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Potential distribution of major plant units under climate change scenarios along an aridity gradient in Namibia

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Abstract

Objectives: Climate change is expected to have major impacts on plant species distribution worldwide. These changes can affect plant species in three ways: the timing of seasonal activities (phenology), physiology and distribution. This study aims to predict the effect of shifting climatic conditions on the major vegetation units along an aridity gradient through Namibia. **Study area:** Namibia's vegetation is characterised by open woodland in the northeast to low open shrubland in the southern part of the country. These differences are a result of increasing aridity from north to south with a rainfall gradient from 100 mm to 600 mm. Namibia is projected to have an increase in annual mean temperature of 2°C by the end of the 21st century. **Methods:** A vegetation classification was done for 1,986 relevés using cluster analysis, a Multi-Response Permutation Procedure and indicator species analysis. The current distribution of the vegetation classes was modelled with Random Forest. Future projections for the most important climate variables were used to model the potential distribution of the vegetation units in 2080. This modelling approach used two scenarios of Representative Concentration Pathways (4.5 and 8.5) from two Global Climate Models – the IPSL–CM5A–LR and HAdGEM2–ES. **Results:** The predicted distribution shows a high expansion potential of *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas, *Combretum africanum-Terminalia sericea* broad-leafed savannas and *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas towards the south under both scenarios. **Conclusions:** The model indicated the ability to classify and predict vegetation units to future climatic conditions. Half of the vegetation units are expected to undergo significant contraction. Overall, RCP8.5 conditions favour the proliferation of certain vegetation types, particularly *Combretum collinum-Terminalia sericea* broad-leafed savannas and *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, potentially displacing other vegetation types.

Taxonomic reference: Klaassen and Kwembeya (2013) for vascular plants, except Kyalangalilwa et al. (2013) for the genera *Senegalia* and *Vachellia* s.l. (*Fabaceae*).

Abbreviations: CDM = Community Distribution Model; CMIP5 = Coupled Model Inter-comparison Project Phase 5; EVI = Enhanced Vegetation Index; GCM = General Circulation Model; IV = Indicator Value; ISA = Indicator Species Analysis; MAP = mean annual precipitation; MAT = mean annual temperature; MRPP = Multi-Response Permutation Procedure; NMS = Non-Metric Multidimensional Scaling; RF = Random Forest; RCPs = Representative Concentration Pathways; SDM = species distribution model.

Keywords

climate change scenarios, distribution, indicator species, Namibia, potential distribution, rainfall gradient, vegetation units, vegetation classification

Introduction

Namibia is the driest country in southern Africa. Despite its arid conditions, Namibia is home to more than 4,500 plant species covering four major biomes: Namib Desert, Succulent Karoo, Nama-Karoo, and tree and shrub savanna (Midgley et al. 2005). The vegetation supports communal and commercial livestock and wildlife farming, the sectors on which Namibia is highly dependent (Reid et al. 2008). Therefore, the tree and shrub savanna that covers up to 84% of the land is economically vital to Namibia. It also provides ecosystem services such as capturing carbon dioxide from the atmosphere and regulating the climate (Snyder et al. 2004). Economically important species in the savanna provide food, traditional medicine, building materials and timber products to local people (Barnes et al. 2012).

However, these savannas are at risk of global climate change that affects many species worldwide (Pounds et al. 2005; Parmesan 2006; Feehan et al. 2009; Lenoir et al. 2010; Chen et al. 2011). It has resulted in species range shifts to cooler areas such as towards the poles and high elevations (Pounds et al. 2005; Feehan et al. 2009; Sintayehu 2018). However, warming challenges species already inhabiting the highest elevations because they do not have new habitats to colonise, leading to possible local extinction (Thuiller et al. 2005; Manish et al. 2016). Species with a low dispersal capability, such as herbs (Ash et al. 2017) are noted to also be at risk as they cannot disperse over a long distance, thus accelerating warming may surpass the rate of migration of these species.

In southern Africa, a change in weather patterns has been noted over the last decennia. For example, the second half of the 20th century observed a reduction in rainfall in mainly Angola, Democratic Republic of Congo and Namibia (Niang et al. 2014). The mean temperature in southern Africa has increased from 1.04°C to 1.44°C between 1961 and 2015 (Trisos et al. 2022).

Midgley et al. (2005) found that 53% of the long–term weather stations in Namibia and the Northern Cape experienced an increased temperature of 0.2°C and a 33% decreased rainfall over a 25 to 60–year period. Future climate projections indicate significant impacts from climate change, including changes in temperature such as a projected mean annual warming between 2°C and 6°C (Reid et al. 2008; Barnes et al. 2012) by the end of the 21st century (Turpie et al. 2010). The projected high temperature will cause an increase in evaporation, resulting in severe water shortages, thereby exacerbating the country's aridity (Reid et al. 2008). The latter is likely to have significant effects on Namibia's vegetation, including changes in species composition and distribution, as well as the overall health and productivity of ecosystems.

By 2050 and 2080, it is expected that the endemic plants in Namibia, such as perennial herbs, geophytes, and trees, will experience adverse effects (Thuiller et al. 2006). Midgley et al. (2005) found that by 2080, a range expansion with 43% of desert–adapted vegetation types, should be expected. A range contraction of desert–adapted species such as *Aloe dichotoma* to higher elevations is also likely. The temperature and rainfall change will result in some plants shifting their ranges towards the north–eastern part of Namibia (Midgley et al. 2005; Thuiller et al. 2006), such as the timber tree *Pterocarpus angolensis* (De Cauwer et al. 2016).

Namibia's vegetation has been studied by several researchers as indicated by Burke and Strohbach (2000) with the most widely accepted classification being the preliminary vegetation map of Namibia by Giess (1998). This map categorizes Namibia's vegetation into 14 different vegetation types. The vegetation varies from desert scrub to woodland. The preliminary vegetation map that is widely used in Namibia is based on ground observations that were then extrapolated to the national level using expert knowledge (Giess 1998; Westinga et al. 2020). A comprehensive vegetation map based on vegetation surveys does not exist yet for Namibia. In addition to the preliminary vegetation map of Namibia, other studies have focused on specific regions or types of vegetation, such as the classification of savanna vegetation in the central parts of Namibia (Strohbach 2002, 2019).

Many studies have used species distribution models (SDMs) to investigate the effects of climate change on species' potential distribution. SDMs are computer algorithms that are widely used to predict species distribution by relating species occurrences to environmental variables at known locations and using this relationship to predict species distribution across space and time (Elith and Graham 2009; Manish et al. 2016). In Namibia, there have been studies on the effect of climate change on species distribution, indicating that the country's vegetation is likely to experience significant shifts in vegetation types and distribution, while others found that the country's savanna ecosystem will change in composition and some species becoming dominant over the others (Midgley et al. 2005).

Unlike SDMs, the examination of large–scale vegetation patterns can be conducted through the application of a community distribution model (CDM) by employing the species compositional approach (Ferrier and Guisan 2006; Potts et al. 2013). Community–level modelling integrates information from various species which are grouped through numerical classification, to provide insights into the spatial distribution at a collective community level which provides an opportunity to integrate a complex dataset (Ferrier and Guisan 2006). Just like SDMs, CDMs are subject to multiple uncertainties such as geographical sampling bias which can limit model generalisation, the assumption of unchanging species interactions, and groups or species that have not been homogeneously described across their distribution range (Thuiller et al. 2004a; Midgley and Thuiller 2011). CDMs share similarities with SDMs in terms of methods and data type (Keane et al. 2020). The CDM's response variable is the vegetation type or community instead of individual species as in SDMs (Franklin 2013). The machine learning models used to predict species distribution also predict community distribution (Jiménez-Alfaro et al. 2018; Keane et al.

2020). An example of an algorithm that has popularly been used in individual species and community modelling is the Random Forest algorithm (Keane et al. 2020).

Namibia exhibits a south–north rainfall gradient. Consequently, the country's vegetation transitions from sparse shrubs with scattered trees in the south to open woodland in the northeast. This rainfall and vegetation gradient offers an ideal national–scale transect for studying vegetation change.

This study aims to use Random Forest models to predict the response of vegetation units along a south–north rainfall gradient to projected global climate change scenarios in Namibia. The above was achieved through the following objectives: classify the vegetation along the gradient, identify the environmental factors responsible for the distribution of vegetation units, model the vegetation for the current climate, and predict the distribution of vegetation units for the future using climate scenarios. The present study used vegetation data collected over many years by various researchers and has therefore the potential to provide a good synthesis of the vegetation distribution in Namibia.

Methods

Study area

The study was conducted along a south-north transect of 1,383 km long and 30 km wide following a rainfall gradient. Rainfall typically begins in the first three months of summer (October to December), but peaks in February (Dreber and Esler 2011). The northern part of the study area receives 600 mm of annual rainfall, while the southern parts of the study area receive 100 to 160 mm, indicating a gradient of decreasing annual rainfall from the north to the south of the transect, as shown in Figure 1a (Mendelsohn et al. 2002). The yearly maximum mean temperature of the hottest month along the study site is 34°C (Turpie et al. 2010). The transect crosses four landscapes: the Kalahari Basin in the north, the Central Plateau, the Khomas Hochland Plateau in the central, and the Nama-Karoo in the south (Figure 1b).

In the far north–east, the topography of the Kalahari basin is flat to nearly flat, with elevations ranging between 900 m and 1,200 m a.s.l. (Mendelsohn et al. 2002) with Ferralic Arenosols as dominant soils. The Central Plateau stretches from the central northeast (near Grootfontein) to the Khomas Hochland (near Okahandja) in central Namibia. For most parts, it is a flat to undulating plain, interrupted by occasional inselbergs and the foot slopes in the north of the Otavi Mountain Land. Altitudes range between 1,100 and 1,600 m a.s.l. In the far north–east, shallow Mollic Leptosols, often with calcrete, prevail, whilst in the central and southern parts deeper Cambisols occur (ICC et al. 2000). The Khomas Hochland forms part of the escarpment and ranges between 1,600 to well over 1,800 m a.s.l. It is a rolling to steep mountainous highland overlaid by lithic Leptosols that are generally shallow and often covered by quarz pebbles (Joubert et al. 2008; Strohbach 2017). The Nama-Karoo forms part of the Central Plateau, however with a distinctly arid climate. It consists of various landforms ranging from dissected plains to mountains and generally lies at approximately 800 to 1,200 m a.s.l. (Mendelsohn et al. 2002).

Data sampling and analysis

This research study used relevé data collected from 1990 to 2016 for the vegetation survey of the Namibia project (Strohbach and Kangombe 2012). The data collection followed the Braun-Blanquet sampling procedure (Strohbach 2014) within a plot size of 20 m × 50 m. This plot size is considered adequate and commonly used for vegetation surveys in Namibia (Burke and Strohbach 2000; Strohbach 2001, 2014). The abundance for each species in a plot was assessed by visually estimating the cover and recorded as a percentage.

The vegetation surveys do not cover the whole country; therefore, a countrywide analysis was not possible. Sufficient data were available for the transect of our study, which represents most of the rainfall gradient in Namibia and hence a wide variety of vegetation units present in the country. The data were grouped into vegetation classes using cluster analysis in PC-ORD version 7 (McCune et al. 2002). Given the length of the gradient, and thus the size and heterogeneity of the data set, it was assumed that less than six groups would not adequately reflect the turnover in habitat and plant diversity. Therefore, the clustering was started with a minimum of six and a maximum of twelve groups. The classification was based on the Sørensen distance measure and Flexible Beta (Beta = -0.25) as a group linkage method (Perrin et al. 2006). There are multiple distance measures available, but all are dependent on the nature of the ecological question to be answered and the type of data collected. For example, the Sørensen distance measure used in this analysis is good for ecological community data analysis because it is less prone to extreme values (outliers) and can retain sensitivity to heterogenous data sets (McCune et al. 2002; Perrin et al. 2006; Peck 2010).

