University of Kent

Kent Academic Repository

Mouafo, Alain D.T., Tédonzong, Luc Roscelin Dongmo, Ingram, Daniel J., Binda, Valery A., Ngwayi, Itoe Constantine Nfor and Mayaka, Theodore B. (2023) ***Maximum entropy modeling of giant pangolin Smutsia gigantea (Illiger, 1815) habitat suitability in a protected forest-savannah transition area of central Cameroon.*** **Global Ecology and Conservation, 43 .**

Downloaded from

https://kar.kent.ac.uk/100850/ The University of Kent's Academic Repository KAR

The version of record is available from

https://doi.org/10.1016/j.gecco.2023.e02395

This document version

Publisher pdf

DOI for this version

Licence for this version

CC BY (Attribution)

Additional information

Versions of research works

Versions of Record

If this version is the version of record, it is the same as the published version available on the publisher's web site. Cite as the published version.

Author Accepted Manuscripts

If this document is identified as the Author Accepted Manuscript it is the version after peer review but before type setting, copy editing or publisher branding. Cite as Surname, Initial. (Year) 'Title of article'. To be published in ***Title of Journal*** , Volume and issue numbers [peer-reviewed accepted version]. Available at: DOI or URL (Accessed: date).

Enquiries

If you have questions about this document contact ResearchSupport@kent.ac.uk. Please include the URL of the record in KAR. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from https://www.kent.ac.uk/guides/kar-the-kent-academic-repository#policies).

Global Ecology and Conservation 43 (2023) e02395

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Maximum entropy modeling of giant pangolin *Smutsia gigantea* (Illiger, 1815) habitat suitability in a protected forest-savannah transition area of central Cameroon

Alain D.T. MOUAFO [a,b,c,*], Luc Roscelin Dongmo TÉDONZONG [d], Daniel J. INGRAM [c,e], Valery A. BINDA [b], Itoe Constantine NFOR NGWAYI [f], Theodore B. MAYAKA [a]

[a] University of Dschang, Faculty of Science, Research Unit of Biology and Applied Ecology, P. O. Box 67, Dschang, West Region, Cameroon
[b] Agriculture and Bio-conservation Organization for Youth Empowerment and Rural Development, Dschang, West Region, Cameroon
[c] IUCN SSC Pangolin Specialist Group, % Zoological Society of London, Regents Park, London NW1 4RY, UK
[d] Centre for Research and Conservation (CRC), Royal Zoological Society of Antwerp (RZSA), Antwerp, Belgium
[e] Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury CT2 7NR, UK
[f] Ministry of Forestry and Wildlife, Yaoundé, Cameroon

ARTICLE INFO

Keywords:
Ecotone
Cameroon
Mammals
Manis gigantea
Species distribution modeling
Suitable habitat

ABSTRACT

Across the planet, biodiversity is facing ever-growing threats including habitat loss, climate change, overexploitation, and pollution. Pangolins of the order Pholidota are the only scaly mammal species worldwide and are considered the most trafficked wild mammals in the world, being widely exploited for their meat and scales. The giant pangolin (*Smutsia gigantea*, GP) is one of the least studied species of this order, with little being known about their response to environmental and anthropogenic variables, as well as their distribution patterns in forest-savannah transition areas. Our study aimed to increase ecological knowledge about GP by investigating the environmental factors associated with the distribution of suitable habitat for GP within a protected forest/savannah transition area of Cameroon. Using data on the locations of GP resting burrows collected using line transects and employing a maximum entropy (MaxEnt) modelling approach, we explored GP habitat suitability within a forest-savannah transition area of Cameroon. Our model revealed a good level of accuracy based on the average test area under the Receiver Operator Curve metric. The jackknife test found that Euclidian distance to the national park's boundaries, normalized difference vegetation index, elevation, and distance to river were the most important predictors determining the distribution of GP burrows. Areas predicted to be suitable for GP burrows were patchily distributed within dense forests, ecotone and savannah, with 19.24% of the study area being suitable and 1% very suitable. Overall, our study shows the possible importance of habitat suitability modeling for understanding GP distribution, as well as planning and prioritising their conservation actions.

* Corresponding author at: University of Dschang, Faculty of Science, Research Unit of Biology and Applied Ecology, P. O. Box 67, Dschang, West Region, Cameroon.

E-mail addresses: alaindelon553@gmail.com (A.D.T. MOUAFO), tedonzongluc@gmail.com (L.R.D. TÉDONZONG), danieljohningram@gmail.com (D.J. INGRAM), bindalery16@gmail.com (V.A. BINDA), iconsty@yahoo.com (I.C.N. NGWAYI), th.mayaka@gmail.com (T.B. MAYAKA).

https://doi.org/10.1016/j.gecco.2023.e02395
Received 1 August 2022; Received in revised form 28 January 2023; Accepted 2 February 2023
Available online 2 February 2023
2351-9894/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Biodiversity is facing ever-growing threats including habitat loss, climate change, overexploitation, and pollution (IPBES, 2019; Pimm et al., 1995). Modern extinction rates have reached a critical point, with extinction rates as a result of human activities being 8–100 times higher than expected, dubbed the "sixth extinction crisis" (Ceballos et al., 2015). The extinction rates of species and the relative effects of factors causing extinction risk vary across regions, particularly in relation to changes in land cover (Rodrigues et al., 2014). Owing to anthropogenic activities, many wildlife species are at risk of extinction (Owens and Bennett, 2000; Thomas et al., 2004), with the extinction risks of vertebrates increasing (Ceballos et al., 2015). Some mammal species have intrinsic traits, such as low reproductive rates and low population densities that make them more susceptible to anthropogenic factors such as overexploitation, habitat loss and degradation (Malakoutikhah et al., 2020; Owens and Bennett, 2000; Sharma et al., 2014; Thomas et al., 2004).

Knowledge of the geographic distribution, ecological and biological characteristics of species, as well as the factors affecting these parameters, are fundamental for conservation planning and forecasting of future actions (Ferrier et al., 2002; Funk and Richardson, 2002; Rushton et al., 2004), and can play a vital role in ecological restoration (Austin and Meyers, 1996; Guisan and Thuiller, 2005; Larson et al., 2004; Martinez-Meyer et al., 2006). This information is also needed to understand the ecological and evolutionary determinants of biodiversity distribution patterns (Brown and Lomolino, 1998; Graham et al., 2006; Ricklefs, 2004; Rosenzweig, 1995).

Species distribution models (SDMs), also called Ecological Niche Models or Climate Envelope Models, are quantitative methods that combine data on the known occurrence of a species with predictor variables, statistical models, and computer algorithms to 1) compute values for each predictor and the way it affects the species of interest at each site of known occurrence, and then 2) identifies suitable areas based on these predictor variables (Carpenter et al., 1993; Duan et al., 2014; Elith and Leathwick, 2009; Fielding and Bell, 1997a; Wisz et al., 2008). Species distribution models are a rapidly growing field of research (Brotons, 2014), which are increasingly used to support decision-making in various fields such as ecology, biogeography, biodiversity conservation and natural resource management (Franklin, 2010, 2013; Guisan and Thuiller, 2005; Guisan et al., 2013; Newbold, 2010). Species distribution models have been proven to assist in directing field surveys (see Peterman et al., 2013), assessing the effects of climate change on species, and improving conservation planning (Fitzgerald et al., 2018; Guillera-Arroita et al., 2015; Zellmer et al., 2019), clearly demonstrating the cornerstone role that SDMs are nowadays occupying in species conservation.

Robust ecological knowledge of the potential distribution and suitable habitats of species whose populations are decreasing over their distribution range is of paramount importance for planning their long-term conservation (Akrim et al., 2017). The giant pangolin (GP; *Smutsia gigantea*), which occurs in parts of West, Central, and East Africa (Kingdon et al., 2015; Hoffmann et al., 2020), is such a species. Of the eight species of pangolins worldwide, the giant pangolin is the largest, with a body mass exceeding 30 kg and a total body length between 140 and 180 cm (Hoffmann et al., 2020; Kingdon, 2015). The GP is classified as Endangered on the IUCN Red List of Threatened Species (Nixon et al., 2019), and is also listed on Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Despite the afforded protection, GP survival is still threatened by two main anthropogenic threats: overexploitation for meat and scales, and the degradation and loss of its primary habitats (Hoffmann et al., 2020; Ingram et al., 2019; Nixon et al., 2019). Given these threats, a general lack of research, and the need to better plan long-term GP conservation, the IUCN Species Survival Commission Pangolin Specialist Group highlighted the urgent need for research to better understand the overall ecology, habitat preferences and current distribution of GPs (Challender et al., 2014).

