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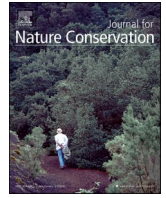
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Habitat suitability modelling to improve conservation status of two critically endangered endemic Afromontane forest bird species in Taita Hills, Kenya

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ABSTRACT

Tropical montane forests are known to support many endemic species with restricted geographic ranges. Many of these species are however, faced with numerous threats, most notably from habitat loss and degradation, invasive alien species, and climate change. Examples include Taita Apalis and Taita Thrush. Taita Apalis (*Apalis fuscicularis*) and Taita Thrush (*Turdus helleri*) are species of birds listed as Critically Endangered by the Government of Kenya and the International Union for Conservation of Nature (IUCN). They are endemic to Taita Hills' cloud forests in southeastern Kenya and protected under Wildlife Conservation and Management Act. As they face high risk of extinction, exploring their habitat suitability is imperative for their protection. To determine the current spatial distribution and the key ecogeographical explanatory factors and conditions affecting species distribution and indirect effects on species survival and reproduction, we employed Maximum Entropy (MaxEnt) modelling. This study was conducted in Ngangao and Vuria forests in June and July 2019 and 2020. Ngangao forest is gazetted as forest reserve and managed by the Kenya Forest Service whereas Vuria is non-gazetted and thus remains without official protection status. Ecogeographical explanatory variables; climatic, remote sensing-, LIDAR-, topography- and landscape-based variables were used in modelling and separate models were produced. 23 occurrence records of Taita Apalis and 30 of Taita Thrush from Ngangao and 21 of Taita Apalis from Vuria forests were used in the modelling. According to the models, less than 7% of the total area of Ngangao and Vuria forests was predicted as suitable habitat for Taita Apalis and Taita Thrush. This shows that these two species are more vulnerable to extinction from demographic stochasticity. Consequently, managing their habitats is critical for their long-term persistence. LIDAR-based canopy height range and elevation greatly influenced Taita Apalis distribution in Ngangao forest, with areas of high elevation (1620–1750 m a.s.l.) and having open middle-storey preferred. Elevation, slope and topographic wetness index (*twi*) were the major determinants of Taita Thrush distribution in Ngangao, where gentle sloping areas with moderately dry surfaces within high elevation (1620–1730 m a.s.l.) were favoured. Mean annual temperature, Euclidean distance to the forest edge, slope and land cover type greatly influenced the distribution of Taita Apalis in Vuria, with gentle sloping areas within forest interior made up of indigenous vegetation preferred. This study proposes reforesting open and degraded sites next to areas predicted as highly suitable for the two species; establishment of agro-forestry belts based on indigenous trees on the boundaries of the two forests to reduce grazing and firewood collection pressure and enhance resilience to the edge effects; and enhancing forest protection through Participatory Forest Management.

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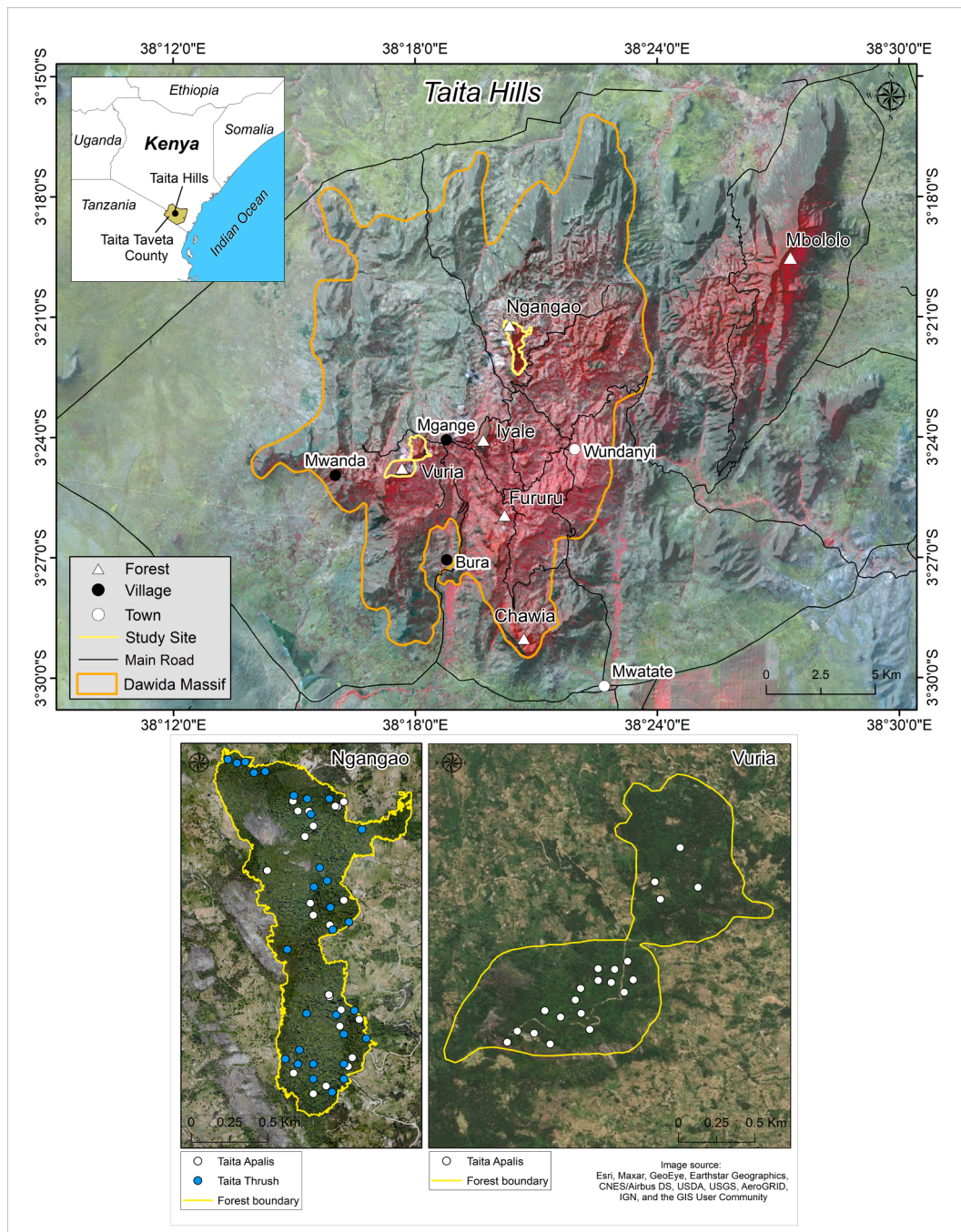


Fig. 1. Montane cloud forest remnants of the Taita Hills and location of Ngangao and Vuria forest. The close-up maps of the Ngangao and southern and northern part of Vuria forest indicate the species points (white points = Taita Apalis, blue points = Taita Thrush). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1. Introduction

The fifth edition of the Global Biodiversity Outlook (GBO 5) by the United Nations Convention on Biological Diversity (CBD) reveals that a significant fraction of wild species is projected to be at risk of extinction due to climate change, natural resource extraction, land use and the impact of other direct drivers (CBD, 2020). Land cover change in Africa is the fastest on Earth since the fastest growing population requires more agricultural land for food, which causes threats to forests and biodiversity (Brink & Eva, 2008).

Besides supporting rich biodiversity and endemism (Kessler & Kluge, 2008), tropical montane forests offer essential ecosystem services

including provision of water, carbon sequestration and storage, and prevention of erosion (Spracklen and Righelato, 2014; Brenning et al., 2015). Many of the species endemic to montane regions are however, threatened with extinction due to habitat loss and degradation, invasive alien species and climate change (Millennium Ecosystem Assessment, 2005; Malcolm et al., 2006; Guo et al., 2013; Le Saout et al., 2013; López-Baucells et al., 2016).

Taita Apalis (*Apalis fuscigularis*) and Taita Thrush (*Turdus helleri*) are endemic bird species to Taita Hills' cloud forests in Taita Taveta County, Kenya, and are listed as Critically Endangered by the Government of Kenya and the International Union for Conservation of Nature (IUCN). They have experienced severe population decline over the last years but,

nevertheless, the reasons behind the decline remain unclear (BirdLife International, 2019). Surveys carried out in 2009–2010 suggested that up to 80% of Taita Apalis population was lost since 2001 (Githiru & Borghesio, 2010; BirdLife International, 2010), with the current global population estimated at 100–150 individuals (BirdLife International, 2010). Taita Thrush population is estimated at 1400 individuals, equivalent to about 930 mature individuals (Waiyaki & Samba, 2000). Their Afromontane forest habitats are severely fragmented and continue to decline in both size and quality (BirdLife International, 2019).

Habitat loss and deterioration, mostly caused by human actions, have reduced global terrestrial habitat integrity (IPBES, 2019), combined with the longstanding relationship between habitat area and species numbers, have led to about 9 per cent of the world's estimated 5.9 million terrestrial species (more than 500,000 species) have insufficient habitat for long-term survival, thus committed to extinction, many within decades (IPBES, 2019). Terrestrial wild species, that are narrowly distributed (endemic) have classically seen larger-than-average changes to their habitats and shown faster-than-average declines (IPBES, 2019). Conservation strategies of threatened and endangered species more often than not begin with the identification of occupied and productive habitat (Margules & Pressey, 2000) and the programs intended to protect them require information about habitat utilisation. For these efforts to succeed, there is need for landscape scale information on species distribution and the environmental factors which underline them (Guisan et al., 2013).

