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Ministère de l'Enseignement Supérieur et de la Recherche Scientifique

UNIVERSITE FELIX HOUPHOUET-BOIGNY

WASCAL
West African Science Service Centre on Climate Change and Adapted Land Use

SPONSORED BY THE
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Graduate Research Program: Climate Change and Biodiversity

Academic year: 2024 – 2025 **Order number: ……../……..**

THESIS

Submitted for the Degree of Doctor of Philosophy of the

University Félix Houphouët-Boigny

Speciality: Climate Change and Biodiversity

Option: Climate Change, Biodiversity, and Ecosystem Services

EFFECTS OF CLIMATE CHANGE AND FOREST FRAGMENTATION ON THE ECOLOGY AND GENETIC DIVERSITY OF WHITE-THIGHED COLOBUS, *Colobus vellerosus*, WEST AFRICA

François Darius Accrombessi

Publicly defended on ……

Members of Jury:

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Academic Year : 2024 - 2025

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THESE

Présentée pour l'obtention du Titre de Docteur en Philosophie de l'Université Félix Houphouët-Boigny

Spécialité: Changement Climatique et Biodiversité

Option: Changement Climatique, Biodiversité et Services Ecosystémiques

EFFECTS DU CHANGEMENT CLIMATIQUE ET DE LA FRAGMENTATION FORESTIERE SUR L'ECOLOGIE ET LA DIVERSITE GENETIQUE DU COLOBE DE Geoffroy, *Colobus vellerosus*, WEST AFRICA

François Darius Accrombessi

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Rapporteur	: Karim Ouattara	Maitre de Conférences	UFHB
Rapporteur	: C. A. M. Sylvestre Djagoun	Maitre de Conférences	UAC

Dedication

To my late parents: A. Lucien Accrombessi and Albertine Ganmadigbe, Posthumously!

To my children: S. Divine, D. Ezekias, and G. Goodness

Foreword

My academic and professional journey toward this dissertation began long before I formally entered doctoral research. With a profound desire to bridge theoretical knowledge and practical applications for socioeconomic development, I pursued a Professional Master's degree in Natural Resource and Biodiversity Management after seven years of teaching Biology, Ecology, and Geology in Benin's high schools. That period of teaching and applied research, including work carried out at the Laboratory of Applied Ecology (LEA) of the University of Abomey-Calavi and the National Institute for Agricultural Research of Benin (INRAB), deepened my awareness of the accelerating loss of biodiversity and the far-reaching consequences this decline holds for ecosystems and human well-being. These experiences strengthened my commitment to wildlife conservation and the sustainable management of natural resources, ultimately shaping the foundations of this doctoral project.

This doctoral project has enhanced my understanding of conservation initiatives and the intricate nature of conservation science. Through my engagement with a critically endangered primate species, I have learned that effective conservation demands not only ecological knowledge but also a comprehensive awareness of the socioeconomic contexts of surrounding communities.

Initially, the project began with five multidisciplinary and ambitious research objectives; however, it subsequently evolved into five refined, achievable goals. I have come to recognise that a successful integrative conservation approach cannot be realised solely through research proficiency; it requires the establishment of a robust, long-term dataset. Achieving this objective necessitates consistent financial resources, collaborative efforts, and active participation from local communities. This underscores the importance of long-term conservation and research endeavours, which serve as the foundation for effective wildlife management.

The research journey was both challenging and rewarding. I navigated various analytical methodologies, proficiently managed various biostatistical software, faced unexpected fieldwork limitations, and addressed conservation issues that reach beyond academia. These experiences deepened my appreciation for how scientific research can provide practical solutions. Providing evidence-based solutions is necessary in regions where biodiversity loss and community livelihoods are inherently intertwined.

I hope the findings of this dissertation will aid in securing the future of *C. vellerosus* and contribute to West African forested ecosystems conservation efforts.

Acknowledgments

This project would not have been possible without the guidance of the Lord, God of the Universe and Creator of Heaven and Earth, to whom I express my deepest honour and reverence. The Lord accomplishes remarkable works through individuals and institutions, for which I am profoundly grateful.

I extend my sincere appreciation to WASCAL and its administrative staff at the Climate Change and Biodiversity Graduate Research Program, represented by Prof. Daouda Koné, Prof. Souleymane Konaté, Prof. Kouassi Edouard, Dr N'golo Koné, Prof. Sorho Fatogoma, Mr Touré, Mr Bamba Hamed, Mr Bamba Inza, Ms Janet Kouassi, and many others whose names I may not be able to mention here. By selecting candidates based solely on merit, you have allowed me to undertake this thesis work, facilitated by the generous financial support from WASCAL, together with the German Federal Ministry of Education and Research (BMBF).

I express my heartfelt gratitude to Prof. Brice Sinsin, who exemplifies humanity and confidence in the potential of the younger generation. Your statement, "Allow him to attend classes and complete his examinations; he will settle all outstanding fees before his thesis defence," has significantly facilitated my pursuit of a professional career. Although I did ensure that my tuition fees were settled before defending my Master's thesis, your intervention prevented an interruption in my professional journey. In particular, I hold a profound admiration for your professional integrity, which motivates countless people to appreciate the value of diligent work.

I would like to express my sincere gratitude to the esteemed Chair and members of my thesis jury for accepting to evaluate this work and contribute to its scientific enhancement.

I am deeply appreciative of my supervisor, Inza Kone, for guiding the development of this thesis, despite his numerous responsibilities. Each moment spent working with you has proven to be more invaluable than years of formal lectures.

I am profoundly grateful to my co-supervisor, Dr Mireille Toyi, for your scientific assessments, continuous guidance, expert advice, and unwavering support since my Master's degree.

I consider myself fortunate to have Dr Dietmar Zinner as my advisor. I could not have wished for a more exemplary mentor. Please be assured that I have acquired considerable knowledge from you, extending beyond scientific understanding, and I am committed to imparting to the younger generation as much as I have received from you.

I express my sincere gratitude to all members of the Cognitive Ethology Laboratory at the German Primate Center, Leibniz Institute for Primate Research in Göttingen, Germany. I

would like to particularly thank Prof. Julia Fisher for providing me with the opportunity to undertake a research internship focused on my genetic work, as well as David Zinner for his invaluable assistance with laboratory tasks. The international professional environment I experienced during this internship was truly enriching.

I would also like to acknowledge the numerous international collaborators I encountered throughout my thesis journey, especially Prof. Christian Roos and Prof. Julie Teichroeb.

I extend my heartfelt thanks to Dr Charles B. Pomalegni, Dr C. A. M. Sylvestre Djagoun, and Dr Fortuné Azihou. Your advice, guidance, and encouragement have been instrumental in the preparation of this document and have significantly influenced my professional development.

I also thank re:wild and the Förderkreis of the German Primate Center for financial support.

I extend my heartfelt thanks to my field guides, Mr Ganiou Adjofè, Mr Roger Hounkanrin and Mr Dramani Gado, who assisted me during data collection. Sadly, Mr Dramani Gado passed away before I completed this work; may his soul rest in peace.

I would like to extend my heartfelt gratitude to my wife, Sabine Agbodainon, for her unwavering support and understanding during my extended periods of absence.

I am also profoundly grateful to my siblings for their continuous support, valuable advice, and encouragement. May God fortify the brotherly love and unity that enable our collective growth each day.

I really appreciate my fellow PhD candidates from WASCAL's fifth batch, as well as my colleagues from PASET, LEA, and CRA-PAH at INRAB. Thank you all for your spirit of collaboration and the amicable professional environment we have fostered together.

I would like to express my gratitude to all persons who, whether directly or indirectly, contributed to the successful completion of this work.

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List of abbreviations

SIGLES	DEFINITION
AIC	Akaike's Information Criterion
AMT	annual mean temperature
ANN	Artificial Neural Network
AOI	area of interest
AUC	area under the receiver operating characteristic curve
BFMS	Boabeng-Fiema Monkey Sanctuary
Bioedit	Biological sequence alignment editor
BSI	Bare Soil Index
CMIP6	Coupled Model Intercomparison Project Phase 6
CNP	Comoé National Park
CR	Critically Endangered
CSRS	Centre Suisse de Recherches Scientifiques
CTA	Classification Tree Analysis
DIVISION	degree of landscape division
EM	ensemble modelling
EPV	ecological predictor variables
ETM+	Enhanced Thematic Mapper Plus
EVI	Enhanced Vegetation Index
FC	forest cover
FDA	Flexible Discriminant Analysis
GAM	Generalized Additive Model
GBIF	Global Biodiversity Information Facility
GBM	Generalized Boosting Model
GCM	Global Climate Model
GEE	Google Earth Engine
GLM	Generalized Linear Model
GPS	Global Positioning System
ha	hectare
HPD	human population density
IPSL	Institut Pierre-Simon Laplace
IsoT	isothermality

Km2	square kilometre
KSF	Kikélé Sacred Forest
LAI	Leaf Area Index
LCF	Lama Classified Forest
LCP	least-cost paths
LULC	land-use and land-cover
m	metre
MARS	Multiple Adaptive Regression Splines
MaxEnt	Maximum Entropy Phillips
MAXNET	Maximum Entropy Phillips2
MDTR	mean diurnal temperature range
MESH	effective mesh size
MESS	multivariate environmental similarity surface
MKF	Monts-Kouffé Forest
MSI	MultiSpectral Instrument
NDBI	Normalised Difference Built-up Index
NDTI	Normalised Difference Tillage Index
NDVI	Normalised Vegetation Index
NDWI	Normalised Difference Water Index
NGO	Non-Governmental Organisation
OA	overall accuracy
OKF	Okuta Kobunan Forest
OSF	Ouémé Supérieur Forest
PA	protected area
PA	producer’s accuracy
PDM	precipitation during the driest month
PFR	Pénéssoulou Forest Reserve
PWM	precipitation during the wettest month
qa_pixel	quality assessment pixel
QGIS	Quantum Geographic Information System
RF	Random Forest
ROC	Receiver Operating Characteristics
RSC	range size change

SATVI	Soil Adjusted Total Vegetation Index
SDM	Species Distribution Modelling
SFF	Surrounding Fragmented Forest
SLC	Scan Line Corrector
SPLIT	splitting index
SRE	Surface Range Envelop
SRTM	NASA Shuttle Radar Topography Mission
SSP	Shared Socio-economic Pathways
TII	transition intensity index
TM	Thematic Mapper
TSS	True Skill Statistic
UA	user's accuracy
UFHB	Université Félix Houphouët-Boigny
UICN	International Union for Conservation of Nature
WASCAL	West African Science Service Centre on Climate Change and Adapted Land Use
WMF	Wari-Maro Forest

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Abstract

The white-thighed colobus (*Colobus vellerosus*), a Critically Endangered primate endemic to West Africa, faces imminent extinction due to rapid habitat loss, intense anthropogenic pressures, and accelerating climate change. For several years, it has been listed among the IUCN's top 25 most endangered primates, underscoring the need for urgent and effective conservation actions. This dissertation presents the first comprehensive, multi-scalar assessment of the species' climatic niche, land-use dynamics within its distribution range, habitat connectivity, and genetic status. By integrating species distribution modelling, long-term landscape analysis, connectivity modelling, and population genetics, this work establishes a robust, spatially explicit foundation for needed conservation interventions. First, using ensemble species distribution models (SDMs) that disentangle climatic from anthropogenic effects, I show that precipitation during the driest month, annual mean temperature, and forest cover are the primary drivers shaping the distribution of *C. vellerosus*. Current anthropogenic pressures have already led to the loss of 36% of climatically suitable habitats, and even under an optimistic climate scenario, suitability is projected to decline by approximately 73% by 2050. Second, a 36-year land-cover analysis (1989-2025, corresponding to four generations of *C. vellerosus*) reveals pervasive landscape transformation across the species' central Benin range. Forest cover has declined by 50% and savannah by 35%, while cropland expanded by 128%. Transition intensity analysis shows that conversions from forest to cropland and forest to settlement are dominant. This aligns with local perceptions, as 60% of surveyed residents acknowledged forest decline, though the accuracy of these perceptions varied only slightly with socioeconomic factors. These findings emphasise that anthropogenic land-use change is both extensive and community-recognised, yet insufficiently integrated into current management strategies. Third, a regional comparison of *C. vellerosus* and its parapatric congener *C. polykomos* demonstrates major mismatches between climatically suitable areas and current distributions, with both species exhibiting severe future range contractions. Although substantial areas of climatically suitable forest persist, 48–83% of these regions fall outside protected areas, underscoring potential opportunities for strategic habitat protection and planning for reintroduction. Fourth, through the modelling of functional connectivity via resistance surfaces in central Benin, least-cost paths, circuit theory, and graph-theoretic metrics, I demonstrate that fragmentation has resulted in a dual landscape: highly permeable corridors in the south (linking Monts-Kouffé, Kikélé, and Wari-Maro) contrasted with isolation in the north. The Monts-Kouffé–Wari-Maro complex emerges as the primary connectivity nucleus, with several medium-sized patches functioning as vital stepping stones, whose loss would

disproportionately impair network integrity. Furthermore, mitochondrial DNA analysis of the two observable populations in central Benin (KSF and OKF) reveals extremely low genetic diversity, characterised by only one cytb haplotype and two nearly identical D-loop haplotypes, indicative of a severe founder effect and prolonged isolation. This significantly low mitochondrial variation highlights the urgent need for a comprehensive species-wide genetic assessment and the exploration of translocation-based genetic rescue strategies. Across all analyses, this dissertation illustrates that *C. vellerosus* faces significant threats from the simultaneous impacts of climate-driven niche contraction, long-term land-use transformation, severe habitat fragmentation, and dramatically reduced genetic diversity. Conservation priorities identified include: (1) protecting and restoring climatically resilient forest refugia, (2) enhancing community-managed and unprotected forests within connectivity networks, (3) establishing ecological corridors informed by functional connectivity outputs, (4) developing reintroduction and genetic rescue programs aligned with IUCN standards, and (5) integrating long-term ecological monitoring with community engagement and adaptive governance. Collectively, this work provides the first comprehensive conservation framework for *C. vellerosus*, from landscape to genome, offering actionable guidelines to prevent the extinction of one of West Africa's most imperilled primates.

Keywords: Species Distribution Modelling, Habitat Fragmentation, Functional Connectivity, Genetic Diversity, *Colobus vellerosus* Conservation.

INTRODUCTION

The Earth's biodiversity is currently undergoing an unprecedented crisis characterised by rapid and widespread decline. This crisis is primarily caused by human activities, such as land conversion, habitat degradation, overexploitation, pollution, and poaching (Barnosky et al., 2011; Teletchea & Robert, 2019). Over the last few decades, the severity of this biodiversity crisis has become increasingly obvious, with current extinction rates of species estimated to be 1,000 times higher than the natural background rates, and future extinction rates projected to reach up to 10,000 times higher (Barnosky et al., 2011; De Vos et al., 2015). Among the taxa most severely affected by this significant biodiversity crisis, more than 66% of the world's primate species are most vulnerable, and more than 19% of them have above critically endangered (CR) conservation status according to the International Union for Conservation of Nature (IUCN) Red List (IUCN, 2025).

For instance, *Piliocolobus waldroni* (Miss Waldron's red colobus) is possibly extinct. Once found in eastern Côte d'Ivoire and western Ghana, the last known specimen was killed in 2002 near the Tanoé Swamp Forest. Despite reports of vocalisations in 2008, there have been no verified sightings for over forty years (McGraw, 2005; Oates et al., 2000, 2020). *Piliocolobus waldroni*'s conservation status highlights the extinction risk and the impact of human activities on primates.

Across Africa, many primate species continue to face similar precarious futures, despite international conservation initiatives, including the establishment of protected area (PA) networks, species action plans, and regional agreements (Morgan et al., 2013), Recent assessments by Mittermeier et al. (2024) identified twenty-three continental Africa primate species among the twelve editions of the World's 25 Most Endangered Primates since 2000, underscoring the continuing vulnerability of Africa's primate fauna (Mittermeier et al., 2022; Schwitzer et al., 2017; Wich & Marshall, 2016; L. Zhang et al., 2019).

The white-thighed colobus, *Colobus vellerosus*, is classified as Critically Endangered and has been listed as one of the top 25 World's primates at risk of extinction for several years (Matsuda Goodwin et al., 2020; Mittermeier et al., 2024). The geographic range of this primate species is extremely fragmented and stretches out from the interfluvial zone between Sassandra and Bandama Rivers and its tributary, the N'zi, in Côte d'Ivoire to the Dahomey Gap countries, Ghana, Togo and Benin. The fact that this colobus monkey still occurs in western Nigeria is uncertain (Matsuda Goodwin et al., 2020). Our investigations through the western Nigeria forests, namely Opara Game Reserve, Old Oyo National Park, and Oba Hill National Park, ended up with no encounter of *C. vellerosus* individuals (Accrombessi and Zinner 2025, unpublished). The species is held sacred at three sites in three different countries in its

geographic range; Kikélé Sacred Forest (KSF) in Benin, Dinaoudi sacred grove in Côte d'Ivoire, and Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana (Djègo-Djossou et al., 2012; Gonedelé Bi et al., 2010; Wong & Sicotte, 2006). Nonetheless, the region it inhabits has a dense and rapidly growing human population. Forest destruction and fragmentation have been extensive, and the hunting of wildlife, including primates, is uncontrolled in most places (Matsuda Goodwin et al., 2019). In KSF in Benin, for instance, hunting in adjacent forests, disposing of garbage and trash, using the forest as a toilet, and regular usage of the forest as grazing ground for cattle are some human activities which have reduced the population size of *C. vellerosus* to just two social groups (Ota, 2020).

Besides these threats, climate change is a delocalised, multi-faceted driver to add to the list because it also exposes forest-dwelling primates to climatically unsuitable conditions (Carvalho et al., 2019, 2021; Kiribou et al., 2024). Moreover, it is obviously known that habitat fragmentation triggers an abrupt decrease in genetic diversity due to isolation and reduced gene flow (Lino et al., 2019; W. Wang et al., 2017). As a result, species' ability to adapt to environmental changes is often compromised, and population and species viability can be hypothecated. Such a situation may even lead to species extinction (de Oliveira, 2017; Frankham, 2005; Frankham et al., 2010; Rodrigues, 2012).

According to Schwitzer et al. (2019), the encounter rate of *C. vellerosus* across seven PAs throughout its geographic range has experienced a staggering decline of 87.2% over the last four decades. Similarly, Matsuda Goodwin et al. (2019) documented a population reduction of more than 80% in *C. vellerosus* during the past three generations from 1992 to 2019. This drastic reduction in the population size has been driven by a combination of intensive hunting pressures and deteriorating habitat quality across its geographic range. These primary threats have undoubtedly contributed to the extinction of the species in Burkina Faso and Nigeria, the greater reduction of the population by more than 90% in Ghana, and the complete disappearance of the population from all national parks in Côte d'Ivoire. However, recent surveys conducted by Matsuda Goodwin et al. (2020) reported that a population of *C. vellerosus* is beginning to recover in the Comoé National Park in Côte d'Ivoire. Since 2004, the species has not been observed in several forests where it was previously found, including Ouémé Supérieur Forest, Mont-Kouffé, Wari-Maro, and Pénéssoulou Classified Forests in Benin, Bosomoa Forest Reserve, Bui National Park, and Digya National Park in Ghana (Djègo-Djossou, 2013; Matsuda Goodwin et al., 2020). The remaining populations in the KSF and the Okuta Kobunan Forest (OKF) in central Benin are now extremely small and isolated (Accrombessi, Toyi, Kone, Zinner, et al., 2025).

The *in-situ* conservation actions that benefit *C. vellerosus* in its inhabiting forests are therefore limited in ensuring its preservation. Urgent conservation measures are then needed to prevent further local extinctions. The research problem thus posed is: "What are the appropriate conservation measures to preclude the global extinction of *Colobus vellerosus* by ensuring its preservation over its geographical range?". This problem justifies the basis of this doctoral research entitled: "Effects of climate change and forest fragmentation on the ecology and genetic diversity of white-thighed colobus, *Colobus vellerosus*, West Africa". To resolve this problem, it is essential to have an in-depth understanding of the ecological niche characteristics of the species, land cover changes and forest fragmentation within the species' geographic range, its genetic diversity and population structure, and the landscape configuration for potential corridor restoration across its habitats. None of these research lines related to the species has yet been explored. The current doctoral research will enable the acquisition of knowledge and techniques necessary for *C. vellerosus* in-situ and ex-situ conservation, and on how climate change can impact the suitable forested areas within the geographic range of *C. vellerosus* populations.

Main objective

The primary objective of this thesis is to examine the combined effects of climate and land-use changes on the distribution of suitable habitats (forested areas), habitat fragmentation and connectivity, and genetic diversity of *Colobus vellerosus* across its distribution range, thereby supporting effective conservation planning and management.

Specific objectives

The specific objectives are:

SO1: to determine the impacts of climate change and anthropogenic factors on the suitable habitats of *C. vellerosus* across its geographic range under current and future climate scenarios;

SO2: to assess historical and contemporary land-use and land-cover (LULC) changes within the distribution range of *C. vellerosus* in central Benin from 1989 to 2025;

SO3: to identify climatically and ecologically suitable habitats, both within and outside protected areas, that could support population persistence and potential reintroduction;

SO4: to evaluate current habitat connectivity and identify potential forest corridors that, if reforested or restored, could enhance population connectivity and reduce extinction risk for *C. vellerosus* in central Benin;

SO5: to analyse the genetic diversity and structure of remnant *C. vellerosus* populations in central Benin to infer gene flow and inform conservation.

Research questions

The research questions which underlie the specific objectives are as follows:

1. What climatic variables determine the distribution of *C. vellerosus* within its geographic range?
2. To what extent have anthropogenic activities reduced the potential distribution of *C. vellerosus*?
3. How will climatically suitable habitats of *C. vellerosus* change over time under optimistic and pessimistic climate scenarios?
4. Which currently forested areas and protected forests provide stable climatic and ecological conditions suitable for the long-term survival or reintroduction of *C. vellerosus* populations under climate change?
5. What are the spatio-temporal patterns and magnitudes of forest loss, conversion, and fragmentation in *C. vellerosus* habitats in central Benin between 1989 and 2025?
6. Are the habitats of *C. vellerosus* currently connected, and what are the potential corridors to restore for creating a meta-population of *C. vellerosus* in central Benin?
7. What are the levels of genetic diversity and differentiation among the remnant *C. vellerosus* populations in central Benin?

Hypotheses

1. Anthropogenic pressures have significantly reduced the extent of suitable habitats of *C. vellerosus*.
2. Climatically suitable habitats of *C. vellerosus* will contract and shift under climate projections.
3. A limited number of refugial areas within and outside the current protected area network maintain stable climatic conditions and high habitat suitability that could serve as strongholds or reintroduction sites for *C. vellerosus*.
4. Forested areas have been significantly fragmented and mainly converted into agricultural lands and settlements between 1989 and 2025 in central Benin.
5. Existing *C. vellerosus* populations in central Benin are isolated by highly fragmented landscapes, but a few remnant forest patches and riparian corridors could provide strategic pathways for restoring population connectivity.

6. Populations of *C. vellerosus* in central Benin experience limited gene flow and low genetic diversity.

Workflow of this doctoral research

The present PhD research combines in an integrative manner species distribution modelling, geographical informatic systems (GIS), land use and land cover change analysis, connectivity and corridors assessment, and genetic analysis (Fig. 1).

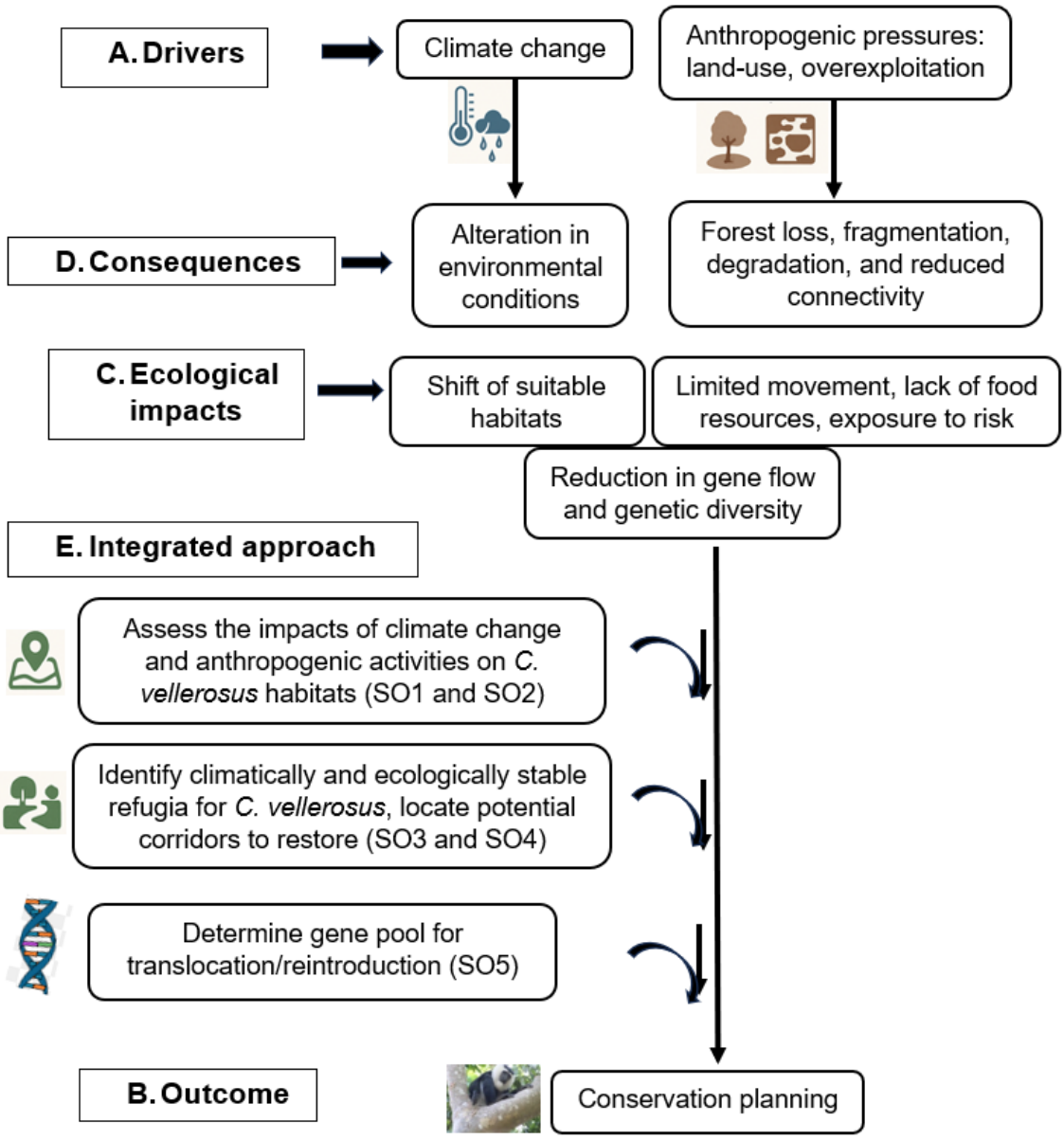

Figure 1. Conceptual workflow of the research

Specific objectives 1 and 2 address the climatic and ecological dimensions by modelling current and future habitat suitability and quantifies spatio-temporal land-use and land-cover changes to

reveal historical drivers of habitat degradation and fragmentation. Specific objective 3 identifies potential refugia under current and projected climate scenarios. Specific objective 4 focuses on landscape connectivity, using resistance-based and corridor modelling to evaluate functional linkages between remaining habitats. Finally, Specific objective 5 assesses genetic diversity and population structure to infer gene flow, providing critical insights into population viability. Together, these objectives form a logical analytical pathway, from climate and land-use pressures to ecological and genetic responses, thereby guiding evidence-based conservation and restoration strategies for *C. vellerosus* across its distribution range.

Structure of the thesis document

Besides the general introduction, the conclusion and perspectives, this thesis is organised into three main parts, encompassing five chapters, which together build a coherent progression from background knowledge to methodological implementation, interpretation and discussion of results, and conservation implications (Fig. 2).

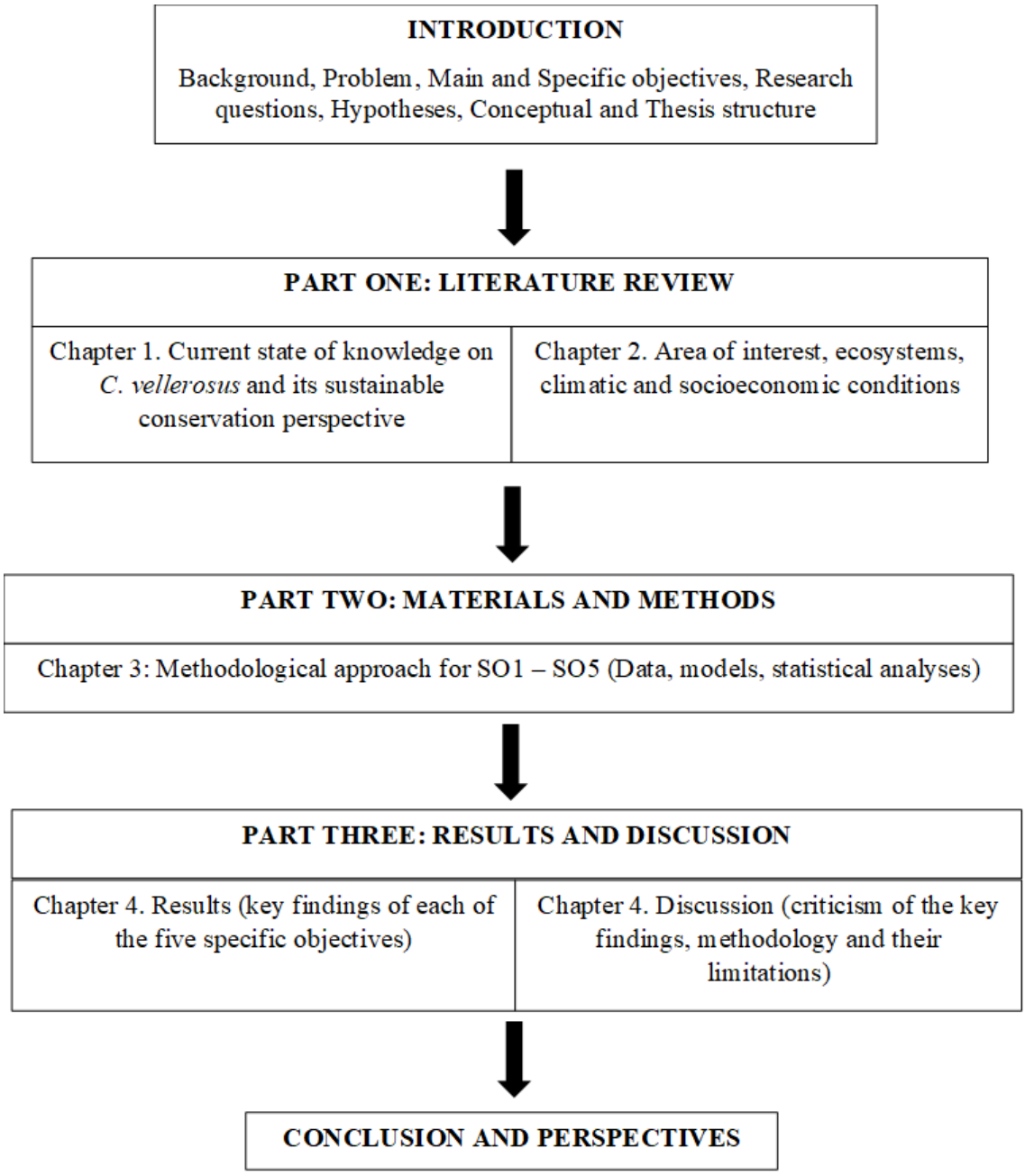

Figure 2. Structure of the thesis

To address the research problem and objectives outlined above, it is essential to first situate the study within the existing body of knowledge on *C. vellerosus*, its ecology, and conservation status. Part One, therefore, presents a comprehensive review of the relevant literature. Chapter 1 presents the current state of knowledge on *C. vellerosus*, including its taxonomy, distribution, ecology, threats, and conservation status, and discusses potential perspectives for its sustainable conservation. Chapter 2 describes the study area, encompassing the ecological, climatic, and socio-economic context of the landscapes where *C. vellerosus* persists, highlighting key environmental and anthropogenic factors influencing its habitats.

Part Two outlines the methodological framework and analytical approaches implemented during this research, drawing on insights from the literature review. Chapter 3 describes the data sources, materials, and methods used for each specific objective. Each subsection aligns with one of the five specific objectives. We, thus, associated each research hypothesis with its corresponding methodological approach.

The analyses described in Part Two form the basis for Part Three, which presents and interprets the key findings of this study. Chapter 4 reports the results obtained for each specific objective, while Chapter 5 is devoted to general discussion, criticism of the methodology and the limitations of the study. It discusses the findings in the context of existing literature, conservation implications, and future perspectives for the sustainable management of *C. vellerosus* populations across West Africa. Similarly, the critical aspects of the study methodology adopted and the limitations of the results obtained are exposed.

PART ONE: LITERATURE REVIEW

Chapter 1. Current state of knowledge on *Colobus vellerosus* and its sustainable conservation perspectives

1.1. Taxonomic history of *Colobus vellerosus*

Colobus vellerosus was originally described by Isidore Geoffroy Saint-Hilaire in 1830 as *Semnopithecus vellerosus*, based on specimens collected in West Africa (Geoffroy Saint-Hilaire, 1830). The species has since been assigned several associated names and has undergone multiple taxonomic revisions (Table 1). In the mid-nineteenth century, when the genus *Colobus* was established by Illiger (1811) to accommodate African leaf-eating monkeys distinct from Asian *Semnopithecus*, *vellerosus* was transferred to this genus, becoming *Colobus vellerosus* (Mammal Diversity Database 2025, https://www.mammaldiversity.org/taxon/1000640/).

Table 1. Different scientific names attributed to *Colobus vellerosus* over time, and their related information

Scientific name	Author	Year	Comments
Semnopithecus vellerosus	I. Geoffroy Saint-Hilaire	1830	First taxonomic name after the original description based on a specimen from West Africa
Semnopithecus bicolor	Wesmael	1835	Early protonym based on an alternative description
Colobus leucomeros	W. Ogilby	1838	Published synonymy circa 1838 and, afterwards, considered a misapplied name
Colobus leucomerus	W. Ogilby	1838	Orthographic misspelling of the above, which was considered a variant
Colobus bicolor	J. E. Gray	1868	Taxonomic attributed name stemming from the combination of previous names
Colobus vellerosus	W.C.H. Peters	1876	Orthographic combination, with the taxon not recognised as valid and distinct.
Pterycolobus vellerosus	A.T. de Rochebrune	1887	Alternative generic name, synonymised afterwards with *Colobus*
Colobus polykomos dollmani	E. Schwarz	1927	Morphology description of a taxon considered as a hybrid of *C. vellerosus* and *C. polykomos*

Source: Groves (2007), and Mammal Diversity Database (2025)

Before 1927, two separate species of black-and-white colobus were believed to exist in West Africa: *Colobus polykomos* (E. A. W. Zimmermann, 1780) and *Colobus vellerosus* (I. Geoffroy Saint-Hilaire, 1830). *C. polykomos* was thought to inhabit regions from southern Senegal, Guinea-Bissau, Guinea, Sierra Leone, and Liberia, to the Sassandra River in Côte d'Ivoire, while *C. vellerosus* was found between the Sassandra and the East of Bandama Rivers in Côte d'Ivoire, extending into Ghana, Togo, and Benin, and reaching south-western Nigeria.

However, in 1927, the description of a colobus variant (*C. polykomos dollmani*) in Côte d'Ivoire led to the reclassification of *C. polykomos* and *C. vellerosus* as a single species (*C. polykomos*) due to presumed significant subspecific variation (Booth, 1954). Thus, during the early twentieth century, taxonomists considered *C. vellerosus* to be a subspecies of *C. polykomos*, referring to it as *C. polykomos vellerosus*. Subsequent studies examining pelage colouration, cranial morphology, and vocalisation patterns revealed consistent diagnostic differences between *C. vellerosus* and *C. polykomos* (Oates & Trocco, 1983). These findings led to the recognition of *C. vellerosus* as a distinct species. Recent research by Groves et al. (1993) further formalised this classification, and modern authorities, including the Mammal Diversity Database and IUCN Red List, now universally recognise *C. vellerosus* (I. Geoffroy Saint-Hilaire, 1830) as a valid and distinct species within the genus *Colobus*. The species is currently placed among the five recognised black-and-white colobus monkeys: *C. guereza*, *C. polykomos*, *C. angolensis*, *C. satanas*, and *C. vellerosus* (T. l. Saj & Sicotte, 2013a). The white-thighed colobus, *Colobus vellerosus* (I. Geoffroy Saint-Hilaire, 1830), is classified within the order Primates, suborder Haplorhini, and family Cercopithecidae, within the subfamily Colobinae and tribe Colobini (Mammal Diversity Database, 2025).

Table 2. Taxonomic classification of *Colobus vellerosus*

Kingdom	: Animalia
Phylum	: Chordata
Class	: Mammalia
Subclass	: Theria
Infraclass	: Placentalia
Magnorder	: Boreoeutheria
Superorder	: Euarchontoglires
Order	: Primates
Suborder	: Haplorhini
Infraorder	: Simiiformes
Parvorder	: Catarrhini
Superfamily	: Cercopithecoidea
Family	: Cercopithecidae
Subfamily	: Colobinae
Tribe	: Colobini
Genus	: *Colobus*

1.2. Description of *Colobus vellerosus*

Initially documented by Geoffroy Saint-Hilaire (1830), *C. vellerosus* is an arboreal colobine known for its distinct morphological traits typical of African leaf-eating monkeys. Adults (Photos 1 and 2) are medium-sized and feature a predominantly black body, accented by a striking white patch on each upper thigh, which has earned them the common name "white-

thighed colobus". The species exhibits a similar colour pattern in both sexes. The white features at the upper thighs, sometimes described as grey by some researchers (Saj & Sicotte, 2013a), extend fully around the ischial callosities in males, and around the ventral and lateral margins with a break at the perineum and under the base of the tail in females. *Colobus vellerosus* has a long, all-white, prominently tufted tail and a wide, bushy, snowy-white circumfacial ruff (Photo 3). There is no whorl on the crown nor white colouration extending far back under the throat. Though there are no epaulettes, males display a few notably longer white hairs of an average of 10 to 15 cm on the shoulder, with shoulder hairs in females being marginally longer (Groves, 2007; Saj & Sicotte, 2013a). The tail length, measuring 124–152% of the head-body length, ranges from 81 to 97 cm, making it shorter than that of the King colobus (*C. polykomos*). The hair on the throat is thick, and the nose is long and convex. Head-body dimensions range from 56 to 64.5 cm for males and 58 to 66 cm for females, with weights of 8.4 to 9.9 kg for males and 7 to 8.3 kg for females (Anandam et al., 2013; Groves et al., 1993).

At birth, infants are completely white (Photo 4), but over the course of 7–11 weeks, they gradually shift to various shades of grey, ultimately developing black-and-white pelage by 12 weeks of age (Saj & Sicotte, 2013a).

