Modelling on the distribution, habitat ecology, suitability and abundance of Djaffa Mountains guereza (*Colobus guereza gallarum*, Neumann, 1902) from Ahmar Mountains, Eastern Ethiopia

By

Chala Adugna Kufa

A Dissertation Submitted to the School of Graduate Studies of the Addis Ababa University, Department of Zoological Sciences in Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Biology (Ecological and Systematic Zoology)

Supervisors

Prof. Afework Bekele (PhD)

Anagaw Atickem (PhD)

Addis Ababa University

College of Natural and Computational Sciences

Department of Zoological Sciences

Addis Ababa, Ethiopia

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Addis Ababa University

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Approved by Examining Board:

Name		Signature
Prof. Afework Bekele	Supervisor	_______________
Dr. Anagaw Atickem	Co-supervisor	_______________
Dr. Fanuel Kebede	External Examiner	_______________
Dr. Mesele Yihune	Internal Examiner	_______________
Dr. Bezawork Afework	Chairman	_______________

Addis Ababa University

School of Graduate Studies

This is to certify that the dissertation prepared by Chala Adugna Kufa, entitled "**Modelling on the distribution, habitat ecology, suitability and abundance of Djaffa Mountains guereza (*Colobus guereza gallarum*, Neumann, 1902) from Ahmar Mountains, Eastern Ethiopia**" and submitted to the School of Graduate Studies of Addis Ababa University in fulfillment of the requirements for the Degree of Doctor of Philosophy in Zoological Sciences (Ecological and Systematic Zoology) complies with the regulations of the Addis Ababa University (AAU) and meets the accepted standards in all aspects.

Signed by the Examining Committee:

Examiner__________________________ Signature_____________ Date ___________

Examiner__________________________ Signature ____________ Date ___________

Supervisors:

Professor Afework Bekele Signature ____________ Date ___________

Anagaw Atickem (PhD) Signature ____________ Date ___________

Head of the Department of Zoological Sciences:

Bezawork Afework (PhD) Signature ____________ Date ___________

Declaration

I hereby declare that this PhD dissertation is my original work and has not been presented for any degree at any other University, and all sources of materials used for this dissertation have been duly acknowledged.

Chala Adugna Kufa Signature________________Date______________.

E-mail: kchalaadugna@gmail.com , chalaadugna@wldu.edu.et

ABSTRACT

Modelling on the distribution, habitat ecology, suitability and abundance of Djaffa Mountains guereza (*Colobus guereza gallarum*, Neumann, 1902) from Ahmar Mountains, Eastern Ethiopia

Chala Adugna Kufa, PhD Dissertation, Addis Ababa University
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Understanding the distribution, abundance, niche use and habitat suitability of little-known primate species in the human dominated landscape is key to guide the conservation and management efforts. Djaffa Mountains guereza (*C. g. gallarum*) is endemic primate of Ethiopia with little information on its ecology and distribution. This study aims to provide the most basic ecological aspects of *C. g. gallarum* focusing on its distribution pattern, population size, habitat suitability and conservation risks. The field study was conducted between 2020 and 2021 both during wet and dry seasons. Population estimate was carried out using line transects method covering a distance of 75.9 km in four forests with varied ecologies. Ecological niche modelling was developed by multiple algorithms. Projected climate of the Representative Concentration Pathways in two scenarios and periods was used. The potential suitable habitats for *C. g. guereza* and *C. g. gallarum* were modelled, identified anthropogenic refugia, analyzed protected anthropogenic refugia, and computed niche overlap. During the surveys, 73 guereza clusters were encountered, resulting in 20,061 individuals (109.6 individuals/km^2). The habitat suitability modelled using MaxEnt for *C. g. gallarum* predicted about 1,336 km^2 within its range. The predicted climate niche for *C. g. guereza* was 168,731 km^2, and for *C. g. gallarum*, it was, 69,542 km^2 as predicted using weighted mean ensemble models. However, closely related taxa of Ethiopia's Guereza exhibit divergent niches. Of the anthropogenic refugia calculated, 53.70% and 39.76% were found within Ethiopia's protected area network for *C. g. gallarum* and *C. g. guereza*, respectively. Habitat ecology analysis showed that height of the trees, variation of tree height and importance value influenced *C. g. gallarum* occupancy. The conservation of *C. g. gallarum* is crucial due to its fragmented habitat and population, necessitating further monitoring and habitat restoration efforts. The study suggests determining *C. g. gallarum*'s geographic distribution and collecting data along the common distribution border between it and other Guereza taxa to check for sympatry and hybridization.

Keywords/phrases: Anthropocene, climate change, ecological niche, Ethiopian highlands, guereza, population estimate, relict forest, species distribution modelling.

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ACRONYMS

ACCNNR	African Convention on the Conservation of Nature and Natural Resources
ASTER	Advanced Spaceborne Thermal Emission and Reflection radiometer
AρρEEARS	Application for Extracting and Exploring Analysis Ready Samples
BA	Basal Area
BCC-CSM	Beijing Climate Centre Climate System Model
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
DAF	Dry Evergreen Afromontane Forest
DEM	Digital Elevation Model
EWCA	Ethiopian Wildlife Conservation Authority
GCMs	Global Circulation Models
HadGEM2-ES	UK met office Hadley centre
HFP	Human Footprint Pressure
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature and Natural Resources
LP DAAC's	Land Processes Distributed Active Archive Centre
LCCS	Land Cover Classification System
OFWE	Oromia Forest and Wildlife Enterprise
ONRS	Oromia National Regional State

PRB	Population Reference Bureau
RCP	Representative Concentration Pathways
SEDAC	Socioeconomic Data and Applications Centre
UEA-CRU	University of East Anglia - Climatic Research Unit
UN FAO	United Nations Food and Agriculture Organization’s
WDPA	World Database on Protected Areas
WPP	World Population Prospects

1. INTRODUCTION

1.1. Background of the study

A significant portion of global biodiversity, including many primates, is at peril of extinction. A recent study has shown that primates currently facing population decline account for about 93% of the species (Estrada and Garber, 2022). IUCN has listed more than 65% of primate species within the threatened category (Fernández *et al*., 2022). From a total of 522 species globally, there is a threatened with extinction of a larger proportion (66.67%) and currently recognised as critically endangered (88 species), endangered (145 species), vulnerable (115 species), and 14 species data deficient by the IUCN (IUCN, 2023). The main reasons for this negative trend are well documented and include destruction, fragmentation, and conversion of primate habitats, besides unsustainable exploitation through trapping, shooting and illegal trade (Estrada *et al*., 2017). It is expected that factors like human population growth, agricultural expansion and changes in climate will further hasten population decline (Estrada *et al*., 2020; Estrada and Garber, 2022; Pinto *et al*., 2023). Climate change, in combination with other human activities, has already influenced the habitat extent of species', leading to changes via reductions, fragmentation, and shifts of suitable habitats for species, mainly species of primate (Walther *et al*., 2005; Korstjens and Hillyer, 2016; Carvalho *et al*., 2019; Sales *et al*., 2020; Winder *et al*., 2023).

Anthropogenic-driven climate change is expected to cause Earth warming, leading to mass extinction of plants and animals (Foden *et al*., 2019). Thus, there are difficulties for vast biodiversity, with habitat loss and fragmentation hindering species' ability to reach suitable areas (Thomas *et al.*, 2004). Primates that inhabit fragmented habitats have already experienced shifts in distribution and reduced range due to global changes in climate and this probably further threatens vulnerable species with extinction. Recent evidence suggests that primates are particularly vulnerable to expected temperature and precipitation changes (Graham *et al*., 2016), as well as life-threatening weather events (Zhang *et al*., 2019). Temperatures in one-quarter of primate habitats at present exceed historical levels (Pinto *et al*., 2023), affecting populations that experienced detrimental effects from worldwide heating (Pacifici *et al*., 2017). These trends will exacerbate the consequences of human activities, pushing vulnerable primate species even closer to extinction (Winder *et al*., 2023). Although primates are known to be adaptable within a limited temperature range (Tewksbury *et al*., 2008), they have low dispersal capacity (Meyer and Pie, 2022) and tend to maintain stable ranges (Gnanadesikan *et al*., 2017; Samplonius *et al*., 2018). Nevertheless, their long generation time makes it difficult for them to develop effective adaptations quickly enough to minimise the detrimental impacts caused by changes in global climate conditions (Bernard and Marshall, 2020). Many studies have been conducted to understand the influences of global change in climate on biodiversity in Ethiopia (Mulugeta Mokria *et al*., 2015; Desalegn Chala *et al*., 2016; Fashing *et al*., 2022; Kandziora *et al*., 2022; Ahmed Seid *et al*., 2023). A study reveals that climate change will increase the minimum altitude of geladas by 500 metres for every 2°C rise in the mean temperature (Dunbar, 1998). A recent review also highlights the need for mega-research on the long-term effects of changes in climate on biodiversity (Fashing *et al*., 2022). Therefore, research on climate change is crucial for understanding how to protect biodiversity (Liu *et al*., 2022), the ways in which species react to the changing climate (Graham and Grimm, 1990), developing approaches that mitigate its effects (Struebig *et al*., 2015), and ultimately conserving species (Thomas *et al*., 2004). Given the magnitude and multitude of threats mentioned above, novel and promising approaches to primate conservation are needed (Wich and Marshall, 2016).

The establishment of Protected Areas (PAs) is widely recognised as one of the most effective strategies for preserving natural habitats, ecological services, and biodiversity conservation. However, in some African countries, these protected areas face numerous challenges. These challenges include inadequate funding and management, security issues, a dearth of facilities and provision from stakeholders, ignorance, and high frequency illicit activities. Over 14% of Ethiopia's landmass is in PAs (> 135 protected areas), threatened by resource access, habitat degradation, agricultural conversion, livestock overgrazing, weak institutional capacity, and invasive species (Fashing *et al*., 2022). As a consequence, these areas are becoming increasingly isolated and fragmented, with little connectivity to other protected areas or private lands. Given the current rapid climate change, connectivity is of utmost importance for gene flow, species migration, and range shifts (Saura *et al*., 2018).

Recognising the urgency of this situation, species distribution modelling or ecological niche modelling of primate species has gained considerable attention in recent years (Duran *et al*., 2013). This modelling approach allows us to comprehend habitat requirements for primate species more clearly, which can then inform conservation efforts and management plans. While many ecologists consider the study of species habitat ecology is to be central (Veech, 2021), understanding the biogeography, abundance, ecological niches, and threats of primates is crucial for developing effective conservation strategies (Chapman *et al*., 1999; Butynski and De Jong, 2022a). To develop species-specific conservation strategies and monitor implemented conservation measures, it is essential to estimate the density, abundance, and distribution of populations (Jachmann, 2001; Marques, 2001; Keeping and Pelletier, 2014; Kiffner *et al*., 2022a). This is particularly important for threatened species that inhabit human-modified landscapes (Cavada *et al*., 2016). Conducting wild animal population surveys, studying distribution patterns, and exploring ecological aspects are therefore crucial contributions to successful species conservation (Ogutu *et al*., 2006; Santini *et al*., 2022). Furthermore, determining the range of potential suitable habitat under various environmental circumstances is essential for identifying priority sites or refugia for species conservation, translocation, and reintroduction, thereby ensuring their long-term survival.

Over significant ecological fluctuations, certain areas might assist as refugia, providing safety and stability for biodiversity, possibly increasing their numbers when situations get favourable (Monsarrat *et al*., 2019). Conservation based on refugias is effective over the long term (Sales and Pires, 2023). In the context of anthropogenic climate change, it is essential to effectively conserve biodiversity (Reside *et al*., 2014; Keppel *et al*., 2015). Historical climatic refugias suggest that areas with remnants of contemporary climates could serve as crucial habitats for current biodiversity in the face of modern climatic change (Michalak *et al*., 2018). Through preservation of important resources and protection of areas shielded from climate change, climate change adaptation research seeks to lessen the effects of human-caused climate change on biodiversity (Morelli *et* *al*., 2017). Since refugia help the biota survive in harsh environments, finding and preserving them is essential for conservation in the face of anthropogenic climate change (Keppel *et al*., 2012; Reside *et al*., 2014).

African colobines are among the primates in danger of extinction on the African continent (Butynski *et al*., 2013). Out of the 79 species of subfamily colobine in the Family Cercopithecidae, 24 are African colobines of which 96% are threatened with extinction. The immediate threats are the loss of forests due to agricultural expansion (Butynski and De Jong, 2022a). However, hunting by humans as a source of bushmeat and skin is also the ultimate threat these primates encountered (Davies and Oates, 1994; Oates, 1994, 1996; Struhsaker, 1997; Fashing, 2011; Linder and Oates, 2011; NGoran *et al*., 2012; Rovero *et al*., 2012). The genus *Colobus*, which belongs to the African colobines, inhabits diversified habitats, altitudes, and climates (Butynski and Koster, 1994; Davies and Oates, 1994; Butynski *et al*., 2013; Groves and Ting, 2013; Butynski and De Jong, 2022a). Apart from a few sympatric species (Oates, 1994; Bocian and Anderson, 2013), most of the species within this genus are allopatric. Allopatric speciation patterns play a crucial role in adapting to changes in climatic conditions and sustaining species populations.

Throughout the 28 tropical African countries where colobines are widespread, human populations have increased by 2.0 to 6.2 times between 1960 and 2018, with population densities ranging from 8 to 499 people/km^2 (Butynski and De Jong, 2022a). Such human population increase followed by agricultural expansion, human settlement and unsustainable natural resource use such as logging and human hunting cause a sharp decline of colobines in Africa, resulting from forest loss (Chapman *et al*., 1999; Chapman *et al*., 2007; Minhós *et al*., 2023).

Forest loss resulting from human population growth has a significant impact on arboreal monkeys. These monkeys rely on forests for their food, shelter, and overall survival as well as reproduction. Unfortunately, they face threats in human-modified landscapes. The late current century is projected to face a significant increase in climate change, more than fivefolds in percentage (Houghton *et al*., 2001; Niang *et al*., 2014), which will cause reduced rainfall and river runoff (IPCC, 1992), affecting forest cover and thereby threatening the colobines (Kaeslin *et al*., 2012; Butynski and De Jong, 2022a). Unfortunately, the majority of African colobines are found outside of protected areas on private property and in forest remnants within agro-ecosystems (Butynski and De Jong, 2022a). These populations play a crucial role as forest engineers and in trophic guilds, but they face significant threats from population reductions and high fragmentation forests occupied. Without effective conservation measures and implementation of management plans, these populations are at high risk of further decline and potential extinction.

Ethiopia is home to 14 species of primates, with its diverse topography, altitude, vegetation type, ecosystem and climate variability (Fashing *et al*., 2022). The study of primates' dates back to 1758 when *Cercopithecus aethiops* (Linnaeus, 1758) and *Papio hamadryas* (L., 1758) were discovered, marking the beginning of primate research. Since then, research has been conducted on various primate species, including *Galago senegalensis* (Lavrenchenko *et al*., 2010), *G. gallarum* (Butynski and De Jong, 2004), *Erythrocebus patas pyrrhonotus* (Solomon Yirga *et al*., 2010), *E. poliophaeus* (Gippoliti, 2017), *Cercopithecus mitis boutourlini* (Addisu Mekonnen *et al*., 2020), *C. neglectus* (Mwenja *et al*., 2019), *Chlorocebus aethiops aethiops* (Willems and Hill, 2009), *C. a. matschiei* (Butynski and De Jong, 2022b), *C. djamdjamensis harennaensis* (Gippoliti, 2020), *C. d. djamdjamensis* (Addisu Mekonnen *et al*., 2018), *C. pygerythrus arenaria* (Butynski and De Jong, 2019), *Theropithecus gelada gelada* (Desalegn Ejigu and Afework Bekele, 2014), *T. g. obscurus*; *T. g. ssp. nov*., *Papio anubis doguera* (Zinner *et al*., 2015), *P. hamadryas* (Shotake, 1981), *P. cynocephalus ibeanus* (Kingdon *et al*., 2016), *Colobus guereza guereza* (Dereje Yazezew *et al*., 2022), and *C. g. gallarum* (Zinner *et al*., 2019). The genus *Colobus*, is predominantly arboreal and folivorous and inhabits a diversity of forest habitats and several of its species are highly threatened (Butynski and Koster, 1994; Davies and Oates, 1994; Butynski *et al*., 2013; Groves and Ting, 2013). Notably, among the genera of the subfamily Colobines, only the genus *Colobus* is found in Ethiopia with only one extant species, *Colobus guereza*. There are seven subspecies of *C. guereza*: *C. g. dodingae*, *C. g. gallarum*, *C. g. guereza*, *C. g. kikuyuensis*, *C. g. matschiei*, *C. g. occidentalis*, and *C. g. percivali* (Wallis, 2023). Two of the seven subspecies, *C. g. gallarum* and *C. g. guereza,* are endemic to Ethiopia (Fashing and Oates, 2013; Zinner *et al*., 2019). In recent decades, there has been a significant increase in attention in primate's studies, probably as a result of increasing pressures and growing recognition of the primates' biological, intellectual, economic, and ecological significance (Wich and Marshall, 2016). Studying Ethiopia's primates' biology, natural history, distribution, ecology, and conservation has also regained interest in recent years.

In Ethiopia two endemic *Colobus* taxa occur, the Omo River guereza *Colobus guereza guereza* and the Djaffa Mountain guereza *Colobus guereza gallarum* (Fashing and Oates, 2013; Zinner *et al*., 2019). They diverged 0.7 Ma ago (Zinner *et al*., 2019). Whereas *C. g. guereza* is widely distributed in Ethiopia, *C. g. gallarum* is restricted to a relatively small area south-east of the Rift Valley (Zinner *et al*., 2019). They seem to be ecologically relatively flexible, and they can be found even in small forest groves around churches or in parks (Dunbar and Dunbar, 1974; Fashing *et al*., 2019).

1.2. Statement of the problem

Our understanding of the taxonomy and distribution of primates remains inadequate in Ethiopia (Yalden *et al*., 1977), thus needs further exploration in remote forests. This exploration may provide an impetus for ecologists to study the conservation status and diverse ecological mechanisms involved in managing populations. Such studies will aids the application of successful management actions (Fashing *et al*., 2022). Despite several studies (Shotake, 1981; Zinner *et al*., 2015; Kingdon *et al*., 2016; Zinner *et al*., 2019; Addisu Mekonnen *et al*., 2020; Dereje Tesfaye *et al*., 2021; Dereje Yazezew *et al*., 2022), knowledge about the biogeography, ecology, behaviour, interspecific relationships, and abundance of primates in Ethiopia is still remains insufficient. One example of this knowledge gap is our understanding of the natural life history, taxonomy, distribution, habitat ecology, behaviour and population size of colobus monkeys in diverse flora types.

