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Article

# *Ecological Niche Modeling of Nuxia capitata and Phyllarthron madagascariensis: Delineating Bioclimatic Envelopes for Sustainable Forest Management in Madagascar*

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**Résumé**

*Nuxia capitata* Baker (Stilbaceae) et *Phyllarthron madagascariensis* K. Schum. (Bignoniaceae) constituent des ressources forestières endémiques de grande valeur à Madagascar, traditionnellement exploitées pour leurs propriétés médicinales et leur bois. Cependant, l'accélération des pressions anthropiques et la fragmentation de leur habitat menacent gravement leurs populations sauvages, freinant la transition vers une gestion durable des ressources. Cette étude utilise la modélisation de niche écologique par entropie maximale (MaxEnt) pour délimiter leurs enveloppes bioclimatiques actuelles, identifier les principaux facteurs environnementaux et évaluer l'efficacité de la conservation par le réseau national d'aires protégées (SAPM). Les modèles ont été calibrés à l'aide de données d'occurrence géoréférencées et de prédicteurs biophysiques non colinéaires filtrés. Les algorithmes générés ont démontré une précision prédictive exceptionnelle, avec des valeurs d'aire sous la courbe (AUC) de 0,951 pour N. *capitata* et de 0,919 pour P. *madagascariensis*. Les évaluations spatiales quantitatives indiquent que l'aire de répartition géographique totale favorable à **N. capitata** s'étend sur 76 188,85 km² (13,35 % du territoire national) et celle de P. *madagascariensis* sur 127 693,60 km² (22,38 %). Les analyses bioclimatiques révèlent que la distribution de *N. *capitata** est fortement contrainte par la température moyenne annuelle (75,6 % de la contribution), ce qui témoigne d'une grande affinité pour les écosystèmes frais d'altitude. À l'inverse, la distribution de P. *madagascariensis* est principalement régie par la saisonnalité des précipitations (43,4 % de la contribution), formant une bande latitudinale continue le long du biome de la forêt humide de l'est. Les superpositions spatiales démontrent que 31,81 % de la niche écologique de N. *capitata* et 36,36 % de l'aire de répartition de P. *madagascariensis* recoupent des aires protégées. Si les populations de la forêt tropicale de l'est sont relativement bien préservées, d'importantes lacunes en matière de protection subsistent dans les hautes terres centrales, notamment dans la région d'Analamanga. Il est urgent de renforcer les transferts de gestion forestière communautaires afin de sécuriser ces réservoirs génétiques fragmentés et de préserver les connaissances ethnobotaniques autochtones associées.

**Keywords:**
Modélisation de niche écologique, MaxEnt, *Nuxia capitata* Baker - *Phyllarthron madagascariensis* K. Schum

**Abstract**

*Nuxia capitata* Baker (Stilbaceae) and *Phyllarthron madagascariensis* K. Schum. (Bignoniaceae) represent high-value endemic forest resources in Madagascar, traditionally exploited for medicinal applications and timber. However, accelerating anthropogenic pressures and habitat fragmentation severely threaten their wild populations, hampering the transition toward sustainable resource management. This study leverages Maximum Entropy (MaxEnt) ecological niche modeling to delineate their contemporary bioclimatic envelopes, identify primary environmental drivers, and evaluate the conservation efficacy of the national Protected Area network (SAPM). Models were calibrated using primary georeferenced occurrence records and filtered, non-collinear biophysical predictors. The generated algorithms demonstrated exceptional predictive accuracy, yielding training Area Under the Curve (AUC) values of 0.951 for N. *capitata* and 0.919 for P. *madagascariensis*. Quantitative spatial assessments indicate that the total suitable geographic range encompasses 76,188.85 km² (13.35% of the national territory) for N. *capitata* and 127,693.60 km² (22.38%) for P. *madagascariensis*. Bioclimatic analyses reveal that the distribution of N. *capitata* is strictly constrained by annual mean temperature (75.6% contribution), showing a high affinity for cool highland ecosystems. Conversely, P. *madagascariensis* is primarily governed by precipitation seasonality (43.4% contribution), tracing a contiguous latitudinal belt along the eastern humid forest biome. Spatial overlays demonstrate that 31.81% of the N. *capitata* niche and 36.36% of the P. *madagascariensis* range intersect protected areas. While the eastern rainforest populations are relatively well-preserved, critical protection gaps exist in the central highlands, particularly within the Analamanga region. Strengthening community-based forest management transfers (VOI) is urgently recommended to secure these fragmented genetic reservoirs and preserve associated indigenous ethnobotanical knowledge.

**Keywords:**
Ecological niche modeling, MaxEnt, *Nuxia capitata* Baker - *Phyllarthron madagascariensis* K. Schum

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# 1. Introduction

Madagascar represents a global biodiversity hotspot of unparalleled ecological significance, characterized by exceptionally high levels of floral endemism (Havinga et *al*., 2024 ; Antonelli, 2022). The island's unique flora comprises approximately 14,000 vascular plant species, exhibiting an endemism rate approaching 90% (Madagascar Catalogue, 2020). Despite this rich evolutionary heritage, the unique botanical diversity of Madagascar faces severe, internationally recognized anthropogenic threats; extinction risk assessments conducted by the IUCN indicate that 35% (approximately 4,500 species) of the documented flora has been evaluated, revealing that nearly 60% of these taxa are currently threatened with extinction (GSPM, 2021). Consequently, identifying and preserving critical centers of plant diversity is imperative, particularly for habitats that harbor unique species assemblages and provide vital ecosystem services for human welfare (Randrianarivony et *al*., 2024 ; Myers, 2019). Although these endemic resources support a wide range of local socio-economic and utilitarian application contexts, their ecological dynamics and sustainable management frameworks remain fundamentally understudied (Randrianarivony et *al*., 2024).

To address these conservation gaps, this study investigates two endemic, multi-purpose forest genetic resources of high socio-economic value: *Nuxia capitata* Baker (Stilbaceae) and *Phyllarthron madagascariensis* K. Schum. (Bignoniaceae). Current scientific literature on *N. capitata* underscores its diverse ethnobotanical, phytochemical, and silvicultural dimensions. Ethnobotanical investigations across various regions have documented numerous traditional therapeutic applications of this species, specifically targeting nine distinct categories of pathologies (Andrianavalonirina & Ramanandraibe, 2023 ; Rasamindrakotroka et *al*., 2022 ; Rakotoarivelo et *al*., 2019 ; Randriamiharisoa et *al*., 2015). These traditional practices have been partially validated by phytochemical assessments, which confirm the species' anti-fatigue and antioxidant properties (Rakotonarivony et *al*., 2024), alongside its pharmacological potential as a diuretic agent (Rasamindrakotroka, 2021). From a silvicultural perspective, empirical research highlights the capacity of N. capitata seedlings to survive and adapt within degraded forest fragments, such as the Ankafobe forest in the central highlands (Birkinshaw et *al*., 2009), reflecting its broad ecological distribution network (Ratolojanahary, 2006).

Simultaneously, *P. madagascariensis* exhibits extensive therapeutic potential within the national pharmacopoeia (Saltier & Razafindravao, 2017 ; Randriamiharisoa et *al*., 2015 ; Razafindraibe et *al*., 2013 ; Ibrahim & Laurence, 2011 ; Debray, 1975). Phytochemical and biological evaluations have verified its antimicrobial efficacy, its inhibitory effects on vascular muscle contraction, and its rich nutrient composition, alongside providing distinct diagnostic botanical markers (Ibrahim & Laurence, 2011 ; Rafidison, 2008). Furthermore, technological assessments of its wood mechanical properties justify its widespread integration into the timber industry, serving locally as a primary source of lumber and fuelwood (Rakotovao et *al*., 2012). Recognizing their ecological and functional importance, the Ministry of Environment and Sustainable Development, in partnership with PAGE/GIZ, has designated these two species as priority candidates for Forest Landscape Restoration (FLR) programs in the western and eastern ecoregions of Madagascar, respectively (Ministère de l'Environnement et du Développement Durable & PAGE/GIZ, 2021).

Despite these multi-disciplinary research efforts, the long-term sustainability of these endemic forest resources remains deeply compromised by severe habitat fragmentation driven by persistent deforestation and anthropogenic pressures (Rakotoarimalala & Ratsimbazafy, 2024). Effectively managing and conserving such vulnerable taxa requires a robust understanding of their potential geographic ranges and the underlying bioclimatic drivers governing their distribution (Fachola et *al*., 2019). However, no comprehensive study has utilized predictive biogeographical frameworks to model the ecological niches of these species, leaving a critical knowledge gap regarding priority conservation sites and the optimal ecological conditions required for reforestation efforts. This problem raises a key ecological question: to what extent are the bioclimatically suitable habitats of *N. capitata* and *P. madagascariensis* adequately represented within Madagascar's current protected area network ?

