

Seasonal distribution model of African elephants (*Loxodonta africana*) under a changing environment and land use in Omo National Park, Ethiopia

Girma Timer Jeza^{1*}, Afework Bekele²

¹Ethiopian Wildlife Conservation Authority, PO Box 386, Addis Ababa, Ethiopia

²Department of Zoological Sciences, Addis Ababa University, PO Box 1176, Addis Ababa, Ethiopia

*Email: girmatimer@gmail.com

Received: 15 February 2023 / Revised: 25 March 2023 / Accepted: 29 March 2023/ Published online: 30 March 2023.

How to cite: Jeza, G.T., Bekele, A. (2023). Seasonal distribution model of African elephants (*Loxodonta africana*) under a changing environment and land use in Omo National Park, Ethiopia, Journal of Wildlife and Biodiversity, 7(3), 96-117. DOI: <https://doi.org/10.5281/zenodo.7783039>

Abstract

Overwhelming anthropogenic activities combined with the effects of climate change pose extreme threats to wildlife resources, resulting in habitat loss and the decline of many mammal species. The African elephant (*Loxodonta africana*) is an endangered large mammal occurring in some protected areas in Africa. In this study, a species distribution model using the spatial maximum entropy algorithm was developed to determine the geographic extent and distribution of the elephant in Omo National Park. Elephant surveys were conducted in the wet and dry seasons in 2021 and 2022. Occurrence data and the 12 predictor variables were processed and framed, and the corresponding models were built for two seasons separately in the Geographic Information System and R software. The modeled seasonal combined results of the elephant range have a total area of 1999 km² (39% of the study area), of which 365 km² (7.2%) is optimal, 748 km² (14.7%) is suitable, and 886 km² (17.5%) is moderately suitable. Distance to the rivers, distance to the canals, and land use/land cover contributed most to predicting habitat suitability (10 and 49%, 40 and 16%, and 34 and 29%, respectively) during the wet and dry seasons. Habitat suitability increases as the mean diurnal range (bio 2) and temperature seasonality (bio 4) increase in both seasons and as the distance to rivers increases and decreases during the wet and dry seasons, respectively. Performance ratings were high, with AUC values (area under receiver operating curves) of 0.877 and 0.952 for the wet and dry seasons, respectively. Changing environmental variables and land use interact to influence habitat suitability and wildlife distribution. Our results are vital for understanding the influence of these variables on elephant distribution and movement and, thus, for adaptive management and migration corridor design to maintain species viability and ecosystem functionality in the study area.

Keywords: Environmental variables, habitat suitability modelling, *Loxodonta africana*, MAXENT model, model prediction

Introduction

Species distribution modeling (SDM) is used in many areas of ecology, climate change research, conservation, and ecosystem management. It uses computer algorithms and environmental data to predict the spatial and temporal distribution of a species and the current and/or future suitability of its habitat and to set priorities for conservation (Baldwin, 2009; Cowley et al., 2000; Elith et al., 2006, 2009; Evangelista et al., 2008; Gibson et al., 2004; Guisa, 2011; Thorn et al., & Zimmermann, 2000; Pearson et al., 2007; Stockwell & Peterson, 2002; Thomaes et al., 2008; Thorn et al., 2009; York et al., 2011). SDM uses geostatistical analysis to establish relationships between species' geographic occurrence points and environmental variables to define the species' ecological niche (Elith et al., 2006). According to Pearson et al. (2007), SDM is very important for determining the spatial and temporal distribution of suitable habitats based on the requirements of target species. Monitoring and evaluation of habitats and species distributions are essential for the appropriate management of wildlife populations and the formulation of conservation actions and strategies (Smeraldo et al., 2021; Su et al., 2021; Zhu et al., 2020). Effective wildlife management and the development of appropriate strategies and plans depend on reliable information about species distributions and the corresponding required environmental variables. Wildlife distribution patterns and habitat use depend on available abiotic and biotic components of ecosystems that influence ecological requirements in their natural geographic ranges. Several statistical modeling algorithms have been used to predict species distribution patterns (Antoine Guisan et al., 2002; Booth et al., 2014; Breiman, 2001; Carpenter et al., 1993; Phillips et al., 2006).

Maximum entropy (MAXENT) is a general method or software that has become a valuable tool for predicting or inferring species distributions (Phillips et al., 2004; 2006). The MAXENT model combines presence-only data with selected environmental variables to create a probability model of species distribution. Several studies on SDMs have shown that MAXENT performs better than other similar models and is widely used to model ecological niches for many species (Elith et al., 2006; Evangelista et al., 2008; Hernandez et al., 2006). In this study, a MAXENT algorithm was used to model the habitat suitability and distribution pattern of the African elephant (*L. africana*) in Omo National Park, Ethiopia.

African elephants (*L. africana*) are an endangered large mammal occurring in some conservation areas in African countries (Gobush & Wittemyer, 2021; IUCN, 2021; Nelleman et al., 2013). In Ethiopia, elephants had a large range in the northern, central, southwestern, and southern areas of the Rift Valley (Dejene, 2016; Yirmed, 2010). However, these populations have been extirpated over time and restricted in some elephant range-protected areas (Chase et al., 2016; Dejene, 2016; Ethiopian Wildlife

Conservation Authority (EWCA), 2015; Lindsay et al., 2017; Thouless et al., 2016). The elephant population in Ethiopia is estimated to be between 1900 and 2151 (Ethiopian Wildlife Conservation Authority (EWCA), 2015). Habitat loss and fragmentation and elephant hunting for ivory are the main reasons for population decline (Dejene, 2016; Ethiopian Wildlife Conservation Authority (EWCA), 2015). Similarly, the number of African elephants has shown declining trends over the past years in Omo National Park (Ethiopian Wildlife Conservation Authority [EWCA], 2015; Largen & Yalden, 1987; Stephenson & Mizuno, 1978).

Understanding the drivers behind the distribution and habitat use of African elephants is fundamental to developing models of suitable habitats and describing their distribution patterns from presence-only data. This study aims to use the MAXENT model to predict the geographic extent of suitable habitats, potential corridors, and distribution of African elephants using predictor variables. The study seeks to understand how the variables affect African elephant dispersal and habitat use in the Omo National Park landscape during both the wet and dry seasons.

Materials and methods

Study area

Omo National Park is one of the 27 national parks in Ethiopia (Gizaw, 2021). It is located in the lower Omo Valley and is the largest protected area in the country. It lies between 05° 30' to 06° 40' N and 35° 20' to 36° 00' E and has a total estimated area of 5,013 km² (Figure 1). The area shows both temporal and spatial variations in precipitation, humidity, and temperature. Rainfall in the area is low and erratic, with a mean annual rainfall below 482 mm (Ethiopian Sugar Corporation (ESC), 2019). A bimodal rainfall period is observed: the long rains usually start in March and last until the end of April, while the short rains fall in October and November. The driest season is from December to January. Limited rain may fall in any month of the year (Cherie Enawgaw, 1996). The seasonal average temperature ranges from 23 to 36 °C, although the maximum daily temperature in February can reach 40 °C and the minimum daily temperature in April can drop to 16 °C (Ethiopian Sugar Corporation (ESC), 2019). The predominant topographic features of the park are flat, grassy plains surrounded by Maji Mountain to the west and the Sai Escarpment to the north; the Omo and Nerube rivers flow to the east and south, respectively (Figure 1). Elevations range from 450 to 1541 m a.s.l. The park is characterized by extensive savannah plains interspersed with wooded grasslands associated with deciduous forests and riparian formations (Lamprey, 1994; Stephenson & Mizuno, 1978). The park comprises extensive open grassland interspersed with woodland and herbaceous and bushy vegetation at the edges.