To find the ideal number of groups for the classification, the statistical outcomes from the Multi-Response Permutation Procedure (MRPP) and Indicator Species Analysis (ISA) in PC-ORD are compared for each number of groups. MRPP was used to test the similarity within groups using the Sørensen distance measure. The difference among the groups was interpreted from a test statistic (T) and the chance–corrected within–group Agreement (A). A high negative T–value indicates a greater separation between the groups, while a low negative T–value indicates less separation (Everhart et al. 2008). The classification with the optimal number of groups would have the lowest negative T–value. The A–value shows how homogenous or heterogenous the groups are (Brinkmann et al. 2009). An optimal number of groups gives a high A–value. The A–value ranges between 0–1, with values between

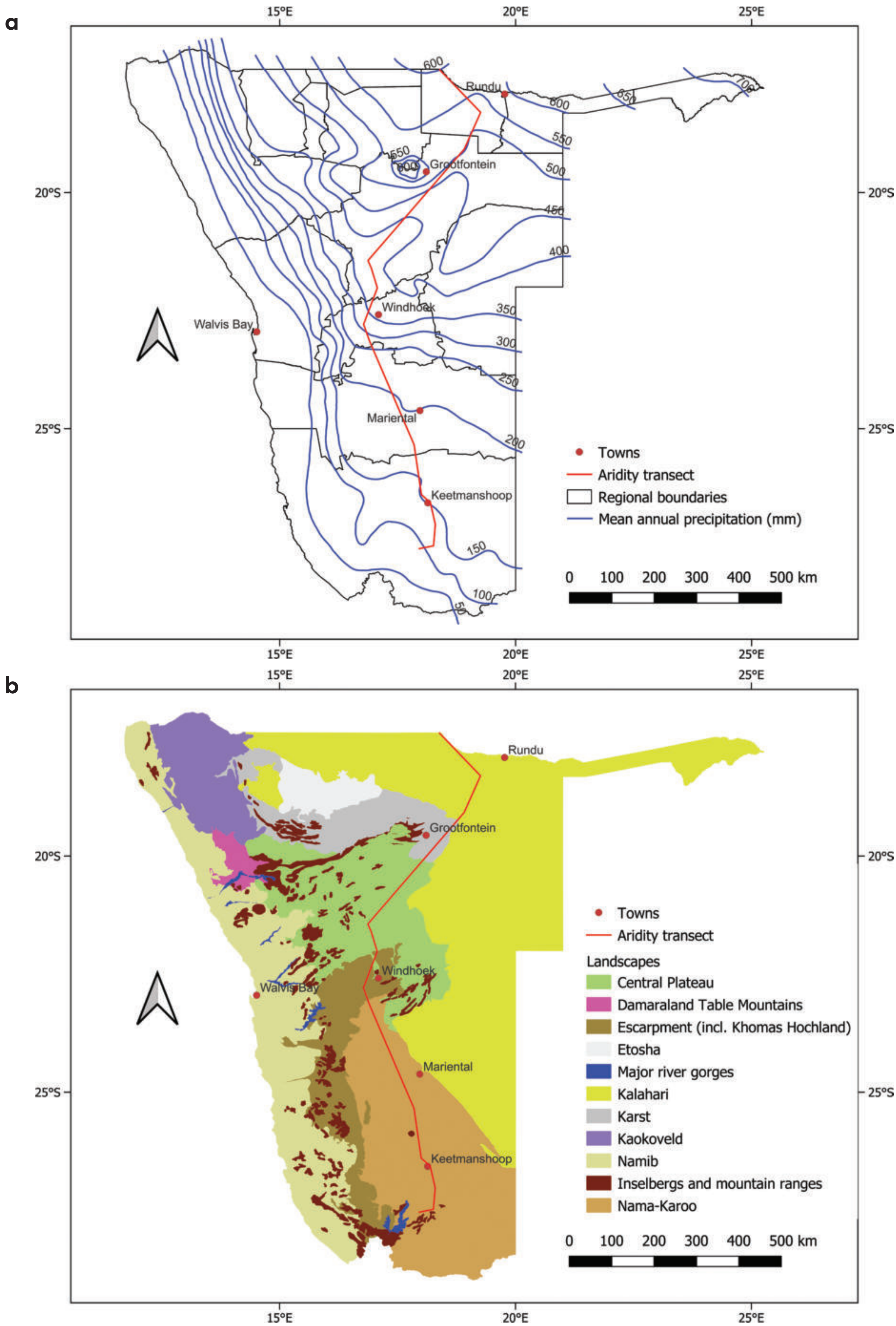

Figure 1. (a) Map of the study area indicating a north–south transect across an aridity gradient. (b) Major landscapes. Maps adapted from De Pauw et al. (1998).

0.3–1 showing that the homogeneity in the groups did not occur by chance (Everhart et al. 2008).

The ISA analysis determined indicator values (IV) for each species, as well as their statistical significance with a Monte Carlo test, to determine species with robust association to specific vegetation groups. A threshold level for IV of 20% with p–value ≤ 0.05 was chosen as the cut–off for identifying indicator species (Dufrêne and Legendre 1997; Khan et al. 2011). ISA contributed to determining the ideal number of vegetation groups in the classification (Brinkmann et al. 2009) by comparing the mean probability (p) value and mean IV for each group. The identified constant and dominant species in each group were used to name the vegetation types. Constant species are species with frequent occurrence, while dominant species frequently occur with a high percentage of cover in a particular vegetation unit (Kusbach et al. 2012). The naming of vegetation units in this study does not follow the International Code of Phytosociological Nomenclature (Theurillat et al. 2021) and are thus named as vegetation units that are not attached to any hierarchical order.

The ISA results were imported into the JUICE program (Tichý 2002) to generate a list of diagnostic species for each vegetation unit through the synoptic table routine. The numbers of relevés were standardised following Tichý and Chytrý (2006). Species with phi ≥ 40 were considered diagnostic. Species above 60% frequency were regarded as constant species and above 10% frequency as dominant species (Marcenò et al. 2018). Diagnostic species have a distinct concentration of occurrence or abundance in a particular vegetation unit and help identify the vegetation units (Chytrý and Tichý 2003). The threshold fidelity value for diagnostic species was 30%, while the cut–off frequency value for constant species was 40%, and 10% for dominant species (Marcenò et al. 2018). This follows standard procedures used for the Vegetation Survey of the Namibia project (Strohbach 2021).

An initial non–parametric ordination technique, non–metric multidimensional scaling (NMS) was performed in PC-ORD using the Sørensen distance measure (McCune et al. 2002). The NMS iterations recommended a two–dimensional ordination space. NMS scores were saved at plot level and correlated to a range of environmental variables

Environmental variables determining the current distribution of the vegetation units

Environmental factors significantly impact vegetation growth and distribution (Anderson and Herlocker 1973; Ahmad et al. 2020). The selection of environmental factors used to define the ecological niche of vegetation units is a critical step in the classification and modelling process because these variables determine the quality of the model output (Guisan and Zimmermann 2000; Araújo and Guisan 2006). A large set of environmental variables (Table 1) was tested for their relevance to the vegetation model. Firstly, highly correlated environmental variables were removed. Spearman's rank correlations were determined in R statistical software version 4.1.0 (R Core Team 2021). For each pair of highly correlated variables (> 0.80) (Pecchi et al. 2019), the variable with the lowest NMS score, explaining the least of the ordination, was removed.

Table 1. Environmental variables used for the current distribution of the vegetation units.

Variable description	Source
Monthly Soil water content (SWC), Priestley–Taylor alpha coefficient (Pt–alpha) – a measure of evapotranspiration rate of water bodies such as lakes and oceans.	CGIAR–CSI (Consortium for Spatial Information, Zomer et al. 2006)
Global aridity index, Monthly potential evapotranspiration (PET).	Global aridity and PET database (Trabucco and Zomer 2018)
19 bioclimatic variables for 1970–2000, with a spatial resolution of 30 arcsec, approximately 1 km at the equator available as GeoTiff files. Data were derived from the average monthly climatic data min, mean, max temperature and precipitation.	WorldClim: version 2 http://www.worldclim.org (Fick and Hijmans 2017; Vega et al. 2017)
Digital soil layer downloaded as GeoTiff at five–arcsecond spatial resolution. Soil digital layers with a spatial resolution of 250 m for 1970–2000 are available in GeoTiff files. The following layer was downloaded:	ISRIC World soil information **http://www.data.isric.org/**
Sand content (60–100 cm) at 5 standard depths in g/100 g was predicted using two sets of African soil profile data.	(Hengl et al. 2015)
Enhanced Vegetation Index (EVI) provides a measure of the greenness of the vegetation and ranges between -1 and 1, where an EVI value close to zero represents less vegetation while a value close to one represents abundant vegetation (Gurung et al. 2009).	Moderate–resolution Imaging Spectroradiometer (MODIS) sensor. African Soil Information Services (AfSIS): Remote Sensing Land Collection
EVI data were obtained as monthly and yearly means between 2000–2018, at a spatial resolution of 250 m.	http://africasoils.net/services/data/remotesensing/land/ Average time–series of Africa
Soil types, and dominant soils (DOM) soil of Namibia	Soil map of Namibia (Coetzee 2020, unpubl.). Accurate soil data for each relevés is not available, and thus the use of a more generalised soil map.
Namibia 2011 census population data. Data extracted from a shapefile.	Namibia Statistic Agency
Cattle density	FAO http://www.fao.org/livestock-systems/global-distributions/en/
Climatic Water Deficit (CWD) downloaded as GeoTiff at 2.5 arcs minute spatial resolution (Chave et al. 2014)	http://chave.ups-tlse.fr/pantropical_allometry.htm
Global Land Cover (GLC) 2006	http://www.landcover.org

Random Forest model

The current and future distribution of vegetation units were modelled with Random Forest. Random Forest uses a collection of computer–grown decision trees (an ensemble of trees) to solve regression and classification problems (Breiman 2001). For this study, environmental variables as predictors and vegetation unit as response were added as input variables into the model. The algorithm selects a group of decision learners in a process known as bagging. Approximately 63% of the data is used for bagging, with the remainder used as an out–of–bag estimate to the test prediction accuracy of the classification (Liaw and Wiener 2002; Cushman and Huettmann 2009). Two parameters (mtry and ntree) are defined as the number of random variables and the number of trees used at each node, respectively (Naidoo et al. 2012). The model of this study used 500 trees (Nguyen et al. 2020) and three randomly chosen variables at each node.

Two models for the current vegetation distribution were fitted with the non–correlated environmental variables as predictors, however, one model used 10 variables, including two satellite–derived Enhanced Vegetation Indices (EVI). Another model was fitted with eight variables, excluding the two EVI variables. Vegetation indices such as the EVI are important predictors for the classification of vegetation and the creation of two models aimed to assess to what extent climate and static data such as topography and soil can predict the current vegetation distribution. Stanton et al. (2012) and Zangiabadi et al. (2021) indicated that using only dynamic climate variables reduces model performance compared to when static variables are included. The model without EVI was the basis for the models that projected the distribution of the vegetation units based on future climate data.

Further selection of the final variables was done through Variable Importance selection under the Random Forest package (Liaw and Wiener 2014) using the Mean Decrease Gini coefficient (MDG) (Naidoo et al. 2012; Han et al. 2016). The MDG measures the decrease in node impurity and how well the data is split among the trees. All variables with an MDG value above 70 were selected to be used in fitting the model. After the selection, the model is rerun with only the selected variables. Partial dependence plots were used to visualise the effect of the most important variables.

Model accuracy assessment

Model calibration was performed using the out–of–bag error. The ratio of 70:30 was used to divide the data into training and testing data, respectively (Duque-Lazo et al. 2016; Sahragard et al. 2018). The confusion matrix was produced to show the correctness of the predicted classes against the actual class values and calculate the misclassification error per class. Additionally, an accuracy score and Kappa statistic (Cohen's Kappa) (Congalton 1991) were used to validate the model from test data. The scale of the statistic ranges as follows; 0.81–1 = almost perfect, 0.61–0.80 = substantial, 0.41–0.60 = moderate, 0.21–0.40 = fair, and 0–0.20 = fail (Heikkinen et al. 2006).

Future climate change scenarios

This study used future climate scenarios for one time period, 2070 (average for 2061–2080) based on emission scenarios from the General Circulation Model of CMIP5, downscaled and calibrated using WorlClim 1.4 as baseline climate. CMIP5 data were used because the CMIP6 downscaled and calibrated data were not available at the time of analysis for this study. The future projection was based on the Representative Concentration Pathways (RCPs 4.5 and 8.5) of IPSL CM5A LR and HadGEM2–ES general circulation models. Future bioclimatic raster layers were reprojected to WGS 84, cropped to the study area, and resampled to ensure that they all have the same extent and resolution. All datasets were resampled to 0.083 degrees resolution, approximately 1 km at the equator.

Results

Vegetation classification along the transect

The grouping statistics of the seven classifications done with PC-Ord Cluster analysis are provided in Table 2. Based on the MRPP and ISA criteria described earlier, a classification of twelve groups was chosen as the best result.

Table 2. The summary of Multi–Response Permutation Procedure (MRPP) and Indicator Species Analysis (ISA) illustrating the statistical values for each classification level or number of classified groups (Gr). The bolded value represents the best result of each statistical test. The values in italic fonts show the second–best value in each category. *T* = Test statistic *T*, *A* = chance–corrected within–group agreement, *p* = mean probability and IV = Indicator Value.

Number of Groups		6 Gr	7 Gr	8 Gr	9 Gr	10 Gr	11 Gr	12 Gr
MRPP	*T*	**-753**	-741	*-744*	-743	-737	-732	-720
	A	0.11	**0.12**	0.13	0.14	0.15	*0.16*	**0.17**
ISA	No. of Indicator species	562	612	*668*	666	**669**	630	642
	Mean *p*	0.25	0.21	*0.20*	***0.20***	0.20	0.21	**0.20**
	Indicator value (IV)	4.9	4.8	5.2	5.2	5.4	*5.5*	**5.5**

Environmental variables and their influence on the distribution of vegetation units along the transect

A description of the twelve vegetation units is described below. A bridged synoptic table of vegetation units, their species composition and species frequency is presented in Table 3.

Unit 1. Senegalia mellifera-Monechma genistifolium *thornbush savanna*

This vegetation unit consists of 138 relevés and 53 species. It occurs sparsely in the south of the Otjozondjupa region as well as towards the north of the Karas region. The vegetation is highly dominated by *Senegalia mellifera* and diagnostic species such as *Monechma genistifolium*, *Leucosphaera bainesii* and *Senegalia tortilis* (Table 3). The probability of occurrence drops as the mean temperature increases above 20°C (Figure 3a). Figure 2a shows a typical example of this unit.

