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Modelling of past, current and future distribution of suitable habitat for Menelik's bushbuck (*Tragelaphus sylvaticus meneliki* Neumann, 1902) in the Ethiopian highlands

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Abstract

Background Wildlife species adapted to the Afro-alpine highlands are vulnerable to loss of habitat due to global warming accompanying potential upward shifts and elevational range contractions of their preferred habitats. Understanding the trends in the shift of suitable habitats of endemic taxa is key to planning the conservation and management of species. Therefore, this study aimed to model the distribution of Menelik's bushbuck, a spiral-horned antelope endemic to Ethiopian highlands across the past (Last Glacial Maximum, and Mid-Holocene), present, and future.

Methods We performed the ensemble modelling implemented in the “sdm” R package using 6 modelling techniques (MaxEnt, Generalized Linear Model, Generalized Additive Model, Random Forest, Boosted Regression Tree, and Multivariate Adaptive Regression Splines). We combined 248 occurrence points of Menelik's bushbuck with 12 climatic, topographic, and anthropogenic variables. We selected these variables from originally 24 variables using the VIF step procedure to avoid highly correlated predictor variables for the final model run.

Results The performance of the ensemble model was excellent having AUC = 0.97 and TSS = 0.88 values. Bio6 (minimum temperature of the coldest month) contributed most to the distribution of Menelik's bushbuck followed by bio12 (annual precipitation) and elevation. The model projection estimated the suitable habitat of Menelik's bushbuck steadily decreases with increasing representative concentration pathways (RCP) scenarios and projection years. The current suitable habitat of this species is estimated to be 25,546 km² whereas the Mid-Holocene and the Last Glacial Maximum potential habitats was about 60,282.24 km² and 33,652 km² respectively. The magnitude of the loss of suitable habitats of Menelik's bushbuck will be highest in 2050 and 2070 under RCP 8.5 climate scenarios showing the loss in the currently suitable habitats of this species is over 95.1% and 99.8% respectively.

Conclusion Menelik's bushbuck has lost suitable habitat since the LGM and the loss will be greatest in the future due to climate change and land use change. The sharp decline of the suitable habitat will greatly threaten the future survival of the species. Our modelling can assist in identifying potential refuge areas for the species to assist in its preservation.

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Keywords Species-distribution-modelling, Climate change, Menelik's bushbuck, Last glacial maximum, High altitude species, Representative concentration pathways

Introduction

Species living at high altitudes will be most likely particularly affected by anthropogenic climate change due to rapid upward shifts of suitable habitats that might lead to mountain top extinctions [1]. This is not only a risk in the mountains of higher latitudes but also for high-altitude species in tropical mountains [2–5]. Ethiopia holds several high-altitude species or subspecies that are endemic to the country such as the Ethiopian long-eared bat (*Plecotus balensis*), gelada (*Theropithecus gelada*), Bale monkey (*Chlorocebus djamdjamensis*), Ethiopian wolf (*Canis simensis*), Mountain nyala (*Tragelaphus buxtoni*), Walia ibex (*Capra walie*), and Menelik's bushbuck (*Tragelaphus sylvaticus meneliki*) [6]. Recent studies on the Ethiopian wolf [7], the Ethiopian long-eared bat [8] and the gelada [9] applying species distribution or ecological niche models stressed the need for taking uphill movement of these species into account for conservation planning. However, these studies also showed that human pressure in mountain ranges, e.g., the expansion of agriculture, poses an additional risk to high-altitude species in Ethiopia [10–15]. In combination with the effects of climate change, this can lead to the extinction of the endemics and other high-altitude taxa.

Among the high-altitude species of Ethiopia, Menelik's bushbuck is probably the most widely distributed taxon [16]. It has been reported to inhabit various habitats such as forested areas with thick undergrowth but also relatively open habitats like Erica scrubland and Afro-alpine grassland [18–20]. According to Yalden et al. [16] this subspecies occupies a limited and disjunct range in the Chercher, Arsi and Bale Mountains, the mountains of western Shoa and areas of high ground in the province of Illubabor, but not, e.g., in the Simien Mountains. Recent surveys, however, have confirmed the taxon in several more mountainous areas, including the Simien Mountains National Park [21, 36]. At lower elevations in Northern, Southern, and Western Ethiopia a second bushbuck taxon occurs, the Ethiopian bushbuck (*Tragelaphus scriptus decula* Rüppell, 1835) [22]. However, the taxonomic status of both Ethiopian *Tragelaphus* taxa, their distribution boundaries, and whether gene flow occurs are not clear.

To understand the distribution of Menelik's bushbuck in Ethiopian highlands, species distribution models (SDMs) can be used for modelling the habitat suitability of the target species in the study area as these models are popular in ecology and used globally to address

fundamental questions like where a species is likely to be found, what factors are involved in the distribution of a species, and what challenges climate change imposes on different species. The advancement in data science has resulted in the development of a number of modelling algorithms, which are being integrated and used to develop more accurate maps and provide advanced decision-making for the conservation of endangered species globally [23–26]. Ensemble modelling, by combining outputs from multiple SDMs, offers a more comprehensive and reliable view of species distributions. It allows for better understanding of the relationships between species and their environment, making it particularly valuable tool in ecology and conservation biology. The ability to integrate and compare different model outputs has made ensemble modelling a preferred choice for predicting the potential impacts of climate change, land use change, or other environmental changes on species distribution patterns [27]. Consequently, ensemble modelling has become instrumental in formulating effective conservation strategies and managing biodiversity under global change scenarios [28].

Therefore, in this study, we performed ensemble modelling using environmental variables across the entire range of Menelik's bushbuck to: (1) predict past, current and future distributions of suitable habitat; (2) identify the climatic factors key to the distribution of the species, and (3) detect the change in suitability area of Menelik's bushbuck under different climate change scenarios.

The results of our SDMs may help to understand the shifts in distribution across time, and to determine the origin and historical dispersal of the target species. We hypothesise that the suitable habitats and distribution of Menelik's bushbuck in the highlands of Ethiopia are influenced by climate, anthropogenic (land use) and other topographic variables. We believe that the precipitation (Annual Precipitation), temperature (Min Temperature of Coldest Month), topographic variables (elevation and slope) and land cover are positively related to the predicted habitat suitability of the target species.

Materials and methods

Study area

Ethiopia is located within the tropics (3° and 15°N latitude and 33° and 48°E longitude). It is the center of the East African region that has eleven Afrotropical ecoregions and has been designated a Global 200, an ecoregion of global importance for biodiversity conservation

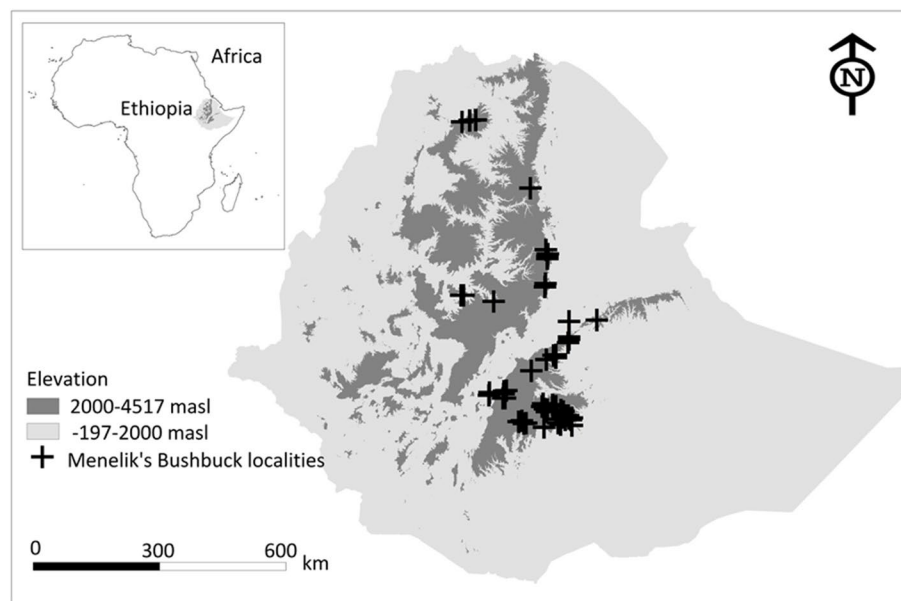


Fig. 1 Topographic map of Ethiopia and occurrence points of Menelik's bushbuck collected between 2018 and 2023

[55]. Our study area comprises the complete Ethiopian highlands above the 2000 m contour line (Fig. 1). The Ethiopian highlands belong to Eastern Afromontane and Horn of Africa biodiversity hotspots [29]. Beside the high altitude endemic mammals [30, 83] they harbour several other endemic vertebrate and plant species [31–33].

