

PREDICTING HABITAT SUITABILITY FOR *VACHELLIA STUHLMANNII* (TAUB.) AND *VACHELLIA TORTILIS* (FORSK.) IN SEMI-ARID AFRICAN SAVANNA USING MAXENT

NKOSI, S. E.

Department of Environmental Sciences, University of South Africa, Private Bag X6 Florida
Science Campus, 1710 Johannesburg, South Africa
(e-mail: nkosise@unisa.ac.za; phone: +27-11-471-2128; orcid.org/0000-0002-4197-2098)

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Abstract. Habitat suitability of *Vachellia stuhlmannii* and *Vachellia tortilis* was evaluated using MaxEnt. Location data was collected, and nineteen bioclimatic variables data downloaded from the WorldClim database. Soils were analysed to investigate their influence on habitat suitability of the two species. MaxEnt effectively predicted current habitat suitability with an average test Area Under Curve value of 0.936 for *V. stuhlmannii* and 0.689 for *V. tortilis*. Key influential variables were BIO-1 (Annual mean temperature) with 71.7% highest gain for *V. stuhlmannii* and BIO-17 (Precipitation of driest quarter) with 65.3% highest gain for *V. tortilis*. However, BIO-14 (Precipitation of driest month) exhibited limited influence in predicting habitat suitability. *V. stuhlmannii* is estimated to cover an area of ~3 255.8 hectares, while *V. tortilis* is estimated to cover ~11 180.7 hectares. Both species predominantly occur on Prisma-cutanic/pedocutanic B-horizons. *V. tortilis* also thrive on Glenrosa and Mispah soils, which are crucial for diverse plant and animal life. These findings have practical implications for conservation efforts aimed at protecting these species. Identifying suitable habitats and preserving soil types is crucial as soil affects microclimate conditions and influences moisture retention. Overall, this study provides insights for the conservation of *V. stuhlmannii* and *V. tortilis* in the semi-arid African savanna.

Keywords: bioclimatic variables, Area Under Curve (AUC), Receiver Operating Characteristic (ROC), prediction, omission rate

Introduction

African elephant (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*) and fire directly influence the structure of woody vegetation by acting as mortality, reversal or growth-retardation agents (Pellew, 1983). Trees taller than 6 meters are not susceptible to fire but may be vulnerable to elephant and giraffe browsing impact. According to Pellew (1983), the impact of giraffe is more observed mainly on trees between 2 – 3 m than any other height class. Increasing elephant populations in confined protected areas and their impact on woody vegetation have received attention for some time and several studies (Coetzee et al., 1979; Waithaka, 1993; O'Connor and Page, 1997; Duffy et al., 2002; Baxter, 2003; Landman et al., 2005; Kerley and Landman, 2006; Rode, 2010; Ndoro et al., 2016) have been conducted to study these effects. According to O'Kane et al. (2011), elephants and giraffes are likely to utilize shared feeding areas, potentially mitigating resource depletion more effectively compared to smaller herbivores. They achieve this by concentrating their foraging efforts in specific regions of their extensive habitats that offer optimal plant parts and a diverse forage mix. This behaviour occurs with a degree of independence from the presence of predators. Elephants have been observed to show seasonal preferences for different parts of certain woody species (Hiscocks, 1999). Similarly, showing preferences for certain tree species (Gadd, 2002; Jacobs and Biggs, 2002; Gandiwa et al., 2011; Mukwashi et al., 2012; Kupika et al., 2014; Seloana et al., 2017).

Vachellia (Acacia) tortilis (Forsk.) is one of the species found to be selected by elephants (Mwalyosi, 1987; MacGregor and O'Connor, 2004; Gandiwa et al., 2011). This species can grow 3 meters height over a period of 3 years in a system where fire and browsing are excluded and would coppice following a fire with good rains (Croze, 1974). *V. tortilis* dominates drier ridge top and upper slopes where dry-season soil moisture is limited (Pellew, 1983). Its natural flat-topped lateral growth form allows the species to shade out competition of other species while developing seedlings provide adequate soil moisture for its survival (Pellew, 1983). The impact of African elephants on *V. tortilis* woodlands have been reported to lead to the transformation of these woodlands into open woodlands (MacGregor and O'Connor, 2004; Gandiwa et al., 2011), and elephants browsing significantly lead to 9.0% mortality of *V. tortilis* per annum, resulting in the replacement of the species (Mwalyosi, 1987) and density reduction (Mwalyosi, 1990). Kalembera (1989) found that *V. tortilis* is generally foraged in proportion to its abundance and forms a large proportion of elephant diet in high-density woodlands and less in lower-density woodlands with a mixture of the availability of other woody species. Elephants are reported to feed mainly on *V. tortilis* during the rainy season than in the dry season (Douglas-Hamilton, 1972). Gandiwa et al. (2011) reported that *V. tortilis* is a species mostly damaged by elephants, and this may be attributed to its high crude protein content (Du Toit, 1990). *V. tortilis* coppice poorly after defoliation, uprooting and debarking but its resilience and vulnerability depend on its recruitment and regeneration rates (MacGregor and O'Connor, 2004).

Vachellia stuhlmannii (Taub.) is a species found to occur in Kenya, Tanzania, Botswana, south Zimbabwe and the northern part of the Limpopo province in South Africa (Mapaura and Timberlake, 2004). This species is poorly studied and yet there are signs that it could be one of the sought-after species by elephants. It is yet to be determined whether *V. stuhlmannii* provide a buffer to other woody species populations. *V. stuhlmannii* was recorded in the top three list of species showing signs of high utilisation by elephants together with *V. tortilis* and the commonly distributed *Colophospermum mopane* in the semi-arid savanna, Venetia-Limpopo Nature reserve (Nkosi et al., 2022a).

