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Modelling a Suitable Habitat for Nigeria–Cameroon Chimpanzees (*Pan troglodytes ellioti*, Matschie, 1914) in Mpem and Djim National Park, Central Cameroon

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ABSTRACT

Tropical forest mammalian communities, particularly those in ecological transition zones, are under constant threat from human activity. In many regions, there is a lack of baseline data on suitable habitats and the environmental factors influencing their suitability. Habitat suitability is a key metric for guiding conservation decisions and is essential for adaptive management of wildlife. These threats mostly affect great apes, including critically endangered Nigeria–Cameroon chimpanzees (*Pan troglodytes ellioti* Matschie, 1914), which is losing much of the suitable habitat required for reproduction and survival across its distribution range, including Central Cameroon. However, little is known about the habitat suitability of this species, particularly those who inhabit the Mpem and Djim National Parks in Central Cameroon. To address this knowledge gap, we used a common species distribution model (MaxEnt) to map and predict suitable habitats based on environmental factors that potentially affect habitat suitability. These environmental factors were related to a dataset of chimpanzee occurrence points recorded during line transect, camera trapping, and reconnaissance surveys (reccee) in the park. After covering an area of approximately 558.671 km^2 on 160.78 km, we found that up to 60% of the study area is unsuitable for chimpanzees. Only 20% of the study area was highly suitable for chimpanzees. Our results also showed that chimpanzees prefer the central and western parts of the study area, which are characterized mainly by high forest density. The MaxEnt model performed well (mean AUC = 0.859 ± 0.086) and identified a clear spatial pattern of suitable habitats. The most important predictors that positively affect habitat suitability for the Nigeria–Cameroon chimpanzee were NDVI (36.7%), canopy height (17.2%), annual mean temperature (16.3%), forest density (4.2%), distance to road (4.2%), and terrain aspect (3.2%). The suitability map identifies areas that are particularly important for conservation management, especially in the central and western parts of the park. Our study provides robust evidence that certain parts of Mpem and Djim National Park remain suitable habitats for chimpanzees. However, much more effort is needed from the government, park managers, national and international policymakers, and local communities to maintain these habitats and prevent severe damage to the survival of this species in the area. While this study provides a robust baseline for the conservation planning and management of chimpanzees in the area, it also fills an existing gap in the scientific literature on the ecology of Nigeria–Cameroon chimpanzee communities in Central Cameroon. Furthermore, it highlights the need for large-scale surveys in the future to evaluate the impact of efforts implemented thus far on the habitat suitability of this species.

1 | Introduction

The growing human population is causing tropical forests and the biodiversity within them to decline rapidly. In order to focus conservation effort on the most important areas, it is crucial to understand how species perceive and respond to their living environment. This includes tropical forests, which support more than 60% of all living species (Tranquilli et al. 2014). Projections of future global change indicate that biodiversity will continue to decline (Pereira et al. 2010). The threats faced by terrestrial mammals worldwide also include a decline in suitable habitats (Hansen et al. 2013). Great apes are among the mammals most affected mainly due to deforestation and habitat degradation (Fotang et al. 2021a; Morgan et al. 2013). Chimpanzees (*Pan troglodytes*) play an essential role in tropical forest regeneration. Their diet primarily consists of fruit, and they disperse the seeds of a wide variety of trees (Chapman 1995). Their extinction would alter ecosystem chains at local and global scales (Tranquilli et al. 2014). For example, Junker et al. (2012) found that there has been a sharp decrease in the amount of suitable habitat for great apes throughout Africa over the past 20 years. In addition to human impact, the occurrence and distribution of chimpanzees are significantly influenced by many environmental factors, including the extent and composition of forest cover (Yuh et al. 2019), topography (Fitzgerald et al. 2018; Jantz et al. 2016), climate (Kosheleff and Anderson 2009; Sesink Clee et al. 2015), and other anthropogenic factors, such as increasing human population density (Strindberg et al. 2018), road construction, and urbanization (Estrada et al. 2017). Therefore, the complexity of the interactions among these factors determines the distribution of great apes and the suitability of their habitats across their range (Junker et al. 2012).

Mammal distribution in Africa is often spatially and temporally heterogeneous, especially in Forest–Savannah Mosaic landscapes (FSM; Graham and Duda 2011). These mosaic habitats, which combine diverse land covers such as savannah and open or closed canopy forests, provide essential resources and conditions for species survival and reproduction (Pletcher et al. 2022). They are considered hotspots that sustain species (Araújo 2002; Hitchman et al. 2018). According to the International Union for Conservation of Nature (IUCN), the *P. troglodytes* taxon has been classified as an endangered species on the Red List since 1995 and all four subspecies (Western *P.t. verus*), Central (*P.t. troglodytes*), Eastern (*P. t. schweinfurthii*), and Nigeria-Cameroon chimpanzee (*P. troglodytes ellioti*; NCC, hereafter) still face population decline (Humle et al. 2016). The NCC is the most endangered of all the currently recognized chimpanzee subspecies, and it still occurs within a range that includes the forest-savannah mosaic of central Cameroon. Its total population is estimated to be between 3500 and 9000 individuals (Abwe et al. 2019), and it is confined to fragmented habitats west of the Sanaga River in Cameroon and eastern Nigeria, as well as isolated forest pockets in the Niger Delta (Abwe et al. 2019; Morgan et al. 2011; Oates et al. 2016). Despite being recognized as a distinct subspecies in 1997 (Gonder et al. 1997), the NCC remains critically understudied relative to its conspecifics. This lack of research severely constrains evidence-based conservation planning (Morgan et al. 2023; Tagg et al. 2013).

In response to the precarious status of this subspecies, the Regional Action Plan for the Conservation of the NCC (hereafter referred to as the 'Action Plan') was published in 2011 by the IUCN/SSC Primate Specialist Group and the Zoological Society of San Diego (Morgan et al. 2011). This landmark document represented a consensus among forestry and wildlife agencies from both nations, international NGOs, and university-based researchers. It formulated a set of priority actions designed to secure the long-term survival of NCC across its range. Crucially, the Action Plan identified specific 'NCC Planning Units' (NCCPUs) and emphasized that implementing its recommended measures would protect over 95% of the remaining population within its range. The Mpem and Djim National Park (hereafter referred to as MNDP) was established in 2004 by the Government of the Republic of Cameroon. It lies within a landscape matrix in central Cameroon. Despite its absence from the action plan, the park can be identified as a priority area for NCC conservation. The park comprises a mosaic of heterogeneous forests and savannahs, including gallery forests, swamp forests, and open woodlands, which favour the maintenance and survival of NCC in different habitats. However, despite its status as a nationally protected area, MNDP remains a poorly studied site. While several recent studies have been conducted in the area, including an assessment of mammals' occupancy and the environmental factors affecting their abundance, richness and detection (Fotsing, Kamkeng, Marcel Senge, et al. 2024; Fotsing et al. 2025; Fotsing, Kamkeng, and Zinner 2024; Fotsing and Kamkeng 2025), baseline information on NCC habitat suitability is virtually absent. The situation is made more urgent by escalating anthropogenic pressures, including subsistence agriculture, livestock grazing and hunting (Fotsing, Kamkeng, Marcel Senge, et al. 2024; Fotsing et al. 2025), as well as cultural beliefs and taboos surrounding NCC among the local population living on the edge of the national park (Fotsing, Kamkeng, and Zinner 2024). The Action Plan's key recommendations included evaluating habitat suitability and identifying NCC priority conservation areas, objectives with which this study aligns.

Great apes are widely used as flagship species to attract funding and attention and increasingly evaluated as umbrella species whose protection can benefit many co-occurring species (Kiribou et al. 2024). To inform conservation decisions, it is necessary to monitor such a population (Nichols and Williams 2006) and infer its habitat suitability with good precision and low bias using a species distribution model (hereafter referred to as an SDMs). Researchers and conservationists alike have employed various methods to map and predict the distribution of mammals across their range (Elith and Leathwick 2009). In the context of our study, the most used SDMs is the maximum entropy (MaxEnt) SDM (Elith et al. 2011; Phillips et al. 2006). This model was recently used to accurately predict the habitat suitability for NCC in the Kom-Wum Forest Reserve in Cameroon (Fotang et al. 2023). Similarly, MaxEnt has been widely used to map habitat suitability across diverse taxa, including pangolins (Kaimo et al. 2026; Mouafo et al. 2023; Sharma et al. 2020), bears and panda (Nazeri et al. 2012; Rather et al. 2021; Su et al. 2021; Sun et al. 2021), Ethiopian wolves (Berhanu et al. 2022), African buffalo (Mwaniki et al. 2025, 2026), and large ungulates

(Boitani et al. 2008; Paudel et al. 2015). It has also been applied to great apes (gorillas and chimpanzees) at both continental and local scales (Junker et al. 2012; Sesink Clee et al. 2015; see Table 1). Although previous studies have improved our understanding, information remains limited for several protected areas within the NCC range. Identifying suitable habitats is therefore important, especially as increasing human activities may contribute to habitat fragmentation and affect population distribution (Crooks et al. 2017; Heinicke et al. 2019a, 2019b; Kiribou et al. 2024). A key challenge for conservation planning is the limited understanding of the environmental and anthropogenic factors shaping species distribution in MNDP. For the NCC, substantial knowledge gaps remain, particularly concerning populations inhabiting the MNDP.