Photo 1. Adult female of *Colobus vellerosus* in Kikélé village

(F. Darius Accrombessi, 2022)

Photo 2. Adult male of *Colobus vellerosus* in Kikélé Sacred Forest

(F. Darius Accrombessi, 2024)

Photo 3. Highlight of the snowy-white circumfacial ruff of the face of an adult *Colobus vellerosus*

(F. Darius Accrombessi, 2022)

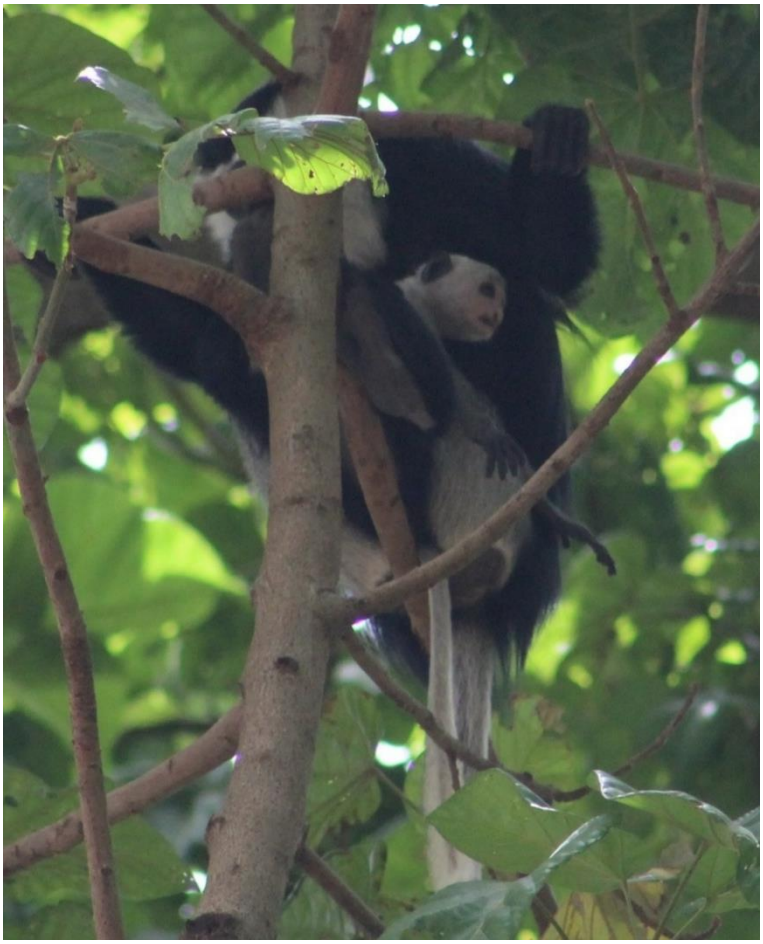

Photo 4. An infant of *Colobus vellerosus*, which is transitioning from white to grey and is carried by its mother in Kikélé Sacred Forest

(F. Darius Accrombessi, 2024)

1.3. Phylogeny and phylogeography

The current understanding of the phylogeny and phylogeography of colobines has been comprehensively documented by Roos and Zinner (2022). Here, we provide a brief overview to contextualise our study within the existing literature. *Colobus vellerosus* is part of the African colobine radiation, a lineage that diverged from Asian colobines approximately 12-10 million years ago (Ma) and is represented today by the genera *Colobus*, *Piliocolobus*, and *Procolobus* (Roos & Zinner, 2022). Molecular genetic studies indicate that olive colobus (genus *Procolobus*) and red colobus (genus *Piliocolobus*) form a cluster, while black-and-white colobus (genus *Colobus*) represents their sister lineage. *Colobus* is believed to have diverged from the *Procolobus*/*Piliocolobus* clade around 9–7.5 Ma. If the retroposon data scenario proposed by Roos et al. (2011) does not contradict the molecular analyses, it suggests a

hybridisation event occurred between the ancestors of *Colobus* and those of *Piliocolobus*/*Procolobus* before their ultimate separation. Phylogenetic relationships within the polytypic genera *Colobus* and *Piliocolobus* remain only partially resolved, with only a single molecular genetic study examining several African colobine species published to date (Ting, 2008). In his study, Ting (2008) employed a fragment of the mitochondrial genome approximately 4000 bp in length, and found strong evidence supporting an early divergence of *C. satanas* from the main lineage about 4 Ma, followed by the successive separations of *C. angolensis* and *C. guereza* around 2 Ma, and finally, the divergence of *C. polykomos* and *C. vellerosus* approximately 0.2 Ma.

From a phylogeographic perspective, *C. vellerosus* shows population structuring that likely results from historical climatic variability. The distribution of its populations reflects alignment with geographic barriers throughout West Africa. The extension of its range eastwards from the Bandama River through the Dahomey Gap corroborates previous hypotheses suggesting that the Bandama and Sassandra rivers functioned as significant biogeographic barriers for its distribution. Researchers argue that these barriers contributed to the differentiation of *C. vellerosus* from the western *C. polykomos* (Booth, 1954; Groves, 2007; Groves et al., 1993). Additionally, the Dahomey Gap, a naturally occurring savannah corridor across Ghana, Togo, and Benin, has long been recognised as a major barrier to the dispersal of forest-dependent mammals (Campbell et al., 2008), likely restricting historical connectivity among *C. vellerosus* populations and constraining the species' east-west expansion. These ecological and historical constraints have likely shaped the species' contemporary phylogeographic structure. Indeed, the most ancient intra-generic splits in *Colobus* are found in western Africa (Roos & Zinner, 2022). Although range-wide genomic data from *C. vellerosus* remain limited, existing evidence suggests reduced gene flow among isolated forest patches (Accrombessi, Toyi, Kone, Zinner, et al., 2025), particularly where fragmentation has eliminated natural corridors. Such patterns highlight the need for maintaining or restoring landscape connectivity to protect the evolutionary resilience of *C. vellerosus* across its range.

1.4. Geographic range and populations

Colobus vellerosus is endemic to West Africa, with a distribution spanning from the Sassandra and Bandama interfluvial areas of Côte d'Ivoire eastwards to Ghana, Togo, and Benin, and possibly extending marginally into southwestern Nigeria (Matsuda Goodwin et al., 2020). The species' historical range was substantially larger, but extensive deforestation and land conversion have resulted in severe range contraction and fragmentation over the past century.

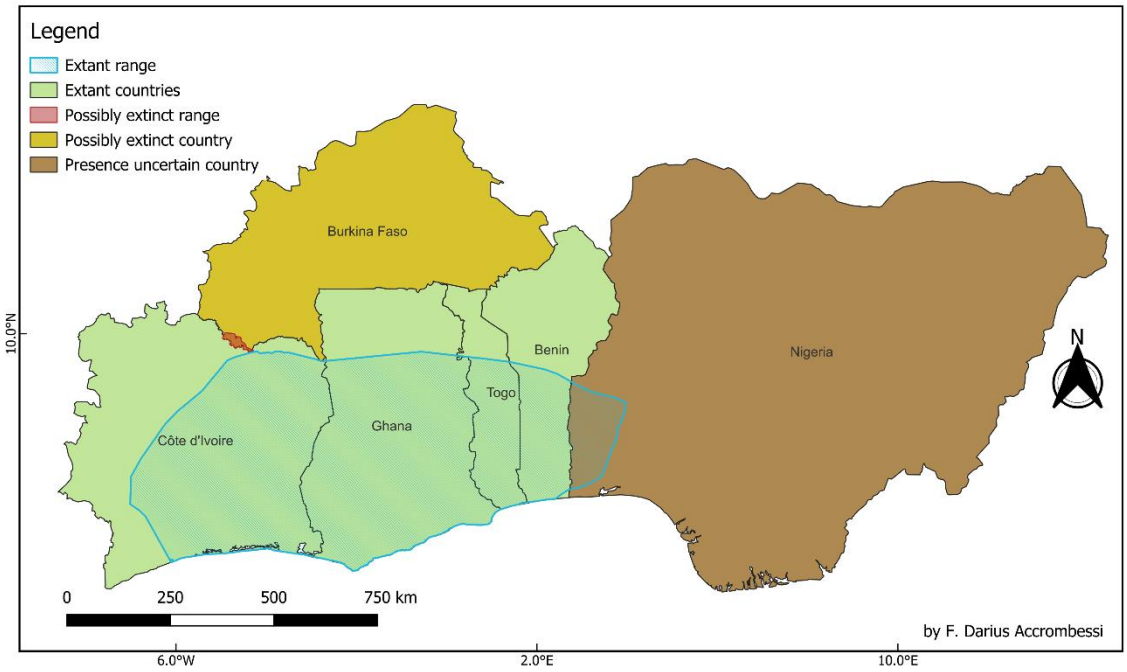

Figure 3. Overview of the IUCN-defined distribution range of *Colobus vellerosus*

To date, *Colobus vellerosus* has largely been extirpated from protected areas in Côte d'Ivoire, except for Comoé National Park, where some groups were observed between December 2018 and January 2019 (Matsuda Goodwin et al., 2020). It also persists in the Tanoé-Ehy swamp forest and two sacred groves, totalling approximately 45 individuals. In Ghana, over 50% of protected areas that once supported this species have experienced significant declines, with an 87% reduction in encounter rates in six forest reserves over the past three decades (Matsuda Goodwin et al., 2020). However, a recent enumeration conducted by Kankam et al. (2023) indicated a growing population of 581 individuals in the BFMS. In Togo, the species is still present in the Togodo protected area and the Yikpa-Dzigbe community forest, although it has disappeared from Missahohe, Assime and Assoukoko forests (Segniagbeto et al., 2017). Our investigations conducted in May-June 2024 resulted in no sightings in the Malfakassa sector of the Fazao-Malfakassa National Park, and the local community reported that their last observations of the species occurred before 2010. In Benin, we identified two groups totalling 29 individuals in the KSF and an additional group of 8 individuals in the OKF during our investigations from March to April 2024. Our surveys, in the framework of this doctoral research, in the Wari-Maro, Pénéssoulou, Lokoli, and Lama Classified Forest over the period from December 2022 to December 2023 did not yield any encounters with *C. vellerosus*. However, we did hear the species' morning calls in the Lama Classified Forest, suggesting that a small number of individuals may still inhabit this forest, and their observation is likely limited

by the forest's evergreen characteristics. In Nigeria, we also conducted surveys at Opara Game Reserve and Old Oyo National Park. However, the existence of the reportedly small populations in Old Oyo NP and Opara Game Reserve remains uncertain. Our investigations in May 2024, which included three western Nigeria forests, namely Opara Game Reserve, Old Oyo National Park, and Oba Hill National Park, did not yield any encounters with the species (Accrombessi and Kazeem, unpublished work). It appears that *C. vellerosus* may be extinct in Burkina Faso (Ginn & Nekaris, 2014). The overall estimated population of *C. vellerosus* ranges from 850 to 1,150 individuals, and is likely to be below 1,500 when accounting for unsurveyed areas (Matsuda Goodwin et al., 2020).

1.5. Ecology, behaviour, and habitat

Colobus vellerosus inhabits a variety of forested ecosystems throughout West Africa, including lowland rainforests, swamp forests, semi-deciduous and dry forests, riparian gallery forests, as well as fragmented forests (Fashing, 2022). This species demonstrates remarkable ecological adaptability, thriving in both minimally disturbed evergreen forests and those that are degraded. However, *C. vellerosus* is strictly arboreal, showing a strong preference for tall-canopy vegetation and depending on continuous arboreal pathways for efficient movement. While colobus monkeys may occasionally descend to the ground to navigate between forest patches or to feed (Teichroeb, 2002), *C. vellerosus* typically does so only infrequently to cross gaps between trees. When they do descend, they tend to be vigilant due to predation risk, often issuing alarm calls in response to small or sudden disturbances (Teichroeb & Sicotte, 2012). *Colobus vellerosus* demonstrates a clear preference for roosting in tall arboreal habitat patches. Typically, the species selects trees with an average height of 22.53 ± 3.76 m and trunk diameters averaging 112.07 ± 14.23 cm. Their selectivity indicates that not all large or tall trees are preferred as sleeping sites (Djègo-Djossou et al., 2015; Nobime et al., 2011). This reliance on specific structural habitat characteristics renders them particularly susceptible to the impacts of habitat fragmentation and edge effects.

Regarding the diet, *C. vellerosus* is the most predominantly folivorous of colobine monkeys (Fashing, 2022). Throughout the year, the species consumes both young and mature leaves from a variety of tree species. The species significantly prefers young leaves. The intake of other plant components, such as fruits and seedpods, is more seasonal. *Colobus vellerosus* relies on mature leaves in the period of food scarcity, further reflecting its dietary flexibility in response to changing resource availability (Saj & Sicotte, 2007). Research conducted at Boabeng-Fiema indicates that *C. vellerosus* is the most predominantly folivorous species

among West African black-and-white colobus, with 79% of its diet comprising leaves (Saj & Sicotte, 2007). However, at the KSF in Benin, its diet appears to be more balanced, with 53% leaves, and incorporates other items such as fruits, seeds, ants, buds, bark, flowers, gum, and inflorescences (Djègo-Djossou et al., 2015). All the dietary studies on *C. vellerosus* were carried out in fragmented forests; therefore, there is no comparison with the diet of the species in continuous forests.

Socially, *C. vellerosus* typically forms multi-male, multi-female groups, although both the composition and size of these groups can vary significantly across different sites. This variation is closely linked to habitat structure and the distribution of food resources (Wong & Sicotte, 2006). Teichroeb (2009) also discovered that within-group scramble competition for food limits group size, while social factors played a larger role in influencing overall group composition, despite the species exhibiting a highly folivorous diet. On average, *C. vellerosus* groups consist of about 15 individuals; however, in heavily fragmented forests, groups tend to have fewer than 10 individuals. Most recent studies reported the maximum observed group sizes as 25 and 21 individuals at BFMS in Ghana (Kankam et al., 2023) and KSF in Benin (Accrombessi, Toyi, Kone, Zinner, et al., 2025), respectively. A summary of the social organisation of *C. vellerosus* populations is provided in Table 3. It is important to note that the study conducted in OKF was exploratory, and the research from the Lama Classified Forest only accounted for clearly observable individuals in a continuous evergreen forest.

Table 3. Social organisation of *C. vellerosus* from available studies

(For BFMS and KSF, the most recent data have been considered since there are several available studies on these sites)

Study site				**Group composition**						**References**
	Group size			**Adult males**		**Adult females**		**Immatures**		
	mean	**range**	**N**	**mean**	**range**	**mean**	**range**	**mean**	**range**	
Bia, Ghana	16	16	2	3.0	2-4	6.5	6-7	6.5		(Olson, 1980)
BFMS, Ghana	16.7	9-25	27	2		5.1		6.4		(Kankam et al., 2023)
SFF to BFMS, Ghana	14.4	9-23	9	1.2		5.2		4.7		(Kankam et al., 2023)
KSF, Benin	14.5	8-21	2	3	2-4	5.5	4-7	2	2	(Accrombessi, Toyi, Kone, Zinner, et al., 2025)
OKF, Benin	8	8	1							(Accrombessi, Toyi, Kone, Zinner, et al., 2025)
Lama, Benin	7.5	5-10	2					1.5	1-4	(Djègo-Djossou, 2013)
Comoé, Côte d'Ivoire	6.8	3-11	5							(Saj & Sicotte, 2013b)

SFF=Surrounding Fragmented Forest

Home range size varies considerably depending on forest type and the extent of anthropogenic disturbance, ranging from 11 hectares in the fragmented BFMS (Teichroeb & Sicotte, 2009; Wong & Sicotte, 2006) to 48 hectares in the continuous Bia Forest (Olson, 1980). The study group in the continuous forest occupied a home range that was more than four times larger than the average home range of five study groups in the fragmented forest (11 hectares). In fragmented landscapes in Ghana, groups in smaller forest fragments tended to spend less time moving, more time resting, and fed more on lianas compared to those groups in BFMS. Additionally, the home ranges of these fragment groups were generally smaller than those of the BFMS groups (Teichroeb & Sicotte, 2009; Wong et al., 2006; Wong & Sicotte, 2007).

Groups of *C. vellerosus* at BFMS exhibit evidence of movement between small forest fragments (Wong & Sicotte, 2006), suggesting that some degree of inter-fragment connectivity can facilitate gene flow, even in heavily disturbed landscapes. Daily travel distances for *C. vellerosus* are reported to be around 359 (Fashing, 2022), illustrating their generally limited yet

variable patterns of displacement in relation to habitat structure and resource availability. The longest mean daily movements typically occur between 1700 and 1730 m (Teichroeb, et al., 2012). Dispersal in this species is notably sex-biased, with males leaving their natal groups, although female dispersal has also been documented. Since these dispersal dynamics can significantly influence gene flow and the preservation of genetic diversity in fragmented habitats, we will further explore these patterns in the upcoming subsection.

1.6. Sex-biased dispersal and genetic diversity in *Colobus vellerosus* populations

Behavioural evidence suggests that dispersal patterns are sex-biased in *C. vellerosus* and might, therefore, influence gene flow within and between their populations. Teichroeb et al. (2009) found at Boabeng-Fiema, Ghana, that most female emigrants are subadult or nulliparous individuals, whereas Sicotte et al. 2017) revealed that female emigration typically results from gradual takeovers involving multiple males. However, successful immigration into established groups is rare and often met with resistance from resident females. This limited female movement constrains the introduction of new maternal haplotypes and hinders mitochondrial gene flow between groups. Further, Wikberg et al. (2012) demonstrated that while some females remain philopatric, instances of female dispersal do occur, though they seldom result in the establishment of new maternal lineages. To date, no dedicated study has yet examined the female dispersal behaviour in the Kikélé population, leaving its extent and success largely unknown. These patterns indicate that the potential for replenishing mitochondrial diversity through female dispersal is exceedingly low. Potential male immigration events do not contribute to mtDNA diversity. However, nuclear genetic markers may retain greater diversity through rare female immigration events or male-mediated gene flow.

In addition to the dynamics of female dispersal, an increasing body of behavioural studies deepens our understanding of the male dispersal system in *C. vellerosus* and its potential effects on genetic structure. Long-term studies conducted at Boabeng-Fiema indicate a male-biased dispersal pattern within this species: males regularly emigrate and immigrate over multi-year periods, and incursions by males into neighbouring groups are an integral aspect of the dispersal process (Teichroeb et al., 2011). Teichroeb et al. (2011) documented numerous instances of male emigration and immigration across seven groups over a decade, and subsequent research (Arseneau-Robar et al., 2024; Teichroeb et al., 2014; Teichroeb et al., 2012) elaborated on how these male incursions vary with age, rank, the presence of all-male bands, between-group encounters, female activism and dominance. Non-alpha males tend to engage in exploratory incursions to evaluate breeding or dispersal opportunities, whereas alpha

males typically undertake shorter, more aggressive incursions aimed at advertising their quality or defending their status (Teichroeb et al., 2011, 2014). Additionally, male coalitions and affiliative relationships among males significantly impact successful immigrations and takeovers (Saj & Sicotte, 2005; Teichroeb et al., 2011). These patterns observed at Boabeng-Fiema suggest that male-mediated nuclear gene flow could play a substantial role in certain populations.

The situation at Kikélé appears to be distinct. Matsuda Goodwin and Chabi Ota (2020) documented only six male incursions over nine months, with most occurring after an instance of infanticide; under stable social conditions, such male incursions were exceedingly rare. This discrepancy indicates that male dispersal and intergroup movement in the Kikélé populations are currently limited, perhaps owing to the very small number of neighbouring groups, significant landscape fragmentation, or anthropogenic pressures that may decrease the frequency or success of male movements. If male dispersal is indeed constrained within the Kikélé populations, likely, nuclear gene flow will also be diminished, in addition to the already low mitochondrial exchange stemming from infrequent female immigration.

1.7. Threats and conservation status

The most important threats the white-thighed black-and-white colobus populations are facing are intensive hunting and habitat destruction, and degradation leading to habitat fragmentation across the species' distribution range. These main threats triggered the species population reduction of more than 80% over the past three generations (1992-2019). This is what prompted the IUCN to upgrade the species' conservation status from "Vulnerable" to "Critically Endangered" in 2019, two categories upgrading justified by the high degrees of threats (Matsuda Goodwin et al., 2020). Of these major threats, uncontrolled hunting has been singled out as the leading cause of the species' disappearance in all range countries (Oates, 2011). Furthermore, the species' distribution range is highly fragmented, and it occurs in only a limited number of protected areas and community forests in each range country (Schwitzer et al., 2019). Although the species is held sacred at Dinaoudi sacred grove in Côte d'Ivoire (Gonedelé Bi et al., 2010), Boabeng-Fiema Monkey Sanctuary in Ghana (Saj et al., 2006) and Kikélé Forest in Benin (Djègo-Djossou et al., 2012), its range countries have a dense and rapidly growing human population; forest destruction and fragmentation have been extensive, and the illegal hunting of wildlife is uncontrolled in most places, even in the vicinity of protected areas (Matsuda Goodwin et al., 2019). Natural predation also contributes to mortality: *C. vellerosus* constituted up to 10% of prey items identified in leopard scats at Comoé National Park in Côte d'Ivoire,

and it made up 5% of prey items found in lion scats at the same site (Bodendorfer et al., 2006). Currently, no protected areas in its distribution range have any in-situ conservation programmes for the species, and there are no ex-situ populations.

In Benin, Djègo-Djossou and Sinsin (2009) revealed a decrease in *C. vellerosus* geographical extent from 56,000 km^2 to 9,000 km^2 between 1984 to 1999, corresponding to a reduction of more than 80% in the species' range. The species' home range in Benin included six classified forests: Monts Kouffé, Wari-Maro, Lama, Pénéssoulou, Ouémé Supérieur, Ouémé Boukou and unprotected forests as follows: Bonou swamp forest, Upper Ouémé River swamp forests, Lokoli swamp forest and Kikélé Forest (Djègo-Djossou, 2013). However, surveys conducted in July 2016 resulted in no encounters of the species in four of these classified forests, namely Pénéssoulou, Monts Kouffé, Wari-Maro, Ouémé Superieur and the Lokoli swamp forest (Matsuda Goodwin et al., 2020). Our surveys during this thesis work also resulted in no encounter of the species in Pénéssoulou, Monts Kouffé, Wari-Maroand the Lokoli swamp forest. As well, Recent wildlife inventory in the Pénéssoulou forest reserve found no white-thighed Colobus groups (Dossa et al., 2021). Very little is known about the species status in Benin, Bonou and the Upper Ouémé River swamp forests. Therefore, it is evident that, in Benin, the white-thighed colobus population is gradually being extirpated from protected and unprotected ecosystems.

1.8. Vulnerability of *Colobus vellerosus* to climate change

Climate change poses an escalating threat to *C. vellerosus*, exacerbating the species' already significant vulnerability to habitat loss, fragmentation, and human encroachment. Globally, climate change is expected to alter habitat suitability, intensify ecological stress, and cause demographic instability in primate populations (Campos et al., 2017; Graham et al., 2016; L. Zhang et al., 2019). The traits associated with heightened vulnerability, such as specialised diets, limited dispersal abilities, and reliance on forested habitats (Kamilar & Beaudrot, 2018; Korstjens & Hillyer, 2016), closely align with the ecological profile of *C. vellerosus* (Korstjens, 2019). As a strictly arboreal and predominantly folivorous species, *C. vellerosus* depends on stable forest structures and predictable leaf availability, both of which are sensitive to climate-induced shifts in precipitation and seasonality (Kalbitzer & Chapman, 2018; Korstjens & Hillyer, 2016).

Climate models for West Africa forecast an increase in the frequency of extreme heat events, persistent drying trends, and disrupted phenological cycles, all of which are likely to diminish both the availability and nutritional quality of leaves (Bernard & Marshall, 2020;

Campos et al., 2017), the primary component of the *C. vellerosus* diet. Reductions in leaf production or alterations in tree species composition may compel the species to expand its foraging range or rely more heavily on lower-quality foods, thereby heightening energetic stress and adversely impacting reproduction and survival. These risks are further intensified by ongoing habitat fragmentation, as isolated groups have limited capacity to adapt to shifting resource distributions across landscapes (Brook et al., 2008; Pacifici et al., 2017). Given that climate change is progressing at a pace that surpasses the climatic niche evolution observed in primates (Meyer & Pie, 2022), *C. vellerosus* is unlikely to adapt physiologically or behaviorally quickly enough to keep pace with rapid environmental changes.

In her study on the climate change effects on the genus *Colobus*, Korstjens (2019) predicted a significant decline in climatically suitable habitats for colobines in West Africa. From this study, West African colobines are expected to experience the contraction of their suitable habitats under both moderate and high emissions scenarios. The semi-deciduous and dry forests inhabited by *Colobus* species were identified as most vulnerable to climatic drying. Several existing suitable habitats for *Colobus* species are predicted to become unsuitable by 2050 due to projected reductions in precipitations and seasonality. *Colobus vellerosus* is thus position as one of the most climate-vulnerable taxa within the *Colobus* genus. This is because its range already falls within the Dahomey Gap, which is anticipated to experience some of the most severe climate driving forest declines. This pattern aligns with broader projections for tropical primates, as Pinto et al. (2023) demonstrate that species across tropical forest hotspots are expected to lose substantial climatically suitable range under future warming scenarios, reinforcing concerns that *C. vellerosus* may face significant range contraction. While Korstjens (2019) further notes that climate-driven shifts in vegetation may result in northward and upslope displacement of suitable habitats for *Colobus* species, this is unlikely for *C. vellerosus* given the highly fragmented or nonexistent forest corridors across Ghana, Togo, and Benin, and its low dispersal capacity (Kankam & Sicotte, 2013). As a result, the species may encounter a range squeeze, as retreating from increasingly unsuitable lowland forests becomes unfeasible due to human-created barriers.

Furthermore, there are evidences that climate change impacts forest regeneration and leaf chemistry. Young leaves are sensitive to water stress and elevated temperatures, which significantly impact their protein-to-fibre. Alterations in these nutritional parameters can significantly affect energy intake and reproductive success in highly folivorous primates (Kalbitzer & Chapman, 2018; Pacifici et al., 2017), , such as *C. vellerosus*. A dimension of particular concern for folivorous vulnerability relates to resting-time requirements. According

to Korstjens et al. (2010), folivorous primates require substantial daily resting periods to process low-quality, fibre-rich foods, leaving limited behavioural flexibility to adjust activity budgets under thermal stress. As temperatures rise, increased resting demands, as well as the need to avoid midday heat, may restrict the ability of *C. vellerosus* to allocate more time to foraging or travelling, thereby exacerbating energetic deficits under climate change. Unlike some tropical primates that utilise behavioural or physiological strategies, such as torpor or extensive microhabitat shifts, to cope with climatic stress (Blanco et al., 2018), *C. vellerosus* demonstrates limited behavioural flexibility. The species primarily increases resting time to satisfy its digestive needs (Wong & Sicotte, 2007), leaving it with little resilience against rising temperatures or declining food quality.

In summary, climate change is anticipated to synergistically interact with current human-induced pressures, leading to accelerated habitat degradation, jeopardising population viability, and complicating conservation efforts. To mitigate the long-term vulnerability of populations of *C. vellerosus*, management strategies should effectively include climate-resilient approach. Therefore, there is a need to identify and protect forest habitats that are likely to maintain suitable microclimates.

1.9. Conservation measures

Effective conservation of Colobus vellerosus requires a multi-layered strategy that integrates legal protection, habitat management and restoration, community participation, cultural stewardship, and long-term monitoring. The species is formally protected under Class A of the African Convention on the Conservation of Nature and Natural Resources and listed in CITES Appendix II, underscoring the need for strict regulation of hunting and trade (Matsuda Goodwin et al., 2020). However, enforcement remains weak across much of its range, making strengthened legal compliance a clear priority.

With many associated limitations, traditional beliefs protection can be considered effective for the conservation of *C. vellerosus*. The populations of *C. vellerosus* in BFMS in Ghana and in KSF in Benin are the only existing strongholds of the species to date. This illustrates how traditional taboos, cultural values, and community involvement can significantly contribute to the long-term survival of the species, even in anthropogenic landscapes (Djègo-Djossou et al., 2012; Saj et al., 2006). The case of the BFMS has proven to be successful when associated with long-term research (Kankam et al., 2023; Wiafe et al., 2023).

The IUCN recommends conducting systematic surveys in targeted protected areas, namely Mole and Digya National Parks in Ghana and Old-Oyo National Park in Nigeria. This

is to refine the population estimates of the species. The existing populations should then constitute the focus of management strategies. One key habitat which also requires investigation is the Lama Classified Forest in Benin (Accrombessi et al., 2025).

Sustained environmental education programmes in key conservation hotspots are essential for reducing hunting pressures, strengthening local stewardship, and increasing community understanding of primate ecology and ecosystem services. Integrating conservation education into local school curricula and community outreach can help foster durable behavioural change. Additionally, conservation strategies must include support for local community development, such as livelihood diversification, alternative protein sources, and small-scale economic initiatives, to reduce dependence on forest resources and ensure that conservation benefits are equitably distributed.

Developing sustainably managed primate-based ecotourism has been proposed for sites such as Kikélé Forest (Benin) and Comoé National Park (Côte d'Ivoire), where it could generate local revenue while incentivising protection of remaining populations. Additionally, because no captive populations currently exist, the IUCN encourages the European Association of Zoos and Aquaria to consider establishing an ex-situ breeding programme as an insurance measure against further declines.

Overall, mitigating the degradation of inhabited habitats and reducing the hunting pressures are the most important conservation actions to ensure long-term survival of *C. vellerosus*. To achieve this, it is indispensable to coordinate actions with local communities. Establishing long-term primate research program in the key habitats will support conservation strategies.

Chapter 2. Area of interest and its environmental and socioeconomic conditions

This chapter provides an overview of the study area, beginning with the extensive geographic area relevant to this research. This wider spatial coverage ensures that ecological models capture the full range of environmental gradients and potential hybrid influence zones pertinent to *C. vellerosus* suitable habitat identification. This broader range was then refined to the specific focus region in central Benin. The chapter describes the area's environmental context, including its climatic and vegetational characteristics, as well as its ecological and conservation relevance to the present research.

2.1. Area of interest (AOI)

The first delineated our area of interest (AOI) for this study encompasses the entire geographic distribution ranges of *C. vellerosus* and *C. polykomos* (Fig. 3). This AOI extends approximately 150 km beyond the terrestrial boundaries of both species' IUCN-defined ranges to capture potential contact or hybridisation zones, given their parapatric distribution. This broader extent ensures that the analysis accounts for all relevant environmental gradients and the potential ecological overlap influencing the realised niche of *C. vellerosus*.

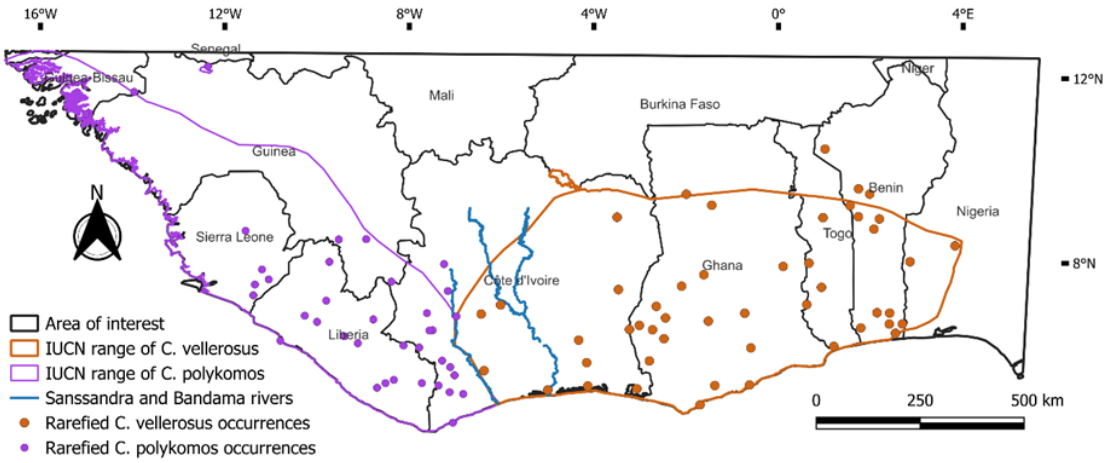

Figure 4. Area of interest, IUCN distribution ranges, and rarefied occurrences of *Colobus vellerosus* and *Colobus polykomos*

2.2. IUCN-defined geographic range of *Colobus vellerosus*

The IUCN-defined geographic range of *C. vellerosus* (Fig. 4) extends longitudinally from latitudes 4.74° N to 9.61° N and longitudes 7.02° W to 3.97° E. From the western end to the eastern end, the range of this colobus monkey extends from the interfluvial zone between the

Sassandra and Bandama Rivers in Côte d'Ivoire through the Dahomey Gap countries, including Ghana, Togo, and Benin, to the Old Oyo National Park in south-western Nigeria (Matsuda Goodwin et al., 2020).

2.3. Central Benin focus area

Within the broader distribution range, the core study area is located in central Benin and covers approximately 15,307 km² (Fig. 5). This zone represents the current stronghold of *C. vellerosus* populations in Benin. The species persists in two community forests: Kikélé Sacred Forest and Okuta Kobunan Forest (Accrombessi, Toyi, Kone, Zinner, et al., 2025), and was encountered in four classified forests: Pénéssoulou, Wari-Maro, Monts Kouffé, and Ouémé Supérieur within the last two decades (Djègo-Djossou, 2013; Djègo-Djossou & Sinsin, 2009).

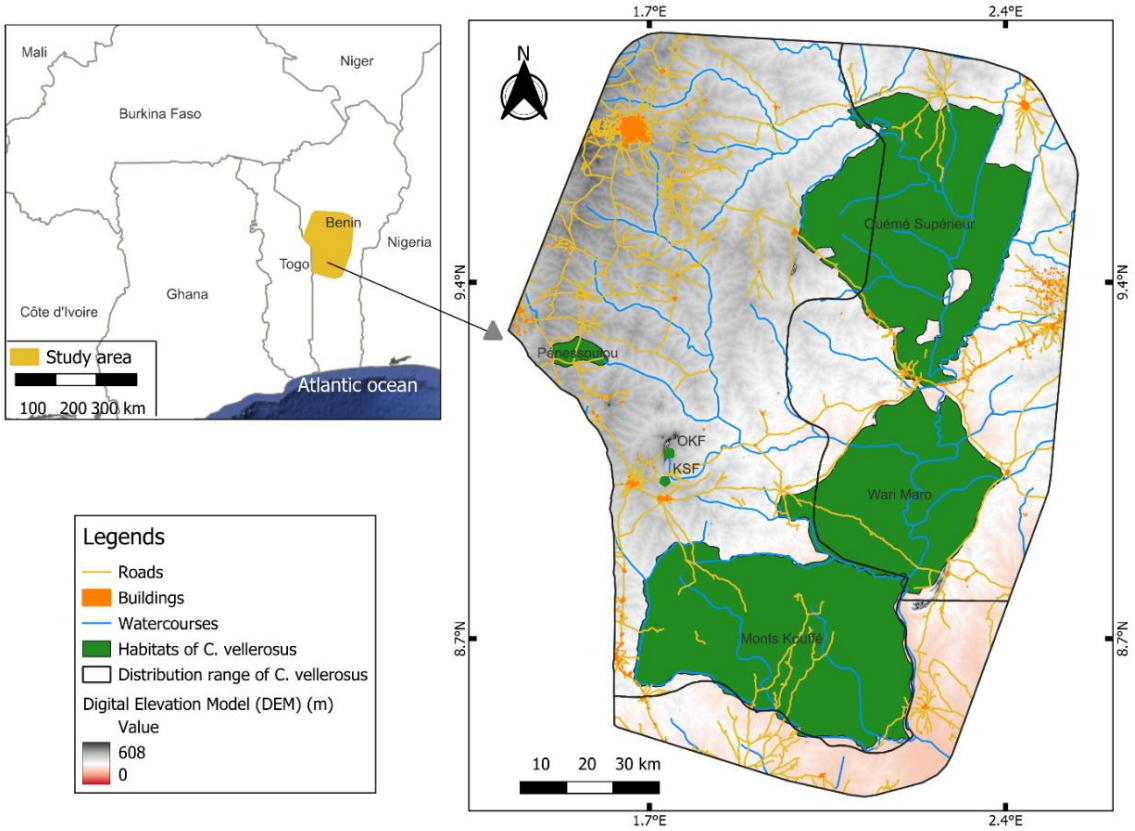

Figure 5. Geographical range of *Colobus vellerosus* in central Benin

Habitats = forests where C. vellerosus *historically (the four classified forests) or currently (the two community forests) occurs.*

To delineate the geographical distribution range of *C. vellerosus* in central Benin, we aggregated and buffered these forests by 10 km, utilising a QGIS-based spatial workflow (Fig. 6).

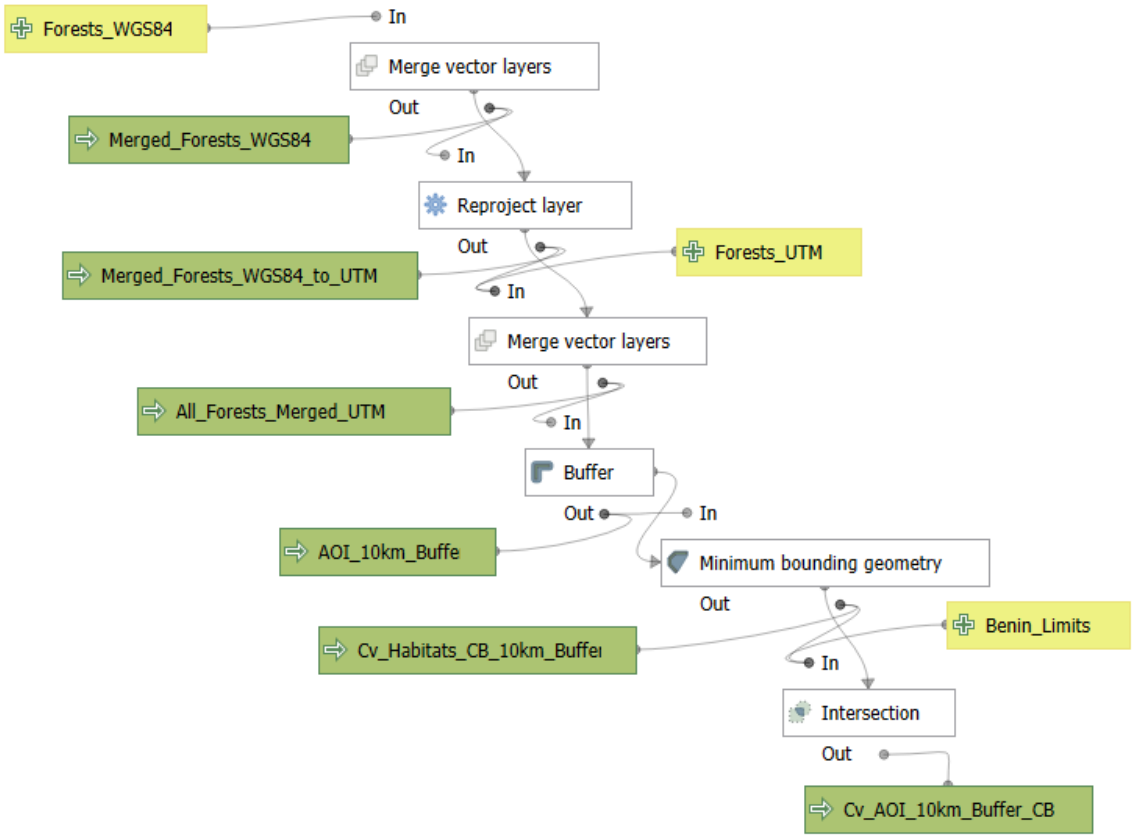

Figure 6. Model workflow to define the geographic range of *Colobus vellerosus* in central Benin

The resulting boundary is geographically located between 1.70° E and 2.90 E longitude and 8.65° N and 10.48° N latitude (Fig. 5), spanning three departments: Donga, Borgou, and Collines. The Donga department includes the Pénéssoulou and Monts Kouffé Forest Reserves, in addition to the Kikélé Sacred and Okuta Kobunan community Forests. The Wari-Maro and Ouémé Supérieur Forest Reserves straddle the boundary between the Donga and Borgou departments, with a predominant area situated within Borgou. The Collines department primarily includes the buffer zone surrounding the Monts Kouffé Forest.

2.4. Environmental parameters

2.4.1. Climate

The wider AOI predominantly experiences an equatorial climate characterised by a pronounced alternation between wet and dry seasons. The climate across the IUCN-defined range of *C. vellerosus* is primarily equatorial. The range features a distinct dry season. Precipitation during the driest month falls below 60 mm. Within the range, the period of dry season varies across

different locations (Berg et al., 2013). Over the past five decades, the region has experienced significant warming. Mean maximum annual temperatures have increased by 0.16°C per decade. Mean minimum annual temperatures have risen by about 0.28°C per decade. Precipitation patterns have exhibited spatial variability. However, precipitation trends are mostly non-significant. This reflects the complexity of the climate dynamics at this region scale (Barry et al., 2018).

