INFLUENTIAL ENVIRONMENTAL PARAMETERS CONTRIBUTING ON TREE SPECIES DISTRIBUTION IN TWO FORESTS OF THE EASTERN AFROMONTANE HOTSPOT, TANZANIA

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ABSTRACT

Understanding the influence of environmental parameters in determining tree species distribution and how it might change over time is a vital issue for species distribution modeling (SDM), yet it is poorly addressed in most of tropical forests and has not been addressed in the Eastern Arc Mountains (EAMs). This study was conducted with the objective of identifying most influencial environmental parameters contributing on tree species distribution in East Usambara Forests (EUF) and Udzungwa Mountain Forests (UMF) of the EAMs, Tanzania. Novel modelling method called Maximum Entropy Distribution (Maxent, version 3.3.3k), was used to model the distribution of eight most dominant tree species based on the frequency of occurence and 11 uncorrelated environmental variables. The drivers of species distribution in EUF and UMF are mainly climatic and edaphic factors. Climate change effects were driven by all climatic variables followed by edaphic variables while topographic factors had no effect. Soil factors have shown stronger effects in the UMF than in the EUF while the effects of temperature and precipitation were strong in both sites. Further studies on physiological responses and range shifts of selected species to environmental change (e.g climate change) within the EAMs are recommended.

Keywords: Climate change - Eastern Arc Mountains - Maxent modeling - Tree species distribution.

INTRODUCTION

The application of Species Distribution Models (SDMs) to plant inventory data can provide useful indications of which areas may be important for biodiversity conservation, and offers a means to estimate the niche-space available for species of conservation concern (Platts *et al*. 2010, Tshwene-Mauchaza and Aguirre-Gutiérrez 2019). Such models estimate the relationship between species records at sites and the environmental and/or spatial characteristics of those sites (Franklin 2009). They are widely used for many purposes in biogeography, conservation biology and ecology (Elith & Leathwick 2009). Species Distribution Models have been advocated as a tool to predict the current and potential distribution of species especially under the influence of climate change.

Since the distribution of many species is determined to a large extent by climatic variables, changes in climate will thus modify their distribution and abundance (Parmesan 2006 & Mahgoub 2019). For example, vegetation zones may move toward higher latitudes or elevations in response to increasing average temperatures (Iverson & Prasad 1998). Such range shifts are predicted to be more pronounced at higher latitudes, where temperatures are expected to rise more than near the equator (Bakkenes *et al*. 2002). Some of the key climatic variables that stress forest ecosystems are changes in precipitation, temperature, evapo-transpiration, and increased frequency of fires and storms (Iverson & Prasad 1998;

Ohlemüller *et al*. 2006). Forests may disappear in certain areas at a faster rate than they can migrate or regrow in new areas (Parmesan 2006).

In the EAMs, a lot of quantitative information has so far been collected on both flora and fauna (Burgess *et al*. 2007). However, the effects of environmental change on species distribution and thus on biodiversity, particularly of plants, are poorly understood. Morever there is no any study that has focused on identifying the most influencial environmental parameters determing tree species distribution. Such knowledge may be acquired through the use of SDM and is useful in planning sustainable biodiversity conservation (Burgess *et al*. 2007, Munishi *et al*. 2007, Platts *et al*. 2013).

Climate is an important determinant of tree species distribution, but its effects are mediated through topographic features and soils apart from biotic factors. Thus, it is important to compare the relative contribution of the environmental factors when making predictions about plant species distribution changes (Lo *et al*. 2010 & Walthert 2017).

The present study aimed at identifying most influential environmental parameters contributing on tree species distribution in EUF and UMF of EAMs. Spatially referenced inventory data (species occurrence records) combined with climate, topography and soil parameters were used to estimate the spatial distribution of dominant tree species using Geographical Information System (GIS) and the Maximum entropy distribution modeling approach (Phillips *et al*. 2006). The modeling results were used to identifying most influential environmental parameters contributing on tree species distribution in two forests under climate change scenarios.

MATERIALS AND METHODS

Description of the study areas

The EAMs are a chain of crystalline mountains near the Indian Ocean coast which run from the Taita Hills in South-East Kenya to Udzungwa Mountains in South-Central Tanzania (Lovett 1993, Burgess *et al*. 2007). They are located approximately between latitudes 3°2'S and 8°51'S and longitudes 34°49'E and 38°20'E (Fig. 1). The EAMs range from sea level up to 2635 m in altitude. There are 13 blocks in EAMs, namely: Taita Hills including Kasigau in Kenya, North Pare, South Pare, West Usambara, East Usambara, Nguu, Nguru, Uluguru, Ukaguru, Rubeho, Malundwe, Udzungwa, and Mahenge in Tanzania. This chain of 13 block-faulted massifs harbour one of the world's most important concentrations of biodiversity across a series of fragile sites (Brooks *et al.* 2002 & Mittermeier *et al.* 2004).

East Usambara Mountains

The East Usambara Mountains (Fig. 1) are located in Korogwe and Muheza districts, in Tanga Region in northeastern Tanzania. They cover an area of 1300 km^2 (Rodgers and Homewood, 1982). It is located between latitudes 4° 48´ and 5° 13´S and longitudes 38° 32´ and 38° 48´E, and altitude of up to 1250 m a.s.l. It has bimodal rainfall averaging to 1500 mm per year. The forests are rich in flora and fauna and the number of endemic species is high (Rodgers & Homewood 1982). Soils in the East Usambaras are acidic at high altitudes and neutral to alkaline near the foothills (Sah 1996).

The East Usambaras are particularly important among the Eastern Arc Mountains for a number of reasons. Firstly, they are close to the Indian Ocean and so have a constant humid climate that has encouraged the growth and maintenance of tropical moist forest over very long periods of time.

