

**Climate Change Impacts on *Apis mellifera L* (1758) Niche in Benin:  
Restriction and Shift of the potential distribution ranges of *adansonii*,  
*scutellata* and *iberiensis* races.**

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**ABSTRACT:** As any biological entity, the honeybee populations are submitted to the worldwide climate change hazards. Mitigation strategies require strong modelling approaches to simulate and anticipate the potential climate change impacts on beekeeping and pollination services. In Benin, as in most tropical African regions, where beekeeping essentially relies on natural swarms, sustainable beekeeping requires deeper control of the environmental factors. We then evaluated the impacts at the 1970-2021 and 2040-2070 horizons prevailing environmental conditions on the potential distribution of *adansonii*, *scutellata* and *iberiensis*, the three *Apis mellifera*

races in Benin. The investigations used 68 occurrences of the three races which were confronted to the bio4, pet, mimq and llds climatic parameters using the maximum entropy modelling. The past distribution areas indicated that 0.43 % of the country territory was favorable to iberiensis races which was restricted to the East-Southern extremity along the Atlantic Ocean. Scutellata and adansonii had larger distribution area, respectively 68.72 % and 75.94 % in the Guineo-Congolian, the Sudano-Guinean and the Sudanian regions. The 2055 horizon predicted a drastic drop of adansonii potential niche (75.94 % to 40 %) which shifted toward the south above the 7th parallel. Scutellata will lose 2.99% of its 1990-2070 horizon niche. On the other hand, iberiensis race was projected to gain 7.04 % of the national territory, restricted to the same past range. Climate change will then shrink and shift Adansonii and scutellata in the best beekeeping areas in Benin. But iberiensis race would be restricted to the poorest honey region, indicating its high extinction risk. We also found that the Sudanian regions above the 10th parallel was unfavorable to the honey bee populations at 2055 horizon. This represents great concerns for beekeeping and pollination service in absence of a long-term strategic beekeeping development plan.

**Keywords:** *Apiculture, Benin, biodiversity, climate change, ecologic niche, honeybee race, MaxEnt modelling.*

## 1. Introduction

Climate change is a worldwide challenge that affects the integrity and distributions of managed and natural ecosystems. It includes phenomenon that involve lasting changes in environmental factors; leading to a disrupted biological equilibrium and the emergence of biotic and abiotic hazards which impact species distribution (Rosenzweig, 1989; 2007). As a consequence of its impacts on the plant species on which the pollinators depend, climate change also deeply affects the performance of the honeybees and determine their distribution in any ecological area (Zapata-Hernández et al., 2024).

The “bees” are made up of more than 18,191 species distributed in the Apidae, Melitideae, Megachilidae, Andrenidae, Halictidae, Stenotrididae and the Colletidae families (Danforth *et al.* 2013; Hedtke *et al.* 2013). The Apidae family,

bearing the domestic bee (*Apis mellifera*) is divided into the Mediterranean and the Western European honeybees ("M" lineage); the North Mediterranean honeybees ("C" lineage); the African honeybees ("A" lineage); the Oriental bees ("O" lineage), and the Ethiopian subspecies ("Y") lineage (Ruttner, 1988; Alburaki et al. 2011). The African honeybees derive from the migration and evolution of the Western honeybee (*Apis mellifera*), which evolved into *adansonii*, *capensis*, *intermissa*, *lamarckii*, *littorea*, *major*, *monticola*, *scutellata*, *unicolor*, *sahariensis*, *simensis*, and *jementica* races with many ecotypes (Ruttner, 1992, Meixner et al. 2011; Hedtke et al., 2013).

According to Villière (1987) and Ruttner (1992) *Adansonii* is widespread and established in the entire Central and Western Africa ecoregions and the honeybee populations of Benin were also classified as *adansonii* race based on morphometric measures. But deeper genetic and morphometric analyses revealed that the honeybee populations in Benin are made up of *adansonii*, *scutellata*, and *iberiensis* genotypes distributed in the benino-dry tropical, the benino Sudanian and the benino-Sudano-Guinean ecotypes under the prevailing bioclimatic conditions of the country (Hounkpe et al. 2006; Amakpe et al. 2015, Gebremedhn et al. 2024).

As any living organism, the honeybees in Benin, are submitted to the biotic and abiotic stresses to which they interact and adapt through morphometric, ethological and behavioural strategies (Matheson, 1996; De Jongh et al. 2022). As found by Abou-Shaara et al. (2017), Southwick & Heldmaier (1987); Beshers (2001), the honeybee colony optimum temperature ranges between 32 °C and 36 °C and high humidity are linked to diseases. Therefore, extreme temperature, humidity and precipitation expected from climate change may lead to a shift of habitat in addition to the adaptation strategies (Becsi et al. 2021; Hosni et al. 2022). As such the honey bee populations in Benin are under permanent geospatial and climatic factor that potentially determine their past, present and future distribution, performance, and strategic adaptation.

At the regional and international levels, the impacts of climate change on the global beekeeping and pest distribution are well documented for the western, mediterranean, south, and East African beekeeping (Ali et al. 2023; Zapata-

Hernandez, 2024; Gebremedhn et al. 2024; Skendzic et al. 2021). But the specific impacts on the honeybee races are poorly covered and almost no relevant publication on climate change impacts on Beninese beekeeping is available (Zapata-Hernandez et al. 2024). Ignoring this specific west African ecoregion where the savannah reaches the Atlantic Ocean coast constitutes a limit for designing and modelling operational approaches for a sustainable worldwide beekeeping and pollinator conservation. This research filled this gap by evaluating the impacts of the past and future climatic conditions on the potential habitat distribution of *adansonii*, *scutellata* and *iberiensis* races of *Apis mellifera* in Benin. Using the geographic positions of these honeybee races (Amakpe et al. 2018) our investigations determined their habitat distribution in 1970-2021 and 2040-2070 horizons prevailing environmental conditions.

## 2. Materials and methods

### 2.1 Study area

The study covered the entire Republic of Benin, a West African Country of 114,760 km<sup>2</sup>. It shares borders with the Republics of Togo, Burkina-Faso, Niger, Nigeria and bears 150 km coast line with the Atlantic Ocean in the south (figure1). According to Akoegninou et al. (2006), the country is characterised by a sub-littoral climatic area from the coast to the 7<sup>th</sup> parallel. From the 7<sup>th</sup> to the 9<sup>th</sup> parallel stands the transitional tropical humid climate while the dry tropical climate stands above the 9<sup>th</sup> parallel.

The honeybees are nationwide distributed, and naturally nest in termite moulds, rock cavities, and trees from which smarms are usually captured by beekeepers in baited hives (Yedomohan et al. 2012). The genetic characterisation of the honeybee populations indicated that they are made up of *adansonii*, *scutellata* and *iberiensis* races (Amakpe et al. 2018). Their specific adaptations to the different ecologic conditions of the country lead to three ecotypes which are i) the giant bees in the extreme north, ii) the small sized bees located in the southern parts, and iii) the intermediate sized honeybees between these two opposite morpho ecotypes (Amakpe et al. 2018). The distribution of these races helped establish the genetic cartography

of the Beninese honeybee races that serves as occurrences of this study (table 1 and figure 1).