Ecological Niche Modeling (ENM) offers a rigorous spatial framework to predict species occurrence probabilities across expansive geographical scales, reconstructing the ecological requirements of a taxon based on georeferenced occurrence points and associated environmental datasets (Vignoles, 2022). Species distribution models have thus become indispensable predictive tools in conservation biology (Paladia et *al*., 2014 ; Phillips et *al*., 2006a ; Peterson et *al*., 1999) and for delineating specific ecological niches (Ayihouenou et *al*., 2016 ; Basille et *al*., 2007), yielding high-resolution cartographic outputs and statistical metrics derived from empirical and environmental data (Vignoles, 2022). Accordingly, the primary objectives of this study are: (1) to delineate the geographical configuration of suitable habitats for *N. capitata* and *P. madagascariensis*, (2) to identify the predominant environmental parameters constraining their distribution, and (3) to evaluate the spatial overlap between

their modeled ecological niches and the national protected area network, utilizing the maximum entropy (MaxEnt) algorithm to guide future strategic conservation and restoration initiatives.

## 2. Material and Methods

### 2.1. Study setting

The study was conducted across the macro-territory of Madagascar, an island nation situated in the southwestern Indian Ocean within Southern Africa. Encompassing a total land area of approximately 587,014 km², the island extends geographically between latitudes 12° and 25° South and longitudes 43° and 51° East, a spatial configuration that corresponds to the Universal Transverse Mercator (UTM) zones 38 S and 39 S (INSTAT, 2020). Due to its evolutionary isolation and bioclimatic heterogeneity, Madagascar is designated as a global biodiversity hotspot of paramount ecological significance, harboring an extraordinarily rich assembly of endemic biota (Ministère de l'Environnement et du Développement Durable [MEDD], 2019).

The island is structurally categorized into four primary biomes dictated by distinct bioclimatic regimes: the Eastern Biome, the Central Highlands Biome, the Western Biome, and the Southern/Southwestern Biome. The Eastern Biome is characterized by a persistently hot and humid tropical climate. Conversely, the Western Biome experiences a dry tropical climate governed by monsoonal influences, which delineate two contrasting seasons and support extensive dry deciduous forest ecosystems across the western and northern regions. Finally, the Southern Biome is dominated by arid and sub-arid climatic conditions, which restrict the vegetation to highly specialized xerophytic formations (Carré et al., 2021).

Recent spatial monitoring assessments estimate Madagascar's total forest cover at approximately 8.9 million hectares, representing 15% of the national territory (Vieilledent et al., 2018). This forest estate comprises 4.4 million hectares of humid rainforests, 2.6 million hectares of dry deciduous forests, 1.7 million hectares of thorny thickets, and 177,000 hectares of mangrove ecosystems (Vieilledent et al., 2018). However, pervasive landscape degradation has profoundly altered the island's primary vegetation, with secondary formations resulting from anthropogenic disturbances now occupying more than half (63%) of the total land surface (Roelens et *al*., 2017).

From a socio-economic perspective, Madagascar is classified as a low-income country, with an estimated gross domestic product (GDP) per capita of 549 in 2024. Despite these financial constraints, the nation maintains positive macroeconomic dynamics driven primarily by the agricultural, textile, ecotourism, and telecommunications sectors (Banque Africaine de Développement [BAD], 2025), underscore the critical dependence of local livelihoods and national development on the sustainable exploitation of natural and forest resources.

### 2.2. Materials

#### 2.2.1. *Nuxia capital* Baker

*Nuxia capitata* Baker is taxonomically assigned to the Stilbaceae family—historically classified under Buddlejaceae—and is currently categorized as Least Concern on the IUCN Red List of Threatened Species (IUCN, 2023). Vernacularly recognized across Madagascar by names such as Lambinana, Valanira, Valanirana, and Valanirandrano, this woody species typically manifests as a tree attaining heights between 6 and 10 meters. Morphologically, it is distinguished by a characteristic fluted trunk covered in pale grey-brown, deeply fissured bark. The twigs support simple, opposite or sub-opposite foliage, with individual leaves presenting an elliptical or oblong apex and notably paler tertiary venation network. The inflorescences consist of flowers with white corollas and distinct bell-shaped calyxes, exhibiting a flowering phenology that spans from October to January. The fruits develop into dehiscent capsules enclosing slender, spindle-shaped seeds that reach maturity between November and July (Ratolojanahary, 2006).


Figure 1 : *Nuxia capitata* Baker : Leafy branches (a), trunk of a mature individual (b), juvenile stage (c), mature stage (d).

These distinct ontogenetic and anatomical phases illustrate the vegetative growth architecture of *Nuxia capitata*, tracking its development from juvenile foliage traits to the deeply fissured bark defining mature forest individuals.

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### 2.2.2. *Phyllarthron madagascariensis* K.Schum

*Phyllarthron madagascariensis* K. Schum., a member of the Bignoniaceae family, is widely identified by several indigenous vernacular names, including Antohiravina, Solohotsy, Zahaina, Zahona, Tononana, Sangy, Tahila, Tokandilana, Zahambe, and most predominantly, Zahana. This canopy-dwelling tree achieves heights ranging from 20 to 40 meters, characterized by a remarkably straight, unbranched bole extending up to 15 meters, which occasionally exhibits fluting at the base and a diameter at breast height (DBH) of up to 80 cm. Ecologically, it is a heliophilous, moderately slow-growing species primarily distributed across the humid and sub-humid evergreen forests of eastern and central Madagascar, spanning an altitudinal gradient up to 1,600 meters, and occasionally reaching 2,200 meters (Rakotovao et *al*., 2012). Mirroring the previous taxon, its global conservation status is designated as Least Concern (IUCN, 2023).

The foliar morphology of *P. madagascariensis* is highly specialized and diagnostic for the genus. The leaves are arranged oppositely and are structurally bipartite, composed of two distinct articulated segments : a basal segment attached directly to the petiole presenting an oval or oblong geometry, and an upper segment characterized by a broadly elliptical outline (Rafidison, 2008).


Figure 2 : *Phyllarthron madagascariensis* K. Schum : adult leafs (a), juvenile stage (b) and mature stage (c).

The unique articulated foliar geometry and structural modifications across ontogenetic stages highlight the anatomical adaptation of *Phyllarthron madagascariensis*, facilitating key diagnostic verification within heterogeneous Malagasy forest canopy ecosystems.

## 2.3. Methods

### 2.3.1. Data collection and environmental predictors

- **Species occurrence records**

The development of robust and reliable species distribution models necessitates high-quality, representative occurrence datasets. While universal guidelines for the absolute minimum threshold of occurrence records do not exist due to variations in species rarity and niche breadths, empirical studies suggest that 10 records can suffice for narrow-ranged endemic species (Scheldeman et *al*., 2007), whereas approximately 50 records are recommended for widespread forest taxa (Van Zonneveld et *al*., 2009). Given that both *Phyllarthron madagascariensis* K. Schum. and *Nuxia capitata* Baker are widely distributed across their respective biomes and categorized as Least Concern (IUCN, 2023), larger sample sizes were leveraged. Specifically, a total of 144 occurrence records for *P. madagascariensis* and 50 records for *N. capitata* were acquired. These georeferenced data were extracted from the Global Biodiversity Information Facility platform (GBIF, www.gbif.org), which consolidates primary digitized geographic coordinates from national and international herbarium collections.

- **Environmental variables**

Vegetation structure and phytogeographical distribution patterns are regulated by an interplay of biotic interactions, dispersal limitations, and abiotic constraints—including solar radiation, soil properties, atmospheric conditions, precipitation regimes, and altitudinal gradients (Peters et *al*., 2019 ; Rahbek et *al*., 2019 ; McCain & Grytnes, 2010 ; Korner, 2007). Predictive ecological niche modeling must therefore integrate environmental predictors that directly constrain the physiological tolerances and geographical boundaries of the target taxa (Peterson et *al*., 2011). These typically comprise macroclimatic parameters (Pearson & Dawson, 2006), edaphic attributes essential for plant growth (Zuquim et *al*., 2020 ; Hengl et *al*., 2017), and topographic factors such as elevation, which strongly correlates with localized temperature gradients and modulates both species richness and life-form distributions (Loiola et *al*., 2023).

To capture these ecological drivers within Madagascar, raster layers representing three categories of environmental factors were gathered. Macroclimatic variables were sourced from the WorldClim database (http://www.worldclim.org/bioclim) at an initial spatial resolution of 30 arc-seconds (~90 meters). The edaphic dimension was represented by soil organic

carbon density at a depth of 0–30 cm, extracted from the high-resolution 250-meter SoilGrids database compiled by the International Soil Reference and Information Centre (ISRIC). Topographic elevation data were derived from the Consortium for Spatial Information of the Consultative Group on International Agricultural Research (CGIAR-CSI) Shuttle Radar Topography Mission (SRTM), featuring an intrinsic accuracy of 30 meters based on NASA Earth relief assessments. Lastly, contemporary forest cover data were integrated from the BioSceneMada project database to account for habitat availability. All environmental raster layers were subsequently clipped to the administrative boundaries of Madagascar and resampled to a uniform spatial resolution within an ArcGIS framework to ensure spatial alignment during maximum entropy modeling.