MaxEnt has emerged as an indispensable tool for addressing these gaps. It can predict the probability of a species occurring in a given landscape based on the relationship between occurrence records and environmental factors (Elith and Leathwick 2009). Studying the NCC population inhabiting the MNDP using MaxEnt could improve our understanding of their habitat requirements and the threats affecting their survival. In light of the limited information available on suitable NCC habitats in the MNDP, mapping these habitats is essential for developing site-specific conservation plans and enabling the long-term monitoring of NCC populations. To the best of our knowledge, no other studies have used three different methods (camera traps, line transects, and reconnaissance walks, hereafter, reccee) to apply MaxEnt to assess suitable NCC habitats in the MNDP. This study therefore aims to assess NCC habitat requirements by:

(1) mapping and predicting suitable NCC habitats using MaxEnt; (2) quantifying habitat suitability and determining the environmental factors affecting it; (3) evaluating the contribution of each environmental variable to predicting NCC habitat suitability in MNDP; (4) assessing the effect of each environmental variable on the probability of finding suitable chimpanzee habitats; and (5) proposing measures for species habitat protection and management.

Chimpanzees and gorillas are large-bodied primate species that frequently occur at high densities in dense tropical forests and wooded savannahs across equatorial Africa (Moore et al. 2018; Tutin and Fernandez 1993). These habitats are therefore areas of specific interest for great ape conservation (Tutin and Fernandez 1993). In Mbam–Djerem National Park, nest-based density estimates revealed higher chimpanzee densities in dense forests than in forest–savannah mosaics (Kamgang et al. 2018, 2020). Nest abundance was found to be associated with steep slopes, dense canopies, and higher altitudes (Kamgang et al. 2018). Based on these previous studies, we predict that dense forest, canopy height, and NDVI will be among the key variables determining NCC habitat suitability, whereas the human footprint will not since this is known to have a negative effect on wildlife distribution (Nickel et al. 2020). However, as the MNDP is a flat area, we do not expect slope to be positively associated with NCC habitat suitability as this has been shown to have a negative effect on mammals' occupancy in the area (Fotsing and Kamkeng 2025).

2 | Methods

2.1 | Study Area

The study was conducted in the Mpem and Djim National Park (MNDP, 5°00′-5°20′N, 11°30′-12°00′E) in the Central Region of Cameroon (Ntui Division) (Figure 1). MDNP was established in 2004 (law no. 2004/0886/PM). The park covers 974.8 km^2, with an average altitude of 640 m above sea level (Fotsing et al. 2025). The park lies in northern Congolian forest savannah mosaic which is home to both forest and savannah species (Fotsing et al. 2025). The annual minimum and maximum temperatures in the park are 22.9°C and 29.1°C, respectively. The average annual rainfall is 1500 mm (Fotsing et al. 2025). The climate is a classic Guinean type with four seasons: a long dry season (from mid-November to mid-March); a long rainy season (from mid-March to the end of June); a short dry season (from July to August); and a short rainy season (from September to mid-November).

2.2 | Data Collection

2.2.1 | Reconnaissance Walks and Line Transect

The study was conducted during the dry season between 16.09.2021 and 11.12.2021. Data collection was restricted to this period due to logistical and financial constraints, and no surveys were conducted during the rainy season. We first established 11 line transects of 2 km length each in the Western sector of the MDNP. The transects ran in the East–West direction and were evenly spaced by 2 km distance, partly in parallel or in a row (Figure 1). We used the reccee to access start-of-line transects and increase encounters with chimpanzee signs by following a predetermined direction (given by the GPS when doing a go to from the last camp position to the starting point of the transect), deviating less than 40 degrees to avoid obstacles and using large mammal tracks where possible to increase our movement speed, cover more area in less time and also reduce environmental impact (Gagbe et al. 2024; White and Edwards 2000); given our experience of working in the area and the limited funds available to cover the entire park with camera traps and line transects during this study, we randomly selected specific areas. We prioritized dense forests because previous studies in Mbam and Djerem, Kom-Wum Reserve and Ebo Forest in Cameroon demonstrated that NCC prefer dense forests to savannahs (Abwe et al. 2019; Fotang et al. 2023; Kamgang et al. 2018, 2020). We selected areas in the North, South and East of the park to ensure our occurrence data were representative. Because reccee can help collect more data in a reduced amount of time, this method is well suited to difficult and remote environments (White and Edwards 2000; Whytock et al. 2021); we then conducted additional reccee in these selected areas, specifically searching for signs of chimpanzee presence (We indicated area covered and reccee road map in Figure S1ab).

Our data collection team consisted of two local guides, a team leader (the first author) and an assistant (MSc student). During the reccee, we looked for NCC, signs of their presence while

TABLE 1 | Relationship between environmental variables of suitable great ape habitats and their occurrence in some study sites across Africa (modified from Fotang et al. 2023).

Predictor variable	Effect	Study Site/Country	Species/Subspecies	References
Elevation/Secondary Forest density/Distance to village/Aspect/Primary Forest density	Positive	Kom-Wum Forest Reserve, Cameroon	Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*)	Fotang et al. (2023)
Road density	Negative	FSC-certified forestry concession, Cameroon	Western lowland gorilla (*Gorilla gorilla gorilla*) and Central chimpanzee (*Pan troglodytes troglodytes*)	Kehou et al. (2021)
Dense forest cover	Positive	Lobéké National Park, Cameroon	Central chimpanzee (*Pan troglodytes troglodytes*)	Yuh et al. (2020)
Hunting pressure	Negative	Lobéké National Park, Cameroon	Central chimpanzee (*P. troglodytes troglodytes*)	Yuh et al. (2020)
Elevation/Forest density/nesting habitat distribution/human features	Positive	Dja Reserve Biosphere, Cameroon	Western lowland gorilla (*Gorilla gorilla gorilla*) and Central chimpanzee (*Pan troglodytes troglodytes*)	Tédonzong et al. (2020)
NDVI/Elevation/surface brightness/slope/distance to rivers	Positive	Greater Nimba Landscape, Guinea	Western chimpanzee (*Pan troglodytes verus*)	Fitzgerald et al. (2018)
Precipitation/food availability	Positive	Nyungwe National Park and Gishwati-Mukura National Park, Rwanda	Eastern chimpanzee (*Pan troglodytes schweinfurthii*)	Tuyishimire et al. (2020)
Elevation/Slope	Positive	Afi-Mbe-Okwangwo protected area of Cross River State, Nigeria	Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*)	Onojeghuo et al. (2015)
Topography/rainfall/temperature/seasonality/vegetation structure	Positive	Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*) range, Cameroon	Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*)	Sesink Clee et al. (2015)
Elevation/Slope/Distance to villages	Positive	Mawambi Hills, Cameroon	Cross River gorilla	Etiendem et al. (2013)