For all pangolin species, occurrence is considered to be determined mainly by food availability (presence of ants and termites), appropriate temperature, and presence of a permanent water source (Chao et al., 2020). In addition, other factors such as distance to human settlement and distance to roads might also be important predictors of pangolin occurrence (Akrim et al., 2017; Bruce et al., 2018; Waseem et al., 2020). For Indian (*Manis crassicaudata*) and Chinese (*Manis pentadactyla*) pangolins for example, elevation, average temperature, distance to human settlements, land cover class, slope, aspect, and precipitation have all been shown to be determinant factors of their distribution (Dorji et al., 2020; Sharma et al., 2014; Thomas et al., 2004). Indian and Chinese pangolins reportedly prefer digging their burrows in areas with moderate canopy cover and slope, not far from human settlements and water-courses, at a moderate elevation between 500 and 1750 m above sea level (Karawita et al., 2018; Suwal et al., 2020; Waseem et al., 2020). Dorji et al. (2020) also found that Chinese pangolins preferred digging their burrows on clay and sandy loam soils as they form soft layers that are easy to dig in, thus highlighting the importance of soil for pangolins as it permits them to find food, shelter, and also regulate their body temperature by retreating into burrows (Redford, 1987; Sun et al., 2021).

The GP distribution range is limited to tropical sub-Saharan Africa, where it is known to inhabit primary and secondary forests, forest-savannah mosaics, swamps, gallery forests, wooded savannah and wet grasslands (Hoffmann et al., 2020; Nixon et al., 2019). It is also considered to prefer areas near permanent water sources with minimal human activities (Hoffmann et al., 2020; Nixon et al., 2019). Khwaja et al. (2019) found that elevation and distance to river affect GP occupancy, however, compared to their Asian relatives, it remains unclear how other environmental variables, such as soil type, temperature, vegetation type, elevation, aspect, precipitation and slope may affect the distribution of the GP. This lack of information has direct consequences on accurately determining this species' conservation status and habitat preferences, thus hindering efforts to map priority areas where conservation actions (e.g., habitat restoration and protection efforts) could be implemented.

Cameroon hosts three of the four African pangolin species, including the GP (Hoffmann et al., 2020; Kingdon, 2015). Studies on the GP in Cameroon have traditionally focused on relative abundance and distribution based on indirect signs and camera-traps (Bruce et al., 2018; Ichu et al., 2017, Mouafo, 2018; Amin et al., 2023). So far, no study has examined the habitat suitability and potential distribution of GP using a SDM approach in mosaic forest-savannah transition areas. In an attempt to fill this gap in knowledge, two main research questions were asked, namely: (i) what are the environmental variables shaping GP distribution, and how do these

variables affect the distribution of GP? and (ii) what is the proportion of suitable habitat for GP and how is it distributed within the study area? From these questions, we hypothesized that:

- the distribution of GP is affected by elevation, vegetation types and distances to human settlements and nearest watercourse (Hoffmann et al., 2020; Waseem et al., 2020), as well as soil type given that GP is a burrowing species, and
- suitable habitat for GP burrowing is patchily distributed across habitat types, with GPs showing a preference for densely forested areas.

Based on these research questions, this study aimed to contribute to a better understanding of GP ecology as pre-requisites to developing area-based and species-specific conservation strategies.

2. Materials and methods

2.1. Study area

This study was undertaken in Mbam et Djerem National Park (MDNP), a 416,512 ha protected area situated between 5°30´and 6°14 N, and 12°20´and 13°15 E in central Cameroon (MINFOF, 2007). Its climate has two seasons of almost equal length: the rainy season from mid-April to mid-October and the dry season from mid-October to mid-April. The average rainfall is 1900 mm/year, with an annual average temperature of 24 °C (MINFOF, 2007). The relief is almost flat, but there is an elevational drop from 930 m to 650 m a.s.l. from the north to the south of the park. The area lies within the Guinea-Congolian/Sudanian regional transition zone, between the Sudanian regional center of endemism in the north and the Guinea-Congolian forest block in the south (Pye, 1985). The park's vegetation varies from savannah in the northwest through forest-savannah mosaics to closed canopy humid forest in the south-west (Mitchard et al., 2009). The fauna thus consists of species from both savannah and forest ecosystems with approximately 65 mammal species recorded (Maisels et al., 2000; MINFOF, 2007). Approximately 30,000 people are distributed in 75 villages bordering the MDNP and depend on farming, fishing, and hunting for their livelihoods (Bobo and Weladji, 2011; MINFOF, 2007; RGPH, 2005).

Our study site (Fig. 1) is located in the southern branch of the MDNP and occupies approximately 507 km^2, representing

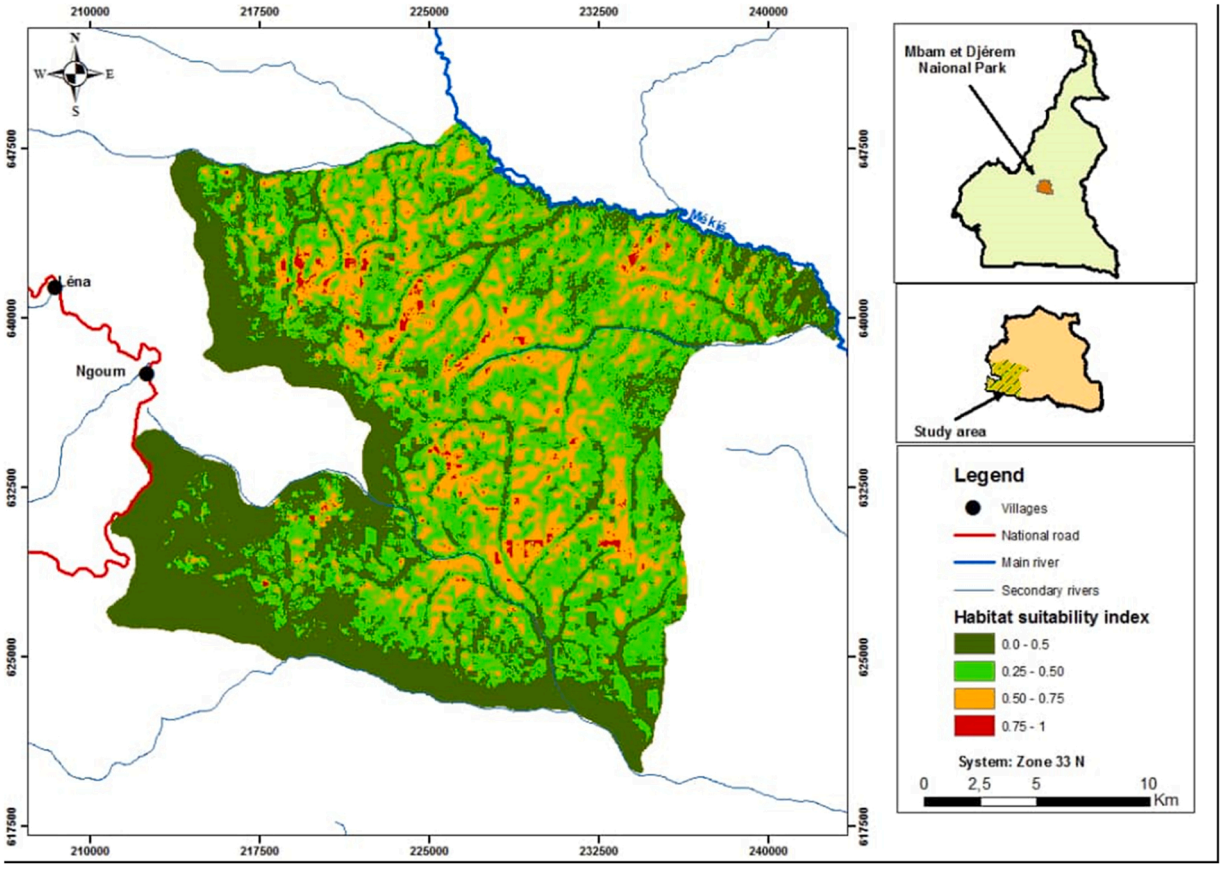


Fig. 1. Study area in the Mbam et Djerem National Park showing human settlements, rivers, and the areas predicted to be suitable for giant pangolins (*Smutsia gigantea*).

approximately 12% of the MDNP.

It is bordered in the North by the Djerem River, in the South by the Gbing River, in the East by the Mékié River and in the West by the Oussomisson River, as well as by the National Road 15 and two villages, Ngoum and Léna. The site is a typical mosaic habitat with the succession of young pioneer forests, gallery forests, wooded savannahs and shrub savannahs. A clear ecotone is evident between the gallery forests and the wooded savannahs or shrub savannahs. Due to its proximity to two villages and the recently constructed National Road 15, our study site has ongoing human disturbance and illegal hunting activities as demonstrated by anthropogenic signs frequently encountered during our surveys.

