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Morphological characterization and habitat suitability modeling of the goat population of Benin under climate change scenarios

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Abstract

Background: Insufficient knowledge of the genetic and phenotypic diversity in the local Beninese goat population combined with the lack of understanding of its adaptive capacity to ongoing environmental and societal changes hampers the development of strategies for better management and genetic improvement. The objective of this study was to establish the current geographical distribution of goats in Benin based on their morphology and model the potential habitat suitability of the three known main goat phenotypes (i.e., Djallonké goat or Type I, Sahelian goat or Type II, and their Crossbreeds or Type III) under climate change scenarios. Ten qualitative and 26 linear body measurements were taken on 2114 adult female goats sampled across the three vegetation zones of the country. Fifteen ratios were generated from the quantitative variables. The data were analyzed using generalized linear model procedures followed by multiple comparisons of least-squares means and multivariate analytical methods, including canonical discrimination analysis and hierarchical ascendant classification. Each goat was then assigned to one of the three aforementioned main goat phenotypes following its morphological characteristics and according to the a priori cluster membership defined in the previous step. The Maximum Entropy algorithm was used to model the current and future distribution of the three goat phenotypes under climate change scenario using the Representative Conservation Pathways 4.5 and 8.5.

Results: All linear body measurements varied among vegetation zones. In the discriminant function analysis, 71% of the measured individuals were correctly classified in their vegetation zone of origin by seven measured variables and three ratios. The cluster procedure analysis revealed two groups of goats subdivided into the three main phenotypes. The modeling results showed that the currently highly favorable habitats were distributed in the South for Type I, in the North for Type II, and both South and North for Type III. However, under climate change scenarios, the favorable habitats for Type I decreased while those of Types II and III increased.

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Conclusions: The results of this study confirm the spatial variation of the goat population in Benin. The habitat suitability model can be used to support decision-making toward better management of goat genetic diversity in Benin.

Keywords: *Capra hircus*, Climate change, Ecological niche modeling, Farm animal species, MaxEnt model, Morphology

Introduction

Worldwide, farm animal genetic resources are the basis of livestock production. They are therefore essential for ensuring food security and sustainable development in rural areas, where livelihoods are mostly based on livestock products. Hence, the implementation of any effective program aiming at sustaining livestock production should be based not only on a good knowledge of the genetic diversity within and among animal populations within species, but also on an understanding of the characteristics of the production environments in which the animals are raised (FAO 2007). However, the management of farm animal genetic resources has always been neglected or poorly organized, especially in developing countries where there is great genetic diversity within livestock species (Molina-Flores et al. 2020). In the face of current environmental and societal changes, linked to the effects of climate change, there is increasing recognition of the need to preserve existing genetic diversity and to review livestock development policies. Phenotypic and genetic characterization of farm animal genetic resources is an important first step towards their national inventory and effective management for sustainable development as called for in the Global Plan of Action for Animal Genetic Resources (FAO 2007).

The provision of more animal-sourced products with fewer resources, to improve the livelihoods of rural households and reduce food insecurity, remains the major challenge for livestock production (FAO 2009). One solution would be to reorient this production towards fast-growing livestock species like small ruminants, especially goats. Indeed, compared with other livestock species, goats are likely less demanding of natural resources such as natural pastures and water (Akinmoladun et al. 2019) and more climate-resilient (Nair et al. 2021).

In West Africa, indigenous goat populations are distributed in different agro-ecological zones, ranging from the most humid to the aridest (Molina-Flores et al. 2020). However, these areas, previously governed by well-known climatic conditions, are increasingly changing under the influence of climatic fluctuations. In Benin, like in other West African countries, goats are kept mostly by women in most households in different production systems (Missohou et al. 2016). This wide distribution of goats in different environments is explained by their relatively

small size, along with their ease of keeping due to their low feed requirements and very high capacity to adapt to all the systems in which they are raised (Lebbie and Ramsay 1999; Alexandre and Mandonnet 2005; Escareño et al. 2013; Missohou et al. 2016). In addition, goat farming provides various monetary (income, financial security) and non-monetary services (self-consumption, sacrifices, celebrations) in both rural and peri-urban areas (Yakubu and Ibrahim 2011; Escareño et al. 2013; Missohou et al. 2016). In West Africa, there are three large groups of local goats: the short-legged known as the West African Dwarf goat or Djallonké (Additional file 1: Figs. S1 and S2), the long-legged goat also called Sahel goat (Additional file 1: Figs. S3 and S4), and diverse crosses of the two (Additional file 1: Figs. S5 and S6). Several subgroups might exist in each group. But unfortunately, as revealed by existing literature, no recent phenotypic characterization of the goat population of Benin that accounts for ecological variations has been carried out. The only previous nationwide morphological characterization study of the Beninese goat population dates from 2007 (Dossa et al. 2007). In the meantime, frequent introductions of new breeds (generally long-legged) from neighboring countries of Sahel have occurred by the different actors of the goat value chain (producers, traders, sellers). These introductions may have had several impacts on the local goat population, which has so far been poorly described. Also, faced with various anthropic actions and environmental challenges, the goat population of Benin has probably undergone changes in its morphology and genetic structure as well as its spatial distribution. Recent case studies were limited, respectively, to the departments of Borgou in the Northeast (Idrissou et al. 2017) and Atacora in the Northwest (Kouato et al. 2021). There is a dearth of updated knowledge on the specific traits of the local goat population from Benin, hampering the design and implementation of any sustainable management program. The spatial distribution of goats in Benin needs to be updated and the existing within-population morphological diversity assessed and confirmed through further genetic characterization studies.

Furthermore, the impacts of climate change on the Beninese goat population are expected to vary considerably across locations and vegetation zones within the country. While efforts to improve local goat populations in West Africa through selection are very limited,

the West African Dwarf goat type is being increasingly crossed with or replaced, in several locations, by the long-legged ones. This uncontrolled or poorly controlled crossbreeding might lead to the loss of adaptive traits in the Djallonké type (Biscarini et al. 2015). But there might be potential habitats suitable for crossbreeds. Therefore, knowing the environmental variables that most determine the productivity of the local goat population will help to predict its future distribution and support the development of programs for its improvement.

Several studies have shown that Geographic Information System (GIS) tools can be used to establish different prediction models in several areas. Indeed, these tools have been used to predict the spatial distribution of species (Booms et al. 2010) and the potential transmission of certain diseases (Simón et al. 2014; Bett et al. 2017; Valiakos et al. 2017), establish conservation priorities (Bertaglia et al. 2007), predict areas of occurrence of livestock breeds (Leta and Mesele 2014; Lozano-Jaramillo et al. 2018; Kebede et al. 2021) and the suitability of a breed for a region based on climatic

and occurrence information (Thuiller et al. 2005; Phillips et al. 2006). We assume that it will be possible to establish models to predict the future distribution of the goat population of Benin based on climate data and population occurrences.

The aim of the current study was twofold. The first objective was to assess the actual morphological diversity within and among goats from the three vegetation zones of Benin, and the second was to establish models to predict current and future distributions of the three main goat phenotypes raised in Benin (i.e., Djallonké, Sahelian and Crossbreeds). We hypothesized that: (1) based on morphological traits it is possible to distinguish the three goat subpopulations as previously identified by Dossa et al. (2007); (2) the current habitats suitable for each goat subpopulation do not change despite future changes in the environmental factors that characterize them.

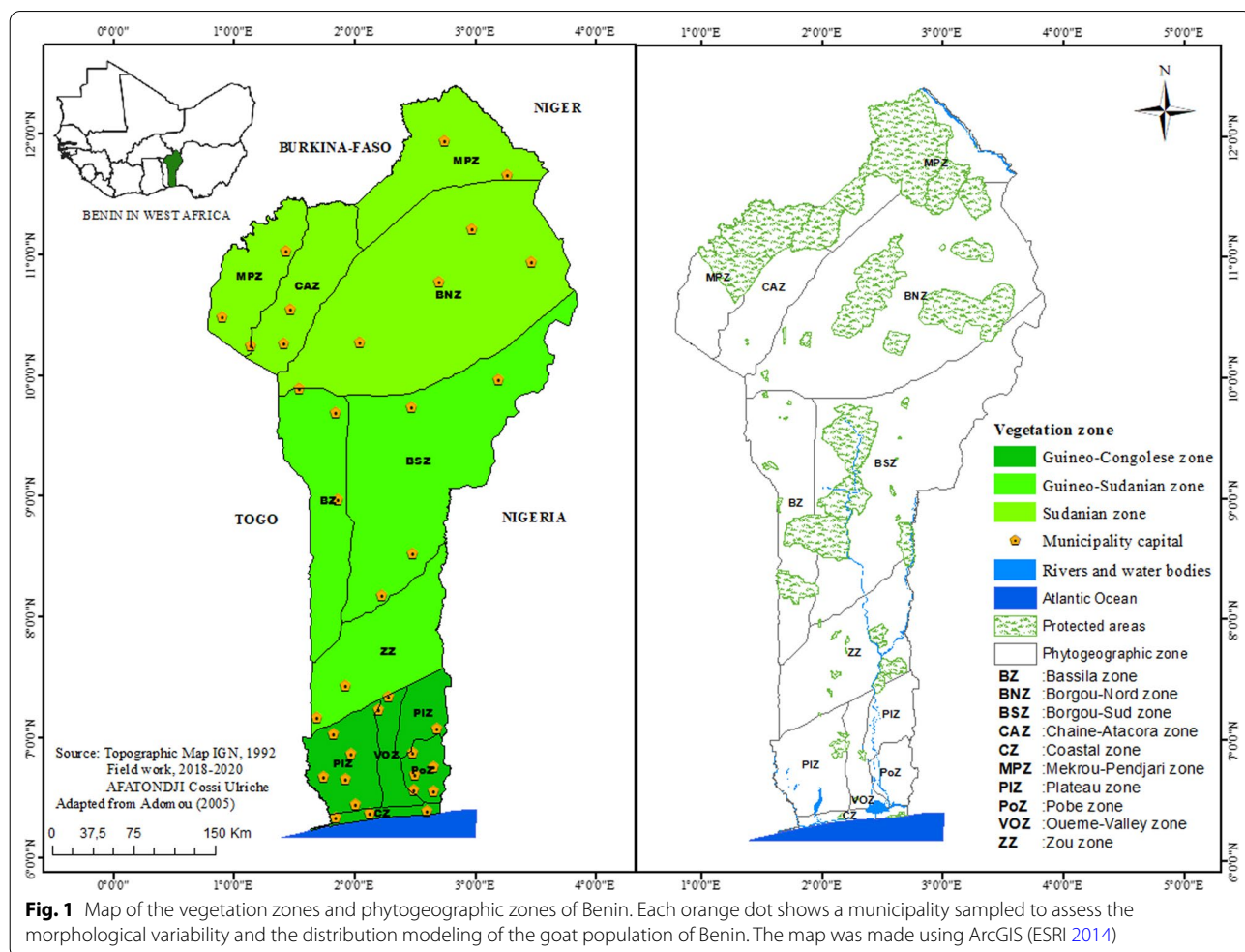


Fig. 1 Map of the vegetation zones and phytoecographic zones of Benin. Each orange dot shows a municipality sampled to assess the morphological variability and the distribution modeling of the goat population of Benin. The map was made using ArcGIS (ESRI 2014)

Methods

Study area

This study was conducted in the three vegetation zones of Benin, namely the Guineo-Congolese zone (GCZ) in the South, the Guineo-Sudanian zone (GSZ) in the Center, and the Sudanian zone (SZ) in the North. These vegetation zones are subdivided into ten phytogeographic zones (Additional file 2: Table S1, Fig. 1) based on similarities or dissimilarities in climatic conditions, temperature, humidity index, soil characteristics, and predominant vegetation (Adomou 2005). The GCZ encompasses four phytogeographic zones (Coastal, Pobe, Plateau, and Oueme Valley), the GSZ three phytogeographic zones (Zou, Borgou-Sud, and Bassila), and the SZ

three phytogeographic zones (Chaîne Atacora, Borgou-Nord, and Mekrou-Pendjari).

