

Ecological-niche modelling of genetically distinct populations revealed Kersting's groundnut [*Macrotyloma geocarpum* (Harms) Maréchal et Baudet] as a resilient orphan crop to present and future climates

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Abstract

Orphan legume crops play an important role in smallholder farmers' food systems. Though less documented, they have the potential to contribute to adequate nutrition in vulnerable communities. Unfortunately, data are scarce about the potential of those crops to withstand current and future climate variations. Using *Macrotyloma geocarpum* as an example, we used genetically informed ecological niche models to explore the role of ecology on the current and future distributions of genetic populations of Kersting's groundnut. Three main conclusions emerged: i) the models had good predictive power, indicating that *M. geocarpum*'s distribution was correlated with both climatic and soil layers; ii) identity and similarity tests revealed that the two genetic groups while overlapping, are each, locally adapted and display differences in climate suitability; iii) by integrating the genetic information in niche modeling, niches projections show divergence in the response of the species and genetic populations to ongoing climate change. This study highlights the importance of integrating genetic data into ecological niche modelling approaches to obtain finer scale information of species' distribution, and explores the implications for agricultural adaptation, with a particular focus on identifying priority actions in orphan crops conservation and breeding.

1. INTRODUCTION

Defining how and where plant varieties will adequately respond to environmental variations is a central topic in plant science research. This is more preoccupying for orphan crops that are largely grown in marginal areas and neglected in the mainstream research agenda (Mabhaudhi *et al.* 2019). Availability of the genetic resources of those crops is still a challenge for many genebanks at national, regional, and international levels. This situation jeopardizes the sustainable utilization of the plant genetic diversity that can be useful for current and future food systems and secured nutrition (Govindarajet *al.* 2015; Litrico & Violle 2015; Singh

et al. 2014). Such genetic resources are important for successful cultivars development and selection of economic and agronomic traits and could confer resilience to evolving climate.

In Kersting's groundnut [*Macrotyloma geocarpum* (Harms) Maréchal and Baudet], a multipurpose staple orphan crop with high nutritional and economic values for smallholder farmers in West Africa (Adu-Gyamfi *et al.* 2011; Ajayi & Oyetayo 2009; Akohoué *et al.* 2019; Assogba *et al.* 2015; Obase & Agbatse 2015), the need to solve the ecological suitability of the extant genetic resources arose despite the significant achievements made recently on the germplasm collection, conservation and crop selection. Kersting's groundnut plays an important role in farming sustainability through its ability to fix atmospheric nitrogen in soil and enhance soil fertility (Mohammed *et al.* 2018). Furthermore, It serves in traditional medicine for local populations (Adu-Gyamfi *et al.* 2011; Assogba *et al.* 2015; Tamini 1995). However, the production of Kersting's groundnut is declining rapidly and the genetic resources were rarely collected and safeguarded for future generation. In addition, environmental stresses are among the main causes for declining Kersting's groundnut production from its cultivated areas (Akohoué *et al.* 2019; Coulibaly *et al.* 2020). Though Kersting's groundnut has relatively good adaptation to low-input conditions (Achigan-Dako & Vodouhe 2006; Mergeai 1993), increased frequency of drought, intense precipitations, elevated temperatures, and increased salt and heavy metals in soils will often be accompanied by increased infestation by pests, and pathogens, are expected to limit the plant growth and productivity, and consequently the crop's yield and production (Long *et al.* 2015).

Recent studies revealed a low variation within the species (Akohoué *et al.* 2020; Mohammed *et al.* 2018) that limits the extent of its genetic diversity and cultivated zones. Kersting's groundnut counts six landraces set mostly within three agroclimatic zones; Northern-Guinean (NG), Northern-Sudanian (NS) and Southern-Sudanian (SS) of Benin, Burkina Faso, Ghana and Togo with the predominance of genetic resources and diversity in Southern-Sudanian zone (Akohoué *et al.* 2019; Coulibaly *et al.* 2020). Overall, the area of cultivation and adaptation of landraces differ among agroclimatic regions. The Black landrace was largely collected in the Northern-Sudanian environmental conditions and was widely preferred, cultivated and maintained by farmers (Coulibaly *et al.* 2020). The White landrace was widely grown in the Northern-Guinean transition zone of Benin (Akohoué *et al.* 2019; Assogba *et al.* 2015) while less cultivated in Burkina Faso (Coulibaly *et al.* 2020) and absent in other countries of West-Africa. The production of the Brown landrace was specifically limited to Ghana farming system (Coulibaly *et al.* 2020).

Kersting's groundnut landraces are the direct results of farmer selection, cultivation and maintenance over the centuries. This continual adaptation of the crop to smallholders farming conditions could continue to play a role in adapting production to climate change. Also, local adaptation of landraces could vary in their climatic response and requirement and therefore, may spread differentially under evolving environmental conditions (Schierenbeck 2017). To find the adequate referendum where the species can thrive, it has become crucial to approximate the potential distribution of the crop and its genetic resources.