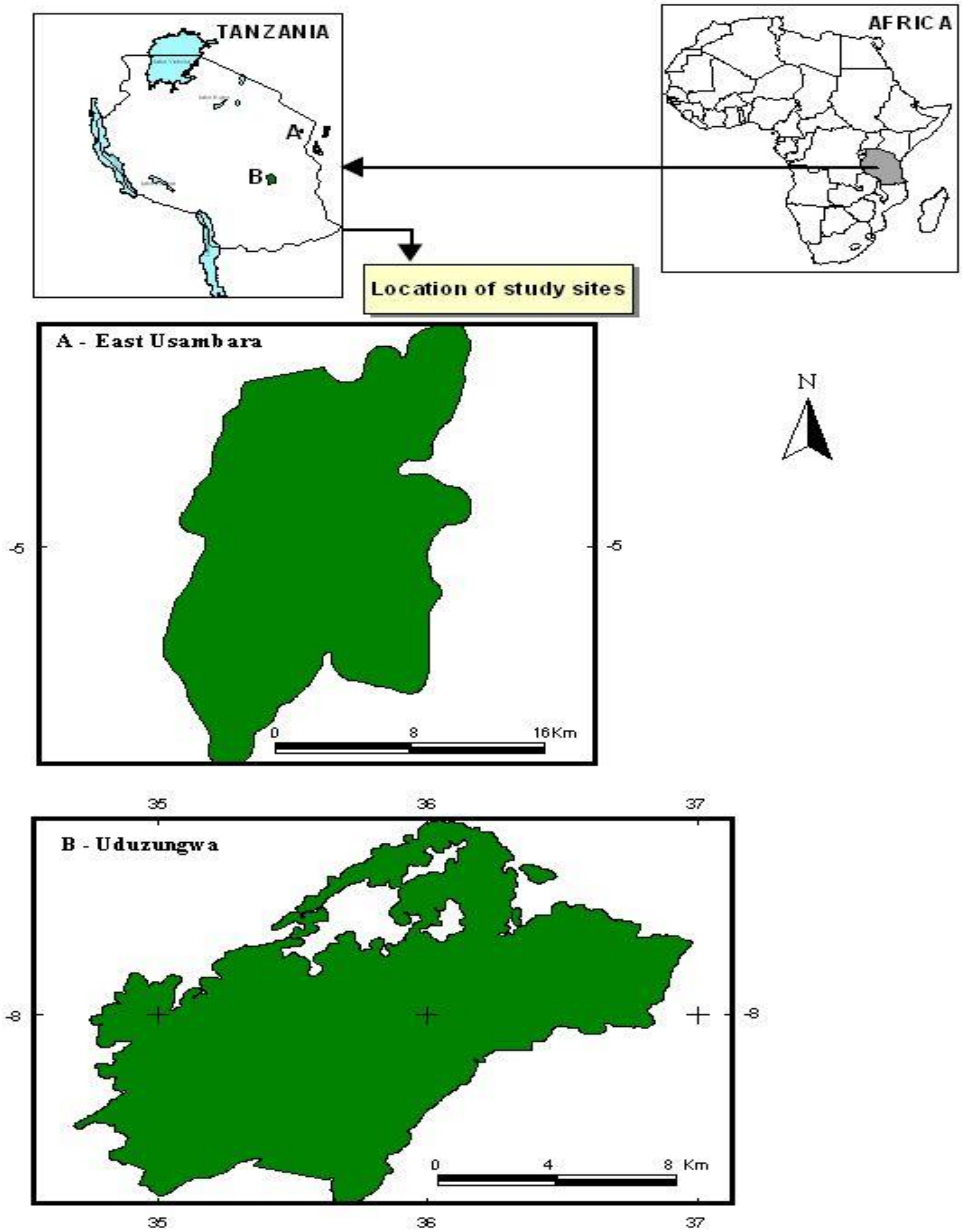

Figure 1: Location of East Usambara and Udzungwa Mountains

Secondly, the Amani plateau in the East Usambaras is at the elevation occupied by species rich sub-montane forest type. Thirdly, there was until recently substantial areas of relatively undisturbed forest in the East Usambaras. Even though the forests have been heavily disturbed in the last two decades and the forest area reduced, there are still fine stands of natural vegetation rich in globally rare species of plants and animals.

Udzungwa Mountains

The Udzungwa Mountains (Fig. 1) are the largest block of the EAMs, covering about 10,000 km^2 (Rodgers & Homewood, 1982). It is found at the southern end of EAMs chain. Udzungwa Mountain's highest point, Luhombero Peak, rises to 2,800 m (Zilihona & Nummelin, 2001). The rainfall varies according to topography and distance from the Indian Ocean. The eastern slopes, facing the Indian Ocean, have annual rainfall of more than 2000 mm, whereas the western slopes are in the rain shadow, receiving about 600 mm precipitation per year. There is a unimodal rainfall pattern between November and May (Lovett 1999). The eastern scarp of the Udzungwa Mountains is one of the few areas left in the Afrotropical region where one can find a continuous moist forest cover from lowland (300 m) to highlands (2500 m). Soils are mostly sandy-loams or sandy-clay-loams (Lovett *et al*).

Tree data

Point distributions for tree species in the EAMs were used. The tree dataset combined own field data with a large dataset contributed by the TROPICOS of Missouri Botanical Garden (http://www.tropicos.org). The field data collection was conducted using common forest field survey (inventory) procedures used in forestry. From the datasets, the most dominant species were selected based on the frequency of occurence in each study site. Nomenclature was standardized by reference to the African Flowering Plants Database (AFPD 2009). A total of 16 dominant tree species (based on the frequency of occurrence), eight each from UMF and EUF were used in modelling (Appendix 2).

Environmental data

Climate is an important determinant of tree species distribution, but its effects are mediated through soils, topographic features, fire and biotic factors. Although most of the modelling approaches lack the capacity to include all variables, it is important that all available information is used to capture the possible sources of variations and address the interaction of the factors. In the present study, the effects of climate on distribution of tree species were modelled by combining climatic, topographic and edaphic predictors.

Environmental predictor variables

Current climate data (bioclimatic variables) were obtained from *https://worldclim.org/version2* (Hijmans *et al*. 2005) based on records from the period 1950-2000, provided as grids at a spatial resolution of 30 arc seconds (1 km).

Climate projections were obtained from the Max Planck Institute for Meteorology (Hamburg). These were provided as monthly grids at 55km resolution. These Regional Climate Models (RCMs) provide high resolution data than the commonly used General Circulation Models (GCM) outputs (~200km resolution). The RCMs were then downscaled to 1 km according to the methods described in Platts (2012) and Platts *et al*. (2013) to better suite ecological niche modelling.

Two IPCC-AR4 scenarios were available for Regional Model (REMO). The first, scenario A1B, describes a world in which economic growth and globalisation prevail, and where energy sources are balanced across fossil-intensive and non-fossil technologies. Global population peaks at mid-century and declines thereafter. The second scenario, B1, assumes similar population and convergence among regions as A1B, but with more rapid improvements in public services and economic structures. The emphasis is on clean and resource efficient technologies, leading to a reduced warming trend (IPCC, 2007). Therefore, scenario B1 mainly focuses in economic issues while scenario A1B mainly focused in environmental sustainability. Temperature is predicted to be high under scenario B1 than A1B. Given recent patterns in global energy consumption and sluggish rates of decarbonisation, both of the scenarios may now be considered optimistic (Peters *et al*., 2012).

From the monthly grids, five climatic gradients known to correlate well with plant distribution in the study region were derived (Greve *et al*. 2011 & Platts *et al*. 2013). These were mean annual temperature; temperature seasonality (annual range); mean annual rainfall; dry season water stress (precipitation of driest quarter); and a moisture index (ratio of annual rainfall to potential evapotranspiration (PET), according to Thornthwaite (1948). Water stress is defined as the cumulative deficit in mean monthly rainfall throughout the longest dry season, where a deficit is <10 mm month^{-1}.