Unit 2. Monelytrum luederitzianum-Senegalia hereroensis *mountain savanna*

The vegetation unit consists of 175 species in 217 plots. The vegetation occurs in the rocky outcrops from the Otavi mountain range to the Omatako mountains of the

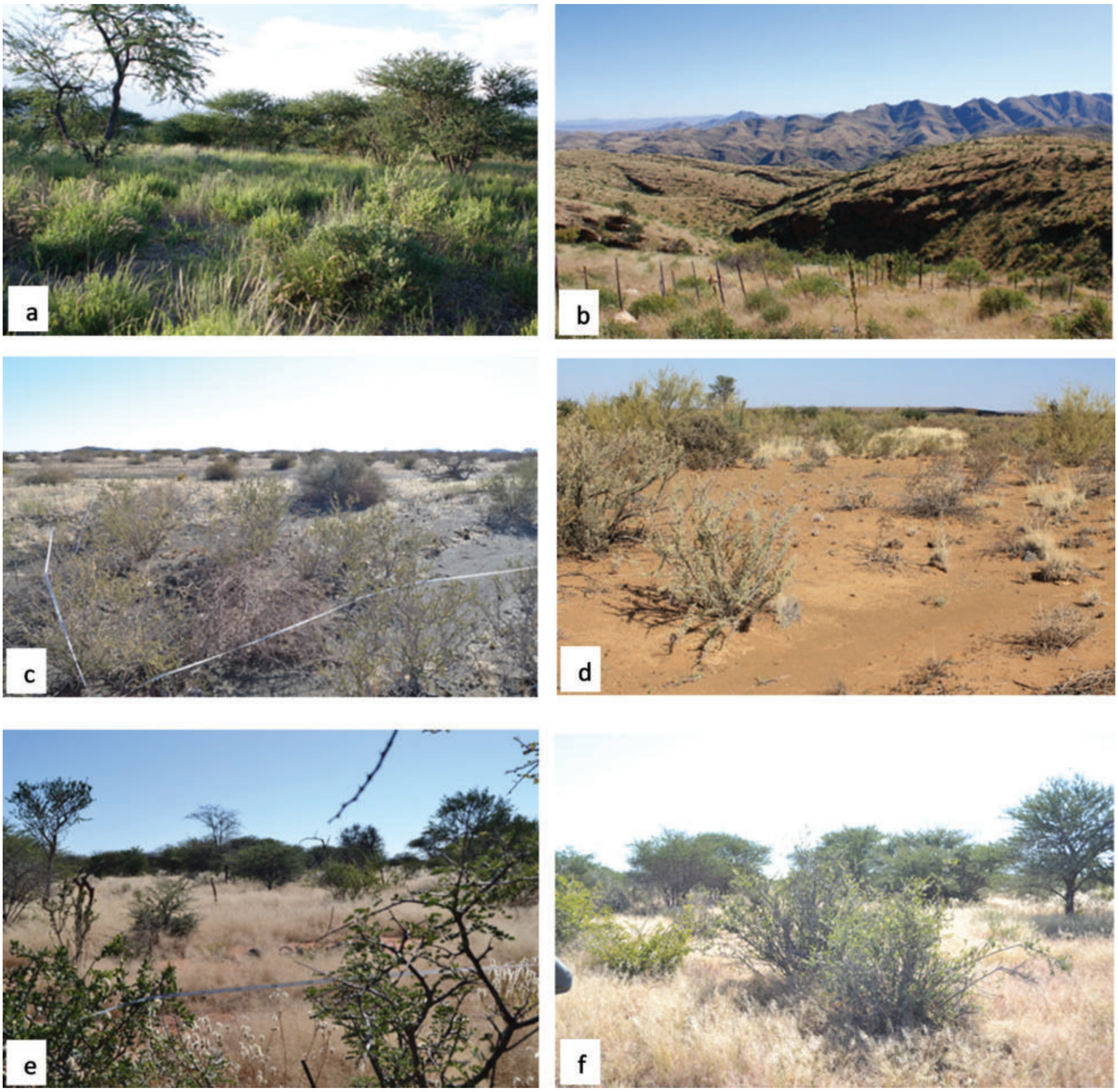

Figure 2. Typical representations of the vegetation units. (a) unit 1, the *Senegalia mellifera-Monechma genistifolium* thornbush savanna; (b) unit 2, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savanna; (c) unit 3, the *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savanna; (d) unit 4, the *Salsola-Tetragonia schenckii* dwarf shrub savanna; (e) unit 5, the *Dichrostachys cinerea-Senegalia mellifera* thornbush savanna; (f) unit 6, the *Stipagrostis uniplumis-Senegalia mellifera* thornbush savanna. Photo credit: (a) and (d) Ben Strohbach; (b), (c), (e) and (f) Leena Naftal.

Table 3. Abridged synoptic table of all the vegetation units along the transect. Vegetation units are labelled as follows: **1**. *Senegalia mellifera-Monechma genistifolium* thornbush savanna, **2**. *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, **3**. *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas, **4**. *Salsola-Tetragonia schenckii* dwarf shrub savannas, **5**. *Dichrostachys cinerea-Senegalia mellifera* thornbush savannas, **6**. *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas, **7**. Thornbush savanna – Nama-Karoo transition, **8**. *Aristida congesta-Senegalia mellifera* thornbush savannas, **9**. *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, **10**. *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas, **11**. *Combretum collinum-Terminalia sericea* broad-leafed savannas, **12**. *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas. **F** = percentage frequency; **P** = the phi coefficient of fidelity × 100. The highlighted values are for species with Phi > 0.30, and Freq > 40%, meeting the predetermined criteria for the respective vegetation units.

Vegetation units	**1**		**2**		**3**		**4**		**5**		**6**		**7**		**8**		**9**		**10**		**11**		**12**	
Number of plots	**138**		**217**		**101**		**173**		**175**		**157**		**115**		**168**		**305**		**84**		**301**		**52**	
	F	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**	**F**	**P**
Monechma genistifolium	73	41	10	---	12	---	21	---	18	---	22	---	23	---	31	9	6	---	12	---	.	---	2	---
Cenchrus ciliaris	74	36	37	10	7	---	10	---	37	10	26	---	16	---	30	---	28	---	10	---	.	---	4	---
Leucosphaera bainesii	88	36	50	11	19	---	17	---	32	---	38	---	37	---	69	24	20	---	14	---	.	---	6	---
Hermannia damarana	19	36	4	---	.	---	.	---	1	---	.	---	.	---	1	---	1	---	.	---	.	---	.	---
Vachellia tortilis	60	35	6	---	.	---	1	---	27	8	24	---	1	---	49	26	19	---	.	---	.	---	13	---
Monelytrum luederitzianum	10	---	39	40	.	---	.	---	9	---	4	---	1	---	5	---	8	---	.	---	.	---	.	---
Hirpicium gazanioides	4	---	40	40	3	---	6	---	7	---	5	---	.	---	2	---	10	---	1	---	.	---	.	---
Eriocephalus luederitzianus	20	16	39	40	1	---	5	---	4	---	4	---	3	---	2	---	1	---	.	---	.	---	.	---
Senegalia hereroensis	.	---	30	40	..	---	.	---	4	---	4	---	.	---	1	---	8	---	.	---	.	---	2	---
Eragrostis nindensis	14	---	71	40	14	---	10	---	11	---	33	11	24	---	10	---	18	---	8	---	2	---	15	---
Microchloa caffra	4	---	39	36	2	---	2	---	8	---	9	---	.	---	11	---	7	---	1	---	3	---	2	---
Hibiscus discophorus	1	---	21	36	.	---	.	---	2	---	3	---	.	---	2	---	1	---	.	---	.	---	.	---
Fingerhuthia africana	13	---	39	35	2	---	5	---	10	---	6	---	2	---	.	---	11	---	5	---	.	---	.	---
Panicum lanipes	.	---	19	34	.	---	1	---	4	---	3	---	.	---	.	---	2	---	.	---	.	---	.	---
Ursinia nana	.	---	18	32	.	---	1	---	2	---	3	---	.	---	.	---	2	---	1	---	.	---	.	---
Hermannia affinis	1	---	24	30	5	---	5	---	1	---	2	---	.	---	.	---	2	---	8	---	.	---	.	---
Plinthus sericeus	.	---	17	30	.	---	2	---	3	---	2	---	.	---	.	---	2	---	.	---	.	---	.	---
Stipagrostis anomala	.	---	.	---	45	56	2	---	.	---	.	---	1	---	.	---	.	---	11	8	.	---	.	---
Zygophyllum simplex	.	---	1	---	30	44	6	---	.	---	.	---	2	---	.	---	1	---	2	---	.	---	.	---
Xerocladia viridiramis	1	---	.	---	19	40	1	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---
Calicorema capitata	.	---	.	---	39	40	4	---	.	---	3	---	2	---	.	---	.	---	30	29	.	---	.	---
Tribulus cristatus	1	---	1	---	37	39	11	6	.	---	3	---	18	15	.	---	.	---	2	---	.	---	.	---
Zygophyllum rigida	1	---	1	---	19	35	6	8	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---
Petalidium parvifolium	.	---	.	---	10	30	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---
Stipagrostis ciliata	7	---	11	---	26	13	68	52	.	---	1	---	21	8	1	---	2	---	10	---	.	---	.	---
Cadaba aphylla	1	---	1	---	6	---	31	33	.	---	9	---	14	10	1	---	1	---	7	---	.	---	.	---
Salsola species	3	---	1	---	17	18	25	31	.	---	.	---	5	---	.	---	1	---	2	---	.	---	.	---
Boscia foetida	27	5	6	---	30	7	27	5	1	---	38	14	74	41	5	---	4	---	29	---	.	---	.	---
Lycium cinereum	.	---	11	---	16	---	9	---	1	---	25	13	48	35	1	---	1	---	25	13	.	---	.	---
Triraphis ramosissima	2	---	6	---	1	---	.	---	1	---	17	16	29	32	.	---	5	---	1	---	.	---	.	---
Vachellia nebrownii	.	---	1	---	10	---	17	10	.	---	16	9	36	30	1	---	.	---	17	9	.	---	.	---
Ondetia linearis	6	---	6	---	.	---	.	---	12	---	3	---	.	---	40	43	2	---	.	---	.	---	4	---
Indigofera rautanenii	5	---	5	---	.	---	.	---	18	9	14	---	2	---	45	38	5	---	.	---	.	---	13	---
Geigeria acaulis	14	---	8	---	1	---	.	---	15	---	16	---	1	---	43	36	5	---	1	---	.	---	2	---
Lycium eeni	57	21	31	---	.	---	1	---	38	9	38	8	7	---	76	35	18	---	12	---	.	---	31	---
Achyranthes aspera	54	21	22	---	.	---	1	---	57	23	25	---	5	---	71	33	26	---	7	---	4	---	21	---
Phaeoptilum spinosum	36	11	32	8	16	---	3	---	24	---	25	---	14	---	65	33	7	---	18	---	.	---	10	---
Eragrostis porosa	51	14	38	---	3	---	5	---	35	---	50	13	42	---	79	32	25	---	20	---	1	---	13	---
Boscia albitrunca	59	15	25	---	3	---	2	---	59	15	46	7	17	---	84	31	39	---	17	---	10	---	62	17
Aristida rhiniochloa	30	12	11	---	.	---	.	---	42	22	9	---	3	---	52	31	23	6	.	---	.	---	17	---
Combretum apiculatum	1	---	6	---	.	---	.	---	3	---	1	---	1	---	2	---	20	30	.	---	.	---	.	---
Schmidtia kalahariensis	7	---	11	---	19	---	17	---	.	---	33	7	62	28	1	---	7	---	93	50	.	---	25	---
Stipagrostis hirtigluma	12	---	22	4	37	16	20	---	6	---	5	---	8	---	5	---	5	---	68	42	.	---	12	---
Eragrostis cylindriflora	.	---	6	---	3	---	1	---	.	---	.	---	.	---	3	---	4	---	27	38	.	---	.	---
Aizoanthemum galenioides	.	---	1	---	.	---	3	---	.	---	.	---	.	---	.	---	.	---	19	38	.	---	.	---
Combretum collinum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	83	85	6	---
Ochna pulchra	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	3	---	.	---	72	79	6	---
Terminalia sericea	.	---	.	---	.	---	.	---	5	---	1	---	.	---	1	---	10	---	.	---	89	79	17	---
Burkea africana	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	62	77	.	---
Baphia massaiensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	70	76	10	---
Bauhinia petersiana	.	---	1	---	.	---	.	---	3	---	.	---	.	---	.	---	9	---	.	---	82	73	23	---
Eragrostis pallens	.	---	.	---	.	---	1	---	.	---	1	---	.	---	.	---	1	---	.	---	55	72	.	---
Aristida stipitata	.	---	.	---	.	---	.	---	2	---	.	---	2	---	2	---	3	---	.	---	62	72	2	---
Combretum psidioides	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	52	68	2	---
Xenostegia tridentata subsp. *angustifolia*	.	---	1	---	.	---	.	---	5	---	1	---	.	---	.	---	5	---	.	---	57	64	6	---