Habitat suitability modelling (HSM), alternatively known as species distribution modelling (SDM), environmental niche modelling or ecological niche modelling (ENM), is a statistical model that uses species occurrence data, together with environmental data, to produce a correlative model of the environmental conditions that meet a species' ecological needs and which can determine the potential habitat of a given species (Guisan & Zimmermann, 2000; Hirzel & Le Lay, 2008; Elith & Leathwick, 2009; Barve et al., 2011; Sillero, 2011; Lyet et al., 2013; Fatima et al., 2016; Guisan et al., 2017; Uusitalo et al., 2019; Zhang et al., 2019).

In this study, we determined the current spatial distribution and the key ecogeographical explanatory factors and conditions that affect Taita Apalis and Taita Thrush distribution in Ngangao and Vuria forests of the Taita Hills using MaxEnt model. MaxEnt model was chosen since many studies have shown that it can solve the problem of presence-only data availability (Elith & Leathwick, 2009; Phillips & Dudík, 2008). The objectives of this study were: (i) to examine which and how ecogeographical factors influence the habitat suitability of Taita Apalis and Taita Thrush; and (ii) to create maps of the predicted occurrences of the two studied species. The predicted occurrence maps will be useful for setting targeted conservation measures at the right locations.

2. Methods

2.1. Study area

Taita Hills (3°25'S, 38°20'E) lie in Taita Taveta County ca. 150 km inland from the coast of the Indian Ocean in the southeastern Kenya and are the northernmost extension of the Eastern Arc Mountains (EAM) of Kenya and Tanzania. EAM is one of the world's 36 biodiversity hotspots based on global concentrations of species endemism (CEPF, 2020). The population of the whole Taita Taveta County has grown from 90,146 persons in 1962 to 340,671 in the year 2019 (KNBS, 2019). This growth has been a central driving factor behind rising environmental pressure in the area (Clark, 2010). Between 1955 and 2004, approximately half of the cloud forests in the Taita Hills had been lost to agriculture (Pellikka et al., 2009). Today, only four larger fragments of indigenous cloud forests, between 100 and 200 ha, and nine smaller patches remain in the area (Siljander et al., 2020). The area receives bi-modal type of rainfall with long rains and short rains occurring between March and May and November and December. The rainfall over 1400 m a.s.l. amounts on

average to 1300 mm annually, based on Kenya Meteorological Department statistics between 1985 and 2005. (Erdogan et al., 2011).

Ngangao (38°20'E, 03°21'S) and Vuria (38°18'E, 3°25'S) forest fragments (Fig. 1) are part of Dawida Hills of the Taita Hills and hold the highest population of the two endemic bird species. Ngangao forest is gazetted as forest reserve and managed by the Kenya Forest Service. It is located on the eastern slope of a north–south oriented mountain ridge with the western slope mainly covered by open rock and patches of *Acacia mearnsii*, *Cypripedium lusitanica* and *Pinus* spp. plantations. The forest can be characterized as moist montane to intermediate montane forest (Aerts et al., 2011), having indigenous trees of about 100 species (Rogers et al., 2008; Schäfer et al., 2016) accompanied by pine and cypress stands and some individual exotic trees within native forest (Omoro et al., 2013; Pellikka et al., 2009). The forest covers an area of approximately 120 ha with the elevation ranging from 1700 to 1952 m a.s.l. (Omoro et al., 2010). Vuria is non-gazetted forest and thus remains without official protection status (Kenya Gazette Supplement No. 155 (Acts No. 34), 2016). It retains a small cover of the montane forest of about 19 ha with mixed forest (exotic and indigenous) totalling to 115 ha (Morara, 2005). It has the largest population of Taita Apalis in the World. It peaks at elevation of 2208 m a.s.l. The northern section of Vuria forest (38°18'E, 3°24'S) covers about 43 ha and is partly on private land.

2.2. Studied species

Endemic to Taita Hills' forests, Taita Apalis and Taita Thrush are listed as Critically Endangered by the Government of Kenya and the International Union for Conservation of Nature (IUCN). The two species are protected under Wildlife Conservation and Management Act (Kenya Gazette Supplement No. 47, 2013). Taita Apalis which is a medium-sized, arboreal warbler inhabits the understorey of montane forest, preferring gaps and edges with thick undergrowth, where it gleans insects from vegetation mainly between 0 and 2 m above ground (BirdLife International, 2019). Data from population monitoring between 2001 and 2015 suggested that the species has undergone a severe decline since 2001, with the population estimates now at 100–150 individuals (Githiru & Borghesio 2010; BirdLife International 2010; BirdLife International, 2019). It had been documented to occur in Mbololo, Ngangao, Chawia, Fururu, and Vuria forest fragments (Brooks et al., 1998; Nature Kenya et al., 2015). However, an intensive survey in 2015 failed to locate the species in Chawia, Fururu and Mbololo forest fragments, an indication that the species might now be either very rare or locally extinct in these forest fragments (BirdLife International, 2019). Taita Apalis' range inside Ngangao forest has reduced significantly (Borghesio et al., 2014), with Vuria population appearing stable in its range (Nature Kenya et al., 2015).

Taita Thrush is also confined to montane cloud forest (Waiyaki & Samba, 2000), not venturing into secondary growth, scrub or cultivated areas, although the areas where it occurs have been heavily logged in the past (Brooks, 1997). Despite much research, very few inter-fragment movements have been recorded (Waiyaki & Samba, 2000). It is confined to four forest patches in the Taita Hills: Mbololo (185 ha), Ngangao (206 ha), Chawia (111 ha) and Iyale (88 ha) (Brooks, 1997), the areas indicating fragment size combined of indigenous and exotic forest from Pellikka et al. (2009). At certain times of the year its diet is primarily fruit, but it also consumes invertebrates (Brooks 1997, BirdLife International, 2019). In 1997, a total population of ca. 1350 birds, with ca. 1060 in Mbololo, ca. 250 in Ngangao and ca. 38 in Chawia was observed (BirdLife International, 2019), although the effective population size is likely to be lower due to a male-biased sex ratio. In 2009 and 2015 surveys confirmed continued presence of the species in Mbololo and Ngangao fragments (BirdLife International, 2019).

Table 1
Ecogeographical variables used in modelling.

Variable abbreviation	Description and source of variable	Type	Resolution (m)
<i>aspect_mean_20m</i>	Aspect (°) based on DTM (0–360)	Topography	20
<i>curvature_mean_20m</i>	Curvature based on DTM data and curvature calculation (second derivative of the DTM)	Topography	20
<i>dtm_mean_20m</i>	Elevation (m a.s.l.) based on DTM	Topography	20
<i>dtmrange_20m</i>	Elevational range (m a.s.l.) based on DTM	Topography	20
<i>slope_mean_20m</i>	Mean slope in 20 m analysis square (derived from DEM in degrees 0–90).	Topography	20
<i>Ngangao_twi_mean20m and vuria_twi_mean20m</i>	Topographic wetness index (TWI) based on DTM and 'TWI' calculation (Ln(a/tanB), Beven & Kirkby (1979))	Topography	20
<i>canopyheight_mean_20m</i>	Mean canopy height (meters) based on LIDAR (ALS) point cloud data	LIDAR point cloud data	20
<i>canopyheight_max_20m</i>	Maximum canopy height (meters) based on LIDAR (ALS) point cloud data	LIDAR point cloud data	20
<i>canopyheight_range_20m</i>	Canopy height range (meters) based on LIDAR (ALS) point cloud data	LIDAR point cloud data	20
<i>canopyrelief</i>	Canopy relief (ratio) based on LIDAR (ALS) point cloud data	LIDAR point cloud data	20
<i>coverreturn4</i>	Cover return 4 (%) based on LIDAR (ALS) point cloud data	LIDAR point cloud data	20
<i>Penetrat</i>	Penetration (%) based on LIDAR (ALS) point cloud data	LIDAR point cloud data	20
<i>aisaband1</i>	Airborne imaging spectroscopy data based on MNF transformed band-1 radiation data	Remote sensing based forest characteristics	20
<i>Species_Diversity</i>	Species Diversity based on AISA and LIDAR (ALS) data (mean species richness integer value)	Remote sensing based forest characteristics	20
<i>forest_edge_Distance</i>	Edge distance to forest edge(meters) based on GPS point data and Euclidean distance calculation	Landscape	20
Annual mean temperature (°C)	Correlated with: Elevation – topography - (Virtanen, 2015)	Climate	20
Annual mean relative humidity (%)	Elevation – topography - (Virtanen, 2015)	Climate	20

2.3. Species data collection

Acquisition of Taita Apalis and Taita Thrush occurrence data in Ngangao and Vuria was undertaken in June and July 2019 and 2020. Standardized Point Counts' technique was used. 100 × 100 m grid for point sampling was developed using ArcGIS 10.5. The grid comprised of 139 and 160 centre points (sampling points) covering the entire of Ngangao and Vuria forests, respectively. At each sampling point, within 50 m-radius plot, coordinate of the location where the bird was sighted was recorded using Garmin eTrex 30 Handheld GPS receiver. At each point, birds were sampled for 10 min on sunny days, both in the early morning (6:00–9:30 a.m.) and late afternoon (15:30–18:00p.m.) by two observers. A total of 23 occurrence records of Taita Apalis and 30 of Taita Thrush were collected in Ngangao forest and 21 of Taita Apalis in Vuria forest, and used in the modelling.

2.4. Ecogeographical explanatory variables

We derived different sets of ecogeographical variables; first set of variables were based on airborne LiDAR data: canopy height and canopy relief, point cloud penetration, and percentage of 4th returns. Second set of variables were topographical: elevation, slope, aspect, topographic wetness index, and profile curvature. Third set of variables describing vegetation of the forests interpreted from airborne hyperspectral remote sensing data. Fourth set of variables were landscape variables based on Euclidean distance calculations, and fifth set were climate based variables annual mean temperature (°C) and annual mean relative humidity (%) (See Table 1).