Unfortunately, with the rapid evolution in climate conditions and the further introduction and adoption of new cash crops with high economic importance, local seed systems alone will likely be insufficient to ensure the endurance of the crop genetic resources and diversity. In these conditions, applying ecological research is required to inform conservation and management decisions in order to mitigate a species genetic erosion (Araújo *et al.* 2005), as Kersting's groundnut at National and Regional levels. Ecological niche modeling (ENM) can identify the environmental parameters that can impact a species' distribution and project its potential distribution area onto new environmental surfaces to examine the effect of present or future environmental change (Araújo & Peterson 2012; Martínez-Meyer 2005).

Several statistical and mechanistic techniques proved effective in quantifying niches and spatial distribution of natural and cultivated species (Blonder 2018; Elith *et al.* 2006; Pironon *et al.* 2019; Ramirez-Cabral *et al.* 2016; Syfert *et al.* 2016). The basic modelling framework of species distribution models (SDMs) in general has been criticized on a number of gaps, such as ignoring heterogeneity in population and genetic structure in different parts of a species geographical range (Hampe & Petit 2005). However, many species are organized into differentiated genetic lineages across their geographical ranges (Hereford 2009; Leimu & Fischer 2008) and populations differ in their adaptive potential to respond to environmental change (Shaw & Etterson

2012). Studies proved that incorporating molecular data into SDMs represents an important step forward for modelling the effects of climate change on species geographical ranges (Alvarado-Serrano & Knowles 2014; Gotelli & Stanton-Geddes 2015; Ikeda *et al.* 2016).

In the case of Kersting’s groundnut (KG), much uncertainty remains concerning the ability of the crop to withstand the changing climate, suggesting that there is a clear need to comprehensively analyze the response of the crop diversity under new environmental conditions of the coming decades.

The present study was undertaken to predict the potential distribution of KG under present and future climate change scenarios. Recent molecular studies involving 281 individuals from Benin and Togo identified two major genetic clusters of KG and these two groups were distributed across Southern-Sudanian and Northern-Guinean agroclimatic zones (Akohoue *et al.* 2020). Kafoutchoni *et al.* (2021) also assessed the genetic structure of the species through GBS approach and Discriminant analysis of principal components (DAPC) and found eight genetically distinct groups from five origins. In this context, the following questions are of high interest: does the agroclimatic niches of KG vary with climate changes? Would KG genetic groups differ in their ability to respond to present and future climatic scenarios? This study examines the response of orphan crops to future climates by using genetic information and ecological niche modeling approach (gENMs) using KG as an example. Therefore, we combined KG population genomics data with ecological niche modeling: 1) to analyze the relationship between climate factors and species populations distribution in agroclimatic zones of Burkina Faso, Benin, Ghana, and Togo, and 2) to predict and examine areas that would be suitable for the species and genetic populations under the future scenarios. We hypothesized that: i) the distribution of KG remains stable under future climates, and ii) genetically distinct populations of orphan crops would respond differently to climate change.

2. MATERIALS AND METHODS

2.1. Genotyping and genetic clustering

For the present work, a total of 361 accessions of KG collected from Benin, Burkina Faso, Ghana and Togo were used. The DNA of each sample was extracted from young leaves of each accession, using the protocol of the Integrated genotyping service and support (IGSS) at the Biosciences Eastern and Central Africa (BeCA: <http://hub.africabiosciences.org/activities/services>) located in Nairobi, Kenya. The quality of the DNA was confirmed by electrophoresis in 0.8% agarose, and the quantification carried out using UVP BioDoc-It2 Imaging System. All of the samples were diluted to 50 ng/ul for the DArT genotyping platform. Genotyping was performed using the DArT-Seq platform at Diversity Arrays Technology (Kilian *et al.* 2012). The quality analysis of the genotypic data was performed using Illumina HiSeq 2500 (Illumina 2015). The SilicoDart calling algorithms (DArTsoft14) was used to score DArTseq markers into a binary format (presence = 1 and absence = 0) for each sample genomic representation. A total of 2844 SNP markers were obtained and processed in TASSEL v5 (Buckler *et al.* 2014), for quality check. SNPs were filtered with TASSEL v5 for further analysis using the parameters Minor Allele Frequency (MAF) >0.05 and proportion of missing data < 30%. A total of 142 SNPs were retained and Nipals model in kdcompute (<https://kdcompute.igss-africa.org>) was used for data imputation.

The program Structure 2.3.4 (Pritchard *et al.* 2010) was used to assign individuals to different genetic clusters based on admixture model. The population structure was evaluated based on Bayesian clustering approach using the following settings: correlated allelic frequencies, burn-in period of 10,000 and 10,000 Markov Chain Monte Carlo (MCMC) interactions; and grouping (K) ranging from 1 to 5 in 10 independent runs. The results generated were used as input to the POPHELPER, an R package (Francis 2016), to predict the best K value based on Evanno method (Evanno *et al.* 2005) and to generate the bar graph and delta K graph.