2.2. Data collection

2.2.1. Survey design and GP occurrence data

Following meetings held with local people, and conservation staff of MDNP, a pilot study was conducted in August 2017 on three 2-km long transects to identify potential sites to place transects. From this pilot study, we decided to adopt a systematic sampling procedure by placing transects perpendicular to rivers where possible, given the variation of habitat types we observed. We first established eight principal transect lines with lengths varying from 14 km to 22 km and separated from each other by a distance of 2–6 km. We then established 2-km long transects following the principal transect line, with each transect separated from the next to ensure independence in our observations. Because of their elusive nature, pangolins in general are difficult to observe directly, and as such, indirect evidence is often used to identify their presence (Mahmood et al., 2014; Perera and Karawita, 2020). Furthermore, to solve the problem of accurate identification of indirect signs of GP, which is sometimes problematic due to their similarity with those of aardvark (*Orycteropus afer*) and the likelihood of GP using an abandoned aardvark burrow (Hoffmann et al., 2020), we relied both on local knowledge and verifiable evidence as employed in previous studies on pangolins (Karawita et al., 2018; Mouafo, 2018; Nash et al., 2020; Newton et al., 2008). This was to ensure that a burrow in question was that of a GP and/or had recently been used by a GP. As the study area is a mosaic of forest and savannah, transects were placed perpendicular to the nearest river so that they crossed different habitat types. Major habitat types crossed by transects were: gallery forests, young pioneer forests (ecotone), savannah (wooded and shrub), closed undergrowth mixed forests and marshes. Between 2018 and 2021, two independent studies were carried out on a set of 34 transects to collect indirect occurrences of GP. The first study (November 2017 and March 2018) focused on the southern part of the study area, targeting 14 transects, while the second study (June and September 2020) targeted the northern part of the study area, and covered 20 transects. Using two observers on both sides of each transect with varying widths depending on the visibility of the habitat surveyed, we searched for the presence of GP through the identification of feeding and resting burrows. This study used only confirmed 'active' resting burrows (i.e., with evidence of use) of GP to be sure to capture information about the species distribution patterns. Sixteen camera-traps placed at a height between 30 and 60 centimeters above the ground, and in different habitat types were also used when collecting data to reduce the likelihood of erroneously recording burrows not used by GP.

This research was approved by the University of Dschang. All required authorizations for field work were obtained from the Ministry of Forestry and Wildlife through the Conservator of MDNP.

2.2.2. Environmental data

Four categories of environmental variables (Table 1) were used for modeling: (i) vegetation variables (Advanced Vegetation Index – AVI, Normalized Vegetation Difference Index – NDVI, Modified Normalized Difference Water Index - MNDWI and Shadow Index - SI); (ii) geophysical variables (Digital Elevation Model - DEM, slope, aspect, hill shade, distance to permanent rivers and streams) (iii) soil variables (bulk density, carbon exchange capacity, clay content, coarse fragments, nitrogen, organic carbon density, pH index

Table 1
Predictor variables retained in the final Environmental Niche model for giant pangolins (*Smutsia gigantea*) with their code description and contribution (%) to the model, ranked from highest to lowest.

Variable code	Variable description (Unit)	Contribution (%)
eucdist_pnmd1	Euclidian distance to MDNP's borders (meters)	41.3
ndvi_pnbd	Normalized difference vegetation index	15.2
pnbd_dem	Elevation (meters)	8.1
eucdist_river_pnmd	Euclidian distance to the nearest river (meters)	6.6
ph_water	pH index measured in water solution	5.9
coarse_fragment	Concentration of coarse fragments in the soil (cm^3/dm^3)	5.1
clay_content	Clay content in a kilogram of soil (g/kg)	4.4
pnbd_asp1	Aspect (degrees)	3
sand	Sand content in a kilogram of soil (g/kg)	2.4
nitrogen	Nitrogen concentration in the soil (g/kg)	2.2
silt	Silt content in a kilogram of soil (g/kg)	2
cec7	Carbon exchange capacity (mmol/kg)	1.5
org_car_density	Organic carbon density (kg/m^3)	1
avi_pnmd	Advanced vegetation index	0.9
pnbd_slop1	Slope (degrees)	0.4
pnbd_hill1	Hills shade	0
soilorgcarb1	Soil organic carbon stock (g/kg)	0

measured in water solution (the value of pH is multiplied by 10; Hengl et al., 2017), sand, silt, soil organic carbon, soil organic carbon stock and organic carbon density), and (iv) anthropogenic variables (distance to human settlements, distance to road, and distance to the park's boundaries). Geophysical and soil variables were chosen for their proven ability to affect species distributions at a broader scale (Austin, 2007; Elith and Leathwick, 2009; Guisan and Thuiller, 2005), while vegetation indices and anthropogenic variables have the ability to affect species distribution at finer scales (Benton, 2009; Lewis et al., 2017; Wiens, 2011), with GP preferring habitats with low human pressure (Bruce et al., 2018; Hoffmann et al., 2020). For example, we chose NDVI as it is commonly used as an indicator of vegetation state in a particular area, and because of its proven ability to predict both herbivore and non-herbivore species distribution and abundance over time and space (Myneni et al., 1995; Pettorelli et al., 2005, Rouse et al., 1973; Running, 1990). In addition, another motivation for the use of these variables was for comparability with models produced for other pangolin species (Dorji et al., 2020; Sharma et al., 2020; Suwal et al., 2020, 2021). Since our study area was relatively small, we anticipated climate to be uniform across the study area, which lead to excluding climatic data from our modeling process.

To obtain distance-based variables (distances to river, human settlements, park boundaries and distance to road), a shapefile of each feature type were created using ArcGIS version 10.3.1 and used to create raster files of Euclidian distance from the corresponding features (Tédonzong et al., 2020). Following the procedure described in Tédonzong et al. (2020), the Landsat 8 scene necessary for deriving vegetation indices and the DEM from the NASA Shuttle Radar Topography Mission (SRTM) version 3.0 were downloaded from the Earth explorer website (https://earthexplorer.usgs.gov), and used at 30 m resolution. For the topographic variables (elevation, aspect, slope and hills), the DEM was used as the base file and processed accordingly in ArcGIS version 10.3.1. Finally, in order to obtain raster files corresponding to our study area, we used the function "*extract by mask*" in ArcGIS to select the corresponding cells.

Soil variables were obtained from the SoilGrids 250 m database (https://www.soilgrids.org; Hengl et al., 2017). We used 11 soil variables that provide predicted values for the surface soil layer (0–15 cm depth). These included: four soil texture variables (proportion of clay, sand, silt, coarse fragment), which are related to soil drainage and seven chemical variables related to nutrient availability (the cation exchange capacity (CEC), bulk density, nitrogen content, organic carbon density, soil organic carbon, soil organic carbon stock and pH).

All environmental data were masked to the full extent of the study area and all layers were resampled at a resolution of 30 × 30 m using ArcGIS. We computed a Pearson correlation coefficient matrix to assess the strength of association among variables, setting the correlation threshold at $r = |0.7|$ (Dormann et al., 2013). When variables were highly correlated ($\geq|0.7|$), we used the *usdm* package in R to calculate the variable inflation factor (VIF) of each variable and sequentially discarded the correlated variable with the highest VIF using a stepwise analysis until the maximum correlation between variables was $< |0.7|$ (Dormann et al., 2013; Naimi et al., 2014). Based on the spatial resolution of 30 m, we conducted the spatial thinning to reduce the spatial autocorrelation of points using the SDMtoolbox in ArcGIS; this analysis considers a single point out of all occurrences in each grid cell (Brown, 2014). Although the selection of the resolution is known to be subjective and arbitrary (Anderson and Raza, 2010), the spatial resolution of 30 m was selected due to the heterogeneity of our study site (variation being in the order of decametres), the size of the study site, and the fact that we wanted to capture variation at the micro level which could not be possible if the standard resolution of 1 km was used.

2.3. Modeling approach

Suitable habitat for GP was estimated using a maximum entropy approach relying on occurrence points and comparisons between predictor variable values at presence localities and those at randomly selected background sites using the software MaxEnt version 3.4.4 (Phillips et al., 2006). MaxEnt is one of the most robust approaches based on a machine-learning process that predicts the presence of a species in a geographic space based on the presence-only occurrence points of the species without considering absence points. To overcome the problem of absence points which are necessary to model a species distribution, MaxEnt creates and randomly selects false absence points (background data) by considering the species to have the same likelihood of occurring across the study area (Lahoz - Monfort et al., 2014; Merow et al., 2013; Phillips and Dudík, 2008). A few limitations of the MaxEnt approach have been discussed, among which are the occurrence sampling bias and the use of false absence points instead of true absence points (Elith et al., 2011; Kramer-Schadt et al., 2013; Phillips and Dudík, 2008; Radosavljevic and Anderson, 2014). Despite these limitations, MaxEnt has many advantages such as the use of few occurrence points to yield good results and the prevention of model over-fitting (Mohammadi et al., 2019; Phillips and Dudík, 2008; Spiers et al., 2018).

Since MaxEnt modeling is a machine learning process which simulates a known real model with potential complexity based on a certain algorithm, its accuracy cannot be determined with precision, thus requiring preventative measures to be taken to reduce model over-fitting (Yan et al., 2021). Preventing over-fitting can then be done by wisely selecting parameters used to set the program. For example, an optimal model might be selected by setting the appropriate regularization multiplier (RM) and the corresponding feature combination (FC) (Phillips et al., 2006; Yan et al., 2021). MaxEnt provide five feature modes (Linear (L), quadratic (Q), product (P), hinge (H), and threshold (T)) which can be used alone or in combination depending on the sample size (Elith et al., 2011). The L feature is always running, the Q feature starts to run with at least 10 occurrences, the H function requires a minimum of 15 occurrences, and the P and T features require > 80 samples (Elith et al., 2011; Yan et al., 2021). Although default MaxEnt settings of the RM are based on 226 species over 6 regions, many studies have shown that it is necessary to select an individual regularization multiplier according to the species of interest and the data structures (Phillips and Dudík, 2008; Elith et al., 2011; Muscarella et al., 2014). The regularization multiplier can affect how focused the output distribution is, with a smaller RM value resulting in a localized output distribution that fits the given occurrence records well, but is vulnerable to over-fitting, while a larger RM value will produce a prediction that can be applied more widely (Merow et al., 2013; Zhu et al., 2018; Yan et al., 2021).