- **Selection of environmental variables**

The total number of predictor variables significantly influences model performance ; incorporating excessive multi-collinear variables increases model complexity and often leads to overfitting, forcing the generated niche to conform artificially to the training data (Peterson et *al*., 2011). It is therefore vital to restrict the modeling inputs to a parsimonious subset of weakly correlated or uncorrelated environmental predictors (Peterson et *al*., 2011). To achieve this, all initial ecological variables were subjected to a pairwise Pearson correlation analysis within ArcMap. Predictors exhibiting a correlation coefficient above a strict threshold ($|r| \geq 0.85$), were excluded, ensuring that only statistically independent variables were retained for the final maximum entropy modeling phase (Elith et al., 2011).

**Table 1. Ecological variables considered for modelling the spatial distribution of *Nuxia capitata* Baker and *Phyllarthron madagascariensis* K. Schum**

| Variable Code | Variable Type | Variable Code | Variable Type |
|---|---|---|---|
| BIO1 | Annual mean temperature | BIO12 | Annual precipitation |
| BIO2 | Mean diurnal range | BIO13 | Precipitation of wettest month |
| BIO3 | Isothermality (BIO2/BIO7) × 100 | BIO14 | Precipitation of driest month |
| BIO4 | Temperature seasonality | BIO15 | Precipitation seasonality |
| BIO5 | Maximum temperature of warmest month | BIO16 | Precipitation of wettest quarter |
| BIO6 | Minimum temperature of coldest month | BIO17 | Precipitation of driest quarter |
| BIO7 | Temperature annual range (BIO5–BIO6) | BIO18 | Precipitation of warmest quarter |
| BIO8 | Mean temperature of wettest quarter | BIO19 | Precipitation of coldest quarter |
| BIO9 | Mean temperature of driest quarter | Sol_mada | Soil organic carbon density (0–30 cm) |
| BIO10 | Mean temperature of warmest quarter | Alt | Altitude |
| BIO11 | Mean temperature of coldest quarter | c_for | Forest cover |

This comprehensive suite of nineteen bioclimatic variables, combined with edaphic, topographic, and vegetative layers, establishes a robust multidimensional matrix critical for accurately delineating the ecological niches of both Malagasy endemics.

### 2.3.2. Data analysis

- **Data preparation**

The georeferenced coordinates representing the known distribution of the target species, initially compiled in decimal degrees, were projected into the WGS 1984 / UTM Zone 38S coordinate system to ensure uniform pixel dimensions and facilitate highly accurate surface area computations (Guisan et *al*., 2017). These cleaned occurrence datasets were subsequently formatted as comma-separated values (.csv). Concurrently, the environmental raster predictors (comprising bioclimatic, edaphic, and topographic layers) were processed utilizing ArcGIS and exported into the ASCII grid format (.asc). To prevent overfitting and enhance spatial rigorousness, duplicate and spatially redundant occurrence records within the same grid cell were systematically removed before executing the predictive algorithms.

- **Ecological niche modeling framework**

**Selection of the MaxEnt model**

The selection of an appropriate algorithm to construct descriptive and predictive ecological niche models depends on the primary research objectives and the structure of the available occurrence data, which typically fall into presence-absence, presence-only, or presence-background categories (Vignoles, 2022). While Generalized Additive Models (GAMs), Generalized Linear Models (GLMs) (Guisan & Zimmermann, 2000), hierarchical occupancy frameworks (Royle & Dorazio, 2006), and Classification Tree Analysis (CTA) (Thuiller et *al*., 2005) rely on explicit presence-absence observations, alternative methods such as BIOCLIM (Booth et *al*., 2014) and DOMAIN (Carpenter et *al*., 1993) are tailored for presence-only datasets.

For this study, the MaxEnt (Maximum Entropy) software package was selected. MaxEnt utilizes a presence-background framework that integrates empirical occurrence points with background environmental data across the study area (Phillips & Dudík, 2008 ; Phillips et *al*., 2006b). This algorithm is highly effective because it simultaneously

handles continuous and categorical environmental datasets (Phillips et *al*., 2006b), performs robustly with small or restricted occurrence samples (Urbina-Cardona & Loyola, 2008), and exhibits superior predictive accuracy regarding species distributions compared to alternative methods (Hernandez et *al*., 2008). Operating on the principle of maximum entropy, the algorithm estimates the most uniform target probability distribution bounded by the constraints of the observed environmental data, thereby avoiding unwarranted ecological assumptions (Peterson et *al*., 2011 ; Phillips & Dudík, 2008 ; Phillips et *al*., 2006b). The resulting outputs map potential geographical suitability based on the statistical properties of the species' bioclimatic profile (Roger, 2009 ; Phillips et *al*., 2006a).

**Validation parameters and model analysis**

**Area under the ROC curve: AUC**

The predictive performance and discriminative capacity of the MaxEnt models were evaluated using the Receiver Operating Characteristic (ROC) curve and the corresponding Area Under the Curve (AUC) metric. The ROC curve determines the probability that a randomly chosen presence site is ranked higher than a randomly selected background point (Phillips et *al*., 2006a). The horizontal axis (1 − specificity) represents the fraction of background points incorrectly predicted as presences, while the vertical axis (sensitivity) represents the fraction of accurately omitted true presences.

To validate the model, the occurrence data were partitioned into a 1:4 ratio: 80% of the occurrence records were utilized for model training and calibration, while the remaining 20% were set aside as independent test data to compute the test AUC (Phillips et *al*., 2006a). Model accuracy based on the resulting AUC values was interpreted using standard thresholds: excellent (AUC > 0.90), good (0.80 < AUC ≤ 0.90), acceptable (0.70 < AUC ≤ 0.80), poor (0.60 < AUC ≤ 0.70), and invalid (AUC ≤ 0.60) (Araújo et al., 2005).

**Threshold selection and variable contribution**

To transform continuous probability surfaces into binary presence-absence and discrete habitat quality maps, a specific decision threshold was implemented. We adopted the "10th percentile training presence" threshold, an approach that establishes the minimum probability required to classify a pixel as suitable habitat while systematically excluding the 10% of training records exposed to extreme or anomalous environmental conditions (Roger, 2009).

The relative influence of each environmental variable on the final distribution models was evaluated through percentage contributions and Jackknife exclusion tests generated natively within MaxEnt. In the percentage contribution assessments, higher values indicate a stronger influence of that variable on habitat constraints. In the Jackknife diagrams, the blue bars reflect the descriptive power of each isolated variable when included alone, whereas the green bars illustrate the loss in total gains when that specific parameter is omitted, highlighting its unique information content.

**Cartography and spatial analysis**

The post-modeling spatial analysis and habitat cartography were executed within an ArcGIS environment. Utilizing the continuous suitability values (p) and the designated 10th percentile training presence threshold (s), three distinct habitat suitability classes were delineated (Roger, 2009) :

Unsuitable habitat : $p < s$
Suitable habitat : $s \leq p < s + \frac{x}{2}$
Highly suitable habitat : $s + \frac{x}{2} \leq p \leq 1$

The total geographic surface area (S) for each suitability class was calculated using the following mathematical formulation:

$$S = \sum_{i=1}^{n} Pi \text{ x } A\text{pixel}$$

This geometric equation quantifies the total spatial extent of each suitability class by multiplying the aggregate number of classified raster pixels by the uniform area metric of an individual pixel.

To assess conservation efficacy, these finalized suitability layers were overlaid with vector shapefiles detailing administrative boundaries, ecoregions, community-based forest management transfer zones, and the national protected area network. The authoritative geospatial layer for the protected area networks was obtained via Africa Geoportal from the Regional Centre for Mapping of Resources for Development under the file name Madagascar_Protected_Areas_July2024.shp. This spatial overlay facilitated an evaluation of the percentage of suitable habitats currently protected under national legislation.

# 3. Results

## 3.1. Environmental variable selection and multicollinearity analysis

To optimize predictive performance and prevent the statistical artifacts associated with overfitting, a parsimonious subset of environmental predictors was established. Following the

pairwise Pearson correlation analysis, highly collinear and redundant variables were systematically excluded from the modeling matrix. This filtration process retained only 11 independent environmental descriptors that conformed strictly to the non-collinearity threshold (|r| < 0.85). The finalized multi-dimensional dataset integrated into the MaxEnt architecture encompasses one edaphic predictor (sol_mada: soil organic carbon density), one vegetative descriptor (c_for: forest cover), and nine specific bioclimatic variables capturing temperature and precipitation regimes (BIO1, BIO2, BIO3, BIO4, BIO6, BIO12, BIO13, BIO15, and BIO18).