The pairwise Fixation index (Fst) and molecular variation (AMOVA) were performed using R package adegenet (Jombart & Ahmed 2011) in order to reveal genetic differentiation among the two distinct groups occupying the three agroclimatic zones of Burkina Faso, Benin, Ghana and Togo. General patterns of genetic diversity were also evaluated by calculating observed (Ho) versus expected (He) heterozygosity and

gene diversity (Hs) within each population.

2.2. Occurrence data

We used two sets of occurrence data, at the species and genetic analysis levels. *M. geocarpum* records were collected from its location points using data of self-collected material and the Global Biodiversity and Informatics Facility (GBIF, www.gbif.org), an online available database. We used both the original population location points and those from GBIF in all subsequent analyses. As the different data sources and a large dataset (>500 occurrence records) would likely carry elevated geographical or environmental space biases (Boria *et al.* 2014; Peterson *et al.* 2011), the number of records were decreased in Wallace package, an online workspace based on R interface (Kass *et al.* 2020) using four complementary approaches: 1) we first removed occurrences collected before 1986 to match with environmental layers and soil properties; 2) considerable ambiguity may exist in GBIF data over the identity of the species due to synonymous names (*M. geocarpum* var. *geocarpum*, *M. geocarpum* var. *Tisserantii*; *Kerstingiella geocarpa*, *Kerstingiella tisserantii*). To avoid any confusion arising from this taxonomic ambiguity, we searched through the online databases using the following keywords: *Macrotyloma geocarpum*, *Kerstingiella geocarpa*, var. *geocarpa* or var. *geocarpum*; orphan legumes. We then harmonized the GBIF database and discarded the reports on var. *tisserantii* and *Kerstingiella tisserantii*; 3) we used spatially filtering occurrences located [?] 10 km from other occurrences using the spThin, an R package (Aiello-Lammens *et al.* 2015); finally, 4) we manually checked isolated locations points in Africa (in ArcGis ver. 10.7.1) and removed occurrences in areas where *M. geocarpum* is not generally grown.

The defined genetic clusters data with their geographic coordinates were also filtered separately to ensure the real distribution of each population within agroclimatic zones. The filtered dataset comprised in total 64 occurrences (Pop1 = 22; Pop2 = 25 and GBIF = 17) that was used in subsequent analyses (Table S1).

2.3. Environmental variables

We used bioclimate layers combined with soil properties to project current and future niches for the species and each genetic group. A total of 14 bioclimate variables were downloaded from Africlim online regional climate models (RCMs) data portal (<https://webfiles.york.ac.uk/KITE/AfriClim/>) (Platts *et al.* 2014). Current and future variables averaged between the time periods 1986-2015 (2000) and 2041-2060 (2055) were downloaded at a 30 arc-second (~1 km) spatial resolution. For future climatic conditions, predictions from the Ensemble model (Platts *et al.* 2014) were used. This model simulates changes based on a set of scenarios. The projections were run under Representative Concentration Pathway (RCP), RCP 4.5 and RCP 8.5 for the 2055 time horizon (Meinshausen *et al.* 2011). In all RCPs, the climatic conditions are extreme in RCP 8.5 scenarios compared to RCP 4.5. RCP 4.5 projects temperatures to rise above industrial levels by at least 1.5°C in West Africa, with atmospheric CO₂ reaching 500 ppm while in RCP 8.5 projections, temperatures are predicted to rise by 2.8°C and atmospheric CO₂ to be over 550 ppm (IPCC 2013). These climate projections were statistically downscaled to match the bioclimatic variables using the delta method, (Ramirez-Villegas & Jarvis 2010).

Data related to soil characteristics were available in the World Soil Information (ISRIC) databases (*Soil-property-maps-of-Africa-at-250-m-resolution*) at 250 m resolution (Hengl *et al.* 2015). These spatial predictions of soil properties were generated based on two predictive approaches such as random forests and linear regression (Hengl *et al.* 2015). Soil characteristics identified as relevant to *M. geocarpum* agricultural management included 11 variables related to the soil physical, chemical and nutritional properties. Soil data were then converted to 30 arcseconds using ArcGis software v 10.7.1 to match with bioclimate layers. Finally, using shapefile boundaries of four West African countries (Benin, Burkina Faso, Ghana and Togo) we cropped all variables to encompass the broad geographic regions that define Kersting's groundnut global distribution.

Jackknife Procedure in Maxent 3.4.4 was used to reduce the number of variables to be included in the prediction models (Phillips *et al.* 2005). The six variables with highest contribution proportions were selected and were used in the final models of the species, and with genetic information.