According to the WorldClim v2.1 Climate dataset from 970 to 2000 (Fick & Hijmans, 2017), the mean annual temperature is about 26.6 °C across this range. Monthly average temperatures fluctuate between 24.6 °C in the coolest months and 28.5 °C in the warmest months (Fig. 7). Average annual precipitation of this range is around 1214 mm. Monthly precipitations range from about 11 mm during the driest months (December and January) to approximately 189 mm during the peak of the rainy seasons (Fig. 8). The resulting temperature–precipitation profile (Fig. 9) illustrates a strong seasonality. It is characterised by significant rainfall peaks, which occur in June and September. Temperatures exhibit slight fluctuations throughout the year.

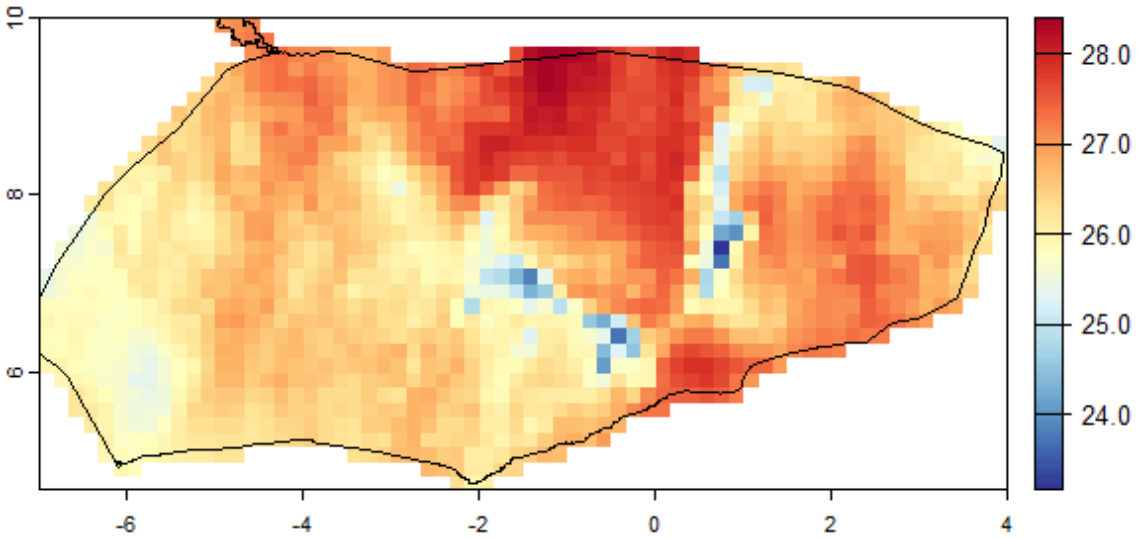

Figure 7. Spatial distribution of annual mean temperature (ºC) across the IUCN distribution range of *Colobus vellerosus* derived from WorldClim v2.1 (1970–2000)

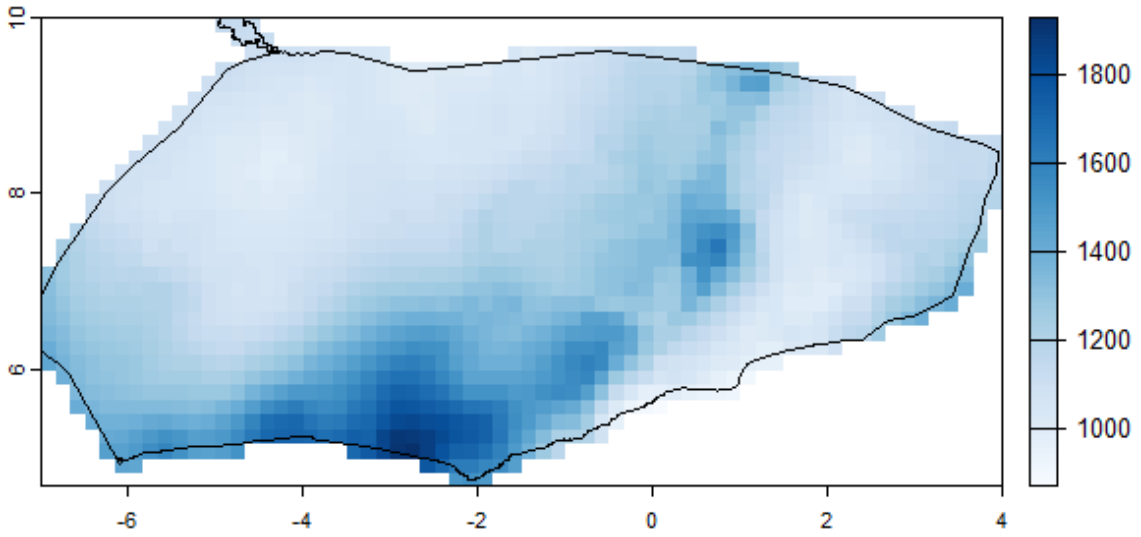

Figure 8. Spatial distribution of annual precipitation (mm) across the IUCN distribution range of *Colobus vellerosus* derived from WorldClim v2.1 (1970–2000)

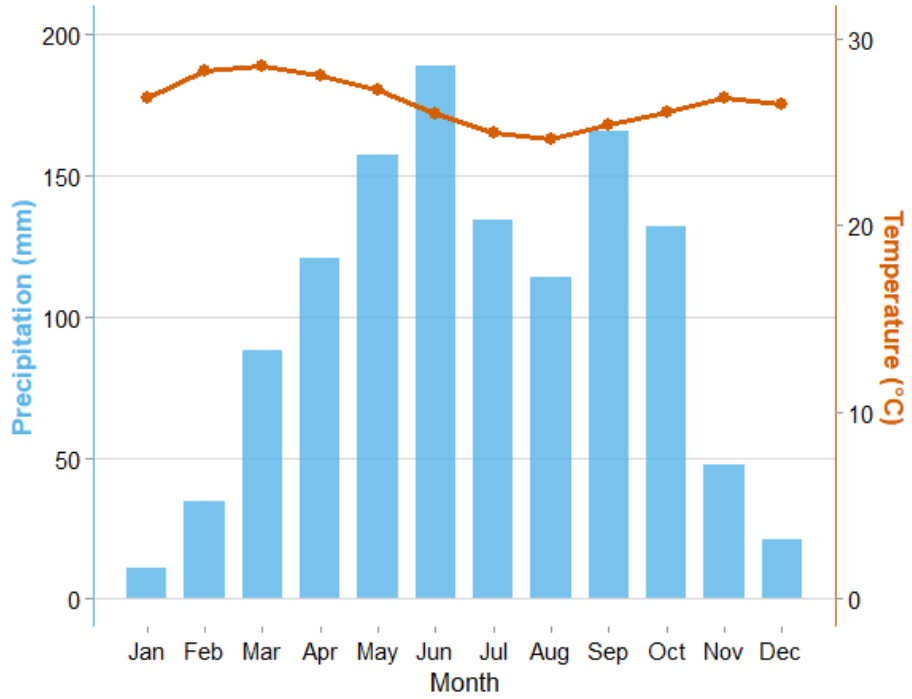

Figure 9. Climate diagram of the IUCN distribution range of *Colobus vellerosus* derived from WorldClim v2.1 (1970–2000)

In central Benin, where the focal populations of *C. vellerosus* are located, the climate transitions between the Sudano-Guinean and Sudanian zones. The Sudano-Guinean zone extends roughly from 7.30° N to 9.45° N. In contrast, the Sudanian zone stretches northward from 9.45° N to 12.25° N. Rainfall follows a unimodal pattern, primarily occurring from May to October, with annual totals ranging between 900 mm and 1100 mm in the Sudano-Guinean zone, and below

1000 mm in the Sudanian zone. Mean annual temperatures fluctuate between 21.2°C and 32.5°C, with the warmest months typically occurring just before the onset of the rainy season (Gnanglè et al., 2011).

2.4.2. Vegetation and Ecosystems

The broader AOI encompasses a diverse mosaic of ecosystems, ranging from relatively well-preserved forest formations to landscapes extensively affected by anthropogenic degradation. Notably, the vegetation within the IUCN-defined range of *C. vellerosus* largely corresponds to that of the Dahomey Gap, a biogeographic region marked by a blend of semi-deciduous forests, wooded savannahs, lowland rainforests, swamp forests, and gallery forests interspersed with agricultural lands (Salzmann & Hoelzmann, 2005; Ugbaje et al., 2017). Except for cultivated areas, these forest formations constitute the preferred ecological habitats of *C. vellerosus.* The species depends on structurally complex forest patches for foraging, movement, and social interactions.

Within central Benin, vegetation structure reflects a forest-savannah transitional character, composed of open and dense forests interspersed with shrub and tree savannahs, gallery forests, and secondary vegetation formations. The forests of Pénéssoulou, Wari-Maro, Monts Kouffé, and Ouémé Supérieur, together with the Kikélé Sacred and Okuta Kobunan community forests, are vital habitat refugia for *C. vellerosus*. These remnant forest patches provide ecologically favourable conditions amid an increasingly fragmented matrix dominated by agricultural expansion, selective logging, and fuelwood extraction. Central Benin also boasts the highest species diversity in the country, particularly among primate taxa (Sinsin et al., 1998), underscoring its ecological and conservation importance within the regional biodiversity network.

2.4.3. Forest of particular interest and their management

The forests of central Benin, of particular interest for this research, constitute the historical and current core habitats of *C. vellerosus*, forming a network of ecological refugia embedded within a landscape undergoing progressive fragmentation. These forest systems include both state-governed classified forests, Pénéssoulou, Wari-Maro, Monts Kouffé, and Ouémé Supérieur, and community-managed forests such as the KSF and the OKF. Although they differ substantially in size, protection status, and degree of anthropogenic pressure, they collectively support the persistence of forest-dependent taxa and maintain the ecological environment for necessary for the survival of *C. vellerosus*.

2.4.3.1. Classified Forests

The classified forests are managed under national forestry regulations and form part of Benin's protected area network, intended to safeguard biodiversity and ensure the sustainable provision of ecosystem services. Among these, the Pénéssoulou Forest Reserve (PFR) is particularly notable for hosting several endangered and vulnerable species, including *C. vellerosus*, duikers (*Cephalophus* spp.), mona monkey (*Cercopithecus mona*), and white-bellied Pangolin (*Phataginus tricuspis*) (Dossa et al., 2021).

A major recent conservation achievement is the designation of the Monts Kouffé–Wari-Maro Forest complex as a National Park in Benin. This decision was ratified by the Council of Ministers on 12 November 2025. This reclassification establishes a more robust legal framework for conservation efforts. This framework facilitates enhanced monitoring protocols. It also facilitates the curtailment of illegal logging and poaching activities. Further, it facilitates the adoption of comprehensive landscape management strategies. This forest complex is important. It represents one of the largest contiguous habitats for *C. vellerosus*. This designation is therefore a pivotal advancement for the conservation of this species in central Benin.

2.4.3.2. Community-Managed and Sacred Forests

In contrast to the state-managed classified forests, community forests such as KSF and OKF (Fig. 10) are governed through traditional authority systems that often yield highly effective conservation outcomes, particularly regarding the protection of culturally important species, e.g. *C. vellerosus* in KSF (Djagoun et al., 2022). The KSF, spanning approximately 13.5 ha, is a well-established sacred site known for its strict local management rules and strong spiritual importance. It is home to at least three primate species, including Senegal bushbaby (*Galago senegalensis*) and mona monkey (*Cercopithecus mona*), in addition to *C. vellerosus* (Dewanou et al., 2023; Matsuda Goodwin & Chabi Ota, 2020).

The OKF encompasses approximately 157 ha. It is a newly established sacred forest. It is gaining recognition for its exceptional biodiversity. The name "Okuta Kobunan" means "mountain forest" in the Nago language. It reflects both its rugged terrain and its cultural roots. Historically, the area was abandoned. This was due to steep hills unsuitable for agriculture or construction. The area naturally regenerated into a dense semi-deciduous forest. Recent surveys conducted during this research revealed a group of eight individuals of *C. vellerosus*. Accrombessi et al. (2025) carried out the first scientific paper on *C. vellerosus* in this forest. Rapid biodiversity assessments indicated the presence of antelopes, duikers, baboons, civets,

monitor lizards, and other wildlife species. Ongoing conservation initiatives supported by local NGOs continue to promote the protection of these species.

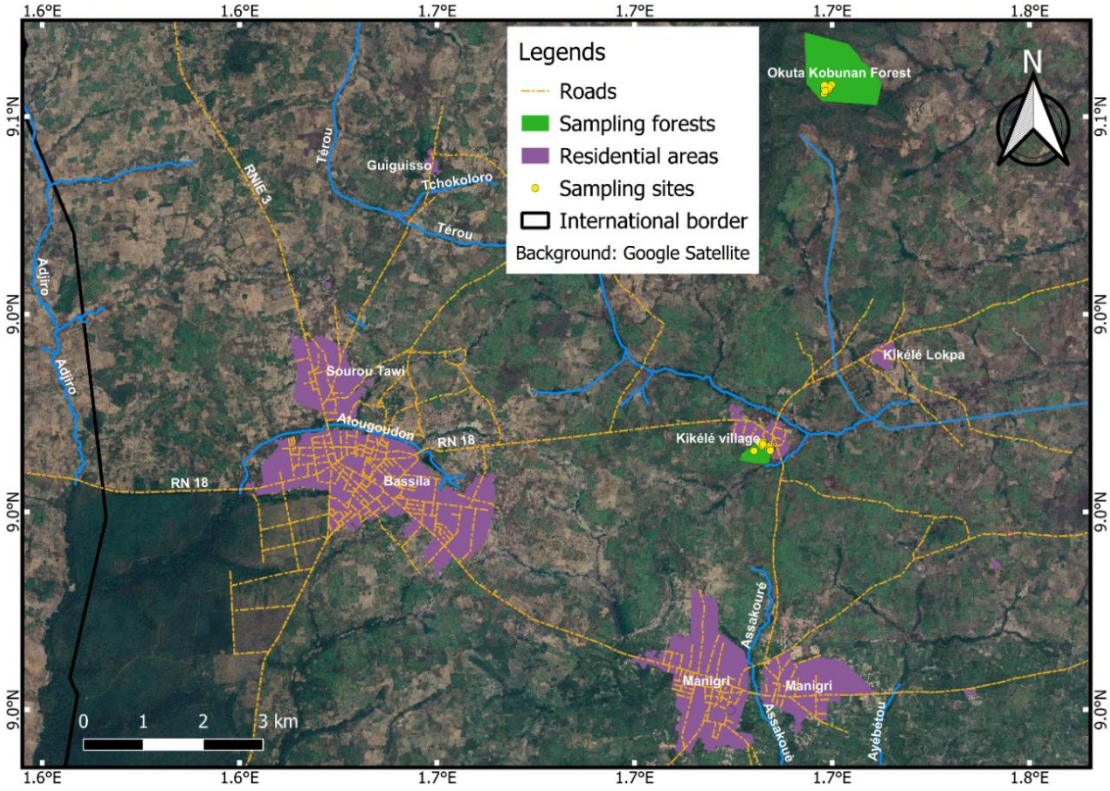

Figure 10. Sampling area around Kikélé village in west-central Benin (Kikélé Sacred Forest, KSF; Okuta Kobunan Forest, OKF).

2.5. Populations and socioeconomic factors in central Benin

The human population within the *C. vellerosus* range in central Benin is ethnically diverse. it includes Anii, Nagot, Kotokoli, Peulh, Otammari, Lokpa, Yom, Waama, Kabyè, and Ditamari. The combined population of the main communes (Bassila: 130,091; Djougou: 267,812; Tchaourou: 223,138) is approximately 621,041, based on the INSAE (2013) census.

The local economy relies heavily on agriculture, livestock, and logging. The expansion of these activities leads to significant habitat loss and fragmentation. This impact is especially pronounced near forest edges (Amagnide et al., 2015; Orekan, 2007a; Sinsin & Kampmann, 2010). However, community involvement in protecting sacred and community-managed sites presents a promising approach. It supports participatory conservation alongside formally protected areas.

PART TWO: MATERIALS AND METHODS

Chapter 3: Methodology

3.1. Global research approach

Globally, each specific objective was executed according to the internal research proposal of the relevant laboratory, and validation was provided by teams focused on the sub-themes. The work was conducted in a sequenced manner within the thesis team, ensuring that the complementarity between the themes was respected. Each objective adhered to a specific methodology, utilising SMART Conservation and Kobotoolbox for data collection in the field in a cross-sectional manner.

3.2. Analytical review

An in-depth literature search was done using scientific search engines for an analytical review of the current state of knowledge on *C. vellerosus* and its sustainable conservation perspectives. An in-depth literature search was done using Scopus (http://www.scopus.com), Google Scholar (www.googlescholar.com), and ResearchGate (www.researchgate.net). Scientific articles, theses, books and all scientific publications deemed useful were collected. We used the scientific name *Colobus vellerosus*, its synonym *Semnopithecus vellerosus*, *Colobus polykomos dollmani*, *Colobus bicolor*, *Semnopithecus bicolor*, the common names white-thighed colobus, Geoffroy's black-and-white colobus, ursine colobus, white-thighed black-and-white colobus, Geoffroy's colobus, and other general expressions related to primates essential to the conservation of the species for documentary research. In addition, we have prospected the distribution areas of the species in Benin to record the conservation actions which favour the preservation of the species in order to correlate priority research axes with real conservation actions.

3.3. Determining the impacts of climate change and anthropogenic factors on the distribution and suitability of *Colobus vellerosus* habitats across its geographic range under current and future climate scenarios

We hypothesised that climate change would reduce the geographical range of the species' ecological niche, and anthropogenic factors would further affect its suitable habitat distribution. To verify this, we developed and compared optimised ensemble models of the species' climatic niche and its habitat suitability, under both optimistic and pessimistic climate scenarios.

3.3.1. Ethical statement

We used non-invasive methods to carry out this research. Thus, the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates does not apply to it. Its protocols were approved by the Research Committee of Wildlife Conservation and Landscape Ecology of the Laboratory of Applied Ecology of the University of Abomey-Calavi of Benin.

3.3.2. Occurrence data of *Colobus vellerosus*

We downloaded the occurrences data of the species from the Global Biodiversity Information Facility – GBIF (https://www.gbif.org/fr/, 2023). We also collected occurrence records from IUCN and retrieved location records from the literature using the following search terms: "*Colobus vellerosus*", "*Semnopithecus vellerosus* ", "*White-thighed Colobus*", "*Geoffroy's Black-and-White Colobus*", "*Ursine Colobus*", "*White-thighed Black-and-White Colobus*", "*Colobe de Geoffroy*". Additionally, we recorded occurrence points using the Global Positioning System (GPS, Garmin 78) during our fieldwork from November 2022 to June 2023 in central and southern Benin. To improve the accuracy of the occurrence dataset, we used Google Earth satellite maps to validate all the records and excluded records that fell outside forested areas (Moraes et al., 2020). We used the map of the IUCN-defined geographic range of *C. vellerosus* to match occurrence points, ensuring all points fell within this range. We checked and removed duplicate data from the historical data, which was also filtered. In this regard, occurrences dated before 2000 without recent observations were discarded. As a result of this filtering process, the oldest occurrence in the database dates to 2004. Afterwards, to account for potential spatial autocorrelation for clustered records, we filtered the occurrence records to only retain single records within a radius of 10 km^2 spatial resolution using the spThin package (Aiello-Lammens et al., 2015) in R version 4.3.1 (R Core Team, 2023). From the overall 321 compiled points, our filtered dataset resulted in 41 retained occurrence records.

3.3.3. Ecological predictors

In our first set of models, we used the nineteen standard bioclimatic variables and topographic attributes (slope and aspect) as predictors. In our second set of models, we added forest cover (FC) and human population density (HPD) as proxies for food resources and human disturbances, respectively. The bioclimatic variables at 30 arc-seconds were obtained from WorldClim v2.1 (Fick & Hijmans, 2017), while slope and aspect at 30 m, and FC data were obtained from NASA Shuttle Radar Topography Mission (SRTM), (2013) and Global Forest

Change v1.10 (Hansen et al., 2013), respectively. In the Global Forest Change dataset, trees are defined as vegetation at least 5 m tall, and forest cover is measured as a gradient of percentage canopy connectivity per grid of 30 m pixels at the equator from 2001 to 2023. We downloaded HPD data estimated as the number of people per cell at 30 arc-seconds from 2000 to 2025 from the Global Human Settlement Layer (Schiavina et al., 2023). Using the spatial analysis toolset in ArcGIS 10.8, we cropped the species' IUCN-defined geographic range from these ecological predictor variables (EPV) rasters. We then converted the cropped rasters to ASCII using the conversion toolset in ArcGis 10.8. Afterwards, we used the "extract" function of the raster package (Hijmans, 2023) in R to obtain the EPV corresponding to the cells matching the filtered occurrences' records. The correlation of these variables was analysed using the "corrSelect function" of the package fuzzySim (Barbosa, 2015) in R. This function selects among correlative variables by computing pairwise correlations among the variables and excluding highly correlated variables based on a threshold value of the correlation coefficient. Here, we chose the Pearson method to exclude variables with a correlation higher than 0.8 (Sillero et al., 2021). The selected EPV after removing colinear variables were: annual mean temperature (AMT), mean diurnal range (MDR), isothermality (IsoT), precipitation during the wettest month (PWM), precipitation during the driest month (PDM), slope, aspect, forest cover (FC), and human population density (HPD).

For the future projections, we considered the IPSL-CM6A-LR Global Climate Model (GCM) of the CMIP6 model for the years 2041 – 2060 and 2061 – 2080 since several studies have suggested it as one of the models that perform better in West Africa (Ajibola et al., 2022; Nkrumah et al., 2022). We built the SDMs based on the optimistic and pessimistic scenarios, corresponding to the Shared Socio-economic Pathways (SSPs): SSP1-2.6 and SSP5-8.5 of the CMIP6, respectively.

3.3.4. Climatic niche characterisation

We computed their mean or median values with standard errors depending on the normal distribution of the selected uncorrelated bioclimatic and topographic variables. We ran principal component analysis (PCA) on them to characterise the climatic niche of *C. vellerosus*. We then performed hierarchical clustering on the PCA result to distinguish climatically characterised habitat clusters. Afterwards, we spatially plotted the filtered occurrence records in ArcGIS 10.8 and matched them with the hierarchical clustering map to identify the climatically significant habitats of the species.

3.3.5. Optimisation of the MaxEnt model and analysis of Multivariate Environmental Similarity Surface (MESS)

We used the ENMeval package (Muscarella et al., 2014) to optimise the MaxEnt (Phillips et al., 2017) model by determining the main tuning parameters: regularisation beta-multipliers and feature class combinations. We tested six feature class combinations (L, LQ, H, LQH, LQHP, LQHPT) with adjusted regularisation multipliers from 0.5 to 2 at 0.5 intervals. The optimal MaxEnt model was selected based on the lowest delta Akaike information criterion (delta AICc = 0) (Muscarella et al., 2014), with the optimal model parameters being the linear (L) feature class and a beta-multiplier of 2.

We employed the "dismo" package in R to compute the multivariate environmental similarity surface (MESS), as outlined by Elith et al. (2010), to investigate the extent of climatic anomalies within the distribution range of *C. vellerosus* under current climatic conditions and projected climate change scenarios. The predictor variables in the current potential distribution areas served as the reference for this analysis. Negative MESS values indicate novel conditions in the projection areas and call for turning "ON" clamping in the modelling process.

3.3.6. Ensemble modelling process: cross-validation, calibrating, training, and evaluation of the models

We developed an ensemble modelling (EM) using the Biomod2 package (Thuiller et al., 2023) and MaxEnt in R version 4.3.1. As our occurrence's dataset represented presence-only data whereas Biomod2 models require both presences and absences to run, two different sets of pseudo-absence points were randomly generated within a buffer with minimum and maximum radii of 5 km and 35 km, respectively, around each retained occurrence. We adopted these radii as *C. vellerosus* closest forest fragments are within a radius of 4.5 km (Wong & Sicotte, 2006), and the mean of the longest distance between fragments is approximately 35 km (Djègo-Djossou, 2013). Each set of pseudo-absence data contained the same number of points as those in our occurrence dataset, N = 41. We used the ENMeval-defined optimal parameter settings for the MaxEnt model and the default settings for the remaining individual algorithms in the ensemble modelling. We adjusted the clamping setting based on the results of the MESS analysis for the current and future models. We computed eleven algorithms, namely: Generalized Linear Model (GLM), Generalized Boosting Model (GBM), Generalized Additive Model (GAM), Classification Tree Analysis (CTA), Artificial Neural Network (ANN), Surface Range Envelop (SRE), Flexible Discriminant Analysis (FDA), Multiple Adaptive Regression

Splines (MARS), Random Forest (RF), Maximum Entropy Phillips (MaxEnt) and Maximum Entropy Phillips2 (MAXNET).

We randomly split 80% of our dataset for calibrating and training the models and the remaining 20% for testing them. We made five cross-validations for each of the eleven modelling algorithms. Presences and pseudo-absences were equally weighted in the model computing process. Each modelling algorithm was evaluated based on the True Skill Statistic (TSS) and the Area Under the Curve (AUC) of a Receiver Operating Characteristics (ROC) plot (Allouche et al., 2006; Barratt et al., 2021). To build the EM, we excluded models with TSS and AUC, respectively, lower than 0.5 and 0.8.

We generated the binary presence-absence maps using the "bm_BinaryTransformation" internal Biomod2 function. We analysed the range size change (RSC) using the "BIOMOD_RangeSize" function of the Biomod2 package. This function requires a binary dataset and is a one-to-one comparison method that allows the calculation of habitat change differences between projections of SDMs (i.e. to make quantitative predictions of range changes in terms of number of pixels, Thuiller et al., 2023).

3.4. Assessing historical and contemporary land-use and land-cover (LULC) changes within the distribution range of *Colobus vellerosus* in central Benin from 1989 to 2025

3.4.1. Imagery data and preprocessing

To assess land cover changes over the past 36 years, corresponding to four generations of *C. vellerosus*, we acquired satellite scenes from Landsat and Sentinel-2 at three distinct periods: 1989, 2007, and 2025 (Fig.). Then, we clipped the images to the study area. We utilised Landsat 5 Thematic Mapper (TM) for 1989 and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) for 2007, both with 30 m spatial resolution. Cloud and shadow contamination were addressed using sensor-specific masking techniques. We applied the quality assessment pixel (qa_pixel) band to eliminate pixels identified as cloudy or affected by cloud shadow, based on bitmask interpretation. We adjusted the surface reflectance values according to the coefficients specified in the metadata (SR = DN × 0.0000275 - 0.2). Although Landsat 7 remained operational after 2003, its data from May 31, 2003 onwards has been compromised by the Scan Line Corrector (SLC) failure, resulting in wedge-shaped gaps between scans (Markham et al., 2004). We addressed these gaps using median compositing techniques to preserve spatial continuity (Griffiths et al., 2013; Luffy, 2019; Roy et al., 2010).

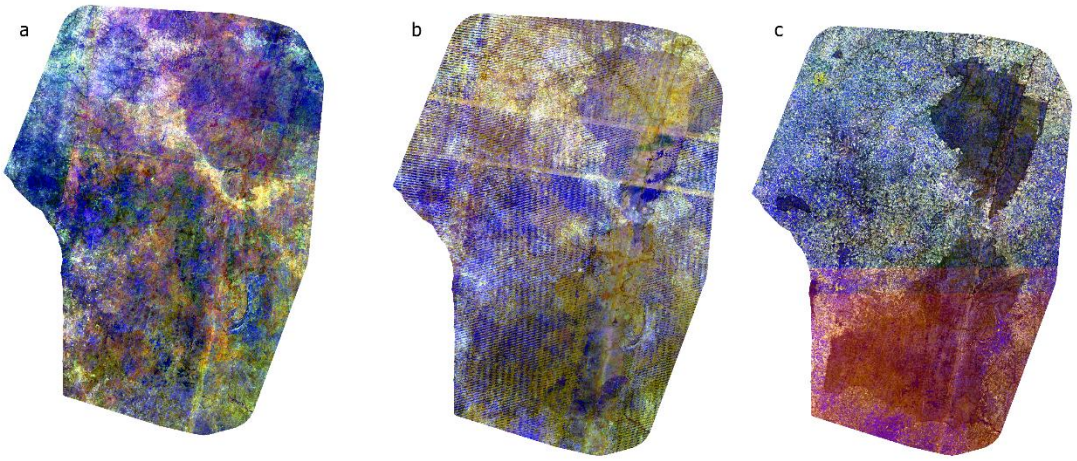

Figure 11. Median composite satellite images of a) Landsat 5 TM FOR 1989, b) Landsat 7 ETM+ for 2007, and c) Sentinel-2's MSI for 2025

For 2025, we utilised imagery from Sentinel-2's MultiSpectral Instrument (MSI), which offers a higher spatial resolution of 10 to 20 meters and a high temporal resolution of 5 days compared to, respectively, 30 m and 16 days for Landsat. This makes Sentinel-2 particularly suitable for current land cover monitoring (Chastain et al., 2019; Phiri et al., 2020). To ensure image quality, we employed the S2_Cloud_Probability product and masked out pixels with a cloud probability exceeding 60%. This threshold was chosen to strike a balance between effective cloud removal and image retention and was confirmed through visual inspection of representative images. Subsequently, we generated a median composite from the filtered, cloud-free images to minimise noise resulting from atmospheric variability and residual cloud contamination.

To ensure radiometric consistency with Landsat surface reflectance data, we used Copernicus/S2_SR surface reflectance for Sentinel-2 images. Then, we harmonised four bands: red, near-infrared (NIR), shortwave infrared-1 (SWIR-1), and shortwave infrared-2 (SWIR-2). These bands were selected based on their optimal accuracy in land cover classification (Fariz & Nurhidayati, 2020). The satellite sensors and corresponding datasets used are summarised in Table 4. Sentinel-2 imagery was resampled from its original resolution of 10 to 20 m to 30 m. Afterwards, we reprojected it to match Landsat’s spatial resolution. This ensured compatibility across datasets. All image processing was conducted using the Google Earth Engine (GEE).

Table 4. Satellite sensors and corresponding spectral bands

Feature	Landstat (TM/ETM+)	Sentinel-2 MSI
Red	SR_B3	B4
NIR	SR_B4	B8
SWIR 1	SR_B5	B11
SWIR 2	SR_B7	B12

3.4.2. Incorporation of Spectral Indices

To improve classification accuracy and spectral separation of various land cover types, we calculated seven spectral indices and analysed their correlation. These indices included the Normalised Vegetation Index (NDVI), Enhanced Vegetation Index (EVI), Bare Soil Index (BSI), Normalised Difference Built-up Index (NDBI), Normalised Difference Water Index (NDWI), Soil Adjusted Total Vegetation Index (SATVI), and Normalised Difference Tillage Index (NDTI). We retained four of these indices with a correlation coefficient less than 0.8: NDWI, which is sensitive to changes in the liquid water content of vegetation canopies (Gao, 1996); NDTI, effective in distinguishing differences in tillage practices (Van Deventer et al., 1997); EVI, a modified version of NDVI that enhances monitoring of the vegetation in high biomass areas (Huete et al., 1999; Liu & Huete, 1995); and SATVI, valuable for quantifying herbaceous vegetation cover (Marsett et al., 2006). We then incorporated these selected indices into the input features. Research has demonstrated that integrating spectral indices significantly enhances the efficacy of classification models in distinguishing similar land cover classes (Arfa & Minaei, 2024; Brendel et al., 2019).

3.4.3. Supervised classification, validation, and accuracy assessment

Numerous studies have shown that the Random Forest (RF) algorithm excels in mapping applications compared to other classifiers, effectively classifying land use and land cover (LULC) (Arfa & Minaei, 2024; Belgiu & Drăgu, 2016; Fariz et al., 2024). In this study, LULC classification was implemented using the RF algorithm in GEE.

Based on the vegetation characterisation within the study area (Sinsin et al., 1998), field surveys, the concerned climatic zones, and the ecology of *C. vellerosus*, six land cover classes were defined: forest land, savannah, plantations, agricultural land, human settlements, and water bodies (Table 5).

Table 5. Description of defined land cover classes

Land cover class	Description
Forest	Forests and woody vegetation with more than 75 trees per hectare
Savannah	Fewer than 75 trees per hectare and features a diverse understory of shrubs and grasses, with some areas dominated by either
Plantation	Cashew, mango, teak, oil palm, eucalyptus, cocoa, citrus—woody crops in blocks/rows
Agricultural land	Fields featuring cultivated crops or that have undergone harvesting
Human settlements	Urban areas and rural settlements, roads, other buildings, and bare soils
Water bodies	Temporal and permanent watercourses (rivers, lakes, and ponds)

We employed a supervised methodology, utilising control samples from the field and high-resolution imagery and auxiliary datasets. For 1989 and 2007, we used 25 digitised sample points per land cover class per year from previous land cover maps of central Benin (Orekan, 2007a, 2007b). For 2025, we used 259 field-validated data points of land cover classes. In addition, we manually digitised 50 auxiliary points per land cover class per each targeted year from high-resolution imagery from GEE, constituting a combined ground-truth and digitised dataset. These control datasets representing major LULC classes were imported into GEE as a table of feature collections and split randomly into 70% for training and 30% for validation to assess classification accuracy.

The RF classifier, known for its robustness to noise and overfitting (Breiman, 2001; Pelletier et al., 2016), has two key tuning parameters: the number of trees and the number of variables considered at each node. Here, we implemented the RF algorithm with 500 decision trees, and the number of variables randomly sampled at each node was set to the square root of the total number of predictor variables ($variablesPerSplit = \sqrt{p}$), where p is the number of predictor variables. We chose the number of trees through trial and error, and the variablesPerSplit is consistent with common recommendations for RF to balance classification accuracy and computational efficiency (Liaw & Wiener, 2002). We applied a fixed random seed of 42 to ensure reproducibility. The RF classifier was trained using the selected spectral bands (Red, NIR, SWIR1, and SWIR2) as predictor variables and the landcover class as the dependent variable. The classification was performed separately for each year to account for differences in spectral responses and class representation over time.

We conducted an accuracy assessment using a confusion matrix. We then evaluated the classification performance and reliability. We did so by calculating the overall accuracy (OA), user's accuracy (UA), producer's accuracy (PA), and the Kappa coefficient. We exported the resulting maps for further spatial analysis.

3.4.4. Land cover change analysis

A comprehensive post-classification approach was used to quantify LULC transitions across the three study periods. These periods were 1989 to 2007, 2007 to 2025, and 1989 to 2025. We conducted this workflow using both GEE and R. It involved computing class-level areas from each classified map. Next, we generated pixel-wise transition matrices and derived change metrics. These metrics included persistence, gross gains, gross losses, and net change. The workflow further involved quantifying transition intensities. Finally, it included visualising landscape transformations through multiple graphical methods.

3.4.4.1. Estimation of class areas in each time period

For each classified image (1989, 2007, 2025), the area occupied by each land-cover class was calculated by summing all pixels assigned to that class and converting pixel counts to hectares based on the 30 m spatial resolution of Landsat imagery. Class-specific totals were used to quantify temporal shifts and supported the subsequent change accounting procedures. These area statistics were later visualised using grouped bar plots to illustrate the temporal dynamics of each land-cover category.

3.4.4.2. Pixel-level transition mapping

To characterise how land-cover types transformed between time periods, pairwise transition maps were generated. For each interval, an image was created in which every pixel received a unique numerical identifier representing its “from earlier year to later year” class combination. The frequency histograms of these identifiers were then compiled to form transition matrices for the three distinct time periods analysed. Each transition matrix quantified the number of pixels corresponding to every possible class conversion. Thus, it offered a complete description of the landscape dynamics.

3.4.4.3. Change accounting: persistence, gross gains, losses, and net change

Transition matrices exported from GEE were analysed in R to derive class-level widely applied land-change accounting metrics: Persistence, Gross Loss, Gross Gain, and Net Change. Persistence refers to the area that remained in the same class over the time interval. In the transition matrix, persistence is indicated along the diagonal. At the same time, the row-wise off-diagonals represent the Gross Loss, which quantifies the area that transitions from one class to another. Conversely, Gross Gain captures the area a class acquired from other classes and is indicated by the column-wise off-diagonal elements. Finally, the Net Change is calculated as

the difference between Gross Gain and Gross Loss. Ecologists used the Net Change to identify the expansion or contraction of classes by measuring the overall shift in area.

3.4.4.4. Computation of the transition intensity index

To identify the most dominant transitions, a transition intensity index (TII) was computed for each "from earlier year to later year" pair. The index represents each observed transition relative to the expected transition magnitude under a hypothetical uniform distribution of change across all classes. The formula is as below:

$$\text{Expected change} = \Sigma_{ij}\, T_{ij} / n(n-1),$$

Where T_{ij} is the area of pixels transitioning from class i to class j, and n is the number of land-cover classes.

$$TII_{ij} = (T_{ij} / \text{Expected change}) \times 100$$

TII values exceeding 100 denote transitions that are occurring with greater intensity than anticipated. Values falling below 100 signify transitions that are less intense than expected. We assessed the transitions for each time period. Then, they were ranked based on their intensity. This allowed for the extraction of the ten most significant transitions. This approach emphasises the key land-cover conversions.

3.4.4.5. Visualisation of land-cover transitions

We employ grouped bar charts, heatmaps, and chord diagrams to effectively illustrate the complex nature of LULC change. Class-level area changes for each year are represented through a grouped bar chart, utilising a harmonised colour palette to facilitate comparisons across different time periods. Transition matrices are visualised as heatmaps with a sequential colour gradient, where persistence values are annotated directly on the diagonal to demonstrate class stability, and off-diagonal intensities highlight the magnitude of conversions.

We illustrate the magnitude and reciprocity of transitions among classes using circular chord diagrams.

3.4.5. Perception of forest-cover change and its determinants

We assessed community perceptions of forest-cover change and the socio-economic and cultural factors influencing these perceptions in the villages of Kikélé and Pénéssoulou, which are adjacent to the Kikélé Sacred Forest (KSF) and the Pénéssoulou Forest Reserve (PFR), respectively. A structured questionnaire was designed to capture key dimensions related to (i)

household socio-demographic characteristics, (ii) livelihood activities and domestic energy use, (iii) conservation awareness and willingness to engage in conservation actions, (iv) perceived trends in forest-cover change, and (v) respondents' understanding of the main drivers of forest change. These variables form the basis of the dataset analysed in this study. The questionnaire was digitised using KoboToolbox to ensure standardised data entry during field surveys. Sample size for each village was calculated using the normal approximation of the binomial distribution (Dagnelie, 1998), a method commonly applied in studies of forest-resources and ecosystem-services in Benin (Djagoun et al., 2022; Lokonon et al., 2019). A total of 140 respondents were interviewed (73 in Kikélé; 67 in Pénéssoulou). Eligible participants were household heads aged 25 years or older, residing in the community for at least five consecutive years to ensure adequate familiarity with local environmental dynamics. Data collection was carried out by two trained field assistants: an MSc researcher responsible for administering the digital questionnaire and a local interpreter who facilitated communication according to each participant's preferred language. Participation was voluntary, and respondents were informed about the purpose of the study, the confidentiality of their responses, and their right to withdraw at any time. Verbal informed consent was obtained before administering the questionnaire.

3.4.5.1. Data preparation and variable coding

All survey responses were exported from KoboToolbox and cleaned in R v4.5.1 (R Core Team, 2023). Variable names were standardised to lower snake case using the janitor package (Firke, 2025). Categorical responses were harmonised to avoid inconsistencies, and socio-demographic variables (education level, profession, domestic energy type, willingness to conserve, and conservation awareness) were recoded as factors.

Annual household income was transformed using a natural log transformation (log1p) to reduce skew. Household size was treated as a continuous variable. Perceived forest-cover change was categorised into three levels: decreasing, stable, or increasing. To assess the correctness of community perception against observed forest-cover trends derived from remote-sensing analysis (1989–2025), we generated a binary variable correct_perception, coded as 1 for respondents reporting decreasing forest cover (the trend consistent with the observed LULC trends), and 0 otherwise. The dataset used for the statistical analyses therefore consisted of:

- socio-demographics: village, education, profession, household size, log-transformed income;
- livelihood and resource dependence: domestic energy source;
- conservation attitudes: willingness to conserve, conservation awareness;

- perceptions: perceived forest-cover change, perceived causes;
- derived variable: correctness of perception

3.4.5.2. Descriptive analyses

We first summarised the distribution of perception categories overall and across the two villages. Differences in perception between villages were assessed using Pearson's Chi-square test, with Fisher's exact test applied when expected counts fell below five. Descriptive summaries for income and household size were computed by village.