Additionally, topographic and edaphic variables were derived from digital elevation model (DEM) and Soil and Terrain Digital Database (SOTER), respectively (Table 1). As elevation is highly correlated with temperature and the latter is a more functional predictor of plant distribution, derived measures such as slope, aspect and topographic wetness index can be useful surrogates for soil moisture and micro-climate. Thus, slope, aspect and topographic wetness index were derived from the digital elevation model. PET was adjusted into the future climate according to the projected changes in temperature under scenarios A1B and B1. On the other hand, the spatial distribution of all climate data below half-degree scale was assumed to be constant through time prior to change-factor technique used in downscaling. Soil was assumed to be constant into the future. Similarly, the topographic wetness index was also assumed to be constant over time. All calculations were done using Raster calculator in ArcMap 10. A detailed description on calculations of environmental predictor variables are shown in Appendix 1.

Boundary definitions for study locations were according to Platts *et al*. (2011).

Table 1: List of environmental predictor variables used in Maxent modelling

Environmental variables/layers	Description
Climatic	Mean Annual Temperature (^{0}C) Temperature Seasonality (Annual Range/ Temperature CV) (^{0}C) Mean Annual Rainfall (mm) Precipitation of Driest Quarter/Dry Season Water Stress (mm) Moisture Index (Rainfall/PET)
Topographic	Slope (degrees) Aspect (cosine transformed) Topographic Wetness Index
Edaphic	Soil Reaction (pH) Effective Cation Exchange Capacity (cmol$_c$kg^{-1}) Available Water Capacity (mm)

Note: CV= Coefficient of Variation

Maximum entropy (Maxent) modelling of species distribution

The Maxent program is based on the maximum-entropy approach for species habitat modeling. It takes as input a set of layers or environmental variables (such as elevation, precipitation, etc.), as well as a set of geo-referenced occurrence locations (presence point locations/presence-only species records), and produces a prediction model of the range of the given species. It is a powerful tool applicable in exploring ecological relationships with fine-scale, raster (gridded) environmental data using spatial information on species occurrence in relation to environmental data to estimate potential (suitable) habitat for species. It is a promising new method for modelling species potential distribution and has proven to perform well in comparison with alternative approaches (Elith *et al*. 2006).

Maxent uses environmental variables represented in GIS layers to predict probability distribution/habitat suitability for the target species by evaluating different combinations of variables and their interactions. Based on the maximum-entropy principle, Maxent finds the probability distribution/habitat suitability for the species that maximizes entropy (is closest to the uniform distribution), using a set of constraints/variables imposed by the modeller (Phillips *et al*. 2006). Maxent calculates the percentage contribution of all environmental factors involved in determining the distribution of tree species under study.

Modelling framework

Prior to modelling, all environmental variables were modified using GIS techniques into formats required by Maxent modelling (Phillips *et al*. 2006). Using boundary layers of the modelled areas, the environmental layers were modified to be in the same extent (geographic bounds and cell size) using GIS tools. Maxent requires all the environmental layers to be in raster format and have the exact same cell size, extent and projection system (e.g., geographic or UTM). Thus, all environmental layers were spatially projected to geographic coordinate system, WGS 1984 zone 37S.

For tree data, point distribution of species occurrence records in longitude and latitude coordinates were converted to comma-separated value (.csv) files in excel spreadsheet for a particular modelled geographic extent. Using Maxent, the samples (*y*-variables) in this case the selected tree species, were modelled with environmental variables (*x*-variables) based on the current conditions and future climatic scenarios A1B and B1 (Fig. 2). Maxent software version 3.3.3k was used to fit the models. The Maxent algorithm was run with default parameters (convergence threshold = 10^{-5}, regularization multiplier = 1, maximum number of background points = 10 000); these default settings have been shown to achieve good performance (Phillips and Dudík 2008).

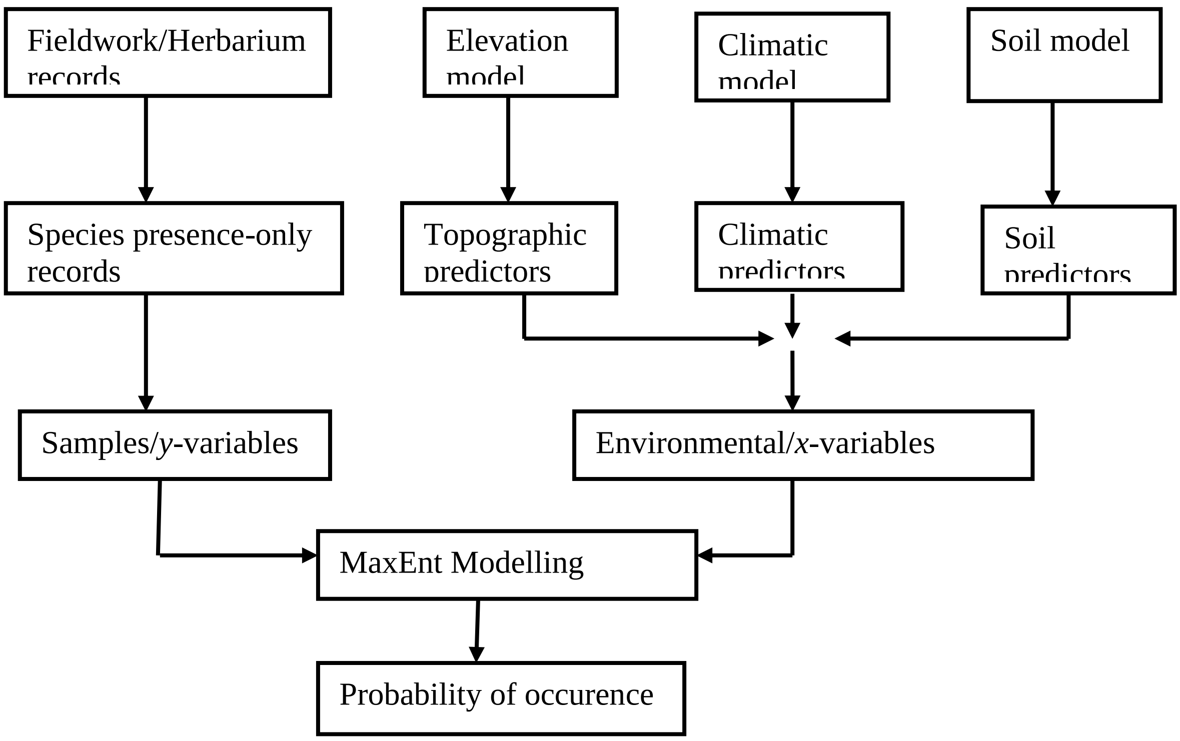

Figure 2: Flow chart of the modelling procedure (modified from Platts *et al*. 2008)

Maximum iteration value was set to 5000 (to give the model adequate time for convergence). A jackknifing procedure was used to examine the importance of each variable (Phillips *et al*. 2006).

Models were created using 75% of the localities for model training and 25% for model testing under current conditions and in the future for both scenarios. Statistical evaluation of the models was based on threshold independent receiver operating characteristic (ROC) analysis (Phillips *et al*. 2006). For presence-only modelling, the ROC curve is a plot of sensitivity (proportion of correctly predicted presences) against the fractional area predicted present.