The Ethiopian guereza is a primate species with unique structures. The difference between *C. g. gallarum* and *C. g. guereza* is grounded on craniometric differences (Hull, 1979), colour differences in the base of the tail (Rahm, 1970; Fashing and Oates, 2013), and mitochondrial markers (Zinner *et al*., 2019). For example, the guereza of the Djaffa

Mountains has a black proximal tail with grey hairs spread distally, and a white, bushy distal tail that makes up about half of its overall length (Butynski *et al*., 2013). But be aware that the guereza of the Bale Mountains National Park's Harenna Forest does not have the same tail feature as *C. g. gallarum* (Carpaneto and Gippoliti, 1994). Therefore, *C. g. gallarum* seems to be confined to the Eastern Arsi and Chercher regions (Groves, 2007). Zinner and colleagues (2019) have verified the authenticity of *C. g. gallarum* and its limited geographical distribution inside the Ahmar Mountains.

In recent decades, Ethiopia has experienced a severe loss of forest habitats in almost all regions of the country. Its rapid human population growth with 3.02% annual growth rate and double the next 30 years (PRB, 2023; WPP, 2021) have significantly threatened biodiversity. These have had a significant impact on the primary habitats for forest-dependent species, including several primate taxa (Yalden *et al*., 1977; Fashing *et al*., 2022). One primate taxon that is particularly at risk of extinction is the *C. g. gallarum* because, within its supposed range, only a few forested areas remain. *Colobus g. gallarum* is monkey endemic to the Arsi and Ahmar Mountains in Ethiopia (Groves, 2001; Fashing and Oates, 2013, 2019a). However, there is uncertainty about its exact distribution, particularly regarding the range boundaries between the closely related taxa of Ethiopian guereza. The occurrence of Djaffa Mountains guereza west of the Arsi and Ahmar Mountains, such as in Dale Forest and the Bale Mountains National Park, Munessa Forest and Wondo Genet Forest is questionable (Israel Petros *et al*., 2018a, b, c; Israel Petros and Sefi Mekonen, 2019; Sefi Mekonen and Mastewal Hailemariam, 2021). These western populations do not exhibit *C. g. gallarum*-specific mitochondrial haplotypes (Zinner *et al*., 2019; Dereje Tesfaye *et al*., 2021). Given the significant loss and degradation of forests within its range, as well as its likely limited distribution, *C. g. gallarum* is facing a severe risk of extinction. However, due to limited knowledge regarding its population size and structure, distribution pattern, and niche characteristics, this study taxon is recently registered as Data Deficient by the IUCN (Fashing and Oates, 2019a). Whereas *C. g. guereza* is listed as Least Concern by IUCN, the conservation status of *C. g. gallarum* is unclear, but according to a recent assessment it is Vulnerable, mainly because of habitat loss due to agricultural expansion. Since particular the pressure on *C. g. gallarum* is high, we modelled the ecological niches of both taxa in a comparative study to identify suitable habitats within and outside of both forested and protected areas that may serve as anthropocene refugia. However, a thorough comparative analysis of the climate niches and extent of suitable habitat of both taxa is missing.

Eastern Africa exhibits several populations of primates in isolated forests 'islands,' per subsequent subspecific divergence (Schwarz, 1929; Hull, 1979). Often, small geographic distances separate recognized subspecies in this region, as is between Omo River guereza and Djaffa Mountains guereza in the Arsi region (Hull, 1979). The Rift Valley was traditionally seen as a barrier preventing gene flow between *C. g. guereza* and *C. g. gallarum*, thus keeping the two subspecies of Ethiopia separate. Neumann (1902), previously reported the presence of *C. g. gallarum* in the Arsi Mountains, near headwaters of the Wabe Shebelle River, as well as in the Djaffa Mountains, Gara Muleta and within forests nearby Burka (Yalden *et al*., 1977). Schwarz (1929) described including Mountains Gara Muleta, Kulubi Hills (60 km southwest of Dire Dawa), Harrar, Burka (between Harrar and Addis Ababa), Abuel Kassim Mountain, and the Djaffa Mountains. Allen (1939) gave the geographic extent of the taxon to the mountain forests east of the Awash River, Shebele River, Gara Muleta, and the Arsi region. Nevertheless, recent work conducted using genetic analysis has provided solid suggestion regarding the classification of Ethiopian guereza, that supports previous research (Hull, 1979). The study by Zinner and colleagues confirmed that the populations previously identified as *C. g. gallarum* were actually *C. g. guereza*. Genetic data show that mitochondrial haplotypes of *C. g. gallarum* are more closely related to *C. g. occidentalis* than to *C. g. guereza*. This suggests that *C. g. gallarum*, in contrast to *C. g. guereza*, might be a remnant of the first colonization of the Ethiopian Highlands by *Colobus*, followed by a second colonization by *C. g. guereza* (Zinner *et al*., 2019).

It was believed that *C. g. gallarum* inhabits forested highland areas east of the Rift Valley and possibly parts of the Rift Valley itself (Yalden *et al*., 1977; Carpaneto and Gippoliti, 1994). It is endemic to the Ahmar Mountains of the Ethiopian Highlands. It may be sympatric with *C. g. guereza* in the Arsi region (Yalden *et al*., 1977; Groves, 2001). The limits of the geographic boundaries are poorly understood (Zinner *et al*., 2019; Butynski and De Jong 2022a, 2022c). However, there is still some uncertainty regarding its exact distribution, population size and structure and ecology, as well as conservation potential threats faced by the *C. g. gallarum*. Thus, it is essential to reevaluate its conservation status once the population size and distribution patterns have been determined. This study aims to enhance conservation efforts for *C. g. gallarum* focusing eastern parts in Ethiopia, specifically in the Hararghe Plateau, an extension of the southeastern highlands. This dissertation focuses on examining the ecological stressors (both species-climate and species-habitat) that govern the abundance and distribution of endemic *C. g. gallarum* to develop conservation management strategies for this subspecies. These studies have incorporated state-of-the-art approaches such as species distribution modelling, ecological factor analysis and line transect distance sampling.

1.3. Objectives of the study

1.3.1. General objective

The main objective of this dissertation was to model the distribution, habitat ecology, suitability and abundance of Djaffa Mountains guereza (*Colobus guereza gallarum*, Neumann, 1902) from Ahmar Mountains, Eastern Ethiopia.

1.3.2. Specific objectives

The specific objectives were to:

- Estimate the population size and structure of the *C. g. gallarum*;
- Estimate the density of *C. g. gallarum* in the study area;
- Develop maps of suitable habitat and distribution of the *C. g. gallarum* in the eastern Ethiopian highlands during periods of climate change;
- Assess the extent of potential suitable habitats for *C. g. gallarum* and its sister taxon, *C. g. guereza*, identify anthropogenic refugia, analyze protected anthropogenic refugia, and compute niche overlap (divergence) to illuminate the similarities and differences in niche requirements between the two taxa;
- Assess abundance-suitability relationships for *C. g. gallarum*;
- Examine the vegetation community composition and structure of forest patches;
- Analyse the habitat association of *C. g. gallarum* and examine the habitat ecology in the remnants of forests in Ahmar Mountains, Eastern Ethiopia.

1.4. Research questions

- What is the distribution range of the *C. g. gallarum*?
- What is the current population size of *C. g. gallarum* in the forests of the Ahmar Mountains?
- What is the density of *C. g. gallarum* in the study area looks?
- What are the ecological factors that dictate the distribution pattern and abundance of *C. g. gallarum* under climate change?
- Do closely related *guereza* taxa have overlapping ecological niches in Ethiopia?

- Does each taxon ecological niche model encompass a variable area of suitable habitat?

- Is a significant percentage of the Anthropocene refugia situated inside protected areas because of the considerable efforts of conservation workers to keep Ethiopia's relict biodiversity? How about the niches that are most likely at substantial peril from human pressures, and does that suitable habitat correlate with pressure intensity?

- Is there correlation between local abundance and habitat suitability predicted by ecological niche models?

- How do the attributes of local habitats affect the occupancy and abundance of Djaffa Mountains guereza among forests from Ahmar Mountains?

1.5. Significance of the study

For decades, the geographic range of *C. g. gallarum* is confused with *C. g. guereza*. Studies carried out on *C. g. gallarum* reported it as *C. g. guereza* (Dereje Tesfaye *et al*., 2021). While the study conducted by Zinner *et al*. (2019) indicated that the distribution of *C. g. gallarum* is significantly lesser against previously documented finding. Its population size in the degraded Ahmar Mountains remains unknown. This study is the first study on *C. g. gallarum* which provides reliable information on its population size, distribution pattern, ecology, potential suitable habitat map and niche selection.

Colobus g. gallarum populations are in danger of extinction risks due its restricted range, which has experienced significant forest loss. Lastly, this dissertation is instrumental in the IUCN assessment of the status of *C. g. gallarum*, providing important baseline data for the reassessment process. It is speculated that this subspecies is vulnerable. If appropriate action is not taken, Ethiopia may face the impending loss of this endemic subspecies. Therefore, this study has utmost importance for conservation managers in guiding their conservation efforts.

The outcome of this dissertation has already contributed to reassess *C. g. gallarum's* conservation status, which is currently in press. The findings are essential for EWCA and other stakeholders in determining priority areas for conservation and starting management initiatives in the area to safeguard the subspecies and its habitat. The impacts of this study are to address the conservation gaps regarding the Djaffa Mountains guereza, *C. g. gallarum*. This is achieved by integrating various research fields, such as abundance, habitat suitability, ecological niche overlap, and the anthropogenic threats faced by this taxon in the relic forests of the Ahmar Mountains

1.6. Scope of the study

This study covers four important subjects on *C. g. gallarum* 1) distribution pattern and population size; 2) the potential suitable habitat of the subspecies and its niche overlap with the *C. g. guereza*; 3) the identification of Anthropocene refugia and its conservation implication; and 4) habitat ecology and association of the subspecies.

2. LITERATURE REVIEW

2.1. General description of Colobine monkeys

Colobines are monkeys from Africa and Asia belonging to the family Cercopithecidae. Over 79 species, grouped into 10 genera, exhibit diverse ecological and social traits, primarily forest-living and arboreal (Matsuda *et al*., 2022). Occupying forest and woodland habitats, colobines vary in size from 4 to 20 kg for adult males (Oates and Davies, 1994) and 5 to 11 kg for adult females (Fashing and Oates, 2013). Colobines are unique among primates in that they possess a complex, multichambered stomach (either tripartite or quadripartite) as part of their foregut fermentation system, setting them apart from all other species (Matsuda *et al*., 2022). For extended fermentation of plant materials consumed as diets, the forestomach (presaccus plus saccus) accumulates ingesta and slows down digesta transit. Hindgut fermentation can also be utilized less in colobines than in folivorous monkeys, such as the Neotropic howlers. However, colobines have complex stomachs than other cercopithecines, which have complex bacterial microflora capable of breaking down cellulose (Oates and Davies, 1994). In contrast to other cercopithecine, colobines feed above ground and pull leaves and fruits (unripe and/or ripe) from branches or climber stems when they procure them as feeding strategies, whereas the cercopithecine use their dexterous thumbs to pick up foraging fruits and insects.

Knowledge of morphology, physiology, demographics, ecology, and behaviour is crucial for understanding African colobine biogeography, abundance, conservation status, and threats and for finding solutions to counter the major threats they face (Davies and Oates, 1994; Butynski *et al*., 2013; Groves and Ting, 2013; IUCN, 2019/2020). The black and white colobus monkeys, one of the genera of African colobines, is endemic to equatorial Africa's forests (Fashing, 2022). The colobus monkeys in the forests of sub-Saharan Africa are medium-sized primates. They are renowned for their strikingly black, black-and-white, or red fur coat, folivorous diet and cooperative social structure (Matsuda *et al*., 2022). They have a specialized arboreal lifestyle, with a reduced thumb for agility. They are agile climbers and are well adapted to life in the forest canopy. Their long tails, provide them with balance and act as a counterbalance while leaping between branches. Colobus monkeys also consume fruits, seeds, and flowers, supplementing their diet when available. The two traits that most obviously distinguish the living African colobines from other Cercopithecoid monkeys are thumbless and nutritional specialism (Kingdon and Groves, 2013).

Colobus monkeys live in small to medium-sized groups, typically averaging 2-15 individuals and never exceeding 23 individuals, with a dominant male, multiple females and offspring (Fashing, 2022). They maintain social bonds through grooming, vocalizations, and communication. Conservation status varies, with some listed as vulnerable resulted from habitat loss, fragmentations, poaching and illegal wildlife trade. However, they play crucial roles in forest ecosystems.

2.2. Historical taxonomy and diversity of African colobines

Colobines or Afroeurasian monkeys, belong to the Cercopithecidae family (Tran, 2014) and originated in Africa, likely western Africa (Roos *et al*., 2011) (Fig.1). They have since spread to South and Southeast Asia and thrived. The Colobine subfamily diverged from Cercopithecinae 14–15 million years ago (Stewart and Disotell, 1998). Two monophyletic Colobinae lineages radiated independently during the latter Miocene (Fleagle and Gilbert, 2006). At present, Colobinae monkeys are native to Africa and southeastern Asia.

Dispersal in biogeography has been a topic of debate. Darwin and Wallace suggested that species disjunctions were due to long-distance movement across barriers, while Lyell, Forbes, and Hooker suggested that ancient corridors disappeared directed disconnections (Brown and Lomolino, 1998). Dispersal benefits species by colonizing new areas, avoiding harsh conditions, feeding and mating (Huggett, 2004). The land bridges and ancient landmass, which are now submerged in the oceans, were the routes through which the species were dispersed (Crisci *et al*., 2003; Sanmartín, 2012).

Stewart and Disotell (1998) suggested that barriers such as water bodies prevent land mammals from dispersing between Africa and Eurasia. However, in the late Miocene inherited genera of Asian colobines dispersed in to Asia from African continent (Delson, 1994; Fleagle and Gilbert, 2006). The invasion process involved the movement of the Arabian Peninsula, the formation and expansion of the Red Sea, and formation of an evolving land-bridge connecting the Arabian Peninsula and Africa. Afterwards, through a route along the northern part of the Himalayas, they diversified into several lineages (Roos *et al*., 2011).

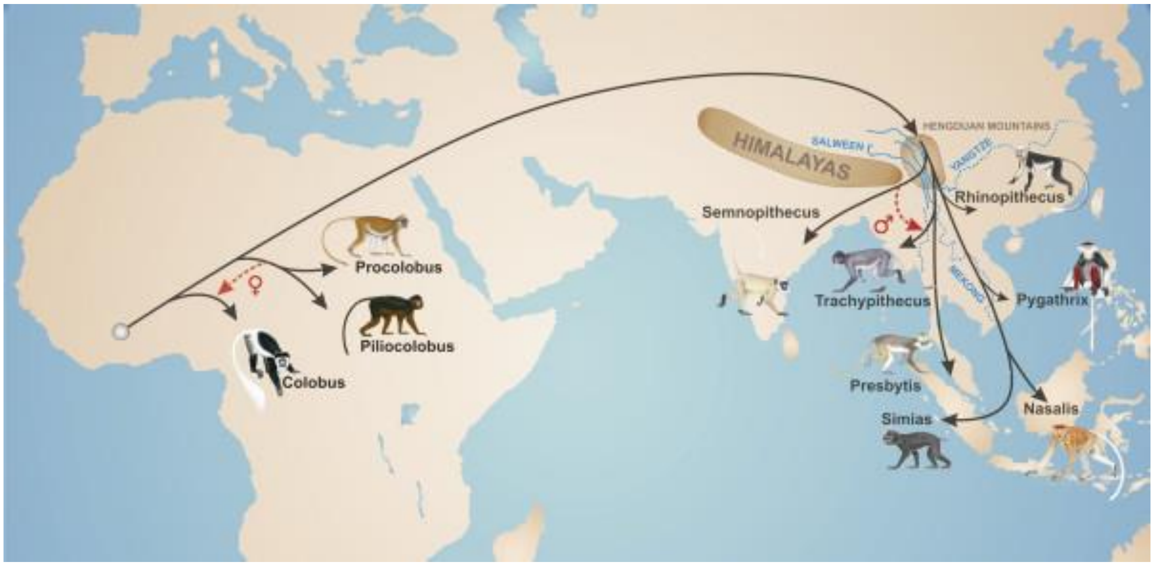


Figure 1. Origin and Dispersal Scenario for the Colobine Monkeys (Source: Roos *et al*., 2011).

African colobines exhibit remarkable diversity in terms of species, distribution, and ecology. They are medium-sized, folivorous, arboreal, and thumbless and rely on forests. They have long limbs, complex social structures, and a specialized digestive system (Kingdon and Groves, 2013). With respect to their ecological roles, African colobines provides support in ecosystem health, seed dispersion and nutrient cycling. However, habitat loss, hunting, and human-induced factors have increased their susceptibility to extinction (Butynski *et al*., 2013; IUCN 2019/2020).

Despite extensive research (Groves and Ting, 2013), the classification and taxonomy of African colobines are still ongoing revision due to inadequate conservation efforts (Butynski and De Jong, 2022a). This could lead to species and subspecies expansion or near extinction, and new discoveries and genetic studies could alter the classification and relationships within the Colobinae subfamily.

The diversification of Africa's colobines is represented by three extant endemic genera, namely, red colobus (*Piliocolobus*; 17 living species), black-and-white colobus monkeys (*Colobus*; 6 living species) and olive colobus (*Procolobus*; 1 living species) (Butynski and De Jong, 2022c; IUCN, 2023; Wallis, 2023). Out of the 79 species of Colobinae that exist, 24 are found only on the African continent, mainly in the rainforests of the African Belt. Despite early diversification, the African colobine lacks radiation due to aridification of suitable tropical rainforest-cover along East Africa, interspecies rivalry for home and nutritional capitals, and constrained morphological variation. These factors have depressed diversification and imperfect chances for speciation through differing assortment (Tran, 2014).

Due to the geographic sympatry of all three genera (*Colobus*, *Piliocolobus*, and *Procolobus*), speciation events in Colobine monkeys occurred in western Africa (Davies and Oates, 1994; Groves, 2001; Ting, 2008). An evolutionary relationship among the modern African colobus monkeys shows their divergence from one another during the latter Miocene as well as the current lineages of the species appeared during Plio-Pleistocene (Ting, 2008). The phylogenetic relationships among African colobines are controversial, with some suggesting that they are paraphyletic. A study suggested that the genus *Colobus* split off first from the ancestor of Asian Colobinae at ~10.9 Mya, followed by the ancestor of *Piliocolobus* and *Procolobus* at ~10.7 Mya (Roos *et al*., 2011). Later work indicates that around 7.5 Mya the genera *Colobus* and *Procolobus* group were diverged, whereas the lasting 2 genera deviated at 6.4 Mya (Ledevin and Koyabu, 2019). This is suggesting that the taxonomy of colobines should be further resolved for conservation reasons, because a study by Roos *et al*. (2011) emphasized the future analyses of various molecular marker to track the occurrences of inbreeding and gain a deeper understanding of evolutionary relationship.