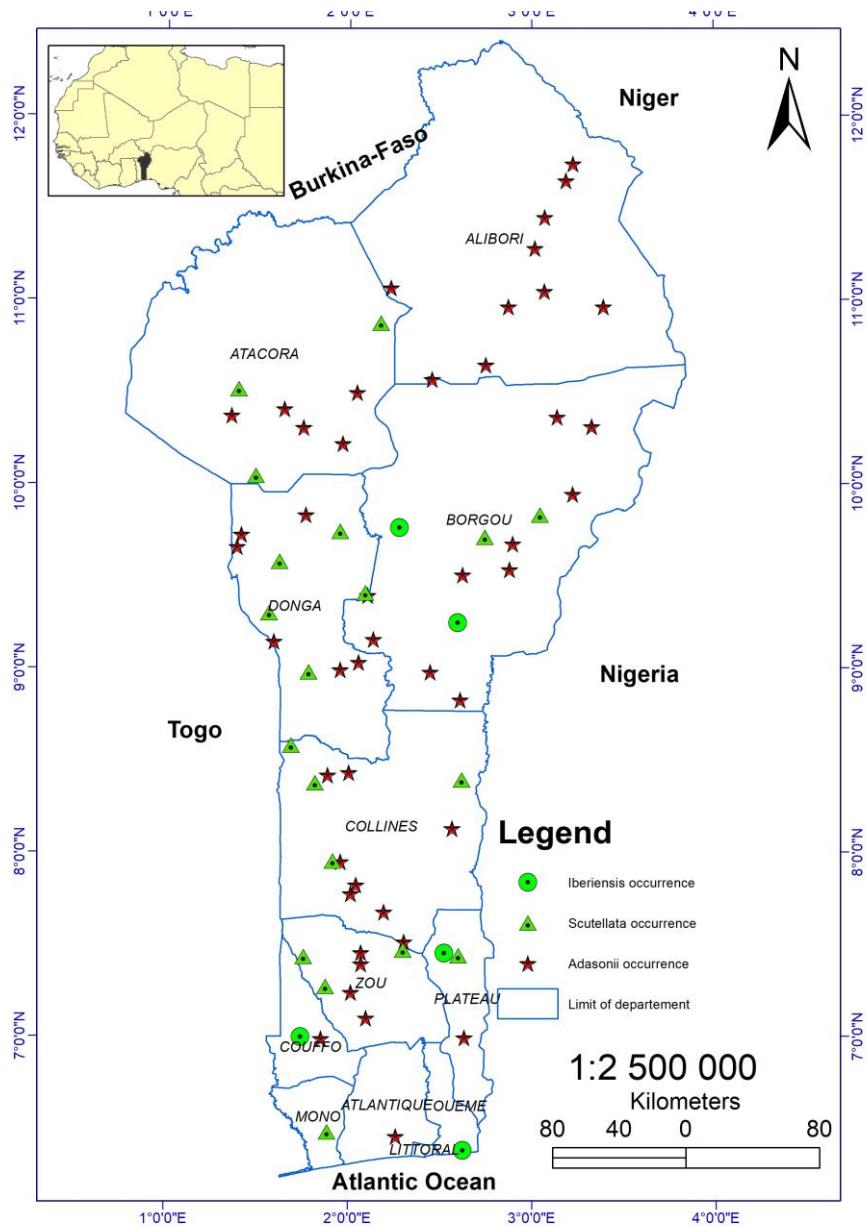
## 2.2 Occurrence data

The GBIF database presented some occurrence points for *Apis mellifera* in Benin. But these data are limited to the studied apiaries with no validated metadata for distinguishing the different races. These investigations were then based on the nationwide genetic characterisation of the honeybees in Benin of Amakpe et al. (2018) who sequenced the mtDNA region including the tRNAleu gene, the COI-COII intergenic region and the 5' end of the COII subunit gene of honeybees in the entire country. 44 colonies were of *adansonii* race, 19 were *scutellata* and only five (5) colonies were classified as *iberiensis* race (table1, figure 1). The geographic position of the colonies served as the occurrence training field points from which the environmental parameters were extracted for modelling the past and future potential distribution range of the three races. The geographic coordinates of the occurrence are presented as supplementary material 1.

The distribution of the honeybee hives was impacted by beekeeping system as the apiaries are established by beekeepers. But beekeeping system in Benin is mainly based on natural swarms that are caught from the nearby natural colonies (Amakpe et al. 2018). The investigated apiaries from which the race occurrence data were obtained represented then the habitat of the bee colony and are representative of the climatic and edaphic optima of the targeted race.

**Table 1:** Distribution of the race occurrence per department in Benin

Race	Alibori	Atacora	Borgou	Collines	Couffo	Donga	Mono	Oueme	Plateau	Zou	Total
<i>Adansonii</i>	10	4	9	8	1	7	0	0	1	4	44
<i>Scutellata</i>	0	2	0	4	0	5	1	0	1	3	16
<i>Iberiensis</i>	0	0	2	0	1	0	0	1	1	0	5
Total occurrence	10	6	11	12	2	12	1	1	3	7	65



**Figure 1:** Geographic occurrence of the focused honeybee races in Benin

### 2.3. Past and future environmental modelling parameters

The environmental data for predicting the suitable geographic distribution of habitat and species were analysed by Platt et al. (2014) and a total of 19 variables are commonly used. Some are highly correlated and we based the analyses on variables with very low multicollinearity (Warren et al., 2010; Fandohan et al. 2016, Toffa et al. 2022). In the same line, data presenting discontinuity for Benin (Biaou et al. 2023) were also discarded. The queen laying capacity, the life span of workers and their foraging performance are highly determined by seasonality and aridity

parameters (Abou-Shaara et al. 2017; Cornelissen, et al., 2019; Skendzic et al. 2021; Gebremedhn et al. 2024). The analyses were finally based on four temperature and aridity (pluviometry) parameters which were less correlated and best determine nectar and pollen producing plants species, honeybee pests' distribution, and their susceptibility to colony collapse disorder (Mwakapeje et al. 2019; Platts et al. 2014; Odony et al. 2019; Toffa et al. 2022). The temperature variables were the temperature seasonality standard deviation over monthly values (Bio4) and the potential evapotranspiration (PET). The pluviometry parameters were the Moisture index moist quarter (MIMQ) for any consecutive three (3) months periods, and the Length of longest dry Season (LIDS in months).

The baseline data covered an average term of 30 year, from 1990 to 2021 which covered the periods of most beekeeping development projects in Benin (Ahoudjinou et al., 2012). Regarding the future environmental data, SSP 1–2.6, SSP 2–4.5, SSP 3–7.0, SSP 5–8 were the validated scenario of the WorldClim. Among them, SSP 2–4.5 (2041 to 2070) is considered as the most realistic and most reflective to the current political and economic trends according to the United Nations framework of global challenges in agriculture and food of agenda 2063 for Africa (Arias et al. 2021; Asamoah et al. 2025; Kabato et al. 2025). Therefore, the predictive future environmental data we used covered the mid-century 2055 term average period, from 2041 to 2070 (Platts et al. 2014). These data were based on the ensembled representative concentration pathways of IPCC-AR5 at 30s (1.0km<sup>2</sup>/pixel) resolution. They were downloaded from the York University web site at [www.york.ac.uk/environment-geography/research/kite/resources/](http://www.york.ac.uk/environment-geography/research/kite/resources/). The specific environmental data of Benin were extracted from the global African GeoTIFF files and converted to the ASCII format of R using the “1a.Extract by mask” and the “2b.Raster to ASCII” of the Species Distribution Model (SDM) tools of Arc ArcMap 10.1 at the same 30' pixel resolutions for their use in Rstudio (Elithn & Leathwick, 2009; Merow et al. 2013; Kass et al. 2022).

### **2.3 Data analysis and habitat prediction**

First, we extracted and prepared the environmental data at the same extent, same spatial resolution, and reported them to the same WGS84 geodesic projection using

the "crop", "resampl" and "mask" functions of RStudio and used the maximum entropy (MaxEnt) in accordance with Okely et al. (2023) for other bee species distribution. As a presence alone model, MaxEnt considers a list of species presence-alone locations as input, integrates the set of environmental factors in the targeted ecological area that is divided into grid cells and a sample of background locations is extracted from this landscape. The extracted sample which is independent to the presence-alone ones are contrasted to the environmental baselines or predictive considered environmental parameters (Elith & Leathwick, 2009; Meraw et al. 2013; Fithian & Hastie, 2012). This model requires few presence-alone records for habitat distribution as in our case where the race occurrences were very limited. The habitat distribution model from the dismo package of R was used for predicting the suitability of the baseline environmental covariate location by assimilating each race occurrence to its "presence-alone" event. This helped determine a natural probabilistic interpretation with a gradation ranging from highly to least or favourable environmental conditions to each race (Phillips et al. 2008; Tesfamariam et al. 2022, Okely et al. 2023).

The delineation of suitable potential habitat of the targeted race from unsuitable areas was done by setting a 10<sup>th</sup> percentile training presence threshold ( $\beta$ ) that represented the probability that 90% of the pixel centres were located in the delimited geographical area (Phillips & Dudik, 2008; Elith & Leathwick, 2009; Merow et al. 2013; Moukrim et al. 2018).

The past and potential future distribution areas of each race were analysed by three probability (P) distribution classes in relation to the set threshold as follow (Moukrim et al. 2018; Toffa et al. 2022):

- Highly favourable habitat for pixels with  $P \geq \beta$ ;
- Moderately favourable habitat for pixels with  $\frac{1}{4}\beta \leq P < \beta$ ;
- Non favourable habitat for pixels with  $P < \frac{1}{4}\beta$ .

From these three distributions we determined the suitable versus non suitable areas for the considered race by adding its highly favourable and moderately favourable areas (Gahounga et al. 2025).