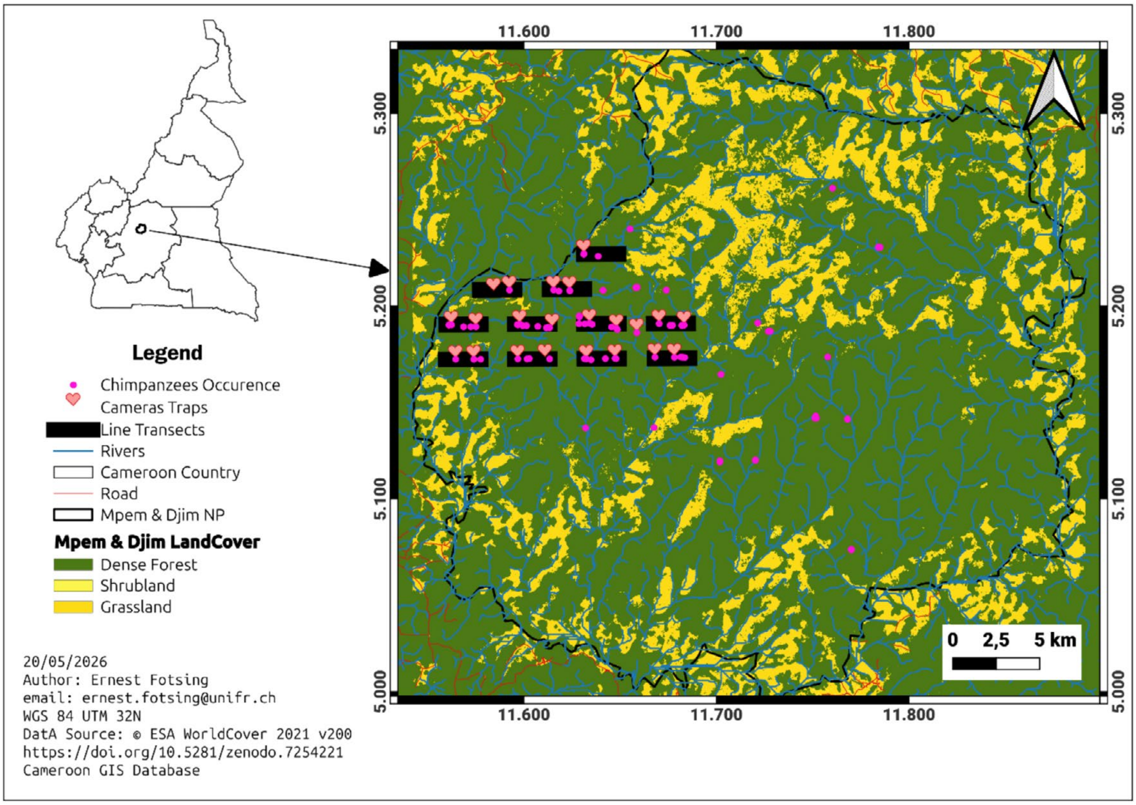

FIGURE 1 | Map of the Mpem and Djim National Park in central Cameroon with the position of the 11 lines transects (black lines) and the positions of the camera traps (orange star) along the lines as well as the occurrence point of chimpanzees recorded (violet dot). Top left inset map of the Republic of Cameroon with the park boundary located in the centre region of Cameroon. The land Cover map appearing is derived from WorldCover 2021 v200 (Zanaga et al. 2021).

data collection on the line transect followed the standing crop nest count (SCNC) method combined with the approach used by (Bessone et al. 2020; Fotsing et al. 2025). More specifically, along each transect and reccee, we recorded for each sign observed the geographic coordinates (using a handheld Global Positioning System, GPS), the type of sign (rest of food, footprint, faeces, nests, vocalization, tracks, tools used, etc.) associated with the number of signs, the distance we travelled, the height of the nest, the age class of each nest following the classification system developed by Tutin and Fernandez (1994), and the trees species used to build the nest was collected for later identification. Tool-use evidence was categorized, as chimpanzees are known to use plant-based tools to extract social insects such as bees, ants, and termites (Fowler and Sommer 2007), stone hammers to crack nuts (Morgan and Abwe 2006), and occasionally hunt vertebrate prey (Klein et al. 2021). At nesting sites, we searched for chimpanzee nests within a 50 m radius (White and Edwards 2000). To avoid replication and double counting of the same sign of presence, each sign/nest and group size was clearly identified based on their age and the distance among them following the methodological approach outlined in (N'Goran et al. 2016).

2.2.2 | Camera Trapping

While walking on transect, we also deployed 22 camera traps (CTs; Bushnell Trophy Trail Camera 20MP, infrared, Model 119717CW) along the 11 established line transects (Figure 1) in the West sector of the park. Two CTs with angle of view $\theta = 45°$, were set at 250 and 1750 m from the western start point of each transect. CTs spent approximately 3 months (81 ± 7 days) at each of the 22 locations (for more information about effort and other details please see Fotsing et al. 2025). To avoid any disturbance caused during data collection along the transects, cameras were systematically positioned 50 m to the north or south of the transect line, oriented north between 40 and 50 cm above the ground (Bessone et al. 2020). The cameras were set with motion sensors on high sensitivity (to increase detection), continuous triggering, that is, 60 s interval between consecutive videos, and the picture quality was set at high resolution (20 M pixels). The date, habitat and time for each camera were recorded during the installation.

2.2.3 | Environmental Covariates

To model the habitat suitability of chimpanzees within the study area, we used 16 enviromentals variables (see Table 2 for covariates description), including Aspect, Bio1, Bio12, Bio7, Bio8, slope, solar radiation, topographic position index (TPI), terrain ruggedness index (TRI), canopy height, Human footprint distance to river (nearest water source), distance to road, Normalized difference vegetation index (NDVI), density of primary forest (number of point per square kilometre) and density of grassland and savannah (number of point per square

TABLE 2 | Definitions, measurements, and descriptions of the 16 covariates used for habitat suitability modelling in MDNP. Some covariates were excluded from the analysis due to multicolinearity.

Covariates	Acronyms	Definition	Type
Human Footprint	HF	Anthrpogenic pressure	Continuous
Canopy height	CH	Global canopy height in metres	Continuous
Slope	Slope	Terrain slope (degree)	Continuous
TPI	TPI	Terrain position index	Continuous
TRI	TRI	Terrain Ruggedness index	Continuous
Distance to river	NeaDistRiv	Distance of camera positions to nearest water sources (m)	Continuous
Distance to raod	DistRoad	Distance of camera positions to nearest road (m)	Continuous
Grassland	Gr	Density of grassland savannah per km square	Continuous
Dense forest	DF	Density of forest per km square	Continuous
NodifvegI	NDVI	Normalized difference vegetation index (NDVI)	Continuous
Temperature	Bio1	Annual mean temperature (°C)	Continuous
Temperature	Bio7	Temperature annual range (BIO5-BIO6) (°C)	Continuous
Temperature	Bio8	Annual mean precipitation (mm^3)	Continuous
Temperature	Bio12	Annual precipitation (mm)	Continuous
Srad	Srad	Solar radiation ($kJ\,m^{-2}\,day^{-1}$)	
Aspect	A	Aspect of the terrain	Continuous

kilometre) derived from a variety of sources using remote sensing. First, we obtained topographic data as Geotif format by calculating TPI, TRI, and slope in degrees in R (V.4.5.2) using digital elevation model (DEM) data from Shuttle Radar Topography Mission 30 m resolution (Jarvis 2008). Similarly, from Bioclim website (Fick and Hijmans 2017), we obtained Geotif files (10 m spatial resolution) of solar radiation (Srad), annual mean temperature (BIO1), temperature annual range (Bio7), mean temperature of Wettest month (Bio8), as well as Annual Precipitation (Bio12).

Again, we obtained the world land cover data (10 m spatial resolution as Geotif file) from ESA WorldCover project [2021] website (Zanaga et al. 2021) that we reproject to our research site and crop it using our site shapefile in R. We also obtained Geotif file of a new, 30 m spatial resolution global forest canopy height map developed through the integration of the Global Ecosystem Dynamics Investigation (GEDI) lidar forest structure measurements and Landsat analysis-ready data time-series (Potapov et al. 2021) that we reprojected, cropped and masked (to ensure spatial extend and resolution fit) to our site (coordinate reference system used was WGS 84 zone 32 N). Using the same approach, we obtained human footprint raster file after dowloading the Global 100 m spatial resolution of Terrestrial Human Footprint (HFP-100) v1.2 as recommended by (Gassert et al. 2023). Secondly, we resampled the raster layers (using bilinear interpolation) of all environmental variables at 30 × 30 m grid cells (pixels) to achieve equal resolution of 30 × 30 m. Thirdly, we converted the raster layers to points data representing pixel centres (number of pixels) and used the Kernel Density estimation interpolation (KDE) trought the kde2d function in R (*MASS* package) with a bandwidth of 1 km to calculate the densities of dense forest, shrubland and grassland savannah per km^2. Following (Tarjuelo et al. 2017), the density of each of these habitats class was calculated as the number of cells of the two-dimensional KDE falling within the 95% defined region. Lastly, we used Google Earth images to digitize roads, rivers and villages, and then measured the distance to each feature as Euclidean distance using google engine code after we georectified the Google Earth images using GPS points collected from recognizable locations in the field, ensuring better alignment with ground truth data. Additionally, Normalized Difference Vegetation Index (NDVI), a widely used vegetation index in ecological studies due to its correlation with biodiversity (Gould 2000; Pettorelli et al. 2011) was computed to measure vegetation greenness. To achieve this, a Geotif Landsat 8 Operational Land Imager (OLI) Collection 2 Surface Reflectance product was obtained from the United States Geological Survey (USGS) for the dry season (22/12/2023), ensuring no cloud contamination (Vermote et al. 2016). The NDVI calculation was therefore performed in Python v3.11.0 using the formula available in (Borowik et al. 2013). Figure 2 illustrate some covariates used in the study.