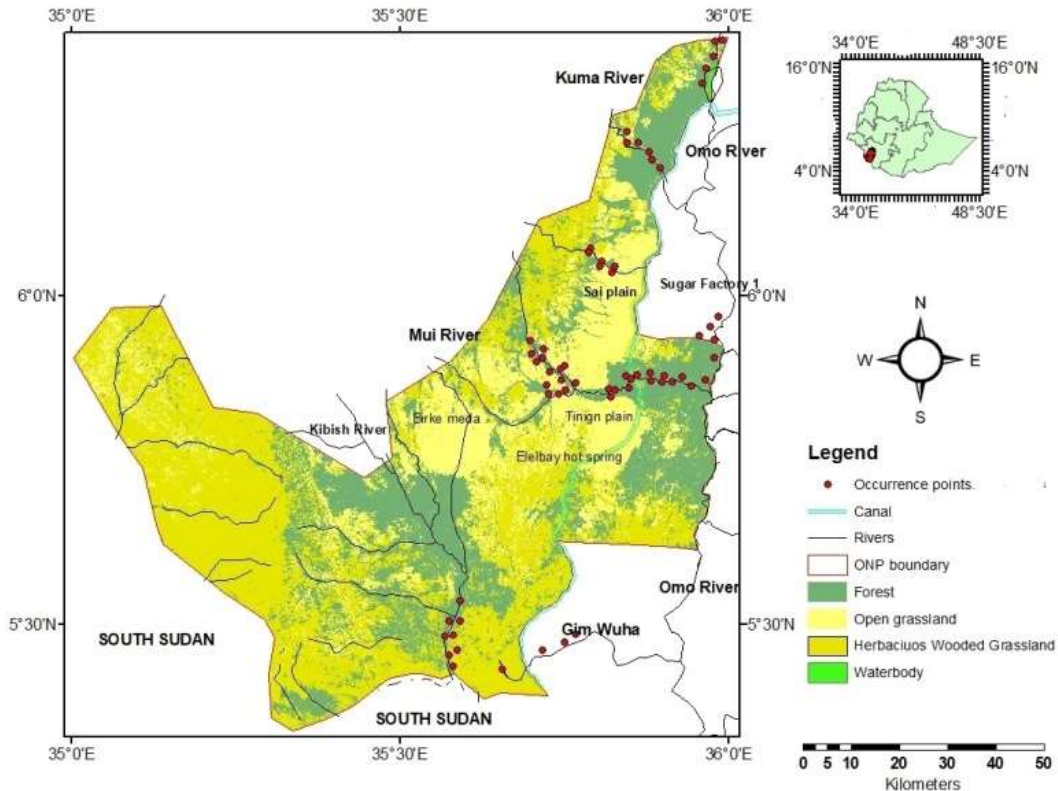


Figure 1. Map of the study area.

Omo National Park was established in the late 1950s, when most of Ethiopia's wildlife-protected areas were designated (Hillman, 1993). The park has numerous water sources and is rich in wildlife resources. So far, 73 large and medium-sized mammals and 312 bird species have been recorded, two of which are endemic to Ethiopia (Asbl & Fortrop, 2008; Cherie Enawgaw, 1996; Ethiopian Wildlife Natural History Society (EWNHS), 1996; Ferguson, 2021). Although there are growing anthropogenic activities that affect natural connectivity, the park has connections and corridors with the adjacent protected areas (Tama Wildlife Reserve and Mago National Park located on the other side of the Omo River) (Asbl & Fortrop, 2008; Cherie Enawgaw et al., 2011; Yirmed, 2010).

In Omo National Park, the number of African elephants was estimated at 700–1000 in 1978 (Stephenson & Mizuno, 1978). Largen and Yalden (1987), estimated 800 elephants, and more recently the Ethiopian Wildlife Conservation Authority (EWCA) (2015), reported 450 elephants. The Park is customary grazing land for the Nagngatom and Surma pastoral communities, resulting in competition with livestock for grass and water, and illegal hunting is considered a major threat to the survival of African elephants and other endangered species. In addition, land grabbing for large-scale agricultural investments, including ongoing sugarcane cultivation and sugar factory development, road construction, and the establishment of temporary and permanent camping villages in the park have led

to extreme fragmentation of the species' natural habitats and loss of connectivity. Connectivity is critical for the conservation and management of species for successful reproduction (Cleary et al., 2017; Keeley et al., 2017; Liu et al., 2018).

Data collection

Two weeks of reconnaissance were conducted in the study area in October 2021 to collect basic information on the location, topography, habitat types, climatic conditions, and approximate size of the different habitats in the area. During this survey, line transects representing the most important habitat types in the National Park were randomly laid (Koster and Hart, 1998).

Surveys were conducted seasonally from 2021 to 2022, during the wet season (March and April) and the dry season (December and January) in both years. The distinction between wet and dry seasons was based on the change in rainfall patterns. To collect basic information on African elephant populations in riverine forests, wooded grasslands, and open grasslands, a line transect census method was used, as used by Ratti et al. (1983) and Sutherland (2006) for various mammals. The stratification and arrangement of transects were based on the vegetation types considered as the sampling unit or survey area, and each of these blocks was divided into different blocks or grids of different sizes depending on vegetation type, visibility, and topography. Transect lines were roughly parallel and systematically spaced 1500–2000 m perpendicular to the main watercourses of the area. Since most of the tributaries (Mui, Kuma, and Sherma) of the Omo River flow from west to east, the transect lines were oriented from north to south, while the transect lines along the Omo River run from east to west as it flows from north to south. This orientation was chosen to maximize data collection while taking into account landscape conditions and minimizing sampling error (Norton-Griffiths, 1978). The length of transects varied between 5 and 16 km, depending on the size and landscape of the survey zone. Transects in each survey zone were fixed (Norton-Griffiths, 1978). The start and end points of each transect, the locations of African elephants, and indirect detections were recorded using a GPS (WGS 1984). The total area sampled was 501 km², representing approximately 20% of the known elephant range in the study area (Asbl & Fortrop, 2008; Cherie Enawgaw et al., 2011). Visibility varied according to vegetation type or census zones. The survey period was between 6:00 and 10:00 in the morning and between 16:00 and 18:00 in the afternoon, when wildlife was most active. In addition to the transect counts, a ground survey was conducted to obtain additional information on water bodies, human settlements and farming, roads, the herd sizes of African elephants, and the recording of dung piles and footprints. Coordinates from indirect and direct observations of African elephants were recorded using GPS. All records were independently checked for spatial auto-correlation in ArcGIS (version 10.8) using analyses of average nearest neighbours (Moran's index = 0.60, z-score = 6.96, P

= 0.00 for the wet season, and Moran's index = 0.84, z-score = 12.95, P = 0.00 for the dry season). Thus, a total of 56 and 51 occurrence points (direct observation 10 and elephant dung piles and footprints count 46; direct observation 7 and elephant dunghill count 44) for the wet and dry seasons, respectively, were independently used for modeling in the study region using the MAXENT algorithm (Phillips et al., 2006) (Supplementary Table 1).

Predictor variables

Ecological predictor variables for the MAXENT models were selected on the basis of their potential impact on determining the movement patterns and distribution of African elephants in Omo National Park. The spatial and temporal distribution of a given species is strongly influenced by certain environmental conditions (Barnard & Thuiller, 2008). Pr'eu et al. (2020) indicate that climate-related factors and landscape composition are important in determining high-priority habitats for the species. Increasing anthropogenic activities, including poaching, human settlement, and agricultural investments, are among the most important factors limiting African elephant habitat use and distribution in Omo National Park (Asbl & Fortrop, 2008; Cherie Enawgaw, 1996; Ethiopian Wildlife Conservation Authority (EWCA), 2015). We used the most recent 19 bioclimatic data sets from Worldclim 2.1 at the 30s (1 km²) resolution for habitat suitability modeling (Fick & Hijmans, 2017; Hijmans et al., 2005; www.worldclim.org). The digital elevation model (DEM) of the study region was processed using the Spatial Analyst tool of ArcGIS 10.8 to generate topographic attributes, including slope, aspect, and elevation, as predictor variables for the target species. Landsat-8 data extracted from USGS Earth Explorer (<https://earthexplorer.usgs.gov/>) was used to prepare land use and land cover using ArcGIS 10.8 software (imagery and supervised classification), which included herbaceous woodland, open grassland, forest, water bodies, and settlement and agricultural areas for inclusion in the final habitat suitability prediction. Other predictor variables, including distance to roads, rivers, and settlements or farms, were also prepared using the Euclidean distance from the ArcGIS 10.8 software spatial analysis tools. All predictor variables were adjusted using R and R Studio software to have a similar extent, projection, and resolution as required to run the MAXENT model (Phillips et al., 2006). Predictor variables were selected using ENMTools software in R 4.2.2 (Table 1) and checked for correlations between variables; the highly correlated variables were removed (<-0.7 and > 0.7)(Kufa et al., 2022) (Supplementary Table 3), followed by the removal of the least contributing variable after the MAXENT run (zero value of contribution) (Fekede et al., 2019, 2021; Landau & Everitt, 2004). Highly correlated variables reduce the efficiency and increase the uncertainty of species distribution models (Dormann et al., 2013; Junior & Nobrega, 2018; Zurell et al., 2019). Therefore, 12 predictor variables were selected to determine the habitat suitability and distribution of African elephants in Omo

National Park under current conditions. The selected predictors include slope, aspect, altitude, and distance from water sources, roads, settlements/farming, and land use land cover, as well as the mean diurnal range of temperature (bio 2), isothermality (bio 3), temperature seasonality (bio 4), and monthly rainfall in March (Table 1).