The generated maps from RStudio were saved as Geotiff which were projected in ArcMap10.1 for elaborating the distribution maps of each race. ,The corresponding covered areas (ha) was determined using the geometry calculation tools.

The dynamics from 1990 to 2070 was analysed by the difference between the covered area (d) of future and past distribution area and the difference between the proportion of these values over the total covered area of the Republic of Benin (Dp%) using the following equations.

$$d=Cf-Ch \text{ and } dp\%=(Cf/S)-(Ch/S).$$

d= dynamic between the historic and future covered area of the considered suitable area of the considered race.

cf: future predicted value of the considered area of the targeted race

ch: historic value of the covered area of the targeted race

dp%: proportion of the distribution area over the national total area

S total covered area of the Republic of Benin (14760km<sup>2</sup>)

## 2.5 Model accuracy and performance

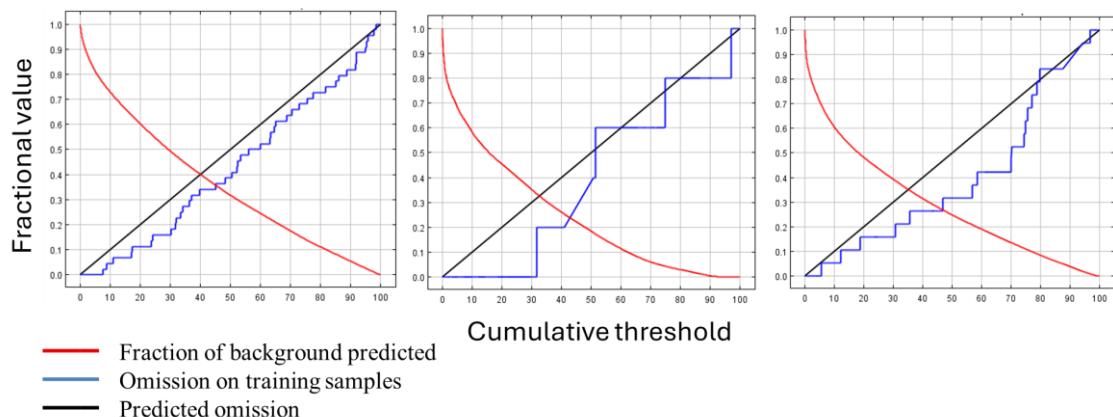
The algorithms converged after 240 iterations for the *adansonii* race distribution analyses, 160 for the *scutellata* and 100 for the *iberiensis* race generated with 116988 training background points. The area under the receiver operating characteristics (ROC) curve (AUC) was first used for evaluating the model accuracy. This varies from 1 for successful model to 0.5 for randomized ones and values above 0.7 are for good and robust models (Hanley & McNeil, 1982, Lobo et al. 2007; Phillips & Dudik, 2008). The contribution of each environmental predictors in the model was evaluated by the jackknife test. The specific effects of each environmental variable on the MaxEnt prediction and how the prediction changes with each environmental

variable average sample value were analysed by the response curves of each parameter. The MaxEnt model performance was also evaluated by the test omission rate. This is good and different from the randomized classification when the omission rate curve is close to the predicted omission line (Ramírez-Rodríguez et al., 2025).

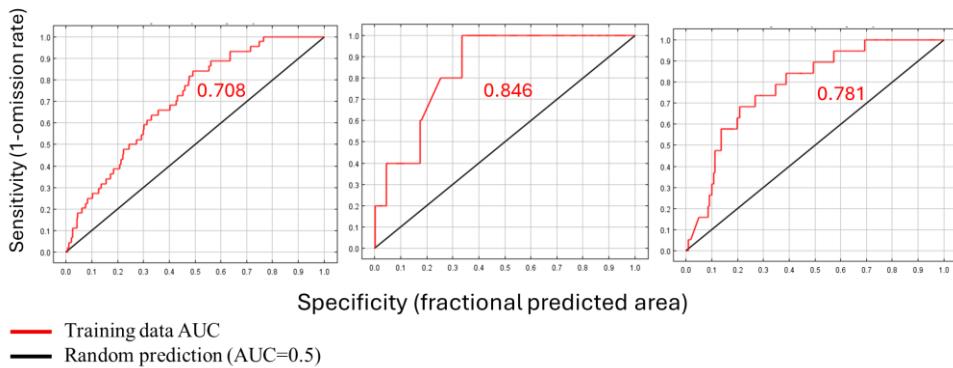
### 3 Results

#### 3.1 Model quality and performance in determining the honeybee races distribution area in Benin

The average probability of presence over background pixels was 0.541 for the *adansonii* race, 0.453 for the *scutellata* and 0.346 for the *iberiensis*. This indicated that the prevalence of each species is low in the country at the past and projected future. The omission rate and predicted area function of the cumulative threshold (figure 2) curves showed that the omission rate line was closest for the *adansonii* race. The AUC are all higher than 0.7 with the highest value (0.82) achieved for the *iberiensis* race predictions (figure 3). The power of the MaxEnt model prediction of the historic and future potential suitable distribution of the honeybee races in Benin is then strongly acceptable. But, with a higher AUC, the *iberiensis* modelling showed a more irregular omission line, indicating that this race which was restricted to the south of the country was race with very limited spatial distribution potential.



**Figure 2:** figure 2 Omission and predicted area for adansonii (left), iberiensis (centre) and scutellata (right)



**Figure 3:** Area under curve for *adansonii* (left), *iberiensis* (centre) and *scutellata* (right).

### 3.2 Contribution of each environmental variable to the model performance

The estimates of the contribution of the difference variables depended on the targeted race (table1). In fact, pet had the highest contribution to the model for *adansonii* (58.88 %); bio4 had the highest contribution for *scutellata* and *iberiensis* with 59.71 % and 35.95 % respectively. The lowest contribution to the model was obtained with mimq for the *adansonii* and *scutellata* races (0.38 % and 2.52 %) and pet for the *iberiensis*. This indicated that pet had almost no impact on the distribution of *iberiensis* race in conjunction with the other environmental parameters and poorly impacted the *scutellata*. On the other hand, it highly determined the past and future potential distribution areas of *adansonii* race.

When considering pet and bio4 which had the highest contribution to the model (table 1 and figure 4), the occurrence probability of *adansonii* exponentially increased from 0 to 12mm values of bio4 followed by a slight increase from 12 to 21 mm. It also highly increased from 21 mm before reaching its maximum values from 24 mm. As far as the pet was concerned, the occurrence probability of *adansonii* was maximum with values ranging from 1200 to 1900 mm. The occurrence probability of *scutellata* and *iberiensis* on the other hand had similar responses. The increase in bio4 negatively impacted the occurrence that dropped as a Goss curve till the lowest values from 22 mm. This occurrence probability was poorly impacted by the pet while an increase in llds and mimq values had contradictory impacts on the occurrence of these two races in Benin.