The climate in the highlands is characterized by a rainy season from June to September, and a dry season from October to April. Rainfall generally increases from north to south and east to west, with an average annual rainfall of 600 mm in the northeast and 2,000 mm in the southwest [34]. In combination with its topography this climate variability is responsible for the wide range of vegetation types across the country, which includes arid and semi-arid *Acacia* woodland and Afro-alpine vegetation.

The highlands are the main area of agriculture and human settlement in Ethiopia with 88% of the human population, 95% of the agricultural area and about 75% of the livestock of Ethiopia found in the highlands [35]. The high human population lead to large-scale conversion of the natural habitat and the impoverishment of natural ecosystems, including deforestation and biodiversity loss.

Data collection

Species occurrence data

We assembled a total of 248 occurrence points for Menelik's bushbuck (Table, S1) from field surveys between December 2018 and July 2023. At each observation site, a minimum distance of 1 km was set between transects to avoid an overlap of sampling points in most highlands of northern, central and south eastern Ethiopia where

the target species is found (Fig. 1). We used Global Positioning System (GPS) to record the coordinates of direct observations of the respective presence points. We also used binoculars to spot the target species from a distance. We filtered these data by removing duplicates. In cases where we detected multiple occurrence points within a 1 km×1 km grid cell, we used only one point per cell. Finally, we retained 132 occurrence points for our modelling (Fig. 1). These points lay between 2000 to 3800 m asl with most localities above 2800 m asl. A study by Hernandez et al. [56] indicated that high model accuracy was observed using several modelling techniques for models based on samples as small as 5, 10 and 25 compared to models based on 100 samples.

Environmental variables

We examined 24 climate, topographical and anthropogenic variables (Table 1). We downloaded data of the 19 bioclimatic variables for the current (1950 – 2000), future, and Paleo climate data for the last glacial maximum (LGM), and the mid-Holocene from the WorldClim version 1.4 (<https://www.worldclim.org>; accessed June 2023) with a spatial resolution of 2.5 arc-minutes (about 4.5 X 4.5 km) at the equator.

Topographical variables such as elevation and slope can be of importance in high-altitude species. We therefore used digital elevation model data, with a resolution of 30 m (SRTM 1 Arc-Second Global) from the United States Geological Survey (<https://earthexplorer.usgs.gov/>). We computed slope and aspect from digital elevation using ArcMap10.8.2. Additionally, we downloaded

Table 1 Environmental variables (variables marked x are those that we selected for our modelling approach)

Code	Variables	Units	VIF values	Selected
Bio1	Annual Mean Temperature	°C		
Bio2	Mean Diurnal Range [Mean of monthly (max temp – min temp)]	°C	5.28	x
Bio3	Isothermality (P2/P7)*(100)	-	2.68	x
Bio4	Temperature Seasonality (standard deviation*100)	C of V		
Bio5	Max Temperature of Warmest Month	°C		
Bio6	Min Temperature of Coldest Month	°C	6.67	x
Bio7	Temperature Annual Range (P5-P6)	°C		
Bio8	Mean Temperature of Wettest Quarter	°C		
Bio9	Mean Temperature of Driest Quarter	°C		
Bio10	Mean Temperature of Warmest Quarter	°C		
Bio11	Mean Temperature of Coldest Quarter	°C		
Bio12	Annual Precipitation	mm	6.16	x
Bio13	Precipitation of Wettest Month	mm		
Bio14	Precipitation of Driest Month	mm		
Bio15	Precipitation of Seasonality (Coefficient of Variation)	-	4.20	x
Bio16	Precipitation of Wettest Quarter	mm		
Bio17	Precipitation of Driest Quarter	mm		
Bio18	Precipitation of Warmest Quarter	mm	1.80	x
Bio19	Precipitation of Coldest Quarter	mm	1.59	x
aspect	Aspect	degree	1.35	x
elev	Elevation	m	8.83	x
Land cover	Land cover	-	1.36	x
slope	Slope	%	1.31	x
Solar rad	Solar radiation	-	3.61	x

solar radiation from www.worldclim.org as standardized tiff formats [23, 37] and it is theoretically proportional to the amount of direct solar radiation striking arbitrarily oriented earth's surface as a function of its aspect, slope and latitude [38].

We also obtained land cover data from the Copernicus Climate Change Service (<https://cds.climate.copernicus.eu/>). Land cover data in the current habitat suitability prediction was used as constant in the past and future projection due to lack of past and future dataset for such variable.

In 2008, many climate modelling groups worldwide come to an agreement to develop the new global climate models (GCMs) which aim to enhance an understanding of past and future climate changes and provide projections of future climate change for the analysis of possible consequences [78]. These developments are currently in the fifth phase of the Coupled Model Intercomparison Project (CMIP5). The four Representative Concentration Pathways (RCPs) of CMIP5 can be used to facilitate the assessment of potential climate change impacts and provide useful information for possible mitigation and adaptation strategies [78, 79]. RCPs were produced based

on comprehensive data on climate change forcing agents such as future concentration and emission of greenhouse gases (GHG), and land cover, to represent a projected radiative forcing level of all major forcing components by the end of 2100 [79].

The commonly used four RCPs (RCP2.6, 4.5, 6.0 and 8.5) indicate varying forcing levels from very low to high. RCP2.6 can be considered a low emission scenario whereas RCP8.5 represents a very high scenario due to increased GHG emission from high fossil fuel/coal consumption to support rapid population growth. RCP4.5 and RCP6.0 are a representative of intermediate/medium mitigation scenarios [79]. In this study, we used the intermediate greenhouse gas scenario (RCP 4.5) and the highest emission scenario (RCP 8.5) for the years 2050 and 2070 from the fifth Report of the Intergovernmental Panel on Climate Change [81].

In the future, the on-going emission of greenhouse gases will likely cause an increase in frequency, severity and magnitude of extreme climate-related events [80], posing ever greater threats to the biodiversity in east Africa. A slight increase in warming can have a significant impact on tropical species that have a narrow

thermal-tolerance range than that of temperate species [82].

To model the past suitable habitat of Menelik's bushbuck, we used two time windows: (1) The last glacial maximum (LGM), about 22,000 years ago, when the air temperature was about 6 °C lower than today [84], and (2) the mid-Holocene period, about 6,000 years ago, when air temperature was similar to the present [39].

Data analysis

Collinearity analysis of predictor variables

Multicollinearity analysis is a critical procedure in SDMs, which addresses the issue of collinearity, or the high correlation among predictor variables [40]. It aims to identify and mitigate the influence of interrelated variables that may otherwise confound the results and interpretations of a model, thereby ensuring robust and credible model outcomes. Within the context of SDMs multicollinearity can lead to an overestimation or underestimation of the effects of different environmental variables on species distributions [41]. This can mislead the interpretation of species-environment relationships and can undermine the predictive performance of the model. Hence, a careful multicollinearity analysis is fundamental to the successful application of species distribution modelling.