Sampling procedure

A longitudinal survey was conducted from November 2018 to February 2020 to describe the morphological characteristics of goats throughout the country. All the three vegetation zones of Benin with their phytogeographic zones were considered. In each phytogeographic zone, three to five municipalities were selected based on the previous work by Dossa et al. (2007), and on the presence and abundance of goat flocks. Thirty-six municipalities (36) out of the 77 of Benin were included in the survey. In each municipality, up to four distinct villages

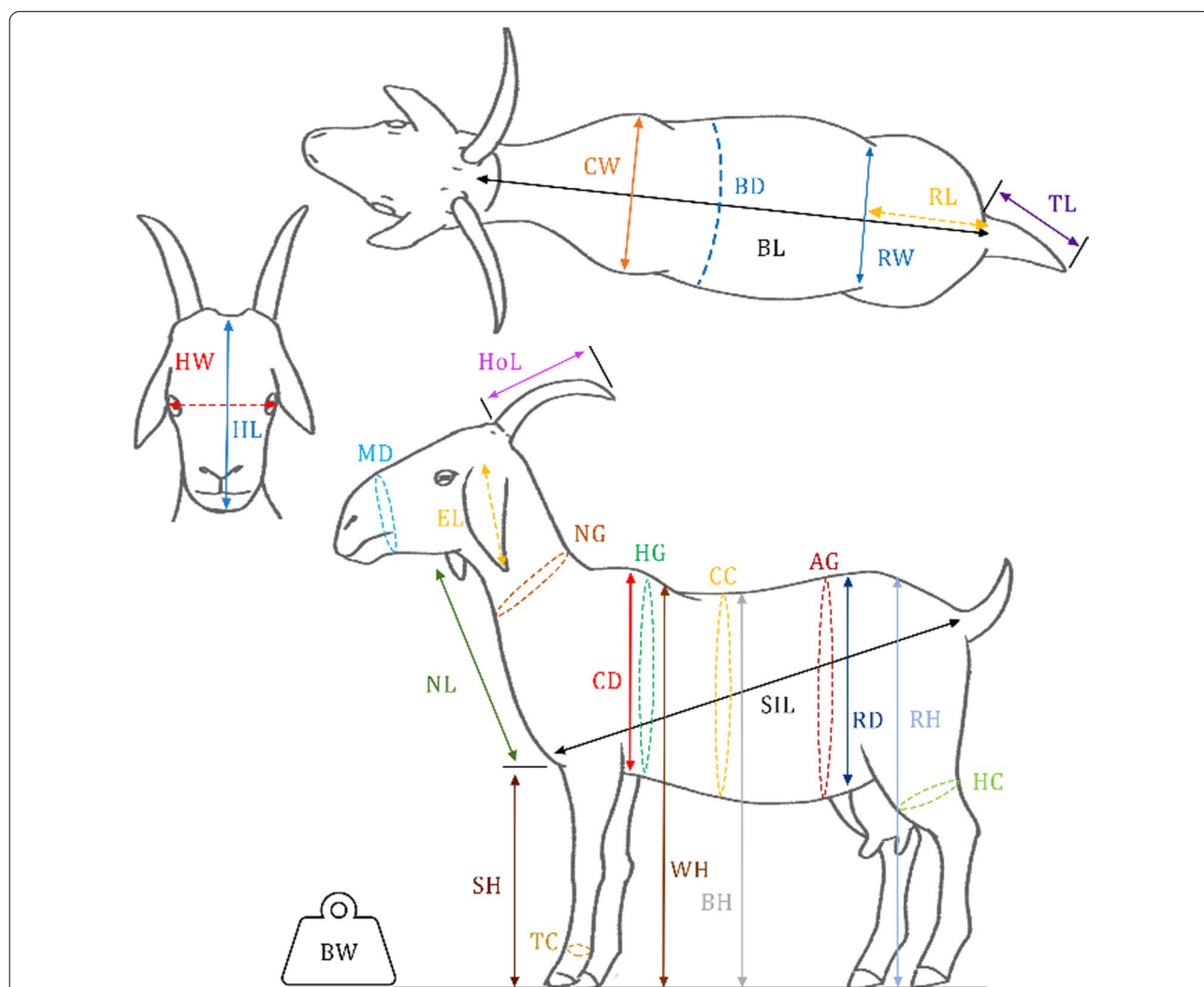


Fig. 2 Illustration of the 26 linear body measurements taken on each sampled goat. WH withers height, RH rump height, SH sternum height, BH back height, CD chest depth, RD rump depth, CW chest width, SIL scapulo-ischial length, BL body length, HL head length, HW head width, EL ear length, HoL Horn length, MD muzzle diameter, NL neck length, NG neck girth, TL tail length, HG heart girth, CC chest circumference, AG abdominal girth, BD bicoastal diameter, RW rump width, RL rump length, TC cannon bone circumference, HC hock circumference, BW body weight

were randomly chosen, and phenotypic information collected from 5 to 20 individual random flocks based on farmers' willingness to participate in the study. A total of 2114 adult female goats (does) of at least two years old and multiparous (at least two kidding) were randomly selected, described, and morphologically characterized. The age of each sampled animal was estimated by its owner and ascertained by examining its teeth according to the procedure described in Ali (1994) and FAO (2013). The sample distribution across vegetation and phytogeographic zones is presented in Additional file 2: Table S1. All individual animals sampled in each vegetation zone were considered as a subpopulation of the Beninese goat population, whereas each phytogeographic zone was considered as a provenance.

Morphological variability

Data collection procedure

Overall 26 quantitative linear body measurements (Additional file 2: Table S2, Fig. 2) and 10 qualitative physical traits (Additional file 2: Table S2) drawn from the FAO guidelines for phenotypic characterization of animal genetic resources (FAO 2013) and a previous study (Chacón et al. 2011), were used to describe the morphological characteristics of each sampled animal. To minimize bias in data collection, all measurements were taken by a three-member team consisting of two young researchers and a trained field assistant. The body weight of each animal was measured using a hanging scale with a sensitivity of 100 g (Kern & Sohn GmbH, Balingen, Germany). The other 25 body linear measurements were taken using a measuring tape and a measuring stick, early in the morning before the animals were fed to avoid biases on certain traits due to feed intake. In addition, the reproductive history of each sampled animal, including the number and type of parities (single, twins, triplet, and quadruplets), was recorded from the animal's owner. The geographic position of each surveyed herd was recorded with a Garmin GPS (Etrex Vista TM).

Data analysis

Fifteen morphological indices (Additional file 2: Table S3) were generated based on the collected quantitative linear body measurements. All statistical analyses were performed using SAS version 9.4 software (SAS Institute Inc., Cary, NC, USA). The procedures 'proc univariate' and 'proc freq' were used to perform descriptive statistics for the quantitative linear body measurements and qualitative physical traits, respectively. The Pearson Chi-square (χ^2) test was used to explore the relationships among qualitative variables. The least-squares means (lsmeans) of the morphometric traits, their standard errors (SE), and related coefficients of variation (CV)

were calculated for each vegetation zone. Comparisons between vegetation zones were performed using Tukey's multiple mean comparison test. Subsequently, the general linear model procedure ('proc glm') was used to analyze the relationships between vegetation zones and goat morphometric traits.

A stepwise discriminant analysis was performed using 'proc stepdisc' to identify the most useful morphometric traits and morphological indices for further discriminant analyses. The relative discriminatory ability of a quantitative variable was assessed using the partial *R*-square, *F*-value, and the level of significance ($P < F$). Then, the canonical discriminant analysis (CDA) function ('proc candisc') was used to perform one-way univariate and multivariate analyses, to derive canonical functions and linear combinations of the quantitative variables that summarize variation between subpopulations with their provenances, and to calculate the associated Mahalanobis distances. The ability of the computed canonical functions to classify each animal to its a priori vegetation zone or provenance group (i.e., phytogeographic zone) was measured using the discriminant procedure ('proc discrim'). The degree of morphological similarity or dissimilarity among individuals from different vegetation zones and provenances was determined based on the ascending hierarchical clustering (AHC) analysis procedure ('proc cluster'). The 'proc tree' procedure was used to build a dendrogram displaying both the interrelationships among individuals within and across vegetation zones and the interrelationships among individuals within and across the provenances. Finally, a multiple correspondence analysis (MCA) using the 'proc corresp' procedure was performed to associate the physical traits with the vegetation zones.

Geographical distribution modeling

Species study and occurrence data

The species distribution modeling focuses on the three major goat phenotypes (Djallonké, Sahelian, and Cross-breeds), as previously identified by Dossa et al. (2007). Indeed, although the results of the morphological characterization performed in Section 'Morphological variability' revealed a trend of two large subpopulations, the existence of some individuals of the Sahelian goat type cannot be ignored, especially since introductions of new individuals of this type are continually occurring from neighboring Sahelian countries. This justifies the consideration of all three groups for the prediction of current and future habitats suitable for their breeding in Benin. Thus, following its morphological characteristics and according to the a priori cluster membership defined by vegetation zones in the morphological characterization, each animal was assigned to one of the three main

phenotypic groups (i.e., Djallonké goat, Sahelian goat, and Crossbreeds, here onwards referred to as Type I, Type II and Type III, respectively). The occurrence data of each animal was then considered according to the geographic position of surveyed herds recorded during the data collection for morphological characterization. Overall, a total of 1222 occurrences were included in the spatial distribution modeling study (Additional file 2: Table S4).

Environmental data and modeling approach

Current and future environmental data were collected from the database of AFRICLIM ensembles 3.0 (www.york.ac.uk/environment/research/kite/resources/). A total of 21 variables (Additional file 2: Table S5) was considered under the Representative Concentration Pathway (RCP) scenarios: RCP 4.5 and RCP 8.5 for the 2055-time horizon as described by Platts et al. (2015). These scenarios, established by the *Intergovernmental Panel on Climate Change* (IPCC) in its Fifth Assessment Report, are likely climate assumptions based on greenhouse gas emissions (i.e., CO₂, CH₄, SO₂) over a period of time. Scenario 4.5 is a baseline prediction of climate change defined by low greenhouse gases emissions (low-concentration scenario), while scenario 8.5 models a climate that will change significantly as a result of high greenhouse gas emissions (high-concentration scenario). In addition, soil data were drawn from the FAO World soil database (Nachtergaele et al. 2012). The 21 environmental variables and soil data were subjected to correlation analysis and, based on a Pearson correlation coefficient lower than 0.8, the highly correlated variables were eliminated using ENM-Tools (Elith et al. 2010) for a better predictive model.

The maximum entropy (MaxEnt) modeling approach (Phillips et al. 2006; Phillips and Dudík 2008), performed with the MaxEnt software (ver. 3.4.1), was used to model the current and potential future distribution of goat subpopulations in Benin. Indeed, the MaxEnt approach predicts species distribution and establishes the relationship between occurrence data of species and environmental parameters (Phillips et al. 2006). This approach offers many advantages and has been shown to perform the distribution modeling relatively better than other modeling methods (Elith et al. 2006, 2011; Phillips et al. 2006; Pearson et al. 2007; Wisz et al. 2008; Kumar and Stohlgren 2009; Rebelo and Jones 2010; Sardà-Palomera et al. 2012; Garcia et al. 2013; Marcer et al. 2013). Thus, 75% of the data were selected for model training, and the 25% remaining used for model testing (Phillips 2008). The Jackknife test inbuilt in the MaxEnt software (Pearson et al. 2007; Shcheglovitova and Anderson 2013) was used to

assess the relative significance and contribution of each independent environmental variable to the model. The models were performed using cross-validation and the option "write background prediction" with ten replicated runs. Furthermore, the overall performance of the models was assessed using the values of the area under receiver operating characteristic (ROC) curve (AUC) and true skill statistics (TSS) (Fielding and Bell 1997; Allouche et al. 2006). Thus, following different thresholds (i.e., 0.9, 0.8, and 0.5), different interpretations were provided. For an $AUC \geq 0.9$, the model was considered very good, when $0.9 > AUC \geq 0.8$, the model was good, and for an $AUC < 0.8$, the model was considered poor (Gassó et al. 2012; Hosmer et al. 2013). Moreover, a model with an $AUC > 0.5$ was considered more powerful than a random prediction ($AUC = 0.5$). AUC test value close to 1 indicates perfect discrimination (Swets 1988; Peterson et al. 2008; Phillips and Elith 2010). However, TSS expressed as: "sensitivity + specificity - 1" was used to measure the capacity of models to detect the true presence (sensitivity) and true absence (specificity) of goat subpopulations. Following Allouche et al. (2006), a model was considered as having a good predictive power when its TSS was close to 1 ($TSS > 0.5$).

The results of the presence prediction models (range 0–1) obtained with MaxEnt were displayed in ArcGIS 10.4.1 (ESRI 2014) to map the a priori distribution under current and future (the year 2055) environmental conditions. Four potential habitat classes (i.e., low suitable, moderately suitable, suitable, and highly suitable) grouped using threshold values following the range 0–1 (i.e., 0–0.25, 0.25–0.50, 0.50–0.75, and 0.75–1) were used to create potential distribution maps as described in Çoban et al. (2020). Spatial analysis tools in ArcGIS software were used for each model to estimate the area of optimal distribution classified as, low, moderate, suitable, or highly suitable habitat. The different distribution areas were calculated by removing areas occupied by protected areas and waterways from the total area of the country. The research design adopted for modeling goat distribution and integrating environmental variables with morphometric variables is presented in Additional file 1: Fig. S7.

