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Testing the forest refuge hypothesis in sub-Saharan Africa using species distribution modeling for a key savannah tree species, *Senegalia senegal* (L.) Britton

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Abstract

Quaternary geographic range dynamics of savannah tree species are still not fully understood. The forest refuge hypothesis postulates that climatic and vegetational upheavals during the Pleistocene fragmented the previously continuous ranges of many species into isolated refuges that would have acted as shelters for rainforest taxa and allowed their survival through the Pleistocene cold stages. This hypothesis has recently been applied to studies of taxa in the African savannahs. We here test this hypothesis using the savannah tree species *Senegalia senegal* (L.) Britton., which is widely distributed across sub-Saharan Africa. Specifically, we ask the following questions: (i) Do we find evidence for savannah refugia during the last 130,000 before-present in sub-Saharan Africa? (ii) Would the climate in West Africa already have been suitable for *S. senegal* prior to the Last Glacial Maximum (LGM)? Using 1,132 occurrence records, we modeled the geographic distribution of *S. senegal* and projected the model into the past using climatic conditions from four time slices spanning the last 130,000 years bp. Our analyses show that the projected geographic extent of *S. senegal* was broader during the Last Interglacial, with a dramatic decline during the LGM and the subsequent recovery through the mid-Holocene to the present day. Our results indicate a range expansion at least from the mid-Holocene to the present and further show that *S. senegal* had similarly continuous distribution during the LGM as found today in sub-Saharan Africa. We also assessed the regional variation of environmental niche occupancy using a principal components analysis (PCA). The PCA reveals variation in the occupancy of environmental space across sub-Saharan Africa, a key indication of a wide ecological amplitude exhibited by the species. This study provides insights into the ancestral distribution and the temporal dynamics of a key savannah species that have shaped its current areas of occupancy.

Highlights

- Suitable climate for *Senegalia senegal* dominated the savannahs of sub-Saharan Africa since the Last Interglacial to the present.

- High suitability area for *Senegalia senegal* indicates that the species occupied a stable and wide possible range to allow its persistence and survival in open habitat rather than isolated refugia during the LGM, thus providing no support for the existence of savannah refugia for this tree species.

- Precipitation of the wettest month, seasonal potential evapotranspiration, soil pH, and the mean temperature of the wettest quarter are important environmental determinants of the distribution of *Senegalia senegal*.

- The insights into range dynamics and historical distribution for *Senegalia senegal* will be useful for predicting future responses to anthropogenic climate change in this species and related taxa.

Introduction

The distribution ranges of most organisms have changed over time subject to historical events that predisposed the Earth to climatic fluctuations throughout its history. Environmental driving forces acting during the Pleistocene, i.e., starting 2.6 Million years ago (Mya; Hampe and Jump 2011), resulted in repeated range contractions and expansions and have been decisive for the present-day geographic distribution of species (Harrison and Prentice 2003). In many cases, the fossil record provides evidence that extant species' ranges can be very different from past distributions, indicating the impact of past environmental changes (Steele 2007).

Several biogeographical hypotheses and mechanisms, including speciation (allopatric and parapatric), historical mountain ridges, climatic disturbance, as well as forest refugia, have been proposed to explain patterns of species distribution (Leite and Rogers 2013) in response to Pleistocene climate change. Earlier studies on palaeoecology, geologic, and climatic history of tropical continents and species highlighted the importance of glacial refugia (Moreau 1963, Ridpath and Moreau 1966). For example, Moreau (1966) investigated the bird faunas of Africa and its islands. These early works altogether inspired studies that resulted to what is today known as the forest refugia hypothesis.

The forest refugia hypothesis was initially formulated to explain species distribution patterns, especially vicariant distributions and high levels of endemism, for South American forest bird fauna (Haffer 1969). It gained wide application for explaining distribution patterns and range dynamics of faunas and floras across other continents, like Africa (Hamilton 1976, Maley 1989), Asia (Tang et al. 2018), Europe and North America (Hewitt 1996, Roberts and Hamann 2015). The hypothesis advocates that fragments of tropical forest would have acted as shelters for rainforest taxa and allowed their survival through the Pleistocene cold stages (Daïnou et al. 2010). Thus, species retreating into smaller patches, reduction in overall range size, and increase in fragmentation were notable events of the Pleistocene refugia (Sosef 1996, Flenley 1998). Several studies have been published in support of refugia during the cold and arid periods of the Quaternary in Africa (Maley 1989, Flenley 1998). These studies employed approaches such as palaeoclimatic analysis (Demenocal 1995), phylogeography and vegetation mapping (Voelker et al. 2010), palaeoecological analysis, and species distribution modeling (Prentice and Jolly 2000) to infer the historical distribution and presence of forest refugia.

In Africa, Pleistocene forest refugia were identified for plants in southwestern Nigeria, the South Cameroon highlands, Central Gabon (lowland), the northeastern Congo region, and the Tanganyika (Nyasa) highland areas (Hamilton 1976, Daïnou et al. 2010). In addition, forest refugia for mammals and birds were found in Upper Guinea, Gabon, the Congo Basin, the Ethiopian Highlands, the eastern African equatorial savannah and the Eastern Arc Mountains (Crowe and Crowe 1982,

Mayr and O'Hara 1986), the Angola–Namibia area, and the southeastern part of South Africa (Grubb 1982, Lorenzen et al. 2010). Further evidence shows that populations of some groups of mammals (Antunes et al. 2008) and reptiles (Kissling et al. 2016) in the African savannahs underwent historical genetic contractions and bottlenecks, likely surviving in refugia during the LGM (Dauby et al. 2010). However, unlike tropical forest species, evidence for savannah refugia for woody plants remain obscure even as some studies have referred to centers of origin and LGM refugia in the African savannahs (Leong Pock Tsy et al. 2009, Odee et al. 2012). Cold and dry climatic conditions were prominent over large parts of Africa during the LGM and may have provided a stable range for savannah tree species (Logossa et al. 2011). In addition, mid-Pleistocene evidence from paleogeomorphology, including recent observations from satellite data, indicated the absence of refugia in the eastern Democratic Republic of the Congo and around Lake Bosumtwi in lowland Ghana, with vegetation structurally similar to the present-day Sahelian grassland (Nichol 1999).

Although suitable climatic conditions pre-dating the LGM have been seen in other savannah tree species in west Africa, e.g., *Vitellaria paradoxa* commonly called the shea tree (Allal et al. 2011, Logossa et al. 2011), recent range expansion from eastern Africa, possibly during the Holocene humid period, has been hypothesized for *Senegalia senegal* based on phylogenetic analyses of ITS data (Odee et al. 2012). This implies that *S. senegal* may not have inhabited western Africa before this period.