We performed a multicollinearity analysis using the Variance Inflation Factor (VIF) rule. Variables with a VIF exceeding 10 are considered highly collinear and thus should be omitted from the model [42]. The stepwise multicollinearity analysis conducted in this study leveraged the VIF step function using the Uncertainty Analysis for Species Distribution Models (USDm) package in R [43]. The outcome of VIF step function is a model with multicollinearity significantly reduced, thereby enhancing the interpretability and credibility of the model results. From the original 24 variables, we considered 12 weakly correlated variables for further analyses of Menelik's bushbuck ensemble modelling (Table 1).

Background data

It has been suggested that when modelling species distribution using presence-only data, the selection of background data approach is as important as the selection of modelling method [59]. The background or pseudo-absence approach has been found to improve model performances in the studies of various species and across geographic areas [59].

In this study, we only used presence or occurrence data. The background or pseudo-absence data were generated using "gRandom" which generates points randomly over geographic space by removing points located in present sites [44]. Additionally, 500 background points were generated from 132 occurrence points of Menelik's bushbuck

representing an error-free and adequately compiled data. Spatial autocorrelation in species occurrences interferes with independence between the test and training data sets if the division of the training and test data is executed randomly [45]. Thus, the Spatially Rarefy Occurrence Data Tool in the SDM toolbox2.5 of ArcGIS 10.8.1 was employed to filter multiple occurrence points to reduce to a single point [46] and all points were mapped using ArcGIS 10.8.1 for observation and check the accuracy of occurrences. The occurrence records were projected on the study area map to ensure that they were within the targeted region.

Species distribution modelling

We used an ensemble of species distribution model algorithms to minimise the uncertainty associated with single modelling techniques [27]. An ensemble model combines the strengths of several SDM approaches while minimizing the weakness of any particular model [47, 48]. We applied an ensemble of six models implemented in the 'sdm' package [44] in R version 4.3.2 [85]. The models include three machine learning algorithms and three regression methods. We selected Maxent, Boosted Regression Tree (BRT), Random Forest (RF), generalized additive model (GAM), Generalized Linear Models (GLM) and Multivariate Adaptive Regression Splines (MARS). These modelling algorithms are among the most commonly employed for species distribution models, depend on the level of complexity, appropriateness, predictive power, and capability to incorporate presence-only data because of limited access to absence data [57, 58]. The algorithms were combined into one ensemble model through by applying a weighted mean approach using true skill statistic (TSS) [49].

For fitting the models together, subsampling and bootstrapping replication methods were used. Ten replications were done for the model object meaning five for each replication method. After preparing the model object we used the "predict" function to predict the distribution of the study species under the past, current, and future conditions using the selected predictor variables. Prediction output maps were also ensembled together using an ensemble function. The ensemble process was done by using a weighted averaging method by taking the value of True skill statistics (TSS) where sensitivity and specificity is maximized as a threshold.

Performance statistics

The value of sensitivity against the random sample of background locations is sufficient to define a Receiver Operating Curve (ROC) [50, 51]. The value of AUC ranges from 0.5 (random prediction) to 1 (perfect accuracy). According to Merckx et al. [17] AUC values are

interpreted as follows 0.6–0.7 as poor, 0.7–0.8 as average, 0.8–0.9 as good, and 0.9–1 as excellent.

Although the Kappa statistic is the most widely used, several studies have criticized it for being inherently dependent on prevalence. The TSS corrects for this dependence while still keeping all the advantages of kappa [52]. Both Kappa and TSS are threshold-dependent measures of model accuracy [53] and their values ranged from -1 to $+1$, where $+1$ indicates perfect agreement between predictions and observations, and values of 0 or less indicate agreement no better than random classification [53]. The following ranges were used to interpret Kappa and TSS statistics: values < 0.4 were poor, 0.4–0.8 useful, and > 0.8 good to excellent.

Examining the impact of climate change on species distributions

The assessment of the impact of climate change on the species distributions was performed by comparing the potential distribution areas in the current climate conditions with the future potential distribution areas based on a species' current climate preferences and future climatic conditions. Areas of habitat gain and habitat loss were calculated in Arc Map 10.8.2 using the ensemble output maps. We classified the pixels into two categories based on the TSS threshold values as suitable or unsuitable habitats. The TSS threshold value for this study was found to be 0.6.

Quantifying and visualizing changes in range shift

Changes in range shift were visualized by producing maps using occurrence probabilities and predicted presence absence data. To quantify and visualize the range shift using occurrence probabilities, we used the worst-case scenarios RCP 8.5 predictions for both 2050 and 2070 and the current prediction. We then calculated the change between the ensemble prediction of RCP 8.5 and current predictions and plotted the change into a map. Secondly, we quantified and visualized the change in range shift using presence and absence data. The presence and absence data were extracted from occurrence probabilities using coordinates from both current and future predictions by setting a threshold for TSS where it is maximized. The threshold converts the probabilities to binary scores, 1 (presence) and 0 (absence) [54]. Then we prepared an empty raster with the same extent and resolution with the other ensemble maps and plotted presence and absence points based on the threshold.

Results

Model performance

Sensitivity and specificity scores were excellent for all models indicating both suitable and unsuitable areas

were well identified and the proportion of correctly classified samples were maximum (Fig. S8). Receiver operator characteristics (ROC) curve using bootstrap and subsampling replication methods for different SDMs showed that sensitivity (true positive rate) of the vertical line and 1-specificity (false positive rate) of the horizontal line describe the proportion of correctly and incorrectly classified samples (Fig. S8). The red and blue curves represent the mean of AUC using training and test data respectively (Fig. S8).

In this study the AUC value achieved was 0.97 (Table 2), indicating an excellent performance of the ensemble model, as values closer to 1 suggest a near-perfect ability of the model to distinguish between presence and absence areas. The TSS value, at 0.88 (Table 2), also demonstrates a high level of accuracy, as values closer to $+1$ denote perfect agreement between observed and predicted species presence [52]. Additionally, the six modeling algorithms performed best resulting in an AUC value ranging from 0.94 to 0.98 and TSS values ranging from 0.86 to 0.92 (Table 2). Generally, the performance of both machine learning and regression algorithms were excellent. The differences in the modelling techniques' performance and prediction ability in this study suggest that, the ensemble model has the potential to model a suitable habitat for the target species, as also suggested by [86]. Random Forest outperformed all other models, with a high COR (0.91) (Table 2) and a comparatively lower deviance (0.24) (Table 2).

Variable importance analysis

The key environmental factors that determined the suitability of habitat for Menelik's bushbuck were bio6 (min temperature of coldest month), followed by bio12 (annual precipitation), elevation, solar radiation, and bio18 (precipitation of warmest quarter) (Fig. 2). The remaining environmental variables had lower effects. Aspect and slope contributed the least to the distribution of the target species.

The response curve also showed the relationships of probability of occurrence of the target species and each

Table 2 Results of model performance

Method	AUC	COR	TSS	Deviance
Maxent	0.98	0.85	0.89	0.35
GLM	0.97	0.83	0.86	0.38
BRT	0.97	0.84	0.87	0.50
RF	0.98	0.91	0.92	0.24
GAM	0.94	0.83	0.86	0.68
MARS	0.97	0.84	0.88	0.56
Ensemble	0.97	0.85	0.88	0.45