Results

Morphological variability

Morphometric traits' variation among vegetation zones

Significant variations among the three vegetation zones were recorded for all quantitative linear body traits (Table 1) and all calculated morphological indices, except mass index (MI) and index of boniness (Bi) (Table 2). The highest mean values of most of the morphological linear

Table 1 Least squares means (lsmeans) and standard errors (SE) and coefficients of variation (CV) of morphological measurements (cm)

Variables	GCZ (n = 893)		GSZ (n = 610)		SZ (n = 611)		Overall (n = 2114)	
	lsmean ± SE	CV	lsmean ± SE	CV	lsmean ± SE	CV	lsmean ± SE	CV
WH	40.1 ^c ± 0.10	7.60	45.7 ^b ± 0.17	9.39	49.8 ^a ± 0.24	11.66	44.5 ± 4.36	9.38
RH	42.6 ^c ± 0.09	6.47	46.7 ^b ± 0.17	8.81	50.5 ^a ± 0.25	12.22	46.1 ± 4.37	9.48
SH	23.1 ^c ± 0.11	14.97	27.0 ^b ± 0.13	11.45	30.7 ^a ± 0.18	14.61	26.4 ± 3.69	13.97
BH	41.0 ^c ± 0.09	6.46	44.9 ^b ± 0.16	8.80	48.9 ^a ± 0.25	12.38	44.4 ± 4.25	9.57
CD	21.3 ^c ± 0.06	7.94	22.3 ^b ± 0.08	9.22	22.7 ^a ± 0.08	8.50	22.0 ± 1.87	8.51
RD	22.7 ^c ± 0.07	9.24	23.9 ^b ± 0.11	11.11	24.6 ^a ± 0.09	9.34	23.6 ± 2.33	9.86
CW	13.4 ^a ± 0.04	9.80	12.9 ^b ± 0.06	10.71	13.0 ^b ± 0.06	11.04	13.2 ± 1.37	10.42
SIL	48.7 ^c ± 0.13	8.18	49.6 ^b ± 0.17	8.63	50.7 ^a ± 0.19	9.02	49.5 ± 4.25	8.57
BL	67.8 ^c ± 0.18	7.77	71.2 ^b ± 0.24	8.20	74.1 ^a ± 0.30	9.94	70.6 ± 6.10	8.64
HL	13.8 ^c ± 0.05	10.94	14.4 ^b ± 0.06	9.46	14.9 ^a ± 0.05	8.61	14.3 ± 1.41	9.83
HW	8.2 ^b ± 0.03	9.72	8.5 ^a ± 0.03	9.31	8.4 ^a ± 0.03	9.67	8.4 ± 0.80	9.59
EL	9.4 ^c ± 0.06	11.3	10.6 ^b ± 0.05	12.71	12.1 ^a ± 0.06	12.77	10.5 ± 1.30	12.35
HoL	7.2 ^b ± 0.07	29.24	7.1 ^b ± 0.09	32.48	8.2 ^a ± 0.10	29.52	7.5 ± 2.26	30.27
MD	16.2 ^a ± 0.05	9.93	16.7 ^b ± 0.07	9.62	17.1 ^a ± 0.05	7.68	16.6 ± 1.53	9.21
NL	15.8 ^c ± 0.08	14.83	18.2 ^b ± 0.10	13.11	19.8 ^a ± 0.10	12.17	17.6 ± 2.37	13.45
NG	21.8 ^c ± 0.07	10.05	22.1 ^b ± 0.08	8.71	22.5 ^a ± 0.08	8.54	22.1 ± 2.04	9.24
TL	10.2 ^c ± 0.05	15.58	10.9 ^b ± 0.06	12.4	11.9 ^a ± 0.07	13.98	10.9 ± 1.55	14.21
HG	55.6 ^c ± 0.16	8.61	56.9 ^b ± 0.20	8.71	59.1 ^a ± 0.22	8.98	56.9 ± 4.99	8.76
CC	70.2 ^b ± 0.23	9.98	69.1 ^c ± 0.28	10.08	71.8 ^a ± 0.28	9.76	70.3 ± 6.99	9.95
AG	62.9 ^c ± 0.21	9.82	64.1 ^b ± 0.26	10.07	66.8 ^a ± 0.27	10.01	64.4 ± 6.41	9.96
BD	24.7 ^c ± 0.08	9.70	27.3 ^b ± 0.13	11.85	29.5 ^a ± 0.13	11.05	26.8 ± 2.92	10.87
RL	11.9 ^b ± 0.05	11.7	11.4 ^c ± 0.05	11.70	12.4 ^a ± 0.08	16.73	11.9 ± 1.61	11.90
RW	10.5 ^a ± 0.08	21.93	9.7 ^b ± 0.08	20.10	9.4 ^c ± 0.08	20.75	9.9 ± 2.11	21.17
TC	6.2 ^c ± 0.02	7.79	6.2 ^b ± 0.02	7.59	6.4 ^a ± 0.02	9.49	6.2 ± 0.52	8.28
HC	15.8 ^b ± 0.06	11.17	15.1 ^c ± 0.05	8.48	16.1 ^a ± 0.09	13.73	15.7 ± 1.79	11.41
BW	16.2 ^c ± 0.12	21.20	18.2 ^b ± 0.18	24.68	20.1 ^a ± 0.21	25.81	17.9 ± 4.31	24.08

^{abc} lsmeans with different letters in rows are significantly different at $P \leq 0.001$; SNK's multiple mean comparison test, GCZ Guineo-Congolese zone, GSZ Guineo-Sudanese zone, SZ Sudanese zone

WH withers height, RH rump height, SH sternum height, BH back height, CD chest depth, RD rump depth, CW chest width, SIL scapulo-ischial length, BL body length, HL head length, HW head width, EL ear length, HoL horn length, MD muzzle diameter, NL neck length, NG neck girth, TL tail length, HG heart girth, CC chest circumference, AG abdominal girth, BD bicoastal diameter, RL rump length, RW rump width, TC cannon bone circumference, HC hock circumference, BW body weight

body measurements and indices were recorded in the SZ zone in the drier North and the lowest in the GCZ zone in the humid South. Relatively low values of CV were recorded for most of the variables except for horn length (HoL), rump width (RW), and body weight (BW), with the least variation for cannon bone circumference (TC). Most of the morphological indices, except boniness index (Bi), pelvic index (IP), chest depth index (CDI), balance index (Ba), cephalic index (IC), and thoracic development (TD), showed also relatively low CV with the least variation for body ratio (BR) and body index (IBR). The highest mean values recorded for rump height (RH), sternum height (SH), back height (BH), body length (BL), neck length (NL), tail length (TL) and bicoastal diameter (BD) were 50.5, 30.7, 48.9, 74.1, 19.8, 11.9, and 29.5,

respectively (Table 1). The highest mean values of the auricular index (IAT), size index (SI), and pectoral index (PI) were 0.5, 98.2, and 1.4, respectively (Table 2).

Significant variations ($P < 0.0001$) were also observed among the three vegetation zones for all the qualitative traits (Table 3). Coat colors and pigment patterns were very diverse. In general, composite coat colors (93.2%) and variegation pigment patterns (64.9%) were the most frequently observed regardless of vegetation zones, with a dominance of spotted white (31.5%) and black (24.5%) colors, and localized variegation (36.5%) pattern. In addition, animals from the Northern Sudanese zone were characterized predominantly by spotted brown coats (27.5%) and other pigment patterns. Irrespective of vegetation zones, supernumerary teats

Table 2 Least squares means (lsmeans) and standard errors (SE) and coefficients of variation (CV) of morphological indices across vegetation zones

Variables	GCZ (n = 893)		GSZ (n = 610)		SZ (n = 611)		Overall (n = 2114)	
	lsmean ± SE	CV	lsmean ± SE	CV	lsmean ± SE	CV	lsmean ± SE	CV
MI	40.2 ± 0.24	18.18	39.6 ± 0.30	18.42	40.1 ± 0.32	19.47	39.9 ± 7.45	18.63
IGS	0.9 ^c ± 0.00	15.13	1.1 ^b ± 0.01	12.99	1.2 ^a ± 0.01	14.04	1.0 ± 0.15	14.20
IAT	0.4 ^c ± 0.00	11.59	0.5 ^b ± 0.00	9.75	0.5 ^a ± 0.00	11.41	0.5 ± 0.05	11.07
USI	46.7 ^c ± 0.13	8.52	50.9 ^b ± 0.17	8.11	54.1 ^a ± 0.14	6.31	50.1 ± 3.87	7.73
BI	11.4 ± 0.20	51.55	11.0 ± 0.04	7.91	10.9 ± 0.17	37.56	11.2 ± 4.45	39.82
IP	89.0 ^a ± 0.62	20.74	85.2 ^b ± 0.60	17.35	76.5 ^c ± 1.21	39.16	84.3 ± 21.59	25.61
CDI	53.3 ^a ± 0.13	6.99	48.9 ^a ± 0.13	6.54	46.6 ^c ± 0.73	38.90	50.1 ± 10.18	20.33
SI	82.8 ^c ± 0.23	8.34	92.2 ^b ± 0.26	6.85	98.2 ^a ± 0.27	6.67	89.9 ± 6.64	7.38
Ba	0.4 ^a ± 0.00	24.38	0.4 ^b ± 0.004	28.07	0.4 ^b ± 0.01	29.63	0.4 ± 0.11	26.88
IBR	87.8 ^a ± 0.19	6.44	87.4 ^a ± 0.21	5.79	86.0 ^b ± 0.19	5.41	87.2 ± 5.21	5.98
PI	1.4 ^a ± 0.00	8.9	1.4 ^b ± 0.00	4.90	1.3 ^c ± 0.00	5.02	1.4 ± 0.10	7.04
IC	60.4 ^a ± 0.29	14.56	60.0 ^a ± 1.03	42.23	56.7 ^b ± 0.22	9.56	59.2 ± 15.05	25.41
BR	0.9 ^c ± 0.001	3.91	0.9 ^b ± 0.00	2.98	0.9 ^a ± 0.00	1.94	0.9 ± 0.03	3.15
TD	2.5 ^a ± 0.00	15.85	2.2 ^b ± 0.03	36.34	1.9 ^c ± 0.01	11.10	2.2 ± 0.50	22.67
WS	0.8 ^a ± 0.00	19.79	0.8 ^b ± 0.01	19.23	0.7 ^c ± 0.01	17.05	0.8 ± 0.14	18.96

^{abc} lsmeans with different letters in rows are significantly different at $P \leq 0.001$, SNK's multiple mean comparison test, GCZ Guineo-Congolese zone, GSZ Guineo-Sudanian zone, SZ Sudanian zone

MI mass index, IGS slenderness index, IAT auricular index, USI sternum index, BI boniness index, IP pelvic index, CDI chest depth index, SI size index, Ba balance, IBR body index, PI pectoral index, IC cephalic index, BR body ratio, TD thoracic development, WS width slope

(28.7%), beard (5.4%), and wattles (18.3%) were rarely observed. Goats with wattles were evenly distributed in all vegetation zones, whereas those with a beard and supernumerary teats were mainly found in the Northern Sudanian and the Southern Guineo-Congolese zones, respectively. Furthermore, straight facial profile (68.0%) and erected ears (93.0%) were more common than concave facial profile (32.0%) and dropped ears (7.0%), which predominated, respectively, in GCZ, and in GSZ with SZ. Curved horns (82.2%) were predominant, with a diversity of horn orientations dominated by backward (44.1%) and lateral (26.0%) orientations.

The proportion of birth type, especially of single and multiple births, varied significantly ($P < 0.0001$) among the three vegetation zones (Additional file 2: Table S6). Irrespective of the vegetation zone, the frequencies of multiple births (i.e., twins and triplet/quadruplet born) appeared to be similar to those of single births (Additional file 2: Table S6). However, multiple births seemed to be more frequent in the GSZ and GCZ zones, and to increase with does' parity number (Additional file 2: Table S6).