2.4. Ecological predictive models’ development and evaluation

To calibrate our models, we employed the maximum entropy method (Elith *et al.* 2010; Phillips *et al.* 2005) implemented in Maxent ver. 3.4.4. The algorithm has been extensively tested and benchmarked (Phillips & Dudík 2008; Richards *et al.* 2007). Many studies have reported Maxent as one of the highest performing presence-background algorithms (Elith *et al.* 2006; Merow *et al.* 2013). As the selection of sample points can influence model performance in Maxent (Phillips *et al.* 2009), we restricted the selection of background points using a regularization of 10,000 background points (Elith *et al.* 2006). For simplification of the modeling algorithms, we used the default settings (feature class and regularization) in Maxent for each of the three models. Models were trained with data from the present and projected in the future. Three Maxent models were generated with different occurrence datasets: first, all accessions location points grouped together without genetic information were used in projecting the entire distribution of KG (model 1); model 2 and model 3 were developed using separately occurrence data of Pop 1 and Pop 2, the genetically defined populations (Supplemental Table S1).

We used a tenfold cross-validation method, which uses 90% of the data for model training and 10% for model testing for 10 iterations (Elith *et al.* 2010).

Each model performance was evaluated using traditional Receiver Operator Characteristics (ROC) - area under the curve (AUC) scores (Merow *et al.* 2013) by specifying 500 iterations with the omission threshold set at ten percent (Peterson *et al.* 2008). A model is considered as having a good fit when its AUC is close to one (AUC[?]0.75) (Elith *et al.* 2006). Minimum training presence (MTP) values were also used as thresholds for testing the performance of each model (Phillips *et al.* 2005).

The outputs from Maxent were processed in ArcGIS ver. 10.7.1 to construct maps of the distribution of Kersting’s groundnut areas cultivability. The continuous probabilities generated by Maxent (Ten Percentile Training Presence) were converted into binary presence-absence maps to identify the levels of areas suitability. Two different levels were therefore, defined: unsuitable and suitable. Finally, we quantified the dynamic of the cultivated zones of the crop in the scenarios RCP 4.5 and RCP 8.5 of the horizon 2055 using the following equation:

$$\Delta(\%) = \frac{(FA_{ij} - CA_j) * 100}{TA}$$

Where, FA_{ij} corresponds to the extent value (in number of pixels) under the scenario i of future horizon in the environment j (area suitability); CA is the extent value of current condition; TA corresponds to the total extend of all cultivated zones of the present day. Negative, null and positive values represent range lost, stable and gained, respectively.

Furthermore, to visualize the potential changes of suitable areas for Kersting’s groundnut production, we compared current and future distribution ranges of the crop and of genetic populations using package “tmap” version 3.3-1 (Tennekes 2018) in R.

2.5. Niche differentiation

To assess the degree of climate niche overlap among species and genetic groups, two randomization tests were executed in ENMTools ver. 1.0.4 (Warren & Dinnage 2021): the niche identity test and the niche similarity test or background test (Warren *et al.* 2008). The identity test was performed to examine whether the habitat suitability scores generated from the ecological niche models of species and genetic populations are significantly different than expected if they were generated from the same distribution. The similarity test was also performed to examine the degree to which environmental niches are conserved over time, between *M. geocarpum* and genetic groups.

To quantify niche overlap for pair-wise comparisons, we used Schoener’s D (Rödder & Engler 2011; Schoener 1968; Warren *et al.* 2008) metric, calculated using generalized linear model (GLM) with 100 randomized

pseudoreplicates following the model below:

$$D(p_x + p_y) = 1 - \frac{1}{2} \sum_i (|p_{x,i} - p_{y,i}|)$$

Where $p_{x,i}$ and $p_{y,i}$ denote the probability assigned in a species distribution model computed for species X and Y to grid cell i . D value ranged from 0 to 1.

The observed values of D in both the niche identity test and the background similarity test were compared to the mean values of five randomized runs using t-test (Warren *et al.* 2008). The environmental niches were considered significantly different if the observed values of niche overlap were less than 95% or 99% (alpha = 0.05 and 0.01, respectively) of the overlap values derived from the pseudo replicates.

3. RESULTS

3.1. Population structure and admixture

Despite low levels of diversity (He = 0.28 and Ho = 0.023, p.value = < 0.001), Kersting's groundnut populations remained genetically well differentiated. Admixture models with a putative number of tested genetic clusters (K) from one to five, showed that the most likely number of inferred members was 2 with $\Delta K = 368.369$ (Figure 1a). The classification of the 361 accessions into populations based on the model-based structure (Figure 1b) showed that 231 accessions belonged to the first population (Pop1) and 130 accessions were included in the second population (Pop2). Table 1 showed the distribution of populations across agroclimatic zones. Most of the accessions were collected in the Southern-Sudanian zone with proportions of 80.519% and 80% comprised in Pop1 and Pop2, respectively. The accessions collected in Northern-Sudanian zone were all counted in the Pop2. In the Northern-Guinean zone, 19.481% of accessions belonged to Pop1 and 14.615% were included in Pop2. The random distribution of landraces (Figure 2) into the genetic groups indicated that Pop1 were mostly characterized by the White landrace (97.403% of individuals in Pop1). Pop1 comprised also the Red and the Black landraces. Pop2 were composed of all the six landraces included in this study with a predominance of Black (43.846%) and Brown ones (30%).