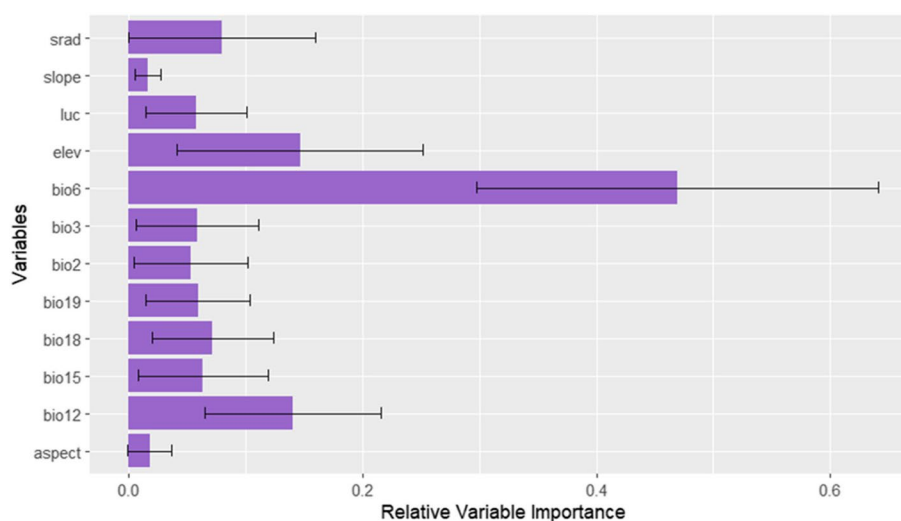


Fig. 2 Relative contributions of environmental variables on the suitability of habitat for Menelik's bushbuck

environmental variable (Fig. S1). The habitat suitability of Menelik's bushbuck decreases, when bio6 (Min Temperature of Coldest Month), bio12 (Annual Precipitation), bio2 (Mean Diurnal Range [Mean of monthly]), bio15 (Precipitation of Seasonality), bio19 (Precipitation of Coldest Quarter), aspect and solar radiation decreases (Fig. S1) however, habitat suitability of the target species increases with an increase in the predictor variables, such as elevation, bio3 (Isothermality), land cover, slope and bio18 (Precipitation of Warmest Quarter) (Fig. S1).

Past, present and future climatic distributions

Dynamics of suitable habitats of Menelik's bushbuck

According to our modelling, the current distribution of suitable habitat for Menelik's bushbuck is in the highlands of Bale, Arsi, Chercher, western Showa, Illubabor, Menz-Guassa, Wof-Washa, Simien and Borena Saint (Fig. 3).

The current extent of suitable habitat is 25,546 km² within an elevation range of 2000 m to 3800 m. Compared to this, the extent during the LGM was 24.1% larger and extended further into the northern, central, and south eastern highlands of Ethiopia. During the Mid-Holocene the area was 57.6% larger than the current area (Table 3).

Compared to the current extent, all future climate scenarios projection under the (2050RCP4.5, 2070RCP4.5, 2050RCP8.5 and 2070RCP8.5) estimated the total area of suitable habitat of Menelik's bushbuck would decline sharply by 81.4%, 96.8%, 95.1% and 99.8% respectively (Table 3). This showed the target species is currently under pressure from climate change and human pressure on its suitable habitat. Thus the species will lose most of

its suitable habitat until 2070 under RCP 8.5 and only a small part of its current distribution south of the Rift Valley mainly in the highlands of Arsi and Bale will remain suitable (Fig. 3).

The magnitude of the loss of potentially suitable habitats of Menelik's bushbuck in 2070 under all future climate scenarios is the highest compared to the current, Mid-Holocene, and Last Glacial Maximum (Table 3). The Mid-Holocene potential habitat of 60,282.24 km² and the LGM potential habitat of 33,652 km² will shrink only 52.4 km² in 2070 in 2070 under RCP 8.5 (Table 3). Generally, the ensemble prediction estimated, the suitable habitats of Menelik's bushbuck will decrease sharply for the year 2070 for both RCP 4.5 and RCP 8.5 scenarios compared to the current projection (Table 3).

The suitable habitats of this species steadily decrease with increasing RCP scenarios and projection years (Table 3). The magnitude of the loss of potential suitable habitats of Menelik's bushbuck will be highest in 2050 and 2070 under RCP 8.5 climate scenarios compared to the current (Table 3). The loss in the current suitable habitats of Menelik's bushbuck is over 95.1% and 99.8% for the years 2050 and 2070 respectively under RCP 8.5 climate scenarios (Table 3).

Range shift visualization

Fundamental assumption in SDM is presuming the modelled species being in equilibrium with its environment [60] as opposed to still spreading in a new habitat (invasive species). However, it can be also argued that the land use and climate change are simultaneously transforming the species ranges. Other basic assumption in SDM is that the habitat is actually dictated by the environmental

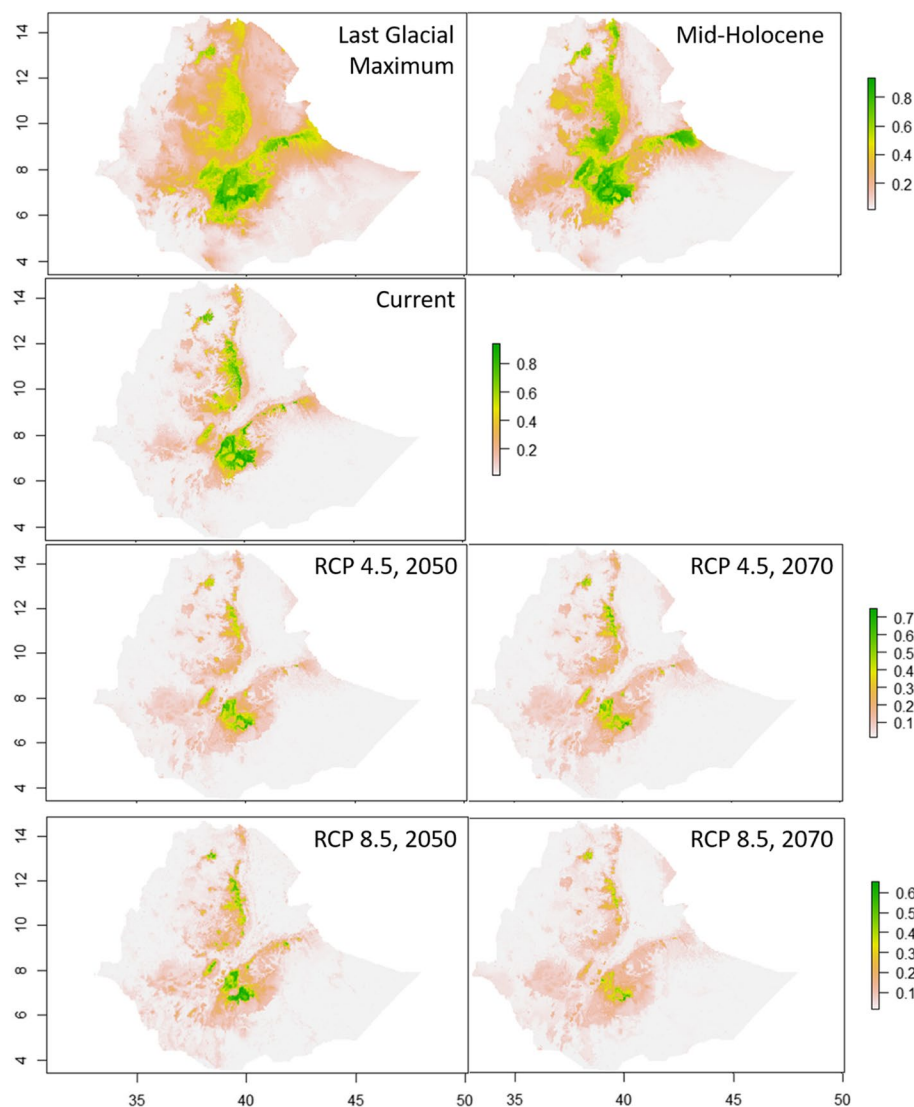


Fig. 3 Distribution of suitable habitat of Menelik's bushbuck under past, current and future (2050; 2070) climate conditions. Suitability classes: (0.00 - 0.2) = unsuitable; (0.2 - 0.40) = least suitable; (0.4 - 0.6) = moderately suitable; (0.6 - 1) = suitable. Green colour denotes potential suitable habitats; yellow indicates moderately suitable habitats; pink shows least suitable habitats and grey denotes unsuitable habitats

requirements and tolerances [60] and the relationships are not just random correlations without causation. Taking spatial autocorrelation into account while working with SDMs is crucial, even if it would mean only pointing out its existence.