Most authors divide colobines into distinct genera or subgenera. Much less agreement exists on the number of species. For purposes of this study, I follow Myers *et al.* (2019) for taxonomic classification of *C. g. gallarum*:

Kingdom: Animalia
Phylum: Chordata
Class: Mammalia
Order: Primates
Family: Cercopithecidae
Subfamily: Colobinae
Genus: *Colobus*
Species: *Colobus guereza*
Subspecies: *Colobus guereza ssp, gallarum*

Human activities such as species removal, ecosystem degradation, climate change, and biodiversity loss often lead to species extinction (Brown and Lomolino, 1998). Extinction is a natural process that reflects the inability of a species to adjust to its environmental dynamics (Ricklefs and Miller, 2000). This is a critical scientific issue due to the threat of anthropogenic global change and its impact on Earth's ecosystem. In the past, several colobine lineages, including *Microcolobus*, *Rhinocolobus*, *Paracolobus*, *Libypithecus*, and *Kuseracolobus* and *Cercopithecoides* became extinct (Leakey, 1982; Delson, 1994; Benefit, 2000; Jablonski *et al.*, 2008). Nevertheless, their relationships with modern subtribes and the phylogenetic relationships of the extinct forms are unclear or not well resolved (Delson, 1994; Ting, 2008).

2.3. Distribution of African colobines

2.3.1. Biogeography of African colobines

Ecologists define biogeography as the patterns of organism distribution across the Earth's surface and the interactions between organisms in their physical environments, whereas biologists define biogeography as the study of the history and geography of animals and plants (Brown and Lomolino, 1998; Huggett, 2004; Posadas *et al.*, 2006). Accordingly, biogeography is the study of how organisms are distributed geographically, and it may take many different forms, from descriptive to interpretive (Posadas *et al*., 2006). While interpretive studies look for causal explanations for these patterns, descriptive studies concentrate on identifying the distributional patterns of the live organism. The former research has yielded two distinct methodologies, namely, ecological and historical biogeography. According to Brown and Lomolino, ecological biogeography studies the present spreading of species and the ecological characteristics where the species dispersed. Historical biogeography aims to reconstruct biota origin, dispersal and extinction while exploring life evolution and environmental factors such as continental drift. Both approaches aim to understand species distributions spatio-temporally, integrating them into a common framework (Brown and Lomolino, 1998; Crisci *et al*., 2003; Huggett, 2004).

African colobines are primarily found in sub-Saharan Africa, inhabiting forests, woodlands, and montane regions (Matsuda *et al*., 2022). *Procolobus*, the olive colobus monkey, is found in West Africa's rainforests, while *Pilicolobus*, the red colobus monkey, is the most threatened group, spanning Senegal to Zanzibar Archipelago. The exact distribution and range of each species may vary within these broader regions, and there may be localized variations and subpopulations within specific countries. They are primarily associated with forested habitats which are found in tropical rainforests. Some species, such as Eastern *C. guereza*, are adapted to subtropical and montane forests, which have cooler temperatures and higher elevations (Fashing, 2022). Some species can also be found in woodlands and savannas, with a more open canopy and a mix of trees and grasses. Some species are specialized for montane regions, with unique adaptations to thrive in these environments. However, anthropogenic factors impacting the populations of African colobines. Ongoing research and field surveys may lead to further discoveries and updates regarding the distribution of African colobines. Overall, understanding the geographic range of African colobines is crucial for conservation efforts, as it helps identify areas of high species richness, prioritize conservation actions and protect their habitats across their range.

The genus *Colobus* (black and white Colobus) contains six species that are widely distributed across Equatorial Africa (Grubb *et al*., 2003; Fig. 2 and 3). These six species include Angolan Colobus, *Colobus angolensis* (VU), Black Colobus, *Colobus satanas* (VU), Guereza Colobus, *Colobus guereza* (LC), King Colobus, *Colobus polykomos* (EN), White-Thighed Colobus, *Colobus vellerosus* (CR), and Mt. Kilimanjaro Guereza, *Colobus caudatus* (VU) (Wallis, 2023).

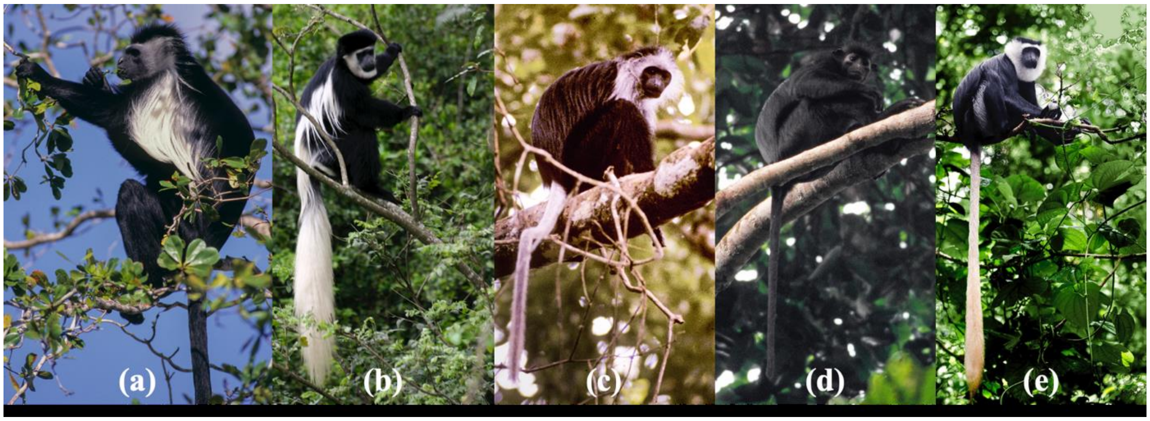


Figure 2. The five species of black-and-white colobus monkeys: (a) *Colobus angolensis*, (b) *C. guereza*, (c) *C. polykomos*, (d) *C. satanas*, and (e) *C. vellerosus* (Source: Fashing, 2022).

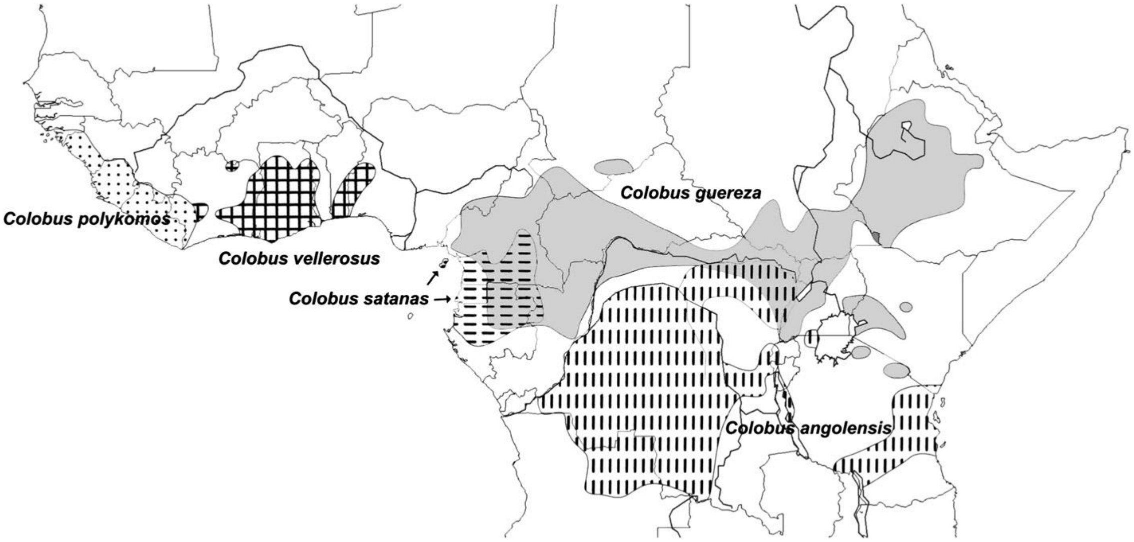


Figure 3. The geographic distribution of African black and white colobus species (Source: Grubb *et al*., 2003).

Arboreal African monkeys known as the black-and-white colobus (*Colobus guereza* Rüppell, 1835) inhabit much of sub-Saharan Africa's deciduous and evergreen forests (Zinner *et al*., 2019; Dereje Tesfaye *et al*., 2021; Fig. 4). There are eight subspecies found within this species. *C. guereza's* first divergence occurred at 0.7 Ma, with lineages like *C. g. occidentalis*, *gallarum*, and *matschiei* splitting from other. These separated at 0.6 Ma and 0.5 Ma in order (Zinner *et al*., 2019). The phylogenetic connections of *Colobus caudatus* with another *Colobus* should be examined because of its recent elevation from the old subspecies level of *C. g. caudatus*.

Previously, eight subspecies of *C. guereza* were identified (*C. g. occidentalis*, *C. g. gallarum*, *C. g. matschiei*, *C. g. caudatus*, *C. g. guereza*, *C. g. dodingae*, *C. g. kikuyuensis*, and *C. g. percivali*) (Mittermeier *et al*., 2013). However, Butynski and De Jong (2018) recently suggested that *C. g. caudatus* warrants elevation to species level as *C. caudatus* due to its geographic isolation and phenotypic distinctiveness (Fashing, 2022). Awaiting a full taxonomic review of *C. guereza*, the researcher here follows Hollister (1924) and Butynski and De Jong (2022c) by treating *Colobus guereza poliurus* as a subspecies that needs assessment.

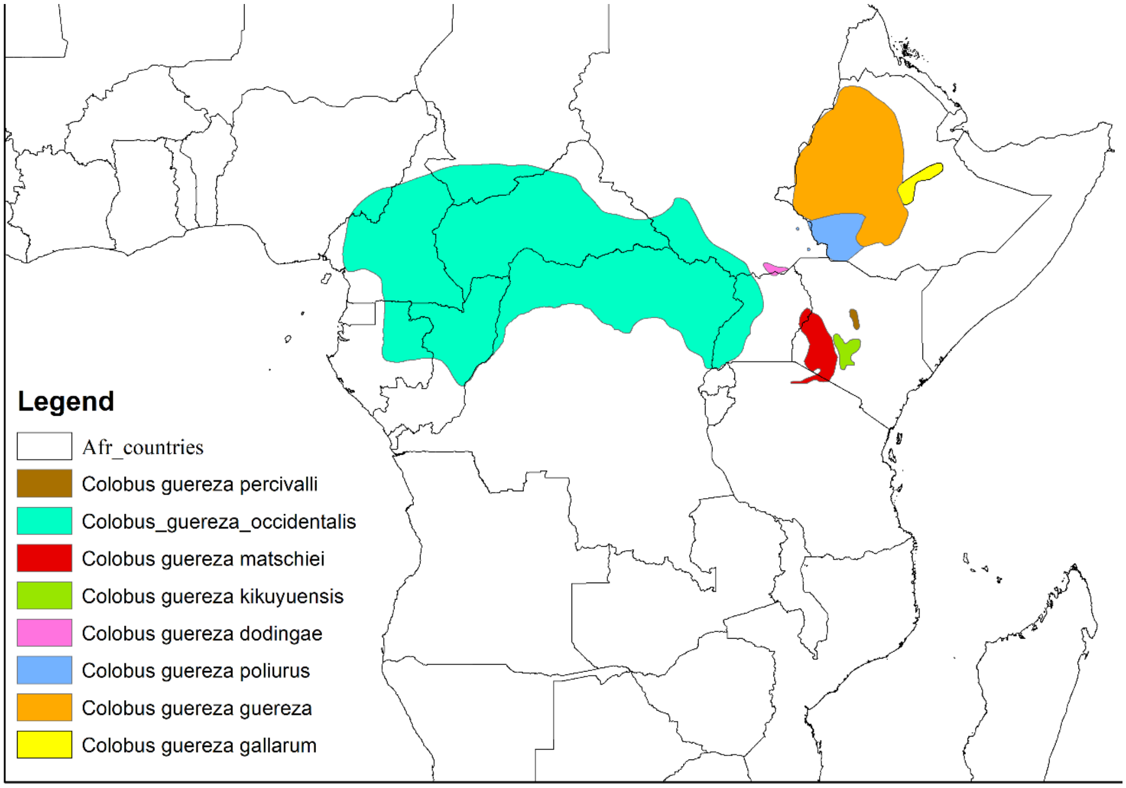


Figure 4. Current phylogeographic distribution of *Colobus gguereza* along the forest belt of Equatorial Africa (Source: Butynski and De Jong, 2022c).

Ethiopia has two endemic black-and-white colobus subspecies (Fig. 5), *C. g. gallarum* and *C. g. guereza*. *Colobus g. gallarum* is found in fragmented Ahmar Mountains forests, while *C. g. guereza* is found in both western and eastern part of the Great Rift Valley. The validity of Ethiopian taxa is debated, and morphological differences are attributed to clinal variation within *C. g. guereza*. A study using mitochondrial DNA markers and orthologous sequence information found two major Ethiopian mitochondrial clades, one congruent with *C. g. gallarum* distribution and the other clustering with *C. g. caudatus* and *C. g. kikuyuensis* from Kenya and northern Tanzania (Zinner *et al*., 2019). Zinner and his colleagues in their study supports the two-taxa hypothesis, making *C. g. gallarum* an Ethiopian endemic and one of the most endangered subspecies of black-and-white colobus. However, its geographic range is poorly known due to a lack of field surveys and uncertainties about its taxonomy.

Figure 5. Illustration of two endemic *Colobus* taxa in Ethiopia. LC is represented for Least concern whereas DD is representing Data Deficient (Source: Butynski and De Jong, 2022c).

2.3.2. Factors affecting the distribution of colobine monkeys

Biogeography focuses on species distribution, which include locations of occurrence, population dynamics, and biodiversity patterns. Factors affecting this distribution include climatic conditions, barriers, island formation, range size, boundaries and shifting abundance patterns. Species grow under suitable environmental conditions and avoid areas lacking essential resources (Darwin, 1859; Brown and Lomolino, 1998). Primates are primarily found in tropical forests. There are factors influencing the ranging patterns of these primates including geographical area, latitude, climatic change, vegetation cover, and anthropogenic factors. Biogeographic regions have distinct fauna, climate, soil, vegetation composition, and animal association (Fleagle, 1998). African colobines distribution patterns are affected by various issues, including climate, vegetation, and anthropogenic activities. Overall, the African colobines' geographic ranging patterns are shaped by the synergistic effects of the previously listed factors. Therefore, novel strategies should be planned to address these factors to protect and preserve the habitats necessary for the survival of these primate species.

Earth's dynamic nature is influenced by the movement of individual plates, including divergent, convergent, and transform plates, which impact animal migration routes. Land-bridge connections between continents, which can act as corridors or filters, vary in their ecological conditions and are often discontinuous, affecting the temporal similarity of fauna (Tarling, 1982; Brown and Lomolino, 1998; Fleagle, 1998). Southeast Asian rivers have served as barriers for arboreal primates since the early Miocene. *Semnopithecus* invaded India, *Presbytis* and *Trachypithecus* migrated to southern mainland Asia, odd-nosed monkeys expanded into Indochina and Sundaland, and *Nasalis* and *Simias* diverged in the Pleistocene (Miller *et al*., 2005).

Continental drift or plate tectonics are the major factors that affect the prolonged organisms' distributional patterns that result from sluggish alterations of the global topography (Cox and Moore, 1993, 2005). This has had profound impacts on the biogeographical pattern of biota. Such a scheme explains the origin and destruction of the earth's plates as well as their lateral movement or drift. The biogeographic impacts of tectonic events include altered opportunities for biotic exchange and climate change on regional and global scales due to the collision, separation, or destruction of continents or oceanic basins (Brown and Lomolino, 1998).

Large areas have more geographic barriers and a wider variety of habitats, which increases species diversity from a biogeographic perspective. Accordingly, the tropical forest cover has a significant impact on primate species on large islands and major continental areas (Fleagle, 1998). Of the 522 known extant primate species that are found in 90 countries, 65% are found in Madagascar, Brazil, the Democratic Republic of the Congo, and Indonesia (Estrada *et al*., 2017; Estrada *et al*., 2018). These species are abundant in tropical regions because of their long history of occupation, a higher number and rate of speciation events, and more dispersal events to other regions (Sterck, 2012; Wich and Marshall, 2016).

Climate changes, including global warming and El Niño intensification, could impact primate populations, but little is known about the quantity and distribution patterns of food resources, dispersal abilities and interactions (Wiederholt and Post, 2010; Wich and Marshall, 2016). Ten percent greater warming than the world average is predicted for primates, with restricted regional distribution features being most affected (Pearson *et al*., 2014; Sesink *et al*., 2015; Estrada *et al*., 2017). Many species will vary their range in response to climate change (Schloss *et al*., 2012), change their dispersion patterns as a result of forest fragmentation (Gouveia *et al*., 2016), and become more susceptible to effects from humans such as hunting (Araújo *et al*., 2004).

In Africa, high primates' diversity exhibits possibly due to increased productivity, solar radiation and long-term species evolution. Factors related to climate and ecology affect primate distribution. These species have smaller geographic ranges and are more generalists with wider habitat tolerances (Fleagle, 1998). Primates and plants are more impacted by seasonal rainfall than by day length or temperature (Fleagle, 1998). Rainfall is closely correlated with species diversity in various regions. Diversity in primate species may represent diversity in plant foods, which in turn reflects productivity in forests. Productivity has a curvilinear connection with rainfall, driving both species diversity and productivity (Fleagle, 1998).

African colobines distribution are significantly influenced by climate change (Butynski and De Jong, 2022a). The abundance of food supplies and overall suitability of the habitat are influenced by variables including temperature, rainfall patterns, and seasonality. Different species have varying tolerances to specific climatic conditions. As primary extrinsic factors climate and soils as well, plants are secondary factors contributing to the structure of primate communities, in turn influences the species distribution. The distribution of African colobines is closely tied to the availability of suitable vegetation and habitat types (Butynski *et al*., 2013). Different species have specific preferences for certain forest types, woodlands, or savannas. For example, *Colobus guereza* is often associated with dense tropical rainforests, where they feed on leaves, fruits, and other plant parts. They are adapted to montane forests, which provide a unique habitat with specific vegetation types and ecological conditions.

Understanding the impact of anthropogenic activities on African colobines is crucial for conservation efforts. Efforts should focus on mitigating deforestation, promoting sustainable land-use practices, and implementing effective anti-poaching measures. Anthropocene Era has led to the near-term extinction of more than half of the global primates due to habitat loss caused by agriculture, logging and livestock farming as well as hunting, trapping, infrastructural development, pollution, and climate change. Colobine monkeys, particularly black and white colobus monkeys, are significantly impacted by habitat loss due to farmland expansion, logging, and settlement, particularly in East Africa (Kingdon *et al*., 2008; Dela, 2011; Liu *et al*., 2015; Ruiz-Lopez *et al*., 2016; Wich and Marshall, 2016; Estrada *et al*., 2017; Estrada *et al*., 2018). The extraction of products also contributes to the loss of habitats. These factors are growing issues for tropical ecosystems and the primates they inhabit, affecting their distribution and survival (Meijaard and Nijman, 2000). The effects vary across regions, with habitat loss and fragmentation being the principal global threats, but also hunting is the primary threat (Wasserman and Chapman, 2003; Estrada *et al*., 2017; Fuentes and Baynes-Rock, 2017; Estrada *et al*., 2018). Anthropogenic activities contribute to restricting the available range for these primates. Some specific factors include deforestation (i.e., clearing of forests for agriculture, logging, or infrastructure development) reduces the suitable habitat for colobines, leading to population decline. Habitat fragmentation can isolate colobine populations, restricting their movement, gene flow and access to resources.