To derive topographical and LiDAR point cloud based variables, we used data from flight campaign carried out with Airborne Laser Scanning (ALS) sensor on 3–8 February 2013. Data vendor (Topscan GmbH, Germany) pre-processed the data and delivered it as a geo-referenced point cloud in UTM/WGS84 coordinate system with ellipsoidal heights. TerraScan software (Terrasolid Ltd., Finland) was used to create digital terrain model (DTM) at 1 m resolution. DTM was imported to ArcGIS 10.3.1 to calculate elevation, slope, aspect, topographic wetness index, and profile curvature. FUSION software (McGaughey, 2016) was utilised to calculate variables from point cloud data. Firstly, *Cloud metrics* function was employed to calculate canopy relief ratio ($(\text{mean elevation} - \text{min elevation}) / (\text{max elevation} - \text{min elevation})$). Canopy relief ratio is a quantitative descriptor of the relative shape of the canopy from altimetry observation (Pike & Wilson, 1971; Parker & Russ, 2004) which describes the degree to which canopy surfaces are in the upper ($\text{crr} > 0.5$) or in the lower ($\text{crr} < 0.5$) portions of the height range. Next, percentage of fourth returns above 2 m height was calculated to estimate point penetration close to the ground. Then, *cover* function was applied for canopy closure estimates with output values ranging from 0.0 to 100.0 percent. The *penetration* parameter that computes the proportion of the pulses that penetrate canopy to reach the ground was selected with 20 m cell size and a ground tolerance of 2 m.

For vegetation characteristic variables hyperspectral imagery acquired using AisaEAGLE VNIR push-broom type sensor (Specim, 2012) simultaneously with LiDAR data was used. Data processing phases included radiometric correction and boresight calibration with CaliGeo 4.9.15 software (Specim, 2009); geometric correction with PARGE software (Schläpfer, 2011); and atmospheric correction with ATCOR-4 (Richter and Schläpfer, 2011). In addition, minimum noise fraction (MNF) transformation (Green et al., 1988) with ENVI 5.0 software to segregate noise in the data, to reduce the number of spectral bands, and to pack the majority of the useful information in the first bands (Petropoulos et al., 2012; Ghosh et al., 2014) was carried out. The first MNF transformed band which best differentiated the vegetation characteristics in Ngangao forest was selected. Geospatial variable describing tree species richness in the Ngangao forest from Schäfer et al., (2016) was applied.

For climate based variables we used annual mean temperature (°C)

Table 2

Three MaxEnt models applied for species distribution of Taita Apalis and Taita Thrush in Ngangao forest.

Model	Description
1	Top 5 of AUC value of training data: <i>slope_mean_20m</i> , <i>dtm_mean_20m</i> , <i>canopyrelief</i> , <i>dtmrange_20m</i> and <i>canopyheight_range_20m</i> (for Taita Apalis) and <i>dtm_mean_20m</i> , <i>aisaband1</i> , <i>canopyheight_mean_20m</i> , <i>penetrat</i> and <i>slope_mean_20m</i> (for Taita Thrush).
2	All the predictor variables: <i>slope_mean_20m</i> , <i>dtm_mean_20m</i> , <i>canopyrelief</i> , <i>dtmrange_20m</i> , <i>canopyheight_range_20m</i> , <i>Ngangao.twi_mean20m</i> , <i>curvature_mean_20m</i> , <i>aisaband1</i> , <i>aspect_mean_20m</i> , <i>forest_edge_Distance</i> , <i>Species_Diversity</i> , <i>canopyheight_max_20m</i> , <i>canopyheight_mean_20m</i> , <i>coverreturn4</i> and <i>penetrat</i> .
3	Top 3 of the highest AUC value of training data per category: <i>slope_mean_20m</i> , <i>dtm_mean_20m</i> , <i>dtmrange_20m</i> , <i>canopyrelief</i> , <i>canopyheight_range_20m</i> and <i>aisaband1</i> (for Taita Apalis) and <i>dtm_mean_20m</i> , <i>slope_mean_20m</i> , <i>dtmrange_20m</i> , <i>aisaband1</i> , <i>penetrat</i> , <i>canopyheight_mean_20m</i> (for Taita Thrush)

Table 3

Two MaxEnt models applied for species distribution of Taita Apalis in Vuria forest.

Model	Description
1	Top 5 of AUC value of training data: <i>Annual mean temperature</i> , <i>slope_mean_20m</i> , <i>aspect_mean_20m</i> , <i>forest_edge_Distance</i> and <i>canopyheight_mean_20m</i> .
2	All the predictor variables: <i>slope_mean_20m</i> , <i>vuria_landcover_2004_20m</i> , <i>vuria.twi_mean20m</i> , <i>canopyheight_mean_20m</i> , <i>forest_edge_Distance</i> , <i>aspect_mean_20m</i> , <i>Annual mean temperature</i> and <i>curvature_mean_20m</i> .

AUC = area under the ROC curve, ROC = receiver operating characteristics.

and annual mean relative humidity (%) data by Virtanen (2015). Euclidean distance calculation from Taita Apalis and Taita Thrush occurrences points to Ngangao and Vuria forest edges was used as landscape variable.

Before modelling, *Zonal Statistics* function (ESRI, 1991) in ArcGIS 10.3.1 was used for all ecogeographical variables to summarize values within each of the 20 m analysis squares across Ngangao and Vuria forests to match with the species occurrence data sets. Ecogeographical variables were harmonized to 20 × 20 m grid cells due to the following reasons: (i) We used 20 m cell size to produce meaningful forest cover estimates from LiDAR data, as it has been pointed out that the analysis cell size must be larger than individual tree crowns and suggestion is to use 15 m or larger grid cell size (McGaughey, 2016), (ii) less than 20 m analysis square size would increase the sample size ending up to pseudoreplication in statistical analysis (Hurlbert, 1984), and (iii) pixel size for climate based variables was 20 m. As a final adjustment, granite outcrops areas in Ngangao forest were masked out from the geospatial data set before modelling process to reduce errors. Taita Apalis and Taita Thrush have not been sighted on the rock outcrops.

3. Habitat suitability modelling

3.0.1. Model calibration

This study used MaxEnt (Maximum Entropy) version 3.3.3e machine-learning algorithm to model the distribution of Taita Apalis in Ngangao and Vuria and Taita Thrush in Ngangao forest. This model uses presence-only machine learning algorithm (Phillips et al., 2006; Gomes et al., 2018) to approximate the probability of occurrence on the basis of species data and different environmental constraints. In our models, we selected 75% of occurrence data for model training and 25% for model testing (Hernandez et al., 2008; Phillips & Dudík, 2008), maintaining other values as default. We used 'bootstrap' approach as a sampling technique (replicated run type) since it has been found to be optimal for studies with few occurrences (Elith et al., 2011). Prior to modelling,

each predictor variable was run in MaxEnt independently in order to get the Area Under the Receiver Operating Characteristics Curve (AUC) value of the training data (Abdullah, 2016). Then, the generated values were used to rank the predictor variables from the highest to the lowest values and this ranking was utilized as a reference for selection of appropriate predictor variables in each model (Abdullah, 2016). The predictor variables were grouped into: (i) topography related (*slope_mean_20m*, *dtm_mean_20m*, *dtmrange_20m*, *twi_mean_20m*, *curvature_mean_20m* and *aspect_mean_20m*), and (ii) vegetation characteristics related (*aisaband1*, *canopyheight_mean_20m*, *penetrat*, *coverreturn4*, *forest_edge_Distance*, *Species_Diversity*, *canopyheight_max_20m*, *canopyrelief* and *canopyheight_range_20m*) to examine the role and influence of each predictor variable based on their categories (Abdullah, 2016). Based on the AUC value of training data, Model1 (the top 5), Model2 (all predictor variables) and model3 (top 3 per category) were generated (Table 2). Fewer models were applied in Vuria forest compared to Ngangao owing to the 'sparse' explanatory data used (Table 3). Jackknife analyses were performed to determine variables that reduce the model reliability when omitted and 10 random partitions were made for each model in order to assess the average behaviour of the algorithms, and to allow for statistical testing of observed differences in performance. Random seed was selected to ensure that replicates were not identical. We used maximum training sensitivity plus specificity to get the threshold value of each model, a promising selection method for presence-only data (Abdullah, 2016; Norris, 2014; Liu et al., 2013).

3.0.2. Model evaluation

We used the Area Under the Receiver Operating Characteristics Curve (AUC) to evaluate model performance. Value of AUC ranges from 0 to 1 (Fielding & Bell, 1997). An AUC value of 0.50 indicates that model did not perform better than random, whereas a value of 1.0 indicates perfect discrimination (Swets, 1988). The model with the highest test AUC value was considered the best performer. In addition, we used response curves to demonstrate the influence of the most important ecogeographical variables on the MaxEnt.

3.0.3. Habitat suitability maps

Habitat suitability maps were generated based on the prediction models. The probability values were reclassified into four habitat suitability classes, i.e. 'unsuitable' (0–0.2), 'low' (0.2–0.4), 'moderate' (0.4–0.6), and 'high suitability areas' (0.6–1). This type of map classification has been applied to large number of studies (Ansari & Ghodousi, 2018; Convertino et al., 2014; Zhang et al., 2019).

4. Results

4.1. Model performance

All models provided reliable estimates of Taita Apalis and Taita Thrush distribution in Ngangao and Vuria forests (AUC > 0.7) and small differences in the test and training AUC values indicated very low overfit in the prediction results (Appendix A, Tables A1 to A8). The model2 produced the highest AUC values of training data: Taita Apalis model2 in Ngangao forest had AUC value of 0.924, Taita Apalis model2 in Vuria forest had AUC value of 0.935 and Taita Thrush model2 in Ngangao forest had AUC value of 0.891. For test data, however, there were mixed results. E.g. While Taita Apalis model2 in Ngangao and Vuria forest had the highest test AUC values (AUC = 0.809 and 0.890 respectively), Taita Thrush model3 in Ngangao forest had the highest test AUC value (AUC = 0.783) (Appendix A, Tables A1 to A8).