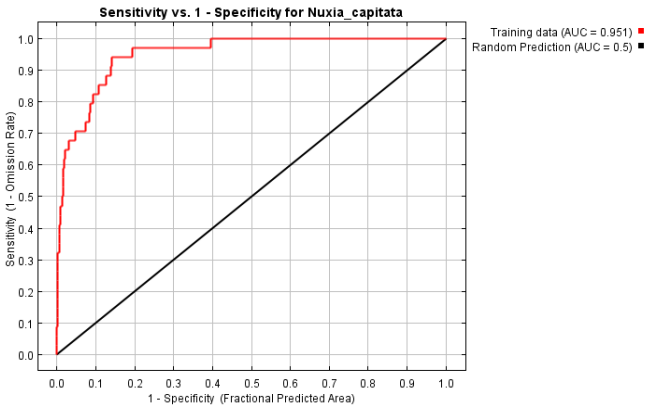


Figure 3 : ROC curve evaluating ecological niche model performance of *Nuxia capitata* Baker

**Table 2 . Pearson correlation coefficients among the selected environmental variables for Madagascar**

| VARIABLE | sol_mada | c_for | BIO1 | BIO2 | BIO3 | BIO4 | BIO6 | BIO12 | BIO13 | BIO15 | BIO18 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| sol_mada | 1 | -0.3 | 0.68 | -0.18 | 0.11 | -0.07 | 0.58 | 0.58 | 0.28 | 0.6 | 0.55 |
| c_for | 0.34 | 1 | -0.05 | -0.15 | -0.07 | 0.08 | 0.01 | -0.02 | -0.14 | 0.09 | -0.01 |
| BIO1 | -0.3 | -0.05 | 1 | 0.17 | 0.28 | -0.42 | 0.84 | -0.09 | -0.14 | -0.77 | -0.4 |
| BIO2 | 0.68 | -0.14 | 0.17 | 1 | 0.2 | 0.32 | -0.34 | -0.78 | -0.46 | -0.77 | 0.63 |
| BIO3 | -0.18 | -0.06 | 0.28 | 0.28 | 1 | -0.06 | 0.26 | -0.14 | 0.28 | -0.49 | -0.69 |
| BIO4 | 0.11 | 0.08 | -0.42 | 0.32 | -0.6 | 1 | -0.65 | -0.44 | -0.79 | 0.04 | -0.79 |
| BIO6 | -0.07 | 0.01 | 0.84 | -0.34 | 0.26 | -0.65 | 1 | 0.35 | 0.47 | 0.21 | 0 |
| BIO12 | 0.58 | -0.02 | 0.09 | -0.78 | -0.14 | -0.44 | 0.35 | 1 | 0.74 | 0.78 | 0.79 |
| BIO13 | 0.28 | -0.14 | 0.18 | -0.46 | 0.28 | -0.79 | 0.47 | 0.74 | 1 | 0.22 | 0.54 |
| BIO15 | 0.6 | 0.09 | -0.18 | 0.77 | -0.49 | 0.04 | 0.21 | 0.78 | 0.22 | 1 | 0.66 |
| BIO18 | 0.55 | -0.01 | 0.4 | -0.69 | -0.19 | -0.17 | 0 | 0.79 | 0.54 | 0.66 | 1 |

The correlation matrix confirms that all eleven selected environmental predictors exhibit multi-collinearity coefficients strictly below the critical threshold (|r| < 0.85). The highest correlation occurs between annual mean temperature (BIO1) and minimum temperature of the coldest month (BIO6) at 0.84, ensuring statistical independence and model parsimony for subsequent maximum entropy modeling executions.

## 3.2. Model validation and predictive performance

The predictive performance and discriminative accuracy of the generated ecological niche models were rigorously evaluated using the Area Under the Receiver Operating Characteristic (ROC) Curve (AUC). The training AUC metrics reached 0.951 for *Nuxia capitata* Baker and 0.919 for *Phyllarthron madagascariensis* K. Schum. These elevated statistical values demonstrate the high robustness and exceptional predictive capacity of the MaxEnt algorithm in reconstructing the bioclimatic envelopes of both endemic taxa in response to multi-dimensional environmental variations. In predictive biogeography, AUC values exceeding the 0.90 threshold represent excellent model performance, confirming that the selected environmental predictors effectively distinguish true presence localities from background pseudo-absences (Araújo et *al*., 2005).

The training receiver operating characteristic curve for *Nuxia capitata* yields an outstanding AUC value of 0.951, demonstrating that the maximum entropy algorithm possesses a 95.1% probability of correctly ranking a randomly chosen presence site above a background site, thereby validating the model's high discriminative capacity.

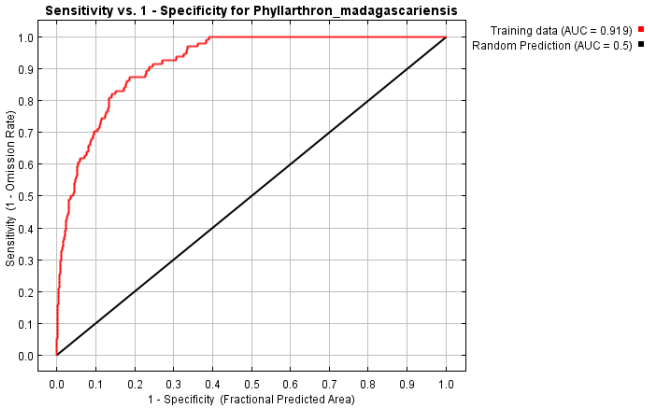


Figure 4 : ROC curve showing the predictive performance of the ecological niche model for *Phyllarthron madagascariensis* K. Schum

The predictive validation curve for *Phyllarthron madagascariensis* achieves a robust training AUC score of 0.919, establishing that 91.9% of the modeled geographic space accurately aligns with known species occurrences,

minimizing commission errors and confirming the statistical reliability of the macroclimatic and edaphic variables utilized.

## 3.3. Environmental variable contributions and predictor importance

### Ecological determinants of *Nuxia* capital Baker distribution

The maximum entropy model identifies annual mean temperature (BIO1) as the predominant macroeconomic driver regulating the geographical distribution of *N. capitata*, accounting for an outstanding percent contribution of 75.6%. This primary role is further substantiated by its high permutation importance score of 45.5%, followed closely by the precipitation of the wettest month (BIO13) at 25.6%. These metrics suggest that macroclimatic thermal thresholds and peak seasonal rainfall volumes constitute the core bioclimatic constraints defining the species' fundamental niche. Consequently, *N. capitata* is ecologically constrained to regions featuring a humid climate with well-defined temperature ranges, requiring substantial moisture availability during the core rainy season.

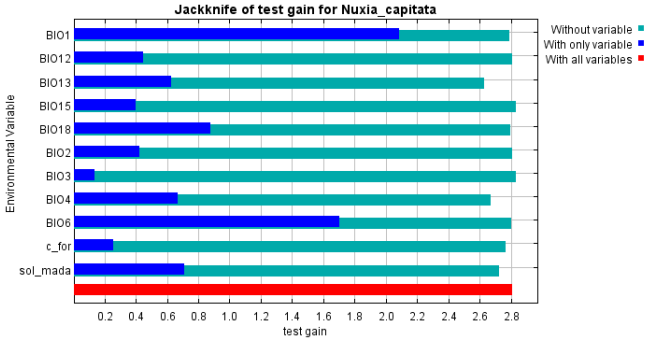


Figure 5 : Diagram of Jackknife test for *Nuxia capitata* Baker distribution model

The Jackknife evaluation indicates that annual mean temperature (BIO1) yields the highest isolated training gain, whereas its omission causes the most significant reduction in model execution gain, confirming that BIO1 contains the most specialized, non-redundant bioclimatic information necessary for accurately predicting the spatial distribution of *Nuxia capitata*.

**Table 3 . Relative contributions and permutation importance of environmental variables for the Nuxia capitata Baker distribution model**

| Variable code | Variable type | Percent contribution | Permutation importance |
|---|---|---|---|
| BIO1 | Annual mean temperature | 75.6 | 45.5 |
| sol_mada | Soil organic carbon density | 6.7 | 6.7 |
| BIO18 | Precipitation of warnest quarter | 5.5 | 0.9 |
| BIO15 | Precipitation seasonality | 5 | 5.3 |
| BIO13 | Precipitation of wettest month | 2.7 | 25.6 |
| BIO4 | Temperature seasonality | 2.4 | 10 |
| BIO3 | Isothermality (BIO2/BIO7)*100 | 1.4 | 0 |
| c_for | Forest cover | 0.4 | 0.7 |
| BIO12 | Annual precipitation | 0.1 | 2.8 |
| BIO6 | Minimale temperature of coldest month | 0.1 | 2.6 |
| BIO2 | Mean dual range | 0 | 0 |

Statistical outputs reveal that annual mean temperature (BIO1) exerts a dominant 75.6% contribution, while the combination of BIO1 and precipitation of the wettest month (BIO13) aggregates a decisive 71.1% of total permutation importance, demonstrating that thermal limits and hyper-humid seasonal moisture govern the macro-ecological boundary of this species.