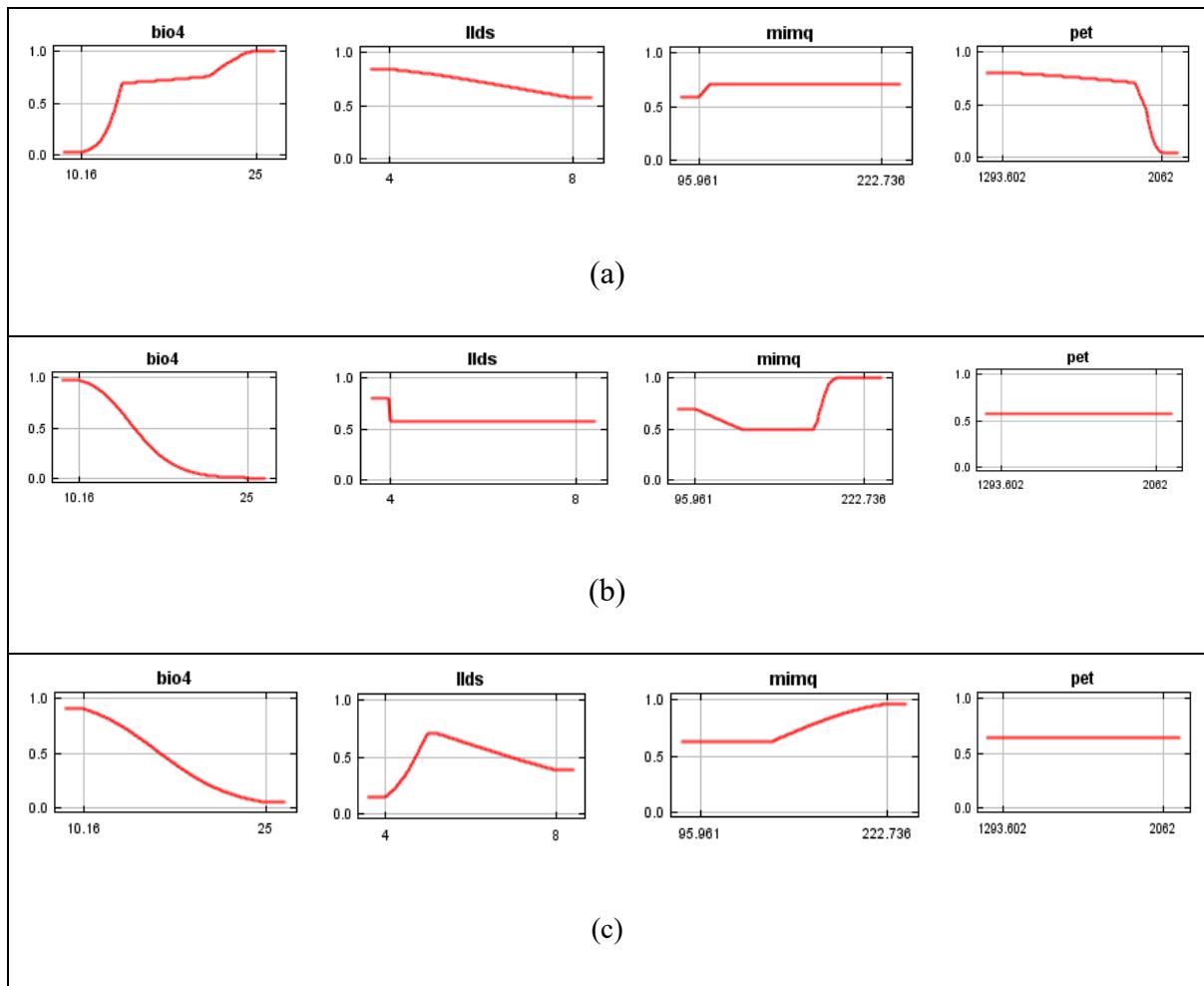
The analysis of the specific impacts of each parameter alone in the ecological area indicated that Bio4 had similar impacts as when the other parameters were kept at their optimum (figure 2.2). But Pet that only impacted the *adansonii* distribution in conjunction with the other parameter had high impact when considered alone on the three races distributions. The optimum environmental ranges for the three races proved that they could share limited ecological areas in Benin. In fact, the optimum pet values for *Adansonii* race ranged from 1600 to 1900 mm, the *scutellata* race would best support any value bellow 1900 while values below 1600mm were optimum for *iberiensis* population.

The permutation that indicated the loss of precision when omitting the environmental parameters showed that bio4 is key in modelling the three races even if it was not the most determinant distribution factor. llds poorly reduced the model performance when omitted for the *adansonii*, while pet was the one poorly reduced the distribution accuracy for *scutellata* and *iberiensis* when omitted (table 2, figure 5).

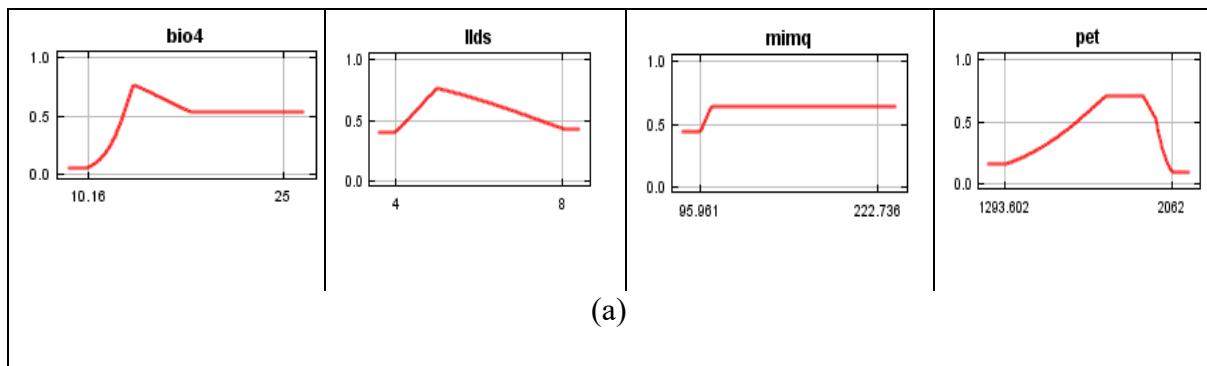
**Table 2: MaxEnt analysis outputs**

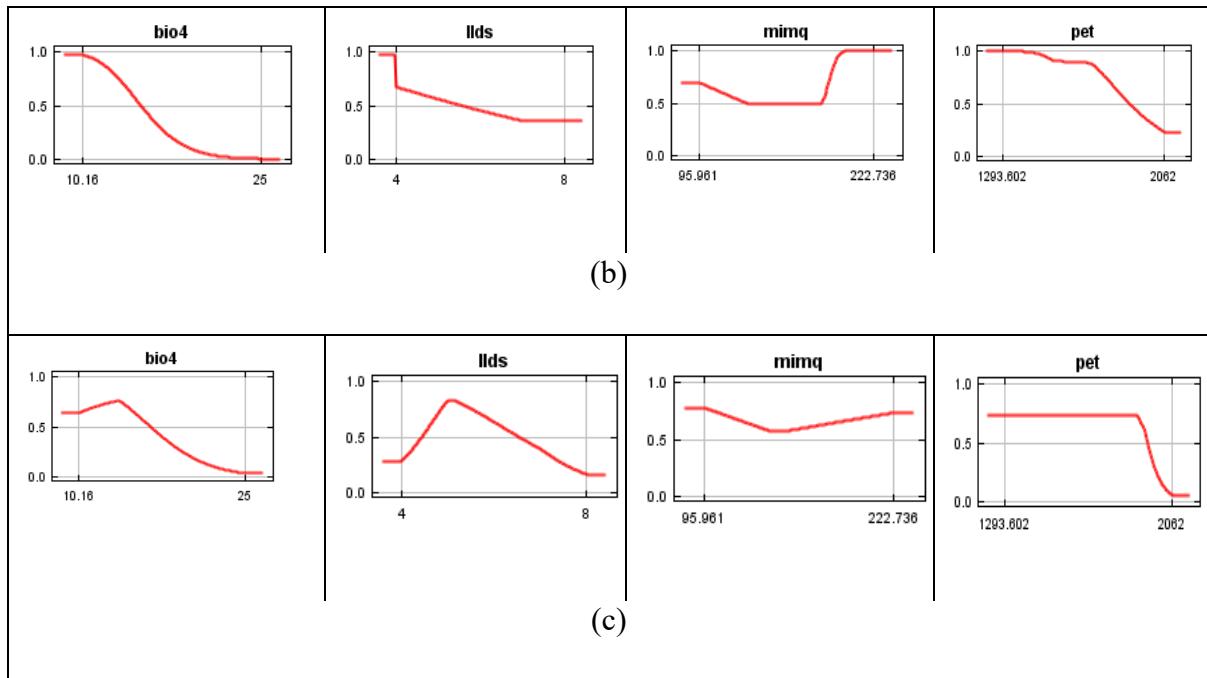
NB: Number of backgrounds points, race; bio4: llds: mimq; pet: cont: contribution; perm permutation, import: importance; AUC: area under curve

Race	AU C	bio4 cont	llds cont	mim q cont	pet cont	bio4 perm impor	llds perm impor	mimq perm impor	pet perm impor	Prevalenc e
<i>Adansonii</i>	0.7 0	34.2 1	6.51	0.38	58.8 8	72.11	0.00	0.70	27.17	0.54
<i>Scutellata</i>	0.7 8	59.7 1	29.6 6	2.52	8.09	51.11	28.81	20.06	0.00	0.45
<i>iberiensis</i>	0.8 4	46.1 6	35.9 5	17.8 8	0.00	93.76	5.52	0.70	0.00	0.34



**Figure 4:** Contribution of each environmental factor to the MaxEnt model when the other ones are kept at their optimum. (a) responses of *adansonii*, (b) responses of *iberiensis*. (c) responses of *scutellata*