Table 1. Ecological predictor variables selected for modeling the habitat suitability of African elephants after the multicollinearity test (correlation analysis using ENM R tools)

	Aspect	bio_2	bio_3	bio_4	dist_canal	dist_cultland	dist_river	dist_road	Elev	lulc_o	prec_03	Slope
Aspect	1.00											
bio_2	0.04	1.00										
bio_3	0.1	-0.1	1.00									
bio_4	-0.03	0.19	-0.64	1.00								
dist_canal	0.09	-0.3	0.36	-0.39	1.00							
dist_cultland	0.01	-0.02	-0.2	0.13	0.24	1.00						
dist_river	0.01	0.19	0.1	0.17	-0.25	-0.27	1.00					
dist_road	0.03	-0.07	0.15	-0.32	0.62	0.24	-0.24	1.00				
Elev	0.11	-0.58	0.42	-0.25	0.75	0.11	-0.11	0.32	1.00			
lulc_o	-0.03	-0.04	-0.06	-0.01	-0.13	0.06	-0.04	-0.1	-0.07	1.00		
prec_03	0.1	-0.61	0.4	-0.12	0.36	0.11	0.01	0.07	0.64	-0.01	1.00	
Slope	0.01	-0.49	0.14	0.03	0.11	0.03	0.04	0.03	0.4	0.02	0.5	1.00

Statistical analyses

MAXENT version 3.4.4K (Available at http://biodiversityinformatics.amnh.org/open_source/MAXENT/) was used to predict the wet and dry season African elephant distribution and habitat suitability in Omo National Park. It is the most preferred method to use either presence or absence-data (if available) or presence-only data to predict the habitat suitability of species (Merow et al., 2014; Morales et al., 2017). MAXENT operates on the principle of maximum entropy, making inferences from available data while avoiding unfounded constraints from the unknown (Phillips et al., 2006). Entropy is the measure of uncertainty associated with a random variable. The greater the entropy is the greater the uncertainty. Adhering to these concepts, MAXENT utilizes presence-only points of occurrence, avoiding the absence of data and evading assumptions on the range of a given species. Thus, it was used to build and calibrate the spatial models based on 10-fold cross-validation with a regularization multiplier ($\beta = 1$) and linear and quadratic features to have smooth models (Anderson & Gonzalez, 2011; Anderson & Raza, 2010; Elith et al., 2010). The occurrence data were

randomly classified into 70% for training and 30% for testing the model(Phillips et al., 2006; Zurell et al., 2019). Five thousand background locations were randomly generated and chosen considering the targeted study area to determine pseudo presence. For the remaining parameters, the MAXENT default settings were considered for the modeling.

Model performance was assessed by analyzing the area under the receiver operating characteristic (ROC) analysis and the area under the curve (AUC) in MAXENT as a measure of model fit. AUC results were rated as 'high accuracy' for AUC values between 0.90-1.00, 'good' for AUC values between 0.80-0.90, 'moderate' for AUC values between 0.70-0.80, 'poor' for AUC values between 0.60-0.70 and 'no chance' for AUC values below 0.50(Elith et al., 2011; Swets, 1988). In addition, the variable response curves and jackknife test were used to evaluate the relative contribution of the predictor variables to the model (Elith et al., 2011; Fekede et al., 2019; Korennoy et al., 2014). We used the percentage contribution, permutation importance, and jackknife test results to estimate the contribution of each variable to the models (Phillips et al., 2006). In addition, the response curve resulting from the model for each environmental variable was used to examine the relative effects of the different environmental variables.

Results

The test omission rate and predicted area as a function of the cumulative threshold were averaged over the ten replicate runs in the MAXENT model for both wet and dry seasons. We observed that the receiver operating characteristic (ROC) curve averaged over the ten replicate runs for the wet and dry seasons of elephants provided higher AUC values of 0.877 ± 0.028 and 0.952 ± 0.006 , respectively. Thus, both the training and test data are greater than that of the random prediction line in both seasons of the MAXENT run (0.5), indicating very-good predictive ability in determining the habitat suitability of the elephant in the study area (Supplementary Fig. 2 and 3).

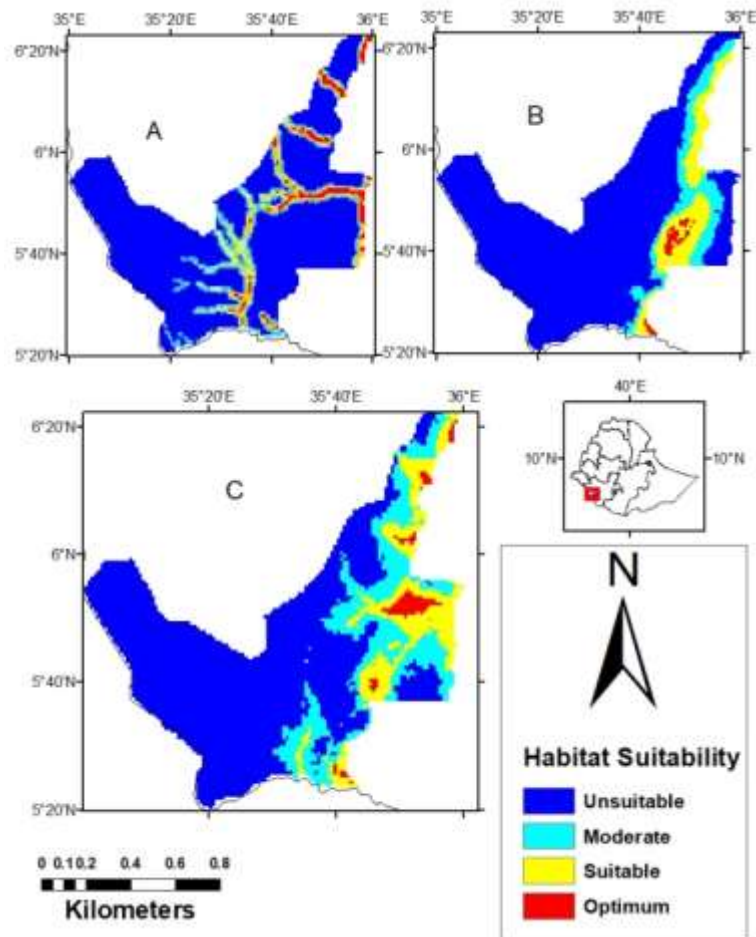


Figure 2. MAXENT model result of African elephant habitat use during the (a) dry season, (b) wet season and (c) both seasons of the year 2020 and 2021.

The prediction maps in Figure 2 (A, B) illustrate the probabilities of elephant occurrence in the wet and dry seasons based on the MAXENT model using the spatially defined variables. In general, the likelihood of elephant occurrence is higher in the dry season near water sources (Figure 2A). In contrast, the elephant occurrence in the wet season and optimum habitats tend to be distant from rivers and scattered toward herbaceous, wooded, and open grassland habitats (Fig. 2 B). Figure 2 C shows the habitat preferences of elephants in the study area for both the wet and dry seasons.

African elephants have a larger area of optimal habitat in the wet season (312 km²) than in the dry season (29 km²). The range of African elephants covered 1215 km² and 191 km² in the wet and dry seasons, respectively. The modeled seasonal combined elephant range results have a total area of 1999 km² (39% of the study area), of which 365 km² (7.2%) are optimum or highly suitable, 748 km² (14.7%) are suitable habitats, and 886 km² (17.5%) are moderately suitable habitats. The remaining area (61% of the total study area) was found unsuitable for or not visited by African elephants in the Omo National Park (Fig. 2) (Supplementary Table 4).