The Jackknife evaluation plots summarize the idiosyncratic predictive power of individual environmental factors. The high gain associated with the isolated inclusion of BIO1 underscores its vital role in model calibration, while its omission significantly diminishes total model gains. Conversely, the high regularized training gain maintained when minimum temperature of the coldest month (BIO6) is excluded reflects a robust tolerance to cold, showing that N. capitata exhibits specialized adaptive traits to navigate winter thermal depressions in the central highlands of Madagascar.

The convergence of the empirical contributions and the Jackknife diagnostics characterizes *N. capitata* as a cool-temperature, hygrophilous specialist. The species thrives within a restricted annual mean thermal envelope ranging from 12°C to 20°C, displaying a remarkable physiological tolerance to sub-zero winter temperatures, provided that peak summer precipitation levels exceed approximately 250 mm.

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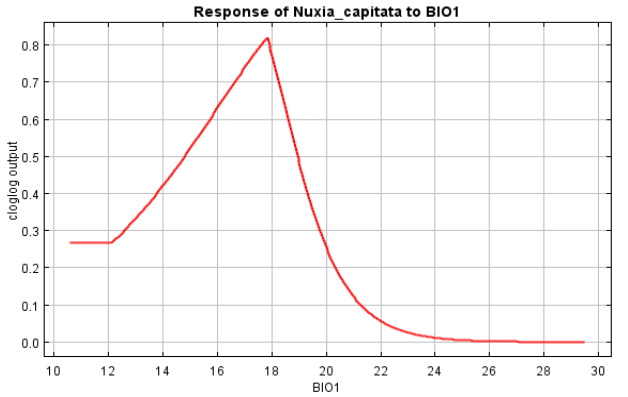


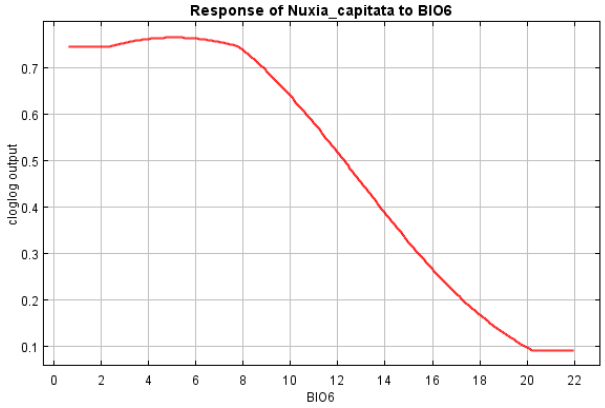


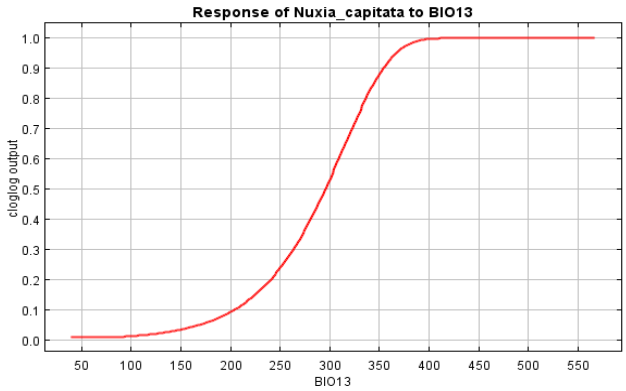


Figure 6 : *Nuxia capitata* Baker response curves according to the main ecological parameters : BIO1, BIO6 and BIO13

The marginal response curves show a peak probability of occurrence for *Nuxia capitata* when annual mean temperature (BIO1) ranges between 12°C and 20°C, coupled with a physiological requirement for peak seasonal precipitation (BIO13) exceeding 250 mm, highlighting its bioclimatic specialization within cold and humid high-altitude Malagasy ecosystems.

**Ecological determinants of Phyllarthron madagascariensis K. Schum distribution**

The spatial distribution of *P. madagascariensis* is primarily governed by precipitation seasonality (BIO15), which exhibits a dominant percent contribution of 43.4%, followed by mean diurnal temperature range (BIO2) at 14.5% and forest cover (c_for) at 13.0%. The model's sensitivity to these drivers is reinforced by their permutation importance rankings, where mean diurnal range (BIO2) accounts for a critical 41.8% and precipitation seasonality (BIO15) represents 15.3%. These metrics indicate that high daily thermal fluctuations and historical rainfall variability are the primary factors shaping the ecological boundaries of this canopy tree.

Table 5 . Relative contributions and permutation importance of environmental variables for the *Phyllarthron madagascariensis* K. Shum distribution model

The data indicate that precipitation seasonality (BIO15) provides the highest percent contribution at 43.4%, while mean diurnal range (BIO2) dominates permutation importance at 41.8%, establishing that a combined 57.9% of model distribution structure depends strictly on spatial variations in rainfall seasonality and localized daily thermal fluctuations across Madagascar.

The Jackknife metrics clarify the specific environmental requirements critical for the growth and development of *P. madagascariensis*. The substantial gains achieved by precipitation seasonality (BIO15), mean diurnal range (BIO2), and soil organic carbon density (sol_mada) reveal that the species' occurrence is closely linked to deep, fertile,

**Table 4 . Relative contributions and permutation importance of environmental variables for the *Nuxia capitata* Baker distribution model**

| Variable | Variable type | Percent contribution | Permutation importance |
|---|---|---|---|
| BIO15 | Precipitation seasonality | **43.4** | **15.3** |
| BIO2 | Mean dual range | **14.5** | **41.8** |
| c_for | Forest cover | **13** | 5.4 |
| sol_mada | Soil organic carbon density | 8.3 | 7.9 |
| BIO3 | Isothermality (BIO2/BIO7)*100 | 6.6 | 2.6 |
| BIO1 | Annual mean temperature | 4.3 | 0.3 |
| BIO13 | Precipitation of wettlest month | 3.2 | 9.2 |
| BIO6 | Minimale temperature of coldest | 1.9 | 8.4 |
| BIO18 | Precipitation of warnest quarter | 1.8 | 1.4 |
| BIO4 | Temperature seasonality | 1.6 | 5.7 |
| BIO12 | Annual precipitation | 1.2 | 2.1 |

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humus-rich soils. These soil conditions are typically found within dense primary forest structures or riparian valley bottoms characterized by seasonal moisture dynamics and pronounced daily thermal variations.

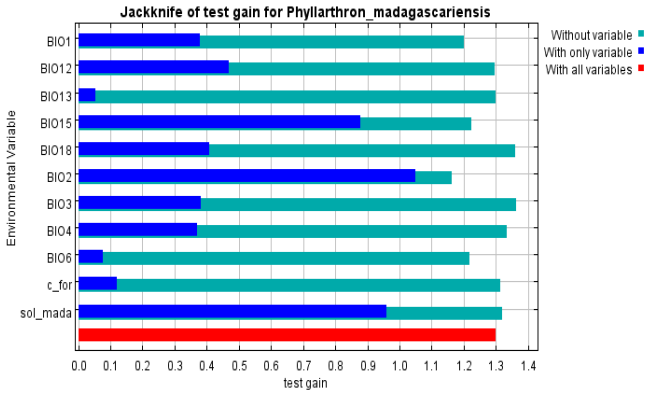


Figure 7 : Ecological profile of *Phyllarthron madagascariensis* K. Schum based on the Jackknife test

The Jackknife diagnostic bars reveal that precipitation seasonality (BIO15) and mean diurnal range (BIO2) maintain the longest individual vectors, indicating that these macroclimatic constraints, along with soil organic carbon density (sol_mada), hold the highest informative value for successfully predicting the suitable forest habitats of *Phyllarthron madagascariensis*.

The response curves show that the distribution of P. madagascariensis depends on edaphic fertility, requiring an organic carbon density greater than 20 kg/m³. The species exhibits an adaptable, bimodal water requirement: it thrives under the constant, high-volume rainfall regimes of eastern Madagascar (low coefficient of variation) but also tolerates more variable, seasonal water regimes. Furthermore, its preferred thermal amplitude is associated with a mean diurnal range between 7°C and 11°C, confirming its affinity for mature, cool forest microclimates.