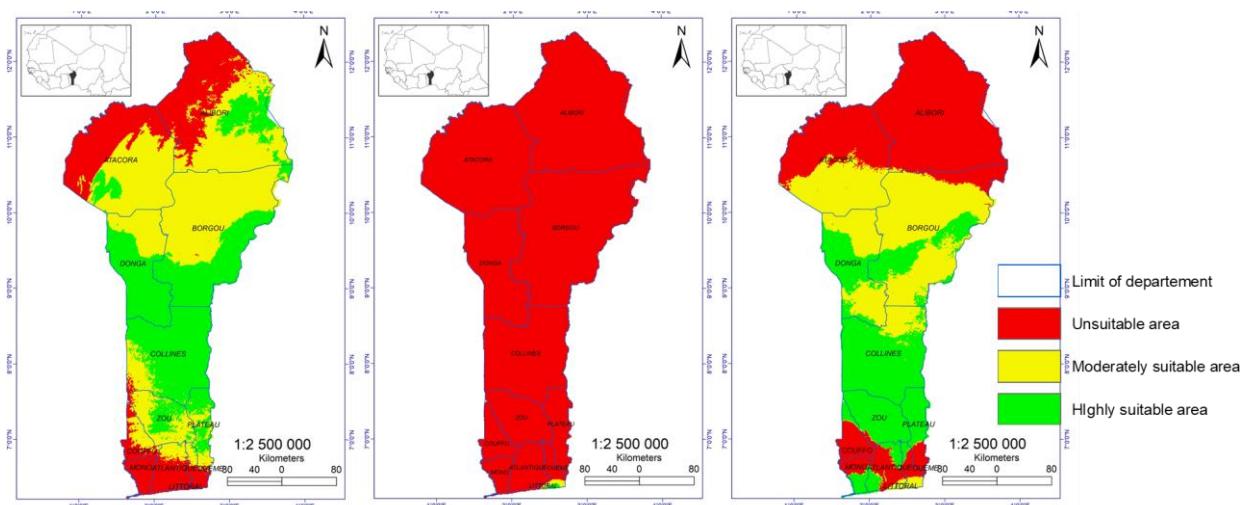
**Figure 5:** Estimated specific contribution of each factor, excluding the interaction of the other ones  
 (a) responses of *adansonii*. (b) responses of *iberiensis*, (c) responses of *scutellata*

### 3.3 Historic habitat distribution of *adansonii*, *iberiensis*, and *scutellata* honeybee races in Benin

The historic distribution ranges of the races indicated that each race had specific potential favourable areas with *iberiensis*, the most restricted honeybee race in Benin (table 2 and figure 6). In fact, its potential distribution area was retracted in a tiny part of only 0.43 % of the national territory located in the East Guineo-Congolian region of the south Benin. This region also benefits from a high rainy season with low Pet values that makes it the poorest honey region in Benin. The *adansonii* race had a larger distribution area where 75.94 % of the country territory was favourable to this race. Its highly suitable area was located in the Sudanian zone from the 7<sup>th</sup> to the 9<sup>th</sup> parallel. There were also some isolated locations in the north East and the central north West. The moderately suitable areas were located in the entire central north covering the department of Alibori, Borgou, Atacora and north Donga. The north unsuitable area was located in the national parcs regions along the borders of Burkina Faso and north Togo. The south unsuitable area to this race covered the departments of Mono, Oueme, Couffo to the borders of the Republic of Togo with

the department of Zou, and Couffo in the Sudano Guinean and the littoral climatic area.

Regarding the *scutellata* race, the entire northern part of the country including the entire department of Alibori and north Atacora are unsuitable area. In the south, the race showed some highly suitable area in the south West in contact with Atlantic Ocean. Above this particular area stood a large unsuitable area that covered the department of Couffo, Mono, Oueme while the Atlantic department is moderately suitable. The unsuitable area covered 37.29 % of the national territory while the moderately suitable distribution area represented 39.93 % of the national territory and was mainly distributed in the north Sudano dry tropical areas. The highly suitable distribution area for this race (28.79 % of the national territory) seemed overlay the one of *adansonii* in the Sudano-Guinean region.



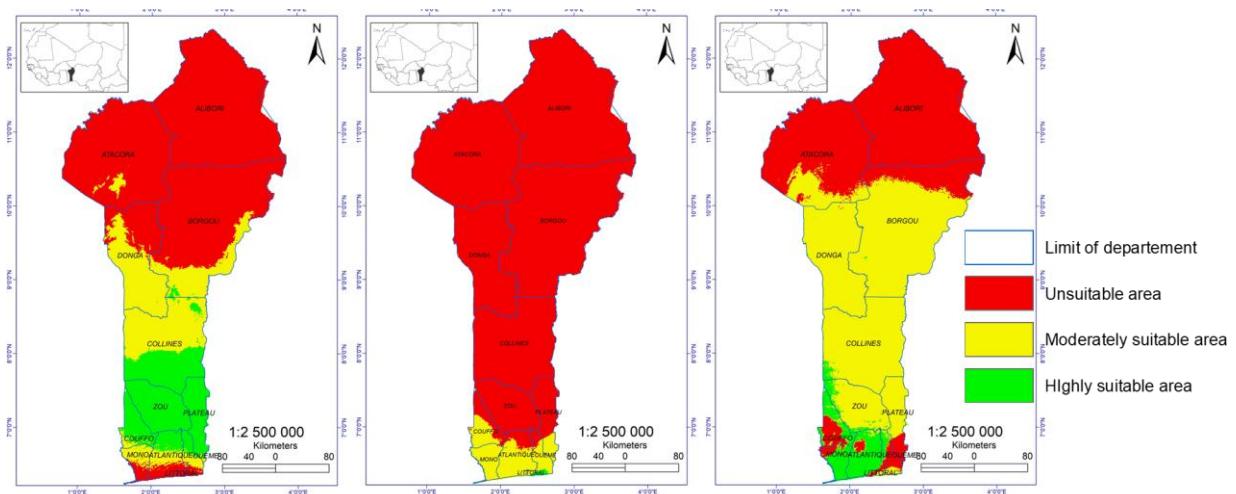
**Figure 6:** Historic potential distribution area of *adansonii* (left), *iberiensis* (centre) and *scutellata* (right) races in Benin

### 3.4 Future potential habitat distribution of *adansonii*, *iberiensis* and *scutellata* races in Benin

The 55-year term predicted a global degradation of the habitat conditions in the north which was predicted to become unsuitable area to the three races (figure 7 and table 2). The predicted future environmental conditions will particularly become hard to the *adansonii* which will lose 35.77 % of its favourable area. The *scutellata* will only register such drop in its highly suitable area that will be converted to 19.69 % of

moderately suitable area and 2.99 % of unsuitable area. *iberiensis* on the other hand will gain in its suitability. In fact, 7.04% of is unsuitable area was predicted to evolve in 6.99 % of moderately suitable area and 0.05 % of highly suitable area in 2055 horizon when larger southern parts were predicted to become favourable for *scutellata* race.

The predicted distribution of the suitable area indicated that the *adansonii* niche will shift to the central parts of the in the Sudano Guinean climatic area. The highly suitable areas for the *scutellata* race seemed more restricted to the southern central western parts excluding the border of the department of Couffo with the Republic of Togo. Though a niche expansion was predicted for the *iberiensis*, it will stay restricted to the eastern costal part of the country and its favourable distribution areas will not exceed the 7<sup>th</sup> parallel.