We initially used the default settings of MaxEnt, but set the output format to logistic, the maximum number of iterations to 1000,

LQHP feature types (since our sample size was greater than 80), and a 20-fold random cross-validation to estimate errors around fitted functions. For the RM, we used a step-by-step approach by successively running models with different RM values (0.5, 1.0, 1.5, 2.0, 2.5 and 3.0) to constrain MaxEnt, and prevent over-fitting of the models (Phillips et al., 2008, Breiner et al., 2015). The individual contribution of environmental predictors was assessed using the jackknife test (Pearson et al., 2007; Thorn et al., 2009), while we used the AUC (which is directly proportional to the accuracy of the model prediction) to assess the predictive power of our modeling process (Fielding and Bell, 1997b; Marmion et al., 2009; Muscarella et al., 2014; Yan et al., 2021). The AUC is generally between 0 and 1 and values of AUC greater than 0.9 were considered as excellent, 0.8 − 0.9 as very good, 0.7–0.8 as good, 0.6–0.7 as fair, and values $\leq$ 0.6 were considered poor (Araújo et al., 2005; Duan et al., 2014).

Prior to running the models, vegetation types were grouped as follow: dense forests (gallery forests, closed undergrowth mixed forests, and marshes), savannah (wooded and shrub) and ecotone (pioneer forests), based on land cover data available for the area. The predicted habitat suitability for GP was grouped into four classes: 0.0–0.25 (highly unsuitable habitat), 0.25–0.5 (unsuitable habitat), 0.50–0.75 (suitable habitat), 0.75–1 (highly suitable habitat); (Campos et al., 2015; Morris et al., 2016). We then overlaid the raster file obtained from the MaxEnt output onto the study site and calculated the total number of cells of each category of habitat suitability within each vegetation type using the raster calculator in ArcGIS 10.5 (Thapa et al., 2018).

3. Results

3.1. Model performance and contribution of environmental variables

A total of 234 burrow occurrences were used to model suitable habitats of GP in our study area, 95% of which were used for training and 5% for testing. Of the 28 variables selected for modelling GP habitat suitability, 11 variables whose correlation coefficient value was $> |0.7|$ were excluded prior to analysis (Supplemental Material 1). Variables that were used in the final model are shown in Table 1.

Estimates of the receiver operating characteristic (ROC) showed that the AUC for the replicates ran were 0.768 $\pm$ 0.043, which revealed a good level of accuracy in the prediction of the model. The jackknife test of the variable's contribution to the model showed

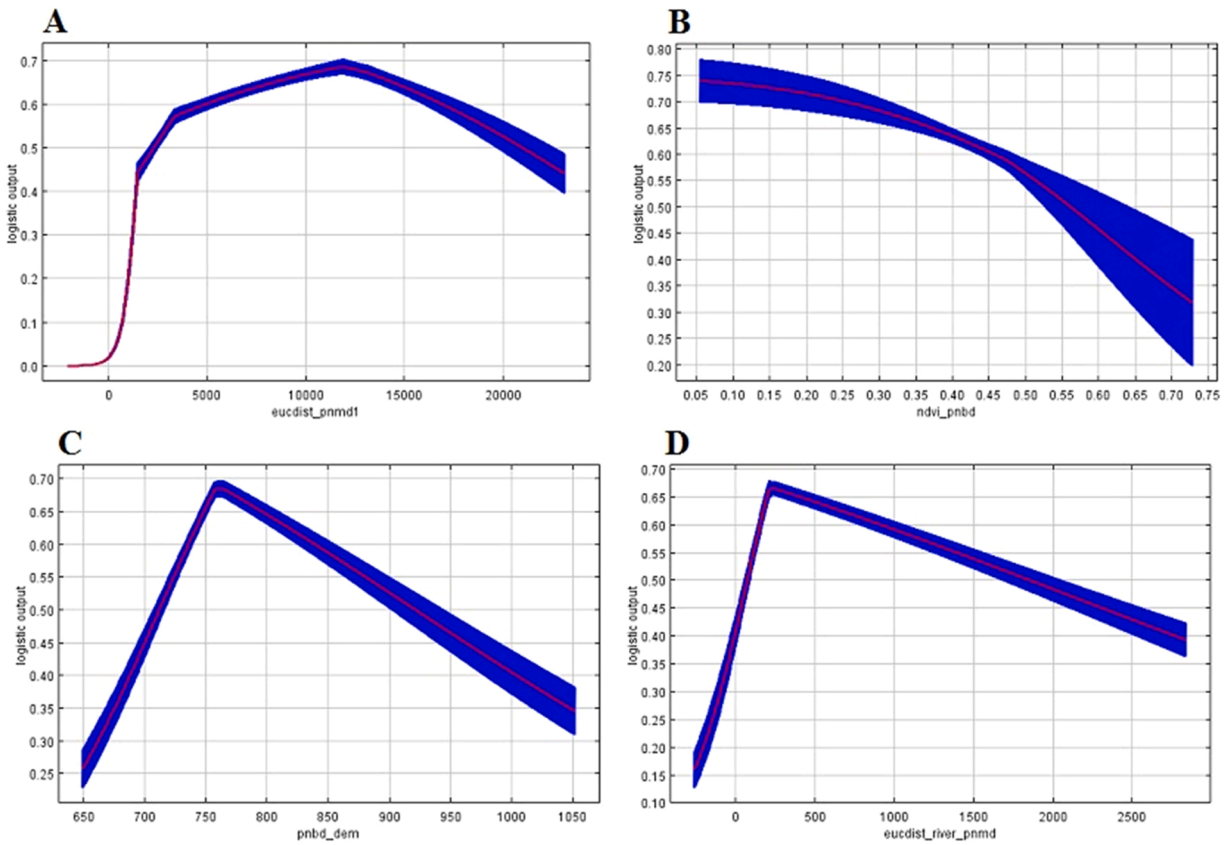


Fig. 2. Response curves (red line) and their standard deviations (blue shade) showing the effects of A) Euclidian distance to park's boundaries (euclid_pnmd1), B) Normalized difference vegetation index (ndvi_pnbd), C) Elevation (pnbd_dem), and D) Euclidian distance to the nearest river (Euclid_river_pnmd) on the predicted habitat suitability for giant pangolins (*Smutsia* gigantea) of giant pangolin burrows in the study area.

that, among the 17 variables used to train the model, Euclidian distance to MDNP's boundaries, NDVI, elevation, Euclidian distance to the nearest river, water pH, and the concentration of coarse fragments in the soil were the environmental variables that contributed the most to the model (>5% contribution; Table 1).

3.2. Response of habitat suitability to environmental variables

Our model predicted suitability for GP burrows between 2.4 km and 23 km from the park's boundaries, with a peak at 12 km from the park's borders (Fig. 2A. Giant pangolins preferred more open habitats (NDVI values of 0.06–0.57), with burrow habitat suitability predicted to decrease with an increase in NDVI value (indicating increasingly forested habitats; Fig. 2B). The model predicted the entire elevational range present at our study site (650–1050 m a.s.l.) to be suitable for GP burrows, with a peak around 760 m a.s.l. (Fig. 2C). Suitable areas for GP burrows were predicted to occur within 100–2000 m from rivers, with a peak around 300 m from rivers (Fig. 2D).

Predicted suitable pH values ranged between 5.252 and 5.52, with the predicted most suitable areas for GP burrows observed when the pH value was 5.35 (Supplemental Material 2 A), suggesting that GPs prefer to burrow in acidic soils. Finally, suitable habitats were predicted for coarse fragment concentration values between 110 and 210 cm^3/dm^3, and the most suitable habitats were observed for concentration values of 155 cm^3/dm^3 (Supplemental Material 2B).

3.3. Prediction of giant pangolin habitat suitability

The study site (MDNP) used to predict the habitat suitability for GP burrows comprised of moderate to dense forests (gallery forests, closed undergrowth mixed forests and marshes; 60.32%), savannah (33.18%) and finally ecotone (6.5%). Predicted suitable habitat for GP burrows was patchily distributed across the study area (Fig. 1), and only 1% of the study area could be considered as highly suitable for GP burrow placement, while 19.24% was predicted to be suitable, 40.53% as unsuitable, and finally 39.23% of the area was predicted to be very unsuitable.

4. Discussion

Giant pangolins are one of the least studied species of the order Pholidota, rendering knowledge about their ecology very scarce (Hoffmann et al., 2020). Our study aimed to contribute to the enhancement of ecological knowledge about GPs by investigating variables affecting the distribution of GP burrows and determining the habitat suitability of GP within a forest-savannah mosaic area of Cameroon. Our modelling approach based on maximum entropy (Phillips et al., 2006) enabled us to better understand how environmental variables shape the distribution of GPs and affect their predicted habitat suitability. Overall, our results suggest that modelling habitat suitability of species can be an approach that conservationists and wildlife managers can take advantage of, especially when it comes to targeting areas where conservation actions are mostly needed under limited resources.