The genus *Senegalia* s.s. comprises about 200 species (Terra et al. 2017), including *Senegalia senegal* (L.) Britton. (Fabaceae, Lindl.), a key savannah tree species of economic and ecological importance, known for its exudate named gum arabic (Fagg and Allison 2004). The most recent ancestor of *Senegalia* dispersed from the Americas during the late Miocene aridification that triggered the spread of open habitats in Africa, and subsequently diversified during the Plio-Pleistocene climate fluctuations (Bouchenak-Khelladi et al. 2010). Today, *S. senegal* is distributed throughout the arid Sudano-Sahelien, Zambezian and Southern regions of Africa where it is known to occur on a variety of soil types and in close proximity with other members of the *Acacia* (syn. *Senegalia*) species complex (Ross 1979). Four varieties have been described within the species: *Senegalia senegal* var. *senegal, S. senegal* var. *kerensis* (Schweinf.) Kyal. & Boatwr., *S. senegal* var. *rostrata* (Brenan.) Kyal. & Boatwr., *S. senegal* var. *leiorhachis* (Brenan.) Kyal. & Boatwr. East Africa is home to all the four varieties, while *Senegalia senegal* var. *senegal* occurs in West and Central Africa, var. *rostrata* and *leiorhachis* occur in southern Africa (Odee et al. 2012).

Inferring the past distribution of *Senegalia senegal*, which is the primary aim of this study, may help to provide clues to whether or not there were refugia for the species in its currently occupied distribution range within the African savannah. The geographical distribution coupled with the species' remarkable ecological characteristics makes it a good candidate

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for investigating range dynamics of savannahs and woodlands of tropical Africa. Therefore, we ask the following questions: 1) Do we find evidence for refugia for *S. senegal* during the last 130 ka BP across sub-Saharan Africa? We expect a reduction in overall range size, disjunct and fragmented geographic distribution during the LGM relative to the present, similar to forest species (both plants and animals) that retreated into smaller patches as their ranges contracted due to local extinctions, driven by the climatic changes of the Pleistocene (Maley 1989, Sosef 1996, Flenley 1998). 2) Would the climate in West Africa already have been suitable for *S. senegal* before the LGM? As it has been shown for the shea tree (Allal et al. 2011), we expect that the climate pre-dating the LGM would already have been suitable to support the distribution and survival of *Senegalia senegal* in West Africa, and that habitat suitability will be continuously high because savannahs throughout Africa are ancient, originating during the late Miocene aridification. To answer these questions, we use a species distribution modeling (SDM) approach to estimate the geographic extent of appropriate climatic conditions in Africa at the Last Interglacial (LIG ~ 130 ka BP), the Last Glacial Maximum (LGM ~ 21 ka BP), and the mid-Holocene (~ 6 ka BP) to potentially sustain populations of *Senegalia senegal.* We then draw inference from the evidence provided by our data.

Material and Methods

Species occurrence records

We compiled occurrence point locations for *S. senegal* in Africa from the Global Biodiversity Information Facility (GBIF[1]), scientific literature and field surveys undertaken between 2013 and 2018. Regions where the species has been introduced (i.e., the non-native range), such as the Middle East or South Asia, were not considered in the study. We cleaned occurrence records (initial number = 4,339) in a stepwise fashion. First, we double-checked all point locations to ensure correct assignment of the coordinates. We removed all occurrence records with imprecise coordinates and excluded all duplicate records, resulting in 2,070 occurrence records.

These 2,070 occurrence records were filtered (Boria et al. 2014) to avoid spatial autocorrelation (Duque-Lazo et al. 2016) and spatial sampling bias (Beck et al. 2014). The final dataset comprised 1,132 occurrence records of *S. senegal* spatially separated by the hypotenuse of pixel resolution ~1,500 meters (Table S1). We then generated ten sets of an equal number of randomly distributed pseudo-absences (Navarro-Cerrillo et al. 2018) within the study area, with a minimum spatial distance of 1500 m, using the *biomod2* R package (Thuiller et al. 2009).

Past and present environmental layers

We used the 19 bioclimatic variables available from the Worldclim database (Hijmans et al. 2005)

and 66 soil-related variables (Hengl et al. 2017), together with thirteen climatic variables derived from the ENVIREM R package (Title and Bemmels 2018), to assess the current potential distribution of *Senegalia senegal* (Table S2). We also downloaded past climatic conditions according to two General Circulation Models (GCMs) from the Worldclim database (Hijmans et al. 2005): the Community Climate System Model Version 4 (CCSM4; see Watanabe et al. 2011) and the Model for Interdisciplinary Research on Climate–Earth System Model (MIROC-ESM; see Gent et al. 2011) for the LIG, LGM and mid-Holocene. We spatially re-sampled current and past datasets by nearest neighbourhood assignment to 30 arc-seconds grids at WGS 84 spatial reference system.

Variable reduction and importance

We reduced the environmental variables (n=98) using variable inflation factor (VIF<10) (Duque-Lazo et al. 2016) and the AUCRF R package (Calle et al. 2011, Kukunda et al. 2018). We considered the non-collinear variables that maximized the AUC value of the Random Forest (RF) model prediction (Kukunda et al. 2018). We considered two important criteria in selecting the variables: variable importance and probability of selection. The variable importance measures how much influence an explanatory variable has on the model while the probability of selection is the probability that a particular variable is statistically selected for inclusion in the modeling (Table 1). Variable importance measurement implemented in the R-package AUCRF offers two different importance measures: the mean decrease Gini (MDG) and mean decrease accuracy (MDA), respectively (Calle et al. 2011). The higher the value, the more influence it has on the model.