Multivariate analysis of morphometric traits

Overall, 31 out of the 41 quantitative variables (i.e., 26 quantitative linear body traits and 15 morphological indices) included in the stepwise discriminant analysis

(Additional file 2: Table S7) significantly contributed to discriminating between the vegetation zones ($P < 0.001$). Nevertheless, the use of the 22 most significant variables ($P > F$ and $F > 10$) in the canonical discriminant analysis generated two significant ($P < 0.0001$) canonical variables (CAN 1 and CAN 2) that explain the total variance as revealed by the standardized coefficients for the discriminant function, the canonical correlation, the eigenvalue, and the shared variance (Additional file 2: Table S8). Figure 3 plots the individual scores for the two canonical variables (CAN 1 and CAN 2). Canonical loadings that measure the simple linear correlations between each independent variable and the canonical variables are reported in Additional file 2: Table S8. All original variables were correlated with CAN 1 which was dominated by positive loadings of size index (SI), sternum height (SH), back height (BH), rump height (RH), neck length (NL), auricular index (IAT), bicoastal diameter (BD), tail length (TL), body length (BL) and a negative loading of the pectoral index (PI).

All pairwise Mahalanobis distances between goat subpopulations, represented by the vegetation zones, were significant ($P < 0.0001$) (Additional file 2: Tables S9 and S10). The largest (9.22) Mahalanobis distance was recorded between the GCZ and SZ zones, whereas the closest (2.49) was between the SZ and GSZ zones. The discriminant functions classified about 71% of the

Table 3 Frequency (%) of qualitative traits of goat subpopulations of three vegetation zones of Benin

Variables	Modalities	Overall (n = 2114)	GCZ (n = 893)	GSZ (n = 610)	SZ (n = 611)	χ^2	P
Incidence of supernumerary teats	Absence	71.3	64.1	71.8	81.3	53.085	0.0001
	Presence	28.7	35.9	28.2	18.7		
Head profile	Straight	68.0	49.8	80.3	82.2	234.269	0.0001
	Concave	32.0	50.2	19.7	17.8		
Ear orientation	Erected	93.0	99.9	94.4	81.5	190.964	0.0001
	Dropped	7.0	0.1	5.6	18.5		
Coat color	Uniform black	1.6	2.4	1.5	0.5	224.243	0.0001
	Uniform brown	2.1	0.3	3.6	3.3		
	Uniform white	2.6	4.6	1.1	1.0		
	Uniform fawn	0.7	0.6	0.5	1.1		
	Spotted white	31.5	40.5	25.9	23.7		
	Spotted fawn	15.9	13.9	24.1	10.6		
	Spotted grey	1.4	1.5	0.3	2.3		
	Spotted brown	17.5	12.4	14.8	27.5		
	Spotted black	24.5	23.0	26.1	25.0		
	Spotted red	2.4	0.9	2.1	4.9		
	Pigment pattern	Eumelanic	10.0	5.7	9.5		
Localized Variegated		36.5	39.1	38.7	30.6		
Generalized Variegated		28.4	42.2	22.8	13.9		
Others		25.1	13.0	29.0	38.8		
Back profile	Straight	25.9	13.0	24.4	46.2	691.9	0.0001
	Dipped	25.5	7.4	38.2	39.3		
	Slopes up towards the withers	48.6	79.6	37.4	14.6		
Incidence of wattles	Presence	18.3	12.7	17.5	27.2	51.504	0.0001
	Absence	81.7	87.3	82.5	72.8		
Incidence of beard	Presence	5.4	2.7	3.9	11.0	52.106	0.0001
	Absence	94.6	97.3	96.1	89.0		
Horn form	Straight	17.8	18.8	18.4	15.9	2.299	0.0001
	Curved	82.2	81.2	81.6	84.1		
Horn orientation	Lateral	26.0	18.3	29.2	34.2	183.401	0.0001
	Slanting	17.8	18.8	18.4	15.9		
	Onward	12.1	5.2	13.9	20.3		
	Backward	44.1	57.8	38.5	29.6		

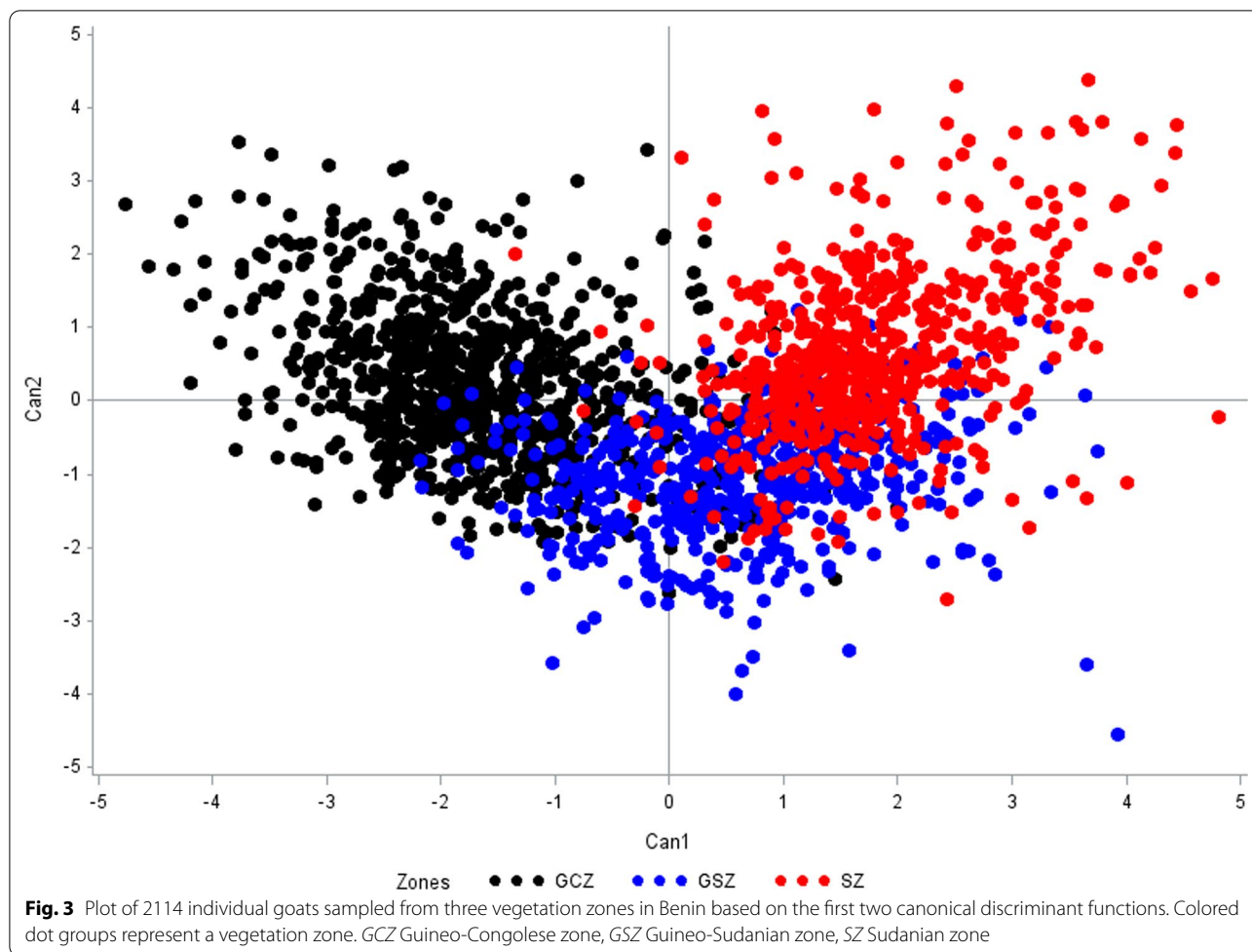
GCZ Guineo-Congolese zone, GSZ Guineo-Sudanian zone, SZ Sudanian zone

P is the probability observed for the qualitative traits, χ^2 expresses independence between variables at 5% level

individual goats in their a priori group (Table 4). The pairwise Mahalanobis distances between the phytogeographic zones, considered as provenances within each vegetation zone, were also significant ($P < 0.0001$) with a correct classification of 56% of individual goats in their a priori phytogeographic zones (Table 5). The dendrograms generated using the squared Mahalanobis distances showed two large groups of goats (Fig. 4a) that can be subdivided into four subpopulations (Fig. 4b) irrespective of the phytogeographic zones. The first group was composed mainly of individuals from the GCZ zone and subdivided into two subpopulations: the first was made

of individuals from Coastal and Pobe zones, whereas the second regrouped individuals from Oueme Valley, Zou, and Plateau zones. The second group of goats was made of individuals from the GSZ and SZ zones and was further subdivided into two subpopulations: the first subpopulation grouped individuals from Bassila, Chaîne Atacora, and Borgou-Sud, whereas the second subpopulation was made of individuals from Mekrou-Pendjari joined by those of Borgou-Nord zone in the other hand.

The association between the different physical traits under consideration and the vegetation zones is shown in Fig. 5. The two dimensions (i.e., Dim 1 and Dim 2)



explained, respectively, (91.06%) and (100%) of the total variation. The right-hand side of the plot shows a close linkage of the GSZ zone with goats that have erected/

Table 4 Percent of individual goats classified into vegetation zones (n = 2114)

Vegetation zones	Posterior probability (%)		
	GCZ	GSZ	SZ
GCZ	80.96	17.25	1.79
GSZ	20.49	59.67	19.84
SZ	0.33	26.19	73.49
Rate	0.19	0.40	0.27
Priors	0.33	0.33	0.33

GCZ Guineo-Congolese zone, GSZ Guineo-Sudanian zone, SZ Sudanian zone
 Values above and/or below the diagonal represent the percentage of individuals from other phyto-geographic zones present in the zone considered by the diagonal value
 Rate: proportion of misclassified observation in each phyto-geographic zone
 Priors: Prior probabilities of group membership

hanging ears, a straight facial head profile, a dipped back, curved horns with lateral orientation, and a composed coat color with the predominance of spotted black and brown patterns. Goats from the SZ zone were characterized by dropped ears, straight head profile and back line, wattles, beard, straight horn oriented laterally, and eumelanic coat pigment pattern. On the left-hand side, the GCZ zone was associated with goats that have erected ears, a concave head profile, a back with slopes up towards the withers, supernumerary teats, a curved horn with different orientations (slanting or backward), and a composite coat color spotted white or uniform white coat.

Geographical distribution modeling
Performances of model and environmental variables contribution

The MaxEnt model results showed that the average AUC of goat Type I, Type II, and Type III were 0.916 (± 0.026), 0.847 (± 0.077), and 0.852 (± 0.024), respectively. These AUC values, close to 0.9, indicate a very

Table 5 Percent of individual goats classified into different phytogeographic zones ($n = 2114$)

Phytogeographic zones	Posterior probability (%)									
	BNZ	BSZ	BZ	CAZ	CZ	MPZ	PIZ	PoZ	VOZ	ZZ
BNZ	52.91	6.80	4.37	14.08	0.49	18.45	0.49	0.97	0.97	0.49
BSZ	7.11	30.96	5.08	25.38	0.51	7.11	10.15	0.00	6.09	7.61
BZ	8.74	5.34	38.83	11.65	9.22	2.91	5.83	3.40	1.46	12.62
CAZ	1.50	10.00	2.00	60.00	0.00	6.50	0.00	0.00	2.50	17.50
CZ	0.00	0.00	2.48	0.00	75.74	0.00	0.00	20.30	0.99	0.50
MPZ	4.88	4.39	0.00	32.68	0.00	55.12	0.00	0.00	0.00	2.93
PIZ	0.00	7.42	3.06	3.93	0.00	0.00	62.45	0.00	2.18	20.96
PoZ	0.00	0.00	0.43	0.00	27.47	0.00	0.43	70.82	0.43	0.43
VOZ	0.00	2.18	3.49	9.17	0.87	0.00	13.54	0.00	61.14	9.61
ZZ	0.97	5.80	7.73	18.84	2.90	0.00	4.83	0.00	6.28	52.66
Rate	0.4709	0.6904	0.6117	0.4000	0.2426	0.4488	0.3755	0.2918	0.3886	0.4734
Priors	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

MPZ Mekrou-Pendjari zone, CAZ Chaîne Atacora zone, BNZ Borgou-Nord zone, BSZ Borgou-Sud zone, BZ Bassila zone, CZ Coastal zone, PoZ Pobe zone, PIZ Plateau zone, VOZ Oueme Valley zone, ZZ Zou zone

Values above and/or below the diagonal represent the percentage of individuals from other phytogeographic zones present in the zone considered by the diagonal value

Rate: proportion of misclassified observation in each phytogeographic zone

Priors: Prior probabilities of group membership

high informative performance of the model. In addition, the values of TSS (0.75, 0.60, and 0.62, respectively, for Type I, Type II, and Type III) also indicate a good predictive power of the MaxEnt models obtained.