The area under the ROC curve (AUC) is subsequently compared with the area under the null expectations line connecting the origin and (1, 1), thus providing a measure of predictive model performance. An AUC approximating 1 would mean optimal discrimination of suitable versus unsuitable sites, whereas an AUC between 0 and 0.5 is indicative of predictions no better than random. (i.e., when comparing predicted value and the observed, the slope should be 1 if the model is good. Greater or less than 1, the prediction is poor).

RESULTS

Model performance

Models of all tree species performed better than random, with average test AUC values greater than 0.5 (Table 2). Except for some few cases where there was evidence of over estimation with higher AUC values of up to one (~1), for example *Didymosalpinx norae*, most of the variables fell within reasonable range.

Species responses to climate change scenarios

(a) East Usambaras

The contribution of predictor variables to current distribution of tree species in the EUF is shown in Table 3. There was pronounced effect of mean annual temperature on the distribution of *Grandidiera boivinii* while precipitation of driest quarter showed stronger influnce to the distribution of *Leptonychia usambarensis*, *Mesogyne insignis*, *Sorindeia madagascariensis*, *Synsepalum msolo* and *Trilepisium madagascariense*. Meanwhile mean annual rainfall was linked to the distribution of *Psychotria leucopoda* and available water capacity linked to the distribution of *Funtumia africana.* Mean annual temperature had highest predictive contribution (77.9%) than other variables and it affected *Grandidiera boivinii*. Soils showed little effects only with available water capacity (Table 3).

The future distribution under scenario 2055 A1B for most species was also dominated by changes driven by precipitation of the driest quarter except for *Mesogyne insignis* and *Psychotria leucopoda* (Table 4). This was followed by predictive contributions by mean annual temperature, moisture index and mean annual rainfall. Soils and topography showed little contribution to the models under this scenario. Precipitation of the driest quarter showed greater influnce (62.1%) on the distribution of *Synsepalum msolo* relative to other species. Thus, increasing dry conditions, temperature, moisture and rainfall will likely drive species distribution.

Under scenario 2055 B1, the distribution of most tree species was mainly governed by moisture index and to a lesser extent by mean annual temperature, precipitation of the driest quarter and available water capacity (Table 5).

Table 2: The average test AUC for the replicate runs in the maxent models

	Current		2055 A1B		2055 B1		2090 A1B		2090 B1	
Species	**AUC**	**STD DEV**	**AUC**	**STD DEV**	**AUC**	**STD DEV**	**AUC**	**STD DEV**	**AUC**	**STD DEV**
East Usambara										
Funtumia africana	0.85	0.06	0.91	0.03	0.79	0.07	0.80	0.11	0.88	0.04
Grandidiera boivinii	0.80	0.08	0.58	0.15	0.67	0.12	0.58	0.13	0.62	0.12
Leptonychia usambarensis	0.83	0.07	0.90	0.04	0.89	0.04	0.81	0.10	0.85	0.07
Mesogyne insignis	0.76	0.08	0.80	0.06	0.77	0.09	0.78	0.08	0.79	0.08
Psychotria leucopoda	0.63	0.08	0.52	0.10	0.58	0.11	0.57	0.12	0.49	0.11
Sorindeia madagascariensis	0.90	0.06	0.83	0.07	0.72	0.11	0.79	0.10	0.80	0.10
Synsepalum msolo	0.86	0.05	0.80	0.07	0.73	0.11	0.74	0.08	0.74	0.10
Trilepisium madagascariense	0.89	0.03	0.77	0.05	0.67	0.14	0.69	0.06	0.72	0.08
Udzungwa										
Coffea mufindiensis subsp. *mufindiensis*	0.87	0.06	0.81	0.06	0.77	0.09	0.81	0.07	0.79	0.06
Didymosalpinx norae	0.99	-1.00	1.00	-1.00	1.00	-1.00	1.00	-1.00	1.00	-1.00
Englerodendron usambarense	0.99	0.00	0.99	0.00	0.99	0.00	0.99	0.00	0.99	0.00
Parinari excelsa	0.90	0.07	0.95	0.04	0.89	0.04	0.93	0.06	0.91	0.06
Pavetta lynesii	0.89	0.05	0.81	0.05	0.82	0.05	0.83	0.05	0.83	0.05
Psychotria goetzei	0.90	0.04	0.82	0.06	0.90	0.04	0.82	0.06	0.86	0.05
Sorindeia madagascariensis	0.99	0.01	0.99	0.00	0.99	0.00	0.99	0.00	0.99	0.00
Tabernaemontana usambarensis	0.99	-1.00	0.97	-1.00	0.99	-1.00	0.87	-1.00	0.99	-1.00

Note: STD DEV denotes the standard deviation, AUC denotes area under receiver operating characteristic (ROC)

Table 3: Percent variable contributions in the maxent models under current conditions in EUF

Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
	Species							
as	0	0.3	1.3	20.7	2.3	0	0.1	0.1
ce	9.3	0.1	8.5	0.4	0.8	0.1	6.5	0
mi	0	0	2.9	10.1	34.4	24.6	1.7	0
mr	0	8.2	0	9.3	**37.7**	0.3	0.1	0
mt	0	**77.9**	0	0	15.8	0	0	0
ph	0	0.5	0	17.1	0.5	0.9	0.1	1.2
pq	40.8	0	**51.9**	**34.9**	1.1	**45**	**65.5**	**59.4**
sl	0.1	10.9	0	1.4	4	6.2	3	1.3
ts	0.3	1.3	0	3	0.3	4.5	3.4	10.4
wc	**48.2**	0.8	34.9	0	2.6	18.1	19.4	27.6
wi	1.3	0.1	0.6	3.1	0.4	0.3	0.2	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. wc=Available Water Capacity; mt=Mean Annual Temperature; pq=Precipitation of Driest Quarter; mr=Mean Annual Rainfall. (a) *Funtumia africana* (b) *Grandidiera boivinii* (c) *Leptonychia usambarensis* (d) *Mesogyne insignis* (e) *Psychotria leucopoda* (f) *Sorindeia madagascariensis* (g) *Synsepalum msolo* (h) *Trilepisium madagascariense*.

Table 4: Percent variable contributions in the maxent models under future conditions (2055 A1B) in EUF

Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
	Species							
as	0.1	0.1	0.1	9.9	9.9	0	0.6	0
ce	1.8	0.6	3.2	0	0.1	0.5	2	0
mi	16.8	0.7	30.7	**36.2**	0.1	11.4	8.2	20.2
mr	0.5	0.5	0.6	3.1	**34**	5.5	4.7	4.3
mt	0	**45.7**	0	2	32.6	2.3	0	0.2
ph	0	1.6	0	15.9	1.3	0.3	0.2	0.9
pq	**45**	18.5	**35.3**	2	5.7	**40.8**	**62.1**	**51.1**
sl	0.1	25.1	0	1.7	3.2	10.2	3.3	8.9
ts	0.2	5.3	1.9	25.5	4.3	10.7	0.5	0
wc	33.4	1.8	27.3	0	5	17.6	17.8	14.4
wi	2.1	0	0.7	3.7	3.7	0.7	0.6	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. pq=Precipitation of Driest Quarter; mt=Mean Annual Temperature; mi= Moisture Index; mr=Mean Annual Rainfall. (a) *Funtumia africana* (b) *Grandidiera boivinii* (c) *Leptonychia usambarensis* (d) *Mesogyne insignis* (e) *Psychotria leucopoda* (f) *Sorindeia madagascariensis* (g) *Synsepalum msolo* (h) *Trilepisium madagascariense*.