Vachellia stuhlmannii and *Vachellia tortilis* are ecologically and economically important plant species in the African savanna ecosystem. They provide food, shelter and habitat for various animal species and play a crucial role in maintaining ecosystem balance. The African savanna is increasingly subjected to habitat fragmentation due to human activities and identifying areas for the species can guide conservation efforts to mitigate negative impacts of habitat fragmentation and promote connectivity of viable populations. On the other hand, the semi-arid African savanna is vulnerable to climate change, which can affect temperature and precipitation patterns. Studying habitat suitability in relation to climatic variables helps the understanding of how these species and any other species might respond to changing conditions, which is vital for adaptive management strategies.

African elephants have an influence on the woody vegetation found in both arid and semi-arid savannas (Guldemon and Van Aarde, 2008) and are known as ecosystem engineers. However, elephants may not be the only factor responsible for changes in woody vegetation or reduction in *V. stuhlmannii* woodlands, other factors such as fire, environmental variables, frost, drought, disease, topography and past human-activities may be responsible (Guldemon and Van Aarde, 2008). *V. tortilis* was selected for this study since it is a highly sought after species by elephants and its density is strongly

influenced by elephants (O'Connor, 1991) in Venetia-Limpopo Nature Reserve and *V. stuhlmannii* was selected due to its high regeneration potential (O'Connor, 2017) and yet their densities decreased between 2013 and 2017 (Nkosi et al., 2022b) in the reserve. The objective of this study was to utilize Maximum Entropy (MaxEnt) model to predict the current habitat suitability of these two *Vachellia* species in the semi-arid African savanna, based on their respective habitat niches.

MaxEnt is a machine learning algorithm commonly used in Species Distribution Modelling (SDM) for predicting the potential distribution of species based on environmental variables (Zhang and Li, 2017). MaxEnt was chosen since it is effective in instances where there is a small sample size or biased sampling (Bean et al., 2012) which is common in ecological studies. It also provides reliable predictions even when data are limited, contributing to its robustness in real-world ecological applications (West et al., 2016). The flexibility and capability of the model to handle complex interactions among variables, and suitability for presence-only data make it a valuable tool for researchers and conservation practitioners interested in predicting species distribution in various ecological contexts.

The use of MaxEnt facilitated the achievement of the objective of this study, which is to understand the current habitat suitability of *V. stuhlmannii* and *V. tortilis* using bioclimatic environmental variables as well as the influence of soils in the distribution of such habitats. The results of this study will help to guide future research in terms of critical habitats that require protection, and for the assessment of the relative impact of environmental variability for long-term survival of the species. This is information that can inform conservation efforts, ensuring that these species and their ecosystems are preserved for future generations.

Materials and methods

Study area

This study is based on two woody species' (*V. stuhlmannii* and *V. tortilis*) presence or occurrence data collected in the semi-arid African savanna of Venetia-Limpopo Nature Reserve (Fig. 1). The reserve covers an estimated area of ~39 000 ha and is situated in the Limpopo Province of South Africa, about ~80 km East of the town, Musina. This semi-arid region is characterised by low annual rain estimated at 366 mm (Hrbar et al., 2009; O'Connor and Page, 2014) and wet, hot summer and dry, mild winter seasons. Mean monthly minimum temperature of 20.3°C and mean monthly maximum temperature of 32.0°C are recorded in summer and 7.2°C and 24.7°C in winter, respectively (MacGregor and O'Connor, 2002).

Mucina and Rutherford (2006) broadly described the vegetation of the reserve as Mucina Mopane Bushveld. The most dominant woody species is the *Colophospermum mopane*, commonly known as the 'Mopane', from which the name of the vegetation type was derived. Old crop areas are dominated by *Vachellia tortilis* species and the alluvial soils that support riparian vegetation types such as *Vachellia* woodland covering about 5% of the reserve (MacGregor and O'Connor, 2004).

Species occurrence and climate data

In 2018, a handheld Geographic Positioning System (GPS) device was used to collect presence records of 110 data points for *V. stuhlmannii* and 29 for *V. tortilis*. Different

bioclimatic variables are key biological variables that determine species' environmental niches (Yi et al., 2016). Historical climatic data of nineteen bioclimatic variables (Table 1) were downloaded from the WorldClim database at approximately 1 km² (30 arc-seconds) spatial resolution (Fick and Hijmans, 2017) from the website: <https://www.worldclim.org/>. This is climatic data for 1970 – 2000, which was released in January 2020. The data include monthly climate data for minimum, mean and maximum temperatures, precipitation, solar radiation, wind speed, water vapour pressure and for total precipitation (Hijmans et al., 2005). These are key limiting factors that are generally used in the modelling of species distribution (Sanchez et al., 2011; Evangelista et al., 2011).

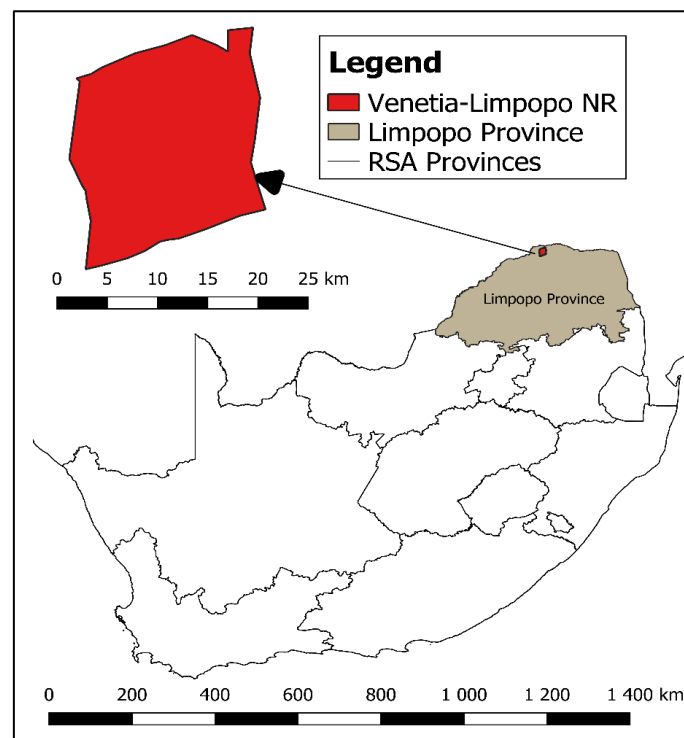


Figure 1. Venetia-Limpopo Nature Reserve location within the South African province of Limpopo