The result of the Jackknife test revealed that seven bioclimatic variables (i.e., mean diurnal range in temp (bio2), isothermality (bio3), maximum temp warmest month (bio5), annual temperature range (bio7), rainfall driest quarter (bio17), annual moisture index (mi), and moisture index arid quarter (miaq)) were less correlated and contributed mostly ($\geq 10\%$) to the variation in the environmental suitability of all goat types (Table 6). The main environmental factors that influenced the habitat suitability of goat Type I were the mean diurnal range in temp (64.8%). The habitat suitability of goat Type II was mainly influenced by isothermality (65.2%) and rainfall driest quarter (19.9%) while that of Type III was influenced by maximum temp warmest month (29.5%), annual moisture index (16.0%), annual temperature range (15.5%), rainfall driest quarter (15.2%), isothermality (12.1%) and mean diurnal range in temp (10.2%).

Furthermore, the Jackknife test allowed to identify the environmental variables that significantly increased the gain in information about the origin of the distribution of the different goat types when used in isolation. Thus, annual temperature range (bio7) and rainfall driest quarter (bio17) were the most determinant environmental variables for the Type I against isothermality (bio3) and maximum temp warmest month (bio5) for the Type II.

The increased gain in information about the origin of distribution of Type III was obtained with rainfall driest quarter (bio17) and the mean diurnal range in temp (bio2) (Fig. 6).

The curves of the most discriminating/explanatory environmental variables of the distribution of the three main goat phenotypes (i.e., Types I, II, and III), obtained with the MaxEnt software, are presented in Fig. 7. These different curves describe the probability of change in each environmental variable when all other environmental variables are kept at their sample average value.

Thus, the probability of occurrence of Type I was obtained in areas where the mean diurnal range in temp (bio2) was below 10.3°C (between 5.2 and 5.9°C), a value from which it drops rapidly (Fig. 7a). The environmental variables isothermality (bio3) and rainfall driest quarter (bio17) provided the highest probability of occurrence, respectively, with values between 550 – 575 and 200 mm, for Type II (Fig. 7b, c). The probability of occurrence of Type III with maximum temp warmest month (bio5) appeared with two extremes of intervals (between 33.1 and 33.3°C) and (between 38.1 and 38.3°C). Likewise, the probability of occurrence of Type III with annual moisture index (mi) was obtained for two extremes, the first was a peak of the order 0.53 and the second that of 0.88 (Fig. 7e). This goat type was found in habitats with two extremes of intervals for annual temperature range (bio7) between (11 and 11.6°C) and (23 and 25°C). As was the case for the variable annual temperature range

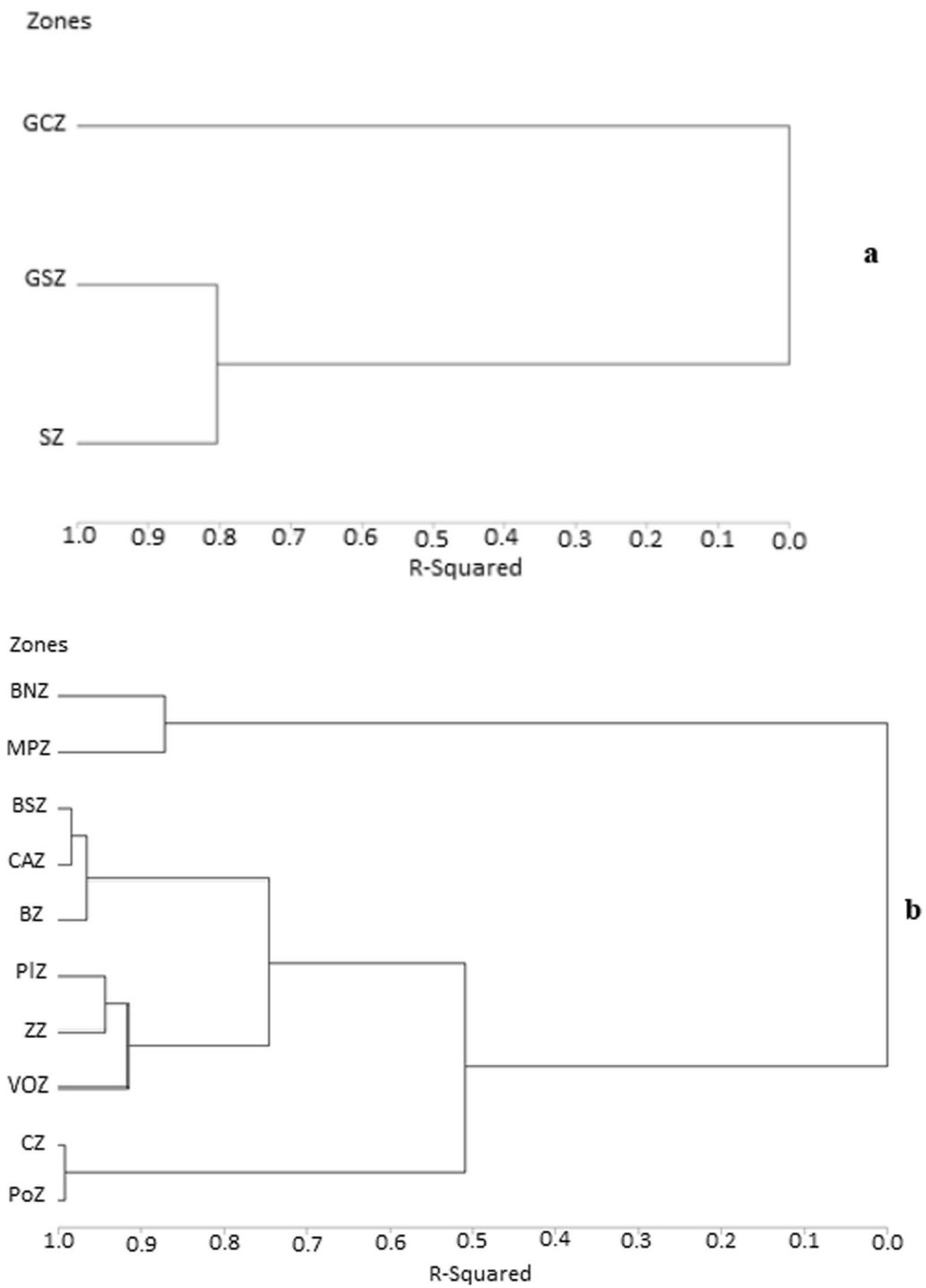


Fig. 4 Clusterdness of goat population in Benin based on Mahalanobis distance. **a** Representation based on vegetation zones model; GCZ Guineo-Congolese zone, GSZ Guineo-Sudanian zone, SZ Sudanian zone. **b** Representation based on phytogeographic zones model; MPZ Mekrou-Pendjari zone, CAZ Chaîne Atacora zone, BNZ Borgou-Nord zone, BSZ Borgou-Sud zone, BZ Bassila zone, CZ Coastal zone, PoZ Pobe zone, PIZ Plateau zone, VOZ Oueme Valley zone, ZZ Zou zone

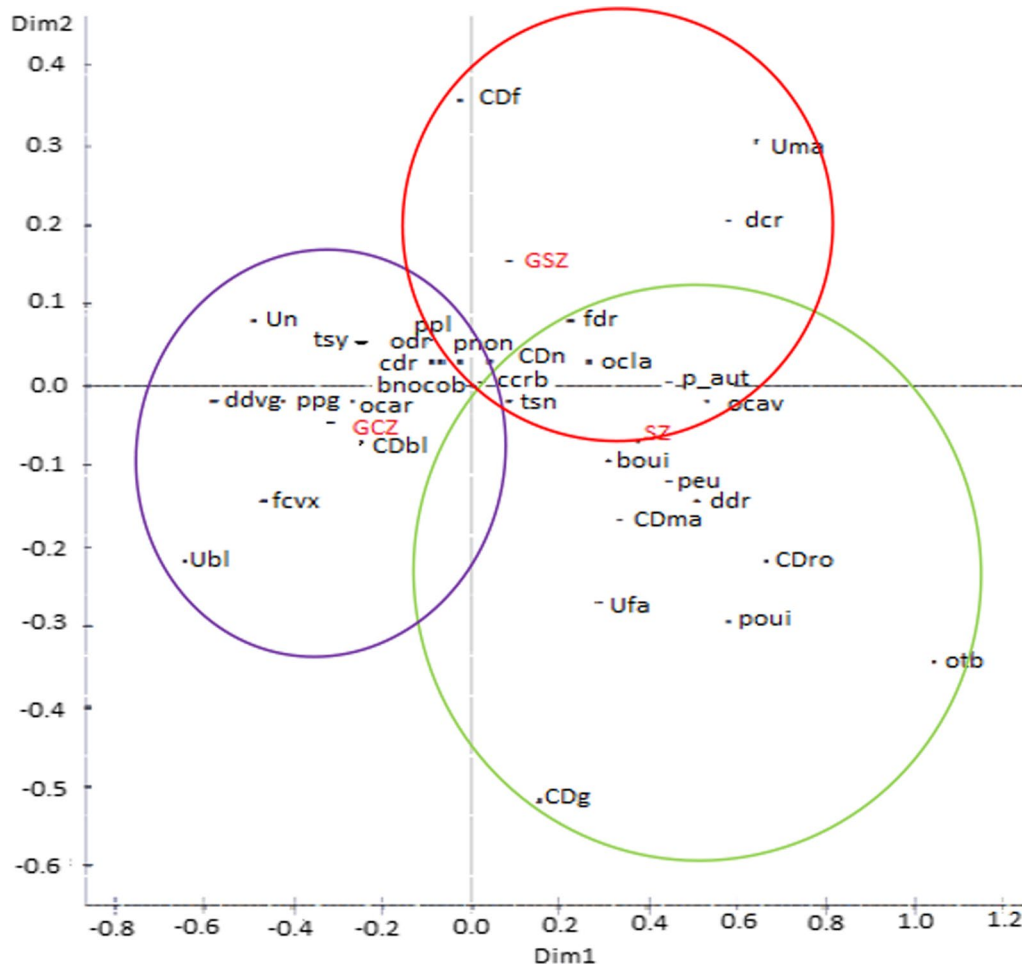


Fig. 5 Multiple correspondence analysis of the morphological physical traits of goat population in Benin; GCZ Guineo-Congolese zone, GSZ Guineo-Sudanian zone, SZ Sudanian zone. *tsn* absence of supernumerary teats, *tsy* presence of supernumerary teats, *fdr* straight facial, *fcvx* concave facial, *odr* erected ear, *otb* dropped ear, *Un* uniform black, *Uma* uniform brown, *Ubl* uniform white, *Ufa* uniform fawn, *CDbl* spotted white, *CDf* spotted fawn, *CDg* spotted grey, *CDma* spotted brown, *CDn* spotted black, *CDro* spotted red, *peu* eumelanic, *ppl* localized variegation, *ppg* generalized variegation, *p_aut* other pigment patterns, *ddr* straight back, *dcr* dipped/curved back, *ddvg* back with slopes up towards the rump, *bnon* absence of beard, *boui* presence of beard, *prnon* absence of wattles, *poui* presence of wattles, *cdr* straight horn, *ccrb* curved horn, *ocla* lateral orientation, *ocob* slanting orientation, *ocav* onward orientation, *ocar* backward orientation