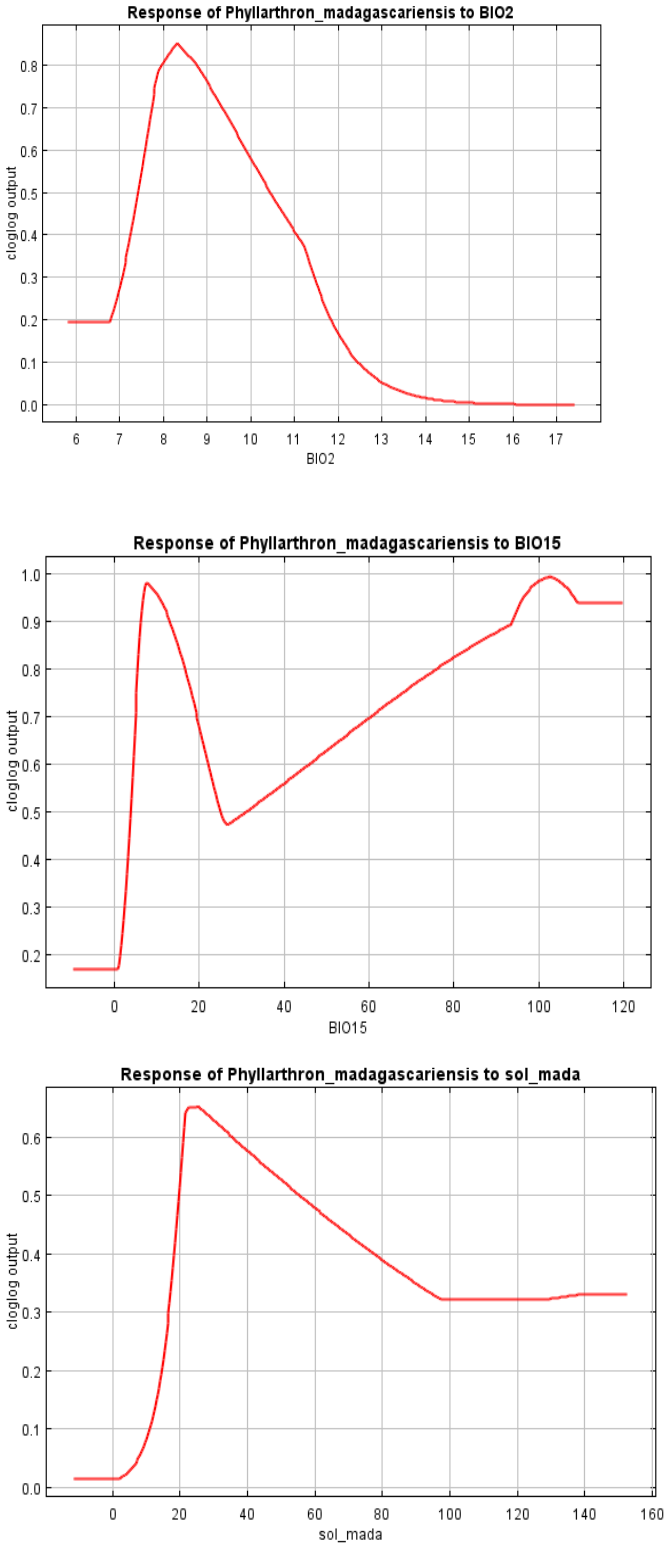


Figure 8 : *Phyllarthron madagascariensis* K. Schum response curves to three key factors : BIO2, BIO 15 et sol-Mada

The probability profiles show that optimal suitability for *Phyllarthron madagascariensis* requires fertile soils with organic carbon density (sol_mada) exceeding 20 kg/m³, a narrow mean diurnal range (BIO2) from 7°C to 11°C, and adaptable rainfall coefficient levels, confirming its ecological

affinity for humid, nutrient-dense forest habitats.

### 3.4. Predicted geographical distribution and habitat classification

To classify the spatial grid cells of the continuous probability map, the "10th percentile training presence" logistic decision threshold was implemented, establishing a critical baseline value of p = 0.218.

predominantly clustered in the central highlands, expanding along northwestern slopes and penetrating inward toward the eastern rainforest margins. Geographically, these high-suitability patches intersect 11 distinct administrative regions, spanning Analamanga, Itasy, Bongolava, Vakinankaratra, Amoron'ny Mania, and Haute Matsiatra in the central plateau, Betsiboka in the northwest, alongside Analanjirofo, Alaotra-Mangoro, Atsinanana, and Vatovavy in the east.

**Table 6 . MaxEnt threshold values utilized for site suitability classification of *Nuxia capitata* Baker**

| Cumulative threshold | Cloglog threshold | Description |
|---|---|---|
| 1 | 0.014 | Fixed cumulative value 1 |
| 5 | 0.076 | Fixed cumulative value 5 |
| 10 | 0.171 | Fixed cumulative value 10 |
| 3.367 | 0.014 | Minimum training presence |
| 13.535 | **0.218** | 10 percentiles training presence |
| 22.526 | 0.244 | Equal training sensitivity and specificity |
| 19.884 | 0.212 | Maximum training sensitivity plus specificity |
| 3.367 | 0.014 | Balance training omission, predicted area and threshold value |
| 10.742 | 0.184 | Equate entropy of thresholded and original distributions |

The statistical threshold values reveal that the 10th percentile training presence criteria successfully establishes a cloglog value of 0.218. This numerical cutoff isolates 90.0% of the active empirical occurrence points, optimizing predictive rigor while allowing for the rigorous delineation of core bioclimatically suitable geographic environments across Madagascar.

Based on this mathematical baseline, the landscape of Madagascar was partitioned into three discrete habitat categories: unsuitable areas ($p < 0.218$, shaded in grey) favorable habitats ($0.218 \leq p < 0.609$, shaded in green and highly favorable core habitats ($0.609 \leq p < 1$, shaded in red) Aligning these results with regional phytogeographical divisions indicates that the potential distribution of *N. capitata* is concentrated within the eastern mid-altitude rainforests, the high-altitude rainforest ecosystems of the central highlands, and the wooded or shrubby grasslands characterizing the central plateau.

The optimum bioclimatic envelopes for *N. capitata* are

**Spatial distribution of *Phyllarthron madagascariensis* K. Schum.**

The spatial configuration of suitable ranges for P. madagascariensis was similarly delineated utilizing a 10th percentile training presence threshold value of p = 0.250.

**Table 7 . MaxEnt threshold values utilized for site suitability classification of *Phyllarthron madagascariensis* K. Schum**

| Cumulative threshold | Cloglog threshold | Description |
|---|---|---|
| 1.000 | 0.024 | Fixed cumulative value 1 |
| 5.000 | 0.122 | Fixed cumulative value 5 |
| 10.000 | 0.198 | Fixed cumulative value 10 |
| 3.367 | 0.087 | Minimum training presence |
| 13.535 | **0.250** | 10 percentiles training presence |
| 22.526 | 0.357 | Equal training sensitivity and specificity |
| 19.884 | 0.326 | Maximum training sensitivity plus specificity |
| 3.367 | 0.087 | Balance training omission, predicted area and threshold value |
| 10.742 | 0.209 | Equate entropy of thresholded and original distributions |

The statistical threshold values show that the 10th percentile training presence option generates a definitive cloglog value of 0.250. This quantitative cutoff optimizes model performance by dividing geographical pixels above 0.250 into macroclimatically validated presences, minimizing potential overprediction within the highly heterogeneous forest ecoregions of Madagascar.

This mathematical threshold categorized the territory into three discrete suitability tiers: unsuitable sites ($p < 0.250$, shaded in grey), suitable habitats ($0.250 \leq p < 0.625$, shaded in green), and highly suitable habitats ($0.62 \leq p \leq 1.000$,

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shaded in red). The predictive niche of *P. madagascariensis* is entirely restricted to forested landscapes, tracing a contiguous north-to-south latitudinal arc along the humid evergreen biome. This distribution encompasses low-altitude coastal rainforests, dense mid-altitude escarpment formations, and high-altitude humid fragments situated along eastern mountain ridges (Carré et *al*., 2021).