Modelling of study species' distribution

Species occupy areas or niches where a set of conditions allow for their long-term survival (Hutchinson, 1957). Niche-based models that require only the presence data are invaluable in predicting species geographic distribution (Graham et al., 2004). MaxEnt is one such model used in making such predictions or inferences from incomplete information by estimating a target probability distribution of maximum entropy (most spread out or closest to uniform) to a set of constraints that represent incomplete information about the target distribution (Phillips et al., 2006). It is a widely used technique in ecology for predicting species distribution using presence records and environmental variables (Phillips et al., 2006). MaxEnt operates by estimating the probability of a species' spatial distribution while considering constraints such as known observations of the species. The method employs entropy to generalize specific

observations of the species and does not necessitate the incorporation of absence points within the theoretical framework. Instead, it relies on the global positioning system (GPS) locations of occurrence or presence points to infer the absence points (Sharma et al., 2018).

Table 1. Bioclimatic variables derived from monthly temperatures and rainfall values

Code	Variable
BIO-1	Annual Mean Temperature
BIO-2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO-3	Isothermality (BIO2/BIO7) (x 100)
BIO-4	Temperature Seasonality (standard deviation x 100)
BIO-5	Max Temperature of Warmest Month
BIO-6	Min Temperature of Coldest Month
BIO-7	Temperature Annual Range (BIO5 - BIO6)
BIO-8	Mean Temperature of Wettest Quarter
BIO-9	Mean Temperature of Driest Quarter
BIO-10	Mean Temperature of Warmest Quarter
BIO-11	Mean Temperature of Coldest Quarter
BIO-12	Annual Precipitation
BIO-13	Precipitation of Wettest Month
BIO-14	Precipitation of Driest Month
BIO-15	Precipitation Seasonality (Coefficient of Variation)
BIO-16	Precipitation of Wettest Quarter
BIO-17	Precipitation Temperature of Driest Quarter
BIO-18	Precipitation Temperature of Warmest Quarter
BIO-19	Precipitation Temperature of Coldest Quarter

To build the model for each of the two *Vachellia* species, partitions were created by randomly selecting 70% of the presence localities as training data with the remaining 30% as test data (Phillips et al., 2006). The MaxEnt software version 3.4.4 was downloaded from https://biodiversityinformatics.amnh.org/open_source/maxent and applied in this study. The bioclimatic data were converted to “ASCII” file format in Quantum-GIS (QGIS Development Team, 2012) for compatibility with MaxEnt. The GPS location data of the two species (*V. stuhlmannii* and *V. tortilis*) were converted into “CSV” format and the converted file was used as input to MaxEnt. MaxEnt generated output results that predict the suitability of a habitat for each species using a scale of 0-1, where the lowest suitability areas are represented by zero, while the highest suitability areas are represented by one (Sharma et al., 2018). Response curves for each predictor variable were generated from MaxEnt. To assess the performance of the model, the metric used was the Area under the ROC (receiver operating characteristic) curve (AUC), which ranges from 0 to 1 and is a measure of the model’s effectiveness (Vanagas, 2004). According to Swets (1988), the closer the AUC value is to 1, the better the model’s performance. The ROC curve plots the true positive fraction (sensitivity) that represents the absence of omission error, against the false positive fraction (1-specificity) that represents the proportion of incorrectly predicted observed absences (commission error). In this case, specificity is defined using the predicted area instead of the true commission. MaxEnt also uses the jack-knife method to highlight the relative influence of each predictor variable (Khanum et al., 2013). To produce the potential habitat maps of the two species, the Venetia-Limpopo Nature Reserve boundary map was overlaid on the grid file generated by MaxEnt in QGIS.

Influence of soils on suitability habitats distribution

The distribution of major soil types broadly described by Mucina and Rutherford (2006) were incorporated into the suitability maps to assess the habitat suitability of the two species in relation to soils. This is because soil type and structure can impact microclimate conditions by affecting moisture retention (Rost et al., 2009). The distribution of habitats could be influenced by the interplay between soil resources and herbivore impact (Skarpe et al., 2004). Moreover, other factors such as variations in soil types could potentially impact the differences observed in the attributes of woody vegetation (Gandiwa et al., 2011). Geology, topography, soil, and water are critical environmental factors that directly affect the structure and composition of vegetation at various scales, ranging from individual plants to landscape levels (Sankaran et al., 2005).

Results

Modelling the distribution of suitable habitats

Continuous raster files were produced in MaxEnt to indicate threshold values from 0 to 1, which represents habitat suitability for the two species. These threshold values are based on several statistical measures in MaxEnt. The 10-percentile training presence logistic threshold was used for this study and the habitat suitability map was produced with two classifications (Suitable and Unsuitable) for each species (Fig. 2). A turquoise colour represents areas with the lowest probability of habitat suitability (unsuitable) for both species (>0.5) while the mustard colour represents areas with high habitat suitability (<0.5) for *V. tortilis*. Additionally, the blue vertical-lined areas represent high habitat suitability for *V. stuhlmannii* (Fig. 2). There is an overlap (~2 944 hectares) in the species habitat, which indicates the extent to which the two species share similar requirements or compete for the same resources such as light, water, nutrients or space (Craine and Dybzinski, 2013). The commonly used threshold includes the minimum training presence logistic threshold, 10 percentile training presence logistic threshold, equal training sensitivity and specificity logistic threshold (Phillips et al., 2006). The current estimated area of suitable habitats for *V. stuhlmannii* covers ~3 255.8 hectares, representing 8% of the study area, while *V. tortilis* has an estimated suitable habitat area of ~11 180.7 hectares, accounting for 28% of the study area.