Vegetation units	1		2		3		4		5		6		7		8		9		10		11		12	
Number of plots	138		217		101		173		175		157		115		168		305		84		301		52	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Baissea wulfhorstii	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	40	60	2	---
Panicum kalaharense	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	37	59	.	---
Pterocarpus angolensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	37	59	.	---
Senegalia ataxacantha	.	---	.	---	.	---	.	---	1	---	1	---	.	---	.	---	4	---	.	---	44	58	4	---
Jacquemontia tamnifolia	.	---	.	---	.	---	.	---	1	---	1	---	.	---	1	---	3	---	.	---	43	56	6	---
Ozoroa schinzii	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	39	56	6	---
Combretum engleri	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	37	55	4	---
Lophiocarpus tenuissimus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	31	54	.	---
Acrotome angustifolia	.	---	.	---	.	---	.	---	4	---	.	---	.	---	1	---	3	---	.	---	38	54	.	---
Cyperus margaritaceus	.	---	.	---	.	---	.	---	2	---	2	---	.	---	.	---	4	---	.	---	50	53	19	---
Megaloprotachne albescens	.	---	.	---	.	---	.	---	2	---	.	---	.	---	.	---	1	---	.	---	31	50	2	---
Commiphora angolensis	.	---	2	---	.	---	.	---	14	---	1	---	.	---	4	---	9	---	.	---	59	49	33	23
Perotis patens	.	---	.	---	.	---	.	---	1	---	.	---	.	---	.	---	1	---	.	---	26	49	.	---
Diplorhynchus condylocarpon	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	25	48	.	---
Croton gratissimus	.	---	1	---	.	---	.	---	19	---	.	---	.	---	.	---	18	12	.	---	50	48	6	---
Ipomoea chloroneura	.	---	.	---	.	---	.	---	3	---	.	---	.	---	.	---	3	---	.	---	33	46	6	---
Tristachya superba	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	22	46	.	---
Indigofera filipes	.	---	.	---	.	---	.	---	.	---	1	---	.	---	1	---	1	---	.	---	28	45	4	---
Syncolostemon bracteosus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	24	44	2	---
Guibourtia coleosperma	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	20	44	.	---
Tephrosia lupinifolia	.	---	.	---	.	---	.	---	2	---	.	---	.	---	1	---	1	---	.	---	25	43	2	---
Strychnos pungens	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	19	42	.	---
Oxygonum alatum	2	---	6	---	.	---	.	---	13	---	26	---	1	---	13	---	18	---	4	---	67	42	40	20
Polydora steetziana	.	---	.	---	.	---	.	---	5	---	4	---	.	---	.	---	5	---	.	---	31	42	2	---
Baikiaea plurijuga	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	19	42	.	---
Limeum fenestratum	.	---	1	---	.	---	1	---	3	---	6	---	3	---	6	---	8	---	.	---	44	42	19	---
Rhynchosia venulose	.	---	2	---	.	---	.	---	1	---	.	---	.	---	.	---	7	---	.	---	27	41	.	---
Phyllanthus omahakensis	.	---	.	---	.	---	.	---	1	---	.	---	.	---	.	---	2	---	.	---	25	41	4	---
Gardenia brachythamnus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	18	41	.	---
Chamaecrista absus	.	---	.	---	.	---	.	---	2	---	.	---	.	---	1	---	1	---	.	---	23	41	2	---
Sesamum alatum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	16	39	.	---
Philenoptera nelsii	.	---	.	---	.	---	.	---	5	---	1	---	.	---	.	---	6	---	.	---	31	39	12	---
Dichapetalum cymosum	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	16	38	.	---
Diospyros chamaethamnus	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	38	.	---
Pavonia clathrate	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	1	---	.	---	19	37	2	---
Indigofera baumiana	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	15	37	.	---
Clerodendrum ternatum	.	---	1	---	.	---	.	---	14	---	5	---	.	---	2	---	16	---	.	---	47	36	38	28
Combretum zeyheri	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	.	---	14	36	.	---
Acanthosicyos naudinuanus	.	---	1	---	.	---	.	---	6	---	13	---	.	---	4	---	8	---	4	---	41	36	23	---
Bulbostylis hispidula	2	---	6	---	.	---	.	---	8	---	9	---	5	---	8	---	15	---	14	---	53	35	44	27
Tephrosia purpurea	1	---	.	---	.	---	.	---	5	---	3	---	.	---	1	---	3	---	.	---	29	35	13	---
Raphionacme velutina	1	---	23	22	.	---	.	---	4	---	3	---	.	---	1	---	5	---	.	---	32	34	.	---
Chamaecrista biensis	.	---	.	---	.	---	.	---	3	---	1	---	.	---	1	---	5	---	2	---	26	34	10	---
Phyllanthus pentandrus	6	---	3	---	1	---	1	---	6	---	10	---	2	---	14	---	15	---	2	---	44	32	31	19
Strychnos cocculoides	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	11	31	.	---
Pogonarthria squarrosa	.	---	2	---	.	---	.	---	7	---	1	---	.	---	.	---	8	---	5	---	31	31	19	---
Grewia flavescens	5	---	4	---	.	---	1	---	22	---	5	---	1	---	15	---	17	---	.	---	46	31	31	---
Triraphis schinzii	.	---	1	---	.	---	.	---	2	---	1	---	.	---	.	---	4	---	.	---	21	31	10	---
Eragrostis dinteri	1	---	1	---	.	---	.	---	6	---	3	---	.	---	4	---	10	---	1	---	27	31	6	---
Tricholaena monachne	.	---	.	---	.	---	.	---	3	---	1	---	.	---	.	---	2	---	1	---	16	31	.	---
Commiphora africana	.	---	1	---	.	---	1	---	12	---	.	---	.	---	1	---	3	---	.	---	32	30	31	29
Psydrax livida	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10	30	.	---
Entada arenaria	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	10	30	.	---
Chamaecrista mimosoides	.	---	.	---	.	---	.	---	.	---	2	---	.	---	.	---	1	---	.	---	13	30	.	---
Gloriosa superba	.	---	.	---	.	---	.	---	1	---	.	---	.	---	1	---	1	---	1	---	15	30	2	---
Eragrostis rigidior	.	---	2	---	1	---	1	---	27	8	23	5	1	---	17	---	19	---	.	---	15	---	98	65
Rhigozum brevispinosum	1	---	.	---	.	---	.	---	12	7	4	---	.	---	4	---	10	5	.	---	1	---	42	45
Urochloa panicoides	.	---	.	---	.	---	.	---	.	---	1	---	.	---	1	---	2	---	.	---	.	---	25	45
Ozoroa paniculosa	.	---	2	---	.	---	.	---	11	---	4	---	.	---	1	---	16	10	.	---	7	---	44	43
Solanum elaeagnifolium	.	---	.	---	.	---	.	---	.	---	.	---	.	---	1	---	4	3	1	---	.	---	23	40
Geigeria schinzii	.	---	1	---	.	---	.	---	.	---	1	---	.	---	1	---	3	---	.	---	.	---	21	40
Pavonia senegalensis	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2	---	4	3	.	---	1	---	21	39
Rhynchosia totta	1	---	1	---	.	---	.	---	7	---	1	---	.	---	1	---	8	---	.	---	15	12	35	38
Peltophorum africanum	.	---	2	---	.	---	.	---	15	8	2	---	.	---	.	---	18	12	.	---	15	8	40	37
Indigofera holubii	1	---	1	---	.	---	.	---	1	---	1	---	.	---	5	---	3	---	.	---	.	---	23	36
Evolvulus alsinioides	9	---	10	---	.	---	.	---	35	11	31	8	1	---	28	---	29	7	1	---	27	5	67	36
Camptorrhiza strumosa	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	12	33
Grewia flava	59	13	27	---	.	---	2	---	74	22	51	8	26	---	61	14	46	5	7	---	15	---	90	32
Commiphora glandulosa	1	---	6	---	.	---	.	---	18	10	6	---	7	---	.	---	18	10	.	---	8	---	38	32

Vegetation units	1		2		3		4		5		6		7		8		9		10		11		12	
Number of plots	138		217		101		173		175		157		115		168		305		84		301		52	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Brachiaria brizantha	.	---	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2	---	.	---	1	---	13	32
Rhus tenuinervis	.	---	1	---	.	---	.	---	6	---	.	---	.	---	.	---	6	5	.	---	3	---	21	31
Combretum hereroense	.	---	6	---	.	---	.	---	26	20	3	---	.	---	.	---	20	13	.	---	7	---	37	31
Lapeirousia otaviensis	.	---	.	---	.	---	.	---	1	---	.	---	.	---	.	---	.	---	.	---	.	---	12	31
Ipomoea hochstetteri	.	---	.	---	.	---	.	---	.	---	.	---	.	---	2	---	2	---	.	---	.	---	13	31
Hibiscus mastersianus	.	---	.	---	.	---	.	---	1	---	.	---	1	---	1	---	2	---	.	---	19	24	23	30
Digitaria seriata	.	---	1	---	.	---	.	---	7	---	3	---	.	---	.	---	11	---	.	---	83	64	48	32
Commelina africana	.	---	12	---	.	---	.	---	10	---	3	---	.	---	2	---	10	---	.	---	53	41	42	30
Senegalia cinerea	1	---	1	---	.	---	.	---	16	---	5	---	.	---	4	---	21	8	2	---	48	32	52	36
Talinum arnotii	30	---	19	---	1	---	1	---	29	---	40	13	1	---	52	22	20	---	12	---	1	---	60	27
Lantana angolensis	14	---	12	---	.	---	.	---	30	16	6	---	.	---	13	---	23	9	2	---	12	---	42	27
Pogonarthria fleckii	8	---	41	10	.	---	2	---	45	13	39	9	3	---	52	18	37	7	8	---	18	---	65	26
Schmidtia pappophoroides	4	---	38	11	1	---	2	---	25	---	32	---	3	---	17	---	32	---	10	---	58	25	58	25
Ehretia rigida	38	11	16	---	.	---	1	---	47	18	18	---	6	---	48	18	25	---	12	---	6	---	54	23
Ziziphus mucronata	23	---	31	---	1	---	2	---	50	20	15	---	17	---	24	---	43	15	1	---	8	---	54	23
Dichrostachys cinerea	17	---	13	---	.	---	.	---	61	21	33	---	2	---	61	21	52	15	13	---	42	8	62	21
Urochloa brachyura	26	---	19	---	.	---	.	---	55	15	42	---	3	---	55	15	49	11	7	---	63	20	63	20
Senegalia mellifera subsp. *dentinens*	91	20	61	---	15	---	17	---	100	26	74	10	35	---	96	23	72	9	42	---	8	---	88	19
Eragrostis trichophora	20	---	23	---	.	---	1	---	54	25	13	---	3	---	39	14	28	---	4	---	16	---	44	18
Phyllanthus maderaspatensis	34	10	24	---	.	---	.	---	39	14	18	---	2	---	42	16	21	---	4	---	20	---	44	18
Aristida congesta	18	---	35	6	11	---	6	---	41	11	37	8	6	---	67	29	24	---	13	---	4	---	48	15
Tragus berteronianus	39	12	28	---	5	---	3	---	30	---	24	---	11	---	42	14	25	---	18	---	3	---	42	14
Stipagrostis uniplumis	72	---	58	---	48	---	18	---	62	---	100	22	97	20	74	---	55	---	39	---	72	---	87	14
Barleria lanceolata	48	23	16	---	3	---	.	---	35	13	17	---	1	---	54	28	12	---	2	---	2	---	31	---
Enneapogon cenchroides	78	24	51	7	10	---	24	---	43	---	75	22	61	13	68	17	32	---	20	---	3	---	12	---
Rhigozum trichotomum	9	---	13	---	63	27	65	28	1	---	29	---	63	26	1	---	5	---	54	20	.	---	.	---
Kyphocarpa angustifolia	25	---	52	18	.	---	8	---	43	13	28	---	4	---	57	22	32	---	12	---	5	---	38	---
Cyperus palmatus	20	---	15	---	.	---	.	---	19	---	21	9	.	---	41	28	9	---	1	---	1	---	15	---
Chloris virgata	28	---	24	---	9	---	7	---	28	7	15	---	8	---	46	21	21	---	15	---	1	---	23	---
Hermannia modesta	18	---	41	22	3	---	3	---	18	---	19	---	10	---	48	27	11	---	4	---	.	---	12	---
Otoptera burchellii	46	20	27	---	1	---	1	---	28	---	43	17	23	---	28	---	17	---	6	---	1	---	17	---
Ptycholobium biflorum	34	7	27	---	7	---	5	---	22	---	48	17	28	---	60	25	12	---	13	---	.	---	40	---
Aristida adscensionis	55	10	68	18	13	---	5	---	59	12	45	---	42	---	79	25	37	---	33	---	8	---	31	---
Melinis repens	33	---	62	12	4	---	10	---	47	---	59	---	30	---	61	11	53	---	20	---	70	17	65	---
Gisekia africana	4	---	12	---	7	---	8	---	17	---	48	15	41	10	29	---	17	---	38	---	55	20	38	---
Vachellia luederitzii	56	19	28	---	1	---	1	---	60	21	26	---	3	---	51	15	42	9	11	---	11	---	48	---
Enneapogon desvauxii	54	22	32	7	50	19	21	---	8	---	20	---	38	11	10	---	10	---	30	---	.	---	.	---
Dicoma capensis	6	---	23	9	33	18	12	---	5	---	13	---	35	20	5	---	3	---	20	---	.	---	.	---
Catophractes alexandrii	52	11	50	10	22	---	24	---	21	---	59	16	70	23	39	---	22	---	39	---	1	---	12	---
Vachellia hebeclada subsp. *hebeclada*	24	---	28	7	.	---	1	---	23	---	31	9	10	---	40	17	26	6	12	---	1	---	27	---

Central Plateau and Khomas highlands, at a mean altitude of 2,000–2,500 m (Strohbach 2017, 2019). Figure 2b shows a typical example of this unit which consists of diagnostic species of grasses such as *Monelytrum luederitzianum*, *Eragrostis nindensis*, *Pogonarthria fleckii*, and bushes such as *Monechma genistifolium*, *Catophractes alexandrii* and *Searsia marlothii* (Table 3), forming semi–open shrublands on shallow soils. The probability of occurrence of this vegetation type increases with the Mean Annual Precipitation (MAP) between 200 mm and 350 mm (Figure 3b).

Unit 3. Calicorema capitata-Rhigozum trichotomum *dwarf shrub savanna*

These are dwarf shrub savannas occurring in the Nama–Karoo (Figure 2c) in areas with mean annual rainfall below 250 mm (Figure 3c). Diagnostic species include *Stipagrostis anomala*, *Tetraena simplex*, *Xerocladia viridiramis*, *Calicorema capitata*, *Tribulus cristatus*, *Zygophyllum rigidum* and *Petalidium parvifolium*. Constant species include *Rhigozum trichotomum* and *Enneapogon desvauxii* (Table 3).

Unit 4. Salsola-Tetragonia schenckii *dwarf shrub savanna*

This vegetation is mainly associated with washes, floodplains, pans and other ephemeral wetland systems of the Nama-Karoo (Strohbach and Jankowitz 2012). The vegetation unit occurs around the mean rainfall of 250 mm per year (Figure 3d). The dwarf Karoo shrubs, mainly *Rhigozum trichotomum* and *Tetragonia schenckii*, but also *Zygophyllum microcarpum*, *Vachellia nebrownii* and *Salsola* species dominate the unit. Grass species such as *Stipagrostis ciliata* and *Stipagrostis obtusa* form part of the dominant species of the unit (Table 3) Figure 2d shows a representation of this vegetation unit.