2.3 | Data Analysis

2.3.1 | Occurrence Data From Camera Traps Data

First, we selected all images and videos containing animals and identified the species present to create a database of all recorded species (see Fotsing et al. 2025 for more details). We then filtered this database to include only camera traps with

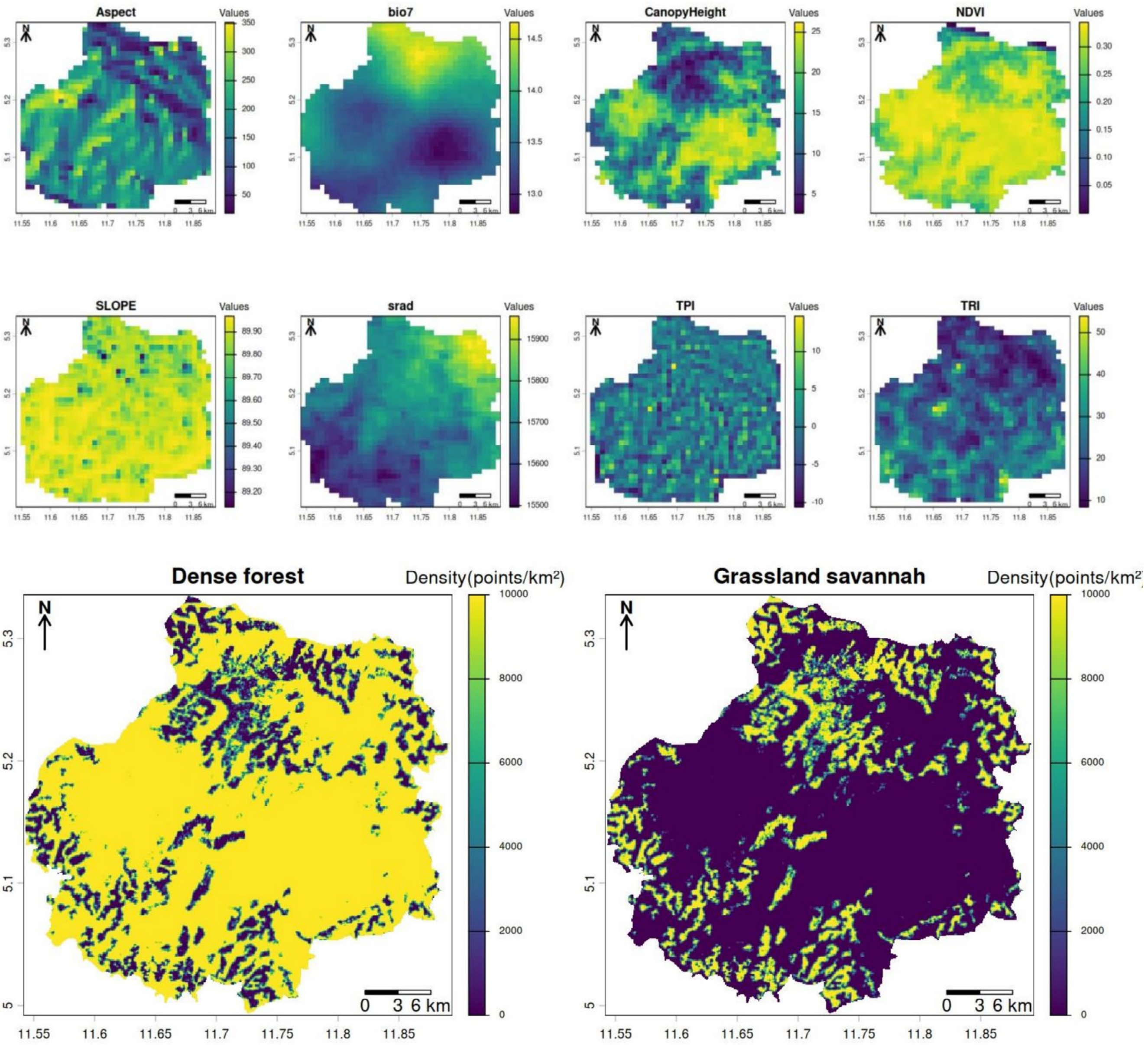

FIGURE 2 | Some environmental variables prepared and used for MaxEnt Modelling. Hint: Variables description and definition can be found in the Table 2 above.

at least one chimpanzee record, counting the number of different species recorded per location. Of the 22 CTs, 19 recorded at least one chimpanzee (Figure 3). After considering factors such as age, sex, morphology, body size, and the time/day interval between each record (at least 7 days in our case), we ultimately identified 36 distinct species across the 19 locations.

2.3.2 | Occurrence Data From Other Signs

In total, we supplemented our CTs data with 125 chimpanzees occurrence points including nesting locations (61), tool used sites (1), dung (7), feeding locations (35), vocalizations (11), tracks and footprints (10) over a survey effort of 160.78 km covering an area of approximately 558.68 km^2 (see Figure S1ab, File S1) for the survey period. All nests detected during the survey were constructed by chimpanzees, as gorillas are not present in this park. Combined with CTs points, we totally obtained 144 chimpanzees occurrence points. However, given the low detectability and conservation status of the species, combining multiple types of evidence (i.e., Different data collection methods) is a common and necessary approach in chimpanzee field studies to increase sample size and improve spatial coverage. Importantly, all recorded signs reliably indicate chimpanzees presence within their home range and are therefore informative for modelling habitat suitability. To reduce spatial autocorrelation and sampling bias, we applied spatial thinning using the *thin* function in the *spThin* R package (Aiello-Lammens et al. 2015). A minimum nearest-neighbour distance of 2.5 km was used, which is consistent with the spatial scale of chimpanzee movements and home range use (e.g., Boesch and Boesch-Achermann 2000; Moore et al. 2018). This procedure reduced the dataset from 144 to 97 occurrence points, which were retained for subsequent modelling.

FIGURE 3 | Image of the chimpanzees recorded by our camera traps. On the top left is the first individual passing through the camera, followed a few seconds later by another member of the family on the top right. The bottom left shows the chimpanzee nest, followed by the first author setting up the camera traps in the field (bottom right).

2.3.3 | Species Distribution Model

Prior to the analysis, we first check for collinearity between variables, using the package usdm in R (Naimi et al. 2014) setting a correlation threshold at 0.7. When the correlation between two variables was greater than a threshold value, we used the VIF (Generalized Variance Inflation Factors, Fox and Monette 1992) with a threshold set at 7 (O'Brien 2007) using the function vif of the package car (version 3.0-13; Fox and Weisberg 2019) to remove the variable with the greatest VIF value (see Table S1, File S3). The correlation matrix was calculated again until the threshold condition was satisfied (Naimi et al. 2014). We discarded distance to village, Elevation, Bio5, Bio6, Bio16, Bio17, Hillness and Roughness after analysing collinearity (see Figure S2a, File S2). Our final models had 16 uncorrelated environmental variables, including density of forest and grassland, Aspect, Bio1, Bio7, Bio8, Bio12, Slope, Solar radiation, TPI, TRI, Canopy height, NDVI, distance to roads and distance to rivers (see Figure S2b, File S2).

Habitat suitability for the Nigeria-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Mpem and Djim National Park in relation to environmental variables was modelled using the Maximum Entropy algorithm implemented in the MaxEnt R package version 3.3.3a (www.cs.princeton.edu/~schapire/maxEnt, Phillips et al. 2006) with the argument args = "biasfile = dens.ras" (see the description how to get this file below) and with default settings following (Kramer-Schadt et al. 2013) approach as follows: random test percentage = 25; regularization multiplier =3 and maximum iterations of 5000; maximum number of background points = 2000. We ran 10 replicates and used mean relative occurrence or suitability probabilities predicted for further analyses.