4.2. Analysis of variable contributions

Tables 4, 5 and 6 show the contribution of each explanatory variable

Table 4
Percentage contribution of predictor variables in three MaxEnt models of Taita Apalis in Ngangao forest.

Taita Apalis in Ngangao forest				
S/No	Variable	Contribution (%)		
		Model1	Model2	Model3
1	Species Diversity	–	2.1	–
2	aisaband1	–	2.5	10.4
3	aspect_mean_20m	–	9.1	–
4	canopyheight_max_20m	–	1.6	–
5	canopyheight_mean_20m	–	0.7	–
6	canopyheight_range_20m	44.3	13.8	38.9
7	Canopyrelief	20.5	8.1	7.8
8	coverreturn4	–	16.4	–
9	curvature_mean_20m	–	1.1	–
10	dtm_mean_20m	21.4	9.7	27.1
11	dtmrange_20m	2.1	0.9	2.5
12	forest_edge_Distance	–	14.9	–
13	Penetrat	–	8.8	–
14	slope_mean_20m	11.7	9.6	13.3
15	Ngangao_twi_mean20m	–	0.8	–

Table 5
Percentage contribution of predictor variables in three MaxEnt models of Taita Thrush in Ngangao forest.

Taita Thrush in Ngangao				
S/NO	Variable	Contribution (%)		
		Model1	Model2	Model3
1	Species_Diversity	–	1.3	–
2	aisaband1	17.4	8.7	12.5
3	aspect_mean_20m	–	7.3	–
4	canopyheight_max_20m	–	0.3	–
5	canopyheight_range_20m	–	6.2	–
6	Canopyrelief	–	2.6	–
7	coverreturn4	–	9.2	–
8	canopyheight_mean_20m	15.1	6.3	18.5
9	curvature_mean_20m	–	2.1	–
10	dtm_mean_20m	31.6	19.0	34.3
11	dtmrange_20m	–	0.4	0.8
12	forest_edge_Distance	–	5.6	–
13	Penetrat	15.7	8.8	11.9
14	slope_mean_20m	20.1	7.6	21.9
15	Ngangao_twi_mean20m	–	14.6	–

Table 6
Percentage contribution of predictor variables in two MaxEnt models of Taita Apalis in Vuria forest.

Taita Apalis in Vuria forest				
S/No	Variable	Contribution (%)		
		Model1	Model2	
1	vuria_aspect_20m	8.5	6.8	
2	vuria_CHM_20m	9.3	9.1	
3	vuria_eucdist_to_edge_20m	28.1	23.6	
4	vuria_mean_temperature_annual_20m	34.5	20.5	
5	vuria_slope_20m	19.6	20.1	
6	vuria_curvature_dem_20m	–	1.0	
7	vuria_landcover_2004_20m	–	12.3	
8	vuria_twi_mean20m	–	6.5	

within the selected MaxEnt models. LIDAR-based canopy height range and mean elevation variables had the highest contributions in all the models for Taita Apalis in Ngangao forest (Table 4). The total contribution rate of variables related to vegetation characteristics was higher than topography in all Taita Apalis models in Ngangao forest. For Taita Thrush in Ngangao forest, elevation was the major ecogeographical contributor for the models followed by slope, topographic wetness index (*twi*) and mean canopy height (Table 5). The total contribution rate of variables related to topography outperformed vegetation characteristics

in all Taita Thrush models in Ngangao forest. In Vuria forest, mean annual temperature, Euclidean distance to the forest edge, slope and land cover contributed greatly to Taita Apalis models (Table 6). The total contribution rate of variables related to vegetation characteristics performed the best followed by variables related to topography and climate.

4.3. Response curves

We focused our examination of the response curve on variables whose contribution rates were more than 10% (Figs. 2, 3 and 4). The occurrence of Taita Apalis in Ngangao forest was found to be negatively correlated with elevation, canopy relief and slope, where the probability of its presence decreased with increase in elevation, canopy relief and slope (Fig. 2). Areas on slopes of less than 5°, within elevation between 1620 and 1750 m a.s.l. and with canopy relief of less than 0.1 were the most preferred. Probability of Taita Apalis occurrence however increased with increase in canopy height range and Euclidean distance to the forest edge. Areas with canopy height range of 47–55 m and were 60 m and above from Ngangao forest edge were the most preferred (Fig. 2).

The occurrence of Taita Thrush in Ngangao forest was positively correlated with mean canopy height and topographic wetness index (*twi*), where the probability of its presence increased with increase in mean canopy height and topographic wetness index (*twi*). Areas with topographic wetness index (*twi*) of 8.3–8.8 and canopy height of 37–41 m were the most preferred (Fig. 3). It showed similar trend with LiDAR penetration and airborne imaging spectroscopy band-1 reflectance, but decreased rapidly after values of about 10% and 1 respectively (Fig. 3). The probability of Taita Thrush occurrence however decreased with increase in elevation and slope. Areas on slopes of less than 5° and within elevation between 1620 and 1730 m a.s.l., were the most preferred (Fig. 3).

The occurrence of Taita Apalis in Vuria forest was found to be negatively correlated with mean annual temperature and slope, where the probability of its presence decreased with increase in mean annual temperature and slope. Areas with mean annual temperature of 11.5 °C–12 °C and on slopes of less than 1° were the most preferred (Fig. 4). The probability of Taita Apalis occurrence increased with increase in distance from the forest edge to about 270 m, beyond which, it decreased rapidly (Fig. 4). Land cover type was also found to have influenced Taita Apalis presence in Vuria forest, where the cover type made up of indigenous tree species was the most preferred (Fig. 4).

4.4. Predicted distribution of bird species in two forests

Predicted probability of the two bird species is displayed by three maps (Figs. 5, 6 and 7). Probability of Taita Apalis presence was found to be high on the southern, eastern and north-eastern parts of Ngangao forest (Fig. 5), whereas for Taita Thrush, the predicted probability of presence was higher on the northern part of Ngangao forest than in the southern part (Fig. 6). In these maps, white colour inside Ngangao forest represents bare granite outcrop. In Vuria, the predicted probability of Taita Apalis presence was high on the southern and eastern sides of the southern patch and on the western side of the northern patch (Fig. 7).

4.5. Percentage of suitable habitat and suitability maps for the two bird species

Based on the model results, 20–50% of Ngangao forest was categorised as unsuitable habitat for Taita Apalis, 37–43% as habitat of low suitability, 4–37% as habitat of moderate suitability and 2–7% as habitat of high suitability (Fig. 8). For Taita Thrush, 16–39% of Ngangao forest was considered as unsuitable habitat, 42–53% as habitat of low suitability, 16–36% as habitat of moderate suitability and 2–6% as habitat of high suitability (Fig. 9). For Vuria forest, 64–67% was classified as

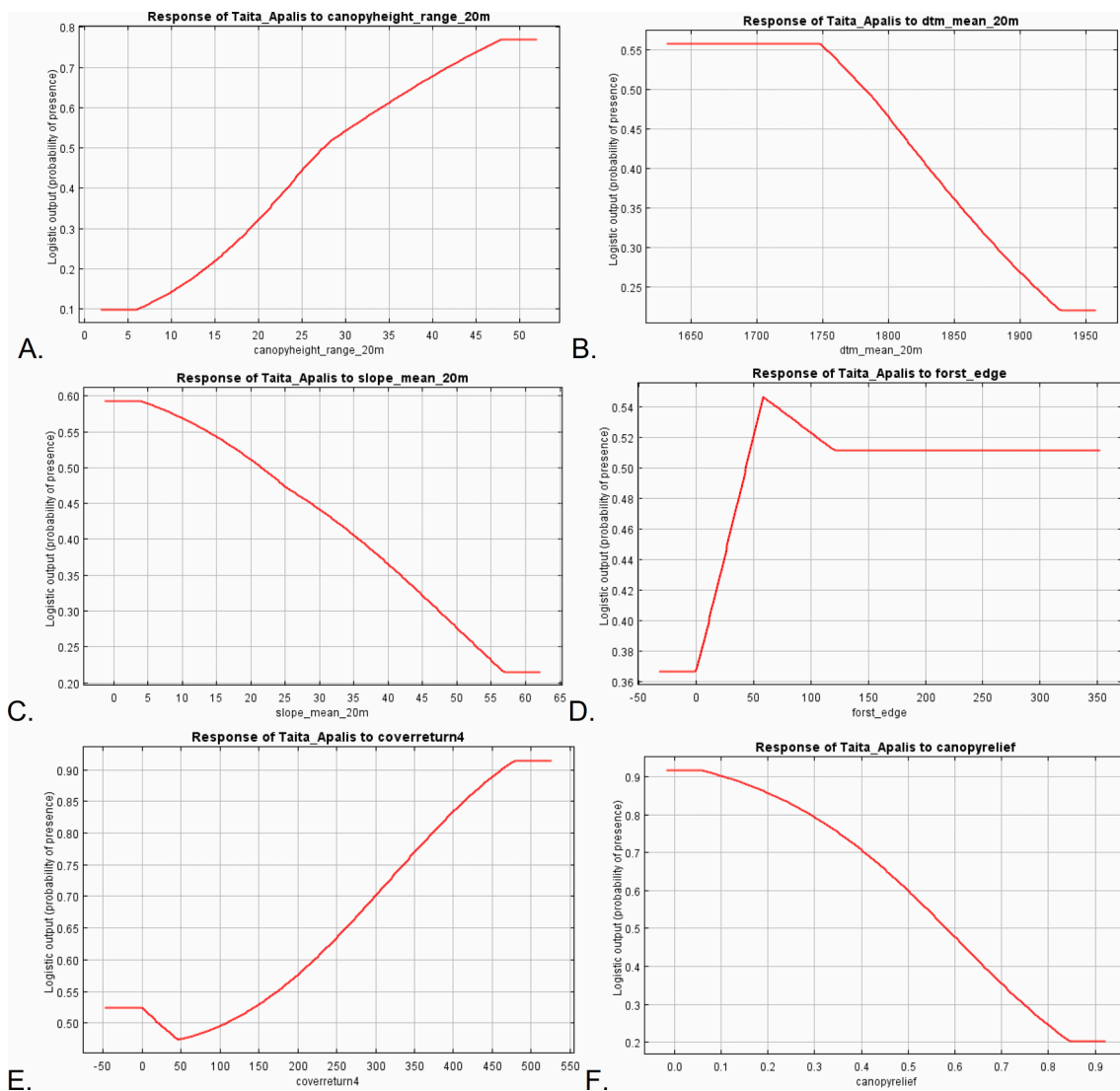


Fig. 2. Response curves of environmental variables of Taita Apalis in Ngangao forest: (A) canopy height range, (B) elevation, (C) slope, (D) Euclidean distance to the forest edge, (E) percentage of LiDAR 4th return, and (F) canopy relief.