Estimation of the current and past potential distribution of Senegalia senegal

The current and past potential distributions of *Senegal senegal* were estimated by ensemble SDMs. We used biomod2 R package, which accounts for inter-model variability by fitting ensembles of forecasts (Araújo and New 2007) and incorporates 10 SDM algorithms (Thuiller 2014, Duque-Lazo et al. 2018a). The ensemble methods employed are based on the statistical combinations of single algorithm predictions, i.e., single algorithm predictions were combined by their median, mean, coefficient of variation (CV), and confidence intervals using the statistical functions. The probability mean weight decay (MWD) and committee averaging (CA) methods preselected the single models based on certain predefined criteria. The CA was achieved by a binary (presence/absence) transformation using the threshold of single model predictions. The threshold is the one that maximized the True Skills Statistics (TSS) evaluation metric. Subsequently, we calculated the probability value of each pixel by the mean of single pixel predictions. The MWD ensemble modelling scaled the individual model predictions according to their accuracy statistic value (AUC) and the sum of all

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1 www.gbif.org; last accessed on 13/11/2019

Table 1. Variable importance ranking of the environmental variables used for modeling the distribution of *Senegalia senegal* in Africa. The final set of variables that were selected to run the model are highlighted in bold. Variable importance measures how much influence a particular variable has on the model. The higher the value, the more influence it has on the model. Probability of selection: the probability that a particular variable is selected during the variable selection procedure of the modeling.

Rank	Variable codes	Importance	Probability of selection	Variables
1	**bio_13**	**59.65**	**1.00**	**Precipitation of wettest month[1]**
2	**petsea**	**58.67**	**1.00**	**Seasonal potential evapotranspiration[3]**
3	**pHikcl_sl1**	**50.42**	**1.00**	**Soil pH[2]**
4	**bio_8**	**41.8**	**1.00**	**Mean Temperature of Wettest Quarter[1]**
5	bio_18	41.75	1.00	Precipitation of Warmest Quarter[1]
6	bio_3	39.06	1.00	Isothermality (BIO2/BIO7) (* 100)[1]
7	bio_9	32.36	1.00	Mean Temperature of Driest Quarter[1]
8	Ncontent	30.03	0.99	Nitrogen content[2]
9	bio_15	28.76	1.00	Precipitation Seasonality (Coefficient of Variation)[1]
10	bdticm	27.44	0.99	Absolute depth to bedrock[2]
11	cecsol_sl7	25.98	0.95	Cation exchange capacity of soil at depth 2.00 m[2]
12	bio_19	24.77	0.98	Precipitation of Coldest Quarter[1]

Note: [1] Hijmans et al. 2005; [2] Hengl et al. 2017; [3] Title and Bemmels 2018.

individual models (Duque-Lazo et al. 2018b). Ensemble model predictions were based on the combination of single models with TSS > 0.70. Finally, it should be noted that the reliability of hindcasted SDMs to past climatic conditions is premised on the assumption of niche conservatism, which is the tendency of species to retain ancestral ecological characteristics over time (Wiens et al. 2010).

Model calibration and validation

We randomly split our dataset into two subsets, 70% of the data to train the model and 30% for model evaluation using cross-validation (100), which yielded 100 different fits per model. Models with higher mean values and smaller variations were considered as being the most accurate ones (Duque-Lazo et al. 2016). We used three evaluation metrics to assess model performance: AUC of the Receiver Operating Characteristic plot (Lins et al. 2018), Cohen's Kappa (Franklin 2010), and True Skill Statistics (TSS; see Allouche et al. 2006). Two of the measures (TSS, Kappa) are threshold dependent and one (AUC) is independent of threshold. The AUC represents the models' discriminative capacity with regard to the data by testing whether the predicted pattern in the other range differs significantly from a random prediction, compared to the prediction achieved in the same range. It is obtained by plotting the omission error (sensitivity; actual or correctly identified positives) against the commission error (1 – specificity; false positives) for numerous thresholds. The closer the AUC value is to 1.0, the better the fit whereas 0.5 or lower indicates that the model is no better than random (Lins et al. 2018). Cohen´s Kappa (κ) was derived from the 2x2-confusion matrix to measure the rate of agreement between actual and predicted values in the spatial space for categorical Kappa values; however, the matrix depends on the defined threshold for presence. Values of κ near to 0.5 indicate no discrimination capacity (random agreement), whereas a value of 1 represents the perfect discrimination model (Franklin 2010). The TSS deals with omission and commission errors and is prevalence independent. It ranges from -1 to +1, where +1 indicates perfect agreement and <0 indicates a random performance. The TSS measures the difference between the actual agreement and the randomly expected agreement. Kappa and TSS were calculated and evaluated, considering a threshold equal to prevalence as described by (Franklin 2010).

Distribution maps

We generated continuous probabilistic maps for the current and past potential distributions of *S. senegal* in its native range in Africa. We also estimated the coefficient of variation (CV), which is a measure of uncertainty of model predictions. To assist the visual interpretation of the model predictions, the probability values were classified into five categories (0 – 20%, very low; 21 – 40%, low; 41 – 60%, moderate; 61 – 80%, high; 81% - 100%, very high). To calculate shifts in the range of the species from the past to the current distributions, we reclassified the probabilities as 0 (unsuitable habitat) and 1 (suitable habitat), with a similar threshold as employed in calculating TSS and Kappa. The changed area was presented as percentage of total area loss (<100%) or gained (>100%). Additionally, we highlight the variance in the probability of occurrence of the species using response curves to provide an overview on habitat

suitability of the species in relation to the tested environmental variable (Elith et al. 2006).

Testing for ecological variations in local environments

To test if niche conservatism may be assumed as a precondition for analyzing our data, we estimated the environmental space (bioclimatic and edaphic) of *Senegalia senegal* in Africa. This step is vital to elucidate whether or not the species occupies a uniform environmental space across Africa, as recent phylogeography of *S. senegal* identified three genetic groups corresponding to geography (west-east-south) in Africa (Odee et al. 2012). However, we included a fourth group (central Africa) in our analysis to correspond with the geographic regions that form part of the species' range in Africa (and since a reasonable number of occurrence records were from this region). We extracted the values of the most important non-collinear variables (obtained from the variable selection procedure mentioned above) for all occurrence points (n=1,132). We grouped these data into four geographical categories: western (WA), central (CA), eastern (EA), and southern (SA) Africa, respectively. In addition, we randomly sampled 500 background points for each region. To evaluate environmental divergences (heterogeneity) within *S. senegal* and compare the realized ecological space within the four regions to the corresponding available environmental space (background data), we performed a principal components analysis (PCA) in R for two independent

sets of data: (1) occurrence records only; (2) combined - occurrence with background points. We also compared the extracted values of seven environmental variables with the highest importance values for each region and plotted the variations on a boxplot.

Results

Variable selection

The variable selection procedure identified 12 variables as the most relevant for estimating the potential current distribution of *Senegalia senegal* within Africa (Table 1). We used four of these variables with the highest importance values (Table 1, in bold) for the final model, assuming that the soil pH did not change through time and because a lower number of variables tends to reduce model complexity, improve extrapolation, and accuracy in space and time (Duque-Lazo et al. 2016).