**Figure 7:** Future potential distribution area of the *adansonii* (left) *iberiensis* (centre) and *scutellata* (right) races in Benin

**Table 2:** Dynamics in the habitat distribution ranges of the three honeybee races in Benin

Race	Parameters	Unsuitable area	Moderately suitable area	Highly suitable area	Favourable area
	Historic covered area km <sup>2</sup>	27615,58	49699,79	37444,63	87144,42
	Historic % of Benin	24,06%	43,31%	32,63%	75,94%

Adanso nii	Future covered area km <sup>2</sup>	68659,75	26119,09	19981,15	46100,25
	Future % of Benin	59,83%	22,76%	17,41%	0,40
	Area dynamics km <sup>2</sup>	41044,18	-23580,70	-17463,48	-41044,18
	Dynamics %	35,77%	-20,55%	-15,22%	-35,77%
	Historic covered area km <sup>2</sup>	42790,49	38935,28	33034,23	71969,51
	Historic % of Benin	37,29%	33,93%	28,79%	62,71%
Scutella ta	Future covered area km <sup>2</sup>	46218,71	61536,92	7004,36	68541,29
	Future % of Benin	40,27%	53,62%	6,10%	59,73%
	Area dynamics km <sup>2</sup>	3428,23	22601,64	-26029,87	-3428,23
	dynamics %	2,99%	19,69%	-22,68%	-2,99%
	Historic covered area km <sup>2</sup>	114267,39	354,89	137,72	492,61
	Historic % of classified	99,57%	0,31%	0,12%	0,43%
Iberiens is	Future covered area km <sup>2</sup>	106191,13	8376,75	192,13	8568,87
	Future % of Benin	92,53%	7,30%	0,17%	7,47%
	Area dynamics km <sup>2</sup>	-8076,27	8021,86	54,41	8076,27
	Dynamics %	-7,04%	6,99%	0,05%	7,04%

## 4 Discussion

### 4.1 Environmental factors and the potential distribution ranges for the three races in Benin

The receiver operating characteristics (ROC) area under the curve (AUC) values we found was in range of most species and biological entity distribution using the MaxEnt model (Redon & Luque, 2010; Favi et al. 2022; Anderson et al. 2023). This indicated a good performance in delineating the suitability areas of the three races

which was different from a randomised distribution. The temperature and pluviometry environmental factors we used are then effective in predicting the past and future potential distribution area of the three honeybee races as also found for other species by Gabglo et al. (2017), Dasso et al. 2024 and Toffa et al. (2023) in Benin. Despite a lower AUC value for the *Adansonii* and *scutellata* races modelling, they had very good omission curve trend, indicating that the two races had broader distribution area than the *iberiensis* that is restricted to the south east extremity of Benin.

The differences in the past favourable area of the three races indicated their specific adaptation or responses to the baseline environmental conditions in Benin. The predicted extremes values of most environmental factors for the Sub-Saharan Africa by the middle century will impose specific responses of the Hymenoptera species or populations to climate change at regional or local scales (Odevn et al. 2019; Okely, 2023). The northern future conditions were predicted to negatively impact the three races habitat while they show contradictory range in the south. In fact, the coastal line was predicted to be unsuitable to *adansonii* in contrast to *scutellata* and *iberiensis*. The predicted shift and restriction of *scutellata* and *iberiensis* to the south-east extremity country proved that these two races would be threaten in the future as their predicted favourable areas are located in the poor honey region with rare apiary that may sustain the bee establishment (Amakpe et al. 2015; Yedomohan et al. 2012). With such very poor beekeeping potential, the natural colonies will be challenged as a consequence of the global environmental degradation on wood, termite huts, and natural cavities in which they may nest.

The honeybees rely on floral resources in the ecological patch and this supports their intimate dependence on the melliferous plant species distribution (Filipiak et al, 2017; Wright et al. 2018; Zapata-Hernández et al. 2024). Living in the same floral resource potential in the country (Yedomohan et al, Amakpe et al. 2015) the three races should have superposable distribution area, linked to the phytogeographic areas. But their showed specific past and future niche distributions (Adomou et al. 2007). Therefore, their establishment and distribution in the country were and will be determined by more complex environmental factors with specific impact on each

race niche beyond the melliferous flora distribution and apicultural system (Alemou et al. 2014 ; Mahhammadian et al. 2024; Singh & Rana, 2025).

#### **4.2 Implications of the niche shift and restriction for the races**

The global drop of the suitable distribution areas is conform to the findings of many other researches on the honeybee and other species or populations to which the environmental factors is predicted to become more challenging in face of climate change (Gebremedhn et al. 2024; Ali et al. 2023; Johnson et al. 2023). This is particularly true for *adansonii* and *scutellata* races in the Benin which will lose 15 % to 22 % of their highly suitable areas in the coming 55 years. In addition to the direct impact of the environmental factors on the bees, the projected negative impacts of climate change on the flora through frequent severe drought, extreme temperatures, and floodings will hinder the availability and diversity of melliferous plants and reduce the bee foraging capacity (Wright et al. 2018; Tadesse et al. 2021). On the other hand, pressures from pesticides and land clearing are also key colony collapse disorder factors that will undermine beekeeping in the entire country (Ellis et al. 2010; Hailu et al. 2024).

The analysis of the dynamics of the distribution areas indicated that *iberiensis* was the least impacted by the past and future environmental conditions which are predicted to improve the for this race. But the total favourable area for this race was less than 7.30 % of the territory and located in the most populated areas with limited beekeeping potential (Amakpe et al. 2015). The global limited present and future niche for *iberiensis* supported its recent introduction in the southern Benin. In fact, *iberiensis* is the Spanish bee, native to the Iberian Peninsula (Franc et al. 1998). Though it belongs to the African honeybee lineage, its presence the West African regions seem be linked to introductions from Spanish beekeepers during colonial period (Franck et al. 1998; Tihelka et al. 2020). As such, it will be very difficult to value this race for a sustainable beekeeping in Benin despitess all its proven performance in the European beekeeping. It will definitely disappear in favour of the *adansonii* and the *scutellata* races that had wider suitable distribution range.

*Adansonii* race is widespread honeybee race in the tropical and semi-arid ecoregions of the entire western Africa from Senegal to Nigeria, the Congo basin and towards the south of Chad and Congo Bassin (Ruttner, 1988). Despite this large natural distribution area, our finding proved that the south west region and the north west regions were unsuitable to this race in the past. The unsuitability of the coastal part to this race was conclusive to the finding of Borst (2015) who reported that humid climatic conditions are not suitable for *adansonii*. The entire Sudanian region was predicted to become unsuitable as the south coastal part. The shift and restriction of the favourable area to the Sudano-Guinean region indicated that *adansonii* race in Benin requires more stable environmental conditions than the one prevailing in the extreme south and north of the country (Akouegninou et al. 2006). As This region also bear good melliferous plant distribution and the highest beekeepers' population, the future beekeeping in Benin will be dominated by *adansonii* race which also share favourable areas with *scutellata*

*Scutellata* race is native to central, southern and eastern Africa (Ruttner, 2008). Its high distribution in Benin where beekeeping is based on natural swarms (Yedomonhan et al. 2012) supported the underestimated natural origine of this race. Though it had smaller highly suitable distribution area than *adansonii*, the two races share the same future potential niche above the 7<sup>th</sup> parallel. The overlaps of their suitable distribution area in the central and southern parts implies a better diversity available for beekeeping in these regions which were also the best beekeeping areas in Benin (Yedomonhan et al. 2012).

#### **4.3 Adaptation and interracial crossing possibilities in the distribution range**

Our investigation proved that the potential past, present, and future distribution ranges of each race is determined by the prevailing environmental factors. But species are under permanent adaptation and potential mutation processes that modulate their population towards a biological dynamic equilibrium (Chevin & Bridle, 2025; Lurgi & Pascual-García, 2025; Zuchang, 2025). The adaptation would lead to specific phenotypic plasticities, and genetic responses for surviving in the hard living conditions from the climate change, anthropogenic destruction factors, pests and diseases pressures (Garland 2006; Pigliucci, 2004) which are likely to

impact the predicted distribution area and the niche stability of each race (Qian & Akçay, 2020; Lurgi & Pascual-García, 2025). But adaptation strategies require structural sustainable ethologic, phenotypic, and genetic modifications which may occur in a progressive worsening of the environmental conditions through natural selection and mutations (Lurgi & Pascual-García, 2025). Even though the domestic bee has a short generational turnover, the 2055 horizon could be insufficient for adaptation strategies to present tangible measurable phenotypic traits on each race for establishing in the modified climate change anthropic landscapes. In fact, the environmental conditions that only serve as inducing factors are not alone, efficient promotor of biological entities evolution in the complex ecologic landscape (Zuchang, 2025).

Beside the mutation and adaptation strategies, the niche overlaps provide an interracial crossing environment in which high hybridization will occur in the shared niches. For that, the three races presented specific hybridization areas (figure xx and xx). The south-East of the Guineo-Congolian regions fits the hybridization area for *scutellata* and *iberiensis* races while the Sudano-Guinean regions between the 7<sup>th</sup> and 11<sup>th</sup> parallels are potential hybridization area for the *adansonii* and *scutellata* races. The high gene flows in these hybridization areas represent strong adaptation factor in face of the climate change and other environmental challenges (Lynch & Conery, 2000; Zuchang, 2025). The north extremity of the country was predicted to stay poorly favourable to the three races and will not benefit from the interracial gene flow. In absence of mutation and special adaptation strategies, only beekeeping would sustain the survival of the honeybee populations in this area through high inputs to compensate the environmental weaknesses in these areas.