We visualised the distribution of perceived forest-cover change between the two communities based on a bar plot.

3.4.5.3. Modelling determinants of accurate perception of forest-cover change

To identify socio-economic and cultural predictors of accurate perception of forest-cover loss, we fitted a binary logistic regression model with correct perception as the response variable. Explanatory variables included village, education level, log-transformed income, household size, domestic energy source, willingness to conserve, conservation awareness, and hunting pressure.

We initially fitted a full model including all predictors and then performed bidirectional stepwise selection using Akaike's Information Criterion (AIC) to build a simpler model. We calculated odds ratios and 95% confidence intervals by exponentiating model coefficients. We used pseudo-R^2 statistics (McFadden and Nagelkerke), AUC, and a confusion matrix at a threshold of 0.5 to evaluate the model performance.

3.4.5.4. Modelling predictors of perception categories

Because perceived forest-cover change has three categories (decreasing, stable, increasing), we further implemented a multinomial logistic regression using the nnet package, with decreasing set as the reference category. This model allowed us to assess how socio-economic variables influence the likelihood of perceiving stable or increasing forest cover relative to the observed trend of decline. We extracted the coefficient estimates, standard errors, z-scores, and p-values to evaluate the direction and significance of predictors.

3.4.5.5. Cross-tabulations between key social variables

Additional cross-tabulations and Chi-square tests were conducted to assess whether conservation awareness was associated with accurate perception, and whether the domestic

energy source was related to the overall perception category. These tests provided further insight into how livelihood dependence and conservation attitudes shape interpretations of local forest dynamics.

3.5. Identifying climatically and ecologically suitable habitats

3.5.1. Occurrence records

We collected the presence records of both species from the Global Biodiversity Information Facility (GBIF), with 157 occurrences for *C. vellerosus* and 700 occurrences for *C. polykomos* (https://www.gbif.org/, 2024). In addition, we screened the literature (Alonso et al., 2019; Djègo-Djossou, 2013; Gonedelé Bi et al., 2014; Guilherme, 2014; Kazeem, 2017; Matsuda-Goodwin et al., 2020; Schwitzer et al., 2019; Segniagbeto et al., 2017; Wiafe, 2021; Wiafe et al., 2023) and consulted the museum catalogues from the Natural History Museums in London and Paris. We also took occurrence points using the SMART Conservation version 7.5.6 (Meadows, 2022) and the Global Positioning System (GPS, Garmin 78) during our fieldwork from November 2022 to June 2023 and from March to April 2024 in central and southern Benin. To improve the accuracy of our dataset, we plotted the occurrences in Google Earth Pro and excluded records that fell outside forested areas. We matched occurrence points with the IUCN ranges of both species and ensured that any records falling outside these ranges originated from scientific research or "colobine experts". Occurrences recorded before 1970 were excluded to reduce temporal biases and ensure occurrence data align with current climate datasets.

We removed duplicates, and to account for spatial autocorrelation, we accepted only occurrence records with a mean Euclidean distance of more than 20 km using SDM Toolbox v2.6 in ArcMap (Brown, 2014). From 711 occurrences for *C. polykomos* and 350 occurrences for *C. vellerosus*, we retained only 39 rarefied occurrences for *C. polykomos* and 48 for *C. vellerosus* for our modelling.

3.5.2. Bioclimatic variables selection

We downloaded the 19 bioclimatic variables at a 30 arc-second (~1 km²) resolution from WorldClim v2.1 (Fick & Hijmans, 2017). We clipped the area of interest from these variables' rasters using QGIS 3.34.11. We used a Pearson correlation running with the "cor" function in R v4.3.1 to select a subset of 10 less correlated bioclimatic variables. The correlation coefficient of the retained variables is smaller than $|r| \leq 0.78$ (Figs. 11 and 12). The selected variables are: annual mean temperature (bio01), mean diurnal temperature range (bio02), maximum temperature during the warmest month (bio05), mean temperature during the wettest quarter

(bio08), mean temperature during the driest quarter (bio09), precipitation during the wettest month (bio13), precipitation during the driest month (bio14), precipitation seasonality (bio15), precipitation during the warmest quarter (bio18), and precipitation during the coldest quarter (bio19).

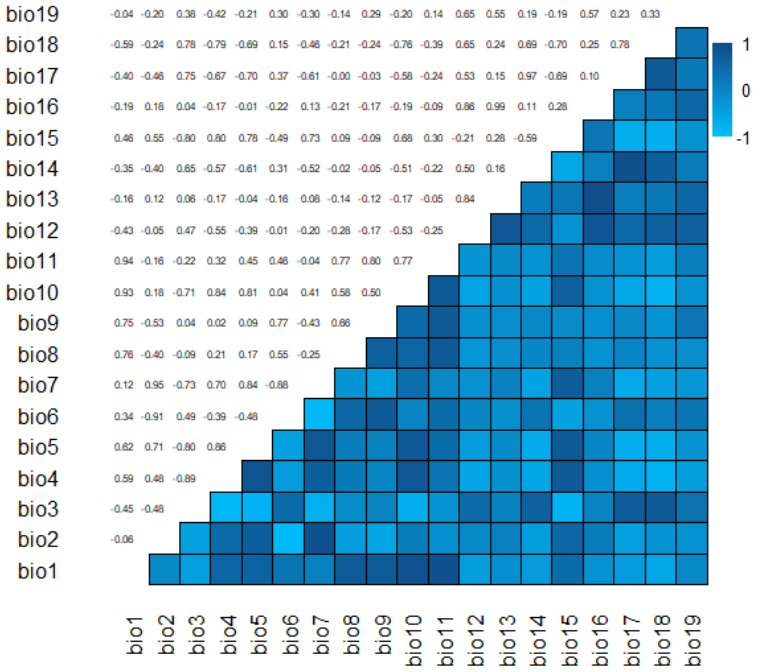

Figure 12. Pairwise Pearson's correlations between bioclimatic variables

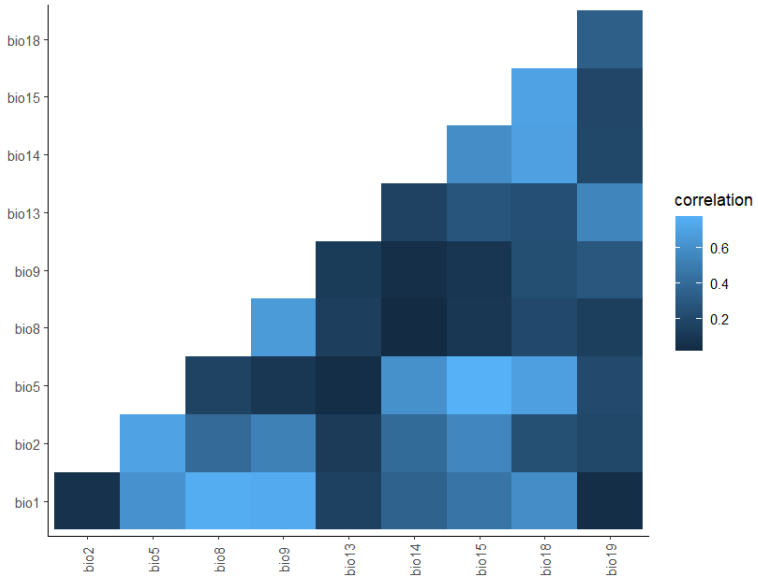

Figure 13. Pairwise Pearson correlation between selected bioclimatic variables with correlation coefficient |r|≤ 0.78

We selected these climatic variables due to their importance in shaping primate distribution patterns. Korstjens (2019) has shown that most of these climatic variables affect the distribution of the genus *Colobus*. In particular, folivorous primates, such as *Colobus*, should inherently counteract the increased cost of leaf digestion for their adaptations to climate change in scenarios of increased temperature and decreased rainfall (Korstjens & Hillyer, 2016). Furthermore, previous studies have highlighted the effects of the climatic predictors on the behavioural and feeding ecology, physiological processes, and biogeographical distribution of folivorous primates (Korstjens et al., 2010; Lehmann et al., 2010; van Schaik & Pfannes, 2005; K.-C. Zhang et al., 2021).

We used the IPSL-CM6A-LR Global Climate Model from CMIP6 to project future climate conditions for 2050. This model is noted for its strong performance in West Africa (Ajibola et al., 2022; Nkrumah et al., 2022). Our projections are based on the low greenhouse gas emission scenario for 2050, corresponding to the SSP1-2.6.

3.5.3. Multivariate environmental similarity surface analysis and MaxEnt optimal parameters selection

The “raster”, “sp”, and "dismo" packages were used in R to analyse the MESS following the method described by Elith et al. (2010). The selected bioclimatic variables serve as a reference for this analysis. The presence of negative MESS values indicates climate conditions outside the species' niche, leading us to enable clamping in the MaxEnt modelling process

The key tuning parameters for MaxEnt, including the regularisation beta-multipliers and feature class combinations, were identified using the ENMeval package (Muscarella et al., 2014). We evaluated six feature class combinations: L, LQ, H, LQH, LQHP, and LQHPT, where L represents linear, Q represents quadratic, P stands for product, T for threshold, and H for hinge. For this analysis, the adjusted regularisation multipliers ranged from 0.5 to 2 in increments of 0.5. Based on the lowest delta Akaike information criterion (delta AICc = 0) (Muscarella et al., 2014), we selected the optimal MaxEnt model, which comprises the linear (L) and quadratic (Q) feature classes with a beta-multiplier of 2.

3.5.4. Climatic niche ensemble modelling and evaluation

We built an ensemble ecological niche model using the Biomod2 package (Thuiller et al., 2023) and MaxEnt (Phillips et al., 2017) in R version 4.3.1. To apply the modelling approach to both species, we developed a wrapper that considered the species’ name as the argument and stored the single niche modelling procedure. We randomly generated two sets of pseudo-absence

points, each containing the same number of rarefied occurrence records. Our ensemble model comprises a presence-background algorithm (MaxEnt), and three widely used presence-pseudo-absence algorithms, namely Generalized Boosting Model (GBM/BRT) (Ridgeway & Developers, 2003), Generalized Linear Model (GLM) (McCullagh & Nelder, 2019), and Random Forest (RF) (Breiman, 2001). We used the ENMeval-defined optimal settings for the MaxEnt model and the default settings for the other individual algorithms.

We randomly split 80% of our dataset for calibrating and training the models and used the 20% remainder for testing them. We made five cross-validations for each of the four modelling algorithms. Presences and pseudo-absences were equally weighted in the model computing process. Each modelling algorithm was evaluated based on the TSS and the AUC of a ROC plot. To build the EM, we excluded models with TSS and AUC, respectively, lower than 0.5 and 0.8 (Allouche et al., 2006; Fielding & Bell, 1997; Swets, 1988).

3.5.5. Range change analysis

We analysed the range size change (RSC) using the "BIOMOD_RangeSize" function of the Biomod2 package. Given that *C. vellerosus* has a low dispersal capacity, which may be exacerbated by habitat fragmentation and tree species richness (Kankam & Sicotte, 2013), we propose that the zero-migration assumption represents the most realistic hypothesis. Nevertheless, we also project the change in range size based on the unlimited migration assumption to estimate potential range size changes in an optimal scenario, where conservation efforts implement corridors to facilitate species dispersal.

3.5.6. Identification of the suitable forests for re-introduction

We downloaded the protected areas and other effective area-based conservation measures of Africa from Protected Planet (UNEP-WCMC & IUCN, 2024) (Figs. 13 and 14).

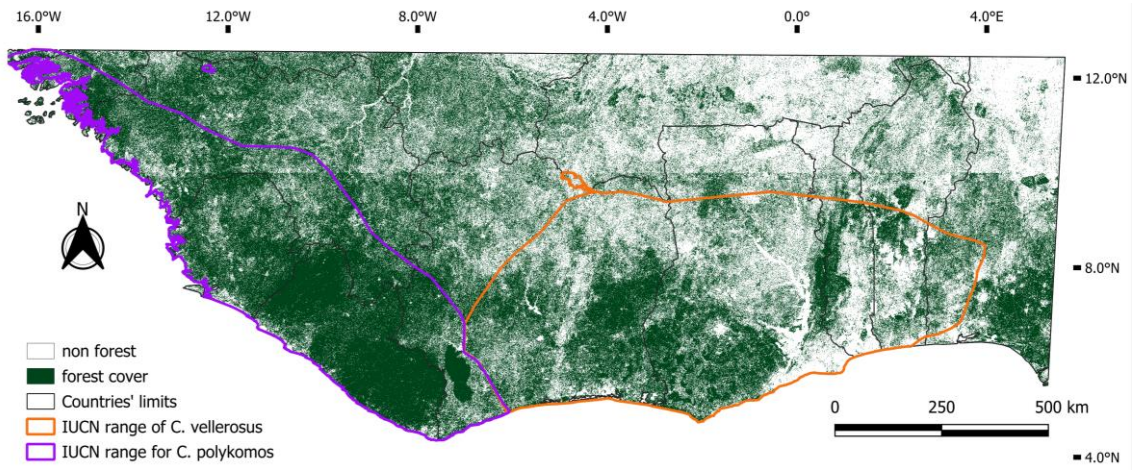

Figure 14. Current forest cover over the area of interest

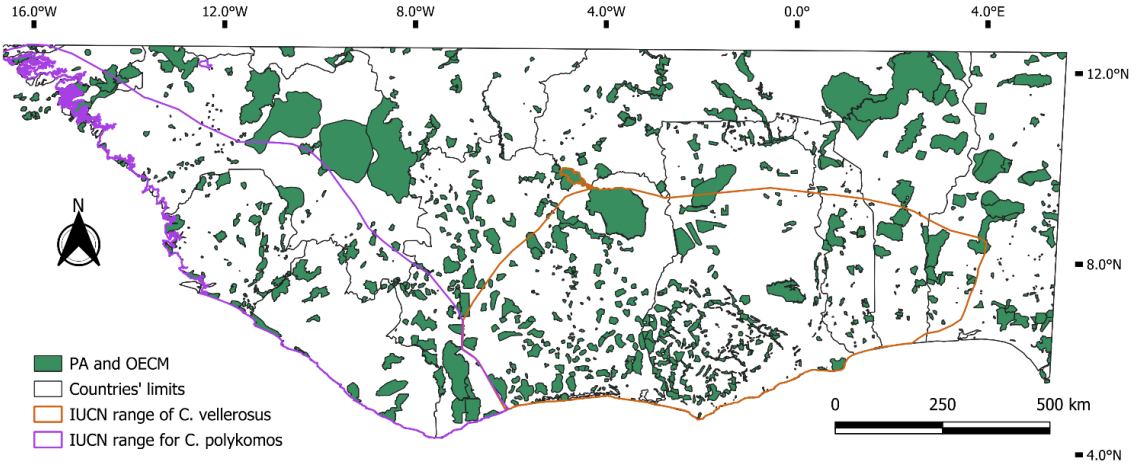

Figure 15. Current protected areas (PAs) and other effective conservation measures (OECM) of at least 1 km^2 within the area of interest

Other effective conservation measures (OECM) refers to a geographically defined area that is not classified as a Protected Area. It is governed and managed to achieve positive and sustained long-term outcomes for in situ biodiversity conservation, along with associated ecosystem functions and services. Additionally, it considers cultural, spiritual, socio-economic, and other locally relevant values where applicable (UNEP-WCMC, 2019).

Additionally, we obtained the land cover raster of Africa with a resolution of 20 meters from the Climate Change Initiative project of the European Space Agency (https://2016africalandcover20m.esrin.esa.int/).

We polygonised the binary rasters generated from our modelling and extracted suitable areas for each taxon. Afterwards, we clipped the land cover raster according to our AOI and extracted the layer representing forested areas. Utilising the modelled suitable areas examined

against the current and future climate change scenarios, we clipped, polygonised, extracted, and calculated the forested areas for each taxon. We then intersected these forested areas with protected areas to determine and calculate the protected forested areas that are suitable for each taxon. Considering that the home range of *C. vellerosus* is about 11 hectares (Fashing, 2022) and the necessity to establish ten groups for sustainable population conservation, we specifically focused on identifying suitably protected forests that encompass at least 1 km². We conducted this analysis for both species, identifying forests that could potentially be used for their reintroductions. All spatial analyses and area calculations were performed using QGIS v3.34.11, and the attribute tables were exported to CSV files for subsequent calculations in R v4.3.1. Additionally, we uploaded our area of interest (AOI) to Global Forest Watch (GFW) (https://www.globalforestwatch.org/dashboards/aoi/67225c0ecb8e690020602a58/) for follow-up and analysis of forest cover change.

3.6. Evaluation of current habitat connectivity and identify potential forest corridors that, if reforested or restored, could enhance population connectivity and reduce extinction risk for *Colobus vellerosus* in central Benin

3.6.1. Landscape metrics analysis

In the fields of species conservation and population dynamics, class-level spatial patterns are essential due to their strong association with fundamental ecological processes. As such, they are a primary focus in ecological research. There are over 64 indices available for assessing habitat fragmentation at the class level (Wang et al., 2014). However, the effective use of these indices depends on the specific niche characteristics of the species under investigation.

In relation to our goal of examining the impact of fragmentation on structural connectivity within the habitat of *C. vellerosus*, we focused on eight class-level landscape metrics: number of patches (N_PATCHES), mean patch size (MP_SIZE), edge density (EDGE_D), patch cohesion index (COHESION) connectance index (CONNECT), coefficient of variation of proximity index (CV_PROX), degree of landscape division (DIVISION), effective mesh size (MESH), and splitting index (SPLIT). These metrics serve as effective proxies for evaluating habitat fragmentation and the dynamics of forest patches (Hargis et al., 1998; Wang et al., 2014).

We selected N_PATCHES, MP_SIZE, EDGE_D, CONNECT, and CV_PROX for their relevance to the migratory capabilities of *C. vellerosus* in establishing a metapopulation. DIVISION, MESH, and SPLIT were also included, as they help assess the ability of animals in

different areas to locate each other. These latter three metrics measure the impacts of human encroachment on landscapes (Jaeger, 2000).

For landscape metrics, we reclassified LULC maps into binary rasters to differentiate forest and non-forest areas. Metrics were calculated using R v4.5.1 with the "raster," "sf," "landscapemetrics," and "dplyr" packages.

3.6.2. Functional connectivity modelling

3.6.2.1. Resistance surface building

Colobus vellerosus is a forest-dwelling and folivorous monkey. To date, there is no literature mentioning evidence of the species frequenting farmland or causing conflict with farmers. Based on the ecology and expert opinion regarding *C. vellerosus*, resistance surfaces were generated by integrating land cover classes, the Enhanced Vegetation Index (EVI), and the Leaf Area Index (LAI) with respective weights of 0.2, 0.4, and 0.4. Resistance values for LULC classes were defined as follows: forest = 1, savannah = 20, plantation=30, agriculture = 70, settlements = 98, and water = 100. EVI and LAI were rescaled and inverted to match resistance values such that greater greenness or foliage resulted in lower resistance. Each layer (LULC, EVI-based resistance, LAI-based resistance) was scaled to 0–1. We then produced a weighted composite resistance surface according to the following integrating formula:

$$\text{Resistance} = (0.2 \times \text{LULC}) + (0.4 \times 1\text{–EVI}) + (0.4 \times 1\text{–LAI})$$

Where LULC = resistance value of land use and land cover classes; EVI = enhanced vegetation index; LAI = leaf area index.

The resulting resistance raster was exported and served as the input for circuit-theory and least-cost path analyses in Circuitscape v5.12.3 (Anantharaman et al., 2020) and gdistance (van Etten, 2017).

3.6.2.2. Habitat patch identification and core forest selection

We first extracted forest habitat from the 2025 LULC classification by reclassifying all forest pixels to a binary raster. The binary raster was converted to vector polygons, and small fragments (< 1 Km2) were removed to avoid noise from extremely small fragments. The resulting polygons were saved as the initial forest habitat layer. For each polygon, the geometric centroid was computed and assigned a unique patch ID.

To characterise landscape-scale connectivity, we first computed pairwise cost distances among all forest centroids derived from the complete forest habitat layer. A preliminary graph-theory analysis was performed using a 7 km cost-distance threshold, chosen to represent the upper limit of biologically meaningful movement for *C. vellerosus*. We defined this threshold because of the short daily path length of *C. vellerosus* of an average 359 m (Fashing, 2022) and the known closest distance between *C. vellerosus* habitats of an average 7 km in central Benin (Accrombessi, Toyi, Kone, Zinner, et al., 2025). Patches with pairwise cost distance greater than 7 km were treated as functionally isolated. Connectivity metrics (degree and betweenness centrality) were mapped to provide an overview of landscape connectivity. The results were exported as GPKG for further investigation in QGIS.

This exploratory assessment has uncovered a significant number of small, isolated forest fragments. These small fragments are not suitable for focal-patch modelling and are likely to be ecologically insignificant in the context of conservation planning. These findings highlight the need to reconsider our conservation strategies. Therefore, subsequent analyses focused on six major community and protected forests representing the largest, most ecologically meaningful, and known habitats of *C. vellerosus* in central Benin. These six forests were treated as core habitat patches for circuit-theory and least-cost modelling steps.

3.6.2.3. Circuit-theory modelling and Pinch Point detection

We modelled functional connectivity among the six core *C. vellerosus* habitat patches using the pairwise mode of Circuitscape v5.12.3 run in Julia 1.8.2. Input rasters consisted of the resistance surface derived from the landscape-scale resistance model. We enabled the conjugate-gradient solver with algebraic multigrid preconditioning (cg+amg) to efficiently handle the large grid. Circuitscape produced current density and voltage maps for each pair of cores, a three-column edge file containing pairwise effective resistances and a square resistance matrix representing pairwise effective resistance among all habitat patches. All Circuitscape outputs were exported and subsequently integrated into the least-cost and Linkage Mapper workflow in R v4.5.1 to identify potential corridors and pinch points, and assess connectivity.

3.6.2.4. Cost-Distance Modelling

Conductance was defined as the inverse of resistance:

$$C=1/(R+\varepsilon)$$

where $\varepsilon = 10^{-6}$ avoids division by zero.

We built an 8-neighbour transition matrix using the "gdistance" package (van Etten, 2017) and applied a geographic correction to ensure that resistance accumulated according to true Euclidean distance. Pairwise least-cost distances between all core centroids were computed using the "costDistance" function, and the resulting symmetric distance matrix was saved and used as the weight attribute for the graph-theory analysis.

3.6.2.5. Least-cost path (LCP) computation

We generated pairwise LCPs for each pair of patches (i, j) using the "shortestPath" function of the "gdistance" package. Each LCP polyline was saved as an individual ESRI Shapefile to match Linkage Mapper's required format.

3.6.2.6. Accumulated cost surfaces and raster corridors

For each patch i, an accumulated cost raster was computed using accCost() function and saved. Pairwise corridors were constructed by aggregating the accumulated cost rasters of two distinct patches. Assuming patch1 and patch2, this can be mathematically expressed as:

$$\text{Corridor}_{(\text{patch1, patch2})} = \text{acCost}_{(\text{patch1})} + \text{accost}_{(\text{patch2})}$$

with acCost designated accumulated cost.

All generated corridors were subsequently exported as GeoTIFF files.

To create a corridor density raster, each LCP line was rasterised onto a unified template raster, followed by the summation of the rasterised lines. This resulting raster effectively quantifies the frequency of LCPs intersecting each grid cell, thereby identifying key movement corridors.

3.6.2.7. Buffered corridor polygons

To obtain vector corridors suitable for visualisation, each LCP shapefile was converted to a sf object and then buffered by 500 m. Buffered polygons were written to disk individually. These represent potential dispersal "bands" around each least-cost path.

3.6.2.8. Graph-theory connectivity network construction

Initially, a least-cost path workflow was employed to construct an undirected weighted graph, where nodes, edges, and edge weights represented core forest patches, pairwise connections, and least-cost distances, respectively. We calculated two centrality metrics: degree centrality, which reflects the number of connections for each patch, and betweenness centrality, indicating

the number of shortest paths that traverse each patch. These metrics were then appended to the spatial dataset of core forests and exported as a polygon of cores with metrics included.

To visualise the functional connectivity among the six core *C. vellerosus* habitats, we created a weighted connectivity network using a Fruchterman-Reingold layout. Nodes represented habitat patches, and edges illustrated least-cost connections. Edge weights are based on the inverse of accumulated movement cost (1/cost) to prioritise lower-resistance pathways. We also used betweenness centrality to identify potential connector patches within the landscape. Transforming the Circuitscape three-column file into an undirected weighted graph with the igraph package in R, we converted effective resistance (R) into conductance (C = 1/R). Finally, we calculated node-level connectivity metrics such as Degree, Strength (sum of incident conductances), and Betweenness centrality.

We employed tidygraph and ggraph packages to generate a connectivity diagram based on a Fruchterman–Reingold layout. Node size was scaled according to betweenness, and node colour by strength. Edge width was proportional to conductance.

3.6.2.9. GIS-ready spatial line network and corridor classification

Habitat patch coordinates, extracted from the Circuitscape node file, were linked to all pairwise edges to create a spatial line network using the sf package. Each linkage was categorised into five quantile-based resistance classes (Q1 representing the lowest resistance and Q5 the highest), facilitating a cartographic representation of corridor quality.

3.6.2.10. Comparison of circuitscape resistances with least-cost path distances

To assess the alignment between circuit-theory connectivity and cost-distance connectivity, we matched the LCP distances to the Circuitscape node pairs and compiled them into a comparison table. We quantified the relationship between the two metrics using Spearman's rank correlation, created a scatterplot with a linear fit, generated a rank-difference table, and developed a Bland–Altman plot to characterise systematic differences between the methods.

3.7. Analyse the genetic diversity and structure of remnant *Colobus vellerosus* populations in central Benin to infer gene flow and inform conservation

3.7.1. Sample collection

We collected 16 faecal samples non-invasively from two groups in the KSF and one group in the OKF between March 16, 2024, and April 2, 2024. We determined group sizes and age-sex class compositions during a preliminary survey (November 2022) and twice during the

sampling period. Sex assignments were based on body size, agonistic loud call of the male, and, when possible, observation of nipples or penis using binoculars and captured photos. Therefore, not all individuals could be sexed with certainty, and we focused on adults and sub-adults in this assignment during our short-term study. Infants were easily identified by their white pelage. The compositions of the sampled groups are summarised in Table 6.

Table 6. Sampling and sequencing summary of *Colobus vellerosus* in Kikélé Sacred Forest (KSF) and Okuta Kobunan Forest (OKF)

group ID	group size	adult		sub-adult		juveniles	infants	NFS	SScytb	SSD-loop
		♀	♂	♀	♂					
KSF1	8	4	2	0	0	0	2	6	0	6
KSF2	21	7	4	2	2	4	2	6	0	6
OKF	8	6		0		2	0	4	4	3
Total	37	23		4		6	4	16	4	15

KSF1: group 1 of the KSF; KSF2: group 2 of the KSF; OKF: group of OKF; NFS: number of faecal samples collected; SScytb: successfully sequenced cytochrome b; SSD-loop: successfully sequenced D-loop.

Both forest sites are located in the Kikélé village area (Fig. 10). In KSF, we monitored each group from dawn at 6:30 AM to 11:45 AM and again in the afternoon from 3:30 PM to 7:30 PM. During our observations, we collected fresh samples as soon as individuals defecated. Based on the characteristics of individuals, we cared not to sample the same individual twice. However, we could not completely rule this out. In OKF, we collected faecal samples from eight confidentially identified individuals of one group. Based on their size, samples were collected in either 15 ml or 50 ml Falcon tubes, stored in 96% ethanol, and transported from the field to the Laboratory of Applied Ecology of the University of Abomey-Calavi, Benin. There, they were preserved using silica gel, following the two-step protocol outlined by Nsubuga et al. (2004) and Roeder et al. (2004), until their transportation to the German Primate Center, Göttingen, Germany, for genetic analysis. For each sample, we recorded date, time, and geographic coordinates (Global Positioning System).

3.7.2. Laboratory work

We extracted total genomic DNA using the NucleoSpin® DNA Stool kit (Machery-Nagel), following the manufacturer's protocols. After extraction, DNA concentrations were quantified with a NanoDrop ND-1000 spectrophotometer (Peqlab). We stored the eluted samples at −20°C until further analysis.

We amplified and sequenced two mitochondrial fragments, the complete cytochrome b gene (cytb; 1140 bp) and a fragment of the hypervariable control region (D-loop). We amplified cytb via two overlapping PCR products with sizes of 727 bp and 663 bp, while D-loop was amplified via a single PCR product with a size of 750 bp. We designed primers (Table 7) within conserved regions of an alignment of whole mitochondrial sequences retrieved from GenBank: *Piliocolobus badius* NC_008219, *Procolobus verus* NC_020666 and *Colobus guereza* NC_006901.

Table 7. Primers used in this study

Primer ID	Sequence 5'-3'
Cytb1-F	ACC AAT GAT ATG AAA AAY CAT C
Cytb1-R	TGG TTG TAT AGT AGG GGT G
Cytb2-F	ACA CCT ACT CTT TCT ACA TG
Cytb2-R	GTT TTG GGT ATT GGY GGT G
D-loop-F	CTC CTC AAA TGA ACT TGC CC
D-loop-R	CAT GCA TTT GGT ATC TTT TAT CT

We performed polymerase chain reaction (PCR) in a total volume of 25 µl containing 2.5 µl 10X buffer, 200 µM dNTPs, 0.4 µM of each primer, 1 Unit FastStart Taq DNA polymerase (Roche), double-distilled water (ddH2O), and 50 ng DNA. Each PCR run included an initial denaturation step at 95°C for 4 minutes, followed by 40 cycles of denaturation at 95°C for 30 seconds, annealing at 54°C (both cytb fragments) or 58°C (D-loop) for 30 seconds, and extension at 72°C for 60 seconds, concluding with a final extension at 72°C for 7 minutes, and subsequent cooling at 8°C. To ensure reproducibility and genotyping success, each sample was amplified at least twice independently. We ran the PCR product in 1% agarose gels stained with ethidium bromide (0.5 µg/mL) to check for PCR performance. We cut PCR products from the gel, cleaned them with the Monarch® DNA Gel Extraction Kit (New England Biolabs), and then sent them to Eurofins Germany for Sanger sequencing.

3.7.3. Data analysis

We checked sequence electropherograms by eye and assembled and manually edited them in BioEdit Sequence Alignment Editor. We aligned the cytb and D-loop sequences using MUSCLE (Edgar, 2004) as implemented in MEGA 12 (Kumar et al., 2024). We also used MEGA12 to check for the correct translation of the cytb sequences into amino acid sequences. To confirm species identity and marker specificity, we employed BLAST (NCBI). However, since no orthologous cytb sequences of *C. vellerosus*, *C. polykomos*, and *C. satanas* are

available in GenBank, we used complete cytb sequences of *C. guereza* and *C. angolensis* to determine the relationship of *C. vellerosus* to these two other Colobus species. In a second step, we downloaded orthologous D-loop sequences from *C. polykomos*, *C. guereza*, and *C. angolensis*. We used *Piliocolobus badius* as an outgroup and reconstructed the phylogenetic trees for cytb and D-loop using the Maximum Likelihood (ML) algorithm with 100 bootstrap replications in MEGA12.

Utilising the aligned cytb and D-loop sequences, we assessed the genetic diversity within the population of *C. vellerosus* inhabiting the KSF and OKF by calculating the number of variable sites (s), total number of mutations (η), haplotype diversity (Hd), and nucleotide diversity (π) with the DnaSP software v6.12 (Rozas et al., 2017).

PART THREE: RESULTS AND DISCUSSION

Chapter 4. Results

4.1. Assessing climate change and anthropogenic impacts on the distribution of suitable habitat for the critically endangered *Colobus vellerosus*

4.1.1. Characterisation of the climate niche of *Colobus vellerosus*

The statistical analysis of the bioclimatic and topographic variables (Table 1) indicated that the climate niche of *C. vellerosus* is defined by averaged median values of 26.10 ºC (±0.74) for AMT, 9.87 ºC (±1.15) for MDR, 68.27 (±2.51) for IsoT, 203.00 mm (±32.09) for PWM, 5.00 (±6.95) for PDM, 2.50 (±1.97) for slope, and 199.00 (±79.46) for aspect.

The response curves of the ensemble climate suitability model (Fig. 15) for bioclimatic variables showed that *C. vellerosus* thrives within a spectrum of climate conditions. These conditions include an AMT ranging from 24.5°C to 27.8°C, a MDR ranging from 7.5°C to 11.5°C, an IsoT ranging from 61 to 74, PWM ranging from 150 mm to 280 mm, PDM ranging from 2 mm to 32 mm, slope ranging from 0 to 10.80, and aspect ranging from 0 to 250.

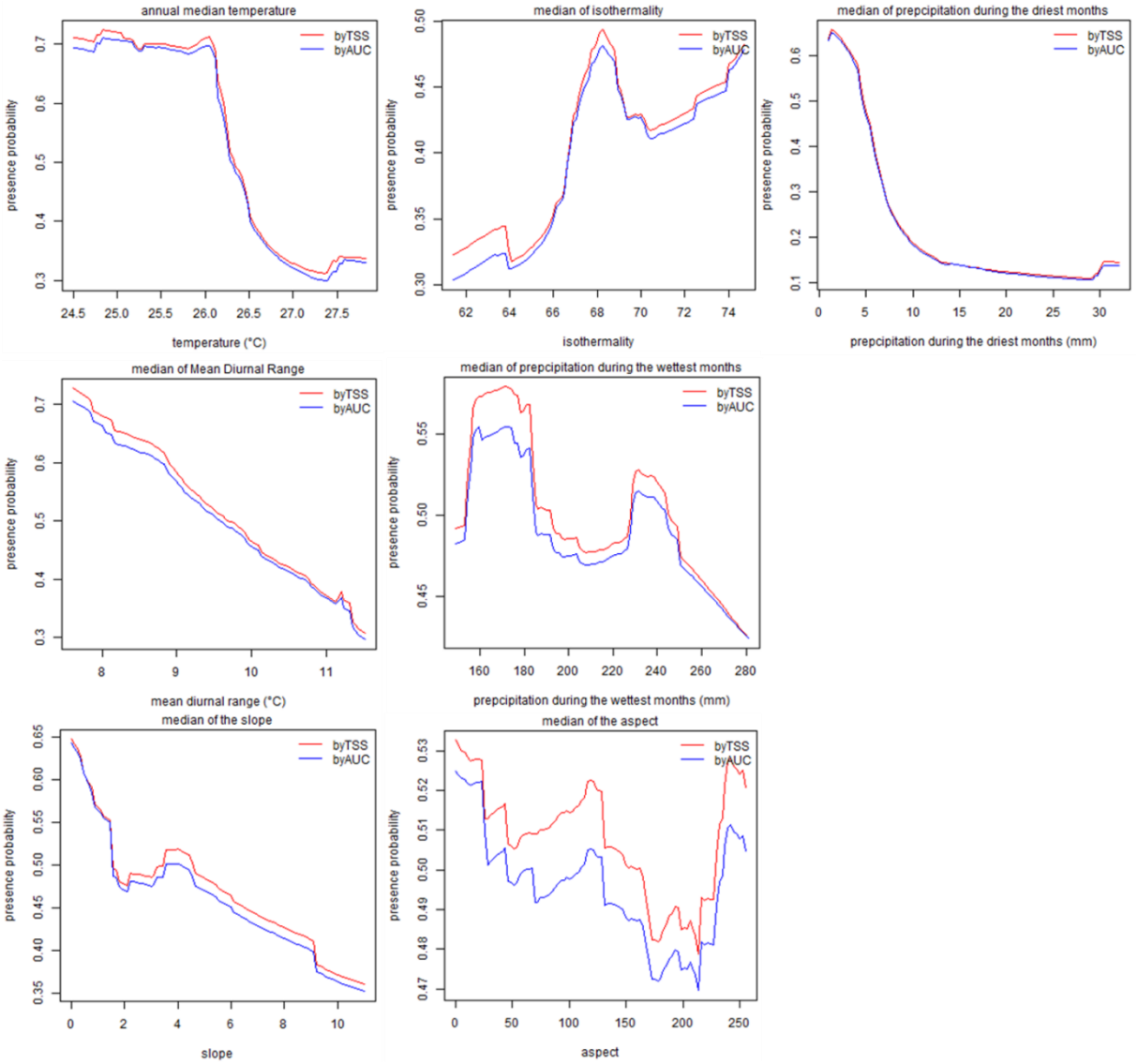

Figure 16. Response curves of the climate suitability ensemble model. Red: TSS; light blue: AUC

The MESS analysis (Fig. 16) highlights areas where the current climate conditions differ from the range of conditions on which the model was trained. In MESS outputs, these differences are called “anomalies.”, and are represented by negative MESS values. An anomaly appears when one or more environmental variables in a location fall outside the range of values the species has historically experienced. In practical terms, this means the model has less confidence in predicting the species’ suitability in those areas because the climate there is unlike anything present in the training data.

In our results, such anomalies occur mainly along the Ghana-Togo border and the southern coast of Ivory Coast along the Gulf of Guinea. Under more severe future climate scenarios (high emission 2070), these anomalous regions are expected to expand, indicating

that larger portions of the landscape may experience climate conditions increasingly unfamiliar to the species' known ecological range.

Conversely, the key predictors (precipitation during the driest months -PDM, precipitation during the wettest months -PWM, and mean diurnal temperature range -MDTR) that determine the distribution of *C. vellerosus* are predicted to become similar to current levels within the species range under future scenarios in the northern areas extending toward the Saharan zone (Fig. 17). This is important to understand, in later result section, why the ensemble models predicted the emergence of new climatically suitable areas in the species' geographical range, particularly in the northern regions towards the Saharan zones under pessimistic scenarios.

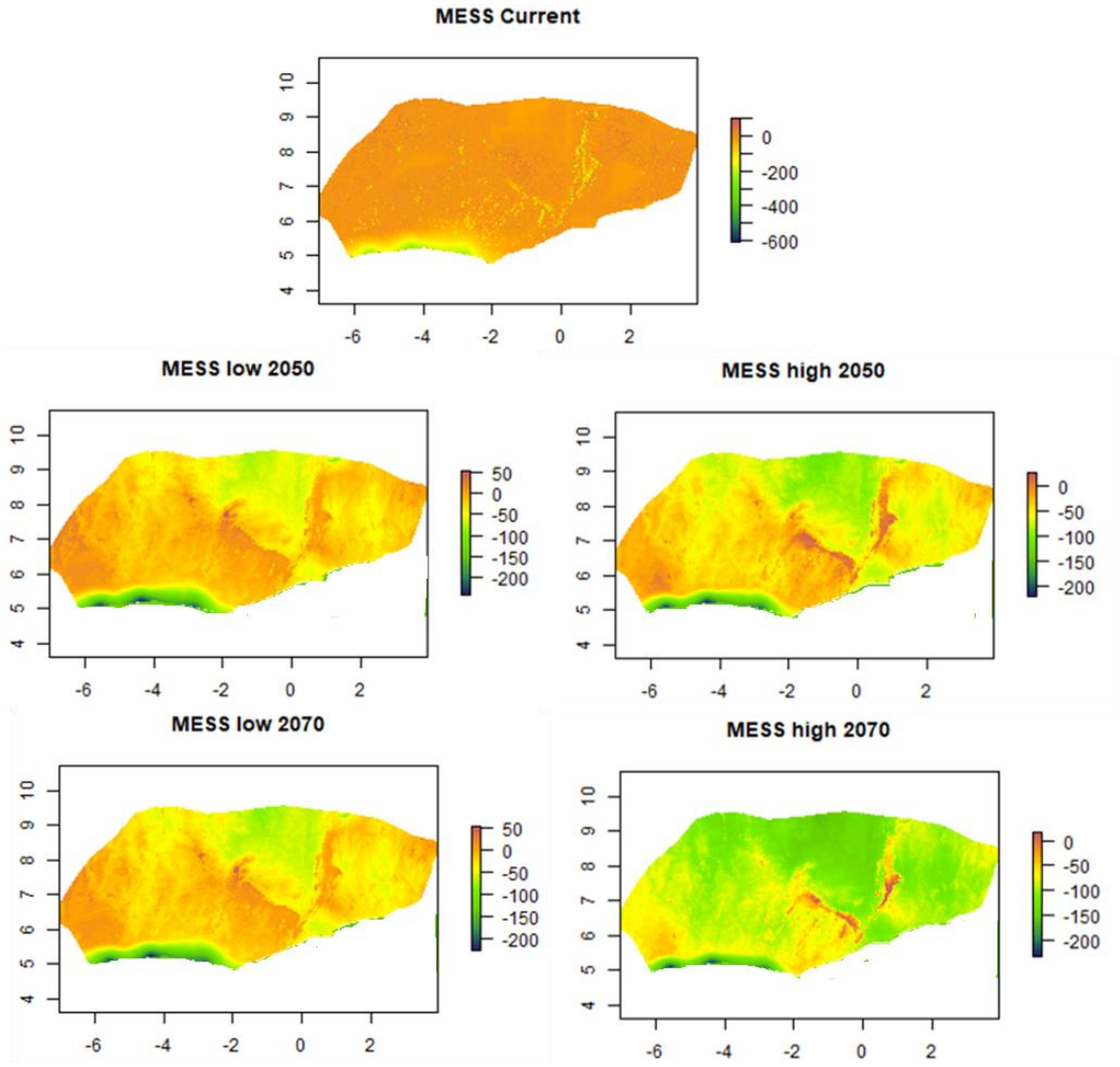

Figure 17. Multivariate Environmental Similarity Surface (MESS) analysis results

Note: The colours in MESS outputs (Figs 16 and 17) represent MESS values, where negative values indicate climate anomalies and positive values indicate climatic conditions within the model's training range. Because *C.*

vellerosus is a terrestrial mammal, these colours should be interpreted solely as indicators of climatic similarity or dissimilarity, not as water bodies or aquatic features.