Unit 5. Dichrostachys cinerea-Senegalia mellifera *thornbush savanna*

These savanna types comprise 175 plots and 90 species, characterised by a woody layer with constant species *Grewia flava*, *Ziziphus mucronata*, *Senegalia mellifera* subsp. *dentinens* and *Dichrostachys cinerea* (Table 3) usually forming open to closed bushland (Figure 2e). The lower strata consist of herb species

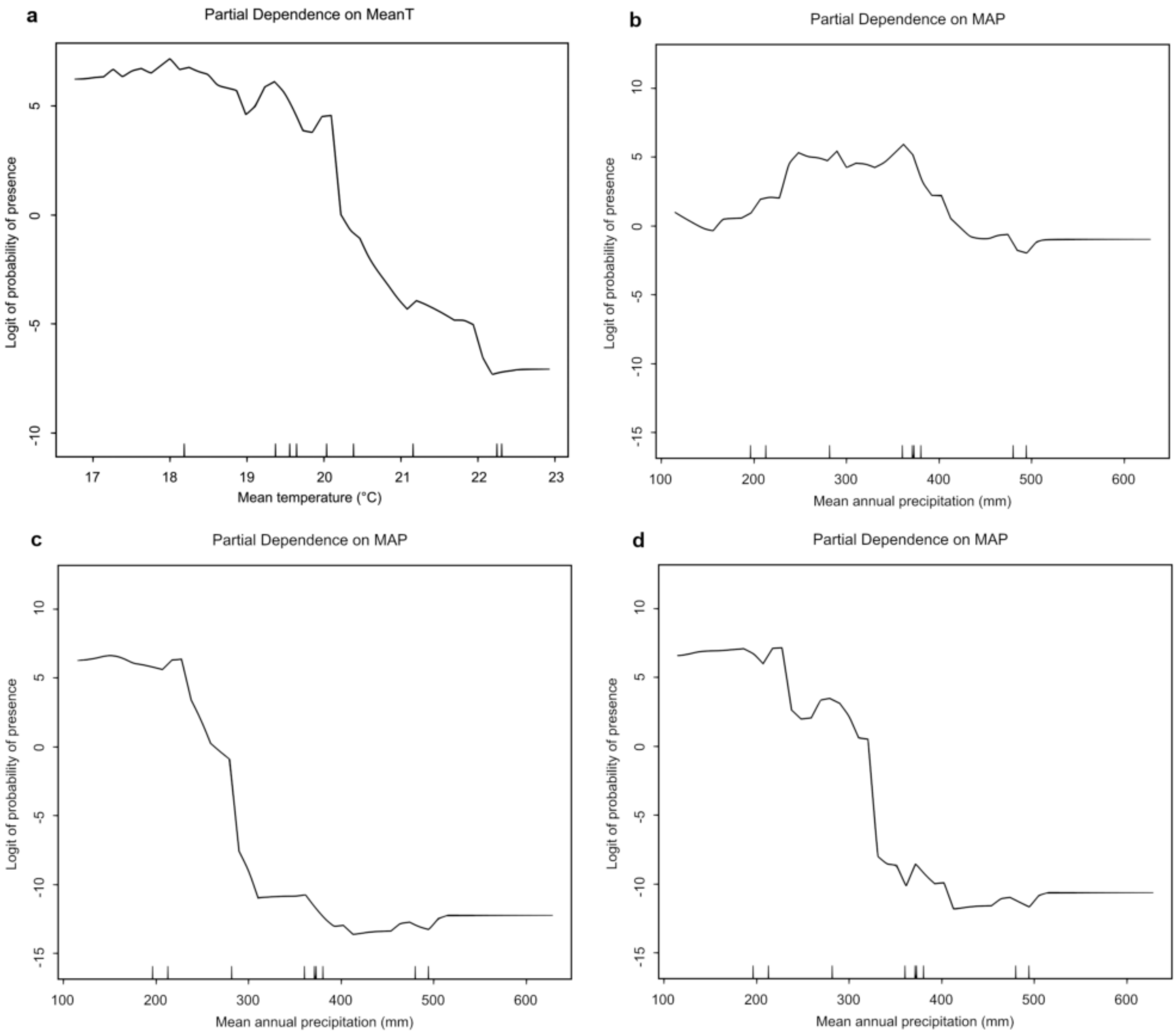

Figure 3. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) Mean annual temperature (MAT) influencing the distribution of unit 1, the *Senegalia mellifera-Monechma* thornbush savanna; (b) Mean annual precipitation (MAP) influencing the distribution of unit 3, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savanna; (c) MAP influencing the distribution of unit 3, the *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savanna; (d) MAP influencing the distribution of unit 4, the *Salsola-Tetragonia schenckii* dwarf shrub savanna.

such as *Achyranthes aspera*, which according to field observation, are mostly shade–loving, taking up cover under trees with big canopies. Other herb species include *Pavonia burchellii* and *Pollichia campestris*. Dominant grass species include *Urochloa brachyura*, *Pogonarthria fleckii* and *Melinis repens* subsp. *grandiflora*. The vegetation occurs in an area with MAP between 250 mm and 500 mm (Figure 4a).

Unit 6. Stipagrostis uniplumis-Senegalia mellifera *thornbush savanna*

This vegetation unit consists of 157 plots and 30 species. The unit is distributed within the mean annual rainfall range of 230 mm and 400 mm (Figure 4b), but also an altitudinal range of between 1100 and 1300 m asl (Figure 4c). The species composition of this vegetation includes the following dominant species: *Catophractes alexandrii*, *Grewia flava*, *Eragrostis porosa*, *Senegalia mellifera* subsp. *dentinens*, *Vachellia reficiens* and *Schmidtia pappophoroides* (Table 3). An overview of the vegetation unit is shown in Figure 2e.

Unit 7. Thornbush savanna – Nama-Karoo transition

This vegetation unit is distributed in areas with MAP below 300 mm (Figure 6a). The vegetation unit comprises 115 plots and 52 species. Diagnostic species of the group include species such as *Boscia foetida*, *Lycium cinereum*, *Triraphis ramosissima* and *Vachellia nebrownii*. Species such as *Stipagrostis uniplumis*, *Catophractes alexandrii*, *Rhigozum trichotomum* and *Schmidtia kalahariensis* dominate the unit (Table 3). An example of the vegetation is shown in Figure 5a.

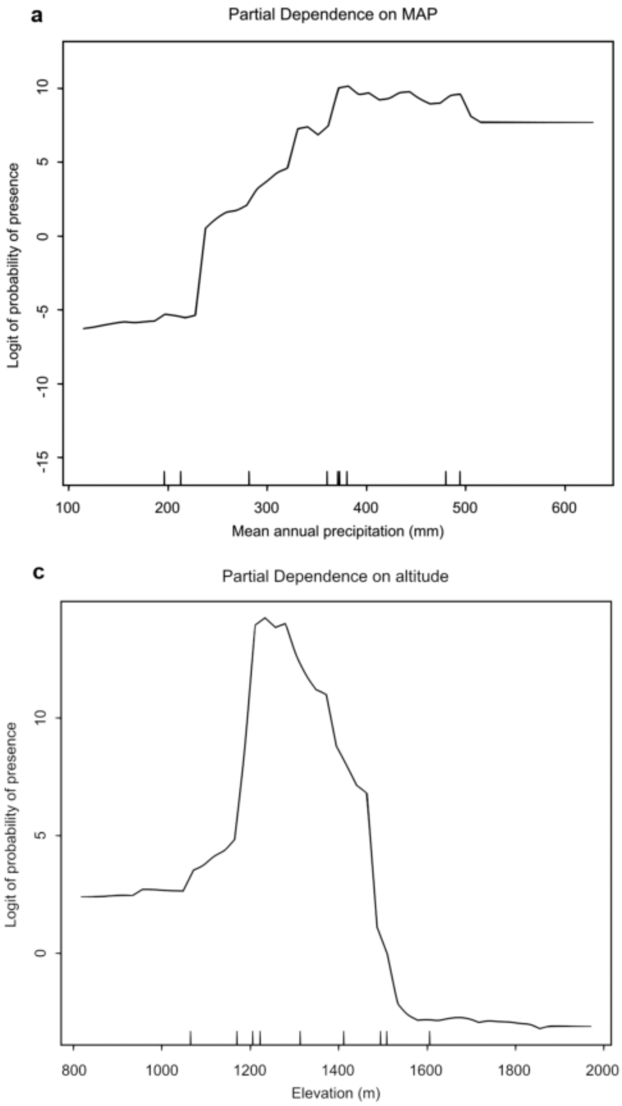

Figure 4. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) MAP influencing the distribution of unit 5, the *Dichrostachys cinerea-Senegalia mellifera* thornbush savanna; (b) MAP influencing the distribution of unit 6, the *Stipagrostis uniplumis-Senegalia mellifera* thornbush savanna; and (c) altitude also influencing the distribution of unit 6, the *Stipagrostis uniplumis-Senegalia mellifera* thornbush savanna.

Unit 8.* Aristida congesta-Senegalia mellifera *thornbush savanna

The distribution of this vegetation unit occurs between the mean rainfall range of 200 mm to 400 mm (Figure 6b). Species diagnostic of the group include *Lycium eenii*, *Achyranthes aspera*, *Phaeoptilum spinosum*, *Eragrostis porosa*, *Boscia albitrunca*, *Aristida rhiniochloa*, with dominating species *Senegalia mellifera* subsp. *dentinens*, *Aristida adscensionis*, *Stipagrostis uniplumis* and *Leucosphaera bainesii* (Table 3). A typical example of the vegetation of this unit can be seen in Figure 5b.

Unit 9.* Senegalia mellifera-Dichrostachys cinerea *degraded thornbush savanna

This unit is the most widely distributed, occurring in areas that receive a mean rainfall of 200 mm to 500 mm (Figure 6c). It occurs in mosaic with many other thornbush savanna units, often associated with a dense shrublayer dominated by the woody species *Senegalia mellifera* subsp. *dentinens*, *Grewia flava*, *Dichrostachys cinerea* and *Vachellia reficiens*, whilst the herb layer is generally sparser with the grasses *Urochloa brachyura*, *Stipagrostis uniplumis*, *Melinis repens* subsp. *grandiflora* and *Eragrostis trichophora.* Bush encroachment is regarded as a serious form of degradation in the savannas of Namibia and southern Africa (De Klerk 2004; Laufs et al. 2024). An example of vegetation occurring in this unit can be seen in Figure 5c. A more detailed species composition can be found in Table 3.

Unit 10.* Schmidtia kalahariensis-Rhigozum trichotomum *arid thornbush savanna

This savanna type is distributed within the mean rainfall range of 100–300 mm (Figure 6d). Constant species of this unit are as follows: *Schmidtia kalahariensis*, *Stipagrostis hirtigluma* and *Eragrostis cylindriflora.* Species such as *Chloris virgata*, *Senegalia mellifera* subsp. *dentinens*,

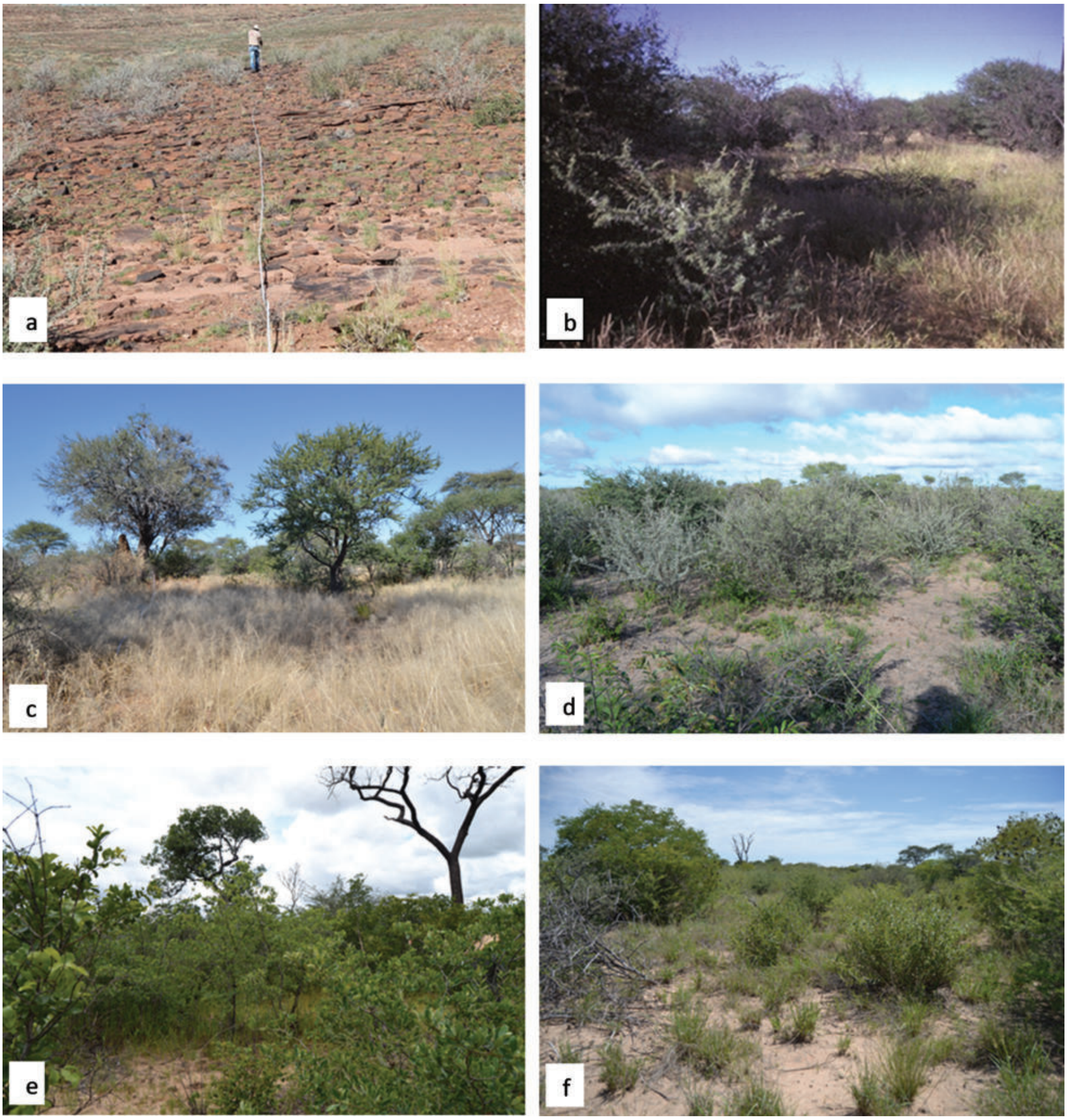

Figure 5. Typical representations of the vegetation units. (a) unit 7, the Thornbush savanna – Nama-Karoo transition, (b) unit 8, the *Aristida congesta-Senegalia mellifera* thornbush savanna, (c) unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savanna, (d) unit 10, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savanna; (e) unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savanna; and (f) unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savanna. Photo credit: (a) Johanna Nghishiko, (b) Ben Strohbach, (c–f) Leena Naftal.