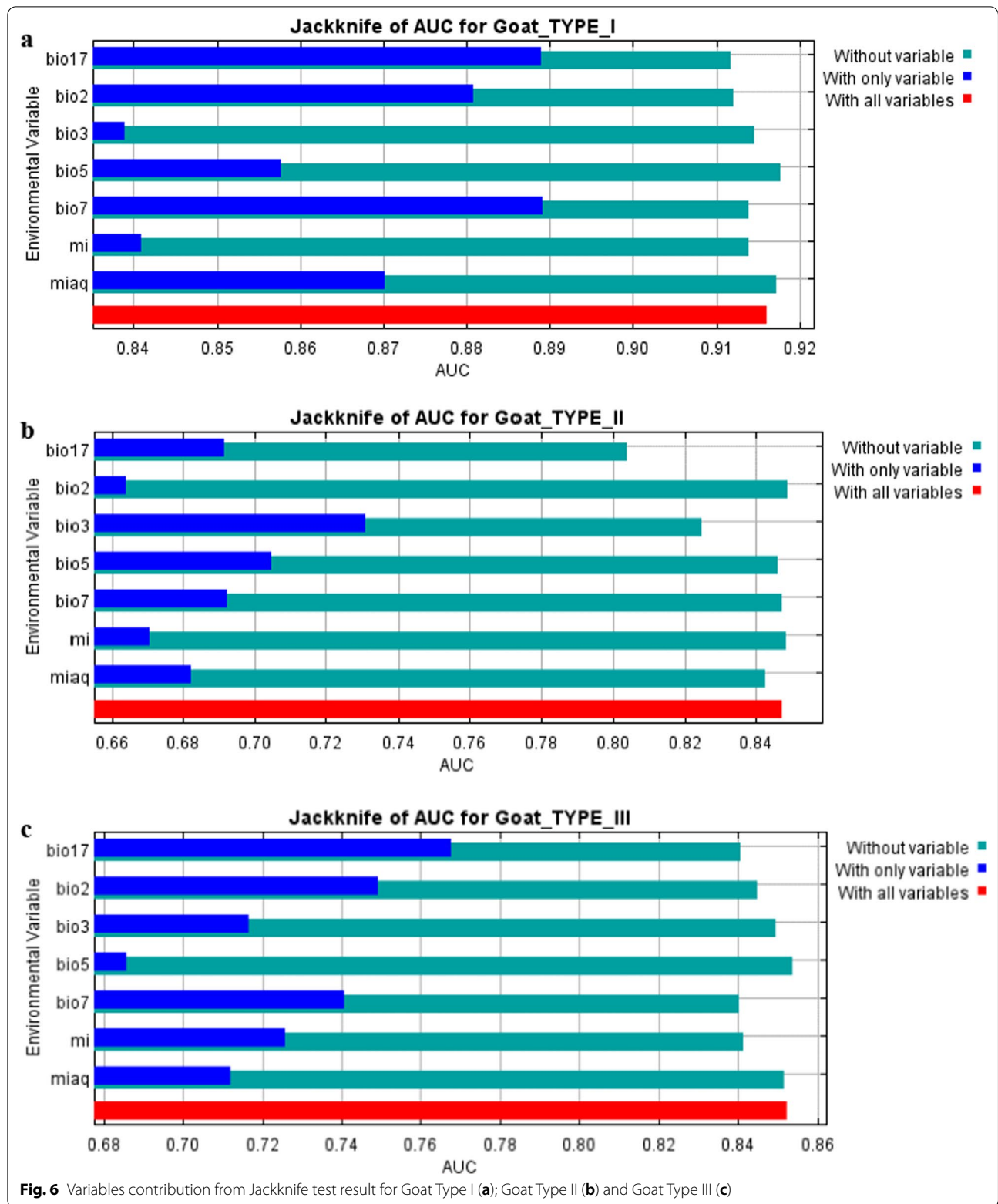
Table 6 Environmental variables less correlated and their contribution to the model

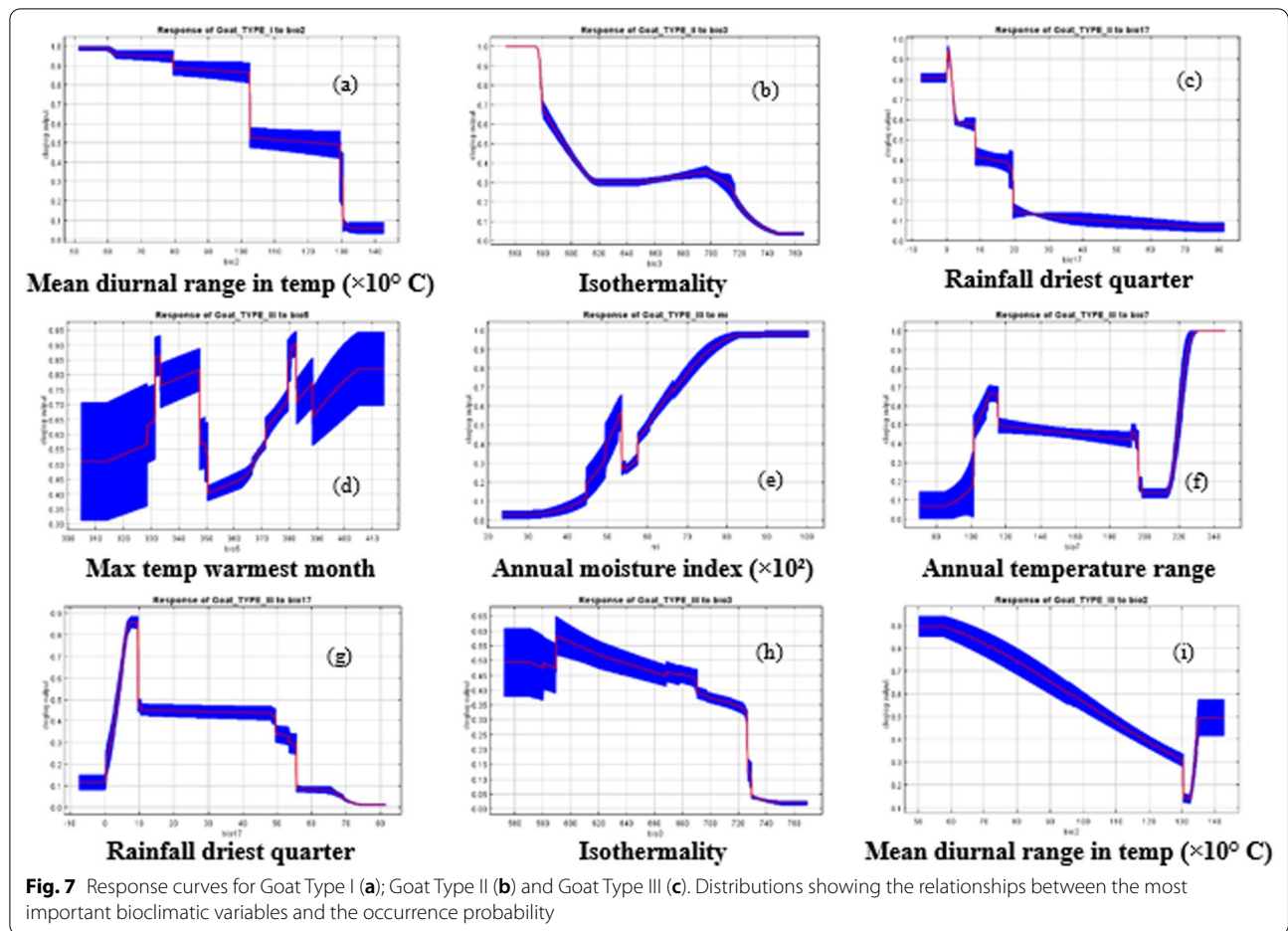
Code	Environmental variables	Contribution (%)		
		Type I	Type II	Type III
bio2	Mean diurnal range in temp	64.8	4.8	10.2
bio3	Isothermality	8.4	65.2	12.1
bio7	Annual temperature range	8.3	0.8	15.5
bio17	Rainfall driest quarter	7.3	19.9	15.2
miaq	Moisture index arid quarter	5.6	3.9	1.6
bio5	Max temp warmest month	4.2	3.9	29.5
mi	Annual moisture index	1.3	1.5	16.0

Type I Djallonké goats, Type II Sahelian goats, Type III Crossbreed goats

(bio7), the highest probability of occurrence of Type III with rainfall driest quarter (bio17) appeared with values between 800 and 1000 mm (Fig. 7i). Habitats with 590 for isothermality (bio3) and mean diurnal range in temp (bio2) between 5 °C and 5.7 °C appear more favorable for the presence of Type III (Fig. 7h).

The current distribution of goat subpopulations in Benin
Highly favorable habitats for Type I and Type II were concentrated in the GCZ and SZ zones, respectively. In contrast, highly favorable habitats for Type III extended across the three vegetation zones of Benin (Figs. 8, 9, 10). However, the habitats less favorable to the three goat types occupied the largest proportions. The results of the

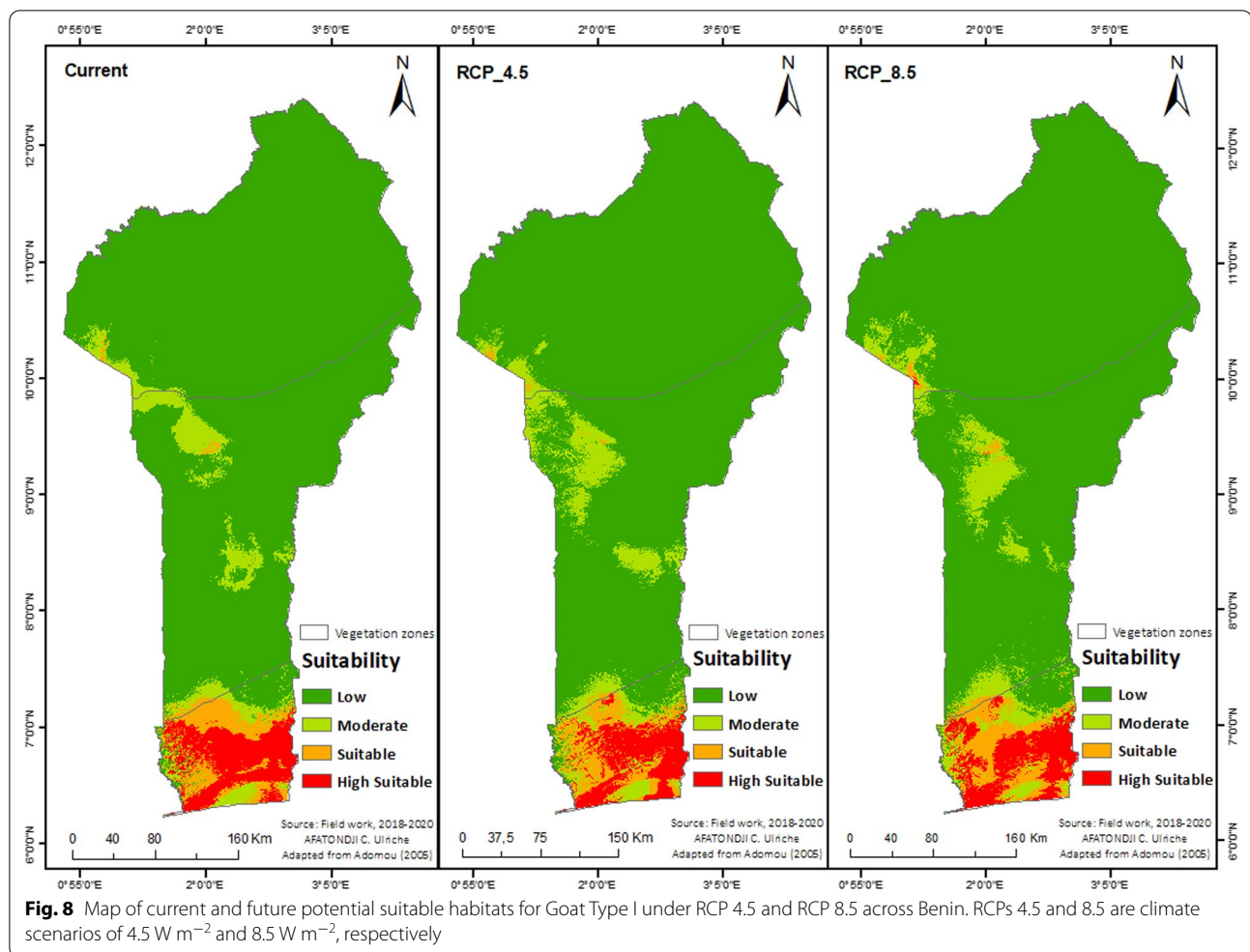




model showed that an area corresponding to a proportion of 4.72% of the total area of land potentially habitable by goats, represents the area of highly favorable habitat for Type I (Additional file 2: Table S11, Fig. 8). This is followed by the area classified only as favorable habitat (3.18%). More than half of the national land area (62.20%) was a low suitable habitat for Type I. Compared to Type I, the proportion of the national land area for both levels of habitat (favorable and high) for Type II and III was greater (over 10%). A significant proportion was recorded as moderately favorable (29.04%) and favorable (8.08%) habitats for Type II. The lowest proportion (2.97%) of highly favorable habitats was recorded for Type II (Additional file 2: Table S11, Fig. 9). The highly favorable habitat (5988.44 km²) for Type III was larger than that of favorable ones (11,295.30 km²). These two levels of habitat were disproportionately distributed across the three vegetation zones of the country (Fig. 10). In general, the proportion of highly favorable habitats for all three goat types was very low, followed by the proportion of favorable habitats.