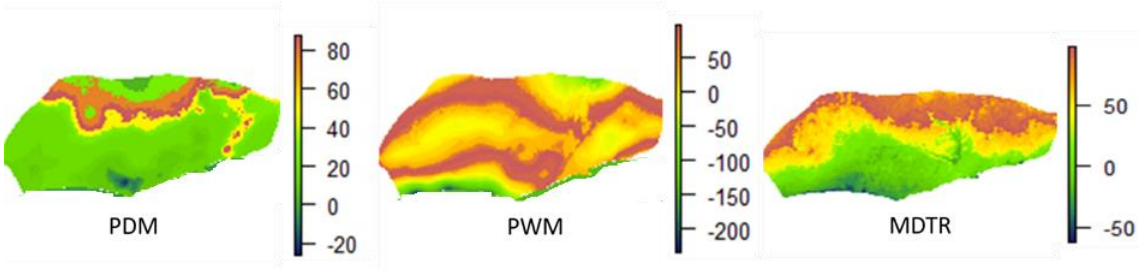

Figure 18. Driving climatic variables

Note: PDM = precipitation during the driest months, PWM = precipitation during the wettest months, and MDTR = mean diurnal temperature range

The clustering analysis showcased three main climatic patterns in the occupancy areas of *C. vellerosus* (Fig. 18). Table 8, Figs. 19 and 20 illustrate that Cluster 1 is characterised by high values of the precipitation during the wettest months, the mean diurnal temperature range and slope, and low values of aspect. Cluster 2 is characterised by high values of the annual mean temperature, and the values of the other variables do not differ significantly from the mean. Cluster 3 is characterised by high values of the isothermality and precipitation during the driest months, and aspects; and low values of the annual mean temperature.

The first two orthogonal dimensions (Dim 1 and Dim 2) of the PCA are highly significant based on eigenvalues and cumulatively explained 67.4% of the variability of the uncorrelated bioclimatic and topographic variables characterising the climate niche of the species (Fig. 21). Dim 1 (38.9% of the total variance) was highly correlated with MDR (r= -0.78, Ctr= 22.03), IsoT (r= 0.89, Ctr= 29.17), PDM (r= 0.90, Ctr= 29.71) and aspect (r= 0.50, Ctr= 9.05). Dim 2 (28.4% of the total variance) was strongly associated with AMT (r= -0.72, Ctr= 26.36), PWM (r= 0.87, Ctr= 37.59), and slope (r= 0.63, Ctr= 20.05).

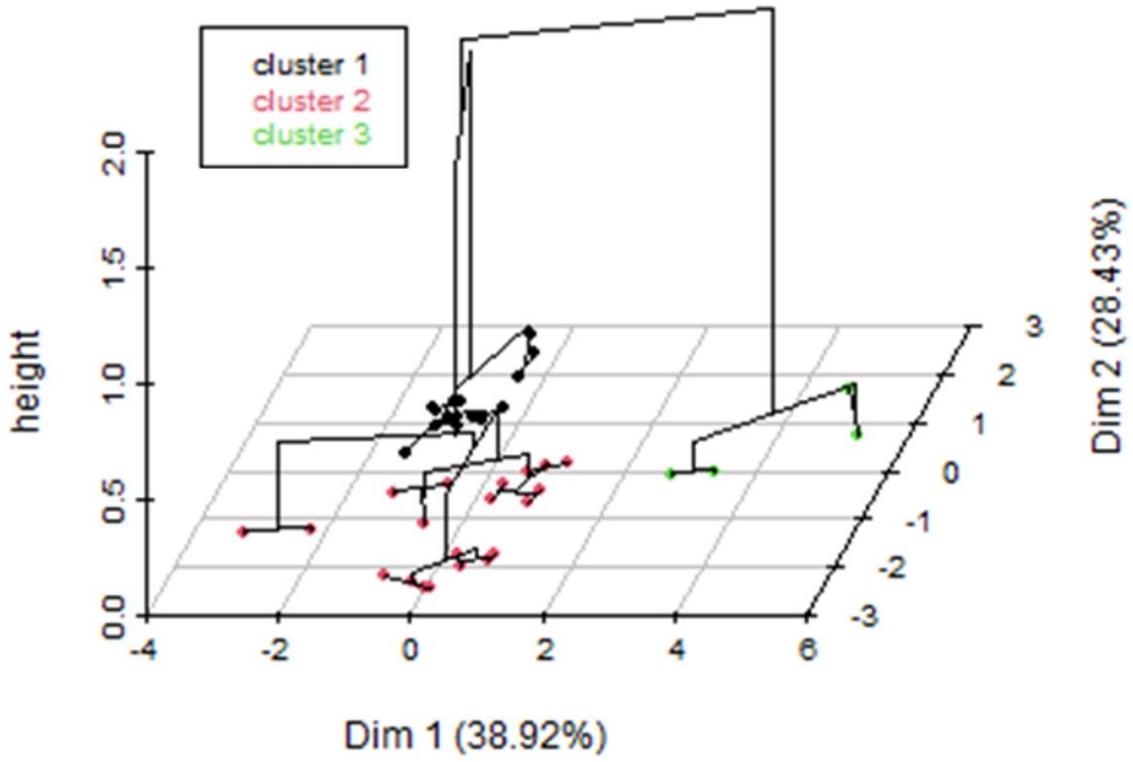

Figure 19. Hierarchical tree drawn on the factorial map, with the occurrences coloured according to their clusters

Table 8. Mean values of variables per cluster

cluster	bio1	bio2	bio3	bio13	bio14	slope	aspect
1	26.1	11.1	66.9	239.1	3	3.5	153.7
2	26.7	9.5	68.3	179.8	5	1.95	179.3
3	25.3	7.9	73.1	235.8	25	3.0	215.0

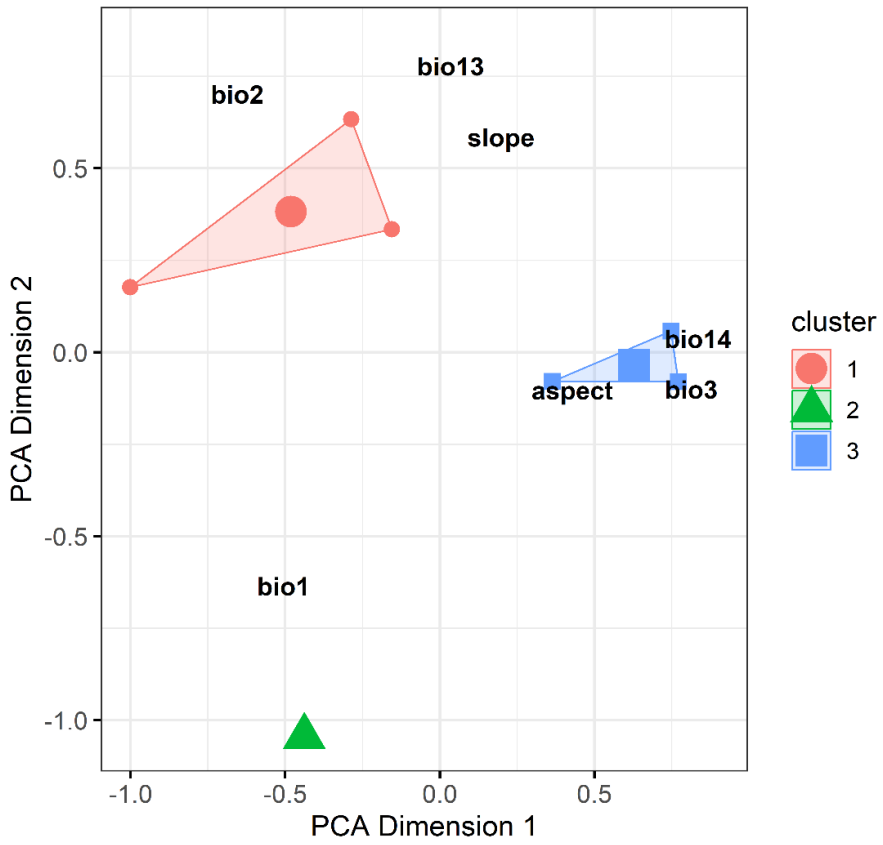

Figure 20. Clusters of environmental variables

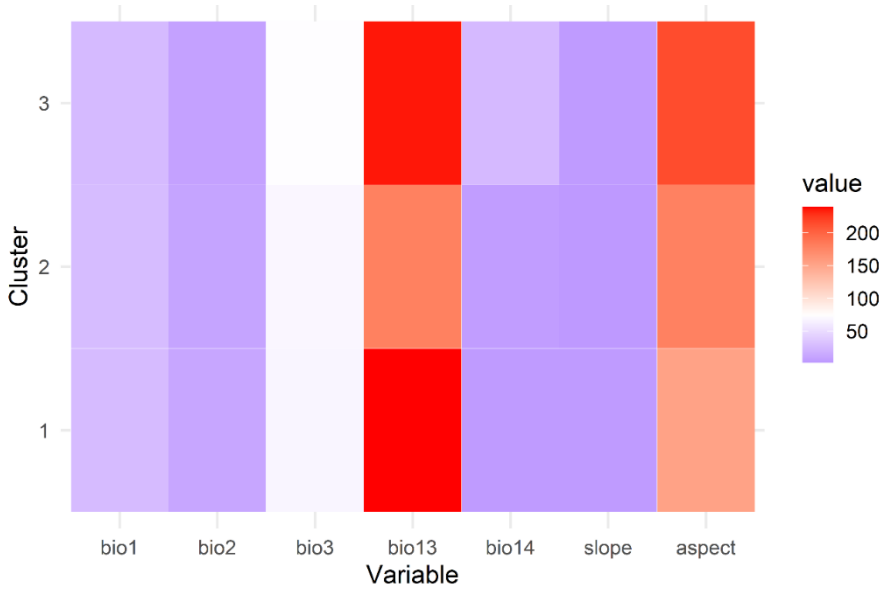

Figure 21. Heatmap of variable values per cluster

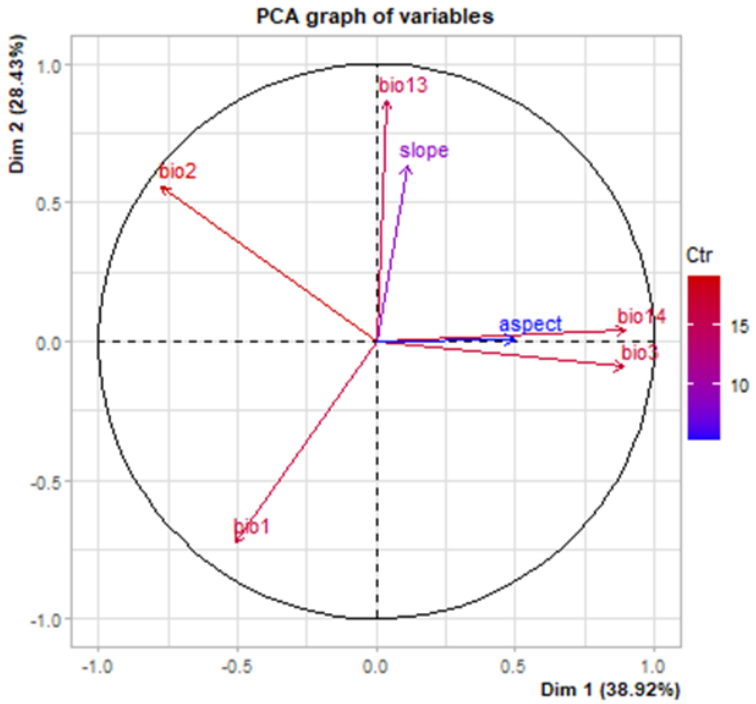

Figure 22. Graph of variables with their contribution (Ctr) to the first two orthogonal dimensions (Dim 1 and Dim 2)

4.1.2. Model performance and variable importance

All the individual algorithms performed well with respect to our defined thresholds. Thus, both our climatic suitability (CS) and habitat suitability (HS) EMs included the eleven initial algorithms and also performed well with higher mean AUC values of 0.92 and 0.93, and mean TSS values of 0.72 and 0.79, respectively (Table 7). These high evaluation scores allow reasonable confidence in the reliability of our EMs, as sufficient model calibration is the most faithful assessment of the model's accuracy (Sillero et al., 2021). Based on the variable importance scores of both EMs, precipitation during the driest month, annual mean temperature, mean diurnal range, and isothermality were respectively the most important bioclimatic variables that best predicted the distribution of *C. vellerosus*, whereas forest cover was the best anthropogenic predictor (Table 8; Figs. 22).

Table 9. Mean evaluation scores of the climatic suitability and habitat suitability EMs

Models	**climatic suitability EM**		**habitat suitability EM**	
Evaluation scores	**ROC**	**TSS**	**ROC**	**TSS**
sensitivity	0.95	0.90	0.85	0.83
specificity	0.77	0.81	0.95	0.95
calibration	0.92	0.72	0.93	0.79

Table 10. Variables' importance in the climatic suitability and habitat suitability EMs

Variables	Climatic suitability EM		Habitat suitability EM	
	ROC	TSS	ROC	TSS
Annual Mean Temperature (°C)	0.50	0.53	0.07	0.08
Mean Diurnal Range (°C)	0.22	0.21	0.16	0.16
Isothermality	0.09	0.08	0.17	0.16
Precipitation during Wettest Month (mm)	0.03	0.02	0.07	0.04
Precipitation during Driest Month (mm)	0.60	0.54	0.64	0.67
Slope	0.06	0.07	0.13	0.16
Aspect	0.01	0.01	0.02	0.02
Forest cover	-	-	0.11	0.10
Population density	-	-	0.07	0.08

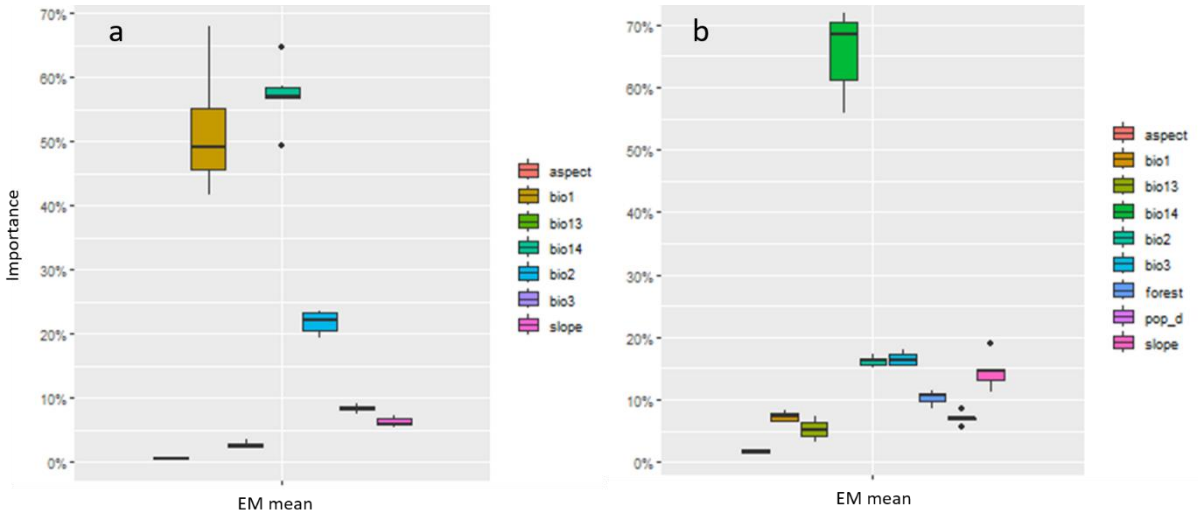

Figure 23. Importance of variables of the climatic suitability EM (a) and the habitat suitability EM. (bio1= annual mean temperature; bio2= mean temperature diurnal range; bio3= isothermality; bio13= precipitation of wettest month; bio14= precipitation of driest month.

4.1.3. Current climatic and anthropogenic habitat suitability

The current suitability maps of the EMs (Fig. 23) showed relatively narrow suitable areas for *C. vellerosus* that correspond to the known inhabited habitats of the species. The climate suitability EM predicted an average of 117,650 km^2 as suitable areas, whereas the habitat suitability EM predicted an average of 117,639 km^2 as the species' current range size. Therefore, *C. vellerosus* exhibited a smaller predicted distribution range when anthropogenic factors were combined with bioclimatic variables. Our analysis of the range size differences between the HS

and the CS models showcased an estimated anthropogenically induced range reduction (percentage of gain minus percentage of loss) of around 36.3% compared to the current climatically suitable areas.

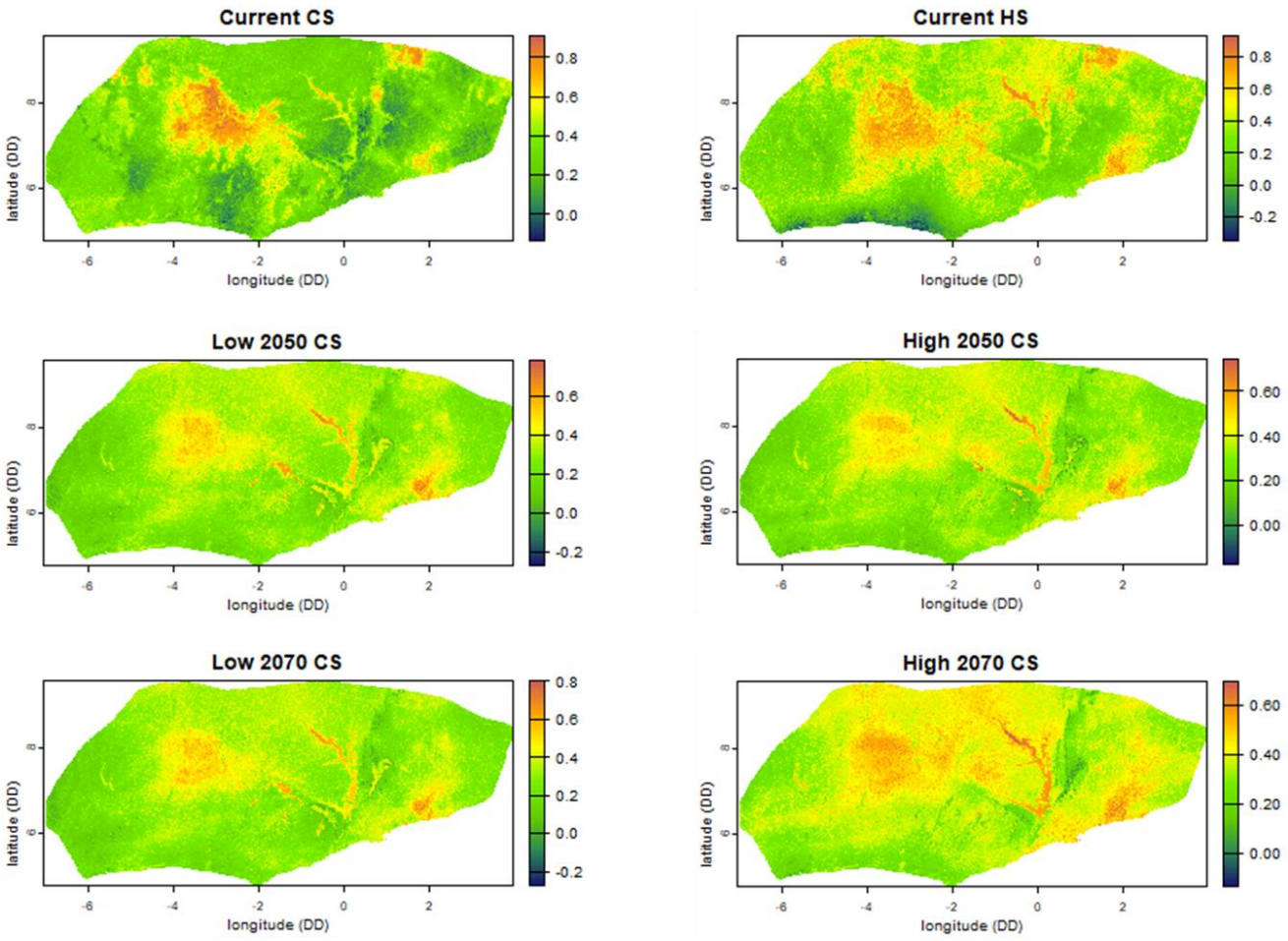

Figure 24. Ensemble model forecasted maps showing the climatic suitability areas for *Colobus vellerosus*

The climatic suitability model was built based on bioclimatic and topographic variables. The habitat suitability model included forest cover and population density as proxies of anthropogenic factors. Higher values indicate higher habitat suitability based on our output BIOMOD2 ensemble model. Low = SSP1-2.6 of the CMIP6; High = SSP5-8.5 of the CMIP6; HS = habitat suitability; DD = decimal degree; low probability value = unsuitable; high probability value = suitable.

4.1.4. Climatic suitability and range change under future scenarios

Under the assumption of zero migration (Table 10, Fig. 24), we determined that the climate suitability for *C. vellerosus* will decrease. The current climatically suitable range is expected to shrink significantly over time, with a projected loss of around 72.9% by 2050, regardless of the scenarios. When considering unlimited migration, our predictions suggested a moderate increase of around 3% to 4% in suitable habitats under the optimistic scenarios for 2050 and 2070, respectively. However, there is still a substantial anticipated reduction in the climatically suitable range, with a higher projected loss of 69.4% by 2050.

Under the assumption of unlimited migration and the pessimistic scenarios (Table 9, Fig. 23), our projections also suggested the emergence of new climatically suitable areas in the species' geographical range, particularly in the northern regions towards the Saharan zones. This could result in new suitable areas ranging from 11.5% to 52.3% in 2050 and 2070, respectively. Therefore, we anticipated a decrease of approximately 58.7% and 2.0% in the climatically suitable range by 2050 and 2070, respectively. Nonetheless, the shift in the climate niche of the species will particularly impact the regions of the KSF in Benin, one of the stronghold habitats of the species, which is predicted to become almost climatically unsuitable by 2050.

Table 11. Range size change computation of the ensemble models filtered by TSS

All entries that are not defined as percentages represent absolute numbers of pixels. CRS: current range size; SRC: percentage of species range change; FRS0D: future range size assuming zero dispersal; FRSFD: future range size assuming full dispersal; Stable 0: unoccupied stable areas; Stable1: occupied stable areas; L50: prediction in 2050 based on SSP1-2.6 of the CMIP6; H50: prediction in 2050 based on SSP5-8.5 of the CMIP6; L70: prediction in 2070 based on SSP1-2.6 of the CMIP6; H70: prediction in 2070 based on SSP5-8.5 of the CMIP6.

TSS (CRS= 117650) climatic suitability									
	Loss	**Stable0**	**Stable1**	**Gain**	**%Loss**	**%Gain**	**%SRC**	**FRS0D**	**FRSFD**
L50	85810	422815	31840	4200	72.937	3.57	-69.367	31840	36040
H50	82644	413436	35006	13579	70.246	11.542	-58.704	35006	48585
L70	79495	421905	38155	5110	67.569	4.343	-63.226	38155	43265
H70	63908	365507	53742	61508	54.32	52.28	-2.04	53742	115250
TSS (CRS= 117639)									
	Loss	**Stable0**	**Stable1**	**Gain**	**%Loss**	**%Gain**	**%SRC**	**FRS0D**	**FRSFD**
CS_HS	56882	412790	60757	14165	48.353	12.041	-36.312	60757	74922

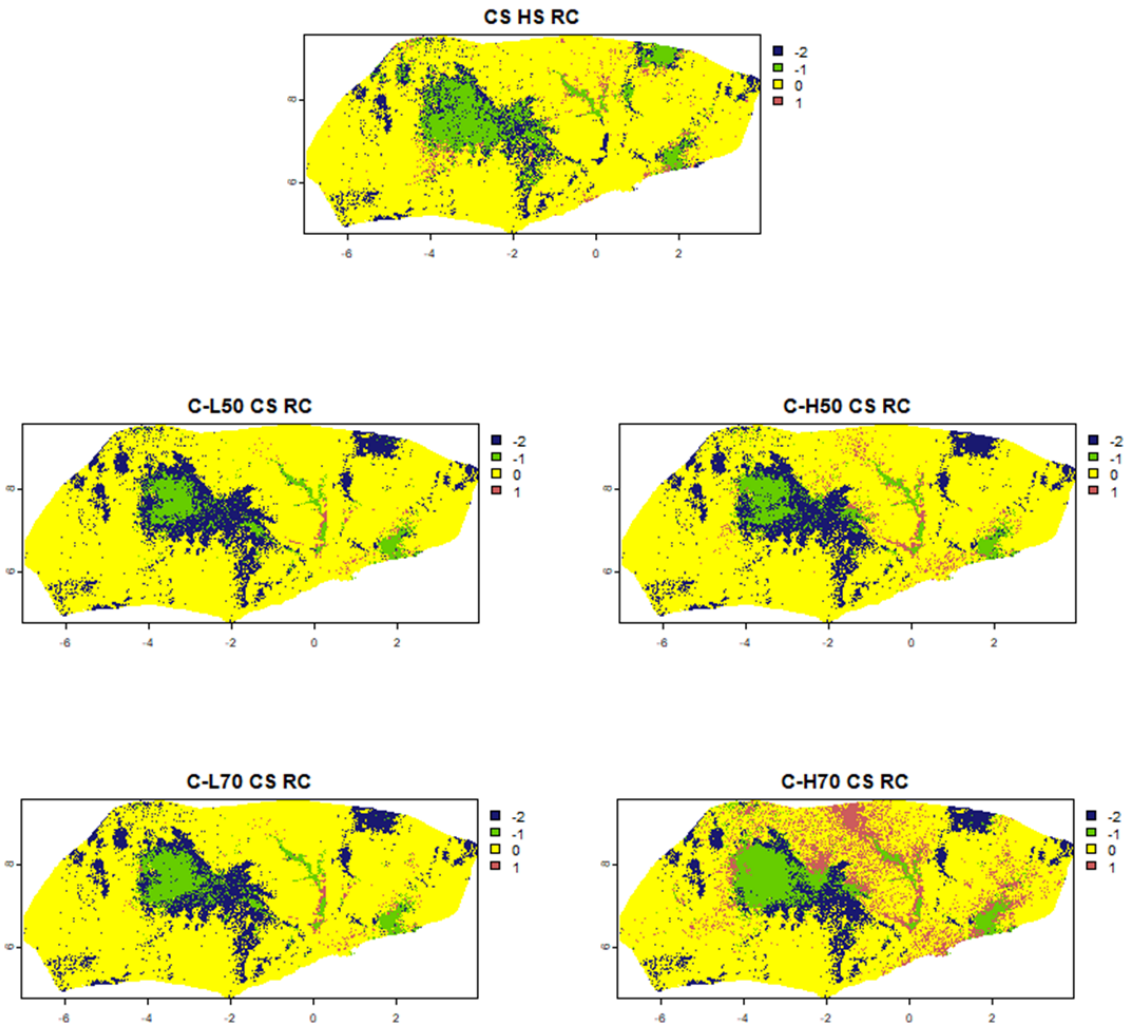

Figure 25. Range size computation maps

HS= habitat suitability; L= SSP1-2.6 of the CMIP6; H = SSP5-8.5 of the CMIP6; 50= 2050; 70= 2070; RSC= range size change; -2= predicted to be lost; -1= predicted to remain occupied; 0= predicted to remain unoccupied; 1= predicted to be gained.

4.2. Spatio-temporal evidence for forest loss and its local socioeconomic drivers within the distribution range of *Colobus vellerosus* in central Benin

4.2.1. Classification Accuracy

The accuracy assessment of the LULC classifications for 1989, 2007, and 2025 demonstrated acceptable to high performance across all study years (Table 12). The overall accuracies were 70.46% for 1989, 86.41% for 2007, and 81.26% for 2025, with corresponding Kappa coefficients of 0.64, 0.83, and 0.77, respectively.

Class-specific accuracies revealed variable performance among LULC categories. The forest class showed high producer's accuracy (0.84–0.94) and user's accuracy (0.73–0.93)

across all periods. Savannah achieved moderate accuracy, with producer's accuracy ranging from 0.44 to 0.76 and user's accuracy from 0.52 to 0.71. Plantations exhibited steady improvement over time, reaching producers' and users' accuracies of 0.77 and 0.89, respectively, in 2025. For cropland, the classification accuracy improved significantly from 1989 (producer's accuracy = 0.17; user's accuracy = 0.37) to 2025 (0.83 and 0.65, respectively). Settlements showed high accuracies, with producers' accuracy between 0.94 and 0.98 and users' accuracy between 0.96 and 0.98. Water bodies were also accurately identified, with both accuracies above 0.91. The highest overall accuracy was in 2007, followed by 2025 and 1989.

Table 12. Confusion matrix based on pixels and classification accuracy metrics for 1989, 2007, and 2025.

PA refers to Producers' Accuracy; UA denotes Users' Accuracy. The grey cells along the diagonal represent the percentage of pixels that have been accurately classified. The off-diagonal cells show the pixels that have been misclassified.

Class	Year	1	2	3	4	5	6	PA	UA
Forest (1)	1989	104	10	5	1	1	1	0.852	0.732
	2007	108	5	1	1	0	0	0.939	0.931
	2025	81	7	1	7	1	0	0.835	0.73
Savannah (2)	1989	12	44	8	12	0	0	0.579	0.524
	2007	0	37	6	6	0	0	0.755	0.712
	2025	17	32	3	19	1	0	0.444	0.696
Plantation (3)	1989	5	6	65	10	2	0	0.739	0.631
	2007	0	8	22	3	0	0	0.667	0.733
	2025	2	0	65	16	1	0	0.774	0.89
Cropland (4)	1989	13	23	25	14	0	4	0.177	0.368
	2007	6	2	0	16	1	0	0.64	0.615
	2025	7	7	1	82	2	0	0.828	0.651
Settlement (5)	1989	3	0	0	1	64	0	0.941	0.955
	2007	0	0	1	0	49	0	0.98	0.98
	2025	2	0	2	2	122	0	0.953	0.961
Water (6)	1989	5	1	0	0	0	62	0.912	0.925
	2007	2	0	0	0	0	35	0.946	1
	2025	2	0	1	0	0	56	0.949	1
1989 – Overall Accuracy = 70.5%; Kappa Coefficient = 0.64									
2007 – Overall Accuracy = 86.4%; Kappa Coefficient = 0.83									
2025 – Overall Accuracy = 81.3%; Kappa Coefficient = 0.77									

4.2.2. Changes quantification

The area extent of major land cover classes exhibited significant temporal variations from 1989 to 2025 (Figs. 26, 27, 28, and 29; Table 13). Forest cover experienced a notable decline, decreasing from 770,281 ha in 1989 to 383,395 ha in 2025, which represents a reduction of 386,886 ha (approximately –50.2%). Similarly, savannah areas diminished from 183,597 ha to 119,268 ha, reflecting a loss of –35.0%.

Between 1989 and 2025, cropland experienced substantial expansion, increasing from 241,585 ha to 551,819 ha. This represents a notable rise of 310,234 ha, or 128.3%. At the same period, settlement areas saw a dramatic increase from 127,974 ha to 352,670 ha, marking a 175.5% increase. In contrast, plantation cover exhibited a more complex trajectory. It decreased sharply from 204,051 ha in 1989 to 40,669 ha in 2007 (80.1% reduction), before rebounding to 121,343 ha in 2025. Despite this rebound, the plantation cover still shows a decrease of 40.5% compared to the initial extent in 1989. Water bodies displayed limited variation throughout the period, with an overall decrease from 3,242 ha in 1989 to 2,235 ha in 2025 (a decline of 31.1%).

Cumulatively, natural vegetation types, specifically forest and savannah, diminished by approximately 46%. Meanwhile, anthropogenic land uses, encompassing cropland, settlements, and plantations, collectively surged by over 60% during the 36-year study period.

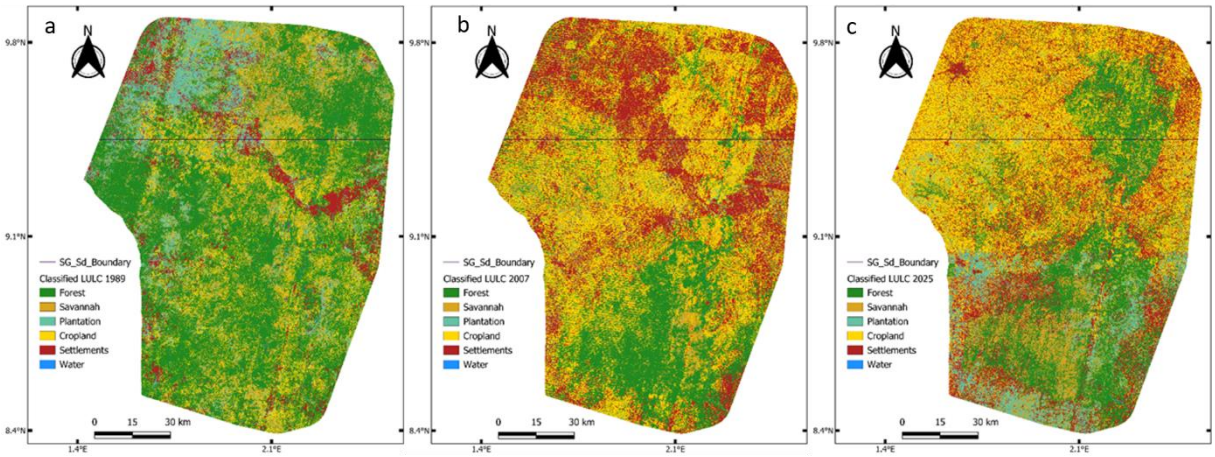

Figure 26. Land use and land cover classification for the year 1989 (a), 2007(b), and 2025

Note: the settlements were overestimated in the 2007 map due to the available satellite image (Landsat 7) for that time period. However, the trajectory of the LULC change is reliable. The depiction of settlement growth from 1989 to 2007, followed by a contraction in 2025, reflects real expansion processes combined with improved mapping techniques rather than an actual decrease in human footprint from 2007 to 2025. See subsection 5.5 for a detailed explanation.

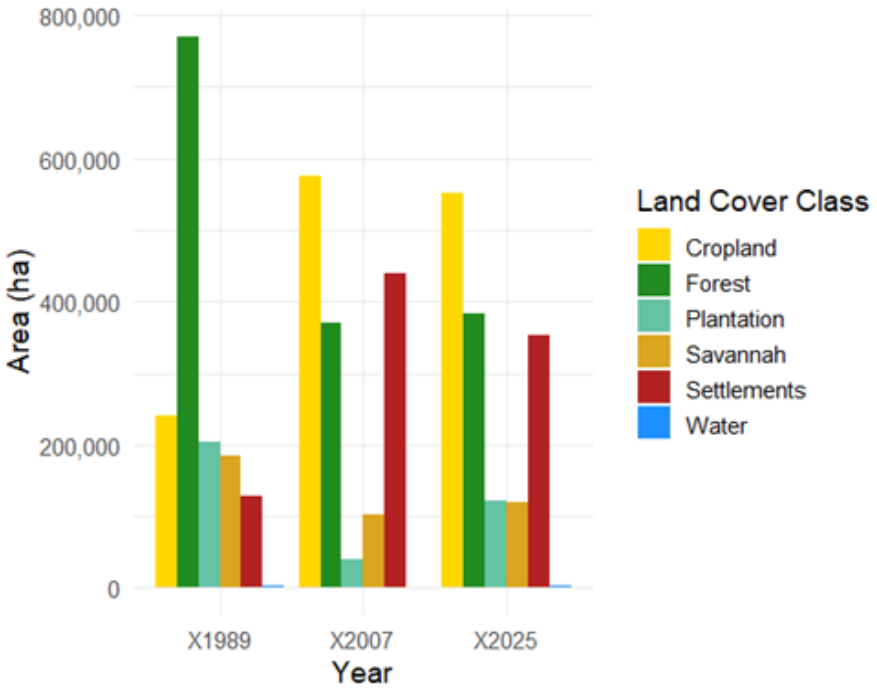

Figure 27. Temporal dynamics of the land cover classes

Table 13. Land-cover area (ha) for each class.

Class	1989	2007	2025
Forest	770,281	370,400	383,395
Savannah	183,597	103,312	119,268
Plantation	204,051	40,669	121,343
Cropland	241,585	575,501	551,819
Settlements	127,974	439,900	352,670
Water	3,242	950	2,235

4.2.3. Land use transition analysis

The analysis of land-cover transitions from 1989 to 2025 revealed significant conversions among dominant classes (Fig. 27; Table 14). Forest areas exhibited the highest transition magnitudes, mainly converting to cropland and settlements. The conversion from forest to cropland accounted for approximately 239,399 ha (30.5% of the forest in 1989), representing the most extensive transition pathway during the study period, with a Transition Intensity Index (TII) of 552.24. The forest-to-settlement transition ranked second, covering 177,095 ha (22.6% of the forest in 1989; TII = 408.52). Together, these two pathways contributed most to the overall reduction in forest extent observed across the landscape.

The transition from plantation to cropland accounted for 111,245 ha, representing 53.4% of the total plantation area in 1989, with a TII of 256.62. Similarly, the conversion from forest to savannah encompassed 69,035 ha, or 8.8% of the forested area in 1989 (TII = 159.25). The

shift from savannah to cropland reached 68,420 ha, equivalent to 36.5% of the savannah area in 1989, with a TII of 157.82.

These quantitative analyses underscore a significant contraction of forested areas from 1989 to 2025 (Fig. 31). In contrast, there has been a notable expansion of cropland-dominated land cover during this same timeframe, both in terms of overall surface area and transition intensity.

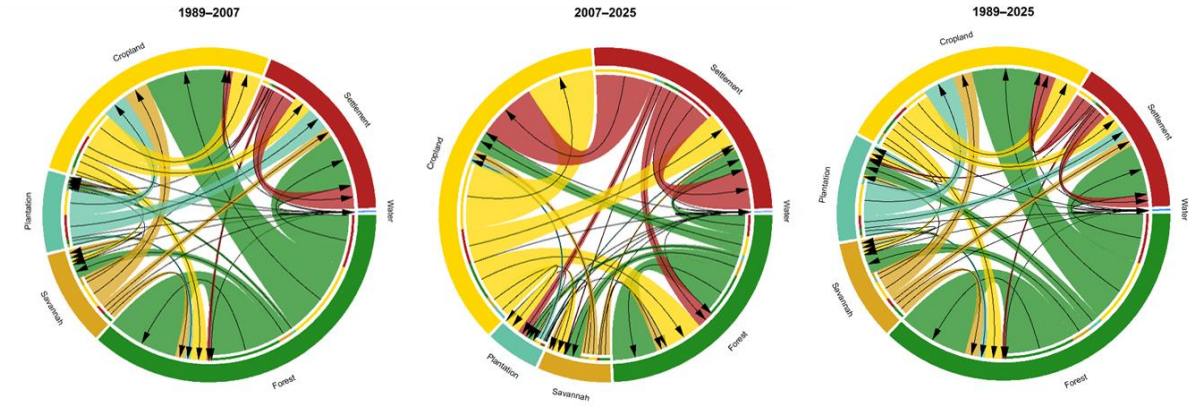

Figure 27. Chord diagram showing the land use land cover transition for the years 1989 to 2007, 2007 to 2025, and 1989 to 2025

Table 14. Transition matrix from 1989 to 2025 in hectares and *percentages*. The letters a, b, c, d, and e indicate the five most dominant land-cover transitions with transition intensity indexes of 552.24, 408.52, 256.62, 159.25, and 157.82, respectively.