To clarify how the geographic distribution patterns of Menelik's bushbuck may change, we calculated the change in suitability compared to current suitability for each grid cell and scenario. Range change differed between past and the two future scenarios depending on Menelik's bushbuck response. For this species, range loss was predicted to be larger than range gain, irrespective of the scenario (Fig. 4), however, the greatest losses were

predicted in 2050 and 2070 under the RCP 8.5 scenario. Specifically, in 2070 under RCP 8.5, Menelik's bushbuck (99.8%), was predicted to lose the largest portions of its suitable ranges. In this regard, the probabilities of occurrence and presence and absence points were extracted from 2050 and 2070 ensemble prediction maps to visualize range shift in Menelik's bushbuck (Fig. 4). This species will lose most of its current suitable habitats in 2050 and 2070 and will occur on a small, fragmented and patchy habitat in the highlands of south of the rift valley (red colour in Fig. 4A and B). Its presence-absence is depicted in Fig. 4C and D showing the likely occurrence of the

Table 3 Projected potential suitable habitats of Menelik's bushbuck in the Last Glacial Maximum, Mid-Holocene, current and future climate conditions

Time		Areas of suitable habitats in km ²	% change compared to current
Last Glacial Maximum—LGM (22,000 BP)	Last Glacial Maximum—LGM (22,000 BP)	33,652	+ 24.1%
Mid Holocene—MDH (6,000 BP)	Mid Holocene—MDH (6,000 BP)	60,282	+ 57.6%
Current	Current	25,546	-
Future	RCP 4.5	2050 4,763	−81.4%
		2070 818	−96.8%
	RCP 8.5	2050 1,259	−95.1%
		2070 52	−99.8%

species with impressive shrinkage of its current suitable ranges.

Discussion

Several studies documented the global warming potentially can lead a significant habitat shifts of suitable habitats of many species in particular those adapted to the afro alpine highlands of Africa [61–63]. The Ethiopian plateau 'roof of Africa' rises 1500 masl above the plateau that lies at 2500 masl and comprises 80% of the

landmass of Africa above 3000 m asl [64]. With this study, we modelled the distribution of Menelik's bushbuck under past (Last Glacial Maximum and Mid-Holocene), current and future climatic scenarios. The study provides important bearings on conservation and management of Menelik's bushbuck under the influence of climate change and human impact effects which in turn will help to develop of strategies and policies for the management and conservation of this endemic high-land species.

We evaluated model discrimination ability using true skill statistic (TSS), Kappa, area under the curve (AUC) of the receiver operator characteristic (ROC), and the deviance statistic. These measures attribute different weights to the various types of prediction errors [52]. To evaluate the performance of the models, AUC (area under the receiver-operating characteristic curve) is an effective, threshold-independent indicator and its values are used as the main evaluator.

Current and future potential distributions

Future distribution models can forecast habitat suitability and provide information on the likelihood of range shifts or population changes [65]. This study showed that Menelik's bushbuck had larger distribution range during period of Mid-Holocene followed by Last Glacial Maximum than the current extent. The reduction of suitable habitat of the Menelik's bushbuck is likely to be further diminished in climate scenarios and projection years. The threshold-independent AUC and threshold-dependent

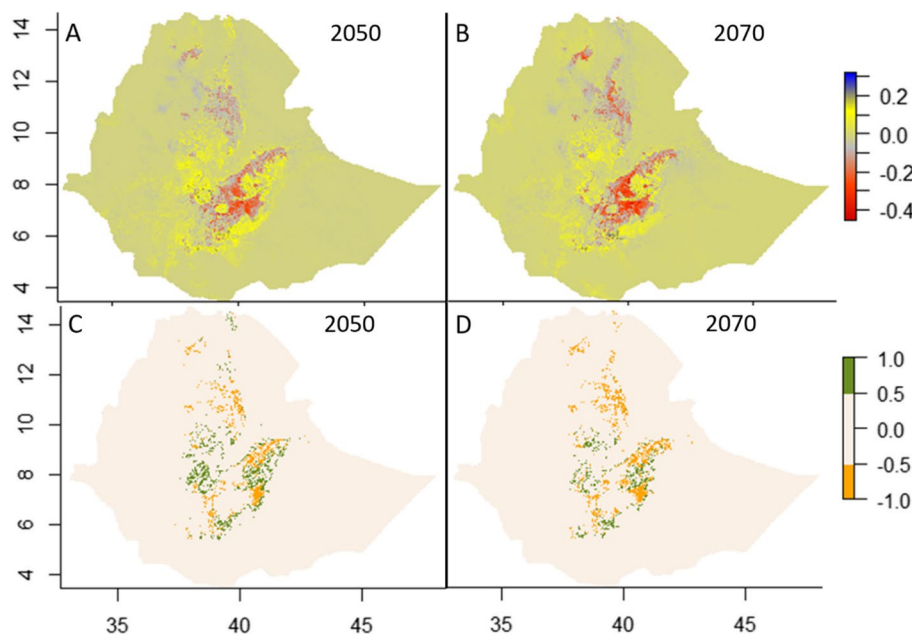


Fig. 4 Probability of occurrence (A and B) and presence-absence (C and D) of suitable habitat for Menelik's bushbuck in 2050 and 2070

TSS performance scores for Menelik bushbuck was performing excellent indicating the performance quality of species distribution models. The current estimated potential habitat of Menelik's bushbuck which is about 25,546 km². The larger proportion of the suitable habitats is found within the protected areas and controlled hunting areas. While protected areas have valuable contribution for the species conservation, they are still under the influence of human activities including unsustainable natural resource use, livestock grazing and encroachment. Supporting the local community to engage with agricultural activities compatible with biodiversity conservation including agroforestry, bee keeping and other off farm activities which can generate additional income may be useful strategy in addition to law of enforcement.

The current potential habitat of Menelik's bushbuck is likely to be diminished to 818 km² and 52 km² for the RCP 4.5 and RCP 8.5 scenarios respectively during 2070 indicating the need for urgent conservation efforts for the sustainable survival of this species in the highlands of Ethiopia. These predictions are relevant to other high-altitude Afromontane biodiversity, and therefore are particularly worrying given the high levels of endemism found in the region [66, 67]. The shrink in habitat due to climate change is predicted to other endemic highlands species of Ethiopia including Ethiopian wolf (*C. simensis*) [7] and *Theropithecus gelada* [9] will have very limited predicted suitable habitats.

Past distributions

SDMs for historical timelines can offer ecological and evolutionary data on the historical changes of species distribution over time [68]. Past models can be used to explain phylogeographic patterns and speciation processes, as well as to predict historical hotspots and potential migration routes [68]. Additionally, studies on how species have adapted to past climate change offer important insights into how species will respond to climate change in the future [69].

During last glacial maximum the suitable habitat of Menelik's bushbuck had expanded to northern, central and south eastern highlands of Ethiopia, covering an area 31.73% larger than the present range but decreased by 79.13% from the time of Mid-Holocene. On the other hand, during the period of Mid-Holocene the area of suitable habitat for Menelik's bushbuck was respectively 135.97% and 79.1% larger than from the current and Last Glacial Maximum.

As a result, the habitat suitability projected for the Last Glacial Maximum and Mid-Holocene scenarios varied for the target species preferring more Mid-Holocene environmental conditions than Last Glacial Maximum. This is because of the suitable areas of Menelik's

bushbuck shifted from low latitudes to high latitudes from the Last Glacial Maximum to the Mid-Holocene. This finding is consistent with those of Saupe et al. [70] about the high-latitudinal migration of tropical species as temperatures rise over geological ages. During the Last Glacial Maximum, the climate was cooler and drier, hence no rainfall, thus, vegetation only occurred in high-elevation refugia regions due to the formation of mist [71]. However, during the Mid-Holocene the temperature became warmer [68], hence the adaptation of Menelik's bushbuck could spread. Most importantly, the difference between the two climate scenarios of the past could be a result of desiccation tolerance speciation, evolution and adaptation for Menelik's bushbuck which would explain the differences in the species responses.