Table 5: Percent variable contributions in the maxent models under future conditions (2055 B1) in EUF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	1.9	0	0.1	13.7	2.9	0.1	0.1	0.2
ce	8.8	0.2	2.1	0.2	0.1	0.1	7.6	0
mi	27.1	0.8	**53**	**49.9**	0.2	27.6	24	**44.3**
mr	4.9	0.1	5.1	1.6	39.4	8.3	10	5.7
mt	0	**61.8**	0.1	0.5	**41.5**	11.2	0.1	0
ph	0	4.2	0	24.4	1.1	0.1	3.6	11.1
pq	6.1	12.9	4.6	0.8	1.6	14	**28.8**	6.1
sl	1.1	18.9	0.1	1.7	5.4	8.9	5.3	12.7
ts	1.2	0	0.1	1.9	2	0.1	2.5	6.7
wc	**46.2**	1.1	33.7	0	5.1	**28.3**	15.8	13.3
wi	2.8	0	1	5.4	0.7	1.4	1.9	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. wc=Available Water Capacity; mt=Mean Annual Temperature; mi= Moisture Index; pq=Precipitation of Driest Quarter. (a) *Funtumia africana* (b) *Grandidiera boivinii* (c) *Leptonychia usambarensis* (d) *Mesogyne insignis* (e) *Psychotria leucopoda* (f) *Sorindeia madagascariensis* (g) *Synsepalum msolo* (h) *Trilepisium madagascariense.*

However, the mean annual temperature showed strongest individual predictive contribution relative to other variables (61.8%). Except for the available water capacity, soil variables showed lower perecentage contributions to the models. Likewise, the topographic variables showed little contribution (Table 5). Therefore, under scenario 2055 B1, increasing moisture, temperature and dry conditions will likely be the main drivers of species distribution.

Under scenario 2090 A1B, environmental predictor variables that showed higher predictive contributions to the models include available water capacity, mean annual temperature, moisture index, mean annual rainfall and precipitation of the driest quarter (Table 6). Mean annual temperature had higher contribution (59.4%) than other variables and affected the distribution of *Grandidiera boivinii*. Similarly, it contributed to the distribution of *Psychotria leucopoda* by 39.5%. Moisture index affected the distribution of *Leptonychia usambarensis* (47.8%) and *Mesogyne insignis* (50.8%) while mean annual rainfall affected the distribution of *Sorindeia madagascariensis* (21.6%) and *Trilepisium madagascariense* (30.1%). On the other hand, precipitation of the driest quarter affected the distribution of *Synsepalum msolo* by 37.6% while available water capacity affected the distribution of *Funtumia africana* by 43.4%. Thus, under scenario 2090 A1B, increasing aridity will likely be the main driver of species distribution.

Under scenario 2090 B1, available water capacity affected the distribution of more species than other variables although with lower contribution (Table 7). Highest contribution of available water capacity was 47.2% and affected the occurence of *Funtumia africana*. Other species affected by high predictive contribution of available water capacity relative to other variables were *Sorindeia madagascariensis* (22.1%) and *Synsepalum msolo* (24%). Overall highest contribution of 56.4% was observed on mean annual temperature and was found to affect the occurence of *Grandidiera boivinii*. Apart from *Grandidiera boivinii*, the mean annual temperature also contributed to the distribution of *Psychotria leucopoda* by 37.2%. Other variables that showed substantial inputs to the models under this scenario were moisture index which contributed by 53.3% to the distribution of *Leptonychia usambarensis* and by 52.6% to *Mesogyne insignis* and the mean annual rainfall which contributed by 27.2% to the distribution of *Trilepisium madagascariense*. Therefore, under this scenario soil water holding capacity, mean annual and rainfall are likely to be the main drivers of species distribution.

Table 6: Percent variable contributions in the maxent models under future conditions (2090 A1B) in EUF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	0.1	0.1	1	12.3	8.4	0	0.6	0
ce	12.3	0.1	5.2	0	0.1	0.6	5.8	0
mi	27.2	0.2	**47.8**	**50.8**	0.3	15.1	10.8	17.7
mr	7	0.4	9.2	1.6	34.5	**21.6**	21.8	**30.1**
mt	0.1	**59.4**	0	1.9	**39.5**	10.6	0.3	0.1
ph	0	5.4	0	18.6	2.3	0.3	2.5	8
pq	6.1	15.1	3.2	0.3	4.2	16.6	**37.6**	9.9
sl	1	16.3	0.2	1.4	3.3	8.3	2.6	15.9
ts	0	1.7	0.1	9.2	4	2.5	0	0.1
wc	**43.4**	1	31.8	0	1.7	23	17	18.2
wi	2.9	0.3	1.4	3.8	1.7	1.5	1	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. wc=Available Water Capacity; mt=Mean Annual Temperature; mi= Moisture Index; mr=Mean Annual Rainfall; pq=Precipitation of Driest Quarter. (a) *Funtumia africana* (b) *Grandidiera boivinii* (c) *Leptonychia usambarensis* (d) *Mesogyne insignis* (e) *Psychotria leucopoda* (f) *Sorindeia madagascariensis* (g) *Synsepalum msolo* (h) *Trilepisium madagascariense*.

Table 7: Percent variable contributions in the maxent models under future conditions (2090 B1) in EUF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	0.9	0.7	0.2	10.5	6.2	0	0	0.2
ce	2.1	0.1	3.6	0.1	0.1	0.7	4.6	0
mi	37.1	0	**53.3**	**52.6**	4.9	19.7	18.2	26
mr	6.9	0	7.6	0.4	31.5	12.8	22.7	**27.2**
mt	0.1	**56.4**	0	4.1	**37.2**	8	0.1	0.2
ph	0.1	3	0.1	16.3	1.7	0.2	3	6.3
pq	1	13.8	0.5	0.1	4.4	12.5	20.9	1.7
sl	1.7	24.3	0.3	1.5	4.6	9.7	3.5	14.8
ts	0	0	0	12.5	4.2	13.1	2.1	0
wc	**47.2**	1.4	32.7	0	2.9	**22.1**	**24**	23.6
wi	2.9	0.2	1.7	1.8	2.4	1.3	0.8	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. wc=Available Water Capacity; mt=Mean Annual Temperature; mi=Moisture Index; mr=Mean Annual Rainfall. (a) *Funtumia africana* (b) *Grandidiera boivinii* (c) *Leptonychia usambarensis* (d) *Mesogyne insignis* (e) *Psychotria leucopoda* (f) *Sorindeia madagascariensis* (g) *Synsepalum msolo* (h) *Trilepisium madagascariense*.