The variance of the probability of occurrence for *Senegalia senegal* based on the range of the tested environmental variables is highlighted in the response curves (Fig. 1A - D). According to these data, *S. senegal* prefers conditions with temperatures ranging from 20°C (during the wettest quarter of the year) to about 35 °C (during the warmest quarter of the year), with an optimum probability of occurrence around 29 ºC and limited rainfall (as low as 100 mm per annum). The soil pH for *S. senegal* ranges between 4.0 and 8.0, indicating that the species thrives in slightly acidic to moderately alkaline soils. Specifically, the response curves showed
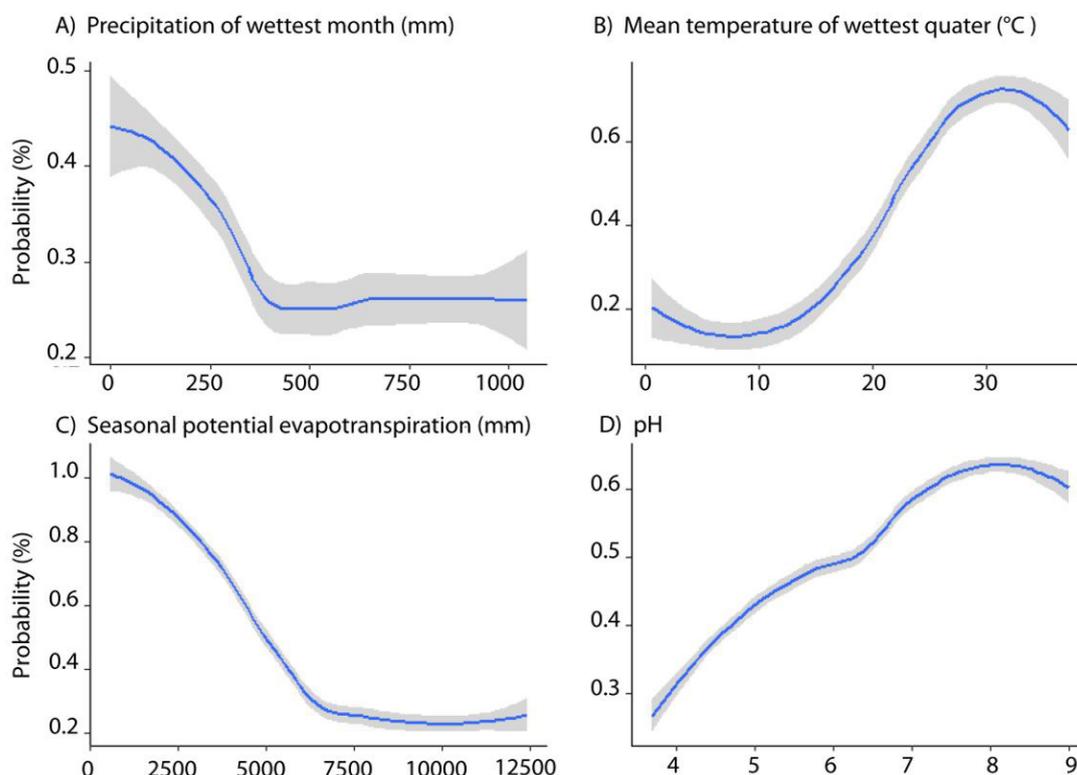

Figure 1. Response curves from the committee averaging ensemble model showing the tolerance of *Senegalia senegal* for the four selected environmental variables (see Table 1) in Africa. Grey band indicates the standard deviation derived from the response curves of different ensemble model predictions.

that the present-day distribution of *S. senegal* is highly controlled by the mean temperature of the wettest quarter, precipitation of the wettest month, seasonal potential evapotranspiration, and soil pH.

Model performances and present potential distribution

Apart from two algorithms (ANN and SRE), all model algorithms performed similarly and produced projections that are supported by good evaluation scores, although BRT and RF slightly outperformed all the others (Fig. 2). The accuracy values obtained for the six ensemble methods indicated a good performance of the model (Table 2). The AUC values ranged between 0.957 (Upper confidence interval) and 0.976 (Lower confidence interval), while the TSS ranged between 0.812 (Upper confidence interval) and 0.865 (Committee averaging - CA), indicating good to very good agreement of the model to the data. The high sensitivity and specificity values (Table 2) produced by the models highlights a very low omission and commission error rate, respectively, being evidence for accurate discrimination between presences and absences in the models. We decided to map the ensemble model with higher TSS accuracy value.

We show the distribution of occurrence records (Fig. 3A) used in this study to project the potential distribution of *Senegalia senegal*. According to the ensemble current potential distribution map (Fig. 3B), areas with high probability of occurrence included northeastern Nigeria and southern Republic of Niger, extending along the Sudano-Sahelian zone.

Also included are Eastern Africa Acacia-Commiphora bushland, South African bushveld, and the north of Naukluft - areas surrounding the Spitzkoppe Mountains extending northwards and covering most parts of the savannah woodland vegetation in Namibia (Fig. 3B). The CV shows the variation between single model prediction (Fig. 3C), and the low values (represented by areas in darker blue) in the CV map indicates an increased certainty of the observed species' presences.

Occurrence of Seneglia senegal from the Last Interglacial to mid-Holocene

Hindcasting the distribution of *Senegalia senegal*, retrieved from present bioclimatic and edaphic variables suggests that, in general, climatic conditions suitable for the survival of *S. senegal* were widespread in the past, extending from East to West and to Southern Africa (Fig. 3D-F). Our result showed that the range size of *S. senegal* at the LIG surpassed the current potential range by at least 4% (CCSM4, Table 3) and that habitat suitability for the species was highest at the LIG. Areas of high suitability declined through the LGM by 12.1%, with a steady recovery of about 9% during the mid-Holocene. There was a more constricted and less dense distribution along the Sudano-Sahelien range of the species during the LGM.