4.1. Relationships between response variables and giant pangolin habitat suitability

Among the 17 environmental variables retained for the model, Euclidian distance to the MDNP's boundaries (EDPB) and Normalized Difference Vegetation Index (NDVI) were the major predictors of GP habitat suitability in our study area, while elevation, Euclidian distance to river (EDR), and possibly water pH and the concentration of coarse fragments in the soil were also found to be predictors to a lesser degree. The distance to the MDNP's boundaries was the most important of these variables, with suitable habitat for GP burrow placement being observed between 2,500 m and 24,000 m. This is contrary to findings in Nepal (Shrestha et al., 2021), where no significant difference between pangolin burrow distribution and distance to a park's boundaries, which can be an indicator of human pressure, was found. Park boundaries are typically closer to human settlements, and therefore often have higher levels of anthropogenic activities, as it is the case in our study site. The apparently unsuitable habitats observed from 0 to 2,500 m from the MDNP's boundaries might be explained by anthropogenic activities carried out around the park. Based on the management plan of MDNP, there is a buffer zone of approximately 6 km from the villages to the park's boundaries within which local people have the right to carry out their daily activities, including farming and hunting (MINFOF, 2007). These anthropogenic activities may disturb GP habitat and behaviour, possibly rendering it unsuitable for GP. Therefore, suitable habitats observed between 2,500 and 23,000 m from the park's boundaries might be due to the edge effect on GP, which has been shown in protected areas to negatively affect some resident wildlife populations (Woodroffe and Ginsberg, 1998), and especially pangolins (Boakye et al., 2016). Beyond 23,000 m, we observed a decrease in habitat suitability, a situation which may be explained by the habitat change from mosaic forest-savannah to dense forest or because we were approaching the limits of our selected study area It would be worth investigating habitat suitability of GPs beyond the limits of our study site to be able to make a clear comparison.

Vegetation structure (here measured using NDVI) has been recognised to affect species distributions and dynamics (Pettorelli et al., 2011), and we found it to be the second most important predictor of GP burrow habitat suitability. Predicted suitable habitats were obtained for NDVI values between 0.06 and 0.57, suggesting that GPs prefer habitat with low to moderate vegetation cover densities. Although they have different ecologies to GP, this is similar to the results obtained for Chinese and Indian pangolins, whose abundance was mainly reported in areas with low to moderate canopy covers (Acharya et al., 2021; Suwal et al., 2020). Giant pangolins are known to inhabit primary and secondary forests, savannah and forest–savannah mosaic habitats of Central, West, and East Africa (Hoffmann et al., 2020; Kingdon, 2015; Nixon et al., 2019). Our study area is a mosaic of forest and savannah, with canopy cover varying from

open to closed. These areas may be preferred by the species because of the high abundance of ants and termites, shown to be important for Temminck's pangolin (*Smutsia temminckii*); (Swart et al., 1999; Pietersen et al., 2016; Panaino et al., 2022), and the ease of digging in such habitats (Hoffmann et al., 2020; Nixon et al., 2019). In addition, aardvark and GP are considered to be ecologically similar species as they share the same habitat types, both feed on ants and termites, and dig burrows in which to rest, with aardvark generally using their burrows for a relatively short period of time, after which time they can be occupied by GP (Hoffmann et al., 2020; Kingdon, 2015). Despite potential direct and indirect interactions between the two species (Morin et al., 2020), it is thought that GP may sometimes use abandoned aardvark burrows for resting (Hoffmann et al., 2020). The correlates of this behavior remain unclear, and it would be worth investigating the interactions between the two species to better understand their ecological interactions for improved planning of conservation actions.

Elevation was the third most important variable predicting the distribution of GP. Similar results were obtained by Khwaja et al. (2019). The same was also observed for the Indian pangolin with elevation being the major variable affecting the species' presence (Dorji et al., 2020; Waseem et al., 2020). The predicted suitable elevation range (710–940 m a.s.l.) falls in the GP species elevation range, which is recognized to vary from slightly above sea level to more than 2,200 m a.s.l. (Hoffmann et al., 2020; Nixon et al., 2019). However, beyond 940 m a.s.l., predicted GP habitat was unsuitable, suggesting that GP would not prefer higher elevation as was observed by Khwaja et al. (2019) for GP occupancy which also decreased with increasing elevation. This differs from results obtained for Indian pangolin whose highest predicted habitat suitability was found at elevations ranging between 1,450 and 1,600 m a.s.l. (Acharya et al., 2021). The apparent unsuitability of such elevations for GP might be explained by the scarcity of permanent water sources at such elevations, as the species is considered to prefer living near permanent water sources (Hoffmann et al., 2020; Nixon et al., 2019). The low suitability of habitat observed at higher elevation for GPs in our study area might also be due to the fact that, at higher elevation, soil was typically rocky, making it hard to dig, thus potentially limiting GP activity.

Euclidian distance to the nearest river was the fourth most important variable contributing to GP burrow occurrence, with the species showing a preference for areas closer to rivers (Fig. 3).

Though this variable contributed only 6.6% to model performance, it might explain observations made during field work, where occurrence of GP decreased with increasing distance to the nearest river. This also supports the notion that the species prefers living near permanent water sources (Hoffmann et al., 2020; Nixon et al., 2019), as was also reported for the Chinese pangolin (Chao et al., 2020), and GP occupancy (Khwaja et al., 2019). In our study, higher predicted habitat suitability was recorded for distances less than 300 m from rivers. This further supports the results of Khwaja et al. (2019) who found a similar trend for GP occupancy, with the highest occupancy being observed for a mean distance from the river of 1.9 km. This may be due to the habitat preference of the species, which prefers mosaic habitats comprising lowland tropical moist and swamp forests (Hoffmann et al., 2020; Nixon et al., 2019). In our study site, high variability of habitat types is observed as one moves away from the river, with a succession of gallery forest and transition habitat types which are rich in resources and have soil suitable for digging both feeding and resting burrows, followed by savannah and dense forests. It is important however to highlight that, as distance to the nearest river was a minor contributing variable to model performance it is possible that these results may be more incidental than explanatory.

Water pH and coarse fragments in the soil also contributed to model performance to a lesser degree. Giant pangolins preferred slightly acidic soil, which may be linked to prey availability. For example, soil pH and type, as well as nutrient availability, are major correlates of ant and termite abundance (Davies et al., 2003; Mugerwa et al., 2011; Roisin and Leponce, 2004). Acidic soils with very low pH have limited nutrients necessary for plant establishment, leading to limited availability of adequate food resources which constrain the survival of termites and ground dwelling ants (Chao et al., 2020; Irshad et al., 2015; Mugerwa et al., 2011; Jacquemin et al., 2012; Staab et al., 2014), thus limit the availability of prey which is a correlate of GP distribution (Hoffmann et al., 2020). Giant



Fig. 3. : A camera-trap photo of a giant pangolin (*Smutsia gigantea*) taken early in the morning in a gallery forest near a river in MDNP (Credit: Alain Delon).

pangolins preferred soils containing moderate to high quantities of coarse fragments. These coarse fragments are important for soil and water management, and presence of higher amounts at the subsurface may improve drainage and aeration, thus increasing the biodiversity of the soil (Khetdan et al., 2017; Zhang et al., 2019), and possibly improving the ease of digging. The diet of GP, consisting primarily of ground-dwelling ant and termite species (Difouo et al., 2020), may explain the apparent preference of GP for areas with such coarse fragments soil concentration for foraging. Given their minor contributions to model performance, it is possible that these results are more incidental than explanatory, and it will be worth investigating in details the effects of these two variables GP's burrow creation.

5. Conclusion and recommendations

Information on the ecology of GP remains scarce over its distribution range, thus preventing their effective conservation planning and management. Despite the caveats of this study, our results clearly showed that species distribution modelling can be used as an important tool to better understand species distribution patterns, and environmental variables responsible for such patterns. We found that habitat suitability of GP burrows was patchily distributed within dense forests, ecotone and savannah habitat types of MDNP, with 20% of the study area being predicted as suitable or highly suitable for the species. This corroborates findings by other authors about GP inhabiting these same habitat types (Hoffmann et al., 2020; Mouafo, 2018; Nixon et al., 2019; Sandri et al., 2022). However, we recommend carrying out similar studies in dense forests and savannah and comparing the findings with ours. Our model predicted GP distribution to be highly affected by the distance to MDNP's boundaries and vegetation density, and to a lesser extent by elevation, distance to the nearest river, water pH, and the concentration of coarse fragments in the soil. The decrease in habitat suitability close to MDNP's edge is an indication that GP distribution is influenced by human activities and edge effects. Giant pangolin distribution is determined by a combination of both abiotic and biotic factors and those identified in this study may be just a small portion of the ecological factors affecting GP distribution in our study area. This study represents only a small part of what is needed to ensure long-term conservation of GP within the MDNP landscape. To better conserve GP in MDNP, we recommend the following research activities:

1) Carry out field surveys to estimate GP abundance within both suitable and unsuitable predicted habitats as a validation process of our model;
2) Carry out the same study in the undisturbed core zone of the park and compare the results with our findings from the disturbed area;
3) Determine the relationship between GP and aardvark habitat suitability as the two species have similar ecologies, and often share the same habitats.