MaxEnt has multiple advantages and these are listed below. (1) First, it only uses a species' presence data and can produce accurate predictions even with incomplete datasets and small sample sizes (Phillips et al. 2006); (2) Rather than using data from only parts of the study area, environmental data derived from the entire area can be used (Phillips and Elith 2013). (3) Because actual absences are extremely difficult to gather, particularly for mobile species (or small population like NCC living within our study area), and require higher levels of sampling effort to ensure their reliability compared with presence data, MaxEnt employs presence data with background data (pseudo-absence data) from the study location (Mackenzie and Royle 2005); (4) In order to avoid overfitting, MaxEnt uses regularization, which is superior than variable-selection techniques frequently employed for regression-based models like general linear models (Phillips and Dudík 2008) (5). MaxEnt can correct for sampling bias by allowing the integration if a bias file in the analysis framework.

Due to unequal sampling effort across the study areas which can be a source of strong inaccuracy in the resulting model and could lead to incorrect predictions, we incorporated a sampling bias layer into the MaxEnt modelling framework. Five methods of bias correction exist in the literature (Fourcade et al. 2014). Following the workflow available in (Fourcade et al. 2014), we used the Bias File option (already implemented in MaxEnt) as our method of sampling bias correction. To achieve this step, we first create a sampling intensity (assuming that areas with higher record density reflect greater survey effort) map across the study area (Figure S3, File S4) and produced a bias grids (dens.ras file) by deriving a Gaussian kernel density surface map of the occurrence locations which was then normalized,

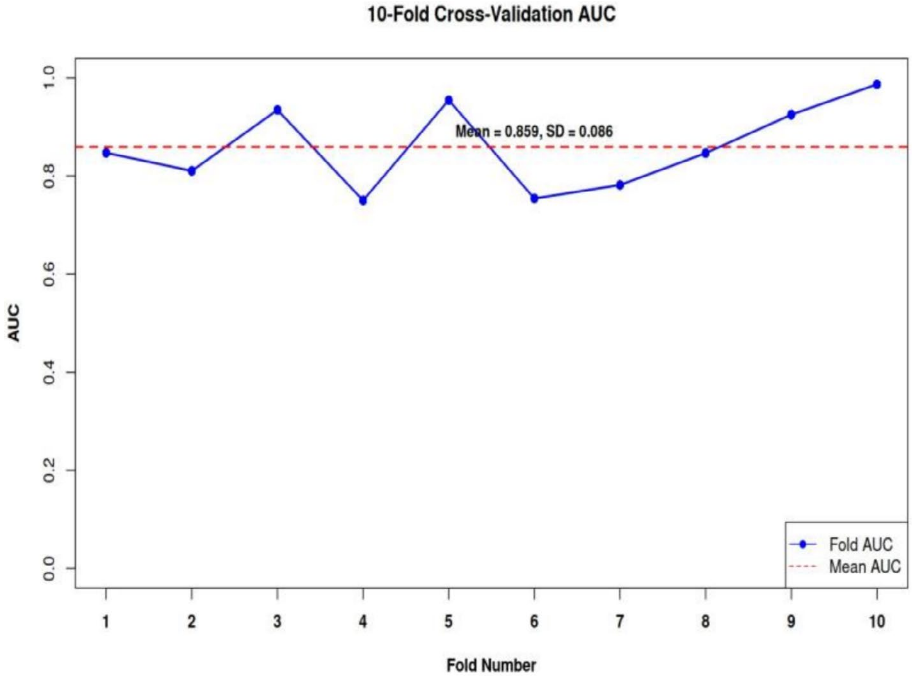

FIGURE 4 | Distribution of AUC values across 10 cross-validation folds for the MaxEnt Model.

following (Elith et al. 2010; Phillips et al. 2009) and used as a bias grid layer in MaxEnt. We further assessed the sensitivity of bias files by assigning values of 0.01 to cells with no records (Kramer-Schadt et al. 2013). This bias layer was provided to MaxEnt using the Bias File option, ensuring that background sampling was weighted according to survey effort (Dudı'k et al. 2005; Elith et al. 2010). The cells values in bias layer reflect sampling effort and give weight to random background data used for modelling. This approach constrains the selection of background points to areas with similar sampling probability as occurrence data, thereby reducing the influence of spatial sampling bias on model predictions. This method is widely used for presence-only models to improve model reliability when sampling effort is uneven across the study area (Dudı'k et al. 2005; Elith and Leathwick 2009; Phillips et al. 2009).

We used the final 97 chimpanzee occurrence points for modelling. The model was trained on 90% of the data (87 points) and tested on the remaining 10% (10 points). We added 2000 generated background points to the 87 training points, resulting in 2087 points in the final model. To evaluate the predictive performance of the MaxEnt model, we performed 10-fold crossvalidation applying spatial partitioning which reduces the effect of spatial autocorrelation and provides a more robust estimate of predictive performance. We then calculated the value of the area under the curve (AUC) of the receiver operating characteristic (ROC) for each fold (Yackulic et al. 2013). Once this was done, we used a raster-based predictor to predict habitat suitability across the study area as a continuous probability surface (0–1) and outputs were exported as Geotiff file. For each continuous predictor retained in the final model, we generated response curves showing the relationship between the variable and predicted habitat suitability, while all other predictors were held at their median values.

We further classify habitat suitability of chimpanzee in the MNDP into three habitat suitability index scores as follows: highly suitable (>0.6–1.0), moderately suitable (>0.4–0.6), low suitable (>0.2–0.4), and unsuitable habitat (>0–0.2). The classification thresholds used above follow previous work conducted in Cameroon on chimpanzees, including *P. troglodytes ellioti* (Fotang et al. 2023) and *Pan troglodytes troglodytes* (Yuh et al. 2020). Although these studies were conducted in predominantly forested environments, whereas our study area represents an ecotonal landscape, both subspecies exhibit broadly similar ecological requirements, particularly in relation to vegetation structure, food resource availability, and nesting behaviour and habitat preference mainly characterized by forest. Consequently, we consider that applying comparable habitat suitability thresholds is ecologically justified, as the key environmental gradients shaping chimpanzee distribution, such as canopy cover and primary productivity, are consistent across these systems. Finally, we measured the percentage of contribution of each environmental variable.

3 | Results

3.1 | Model Performance and Evaluation

Our predicted results show that MaxEnt models performed relatively well (i.e., better than fit) after 10 replicates. Despite some variability among folds, the MaxEnt model demonstrated good predicting performance with an AUC mean value of 0.859 ± 0.086 after 10 folds (Figure 4).

3.2 | Per Cent Contribution of Each Environmental Variable to the MaxEnt Model

The model outputs (Figure 5) show that the key factors contributing most to chimpanzee habitat suitability were NDVI (36.7%), canopy height (17.2%), Bio1 (mean annual temperature,

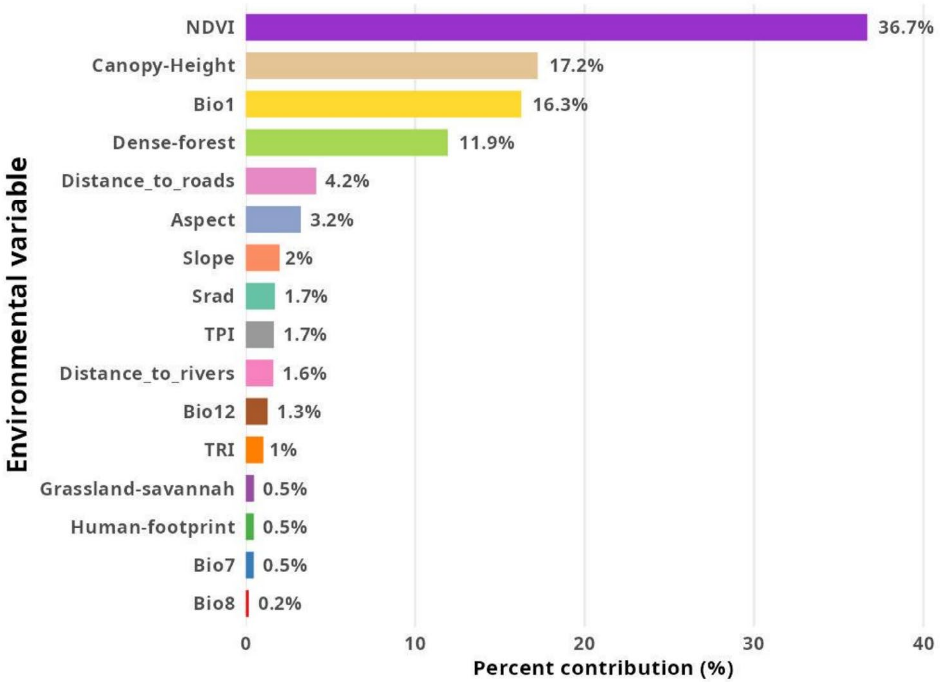

FIGURE 5 | Percent contribution of environmental variables to the MaxEnt habitat suitability model, ranked from highest to lowest importance.