However, habitat suitability appears to be reduced from the easternmost edge of western Africa to the northern range of central Africa, as well as reduced geographic connectivity between the East and Southern ranges during the mid-Holocene, as shown by the light green colours. In addition, hindcasting
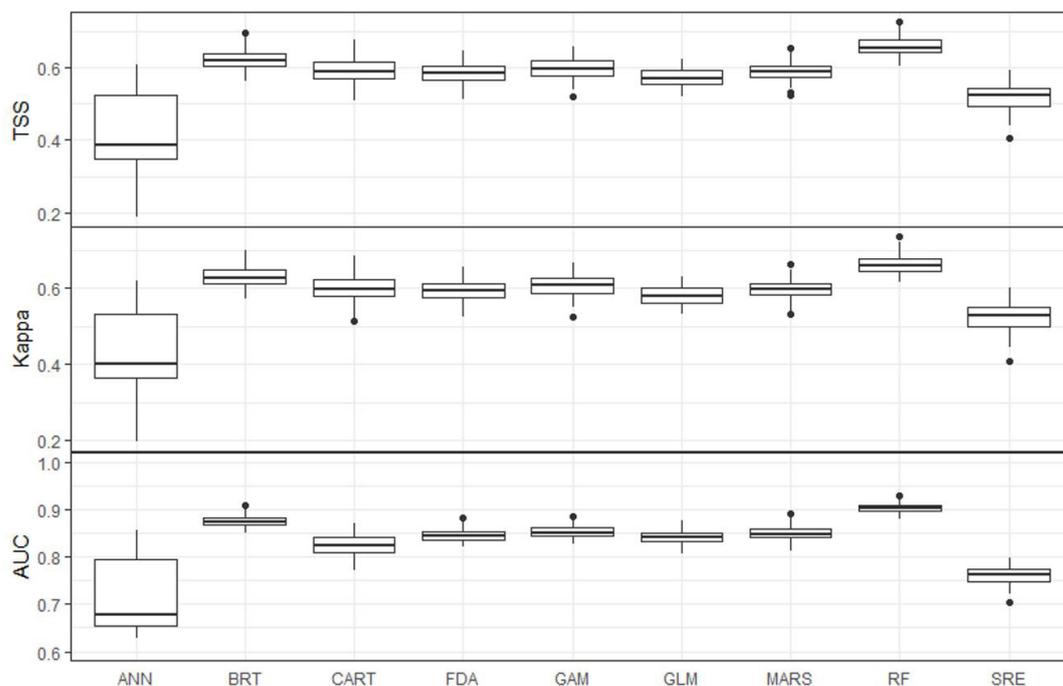

Figure 2. Plot of model performance (TSS, Kappa, AUC) for 100 repetitions of each algorithm, including Artificial Neural Networks (ANN), Boosted Regression Trees (BRT), Classification and Regression Trees (CART), Flexible Discriminant Analysis (FDA), Generalize Additive Models (GAM), Generalized Lineal Models (GLM), Multivariate Adaptive Regression Splines (MARS), Random Forests (RF), and Surface Range Envelop (SRE).

Table 2. Accuracy values obtained from the ensemble models of *Senegalia senegal* habitat suitability prediction in Africa: Cohen´s Kappa (Kappa), Area Under the Curve (AUC), True Skills Statistics (TSS), Sensitivity (true positive rate), Specificity (true negative rate).

Ensemble model	Kappa	TSS	AUC	Sensitivity	Specificity	Threshold
Mean	0.822	0.821	0.974	0.924	0.926	0.594
Lower Confident interval	0.831	0.830	0.976	0.935	0.896	0.500
Upper Confident interval	0.814	0.812	0.957	0.930	0.881	0.771
Median	0.820	0.865	0.973	0.908	0.956	0.785
Committee averaging	0.861	0.865	0.973	0.903	0.956	0.783
Probability mean weight decay	0.822	0.822	0.974	0.920	0.903	0.599

Table 3. Result of Committee Averaging and Mean Weight Decay ensemble models for the CCMS4 scenario showing changes in distribution area of *Senegalia senegal* through time, relative to the present-day.

Time Period	Committee Averaging (%)	Mean Weight Decay (%)
LIG	101.94	103.31
LGM	89.52	90.86
mid-Holocene	98.85	98.26
Current	100	100

Predicted area percentage with % > 100% = Area gained and % < 100% = Area loss. Model evaluation is by the TSS.
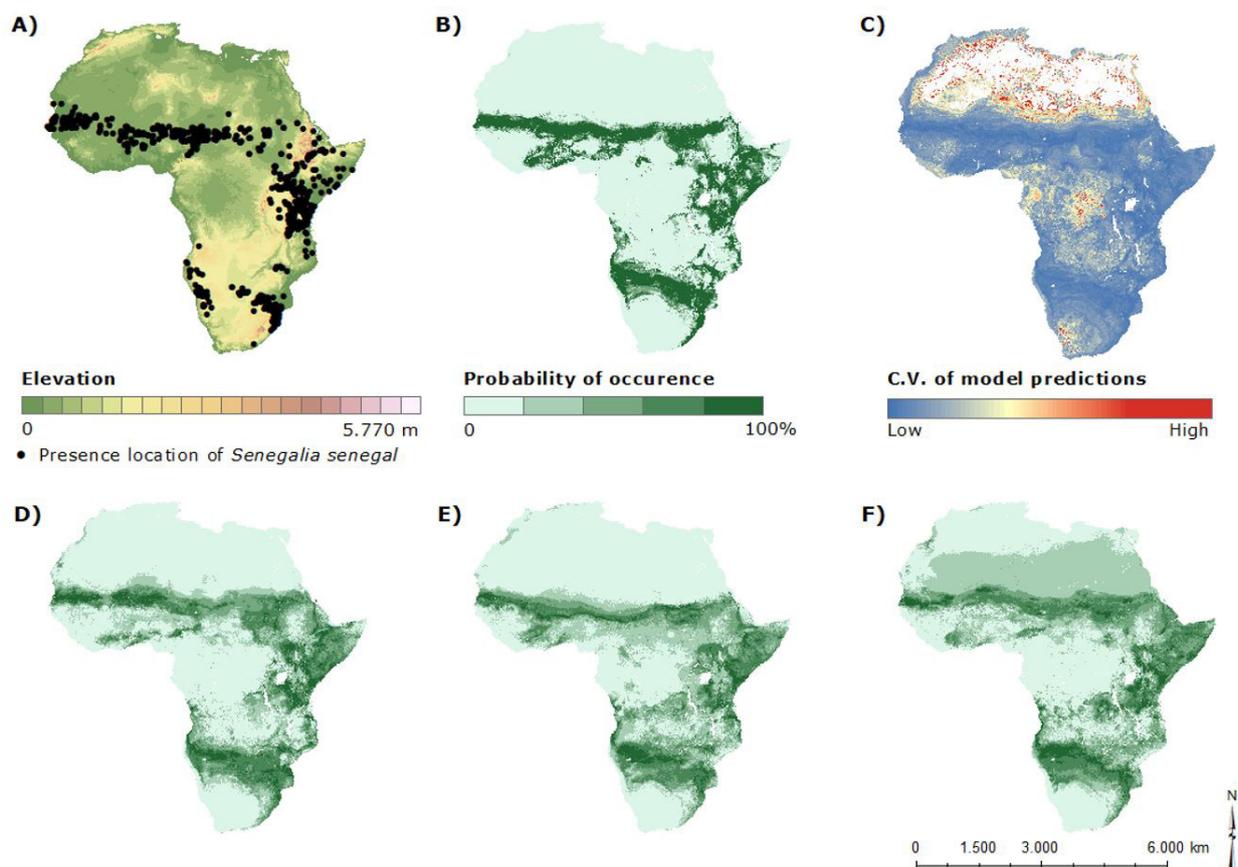