The analysis of genetic distance revealed relatively strong genetic differentiation among the two distinct groups of KG with pairwise Fst value of 0.704 (Table 2). The estimates values of gene diversity (Hs) showed overall, low genetic divergence between individuals within each Group. Meanwhile, the heterozygosity analysis showed a greater genetic divergence between individuals in Pop2 (Hs = 0.323).

3.2. Occurrences dataset construction

After data cleaning steps, the final occurrence dataset contained 53 locations points for the species (including 17 from GBIF), 22 for Pop 1 and 25 for Pop 2, distributed across three agroclimatic zones of Benin, Burkina Faso, Ghana and Togo. The Fig 3 shows Pop1 distributed across two agroecologies, the Northern-Guinean and Southern-Sudanian zones whereas the Pop2 and GBIF points were represented in all agroecologies. At the country level, Pop2 was distributed across the four countries while the Pop1 was located in Benin and Togo.

3.3. Niche overlap and conservatism among *M. geocarpum* and genetic populations

The results of the niche overlap (D) indicated that the current distribution of Kersting's groundnut species and its genetic groups was not significantly different. For all pairwise comparisons, between niches of the species and Pop1, Pop2 and between niches of the two genetic groups, we found Schoener's D values of 0.935, 0.907 and 0.878, respectively.

In addition, our results suggested that niche overlap tests performed differently based on D Values obtained from identity and similarity tests. We rejected the null hypothesis ($P < 0.01$, Fig. 4a) that niches between the species and genetic Pop 1 were identical, but they were similar ($P > 0.05$, Fig. 4d). Predicted niches between *M. geocarpum* and genetic Pop 2, while identical ($P > 0.05$, Fig. 4b), were not conserved ($P <$

0.01, Fig. 4e). We rejected both the null hypothesis that niches were identical ($P < 0.01$, Fig. 4c) and that niches were conserved ($P < 0.05$, Fig. 4f) between the two genetic groups.

3.4. Ecological niche modelling

3.4.1. Climatic variables analogy

The initial run in Maxent with *M. geocarpum* without genetic information showed that the most important environmental variables contributing to the predictive model included temperature seasonality, rainfall wettest month, rainfall driest quarter, Bulk density of soil in kg / cubic-meter for 22.5 cm depth and soil texture fraction of clay at 10 cm. Based on the percent contribution values, the selected climatic variables were more or less important in the three distribution models of Kersting's groundnut (Fig 5a), its genetic Pop1 (Fig 5b) and Pop2 (Fig 5c). Precipitation during the driest quarter was the most influential predictor for *M. geocarpum* and Pop2. Soil texture fraction clay at 10 cm was the variable contributing mostly to Pop1 model whereas for the model of Pop2, it was the less important (0.3%). In general, soil texture fraction sand at 10 cm presented the least contribution values to the different models.

3.4.2. Models' outputs and performance evaluation

The environmental predictive models displayed high predictive power according to the AUC values of 0.86, 0.93 and 0.84 for the species, Pop1 and Pop2, respectively (Table 3). These results suggest that the predictions effectively captured relationships between environmental variables and locations points of Pop1 comparing to Pop2 and the species.

Based on the Minimum training presence (MTP), suitable areas for Kersting's groundnut and population groups were defined. We found that current distributions were significantly different between populations and species. The Maxent model for the species predicted a large area of cultivable conditions across the three agroclimatic zones, Southern Sudanian (SS), Northern Sudanian (NS) and Northern-Guinean (NG) (Fig. 6a1). The SS and NG zones were the areas forecasted to have high suitable climatic conditions for the species production. For the Pop1, the areas predicted to have high likely cultivability conditions were concentrated in NG zone of Benin, but very less and sparsely distributed in SS zone (Fig6b1). The Pop2 was projected across the three studied agroclimatic zones of the four countries with highest cultivable areas in SS and NS zones (Fig6c1).

Furthermore, the potential distribution maps under future (in 2055) climatic conditions revealed varied patterns in KG and genetic populations cultivable areas (Fig 6 and Fig 7, see supplemental Figures).

Under the two future climatic scenarios RCP4.5 and RCP8.5, an increase in the species cultivable areas for about 2.75%, were observed due to the decrease of the non-suitable areas (Fig 6a2, a3, Fig 7). This areas expansion was observed mainly in the NG zone of Southern Benin, also in SS and NS zones of Burkina Faso, Ghana and Togo. Similarly, an increase of the cultivability areas of Kersting's groundnut was observed in the SS zone of the Northern Benin. On the other hand, the SS zone of Central Benin became climatically unsuitable to the crop production. The Pop1 showed to be more vulnerable to future scenarios as the suitable areas slightly decreased (0.504 % under RCP4.5 and 0.779 % under RCP8.5), while the unsuitable ranges increased (Fig 6b2, b3, Fig 7). The model of this genetic group predicted an increase in the suitable areas of NG zone of Benin, Ghana and Togo while a decrease was observed in the NS and SS zone of the four countries. The potential cultivable areas of the Pop2 (Fig 6c2, c3, Fig 7) slightly decreased by 0.322% under RCP4.5 while increased with extreme conditions of RCP8.5 (0.519%). The future climatic conditions of the SS zone of Central Benin would constitute constraints to this population cultivation. In contrast, the NG zone of Southern Benin and Togo and the SS zone gained in cultivable areas for Pop2.