Analysis of contributing variables

Climate plays a significant role in influencing plant distribution across various scales, ranging from regional to global (Carpenter et al., 1993). To determine the most important variable in predicting current habitat suitability for the two species, the MaxEnt model was subjected to a jack-knife test. Through the jack-knife procedure, several models were constructed by excluding one variable at a time and creating a model with the remaining variables. This resulted in models created using each variable in isolation (Phillips, 2010) (Fig. 3). For *V. stuhlmannii*, the environmental variable with the highest gain when used by itself in the model is BIO-1 (mean annual temperature), which means it contributes the most to the model's predictive power. Again, the environmental variable that decrease the gain the most when it is omitted is BIO-1. This indicates that when BIO-1 is excluded or omitted from the model, it results in the most significant reduction in the model's performance in predicting habitat suitability for the species (Fig. 3).

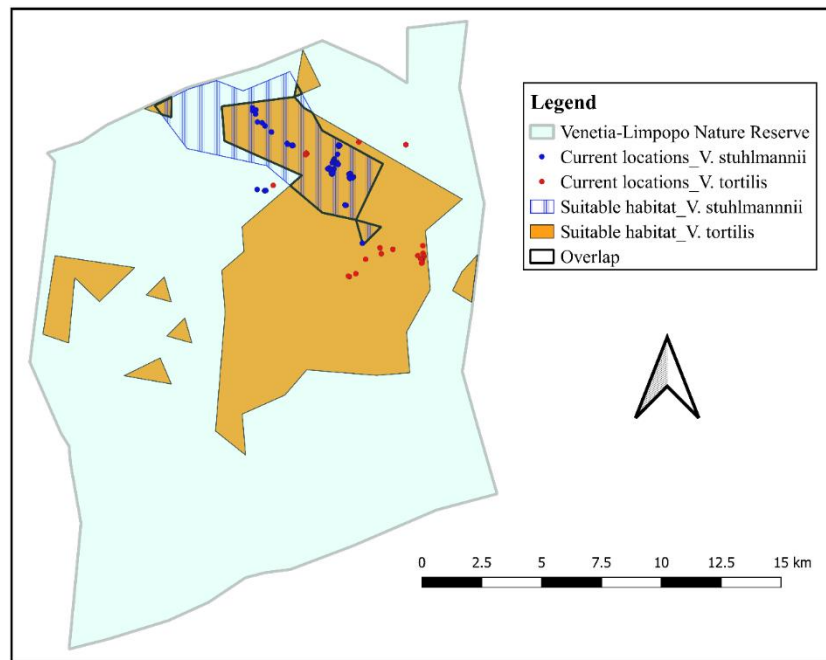


Figure 2. Current locations and predicted habitat suitability map for *V. stuhlmannii* and *V. tortilis*

For *V. tortilis*, the environmental variable with the highest gain when used in isolation is BIO-17 (precipitation during the driest quarter). This means that if BIO-17 is used by itself in the model, it contributes the most to the model's predictive power, making it the influential variable in predicting habitat suitability for the species (Fig. 3). The environmental variable that decreases the gain the most when it is omitted is BIO-5 (maximum temperature during the warmest month). This indicates that when BIO-5 is omitted from the model, there is a significant reduction in the model's performance. It can be deduced that BIO-5 contains information that is not adequately captured by the other variables and is crucial for the model's accuracy.

Nine out of the 19 (bioclimatic variables) used to develop the model were found to have a major impact on the data's variability, including BIO-1 (mean annual temperature, 71.7%), BIO-17 (precipitation of driest quarter, 65.3%), and BIO-5 (Maximum temperature of warmest month, 21.2%) (Fig. 4).

Model validation and performance assessment

The predictive capacity of the models was compared with real observations using area under curve (AUC) of the receiver operating characteristic (ROC). The ROC measures performance using the area under the curve (AUC). The results indicate that the lines of omission from the training data are close to predict omission and this is proven by the AUC value of 0.94 for *V. stuhlmannii*, which indicates a strong performance and a high degree of accuracy in distinguishing between suitable and unsuitable habitats for the species. Similarly for *V. tortilis*, the AUC value of 0.69 suggest a reasonable level of accuracy, although it may be somewhat lower compared to *V. stuhlmannii* (Fig. 5).