Compared with the current and LGM times, the Mid-Holocene projection estimated the presence of more suitable habitats in the northern, central and south eastern highlands of the country, majority of the distributions located south of the rift valley (Bale and Arsi) highlands and central highlands showing the target species had different extents of suitable habitats during the period of Last Glacial Maximum and Mid-Holocene. As a result, this species had larger distribution range during period of Mid-Holocene followed by Last Glacial Maximum than the current extent.

Environmental factors affecting the distribution of Menelik's bushbuck

Ecological factors determine the distribution of species. Temperature, precipitation, topographic and anthropogenic (land cover) variables are mostly discussed ecological factors to shape the distribution of flora and fauna. Temperature decreases as altitude increases, while precipitation and altitude have a direct relationship. As a result of climate change, temperature is expected to increase from 0.3°C to 1.7°C for emission mitigation scenario (RCP 2.6), 1.4°C to 3.1°C for the intermediate emission scenario (RCP 4.5) and 2.6°C to 4.8°C for high emission scenario (RCP 8.5) by 2100 [72].

The study's findings show that environmental variables play a vital role in this species' distribution with bio6 contributing the most to the distribution of Menelik's bushbuck followed by bio12, elevation and bio18 under the examined climate change scenarios. Bio6 gives the highest response to climate change for all algorithms used for modelling. These variables are expected to alter significantly under the RCP8.5 scenario, causing substantial portions of the current distribution area to become unsuitable by 2050. This study predicts more range contraction under RCP8.5 by 2070, a comparatively more extreme scenario. The interaction between temperature, precipitation, topographical and anthropogenic variables

will influence the habitat requirements of the target species.

Response curves generated for this species estimated different variables giving responses for each algorithm. For example; for BRT and RF the environmental variable that gave a high response was elevation (Fig. S2 and S7), while for GAM four variables showed a high response (land cover, slope, bio3 and aspect) among those land cover and bio3 showed the highest response (Fig. S3). Similarly, for GLM four variables showed a high response (bio18, Bio3, slope and land cover) among those bio18 showed the highest response (Fig. S4) while for MARS four variables showed a high response (bio3, elevation, land cover, Bio18 and slope) among those bio3 showed the highest response (Fig. S5). Lastly, for MaxEnt four variables showed a high response (bio18, elevation, Bio3, slope and bio3) among those bio18 showed the highest response (Fig. S6).

Land cover was also included in our model projections and then the response curve showed that habitat suitability of Menelik's bushbuck increases with an increase in land cover among the other predictor variables (Fig. S1). This indicates, land use change can significantly increase the spatial extent of unsuitable habitats [73]. A pronounced negative influence of rural human population growth on several mammal species was indicated in the highlands of southwestern Ethiopia [74]. This implies, climate change coupled with land use changes as a result of human pressure and associated perturbations are posing a risk of suitable habitat loss for the highland species. Given that Ethiopian highlands are isolated and human alteration is highly increasing, conservation strategies should be prepared to tackle the potential habitat loss and risk of extinction. As the climate gets warmer species give response by shifting their range or by adapting to the changes. Range shifts can result to habitat contraction or expansion.

Limitation of the study

The model predictions of Menelik's bushbuck did not consider factors such as dispersal ability and biotic interactions that may restrict species range shifts due to absence of data availability. Furthermore, biotic interactions have been suggested to influence species geographic distribution at all spatial extents across and within trophic levels [75]. They have been found to shape species' spatial patterns by the operation of multiple mechanisms, notable examples are competition, predation and host-parasite [76, 77]. The development of these environmental data over large spatial extents and the addition of these factors into the models will improve the robustness of the predictions of SDMs.

Conclusion

This is the first study using background data and ensemble modelling methods to improve the accuracy in the model predictions combining climate, topography and land cover data to simulate the distribution of potential suitable areas of Menelik's bushbuck in the highlands of Ethiopia across the past, current and future climate changes, and analyze the dominant environmental factors affecting the target species distribution. As a result, the study showed that the ensemble model performed better than single models, and it is good enough at predicting the potential suitable habitat of Menelik's bushbuck with excellent accuracy. The majority of the current suitable habitats for this species were found in the highlands of south eastern, central and northern Ethiopia indicating the target species in the study area is highly vulnerable to environmental change.

The study also showed temperature, precipitation and elevation had an impact on the targeted species' present distribution, which was consistent with the trend seen at both the global and regional scales. Min Temperature of Coldest Month contributing the most to the distribution of Menelik's bushbuck followed by Annual Precipitation and elevation under the examined climate change scenarios. The remaining variables had lower contribution to the habitat suitability of this species. Aspect and slope contributed the least to the distribution of this species.

Our research highlights the negative impacts of climate change on the Menelik's bushbuck, as it is expected to experience a sharp decline in its geographic range under future climate change scenarios. These findings provide valuable insights in identifying areas that are likely to remain suitable for this species in future climate change scenarios. To ensure the survival of the Menelik's bushbuck, it is crucial to enhance the protection of its habitats. We recommend the development and implementation of a species conservation action plan to mitigate the climate change effects and human disturbance on its distribution.

Abbreviations

AUC	Area Under the Curve
BRT	Boosted Regression Tree
CCSM4	Community Climate System Model version 4
CMIP5	Coupled Model Intercomparison Project 5
EBI	Ethiopian Biodiversity Institute
EFAP	Ethiopian Forestry Action Program
EWCA	Ethiopian Wildlife Conservation Authority
GAM	Generalized Additive Model
GCMs	Global Climate Models
GLM	Generalized Linear Model
IPCC	Intergovernmental Panel on Climate Change
LCCS	Land Cover Classification System
MARS	Multivariate Adaptive Regression Splines
Maxent	Maximum Entropy
RCP	Representative Concentration Pathways
RF	Random Forest
SDMs	Species Distribution Models

SRTM Shuttle Radar Topography Mission
 TSS True Skill Statistic
 USDM Uncertainty Analysis for Species Distribution Models
 USGS United States Geological Survey
 VIF Variance Inflation Factor

Supplementary Information

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Supplementary Material 1.

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Authors' contributions

Conceptualization: Zeleke Tigabe Abuhay, Anagaw Atickem. Data curation: Zeleke Tigabe Abuhay, Arega Mekonen Ali. Formal analysis: Zeleke Tigabe Abuhay. Methodology: Zeleke Tigabe Abuhay, Anagaw Atickem, Dietmar Zinner. Supervision: Anagaw Atickem, Dietmar Zinner. Validation: Zeleke Tigabe Abuhay. Visualization: Zeleke Tigabe Abuhay. Writing original draft: Zeleke Tigabe Abuhay. Writing - review and editing: Zeleke Tigabe Abuhay, Dietmar Zinner, Anagaw Atickem.

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Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

Ethical review and approval were not required for the animal study because the study didn't require animal handling. The field survey and data collection were conducted without disturbing the animals.

Consent for publication

Not applicable.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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References