To support GP conservation actions at MDNP, we additionally recommend that the following actions be implemented: 1) involve local communities bordering the study in the management and conservation process; and, 2) raise awareness in local communities on a regular basis about the importance of GP in the ecosystem and the necessity to preserve them.

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.

Data availability

Data will be made available on request.

Acknowledgements

We thank the Cameroonian Ministry of Forests and Wildlife, Mbam et Djerem National Park staff and Agriculture and Bio-Conservation Organization for Youth Empowerment and Rural Development (ABOYERD) for permission to conduct this study and assistance during field work. This work was supported by the Mohamed bin Zayed Species Conservation Fund [Grant ID: 190520489], Chicago Board of Trade, Chicago Zoological Society, and Idea Wild. We acknowledge SMACON Nigeria and the *Mecistops* Project whose assistance through the West African Mammals Fellowship Program (WAMF) permitted us to improve on the quality of this manuscript. We also acknowledge Edgar Désiré Ambassa Ongono, Tsetagho Guilain, Iya Paul, Kengne Paulin, Ndore Ghislain and the village chiefs and local communities for their collaboration during the course of this work.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02395.

References

Acharya, S., Sharma, H.P., Bhattarai, R., Poudyal, B., Sharma, S., Upadhaya, S., 2021. Distribution and habitat preferences of the Chinese Pangolin Manis pentadactyla (Mammalia: Manidae) in the mid-hills of Nepal. J. Threat. Taxa 13 (8), 18959–18966.

Akrim, F., Mahmood, T., Hussain, R., Qasim, S., Zangi, I.D., 2017. Distribution pattern, population estimation and threats to the Indian Pangolin Manis crassicaudata (Mammalia: Pholidota: Manidae) in and around Pir Lasura National Park, Azad Jammu & Kashmir, Pakistan. J. Threat. Taxa 9 (3), 9920–9927. https://doi.org/10.11609/jott.2914.9.3.9920-9927.

Amin, R., Wacher, T., Fankem, O., Bruce, T., Gilbert, O.N., Ndimbe, M.S., Fowler, A., 2023. Giant pangolin and white-bellied pangolin observations from a World Heritage site. Mammalia. https://doi.org/10.1515/mammalia-2021-0173.

Anderson, R.P., Raza, A., 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. J. Biogeogr. 37 (7), 1378–1393. https://doi.org/10.1111/j.1365-2699.2010.02290.x.

Araújo, M.B., Pearson, R.G., Thuiller, W., Erhard, M., 2005. Validation of species–climate impact models under climate change. Glob. Change Biol. 11 (9), 1504–1513.

Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecol. Model. 200 (1–2), 1–19.

Austin, M., Meyers, J., 1996. Current approaches to modelling the environmental niche of eucalypts: implication for management of forest biodiversity. For. Ecol. Manag. 85 (1–3), 95–106.

Benton, M.J., 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. Science 323 (5915), 728–732. https://doi.org/10.1126/science.1157719.

Boakye, M.K., Kotzé, A., Dalton, D.L., Jansen, R., 2016. Unravelling the pangolin bushmeat commodity chain and the extent of trade in Ghana. Hum. Ecol. 44 (2), 257–264.

Bobo, K.S., Weladji, R.B., 2011. Wildlife and land use conflicts in the Mbam and Djerem conservation region. In: Human Dimensions of Wildlife, 16. status and mitigation measures,, Cameroon, pp. 445–457.

Breiner, F.T., Guisan, A., Bergamini, A., Nobis, M.P., 2015. Overcoming limitations of modelling rare species by using ensembles of small models. Methods Ecol. Evol. 6, 1210–1218 https:// doi.org/10.1111/2041-210X.12403.

Brotons, L., 2014. Species distribution models and impact factor growth in environmental journals: methodological fashion or the attraction of global change science. PLoS ONE 9 (11), e111996.

Brown, J., Lomolino, M., 1998. Biogeography. Sinauer Assoc. *Inc., Sunderland, Ma.*

Brown, J.L., 2014. SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. Methods Ecol. Evol. 5, 694–700. https://doi.org/10.1111/2041-210X.12200.

Bruce, T., Kamta, R., Mbobda, R.B.T., Kanto, S.T., Djibrilla, D., Moses, I., Deblauwe, V., Njabo, K., Lebreton, M., Ndjassi, C., Barichievy, C., Olson, D., 2018. Locating giant ground pangolins (Smutsia gigantea) using camera traps on burrows in the dja biosphere reserve, Cameroon. Trop. Conserv. Sci. *11*. https://doi.org/10.1177/1940082917749224.

Campos, V.E., Gatica, G., Bellis, L.M., 2015. Remote sensing variables as predictors of habitat suitability of the viscacha rat (Octomys mimax), a rock-dwelling mammal living in a desert environment. Mammal. Res. 60 (2), 117–126. https://doi.org/10.1007/s13364-015-0215-3.

Carpenter, G., Gillison, A., Winter, J., 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. Biodivers. Conserv. 2 (6), 667–680.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1 (5), e1400253.

Challender, D., Waterman, C., Baillie, J., 2014. Scaling up pangolin conservation. IUCN SSC pangolin specialist group conservation action plan. Pap. Presente Zool. Soc. Lond.

Chao, J.-T., Li, H.-F., Lin, C.-C., 2020. Chapter 3 - The role of pangolins in ecosystems. In: Challender, D.W.S., Nash, H.C., Waterman, C. (Eds.), Pangolins. Academic Press, pp. 43–48.

Davies, R.G., Hernández, L.M., Eggleton, P., Didham, R.K., Fagan, L.L., Winchester, N.N., 2003. Environmental and spatial influences upon species composition of a termite assemblage across neotropical forest islands. J. Trop. Ecol. 19 (5), 509–524.

Difouo, G.F., Simo, F.T., Kekeunou, S., Titti Ebangue, G., Ndoh, L.G., Olson, D., 2020. Ant and termite prey of the giant pangolin Smutsia gigantea Illiger, 1815 in forest–savannah mosaics of Cameroon. Afr. J. Ecol. https://doi.org/10.1111/aje.12829.

Dorji, D., Jambay, Chong, J.L., Dorji, T., 2020. Habitat preference and current distribution of Chinese Pangolin (Manis pentadactyla L. 1758) in Dorokha Dungkhag, Samtse, southern Bhutan. J. Threat. Taxa 12 (11), 16424–16433. https://doi.org/10.11609/jott.5839.12.11.16424-16433.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46.

Duan, R.-Y., Kong, X.-Q., Huang, M.-Y., Fan, W.-Y., Wang, Z.-G., 2014. The predictive performance and stability of six species distribution models. PLoS ONE 9 (11), e112764.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol., Evol., Syst. 40, 677–697.

Elith, J., Phillips, S., Hastie, T., 2011. In: Dudik, M., Chee, Y.E., Yates, C.J. (Eds.), A statistical explanation of MaxEnt for ecologists, 17. Diversity and Distributions, pp. 43–57.

Ferrier, S., Watson, G., Pearce, J., Drielsma, M., 2002. Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. I. Species-level modelling. Biodivers. Conserv. 11 (12), 2275–2307.

Fielding, A.H., Bell, J.F., 1997a. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 24 (1), 38–49.

Fielding, A.H., Bell, J.F., 1997b. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environ. Conserv. 38–49.

Fitzgerald, M., Coulson, R., Lawing, A.M., Matsuzawa, T., Koops, K., 2018. Modeling habitat suitability for chimpanzees (*Pan troglodytes verus*) in the Greater Nimba Landscape, Guinea, West Africa. Primates 59 (4), 361–375. https://doi.org/10.1007/s10329-018-0657-8.

Franklin, J., 2010. Moving beyond static species distribution models in support of conservation biogeography. Divers. Distrib. 16 (3), 321–330.

Franklin, J., 2013. Species distribution models in conservation biogeography: developments and challenges. Wiley Online Library.

Funk, V.A., Richardson, K., 2002. Systematic data in biodiversity studies: use it or lose it. Syst. Biol. 51 (2), 303–316.

Graham, C.H., Moritz, C., Williams, S.E., 2006. Habitat history improves prediction of biodiversity in rainforest fauna. Proc. Natl. Acad. Sci. 103 (3), 632–636.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R., Wintle, B.A., 2015. Is my species distribution model fit for purpose? Matching data and models to applications. Glob. Ecol. Biogeogr. 24 (3), 276–292.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8 (9), 993–1009.

Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I., Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., 2013. Predicting species distributions for conservation decisions. Ecol. Lett. 16 (12), 1424–1435.

Hengl, T., de Jesus, Mendes, Heuvelink, J., Ruiperez Gonzalez, G.B., Kilibarda, M., Blagotić, M., Shangguan, A., Wright, W., Geng, X, M.N., Bauer-Marschallinger, B., 2017. SoilGrids250m: Global gridded soil information based on machine learning. PLoS ONE 12 (2), e0169748.