4. DISCUSSIONS

This study provided evidence of incorporating genetic information in ENM to characterize the adaptation potential of *M. geocarpum* in four West-African countries (Benin, Burkina Faso, Ghana and Togo) and

suggested implications for sustainable management and breeding perspectives under current and future climate change.

4.1. Current potential distribution ranges of Kersting’s groundnut and genetic groups

We used two approaches to model KG distributions across agroclimatic zones of four West African countries: a traditional species SDM using a species wide cultivated areas, and intraspecific models based on genetic information. We found that decomposing a species into intraspecific genetic groups increases our understanding of potential distribution of KG, which is consistent with results from the previous few studies (Gotelli & Stanton-Geddes 2015; Ikeda *et al.* 2016; Marcer *et al.* 2016; Oney *et al.* 2013). The SDMs for Pop1 performed more accurately in estimating potential cultivation areas of KG rather than the genetic Pop2, which showed lower prediction accuracy. The Pop2 is found in the three agroclimatic zones of all countries; it displays a wide distribution range like the whole-species. Indeed, Allouche *et al.* (2006) reported that the values of predictive accuracy tend to be lower when species are more common within the distribution ranges. Our results reinforce the view that it is necessary in SDMs evaluation, to consider not only the use of genetic data but also the population sizes and the cultivated ranges of each genetic unit (Marcer *et al.* 2016; Milanesi *et al.* 2018).

4.2. Environmental variable contribution

Our approach allowed to identify six environmental variables correlated with the potential distribution ranges of the species and populations. Clearly, the rainfall wettest month, rainfall driest quarter and temperature seasonality were mostly involved in fitting the models. The ecological weight that precipitations may have in KG’s distribution is also supported by a recent ethnobotanical study where farmers identified drought and high moisture during the reproductive stage as main factors hindering the species production (Akohoué *et al.* 2019; Coulibaly *et al.* 2020). Tamini (1997) also showed that the different sowing dates and seasons with varied temperatures influenced KG growing cycle by delaying or accelerating the flowering time. In order to cope with these weather issues, farmers managed their cropping calendar by advancing (in June) or delaying (in August) the date of planting KG. The change in temperature and moisture levels are not only determined by climatic parameters but may also lead to a change in the absorption rate of water, fertilizers and other minerals in soils, which determine yield output (Padi & Ehlers 2008; Sileshi *et al.* 2010; Yohannes 2015). Therefore, the consideration of both climate and soil type was essential to better predict the species and genetic groups’ distribution. The physical composition of soil such as bulk density of soil in kg / cubic-meter for 22.5 cm depth also had a relevant role in KG and populations distribution. Furthermore, based on variables importance shown by Jackknife measures, soil texture fractions clay and sand in percent, at 10 cm depth accounted for the potential distribution ranges of *M. geocarpum* and the genetic Pop1 while less for Pop2. Kouelo *et al.* (2012) reported that the soil texture and preparation (type of tillage) influenced the crop productivity in Benin. Although applying SDM to intraspecific genetic groups allowed the detection of environmental variables, a multidisciplinary approach involving agronomists and biologists would allow a clear understanding of the weight that each of these components may have on the crop growth and development.

4.3. Niche overlapping

We found important geographic overlap among the projected distributions of the species genetic populations. The clusters did not show strict cluster-specific ecological niches. Our results did not support the view that a given species could be considered as an assemblage of genetic units differing in their spatial distribution (Ikeda *et al.* 2016; Marcer *et al.* 2016). Populations of KG are both cultivated in the Northern-Guinean and the Southern-Sudanian zones of Benin, characterized by a bimodal (rainfall [?] 1500mm) and unimodal (rainfall [?] 1100mm) growing seasons, respectively. However, the Pop 2 showed wide cultivable areas rather than the Pop1, as it is also grown in the Northern-Sudanian zone, where rainfalls are relatively low (rainfall [?] 900mm). The null hypothesis was rejected as climatic niches between the two populations were identical and similar (niche identity test $p < 0.01$ and niche similarity $p < 0.05$), suggesting variation in their environmental niches and adaptation to different climate conditions, as previously reported by Wellenreuther

et al. (2012) who analyzed the ecological causes of the ranges limits and the coexistence of two congeneric damselflies (*Calopteryx splendens* and *C. virgo*). In addition, Maxent’s outputs also revealed that climatic niches of the two genetic populations of *M. geocarpum* are relatively different in the distribution areas. This finding is in accordance with other studies which reported environmental niche dissimilarity at the intraspecific level (Banerjee *et al.* 2019; Gorel *et al.* 2019; Ikeda *et al.* 2016; Milanesi *et al.* 2018).