Illegal hunting and trade for subsistence, medicine, pets, and bushmeat are increasing, contributing to biodiversity loss in Africa and to primate population reduction (Fichtel, 2012; Estrada *et al*., 2017; Estrada *et al*., 2018). Target hunting for bushmeat or the pet trade poses a significant threat to colobine populations (Mittermeier, 1973; Dunbar and Dunbar, 1975). Colobine monkeys are vulnerable due to their large bodies and loud calls (Dela, 2011). Illegal, unsustainable trade intensifies the need for consumption, biomedical research, wildlife collection, and traditional medicine (Alves *et al*., 2010; Nijman *et al*., *2*011).

The effects of predation on primate evolution are not well understood (Zuberbuhler and Jenny, 2002). More studies are needed to understand the ecological and evolutionary consequences of predation on primate distribution (Isbell, 1992; Fichtel, 2012; Sterck, 2012). Predators include carnivores, birds, and reptiles. Variations in predator geographic distribution and prey size could influence attacks on primates. Parasites and pathogens have unintended consequences for primate ecology, evolution, population growth, and biodiversity. Degraded or disturbed forests, habitat overlap, coexistence between humans and wild primates, expanded ecotourism and forest encroachment lead to high-risk interfaces for parasite and pathogen infestation (Wolfe *et al*., 1998; Schaumburg *et al*., 2012). This might be due to their close phylogenetic relationships and geographical proximity to humans (Davies and Pedersen, 2008; Calvignac-Spencer *et al*., 2012; Cooper and Nunn, 2013). Gillespie *et al*. (2005) reported that anthropogenic habitat changes affect parasite infection patterns in primates, with a greater prevalence in fragmented forests and a greater risk in fragmented areas. Nutritional stress also increases parasite prevalence in fragmented forests (Chapman *et al*., 2006).

2.3.3. Distribution and environmental suitability

Understanding environmental variables that can impact how species spread and forecast how the global biota will react to disturbances, climate change, and other factors is crucial for the use of species distribution models, or SDMs (Guisan *et al*., 2017). These models assess taxon habitat suitability, identifying ecological requirements, and determining suitable environmental conditions, which is crucial for wildlife management and conservation policy formulation (Smeraldo *et al*., 2021; Su *et al*., 2021). Thus, choosing priority conservation sites and devising successful management strategies mainly depend on reliable data on species distribution and environmental stress (Addisu Mekonnen *et al*., 2020).

Many threatened species have lost their geographical ranges are now restricted to tiny and fragmented forest areas (Nüchel *et al*., 2018). These distribution patterns are determined by landscape fragmentation and modification (Rondinini *et al*., 2011; Newbold *et al*., 2015; Galán-Acedo *et al*., 2018), ecoregions (Olson *et al*., 2001), climate changes (Zhao *et al*., 2019; Préau *et al*., 2020; Gusmão *et al*., 2021), biotic factors (Araújo and Luoto, 2007), topographic attributes (Singh *et al*., 2018), and human disturbances (Mangiacotti *et al*., 2013; Singh *et al*., 2018). These factors affect the ecological requirements of the species in their natural habitats, which in turn limit their distribution and survival and may ultimately lead to extinction, either local or global. The distribution patterns of primates are described by many parameters, including geographical or continental region, latitude, climate and vegetation cover, as well as anthropogenic causes. Even though primates live in tropical regions, there are considerable variances in forest habitats within and across these areas. Climate and seasonality, geology and soil, floristic composition and animals living close to primates all change as a result of these variations (Fleagle and Gilbert, 2006).

Since the 20th century, ecologists have explained and understood species distribution at various spatial-temporal scales. The predictive distribution model has applications in diverse fields of study (Zurell *et al*., 2020). It is commonly applied to predict species ranges under changing climate conditions as predictors or to associate species occurrence with environmental variables. Moreover, describing what environmental conditions are suitable for a species and then identifying where they are distributed in space are also answered through a predictive model. As an active area of research, modelling species distribution patterns is central to understanding the world's biota's reaction to disturbances and climate change (Guisan *et al*., 2017). Understanding species distribution drivers is crucial for modeling associations between biological individuals and environmental conditions. Utilizing detailed data and powerful computers, predictive modeling of species' environmental requirements and geographic distributions has increased (Phillips *et al*., 2006).

An organism can only survive in its ecological niche if certain requirements are met (Hending *et al*., 2023). As one of these conditions, global climate change is a significant problem to biodiversity (Thapa *et al*., 2022). Its effects have intensified in the Anthropocene when coupled with anthropic land cover modification (Auffret and Svenning, 2022). As a result, species distributional shifts, contractions and expansions are triggered (Pinto *et al*., 2023).

Primate taxa with significant ecological and anthropological relevance, live in fragmented habitats. With respect to the majority of primate taxa modelled thus far, significant suitable habitat reductions are predicted to occur by 2100 under projected climate change (Winder *et al*., 2023). In particular, many Atlantic Forest primates in tropical forest hotspots will lose a climatically suitable geographical range, undergo a latitudinal shift to the south in the 2100s under the worst-case (SSP5-8.5) scenario (Pinto *et al*., 2023), and will reshuffle within its range (Antao *et al*., 2022). For example, climate refugia for *Saguinus leucopus* and *S. oedipus* primates are critically underprotected (Arias-González *et al*., 2021). The suitable range size of *C. g. gallarum* is more limited under current climate conditions; and the *Pygathrix cinerea* range has shrunk in the future (Vu *et al*., 2020). Range shifts may have also resulted in the isolation of suitable habitats, affecting gene flow among *Papio* populations (Desalegn Chala *et al*., 2019).

Information on species taxonomy and biogeography can be obtained from a comprehensive considerate of an organism's ecological niche (Hending *et al*., 2023). This information is extensively used concepts in ecology, evolution and conservation (Merow *et al*., 2019). The estimated species' niches and the distribution of suitable habitats are used to aid conservation decisions and study niche evolution. The optimal conditions for a given species are used for conservation (Kling *et al*., 2020) and to prioritize areas to protect the species (Wiens *et al*., 2011). One can assume that, as a result of taxonomic divergence, niche of inherently related but geographically isolated species can be different, in contrast to niche differences that favour species coexistence. McDonald *et al*. (2019) reported that *C. angolensis sharpei* and *C. a. palliatus* in Kenya and Tanzania have only 1.2% overlap, indicating distinct niches. Similarly, the niche divergence between the specific species remained high (range: under current (0.170–0.310) and Last Glacial Maximum (LGM, 0.00–0.228) conditions), signifying only a small intersection of suitable habitats between baboons (genus *Papio*) (Desalegn Chala *et al*., 2019). The study suggests that habitat shifts may have caused population isolation and reconnection, potentially impacting gene flow among them.

Ecological niche modelling is now widely used for predicting species niches and for estimating and understanding the connections between a species' distribution and its surroundings (McDonald *et al*., 2019); however, this approach requires robust estimations of model performance and significance (Bohl *et al*., 2019). Ecological niche models aid researchers in studying species coexistence, determining habitat requirements and mapping distributions, while also aiding conservationists in assessing threats (Hending *et al*., 2023). Demography, taxonomy, and species conservation studies are enhanced by their ability to evaluate species protection and their vulnerability to anthropogenic pressures (Elith *et al*., 2006; Thorn *et al*., 2009). Thus, ecological niche models offer insights into the species potential geographic range, niche divergence between parapatric and sympatric species, closely related taxa as well as integrated taxonomy.

2.4. Abundance and associated factors of African colobines

2.4.1. Population ecology

Understanding population abundance is crucial for conservation because it provides a scientific basis for decision-making, prioritizes conservation efforts and supports species and ecosystem survival. Understanding population sizes could be critical in wildlife ecology. Estimates of animal density and abundance are used to monitor the status of a range of species as well as devise management strategies for particular ecosystems and/or populations (Marques, 2001). This reliable information is necessary to sustainably manage and conserve wildlife (Buckland *et al*., 2015) and its success depends on proper wildlife population assessment (Ogutu *et al*., 2006).

Accurate species abundance is crucial for wildlife studies, primate conservation, and management (Hassel-Finnegan *et al*., 2008). Surveying primates over time helps monitor trends, design conservation plans, and determine threatened species status. Appropriate methods are essential for assessing population sizes and carrying capacity (Chiarello and De Melo, 2001). Ecologists have developed a variety of ways to determine the number and density of primates (NRC, 1981; Peres, 1999). The density of primates can be estimated using methods such as census techniques, home range analysis, nesting or resting structure, individual recognition, counting calls, feeding signs and line transect surveys (Krebs, 2006). Ecological determinants include food quantity, habitat diversity, parasites and diseases, predators, forest type, rainfall, elevation and latitude. Line-transect sampling technique has been widely employed to assess the densities of diurnal arboreal primates in tropical forests (Ogutu *et al*., 2006; Buckland *et al*., 2010; Höing *et al*., 2013; Leca *et al*., 2013). It is well-thought-out fairly simple, fast, and cost-effective in terms of accurateness and precision, in addition to generating systematic data quickly (Peres, 1999). Research shows that guereza populations reached high densities in small East African forest fragments (Dunbar, 1987), suggesting that they are well adapted to disturbed forests (Fashing, 2011). However, colobus monkey population in Ethiopia is declining due to forest clearance, despite the traditional belief that guerezas are adapted to habitat degradation.

2.4.2. Abundance–suitability relationship

Understanding how population dynamics and environmental factors affect species distribution and abundance is essential in ecology and biogeography (Brown, 1984). Many authors have proposed using abundance data to confirm the relevancy of distribution models since they have identified the association between ecological suitability estimated from presence-only data and local abundance (VanDerWal *et al*., 2009; Fuente *et al*., 2021; He and Gaston, 2007). However, this assumption is far from generalization and further studies need to be conducted.

Environmental and ecological factors significantly impact a species' capacity to maintain in a specific habitat. Local abundance might serve as an indicator of how well the local circumstances fit the species, with more suitable places holding more populations of the species (Brown, 1984; Holt, 2009). The distribution of species is not uniform, with low abundance in less suitable locations and high abundance in preferred habitats. Although the abundance-suitability relationship may have implications (Fuente *et al*., 2021), little study has been done on its prediction ability and so the extent of its impact remains unclear.

Thoughtful association between species and their surroundings may be crucial for anticipating biological incursions (Kulhanek *et al*., 2011) or responses of species to changing climate (VanDerWal *et al*., 2009). However, predicting abundance from species distribution is still an open issue (He and Gaston, 2007), especially in regard to primates. Relationships may be inferred from the density of individuals in a certain location (abundance) and the extent of their spatial distribution (range).

Using occurrence data to evaluate habitat suitability against environmental factors, ENMs or SDMs are used to predict species distribution (Hijmans and Graham, 2006). Population demography serves as the fundamental process determining the occurrence of a species (Thuiller *et al*., 2014). In this sense, populations should thus be high in locations with better environmental adaptability and vice versa. The abundance-suitability connection postulates that the regional variation in the abundance of a species should be explained by environmental suitability, which is obtained from ecological niche models (Weber *et al*., 2017). Although points to as potential generalization (Weber *et al*., 2017), the prevalence of this relationship is called into question by a number of studies that did not find an effect (Dallas and Hastings, 2018).

Some studies found weak relationships between abundance and suitability (Nielsen *et al*., 2005; Estrada and Arroyo, 2012; Martínez-Meyer *et al*., 2013; Weber *et al*., 2017; Dallas and Hastings, 2018). The suitability of habitat for a particular specie may depend on a number of factors, including species interactions (Braz *et al*., 2020), the presence of ecologically relevant occurrences and species detectability (Jiménez-Valverde, 2011). Therefore, the link between ecological suitability and the upper bounds of abundance might be useful in drawing conclusions on a large regional scale without requiring the determination of abundance everywhere. Based on ecological niche models, population abundance may be precisely predicted at a fine scale in relation to environmental suitability (Jiménez-Valverde *et al*., 2021).

2.5. Habitat ecology

In ecological research, habitat analysis is essential for comprehending the relationships, interactions, and population dynamics of species (Veech, 2021). The long-term survival of colobus monkeys, which are arboreal primates found in sub-Saharan Africa, depends on safeguarding their forest habitats, promoting sustainable land use and combating illegal hunting and pet trade. Their particular food, social structure and behavioural adaptations are intimately associated with the ecology of their habitat. According to Veech (2021), habitat refers to the physical environmental factors that a species is associated with, omitting predators, climate and food supplies. When comparing the impacts of habitat with other variables that may affect species distribution and abundance, such as food supplies, predators, climate and illness, this term is used in habitat analysis. Tropical rainforests, montane and gallery forests, and riverine forests are home to colobus monkeys. For safety and sustenance, they favour thick, closed-canopy trees.

Understanding the responses of biodiversity to human modification of landscape structure has been challenging (Garmendia *et al.*, 2013). This modification forces numerous animals to occupy forests, which impend their existence and reproductive success (Arroyo-Rodriguez *et al.*, 2013). Species-specific future conservation and management plans will depend on studies of animals in modified landscapes. This alteration of landscape structure can lead to habitat fragmentation, which can have negative impacts on biodiversity. Fragmented habitats can limit the movement and dispersal of species, disrupt ecological processes and increase the risk of local extinctions. Additionally, altered landscapes may also result in changes in resource availability and competition dynamics among species, further affecting their ability to survive and reproduce. Future conservation and management strategies for individual species will be based on research conducted on animals living in altered landscapes. These disruptions to the habitat have an impact on monkeys' responses, including species richness, abundance and dispersion. The biological needs of arboreal monkeys, who depend on trees and forest patches for habitat, food, cover, shelter and territory, mean that the consequences of rainforest fragmentation on these species are diverse (Anzures-Dadda and Manson, 2007).

Due to deforestation for agriculture and human settlements, the habitat of colobus monkeys is being lost or fragmented. This causes the monkeys to become isolated, interrupt their migration, and have less gene flow, which puts many species at risk of extinction. The clearance of agricultural forests (Kingdon *et al.*, 2008), farmland expansion, and settlement are the main observed threats to colobus monkeys (Israel Petros *et al.*, 2018a). For instance, a loss of canopy cover due to habitat destruction is the most significant threat in human-modified environments (Dela, 2011). These threats were shown to be experiencing population declines, population restructuring, and eroding the gene variety (Ruiz-Lopez *et al.*, 2016).

The main factors affecting a species survival are the size of its habitat, the size of its home range and diets, the distance between patches and the kind of environment in which the habitat fragments are rooted. According to Estrada *et al*. (2017), prolonged tropical deforestation causes forest fragmentation, which increases the risk of extinction in nearby populations. As a result, the ecological and behavioural resistance of monkeys to habitat disruptions varies. Due to the degradation of tropical forests, studies on primates' response towards shift in climate change is increasingly important (Barelli *et al.*, 2015).

2.6. Subspecies concept and conservation

During the past three decades, primatologists have identified a greater number of primates which is grown significantly, from approximately 200 in the 1990s to 522 in 2023, adding an estimated 182 subspecies (IUCN, 2023). In the fields of taxonomy and conservation biology, subspecies are common units of biological structures (Braby *et al.*, 2012). The subspecies concept, initially intended to document geographic diversity, has faced challenges such as conceptual inconsistencies, objective standards and inaccurate representations of distinct evolutionary units. Groves (2016) defined subspecies as geographic divisions of a species that have different average sizes, gene frequencies, or colour variations. These divisions are frequently given trinomial scientific names.

One pressing issue is the utility of subspecies for the reason that the taxonomical position of numerous categories is debatable and unpredictable among experts. The reviews of systematic and conservation issues related to subspecies in mammals have been extensive (Stanford, 2001; Gippoliti and Amori, 2007). The review by Gippoliti and Amori (2007) highlights the bias in scientific and political communities regarding the taxonomy of living organisms, particularly subspecies and the insufficient scientific scrutiny of their inclusion in conservation lists, particularly in the Mammalia class, resulting in a biased view of mammalian endangerment. Similarly, Standford (2001) reviews the application of subspecies in primatology, focusing on the critically endangered mountain gorilla, *Gorilla gorilla beringei*, advocates for a cautious approach to subspecies conservation management policies for endangered primate populations.

The species concept in biodiversity science is evolving to recognize the heterogeneity in classification. Cryptic species, which are underrepresented in ecological and evolutionary theory tests (Fišer *et al*., 2018) have posed a taxonomic challenge for nearly 300 years. They are highly similar and could influence future conservation decisions (Bickford *et al*., 2007). Inconsistency in descriptions and classifications makes understanding their coevolutionary relevance difficult (Struck and Cerca, 2019). In colobines, cryptic species result from their morphological colorations (Yeager and Kirkpatrick, 1998; Groves, 2007; Nokelainen *et al*., 2024) and vocalizations (Clarke, 1990). The closely related parapatric taxa of Ethiopia's guereza, particularly between Omo River guereza and Djaffa Mountains guereza, use black and white pelage as visual coloration, making the conservation of the taxa more difficult.

Scientists struggle with defining subspecies concepts and criteria, which impacts resource optimization for management and protection (Stanford, 2001; Gippoliti and Amori, 2007). For reasons related to the ecological, economic, scientific, and cultural roles, primate taxonomy is important to focus on conservation efforts (Wich and Marshall, 2016). Thus, conservation is a viable endeavour, despite population declines due to environmental and human factors. Immediate action is needed to prevent primate extinction (Estrada *et al*., 2017).

3. METHODOLOGY

3.1. Study area

3.1.1. Location of the study sites

This present study on the distribution, ecology as well as abundance of *C. g. gallarum* was conducted in the Ahmar Mountains, a mountain range of the Ethiopian Highlands southeast of the Rift Valley in Oromia Region. It is an extended highland from the eastern Arsi Mountains to Jigjiga city in Somali Regional State, flanked between 8°30'–10°00'N latitude and 40°00'–42°30' E longitude (Fig. 6). These highlands slope slightly to the southeastern lowlands, further extending to Indian Ocean (Friis *et al*., 2010). The study area is located within Eastern Afromontane Biodiversity hotspots. This chain of the study area was based on geographic range drawn by Zinner *et al*. (2019) and IUCN for *C. g. gallarum*. The total geographic extent considered in this study was 75,307.49 km^2.