(b) Udzungwas

The current distribution of most species in the UMF were mainly predicted by precipitation of the driest quarter. Moisture index, pH and effective cation exchange capacity also showed substantial contribution relative to other variables (Table 8). Precipitation of the driest quarter had highest predictive contribution (66.3%) than other variables and had a stronger effect on distribution of *Pavetta lynesii*. Apart from *Pavetta lynesii*, the effect of precipitation of the driest quarter was also pronounced for the distribution of *Coffea mufindiensis* by 52.3%, *Englerodendron usambarense* by 38.1% and *Psychotria goetzei* by 46.5%. On the other hand, the effect of soils was also evident. The effect of effective cation exchange capacity was observed on the distribution of *Didymosalpinx norae* by 38.9% and on *Sorindeia madagascariensis* by 32.5% while that of pH was observed on *Tabernaemontana usambarensis* by 35.8%. Therefore the distribution of species in the Udzungwas under current climatic conditions are likely to be controlled by dry conditions, soil chemical properties and moisture.

Table 8: Percent variable contributions in the maxent models under current conditions in UMF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	0.7	0.3	0	3.8	2.1	2.5	0	0
ce	5.6	**38.9**	31.6	2	0	20.5	**32.5**	23.9
mi	3.1	1.3	20.1	**37.5**	0	0.1	13.1	0.6
mr	1.9	32.3	1.8	1.4	1.8	0.5	5.2	22.6
mt	19.5	0	0	0.1	14.3	19.2	0.6	0
ph	0.4	13.1	3.4	17.2	1.4	0	1.4	**35.8**
pq	**52.3**	5.8	**38.1**	14.9	**66.3**	**46.5**	23.8	0
sl	11	8.2	4.6	5.6	5	1.8	1.5	16.7
ts	4.2	0	0	17.3	5.7	3.7	20.5	0.4
wc	0.9	0	0.4	0.2	2.7	2.5	1.3	0
wi	0.4	0	0	0.2	0.7	2.6	0.1	0.1

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. pq=Precipitation of Driest Quarter; ce= Effective Cation Exchange Capacity; mi= Moisture Index; ph= Soil Reaction (pH). (a) *Coffea mufindiensis* subsp. *mufindiensis* (b) *Didymosalpinx norae* (c) *Englerodendron usambarense* (d) *Parinari excelsa* (e) *Pavetta lynesii* (f) *Psychotria goetzei* (g) *Sorindeia madagascariensis* (h) *Tabernaemontana usambarensis*.

Under scenario 2055 A1B, soils showed stronger influence on four species of the eight modelled. Effective cation exchange capacity had higher predictive contribution on *Didymosalpinx norae* (35.5%), *Englerodendron usambarense* (37.1%) and *Psychotria goetzei* (43.4%) while pH had higher contribution (36.7%) on *Tabernaemontana usambarensis* (Table 9). Among the climate variables, moisture index showed higher effects than other variables. It attained a contribution of 56.5%, which was highest relative to all variables in the scenario. The moisture index had a stronger effect on the distribution of *Pavetta lynesii*. It was also observed to affect the distribution of *Coffea mufindiensis* by contributing 46.7% of the model (Table 9). Apart from moisture index, another climate variable that showed higher effects was temperature seasonality. Temperature seasonality had predictive contributions of 54.3% and 35.8% to the distribution of *Parinari excelsa* and *Sorindeia madagascariensis*, respectively (Table 9). Therefore, the distribution of species under this scenario is likely to be driven by changes in soil conditions, moisture and variations in temperature.

Table 9: Percent variable contributions in the maxent models under future conditions (2055 A1B) in UMF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	2.2	0.5	0.5	5.1	2.3	4.3	0.1	0
ce	20.2	**35.5**	**37.1**	0.2	0.2	**43.4**	35.1	25.5
mi	**46.7**	23	0.1	3.9	**56.5**	25.4	0	20.9
mr	1.4	8.4	11.8	9.3	3.1	6.9	15.4	5.2
mt	5.2	6.2	0.6	0.2	1.4	5.8	3.1	3.8
ph	2.2	20.3	15.3	20.5	13	0	8.9	**36.7**
pq	0.3	2.8	9.3	3.2	10.5	5.4	0.5	0.2
sl	20.3	1.7	3.3	3.2	7.2	3.4	0.3	7.7
ts	0.6	1.5	21.6	**54.3**	0.8	1.2	**35.8**	0.1
wc	0.8	0	0.4	0.2	3.7	2.2	0.8	0
wi	0.1	0	0	0	1.3	2.1	0	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. mi=Moisture Index; ce=Effective Cation Exchange Capacity; ts=Temperature Seasonality; ph=Soil Reaction (pH). (a) *Coffea mufindiensis* subsp. *mufindiensis* (b) *Didymosalpinx norae* (c) *Englerodendron usambarense* (d) *Parinari excelsa* (e) *Pavetta lynesii* (f) *Psychotria goetzei* (g) *Sorindeia madagascariensis* (h) *Tabernaemontana usambarensis*.

The effects of soil properties were also apparent under scenario 2055 B1. This was indicated by higher variable contributions by effective cation exchange capacity and pH. For effective cation exchange capacity, higher contribution of 32.7% and 36.8% had strong effects on the distribution of *Didymosalpinx norae* and *Englerodendron usambarense* respectively. For pH, the predictive contribution of 37.6% had strong effect on *Tabernaemontana usambarensis* (Table 10). The influence of moisture index on distribution of tree species was also evident under this scenario. Moisture index contributed to occurence of *Coffea mufindiensis* (47.3%), *Pavetta lynesii* (73.4%) and *Psychotria goetzei* (55.4%) (Table 10). The predictive contribution of 73.4% observed was the highest of all variables under this scanario. Temperature seasonality was another climate variable with high contribution to tree distribution. It accounted for 42.7% and 39.7% in predicting distribution of *Parinari excelsa* and *Sorindeia madagascariensis*, respectively (Table 10). Thus, the distribution of species under this scenario will likely be controlled by soil factors, moisture and variation in temperature.

Under scenario 2090 A1B, temperature seasonality had highest contribution (49.6%) relative to other variables in the models and had strong effect on *Parinari excelsa* (Table 11). Six out of eight modelled species were affected by soil factors. The effective cation exchange capacity contributed by 35% to the distribution of *Didymosalpinx norae*, 35.1% to *Englerodendron usambarense*, 41.3% to *Psychotria goetzei* and 34.9% to *Sorindeia madagascariensis* while the effect of pH was evident on *Pavetta lynesii* and *Tabernaemontana usambarensis*. Slope was the only strongest topographic predictor and had effect on the distribution of *Coffea* *mufindiensis* (Table 11). The effective cation exchange capacity had a negative effect on the distribution of *Didymosalpinx norae*, *Englerodendron usambarense* and *Sorindeia madagascariensis* while it showed a positive effect to *Psychotria goetzei*.