16.3%) and dense forest (11.9%). These four factors accounted for a total of 82.1% of the total contribution. The contribution of distance to roads (4.2%), Aspect of the terrain (3.2%) and slope (2%) summed up to 9.4%, indicating a low contribution of these variables to habitat suitability prediction. Meanwhile, the contribution of the remaining variables summed up to 8.5%, indicating a very low contribution (Figure 5).

3.3 | Mapping and Quantification of Suitable Habitat

The results of our study show that suitable and moderately suitable chimpanzee habitats cover 20% and 10% of the entire national park, while low and unsuitable habitats cover 10% and 60%, respectively (Figure 6).

3.4 | Effects of Environmental Predictors: Variable Response Curves

The variable response curves from the MaxEnt model outputs (Figure 7) show that the effect of the predictor variables on the probability of finding suitable chimpanzee habitats varies with some having a positive effect and others a negative effect. The predicted suitability of chimpanzee habitats increased with aspect, Bio12, canopy height, and NDVI (positive effect). However, as these variables exhibited a positive slope, the probability of finding suitable chimpanzee habitats also increased as the values of these predictors increased. This suggests that chimpanzees are most likely to be found in areas that meet these conditions. Furthermore, the predicted habitat suitability value was higher below 24.3°C, 13.2°C, 15,700 kJ m^{-2} day^{-1} and 10 and 5 threads per inch for Bio1, Bio7, the human footprint, Srad, TPI and TRI, respectively. Conversely, the probability of chimpanzee occurrence decreased above these thresholds for each variable, indicating that the probability of finding a suitable chimpanzee habitat is high only below these threshold values. In contrast, chimpanzee occurrence decreased with slope that appears to be negatively correlated with the probability of finding a suitable chimpanzee habitat, indicating that chimpanzees do not inhabit areas with steep slopes. The probability of occurrence also increased in areas with a high number of forest density points (i.e., number of pixels) per square kilometre, and decreased in areas with a high number of grassland savannah points (i.e., number of pixels) per square kilometre, indicating that chimpanzees are more likely to be found in dense forests than in savannahs. Similarly, the probability of chimpanzee occurrence was higher closer to rivers, but not closer to roads.

4 | Discussion

The Nigeria-Cameroon chimpanzee (*P. troglodytes ellioti*) is the most endangered of all chimpanzee subspecies. Fewer than 6000 individuals remain in the wild throughout its range, which appears to be the Gulf of Guinea biodiversity hotspot in western Equatorial Africa (Sesink Clee et al. 2015). This subspecies is facing severe habitat fragmentation, primarily due to anthropogenic effects and climate change (Sesink Clee et al. 2015), which justifies the urgent action needed for its conservation. Among the actions that need to be taken are understanding their suitable areas and which environmental factors best predict their optimal habitats. SDMs such as MaxEnt have become central tools in primate conservation for achieving this goal, as this tool can translate presence data, which is usually obtained directly from the field, into spatially explicit predictions of current and future habitat suitability. Although MaxEnt models have been widely used to map suitable habitat

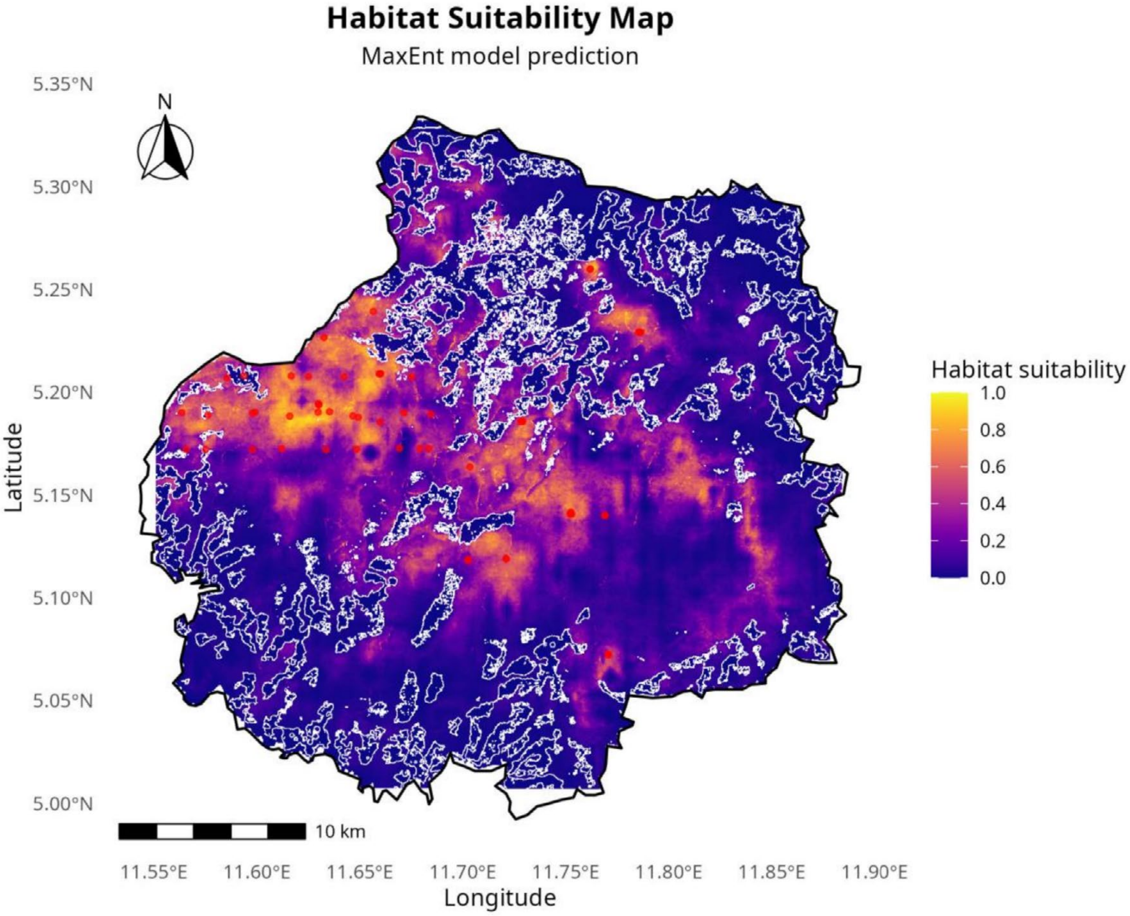

FIGURE 6 | Predicted habitat suitability map for chimpanzees in Mpem and Djim National Park (predicted value exhibited as continuous values on the map).

and key environmental drivers for Nigeria–Cameroon chimpanzees and other great apes across site, landscape, and continental scales (Abwe et al. 2019; Etiendem et al. 2013; Fitzgerald et al. 2018; Fotang et al. 2023; Yuh et al. 2020; Sesink Clee et al. 2015), substantial knowledge gaps remain, particularly with regard to populations inhabiting the ecotonal areas of Mpem and Djim National Parks in central Cameroon. This study was therefore undertaken to address this gap in literature. We then model in this study the habitat suitability and identified the most important biophysical variables contributing to habitat suitability of NCC in MNDP.

The results of our MaxEnt model demonstrated strong performance (AUC = 0.859), indicating a high capacity for distinguishing between suitable and unsuitable habitats. While this value is relatively high compared to other studies, it is slightly lower than the very strong performance reported for *P. t. ellioti* in Kom-Wum (AUC = 0.958) by Fotang et al. (2023). However, it is higher than the results obtained for NCC in Mount Cameroon National Park (AUC ≈ 0.70) and Greater Nimba (*P. t. verus*, AUC = 0.721) by (Mwambo 2010; Fitzgerald et al. 2018), respectively. Our result is, however, closely comparable to that for Western Rwanda (*P. t. schweinfurthii*, AUC = 0.87) reported by (Tuyishimire et al. 2020). The lower values reported for Lobéké (AUC ≈ 0.712 for chimpanzees and AUC ≈ 0.655 for gorillas) by Yuh et al. (2020) further highlight the variability across studies. Overall, model performance is generally good across studies, and our model falls within the upper range of reported performances, supporting its reliability and the usefulness of MaxEnt tool in providing accurate and reliable results. The use of spatial partitioning in cross-validation provides a more conservative and reliable evaluation compared to random partitioning, particularly when occurrence data are spatially clustered as in our case. While additional metrics such as omission rates and threshold-dependent indices were not computed, we now explicitly acknowledge this limitation in this manuscript and further study will need to take that into account.