Figure 3. Past and present potential distribution of *Senegalia senegal* in Africa. A) Occurrence records; B) Present-day habitat suitability; C) Coefficient of variation of model predictions. Habitat suitabilitys for the, D) mid-Holocene; E) Last Glacial Maximum; F) Last Interglacial. Dark green shading in (A) indicates lower elevation and light shading indicate higher elevation; black dots in (A) show the occurrences of *S. senegal* used in this study. (B; D-F) Darker colours indicate higher habitat suitability. Prediction maps of habitat suitability are based on ensemble model predictions.

indicates that *Senegalia senegal* potentially inhabited geographic areas (e.g., Central part of the Guinean savanna in present day Ghana, Togo and Benin) that are not occupied by the species in the present-day. We observed similar patterns of distribution for both CCSM4 and the MIROC-ESM scenarios, therefore we present results for the CCSM4 scenario.

Environmental variation

The first two axes of the principal components analysis (PCA) cumulatively explained 59.6% of the variance (Fig.4). Factor loadings of PC1 (explaining 41.1% of the variance) are associated with a gradient in temperature, precipitation, and soil fertility, with the strongest correlates being mean temperature of the wettest quarter (Bio 8), precipitation seasonality (Bio 15), seasonal potential evapotranspiration (Petsea), Isothermality (Bio 3), precipitation of the warmest quarter (Bio18), and nitrogen content (N-content). The positive loading of precipitation seasonality (Bio 15) on the first axis shows that at warmer temperatures, rainfall is more seasonal in West and Central than in the East and South of Africa. In addition, temperature during

the wettest quarter ranging from 17.4 °C in East Africa to 30.2°C in West Africa indicates that temperature decreases with wetness. PC2 explained 18.5% of the variation and mainly corresponded to variation in precipitation, temperature, soil cation exchange capacity (CECSOL_sl7) and soil pH. Precipitation of the wettest month (Bio 13), mean temperature of the driest quarter (Bio 9) precipitation of coldest quarter (Bio 19) loaded positively on PC2 axis and correlate with an increase from drier environment in southern Africa to more humid in eastern Africa (Fig. 4). Soil pH (PHIKCL_sl1) loaded negatively on this axis with a decrease in pH as one moves from the South towards the East of the distribution range. Furthermore, the data revealed Eastern Africa as the only region overlapping with all other regions, and West Africa almost entirely overlapping with Central Africa, and a strong spatial discontinuity, discriminating occurrence records from Southern Africa (blue) from those of Western Africa - in purple (Fig 4). However, Western and Southern Africa are the most distinct observed environmental spaces in the PCA graphic, and this is supported by the boxplot showing the distribution of environmental variables
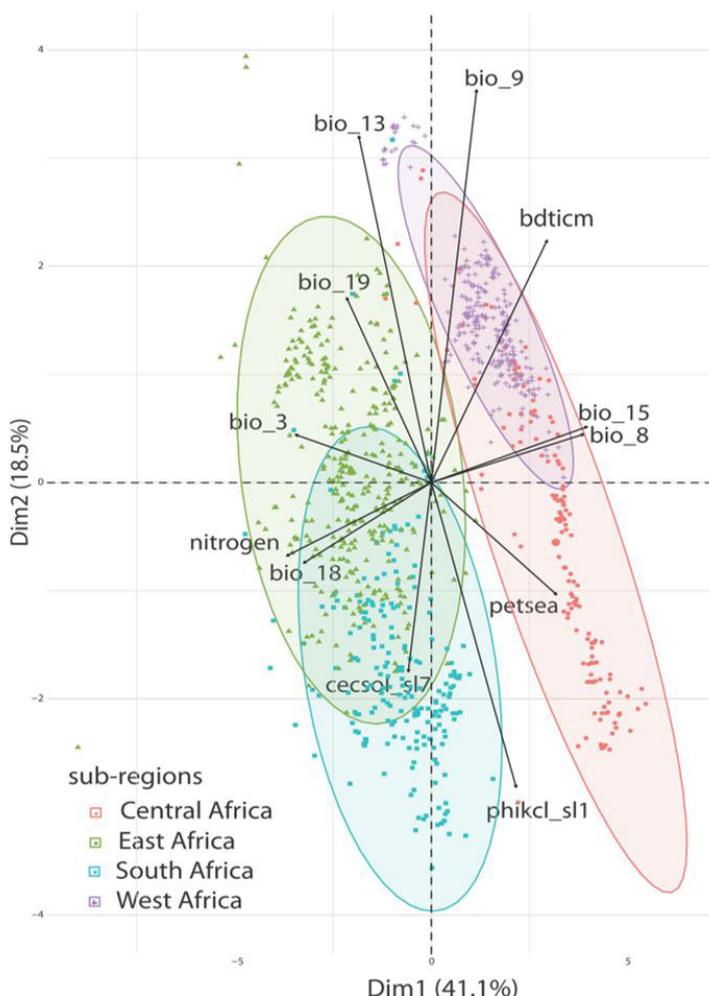