The response curves show how each environmental variable affects the MAXENT prediction in both seasons (Fig. 3 & Fig. 4) (Supplementary Fig. 4). During the dry season, the habitat suitability of elephants increases as predictor variables like isothermality (bio3) and the distance to (canals, rivers, roads,) and elevation decrease. In contrast, suitability increases with an increase in the predictor's variables, such as the mean diurnal range temperature (bio 2) and temperature seasonality (bio 4). The influence of distance to cultivated land, slope, and aspect somewhat fluctuated but still had a limited impact on the habitat suitability of elephants (Fig. 3 & Fig. 4; Supplementary Fig. 4).

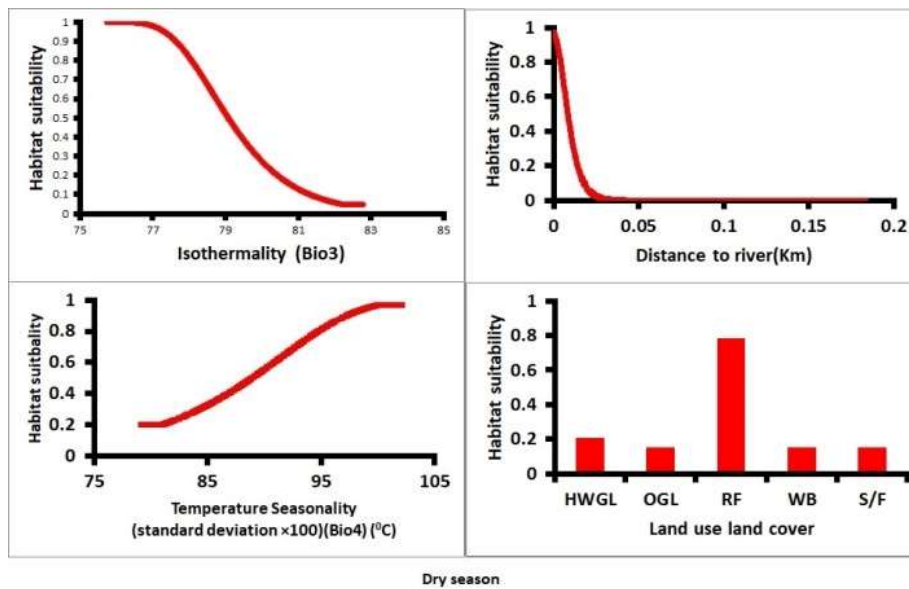


Figure 3. The response curve of the most important variables showing African elephant habitat suitability to predictor variables in the dry season. (HWGL: Herbaceous Wooded Grassland; OGL: Open Grassland; RF: Riverine Forest; WB: Water Bodies; F/S: Farming and Settlement)

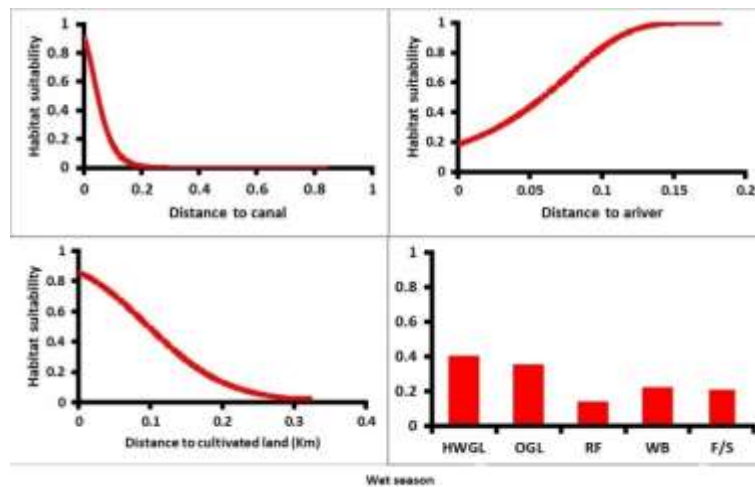


Figure 4. The response curve of the most important variables showing African elephant habitat suitability to predictor variables in the wet season. (HWGL: Herbaceous Wooded Grassland; OGL: Open Grassland; RF: Riverine Forest; WB: Water Bodies; F/S: Farming and Settlement)

However, during the wet season, the habitat suitability of elephants increases as most of the predictor variables decrease except for the mean diurnal range temperature (bio 2), temperature seasonality (bio 4), and distance to the river. The land use and land cover categorical variables indicate the highest habitat suitability in the herbaceous woodland (0.2) and riverine association (forest) (0.79) during the dry season; in contrast, it was highest in the herbaceous wooded grassland (0.40) and open grassland habitats (0.39) during the wet season (Fig. 3 & Fig. 4 bar graphs).

Regarding the relative contribution of the environmental variables to the MAXENT model (Table 2), three variables—distance to rivers, land use land cover and distance to canal—were the most important predictors, having the greatest contribution (> 10%) to the model results but each with a different percent contribution for both the wet and dry seasons.

Table 2. Relative contribution and importance of predictor variables to the MAXENT model in the habitat of African elephants in both the wet and dry seasons (average results of 10 replicates).

Predictor variables	Code	Percent contribution	Permutation Importance	Percent contribution	Permutation Importance
		Dry season		Wet season	
Distance to river	dist_river	49.2	44.8	10	2.3
Land use land cover	Lulc_o	28.7	0.6	33.8	0.9
Distance to canal	dist_canal	16.3	52.3	40.1	50.8
Temperature Seasonality	bio4	2.6	0.6	0	0.1
Elevation	Elev	1.1	0.4	5	0
Distance to roads	dist_road	0.9	0.7	0.5	5.6
Isothermality	bio3	0.7	0	0.1	1.7
Slope	Slope	0.3	0.1	0.3	0.5
Mean diurnal range of temperature	bio2	0.1	0.1	7.2	13
Distance to cultivated land	dist_cultland	0.1	0.4	1.5	6.9
Aspect	Aspect	0	0	0.2	0.1
Precipitation (March)	Prec 3			1.3	18.2

Elephant populations tend to congregate closer to river valleys. The model showed a higher percentage contribution for distance to rivers (49%), followed by land use and land cover (29%), and distance to the canal (16%) during the dry season. In contrast, during the wet season, the elephant tended to disperse in the herbaceous, wooded, and open grassland habitats or move away from the lowland river valleys. Thus, the MAXENT model showed a higher percentage contribution for distance to the canal (40%), followed by land use land cover (forest) (34%), and distance to the river (10%) during the wet season (Table 2).

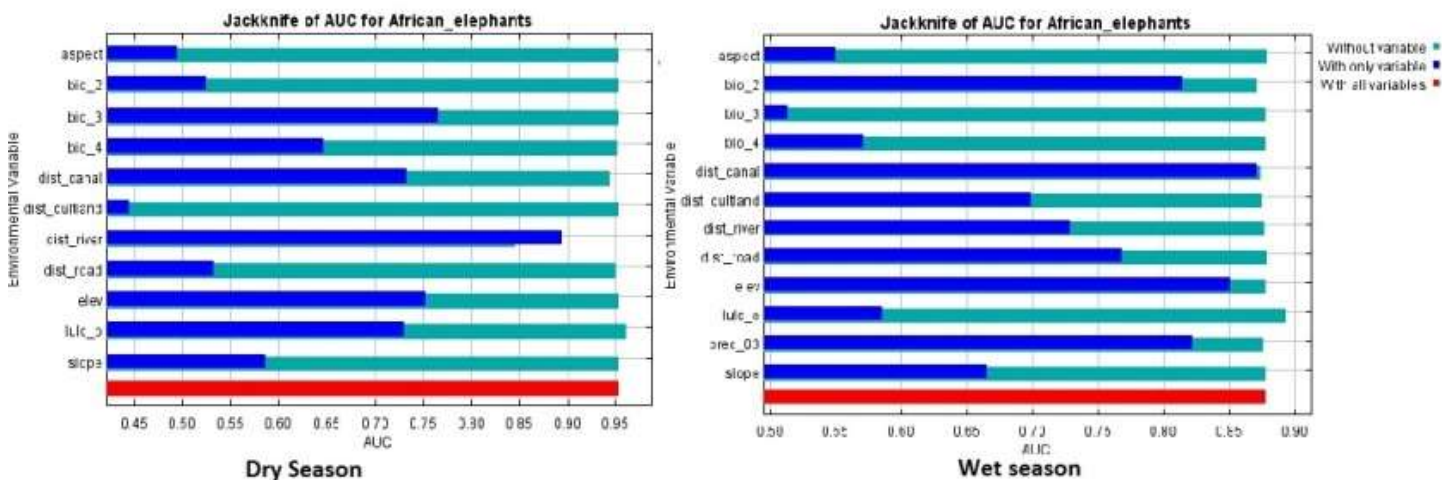


Figure 5. Jackknife of AUC (area under the receiver operating curve) for the African elephant, showing average AUC gains for each variable (abbreviation of variables are in Table 2 above)