FromTo	Forest	Savannah	Plantation	Cropland	Settlement	Water	Total 1989
Forest	245,951 (31.3)	69,035[d] (8.8)	53,093 (6.8)	239,399[a] (30.5)	177,095[b] (22.6)	604 (0.1)	785,177 (100)
Savannah	47,878 (25.6)	20,784 (11.1)	15,010 (8.0)	68,420[e] (36.5)	34,933 (18.7)	196 (0.1)	187,221 (100)
Plantation	22,662 (10.9)	9,719 (4.7)	19,635 (9.4)	111,245[c] (53.4)	44,772 (21.5)	127 (0.1)	208,160 (100)
Cropland	59,914 (24.3)	19,105 (7.8)	24,750 (10.1)	84,845 (34.5)	57,491 (23.3)	147 (0.1)	246,251 (100)
Settlement	13,329 (10.2)	2,522 (1.9)	10,915 (8.4)	58,656 (44.9)	45,067 (34.5)	10 (0.0)	130,500 (100)
Water	1,024 (31.0)	334 (10.1)	212 (6.4)	329 (10.0)	212 (6.4)	1,194 (36.1)	3,305 (100)
Total 2025	390,758 (25.0)	121,498 (7.8)	123,615 (7.9)	562,894 (36.1)	359,570 (23.0)	2,278 (0.1)	1,560,613 (100)

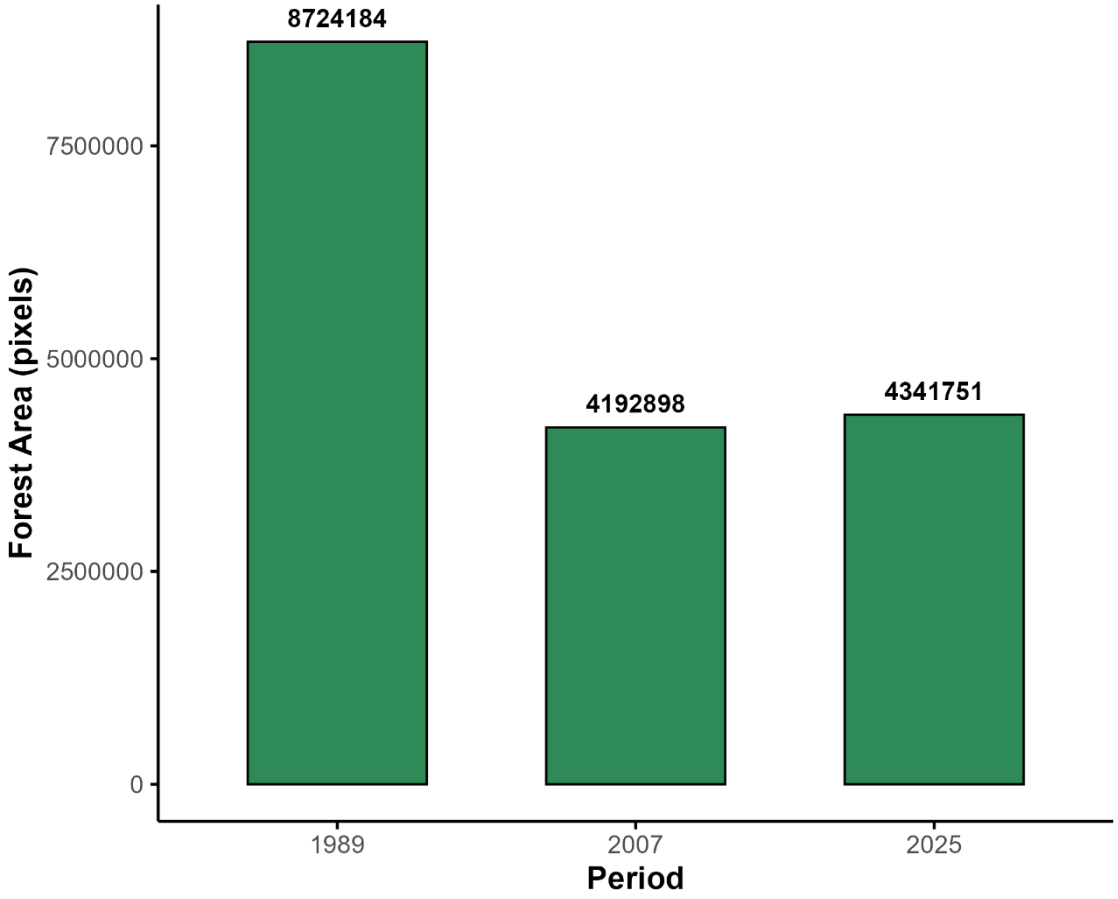

Figure 28. Forest area across 1989, 2007, and 2025 and its net change

4.2.4. Perception of Forest Change and its Determinants

4.2.4.1. Local Perceptions of Forest-Cover Change

Across the Kikélé and Pénéssoulou communities, a majority of respondents (60.7%) perceived a decrease in forest cover over the past decades, while 35.7% perceived an increase, and only 3.6% considered the forest to be stable. When disaggregated by village, similar proportions were observed: in Kikélé, 58.9% perceived decreasing forest cover, 36.9% increasing, and 4.1% stable; in PFR, 62.7% perceived decreasing forest cover, 34.3% increasing, and 3.0% stable (Fig. 28).

A Pearson's chi-square analysis indicated that there was no statistically significant difference in perception patterns between the two villages ($\chi^2 = 0.275$, df = 2, p = 0.87). This finding was corroborated by Fisher's Exact Test, which also showed no significant differences (p = 0.91), suggesting that any variations at the village level lack statistical significance.

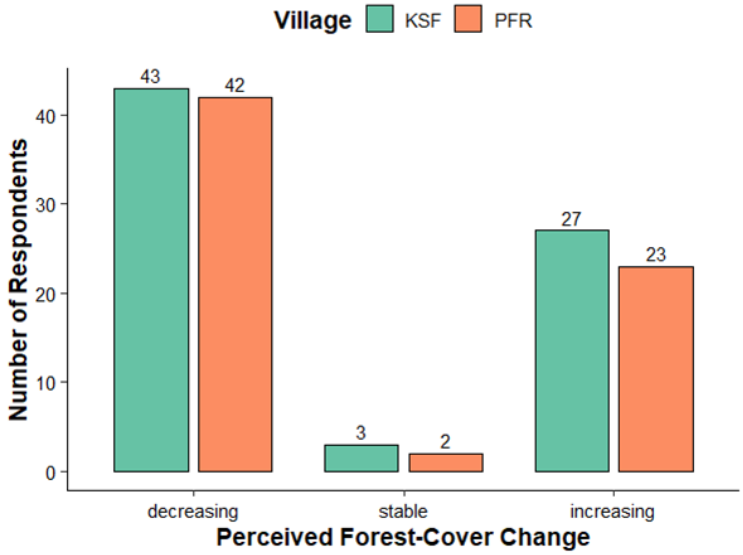

Figure29. Perceptions regarding forest cover change in Kikélé and Pénéssoulou communities

Although the statistical tests revealed no significant difference in perception of forest-cover change between the two communities, it is important to recognise their distinct forest governance contexts. The KSF represents a community-managed sacred landscape governed by local customary rules and taboos, whereas the PFR is a state-managed forest subject to national forestry regulations. Despite these contrasting management regimes, the similarity in perception suggests that both governance systems face comparable external pressures, such as agricultural expansion and resource extraction, which are visibly transforming the surrounding forest matrix. The absence of perceptual divergence also implies that local ecological knowledge in both settings remains strongly attuned to on-the-ground environmental change.

4.2.4.2. Socioeconomic characteristics

Median annual household income in the communities adjacent to the PFR was significantly higher, recorded at 1,000,000 FCFA, compared to 750,000 FCFA in the KSF area. Additionally, there was a notable difference in mean household size, with PFR exhibiting larger households (7.8 ± 5.2) relative to KSF (5.9 ± 4.5). These variations indicate a degree of socioeconomic heterogeneity between the two study sites.

4.2.4.3. Determinants of correct perception

To evaluate factors associated with accurate perceptions of forest decline (i.e., respondents perceiving "decreasing" where satellite analysis confirmed actual forest loss), a binary logistic regression was performed.

The full model, including socioeconomic, attitudinal, and contextual predictors, was not statistically significant overall (Nagelkerke $R^2 = 0.04$; AIC = 196.8). None of the predictors, including education, income, household size, or domestic energy source, was significant ($p > 0.05$). A marginal negative association was observed for respondents expressing willingness to conserve forests ($\beta = -0.99$, $p = 0.065$), suggesting that these individuals were somewhat less likely to perceive the direction of forest-cover change correctly. This relationship was consistent across both villages, implying that differences in forest governance (community- versus state-managed) did not significantly alter how individuals perceived ongoing forest dynamics.

Model selection via stepwise AIC reduction identified willingness to conserve as the only significant predictor. The reduced model (AIC = 185.9) showed that those willing to conserve were less likely to accurately perceive forest decline ($\beta = -1.11$, $p = 0.026$). Their odds of correct perception were 0.33 times lower (95%, CI = 0.12 - 0.87) than those of unwilling to conserve, who were 3.0 times more likely to recognise decreasing forest cover. This suggests a cognitive dissonance effect: conservationists may feel their efforts stabilise forests, while those less engaged see degradation more clearly. The final model's explanatory power was modest (Nagelkerke $R^2 = 0.04$; McFadden $R^2 = 0.03$) and had limited discriminative capacity (AUC = 0.58), indicating that socioeconomic factors alone weakly predict perception accuracy. Broader experiential or cultural factors likely influence forest change perceptions beyond socio-economic variables.

4.2.4.4. Predictors of perception categories

A multinomial logistic regression model was employed to analyse the three perception outcomes: decreasing (reference category), stable, and increasing forest trends. The model converged successfully with an AIC of 244.1. After accounting for all predictors, none of the explanatory variables exhibited statistical significance ($p > 0.05$). Notably, there was a marginal trend indicating a higher probability of respondents perceiving an increasing forest trend among those expressing a willingness to engage in conservation efforts ($\beta = 0.55$, $p = 0.053$). Additionally, factors such as education level, income, household size, and village affiliation did not demonstrate a significant effect on the perception categories.

4.2.4.5. Association tests and categorical relationships

A chi-square test revealed a significant association between conservation awareness and correct perception of forest change ($\chi^2 = 4.37$, df = 1, p = 0.037), indicating that awareness campaigns may enhance accurate understanding of forest trends. Conversely, the relationship between the domestic energy source and perceived forest-cover change was not significant ($\chi^2 = 5.42$, df = 4, p = 0.25).

4.3. Identifying suitable forested areas and protected forests for the conservation of white-thighed (*Colobus vellerosus*) and king (*C. polykomos*) colobus monkeys under climate change in West Africa

4.3.1. Model accuracy and contribution of the climatic variables

The ensemble model demonstrated high accuracy, with AUC and TSS values of 0.96 and 0.81 for *C. vellerosus*, and 0.99 and 0.95 for *C. polykomos*, respectively (Table 15). The selected climatic variables contributed an average of 71.8% (TSS) to the habitat suitability of *C. vellerosus* and 42.1% (TSS) to that of *C. polykomos*. The mean diurnal temperature range, precipitation during the coldest quarter, precipitation seasonality, precipitation during the wettest month, and precipitation during the warmest quarter accounted for 82.7% of the climatic suitability for *C. vellerosus*. For *C. polykomos*, the maximum temperature during the warmest month, mean diurnal temperature range, precipitation during the driest month, precipitation during the wettest month, precipitation during the warmest quarter, and annual mean temperature accounted for 83.8% of its climatic suitability (Tables 16 and 17).

Table 15. Mean evaluation values of the ensemble model

Species	***Colobus vellerosus***		***Colobus polykomos***	
Metric of evaluation	**AUC**	**TSS**	**AUC**	**TSS**
Sensitivity	0.98	0.94	0.97	0.97
Specificity	0.83	0.88	0.99	0.97
Calibration	0.96	0.81	0.99	0.95

Table 16. Variables' importance based on the ensemble model of *Colobus vellerosus*

Variables	**AUC**			**TSS**		
	Mean per. imp (%)	**Rel. contr. (%)**	**Cum. contr. (%)**	**Mean per. Imp. (%)**	**Rel. contr. (%)**	**Cum. contr. (%)**
bio02: Mean Diurnal Range Temperature)	35.8	50.7	50.7	36.5	50.8	50.8
bio19: Precipitation of Coldest Quarter	8.4	11.9	62.6	7.4	10.3	61.1

bio15: Precipitation Seasonality	5.8	8.3	70.9	6.1	8.4	69.6
bio13: Precipitation of Wettest Month	4.3	6.2	77.0	4.9	6.8	76.4
bio18: Precipitation of Warmest Quarter	4.0	5.6	82.6	4.6	6.4	**82.7**
bio5: Maximum Temperature of Warmest Month	3.4	4.8	87.4	3.5	4.9	87.7
bio08: Mean Temperature of Wettest Quarter	2.6	3.7	91.2	2.7	3.8	91.5
bio09: Mean Temperature of Driest Quarter	2.3	3.3	94.5	2.4	3.3	94.8
bio14: Precipitation of Driest Month	2.1	3.0	97.5	2.1	2.9	97.7
bio01: Annual Mean Temperature	1.8	2.5	100.0	1.6	2.3	100.0
Total	70.5	100.0		**71.8**	100.0	

Table 17. Variables' importance based on the ensemble model of Colobus polykomos

Variables	AUC			TSS		
	per. Imp. (%)	rel. contr. (%)	cum. Contr. (%)	per. Imp. (%)	rel. contr. (%)	cum. Contr. (%)
bio05: Max Temperature of Warmest Month	10.1	22.3	22.3	9.1	21.6	21.6
bio02: Mean Diurnal Range (Temperature)	8.5	18.7	41.0	7.1	16.8	38.5
bio14: Precipitation of Driest Month	6.0	13.1	54.1	5.9	13.9	52.4
bio13: Precipitation of Wettest Month	4.8	10.5	64.6	4.8	11.3	63.7
bio18: Precipitation of Warmest Quarter	4.7	10.4	75.0	4.9	11.6	75.2
bio01: Annual Mean Temperature	4.0	8.9	83.9	3.6	8.5	**83.8**
bio08: Mean Temperature of Wettest Quarter	2.5	5.6	89.4	2.5	6.1	89.8
bio15: Precipitation Seasonality	1.8	4.0	93.4	1.7	4.1	93.9
bio09: Mean Temperature of Driest Quarter	1.5	3.3	96.8	1.4	3.2	97.2
bio19: Precipitation of Coldest Quarter	1.5	3.2	100.0	1.2	2.8	100.0
Total	45.5	100.0		**42.1**	100.0	

4.3.2. Current climatically suitable areas

The climatically suitable area for *C. vellerosus* spans 520,193 km² (Table 18; Fig. 30), exceeding its IUCN-defined distribution range of 478,687 km². The predicted suitable area overlaps with the IUCN range by 71%, amounting to 366,822 km² of the total 520,193 km². The 29% of the predicted suitable area that lies outside the IUCN distribution range encompasses the Tai National Park to the southwest, significantly surrounds the region where the species is probably extinct in Burkina Faso to the northwest, and extends southeast to include Okomu National Park and Ologbo Game Reserve in Nigeria. Suitable areas for *C. vellerosus* have also been identified in the Fouta Djallon Highlands of Guinea.

For *C. polykomos*, the estimated climatically suitable area is 240,398 km², which is smaller than the IUCN-defined distribution range of 343,041 km². This predicted suitable area overlaps with the IUCN-defined distribution range of *C. polykomos* by 78%, representing 186,728 km² of the total predicted area of 240,398 km². The remaining 22% of the predicted suitable habitat, which does not overlap with the known range, extends into the Bandama and Sassandra interfluvial zone, encompassing the vicinity of the Yikpa waterfall in Togo and

covering the western portions of Okomu National Park and Ologbo Game Reserve in Nigeria (Table 2 and Fig. 33).

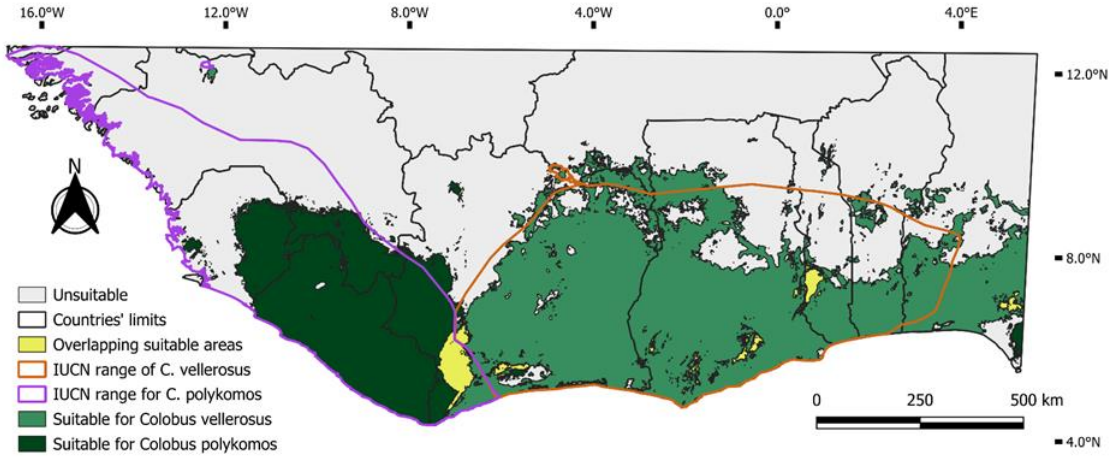

Figure 28. Current climatically suitable and overlapping areas for *Colobus vellerosus* and *C. polykomos*

4.3.3. Future climatically suitable areas

Based on the low greenhouse gas emission scenario and projections for the years 2040 to 2060, climatically suitable areas for *C. vellerosus* are expected to decrease by approximately 21.7% (113,000 km²), while those for *C. polykomos* are projected to decline by 75.7% (181,971 km²) under the zero-migration assumption (Fig. 25). In the case of the unlimited migration assumption, *C. vellerosus* will gain 3.6% (18,886 km²), and *C. polykomos* 1.2% (2,857 km²). Therefore, for *C. vellerosus*, we anticipate a reduction in the suitable area of 18.1%, while for *C. polykomos*, a decrease of around 74.6% is expected (Table 18 and Fig. 31).

Table 18. Computation of range size changes for the ensemble forecasting of *C. vellerosus* and *C. polykomos*.

CCSA: current climatically suitable areas; Loss: currently suitable areas predicted to be lost, Stable: occupied stable areas; Gain: areas predicted to become suitable; %SRC: percentage of species range change; FRS0D: future range size assuming zero dispersal; FRSFD: future range size assuming full dispersal. Projections are based on the low greenhouse gas emission scenario for 2050.

Taxon	CCSA km²	Loss km²	Stable km²	Gain km²	Loss %	Gain %	SRC %	FRS0D km²	FRSFD km²
C. vellerosus	520,193	113,000	407,193	18,886	21.7	3.6	-18.1	407,193	426,079
C. polykomos	240,398	181,971	58,427	2,857	75.7	1.2	-74.5	58,427	61,284

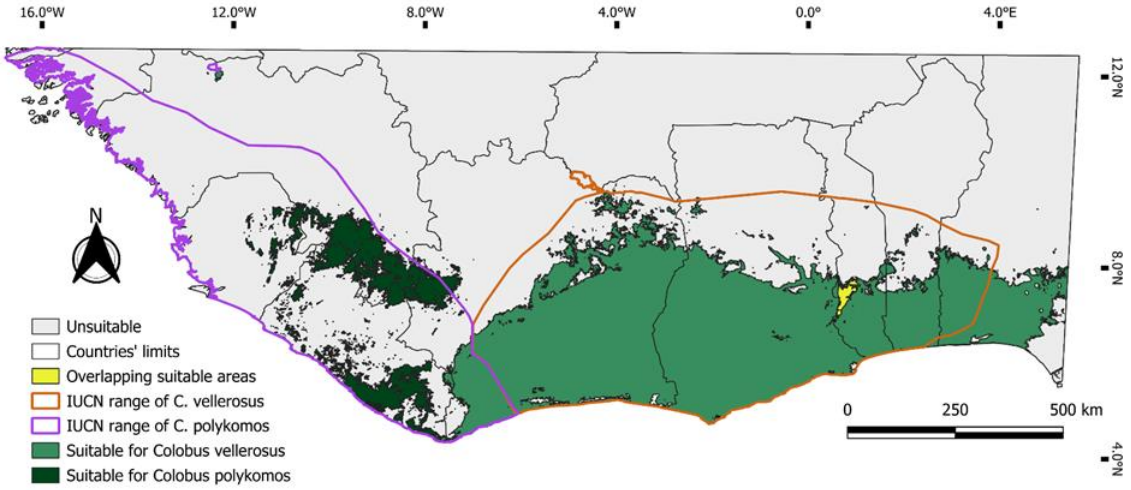

Figure 29. Climatically suitable areas and overlapping areas for *Colobus vellerosus* and *C. polykomos* based on the low greenhouse gas emission scenario by 2050

4.3.4. Current and future overlapping suitable areas

Under present climatic conditions, the total climatically suitable area for the two species amounted to 740,923 km^2 (Fig. 31), with 500,525 km2 for *C. vellerosus* and 220,730 km^2 for *C. polykomos*. The spatial overlap of both species encompassed an area of 19,668 km^2, which represents 2.7% of the total suitable area for both taxa.

Under the low greenhouse gas emission scenario, the projected climatically suitable area for both taxa was 485,313 km^2 (Fig. 25), 424,029 km^2 for *C. vellerosus*, and only 59,234 km^2 for *C. polykomos*. Most currently overlapping areas are predicted to become unsuitable for *C. polykomos*, reducing the overlapping area to just 2,050 km^2 (0.4 % of the total projected suitable area for both species).

4.3.5. Forested and protected forested areas within the suitable range for long-term conservation

Covering an area of approximately 1,624,800 km², representing our study's focus, there was about 370,000 km² of tree cover. From 2001 to 2023, this area has lost 127,000 km² of its tree cover, amounting to a 26% reduction since the 2000s. Only 7.3% (27,066 km²) and 43.3% (160,189 km²) of this tree cover were suitable forested areas for *C. vellerosus* and *C. polykomos*, respectively. Furthermore, we found that 52.1% (14,102 km²) and 17.1% (27,385 km²) of these suitable forested areas were located within protected zones of at least 1 km² for *C. vellerosus* and *C. polykomos*, respectively (Table 19, Fig. 35, Fig. 36). Our modelling predicted that by 2050, 41.3% (11,188 km2) of the current suitable forested areas will remain viable for *C. vellerosus*, while only 28.1% (45,019 km2) will remain suitable for *C. polykomos*. Almost all current overlapping areas were expected to become unsuitable for *C. polykomos*.

Table 19. Sizes (km^2) of the IUCN defined-ranges, climatically suitable areas, suitable forested areas, and suitable forested areas within protected areas for *Colobus vellerosus* and *C. polykomos*

Taxa	IUCN range size	climatically suitable area	suitable forested area	suitable forested area within PAs
C. vellerosus	478,687	520,193	27,066	14,102
C. polykomos	343,041	240,398	160,189	27,385

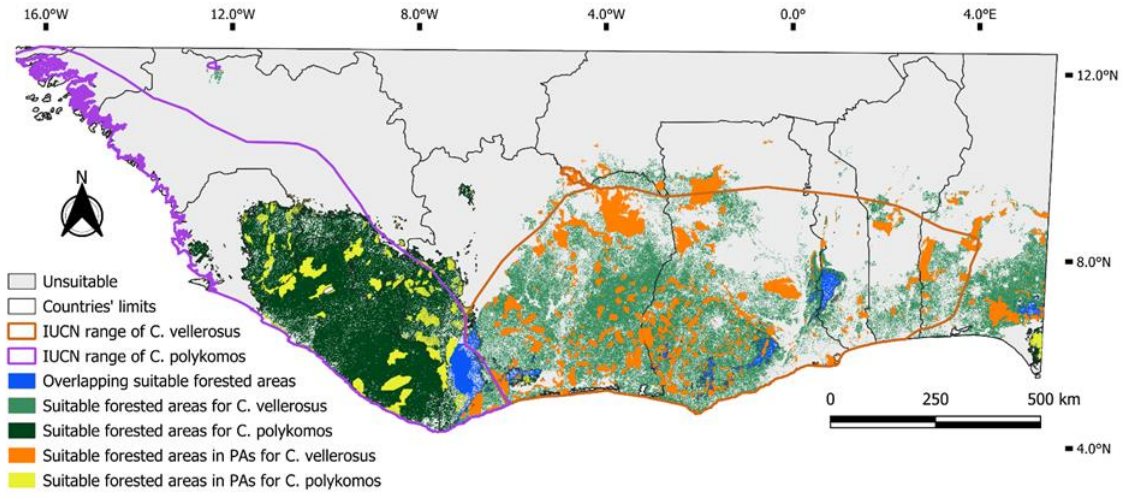

Figure 30. Suitable forested areas for *Colobus vellerosus* and *C. polykomos* based on current climate conditions

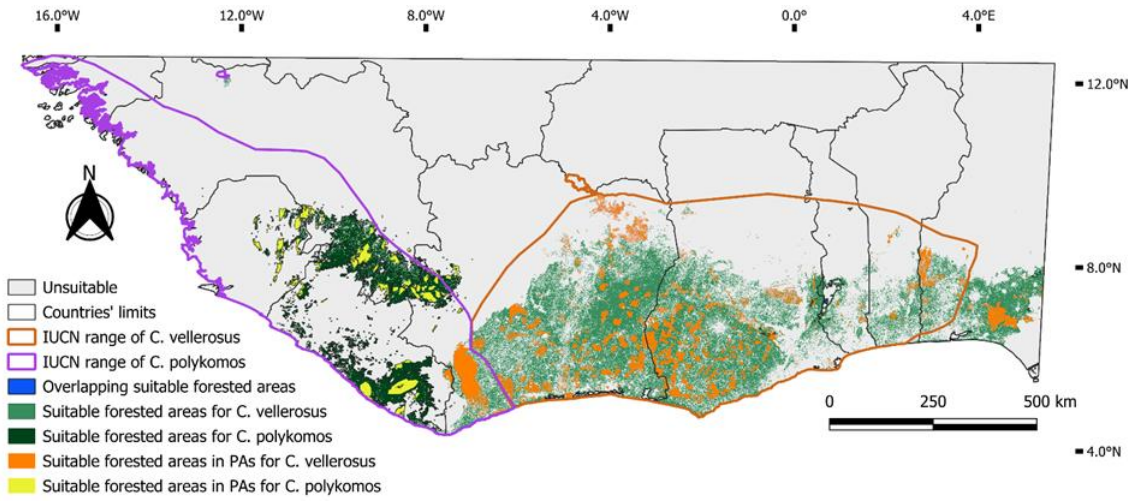

Figure 31. Suitable forested areas for *Colobus vellerosus* and *C. polykomos* according to the low greenhouse gas emission scenario for 2050

4.3.6. Identified suitable protected forests for *Colobus vellerosus*

We identified 527 protected areas (PAs) and other effective conservation measures (OECMs, Fig. 35) that were suitable for *C. vellerosus*, each containing at least 1 km² of forest under the current climate conditions. Within these PAs and OECMs, *C. vellerosus* has been observed in eight forests over the past two decades (from 2004 to 2024), specifically: Lama Classified Forest, Comoe National Park, Boabeng-Fiema Monkey Sanctuary, Kakum National Park, Mole National Park, Opara (Okpara) Forest/Game Reserve, Old Oyo, and Fazao-Malfakassa. However, since 2004, *C. vellerosus* has not been recorded in four of the identified forests: Ouémé Supérieur Classified Forest, Bosomoa Forest Reserve, Bui National Park, and Digya National Park, and it may have possibly gone extinct in four others: Mont-Kouffé Classified Forest, Wari-Maro Classified Forest, Pénéssoulou Classified Forest, and Comoé-Léraba Partial Wildlife Reserve. No sightings of *C. vellersosus* have been documented in the remaining 511 forests. Of the 527 identified PAs, 437 were expected to remain suitable for *C. vellerosus*, based on the low greenhouse gas emission scenario in 2050.

4.4. Current habitat connectivity and potential forest corridors

4.4.1. Changes in forest fragmentation and connectivity between 1989 and 2025

The map of the binary forest raster illustrates two main connected forest patches: a southern patch encompassing the Pénéssoulou Forest Reserve, the Kikélé Sacred Forest, and the Mont-Kouffé-Wari-Mari Forest complex, and a northern patch mainly comprising the Ouémé Supérieur Forest. Thus, “landscapemetrics” internally treats them as separate classes when

certain metrics are calculated, certainly due to different connected components. This results in two contrasting but complementary 2025 scenarios. Here, the southern patch corresponds to 163,142 forest patches, and the northern patch corresponds to 126,821 forest patches in 1989.

Class-level landscape metrics derived from the binary forest rasters indicate a substantial decline in forest structural configuration and connectivity across the distribution range of *C. vellerosus* between 1989 and 2025 (Table 20, Figs 34).

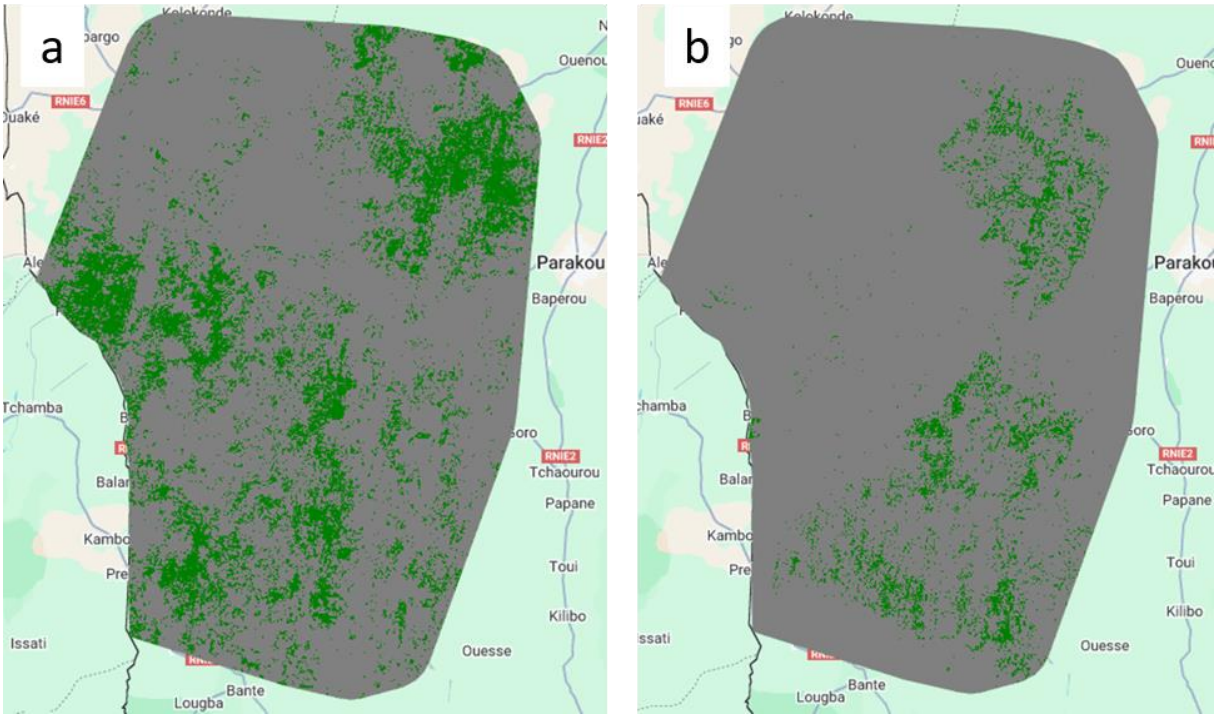

Figure 32. Binary forest map in 1989 (a) and 2025 (b) of the distribution range of *Colobus vellerosus* in central Benin

Table 20. Class-level forest fragmentation metrics for forest cover in 1989 and 2025 within the range of *Colobus vellerosus* in central Benin.

N_PATCHES = Number of Patches; MP_SIZE = Mean Patch Size; EDGE_D = Edge Density; COHESION = Patch Cohesion Index; DIVISION = Landscape Division Index; MESH = Effective Mesh Size; SPLIT = Splitting Index.

Year	N_ PATCHES	MP_SIZE (10^{-5} ha)	EDGE_D	COHESION	DIVISION	MESH (ha)	SPLIT
1989	126,821	77.7	77.8	99.9	0.7	40.97	3.3
1989	163,142	22.8	129.5	99.5	0.9	0.33	416.7
2025	60,606	237.3	65.1	99.9	0.4	105.79	1.5
2025	87,900	21.9	36.9	98.7	0.9	0.04	4421.1

In 1989, the forest landscape of central Benin exhibited a relatively cohesive and spatially structured configuration. The landscape metrics revealed high cohesion values (99.5 and 99.9%), moderate edge density (77.8 and 129.5 m/ha), and low splitting (3.3 and 416.7), which together indicate that the forest cover was highly aggregated and only weakly fragmented. The large mesh size (up to 40.97 ha) further demonstrates that forested areas were spatially continuous at the landscape scale, forming broad and internally connected clusters. These "spatially continuous forest clusters" refer to large, cohesive forest masses separated by limited non-forest gaps, rather than a single uninterrupted forest block. This structural pattern is consistent with the ground-truth configuration of two main connected forest systems: the PénéssoulouForest Reserve, the Kikélé Sacred Forest, the Okuta Kobunan Forest associated with the Mont-Kouffé–Wari-Maro complex in the southern and the Ouémé Supérieur Forest in the northern. Together, these two forest blocks functioned as extensive, internally connected forest clusters, ensuring ecological continuity and potential habitat connectivity for forest-dependent species such as *C. vellerosus*.

By contrast, the 2025 results revealed contrasting fragmentation trajectories between the two main forest clusters identified in the binary raster. The southern cluster (87,900 patches) exhibited a much smaller mean patch size (0.00022 ha), a reduced mesh size (0.037 ha), a very high splitting value (4,421.12), and a slight decline in cohesion (98.7), signalling a transition from large, cohesive clusters to smaller, isolated forest fragments. This area of the landscape has therefore evolved from a configuration dominated by a few large, connected forest complexes to a mosaic of smaller, disconnected patches. This implies a loss of structural connectivity and functional continuity between the major forest systems, reducing potential dispersal pathways and increasing isolation among primate populations. In the northern cluster, represented by 60,606 patches, the mean patch size and the mesh size increased substantially to 0.00237 ha and 105.79 ha, respectively, and the splitting index dropped to 1.5, suggesting the persistence of relatively large, cohesive forest blocks.

The trends observed over the past 36 years in central Benin (Figs. 39 and 40) indicate two contrasting fragmentation scenarios for 2025: one of severe disaggregation and isolation in the southern forest complex, and another of partial consolidation in the northern forest block. This has led to a dual structure of localised fragmentation versus residual connectivity, resulting in uneven habitat quality for *C. vellerosus* and potential risks of population isolation in the fragmented southern area.

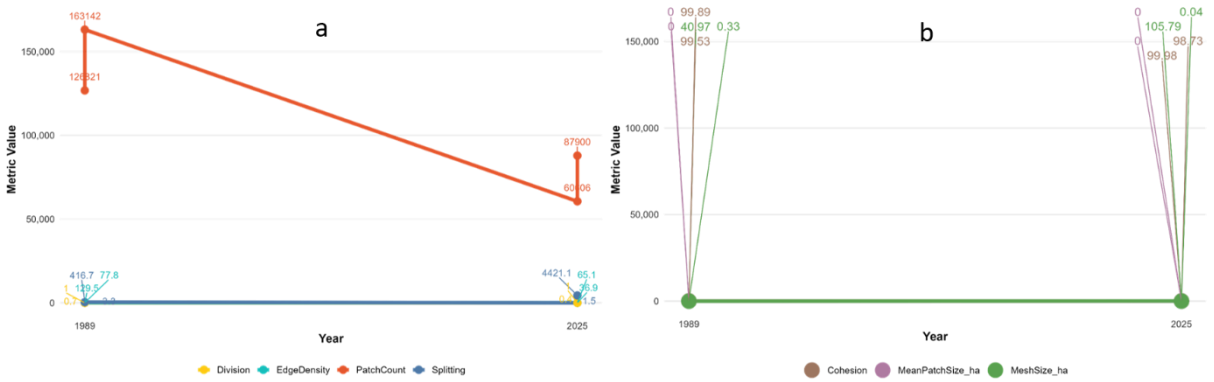

Figure 33. Dual fragmentation trend in central Benin from 1989 to 2025 (a), dual isolating trend in central Benin from 1989 to 2025 (b)

4.4.2. Landscape-scale connectivity patterns in central Benin

The landscape-wide graph analysis (Table A1, Figs. 41 and 42), conducted across all 119 forest patches, revealed strong heterogeneity in both patch size and their structural roles within the forest network. Patch areas spanned several orders of magnitude, ranging from an average 1 km² to more than 966 km², indicating a mosaic of small fragments embedded within a matrix dominated by a few very large forest blocks (notably patches 35 within Ouémé Supérieur, 113, 118 within Monts-Kouffé). Despite their size, most patches exhibited low degree centrality, with 41% of patches (n = 49) showing degree = 0, suggesting that a substantial portion of the forest landscape consists of functionally isolated remnants with no direct topological links to surrounding habitat and highlighting widespread fragmentation.

All the patches were connected with degree centrality values ranged from 1 to 19. However, the patches with high degree centrality were geographically clustered. All patches with degree centrality equal or higher than to 16 were located within the Monts-Kouffé forest complex. This points Monts-Kouffé functions as the central structural nucleus of the entire landscape. This forest hosts both the most well-connected patches and the densest internal network of forest patches.

Most patches exhibited low or zero values of betweenness centrality. However, a few fragments displayed high betweenness. Similarly to degree centrality, most of these are within the Monts-Kouffé-Wari-Maro Forest complex. Thus, they serve as key stepping stones for global movement within the landscape. Patch 70, the only outlier, acts as a gateway between the core and peripheral fragments, highlighting its crucial role of connectivity.

Importantly, many of these high-betweenness connectors were medium-sized fragments rather than the largest forest blocks, underscoring that spatial position, rather than patch size,

primarily determines their centrality within the network. For example, patch 65 (betweenness = 420) and patch 72 (454), both within the Wari-Maro Forest, represent medium-sized forest remnants positioned at key bottlenecks. Conversely, the extremely large patches, such as 35 (Ouémé Supérieur), 113, and 118 (Monts-Kouffé), show contrasting roles: patch 118 serves as a major connectivity broker (betweenness = 772), whereas patches 35 and 113 play minimal or moderate topological roles despite their size. Their roles are analogous to ecological linchpins: the loss of any one of these fragments would disproportionately reduce landscape-scale connectivity.

In summary, these results showed: a widespread isolated fragments with no graph connections; a single, highly cohesive connectivity nucleus within Monts-Kouffé; and a small number of critical stepping-stones that maintain forest cohesion. The key stepping-stones mostly clustered within the Monts-Kouffé–Wari-Maro complex. These results emphasised that conserving or restoring connectivity hinges on protecting both large patches and specific medium-sized fragments.