unsuitable habitat for Taita Apalis, 23–25% as habitat of low suitability, 6–10% as habitat of moderate suitability and 1–4% as habitat of high suitability (Fig. 10). Based on these modelling results, suitable habitat for Taita Apalis covers less than 7% of Ngangao forest and less than 4% of Vuria forest. The results further show that Taita Thrush occupies less than 6% of Ngangao forest.

5. Discussion

The habitat suitability of Taita Apalis and Taita Thrush models produced interpretable predictions of the species distribution. Where suitable conditions were predicted, the species distribution patterns were uniformly clustered. This pattern of distribution might be related to the small sample size of occurrence data as well as clustered data of the two species sightings. This issue had also been observed by Falck et al. (2016). In addition, clustered data has shown to cause MaxEnt to over-fit models to the environmental conditions at those limited locations see for example Syfert et al. (2013). The stability of the models was verified by 10 repeated AUC values and all were found to have mean AUC values above 0.755 and the small differences in the test and training AUC values indicate very low over fit in the prediction results verifying that all the MaxEnt models were robust. *Model2* (all predictor

variables) produced the highest AUC values of training data. This outcome is in agreement with the findings of Abdullah (2016).

5.1. Importance of environmental factors

LIDAR-based canopy height range, elevation, percentage of LiDAR 4th return, Euclidean distance to the forest edge and slope appeared to be the major environmental variables contributing to the current distribution of Taita Apalis in Ngangao forest; elevation, slope, topographic wetness index (*twi*), mean canopy height, Airborne imaging spectroscopy band-1 reflectance and LiDAR penetration were major determinants of Taita Thrush current distribution in Ngangao while mean annual temperature, Euclidean distance to the forest edge, slope and land cover type appeared to be the major environmental variables influencing the current distribution of Taita Apalis in Vuria forest.

Basic topographic factors (e.g. slope, elevation) alter microclimatic conditions and indirectly influence the growth and distribution of land cover, consequently affecting bird distribution and abundance. Slope has a significant contribution towards microclimatic conditions which influence the growth and distribution of vegetation. It affects the amount of solar radiation received by vegetation, soil moisture, and microclimatic variables (Bennie, Huntley, Wiltshire, Hill, & Baxtera,

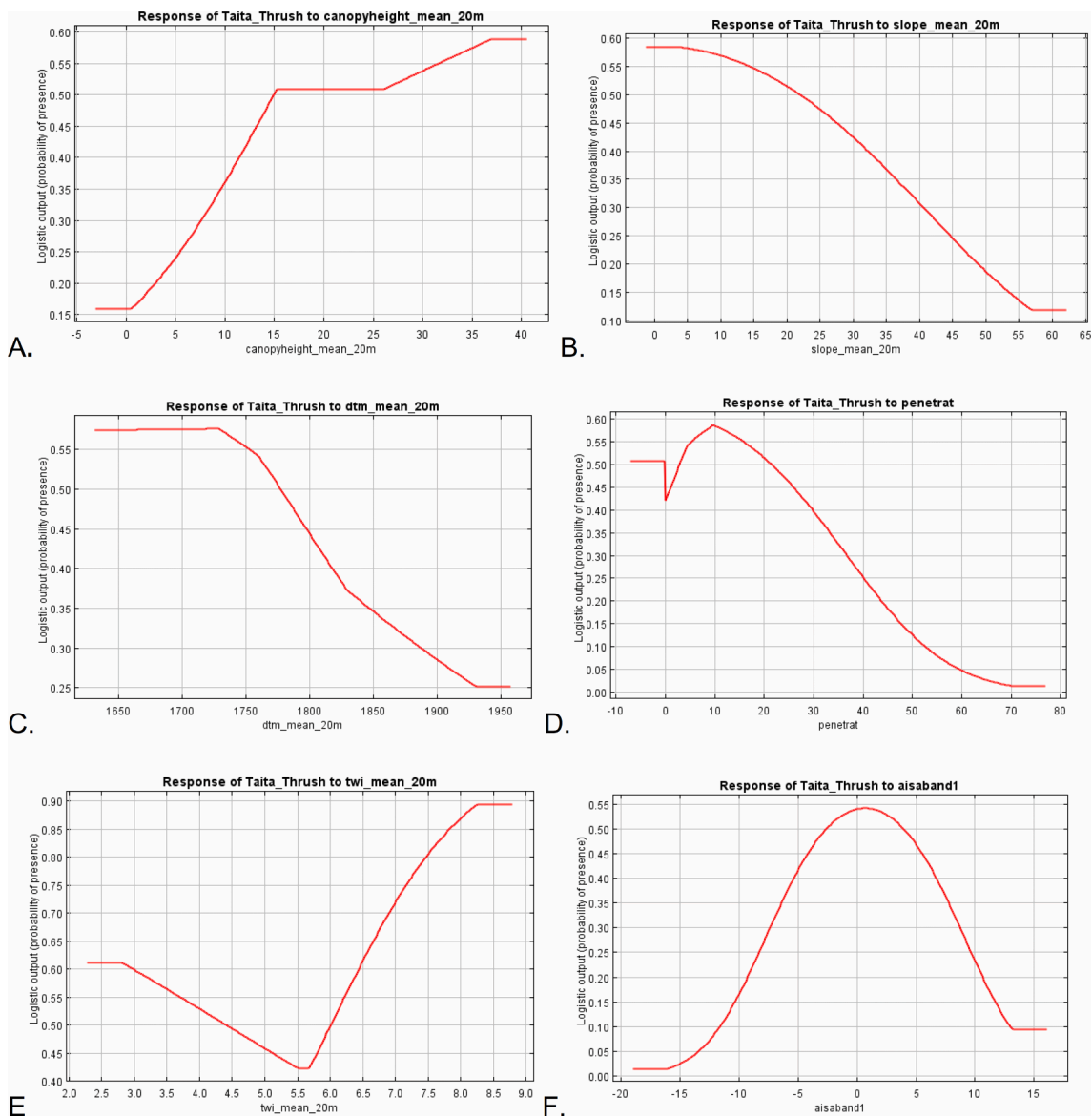


Fig. 3. Response curves of environmental variables of Taita Thrush in Ngangao forest: (A) mean canopy height, (B) slope, (C) elevation, (D) percentage LIDAR penetration, (E) topographic wetness index (*twi*), and (F) airborne imaging spectroscopy band-1 reflectance.

2008), ultimately affecting birds' abundance and distribution. As demonstrated by this study, Taita Apalis and Taita Thrush prefer gentle sloping areas inside Ngangao and Vuria forests. Gentle slopes could be helping them to avoid nest predation. Although elevation may have an indirect effect on the distribution of species, it can largely influence the availability of food resources. Food supply has been shown to have the most direct impact on animal survival, reproduction success and population size (Newton, 2003). Our results indicated that Taita Apalis and Taita Thrush favour high elevations in Ngangao and Vuria forests. High elevation areas could be offering them better foraging, nesting and roosting opportunities.

Topographic wetness index (*twi*) is as an index that is capable of predicting areas susceptible to wetted land surfaces and areas that have strong potential to produce overland flow (Beven et al., 1984), and a good proxy of soil moisture (Chen & Yu, 2011). As shown, Taita Thrush prefers areas of Ngangao forest with topographic wetness index of 8.3 – 8.8 (Fig. 3) indicating that they favour areas with moderately dry surfaces.

Forest canopy height is one of the most significant indicators of forest biomass, site quality, species diversity, and other ecosystem functions

(Fang et al., 2006; Moles et al., 2009). In Ngangao forest, Taita Apalis was found to prefer areas with open middle-storey as indicated by canopy height range of 47–55 m (Fig. 2). Open middle-storey allows light and space for the development of thick undergrowth. Taita Thrush was found to favour areas with fairly closed canopies and having mean height of 37–41 m (Fig. 3).

Taita Apalis showed strong association with Euclidean distance to the forest edge in both Ngangao and Vuria forests. However, the distance preference was varied. For example while there was high probability of Taita Apalis presence at Euclidean distance to the forest edge of 60 m and above in Ngangao forest, about 270 m to the forest edge was preferred in Vuria forest. Possible reason for this variation could be the higher numbers of Taita Apalis predators in Vuria compared to Ngangao forest and therefore the interior of Vuria forest provide much needed protection from the potential predators.