Table 10: Percent variable contributions in the maxent models under future conditions (2055 B1) in UMF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	0.9	0.2	0	4	1.9	4	0	0
ce	23.7	**32.7**	**36.8**	2.2	0	25.1	32.1	20
mi	**47.3**	9.8	1.6	0.1	**73.4**	**55.4**	0.3	7.5
mr	0.3	22.5	16.4	19.3	0	3.4	15.9	19.3
mt	8.5	7	1.7	0.5	0.9	2.6	0.6	4.3
ph	2.3	19.5	16.1	22.3	9.9	0	8.7	**37.6**
pq	1.1	2.1	5.8	3.7	5.7	3.3	0.5	0.2
sl	15	5.9	5.1	5.2	5.2	1.4	1.3	10.7
ts	0	0.2	16.1	**42.7**	0.4	0.7	**39.7**	0
wc	0.4	0	0.2	0	2	1.6	0.8	0
wi	0.5	0	0	0	0.7	2.6	0	0.3

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. mi=Moisture Index; ce=Effective Cation Exchange Capacity; ts= Temperature Seasonality; ph= Soil Reaction (pH). (a) *Coffea mufindiensis* subsp. *mufindiensis* (b) *Didymosalpinx norae* (c) *Englerodendron usambarense* (d) *Parinari excelsa* (e) *Pavetta lynesii* (f) *Psychotria goetzei* (g) *Sorindeia madagascariensis* (h) *Tabernaemontana usambarensis.*

Table 11: Percent variable contributions in the maxent models under future conditions (2090 A1B) in UMF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	1.2	1	0.5	5.8	5.2	3.3	0.2	0
ce	27.9	**35**	**35.1**	0.1	3.5	**41.3**	**34.9**	19.2
mi	1.2	0	0	0.1	1.8	0.5	0	1.4
mr	5.8	26.7	10	6.5	7	0.6	9.9	17
mt	20.2	6.2	2.8	0.3	10.1	4.6	5.2	1.2
ph	3.9	19.5	11.3	18	**18.7**	0	8.5	**43.5**
pq	0.7	8	21.8	11.8	18.5	13.6	11.9	0.7
sl	**28.7**	3.6	4.6	7.4	15.2	6.1	1.2	16.8
ts	9.7	0	13.8	**49.6**	14.6	21.7	27.1	0.2
wc	0.4	0	0.2	0.1	2.9	2.7	1	0
wi	0.3	0	0	0.4	2.5	5.7	0.1	0

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. sl=Slope; ce=Effective Cation Exchange Capacity; ts= Temperature Seasonality; ph= Soil Reaction (pH). (a) *Coffea mufindiensis* subsp. *mufindiensis* (b) *Didymosalpinx norae* (c) *Englerodendron usambarense* (d) *Parinari excelsa* (e) *Pavetta lynesii* (f) *Psychotria goetzei* (g) *Sorindeia madagascariensis* (h) *Tabernaemontana usambarensis.*

Thus, increasing variation in temperature is likely to be the key driver of species distribution under scenario 2090 A1B. The distribution of species under this scenario will largely depend on variations in monthly mean temperatures and soil conditions.

Soil pH and effective cation exchange capacity showed stronger effects under scenario 2090 B1. Of the eight species modelled, five were affected by soil properties

The effect of effective cation exchange capacity was highest (48.2%) on the distribution of *Psychotria goetzei* followed by 33.5% on *Sorindeia madagascariensis*, 33.4% on *Englerodendron usambarense* and 33.3% on *Didymosalpinx norae*.

On the other hand, pH showed stronger effect on *Tabernaemontana usambarensis* with percentage contribution of 37.7% (Table 12). In regard to climate variables, temperature seasonality had strongest effect and had highest percentage contribution of 49.1% relative to other variables in scenario 2090 B1. Apart from temperature seasonality, moisture index showed stronger effects and contributed by 40.8% and 37.8% to the predicted distribution of *Coffea mufindiensis* and *Pavetta lynesii* respectively (Table 12). Thus, the interactive effects of soil and climate are likely to be key drivers of species distribution under this scenario

Table 12: Percent variable contributions in the maxent models under future conditions (2090 B1) in UMF

	Species							
Variables	(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)
as	0.9	0.1	0.2	5	2.4	3.1	0.2	0
ce	25.3	**33.3**	**33.4**	0.2	0	**48.2**	**33.5**	20.1
mi	**40.8**	21.5	0.3	1.2	**37.8**	12.7	0	21.6
mr	1.4	8.8	11.9	13	7	10.9	16.9	1.7
mt	6.4	8.3	0.3	0.7	1.9	5.4	4.3	9.2
ph	2.2	20.8	13.2	18.3	18.4	0	10.2	**37.7**
pq	0.2	1.6	9.9	5.7	11.8	5.3	1.6	0.4
sl	21.4	2.4	7.4	6.8	13.4	3.1	1.6	8.3
ts	0.6	2.9	23.5	**49.1**	3.2	6.9	30.5	0
wc	0.4	0	0	0	2.9	1.7	0.9	0
wi	0.4	0.3	0	0.2	1.2	2.7	0.3	1

Note: Values shown are averages over 15 replicate runs. Bold numbers are the variables with highest contribution for each model per species. mi=Moisture Index; ce=Effective Cation Exchange Capacity; ts= Temperature Seasonality; ph= Soil Reaction (pH). (a) *Coffea mufindiensis* subsp. *mufindiensis* (b) *Didymosalpinx norae* (c) *Englerodendron usambarense* (d) *Parinari excelsa* (e) *Pavetta lynesii* (f) *Psychotria goetzei* (g) *Sorindeia madagascariensis* (h) *Tabernaemontana usambarensis*.

DISCUSSION

Variable importance

In regard to variable importance analysis, modelling results under current conditions revealed some variables having stronger predictive contribution than others. The observed mixed-predictive contributions of environmental parameters on the distribution of tree species in the two forests suggest the need for site-specific assessments in the EAMs forests. Contrally to the results reported in the temperate forests where soils were found to have greater influence on the distribution of trees than climate (Walthert 2017), in the present study climate has indicated to be the strongest driver of tree species distribution in the tropics. Elsewhere in tropics, climate has been reported to be the strongest driver of tree species distribution relative to other environmental parameters (Toledo *et al*. 2011). A study by Zhang *et al*. (2016) conducted in subtropical mountain forests in China revealed elevation (which is surrogated to temperature) to be the most important parameter in plant species distribution. In the Atlantic-Mediterranean environmental gradient, distribution patterns of forest tree species were mainly determined by the north–south topographic-climatic differences (Olthoff 2016).