Our findings also show that habitat suitability is strongly influenced by several environmental variables. The results indicate that only 20%, 10% and 10% of the area is highly, moderately or low suitable for chimpanzees, respectively. This suggests that suitable habitat for chimpanzees is spatially limited within the landscape. However, habitat suitability alone does not allow inference about population viability or extinction risk. Additional data on population size, connectivity, and demographic parameters would be required to assess long-term persistence. Nonetheless, the restricted extent of highly suitable habitat highlights the level of habitat degradation in the site and the importance of targeted conservation and habitat management efforts. While these values are not the lowest in comparison with those reported at other sites across this subspecies distributional range (e.g., 9% suitable area in Kom-Wum Reserve, Cameroon, 1.9% in Afi River Forest Reserve, Nigeria and 14.3% in Mbe

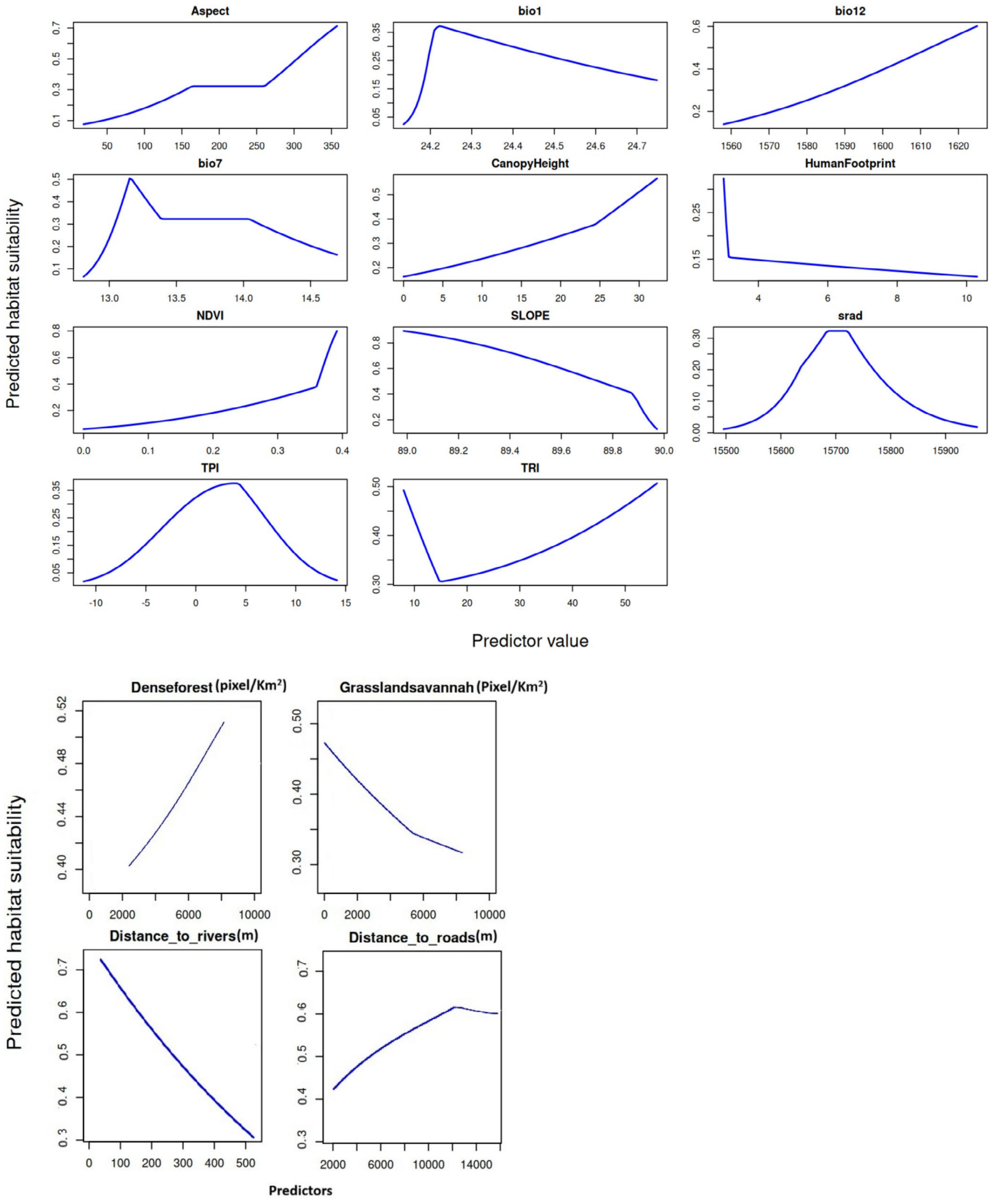

FIGURE 7 | Response curves showing the relationship between chimpanzee habitat suitability and the environmental variables used in the MaxEnt model.

Mountains, Nigeria), other studies have exhibited a greater size of suitable habitat, including 67%, 28%, 35%, 63%, 54.4% and 61% obtained by (Mwambo 2010; Fitzgerald et al. 2018; Tuyishimire et al. 2020; Yuh et al. 2020; Onojeghuo et al. 2015; Kehou et al. 2021) respectively. Nevertheless, these observations are alarming, in line with the prediction of Sesink Clee et al. (2015), who predicted that suitable habitat for *P. t. ellioti* in North-West Cameroon and Eastern Nigeria would remain largely unchanged until 2080 in all scenarios considered in his study, but that *P. t. ellioti* in Central Cameroon (half of the total population of this subspecies) would experience drastic reductions in its ecotone habitat over the next century. This highlights the urgent need for improved management of this protected area.

As predicted, we were able to identify important environmental factors that influence the probability of chimpanzee occurrence in the MNDP. Unlike the results of Fotang et al. (2023), our study showed that NDVI made the greatest contribution to predicting suitable chimpanzee habitats, with an increase in NDVI values coinciding with an increase in chimpanzee occurrence, suggesting a preference for greener habitats with higher food availability, as reported by (Tutin and Fernandez 1993). This finding is consistent with our previous studies demonstrating the positive relationship between species detection event and NDVI (Fotsing et al. 2025) and with that of Fitzgerald et al. (2018), who also identified NDVI as the most significant predictor of chimpanzee presence in the Greater Nimba Landscape in Guinea. In general, the NDVI index indicates active green vegetation (Campbell and Wynne 2011). The positive relationship between NDVI and the probability of occurrence suggests that chimpanzees may prefer areas with dense, healthy vegetation (Fitzgerald et al. 2018). Similarly, canopy height was the second-highest contributor to suitable chimpanzee habitat, and the probability of chimpanzee occurrence increased where the canopy was high, corroborating the observations of Koops (2011) and Koops et al. (2012), who showed that chimpanzees prefer larger trees with dense leaf cover in primary forests in which to build nests. Junker et al. (2012) have also demonstrated on a much larger scale that vegetation influences the behaviour of great apes, including chimpanzees.

The annual mean temperature was the third most important variable in predicting the presence of chimpanzees, with the probability of occurrence decreasing at higher temperatures. This corroborates the observations of Tuyishimire et al. (2020), who found that the high probability of chimpanzee occurrence in southern and northern Rwanda could be explained by climatic conditions such as high rainfall, humidity, and low temperatures. The effect of climate change on chimpanzee habitat suitability confirms the findings of Sesink Clee et al. (2015), who predicted under different scenarios that the optimal habitat of the Central *P. t. ellioti* subspecies is expected to undergo drastic losses and become less suitable over time.