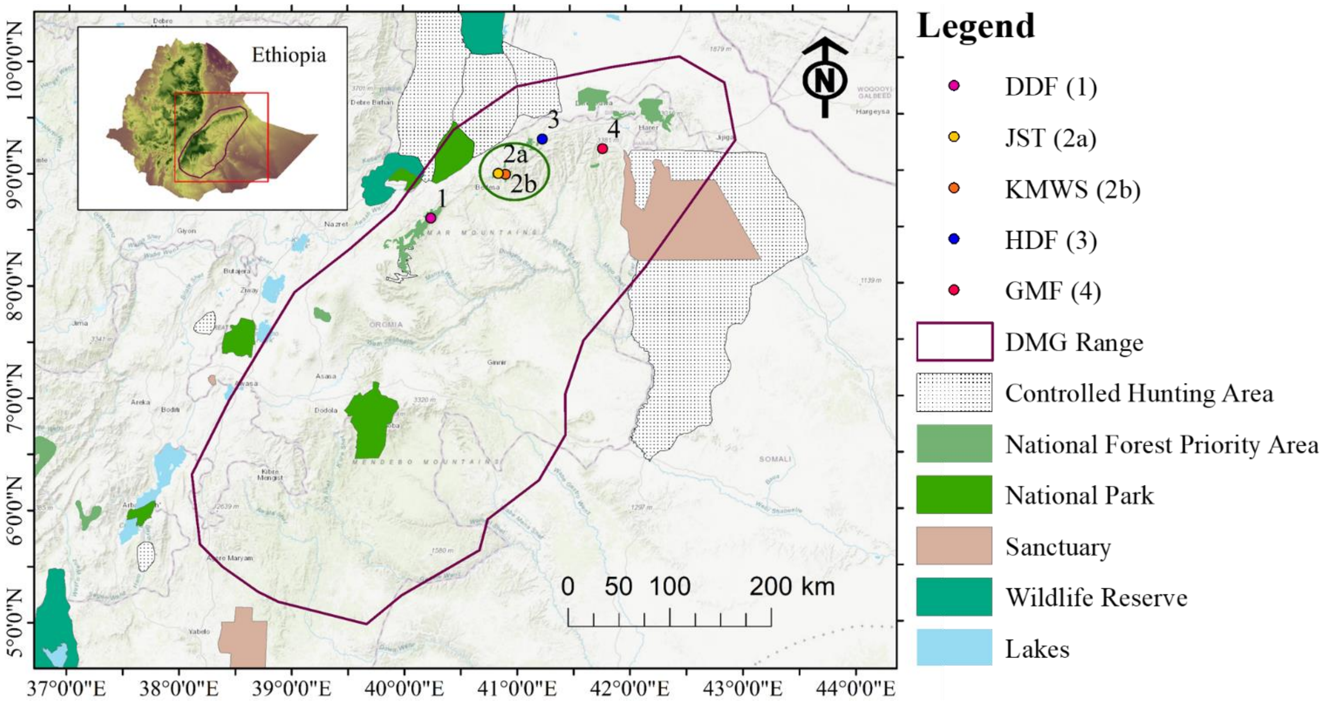


Figure 6. Geographic position of the Ahmar Mountains, Ethiopia and locations of the four forest sites where we did the line transect surveys on the *C. g. gallarum*.

3.1.2. Topography and geomorphology

The topography of the Ahmar Mountains is characterized by grasslands, rugged divided massifs, plateaus, deep gorges, and sloppy hillsides (Tahir Abdala *et al*., 2017). Some of the topographic views of the forests where this study was conducted are given in Plate 1. Geologically, it is characterized by Mesozoic rocks consisting of sandstone, limestone deposits, gypsum, and related rocks (Friis *et al*., 2010). From the perspective of hydrology, the study area is found at the junction between the two major drainage systems of Ethiopia, namely the south-eastern and Rift Valleys. Southeastern Ethiopia's physiographic region is drained by two basins, Wabi Shebelle and Genale, which cross the border into Somalia (Billi *et al*., 2015). The largest river, Wabi Shebelle, drains parts of Oromia, Harari, and Somali regions.

A. Dindin Forest

B. Kuni-Muktar Wildlife Sanctuary

C. Gara Muleta Forest

D. Hades Forest

Plate 1. Topographic views of the study locations where the populations of *C. g. gallarum* were surveyed (Photo by: Chala Adugna, 2021).

3.1.3. Climate

The climate of this area obtains a bimodal rainfall distribution, per a small raining period from February to May, large rains from July to September, and dry periods between October and January. The 30-year (1989–2019) period climate data shows slight variation in the annual precipitation across the surveyed sites (Fig. 7a–d). Averaged annual precipitation of surveyed sites over thirty years (1989–2019) ranges from 957–1007 mm. The mean annual temperatures for each site vary between 18.8 and 21.8°C.

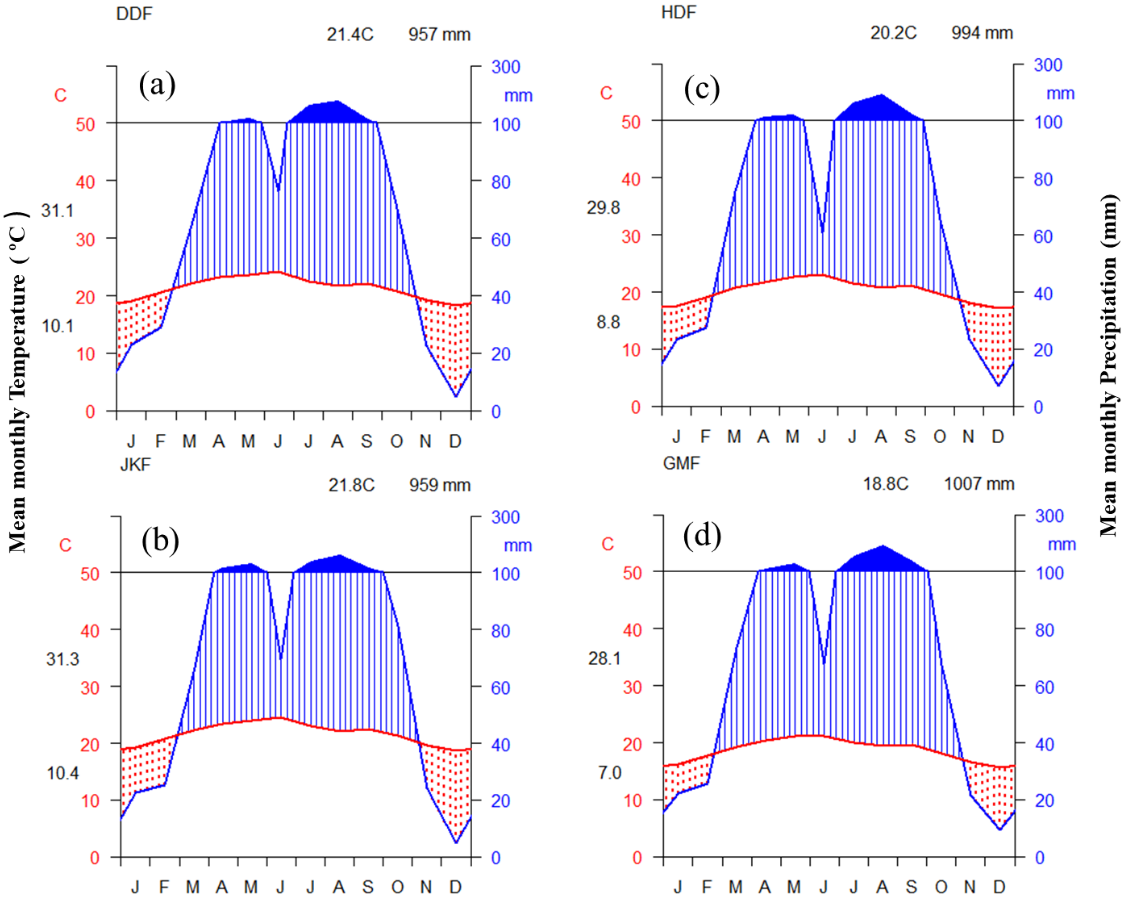


Figure 7. Climate data of the four study sites, Dindin Forest (DDF), Hades Forest (HDF), Gara Muleta Forest (GMF), Jallo Kuni Forest (JKF) in the Ahmar Mountains, Ethiopia, from 1989-2019.

These climate diagrams include monthly mean temperature and precipitation. We downloaded the climate data from the Centre for Environmental Data Analysis (CEDA) datasets of the Climate Research Unit (Source: UEA-CRU; Harris *et al*., 2020).

3.1.4. Vegetation

The Ahmar Mountains, unfortunately, are the most degraded with limited forest coverage. A forested area in the Hararghe highland reflects the trees that once covered most of southeastern Ethiopia's highland. Most of these highlands landscape are roofed by the dry evergreen Afromontane forest and grassland complex vegetation type (Mengesha Asefa *et al*., 2020), and it is also dominated in the range of the Ahmar Mountains (Friis *et al*., 2010). Due to deforestation, most of the highlands have recently been covered by wooded grasslands, where secondary tree species have replaced (Badege Bishaw, 2001). Originally, dry evergreen Afromontane Forest dominated the region (Badege Bishaw, 2001; Friis *et al*., 2010). However, most parts of the Ahmar Mountains are now covered by wooded grasslands, with stands of tree species which is exotic like *Eucalyptus* and bushland (Friis *et al*., 2010). The remaining forests in the region are often fragmented and degraded due to unsustainable use and persistent drought (Tahir Abdala *et al*., 2017).

Four selected forests were surveyed (Fig. 6; Table 1 and 2). These forests have been managed at the regional level by the OFWE, which is promoting a participatory forest management approach in order to conserve and protect of the natural forests of the area. As a restoration practice, *Croton macrostachyus, Cupressus lusitanica, Hagenia abyssinicus and Juniperus procera* have been planted by the OFWE in collaboration with the local community.

Dindin Forest (DDF) is a large, continuous forest that forms part of the watershed between the Awash and Wabe Shebelle catchments. It is one of the remnants of the natural forests, marking a large continuous forest in the eastern part of the country (Simon Shibru and Gizachew Balcha, 2004). The dominant woody vegetation found in the forest includes *J. procera*, *Olinia rochetiana*, *Maytenus addat*, *Podocarpus falcatus*, *Myrsine africana*, *Olea europaea*, *M. undata*, *Maesa lanceolata*, *M. melanophloeos* and

Schefflera volkensii (Simon Shibru and Gizachew Balcha, 2004). The conservation threats that need serious attention include agricultural expansion, livestock grazing, tree harvesting for beehive production and logging for timber production as input for the sawmill established at the eastern part of the Dindin Forest (Plate 2).

Plate 2. Images of the features and timber production of the Dindin Forest (Photo by: Chala Adugna, 2021).

Jallo-Kuni Forest (JKF) is a concession-controlled hunting area that comprises two fragmented forests, the Jallo Sorroro Torgam (JST) and the Kuni Muktar Wildlife Sanctuary (KMWS). The Kuni-Muktar Mountain Nyala Sanctuary was established in 1989 by the Zoological Society of London to protects the critically endangered Mountain nyala population. However, in 2000 the site was designated as controlled hunting area and represented as Sororo-Torgam-Gara-Muktar, which is administered by OFWE (UNEP-WCMC and IUCN, 2023). The areal distance between the two forests is about 3.35 km obtained from Google Earth Online. The concession area is represented by woody tree species such as *M. lanceolata, J. procera, C. macrostachyus, Rhus glutinosa* and *Acacia abyssinicus* (Muktar Reshad *et al*., 2020). Some of the conservation threats found in this concession area are grazing and deforestation for agricultural expansion along the sloppy areas of the mountains (Plate 3).

Plate 3. Livestock grazing and deforestation for agricultural expansion are two threatening factors of *C. g. gallarum* and its habitat in JKF (Photo by: Chala Adugna, 2021).

Hades Forest (HDF) consists mainly of dry Afromontane Forest, comprising 40–48 woody species (Demel Teketay, 1997; Dereje Atomsa and Duguma Dibbisa, 2019). The dominant species of trees are *Prunus africana*, *Schefflera abyssinica*, *A. gracilior*, *H. abyssinica* and *C. macrostachyus*. Crop, grasslands as well as coffee agroforestry are intensified in this site. Thus, degradation is the continuous disturbance challenge of this forest.

Gara Muleta Forest (GMF) harbours a diverse flora, with about 361 vascular plants that include 45 (13%) endemics to Ethiopia (Demel Teketay, 1996). A multi-story mixed deciduous woodland dominated by *O. hochstetteri*, *Ekebergia capensis* and *P. africana* related to intermediate and lower-story species that include *Bersama abyssinica*, *C. macrostachyus*, *Dioscorea schimperiana*, *Erythrina brucei*, *H. abyssinica*, *Nuxia congesta*, *O. africana* and *S. abyssinica* covered southern side of GM Mts (Demel Teketay, 1996). Based on the intact forest canopy availability and inaccessibility of the whole area, this study only focused on the southern side of the mountains. The vegetation of Gara Muleta on the southern side is more diverse than on the northern side (Demel Teketay, 1996). One of the landscape features of this area is indicated in Plate 4.

Plate 4. Picture of southern part of Gara Muleta mountain dominated by *P. africana* tree, where *C. g. gallarum* was surveyed (Photo by: Chala Adugna, 2021).

3.2. METHODS

3.2.1. Preliminary study

Between December 2019 and January 2020, a preliminary survey was carried out in the Ahmar Mountains to map out the forest fragments and validate the existence of *C. g. gallarum* in the forests. Only five accessible forest fragments that contained the study subjects were chosen from a variety of forest patches based on some of their ecological differences. The locations of the transects, the topography of the selected forest patches, and the sites' accessibility were all investigated during the reconnaissance study.

3.2.2. Abundance and density estimates

As with all *Colobus guereza* subspecies, *C. g. gallarum* is highly arboreal and forest is the general type of habitat for this subspecies (Plate 5). Therefore, four forests were selected and surveyed (Fig. 8), where *C. g. gallarum* was reported (Zinner *et al*., 2019) and where their presence was confirmed in a pilot study (unpublished data). The four forests differ slightly in their ecology (Table 1).

Plate 5. Some pictures of *C. g. gallarum* captured during field surveys within the four forests (Photo by: Chala Adugna, 2021).

Table 1. Ecologies of the selected forests in the Ahmar Mountains, (geographic coordinates in decimal degrees; elevation in m asl; size in km^2; mean (± SD) annual precipitation in mm; mean (± SD) annual temperature in °C.

Name of site	Lat	Long	Elevation	Size (km^2)	Veg.	Prec.	Temp.	Legal status*
DDF	8.61581	40.26009	1980–3070	83	LCF	957 ± 130	21.4 ± 0.37	NFPA, CHA
JST	9.01547	40.85807	1945–3025	48.3	SCF	836 ± 116	23.3 ± 0.37	NFPA
KMWS	8.98885	40.92519	2165–2950	16.8	SCF	959 ± 147	21.8 ± 0.36	CHA, WS
HDF	9.31768	41.24319	2050–2750	6	LSF	994 ± 144	20.2 ± 0.36	NFPA
GMF	9.25486	41.75294	2450–3370	29	SCF	1007 ± 154	18.8 ± 0.36	NFPA

Veg = Vegetation type, Prec = Precipitation, Temp = Temperature, NFPA = National Forest Priority Area; CHA = Controlled Hunting Area; WS = Wildlife Sanctuary; LSF = large forest fragment (1-10 km^2); SCF = small continuous forests (11-50 km^2); LCF = large continuous forest (>50 km^2) (*source: UNEP-WCMC and IUCN, 2023).

3.2.1.1. Study design and method of data collection

The population size and density of *C. g. gallarum* were estimated in four of the remaining forests in the Ahmar Mountains. Line transect method was used. This method has been extensively employed for diurnal arboreal primates density estimation in tropical forests (González-Solís *et al*., 2001; Buckland *et al*., 2010; Höing *et al*., 2013; Leca *et al*., 2013; Araldi *et al*., 2014; Omifolaji *et al*., 2020; Kiffner *et al*., 2022a, b). This method is relatively simple, rapid, and cost-effective (Buckland *et al*., 2001; Thomas *et al*., 2010). Furthermore, it is also used for sparsely dispersed populations, for populations that occur in distinct groups at small or intermediate cluster density and populations that are detected through a flushing response (Buckland *et al*., 2001).

As a method of estimating abundance, line-transect surveys were conducted in four forest sites in Ahmar Mountains, employing a Distance Sampling (DS) approach (Buckland *et al.*, 2001). This approach considers the perpendicular distance to estimate the detection probability, thus in turn inferring the population size and density estimate of an animal detected (Buckland *et al.*, 1993).

Nineteen transect lines (Fig. 8; range: 1.8–7.0 km) were generated on topological maps of the four forest fragments using ArcGIS 10.4.1 in systematic random sampling design (Thomas *et al.*, 2010; Buckland *et al.*, 2015). Of the 19 transects, 9 were in DDF, 2 in Jallo-Kuni Forest, 4 in Hades Forest and 4 in Gara Muleta Forest, covering a total distance of 75.9 km (Table 2). Transects were positioned in parallel wherever possible to ensure equal coverage, with 1 km between adjacent transects, except for transects 3 and 4 of the GMF, where the distance is approximately 5 km.

Table 2. Number of transects per study site, lengths of transects, encounter rates and mean cluster sizes per study site.

Site ID	Name of study sites	Number of transects	Transect length (km)	Number of encounters	Encounters km^{-1}	Mean cluster size (±SD)	Number of plots
DDF	Dindin Forest	9	39.3	41	1.04	5.5±2.8	17
JST	Jallo-Sorroro Torgam	1	7	3	0.43		
KMWS	Kuni-Muktar Wildlife Sanctuary	1	5.2	4	0.78		
Combined	JKF	2	12.2	7	0.57	4.3±2.0	13
HDF	Hades Forest	4	12.0	15	1.25	4.5±1.9	20
GMF	Gara Muleta Forest	4	12.5	10	0.80	6.5±1.7	14
all		19	75.9	73	0.96	5.3±2.5	64

The fieldwork was carried out from December 2020 to September 2021 (Appendix 7). From 07.00 h to 18.00 h, a team of three well-trained persons led by the researcher walked slowly along each transect (1 km/h) (Peres, 1999; Plumptre *et al.*, 2013) while visually scanning the forest canopy. This is assumed that the target subspecies had daily travel distances similar to a closely related taxon *C. g. occidentalis* (62 m to 1360 m; Fashing, 2001a). Each transect was surveyed once per season, twofold per study period.