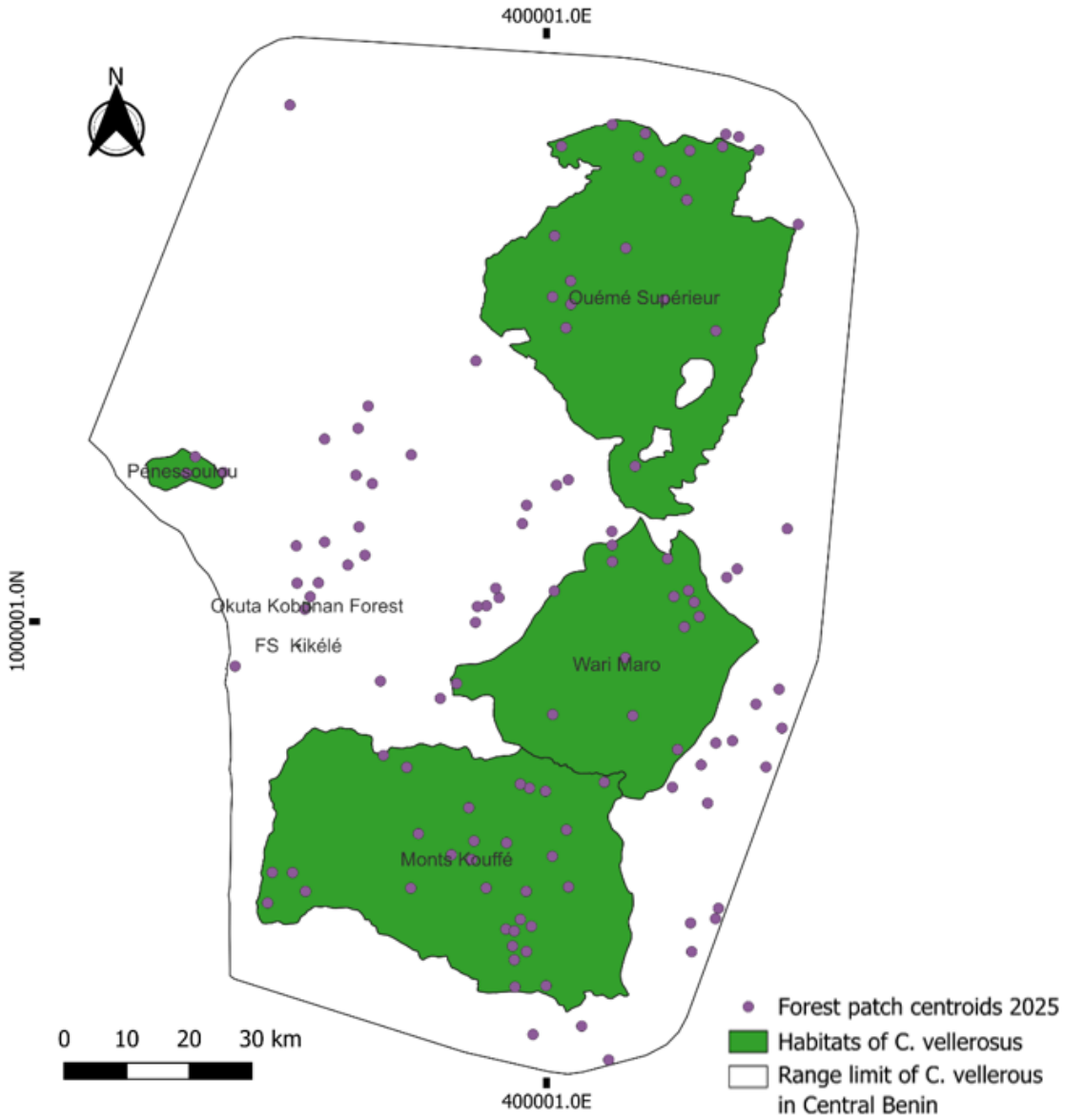

Figure 36. Landscape-scale forest centroids 2025

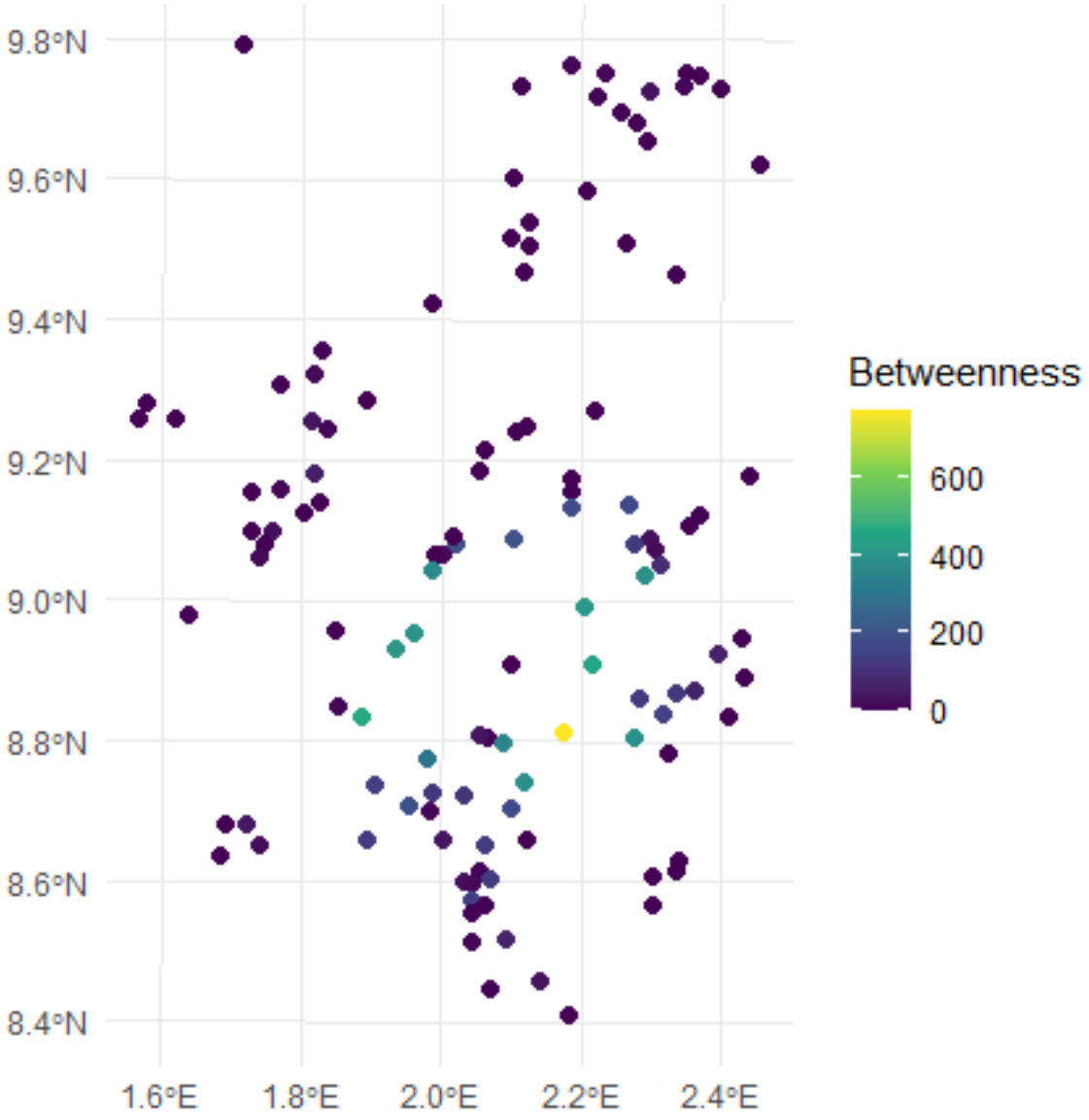

Figure 37. Landscape scale functional connectivity (2025) (7 km cost-distance threshold / Betweeness Centrality)

4.4.3. Circuitscape resistance patterns

Circuitscape returned a symmetric 6 × 6 effective resistance matrix (Fig. 43), with resistance values ranging from 0.468 to 0.908 among distinct habitat pairs (Table 21). The lowest resistances occurred between patches the KSF and OKF and the KSF and Monts-Kouffé Forest (MKF), whereas the highest occurred between Ouémé Supérieur Forest (OSF) and PFR and OSF and Wari-Maro Forest (WMF), indicating strong variation in landscape permeability.

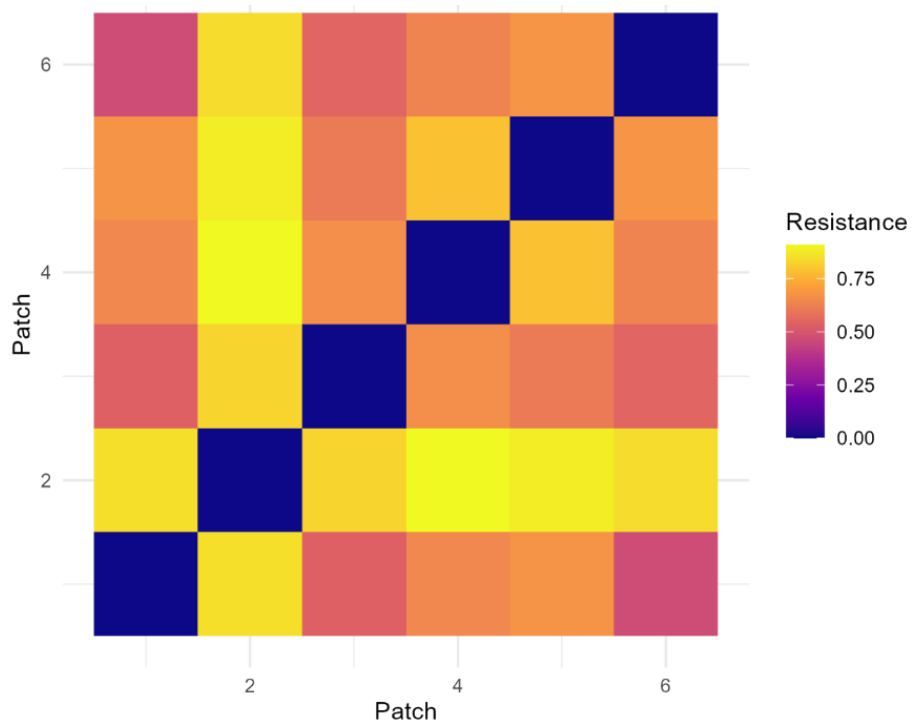

Figure 38. Circuitscape effective resistance heatmap

Table 21. Corridor quantile classification from Circuitscape workflow

from	to	resistance	conductance	res_rank	corridor_class
1	2	0.84981534	1.17672622	5	Q5
1	3	0.53291083	1.87648653	1	Q1
1	4	0.64182167	1.55806518	2	Q2
1	5	0.67525441	1.48092331	3	Q3
1	6	0.46780522	2.13764183	1	Q1
2	3	0.82607693	1.21054101	4	Q4
2	4	0.90849789	1.10071802	5	Q5
2	5	0.88148668	1.13444709	5	Q5
2	6	0.84289973	1.18638073	4	Q4
3	4	0.66235888	1.50975556	3	Q3
3	5	0.6067261	1.64819019	2	Q2
3	6	0.54640677	1.83013839	1	Q1
4	5	0.78417332	1.27522828	4	Q4
4	6	0.63168139	1.58307657	2	Q2
5	6	0.678149	1.47460218	3	Q3

4.4.4. Connectivity network structure

Graph analysis results (Table 22) revealed that each of the six core habitats of *C. vellerosus* in central Benin is directly connected to the others (degree = 5 for every node). Betweenness centrality was zero for all nodes, indicating an absence of unique intermediary stepping-stones

in this fully connected system. Node strength values ranged from 5.81 to 8.23, reflecting differences in cumulative conductance.

The network diagram (Fig. 44) visually reflected these patterns: nodes differed strongly in strength (node colour), but no patch acted as a bottleneck given universal direct connectivity.

Table 22. Summary of node-level metrics from graph analysis for both Circuitscape and Least-Cost Path modelling

NODE ID	NAME	AREA (km^2)	STRENGTH	DEGREE	BETWEENNESS
1	KSF	0.136	**8.22984308**	5	0
2	Ouémé Supérieur	1175.42	5.80881307	5	0
3	Monts-Kouffé	1803	**8.07511168**	5	0
4	Pénéssoulou	54.7	7.02684361	5	0
5	Wari-Maro	1075	7.01339105	5	0
6	OKF	1.57	**8.2118397**	5	0

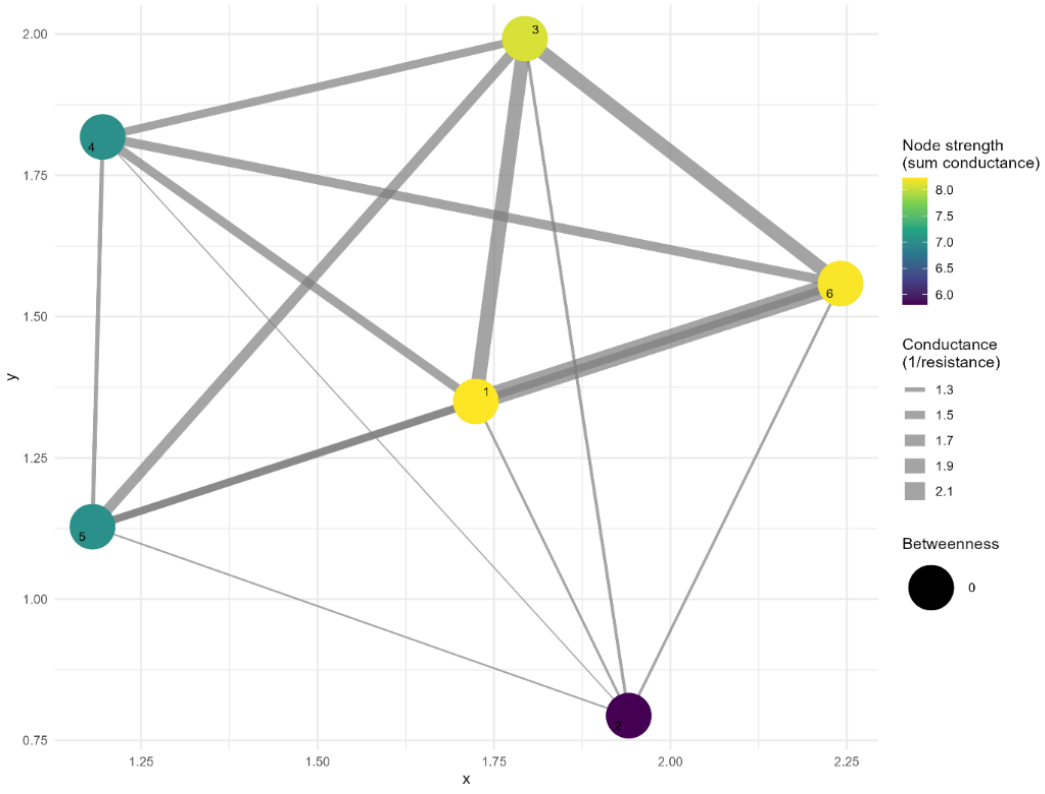

Figure 39. Circuitscape-based connectivity *network.* Nodes = core patches; Edge width = conductance (1/resistance)

4.4.5. Resistance-based corridor classification

Pairwise resistances were divided into five quantile classes (Q1–Q5) (Tables 21 and 23). Class Q1 represented the most permeable linkages (median resistance = 0.533), including connections KSF – MKF (1–3), KSF – OKF (1–6), and MKF – OKF (3–6), whereas Q5 contained the least

permeable linkages (median = 0.881). Each class contained three linkages, illustrating an even distribution of structural connectivity variation across the landscape.

Table 23. Corridor classification summary

corridor_class	n_links	median_res	mean_res
Q1	3	0.533	0.516
Q2	3	0.632	0.628
Q3	3	0.675	0.672
Q4	3	0.826	0.818
Q5	3	0.881	0.880

4.4.6. Comparison between Circuitscape and Least-Cost Path Distance

Spearman's rank correlation showed a strong, positive association between Circuitscape resistance and LCP distance ($\rho = 0.743$, $p = 0.002$; Fig. 45), indicating that pairs of patches separated by long least-cost distances also tended to have high effective resistance. For example, connections OSF - MKF and OSF - PFR exhibited simultaneously high resistance ($\geq$ 0.78) and long cost distances ($\geq$85 km), reflecting the cumulative difficulty of movement between these landscapes.

Rank comparisons showed moderate mismatches between the two approaches (Table 21). The largest divergence was for the Monts-Kouffé to Pénéssoulou connections, ranked 7th in resistance but 14th in LCP distance (a rank difference of 7). This discrepancy reflects the landscape's structure; although the two forests are distant, numerous small intermediate fragments likely offer multiple movement pathways. Circuit theory accounts for these alternatives, lowering the effective resistance more than the single optimal path in LCP analysis.

A similar pattern occurred for the link 2–3 (linking Ouémé Supérieur and Monts-Kouffé, rank difference = 4). This pair showed a long LCP distance ($\geq$ 102 km) but moderate circuit resistance (0.83) in comparison with link 2-4 (Ouémé Supérieur to Pénéssoulou, rank difference 2, Table 21). In the case of the link Ouémé Supérieur to Monts-Kouffé, both of them are connected indirectly through the Wari-Maro Forest, which provides ecologically lower cumulative resistance in Circuitscape even though the overall least-cost distance remains high. Alternative mismatch pattern is the link 2-5, from Ouémé Supérieur to Wari-Maro, which are separated by a short LCP distance but showed high circuit resistance. The landscape configuration indicated that there are very few forest fragments between these two forest centroids. These observations highlight how circuit theory is more sensitive to the redundancy

and distribution of alternative movement routes than LCP modelling, which relies on a single optimal path.

The Bland–Altman plot (Fig. 46) detected no proportional bias, confirming that discrepancies between the two methods were consistent across the distance range. Circuitscape values were systematically lower than LCP distances (mean difference = −63,097), reflecting the fundamental difference between ohmic resistance and cumulative cost distance rather than methodological error. Together, these results indicate that the two approaches are broadly concordant but retain complementary sensitivities to landscape structure.

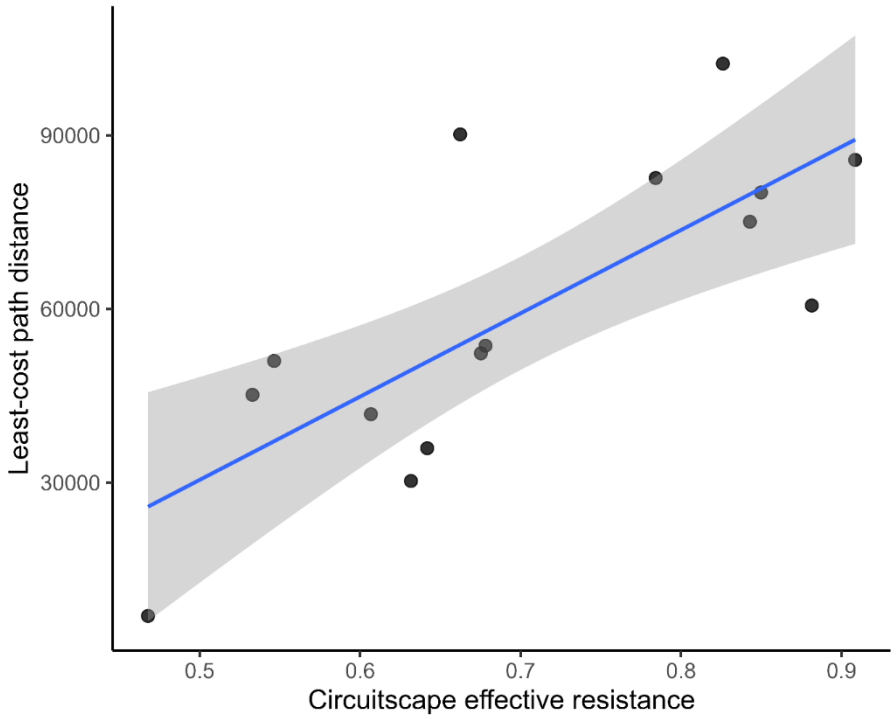

Figure 34. Relationship between Circuitscape and Least Cost Path (r^2 = 0.743, p = 0.002)

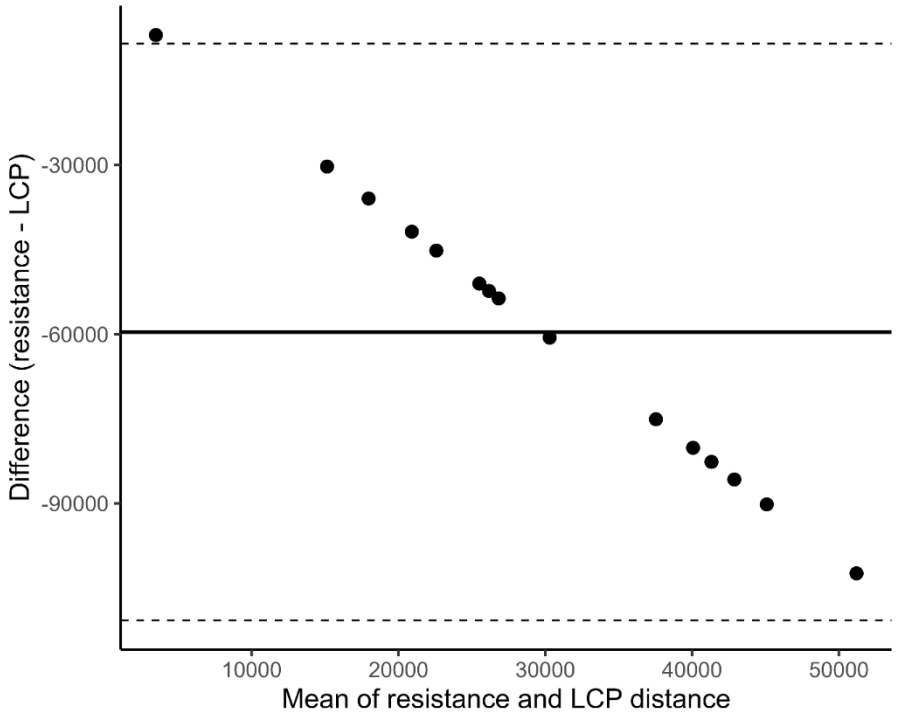

Figure 35. Agreement between Circuitscape resistance and Least Cost Path distance

4.5. Genetic diversity of remnant *Colobus vellerosus* populations in central Benin

From samples collected with a primary target of adult individuals, we successfully generated complete cytb from four samples collected in the Okuta Kobunan Forest and partial D-loop sequences from fifteen samples from both Okuta Kobunan and Kikélé Sacred Forests. Among them, we found only one haplotype for cytb and two haplotypes for D-loop.

As expected, the ML tree (Fig. 47) showed that the cytb haplotype from the *C. vellerosus* population in the Kikélé village forests forms a sister lineage to *C. guereza*, albeit with low statistical support (79%). The D-loop sequences form a sister clade to C. polykomos from Guinea-Bissau, but also with low bootstrap support of only 64%. *Colobus guereza* is sister to the *C. vellerosus* + *C. polykomos* clade, while *C. angolensis* represents to most basal species among the investigated Colobus species.

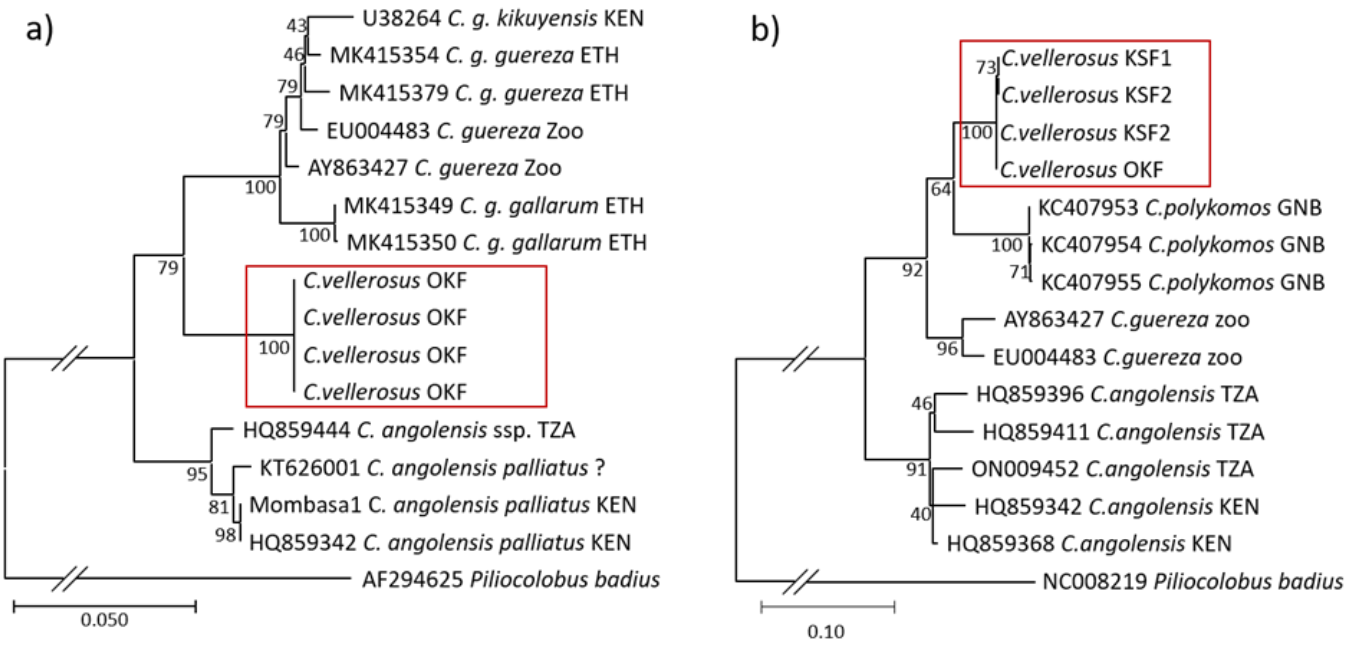

Figure 36. Phylogenetic relationships of *Colobus vellerosus* based on a) the complete cytochrome b gene 1140 bp and b) a 484 bp long fragment of the D-loop.

Orthologue sequences were downloaded from GenBank, *Piliocolobus* was used as an outgroup. The phylogeny was inferred using the Maximum Likelihood method and the HKY+G+I model (Hasegawa et al., 1985). The percentage of replicate trees in which the associated taxa clustered together (100 bootstrap replicates) is shown next to the branches. For the D-loop, we used shorter sequences than 750 bp due to the shorter lengths of the orthologue sequences from GenBank. The bar below the trees indicates substitutions per site.

The two D-loop haplotypes differ only at one position. One haplotype was found in three individuals of the group from the OKF, and one of the second group (group 2) from the KSF. The second haplotype was found in six individuals from the first group (group 1) of the KSF and five individuals from group 2 of the KSF. The estimated haplotype diversity (Hd) was 0.419 ± 0.113, while nucleotide diversity (π) was 0.00056 ± 0.00015, indicating very low genetic diversity in the mitochondrial non-coding region.

Chapter 5 . Discussion

Understanding the long-term survival of *C. vellerosus* requires a synthesis of the ecological, landscape, and genetic processes influencing its persistence. The findings presented in this dissertation collectively inform conservation strategies by identifying the species' most pressing vulnerabilities and the conditions under which recovery may be achievable.

5.1.Overview of key findings

Our research provides the most comprehensive analysis of the niche of *C. vellerosus* and predicts its current and future habitat suitability using an ensemble modelling approach. We identified the uncorrelated environmental variables that determine the niche of *C. vellerosus*. These variables define three major environmental clusters across the species' occupancy areas. Our modelling approach revealed that annual mean temperature (AMT), mean temperature diurnal range (MDR), and isothermality (IsoT) were the most important temperature-related climatic variables that predicted the distribution of *C. vellerosus*. The precipitation during the driest months (PDM) was the most important precipitation-related variable. Overall, precipitation-related predictors held more significance than temperature-related predictors. Our modelling results showed that the overall suitability values of *C. vellerosus* are likely to decline consistently, and its current climate niche may be dramatically reduced by up to 72.94 % by 2050 (approximately three future generations of the species - Matsuda Goodwin et al., 2020) under the optimistic emission scenario. Importantly, by comparing climate-only and climate–anthropogenic models, the results show that human pressures significantly intensify habitat loss beyond what climate alone predicts, highlighting the joint contribution of environmental and anthropogenic change to the species' distribution contraction.

The long-term analysis of LULC in central Benin over the past 36 years revealed that forest cover has halved, savannah has decreased by over one-third, and cropland has expanded by 128%. The main changes involved conversions from forest to cropland and settlements, consistent with community observations of forest decline. However, the accuracy of these perceptions is only weakly correlated with socioeconomic factors and is not significantly influenced by the management status of forests, whether community-managed or state-managed. This integration of biophysical and social evidence highlights the intense human pressures on the landscape and emphasises the limited natural and socio-environmental protections currently available to mitigate ongoing degradation.

Expanding beyond central Benin, the comparative suitability modelling for *C. vellerosus* and *C. polykomos* further highlights the precarious status of both parapatric species.

Through this comparative workflow, we identified protected suitable habitats of adequate size that could serve for *C. vellerosus* reintroduction or support its long-term conservation efforts over its next three generations.

Wide-scale habitat suitability suggests the potential for species persistence, but connectivity modelling shows that forest networks in central Benin have significantly degraded over the past three decades. The Pénéssoulou - Kikélé - Monts-Kouffé - Wari-Maro forest network has become highly fragmented. While some low-resistance pathways exist between MKF, KSF, and OKF, most high-betweenness centrality forest fragments are clustered within Monts-Kouffé. Field evidence showed that these linkages have collapsed due to prolonged hunting pressure. Consequently, *C. vellerosus* survives only in KSF and OKF, which are small and isolated community forests. The gap between potential corridors and the species' absence from these forests illustrates a decoupling between landscape structure and biological reality. This has considerable implications for the genetic exchange, dispersal, and long-term viability of the species.

Genetic analysis reveals extremely low mitochondrial diversity in Kikélé and Okuta Kobunan populations of *C. vellerosus*, with only one cytb haplotype and minimal D-loop polymorphism. These patterns suggest a potential recent bottleneck, founder effects, or genetic drift typical of isolated populations (Ellegren & Galtier, 2016; Mayr, 1966; Nei et al., 1975). This low genetic diversity raises concerns about the species' adaptive potential and underscores the need for broader genetic assessments and potential rescue interventions.

5.2.Climatic niche of *Colobus vellerosus*

The geographic range of *C. vellerosus* is entirely within the equatorial savannah with a dry winter climate defined by the recently updated Köppen-Geiger climate classification (Beck et al., 2018, 2020). Here, we have defined the climatic niche of *C. vellerosus* as a particular range of climatic conditions where this species inhabits. Our analysis showed that the climatic niche for this species typically reflects a tropical environment, with many areas within the IUCN-designated distribution range exhibiting unsuitable environmental conditions. As an endemic species to West Africa, this is in line with previous studies which have shown that tropical animals, especially primates, have a very limited climatic niche due to living in constant shade (Lovegrove et al., 2014; Tewksbury et al., 2008). We found that the annual mean temperature (AMT) is the most significant temperature-related variable that drives future changes in the climatic niche for this species. Notably, due to being folivorous, *C. vellerosus* is particularly sensitive to changes in temperature. Although our results are not directly related to physiological tolerances, there may be strong relationships between climatic distributions and

physiological measurements since species cannot survive under macroclimatic conditions that they cannot tolerate (Quintero & Wiens, 2013). However, behavioural thermoregulation (Kearney et al., 2009) and microhabitats' structures (Marsh et al., 2022) may modulate these relationships.

We found that the distribution of *C. vellerosus* populations aligns with three distinct climatic clusters. This suggests that climatic conditions vary across different locations within the species' geographic range, and the species' responses to global warming and other environmental changes may consequently vary. Meanwhile, studies examining the relationship between the climatic niche distributions of primates and their various populations are rare (Bernard & Marshall, 2020). Quintero and Wiens' (2013) research on three vertebrate clades revealed that among and within localities, seasonal fluctuations explain most variation in climatic niche breadth. Furthermore, our work emphasises that, among and within localities, the *C. vellerosus* climatic niche change is driven by a significant increase in AMT. Temperature variation is highly spatio-temporal scale-dependent and a critical driver of microhabitat changes in relation to vegetation structure at a scale relevant to tropical species (Marsh et al., 2022).

5.3.Ecological predictor variables' relationship with *Colobus vellerosus*

Our EMs have outlined ecological predictors that influence the behavioural and feeding ecology, physiological processes, biogeographical distribution, and evolution of primate species. For instance, the white-headed langurs, highly folivorous primates like *C. vellerosus*, reduced their moving time and travel distance under high-temperature environments (Zhang et al., 2021). In this respect, Korstjens and Hillyer (2016) reported that specialist folivores should inherently counteract the increased cost of leaf digestion for their adaptations to climate change in the event of an increase in temperature and a decrease in rainfall. Similarly, Korstjens et al. (2010) highlighted that a rise of 2 – 4 ºC in annual temperatures could impact the enforced resting time for various primate species, ultimately resulting in time-budgeting issues. The precipitation during the driest months (PDM) is closely linked to food availability and nutritional value of leaves, which in turn affects the feeding habits of *C. vellerosus*. Indeed, tropical semi-deciduous forests (key habitats for *C. vellerosus*) show increased phenological variability in areas with longer dry seasons, and most deciduous species are subjected to seasonal water stress and change their leaves once a year (van Schaik & Pfannes, 2005). Research conducted in two tropical semi-deciduous forests by Djègo-Djossou et al. (2015) and Teichroeb (2002), respectively, revealed that *C. vellerosus* feeds on 35 tree species from 16 families in KSF in Benin and 55 tree species from 21 families in Boabeng-Fiema Monkey

Sanctuary (BFMS) in Ghana. Most of these tree species belong to the families of Leguminosae and Moraceae. *Colobus vellerosus* consumes young leaves, fruits, and seedpods more commonly according to the seasonal availability of these plant items. However, when these foods are scarce, mature leaves become the primary food source, indicating their value as a fallback (Saj & Sicotte, 2007). Interestingly, the nutritional quality of leaves may be influenced by both seasonality and leaf longevity (Chanida, 2006). For instance, when studying the nutrient content of red colobus (*Piliocolobus tephrosceles*) and black-and-white colobus (*Colobus guereza*), it was found that the high intraspecific variation in nutritional content may also impact studies of seasonality in nutrient content (Chapman et al., 2003). Furthermore, *C. vellerosus* populations inhabiting the BFMS have shown some between-group activity budget differences during dry seasons (Teichroeb, 2002), while statistically significant seasonal fluctuations were found in feeding and moving within its populations living in the KSF (Djègo-Djossou et al., 2015).

5.4.Predicted shift and range reduction

Our EMs suggest a decline in the quality of current habitats for *C. vellerosus*. These results dovetail with those of Korstjens (2019), who suggested, at the genus level, that future sites' suitability values are only more likely to be consistently lower where colobus genera is currently present. As per the same study, this author used generalised linear models based uniquely on bioclimatic data to predict that colobus genera would lose some areas of suitable habitats in Western Africa. This aligns with our findings of the significant reduction of *C. vellerosus*' geographical ranges. (Korstjens, 2019; Korstjens et al., 2010) explained this retraction as a consequence of the predicted rise in temperatures and decreased precipitation in southern and western Africa. Conversely, while Baker and Willis (2015) reported "no consensus" for *C. vellerosus*, our EMs forecasted range reduction for the species under the zero-migration assumption and range shift under the unlimited migration assumption. Although Baker and Willis (2015) made a species-specific prediction, they used multi-taxa metadata and made their prediction within West Africa's existing PA network. Their result may differ from ours because *C. vellerosus* is found in very few PAs, and there is a lack of data on its populations inhabiting these habitats. This underscores the importance of using pertinent data in species distribution modelling. Our findings from modelling at the species level are consistent with those of Korstjens (2019), who also forecasted that a few areas would become more suitable for colobus at the genus level.

Our HS model indicated that forest cover is the main anthropogenic factor associated with *C. vellerosus*' range reduction. This finding confirms the first cause justifying the "Critically Endangered" status recently attributed to the species by IUCN (Matsuda Goodwin et al., 2020).

5.5.Land use and land cover trajectories in central Benin

The loss of forests due to cropland expansion is a notable trend in West Africa. Studies indicate that agricultural expansion is the main cause of forest conversion (Acheampong et al., 2019; FAO & AfDB, 2015). Our observed transitions from forest and savannah to cropland are significantly consistent with regional analyses identifying agricultural conversion as a major driver of tropical forest loss (Kalischek et al., 2023; Sanogo et al., 2022). Regarding the plantation area, we found a sharp decline until 2007 and a partial recovery by 2025. This corroborates with cycles of clearing and re-establishment influenced by market forces, land tenure changes, and policy interventions (UNDP, 2015).

The study outlines a trajectory of settlement expansion in central Benin, with growth from 127,974 ha in 1989 to 439,900 ha in 2007, followed by a decline to 352,670 ha in 2025. The increase until 2007 aligns with rapid population growth and agricultural expansion during the 1990s and early 2000s, as detailed by Orekan (2007a) and Amagnide et al. (2015). The construction of the Ouberou–Kikélé road in 1997 facilitated settlement along transport corridors, resulting in a shift from clustered village patterns to more dispersed settlements. Field observations also noted a rise in temporary agricultural camps evolving into permanent communities (Orekan, 2007a).

The use of Landsat 7 ETM+ imagery in 2007 presented challenges due to SLC-off data gaps. However, median compositing in GEE and high accuracy metrics (Producers' Accuracy = 0.98; Users' Accuracy = 0.98) suggest that settlement identification was largely effective. Although the training samples for 2007 were smaller in comparison to those for 2025, they were adequate for RF modelling, especially given the distinct spectral signatures of settlements.

The decline in mapped settlement area from 2007 to 2025 does not indicate true demographic contraction. Instead, it likely stems from improved classification with Sentinel-2 imagery in 2025, which offers finer resolution and better distinguishes between settlements and other land-use types. This corroborates Orekan's (2007a) findings related to the small size of many rural settlements. In sum, the depiction of settlement growth from 1989 to 2007, followed by a contraction in 2025, reflects real expansion processes combined with improved mapping techniques rather than an actual decrease in human footprint. This suggests a landscape-level

intensification of human occupation, followed by corrections in mapping accuracy, enhancing confidence in the study's conclusions on settlement change.

5.6.Identifying climate refugia for *Colobus vellerosus* conservation

Our results show a significant gap between the climatically suitable areas and the current known distributions of both taxa. Moreover, there are overlapping regions for both taxa that contrast with their reported parapatric distribution. This discrepancy suggests that both species face limitations in their natural expansion, despite the availability of suitable habitats at present. Such constraints on expansion may be attributed to a variety of factors, including ancient ecological and historical barriers, differing habitat preferences, phylogeographic and evolutionary influences, and anthropogenic pressures. Previous research has highlighted the probable geographic barrier posed by the Sassandra and Bandama rivers concerning *C. vellero*sus and *C. polykomos* (Booth, 1954), separating *C. polykomos* west of the Sassandra River and *C. vellerosus* east of the Bandama River (Groves, 2007; Groves et al., 1993). Groves et al. (1993) hypothesized that *C. polykomos* once extended as far east as the Bandama River. Whether this was the case remains currently an open question, because genetic studies on the interfluvial form "*Colobus polykomos dollmani*", which might be a hybrid, are still missing (Gonedelé Bi et al., 2006; Oates & McGraw, 2009).

Furthermore, the Dahomey Gap, which stretches across Ghana, Togo, and Benin, is believed to have served as a major natural barrier to the distribution of forest-dwelling mammals (Campbell et al., 2008), such as colobine monkeys. While both species are folivorous, the diet of *C. polykomos* contains a greater proportion of fruit (Korstjens et al., 2009) than *C. vellerosus*, which is regarded as the most folivorous species among the West African black-and-white colobus (Fashing, 2022). *Colobus polykomos* relies more on rainforest and gallery forest (Gonedelé Bi et al., 2020), whereas *C. vellerosus* inhabits lowland rainforest, swamp forests, semi-deciduous forests, and gallery forests within the savannah zone (Matsuda Goodwin et al., 2020). Climate-only models do not account for the above-mentioned ecological constraints (Soberón & Nakamura, 2009), which could explain the parapatric distribution of the two species, despite our climatic model showing overlapping areas.