Catophractes alexandrii and *Vachellia reficiens* dominate the unit (Table 3). An example of this vegetation unit is shown in Figure 5d.

Unit 11. Combretum collinum-Terminalia sericea *broad-leafed savanna*

This vegetation unit has a high species diversity compared to other vegetation units. The diagnostic species forming up the woody layer include *Combretum collinum*, *Ochna pulchra*, *Terminalia sericea*, *Burkea africana*, *Baphia massaiensis*, *Bauhinia petersiana* and *Pterocarpus angolensis*, amongst others (Figure 5e). Herbs and grasses such as *Xenostegia tridentata* subsp. *angustifolia*, *Digitaria seriata* and *Panicum kalaharense* are also found. Species within these savannas occasionally form open to close woodlands and shrublands (Strohbach and Petersen 2007). The unit occurs on deep Kalahari sand, mostly on Ferralic Arenosols (Strohbach and Petersen 2007). The probability

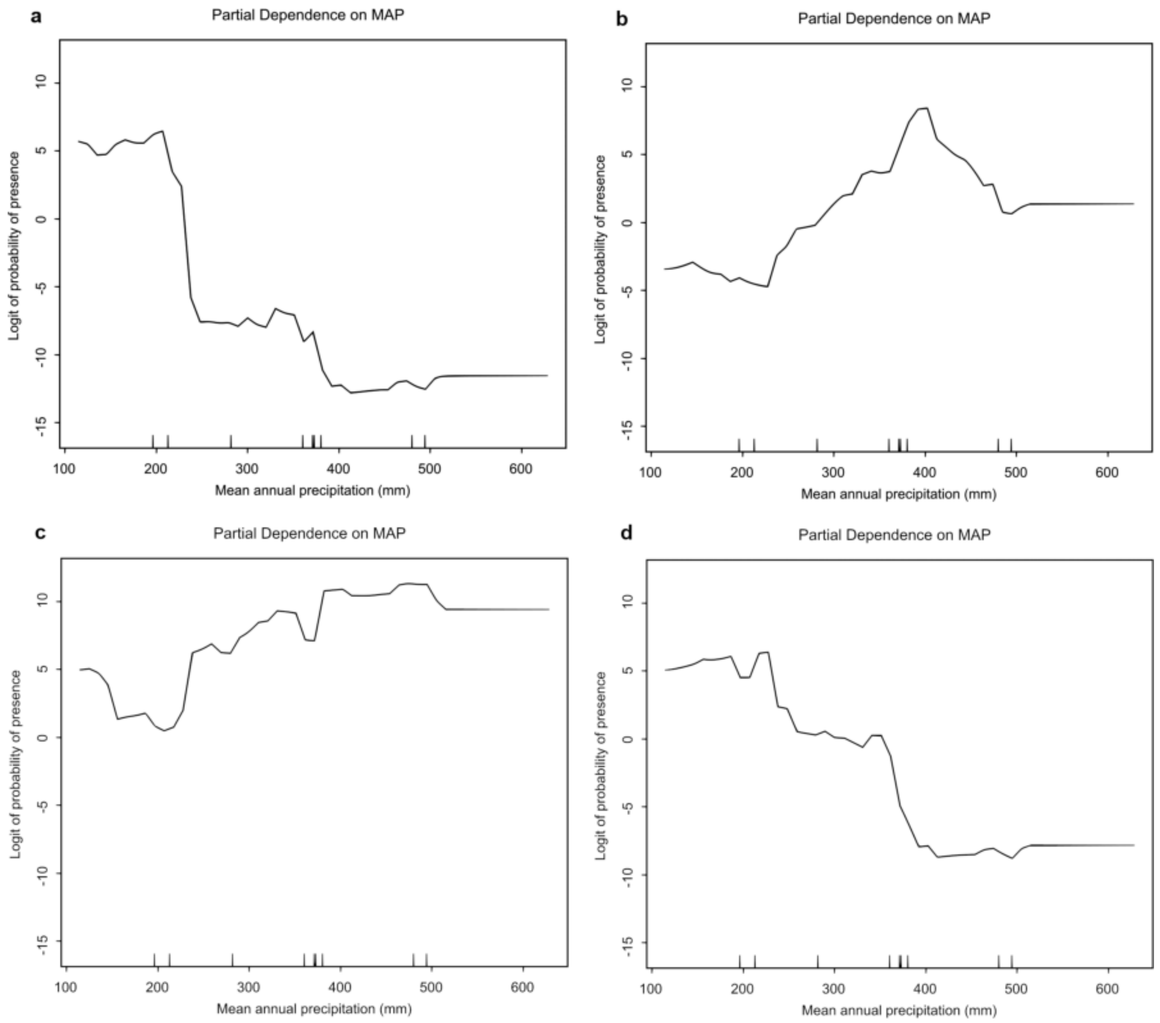

Figure 6. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) MAP influencing the distribution of unit 7, the Thornbush savanna – Nama-Karoo transition; (b) MAP influencing the distribution of unit 8, the *Aristida congesta-Senegalia mellifera* thornbush savanna; (c) MAP influencing the distribution of unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savanna; (d) MAP influencing the distribution of unit 10, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savanna.

of occurrence increases when the mean annual rainfall is above 400 mm (Figure 7a).

Unit 12.* Eragrostis rigidior-Peltophorum africanum *mesic thornbush savanna

This vegetation unit is distributed in areas with MAP of 350 mm to 500 mm and a Mean Annual Temperature (MAT) of over 25°C (Figure 7b, c). The composition of this vegetation unit includes woody species such as *Rhigozum brevispinosum*, *Senegalia cinerea*, *Vachellia erioloba* and *Peltophorum africanum*. Grass species such as *Urochloa panicoides*, *Eragrostis rigidior* and *Schmidtia pappophoroides* (Figure 5f). A detailed list of species occurring in this unit is presented in Table 3.

Modelling vegetation classes with Random Forest

Model performance evaluation

The model prediction with EVI indices had an overall classification accuracy of 94%, a Kappa value of 94% (Suppl. material 1), and an out-of-bag error of 17.1%. The accuracy of the model without EVI indices was 82% and Kappa 80%, as well as an out-of-bag error rate of 17.4% (Suppl. material 2). The environmental variables driving the current distribution and therefore used to predict the future distribution of the vegetation units are shown in Table 4.

The potential distribution of the vegetation units for the current and future under climate change scenarios

The current vegetation distribution results show that some vegetation units have a broad distribution, such as unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, unit 2, *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas and unit 4, *Salsola-Tetragonia schenckii* dwarf shrub savannas. While others such as unit 12, *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas and unit 1, the *Senegalia mellifera-Monechma genistifolium* thornbush savanna, have a restricted distribution (Figure 8). The total area covered by the current distribution for each

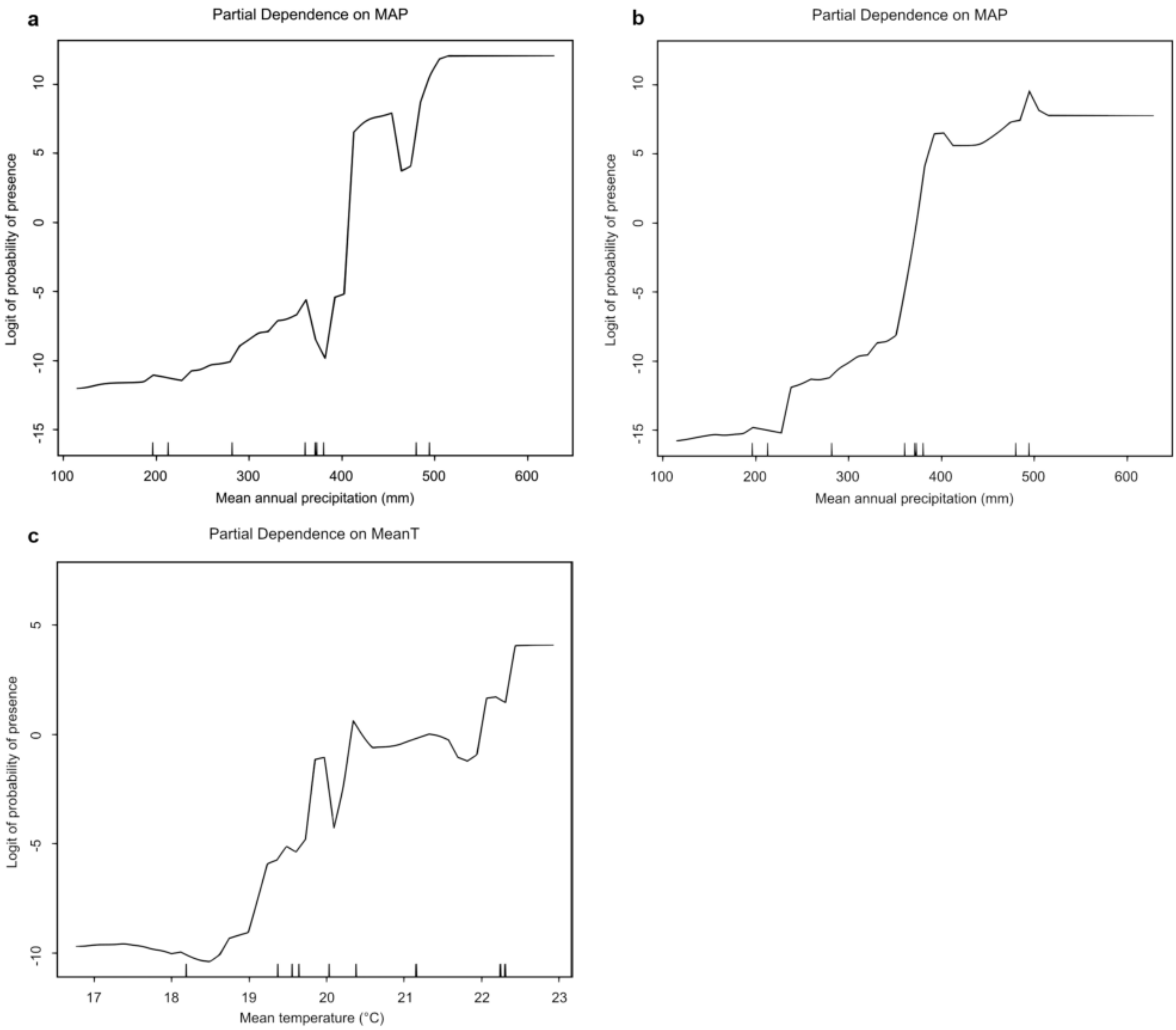

Figure 7. Partial dependence plots showing the effect of various environmental factors on the distribution of vegetation units. (a) MAP influencing the distribution of unit 11, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savanna; (b) MAP influencing the distribution of unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savanna; (c) MAT influencing the distribution of unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savanna.

Table 4. The Mean Decrease Gini (MDG) index and the importance per unit for the predictor variables used to fit the final model. Vegetation units are labelled as follows; unit **1**. *Senegalia mellifera-Monechma genistifolium* thornbush savanna, unit **2**. *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, unit **3**. *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas, unit **4.** *Salsola-Tetragonia schenckii* dwarf shrub savannas, unit **5**. *Dichrostachys cinerea-Senegalia mellifera* thornbush savannas, unit **6**. *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas, unit **7**. Thornbush savanna – Nama-Karoo transition, unit **8**. *Aristida congesta-Senegalia mellifera* thornbush savannas, unit **9**. *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, unit **10**. *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas, unit **11**. *Combretum collinum-Terminalia sericea* broad-leafed savannas, and unit **12**. *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas.