## 5. Conclusions

Our results showed that climate change was predicted to have specific impacts on the potential niches of the three honeybee races of Benin. While *adansonii* and *scutellata* niches will shift and shrink to the Sudano-Guinean regions, the *iberiensis* is predicted to have limited viability in the past and future challenging environmental conditions. The central parts seemed the best past and present beekeeping regions in Benin and such potential need to be improved by strong capacity building programs for the

involved actors in apiary management and securing the bee landscapes, hive products quality and marketing. On the other hand, the poor status of the northern regions for all three bee races in the future is of great concern regarding the sustainability of beekeeping and pollinator services in these fragile ecosystem areas in Benin. The same situation was predicted in the southern parts with its high population density and poor land use system. Beekeeping in these two extremities of the country requires then specific operational strategies for securing a better floral availability, friendly agricultural system and greener urbanization that fully integrate bees and pollinator habitats. This will also require deeper long term researches programs for developing drought, diseases and pesticides tolerant honeybees for a sustainable beekeeping in face of the worldwide climate change hazards.

The model successfully predicted the potential niche distribution of the three honeybee races in Benin with the key environmental factors. But beekeeping is also determined by the managerial capacities of beekeepers. The establishment of a particular race in a landscape is also highly determined by its introduction and the care it receives from the beekeepers. Such factors will act as selection systems that favour targeted races against neglected one. Modelling the future distribution area of honeybee race in an area should then integrate more complex factors such as race preference, their productivity and available knowledge on the race in addition to the bioclimatic factors we usually focused on.

## 7. Reference

1. Abou-Shaara HF, Darwish AAE. 2021. Expected prevalence of the facultative parasitoid *Megaselia scalaris* of honey bees in Africa and the Mediterranean region under climate change conditions. International Journal of Tropical Insect Science. 41: 3137–3145. <https://doi.org/10.1007/s42690-021-00508-5>
2. Adomou AC, Sinsin B, Akoègninou A, Van der Maesen LJG. 2007. Les patrons de végétation et gradients environnementaux au Bénin: Implications pour la biogéographie et la conservation. Notes of the Laboratory of Applied Ecology, 1 : 1-17.

3. Akoegninou A, Van der Burg WJ, Van der Maesen LJJ, Adjakidjè VJPE, Sinsin B, Yédomonhan H. 2006. Flore analytique du Bénin, Backuys Publishers, Leiden, the Netherlands.
4. Alburaki M, Moulin S, Egout H, Alburaki A, Garnery L. 2011 Mitochondrial structure of Eastern honeybee populations from Syria, Lebanon and Iraq. *Apidologie* 42 : 628–641 DOI: 10.1007/s13592-011-0062-4
5. Ali MA, Abdellah IM, Eletmany MR. 2023 Climate change impacts on honeybee spread and activity: A scientific review. *Chelonian Conservation and Biology* 18(2) : DOI: doi.org/10.18011/2023.10(2).531.554.
6. Amakpe F, De Smet L, Brunain M, Jacobs JF, Sinsin B, De Graaf DC. 2018 Characterization of the native bee subspecies in Republic of Benin using morphometric and genetic tools. *J. Apic. Sci.* DOI 10.2478/JAS-2018-0006.
7. Amakpe F, Akouehou GS. de Graaf DC, Sinsin B. 2015. Determination of the silvo-melliferous regions of Benin: a nationwide categorisation of the land based on melliferous plants suitable for timber production. *J. Agric. Rural Dev* 116 (2). 143–156. <http://nbn-resolving.de/urn:nbn:de:hebis:34-2015061048473>
8. Becsi. B.. Formayer. H.. & Brodschneider. R. (2021). A biophysical approach to assess weather impacts on honey bee colony winter mortality. *Royal Society Open Science*. 8: 210618. <https://doi.org/10.1098/rsos.210618>
9. Beshers SN, Huang ZY, Oono Y, Robinson GE. 2001. Social inhibition and the regulation of temporal polyethism in honey bees. *J Theor Biol* 213: 461–479
10. Biaou S, Gouwakinnou GN, Noulekoun F, Salako KV, Houndjo KJM, Houehanou TD, Biaou HS. 2023. Incorporating intraspecific variation into species distribution models improves climate change analyses of a widespread West African tree species (*Pterocarpus erinaceus* Poir, Fabaceae). *Glob. Ecol. Conserv.* 45: 02538. <https://doi.org/10.1016/j.gecco.2023.e02538>
11. Borst P.L. 2015. The origin and distribution of honeybees. *Am. Bee J.*, 161: 565–568.

12. Chevin LM, Bridle J. 2025 Impacts of limits to adaptation on population and community persistence in a changing environment. *Phil. Trans. R. Soc. B* 380: 20230322. <https://doi.org/10.1098/rstb.2023.0322>
13. Cornelissen B, Neumann P, Schweiger O. 2019. Global warming promotes biological invasion of the honey bee pest. *Global Change Biology*. 25(11): 3642-3655. DOI: 10.1111/gcb.14791
14. Danforth BN, Cardinal S, Praz C, Almeida EAB, Michez D. 2013. The Impact of Molecular Data on Our Understanding of Bee Phylogeny and Evolution. *Annu. Rev. Entomol.* 58: 57-78
15. de Jongh EJ, Harper SL, Yamamoto SS, Wright CJ, Wilkinson CW, Ghosh S, Otto SJG. 2022. One health, one hive: A scoping review of honey bees, climate change, pollutants, and antimicrobial resistance. *PLoS One*. 17(2): e0242393. <https://doi.org/10.1371/journal.pone.0242393>
16. Elith J, Leathwick JR. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst.* 40: 677-97
17. Ellis JD, Evans JD, Pettis JS. 2010. Colony losses, managed colony population decline and Colony Collapse Disorder in the United States. *Journal of Apicultural Research* 49(1): 134-136. DOI: 10.3896/IBRA.1.49.1.30.
18. Filipiak M, Kuszewska K, Asselman M, Denisow B, Stawiarz E, Woyciechowski M, Weiner J. 2017. Ecological stoichiometry of the honeybee: Pollen diversity and adequate species composition are needed to mitigate limitations imposed on the growth and development of bees by pollen quality. *PLoS ONE*. 12.. <https://doi.org/10.1371/journal.pone.0183236>
19. Fithian W, Hastie T. 2012. Finite-sample equivalence of several statistical models for presence-only data. <http://arxiv.org/abs/1207.6950v1>. <https://doi.org/10.48550/arXiv.1207.6950>
20. Franck P, Garnery L, Solignac M, Cornuet JM. 1998. The origin of west European subspecies of honeybees (*Apis mellifera*): new insights from microsatellite and

mitochondrial data. *Evolution*, 52(4): 1119-1134. doi:10.1111/j.1558-5646.1998.tb01839.x. JSTOR 2411242. PMID 28565209

21. Garland T, Jr, Kelly SA. 2006. Phenotypic plasticity and experimental evolution. *J. Exp. Biol.* 209: 2344–2361 (doi:10.1242/jeb.02244)
22. Gebremedhn H, Gebrewahid Y, Hadgu G, De Graaf D. 2025. Projecting the impacts of climate change on habitat distribution of Varroa destructor in Ethiopia using MaxEnt ecological modeling. *Science of the Total Environment* 968: 178904. <https://doi.org/10.1016/j.scitotenv.2025.178904>
23. Gebremedhn H, Gebrewahid Y, Haile GG, Hadgu G, Atsbeha T, Hailu TG, Bezabih G. 2024. Projecting the impact of climate change on honey bee plant habitat distribution in Northern Ethiopia. *Scientific Reports*, 14(1): 15866.
24. Hailu TG, Atsbeha AT, Wakjira K, Gray A. 2024. High rates of honey bee colony losses and regional variability in Ethiopia based on the standardised COLOSS 2023 survey. *Insects* 15(6): 376. DOI: <https://doi.org/10.3390/insects15060376>.
25. Hanley JA. McNeil BJ. 1982. The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Diagn Radiol.* 143: 29–36. DOI: <http://dx.doi.org/10.1148/radiology.143.1.7063747>.
26. Hedtke SM, Patiny S. Danforth BN. 2013. The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC Evolutionary Biology*: 13:138
27. Hosni EM, Al-Khalaf AA, Nasser MG, Abou-Shaara HF, Radwan MH. 2022. Modeling the potential global distribution of honeybee pest. *Galleria mellonella* under changing climate. *Insects*. 13: 484. <https://doi.org/10.3390/insects13050484>
28. Hounkpe NUH, Mensah GA, Koutinhouin B, Pomalegni SCB, Goergen G, 2007 Typisation des abeilles mellifères dans le Nord Bénin. *Bul. Rec. Agr. Bénin*. 58: 56-59

29. Johnson MG, Glass JR, Dillon ME, Harrison JF. 2023. How will climatic warming affect insect pollinators? *Adv. Insect. Physiol.* 64: 114. ISSN 0065-2806. <https://doi.org/10.1016/bs.aiip.2023.01.001>

30. Kass JM, Pinilla-Buitrago GE, Paz A, Johnson BA, Grisales-Betancur V, Meenan SI, Attali D, Broennimann O, Galante PJ, Maitner BS, Owens HL, Varela S, Aiello-Lammens ME, Merow C, Blair ME, Anderson RP. 2023. *wallace 2*: a shiny app for modeling species niches and distributions redesigned to facilitate expansion via module contributions. *Ecography*. 3: e06547. DOI: 10.1111/ecog.06547

31. Lobo JL, Jimenez-Valverde A, Real R. 2007. AUC: a misleading measure of the performance of predictive distribution models. *Global Ecol Biogeogr* 1-7. DOI: 10.1111/j.1466-8238.2007.00358.x.