We found a southward reduction in climatically suitable areas for *C. vellerosus*, indicating that favorable conditions may only persist in southern regions. Our projections suggest that the Mole National Park in Ghana, Fazao-Malfakassa in Togo, and the Kikélé Sacred Forest in Benin will likely become unsuitable for *C. vellerosus*. It is noteworthy to mention that the KSF currently offers some protection from illegal hunting due to the traditional

beliefs of the Kikélé villagers (Djègo-Djossou et al., 2012). (Djègo-Djossou et al., 2012). This underscores the need to extend and restore the KSF to protect *C. vellerosus* and its ecosystem.

Currently, only a small number of existing forested habitats are suitable for *C. vellerosus*. A significant proportion of these viable habitats are located outside protected areas. Under a best-case climate scenario to 2050, we anticipate a substantial reduction in suitable habitats for both species. In light of this, it is vital to enhance conservation efforts beyond the current boundaries of protected areas by incorporating secondary forests and community-managed forested areas deemed suitable in the medium term. Yet *C. vellerosus* is predominantly found in community forests (Matsuda Goodwin et al., 2019), and many protected areas continue to face threats from illegal hunting (Djagoun et al., 2018). Priorities should include expanding the protected area network, implementing sustainable management practices for unprotected forests, and establishing ecological corridors. Furthermore, the case of *C. vellerosus*, which may have already vanished from eight historically occupied forests, underscores the urgent need for field monitoring programs and reassessment of the status of remaining populations.

Identifying potentially suitable forested areas for the reintroduction of *C. vellerosus* is a vital strategy for its survival. Such areas could serve not only to re-establish viable populations but also to enhance ecological connectivity between fragmented habitats, particularly among the 437 sites projected to remain suitable by 2050. This connectivity is useful for mitigating genetic isolation and preventing inbreeding (Bergl & Vigilant, 2006; Lawes, 2005). However, illegal hunting (Oates, 2011; Refisch & Koné, 2005) and habitat fragmentation (McGraw, 2005; Minhós et al., 2023) are the most significant anthropogenic pressures likely affecting the distribution of both species. Particularly, these two threats are important drivers of *C. vellerosus* declines across West Africa (Djègo-Djossou & Sinsin, 2009; Gautier-Hion et al., 1999; Oates, 2011; Ota, 2020). Therefore, any reintroduction program for *C. vellerosus* must effectively address hunting risk and establish long-term habitat protection to ensure success.

The IUCN reintroduction guidelines explicitly require that the major threats, which caused declines, be effectively controlled at release sites (IUCN/SSC, 2013). Consistent with IUCN reintroduction standards and existing evidence-based successful reintroductions (Brando et al., 2020; Imam et al., 2002; King et al., 2012; Soorae, 2021), any conservation reintroduction program should align with national and regional conservation frameworks and recognize the roles of existing agencies and legal guidelines. It must consider the legitimate interests of local communities, addressing their socio-economic circumstances, values, expectations, and the expected costs and benefits of the translocation. In practice for *C. vellerosus*, that means

prioritizing sites with demonstrably effective protection (e.g., areas with long-standing traditional taboos), co-designing no-hunting agreements with local communities backed by clear benefits (employment as guardians, tourism revenue-sharing), law-enforcement and biomonitoring capacity building, and post-release monitoring with adaptive responses to any hunting incidents.

The experience at BFMS in Ghana shows that when hunting is socially or legally suppressed, *C. vellerosus* populations can stabilise and even increase (Kankam et al., 2023; Wiafe et al., 2023). Before any reintroduction takes place, it becomes obligatory to ensure that hunting is suppressed. It is only under this condition that costly conservation interventions will achieve lasting results.

Our research examines the climatic suitability and the presence of forests within areas deemed suitable for the species. However, selecting appropriate habitats for a species reintroduction necessitates comprehensive ecological assessments of potential sites, a thorough evaluation of anthropogenic impacts, engagement with local communities to gauge their support, and population genetic studies of the source animal populations. Importantly, the cessation of hunting activities is a prerequisite for any successful reintroduction of *C. vellerosus* or any conservation efforts for both taxa. One viable conservation strategy involves promoting ecotourism and facilitating the development of sustainable livelihoods within local communities. By generating alternative income sources and enhancing livestock production, we can help secure a stable protein supply while simultaneously fostering awareness and support for primate conservation initiatives in local communities.

5.7.Dual fragmentation trajectories and implications for habitat integrity

Our analysis indicates a significant deterioration in the forest structure and spatial configuration of *C. vellerosus* habitats over the past three decades, revealing starkly contrasting regional trends. In 1989, the landscape comprised two extensive, internally cohesive forest clusters: the Pénéssoulou–Kikélé–Mont-Kouffé–Wari-Maro complex in the south, and the Ouémé Supérieur Forest block in the north. Both of these clusters formed a low-fragmentation system that typically supports high ecological continuity, facilitates wildlife movement, and shields species from edge-driven disturbances (Benítez-Malvido & Arroyo-Rodríguez, 2008; Gestich et al., 2022).

By 2025, the southern forest complex underwent significant disaggregation, with a considerable decline in mean patch size, increased fragmentation, and a collapse of effective mesh size. These changes indicate a structurally eroded forest mosaic that threatens the survival

of forest-dependent primates, particularly sensitive species like *C. vellerosus* (Frazier et al., 2021). Persistent anthropogenic pressures, such as agricultural conversion, charcoal extraction, and selective logging, have contributed to this severe fragmentation (Amagnide et al., 2015; Orekan, 2007b) and help explain this observed fragmentation.

In contrast, the northern Ouémé Supérieur block has shown relative structural stability, with larger and more cohesive remnants surviving through 2025. This asymmetric pattern of landscape change emphasises that the loss of connectivity is not uniform across central Benin; rather, it reflects localised socio-ecological dynamics, consistent with trends reported in other West African forest systems (Frazier et al., 2021).

5.8.Structurally hierarchical connectivity network dominated by Monts-Kouffé

Graph-based connectivity metrics further underscore the highly uneven distribution of structural importance among forest fragments. Measures of degree and betweenness centrality converge to identify Monts-Kouffé and, to a lesser extent, Wari-Maro, as the central connectivity hubs within the entire forest network. Nearly all patches exhibiting very high betweenness values (≥300) reside within this complex, serving as irreplaceable stepping-stones and regional bottlenecks. Notably, several of these connector patches are not the largest in size, emphasising that spatial position, rather than size alone, determines a fragment's functional role (Baguette & Van Dyck, 2007; Dutta et al., 2016). Losing even a few of these medium-sized connectors could significantly reduce connectivity, disrupting movement pathways for *C. vellerosus* within the landscape. This fragility is evident for other tropical forest-specialist primates, for which loss of key habitat connections quickly diminishes dispersal and gene flow (Gestich et al., 2022).

5.9. Connectivity and field reality

Circuitscape analysis indicated substantial variability in landscape permeability among core habitat pairs. Minimal resistance levels were recorded between KSF, MKF, and OKF. This reflects their historically cohesive habitat structure. Conversely, the highest resistance values were observed between OSF, Pénéssoulou, and Wari-Maro. This underscores the extensive, partially degraded interstitial matrix that acts as a barrier to these forests.

The quantile-based resistance classification further identified three prominent corridors with high conductivity: from KSF to MKF, from KSF to OKF, and from OKF to MKF. These corridors indicate priority areas for maintaining functional connectivity. While these findings support earlier studies that emphasise the value of electrical circuit theory in identifying diffuse

movement pathways within tropical forest landscapes (Dutta et al., 2016), it is noteworthy that most of the stepping-stone forest patches and least-cost path (LCP) corridors traverse the Manigri village. Previous research has indicated that *C. vellerosus* faces significant hunting pressure when entering Manigri (Djègo-Djossou, 2013; Ota, 2020), underscoring the critical need to incorporate comprehensive environmental education into any corridor management plan to persuade local populations against harming the species.

5.10.Complementarity and divergence between Circuitscape and Least-Cost Path modelling

The strong positive correlation between circuit resistance and LCP distance indicates broad agreement regarding which habitat pairs are most difficult to connect structurally. This pattern is consistent with studies showing that both approaches capture major axes of landscape resistance (Dutta et al., 2016; Frazier et al., 2021). Nonetheless, several key mismatches were informative: Link Monts-Kouffé and Pénéssoulou had a relatively low circuit resistance but a high LCP distance, driven by numerous small forest fragments between the two regions. Circuitscape is based on multiple pathways, while LCP relies on a single optimal path. This allows circuit theory to better reflect the effects of intermediate habitat fragments that reduce resistance (Dickson et al., 2018; McRae & Beier, 2007). For the Link OSF to MKF, moderate circuit resistance was observed despite long LCP distances due to WMF offering an ecologically low-resistance route. Conversely, the Link OSF to WMF showed short LCP distances but high circuit resistance, as the matrix had few intermediate fragments, limiting alternative pathways. These differences highlight how LCP and circuit theory complement each other. LCP identifies the least-effort route, while circuit theory shows the landscape's redundancy and connectivity.

The Bland–Altman plot indicated no proportional bias between Circuitscape and LCP, suggesting that differences are consistent across distances. The lower Circuitscape values represent unit differences (ohmic resistance vs cumulative cost) rather than methodological disagreement. This implies that the methods reveal interpretable ecological signals influenced by landscape structure, not measurement error. Other connectivity studies have reported similar interpretations (Dutta et al., 2016; Frazier et al., 2021).

5.11.Founder origins and the limitations of mitochondrial evidence

Historically, the Kikélé colobus population is believed to originate from a small founding group, possibly a single pair of C. vellerosus (Djègo-Djossou et al., 2012). While this scenario

is consistent with the observed low mitochondrial genetic diversity, it remains one of several possible explanations alongside recent bottlenecks, genetic drift, or incomplete sampling. Given that mitochondrial DNA is inherited through the maternal lineage (Giles et al., 1980; Gutierrez et al., 2024), the monomorphic mitochondrial DNA indicates a common maternal ancestor among individuals, supporting the founder effect hypothesis. The forests adjacent to the Kikélé village, including the Pénéssoulou Forest Reserve, Wari-Maro, Ouémé Supérieur, and Monts Kouffé, served as habitats for *C. vellerosus* (Djègo-Djossou & Sinsin, 2009), most likely harbouring additional mitochondrial haplotypes. These haplotypes have most likely gone lost when *C. vellerosus* became extinct, due to the degradation of these forests and hunting (Djègo-Djossou & Sinsin, 2009; Orekan, 2007a; Ota, 2020). The fur of *C. vellerosus* was used in the production of local shoes and drums (Gautier-Hion et al., 1999; Oates, 2011), and their bones were utilised in traditional medicine and magic (Djagoun et al., 2018).

Another consideration is that our current sampling may not have captured all haplotypes present within the Kikélé population. Nonetheless, relying solely on mitochondrial DNA analysis is insufficient to conclude about the genetic diversity of wild animal populations (Lynn et al., 2016; Roos & Zinner, 2017). This limitation arises because mitochondrial DNA reflects only maternal lineages and does not capture recombination or male-mediated gene flow, which are often key components of overall genetic diversity.

5.12.Mitochondrial genetic diversity

In our study, we identified two haplotypes that differ at a single site within the mitochondrial D-loop. Similarly, Ting (2008) found only a single mitochondrial haplotype in four samples from the *C. vellerosus* population at the Boabeng Fiema Monkey Sanctuary in Ghana. If this locally low mitochondrial genetic diversity is a general characteristic of the species, its conservation status might be even worth than reported.

However, the low mitochondrial genetic variability within local populations of *C. vellerosus* seems not to be an exception among colobines. Several populations of Asian colobines show very low to no mitochondrial genetic variability. Ang et al. (2012) reported only two haplotypes in the Raffles' banded langur (*Presbytis femoralis*) population in Singapore, differing by a single nucleotide in the D-loop. In 201 samples of the largest population of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*), Ang et al. (2016) did not find any mitochondrial genetic variability. Similarly, in 128 samples of the grey or Guizhou snub-nosed monkey (*Rhinopithecus brelichi*), only one mitochondrial haplotype was found (Pan et al., 2011). However, in contrast to the low mitochondrial genetic variability, in this

species, the nuclear genetic diversity, as determined by allele numbers of microsatellites, was significantly higher (Kolleck et al., 2013). The contrast might be the result of interspecific gene flow between *R. roxellana* and the ancestor of *R. bieti* and *R. strykeri* (Wu et al., 2023). That most likely led to hybrid speciation where males of only one lineage introgressed the population of the other lineage and thus importing nuclear variability but not mitochondrial variability. To obtain a complete picture of the genetic diversity in these endangered species, population genetic analyses based on nuclear markers are needed.

Within other species of the genus *Colobus*, McDonald et al. (2022) detected a minimum of one mitochondrial haplotype in two distinct populations and a maximum of seven haplotypes in one population from 140 sequenced samples collected from nine *C. angolensis* populations in southern Kenya and the Southern Highlands of Tanzania. In total, 26 haplotypes were identified across these nine studied populations (McDonald et al., 2022; McDonald & Hamilton, 2010). Although details regarding mitochondrial genetic diversity at the population level in *C. g. guereza* and *C. g. gallarum* are limited; Zinner et al. (2019) listed 76 sequences, including 31 haplotypes for cytb from samples collected across Ethiopia. For *C. polykomos*, three different mitochondrial haplotypes were detected in the Cantanhez Forests National Park in Guinea-Bissau (Minhós et al., 2013), while five different haplotypes were found in the Taï National Park in Ivory Coast (Minhós et al., 2023). Currently, no genetic data is available for *C. satanas*.

5.13.Sex-biased dispersal patterns and genetic diversity in *Colobus vellerosus* populations

Dispersal in *C. vellerosus*, as in most other colobine monkeys, is male biased (Saj & Sicotte, 2005; Teichroeb et al., 2011), i.e., female dispersal is rare (Teichroeb et al., 2009, 2011; Wikberg et al., 2012). Since dispersing males do not pass on their mitochondria to their offspring, they do not bring any ‘new’ haplotypes into the group they migrate to. The result of such male-biased dispersal is a spatial or geographical pattern in the distribution of mitochondrial haplotypes. This means for the situation in the Kikéle Forest that if no new females move in, the mitochondrial genetic diversity will remain low. However, immigrating males that reproduce successfully will bring in their autosomes and gonosomes, which will increase nuclear-genomic diversity. Therefore, to understand the complete genetic diversity of the small population in Kikéle Forests, we need to explore also the genetic diversity on a nuclear-genomic level.

5.14.Implications for the conservation of *Colobus vellerosus*

Our findings demonstrate that climate change is an additional factor leading *C. vellerosus* to a looming extinction. We recommend implementing restoration, reforestation, or afforestation projects as climate change mitigation measures at the occurrence sites of the species and in the predicted emerging areas. The regressive trend in suitability values may require genetic and behavioural adaptations for the species to cope with climate change. These adaptations may involve evolving to thrive in different climatic conditions. However, small populations of threatened species are at risk of inbreeding and loss of genetic diversity (Frankham et al., 2010), which could limit their capacity to adapt. As the species is critically endangered with a tiny and fragmented population, it is crucial to preserve its genetic diversity and develop habitat connectivity at the local scale to connect fragmented forests and create meta-populations for gene flow.

Another major anthropogenic factor that threatens the species' survival is hunting (Matsuda Goodwin et al., 2020), which demands urgent attention in the species' conservation. Therefore, it is crucial to enhance awareness of primate conservation through environmental education among local communities and emphasize the legal rights and obligations of endangered primates in all range countries of the species. Additionally, we recommend establishing a long-term collaborative project, similar to the blend of traditional and conventional conservation efforts at BFMS in Ghana (Kankam et al., 2023; Wiafe et al., 2023), at the other two strongholds of the species, namely Comoé National Park in Côte d'Ivoire and Kikélé Sacred Forest in Benin. In Benin, such a program should also encompass the Lama Classified Forest, which is projected to remain relatively less affected by future climate change. To ensure continuity, the project in Ghana should receive support and be linked with a wider-ranging project on maintaining connectivity between isolated populations, while enhancing genetic diversity if possible.

While our analysis considered both bioclimatic and anthropogenic factors, we acknowledge that there may be other threats to primates' survival, such as diseases, interspecific competition, and predation, that we did not include in our modelling. Conservation programs for wild animals should take all these factors into account. Our work is one of the few studies that examine anthropogenic impacts on the distribution of West African primate species. We used the two most common human predictors (Frans & Liu, 2024) in our modelling. Despite the fact that the forest cover data may ambiguously reflect both anthropogenic and environmental factors, our habitat suitability model offers strong predictions to support species conservation efforts.

The movement ecology of *C. vellerosus* aligns with the patterns described by circuit theory. As an arboreal, canopy-dependent colobine with limited ability to cross open landscapes or cover long distances (Wong et al., 2006; Wong & Sicotte, 2006), *C. vellerosus* is likely to benefit significantly from stepping-stone patches, strips of secondary forest, and any canopy-connected pathways. Circuit theory, which accounts for multiple diffuse routes, may therefore better capture the movement potential in highly fragmented landscapes where the species relies on small, scattered forest fragments for dispersal.

Our landscape analysis highlights some conservation priorities:

- the central Benin range of *C. vellerosus* faces functional collapse and requires intervention to prevent further ecological isolation and genetic erosion of populations of *C. vellerosus*;
- the Monts-Kouffé and Wari-Maro National Park serve as irreplaceable connectivity anchors and should be prioritised as core conservation areas;
- the medium-sized patches with high betweenness in central Benin are equally important as the largest blocks and will help maintain network cohesion.
- the corridors from KSF to MKF, KSF to OKF, OKF to MKF, and KSF to PFR must be preserved to ensure long-term connectivity.

In summary, integrating fragmentation metrics and various analytical approaches provides a comprehensive view of the forest dynamics. Protecting high-centrality patches, reinforcing corridors, and restoring degraded landscapes are essential for the long-term survival of *C. vellerosus*. Genetic rescue in Kikélé and Okuta Kobunan populations of *C. vellerosus* is necessary to enhance long-term viability and adaptability. Several studies have shown that fostering genetic variability supports adaptability and disease resilience within animal taxa (Ostridge et al., 2025; Schwensow et al., 2007; Tallmon et al., 2004; Warren et al., 2025; Zhang et al., 2024).

To address this issue, comprehensive conservation strategies must be employed that encompass several key components. Firstly, improving habitat connectivity is essential to facilitate gene flow between populations, thereby minimising genetic isolation. This can be achieved through the creation and maintenance of ecological corridors that enable individual movement across fragmented landscapes. Regular population monitoring is vital for understanding population dynamics over time, allowing for the identification of potential demographic decline. Moreover, a comprehensive study on the global genetic diversity utilising both mitochondrial and nuclear markers should be carried out. Management decisions, such as translocations, should be guided by nuclear data that can highlight genetic connectivity across

various regions of the species' range. This approach will provide a detailed understanding of the genetic structure of the species. Establishing a localised genetic database would greatly enhance conservation efforts, serving as a critical repository for genetic information that can inform management strategies, such as defining management units, genetic rescue by outcrossing or translocation, reintroduction, and connectivity network for meta-population.

For populations of *C. vellerosus* in Kikélé village, managing strategies should consider the combined effects of demographic bottlenecks and sex-biased dispersal on both mitochondrial and nuclear variation.

CONCLUSION AND PERSPECTIVES

Conclusion

The main objective of this thesis: “examine the combined effects of climate and land-use changes on the distribution of suitable forested areas, forest-habitat fragmentation and connectivity, and genetic diversity of *C. vellerosus* across its distribution range” has been achieved. As expected, the outcomes from the present research support effective conservation planning and management of the species.

This dissertation delivers the first integrative, multi-scalar assessment of the climatic niche, habitat dynamics, landscape connectivity, and genetic status of the critically endangered white-thighed colobus, *C. vellerosus*, with particular emphasis on its population in central Benin. Our findings suggest that the survival of *C. vellerosus* is threatened by interacting climatic, ecological, and anthropogenic pressures.

This thesis demonstrates that *C. vellerosus* occupies a narrow climatic niche influenced mainly by precipitation during the driest months, annual mean temperature, and mean diurnal temperature range. Climate-driven habitat suitability is predicted to contract significantly by mid-century, even under optimistic emission scenarios. This emphasises that climate change is an underestimated threat to the species. Additionally, current habitat loss is primarily due to human-induced forest decline, which has reduced climatically suitable areas by over one-third.

Land-cover analyses over 36 years reveal alarming deforestation trends in central Benin, driven by cropland expansion and settlement growth. This compromises forest extent and ecological function.

The thesis also examines landscape fragmentation's impact on functional connectivity and identifies the Monts-Kouffé-Wari-Maro National Park as a pivotal connectivity hub for *C. vellerosus*. Yet functional isolation is intensifying across the landscape. The connectivity modelling framework established here provides a basis for corridor planning and identifies essential stepping-stone habitats for future conservation efforts.

Mitochondrial analyses of C. vellerosus populations in Kikélé and Okuta Kobunan community-managed forests show extremely low genetic diversity, consistent with a founder effect, historical bottlenecks, or sustained genetic drift. These results are concerning for a species already experiencing demographic contraction and habitat isolation. They reinforce the need for broader range-wide genetic sampling and the urgency of evaluating translocation as a potential genetic rescue strategy.

In summary, the findings of this doctoral research highlight that C. vellerosus is experiencing climate-driven niche collapse, widespread habitat degradation and fragmentation, and low genetic variation. However, they also point to promising opportunities such as

strategically located forest patches for connectivity, community-managed forests for local protection, and stable forested areas that could serve as refugia or reintroduction sites.

Perspectives

Based on the thesis findings and the limitations discussed, several suggestions for future research, as well as conservation projects, are important. The future research axes are related to further climate-ecology integration, multi-species and multi-scale connectivity design, comprehensive genetic assessments, and local ecological knowledge integration. The conservation projects refer to long-term community-based ecological monitoring, evidence-based reintroduction and adaptive management, and integrating conservation with local livelihoods. The future research axes are as follows:

1. future modelling should include microclimatic buffering and vegetation structure to refine predictions of species persistence. There is a need to incorporate behavioural and physiological data to understand the connection between climatic exposure and biological vulnerability;
2. the connectivity framework presented here should be expanded to include other forest-dependent mammals and to assess climate-resilient corridor pathways. Priority should be given to protecting the Monts-Kouffé–Wari-Maro complex, now designated as a National Park, and to restoring linkages toward the Kikélé, Okuta Kobunan, and this complex.
3. distribution range scale genetic diversity assessment is required to effectively characterize nuclear diversity and deepen mitochondrial analysis, identify management units, and assess the practicality of genetic rescue via translocation.

The conservation projects are as follows:

1. establishing long-term community-based monitoring programs. This would help track land-use dynamics, primate presence, and hunting pressure in real time. Subsequently, conservation strategies will be adapted for efficiency and effectiveness.
2. reintroduction of *C. vellerosus* into climatically and structurally suitable forests remains a viable long-term conservation option. However, such a program should take place only where threats, especially hunting, are demonstrably controlled. The program should also integrate habitat quality assessments, socio-cultural acceptability, corridor restoration, and population reinforcement plans guided by IUCN reintroduction best practices.

3. Expanding primate ecotourism, supporting agroforestry, and reinforcing cultural taboos, especially in sacred forests, can create durable community incentives for conservation.

This dissertation offers the most comprehensive and interdisciplinary assessment to date of the ecological, climatic, landscape, and genetic factors essential for the conservation of *C. vellerosus*. By bridging spatial modelling, field ecology, community engagement, and molecular genetics, it establishes a solid scientific foundation for targeted and transformative conservation efforts.

Despite the considerable challenges presented in this work, the future of *C. vellerosus* is not predetermined. The case of the BFMS in Ghana showed that in areas where committed communities, culturally embedded protection systems, continuous institutional frameworks, and long-term research were settled, populations of *C. vellerosus* can recover. Community-managed forests, such as the Kikélé Sacred Forest and the newly established Okuta Kobunan Forest, exemplify how local stewardship can safeguard populations, even amid significant anthropogenic pressures. Moreover, the recent designation of the Monts-Kouffé-Wari-Maro complex as a National Park represents a milestone, providing a strengthened legal foundation for coordinated habitat restoration and connectivity planning.

Ultimately, the long-term recovery of *C. vellerosus* will hinge on conservation strategies that merge ecological science with the socioeconomic realities of the communities inhabiting the species' range. This entails prioritising local livelihoods, cultural values, land-rights systems, and community aspirations within conservation planning. When forest protection aligns with economic opportunity and social values, community stewardship can transform fragmented landscapes into networks of interconnected, climate-resilient habitats. With adequate support, equitable partnerships, and evidence-based decision-making, there is a genuine opportunity for *C. vellerosus* to recover. Successful *C. vellerosus* conservation must serve as a symbol of how biodiversity conservation and human development can harmoniously coexist.

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APPENDIX

Table A1: Summary of node-level metrics from landscape-wide graph analysis

patch_id	area_m^2	degree	betweenness
1	1039410	0	0
2	1565752	3	10
3	2475903	4	0
4	1760849	4	10
5	1452011	4	0
6	1035264	1	0
7	1930407	4	8
8	1017742	3	0
9	4313541	8	28
10	2639055	5	6
11	2908299	5	5
12	5110534	4	0
13	4323243	3	0
14	1103385	0	0
15	1174705	1	0
16	2350416	0	0
17	3750982	4	3
18	1355630	3	0
19	2831330	3	0
20	2292063	3	0
21	1017718	0	0
22	1095202	0	0
23	6284630	3	0
24	2163684	5	13
25	3256000	4	0
26	1293383	2	0
27	2145267	4	0
28	1632466	5	30
29	4938287	0	0
30	1118735	2	0
31	1129706	3	0
32	1262081	3	0
33	2340201	6	10
34	11952627	2	0
35	750977739	0	0
36	1151732	3	0
37	1145550	3	0
38	1057135	7	52
39	1081312	0	0
40	1509265	3	0
41	1072980	8	7
42	1007942	3	0
43	1926186	8	0
44	3018766	9	0

45	3439663	6	167
46	1414498	8	0
47	3049421	4	179
48	1908355	4	0
49	2020444	5	0
50	2411485	7	0
51	1561811	8	21
52	1134212	7	29
53	1996380	4	194
54	1175687	6	128
55	1450884	5	183
56	1237967	7	0
57	5536997	5	0
58	2070717	7	13
59	1041378	5	13
60	1868287	4	0
61	1637671	8	14
62	1056546	6	94
63	1345835	5	364
64	7186563	5	390
65	1383947	2	420
66	7822432	1	0
67	1061570	4	0
68	1598208	3	396
69	2384172	2	0
70	1670548	4	409
71	1683289	4	63
72	1188012	3	454
73	1262960	3	0
74	2532404	6	62
75	6710294	4	2
76	1856255	7	124
77	1005338	6	126
78	4347775	5	6
79	1000975	4	0
80	3153752	6	148
81	1594778	10	0
82	1396192	11	30
83	1546257	9	347
84	2045092	5	387
85	1073132	12	299
86	20171243	7	466
87	6311942	4	0
88	1309584	11	144
89	1440263	17	118
90	12267878	9	384

91	1613203	16	190
92	1127850	17	11
93	10632826	19	108
94	5463117	16	172
95	1899190	18	34
96	12050306	5	41
97	6666030	4	0
98	1819440	5	17
99	2028107	17	135
100	4074884	12	0
101	1064501	3	0
102	4244002	4	0
103	1804812	17	5
104	1842132	3	0
105	1037004	16	128
106	1229376	18	29
107	3872215	3	0
108	1178197	18	12
109	1298221	18	143
110	1608012	14	5
111	1264686	13	0
112	6245683	3	0
113	293036092	15	130
114	2949539	12	68
115	4861057	12	6
116	1447450	7	29
117	1665387	10	0
118	966380999	6	772
119	1178283	3	0

Table A2: Protected areas with at least one square kilometer of woodland forest that are suitable for *Colobus vellerosus*.

NAME	DESIGNATION IN ENGLISH	GIS AREA	COUNTRY	CALCULATED AREA	PFarea	OCCURRENCE STATUT
Agoua	Classified Forest	659.3	BEN	669	1	not documented
Dogo	Classified Forest	311.1	BEN	315	6	not documented
Kétou	Classified Forest	131.7	BEN	133	1	not documented
Lama Classified Forest	**Classified Forest**	**172.97**	**BEN**	**168**	**43**	**present**
Monts Kouffé	**Classified Forest**	**1908.1**	**BEN**	**1940**	**892**	**possibly extinct**
Ouari Maro	**Classified Forest**	**1184.4**	**BEN**	**1206**	**400**	**possibly extinct**
Ouémé Superieur	**Classified Forest**	**2236.8**	**BEN**	**2286**	**42**	**no recent verification**
Pénessoulou	**Classified Forest**	**53.0**	**BEN**	**54**	**39**	**possibly extinct**
Tchatchou Gokana	Classified Forest	20.2	BEN	21	1	not documented
Toui-Kilibo	Classified Forest	479.5	BEN	487	6	not documented
Comoé-Léraba	**Partial Wildlife Reserve**	**1233.1**	**BFA**	**1262**	**36**	**possibly extinct**
Dida	Classified Forest	804.4	BFA	824	48	not documented
Kongouko	Classified Forest	301.0	BFA	309	6	not documented
Koulbi	Classified Forest	400.7	BFA	410	21	not documented
Badikaha	Classified Forest	145.2	CIV	148	9	not documented
Bandama-Blanc	**Classified Forest**	**482.0**	**CIV**	**489**	**56**	**historical**
Bere	Classified Forest	152.6	CIV	155	3	not documented
Classified Forest Name Unknown (CIV) No.11	Classified Forest	29.8	CIV	30	6	not documented
Classified Forest Name Unknown (CIV) No.13	Classified Forest	60.3	CIV	61	16	not documented
Classified Forest Name Unknown (CIV) No.15	Classified Forest	18.6	CIV	19	1	not documented
Classified Forest Name Unknown (CIV) No.16	Classified Forest	1480.1	CIV	1504	114	not documented
Classified Forest Name Unknown (CIV) No.18	Classified Forest	171.5	CIV	174	40	not documented
Classified Forest Name Unknown (CIV) No.19	Classified Forest	25.0	CIV	25	4	not documented
Classified Forest Name Unknown (CIV) No.20	Classified Forest	88.1	CIV	89	3	not documented
Classified Forest Name Unknown (CIV) No.23	Classified Forest	8.7	CIV	9	1	not documented
Classified Forest Name Unknown (CIV) No.24	Classified Forest	74.6	CIV	76	12	not documented

Classified Forest Name Unknown (CIV) No.28	Classified Forest	47.0	CIV	48	3	not documented
Classified Forest Name Unknown (CIV) No.32	Classified Forest	69.7	CIV	70	1	not documented
Classified Forest Name Unknown (CIV) No.37	Classified Forest	37.8	CIV	38	1	not documented
Classified Forest Name Unknown (CIV) No.7	Classified Forest	22.1	CIV	23	1	not documented
Comoe National Park	**UNESCO-MAB Biosphere Reserve**	**11756.2**	**CIV**	**11980**	**528**	**present**
Dora Diaro	Classified Forest	81.4	CIV	82	3	not documented
Foro Foro	Classified Forest	56.1	CIV	57	3	not documented
Kamesso	Classified Forest	363.9	CIV	368	2	not documented
Kinkene	Classified Forest	518.1	CIV	527	36	not documented
Kobo	Classified Forest	126.2	CIV	128	18	not documented
Kogha	Classified Forest	136.8	CIV	140	6	not documented
Laka	Classified Forest	66.7	CIV	67	1	not documented
Log-boyo	Classified Forest	75.4	CIV	77	26	not documented
Mafa	Classified Forest	189.7	CIV	191	4	not documented
Nangbyon	Classified Forest	205.1	CIV	208	98	not documented
Nyellepuo	Classified Forest	660.3	CIV	672	240	not documented
N'Zi River Lodge Voluntary Nature Reserve	Voluntary Nature Reserve	241.9	CIV	245	10	not documented
N'zi Superieure	Classified Forest	824.2	CIV	839	144	not documented
Ouarigue	Classified Forest	663.5	CIV	678	13	not documented
Réserve de faune et de flore du Haut Bandama	Natural Reserve	1220.3	CIV	1247	36	not documented
Silue	Classified Forest	430.6	CIV	439	44	not documented
Suitoro	Classified Forest	432.6	CIV	439	148	not documented
Ambalara	Forest Reserve	125.2	GHA	128	8	not documented
Apepesu River	Forest Reserve	67.6	GHA	68	1	not documented
Awura	Forest Reserve	131.7	GHA	133	1	not documented
Boabeng-Fiema	**Wildlife Sanctuary**	**153.1**	**GHA**	**155**	**1**	**present**
Bosomoa	**Forest Reserve**	**126.5**	**GHA**	**128**	**1**	**no recent verification**
Bui	**National Park**	**1871.8**	**GHA**	**1901**	**48**	**no recent verification**

Buru	Forest Reserve	323.0	GHA	328	6	not documented
Chai River	Forest Reserve	184.2	GHA	187	1	not documented
Digya	**National Park**	**2789.5**	**GHA**	**2818**	**152**	**no recent verification**
Gambaga Scarp East	Forest Reserve	346.1	GHA	356	10	not documented
Gambaga Scarp West	Forest Reserve	158.8	GHA	163	6	not documented
Kakum	**National Park**	**212.2**	**GHA**	**213**		**present**
Kani Kani	Forest Reserve	609.7	GHA	622	45	not documented
Laboni	Forest Reserve	259.4	GHA	264	168	not documented
Mole	**National Park**	**4769.9**	**GHA**	**4876**	**2255**	**present**
Nuale	Forest Reserve	52.6	GHA	54	45	not documented
Pamu Berekum	Forest Reserve	196.4	GHA	198	8	not documented
Pru Shelterbelt	Forest Reserve	49.9	GHA	50	14	not documented
Red Volta East	Forest Reserve	294.6	GHA	303	4	not documented
Red Volta West	Forest Reserve	304.7	GHA	314	14	not documented
Sawsaw	Forest Reserve	65.4	GHA	66	1	not documented
Sephe	Forest Reserve	375.4	GHA	384	130	not documented
Tain Tributaries II	Forest Reserve	536.7	GHA	543	9	not documented
Yakombo	Forest Reserve	1084.6	GHA	1103	157	not documented
Yerada	Forest Reserve	654.2	GHA	665	10	not documented
Mt. Loura	Classified Forest	9.2	GIN	10	6	not documented
N'Guidou	Classified Forest	1.9	GIN	2	1	not documented
Duma	Forest Reserve	14.6	NGA	14	1	not documented
Gwanara	Forest Reserve	704.7	NGA	719	197	not documented
Igangan	Forest Reserve	394.1	NGA	399	106	not documented
Ijaiye	Forest Reserve	246.6	NGA	249	14	not documented
Iwa River	Forest Reserve	376.0	NGA	383	54	not documented
Kusoziko	Forest Reserve	7.8	NGA	8	2	not documented
Lafiagi Oro	Forest Reserve	744.8	NGA	757	24	not documented
Lanlate	Forest Reserve	106.9	NGA	108	56	not documented

Lower Kaduna-Middle Niger Floodplain	Ramsar Site	2299.8	NGA	488	150	not documented
Meko	Game Reserve	751.5	NGA	760	332	not documented
Odo Ogun	Forest Reserve	15.4	NGA	16	1	not documented
Odugebe	Forest Reserve	170.2	NGA	172	1	not documented
Opara (Okpara) Forest/Game Reserve	**Forest Reserve**	**2549.8**	**NGA**	**2588**	**1316**	**present**
Old Oyo	**National Park**	**2384.5**	**NGA**	**2423**	**1225**	**present**
Olla Hill	Forest Reserve	23.7	NGA	24	6	not documented
River Moshi	Forest Reserve	2708.1	NGA	2760	98	not documented
Teshi	Forest Reserve	296.9	NGA	303	51	not documented
Upper Ogun	Forest Reserve	2384.5	NGA	2423	1225	not documented
Vobera	Forest Reserve	994.4	NGA	1015	1	not documented
Abdoulaye	Faunal Reserve	312.3	TGO	317	18	not documented
Alibi 1	Community Forest	54.5	TGO	55	10	not documented
Assoukoko	**Forest Reserve**	**91.8**	**TGO**	**93**	**1**	**extinct**
Bago	Community Forest	31.3	TGO	32	8	not documented
Fazao-Malfakassa	**National Park**	**2209.4**	**TGO**	**2247**	**39**	**present**
Monda	Forest Reserve	13.2	TGO	13	1	not documented
Mt Amalo	Forest Reserve	5.4	TGO	5	1	not documented
Natiwah	Forest Reserve	22.0	TGO	23	1	not documented
Oti-Kéran	National Park	847.2	TGO	869	3	not documented

Table A3: Recent sightings, historical sightings, and forest sites where the *Colobus vellerosus* is possibly extinct

NAME	DESIGNATION IN ENGLISH	GIS AREA	COUNTRY	CALCULATED AREA	PFarea	OCCURRENCE STATUT
Lama Classified Forest	Classified Forest	172.97	BEN	168	43	present
Comoe National Park	UNESCO-MAB Biosphere Reserve	11756.2	CIV	11980	528	present
Boabeng-Fiema	Wildlife Sanctuary	153.1	GHA	155	1	present
Kakum	National Park	212.2	GHA	213		present
Mole	National Park	4769.9	GHA	4876	2255	present
Opara (Okpara) Forest/Game Reserve	Forest Reserve	2549.8	NGA	2588	1316	present
Old Oyo	National Park	2384.5	NGA	2423	1225	present
Fazao-Malfakassa	National Park	2209.4	TGO	2247	39	present
Ouémé Superieur	Classified Forest	2236.8	BEN	2286	42	no recent verification
Bosomoa	Forest Reserve	126.5	GHA	128	1	no recent verification
Bui	National Park	1871.8	GHA	1901	48	no recent verification
Digya	National Park	2789.5	GHA	2818	152	no recent verification
Bandama-Blanc	Classified Forest	482.0	CIV	489	56	no recent verification
Monts Kouffé	Classified Forest	1908.1	BEN	1940	892	possibly extinct
Ouari Maro	Classified Forest	1184.4	BEN	1206	400	possibly extinct
Pénessoulou	Classified Forest	53.0	BEN	54	39	possibly extinct
Comoé-Léraba	Partial Wildlife Reserve	1233.1	BFA	1262	36	possibly extinct
Assoukoko	Forest Reserve	91.8	TGO	93	1	possibly extinct

Scientific publications

Accrombessi, F. D., Toyi, S. S. M., Kone, I., & Zinner, D. (2025). Identifying suitable forested areas and protected forests for the conservation of white-thighed (*Colobus vellerosus*) and king (*C. polykomos*) colobus monkeys under climate change in West Africa. Global Ecology and Conservation, 62, e03820. https://doi.org/10.1016/j.gecco.2025.e03820

Accrombessi, F. D., Toyi, S. S. M., Kone, I., Zinner, D. J., Djimenou, D., Djagoun, C. A. M. S., Roos, C., & Zinner, D. (2025). Low genetic diversity in *Colobus vellerosus* populations in Kikélé Sacred and Okuta Kobunan Forests, Benin. In bioRxiv. https://doi.org/10.1101/2025.07.30.667755. In revision in *Primates*.

Published nucleotide sequence data

Nucleotide sequence data from this study are deposited in NCBI GenBank. Accession numbers for cytb PV963062 - PV963065 and D-loop PV963066 - PV963080.

Presented conferences

Accrombessi F.D., Toyi S.S.M., Djagoun C.A.M.S, and Kone I. (2024). Effects of anthropogenic climate change on the potential distribution of the critically endangered Colobus vellerosus (Geoffory, 1834). 46th annual meeting, American Society of Primatology (ASP), Riviera Maya, Mexico, September 9-11.

Accrombessi F.D., Djimenou D., Toyi S.S.M., Zinner DJ, Djagoun CAMS, Pomalegni CB, Kone I, Roos C, Zinner D. (2025). Evidence of extremely reduced mitochondrial genetic diversity in globally endangered Colobus vellerosus populations in central Benin. Atelier Scientifique National 2025, Benin.

Accrombessi, F. D., Toyi, S. S. M., Kone, I., & Zinner, D. (2025). Identifying suitable forested areas and protected forests for the conservation of white-thighed (*Colobus vellerosus*) and king (*C. polykomos*) colobus monkeys under climate change in West Africa. Atelier Scientifique National 2025, Benin