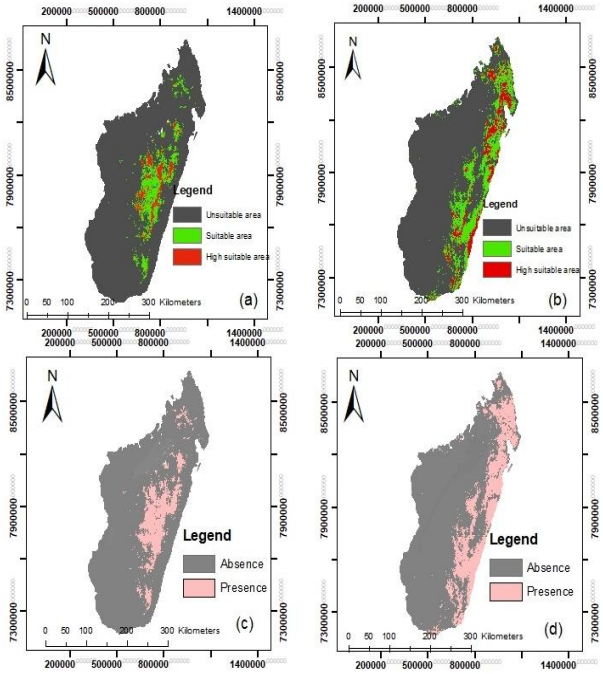


Figure 9 : Distribution model of *Nuxia capitata* Baker (a), *Phyllarthron madagascariensis* K. Schum(b) and binary map of *Nuxia capitata* Baker (c) and *Phyllarthron madagascariensis* K. Schum(d)

The multi-panel cartographic outputs reveal that suitable habitats for *Nuxia capitata* dominate the central highlands ($p \geq 0.218$), whereas the ecological niche of *Phyllarthron madagascariensis* ($p \geq 0.250$) forms a strict latitudinal belt along the eastern humid forest biome, outlining the geographic division between these two endemic tree species.

The model predicts occurrences across a vast network of administrative jurisdictions, specifically including Diana, Sava, Sofia, Analanjirofo, Alaotra-Mangoro, Analamanga, Atsinanana, Vakinankaratra, Amoron'ny Mania, Vatovavy, Fitovinany, Haute Matsiatra, Ihorombe, Atsimo-Atsinanana, Anosy, and Androy.

Crucially, a substantial proportion of the predicted niche for P. *madagascariensis* overlaps with Madagascar's national protected area network along the eastern escarpment. These spatial intersections include key biodiversity targets, such as the Marojejy, Masoala, Ranomafana, Andringitra, Befotaka-Midongy, and Andohahela National Parks, alongside the Analamazaotra and Maromizaha Special Reserves.

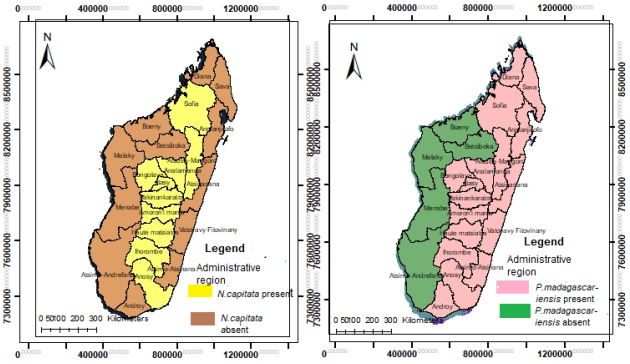


Figure 10 : Distribution of *Nuxia capitata* Baker and *Phyllarthron madagascariensis* K. Schum by administrative region

The regional administrative maps confirm that suitable habitats intersect 11 regions for *Nuxia capitata* and 16 regions for *Phyllarthron madagascariensis*. This spatial distribution emphasizes that the latter possesses an extensive latitudinal coverage, crossing both northern humid forests and southeastern coastal systems under variable regional land management frameworks.

### 3.5. Quantitative spatial distribution and protected area network overlap

The predictive maximum entropy models provide high-resolution quantitative estimates of the total geographical surface area suitable for both endemic species across Madagascar. The aggregate bioclimatically suitable habitat (combining suitable and highly suitable areas) encompasses 76,188.85 km² for *Nuxia capitata* Baker, representing 13.35% of the modeled national territory. For *Phyllarthron madagascariensis* K. Schum., the total projected occurrence zone expands significantly to 127,693.60 km², covering 22.38% of the country. Delineating the core optimal environments reveals that highly suitable habitats occupy 21,010.47 km² (3.68% of the national area) for N. *capitata*, and 36,306.47 km² (6.36% of the national area) for P. *madagascariensis*.

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**Table 7 . Quantified geographic surface areas and proportional distribution of suitable and optimal ecological niches within Madagascar's national territory and Protected Area (PA) network**

| Species | Ecological niche type | Total surface ($km^2$) | Total combined ($km^2$) | Surface included in PA ($km^2$) | Total PA combined ($km^2$) | Pourcentage national (%) | Total national (%) | Pourcentage of niche included in PA (%) | Total niche in PA (%) |
|---|---|---|---|---|---|---|---|---|---|
| *Nuxia* | Suitable area | 55178.38 | | 16081.23 | | 9.67 | | 21.1 | |
| *capitata* Baker | High suitable area | 21010.47 | 76188.85 | 8160.49 | 24241.72 | 3.68 | 13.35 | 10.71 | 31.81 |
| *Phyllarthron madagascariensis* K.Schum | Suitable area | 91387.12995 | | 22773.67 | | 16.02 | | 17.83 | |
| | High suitable area | 36306.47 | 127693.6 | 23667.68 | 46441.35 | 6.36 | 22.38 | 18.53 | 36.36 |

The spatial data quantify that Madagascar's protected networks restrictively encompass 24,241.72 km² of the *Nuxia capitata* niche and 46,441.35 km² for Phyllarthron madagascariensis, securing respectively 31.81% and 36.36% of their total potential ranges, while leaving the remaining major fractions unprotected across multiple anthropogenic land-use matrix zones.

From a strategic conservation perspective, the highly favorable core ecological niches modeled for *N. capitata* exhibit a high degree of spatial intersection with Madagascar's Protected Area System (SAPM) inside the eastern humid rainforest strip. This geographic overlap is particularly concentrated within the Andasibe-Mantadia forest complex—which structurally includes the Analamazaotra and Maromizaha Special Reserves—as well as the Marolambo National Park. These formal legal conservation units are supported by critical regional biodiversity corridors, most notably the Ankeniheny-Zahamena Corridor (CAZ) and the contiguous forest blocks of Mangabe-Ranomena, Sahasarotra, and Ampotaka-Ankorabe (Ministère de l'Environnement et du Développement Durable [MEDD] 2024). Consequently, a total area of 24,241.72 km² of the predicted *N. capitata* range is integrated within protected boundaries, securing 31.81% of its ecological niche.

In stark contrast, within the central plateau and across the western escarpments, formal species protection remains deeply inadequate due to a fragmented conservation framework. In these regions, formal preservation is restricted to a small number of isolated conservation sites, such as the Ambohitantely Special Reserve, the Anjozorobe-Angavo forest corridor, and the highly threatened Ankaratra-Manjakatompo Massif. However, alternative community-based forest management transfer zones (known locally as VOI or TGR) provide a secondary conservation layer, covering a cumulative area of 3,048.18 km² with a strong presence in the Amoron'ny Mania region (MEDD, 2024).

The natural distribution of *N. capitata* within the central part of the island aligns with dense, high-altitude rainforest remnants and central highland forest patches; due to historical topsoil erosion, widespread burning, and severe landscape fragmentation, these unique ecosystems are formally assessed as Endangered (EN) (Carré et *al.*, 2021).

Regarding *P. madagascariensis*, the predictive model shows that 36.36% (46,441.35 km²) of its potential habitat overlaps with national protected networks. This species' range forms a continuous belt within the eastern rainforest biomes, where extensive tracts of its suitable habitats are managed under strict national conservation frameworks.

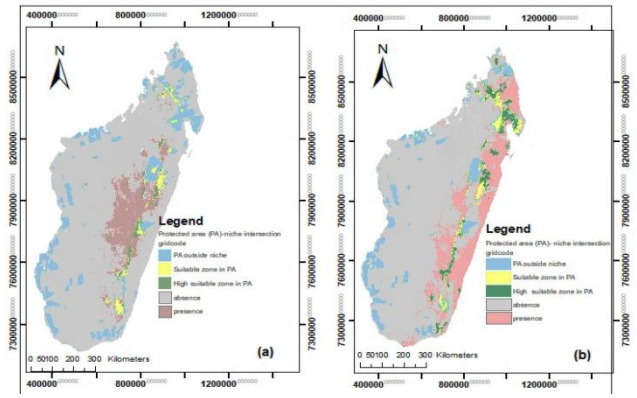


Figure 4 : Spatial correspondence between the national protected area system (SAPM) and the predicted ecological distributions of *Nuxia capitata* Baker (a) and *Phyllarthron madagascariensis* K. Schum. (b)

The overlay maps illustrate that while 31.81% of Nuxia capitata and 36.36% of *Phyllarthron madagascariensis* habitats are situated within eastern rainforest reserves, the central highlands populations face extensive protection gaps, emphasizing a critical structural vulnerability that requires the implementation of community-managed corridors to mitigate regional habitat loss.