The results of the jackknife test of variable importance for the model were vital to evaluate the relative importance of single predictor variables in the model in predicting elephant presence (habitat

suitability). During the wet season, the environmental variable with the highest gain when used in isolation was the distance to the canal, which thus appeared to have the most useful information in and of itself. Following: elevation, mean diurnal range of temperature (bio2), monthly precipitation for March, distance to (roads, rivers, canals, cultivated land/farming), and slope. Land use Land cover, temperature seasonality (bio 4), aspect, and isothermality (bio 3) have low gains in this sequence when used in isolation. The environmental variable that decreases the gain the most when excluded from the model is the distance to the canal, which therefore appears to have the most useful information that is not present in the other variables. Isothermality (bio 3) does not significantly affect the overall training gain when excluded from the model. The dry season, on the other hand, was the environmental variable with the highest gain when used in isolation and the one that reduced gain the most when the distance to the river was left out; thus, this variable appeared to contain the most useful information on its own and the most information that was not present in the other variables (Figure 5). Distance to cultivated land or farming does not significantly affect the overall training gain when excluded from the model. The model also produced the same jackknife tests of variable importance for the African elephant dataset for the regularized training gain and test gain (Supplementary Fig. 5). Similarly, the result shows the variables with the highest training and test gains when used in isolation, the variables that decrease the overall gain when excluded from the model, and the variables that do not significantly reduce the total training and test gains when they were left out.

Discussion

MAXENT mapping of this study indicates a higher probability of elephant presence and habitat suitability, consistent in the north, northeast, east, southeast, and central portions of the parkland (Fig. 2 C). The southwestern forested habitat and western upland slopes were found to be relatively unsuitable habitats for elephants due to the lack of permanent water sources and the higher elevation and rugged nature of the landscape.

Omo National Park is fortunate to have several rivers and streams that flow into the great Omo River within the park (Fig. 1). Elephants tend to be more likely to be near riverine areas that provide water, shade, and quality forage during the dry season in the park. In general, elephants are more likely to be present near water sources during the dry season, suggesting that target species have optimal habitats along riverine forests, such as along the Shorum, Kuma, Mui, Neruze, Kibish, and Omo rivers, where they can find vegetation that provides food and cover in addition to water (Fig. 2 A). Elephant movement patterns in relation to surface water indicate that they are a water-dependent species (Boitani et al., 2008; Dunkin et al., 2013; Xu et al., 2020). Elephants change their movement behavior in

response to both a seasonal change in precipitation (from dry to wet) and wet episodes that occur during the dry season (Garstang et al., 2014). The availability of water influences elephant foraging behavior as they approach water to forage during the dry season (de Beer & van Aarde, 2008; Pittiglio et al., 2011; Robin et al., 2013). Elephant movement patterns in relation to surface water show that they are a water-dependent species and have high evaporative and respiratory losses, drink more frequently, and minimize their distance to the nearest water source (Owen-Smith, 1988; Robin et al., 2013; Ryan & Jordaan, 2005; Smit et al., 2007; Traill & Bigalke, 2006).

The distribution of most wildlife is often more widely dispersed during the wet season due to the greater availability of resources across the landscape (Bergstrom & Skarpe, 1999; Hema et al., 2010; Jachmann, 1988; Kebede et al., 2012). Similarly, the likelihood of elephant occurrence during the wet season tends to be further from the rivers and toward the extensive herbaceous, forested, and open grassland habitats in Omo National Park. The herbaceous wooded and open grassland habitats crossed by the Kuraz Sugar Development Project irrigation canal (one of the environmental variables considered in this study) extend for more than 134 km from north to south in the park (EWCA, 2017; ESC, 2019). Elephants are less selective during the wet season because water is readily available (de Beer & van Aarde, 2008; Pittiglio et al., 2011; Robin et al., 2013). This switches elephants from restrictive movements (during the dry season) to more flexibility (during the wet season), resulting in an expansion of their habitat (Ashiagbor & Danquah, 2017; Cushman et al., 2005).

The Mui River and associated woodland forests are surrounded by visible ecotone habitats. These are the most suitable habitats for elephants in both the wet and dry seasons and are also known as elephant corridors to Tama Wildlife Reserve and Mago National Park (Ethiopian Wildlife Conservation Authority (EWCA), 2015). The MAXENT distribution map shows the presence of seasonal elephant movements in the adjacent Tama Wildlife Reserve and Mago National Park. However, important corridors are altered, and natural connectivity is hindered by the ongoing Kuraz Sugar Development Project in the area (Ethiopian Wildlife Conservation Authority (EWCA), 2017a). The MAXENT map also shows the presence of transboundary seasonal elephant movements in the south between Omo National Park and the adjacent Ilmi Triangle (No Man's Land) and Badingelo and Boma National Parks in South Sudan (personal communication with the Chief Warden and rangers).

Although there are no previous comparable studies, suitable elephant habitats have been significantly reduced due to severe habitat fragmentation and obstruction of seasonal movements of the species in Omo National Park (Ethiopian Wildlife Conservation Authority (EWCA), 2017a; Cherie Enawgaw, 1996). MAXENT model results indicate that new large-scale sugar development projects and sugar plantations adjacent to suitable elephant habitats have negatively impacted habitats suitable for

elephants. In the near past, the northeastern forest areas along with the Shorum and Kuma Rivers and the grasslands and forests of the Sai Plains were the preferred habitats for elephants in both the wet and dry seasons; these were later converted to sugarcane plantations (Ethiopian Wildlife Conservation Authority (EWCA), 2017a). In addition, in the southern part of Omo National Park, an area of about 63 km² that was once part of the park (before 2010) is now being prepared for conversion to sugarcane plantations by the Ethiopian Sugar Corporation project (Cherie Enawgaw, 2013; Ethiopian Wildlife Conservation Authority (EWCA), 2017b). Although this area (the latter) is legally outside the national park, it is a suitable habitat and a migration corridor to Tama Wildlife Reserve and Mago National Park. Continued discussions are needed between the Ethiopian Wildlife Conservation Authority, the Ethiopian Sugar Corporation, and the local communities of Nagngatom to conserve this important habitat for the benefit of elephants and local communities.

Due to high water loss through evaporation and respiration, distance to water is an important factor in elephant movement and dispersal (Smit et al., 2007; Stokke & Du Toit, 2002; Western & Lindsay, 1984). During the rainy season, distance to the canal showed the highest percentage contribution (40%), land uses land cover (herbaceous woodland and open grassland) (34%), and distance to water (10%). The artificial canal built from the north to the south of the national park was intended to divert the Omo River for large-scale irrigation projects in the area. Currently, the canal has not been completed, but the excavated canal is already carrying water as most of the western perennial rivers and seasonal streams that used to drain into the Omo River drain into the canal. Most of the irrigation canal crosses herbaceous woodland and open grassland vegetation, which are preferred habitats for elephants in the model during the wet season. The ecological impacts of canal construction were not considered part of the project and require further investigation to determine the likely negative impacts and mitigation measures.

The other environmental variables that were included in the model, namely rainfall during the wet season (March), mean-diurnal range of temperature (bio 2), and isothermally (bio 3), had varying impacts on elephant habitat suitability depending on the time of year (season). Ecological studies have shown that climatic conditions (seasonal rainfall, temperature) affect behavior, physiology, and species interaction and are among the factors that influence habitat suitability (Ashiagbor & Danquah, 2017; Mole et al., 2016). Kinahan et al. (2007) suggested that elephants' landscape use may be limited by their thermal physiological requirements in addition to food and water. Thermal stress is a major problem for savanna elephants (*Loxodonta africana*), posing a major challenge for heat dissipation in hot and dry environments (Thaker et al., 2019). During the rainy season, elephants tend to spread out

and cover large areas because water is not limited, while in the dry season, they remain closer to water in Omo National Park.