Variable	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	Unit 6	Unit 7	Unit 8	Unit 9	Unit 10	Unit 11	Unit 12	Mean decrease gini
Precipitation of the wettest month	15.7	19.2	29.6	33.5	18.3	15.8	21.7	16.3	15.9	25.4	24.2	17.8	191.71
Mean annual precipitation	18.9	15.2	18.8	26	18	15.6	24.1	16.1	14.5	24.1	18.7	17	195.21
Mean temperature of driest quarter	17.7	24.7	9.2	11.9	18.6	9.5	10.5	10.9	11.5	19.7	15.4	20.6	189.68
Mean temperature	19.6	28.9	12.6	15.3	15	13.5	16.4	14.8	10.7	22.7	11.5	19.9	205.95
Sand_sl4	16.6	6	9.4	8.7	7.5	5.9	7.2	7.5	4.4	7.7	13.3	16.3	168.08
Precipitation of February	17.5	16.9	26.7	29.1	18.1	16.7	24.2	18.5	13.8	28.1	20.7	18.3	182.97
Dominant soil	12.2	18.1	21.2	18.4	25.6	27.8	37	11.7	24.9	20.6	5	11.9	238.19
Altitude	26.1	25.8	25.8	20.6	37.1	32.1	29	24.4	29.2	29.4	12	26.3	366.27

Table 5. A comparison of the percentage change in the future distribution of the vegetation units relative to the current distribution using projected (2061–2080) climatic conditions for moderate (RCP4.5) and high (RCP8.5) scenarios under the IPSL–CM5A–LR and HadGEM2–ES General Circulation Models relative to the current potential distribution.

vegetation type name	Number of relevés	Area covered Current km²	Area covered Current %	RCP4.5 IPSL–CM5A–LR % Change	RCP4.5 HadGEM2–ES % Change	RCP8.5 IPSL–CM5A–LR % Change	RCP8.5 HadGEM2–ES % Change
Unit 1. *Senegalia mellifera-Monechma genistifolium* thornbush savannas	138	469.15	0.36	-99.46	-70.71	-100	-99.82
Unit 2. *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas	217	16,228.09	12.56	-70.56	-85.91	164.10	-98.77
Unit 3. *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas	101	6,985.11	5.41	-98.26	-91.09	-99.29	-10.95
Unit 4. *Salsola-Tetragonia schenckii* dwarf shrub savannas	173	18,648.03	14.44	-76.79	-34.85	-86.32	6.60
Unit 5. *Dichrostachys cinerea- Senegalia mellifera* thornbush savannas	175	5,514.37	4.27	-95.06	-98.35	-100	-100
Unit 6. *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas	157	2,829.78	2.19	-85.67	22.94	-100	-95.75
Unit 7. Thornbush savanna – Nama-Karoo transition	115	12,003.75	9.29	-98.29	-90.96	-100	-100
Unit 8. *Aristida congesta-Senegalia mellifera* thornbush savannas	168	8,632.81	6.68	-13.99	63.30	-83.24	2.14
Unit 9. *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas	305	34,049.07	26.36	-10.50	68.44	-18.19	65.77
Unit 10. *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas	84	1,624.7	1.25	-77.79	49.20	-100	-95.91
Unit 11. *Combretum collinum-Terminalia sericea* broad-leaved savannas	301	21,987.78	17.02	267.30	60.06	336.04	70
Unit 12. *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas	52	162.13	0.13	-97.40	32.94	-66.76	-96.88

vegetation unit is presented in Table 5, and the potential current distribution map is presented in Figure 8.

The HadGEM2–ES under the RCP4.5 predicted a potential expansion in unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, unit 1, *Senegalia mellifera-Monechma genistifolium* thornbush savannas, unit 10, *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas, unit 12, *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas and unit 6, *Stipagrostis uniplumis-Senegalia mellifera* thornbush savannas, towards the south of the transect (Figure 9a). Half of the vegetation types in the HadGEM2–ES are predicted to highly contract relative to the current distribution (Table 5).

The IPSL–CM5A–LR (RCP4.5) (Figure 9b) predicts a high potential expansion of mostly unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, are projected to cover most of the transect from the north to the central parts of the Khomas Highland in the Khomas region as well as sparsely down south. Most of the vegetation types are predicted to lose over 70% of their habitats and will be forced to live in restricted areas under this scenario.

The IPSL–CM5A–LR under the RCP8.5 (Figure 10b) predicts harsher conditions with five vegetation units predicted to go extinct while most of the vegetation types are predicted to lose up to 70% of their habitats. On the other hand, under the HadGEM2–ES (RCP8.5), only two vegetation types are predicted to go extinct while others will be on the verge of losing all their areas of occupancy (Table 5).

The HadGEM2–ES under the business–as–usual scenarios (RCP8.5) (Figure 10a) indicates an expansion shifting a bit towards the south of the transect with a few patches of unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savannas, down south. of Vegetation units such as unit 8, *Aristida congesta-Senegalia mellifera* thornbush savannas, unit 4, *Salsola-Tetragonia schenckii* dwarf shrub savannas, and unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas are predicted to expand.

The RCP8.5 conditions will favour the vegetation types such as the widely spread unit 11, *Combretum collinum-Terminalia sericea* broad-leafed savannas, and unit 9, *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, will expand at the expense of the other vegetation types.

Discussion

Comparison of the vegetation units to existing classification

The vegetation units derived from this analysis can be compared with existing classifications. Giess (1998) broadly described the vegetation of the whole Nama-Karoo as dwarf shrub savanna. Two vegetation units (*Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas and *Salsola-Tetragonia schenckii* dwarf shrub savannas) can be associated with Giess' (1998) classification of the dwarf shrub savanna. The same unit is similar to *Salsolo-Tetragonietum schenckii* as Strohbach and Jankowitz (2012) described for the phytosociology classification of farm Haribes in the Nama-Karoo biome.

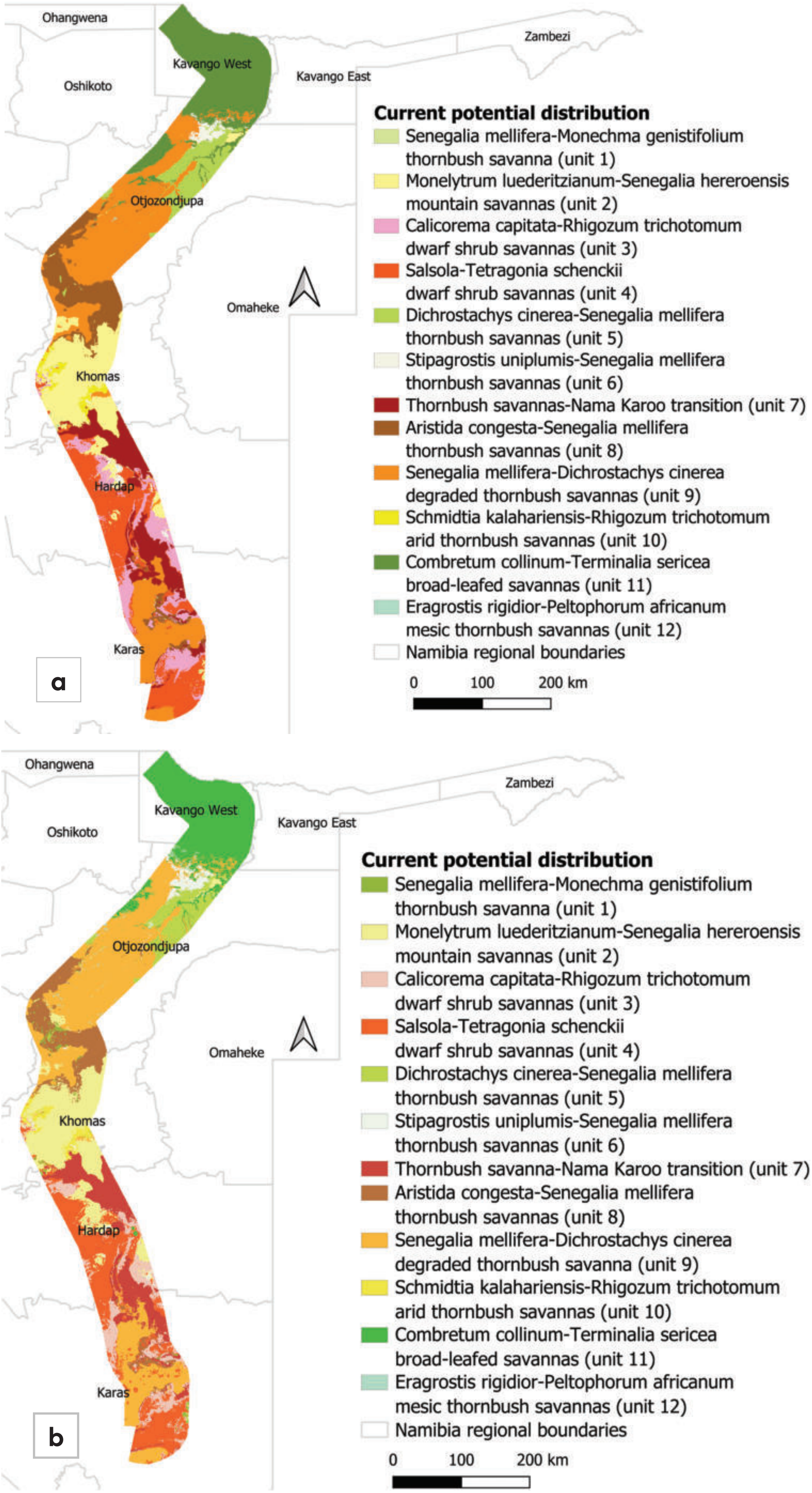

Figure 8. The current potential distribution of the vegetation units modelled under existing environmental conditions. The climate variables are averaged over 1970–2000. Two models were performed for the baseline classification: (a) a classification excluding EVI variables, (b) a classification including EVI of August and EVI of March as variables.

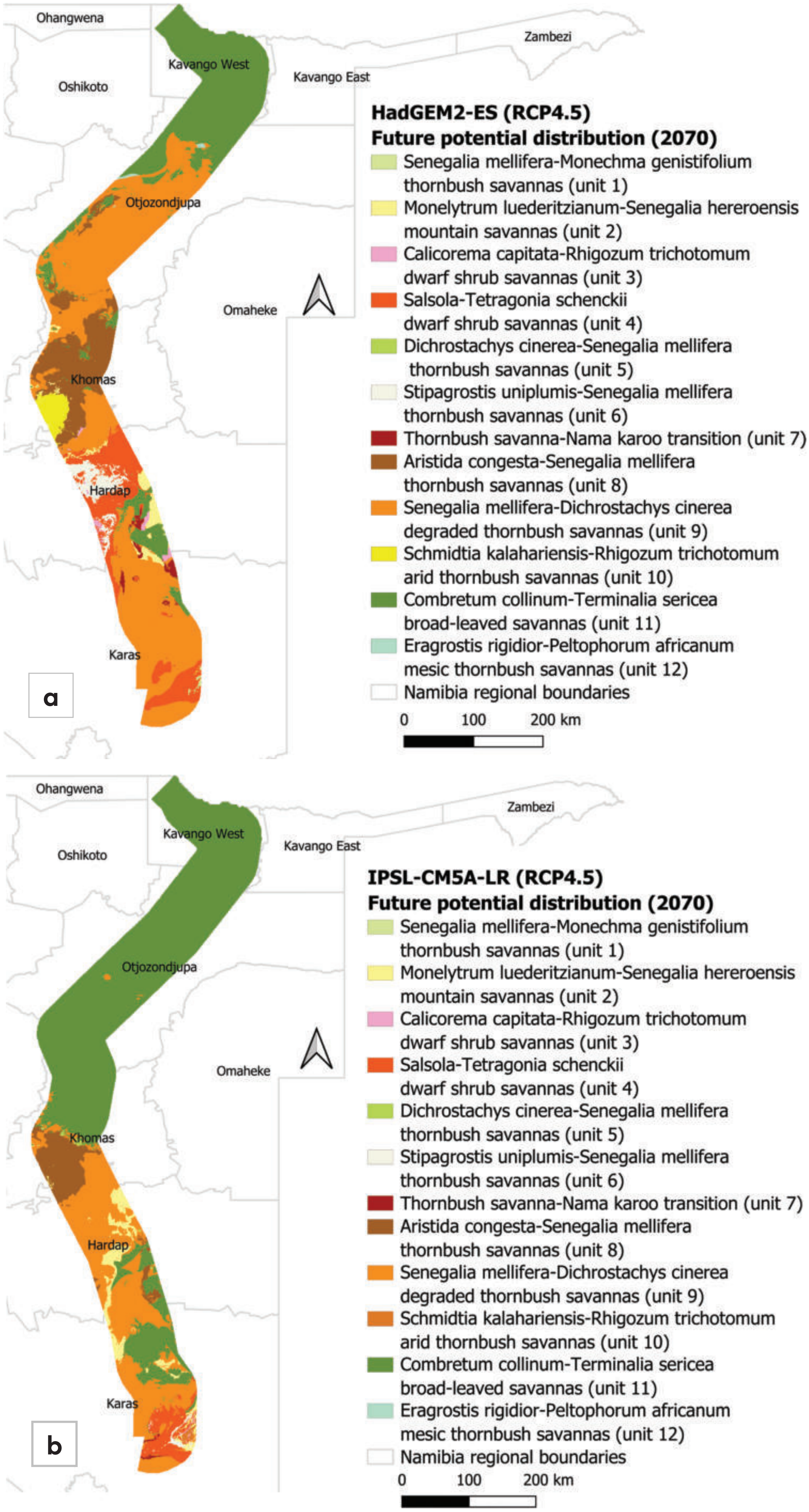

Figure 9. Potential future distribution of the vegetation units using projected (2061–2080) climatic conditions for moderate scenarios (RCP4.5) under the (a) HadGEM2–ES and (b) IPSL–CM5A–LR General Circulation Models.