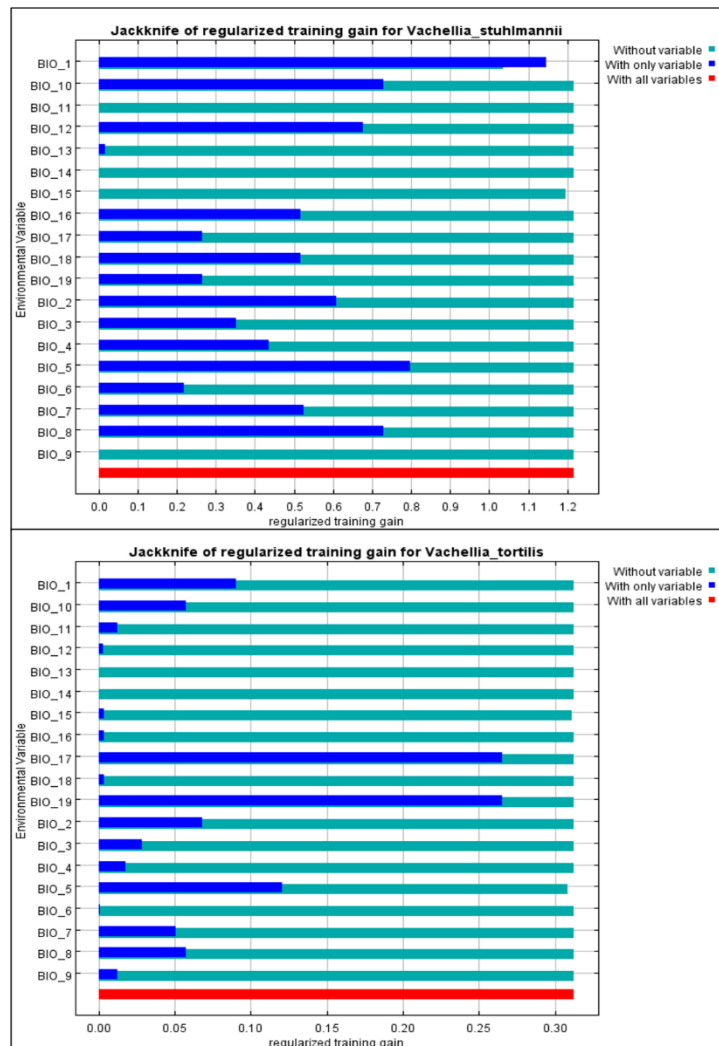


Figure 3. Jack-knife plots showing training gain results for *V. stuhlmannii* and *V. tortilis*. The dark blue bars indicate the gain from using each variable in isolation and the light blue bars indicate the gain lost by removing a single variable from the full model. The red bar indicates the gain using all variables

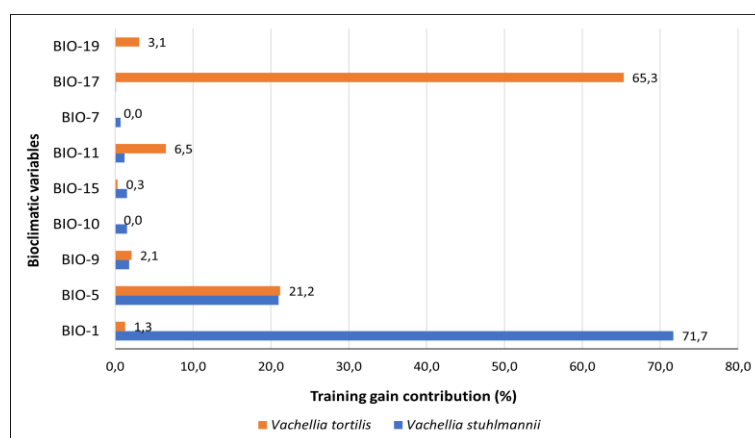


Figure 4. The bioclimatic variables' percentage contributions to the MaxEnt models for both species calculated as averages over ten replicate runs

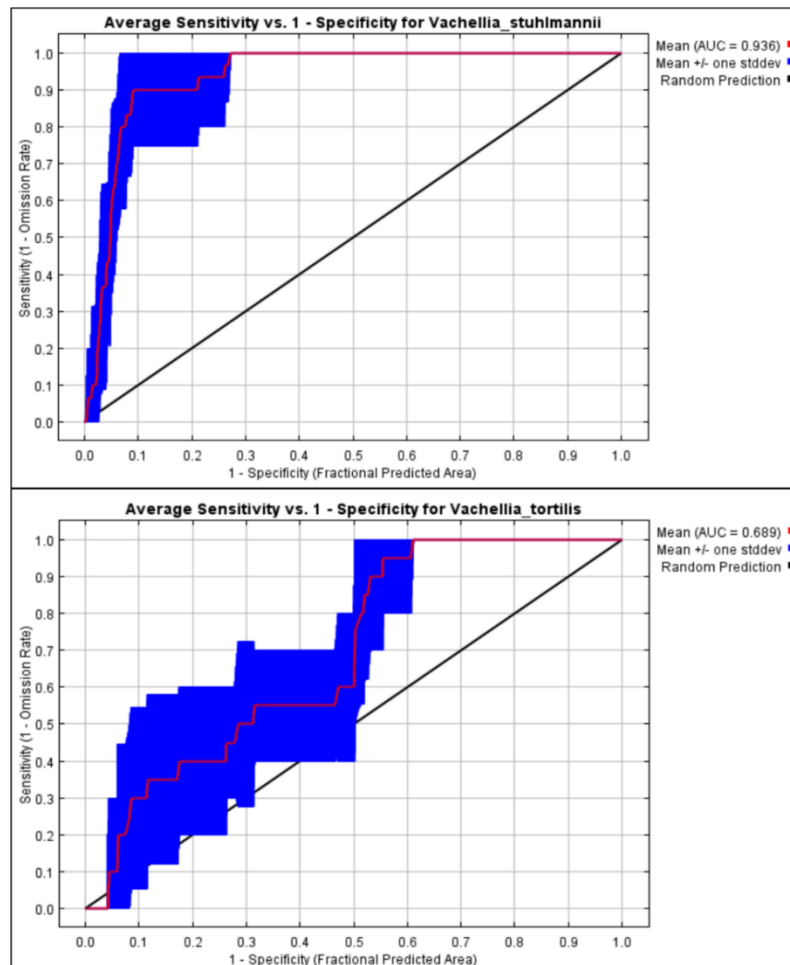


Figure 5. ROC curve demonstrating proximity in training data for *V. stuhlmannii* and *V. tortilis*, supported by High AUV values

The validation of the model, using solely the present data, was also carried out through the binomial test rooted in the training omission rate. This process encompassed both the omission and commission rates, utilizing a binomial test dependent on the threshold rate derived from both predicted area and omission (Phillips and Dudík, 2008). The mean area is represented by the red line, while the predicted omission is shown by the black line. The omission rate for the training samples is depicted by the light blue line (Fig. 6). Additionally, the omission rate was calculated for both the training presence records and the test records for both species. The cumulative thresholds depicted in Fig. 6 represent different levels of confidence or certainty in predicting habitat suitability while fractional predicted area indicates the proportion of the total study area predicted to be suitable for both *V. stuhlmannii* and *V. tortilis*.