# 4. Discussion

## 4.1. Methodology considerations and algorithm performance

In alignment with the current predictive modeling frameworks, which restrict analysis to 11 independent descriptors out of the initial suite of ecological parameters, numerous phytogeographical investigations emphasize the pre-selection of environmental variables prior to MaxEnt processing to mitigate multicollinearity. For instance, in modeling the distribution of *Lantana camara*, the initial environmental matrix was reduced to ten non-collinear predictors, including minimum temperature of the coldest month (BIO6), temperature annual range (BIO7), annual precipitation (BIO12), alongside topographic and edaphic variables (Gebrewahid et *al*., 2025). Conversely, alternative approaches accommodate a larger number of environmental layers provided they leverage significantly larger occurrence datasets, as demonstrated by the integration of 21 environmental variables alongside 1,537 occurrence points to model the distribution of *Blighia sapida* (Kassegne et *al*., 2025).

The derivation of robust ecological niche maps through maximum entropy algorithms relies fundamentally on estimating occurrence probabilities from empirical presence data and background environmental variables, while carefully avoiding spatial autocorrelation and sampling bias (Friedlaender et *al*., 2011). The predictive distribution models developed in this study for *Nuxia capitata* Baker and *Phyllarthron madagascariensis* K. Schum. strictly integrated these spatial recommendations. In Madagascar, multiple predictive modeling studies leveraging the MaxEnt algorithm have yielded decisive conclusions for the conservation and sustainable management of the island's botanical resources. Notable examples include spatial analyses conducted on endangered endemic palms such as *Dypsis lokohoensis*, *Dypsis coursii*, and *Dypsis pumila* (Rajaonarivotantely, 2008), wild pepper resources (*Piper* spp. or Tsiperifery) (Raherinjatovoarison, 2017), as well as threatened succulents like *Aloe analavelonensis* and *Aloe helenae* (Letsara, 2020). Across the African continent, maximum entropy frameworks have similarly been deployed to map high-priority species, including *Blighia sapida* in Togo (Kassegne et *al*., 2025), *Vitellaria paradoxa* (shea tree) in Burkina Faso and Benin (Dimobe & Bayla, 2023 ; Saliou et *al*., 2015), and *Podocarpus falcatus* in Ethiopia (Tesfariam et *al*., 2022).

## 4.2. Implications of niche modeling for biodiversity management strategies

Ecological niche modeling serves as an indispensable tool for designing proactive conservation and management strategies tailored to the specific threat status of vulnerable flora. For instance, the spatial distribution of *Anoectochilus roxburghii*, a threatened medicinal orchid, is strongly constrained by the mean temperature of the coldest quarter (BIO11) and annual precipitation (BIO12). Predictive models for this orchid highlight the necessity of implementing in-situ protection across stable southern refugia, while prioritizing germplasm collection from declining northern populations (Hou et *al*., 2025). Similarly, for *Vitellaria paradoxa* in Côte d'Ivoire—currently classified as vulnerable—predictive modeling underpins the formulation of climate-adaptive agroforestry systems (Pagny et *al*., 2026).

In the context of biological invasions, ENM frameworks reveal that regions characterized by moderate elevations, elevated temperatures, and adequate precipitation are highly susceptible to invasion by *Lantana camara* in Ethiopia (Gebrewahid et *al*., 2025). Furthermore, under future climate change scenarios, the invasive woody weed *Vernonanthura polyanthes* is projected to occupy up to 72% of its study area in Zimbabwe, driven predominantly by mean temperature of the coldest month (BIO6; 34.7% contribution) and annual precipitation (BIO12; 65.3% contribution) (Washaya et *al*., 2025). These parallel investigations underscore the versatility of MaxEnt outputs for structuring both the preservation of endemic genetic resources and the mitigation of ecological threats.

## 4.3. Ecological interpretations of the modeled target species niches

This study modeled the contemporary geographical distribution of *N. capitata* and *P. madagascariensis* in relation to Madagascar's protected area network, addressing a critical priority in national forest management : the ongoing loss of natural habitats driven by deforestation and unregulated anthropogenic exploitation (Rakotoarimalala & Ratsimbazafy, 2024).

The MaxEnt algorithm demonstrated that macroclimatic thermal conditions exert a predominant influence on the distribution of *N. capitata*, with annual mean temperature (BIO1) yielding a substantial percent contribution of 75.6%. This bioclimatic profile is consistent with empirical ecological field assessments conducted along the Andringitra–Ranomafana forest corridor, which characterize the species as heliophilous, without highly restrictive edaphic

or moisture preferences (Ratolojanahary, 2006). Field observations confirm that *N. capitata* successfully colonizes diverse ecological formations, including rocky outcrops, riparian zones, mature secondary forests, and primary dense humid forests, resulting in an extensive geographical range across the central plateau (Ratolojanahary, 2006). This broad ecological amplitude explains the relatively large suitable area predicted by our model, which covers 13.35% of the national territory.

Regarding *P. madagascariensis*, its strict association with the humid forest biome—where precipitation seasonality (BIO15) contributes 43.4% to the model—aligns with its biological requirements as a slow-growing canopy specialist (Carré et *al*., 2021 ; Rakotovao et *al*., 2012). The high spatial overlap between its predicted niche and the eastern protected areas (36.36%) offers a robust framework for in-situ conservation, provided that structural connectivity between fragmented national parks is legally maintained.

### 4.4. Localized distribution analysis and restoration framework in the Analamanga Region

The baseline bioclimatic conditions of the Analamanga region—spanning both seasonal thermal parameters and moisture regimes—are highly suitable for supporting viable populations of *N. capitata* and *P. madagascariensis*. Consequently, implementing large-scale forest landscape restoration (FLR) initiatives within this central jurisdiction is highly feasible.

However, given the severe depletion of primary natural forest cover in the central highlands, immediate and stringent landscape management policies must be adopted. Several geographical zones identified by the MaxEnt algorithm as bioclimatically suitable for these species are currently degraded, fragmented, or transformed into agricultural and urban settlements. In this fragmented landscape, the primary forest remnants of Ankafobe and Ambohitantely (Ankazobe district), the Anjozorobe–Angavo forest corridor (spanning the districts of Anjozorobe, Manjakandriana, and Andramasina), and isolated community-managed forest patches serve as vital biological, genetic, and cultural reservoirs for both endemic tree species. Consequently, strengthening and expanding community-based forest management transfers (VOI) represents an essential strategy to mitigate habitat loss, prevent genetic erosion, and optimize the long-term success of reforestation efforts in the region.

## 5. Conclusion

Faced with the increasing vulnerability of Madagascar's unique botanical heritage, ecological niche modeling (ENM) was deployed to delineate the bioclimatic envelopes of *Nuxia capitata* Baker and *Phyllarthron madagascariensis* K. Schum.—two highly valued endemic forest resources extensively exploited for traditional medicine and timber. This predictive framework successfully characterized their spatial structures and quantified the efficacy of the national protected area system (SAPM) in securing their contemporary populations. The maximum entropy models reveal that N. capitata and *P. madagascariensis* occupy total potential distribution ranges of 76,188.85 km² and 127,693.60 km², representing 13.35% and 22.38% of the national territory, respectively. Crucially, 24,241.72 km² (31.81%) of the *N. capitata* niche and 46,441.35 km² (36.36%) of the *P. madagascariensis* range overlap directly with designated protected areas, providing vital baseline indicators for national conservation planning.

The geographical range of *N. capitata* is strictly restricted to the central highlands and the inland eastern escarpment, aligning with high- and mid-altitude primary rainforest remnants as well as mature secondary formations. Its spatial distribution is predominantly governed by annual mean temperature (BIO1), which yields a high model contribution of 75.6%. This primary driver, coupled with a permutation importance score of 45.5% for BIO1 and 25.6% for the precipitation of the wettest month (BIO13), establishes that stable macroclimatic thermal limits and high seasonal moisture volumes are the fundamental requirements constraining this species' ecological niche.

Conversely, the environmental factors regulating the presence of P. *madagascariensis* are driven by precipitation seasonality (BIO15; 43.4% contribution), mean diurnal temperature range (BIO2; 14.5% contribution), and existing forest cover (13.0% contribution). The functional sensitivity of the model to these predictors is confirmed by Jackknife tests and permutation importance metrics, where the exclusion of mean diurnal range (BIO2) and precipitation seasonality (BIO15) reduces model predictive capacity by 41.8% and 15.3%, respectively, highlighting the species' specialized affinity for stable, humid forest microclimates.

At the regional scale, the Analamanga region encompasses a highly suitable bioclimatic matrix capable of supporting the long-term survival and ecological restoration of both endemic taxa. Given the high fragmentation of natural forest patches in this central jurisdiction, strengthening the protection of primary genetic reservoirs through community-based forest

management transfers (VOI) constitutes an essential strategy to prevent localized extinctions. Ultimately, securing the geographic ranges of these multi-purpose tree species across the region will not only ensure ecosystem stability but also safeguard the invaluable ethnobotanical knowledge linked to traditional medicine, thereby bridging ancestral heritage with sustainable, community-led forest conservation.

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