32. Lurgi M, Pascual-García A. 2025 Structural stability estimated through critical perturbation determines evolutionary persistence in mutualistic model ecosystems. *R. Soc. Open Sci.* 12: 250123. <https://doi.org/10.1098/rsos.250123>.

33. Lynch M, Conery JS. 2000. The evolutionary fate and consequences of duplicate genes. *Science* 290(5494): 1151-1155. 10.1126/science.290.5494.1151.

34. Matheson A. 1996 World bee health update. *Bee World* .77: 45-51.

35. Meixner MD, Leta MA, Koeniger N, Fuchs S. 2011 The honeybees of Ethiopia represent a new subspecies of *Apismellifera*-*Apismellifera simensis* n. ssp. *Apidologie* 42: 425-437

36. Merow C, Smith MJ, Silander Jr JA. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does. and why inputs and settings matter. *Ecography*. 36(10): 1058-1069. DOI: 10.1111/j.1600-0587.2013.07872.x

37. Moukrim S, Lahssini S, Alaoui HM, Rifai N, Arahou M, Rhazi L. 2018. Modélisation de la distribution spatiale des espèces endémiques pour leur conservation : cas de l'Argania spinosa (L.) Skeels. *Revue d'Écologie*. 2018. 73 (2) :153-166. hal-03532905

38. Mwakapeje ER, Ndimuligo SA, Mosomtai G, Ayebare S, Nyakaruhuka L, Nonga HE, Mdegela RH, Skjerve E. 2019. Ecological niche modeling as a tool for prediction of the potential geographic distribution of *Bacillus anthracis* spores in Tanzania. *International Journal of Infectious Diseases.* 79:142-151 <https://doi.org/10.1016/j.ijid.2018.11.367>

39. Okely M, Engel MS, Shebl MA. 2023. Climate Change Influence on the Potential Distribution of Some Cavity-Nesting Bees (Hymenoptera: Megachilidae). *Diversity* 15: 1172. <https://doi.org/10.3390/d15121172>

40. Phillips SJ, Dudik M. 2008. Modeling of Species Distributions with Maxent: New Extensions and a Comprehensive Evaluation. *Ecography.* 31: 161-175. <https://doi.org/10.1111/j.0906-7590.2008.5203.x>

41. Pigliucci M, Schmitt J. (2004). Phenotypic plasticity in response to foliar and neutral shade in gibberellin mutants of *Arabidopsis thaliana*. *Evol. Ecol. Res.* 6: 243-249.

42. Platts PJ, Omeny PA, Marchant R 2014. AFRICLIM: High-Resolution Climate Projections for Ecological Applications in Africa. *African Journal of Ecology.* 53: 103-108. <https://doi.org/10.1111/aje.12180>

43. Qian JJ, Akçay E. 2020. *The balance of interaction types determines the assembly and stability of ecological communities.* *Nat. Ecol. Evol.* 4: 356–365. DOI:10.1038/s41559-020-1121-x.

44. Ramírez-Rodríguez R, Rocha J, Crespi AL, Amich F. 2025. Modelling the present potential habitat distribution of the near-threatened endemic species *Silene marizii*: implications for conservation. *Plant Biosystems - An International Journal Dealing with All Aspects of Plant Biology.* 159(1): 154–163. <https://doi.org/10.1080/11263504.2025.2449928>

45. Rosenzweig. C. 1989. Global climate change: Predictions and observations. *Am. J. Agric. Econ.* 71: 1265–1271. DOI: <https://doi.org/10.2307/1243119>

46. Rosenzweig C, Casassa G, Karoly DJ, Imeson A, Liu C, Menzel A, Rawlins S, Root TL, Seguin B, Tryjanowski PV . 2007. Assessment of observed changes and

responses in natural and managed systems. In Climate Change 2007: Impacts. Adaptation and Vulnerability; Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE. Eds. Cambridge University Press: Cambridge. UK. pp. 79–131.

47. Ruttner F. 1988. Biogeography and Taxonomy of Honeybees (1 ed.). New York: Springer-Verlag Berlin Heidelberg GmbH. pp. 216–218. ISBN 9783642726514.

48. Singh G, Rana A. 2025. Honeybees and colony collapse disorder: understanding key drivers and economic implications. Proc. Indian. Natl. Sci. Acad 1-17. DOI: <https://doi.org/10.1007/s43538-025-00399-x>.

49. Skendzic S, Zovko M, Pajac Zivkovic I; Lesic V, Lemic D. 2021. Effect of Climate Change on Introduced and Native Agricultural Invasive Insect Pests in Europe. Insects 12: 985. <https://doi.org/10.3390/insects12110985>

50. Southwick EE, Heldmaier G. 1987. Temperature control in honey-bee colonies. Bioscience 37:395-399

51. Tadesse T, Abera D, Feyisa T, Assefa A. 2021. Effect of environmental factors on honeybee colony performance and bee flora availability in the Southern Ethiopia. Open Access Library Journal, 8(3): 1-16. <https://doi.org/10.4236/oalib.1107077>

52. Tesfamariam BG, Gessesse B, Melgani F. 2022. MaxEnt -based modeling of suitable habitat for rehabilitation of Podocarpus forest at landscape-scale. Environmental System Research 11:4. 2-12. <https://doi.org/10.1186/s40068-022-00248-6>

53. Tihelka E, Cai C, Pisani D. 2020. Mitochondrial genomes illuminate the evolutionary history of the Western honey bee (*Apis mellifera*). Scientific Reports. 10 (1): 14515. Bibcode:2020NatSR..1014515T. doi:10.1038/s41598-020-71393-0. PMC 7471700. PMID 32884034.

54. Toffa Y, Idohou R, Fandohan AB. 2022. Modélisation de la distribution des espèces en Afrique: état de l'art et perspectives. Physio-Géo. Géographie physique et environnement 17 : 43-65. <https://doi.org/10.4000/physio-geo.13738>

55. Warren DL, Glor RE, Turelli M. 2010. ENM Tools: a toolbox for comparative studies of environmental niche models. *Ecography*. 33(3): 607–11. DOI: <http://dx.doi.org/10.1111/j.1600-0587.2009.06142.x>

56. Wright GA. Nicolson SW. Shafir S. 2018. Nutritional physiology and ecology of honey bees. *Annu. Rev. Entomol.* 63(1): 327–344. <https://doi.org/10.1146/annurev-ento-020117-043423>

57. Yedomonhan H, Houenon GJ, Akoegninou A, Adomou AC, Tossou GM, Van der Maesen LJG. 2012) The woody flora and its importance for honey production in the Sudano-Guinean zone in Benin. *Int. J. Adv. Sci.*. 2(3)): 64-74.

58. Zapata-Hernandez G, Gajardo-Rojas M, Calderon -Seguel M, Munoz AA, Yanez KP, Requier F, Fonturbel F, Ormeno-Arriagada PI, Arrieta H. 2024. Advances and knowledge gaps on climate change impacts on honeybees and beekeeping: A systematic review. *Glob Change Biol.* 30: e17219. <https://doi.org/10.1111/gcb.17219>

59. Zuchang P. 2025. Biological evolution cybernetics vs. neutral mutation: Random drift hypothesis. *Academic journals* 9(1): 1-11. DOI: 10.5897/JEPR2025.0068