The results indicate that as the cumulative threshold decreases, the model becomes more conservative in predicting suitable habitat, resulting in a smaller predicted area (Fig. 6). *Vachellia tortilis* has higher fractional predicted areas across all thresholds, indicating a larger predicted suitable habitat compared to *V. stuhlmannii*. Again, the results of the cumulative thresholds and corresponding omission rates resulted in relatively high *p*-values for both species, indicating a lack of statistical significance in the model's performance (Table 2).

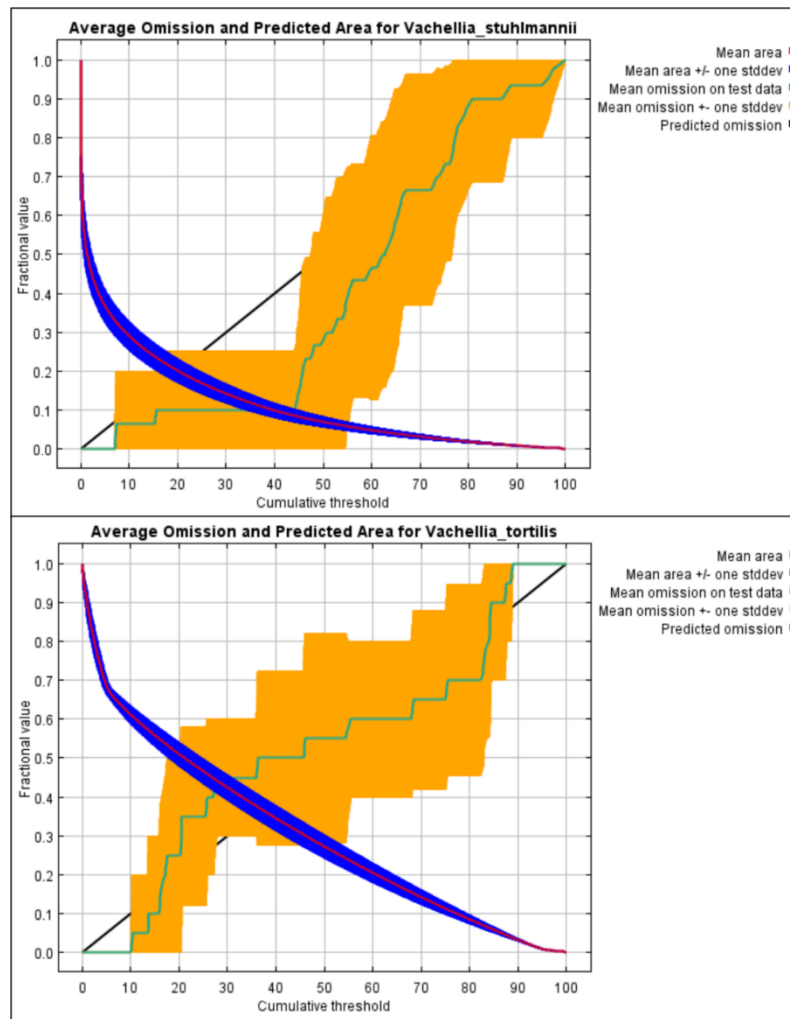


Figure 6. Omission versus predicted area for *V. stuhlmannii* and *V. tortilis*

Table 2. Comparison of Common Thresholds and Omission rates between *V. stuhlmannii* (V.s.) and *V. tortilis* (V.t.) in MaxEnt Model Analysis

Cumulative threshold		Logistic threshold		Description	Fractional predicted area		Training omission rate		Test omission rate		P-value	
V. s.	V. t.	V. s.	V. t.		V. s.	V. t.	V. s.	V. t.	V. s.	V. t.	V. s.	V. t.
1.000	1.000	0.037	0.077	Fixed cumulative value 1	0.578	0.89	0.000	0.000	0.000	0.000	0.1927	0.7917
5.000	5.000	0.139	0.189	Fixed cumulative value 5	0.412	0.676	0.000	0.000	0.000	0.000	0.0701	0.4563
10.000	10.000	0.235	0.348	Fixed cumulative value 10	0.333	0.582	0.000	0.000	0.000	0.000	0.0368	0.3383
17.862	15.591	0.322	0.387	Minimum training presence	0.259	0.518	0.000	0.000	0.000	0.000	0.0174	0.2687
17.862	15.591	0.322	0.387	10 percentile training presence	0.259	0.518	0.000	0.000	0.000	0.000	0.0174	0.2687
31.925	42.058	0.408	0.491	Equal training sensitivity and specificity	0.167	0.29	0.143	0.286	0.000	0.500	0.0047	0.4956
17.862	41.499	0.322	0.488	Maximum training sensitivity plus specificity	0.259	0.294	0.000	0.143	0.000	0.500	0.0174	0.5014
65.416	17.280	0.631	0.397	Equal test sensitivity and specificity	0.051	0.5	0.571	0.143	0.000	0.500	0.0001	0.7500
65.416	15.562	0.631	0.392	Maximum test sensitivity plus specificity	0.051	0.514	0.571	0.143	0.000	0.000	0.0001	0.2645
4.410	5.169	0.126	0.21	Balance training omission, predicted area and	0.427	0.671	0.000	0.000	0.000	0.000	0.0776	0.4508
7.719	4.297	0.2	0.151	Equate entropy of thresholded and original	0.363	0.7	0.000	0.000	0.000	0.000	0.0479	0.4900

Habitat suitability as results of soil types

The current habitat suitability areas for both *V. stuhlmannii* and *V. tortilis* were mainly found on soil types with Prisma-cutanic/pedocutanic diagnostic B-horizons (Fig. 7). Habitat suitability areas for *V. tortilis* were also observed on Glenrosa and/or Mispah soils located on the eastern to southern side of the study area (Fig. 7).