5.2. Potential distribution and habitat suitability

Habitat suitability area of Taita Apalis and Taita Thrush was classified to unsuitable, low, moderate and high suitability. Generally, the

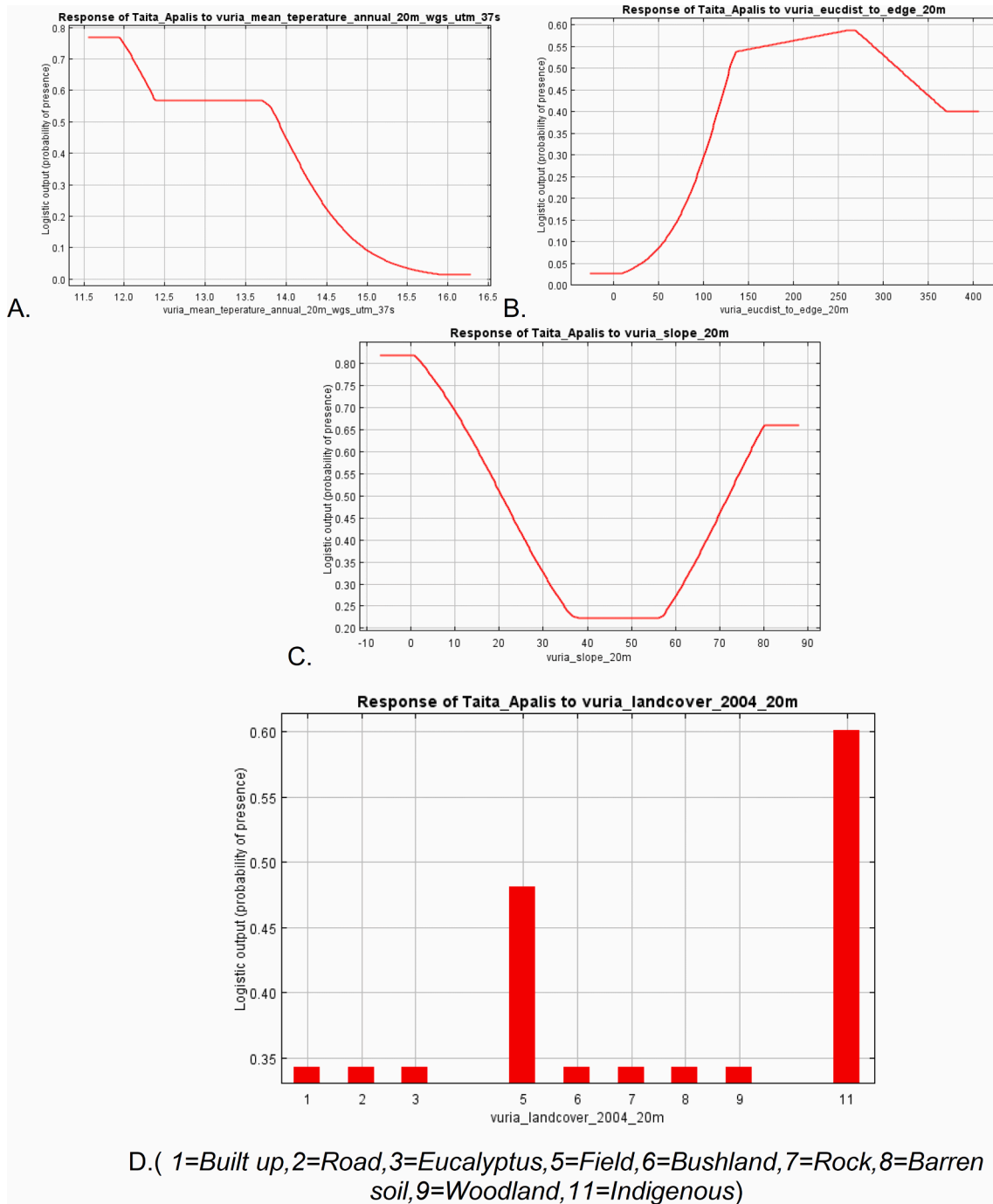


Fig. 4. Response curves of environmental variables of Taita Apalis in Vuria forest: (A) mean annual temperature, (B) Euclidean distance to the forest edge, (C) slope and (D) land cover type.

habitat suitability rate produced by each model was varied, and unsuitable and low classes were always given the highest suitability in each MaxEnt model. The models predicted that less than 7% of Ngangao and less than 4% of Vuria forest might be suitable for the activities of Taita Apalis and less than 6% of Ngangao forest being suitable for the activities of Taita Thrush.

Suitable habitats for Taita Apalis were predicted on the southern, eastern and north-eastern sides of Ngangao forest (Fig. 5), and on the southern and eastern sides of southern patch and on the western sides of northern patch of Vuria forest (Fig. 7). For Taita Thrush, suitable habitats were predicted mainly on the northern parts of Ngangao forest. High presence of Taita Apalis on the north and south of Ngangao forest has in

reality been recorded, with the south supporting densities three times lower than the north (Borghesio et al., 2010). Unsuitable habitats were, however, predicted mainly on the western sides of Ngangao for both species and on the western sides and towards the forest edges of the southern patch and on the northern and southern parts of the northern patch of Vuria forest. Suitable habitats were predicted within the indigenous vegetation whereas unsuitable habitats were predicted mainly in the exotic tree plantation. This conforms to records in literature on preferred habitats for Taita Apalis and Taita Thrush (Borghesio et al., 2015; Borghesio et al., 2017). Although exotic tree plantations are strongly avoided by Taita Apalis (Borghesio et al., 2015), foraging individuals of Taita Apalis and Taita Thrush had occasionally been

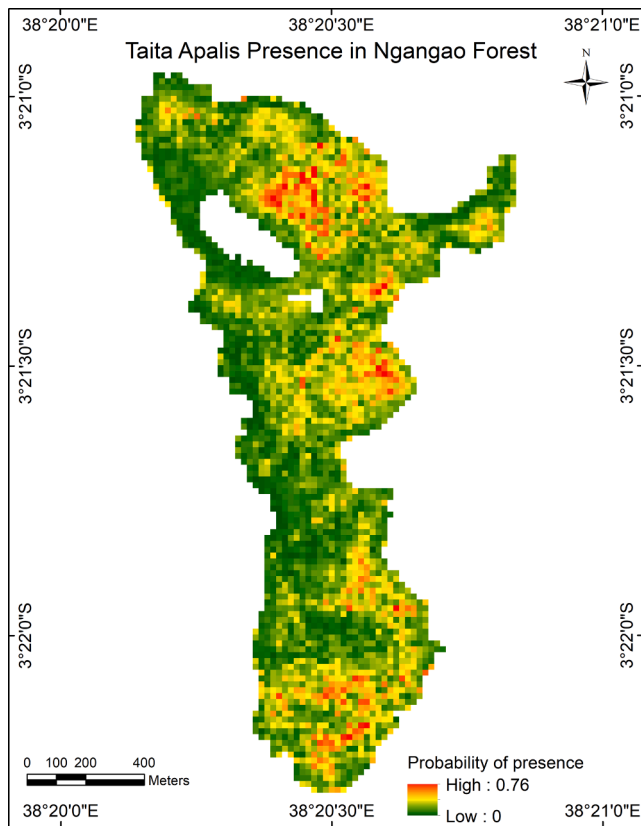


Fig. 5. Predictive occurrence map of Taita Apalis in Ngangao forest in Taita Hills based on model 2. Warmer colours represent areas of higher probability. White colour inside the forest are bare granite outcrop.

observed within some exotic plantation patches in Ngangao forest (Borghesio et al., 2017), underscoring their significance.

5.3. Conservation implications

The models utilized herein produced high AUC values for Taita Apalis in Ngangao forest, Taita Thrush in Ngangao forest and Taita Apalis in Vuria forest, indicating reliable estimations and hence can be applied in detecting highly suitable areas for the two species in other parts of the Taita hills. In addition, the small differences in AUC values for Taita Apalis and Taita Thrush models, indicating that one model can reliably predict the distribution of another species.

This study has shown that less than 7% of the two forests was suitable for the activities of Taita Apalis and Taita Thrush. The small habitat sizes as predicted are expected to influence extinction risk of these two species by reducing their carrying capacity, thus reducing the buffer that exists between the long-run average population size and extinction. Accordingly, populations in smaller habitats are more vulnerable to extinction from demographic stochasticity, which is strongest for small populations (Desharnais et al., 2006; Griffen & Drake, 2008; Lande et al., 2003). Efforts should therefore be put on preventing further habitat loss and disturbance, restoring habitat quality and increasing connectivity between the two forest fragments (Van de Peer, 2013). Our conservation recommendations focus on habitat expansion, connectivity and protection.