Hoffmann, M., Nixon, S., Alempijevic, D., Ayebare, S., Bruce, T., Davenport, T.R., Hart, J., Hart, T., Hega, M., Maisels, F., 2020. Giant pangolin *Smutsia gigantea* (Illiger, 1815) *Pangolins*. Elsevier,, pp. 157–173.

Ichu, I., Nyumu, J., Moumbolou, C., Nchembi, F., Olson, D., 2017. Testing the efficacy of field surveys and local knowledge for assessing the status and threats to three species of pangolins in Cameroon. *A Report of the MENTOR-POP (Progress on Pangolins) Fellowship Program*. Zool. Soc. Lond. Cameroon, Yaoundé, Cameroon.

Ingram, D.J., Cronin, D.T., Challender, D.W., Venditti, D.M., Gonder, M.K., 2019. Characterising trafficking and trade of pangolins in the Gulf of Guinea. Glob. Ecol. Conserv. 17, e00576.

IPBES. (2019). UN Report: Nature's Dangerous Decline 'Unprecedented'; Species Extinction Rates 'Accelerating' – United Nations Sustainable Development.: United Nations. https://www.un.org/sustainabledevelopment/blog/2019/05/nature-decline-unprecedentedreport/.
Irshad, N., Mahmood, T., Hussain, R., Nadeem, M.S., 2015. Distribution, abundance and diet of the Indian pangolin (*Manis crassicaudata*). Anim. Biol. 65 (1), 57–71. https://doi.org/10.1163/15707563-00002462.
Jacquemin, J., Drouet, T., Delsinne, T., Roisin, Y., Leponce, M., 2012. Soil properties only weakly affect subterranean ant distribution at small spatial scales. Appl. Soil Ecol. 62, 163–169.
Karawita, H., Perera, P., Gunawardane, P., Dayawansa, N., 2018. Habitat preference and den characterization of Indian Pangolin (*Manis crassicaudata*) in a tropical lowland forested landscape of southwest Sri Lanka. PLoS ONE 13 (11). https://doi.org/10.1371/journal.pone.0206082.
Khetdan, C., Chittamart, N., Tawornpruek, S., Kongkaew, T., Onsamrarn, W., Garré, S., 2017. Influence of rock fragments on hydraulic properties of Ultisols in Ratchaburi Province, Thailand. Geoderma Reg. 10, 21–28.
Khwaja, H., Buchan, C., Wearn, O.R., Bahaa-el-din, L., Bantlin, D., Bernard, H., Bitariho, R., Bohm, T., Borah, J., Brodie, J., Chutipong, W., Preez, B.D., Ebang-Mbele, A., Edwards, S., Fairet, E., Frechette, J.L., Garside, A., Gibson, L., Giordano, A., Veeraswami Gopi, G., Granados, A., Gubbi, S., Harich, F., Haurez, B., Havmøller, R.W., Helmy, O., Isbell, L.A., Jenks, K., Kalle, R., Kamjing, A., Khamcha, D., Kiebou-Opepa, C., Kinnaird, M., Kruger, C., Laudisoit, A., Lynam, A., Macdonald, S.E., Mathai, J., Sienne, J.M., Meier, A., Mills, D., Mohd-Azlan, J., Nakashima, Y., Nash, H.C., Ngoprasert, D., Nguyen, A., O'Brien, T., Olson, D., Orbell, C., Poulsen, J., Ramesh, T., Reeder, D., Reyna, R., Rich, L.N., Rode-Margono, J., Rovero, F., Sheil, D., Shirley, M.H., Stratford, K., Sukumal, N., Suwanrat, S., Tantipisanuh, N., Tilker, A., Van Berkel, T., Van der Weyde, L.K., Varney, M., Weise, F., Wiesel, I., Wilting, A., Wong, S.T., Waterman, C., Challender, D.W.S., 2019. Pangolins in global camera trap data: implications for ecological monitoring. Glob. Ecol. Conserv. 20, e00769 https://doi.org/10.1016/j.gecco.2019.e00769.
Kingdon, J., 2015. The Kingdon field guide to African mammals. Bloomsbury Publishing.
Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Distrib. 19 (11), 1366–1379.
Lahoz - Monfort, J. J., Guillera - Arroita, G., & Wintle, B. A, 2014. Imperfect detection impacts the performance of species distribution models. Glob. Ecol. Biogeogr. 23 (4), 504–515.
Larson, M.A., Thompson III, F.R., Millspaugh, J.J., Dijak, W.D., Shifley, S.R., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. Ecol. Model. 180 (1), 103–118.
Lewis, J.S., Farnsworth, M.L., Burdett, C.L., Theobald, D.M., Gray, M., Miller, R.S., 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Sci. Rep. 7 (1), 44152. https://doi.org/10.1038/srep44152.
Mahmood, T., Irshad, N., Hussain, R., 2014. Habitat preference and population estimates of Indian pangolin (*Manis crassicaudata*) in district Chakwal of Potohar Plateau, Pakistan. Russ. J. Ecol. 45 (1), 70–75. https://doi.org/10.1134/S1067413614010081.
Maisels, F., Fotso, R.C., Hoyle, D., 2000. Mbam Djerem National Park. Unpublished report: NYZS/WCSCameroon. Conservation status, Large mammals and human impact, Cameroon.
Malakoutikhah, S., Fakheran, S., Hemami, M.R., Tarkesh, M., Senn, J., 2020. Assessing future distribution, suitability of corridors and efficiency of protected areas to conserve vulnerable ungulates under climate change. Divers. Distrib. 26 (10), 1383–1396.
Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Divers. Distrib. 15, 59–69 https:// doi.org/10.1111/j.1472-4642.2008.00491.x.
Martinez-Meyer, E., Peterson, A.T., Servín, J.I., Kiff, L.F., 2006. Ecological niche modelling and prioritizing areas for species reintroductions. ORYX 40 (4), 411–418.
Merow, C., Smith, M.J., Silander Jr, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36 (10), 1058–1069.
MINFOF (2007). Plan d'aménagement du Parc National de Mbam et Djerem et sa zone périphérique 2007–2011. 127p.
Mitchard, E.T., Saatchi, S.S., Gerard, F., Lewis, S., Meir, P., 2009. Measuring woody encroachment along a forest–savanna boundary in Central Africa. Earth Interact. 13 (8), 1–29.
Mohammadi, S., Ebrahimi, E., Moghadam, M.S., Bosso, L., 2019. Modelling current and future potential distributions of two desert jerboas under climate change in Iran. Ecol. Inform. 52, 7–13.
Morin, D.J., Challender, D.W.S., Ichu, I.G., Ingram, D.J., Nash, H.C., Panaino, W., Panjang, E., Sun, N.C.-M., Willcox, D., 2020. Chapter 35 - Developing robust ecological monitoring methodologies for pangolin conservation. In: Challender, D.W.S., Nash, H.C., Waterman, C. (Eds.), Pangolins. Academic Press, pp. 545–558.
Morris, L.R., Proffitt, K.M., Blackburn, J.K., 2016. Mapping resource selection functions in wildlife studies: concerns and recommendations. Appl. Geogr. 76, 173–183. https://doi.org/10.1016/j.apgeog.2016.09.025.
Mugerwa, S., Nyangito, M., Mpairwe, D., Nderitu, J., 2011. Effect of biotic and abiotic factors on composition and foraging intensity of subterranean termites. Afr. J. Environ. Sci. Technol. 5 (8), 579–588.
Muscarella, R., Galante, P.J., Soley, -, Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M., Anderson, R.P., 2014. ENM eval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol. Evol. 5 (11), 1198–1205.
Myneni, R.B., Hall, F.G., Sellers, P.J., Marshak, A.L., 1995. The interpretation of spectral vegetation indexes. IEEE Trans. Geosci. Remote Sens. 33 (2), 481–486.
Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37 (2), 191–203.
Nash, H.C., Lee, P.B., Lim, N.T.L., Luz, S., Li, C., Chung, Y.F., Olsson, A., Boopal, A., Strange, B.C.N., Rao, M., 2020. Chapter 26 - The Sunda pangolin in Singapore: a multi-stakeholder approach to research and conservation. In: Challender, D.W.S., Nash, H.C., Waterman, C. (Eds.), Pangolins. Academic Press, pp. 411–425.
Newbold, T., 2010. Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. Prog. Phys. Geogr. 34 (1), 3–22.
Newton, P., Van Thai, N., Roberton, S., Bell, D., 2008. Pangolins in peril: using local hunters' knowledge to conserve elusive species in Vietnam. Endanger. Species Res. 6 (1), 41–53. https://doi.org/10.3354/esr00127.
Nixon, S., Pietersen, D., Challender, D., Hoffmann, M., Godwill Ichu, I., Bruce, T., Ingram, D.J., Matthews, N., Shirley, M.H., 2019. Smutsia Gigante IUCN Red. List Threat. Species doi: 2019: e.T12762A123584478.
Owens, I.P., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc. Natl. Acad. Sci. 97 (22), 12144–12148.
Panaino, W., Parrini, F., Phakoago, M.V., Smith, D., van Dyk, G., Fuller, A., 2022. Do seasonal dietary shifts by Temminck's pangolins compensate for winter resource scarcity in a semi-arid environment? J. Arid Environ. 197, 104676.
Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34 (1), 102–117.
Perera, P., Karawita, H., 2020. An update of distribution, habitats and conservation status of the Indian pangolin (*Manis crassicaudata*) in Sri Lanka. Glob. Ecol. Conserv. 21, e00799 https://doi.org/10.1016/j.gecco.2019.e00799.
Peterman, W.E., Crawford, J.A., Kuhns, A.R., 2013. Using species distribution and occupancy modeling to guide survey efforts and assess species status. J. Nat. Conserv. 21 (2), 114–121. https://doi.org/10.1016/j.jnc.2012.11.005.
Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol. Evol. 20 (9), 503–510.
Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M., Kausrud, K., 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Clim. Res. 46 (1), 15–27.
Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31 (2), 161–175.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190 (3–4), 231–259.