Changes in variable contribution over time

Some variables e.g. mean annual temperature (mt) showed a decrease in variable contribution with time. In EUF for example the contribution of mean annual temperature in determining the distribution of *Grandidiera boivinii* was 77.9% under current condition. But the value decreased to 45.7% under 2055 A1B and to 61.8% under 2055 B1 for the same species *Grandidiera boivinii*. An increase in temperature may change other ecological processes that in turn may have a stronger influence in species distribution than temperature itself. For example, under 2055 A1B Precipitation of Driest Quarter (pq), a parameter which is a function of temperature had a stronger influence in governing species distribution than other variables by contributing to the distribution of *Synsepalum msolo* by 62.1% and *Trilepisium madagascariense* by 51.1%. On the other hand, temperature again had a higher variable contribution under 2055 B1 in EUF, which is in agreement with IPCC Assessment Report (IPCC-AR4) whereby temperature is predicted to be high under scenario B1 than A1B. Similar patterns have exhibited by other variables. These mixed trends apparently are mainly due to the changes of ecological process as a result of rise in temperature and the difference in predicted temperatures between the two scenarios used in the present study. Climate is an important determinant of tree species distribution, but its effects are mediated through topographic features and soils apart from biotic factors. Thus, it is important to compare the relative contribution of the environmental factors when making predictions about plant species distribution changes (Lo *et al*. 2010; Walthert, 2017).

Environmental predictors can exert direct or indirect effects on species along a gradient. They can act as *limiting factors* (or *regulators*), by controlling species eco-physiology (e.g. temperature, water, soil composition); they can act as *disturbance*, defined as all perturbations affecting environmental systems and they can act as *resources*, defined as all compounds that can be assimilated by organisms (e.g. energy and water). Temperature increases may initially drive forest productivity (Boisvenue and Running, 2006), but as it increases further, productivity can fall (Fischlin *et al.* 2007). Moreover, seasonal climate variability may have a strong influence on forest productivity in the long-term (Williamson *et al.* 2009). Furthermore, temperature changes have a direct influence in the processes that determine local weather, chiefly precipitation, wind and the frequency and/or intensity of extreme weather events (IPCC 2007). The single or combined result of these climatic changes will drive changes in forest ecosystem resources, site conditions, disturbances, and individual tree variables (Williamson *et al.* 2009).

CONCLUSION AND RECOMMENDATIONS

This study has revealed that the influencial parameters in tree species distribution in EUF and UMF are mainly climatic and edaphic factors. Topographic derivatives showed little impact on species distribution. Soil factors showed stronger effects in the UMF than EUF. Thus, tree species were predicted to respond uniquely in both scenarios.

Some variables e.g. mean annual temperature (mt) showed a decrease in variable contribution with time with the contribution being compensated by other parameters e.g., precipitation of driest quarter. These mixed trends have been related to the changes in ecological process as a result of rise in temperature and the difference in predicted temperatures between the two scenarios used in the present study.

The study provides a benchmark for future studies within and ouside the Eastern Arc Montanis. The observed mixed-predictive contributions of environmental parameters on the distribution of tree species in the two forests suggest the need for site-specific assessments in the EAMs forests.

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Appendix 1: Description of environmental predictor variables used in modelling tree species' distribution

Environmental variables/layers	Description	Definition/Source of data
Climatic	Mean Annual Temperature (^{0}C)	The mean of all the monthly mean temperatures in a year. Each monthly mean temperature is the mean of that months's maximum and minimum temperature
	Temperature Seasonality (^{0}C)	The difference between the maximum temperature of warmest period and the minimum temperature of coldest period. It can also be calculated as the standard deviation or a coefficient of variation
	Mean Annual Rainfall (mm)	The mean of all the monthly precipitation estimates
	Precipitation of Driest Quarter (mm)	It is surrogate to dry season water stress. The driest quarter of the year is determined (to the nearest month), and the total precipitation over this period is calculated. A quarter is a period of three months (1/4 of the year)
	Moisture Index (Rainfall/PET)	The ratio of annual rainfall to potential evapotranspiration. This is therefore an estimate of actual water balance (rainfall input / moisture output) at ~1km resolution. PET is derived from WorldClim temperature data according to the Hargreaves method (Hargreaves *et al*., 1985).
Topographic	Slope (degrees)	In the present study it was generated in GIS using DEM
	Aspect (cosine transformed)	This was also generated in GIS using DEM
	Topographic Wetness Index	It is a 90m raster dataset showing zones of increased soil moisture where the landscape area contributing runoff is large and slopes are low. Local upslope contributing area and slope are combined to determine the wetness index. (WI): $WI = In\left(\frac{As}{\tan(b)}\right)$ where *As* is flow accumulation or effective drainage area and b is slope gradient. It differs from moisture index as it is derived solely from the complexity of the terrain (DEM elevation data), with no explicit inclusion of rainfall per se. It was obtained from AfSiS database.
Edaphic	Soil Reaction (pH)	pH measured in water (pH_{H2O}). It was derived from SOTER data.
	Effective Cation Exchange Capacity ($cmol_c kg^{-1}$)	Defined as exchangeable (Ca^{++} + Mg^{++}+ K^+ + Na^+) + exchangeable (H^+ + Al^{+++}). It was also derived from SOTER database.
	Available Water Capacity (mm)	Available Water Capacity (mm, -33 to -1500 kPa conform to USDA standards). It was derived from SOTER database

Appendix 2: List of tree species used in Maxent modelling

	Family	Scientfic name	Sample size	Source	Location
1	Rubiaceae	*Didymosalpinx norae* (Swynn.) Keay	40	1	1
2	Fabaceae	*Englerodendron usambarense* Harms	93	1	1
3	Chrysobalanaceae	*Parinari excelsa* Sabine	101	1	1
4	Anacardiaceae	*Sorindeia madagascariensis* Thouars ex DC.	123	1	1
5	Apocynaceae	*Tabernaemontana usambarensis* K. Schum. ex Engl.	123	1	1
6	Apocynaceae	*Funtumia africana* (Benth.) Stapf	62	1	2
7	Sterculiaceae	*Leptonychia usambarensis* K. Schum.	110	1	2
8	Anacardiaceae	*Sorindeia madagascariensis* Thouars ex DC.	74	1	2
9	Sapotaceae	*Synsepalum msolo* (Engl.) T.D. Penn.	56	1	2
10	Moraceae	*Trilepisium madagascariense* Thouars ex DC.	51	1	2
11	Flacourtiaaceae	*Grandidiera boivinii* Taub.	17	2	2
12	Moraceae	*Mesogyne insignis* Engl.	25	1	2
13	Rubiaceae	*Psychotria leucopoda* E. Petit	27	1	2
14	Rubiaceae	*Coffea mufindiensis* Bridson subsp. mufindiensis	31	2	1
15	Rubiaceae	*Pavetta lynesii* Bridson	33	2	1
16	Rubiaceae	*Psychotria goetzei* (K. Schum.) E.M.A. Petit	29	2	1

Source: 1=Field survey, 2=TROPICOS database; Location: 2=East Usambara Mountains, 1= Udzungwa Mountains