4.4. Predicting evolutionary change based on genetic variation

We assumed that KG species will conserve its cultivated areas over space and time. Our results however, found evidence of variability in the species response to future environmental conditions. This corroborates many other studies which showed the impact of future climatic conditions on crops production, such as cereals, legumes, vegetables (Burke *et al.* 2009; Pironon *et al.* 2019; Ramirez-Cabral *et al.* 2017; Ramirez-Cabral *et al.* 2016; Syfert *et al.* 2016).

We also combined genetic information to ENM to test hypothesis that genetic divergent groups differ in their adaptive potential to respond to environmental change. The projection under future climatic scenarios RCP4.5 and RCP8.5 clearly indicate that the response of Kersting’s groundnut and genetic groups varied significantly across agroclimatic zones. Our results confirmed the idea that different genetic clusters potentially showed adaptive variation to different abiotic conditions within the geographical range of the species (Hancock *et al.* 2011). Globally, although Central Benin is presumed to be a centre of origin for the crop, we observed a loss in suitable areas for the species production in the Southern-Sudanian zone of the country. The genetic Pop 1 is the mostly concerned by the negative impact of environmental evolution as it was generally found in these regions of the country. Similarly, Ikeda *et al.* (2016) tested and demonstrated the hypothesis that species locally adapted to current environments are likely to become maladapted in the future. The same trends were reported on other cereals such as maize, wheat, sorghum and barley which tend to decrease their area of suitability in their centres of origin (Bellon & van Etten 2014; Lane & Jarvis 2007). In the context of an inevitable agricultural reduction in these agroclimatic zones, the earlier the mitigation actions are taken, more successful will be the collection and conservation efforts of KG’ resources. On the other hand, severe environmental conditions (RCP8.5) of the Northern-Guinean zone in Southern Benin and Togo remain, even become more favorable to the species cultivation (Pop2). Likewise, the Southern-Sudanian zone of Ghana, Burkina Faso, Togo and Northern Benin, and Northern-Sudanian zone increased in cultivable areas of Pop2. Out of the 361 individuals included in this study, 101 belong to the genetic Pop2, distributed mostly in the Southern-Sudanian zone and counts all the landraces grown - diversity based on seed coat color - (Akohoue *et al.* 2019; Coulibaly *et al.* 2020). Such diversity in this population may explain the adaptive response of the Pop2 to climate variation. This is supported by the conclusion of Vigouroux *et al.* (2011) who described the evolution and adaptation of pearl millet in West-Africa. However, the cultivable area of this genetic Pop2 is predicted to decline in the Southern-Sudanian zone of Central Benin. With regards to these results, significant headway can be made by creating more favorable policy environments. Two strategies proposed by Ramirez-Cabral *et al.* (2016) can be used in order to mitigate loss in KG resources and diversity: first, the use of all the resources of Pop2 in regions where the stress of climate conditions become unsuitable for the species production. Examples of this is the Southern-Sudanian zone of Central Benin, where the use of KG is more important than other regions. And the second option was to address future loss of suitability by shifting the current cultivation areas of Pop1 to new regions, where the future climatic conditions is projected to become more cultivable for KG, the Northern-Guinean zone of Southern Benin, the southern-Sudanian and northern-Sudanian zones.

4.5. Conservation implications

Successful management of an endangered species often depends on accurate identification of current and future cultivable areas. Thus, we combined genetic diversity and ecological niche modeling to understand the evolutionary dynamics in Kersting’s groundnut species across its cultivated regions. Although the predictive models showed that future climatic conditions will be more favorable to KG production, areas of the Southern-Sudanian and Northern-Guinean zones of Benin were identified as climatically unsuitable for the species and genetic groups. Notwithstanding the above results, this approach may provide a valuable tool for

genetic resources managers for implementing collection and conservation strategies of this orphan legume, as sustained by Sohn *et al.* (2013) in their study on endemic bird in South America. In particular, our suggestion is to focus on the Pop1 with particularly high conservation value. This genetic group is composed mainly of the white landrace mostly preferred, grown and sold by farmers in Benin (Akohoue *et al.* 2019; Assogba *et al.* 2015). However, the local seed system alone will likely be insufficient to adapt the crop production to changing climate. Formal seeds management efforts can improve the decision-making process that would greatly help in the collection and conservation of those populations at higher risk of extinction but also those that may thrive with climate change. In general, African crop genetic resources conservation is unfortunately poorly supported by National Governments, and material from the regions is not fully represented in the important international genebanks which afford the baseline for sustained public breeding efforts (Burke *et al.* 2009).