Figure 4. Principal Components Analysis (PCA) of all 1132 occurrences of *Senegal senegal* across four subregions of Africa. Colors correspond to the four geograhic regions: West (purple), Central (red), East (green), and South Africa (blue), details of the 12 environmental variables used for the PCA can be found in Table 1.
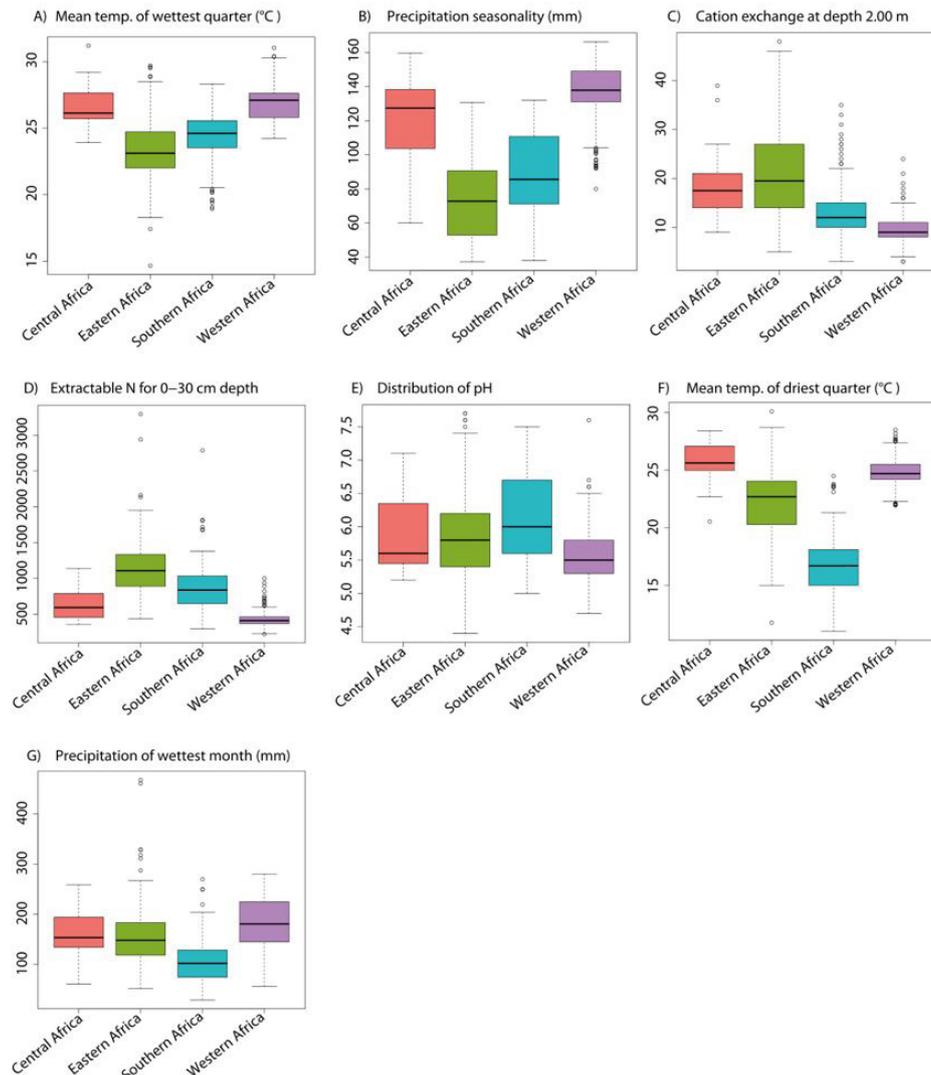
Figure 5. Boxplot showing the distribution of A). mean temperature of wettest quarter; B). precipitation seasonality; C). cation exchange at depth 2.0; D). extractable nitrogen for 0-30 cm depth; E). soil pH; F). mean temperature of driest quarter; G). precipitation of wettest month based on all 1,132 occurrences of *Senegalia senegal* in the four subregions of Africa (West, Central, East, South Africa).

for the four regions (Fig. 5A-G). Finally, the sampled background points (Fig. S1) show that the observed differences in occupied environmental space throughout the native range of *Senegalia senegal* (Fig. 4) are due to regional environmental differences rather than to differential occupation of a shared fundamental niche (i.e., populations occupy the environmental space available to them within each subregion). While this of course does not rule out local adaptation, these data should not be interpreted as conclusive evidence for an ecological divergence between populations of *S. senegal* across sub-Saharan Africa. More data (e.g., transplantation experiments) would be needed to further understand this pattern

Discussion

The projected palaeodistribution of *Senegalia senegal* during the pre-glacial and postglacial period

indicates that the species generally should have had a wide and stable geographic distribution, with only slight changes in range size in relation to the present geographic distribution. Our results are interpreted within the framework of prediction while acknowledging the limitations of the SDM approach (Araújo and Guisan 2006, Araújo and Peterson 2012). We note that *S. senegal* is an important economic species (utilized in the food industry for making food additives, source of fodder for animals; used in the manufacture of lithographic inks and dyes, as well as its ecological relevance in agroforestry, land degradation and desertification control). Therefore, its current distribution might have been influenced by human activities. However, we view human management as an advantage because it brings the current distribution (realized niche) fairly close to the fundamental niche. We here discuss the range dynamics and factors that might have acted during the Quaternary to drive distribution of *S. senegal* and

whether or not the African savannahs once acted as refugia for *S. senegal* during the LGM.

Quaternary climatic fluctuations and suitable areas for Senegalia senegal

Previous phylogeographic studies of savanna species, such as the African locust bean (*Parkia biglobosa* G. Don) and the Shea tree (*Vitallaria paradoxa*), showed a narrow distribution range during the LGM and a post-glacial expansion of suitable habitat (Allal et al. 2011, Lompo et al. 2018). Historical distribution of *Cedrus atlantica* in the North African montane ecosystem using SDM also showed a reduced distribution range during the LGM and a recovery in the mid-Holocene (Benito-Garzón et al. 2007). Range changes found in these studies are vital and comparable with our study where climatically suitable areas for *Senegalia senegal* underwent a cyclic reduction and expansion throughout the four time slices (Table 3). Our model highlighted a broad LIG suitability area distribution, followed by a retreat during the LGM and a progressive expansion through the mid-Holocene, also known as the African Humid Period (hereafter AHP: between ca. 12 000 and ca. 5500 cal yr BP), towards the present.

The highly climatically suitable areas predicted during the LIG suggest that *Senegalia senegal* could have occupied wider ranges (including western Africa) than previously thought and this is consistent with the findings from ENMs of other savannah tree species, such as *Vitellaria paradoxa* (Allal et al. 2011). Given the potentially wide palaeodistribution as inferred by our data, different species of *Senagalia* could have been widely distributed from the LIG, since *S. senegal* is known to co-habit with other members of the *Acacia* (syn. *Senegalia*) *senegal* complex, or it simply could have occupied a diversity of habitats (moist-dry woodland to shrublands) (Bouchenak-Khelladi et al. 2015). It is evident that local glacial refugia were fundamental in preserving and safeguarding the vegetation (Vessella et al. 2015). However, the broad areas of high suitability predicted by our hindcasting suggest a stable and wide possible range for *S. senegal,* which negates the existence of savannah refugia in sub-Saharan Africa, particularly for species adapted to the arid environment. This finding is consistent with previous studies where stable and wide distributional ranges were observed for other African savannah woody species, such as the shea tree, through time, providing no support for refugia or large scale range expansion (Logossa et al. 2011).