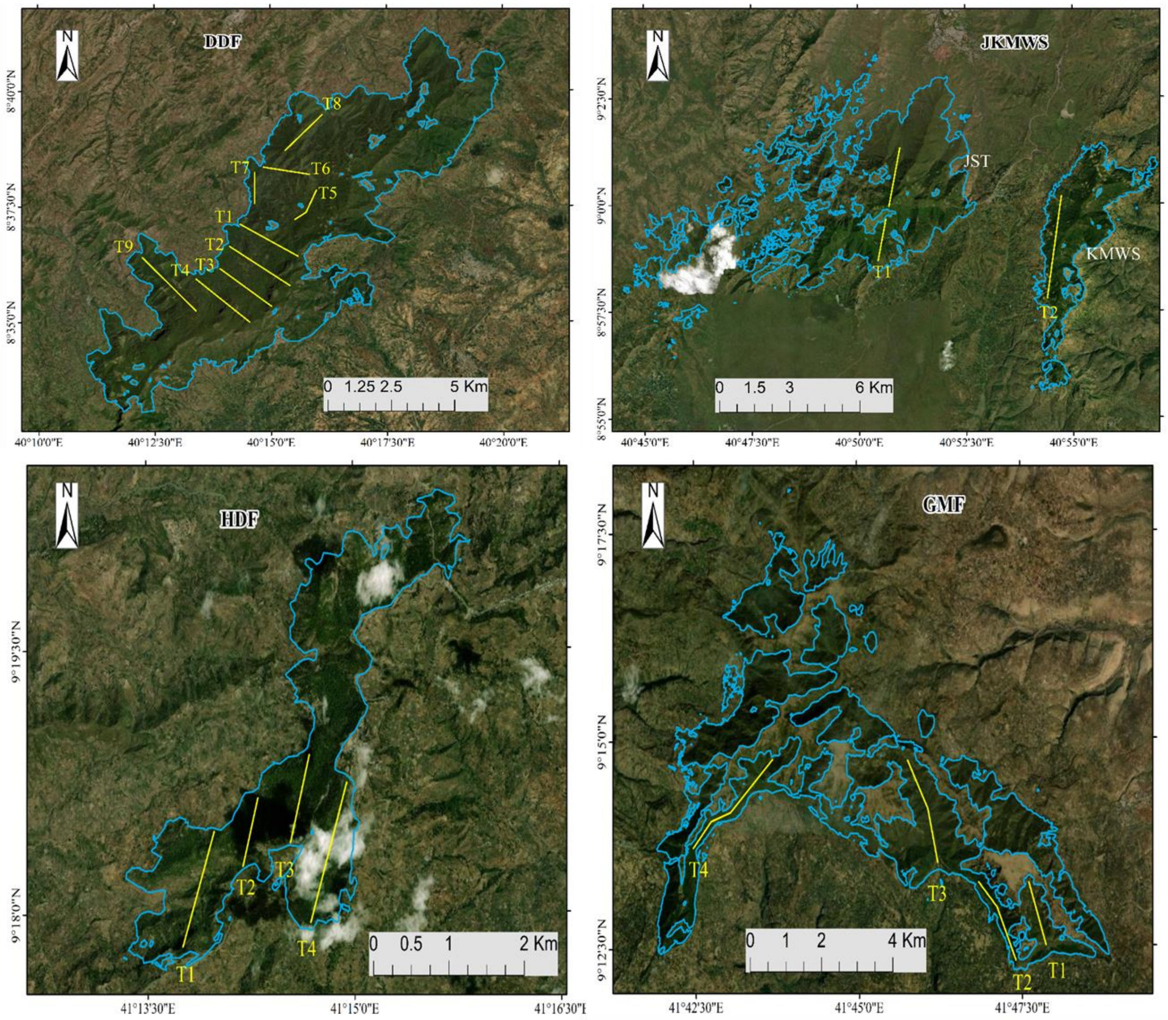


Figure 8. Positions of transects (yellow lines) within the four forests used for *C. g. gallarum* surveys. Dindin Forest (DDF), Jallo Kuni-Muktar Wildlife Sanctuary (JKF), Hades Forest (HDF), and Gara Muleta Forest (GMF). [Base map: Google Earth]

Colobus monkeys are relatively easy to detect because their movements, loud calls, and pelage make them conspicuous (Plate 5 and 6). They often indicate their presence with loud calls that may be heard far more than a kilometer. For each encounter, (1) transect ID, (2) date and time of the sighting, (3) weather conditions, (4) sighting location along the transect using the Global Positioning System (Garmin® GPSmap 76CSx), (5) number of individuals (cluster size), (6) perpendicular distance (visually estimated), (7) first sighting sign (auditory, pellets or visual), and (8) age and sex of the individuals was documented. Assigned individuals estimated the perpendicular distance after they were carefully trained in how to estimate distances and until the errors in distance estimation were reduced to less than 2 m. The perpendicular distances were visually estimated to the centre of each cluster at their first detection (Kiffner *et al*., 2022a).

Plate 6. Male Djaffa Mountains guereza (*Colobus guereza gallarum*) in Hades Forest, 2021. (Photo by: Chala Adugna, 2021).

The home range size of *C. guereza* ranges from 0.075 km^2 to 1 km^2 (Fashing, 2011). Their daily travel distances vary from 390 m to 600 m (Fashing, 2011). Core areas are usually defended and groups keep a certain distance from each other (Von Hippel, 1996). Therefore, the researcher defined individuals >50 m apart as members of different clusters (Teelen, 2007; Kiffner *et al*., 2022b).

With a few adjustments, the criteria for the age-sex groups of individuals were the same as those employed by Dunbar and Dunbar (1974). Based on their size and sex, individuals were categorized into 4 classes: adult males, adult females, juveniles and infants.

3.2.3. Distribution and habitat suitability modelling

Ecological model construction was initiated to understand the ecology of the target species and the overall goal of the study. The selection of important conceptual aspects depends on many factors within the distributional range of the species, including ecological, climatic conditions, and indirect factors (Guisan and Zimmermann, 2000). A research framework on habitat suitability models of the target subspecies was presented by incorporating ecological predictors with the subspecies occurrence data (Fig. 9).

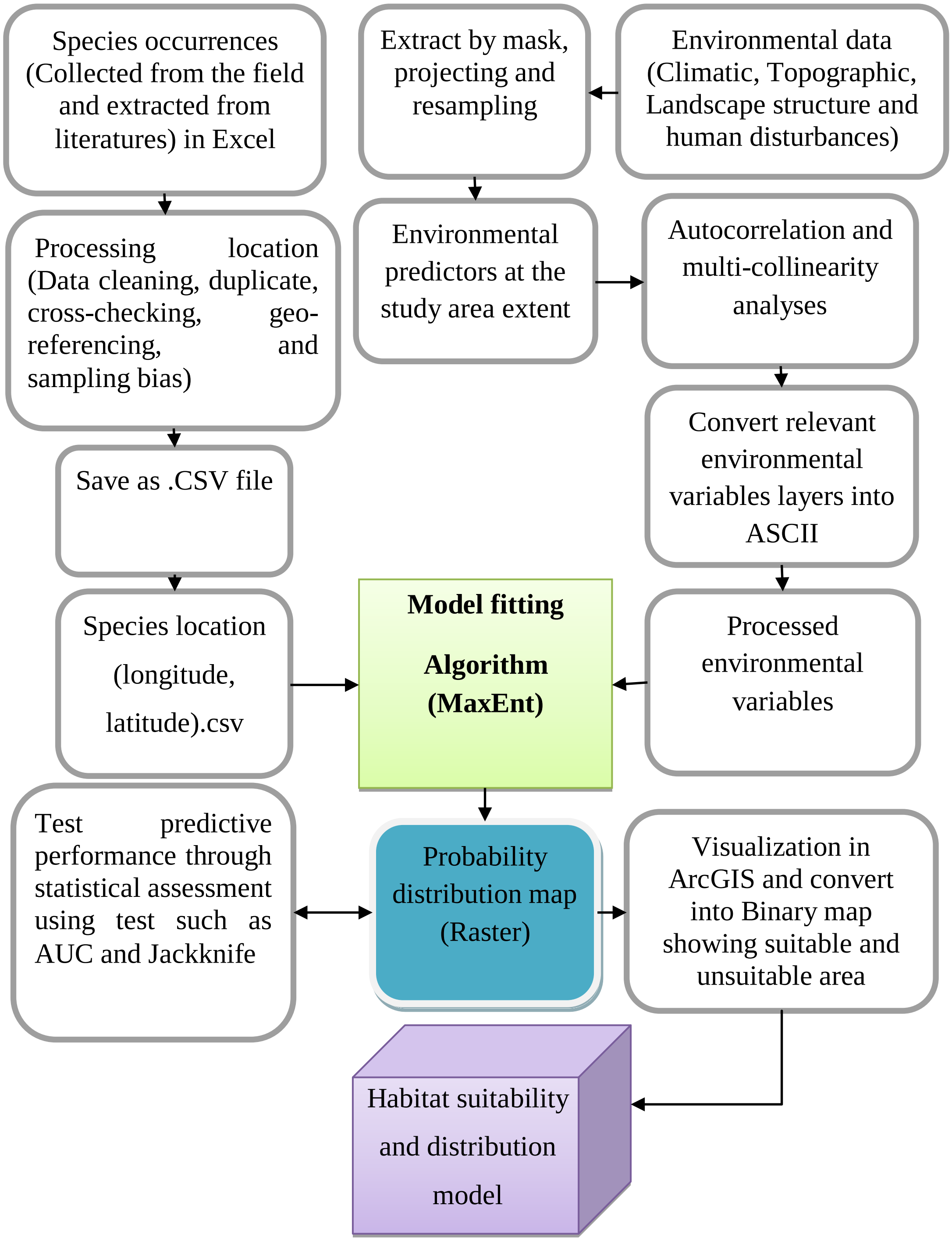


Figure 9. Conceptual research framework developed on which habitat suitability and distribution model was built for the *C. g. gallarum* in the Arsi and Ahmar Mountains.

3.2.3.1. Occurrence data

Occurrence records for each taxon of Ethiopia’s guereza were collected from different sources. To model the habitat suitability of *C. g. gallarum*, 126 occurrence data were assembled through field collections (n = 105), extracted from GBIF (n = 4) (GBIF.org, 2021) and from published articles (n = 17) (Yalden *et al*., 1997; Zinner *et al*., 2019) (Appendix 1). In addition, own field collection for *C. g. gallarum* occurrence data across the forest fragments in the Arsi zone was used. These assembled presence locations were referenced to a 1 × 1 km grid, and outliers and duplicates were removed. The precision of the occurrence data was confirmed by means of Google Earth satellite maps. Then occurrence points outside forests were excluded (Moraes *et al*., 2020). Spatial autocorrelation of occurrence data was screened in ArcGIS version 10.4 by using average nearest neighbour analyses (Moran's Index = 0.35, z-score = 169.44, $P = 0.00$). Thus, a total of 47 occurrences were used to develop both the habitat suitability and ecological niche models of *C. g. gallarum*.

For modelling the ecological niche of *C. g. guereza*, occurrence data were compiled from previously published articles (Zinner *et al*., 2019; Zewdu Kifle and Afework Bekele, 2023; Dereje Tesfaye *et al*., 2021). We included only sightings of Ethiopia’s guereza that occurred after 1970 to match the data with the temporal coverage of the current climate. We removed duplicates and spatially rarified or thinned the data to minimize the effects of spatial bias or autocorrelation (Dormann *et al*., 2007; Zizka *et al*., 2019) via SDMTools v2.4 using ArcGIS 10.4.1. Finally, a total of 116 and 47 occurrence datasets were retained for *C. g. guereza* and *C. g. gallarum*, respectively, for developing ecological niche models of the two closely related taxa (Fig. 10; Appendix 2).

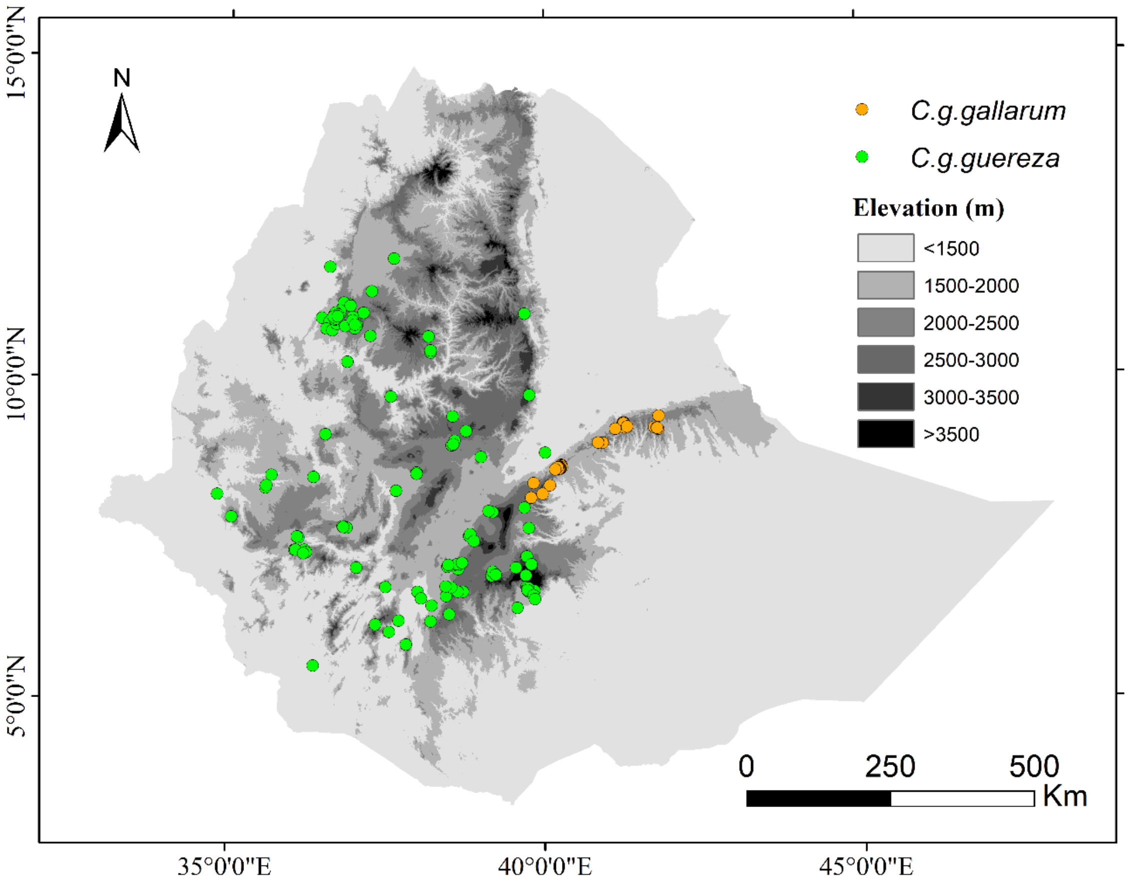


Figure 10. Topographic map of Ethiopia and presence locations of *C. g. guereza* (green circles) and *C. g. gallarum* (orange circles).

3.2.3.2. Ecological predictor variables

Habitat suitability is modeled by combining landscape composition and climate-related factors, which are key in determining habitat patches with high priority for the species (Préau *et al*., 2020). Depending on the roles they play in defining the physiological, ecological, geographic and behavioural characteristics of the species, environmental predictors were chosen to model habitats of *C. g. gallarum*. With this in mind, 27 predictor variables were selected (Appendix 3), gathering them into four classes: climatic condition, landscape compositions, topographic attributes and human disturbances (Table 3).

Nineteen bioclimate from a world climate with spatial resolution of 1 km^2 (Hijmans *et al*., 2005; Fick and Hijmans, 2017) were extracted. The current climate represented for the year 2000 (average for 1970–2000) was taken from Worldclim version 2.1, whereas future climate scenarios of two representative concentration pathways (RCP 2.6 and RCP 8.5) for the periods 2050 and 2070 were found from Worldclim version 1.4. These future climate data were derived from two global circulation models (GCMs): BCC-CSM-1.1 developed by the Beijing Climate Centre Climate System Model (Zhou *et al*., 2014) and HadGEM2-ES developed by the UK Met Office Hadley Centre (Jones *et al*., 2011). The latest current climate data from Worldclim2.1 at a 30 sec (1 km^2) resolution was considered as reference climate data to assess current habitat suitability of *C. g. gallarum* and to provide prompt conservation suggestions with an updated condition. However, at the time of processing, the WorldClim 2.1's 30-second resolution for future climatic data was not released. Therefore, the future projected climate data available from WorldClim1.4 with the same grid resolution as the present climate data were considered to see the consequences of future climate change scenarios. Then, using ArcGIS 10.4.1, climatic data from Worldclim1.4 were re-sampled to match the dimensions of Worldclim2.1-derived data, allowing pixel-by-pixel comparison throughout the study region (Cerasoli *et al*., 2022).

ASTER Global Digital Elevation Model v3 (30 m) with transformation services via the LP DAAC's Application for Extracting and Exploring Analysis Ready Samples (AρρEEARS) was used to generate Digital Elevation Model (DEM) of the study region. This DEM was processed in ArcGIS 10.4.1 to produce topographical characteristics, including altitude, slope and aspect that were used as inputs for the MaxEnt algorithm to inspect their impacts on the taxon's habitat suitability. Global land cover map was found from the Copernicus Climate Change Service (https://cds.climate.copernicus.eu/), which describes land surface into 22 groups well-defined by UN FAO-LCCS. From this land cover map, the land cover classes that included cropland, broad-leaf evergreen forest, broad-leaf deciduous forest, shrubland, grassland, urban areas, bare lands and water bodies of the study region were clipped and processed in the ArcGIS. Human disturbance such as distance to rivers, roads as well as settlements were to used execute models. These human disturbance layers were calculated using the Euclidean distance of the spatial analyst tools of ArcGIS. All analyses were carried out with a 1 km^2 spatial resolution, considering them to have similar extent, projection and resolution (Phillips *et al*., 2006).

Table 3. Ecological factors selected for modelling habitat suitability of *C. g. gallarum* and their code, units of measurement and variable inflation factors (VIF).

Category	Variables	Code	Units	VIF
Bioclimatic	Mean Diurnal Range	BIO2	°C	3.32
	Temperature Seasonality	BIO4	°C	3.31
	Precipitation Seasonality	BIO15	mm	2.83
	Precipitation of Wettest Quarter	BIO16	mm	3.02
	Precipitation of Coldest Quarter	BIO19	mm	2.26
Human disturbance	Distance to roads	DistRod	m	2.12
	Distance to settlements	DistPopD	m	1.20
	Distance to River ways	DistRvr	m	1.36
Landscape attribute	Land cover class	Lulc	Unitless	1.27
Topographic attribute	Aspect	Asp	°degree	1.18

The pairwise correlation between the predictors at $r \leq |0.80|$ (Zhao *et al*., 2019) (Appendix 4) and variance inflation factor (VIF) (Guisan *et al*., 2017)$\leq$ 10 was performed to choose the set of predictors. A variable selection was made by means of R version 4.0.5 (R Development Core Team, 2021). This is done because highly correlated variables in the model predictions result in a confusing model that is difficult to understand (Zurell *et al*., 2020), which decreases the competence and increases doubt of SDMs (Dormann *et al*., 2013). Only ten predictors were used to model habitats of *C. g. gallarum* (Table 3).

For inclusion in the ecological niche modelling of the closely related taxa of Ethiopian guereza, climate data comprising 19 bioclimate variables with the highest spatial resolution (i.e., ~1 km) were found from WorldClim version 2.1 (Fick and Hijmans, 2017) and processed using ArcGIS 10.4.1. Ten thousand random points from the background extent after cropping the candidate covariates were generated. Two datasets were used to construct niche models: training and testing for both the presence and pseudoabsence datasets (Appendix 5). The predictor values at the presence and pseudoabsence locations were extracted from the spatial data layers of the predictor sources. The multi-collinearity computed by means of ‘usdm’ package in R 4.1.2 (R Development Core Team, 2023) and retained only one variable among those pair that are correlated > |0.8| and the variables with the lowest VIF (less than 10) to avoid multi-collinearity problems among predictors (Guisan *et al*., 2017). The selection of one variable from a pair of variables is objectively decided using the variable's contribution to the model fit. Overall, 9 bioclimatic variables were selected (Fig. 11) to calibrate the models and create the ecological niches of the two taxa. These nine bioclimatic variables such as Mean Diurnal Range (Biol 2), Temperature Seasonality (Biol 4), Max Temperature of Warmest Month (Biol 5), Min Temperature of Coldest Month (Biol 6), Temperature Annual Range (Biol 7), Annual Precipitation (Biol 12), Precipitation of Driest Month (Biol 14), Precipitation Seasonality (Coefficient of Variation) (Biol 15), and Precipitation of Wettest Quarter (Biol 16) were used for both taxa.