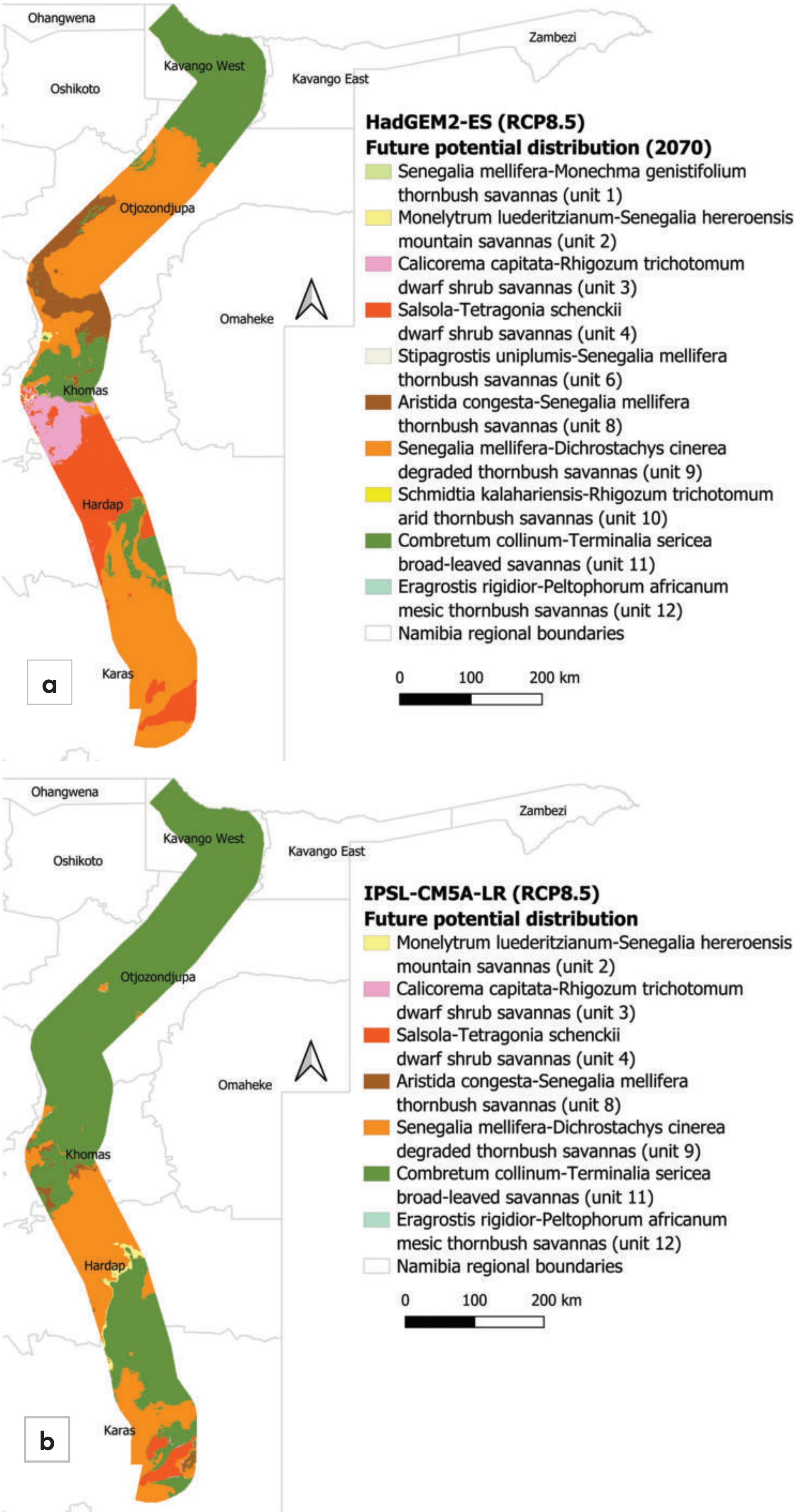

Figure 10. Potential future distribution of the vegetation types using projected (2061–2080) climatic conditions for high scenarios (RCP85) under the (a) HadGEM2–ES and (b) IPSL–CM5A–LR General Circulation Models.

Unit 2, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, include the vegetation orders *Brachiario nigropedatae-Senegalietalia hereroensis* and *Senegalio hereroensis-Tarchonanthoetalia camphorati* as described by Strohbach (2021). This unit is also referred to as the Highland Savanna *sensu* Giess (1998).

Unit 1, the *Senegalia mellifera-Monechma genistifolium* thornbush savanna, occurs in what Giess (1998) referred to as the Thornbush savanna. It includes the *Senegalia mellifera-Monechma genistifolium* association and *Boscia foetida-Leucosphaera bainesii* association, but also elements of the *Monechma genistifolium-Vachellia tortilis* association described by Strohbach (2002, 2019).

Unit 7, Thornbush savanna – Nama-Karoo transition, is similar to *Acacio senegal-Catophractetum alexandri* described by Strohbach and Jankowitz (2012). This unit forms a transition between the Nama-Karoo (Dwarf Shrub Savanna *sensu* Giess 1998) and thornbush savanna, with elements of both biomes present.

Unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas are closely related to various other thornbush savanna units, especially units 5, 6 and 8. The composition of the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas is a highly variable, but generally depauperated form of the related thornbush savannas and may have been impacted by overgrazing, severe bush encroachment and/or injudicious bush control interventions.

Unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savannas, are similar to the Northern Kalahari dry forests and woodlands described by Giess (1998). The vegetation unit consists of elements of small–scale studies such as the classes *Burkeo-Pterocarpetea* described by Strohbach and Petersen (2007) and the *Combreto-Terminalietea sericeae* as proposed by Strohbach (2014). De Cauwer et al. (2016) described this vegetation unit as part of southern Africa's tropical dry forest transition zone, which forms part of the WWF ecoregions Zambesian-*Baikiaea* Woodlands (Vetter 2001) and Kalahari *Acacia-Baikiaea* woodlands (Spriggs 2001).

Unit 12, the *Eragrostis rigidior-Peltophorum africanum* mesic thornbush savannas, is a *Senegalia*–dominated savanna with several mesic species, including broad-leafed species such as *Philenoptera nelsii* and *Terminalia sericea* on sandy soils (Giess 1998). It includes elements of the *Acacia erioloba-Stipagrostis uniplumis* bushlands and the *Lonchocarpus nelsii-Eragrostis rigidior* bushlands described by Strohbach (2002), as well as the *Stipagrostio uniplumis-Acacietum melliferae* described by Strohbach (2014).

Modelling the vegetation units with the current climate

Model accuracy assessment

The model obtained a prediction accuracy of 82%. According to the accuracy scale statistic range (Heikkinen et al. 2006), this accuracy is very good for such a large area and in comparison to other studies such as the classification of eight peatland communities by Thomas et al. (2003) that obtained a classification accuracy of 62%. Other classification studies obtained prediction accuracies of 69% (Dirnböck et al. 2003) and 75% (Dobrowski et al. 2008). However, the prediction accuracy for this study would have been much higher (94%) with the inclusion of EVI indices.

Environmental variables responsible for the distribution of the vegetation units along the transect

Overall, the distribution of the vegetation units is controlled by altitude and soil as indicated by the Mean Decrease Gini. However, each vegetation unit has different variables that control its distribution. In other studies, MAP and MAT were the main factors in plant species distribution, such as in Ghana (Amissah et al. 2014). Another study has found mean temperature to be the leading factor in the distribution of plant species along an elevational gradient in the Himalayas (Maharjan et al. 2022).

Namibia has a high climatic variability, especially in mean annual rainfall. When creating a classification along an extended transect, it is important to choose a classification with many groups to accurately account for climatic variability. This approach prevents grouping species in a manner that does not truly reflect their specific current climatic requirements. The partial plots indicate that three vegetation units occur at the much drier end of the transect, namely unit 4. *Salsola-Tetragonia schenckii* Dwarf shrub savannas, unit 3, *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas, and unit 7, Thornbush savanna – Nama-Karoo transition. The occurrence of vegetation units in these dry areas is facilitated by the heterogeneity of the local topography and landform patterns. The degree of slope and rivers create microhabitats with distinct microclimatic conditions (Abd El-Ghani 1996), allowing for different plant species communities to coexist. The species within these units possess sclerophyllous leaves, an adaptive characteristic enabling them to withstand high evapotranspiration rates induced by high evaporation in the area. Additionally, species in more arid areas tend to have smaller leaves as an adaptive mechanism to limit water loss by reducing the exchange area with air, as stated by Thuiller et al. (2004b).

Other vegetation types presented occur at the wetter end of the gradient, where the MAT and rainfall are high. On the northern end of the transect, the vegetation unit comprises mesophyll-leaved tall trees and high shrubs, which are believed to be influenced by the deep, coarse sands of the Kalahari basin (Strohbach 2014). The broad leaves of the species in this unit allow for maximum light absorption.

Prediction of the future distribution of the vegetation types

The projected expansion for the *Combretum collinum-Terminalia sericea* broad-leafed savannas around the high altitude areas such as the Karstveld towards the Khomas highland under the IPSL–CM5A LR (RCP4.5) may be due to the overestimation of precipitation south of the equator in the IPSL–CM5A LR model (Boucher et al. 2020). Boucher et al. (2020) explain that the overall global rainfall rate in the IPSL–CM5A LR model was generally overestimated, which explains the shift of all the other vegetation units towards the south of the transect following the high predicted rainfall in the RCP8.5 (Suppl. material 3: A).

A southward expansion of several vegetation units for both models under the RCP4.5 and RCP8.5 scenarios towards the central areas with high mean annual rainfall (Suppl. material 3: B–D) and projected low mean temperature (Suppl. material 3: E–F) is surprising, as it does not agree with models used in other studies which predict species to be shifting their distributional range towards the north because of the predicted lower rainfall (Midgley et al. 2005; De Cauwer 2016; Zhang et al. 2019). However, several authors have discovered that not all species are shifting their distribution because of projected changes in rainfall, but some are moving to higher elevations where the temperature is less high (Parmesan 2006; Feehan et al. 2009; Lenoir et al. 2010; Harsch and HilleRisLambers 2016; Sintayehu 2018). The extinction of vegetation units such as *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas in both GCMs supports the idea that warming challenges species at high elevation as they may not have a place left to migrate to when the high elevation areas become warmer (Manish et al. 2016).

Because of the potential human impact on the composition of the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, it is possible that the predicted expansion includes that of unit 5 with which many species are shared.

The projected distributions of vegetation units such as the *Combretum collinum-Terminalia sericea* broad-leafed savannas in the RCP4.5 and RCP8.5 of both GCMs may not be possible because of distributional barriers such as the rate of dispersal, soil type and terrain. Species within the *Combretum collinum-Terminalia sericea* prefer deep sand, high rainfall and high temperature, contradicting the predicted future distribution.

SDMs assume that a model trained in one location can make reliable predictions in another. These models work on the assumption that species are in sync with their surroundings, thriving where conditions are optimal and dying off where conditions are less favourable. However, transferability tests indicate that most statistical models may fail to accurately extrapolate beyond the climate data range used during model training (Higgins et al. 2021; Meyer and Pebesma 2021). The future projections must therefore be interpreted with caution because some of the variables, notably the expected rainfall patterns derived from HadGEM2–ES, exceed the range of the data the models were trained on. For instance, the forecast from the HadGEM2—ES indicates a potential increase of up to 550 mm in northeastern Namibia (Figure 3d), resulting in a MAP exceeding 1000 mm well beyond the 0 to 600 mm rainfall range historically observed in Namibia.

While SDMs predict individualistic responses exhibited by individual species (Baselga and Araújo 2009), this study focuses on CDMs whereby changes in vegetation units, characterised by a group of dominant and indicator species, in response to climate change are predicted. The underlying assumption is based on the idea that species sharing similar ecological niches are likely to have analogous distributions and, consequently, co-occur. This approach considers not only the individual responses of species but also acknowledges the potential influence of ecological interactions such as facilitation and symbiosis within vegetation units (Brooker et al. 2008). As a result, some scientists began modelling higher levels of ecological organization, such as communities (Maguire et al. 2015). Analysing vegetation units or communities offers several advantages, including more efficient processing of species distribution data, increased ability to detect shared patterns of environmental response across species, and improved capacity to synthesize complex data into formats readily interpretable by scientists and decision-makers (Ferrier and Guisan 2006). A limitation is that the interactions between species in a vegetation unit may change under different climate scenarios.

There is a need for the development of projected vegetation indices data, for example, EVI, because they proved to be important in this model. This can be done by averaging the EVI data over many years and interpolating the data similarly to the projection for climate variables.

Despite the limitations, our vegetation predictions provide useful insights into potential future scenarios and can feed into initial risk assessment, future research, and the design of monitoring programs (Midgley and Thuiller 2011).

Conclusion

Vegetation along the aridity gradient was successfully classified into twelve vegetation units. These units were mapped under current climate conditions with very high accuracy (94%) and modelled to assess the influence of future climatic conditions using a Random Forest machine learning algorithm. The projected shift in vegetation units suggests a movement towards the southern end of the transect. Specifically, it is expected that unit 11, the *Combretum collinum-Terminalia sericea* broad-leafed savannas, and unit 9, the *Senegalia mellifera-Dichrostachys cinerea* degraded thornbush savannas, will exert a notably higher dominance compared to other units currently confined to specific habitats, especially the mountainous areas. This includes units like unit 2, the *Monelytrum luederitzianum-Senegalia hereroensis* mountain savannas, unit 3, the *Calicorema capitata-Rhigozum trichotomum* dwarf shrub savannas and unit 10, the *Schmidtia kalahariensis-Rhigozum trichotomum* arid thornbush savannas. Consequently, these latter units are projected to experience a reduction in their area of occupancy, potentially bordering on imminent loss.

Data availability

The data used for this publication forms part of the Namibian Phytosociological Database (GVID ID AF–NA–001) and can be provided on request by Ben Strohbach. All data of GVID ID AF–NA–001 has been shared with the sPlot database as well as the GBIF database.

Author contributions

All authors planned the research, worked on the vegetation classification and revised the manuscript, LN and BS conducted the field sampling, LN performed the modelling assisted by VDC, LN led the writing.

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Supplementary material

Supplementary material 1
Confusion matrix for Random Forest classification with EVI indices (pdf)
Link: https://doi.org/10.3897/VCS.99050.suppl1

Supplementary material 2
Confusion matrix for Random Forest classification without EVI indices (pdf)
Link: https://doi.org/10.3897/VCS.99050.suppl2

Supplementary material 3
Projected change in MAP and MAT in Namibia for the IPSL–LR and HadGeM2–ES general circulation models (pdf)
Link: https://doi.org/10.3897/VCS.99050.suppl3