species (Estrada *et al.* 2006; Riley and Fuentes 2011; Setchell *et al.* 2017; Strindberg *et al.* 2018).

Seasonality of Dietary Diversity, Habitat Use, and Spatial Distribution

During the dry season, bonobos consumed a lower diversity of fruit/ha/h, spent more time in SFM, and used fewer and more aggregated hotspots near the seasonal weighted home range center than during the rainy season. These results confirm our predictions about seasonal variation in bonobo diet, habitat use, and space use. These patterns may be in line with the consumption of fallback foods in SFM during the dry season. However, most of the fallback foods previously identified in neighboring bonobo communities in another forest patch of the region are not more abundant in SFM than in other forest types in the Manzano forest (Pennec *et al.* 2016; Serckx *et al.* 2015). Thus, bonobos may preferentially use SFM during the dry season to consume fallback foods other than those identified by Serckx *et al.* (2015) or this habitat preference could be due to other

parameters (for example, preferred foods may be present in SFM during the dry season). To explore the influence of spatiotemporal variation of food availability on diet, habitat use and space use in this forest–savanna mosaic more deeply, we need to test for preferred foods and potential fallback foods in Manzano forest using relevant data including feeding time and phenology, then determine if preferred foods and fallback foods are consumed more in specific habitat types. At Wamba, a more forested site, seasonal variability of food availability probably influences habitat use but not ranging patterns (Furuichi *et al.* 2008; Hashimoto *et al.* 1998; Terada *et al.* 2015). Therefore, gaps remain in our understanding of bonobo ecology concerning the effect of food availability on habitat use and space use, and their variation in relation to the environmental context.

Conclusion

Our findings provide insights into the ecology of bonobos living in a forest–savanna mosaic. The Manzano bonobos inhabit the most fragmented and open conditions known for this species, but have a similar home range size, density, and dietary diversity to those in continuous forest sites. Bonobos spent almost all their time in forest patches and selected the least fragmented areas in this forest–savanna mosaic, highlighting the need to focus conservation effort on the largest forest patches. However, we need to further explore the complex effect of fragmented habitats on bonobos and include more comprehensive landscape metrics and patch metrics in future studies. The seasonal patterns we observed in habitat use, dietary composition and spatial dispersion may be due to spatiotemporal variation in food availability, as shown in chimpanzees and many other primates species (e.g., Albert *et al.* 2013; Fiore 2003; Hanya *et al.* 2006; Porter *et al.* 2007; Robbins and McNeilage 2003; Twinomugisha and Chapman 2008). However, we need to explore the potential influence of spatiotemporal variation in food availability on diet, habitat use, ranging pattern, and activity budget, for example, by testing for preferred foods, fallback foods, and their distribution in specific habitat types. Such data will fill gaps in our understanding of bonobo ecology and help to improve bonobo conservation strategies, especially in this region where the community-based conservation approach maintains spatial overlap between humans and bonobos. Moreover, we need cross-site comparisons at several scales (between groups from a same subpopulation and between populations, Strier 2017) to improve interspecific comparisons, both for the *Pan* genus and for primates in general, to contribute to socioecological models and a more accurate assessment of the conservation status of these species.

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Authors Contribution FP and VN conceived and designed the study, encoded data, analyzed data, and wrote the manuscript. CG participated in the writing of the manuscript. LM encoded and analyzed data. CM and JCB supported data collection and protocol design. RL participated in data analyses.

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