In general, habitats suitable for elephants in both the wet and dry seasons are predominantly in the lower elevation areas, although there are slight differences in elevation. The influence of elevation on elephant movements and dispersal is clear in that elephants tend to congregate in the low-elevation areas (near water along river valleys) during the dry season and move slightly upward and disperse into the herbaceous woodland and grassland areas during the wet season. Although we saw some contribution to the model that varied with the observed season in predictor variables such as aspect and slope, little can be concluded from the analysis of elephant observations because most suitable habitats in the study area are in lowland areas with minimal slope.

Conclusion

In this study, the machine learning algorithm provides notable information on the habitat suitability of elephants given the current environmental constraints in the Omo National Park. The results of habitat suitability and distribution models indicate the importance of distance to rivers, canals, and LULC (herbaceous woodland forest and grassland) during the dry and wet seasons, respectively. The results clearly show the reduction in elephants' suitable habitats and obstruction of the natural corridors affecting the elephant's movement between conservation areas in the region. The Omo National Park elephants are not able to use most of the available home ranges, resulting in a visible population size decline that requires further specific study. Currently, vast areas of elephant-suitable habitats are converted to sugar cane plantations. The ongoing large-scale sugar development projects and their associated activities pose threats to the remaining elephant habitats and their seasonal movements. In addition, the prevailing factors of increasing human population density, poaching, ineffective law enforcement, and poor governance require strong attention. Due to budget and logistics constraints, the park wardens are not in a position to conduct regular patrols and surveillance against illegal activities to safeguard the park's ecological integrity. Concerted efforts are required with stakeholders to reduce the negative impacts of the sugar development project and maintain the natural connectivity between the nearby conservation areas. Besides, halting poaching for ivory and pastoral encroachment for grazing and agricultural expansion in the core elephant habitat must be among the priorities of the management actions.

Acknowledgements

We extend our deep thanks to the Ethiopian Wildlife Conservation Authority for their support and provision of permits, especially Ato Kumara Wakjira, Solomon Mekonnen, Dr. Fanuel Kebede, Dr. Fekede Regassa, Dr. Adane Tsegaye, and Mr. Oliver Nelson. We are grateful to the Omo National Park Chief Warden, Ato Nuru Ahmed, and all rangers who participated in data collection during the study period. Department of Zoological Sciences, Addis Ababa University, Bezawork Afewrook, Professor Abebe Getahun, Habte Jebessa, Mesele Yihune, and Anagawu Atickem are highly appreciated for their constructive advice during the study period.

References

- Anderson, R. P., & Gonzalez, I. (2011). Species specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling*, 222, 2796–2811. <https://doi.org/10.1016/j.ecolmodel.2011.04.011>
- Anderson, R. P., & Raza, A. (2010). The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: Preliminary tests with montane rodents (*genus Nephelomys*) in Venezuela. *Journal of Biogeography*, 37, 1378–1393. <https://doi.org/10.1111/j.1365-2699.2010.02290.x>
- Antoine Guisan, Thomas C Edwards Jr, & Trevor Hastie. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, 157(2–3), 89–100.
- Asbl, C. N., & Fortrop, O. (2008). Omo National Park report for the wet season aerial survey by Pierre-Cyril Renaud for African Parks Ethiopia On behalf of Nature+. www.fsagx.be
- Ashiagbor, G., & Danquah, E. (2017). Seasonal habitat use by Elephants (*Loxodonta africana*) in the Mole National Park of Ghana. *Ecology and Evolution*, 7(11), 3784–3795. <https://doi.org/10.1002/ece3.2962>
- Baldwin, R. A. (2009). Use of maximum entropy modeling in wildlife research. *Entropy*, 11, 854–866. <https://doi.org/10.3390/e11040854>
- Barnard, P., & Thuiller, W. (2008). Introduction. Global change and biodiversity: future challenges. *Biol Lett*, 4, 553–555. <https://doi.org/10.1098/rsbl.2008.0374>. PMID: 18664413; PMCID: PMC2610103.
- Bergstrom, R., & Skarpe, C. (1999). The abundance of large wild herbivores in a semi-arid savanna in relation to seasons, pans and livestock. *Afr J Ecol*, 37: 12–26. <https://doi.org/10.1046/j.1365-2028.1999.00165.x>
- Boitani, L., Sinibaldi, I., Corsi, F., De Biase, A., C., Carranza, I. D. I., Ravagli, M., Reggiani, G., Rondinini, C., & Trapanese, P. (2008). Distribution of medium to large-sized African mammals based on habitat suitability models. *Biodivers. Conserv*, 17(3), 605–621. <https://doi.org/10.1007/s10531-007-9285-0>
- Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). Bioclim: The first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Divers. Distrib.*, 20(1), 1–9. <https://doi.org/10.1111/ddi.12144>
- Breiman, L. (2001). Random forests. *Mach. Learn.*, 45, 5–32. <https://doi.org/10.1023/A:1010933404324>, Corpus ID: 89141
- Carpenter, G., Gillison, A. N., & Winter, J. (1993). DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodivers. Conserv.*, 2, 667–680. <https://doi.org/10.1007/BF00051966>
- Chase, M. J., Schlossberg, S., Griffin, C. R., Bouché, P. J. C., Djene, S. W., Elkan, P. W., Ferreira, S., Grossman, F., Kohi, E. M., Landen, K., Omondi, P., Peltier, A., Jeanetta Selier, S. A., & Sutcliffe, R.

- (2016). Continent-wide survey reveals massive decline in African savannah elephants. PeerJ, (8). <https://doi.org/10.7717/peerj.2354>
- Cherie Enawgaw. (2013). Reconciling conservation and investment in the Gambella-Omo Landscape, Ethiopia. Ethiopian Wildlife Conservation Authority.
- Cherie Enawgaw, Derbe Deksios, & Girma Timer. (2011). Existing challenges: plantation development versus wildlife conservation in the Omo-Tama-Mago Complex. Ethiopian Wildlife Conservation Authority, Addis Ababa, Ethiopia.
- Cherie Enawgaw. (1996). Distribution, abundance and age structure of elephants in Omo National Park, Ethiopia. *Walia*, 17, 1-10.
- Cleary, K. A., Cleary, K. A., W. L. P., & Finegan, B. (2017). Comparative landscape genetics of two frugivorous bats in a biological corridor undergoing agricultural intensification. *Molecular Ecology*, 26(18), 4603–4617. <https://doi.org/10.1111/mec.14230>. Epub 2017 Aug 8. PMID: 28672105.
- Cowley, M. J. R., Wilson, R. J., Leon-Cortes, J. L., Gutierrez, J. L., Bulman, C. R., & Thomas, C. D. (2000). Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *J Appl Ecol*, 37, 60–72. <https://doi.org/10.1046/j.1365-2664.2000.00526.x>
- Cushman, S. A., Chase, M., & Griffin, C. (2005). Elephants in space and time. *Oikos*, 109(2), 331-341. doi.10.1111/j.0030-1299.2005.13538.x
- de Beer, Y., & van Aarde, R. J. (2008). Do landscape heterogeneity and water distribution explain aspects of elephant home range in southern Africa's arid savannas? *Journal of Arid Environment*, 72:, 2017–2025. <https://doi.org/10.1016/J.JARIDENV.2008.07.002>, Corpus ID: 56371550
- Dejene, S. W., Mpakairi, K. S., Kanagaraj, R., Wato, Y. A., & Mengistu, S. (2021). Modelling Continental Range Shift of the African Elephant (*Loxodonta africana*) under a Changing Climate and Land Cover: Implications for Future Conservation of the Species. *African Zoology*, 56(1), 25–34. <https://doi.org/10.1080/15627020.2020.1846617>
- Dejene, S. W. (2016). The African Elephant (*Loxodonta africana*) in Ethiopia: A Review. *European Journal of Biological Sciences*, 8(1), 8–13. <https://doi.org/10.5829/idosi.ejbs.2016.8.01.1112>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Garc, J. R., Gruber, B., Lafourcade, B., Leit, P. J., Tamara, M., McClean, C., Osborne, P. E., Der, B. S., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36, 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Dunkin, R. C., Wilson, D., Way, N., Johnson, K., & Williams, T. M. (2013). Climate influences thermal balance and water use in African and Asian elephants: Physiology can predict drivers of elephant distribution. *Journal of Experimental Biology*, 216(15), 2939–2952. <https://doi.org/10.1242/jeb.080218>
- Elith, J., Graham, C. H., Anderson, R. P., & Dudik, M. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range shifting species. *Methods in Ecology and Evolution*, 1, 330–342. <https://doi.org/10.1111/j.2041-210X.2010.00036.x>
- Elith, J., Leathwick, & John, R. (2009). “Species Distribution Models: Ecological Explanation and Prediction Across Space and Time”. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697. <https://doi.org/10.1146/ANNUREV.ECOLSYS.110308.120159>, Corpus ID: 86460963
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity Distrib.*, 17, 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Ethiopian Sugar Corporation (ESC). (2019). Kuraz Sugar Development Project EIA Feasibility Report. Ethiopian Sugar Corporation Addis Ababa, Ethiopia.