Future potential distribution for 2055

The future distribution of potential habitats for the three goat types varied under the two RCP scenarios and between vegetation zones (Figs. 8, 9, and 10). For Goat Type I, the range of the most favorable habitats was predicted to decrease by 17.69% under RCP 4.5 and by 9.53% under RCP 8.5 (Additional file 2: Table S12, Fig. 8). The model also predicted the range of favorable habitats to increase slightly under both scenarios, respectively, by 3.03% under RCP 4.5 and by 6.96% under RCP 8.5. In contrast to a slight decrease for low suitable habitat levels, the prediction showed a considerable increase (31.11% and 16.50%), respectively, under RCP 4.5 and RCP 8.5 for moderately suitable habitat levels. For Type II, the joint losses recorded for moderate levels under both scenarios (− 6.46% for RCP 4.5 and − 5.53% for RCP 8.5) were to the benefit of an increase in the suitable and highly suitable levels from RCP 4.5, and an increase in the highly suitable and low suitability levels from RCP 8.5. The future distribution predicted an increase of the highly suitable areas under the RCPs 4.5 and 8.5 scenarios by 4.31% and 20.78%, respectively. Regarding Type III,



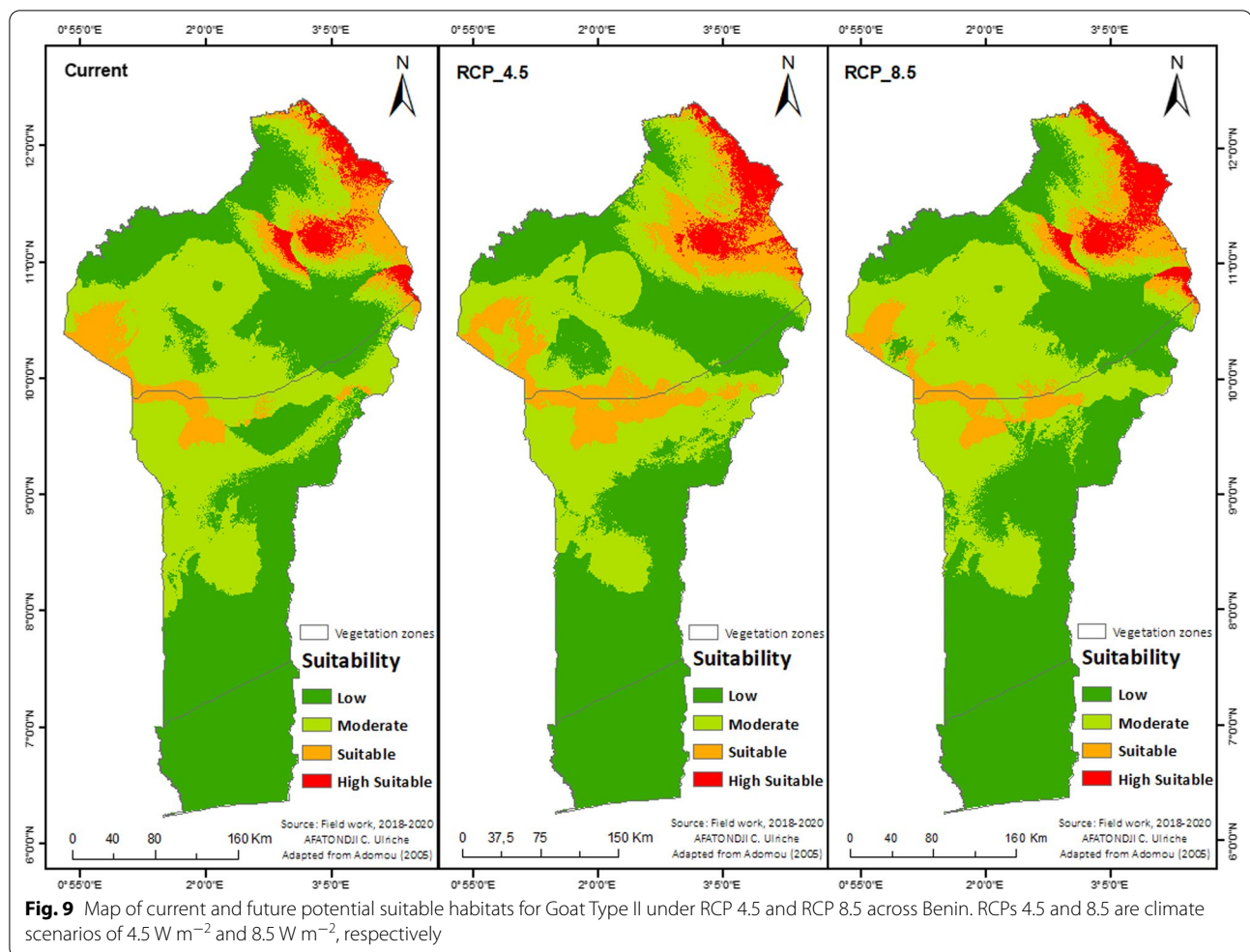
the future distribution predicted an increase in the range of highly suitable habitats of 8.46% and 12.83%, respectively, under the RCPs 4.5 and 8.5 scenarios (Additional file 2: Table S12, Fig. 10). In contrast, a decrease in the range of suitable habitats was predicted under both RCP 4.5 (− 5.85%) and RCP 8.5 (− 19.01%) scenarios. Similar to Type II, a decrease in moderately suitable habitats was predicted for Type III under both RCP 4.5 (12.67%) and RCP 8.5 (23.26%) scenarios (Additional file 2: Table S12, Fig. 9).

Discussion

Morphological variability

In general, the results of univariate analyses revealed a high-to-moderate variability for all morphological and physical qualitative traits measured in the Beninese goat population, within and among vegetation zones. Thus, goat subpopulations of the three vegetation zones might be considered ancestrally distinct from each other. Furthermore, the recorded diversity of the coat color in all

vegetation zones could be a result of climatic factors and anthropogenic pressure on animal phenotype (Ahozonlin et al. 2019; Berihulay et al. 2019; Gaughan et al. 2019; Ofori et al. 2021). The predominance of erected ears, composite coat colors with dominance of spotted white and black coats associated with variegation (localized and generalized) observed in all vegetation zones could support the hypothesis that the subpopulations have the same origin but have probably undergone changes in their morphology and genetic structure. The straight facial head profile, mainly observed in the GSZ and SZ zones, suggests that these goat subpopulations are closer to each other. Regarding the incidence of wattles and beard, the finding of the present study is in line with those by Dossa et al. (2007) and Traoré et al. (2008) who reported a low prevalence of wattles and beard in indigenous goat populations of West Africa. Ofori et al. (2021) also reported the same observations in a recent study on the phenotypic and genetic characterization of qualitative traits in the West African Dwarf goat from

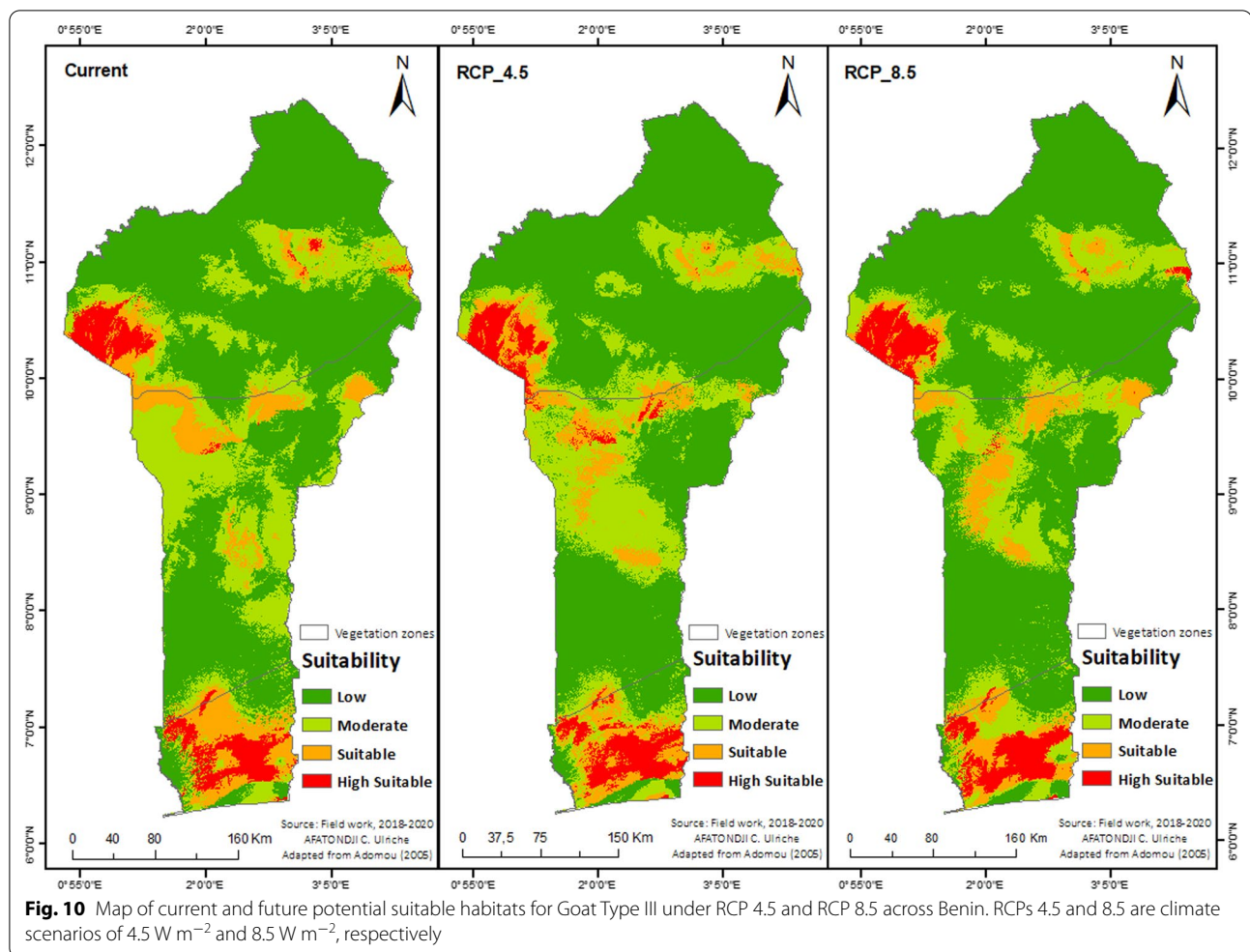


Ghana. Despite the general rarity of wattles in the goat population of Benin, a relatively high proportion of wattles was recorded in the SZ zone. This result, associated with a high incidence of dropping ears, characteristics of long-legged goats and crossbreeds (long-legged \times short-legged breeds), suggests that goats in the SZ zone are closely related to the latter as previously suggested by Dossa et al. (2007). Indeed, the northern part of the SZ zone shares boundaries and ecological conditions with the Sahel countries of Niger and Burkina-Faso. Mani et al. (2014) also reported a high prevalence of wattles in the long-legged goat population from Niger. On the other hand, the lower presence of wattles associated with the prevalence of erected ears (characteristic of African Dwarf goat) in the GCZ zone is evidence of the dominance of short-legged in this zone as previously reported by Dossa et al. (2007).

The multiple correspondence analysis separated the goats from the vegetation zones of SZ and GCZ but revealed an overlap between each of them with those

from the GSZ zone (Fig. 5). These results confirm that goats from the SZ and GCZ zones are phenotypically different, and suggest that those from the GSZ zone may represent an intermediate subpopulation of the first two. In addition, the association of phenotypic traits with goat subpopulations, as shown in Fig. 5, might confirm the dominance of a goat subpopulation in the SZ zone that is close to the long-legged type and characterized by a straight head profile, dropping ear, back line, a diversity of coat color with a dominance of spotted brown, red, fawn or grey colors, presence of beard and wattles with an absence of supernumerary teats.