- Chan WP, Lenoir J, Mai GS, Kuo HC, Chen IC, Shen SF. Climate velocities and species tracking in global mountain regions. *Nature*. 2024;629:114–20.
- Marris E. The escalator effect. *Nat Clim Change*. 2007;1:94–6.
- Sekercioglu CH, Schneider SH, Fay JP, Loarie SR. Climate change, elevational range shifts, and bird extinctions. *Conserv Biol*. 2008;22:140–50.
- Laurance WF, Useche DC, Shoo LP, Herzog SK, Kessler M, Escobar F, et al. Global warming, elevational ranges and the vulnerability of tropical biota. *Biol Conserv*. 2011;144:548–57.
- Chala D, Gizaw A, Thorn JPR, Sanchez AC, Eilu G, Demissew S, et al. The sky islands in eastern Africa: biodiversity, opportunities, and risks. In: Schneiderbauer S, Fontanella Pisa P, Shroder JR, Szarzynski J, editors., et al., Safeguarding mountain social-ecological systems, vol. 2. Amsterdam: Elsevier; 2024. p. 97–107.
- Ethiopian Biodiversity Institute (EBI). Ethiopia's fifth national report to the convention on biological diversity. Addis Ababa: Ethiopian Biodiversity Institute (EBI); 2014.
- Berhanu Y, Tassie N, Sintayehu DW. Predicting the current and future suitable habitats for endemic and endangered Ethiopian wolf using MaxEnt model. *Heliyon*. 2022;8(8):e10223.
- Razgour O, Kasso M, Santos H, Juste J. Up in the air: threats to afro-montane biodiversity from climate change and habitat loss revealed by genetic monitoring of the Ethiopian Highlands bat. *Evol Appl*. 2021;14(3):794–806.
- Ahmed AS, Chala D, Kufa CA, Atickem A, Bekele A, Svenning JC, Zinner D. Potential changes in the extent of suitable habitats for geladas (*Theropithecus gelada*) in the Anthropocene. *BMC Ecol Evol*. 2023;23(1):65.
- Stephens PA, d'Sa CA, Sillero-Zubiri C, Williams NL. Impact of livestock and settlement on the large mammalian wildlife of Bale Mountain National Park, southern Ethiopia. *Biol Conserv*. 2001;100:307–22.
- Debela H. Human influence and threat to biodiversity and sustainable living. *Eth J Educat Sci*. 2007;3(1):85–95.
- Belay S, Amsalu A, Abebe E. Land use and land cover changes in Awash National Park, Ethiopia: impact of decentralization on the use and management of resources. *Open J Ecol*. 2014;4:950–60.
- Kasso M, Bekele A. Threats to mammals on fragmented habitats around Asella Town, Central Ethiopia. *Int J Biodivers*. 2014;2014(1):903898. <https://doi.org/10.1155/2014/903898>.
- Gebretsadik T. Causes for biodiversity loss in Ethiopia: A review from conservation perspective. *J Nat Sci Res*. 2016;6(11):32–40.
- Elsen PR, Monahan WB, Merenlender AM. Topography and human pressure in mountain ranges alter expected species responses to climate change. *Nat Commun*. 2020;11(1):1974.
- Yalden DW, Lagen MJ, Kock D. Catalogue of the mammal of Ethiopia: 5 Artiodactyla. *Ital J Zool*. 1984;19:140–5.
- Merckx B, Steyaert M, Vanreusel A, Vincx M, Vanaverbeke J. Null models reveal preferential sampling, spatial autocorrelation and overfitting in habitat suitability modelling. *Ecol Model*. 2011;222(3):588–97.
- Yazew D, Mamo Y, Bekele A. Population ecology of Menelik's bushbuck (*Tragelaphus scriptus meneliki*, Neumann, 1902) from Donkoro Forest proposed National Park, Northern Ethiopia. *Int J Ecol Environ Sci*. 2011;37:1–13.
- Girma Z, Bekele A, Graham H. Large mammals and mountain encroachments on Mount Kaka and Hunkolo Fragments, Southeast Ethiopia. *Asian J Appl Sci*. 2012;5(5):279–89.
- Zerihun M. Population status, habitat association, feeding behaviour and diurnal activity of Menelik's Bushbuck (*Tragelaphus scriptus meneliki*) in Dinsho, Bale Mountains National Park, Ethiopia. MSc Thesis, Addis Ababa University, Addis Ababa. 2012.
- Ethiopian Wildlife Conservation Authority (EWCA). Unpublished census report in controlled hunting areas. Addis Ababa, Ethiopia. 2022. <https://www.ewca.gov.et>.
- Plumptre AJ, Wronski T. *Tragelaphus scriptus* Bushbuck. In: Mammals of Africa: v. VI: Pigs, Hippopotamuses, Chevrotains, Giraffes, Deer and Bovids, ed. by J. Kingdon and M. Hoffmann (London: Bloomsbury Publishing). 2013.
- Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, et al. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*. 2006;29:129–51.
- Kindt R. Ensemble species distribution modelling with transformed suitability values. *Environ Model Softw*. 2018;100:136–45.
- Mi C, Huettmann F, Guo Y, Han X, Wen L. Why choose random forest to predict rare species distribution with few samples in large under sampled areas? Three Asian crane species models provide supporting evidence. *PeerJ*. 2017;5: e2849.