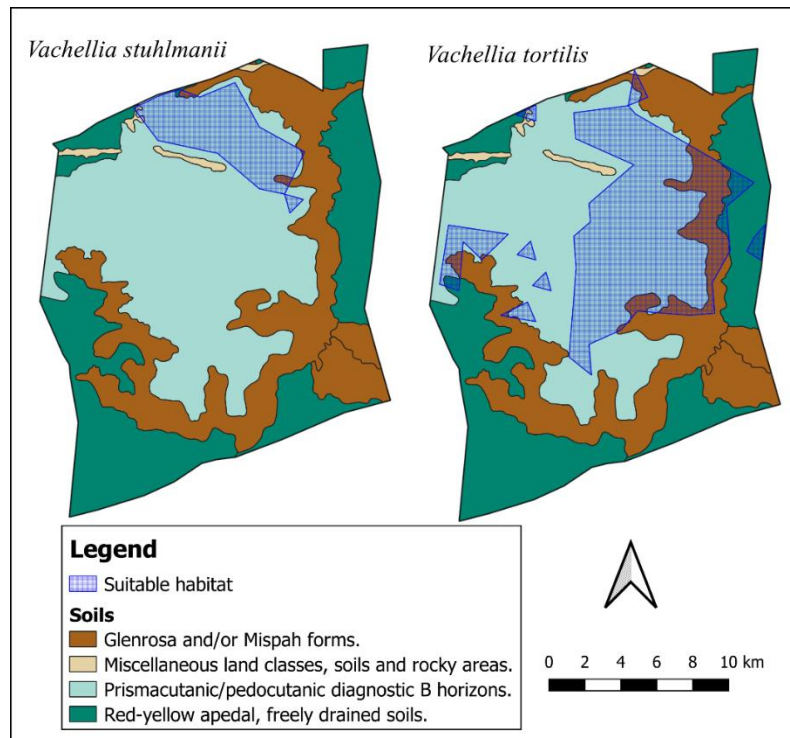


Figure 7. Habitat suitability map for *V. stuhlmannii* and *V. tortilis* based on soil distribution

Discussion

While many studies (Li et al., 2023; He et al., 2023; Waheed et al., 2023) have recently used MaxEnt modelling approach within a climate change context, this study is species-specific and provide detailed insights into the ecological preferences and needs of *V. stuhlmannii* and *V. tortilis* potentially serving as a reference or case study for other species-specific assessment. Incorporating soil analysis added a unique dimension to this study as soil-focused approached contribute valuable information about the relationship between plant distribution and soil types, which may not be as prominent in other MaxEnt-based studies.

In this study, BIO-1 (Annual mean temperature) is identified as a crucial environmental variable in the MaxEnt model both in terms of its individual predictive power and the unique information it contributes that is not present in the other variables. This also suggests that BIO-1 is a key determinant in predicting habitat suitability for *V. stuhlmannii* (Fig. 3). Based on the jackknife test results for *V. tortilis*, BIO-17 appears to be highly informative when used independently, while BIO-5 contained unique information that significantly contributes to the model when other variables are excluded (Fig. 3). These findings highlight the importance of these specific variables in predicting habitat suitability for the two study species.

Again, BIO-1 (Annual mean temperature) proved to be most influential, contributing the highest 71.7% gain to the model's predictive power for *V. stuhlmannii*. The omission of this variable resulted in the lowest decrease in model performance, highlighting its significance in explaining the plant's distribution and growth patterns. This fundamental role of the annual mean temperature underscores its prominence as a key explanation factor within the model. BIO-14 (Precipitation of driest month), BIO-15 (Precipitation

seasonality), and BIO-9 (Mean temperature of driest quarter) did not prove to be useful in predicting the current habitat suitability for the species (Fig. 4). The annual mean temperature was found to be the most important variable contributing to the model's predictive power, indicating that it was the most important variable in explaining the distribution and growth of the plant. Furthermore, when the annual mean temperature was omitted from the model, the decrease in the model's predictive power was the lowest compared to other factors, suggesting that the annual mean temperature was the most crucial variable in the model. Environmental factors, including temperature, have a significant impact on the growth and development of trees (Begum et al., 2013). However, the specific effects depend on the species of tree and other environmental factors, and there may be limits to the positive effects of temperature on tree growth. Given that *V. stuhlmannii* is adapted to survive in areas with low rainfall and can reach underground water sources with its deep root system, it is likely that the temperature plays an important role in its ability to access and utilize water. This information can be useful in understanding the habitat requirements of *V. stuhlmannii* and how it responds to changes in temperature. It also highlights the importance of considering multiple environmental factors when studying plant habitats, as the omission of any important factor can result in a significant decrease in the model's predictive power (Phillips et al., 2004).

On the other hand, when used in isolation, BIO-17 (Precipitation of driest quarter) contributed the highest gain of 65.3%, and the environmental variable that had partial impact on decreasing the gain was BIO-5 (Maximum temperature of warmest month) for *V. tortilis* (Fig. 4). The most significant factor in explaining the *V. tortilis*'s distribution and growth was shown to be the precipitation levels during the driest quarter. Additionally, the statement suggests that the maximum temperature of the warmest month had a partial impact on decreasing the gain of the model, indicating that it also plays a role in the plant's habitat requirements. This means that changes in temperature during the warmest month could potentially limit the *V. tortilis*'s distribution or affect its growth, even if the precipitation is optimal. Similarly, BIO-14 (Precipitation of driest month) did not contribute significantly to predicting current habitat suitability for either of the two species.

The AUC values close to 1 for both *V. stuhlmannii* (.94) and *V. tortilis* (.69) indicate that the MaxEnt model performed well in predicting current habitat suitability (Fig. 5). These results validate the reliability of the model's predictions and provide confidence in its ability to accurately assess the habitat suitability for the two species in the study area. Again, *V. stuhlmannii* appears to have lower omission rates and higher AUC values across various thresholds compared to *V. tortilis* (Fig. 6) and the model seems to have performed more consistently across different thresholds, with smaller predicted suitable areas. Both species exhibit reasonably high AUC values and low *p*-values (Table 2), which suggest that the model for *V. stuhlmannii* may perform slightly better in terms of accuracy and consistency in predicting habitat suitability.