Forest cover (%) is a key covariate influencing occupancy for many species and appeared in most top models (Downs et al. 2016; Zungu et al. 2020). Consistent with our recent study (see Fotsing et al. 2025) as well as those in Nigeria (Fasona et al. 2024) and Rwanda (Madsen and Broekhuis 2020), our findings highlight the importance of forest habitat (due to its shelter for many species) in shaping chimpanzee habitat suitability in MDNP. As Yuh et al. (2020) reported in Lobéké National Park, Cameroon, and Fotang et al. (2023) in Kom-Wum Reserve, Cameroon, our findings reveal that dense forest is the fourth landscape factor supporting chimpanzee habitat suitability. The positive relationship between chimpanzee occurrence and primary forest density could be explained by the fact that great apes, especially chimpanzees, usually prefer to build their nests in dense vegetation that is also rich in their preferred food (Koops 2011; Koops et al. 2012). According to Fotang et al. (2021a, 2021b) and Kamgang et al. (2020), chimpanzees typically select tall nesting trees with high first branches in inaccessible terrain, seemingly as a strategy to minimize their exposure to hunters. However, in Sebitoli, Kibale National Park in Uganda, MaxEnt models linked the presence of chimpanzees to three food-related variables: proximity to forest edges with crop fields, proximity to a road bordered by herbaceous vegetation, and the distribution of wild fruit trees, which illustrates a lack of avoidance of human hyperproximity when high-value foods are available (Bortolamiol et al. 2016). However, in Mbam Djerem National Park in Cameroon, nest-based density estimates showed that chimpanzee density is higher in dense forest than in forest-savannah mosaics (Kamgang et al. 2020). Nest abundance was also found to be associated with steep slopes, dense canopies, and higher altitudes (Kamgang et al. 2018). A ground-truthing study of three *P. t. ellioti* sites across rainforest, ecotone, and human-modified forest demonstrated that ecotones and anthropogenic habitats can provide abundant fruit resources, challenging the assumption that only intact rainforest offers a viable habitat (Abwe et al. 2019). Together, these studies reinforce the idea that conservation planning for *P. t. ellioti* should encompass ecotones and human-modified landscapes, as well as protected forests (Sesink Clee et al. 2015; Abwe et al. 2019; Fotang et al. 2023).

Other factors that support chimpanzee habitat suitability, albeit less importantly, were distance to roads and rivers, human footprint, grassland savannah density, TPI, Bio12 (annual precipitation), and TRI. These factors have also been reported in many studies as influencing the probability of occurrence or detectability of chimpanzees. For instance, a recent study in MNDP revealed positive correlations between TPI, distance to rivers, and roads to species detection events (Fotsing and Kamkeng 2025). Our results are consistent with those of Vanthomme et al. (2013) in Gabon, who argued that road construction facilitates hunter access to the park, and with those of Fotang et al. (2023), who reported that chimpanzees avoided roads in the Kom-Wum reserve in Cameroon because roads lead to rice fields and are usually surrounded by maize and bean fields, which are frequently used by people. Our results also align with data from south-western Sierra Leone, where chimpanzees avoid roads (Garriga et al. 2019), though this was not observed in Cantanhez National Park, Guinea-Bissau (Bersacola et al. 2021). Although Koerner et al. (2018) demonstrated that the impact of human-related factors varies significantly between species, our study is consistent with the findings of Fitzgerald et al. (2018), who observed an increased occurrence probability of chimpanzees in proximity to rivers, as well as the study of Hawkins et al. (2003), which revealed that distance to rivers influenced the presence of lions, leopards, wild dogs, and elephants. The human footprint was also among the predictors of chimpanzee occurrence in line with the observation of Yuh et al. (2020) who also found hunting pressure among the key variable shaping chimpanzees and gorilla occurrence in Lobeke National Park, Cameroon.

Although MaxEnt is now the most common and useful tool for conservation practitioners using occurrence data to train SDMs, these data are often spatially biased probably due to uneven sampling effort, easily accessed areas or geographical sampling bias (Fourcade et al. 2014; Kramer-Schadt et al. 2013). This spatial bias generally leads to inaccurate models or affects variable importance in the model. Incorporating a bias file into the modelling framework can substantially improve predictions of species distributions (Dudík et al. 2005; Elith et al. 2010; Fourcade et al. 2014; Kramer-Schadt et al. 2013; Phillips et al. 2009). For chimpanzees, habitat use is strongly linked to the availability of key resources such as fruiting trees, nesting sites, and canopy structure, as well as to anthropogenic pressures (Fotang et al. 2023; Fotsing and Kamkeng 2025; Kamgang et al. 2018, 2020; Tutin and Fernandez 1993). In our study, the concentration of occurrence records in the more intensively sampled western sector may have probably biased model outputs and is considered as the main limitation of this study. Nevertheless, the use of a bias file helps account for these limitations; we consider the current results to be reliable, while acknowledging that larger datasets would further strengthen conclusions. Although the bias correction file reduces sampling bias, some residual effects may persist. This likely overrepresents environmental conditions from that area. Consequently, variables such as NDVI and canopy height, which are good proxies of mammals' occupancy including chimpanzees' occurrence in the site (see Fotsing et al. 2025), may appear as stronger predictors than under a more balanced sampling design. Such bias can lead to inflated suitability predictions in well-sampled areas while underestimating suitability in less-sampled regions of the park (Elith et al. 2011). However, chimpanzees may also use a broader range of habitats, including ecotones or more open areas, which are often under-sampled due to accessibility or logistical constraints. Therefore, the predicted habitat suitability patterns should be interpreted with caution, particularly in under-sampled areas. Data were collected only during the dry season. Absence of the raining season data may have also had an impact on our prediction. Future work should prioritize more systematic and spatially balanced surveys during both seasons to re-evaluate model accuracy and support more robust conservation planning. From our field experience, the northern sector of the park is dominated by tall savannah grasslands (most often inaccessible and difficult to monitor), which are rarely used by chimpanzees. In contrast, the rest of the park consists mainly of forest, ecotone, and gallery forest habitats where chimpanzee activity is concentrated. Therefore, the identification of NDVI and canopy height as key predictors likely reflects genuine ecological preferences and would remain robust even with more spatially balanced sampling.

The occurrence dataset combined multiple sign types (e.g., nests, dung, vocalizations, tracks, and camera trap detections) to improve sample size and spatial coverage. These indicators reflect chimpanzee presence across different temporal scales and are commonly used for elusive species. However, combining them may introduce temporal and ecological heterogeneity, as they represent different behavioural processes. Therefore, model outputs should be interpreted as general habitat use patterns rather than fine-scale habitat selection.

In conclusion, this study demonstrates that species distribution modelling is an effective approach for identifying suitable habitat for chimpanzees in MDNP, as well as the key environmental predictors (e.g., NDVI, canopy height, temperature, and dense forest density) shaping their distribution. With only a limited proportion of MNDP classified as highly suitable (only 20%), our findings highlight the need to strengthen habitat protection and management, while exploring complementary conservation strategies in collaboration with local communities to support long-term chimpanzee persistence. Given the challenges of maintaining suitable habitat, we recommend further investigation of chimpanzee feeding ecology and habitat use to better inform conservation strategies. We also suggest regular monitoring through repeated surveys (every 3–5 years) to track changes in population trends and habitat suitability over time.

This study provides a robust baseline for future research. Further work should expand surveys to cover the entire park and improve habitat models by incorporating additional anthropogenic and ecological variables such as livestock farming and poaching (Fotsing et al. 2025), hunting pressure (e.g., Yuh et al. 2020), population density, food availability, disease, presence or absence of guards, density of trees per square kilometre (Morgan et al. 2018; Tranquilli et al. 2012, 2014), as well as other conservation activities aimed at reducing human impacts (Tranquilli et al. 2012). Increasing occurrence data through complementary methods such as bioacoustic surveys would also strengthen analyses. Finally, year-round data collection is needed to assess seasonal variation in habitat use and better understand chimpanzee responses to environmental change.

Author Contributions

Ernest D. B. Fotsing: conceptualization, data curation, methodology, data collection, data analysis, writing grant proposal, preparing the original and final draft and supervision. **Meigang M. F. Kamkeng:** conceptualization, methodology, data curation, data collection, data analysis, project administration, writing and editing the draft. **Ogenrwot Ronald:** data curation. All authors gave their final approval for publication.

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Ethics Statement

This research was also conducted following the principles of the American Society of Primatologists and the International Society of

Ethnobiology (ISE) Code of Ethics (ISE. 2006) for the ethical treatment of nonhuman and human primates.

Conflicts of Interest

The authors declared no conflicts of interest.

Data Availability Statement

All data are archived in the first author Github repository account and can be found at https://github.com/Fotsing2023/Mesocarnivores-ecology-in-MDNP-Cameroon.git.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1a:** Total area surveyed (558.671 km^2). **Figure S1b:** Total length of reccee walked by the research team (160.78 km in total). **Figure S2a:** Correlation plot among all predictors. **Figure S2b:** Correlation plot among all predictors after removed correlated variables. **Figure S3:** Survey effort intensity (Kernel Density estimation). **Table S1:** Covariates, VIF values, definitions and measurements used to model chimpanzee habitat suitability in MDNP. Note: some covariates (elevation and distance to village) were excluded from the analysis due to multicollinearity.