26. Woodman SM, Forney KA, Becker EA, DeAngelis ML, Hazen EL, Palacios DM, Redfern JV. ESDM: a tool for creating and exploring ensembles of predictions from species distribution and abundance models. *Methods Ecol Evol.* 2019;10:1923–33.
27. Buisson L, Thuiller W, Casajus N, Lek S, Grenouillet G. Uncertainty in ensemble forecasting of species distribution. *Glob Change Biol.* 2010;16:1145–57.
28. Araújo M, New M. Ensemble forecasting of species distributions. *Trends Ecol Evol.* 2007;22(1):42–7.
29. Mittermeier RA, Gil PR, Hoffman M, Pilgrim J, Brooks T, Mittermeier CG, Lamoreux J, da Fonseca GAB. Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. Washington: Conservation International; 2004.
30. Yalden DW, Largen MJ. The endemic mammals of Ethiopia. *Mammal Rev.* 1992;22:115–50.
31. Large M, Spawls S. The amphibians and reptiles of Ethiopia and Eritrea. Edition. 2010. Chimaira, Frankfurt am Main.
32. Redman N, Stevenson T, Fanshawe J. Birds of the horn of Africa: Ethiopia, Eritrea, Djibouti, Somalia and Socotra. 2011.
33. Enquist BJ, Feng X, Boyle B, Maitner B, Newman EA, et al. The commonness of rarity: Global and future distribution of rarity across land plants. *Sci Adv.* 2019;5:eaa20414.
34. Aerts R, Overtveldt VK, November E, Alemayehu W, Abrham A, Sebsebe D, Desalegn D, et al. Conservation of the Ethiopian church forests: threats, opportunities and implications for their management. *Sci Total Environ.* 2016;551–552(2016):404–14.
35. EFAP (Ethiopian Forestry Action Program). Volume II - The Challenge for development. Ministry of National Resources Development and Environmental Protection. Addis Ababa, Ethiopia. 1993.
36. Ethiopian Wildlife Conservation Authority (EWCA) census report in the Simien Mountains National Park (SMNP). Un published. Addis Ababa, Ethiopia. 2022. <https://www.ewca.gov.et>.
37. Poloczanska E, Brown C, Sydeman WJ, Kiessling W, Schoeman D, Moore P, Brander K, Bruno JF, Buckley LB, Burrows M, et al. Global imprint of climate change on marine life. *Nat Clim Chang.* 2013;3:919–25.
38. Keating KA, Gogan PJ, Vore JM, Irby LR. A simple solar radiation index for wildlife habitat studies. *J Wildl Manag.* 2007;71:1344–8.
39. Gagan MK, Ayliffe LK, Hopley D, Cali JA, Mortimer GE, Chappell J, McCulloch MT, Head MJ. Temperature and surface-ocean water balance of the mid-Holocene tropical western Pacific. *Science.* 1998;279:1014–8.
40. Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, et al. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography.* 2013. 36(1), 27 - 46.
41. Elith J, Kearney M, Phillips S. The art of modeling range-shifting species. *Methods Ecol Evol.* 2011;2(4):330–42.
42. O'Brien RM. A Caution Regarding Rules of Thumb for Variance Inflation Factors. *Qual Quant.* 2007;41:673–90.
43. Naimi, B. Package 'usdm'. Uncertainty analysis for species distribution models. Wien; 2017. <http://www.cran.r-project.org>.
44. Naimi B, Araújo MB. sdm: a reproducible and extensible R platform for species distribution modeling. *Ecography.* 2016;39(4):368–75.
45. Mbatudde M, Mwanjolo M, Kakudidi EK, Dalitz H. Modelling the potential distribution of endangered *Prunus africana* (Hook. f.) Kalkm. in East Africa. *Afr J Ecol.* 2012;50:393–403.
46. Brown JL. SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol Evol.* 2014;5:694–700.
47. Stohlgren TJ, Ma P, Kumar S, Rocca M, Morissette JT, Jarnevich CS, Benson N. Ensemble habitat mapping of invasive plant species. *Risk Anal.* 2010;30:224–35.
48. Capinha C, Anastácio P. Assessing the environmental requirements of invaders using ensembles of distribution models. *Divers Distrib.* 2011;17:13–24.
49. Hu XY, Fang L, Ying J, Da Yuan X. The effects of climate change on the distribution of snub-nosed monkey in China. *Adv Mater Res.* 2015;1092–1093:645–50.
50. Wiley EO, McNyset KM, Peterson AT, Robins CR, Stewart AM. Niche modeling and geographic range predictions in the marine environment using a machine-learning algorithm. *Oceanography.* 2003;16(3):120–7.
51. Phillips SJ, Anderson R, Schapire R. Maximum entropy modelling of species geographic distributions. *Ecol Model.* 2006;190:231–59.
52. Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J Appl Ecol.* 2006;43:1223–32.
53. Zhang L, Liu S, Sun P, Wang T, Wang G, Zhang X, Wang L. Consensus forecasting of species distributions: The effects of niche model performance and niche properties. *PLoS One.* 2015;10(e012):0056.
54. Breugel VP, Friis I, Demissew S. The transitional semi-evergreen bushland in Ethiopia: characterization and mapping of its distribution using predictive modeling. *Appl Veg Sci.* 2016;19:355–67.
55. Olson DM, Dinerstein E. The global 200: priority ecoregions for global conservation. *Ann. Mo. Bot. Gard.* 2002. p. 89 - 199. <https://doi.org/10.2307/3298564>.
56. Hernandez PA, et al. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography.* 2006;29:773–85.
57. West AM, Evangelista PH, Jarnevich CS, Young NE, Stohlgren TJ, Talbert C, Talbert M, Morissette J, Anderson R. Integrating remote sensing with species distribution models; mapping tamarisk invasions using the software for assisted habitat modeling (SAHM). *J Vis Exp.* 2016;116: e54578.
58. Ahmed N, Atzberger C, Zewdie W. Species distribution modelling performance and its implication for Sentinel-2-based prediction of invasive *Prosopis juliflora* in lower Awash River Basin, Ethiopia. *Ecol Process.* 2021;10:18. <https://doi.org/10.1186/s13717-021-00285-6>.
59. Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol Appl.* 2009;19:181–97.
60. Franklin J, Miller JA. Mapping species distributions (Reprinted ed.). U.K.: Cambridge University Press; 2010. p. 320.
61. Barry RG, Seimon A. Research for mountain area development: climatic fluctuations in the mountains of the Americas and their significance. *Ambio.* 2000;29:364–70.
62. Lovejoy TE, Hannah L. Climate change and biodiversity. NH: Yale University Press; 2005.
63. McCormack JE, Huang H, Knowles LL. Sky islands. In: Gillespie RG, Clague DA, editors. *Encyclopedia of Islands*. Berkeley: University of California Press; 2009. pp. 841–3. <https://doi.org/10.1525/j.ctt1pn90r.203>.
64. Monasterio M, Vuilleumier F. Introduction: high tropical mountain biota of the world. In: *High mountains tropical biogeography*. Eds. Vuilleumier, F. and Monasterio, M. Published by Oxford University Press and the American Museum of Natural History. Oxford University Press. New York. USA. 1986.
65. Sinclair SJ, White MD, Newell GR. How useful are species distribution models for managing biodiversity under future climates? *Ecol Soc.* 2010;15: 8.
66. Williams SD, Vivero JL, Spawls S, Anteneh S, Ensermu K. Ethiopian Highlands. In: *Hotspots revisited: earth's biologically richest and most endangered ecoregions*. Chicago: University of Chicago Press; 2004. pp. 262–73.
67. Gizaw A, Brochmann C, Nemomissa S, Wondimu T, Masao CA, Tusiime FM, Abdi AA, Oxelman B, Popp M, Dimitrov D. Colonization and diversification in the African 'sky islands': Insights from fossil-calibrated molecular dating of *Lychnis* (Caryophyllaceae). *New Phytol.* 2016;211(2):719–34.
68. Park HS, Kim SJ, Stewart AL, et al. Mid-holocene northern hemisphere warming driven by arctic amplification. *Sci Adv.* 2022;5:eaa8203. <https://doi.org/10.1126/sciadv.aax8203>.
69. Pearson RG, Thuiller W, Araújo MB, Martinez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC. Model-Based Uncertainty in Species Range Prediction. *J Biogeogr.* 2006;33:1704–11.
70. Saupe EE, Myers CE, Peterson AT, Soberón J, Singarayer JS, Valdes PJ, Qiao H. Spatio-temporal climate change contributes to latitudinal diversity gradients. *Nature Ecology & Evolution.* 2019. <https://doi.org/10.1038/s41559-019-0962-7>.
71. Leal M. The African rain forest during the last glacial maximum, an archipelago of forests in a sea of grass. Ph.D. thesis. University, Wageningen. 2004.
72. IPCC. Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the

- Intergovernmental Panel on Climate Change. Core Writing Team, Pachauri RK, Meyer LA, editors. Geneva: IPCC; 2014.
73. Hu J, Liu Y. Unveiling the conservation biogeography of a data-deficient endangered bird species under climate change. *PLoS One*. 2014;9: e84529.
74. Rodrigues P, Dorresteijn I, Guilherme JL, Hanspach J, Beenhouwer MD, Hylander K, Bekele B, Senbeta F, Fischer J, Nimmo D. Predicting the impacts of human population growth on forest mammals in the highlands of southwestern Ethiopia. *Biol Conserv*. 2021;256: 109046.
75. Wisz MS, Pottier J, Kissling WD, Pellissier L, Lenoir J, et al. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol Rev*. 2013;88:15–30.
76. Álvarez-Loayza P, White JF, Torres MS, Balslev H, Kristiansen T, Svenning JC, Gil N. Light Converts Endosymbiotic Fungus to Pathogen, Influencing Seedling Survival and Niche- Space Filling of a Common Tropical Tree, *Iriartea deltoidea*. *PLoS One*. 2011;6:1–8.
77. Bellingham PJ, Towns DR, Cameron EK, Davis JJ, Wardle DA, Wilmshurst JM, Mulder CPH. New Zealand Island restoration: seabirds, predators, and the importance of history. *N Z J Ecol*. 2010;34:115–35.
78. Taylor KE, Stouffer RJ, Meehl GA. An overview of CMIP5 and the experiment design. *Bull Am Meteorol Soc*. 2012;93:485–98.
79. van Vuuren DP, Edmonds J, Kainuma M, Riahi K, Thomson A, Hibbard K, Hurtt GC, Kram T, Krey V, Lamarque JF, Masui T, Meinshausen M, Nakicenovic N, Smith SJ, Rose SK. The representative concentration pathways: an overview. *Clim Change*. 2011;109:5–31.
80. IPCC. Climate change 2013: the physical science basis. In: The fifth assessment report of the intergovernmental panel on climate change. Cambridge and New York: Cambridge University Press; 2013.
81. IPCC. Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Cambridge: Cambridge University Press; 2019.
82. Brodie J, Post E, Laurance WF. Climate change and tropical biodiversity: a new focus. *Trends Ecol Evol*. 2012;27:145–50.
83. Melaku T. Wildlife in Ethiopia: large endemic mammals. *Curr Zool*. 2011;6:108–16.
84. USGS (United State Geological Survey). Glacier and landscape change in response to changing climate. *Glaciers and sea level*. 2012. <https://pubs.usgs.gov/fs/fs2-00/>.
85. R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. 2023. <https://www.R-project.org/>.
86. Montoya-Jiménez JC, Valdez-Lazalde JR, Ángeles-Perez G, De Los Santos-Posadas HM, Cruz Cárdenas G. Predictive capacity of nine algorithms and an ensemble model to determine the geographic distribution of tree species. *iForest*. 2022;15:363–71. <https://doi.org/10.3832/for4084-015>.

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