- Ethiopian Wildlife Conservation Authority (EWCA). (2015). Ethiopian Elephant Action Plan. Ethiopian Wildlife Conservation Authority, Addis Ababa, Ethiopia.
- Ethiopian Wildlife Conservation Authority (EWCA). (2017a). Ethiopian Wildlife Reconciling Conservation and development project a case of Omo National park and sugar development project (report). Addis Ababa, Ethiopia.
- Ethiopian Wildlife Natural History Society (EWNHS). (1996). Ethiopian Wildlife Important Bird Areas of Ethiopia: A First Inventory. Ethiopian Wildlife and Natural History Society (EWNHS), Addis Ababa, Ethiopia.
- Evangelista, P., Kumar, S., Stohlgren, T.J., Jarnevich, C.S., Crall, A. W., Norman, J. B. I., & Barnett, D. (2008). Modeling invasion for a habitat generalist and a specialist plant species. *Divers. Distrib.*, 14, 808–817. <https://doi.org/10.1111/j.1472-4642.2008.00486.x>
- Evangelista, P., Norman, J., Berhanu, L., Kumar, S., & Alley N. (2008). Predicting habitat suitability for the endemic mountain nyala (*Tragelaphus buxtoni*) in Ethiopia. *Wildl Res.*, 35, 409–416. <https://doi.org/10.1071/WR07173>
- Fekede, R. J., HaoNing, W., Hein, V. G., & XiaoLong, W. (2021). Could wild boar be the Trans-Siberian transmitter of African swine fever? *Transboundary and Emerging Diseases*, 68(3), 1465–1475. <https://doi.org/10.1111/tbed.13814>
- Fekede, R. J., van Gils, H., Huang, L. Y., & Wang, X. L. (2019). High probability areas for ASF infection in China along the Russian and Korean borders. *Transboundary and Emerging Diseases*, 66(2), 852–864. <https://doi.org/10.1111/tbed.13094>
- Ferguson, A. (2021). Mammals of Ethiopia, Eritrea, Djibouti and Somalia: field guide to the larger mammals of the Horn of Africa. *Journal of Mammalogy*, 102, 1203–1204 <https://doi.org/10.1093/jmammal/gyab065>
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, 37(12), 4302–4315. <https://doi.org/10.1002/joc.5086>
- Garstang, M., Davis, R. E., Leggett, K., Frauenfeld, O. W., Greco, S., Zipser, E., & Peterson, M. (2014). Response of African elephants (*Loxodonta africana*) to seasonal changes in rainfall. *PLoS ONE*, 9(10). <https://doi.org/10.1371/journal.pone.0108736>
- Gibson, L. A., Wilson, B. A., Cahill, D. M., & Hill, J. (2004). Spatial prediction of rufous bristle bird habitat in a coastal heathland: a GIS-based approach. *J ApplEcol*, 41, 213–223.
- Gizaw, G. (2021). Updating Protected Areas database of Ethiopia! @ WDPA www.iucnprotectedareaplanet.net. www.iucnprotectedareaplanet.net
- Gobush, K., & Wittemyer, G. (2021). *Loxodonta africana*, African Savanna Elephant Forest elephant behavior and conservation View project Great Elephant Census-First Initiative View project. <https://doi.org/10.2305/IUCN.UK.2021-1.RLTS.T181008073A181022663.en>
- Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling*, 135(2–3), 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)
- Hema, E. M., Barnes, R. F. W., & Guendal, W. (2010). The seasonal distribution of savannah elephants (*Loxodonta africana africana*) in Nazinga Game Ranch, southern Burkina Faso. *Pachyderm*, 48:, 33–40. UR - <https://pachydermjournal.org/index>.
- Hernandez, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, 29, 773–785. <https://doi.org/10.1111/j.0906-7590.2006.04700.x>
- Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25(15), 1965–1978. <https://doi.org/10.1002/joc.1276>

- Hillman, J. C. (1993). Ethiopia: compendium of wildlife conservation information. Ethiopian Wildlife Conservation Organization and New York Zoological Society, Addis Ababa.
- IUCN. (2021; March 25). African elephant species now Endangered and Critically Endangered - IUCN Red List. . IUCN Press Release. .
- Jachmann, H. (1988). Numbers, distribution and movements of the Nazinga elephant. *Pachyderm*, 10, 16–21.
- Junior, P. D. M., & Nobrega, C. C. (2018). Evaluating collinearity effects on species distribution models: an approach based on virtual species simulation. *PLOS ONE*, 13(9). <https://doi.org/10.1371/journal.pone.0202403>
- Kebede, F., Bekele, A., Moehlman, P., & Evangelista, P. (2012). Endangered Grevy's zebra in the Alledeghi Wildlife Reserve, Ethiopia: species distribution modeling for the determination of optimum habitat. *Endangered Species Research*, 17(3), 237–244. <https://doi.org/10.3354/esr00416>
- Keeley, A. T. H., Beier, P., Keeley, B. W., & Fagan, M. E. (2017). Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. *Landscape and Urban Planning*, 161, 90–102. <https://doi.org/10.1016/j.landurbplan.2017.01.007>
- Kinahan A.A, Pimm S.L, & van Aarde R.J. (2007). Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta Africana*. *Journal of Thermal Biology*, 32,(1), 47–58. <https://doi.org/10.1016/j.jtherbio.2006.09.002>
- Korennoy, F. I., Gulenkin, V. M., Malone, J. B., Mores, C. N., Dudnikov, S. A., & Stevenson, M. A. (2014). Spatio-temporal modeling of the African swine fever epidemic in the Russian Federation, 2007-2012. . *Spatial and Spatio-Temporal Epidemiology*, 11, 135-141. <https://doi.org/10.1016/j.sste.2014.04.002>
- Kufa, C. A., Bekele, A., & Atickem, A. (2022). Impacts of climate change on predicted habitat suitability and distribution of Djaffa Mountains Guereza (*Colobus guereza gallarum*, Neumann 1902) using MaxEnt algorithm in Eastern Ethiopian Highland. *Global Ecology and Conservation*, 35. <https://doi.org/10.1016/j.gecco.2022.e02094>
- Lamprey, R. H. (1994). Aerial census of wildlife in Omo and Mago National Parks, Ethiopia: July 29 to August 4, 1994. London and Cambridge: Ecosystems Consultants / EDG.
- Landau, S., & Everitt, B. S. (2004). A handbook of statistical analyses using SPSS. Boca Raton: Chapman & Hall/CRC. Press LLC.
- Largen, M. J., & Yalden, D. W. (1987). The decline of elephant and black rhinoceros in Ethiopia. *Oryx*, 21(2), 103–106. <https://doi.org/10.1017/S0030605300026636>
- Lindsaya, K., Chaseb, M., Landenb, K., & Nowack, K. (2017). The shared nature of Africa's elephants. *Biological Conservation*, 215, 260–267. <https://doi.org/10.1016/j.biocon.2017.08.021>
- Liu, S., Yin, Y., Li, J., Cheng, F., Dong, S., & Zhang, Y. (2018). Using cross scale landscape connectivity indices to identify key habitat resource patches for Asian elephants in Xishuangbanna, China. *Landscape and Urban Planning*, 171, 80–87. <https://doi.org/10.1016/j.landurbplan.2017.09.017>
- Merow, C., Smith Jr., M.J., T. C. E., Guisan, A., McMahon, S. M., Thuiller, W., Wüest, R.O., & Zimmermann, N. E. (2014). What do we gain from simplicity versus complexity in species distribution models? . *Ecography*, 37, 1267-1281. <https://doi.org/10.1111/ecog.00845>
- Mole, M. A., D'Áraujo, S. R., van Aarde, R. J., Mitchell, D., & Fuller, A. (2016). Coping with heat: Behavioural and physiological responses of savanna elephants in their natural habitat. *Conservation Physiology*, 4(1). <https://doi.org/10.1093/conphys/cow044>
- Morales, N. S., Fernández, I. C., & Baca-González, V. (2017). MaxEnt's parameter configuration and small samples: Are we paying attention to recommendations? A systematic review. *PeerJ*, 2017(3). <https://doi.org/10.7717/peerj.3093>