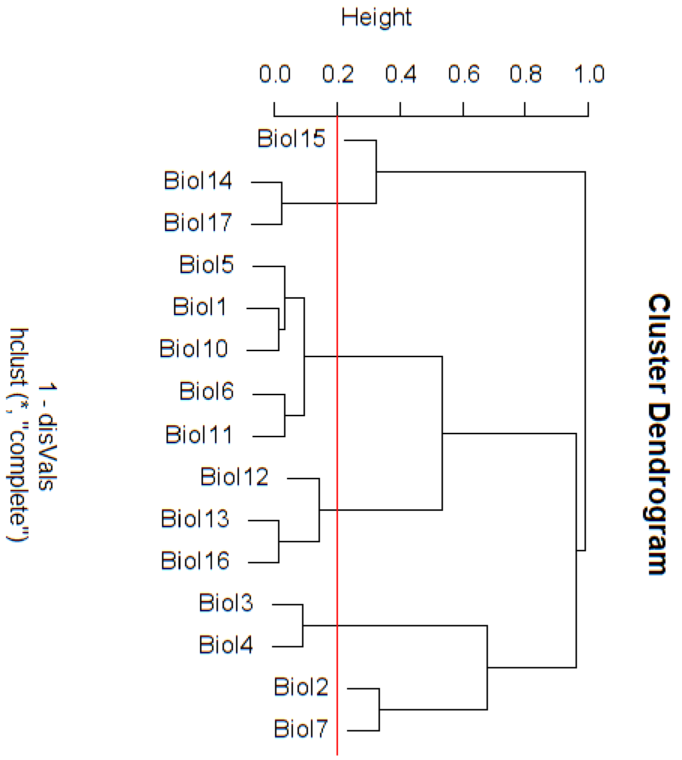


Figure 11. Plot of multicollinearity test computed at correlation coefficient to be set 0.8 with a redline for data sets of both subspecies.

3.2.4. Vegetation community ecology

The study of vegetation ecology is very beneficial for thoughtful the position of tree populations, regeneration and variety for preservation determinations (Abyot Dibaba *et al*., 2022). It is assumed that forests are not only the lungs of the world but also home to a myriad of living creatures. The vegetation community provides food, shelter and support for animals, particularly arboreal primates.

Vegetation data were collected across the remnants of forests in the Ahmar Mountains through purposive sampling method. The collection was employed along the transect lines generated for population surveys. We considered sampling plots established at the sites where *C*. *g*. *gallarum* groups and their faecal samples were detected and absent. The number of plots per site was varied depends on the variation in encounters and ecologies.

Overall, 64 plots, individually 400 m^2 (20 × 20 m), were used across the forests (Table 2). Assuming that *C*. *g*. *gallarum* may require trees with dense canopies that provide support in terms of food and shelter, only woody plant species and lianas were recorded. In each plot, the following parameters were measured: (1) types of trees or climbers, 2) diameter at breast height (DBH, tree with DBH $\geq$12 cm and climber $\geq$ 5 cm) using measurement instrument such as caliper and metre taps (50 m); (3) heights of tree and climber (HEIGHT, m) estimated using naked eye aided by a clinometer; (4) number of trees and/or climbers and growth forms.

Every plant species recorded was taxonomically identified on field at each respective forest by experts from the forestry department of the OFWE of Hararghe Branch, Chiro Office, namely, Olana Badada, Aliyi Oda, and Mumme Ebro, by means of plant identification guides using Flora of Ethiopia and Eritrea (Hedberg, 1996, Hedberg *et al*., 2009).

3.3. Data analyses

3.3.1. Estimating abundance

Since forest ecology and season (more or less good visibility) can affect detection distance (perpendicular distance), first tested whether forest strata (ID) or season (wet and dry) affected the perpendicular distances. Second, cluster sizes among the four forests and seasons were compared and tested to see whether cluster size affected the perpendicular distances since larger groups might be easier to detect. Comparison of perpendicular distances and cluster sizes among the four forests were computed using Kruskal-Wallis (H) test whereas the two seasons and the correlation between cluster size and perpendicular distance were analysed by Mann–Whitney U test. All these tests were computed using R 4.3.1 (R Development Core Team, 2023) and found no effects of forest ID, season, or cluster size on detection distances (Fig.13a-e) and, therefore, combined all our encounters in a single analysis.

Since the perpendicular distances were recorded to the nearest metre, subsequently ordered them into four distance classes to better fit the detection function: 0 m–10 m, >10 m–20 m, >20 m–30 m, and >30 m–50 m. Only two encounters with perpendicular distances larger than 50 m (one with 75 m and a cluster size of 5 and one with 100 m and a cluster size of 2) were found. Therefore, the distribution at 50 m was truncated to enhance detection function robustness (Buckland *et al*., 1993; Buckland *et al*., 2001). To establish the detection models on a large enough sample size since 60–80 detections are advised to consistently produce accurate density estimations (Peres, 1999; Buckland *et al*., 2001) and these sample sizes do not support separate fitting of the detection function to the data in each stratum of the forest, all data were combined across the study sites for fitting a detection function.

Using the pooled encounters across the forests, four candidate detection models were fitted to check key functions performance (uniform (UN), half-normal (HN), hazard-rate (HR), and negative exponential (NE)) on conventional distance sampling (CDS) in Distance 7.3 Release 2 (Thomas *et al*., 2010) (Table 5; Fig.14a-d). This determines the basic model shape. Three series expansions or adjustment terms such as cosine, hermite polynomial and simple polynomial (Table 5) were considered to make models more robust.

Akaike Information Criterion AIC (Akaike, 1973) was used to carefully pick the best model and retained the half-normal key function with no adjustment term (ΔAIC = 0.0; AIC =186.75; Table 5). In addition, chi-squared test and visual fit of models as additional model selection criteria were considered (Buckland *et al*., 2001). Using chi-squared test, the number of observations in a given distance interval was compared to the number expected under the fitted detection function (Appendix 6). Then, the probability was computed to detect a cluster given that it is in the covered area, which is used to correct the density estimation (i.e., number of clusters per km^2) across the study periods and determine effective strip width (ESW, which is the distance at which as many objects are seen) (Thomas *et al*., 2010).

The average size of groups in population, density of groups/clusters, population density, and abundance of *C. g. gallarum* for all data combined were computed. Since predicted cluster size estimation based on the size-biased regression method indicated warnings, the average of the detected clusters was used as the basis for expected cluster size estimation. Relative abundance (i.e., abundance index, typically offered as an encounter rate [ER] of objects recorded per unit of distance (Fewster *et al*., 2009; Campbell *et al*., 2016) was also computed. Finally, the population size of the study taxon was assessed by multiplying the global lumped density of population by the studied forests' total area (183 km^2). The parameter estimates quantified uncertainty or variance using percent of coefficient of variation (CV), standard error (SE) and 95% confidence intervals (CIs) in the analytic variance estimation method in Distance.

3.3.2. Modelling habitat suitability of *C. g. gallarum*

A general-purpose machine learning method, Maximum Entropy (MaxEnt) v. 3.4.4 (Phillips *et al*., 2006), was applied to model habitat suitability of *C. g. gallarum* using the selected predictors. It's widely used in wildlife habitat assessments and shows better model accuracy, transferability and reliability under a small sample size (Elith *et al*., 2006; Phillips and Dudik, 2008; Elith and Graham, 2009; Elith and Leathwick, 2009;

Elith *et al*., 2011; Merow *et al*., 2014). A total of 47 presence points were used for the model. Before fitting a model, the occurrence data were randomly classified (Zurell *et al*., 2020), with 70% of the occurrences designated as training data and the remaining 30% used to test the model (Phillips *et al*., 2006). Besides MaxEnt default settings, the following settings were used: feature class combinations of linear, quadratic, product, and hinge and 10 times replicate with "subsample" as the replicated run type to reduce the model overfitting (Phillips and Dudik, 2008; Elith *et al*., 2011). Ten thousand background positions were also generated randomly from the whole area of the study region to model the habitat suitability map.

The model's performance was evaluated using Area Under the Curve (AUC). It is a threshold-independent measure and is used to assess the model's predictive ability for generating the suitable habitat map (Guisan and Zimmermann, 2000). It portrays the association among the proportion of correctly predicted presence (sensitivity) and the proportion of wrongly predicted absence (specificity) (Phillips *et al*., 2006). A model that predicts correctly will generate a ROC curve that follows the left axis and the top of the figure, whereas a model that is unable to reliably categorize places where the species is present and missing will generate a ROC curve that follows the 1:1 line. The value of AUC varies between 0.5 and 1, in which AUC values above 0.90 are 'high accuracy/excellent'; $0.70 < AUC < 0.90$ 'good accuracy'; $0.50 < AUC < 0.70$ 'low accuracy'; and $AUC < 0.50$ 'no better than random' (Swets, 1988; Elith *et al*., 2011).

The relevance of variables and the influence of each predictor were estimated using percent contribution, permutation importance, and Jackknife tests (Phillips *et al*., 2006). Moreover, univariate response curve for each variable was plotted to see how some of the most relevant variables reacted to predicted habitat suitability and whether they had a positive or negative impact on the subspecies' habitat suitability (Hosni *et al*., 2020).

The suitable habitat distribution of *C. g. gallarum* was predicted for the current environmental conditions and projected for future climate change scenarios. The logistic output of the MaxEnt is continuous, allowing fine distinctions to be made between the modelled suitability of different areas with values between 0 and 1, an indication of a likelihood of occurrence (Phillips *et al*., 2006). Binary prediction of the model was done using 10-percentile training presence Logistic threshold (n = 0.143), which makes the distinction between suitable and unsuitable areas. Then, a distribution map was created using ArcGIS 10.4.1, and the binary prediction was reclassified based on the suitability scores. These habitat suitability scores were categorized as unsuitable (i.e., not specifically cited), moderately suitable (i.e., frequently cited as secondary habitat and presence of low populations with patchy distribution), and highly suitable (i.e., frequently cited as main or preferred habitat and presence of major populations with higher densities) (Boitani *et al*., 2008). Subsequently, the change in the predicted habitat distribution of *C. g. gallarum* under the two scenarios for the years 2050s and 2070s by two GCM was measured. Finally, the map of suitable habitat distribution showing the area of habitat considered stable, lost, and gained was created using ArcMap 10.4.1.

3.3.3. Ecological niche modelling (ENM) for closely related taxa

Multiple algorithms were used to run the models. These include the generalized additive model (GAM; Wood *et al*., 2016; Pedersen *et al*., 2019), general linear model (GLM; Hastie *et al*., 2009), maximum entropy approach (MaxEnt default; Phillips *et al*., 2006; Elith *et al*., 2011), maximum entropy adjusted (MaxEnt tuned; Radosavljevic and Anderson, 2014) and random forest (RF; Breiman, 2001). They were selected basing on their suitability of assumptions for the datasets, the use of various parameters and pseudo-absence points, their variation in the model fitting function (Hastie *et al*., 2009; Merow *et al*., 2014). During model fitting, case weights were applied to the presence and background points. The weights were generated by giving a weight of 1 to every presence location and giving the weights to the background as the summation of the weights for the presence and background samples is equal, i.e., number of presences/number of background (163/10000) (Desalegn Chala *et al*., 2016). All predictors were normalized or standardized to meet a mean of zero as well as a standard deviation of one for all the models, except for the MaxEnt models, which have internal normalization (Valavi *et al*., 2022).

To fit GLMs, forward and backward model selection was used with options for dropping variables or including them, considering only linear or linear plus quadratic terms. No interaction terms were tested, and selection was based on changes in the AIC (Hastie *et al*., 2009). During our model fitting, the maximum likelihood (ML) method was used (Guisan *et al*., 2002). Both linear and quadratic terms in GLMs were allowed for model fitting to develop niches of the taxa. To account for nonlinearity in the fitted functions, GAMs employ nonparametric smooth functions (Merow *et al*., 2014). There is a persistent need to prevent overfitting in model fitting by taking the bias-variance trade-off into account (Hastie *et al*., 2009). A number of models were modified using the presence-background training data in order to prevent overfitting. This was accomplished using AIC for GLM and cross-validation for other approaches (MaxEnt adjusted).

As the most common modelling tool, the "dismo: MaxEnt" R package was used due to its non-stochastic model and computational speed (Valvai *et al*., 2022). Both MaxEnt and MaxEnt optimized as implemented in dismo package were used. As suggested by recent studies (Radosavljevic and Anderson, 2014), MaxEnt can perform better when its regularization multiplier and feature classes (i.e., L, Q, H, and P for linear, quadratic, hinge, and product, respectively) are adjusted. These parameters can control the complexity or generality of the model. The default value of the regularization multiplier is 1, and the lower the value, the more complex a model can be fit (Elith *et al*., 2011). In this study, the multiplier and feature classes were simultaneously adjusted using 5-fold cross-validation (CV) using the presence and pseudo-absence training dataset. Five different regularization multipliers (0.5, 1, 2, 3, and 4) in combination with different features (L, LQ, H, LQH, and LQHP) were used to find the best parameters that maximize the average AUC in the CV.

Since RFs are frequently utilized for SDMs (Zhang *et al*., 2019; Valavi *et al*., 2022), regression trees were used to fit and predict the ecological niches in this study. It combines many trees to create an ensemble. Although it is parameterized to address many pseudo-absence samples, it substantially outperforms other random forest implementations (Valavi *et al*., 2022). To fit the RF model with the default parameter, the "random forest" package was used.

Two threshold-independent measures were used to assess the model's predictive performance (Table 8). These metrics include (1) AUC (Swets, 1988; Philips *et al*., 2006; Desalegn Chala *et al*., 2019) and (2) Pearson correlation coefficient (COR) among predicted probability of occurrence and presence-pseudo-absence testing data (Valavi *et al*., 2022). The COR was employed, which measures the difference between prediction and observation values (0 s and 1 s; Elith *et al*., 2006), provided that understanding into how well estimates are standardized in relative terms. The COR information on about aspects of adjustment since it considers real prediction values. Even in relative terms, a model that performs well in terms of the AUC but poorly in terms of the COR is expected to be under-calibrated. To create binary maps, maxSS (maximum sum threshold), which is the threshold at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) is highest, was utilized (Desalegn Chala *et al*., 2019). This threshold divides all model predictions into binary maps of the suitable and/or unsuitable of each examined subspecies.

3.3.3.1. Ensemble model predictions

The predictions from five algorithms were averaged to create one ensemble map using weighed mean of all five current models' average score. By averaging the optimisation thresholds across the five models, the probabilistic occurrence prediction maps were transformed into binary presence-absence maps. This was done because an ensemble model would perform well in the SDM (Valavi *et al*., 2022). In order to create a binary map, the five separate model predictions were compiled based on AUC values greater than 0.7. The mean predicted values were then computed.

3.3.3.2. Niche overlap between closely related taxa

In order to find evidence for taxa's response to climate data, principal component analysis (PCA) was used to examine the subspecies' appearances in multivariate climate space using the 'ggbiplot' package in R 4.3.2. Identity test metrics such as *Schoener's **D*** and *Warren's **I*** (Broennimann *et al*., 2012) were used to compare the niches between Ethiopian guereza based on ecological niche models. Both statistics range from zero (when the habitat associations of the taxa are completely different) to one (when the habitat associations of the taxa are identical), with pairwise values > 0.8 frequently indicating substantial niche intersection (Warren *et al*., 2008). A background test was then performed using the MaxEnt in dismo package, to determine whether niche resemblance was minor or bigger than anticipated for the taxa's range or to determine whether niche overlaps were equivalent because the background test is suitable for comparing niche overlaps (Warren *et al*., 2010). *Schoener's D* and *Warren's I* were estimated using MaxEnt model layers and 100 pseudo-replicates' expected values. In order to conduct the test, occurrence data for each subspecies pair are pooled, two fresh samples are randomly assigned locales, and 100 repetitions of randomly selected subspecies pairs with niche overlap are used. The null distribution of the pseudo-replicated niche overlap values was compared to the initial subspecies-pair niche overlap values. If the original subspecies-pair overlap values were within the bottom 5% of the null distribution, the ENMs of the two subspecies were determined as not equivalent and significantly more diverged than expected considering the habitat available to each subspecies.

3.3.3.3. Abundance-environmental suitability association

The present study explored the potential predictive power of the abundance-suitability association. It predicts that habitat suitability predicted by SDMs or ENMs would describe the spatial difference in abundance. Hence, this study tested this relationship for *C. g. gallarum* in along the Ahmar Mountains. The estimated habitat suitability obtained by implementing ensemble ecological niche models was used to explore the relationship with the local abundance (i.e., corresponds to group or cluster size) of *C. g. gallarum* recorded during the population surveys. Furthermore, the study also explored the models' predictive power. The fitted association among abundance and habitat suitability is utilised to extrapolate abundance or precisely forecast abundance at a fine scale across the subspecies distribution.

GAM was used to relate the empirical abundance estimate to the predicted ecological niche or suitability. Tweedie distribution and a log-link function was used to fit the model and address the non-linear nature of the relationship (Fuente *et al*., 2021). The selection was made due to the increasing abundance trend in high suitability values and the cluster of zeroes in low suitability values (Weber *et al*., 2017; Jiménez-Valverde *et al*., 2021). The ‘mgcv’ R package was used to fit the GAM model. The deviation that the model was able to explain was reported as the predictive power of the fit. The link between abundance and the suitability was measured in terms of degree or strength, sign, and significance using Spearman rank correlation coefficients (ρ).

Furthermore, Ordinary least squares (OLS) and quantile regression were used (Cade *et al.*, 1999; Cade and Noon, 2003) to analyze the association or relationship between ecological niche suitability and abundance for *C. g. gallarum*. This tests the hypothesis that ecological niche suitability predicts a taxon spatial abundance pattern, particularly, abundance of the upper limits, by regressing predicted ecological niche suitability against abundance. In the analysis, ecological niche suitability was used as a predictor. The abundance values were re-scaled before model regressing to signify the abundance as a proportion of the maximum stated for a taxon. While quantile regressions were used to investigate the relationship between suitability and the upper bounds of abundance (10th, 25th, 50th (median), 75th, and 95th percentiles for linear quantile regressions), ordinary least squares regression was utilised to investigate mean abundance as predicted by suitability. The packages “quantreg” and “olsrr” were used in the R software version, 4.3.2.

3.3.3.4. Identification of Anthropocene refugia

The Anthropocene refugia was defined based on the ecological niche models generated for both taxa as suitable habitats in areas where anthropogenic impacts are less. For each subspecies, two types of Anthropocene refugia were identified: 1) suitable habitats unaffected by human impacts or suitable habitats in forest land cover was mapped as anthropogenic refugia whereas 2) suitable habitats within protected areas network was mapped as protected anthropogenic refugia. The potential suitable habitats within forested areas were identified by overlaying potential suitable habitat maps with forest land cover and identifying their intersections. Indeed, Ethiopian guerezas are dependent on forest habitats for their survival and layer of forest cover (resolution 30 m^2, Fig. 12a) were downloaded and clipped using binary ensembled prediction models to eliminate areas external to forest cover. The raster layer of Ethiopia's forest cover was obtained from https://cds.climate.copernicus.eu/. Then, area of the niche model was measured to calculate the Anthropocene refugia for each subspecies.