5.3.1. Habitat expansion and connectivity

Previous studies showed that forest gene bird species such as Taita Apalis and Taita Thrush display only restricted gene flow among forest patches (Lens et al., 1999; Callens et al., 2011; Teucher et al., 2020). Consequently, it is fundamental to increase cloud forest connectivity to protect

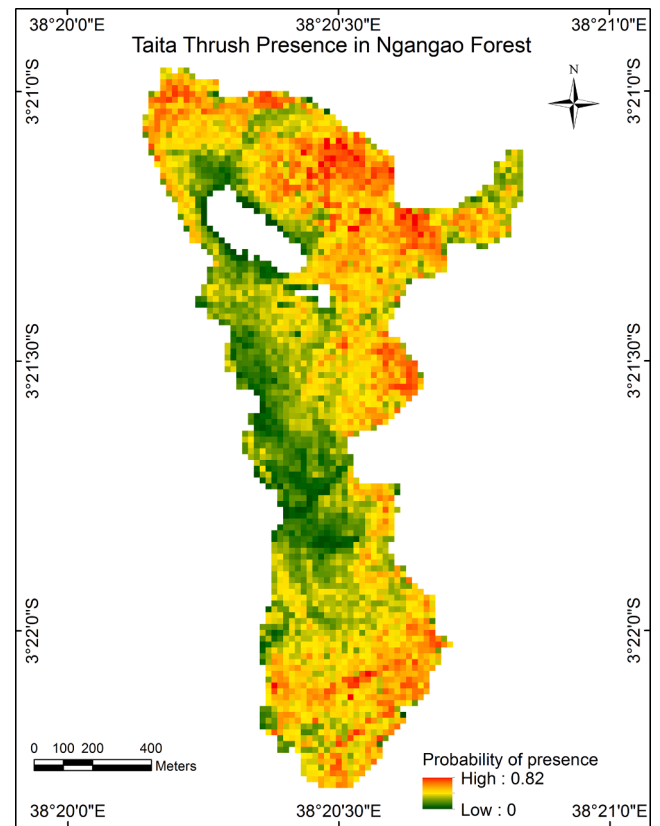


Fig. 6. Predictive occurrence map of Taita Thrush in Ngangao forest in Taita Hills based on model 3. Warmer colours represent areas of higher probability. White colour inside the forest are bare granite outcrop.

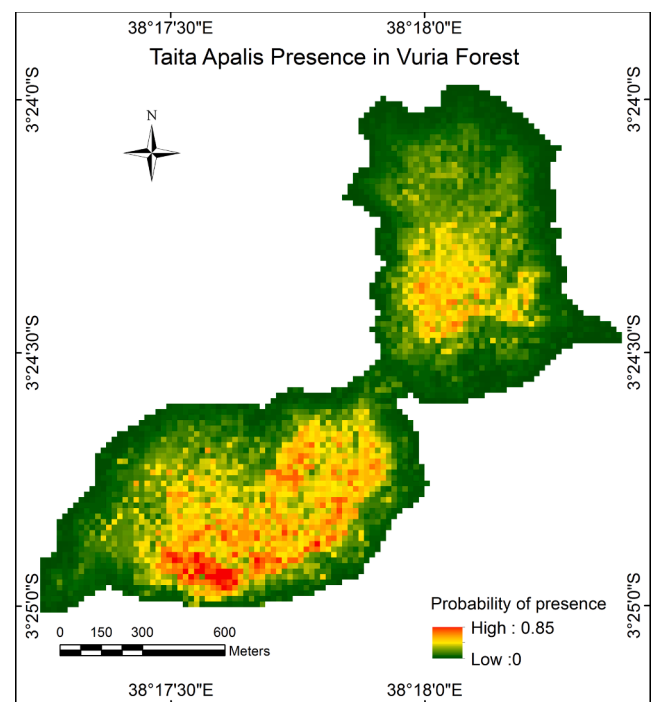


Fig. 7. Predictive occurrence map of Taita Apalis in Vuria forest in Taita Hills based on model 2. Warmer colours represent areas of higher probability.

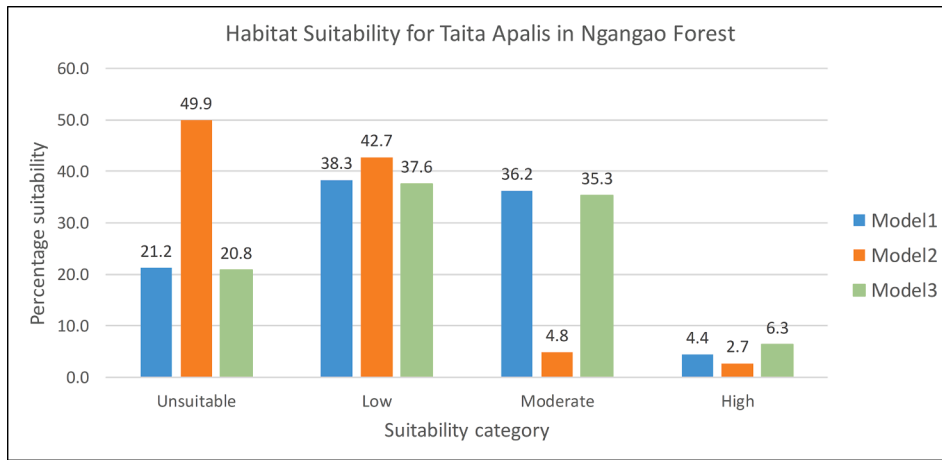


Fig. 8. Graph of habitat suitability for Taita Apalis in Ngangao forest based on three models.

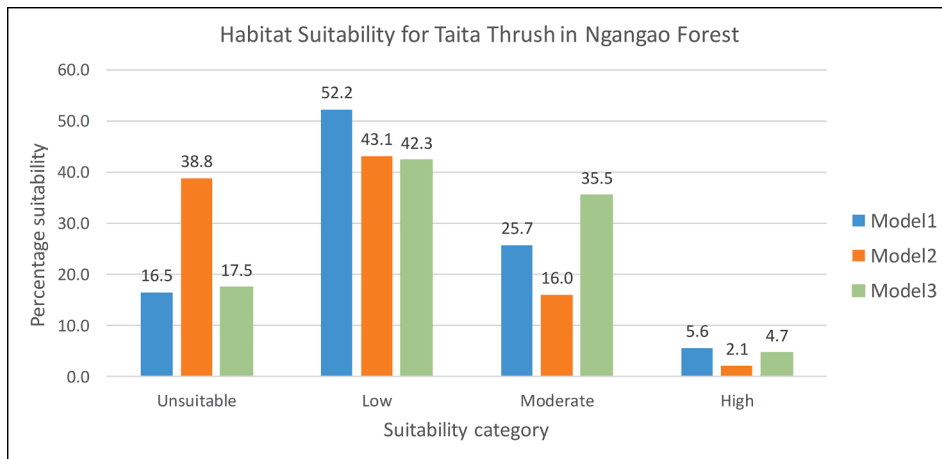


Fig. 9. Graph of habitat suitability for Taita Thrush in Ngangao forest based on three models.

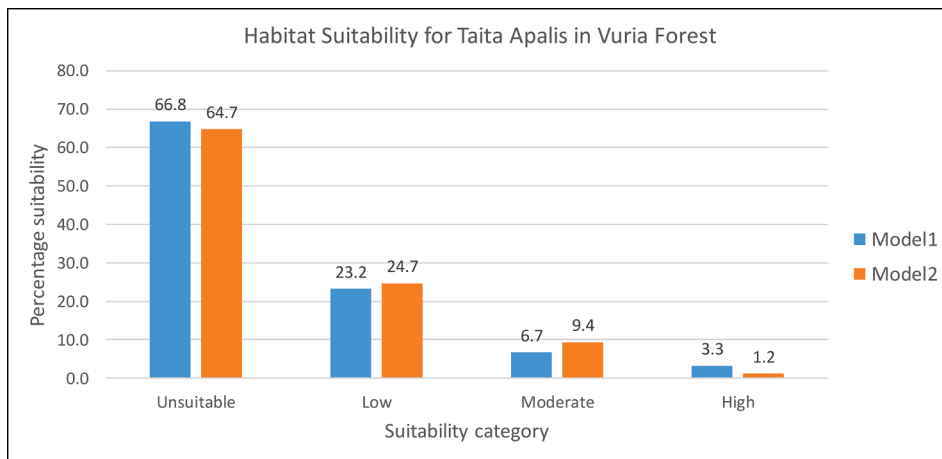


Fig. 10. Graph of habitat suitability for Taita Apalis in Vuria forest based two models.

populations and species (Lens et al., 2002; Aben et al., 2012; Haddad et al., 2015; Teucher et al., 2020). The forest corridor connecting Vuria and Ngangao could be the most efficient through Iyale forest enabling breeding in Iyale, a proposed stepping stone between Ngangao and Chawia by Githiru et al. (2011). This will significantly improve habitat networks for diverse species and forest-related ecosystem services

(Teucher et al., 2020). However, the smallholding land ownership in the study area limits the realization of this dream. We recommend connecting Vuria and Ngangao through Iyale forest using agroforestry system based on indigenous trees (Teucher et al., 2020). The community forests within the proposed corridor should also be targeted for conversion into indigenous vegetation.

As illustrated, less than 7% of the two forests was predicted as being suitable for the activities of Taita Apalis and Taita Thrush, and thus the need for habitat expansion. To achieve this, we propose reforestation with indigenous tree species of open and degraded sites next to areas predicted as highly suitable for the two birds. The targeted sites for reforestation should be the ones on the southern, eastern and north-eastern sides of Ngangao forest and the southern and eastern sides of southern patch and the western sides of northern patch of Vuria forest. In addition, such areas should be within elevation range of 1620–1750 m a.s.l., gentle slopes and having moderately dry surfaces in case of Ngangao forest. Our results will support restoration efforts by organizations such as Nature Kenya which is in the process of restoring 115 ha of forest adjacent to the northern patch of Vuria (BirdLife International, 2021).

Although 6.28 ha has been secured from land owners through land lease and purchase for Taita Apalis within the northern patch of Vuria forest (BirdLife International, 2021), the remaining indigenous forest on the private land might not survive for long without active protection (Borghesio & Wagura, 2012). This study proposes compensation scheme/easement for land owners within the northern patch of Vuria forest to preserve the remaining native vegetation on their land for Taita Apalis. Urgent protection of remaining native vegetation, particularly on privately owned plots between the southern and northern patch of Vuria forest, through the purchased/leased land where Taita Apalis had been documented is also vital (BirdLife International, 2021).