The best discriminant function model used to discriminate goat population in this study included ten body measurements (i.e., RH, SH, BH, BL, NL, TL, BD, IAT, SI, and PI) out of the 31 pre-selected after the stepwise analysis. This result showed that new variables other than those retained by Dossa et al. (2007) (i.e., HW, NL, HS, TL, and IAT) could be used to distinguish subpopulations within the goat population of Benin if they are taken into



account consistently. Furthermore, the mean values of the ten discriminant variables (7 body measurements and 3 morphological indices) recorded for each goat subpopulation (Additional file 2: Table S13) showed a morphological difference among the vegetation zones. Thus, the small to large size variations observed from the GCZ to the SZ zone reveals that goats tend to have larger features following a geographical gradient South–North. These results corroborate previous findings of Traoré et al. (2008), Mani et al. (2014), and Djagba et al. (2019), who reported an increase in goat body size along an aridity gradient. This morphological variability observed among vegetation zones might be due to adaptations to specific environmental conditions (Ibnelbachyr et al. 2015). However, the intermediate size of goats in GSZ supports the occurrence of inbreeding in this vegetation zone. The GSZ zone seems thus to be a favorable zone for crossbreeding of goats. This result, which contrasts with the finding by Dossa et al. (2007), who reported the Southern Sudanian zone (SSZ) as a great crossbreed zone, suggests

a recent expansion of the long-legged type southwards. The SSZ in Dossa et al. (2007) was included in the SZ zone in the current study. This shift of the crossbreeding zone from the SZ zone to the GSZ zones further suggests that recent morphological changes may have occurred in the indigenous goat population of Benin and could probably be the result of both environmental and anthropological factors. As the phenotype is the expression of the genotype–environment interaction (Leroy et al. 2015), the small size of individuals in the GCZ could be an expression of natural selection related to the high humidity and abundance of forage resources in this area. In an area where natural resources are abundant, animals have less distance to travel in search of feed, spend less energy, and therefore easily take a stocky appearance. In contrast, in dry and hot zones characterized by shortages of forage resources during periods of drought (as is the case for goats in the SZ zone of Benin), animals would tend to deposit less fat because of the long walks in search of forage and water. Consequently, they would tend to be

slender and thin, features which also allow them to support heat stress. As pointed out in several studies (Berihulay et al. 2019; Gaughan et al. 2019), different natural adaptation mechanisms are observable in animal populations when subjected to different environmental pressures. However, further studies are needed to confirm the influence of environmental factors on the morphological diversity of goat populations. Anthropological factors could include farmers' breed preference and consumers' demands, as well as the frequent mobility of some herds-men with their cattle and goats, favoring crossbreeding (Dossa et al. 2007). In addition to the frequent introduction by farmers of new goat breeds (mostly long-legged individuals) in their goat flocks, it is worth mentioning recent introductions of the Red Sokoto goat, a variety of West African long-legged goat, by the World Bank-funded project PPAAO/WAAPP (*Projet de Productivité Agricole en Afrique de l'Ouest/West Africa Agricultural Productivity Project*) to improve goat productivity in the Northern zones (Dosseh et al. 2021). We can argue that these aforementioned anthropic factors are very determinant in the increasing crossbreeding practices observed in the GSZ zone.

Geographical distribution modeling

Model performances and environmental variables contribution

For sustainable goat farming, as for the production of any other farm animal species, it is necessary to use genotypes or locally available phenotypes that are better adapted to the deleterious effects of climate change. To do so, it is necessary to know the environmental factors at the origin of the diversity. There has been no previous study aiming at modeling the current and future distribution of farm animal genetic resources in Benin. Indeed, previous work on modeling species distribution in Benin has focused on forest plant species (Salako et al. 2019; Favi et al. 2022). In general, the strong contributions of the environmental variables, for instance, isothermality (bio3) and mean diurnal range in temp (bio2) (65.2% and 64.8%, respectively) revealed the high explanatory power of these variables for modeling the habitat suitability of the Beninese goat population. This result disagrees with the majority of recent studies on species distribution modeling in Benin, which reported soil as one of the key explanatory variables (Salako et al. 2019; Favi et al. 2022). This could be explained by the fact that these studies focused on plant species, as soil plays an important role in their development (Pearson and Dawson 2003; Gbemavo et al. 2020). The fact that soil was less important in predicting the diversity of goat population with environmental variables aligns well with findings from a previous goat distribution modeling study in Greece (Valiakos

et al. 2017) but contrasts with those obtained by Kebede et al. (2021) who reported the soil variable as one of the important variables in the prediction of the distribution of different local poultry ecotypes in Ethiopia.

The variables that contributed to the distribution patterns varied according to goat type. The climatic variable "the mean diurnal range in temp" (bio2) was of utmost importance in explaining the distribution of the Djallonké type. According to Sinsin and Kampmann (2010), the GCZ zone is characterized by a subequatorial climate with a bimodal rainfall regime (two rainy seasons and two dry seasons). Climatic conditions of the GCZ zone provide this goat type with a good level of environmental adaptation and resistance to trypanosomes (Wilson 1991; Molina-Flores et al. 2020). Isothermality (bio3) and rainfall driest quarter (bio17) were the most important environmental factors determining favorable habitats for the Sahelian goat. The presence of temperature variables was consistent with the description of the known distribution areas for this goat type. Indeed, the very low value of rainfall driest quarter confirms the Sahel origin of this goat type, which is often considered adapted to semi-arid or arid areas depending on the breed (Molina-Flores et al. 2020).

Furthermore, the environmental factors defining a favorable habitat for the crossbreeds between Djallonké and Sahelian goats are the maximum temp warmest month (bio5), the annual moisture index (mi), the annual temperature range (bio7), the rainfall driest quarter (bio17), the isothermality (bio3) and the mean diurnal range in temp (bio2), sometimes with two intervals for some variables. Kebede et al. (2021) also identified the variable rainfall driest quarter (bio17) as an important explanatory variable for predicting the local poultry distribution in Ethiopia, in contrast to isothermality (bio3) which was found to be less important. The multiplicity of variables predicting the probability of occurrence of crossbreed individuals (Goat Type III) could be due to the high representativeness of this goat type along the South–North gradient in the three vegetation zones characterized by different environmental characteristics (Adomou 2005).

The potential impact of climate change on the future environment suitability for the Beninese goat population

The modeling results show almost no unfavorable habitats for the three goat types (i.e., Djallonké goat, Sahelian goat, and their crossbreeds) under climate change scenarios. On the contrary, the model predicts an expansion of their breeding areas, from their usual habitat to habitats that were less favorable or almost unfavorable to them. This is in line with findings of several recent studies

(Rojas-Downing 2017; Valiakos et al. 2017; Lozano-Jaramillo et al. 2018; Kebede et al. 2021), which suggest that climate change does impact the distribution of favorable habitats for animal species.

All vegetation zones of Benin could be favorable for the presence of goats at different levels ranging from least favorable to most favorable. The model confirms the GCZ zone as a highly suitable habitat for the small-sized Djallonké goat. It predicts a slight expansion of its favorable habitat in the SZ zone under the RCP 8.5 scenario by 2055. This expansion, specifically in the phytogeographic zone of Chaîne Atacora, could be explained by the striking similarity between this zone and the GCZ zone in environmental conditions (Sinsin and Kampmann 2010).

Currently, the extreme North of Benin represented by the SZ zone is identified as a favorable area for the Sahelian goat (Type II). However, under both RCP 4.5 and RCP 8.5 scenarios, this Goat Type expands much further South along the North–South gradient. By 2055, the Sahelian goat will expand more towards the Guineo-Sudanian zone. This southward expansion could be explained by a probable change in the predominant climatic and environmental conditions in the GSZ zone, making it suitable for the breeding of Sahelian goats.

In contrast to the Djallonké and Sahelian goats, all three vegetation zones of Benin represent favorable habitats for the distribution of Crossbreeds. The current representation of Crossbreed individuals in the three vegetation zones shows that crossbreeding, which occurs throughout the country, is not characteristic of a particular vegetation zone, as its distribution remains unchanged by 2055 under both RCPs scenarios. Yet, as goats are domesticated animal species, their future distribution might be determined not only by changing environmental variables but also by anthropogenic action through a modification of farmers' animal management practices, for instance, their breeding and feeding strategies (Kebede et al. 2021).

The joint presence of highly favorable habitats for both Djallonké and Sahelian goats in the GCZ zone could be explained by the increasing introduction of large-framed goats in this region of the country. The GCZ zone is likely the most densely populated in the country. Faced with the growing needs and demands of consumers for meat, farmers are inclined to engage in practices to improve their animals for meat production. Among these practices, crossbreeding of small-sized with large-framed goats is common. This explains the presence of highly favorable habitats for these two populations in the south of the country.

Contribution of our results and implication

This study has the merit of documenting the current distribution of the main types of goats raised in Benin and

predicting their future potential habitat in the context of climate change. Thus, knowledge of suitable habitats for each of these goat types could allow the design and implementation of effective goat genetic improvement and conservation programs in Benin. In addition, the methodology used in this study can be widely replicated and implemented for predicting the distribution of other farm animal species in Benin or other countries in the subregion.

Conclusion

This study aimed to investigate the morphological variability and model the distribution of the existing goat population in the vegetation zones of Benin. The results revealed on the one hand the existence of three major goat types across the three vegetation zones of the country: a small-sized type with erected ears in the Guineo-Congolese zone, a relative large-framed type in the Guineo-Sudanian and Sudanian zones, and an intermediate type, result of crossbreeding between the two previous types, and predominantly found in the latter two vegetation zones. The presence of this third goat type underlies changes in farmers' management practices and breeding strategies. Indeed, farmers' increasing practice of crossbreeding in certain phytogeographic zones might probably be influenced by their proximity to neighboring Sahelian countries, where Sahelian long-legged goats are predominant. On the other hand, the results of modeling distribution carried out on these three goat types showed the current suitability of the Guineo-Congolese zone and the Sudanian zone for breeding the small-sized Djallonké and large-framed Sahelian goat, respectively. An expansion of the range of these goat types was noted under RCP scenarios 4.5 and 8.5. The suitable habitats for crossbreed individuals, currently found mainly in the Guineo-Sudanian and Sudanian zones, substantially increased and covered all vegetation zones, irrespective of the RCP scenario. Climate change will likely create additional challenges in the management of the existing genetic diversity within the Beninese local goat population. Hence, efforts toward sustainable goat farming in Benin should combine genetics and ecology.

Abbreviations

FAO: Foods and Agriculture Organization; GIS: Geographic Information System; GCZ: Guineo-Congolese zone; GSZ: Guineo-Sudanian zone; SZ: Sudanian zone; GPS: Global Positioning System; RCP: Representative Concentration Pathway; IPCC: Intergovernmental Panel on Climate Change; MaxEnt: Maximum entropy; AUC: Area under curve; ROC: Receiver operating characteristics; TSS: True skill statistics; MPZ: Mekrou-Pendjari zone; CAZ: Chaîne Atacora zone; BNZ: Borgou-Nord zone; BSZ: Borgou-Sud zone; BZ: Bassila zone; CZ: Coastal zone; PoZ: Pobe zone; PIZ: Plateau zone; VOZ: Oueme Valley zone; ZZ: Zou zone; SSZ: Southern Sudanian zone; PPAAO/WAAPP: Projet de Productivité Agricole en Afrique de l'Ouest/West Africa Agricultural Productivity Project.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-022-00392-y>.

Additional file 1: Fig. S1. Djallonké buck. **Fig. S2.** Djallonké doe. **Fig. S3.** Sahelian bucks. **Fig. S4.** Sahelian does. **Fig. S5.** Crossbreed buck. **Fig. S6.** Crossbreed doe.

Additional file 2: Table S1. Characteristics of the ten phytogeographic zones of Benin. **Table S2.** Description of linear body measurements (in centimeters) and qualitative traits taken on 2114 adult female goats in Benin. **Table S3.** Morphological indices calculated from linear body measurements taken on 2114 adult female goats in Benin. **Table S4.** Goat types, occurrence numbers, and most discriminating variables. **Table S5.** Environmental variables used and their description. **Table S6.** Incidence of vegetation zone, doe's parity number, and presence or absence of supernumerary teats on birth type. **Table S7.** Stepwise selection summary. **Table S8.** Total canonical coefficients for the canonical function, the adjusted canonical correlation, the eigenvalue, and the percentage total variance accounted for. **Table S9.** Mahalanobis distances between goat subpopulations identified by vegetation zones ($n=2114$). **Table S10.** Mahalanobis distances between goat subpopulations identified by phytogeographic zones ($n=2114$). **Table S11.** Dynamic of distribution of suitable habitat for the distribution of goat subpopulations GCZ, GSZ, and SZ under two RCPs scenarios in Benin **Table S12.** Percentage change of the suitability levels (low, moderate, suitable, high) for the distribution of GCZ, GSZ and SZ goat subpopulations. **Table S13.** Morphometric characteristics of the goat types of Benin.

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Author contributions

Conceptualization: LHD, HRVW, CUA. Investigation: HRVW, CUA. Data curation: HRVW, CUA. Formal analysis: HRVW, CUA, GAF, CAL. Writing—original draft: HRVW, CUA. Writing—review and editing: HRVW, CUA, CAL, TTN, MRBH, LHD. All authors read and approved the final manuscript.

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Availability of data and materials

All relevant data are within the paper and its Supporting Information files.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no potential conflicts of interest.

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