Temperature and precipitation are the two main and universal variables that influence species range (Häkkinen et al., 2022). Given the importance of temperature and precipitation in influencing species range, it is unsurprising that these two bioclimatic variables contributed the most to the distribution of current habitat suitability for the two studied species. According to Häkkinen et al. (2022), the covariance between temperature and precipitation suggests that the climatic niches of species are not necessarily limited by precipitation alone. Rather, it may be that precipitation conditions always occur in

conjunction with the thermal limit of a species' niche, leading to a correlation between the two variables.

The species *V. tortilis* is widely distributed and commonly favoured by African elephants (Mwalyosi, 1987; Kalembera, 1989). In the study area, elephants were reported to utilize selected riparian areas and *V. tortilis* woodlands of limited size, in vegetation dominated by *Colophospermum mopane* (O'Connor, 1991). The estimated current suitable habitat distribution of *V. tortilis* occupies a relatively small portion, approximately 28%, or 11 180.7 hectares of the total study area as compared to 8%, which is approximately 3 255.8 hectares for *V. stuhlmannii* (Fig. 2). According to MacGregor and O'Connor (2004), the utilization of *V. tortilis* and the resulting tree mortality may be density-dependent or directly proportional to the presence of the species. It is no doubt that several *Vachellia* species are a dominant part in the diet of African elephants (Biru and Bekele, 2012). Climate change and habitat fragmentation are expected to have significant impacts on the distribution and abundance of species (Mantyka-pringle et al., 2012; Holyoak and Heath, 2016; Sirami et al., 2017), including *Vachellia* species. This can have cascading effects on elephant and giraffe populations and their habitats. Studying the importance of *Vachellia* species as part of these browsers' diet can provide insights into how these ecosystems may respond to future environmental changes.

The spatial distribution of current habitat suitability areas for both *V. stuhlmannii* and *V. tortilis* was primarily dominated by Prisma-cutanic/pedocutanic diagnostic B-horizons. This is the most prevalent soil type that is distributed across expansive plains (Neville, 1996) and also found in the centre of the study area falling within the 'Unit F' soils of Ellis and Lambrechts (1986). Additionally, *V. tortilis* was also observed to occur on Glenrosa and Mispah soils (Fig. 7). Glenrosa and Mispah soils are associated with shallow depths of grey to dark brown topsoil over hard rock (Land Type Survey Staff, 1988). Both soils are important for their ability to support plant growth and sustain biodiversity in their respective regions. Glenrosa soils are known for their high clay content, which makes them good at retaining water and nutrients (Matlou, 2006). This makes them an important soil type for agriculture, particularly for growing crops such as wheat and vineyards for wine production (Zörb et al., 2014). However, the high clay content also makes them more susceptible to erosion, which can have negative ecological impacts (Couper, 2003). Mispah soils, on the other hand, are generally poorer in nutrients than Glenrosa soils, which makes them better suited for grazing livestock such as sheep and goats (Mudau et al., 2021). These soils are important for sustaining biodiversity in the semi-arid regions where they are found. However, Mispah soils are also more susceptible to desertification and degradation (Meyer et al., 1996), which can have negative ecological impacts on the surrounding ecosystems. Overall, both Glenrosa and Mispah soils are important for their ecological functions and their ability to support different types of plant and animal life in their respective regions.

Conclusion

This study aimed to identify the significant bioclimatic predictors that influence the current habitat suitability of *V. stuhlmannii* and *V. tortilis*, using the two species' point location data. The results have led to the conclusion that: the distribution of current suitable habitat for *V. stuhlmannii* and *V. tortilis* is significantly influenced by the annual mean temperature and precipitation of the driest quarter, respectively; the most suitable current habitat distribution for the two species in this study was identified on

Prismacutanic/pedocutanic diagnostic B-horizon soils. These are broad classification of soil types according to Mucina and Rutherford (2006) and was used to assess their influence on the habitat suitability of the two species. Soil properties have significant effect on the distribution of plant species. It is recommended for future research endeavours to conduct detailed analysis of soil properties as these properties are influenced by various factors including terrain, slope angle and aspects. Additionally, future studies could utilize satellite imagery to classify the spatial distribution of both species and enhance the predictions of their habitat suitability based on bioclimatic variables.

However, this information is relevant to understanding the two species' ability to grow and survive in dry and arid environments, such as deserts, semi-arid grasslands, and savannas. The extensive root system of *V. tortilis* can reach underground water sources, allowing it to survive prolonged periods of drought. However, this adaptation may not be sufficient if the precipitation levels are too low. Therefore, understanding the variables that are most crucial in explaining species' habitat requirements can aid in identifying areas where species are likely to thrive and predicting how they may respond to changes in climate patterns. It is also essential information for conservation efforts to protect the species and their habitat. Although this study was conducted on a relatively small scale, it establishes a foundation for future research in exploring the habitat suitability of both *V. stuhlmannii* and *V. tortilis*, as well as other species within the *Vachellia* genus, on a larger scale.

MaxEnt performed well in predicting current habitat suitable for the two species with the results validating the reliability of the model's predictions, providing confidence in its ability to accurately assess the habitat suitability for *V. stuhlmannii* and *V. tortilis*. The results collectively provide insight into the model's performance under different conditions and thresholds, aiding in selecting an appropriate threshold for practical applications. Further studies could investigate the potential impact of climate change on the future distribution of suitable habitats for not only *V. stuhlmannii* and *V. tortilis*, but also for other species within the study area or other protected areas. Overall, *Vachellia* species are important species for many ecosystems, playing a vital role in maintaining biodiversity and ecosystem health in arid and semi-arid regions.

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