5.3.2. Habitat protection

Management of Ngangao and Vuria forest should focus on preventing or reducing severe human impacts such as grazing, forest fire incidences and firewood collection. This should be regarded as a complementary measure with long-term effects on bird richness (Santos et al., 2002). This study proposes the establishment of agroforestry belts based on indigenous trees on the boundaries of Ngangao and Vuria forests to create favourable conditions for secondary forest growth and thus, enhancing resilience of the forest fragments to the edge effects and conserving the remaining biodiversity (Wekesa et al., 2018). The belt will also reduce human impacts such as grazing and firewood collection, the practices which destroy the preferred foraging habitat of insectivorous bird species (Nature Kenya et al., 2015; Van de Peer, 2013). Several Taita Apalis territories have been lost in Ngangao and Vuria forests to these practices (Nature Kenya et al., 2015).

Community involvement in protection of these two forests should be enhanced through Participatory Forest Management (PFM), an approach which deliberately involves the forest adjacent communities and other stakeholders in sustainable management of forests within a framework that contributes to community's livelihoods (Kenya Forest Service—KFS, 2015). In this arrangement, each forest is required to have a management plan (Kenya Gazette Supplement No. 155 (Acts No. 34), 2016) and the forest adjacent community to sign forest management agreement with Government to formalize what has been agreed on in the management plan. Currently Vuria forest has forest management plan and in the process of signing forest management agreement with the County Government of Taita Taveta, the forest being under County Government. This forest management plan provides for rehabilitation, tree nursery development and seedlings production as means for providing forest products and facilitating rehabilitation of degraded areas in the forest, ecological monitoring, forest protection and community livelihoods' enhancement. Ngangao forest on the other hand, lacks forest management plan and therefore efforts be made to prepare one. Where it is practiced, PFM has ensured high forest quality and species richness (Matiku et al., 2012). However, without sufficient education and awareness, the forest adjacent communities may misinterpret PFM to mean free and unlimited access into the forest to extract forest resources (Matiku et al., 2013). We recommend that Vuria forest adjacent communities be supported to implement their forest management plan and Ngangao to formulate forest management plan.

Alternative funding mechanisms for the implementation of PFM need to be devised so that it is less burdensome to participating forest adjacent communities.

6. Conclusion

This study aimed to; determine the current spatial distribution of Taita Apalis and Taita Thrush in Ngangao and Vuria forests of the Taita Hills using MaxEnt model; to examine which and how ecogeographical factors influence the habitat suitability of Taita Apalis and Taita Thrush; and create maps of the predicted occurrences of the two studied species. Ecogeographical explanatory variables; climatic, remote sensing-, LiDAR-, topography- and landscape-based variables were used in the modelling, and separate models produced. The outcomes demonstrated that maximum entropy modelling, implemented through MaxEnt was an efficient method in generating meaningful results albeit the small sample size of species occurrence data. Variables related to vegetation characteristics greatly influenced Taita Apalis presence in both Ngangao and Vuria forests, whereas topographical factors were the major determinants of Taita Thrush presence in Ngangao forest. The proportion of the two forests predicted as suitable for the activities of the two species was less than 7%. This study therefore proposes habitat expansion through reforesting open and degraded sites next to areas predicted as highly suitable for the two species and establishment of agroforestry belts based on indigenous trees on the boundaries of the two forests to reduce grazing and firewood collection pressure; and to enhance forest protection through Participatory Forest Management. In future, comparative studies could be undertaken utilizing additional explanatory variables to be able to evaluate how Taita Apalis would respond to various environmental factors in Ngangao and Vuria and Taita Thrush in Ngangao and Mbololo forests. Models should be extrapolated to the other cloud forest fragments in Taita Hills to extend knowledge to find suitable habitats for these two critically endangered species. Future studies should also incorporate climate change variables into species distribution models as Taita Apalis and Taita Thrush populations in Taita Hills will likely decline or even become extinct due to climate change related habitat loss.

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CRedit authorship contribution statement

Gilbay Obunga: Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Mika Siljander:** Conceptualization, Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Marianne Maghenda:** Writing – review & editing, Supervision. **P.K.E. Pellikka:** Writing – review & editing, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Tables A1 to A8.

Table A1

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Apalis model 1 in Ngangao forest.

Species Prediction Model	Training AUC	Test AUC
Taita Apalis model run 1	0.7671	0.7924
Taita Apalis model run 2	0.8152	0.7793
Taita Apalis model run 3	0.8023	0.7418
Taita Apalis model run 4	0.8065	0.7512
Taita Apalis model run 5	0.7978	0.8384
Taita Apalis model run 6	0.7762	0.8172
Taita Apalis model run 7	0.7839	0.6839
Taita Apalis model run 8	0.7527	0.7458
Taita Apalis model run 9	0.8244	0.9177
Taita Apalis model run 10	0.8873	0.7893
Taita Apalis (average)	0.8013	0.7857

Table A2

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Apalis model 2 in Ngangao forest.

Species Prediction Model	Training AUC	Test AUC
Taita Apalis model run 1	0.9198	0.8033
Taita Apalis model run 2	0.9147	0.8961
Taita Apalis model run 3	0.9504	0.7587
Taita Apalis model run 4	0.9282	0.8017
Taita Apalis model run 5	0.8901	0.9089
Taita Apalis model run 6	0.8994	0.9295
Taita Apalis model run 7	0.8977	0.5965
Taita Apalis model run 8	0.9460	0.6886
Taita Apalis model run 9	0.9825	0.9138
Taita Apalis model run 10	0.9091	0.7922
Taita Apalis (average)	0.9238	0.8089

Table A3

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Apalis model 3 in Ngangao forest.

Species Prediction Model	Training AUC	Test AUC
Taita Apalis model run 1	0.8786	0.8016
Taita Apalis model run 2	0.7892	0.7989
Taita Apalis model run 3	0.8393	0.7516
Taita Apalis model run 4	0.8806	0.9193
Taita Apalis model run 5	0.8786	0.7057
Taita Apalis model run 6	0.7325	0.8059
Taita Apalis model run 7	0.8505	0.8813
Taita Apalis model run 8	0.7998	0.6609
Taita Apalis model run 9	0.7772	0.8019
Taita Apalis model run 10	0.7904	0.8987
Taita Apalis (average)	0.8217	0.8026

Table A4

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Apalis model 1 in Vuria forest.

Species Prediction Model	Training AUC	Test AUC
Taita Apalis model run 1	0.9398	0.9409
Taita Apalis model run 2	0.9557	0.9659
Taita Apalis model run 3	0.9064	0.8109
Taita Apalis model run 4	0.9253	0.8521
Taita Apalis model run 5	0.9119	0.9528
Taita Apalis model run 6	0.9409	0.8568
Taita Apalis model run 7	0.8865	0.8905
Taita Apalis model run 8	0.8874	0.9563
Taita Apalis model run 9	0.9094	0.7908
Taita Apalis model run 10	0.8991	0.8003
Taita Apalis (average)	0.9162	0.8817

Table A5

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Apalis model 2 in Vuria forest.

Species Prediction Model	Training AUC	Test AUC
Taita Apalis model run 1	0.9297	0.8600
Taita Apalis model run 2	0.9299	0.8842
Taita Apalis model run 3	0.9150	0.8900
Taita Apalis model run 4	0.9198	0.9326
Taita Apalis model run 5	0.9592	0.9180
Taita Apalis model run 6	0.9256	0.7820
Taita Apalis model run 7	0.9339	0.9317
Taita Apalis model run 8	0.9582	0.8707
Taita Apalis model run 9	0.9525	0.9027
Taita Apalis model run 10	0.9270	0.9250
Taita Apalis (average)	0.9351	0.8897

Table A6

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Thrush model 1 in Ngangao forest.

Species Prediction Model	Training AUC	Test AUC
Taita Thrush model run 1	0.8441	0.6902
Taita Thrush model run 2	0.8662	0.7154
Taita Thrush model run 3	0.8824	0.7562
Taita Thrush model run 4	0.8237	0.9207
Taita Thrush model run 5	0.8131	0.9046
Taita Thrush model run 6	0.8832	0.6608
Taita Thrush model run 7	0.7838	0.6100
Taita Thrush model run 8	0.8046	0.8138
Taita Thrush model run 9	0.7956	0.6699
Taita Thrush model run 10	0.7911	0.8181
Taita Thrush (average)	0.8288	0.7560

Table A7

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Thrush model 2 in Ngangao forest.

Species Prediction Model	Training AUC	Test AUC
Taita Thrush model run 1	0.9034	0.8780
Taita Thrush model run 2	0.8650	0.8689
Taita Thrush model run 3	0.9177	0.8663
Taita Thrush model run 4	0.8715	0.6320
Taita Thrush model run 5	0.8990	0.7678
Taita Thrush model run 6	0.9201	0.7087
Taita Thrush model run 7	0.9103	0.6118
Taita Thrush model run 8	0.8276	0.7562
Taita Thrush model run 9	0.8764	0.6952
Taita Thrush model run 10	0.9140	0.7618
Taita Thrush (average)	0.8905	0.7547

Table A8

Training and testing area under the curve (AUC) values for 10 random model runs for Taita Thrush model 3 in Ngangao forest.

Species Prediction Model	Training AUC	Test AUC
Taita Thrush model run 1	0.8277	0.7041
Taita Thrush model run 2	0.7979	0.7722
Taita Thrush model run 3	0.7798	0.7341
Taita Thrush model run 4	0.8265	0.7164
Taita Thrush model run 5	0.7932	0.7789
Taita Thrush model run 6	0.8997	0.9211
Taita Thrush model run 7	0.8663	0.8411
Taita Thrush model run 8	0.8313	0.8808
Taita Thrush model run 9	0.7616	0.6610
Taita Thrush model run 10	0.8144	0.8187
Taita Thrush (average)	0.8198	0.7828

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