Pietersen, D.W., Symes, C.T., Woodborne, S., McKechnie, A.E., Jansen, R., 2016. Diet and prey selectivity of the specialist myrmecophage, Temminck's ground pangolin. J. Zool. 298 (3), 198–208.
Pietersen, D.W., Fisher, J.T., Glennon, K.L., Murray, K.A., Parrini, F., 2021. Distribution of Temminck's pangolin (*Smutsia temminckii*) in South Africa, with evaluation of questionable historical and contemporary occurrence records. Afr. J. Ecol. 59 (3), 597–604.
Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. Science 269 (5222), 347–350.
Pye, N., 1985. Veg. Afr.: A Descr. Mem. Acco. UNESCO/AETFAT/UNSO Veg. Map Afr.: Jstor.
Radosavljevic, A., Anderson, R.P., 2014. Making better Maxent models of species distributions: complexity, overfitting and evaluation. J. Biogeogr. 41 (4), 629–643.
Redford, K.H., 1987. Ants and termites as food. Current mammalogy. Springer, pp. 349–399.
RGPH, 2005. Recensement Général de la Population et de l'Habitat du Cameroun 2005. Ministère de l'Economie, de la Planification et de l'Aménagement du Territoire. Yaoundé. Cameroon: BUCREP,.
Ricklefs, R.E., 2004. A comprehensive framework for global patterns in biodiversity. Ecol. Lett. 7 (1), 1–15.
Rodrigues, A.S., Brooks, T.M., Butchart, S.H., Chanson, J., Cox, N., Hoffmann, M., Stuart, S.N., 2014. Spatially explicit trends in the global conservation status of vertebrates. PLoS ONE 9 (11), e113934.
Roisin, Y., Leponce, M., 2004. Characterizing termite assemblages in fragmented forests: a test case in the Argentinian Chaco. Austral Ecol. 29 (6), 637–646.
Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge University Press,.
Rouse Jr, J., Haas, R., Schell, J., Deering, D., 1973. *Pap. a 20.* Pap. Presente Third Earth Resour. Technol. Satell. -1 Symp. .: Sect. Ab. Tech. Present.
Running, S.W., 1990. Estimating terrestrial primary productivity by combining remote sensing and ecosystem simulation *Remote sensing of biosphere functioning.* Springer,, pp. 65–86.
Rushton, S., Ormerod, S.J., Kerby, G., 2004. New paradigms for modelling species distributions? J. Appl. Ecol. 41 (2), 193–200.
Sandri, T., Okell, C., Nixon, S., Matthews, N., Omengo, F., Mathenge, J., Ndambuki, S., Challender, D.W.S., Chepkwony, R., Omondi, P., Ngene, S., Cain, B., 2022. Three spatially separate records confirm the presence of and provide a range extension for the giant pangolin *Smutsia gigantea* in Kenya. Oryx 1–4. https://doi.org/10.1017/S0030605322000126.
Sharma, H.P., Belant, J.L., Swenson, J.E., 2014. Effects of livestock on occurrence of the Vulnerable red panda *Ailurus fulgens* in Rara National Park, Nepal. ORYX 48 (2), 228–231.
Sharma, H.P., Rimal, B., Zhang, M., Sharma, S., Poudyal, L.P., Maharjan, S., Kunwar, R., Kaspal, P., Bhandari, N., Baral, L., Dhakal, S., Tripathi, A., Karki, N., Khadki, B., Thapa, P., Acharya, B.K., Acharya, S., Baral, K., Katuwal, H.B., 2020. Potential distribution of the critically endangered Chinese pangolin (*Manis pentadactyla*) in different land covers of Nepal: Implications for conservation. Sustain. (Switz.) 12 (3). https://doi.org/10.3390/su12031282.
Shrestha, A., Bhattarai, S., Shrestha, B., Koju, N.P., 2021. Factors influencing the habitat choice of pangolins (*Manis* spp.) in low land of Nepal. Ecol. Evol. 11 (21), 14689–14696. https://doi.org/10.1002/ece3.8156.
Spiers, J.A., Oatham, M.P., Rostant, L.V., Farrell, A.D., 2018. Applying species distribution modelling to improving conservation based decisions: a gap analysis of Trinidad and Tobago's endemic vascular plants. Biodivers. Conserv. 27 (11), 2931–2949.
Staab, M., Schuldt, A., Assmann, T., KLEIN, A.M., 2014. Tree diversity promotes predator but not omnivore ants in a subtropical Chinese forest. Ecol. Entomol. 39 (5), 637–647.
Sun, S., Dou, H., Wei, S., Fang, Y., Long, Z., Wang, J., An, F., Xu, J., Xue, T., Qiu, H., 2021. A review of the engineering role of burrowing animals: implication of Chinese Pangolin as an ecosystem engineer. J. Zool. Res. 3 (3).
Suwal, T.L., Thapa, A., Gurung, S., Aryal, P.C., Basnet, H., Basnet, K., Shah, K.B., Thapa, S., Koirala, S., Dahal, S., Katuwal, H.B., Sharma, N., Jnawali, S.R., Khanal, K., Dhakal, M., Acharya, K.P., Ingram, D.J., Pei, K.J.C., 2020. Predicting the potential distribution and habitat variables associated with pangolins in Nepal. Glob. Ecol. Conserv. 23, e01049 https://doi.org/10.1016/j.gecco.2020.e01049.
Swart, J., Richardson, P., Ferguson, J., 1999. Ecological factors affecting the feeding behaviour of pangolins (Manis temminckii). J. Zool. 247 (3), 281–292.
Tédonzong, L.R.D., Willie, J., Makengveu, S.T., Lens, L., Tagg, N., 2020. Variation in behavioral traits of two frugivorous mammals may lead to differential responses to human disturbance. Ecol. Evol. 10 (8), 3798–3813.
Thapa, A., Wu, R., Hu, Y., Nie, Y., Singh, P.B., Khatiwada, J.R., Yan, L., Gu, X., Wei, F., 2018. Predicting the potential distribution of the endangered red panda across its entire range using MaxEnt modeling. Ecol. Evol. 8 (21), 10542–10554.
Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., 2004. Extinction risk from climate change. Nature 427 (6970), 145–148.
Thorn, J.S., Nijman, V., Smith, D., Nekaris, K., 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: *Nycticebus*). Divers. Distrib. 15 (2), 289–298.
Waseem, M., Khan, B., Mahmood, T., Hussain, H.S., Aziz, R., Akrim, F., Ahmad, T., Nazir, R., Hameed, S., Awan, M.N., 2020. Occupancy, habitat suitability and habitat preference of endangered indian pangolin (*Manis crassicaudata*) in Potohar Plateau and Azad Jammu and Kashmir, Pakistan. Glob. Ecol. Conserv. 23, e01135 https://doi.org/10.1016/j.gecco.2020.e01135.
Wiens, J.J., 2011. The niche, biogeography and species interactions. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366 (1576), 2336–2350. https://doi.org/10.1098/rstb.2011.0059.
Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14 (5), 763–773.
Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. Science 280 (5372), 2126–2128.
Yan, H., He, J., Xu, X., Yao, X., Wang, G., Tang, L., Feng, L., Zou, L., Gu, X., Qu, Y., Qu, L., 2021. Prediction of potentially suitable distributions of *Codonopsis pilosula* in China based on an optimized MaxEnt model. Front. Ecol. Evol. *9*. https://doi.org/10.3389/fevo.2021.773396.
Zellmer, A.J., Claisse, J.T., Williams, C.M., Schwab, S., Pondella, D.J., 2019. Predicting optimal sites for ecosystem restoration using stacked-species distribution modeling. Front. Mar. Sci. 6 (3) https://doi.org/10.3389/fmars.2019.00003.
Zhang, Y., Hartemink, A., Huang, J., 2019. Quantifying coarse fragments in soil samples using a digital camera. Eurasia Soil Sci. 52 (8), 954–962.
Zhu, G., Yuan, X., Fan, J., Wang, M., 2018. Effects of model parameters in MaxEnt modeling of ecological niche and geographic distribution: case study of the brown marmorated stink bug. Halyomorpha haly. J. Biosaf. 27 (2), 46–51.