4.6. Implications of SDM results for selection for adaptation

An assessment of staple crop productivity, quality and environmentally suitable areas under climate change is necessary to undertake any global initiatives to overcome food insecurity challenges (Ramirez-Cabral *et al.* 2016). KG is a staple food crop and a source of proteins and nutrients for smallholder farmers in West Africa. In this research, we expected to identify the intraspecific genetic group that would be resilient under future climate scenarios, and which areas are concerned by changes in KG diversity. The model projections indicate that a shift in the Kersting's groundnut productive areas is slightly and likely with a loss of cultivability of the Pop1 cultivation areas and an increase for Pop2 in two agroecologies (Northern-Sudanian and Southern-Sudanian). Although KG is predicted to gain in suitable area in future environmental changes, its cultivation is however decreasing year to year from its cultivated areas (Akohoue *et al.* 2019; Amujoyegbe *et al.* 2007). Therefore, it will be crucial to adapt *M. geocarpum* species to the increasingly challenging environmental conditions through development of new resilient cultivars that meet farmers' needs. The Pop2 comprises all landraces (diversity) of the species and can serve as a potential source for diversity on which breeding efforts could be based to confer resilience to changing climates and increase sustainability, growth and yield of genetic Pop1. Advancements in molecular plant breeding would be an importance of paramount to increase the genetic gains and make more accurate the breeding process. In the particular case of KG, currently, available partial GBS data (Akohoue *et al.* 2020; Kafoutchoni *et al.* 2021) would allow the analyses of intraspecific genetic clusters based on gene network variation for various important phenotypic traits (e.g.: grain yield, yield related traits, flowering time). This novel approach would provide possibilities to assess the extent to which key functional genes and genetic variation may be threatened under future ecological conditions (Banta *et al.* 2012). Plant breeders have widely and successfully implemented genome wide breeding approach for the development of climate resilient varieties (Bohra *et al.* 2020; Gobu *et al.* 2020; Kumar *et al.* 2019), through marker assisted selection and genomic selection. Another approach is to increase variability within the species, particularly in Pop1, through mutation methods (using physical or chemical mutagens) combined with molecular markers (Targeted Induced Local Lesions in Genomes (TILLING)). Such techniques have been successfully used in breeding of many legume crops to enhance diversity and to develop mutant cultivars (Al-Khayri *et al.* 2019; Aliyu *et al.* 2016; Singh *et al.* 2014).

5. CONCLUSION AND PERSPECTIVES

This study assessed the potential impacts of climate variations on environments suitability for Kersting's groundnut cultivation, and consequently its distribution around four West-African countries. The use of Maxent' models and genetic information allowed a preliminary understanding of the stress factors influencing the climate suitability of the species and genetic populations under future scenarios (2055, RCP4.5 and RCP8.5). The overall trend shown by our results indicates an increase in climate suitability for the species cultivation in the Northern-Guinean zone of Southern Benin and Togo, the Northern-Sudanian and Southern-Sudanian zones of Burkina Faso, Ghana, Togo and Northern Benin. A decrease was observed in the Southern-Sudanian zones of the Central Benin, which is the major production area. Our findings illustrate also that projected areas of environments cultivability for *M. geocarpum* and the two populations are on different climate change trajectories. The projected distribution maps presented in this paper have been hence, used

to identify strategic measures to manage the impacts of reduced climate cultivability while taking advantage of the opportunities in areas of improved suitability for Kersting’s groundnut cultivation in the future. Our findings could be downscaled to a country level to assist national policy makers in developing of strategic control initiatives to prevent the scarcity of this legume.

Although this study represents a first insight into the examining the potential of Kersting’s groundnut as resilient crop under climate change, several limitations are to be noted in order to develop the right tools to reduce model uncertainty and make better predictions in future research. First, the global distribution of the species and its wild relatives is still incompletely documented online: collecting more and finer occurrence data, especially in regions where its production was previously reported would greatly help in refining or confirming our results. Second, our models identified rainfall, temperature and soil variables that contributed significantly to their fits. However, socioeconomic factors such as local market value of the species and cultural preferences must also be considered in the predictions. Combining also measures of key phenotypic traits in modeling process would contribute to improve predictions of the impact of climate change on this legume crop. Third, the non-availability of whole genome-wide data in the case of Kersting’s groundnut limited access to phylogenetic information and identification of key functional genes for various important phenotypic traits. That may provide means to assess response of key functional genes under evolutionary climate change.

Nevertheless, using our approach, we identified species, genetic populations and cultivable areas for further germplasm collecting to enhance available germplasm and better direct Kersting’s groundnut breeding priorities in the future.

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Author contributions

MC : Conceptualization, Investigation, Data curation, Methodology, molecular data analysis, Writing - Review & Editing; **EGAD** : Conceptualization, Writing - Review & Editing, Visualization, Supervision, Funding management, Project administration; **RI** : Software, data analysis, Review & Editing; **FA** : Additional molecular data resources, Review & Editing; **ATP** : Review & Editing; **MS**: Review & Editing, Supervision.

Data accessibility

Supplementary material related to this article can be found, in CSV file: Supplementary Table S1 and Figures.

Conflict of Interest

None declared

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