The small area of suitable climate observed between the Western and Eastern ranges (with paleo-Lake Chad as a barrier) and those of the South (with a barrier from southern Cameroon up to northern Angola) during the mid-Holocene (Fig. 3D; Table 3) partly corresponds to the phylogeographic divisions for the species in the region (Odee et al. 2012). However, this can be linked to the vegetation history of the African savannah flora. After the LGM, there was evidence of active sand dunes in parts of the modern-day Sahel (Bristow and Armitage 2016), whereas *Senegalia senegal* was more likely distributed in the southern parts of the Sahel into the Sudanian savannah (Fig. 3D-E). The most prominent environmental change in Africa (particularly in the North) over the past 10,000 years has been the mid-Holocene transition from the "green Sahara" to the present hyper-arid desert (Amaral et al. 2013). This change had an impact on ecosystem responses, including for the vegetation belts below the Sahara such as the Sahel. For instance, sedimentary records show that the modern Sahel and parts of the Sahara region were moister during the AHP (Hoelzmann et al. 2004). Phytogeographic studies and pollen analyses from the West African Sahel pointing towards widespread Sudanian elements in the Sahelian zone are the most compelling evidence that the Saharan vegetation has been expanding and retreating (Lézine 1989, Dupont 1993). The heterogeneity of the Sahel vegetation during the mid-Holocene was further supported by pollen and charcoal evidence (Ballouche and Neumann 1995). These ecosystem and vegetation dynamics may explain the small projected suitable area for *Senegalia senegal* in the mid-region of the Sudano-Sahelien range, near the lake Chad during this time period (Fig. 3D), as the species is known to be intolerant to high soil moisture or waterlogged soils (Ross 1979). Furthermore, the expansion and contraction of the moist rainforest across East Africa (Cowling et al. 2008) spurred the reduced geographic connectivity between the East and southern suitable areas. The aridification following the AHP created opportunities for new habitats, with the accompanying wind (monsoons) potentially exacerbating dispersal and reconnecting previously separated populations of *Senegalia senegal* by the end of the AHP. Potential, Sudanian populations could have migrated westwards, while the populations from Northeastern Nigerian could have migrated eastwards. As an arid-adapted species, *S. senegal* could have taken advantage of its dispersal capabilities and expanded along the Sudano-Sahelian zone, as seen in the present-day potential distribution. The potential distribution of *S. senegal* observed in the hindcast in areas not occupied by the species today is supported by palaeogeomorphological evidence from humid forest showing that most of today's west African forest zones were semi-arid, seasonal climate with open woodland and grassland (Burke et al. 1971, Thomas and Thorp 1992). As it has been shown for *Vitellaria paradoxa*, northward shifts of the African vegetation zones during wetter periods (Fontaine et al. 2004) might have led to the loss of centrally located populations of *S. senegal* due to out-competition by plant species tolerant of excess water during episodes of wetter climate.

Regional variation in the environmental space

As much as the realized environmental space for *Senegalia senegal* throughout Africa may share some common ecological conditions, there are variations along climatic and edaphic regimes separating the eastern and southern from the western and central African populations (Figure 5A-G). This suggests that populations of *S. senegal* might have undergone some degree of environmental differentiation throughout

Africa that subsequently led to its wide and remarkable ecological amplitude. However, it should be noted that populations fill the regionally available environmental space (Fig. S1), suggesting that the observed divergences may be non-adaptive. Furthermore, the occurrence clouds in the PCA graph of all 12 variables (Table 1; Fig. 4; Fig. S1) clearly reflect a pattern of environmental connectivity that is in keeping with the connection of vegetation belts across the species' range in Africa, i.e., West-Central-East-South. Finally, the central position occupied by eastern Africa (as shown by the overlap in the PCA) highlights the importance of this region in population connectivity across the range of *S. senegal* in Africa. This finding is supported by phylogenetic data of the species (Odee et al. 2012).

Conclusion

Contrary to our initial expectation, our hindcasting results support the idea that *Senegalia senegal* may have prevailed in parts of the species' native range in Africa during the Quaternary. In addition, we found no clear range disjunctions between the savannah vegetation block throughout the species' range in Africa, which would suggest range fragmentation, especially where once widespread savannah habitats persisted only as fragments throughout the LGM (Donkpegan et al. 2020). Therefore, our data do not support the existence of isolated African savannah refugia for *S. senegal* at the LGM. We show that the areas currently inhabited by *S. senegal* in Africa were climatically already suitable and may have supported populations since at least 130 ka. Given that the LGM represents an extreme scenario of the Pleistocene climatic fluctuations, with intermediate states appearently being more common (Morley 2012, Flantua et al. 2019), populations of *S. senegal* may have thus persisted substantially longer.

Furthermore, the range-wide suitability area maps from the LIG obtained from this study support our expectation that *S. senegal* may already have been present in western Africa before the Holocene. Additionally, our study provides the potential for investigating spatio-temporal ecological connectivity between regions (West-East and East-South) for tropical savannah tree species. Future studies should incorporate population genetic data to investigate the role of historical range dynamics in shaping the contemporary genetic structure of *S. senegal* in Africa and the implications for biodiversity conservation. Finally, an understanding of whether or not genetic diversity of *S. senegal* was preserved during climatic changes of the past should be investigated as this could give insights into the impact of such changes on current genetic diversity patterns and the fate of the species under a changing future climate.

Acknowledgments

Author contributions

PTL and ANM-R conceived of the research idea; PTL, JS, and FH, designed the research; PTL conducted fieldwork and data sampling; PTL and JD generated and analyzed data; PTL interpreted the results and drafted the manuscript; all authors discussed the results and contributed critically to the draft. ANM-R and JS supervised the research.

Supplementary Materials

The following materials are available as part of the online article from https://escholarship.org/uc/fb
Supplementary Table S1. Sampled occurrence records used in the study.
Supplementary Table S2. Variables used in the study.
Supplementary Figure S1. PCA for the background points and occurrence records for the distribution of Senegalia senegal across the four geographic regions (Central, East, South and West) of Africa.

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