- Nelleman, C., Formo, R. K., Blanc, J., Skinner D, Milliken, T., & De Meulenaer T. (2013). Elephants in the dust—the African elephant crisis. A rapid response assessment. United Nations Environment Programme. United Nations Environment Programme, GRID–Arendal.
- Norton-Griffiths, M. (1978). Counting Animals. Handbook Number 1. African Wildlife Leadership Foundation, Nairobi.
- Owen-Smith, N. R. ., (1988). Mega herbivores: The Influence of Very Large Body Size on Ecology. Cambridge University Press, London, Britain.
- Pearson, R. G., Raxworthy, C. J., Nakamura, M., & Peterson, A. T. (2007). Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr*, 34, 102–117.
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecol. Model.* , 190, 231–259. Doi:10.1016/j.ecolmodel.2005.03.026
- Phillips, S. J., Dudik, M., & Schapire, R. E. (2004). Maximum entropy approach to species distribution modeling. In: Proceedings of the 21st international conference on machine learning. . ACM Press, New York, NY, 655–662.
- Pittiglio, C., Skidmore, A. K. , van Gils Hamj, & Prins, H. H. T. (2011). Identifying transit corridors for elephant using a long time-series. . *International Journal of Applied Earth Observation and Geoinformation*, 14, 61–72. <https://doi.org/10.1016/j.jag.2011.08.006>
- Pr´eau, C., Grandjean, F., Sellier, Y., Gailledrat, M., Bertrand, R., & Isselin-nondedeu, F. (2020). Habitat patches for newts in the face of climate change: local scale assessment combining niche modelling and graph theory. *Sci. Rep.*, 10, 1–13. <https://doi.org/10.1038/s41598-020-60479-4>
- Ratti, J. T., Smith, L. M., Hupp, J. . W., & Looke, J. L. (1983). Line transect estimates of density and the winter mortality of Gray partridge. . *J. Wildl. Mangt.* , 47, 1088–1096.
- Robin, C., Dunkin,I, Wilson, D. , Way, N., Johnson, K. , & Williams, T. M. (2013). Climate influences thermal balance and water use in African and Asian elephants: physiology can predict drivers of elephant distribution. Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA, Wildlife Safari, Winston, OR, USA, Six Flags Discovery Kingdom, Vallejo, CA, USA and Have Trunk Will Travel, Perris, CA, USA. Author for correspondence (dunkin@biology.ucsc.edu).
- Ryan, S. J., & Jordaan, W. (2005). Activity patterns of African Buffalo (*Syncerus caffer*) in the Lower Sabie region, Kruger National Park, South Africa. *Koedoe* , 48, 117–124. Pretoria. ISSN 0075-6458.
- Smeraldo, S., Bosso, L., Salinas-Ramos, V. B., Ancillotto, L. , S´anchez-Cordero, V., Gazaryan, S., & Russo, D. (2021). Generalists yet different: distributional responses to climate change may vary in opportunistic bat species sharing similar ecological traits. *Mammal. Rev.*, 51(4), 551–584. <https://doi.org/10.1111/mam.12247>
- Smit, I. J., Grant, C. C., & Whyte, I. J. (2007). Landscape-scale sexual segregation in the dry season distribution and resource utilization of elephants in Kruger National Park, South Africa. *Diversity & Distributions*, 13(2), 225–236. <http://www.jstor.org/stable/4539914>
- Stephenson, J., & Mizuno, A. (1978). .Recommendations on the conservation of wildlife in the Omo-Tama-Mago Rift Valley of Ethiopia. Ethiopian Wildlife Conservation Organization, Addis Ababa. Mimeo, 56.
- Stockwell, D. R. B., & Peterson, A. T. (2002). Effects of sample size on accuracy of species distribution models. *Ecol Modell* , 148, 1–13. [https://doi.org/10.1016/S0304-3800\(01\)00388-X](https://doi.org/10.1016/S0304-3800(01)00388-X)
- Stokke, S., & Du Toit, J. T. (2002). Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology*, 1., 40(4), 360-371. <https://doi.org/10.1046/j.1365-2028.2002.00395.x>

- Su, H., Bista, M., & Li, M. (2021). Mapping habitat suitability for Asiatic black bear and red panda in Makalu Barun National Park of Nepal from Maxent and GARP models. *Sci. Rep.* , 11,14135. <https://doi.org/10.1038/s41598-021-93540-x>.
- Sutherland, W. J. (2006). *Ecological Census Techniques: A Handbook*. (2nded.). Cambridge University Press, New York, NY, USA,
- Swets, J. A., (1988). Measuring the accuracy of diagnostic systems. *Science*, 240(4857), 1285–1293. <https://doi.org/10.1126/science.3287615>
- Thaker, M., Gupte, P. R., Prins, H. H. T., Slotow, R., & Vanak, A. T. (2019). Fine-scale tracking of ambient temperature and movement reveals shuttling behavior of elephants to water. *Frontiers in Ecology and Evolution*, 7(JAN). <https://doi.org/10.3389/fevo.2019.00004>
- Thomaes, A. , Kervyn, T. , & Maes, D. (2008). Applying species distribution modeling for the conservation of the threatened saproxylic stag beetle (*Lucanus cervus*). . *BiolConserv* , 141, 1400–1410. <https://doi.org/10.1016/j.biocon.2008.03.018>
- Thorn, J. S., Nijman, V. , Smith, D., & Nekaris, K. A. I. (2009). Ecological niche modeling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (*primates:Nycticebus*). *Divers.Dist.*, 15, 289–298. <https://doi.org/10.1111/j.1472-4642.2008.00535.x>
- Thouless, C. R., Dublin, J. J., Blanc, D. P., Skinner, T. E., Daniel, R. D., Taylor, F., Maisels, H. L., & FrederickandBouché, P. (2016). African Elephant Status Report 2016: an update from the African Elephant Database. Occasional Paper Series of the IUCN Species Survival Commission, No. 60 IUCN / SSC African Elephant Specialist Group. IUCN, Gland, Switzerland. vi + 309pp. vi(309).
- Traill, L. W., & Bigalke, R. C. (2006). A presence-only habitat suitability model for large grazing African ungulates and its utility for wildlife management. *African Journal of Ecology*, 45, 347–354. <http://dx.doi.org/10.1111/j.1365-2028.2006.00717.x>
- Western, D., & Lindsay, W. K. . (1984). Seasonal herd dynamics of a savanna elephant population. *Afr. J. Ecol.*, 22, 229–244. <https://doi.org/10.1111/j.1365-2028.1984.tb00699.x>
- Xu, W., Fayrer-hosken, R., Madden, M., Simms, C., Mu, L., & Presotto, A. (2020). Coupling African elephant movement and habitat modeling for landscape availability-suitability-connectivity assessment in Kruger National Park. *Pachyderm*, 58, 97–106. Retrieved from <https://pachydermjournal.org/index.php/pachyderm/article/view/422>
- Yirmed, D. (2010). *The Ecology and Conservation of the Relic Elephant Population in the Horn of Africa*. PhD Thesis, University of Melbourne, Australia.
- York, P., Evangelista, P., Kumar, S., Graham, J., Flather, C., & Stohlgren, T. (2011). A habitat overlap analysis derived from Maxent for Tamarisk and the south-western willow flycatcher. . *Front Earth Sci* , 5, 120–129. <http://dx.doi.org/10.1007/s11707-011-0154-5>
- Zhu, B., Wang, B., Zou, B., Xu, Y., Yang, B., Yang, N., & Ran, J. (2020). Assessment of habitat suitability of a high-mountain Galliform species, buff-throated partridge (*Tetraophasis szechenyii*). *Glob. Ecol. Conserv.* <https://doi.org/10.1016/j.gecco.2020.e01230>
- Zurell, D., Zimmermann, N. E., Gross, H., Baltensweiler, A., Sattler, T., & Wüest, R. O. (2019). Testing species assemblage predictions from stacked and joint species distribution models. *J. Biogeogr.*, 47, 101–113. <https://doi.org/10.1111/jbi.13608>