Finally, using all areas confirmed as Anthropocene refugia for both taxa, the researcher overlapped those refugia in Ethiopia's Protected Areas (PAs) network to calculate the refugia under protection. Using the stacked protected area layers overlaid with the Anthropocene refugia for each subspecies, the total area within Ethiopia's PA network was calculated. Ethiopia's PAs network was obtained by merging established PAs in Ethiopia, obtained from the WDPA (UNEP-WCMC and IUCN, 2023; Fig. 12b). The potential suitable habitats within PAs were also examined by overlaying potential suitable habitat maps with PA boundaries and identifying their intersections in ArcGIS.

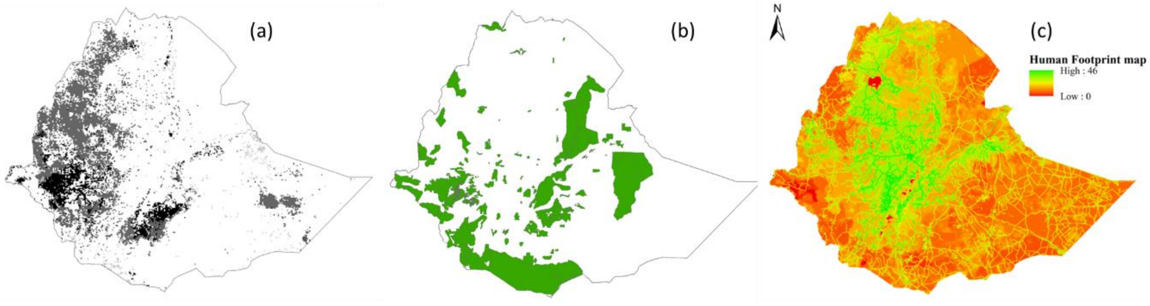


Figure 12. Ethiopia's remaining forest cover (a), protected area distribution (b) and human footprint pressure (HFP) map (c) illustrate the extent of anthropogenic activity. Light green colours show the higher intensity of anthropogenic pressure (c). Maps were created at a scale of 1:7,500,000 for Ethiopia.

3.3.3.5. Conservation and Anthropogenic threat

Whether anthropogenic disturbance has an impact on the potential suitable habitats of both closely related taxa was not studied. Habitat suitability scores predicted using ecological niche models were regressed against the human footprint pressure values using a linear regression analysis. This is used to evaluate the peril of human pressures on the Anthropocene refugia of both taxa. A human footprint pressure (HFP) raster (Venter *et al.*, 2016), a representation of human disturbance (Di Marco *et al.*, 2018; Campera *et al.*, 2020), was obtained from SEDAC (https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint). The raster layer maps human activities like roads, settlements, agricultural areas, and buildings, ranging from 0 to 50 intensity levels, at 1 km^2 resolution (Hending *et al*., 2023; Fig. 12c).

The human footprint pressure index and ecological niche model raster layers were trimmed to the Anthropocene refugia area of each taxon. Using 100 randomly generated points, the scores of HFP and ENMs were retrieved. The Shapiro-Wilk test was run, and the human footprint index and niche score datasets were log transformed to account for linearity, homoscedasticity, and normal distribution requirements for linear regression. The analysis was bootstrapped to 10,000 repetitions using the R package "boot" and bias-corrected and accelerated confidence intervals, with an alpha level of 0.05 indicating significance (Canty and Ripley, 2020).

3.3.4. Vegetation community analysis

Data tables with three columns that includes plots, name of species and the abundance of the species were created and saved. Subsequently, a data matrix containing of 64 plots was produced by creating a dataframe with Labdsv package in R 4.3.1. The number of species missed during sampling was estimated using the vegan package.

3.3.4.1. Cluster analysis

Using hierarchical clustering technique, plant and climber species-containing plots were categorized according to floristic similarities (Kent, 2012). Prior to cluster analysis, an objective method was used to calculate the ideal number of clusters using techniques outlined by Zerihun Woldu (2017). The number of clusters was determined by looking at the abrupt bend at a particular cluster in the plot. Using the Ward technique (minimum-variance clustering) and a similarity ratio (SR) in R 4.3.1, coupled with the Cluster and Vegan packages (Oksanen *et al*., 2013; Zerihun Woldu, 2017), agglomerative hierarchical clustering (AHC) was used to identify plant communities.

To understand the types of vegetation communities where *C. g. gallarum* occurs (i.e., used as a proxy for habitat use), an indicator species analysis (i.e., a diagnostic species for plant community naming) was carried out using the indicator value (IndVal) method in the R packages such as Cluster, Vegan, and Labdsv (Zerihun Woldu, 2017). The dominating species of each community type were determined, and the community types were given their names in honour of the dominant species. A randomization strategy was used to examine the statistical significance of the indicator values. The abundance and presence of a certain species within a specific set of plots serve as the basis for the indicator value index (IndVal). An indicator species of a community was defined as a plant species with a significant indicator value of $p < 0.05$. After determining that three of the dominating species had $p < 0.05$, the community kinds were given names.

3.3.4.1. Diversity indices

Diversity indices were computed to measure variations of species in a clustered plant community. The Shannon-Wiener (1949) index was computed to describe the species diversity using the formula described in Kent (2012):

$$H' = -\sum_{i=1}^{s} pi \ln (pi)$$

where *H'* is the Shannon-Wiener index of woody plant species, which ranges from 0 to *Hmax* and depends on species richness and evenness. In real ecological data, H values range from 1.5 to 3.5, with the maximum value occurring when the community is perfectly even.

Shannon's evenness index, also known as Pielou's J, is calculated by dividing the Shannon diversity index from the real community by ln of the number of species for the same community with the same richness *Hmax*, which decreases with increasing species abundance:

$$J' = \frac{H'}{\ln s}$$

where H' is the Shannon-Wiener index and lns signifies the number of species in the cluster.

3.3.4.2. The similarity between communities

As Zerihun Woldu (2017) enlightens ecological resemblance as the similarity or dissimilarity between samples in terms of their species composition, with similarity decreasing and dissimilarity increasing as species composition differs. The Sorensen similarity index is a widely used metric for comparing plant communities, forest patches, and study areas in R statistical programs. This statistics was done using the following formula:

$$\mathrm{Ss} = \frac{2a}{2a + b + c}$$

where a is the number of species common to both communities, b is the number of species in sample 1, and c is the number of species in sample 2.

Additionally, each plot's total basal area (BA, m2) was computed. To quantify the height dispersion, the standard deviation of tree height (SDHeight) was computed for each plot. The stem density (individual trees/ha) and cluster basal area (m2/ha) were calculated for each plant community (Mbora and Meikle, 2004). BA per hectare was estimated from the DBH following Fashing's (2001b) method:

$\mathrm{BA} = [0.5\mathrm{xDBH}]^2\mathrm{X}\ \pi$, where BA is the basal area and DBH is the diameter at breast height and *pi* is constant.

Analysis of species composition and structure were also calculated using the following formula (Husch *et al*., 2002):

$$\text{Stand density} = \frac{\text{individuals of species A}}{\text{area sampled in hectare basis}}$$

$$\text{Relative density of species (RDe)} = \frac{\text{density of species A}}{\text{total density}} * 100$$

$$\text{Relative frequency of species (RF)} = \frac{\text{frequency of species A}}{\text{total frequency}} * 100$$

$$\text{Relative dominance of species (RDo)} = \frac{\text{basal area of species A}}{\text{total basal area of species}} * 100$$

$$\text{An importance value index (IVI)} = \text{RDe} + \text{RF} + \text{RDo}$$

3.3.4.3. Species-habitat association analyses

The structural complexity and floristic composition were assessed to evaluate how local-scale habitat characteristics influence the occupancy and abundance of *C. g. gallarum* at the local scale. Thus, the variables assessed the structural complexity and floristic composition of the habitat at the exact locations of the *C. g. gallarum* presence and in the 400-m^2 plots where the *C. g. gallarum* was recorded as absent. The value of candidate variables was log-transformed prior to analyses to compute the mean differences among the community types. The differences in the structural complexity among community types were analyzed and verified by One-way ANOVA, followed *post hoc* comparisons.

Habitat analysis was conducted to identify and quantify the strength of the relationships (Veech, 2021) between the subspecies response variables (i.e., occupancy and abundance) and the local habitat characteristics (predictor variables). Normality and multicollinearity tests were performed prior to statistical testing and log-transformed to achieve normality and homoscedasticity. A threshold value for Pearson correlation coefficients (r) was 0.8 (i.e., to measure the correlation between two variables) and the variance inflation factor was set at 10. Standardisation was crucial for comparing forest structural complexities and floristic compositions due to their diverse units of measurement and variances. To standardise the variables, a scale function was used in the package of R software "*statistics*" to make the mean zero and the standard deviation 1 for all variables.

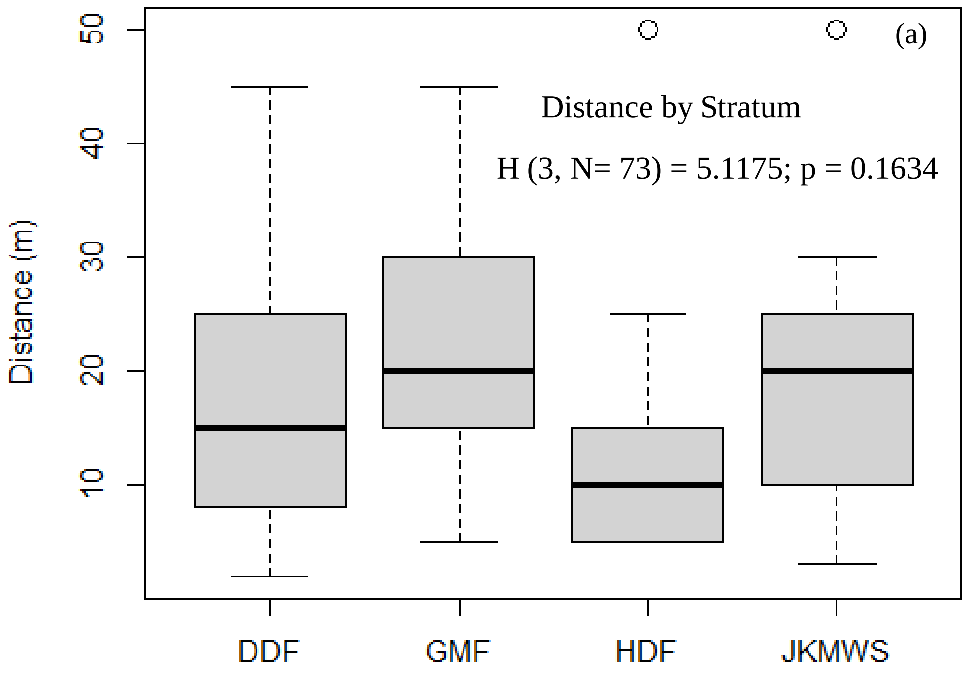
T-test was computed to compare the mean difference between the presence plots and absence plots for the predictors measured. The presence/absence plots were utilized as a grouping variable rather than a response variable. The study employed stepwise multiple logistic regression to examine the influence of the local habitat characteristics on occupancy of *C. g. gallarum*. *C. g. gallarum* presence/absence (coded as 1/0) against local habitat characteristics (e.g., tree basal area, mean height of trees, SD tree height, importance values of trees and various indices of species diversity). The model selection process involved a stepwise approach until non-significant parameters were removed, primarily to reduce the model's fit to the data. Furthermore, a stepwise GLM with Poisson distribution model was performed to analyze whether *C. g. gallarum* abundance is influenced by the habitat variables in the occupied plots. A p-value of 0.05 considered to indicate statistical significance.

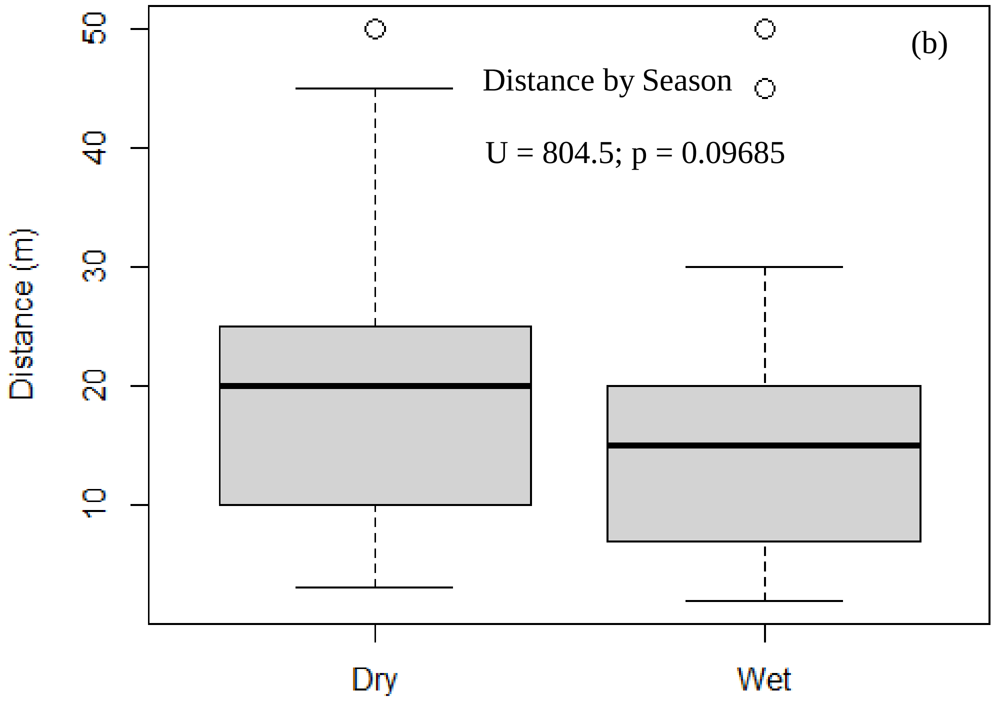
4. RESULTS

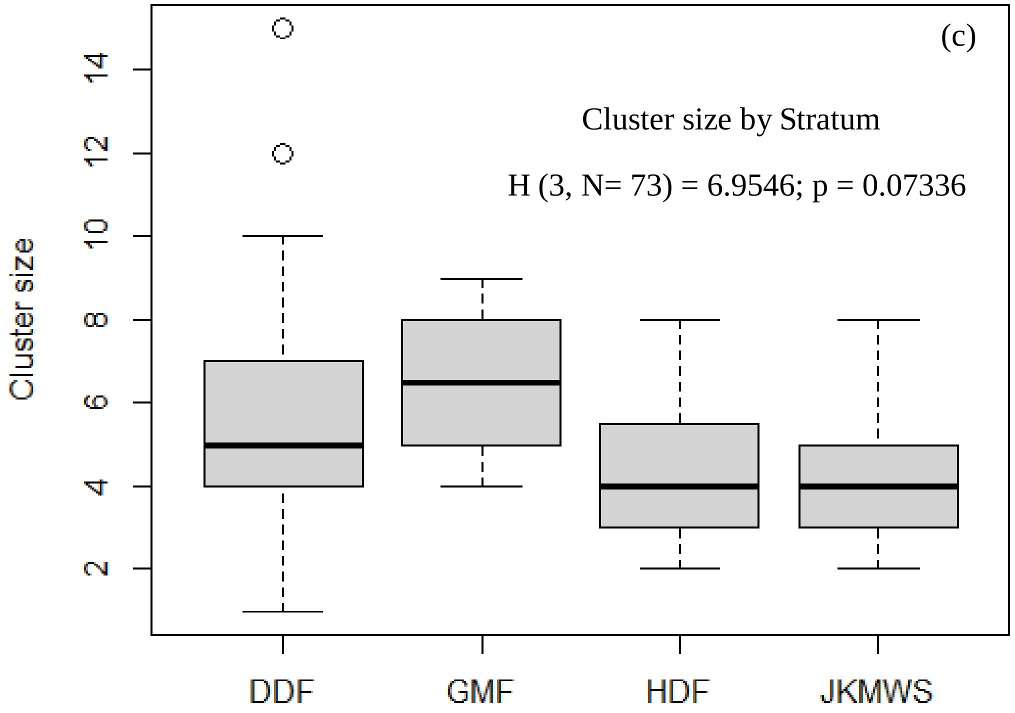
4.1. Population size and density estimates

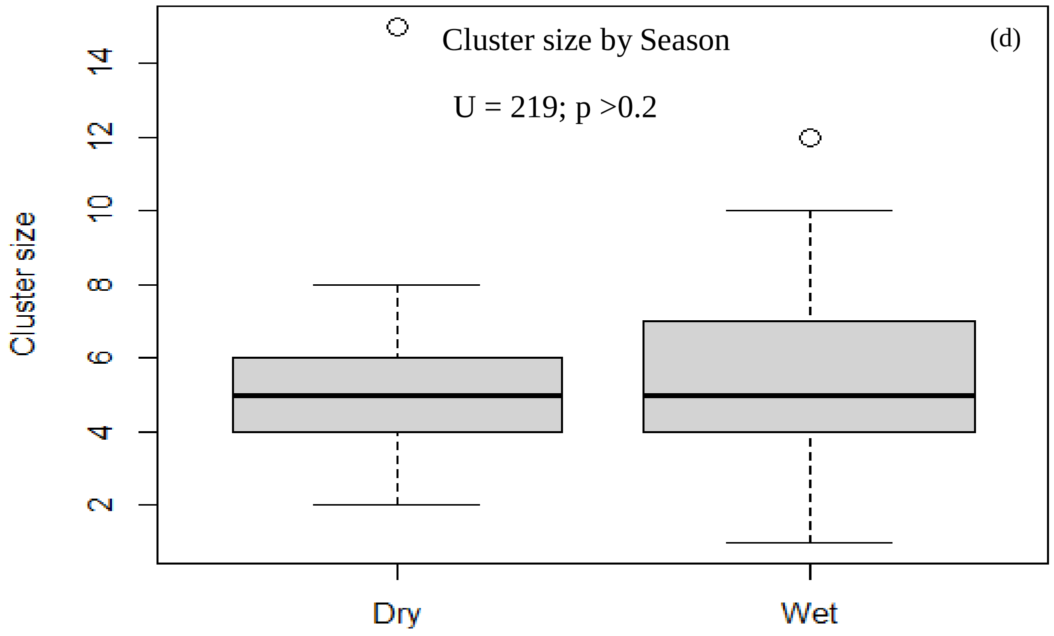
4.1.1. Encounter rate

In total, Djaffa Mountains guereza groups or clusters encountered 73 times (Table 2). The highest encounter rate was in HDF (1.25/km) followed by DDF (1.04/km), GMF (0.80/km) and JKF (0.57/km). The overall encounter rate was 0.96/km. The comparison of perpendicular distances and cluster sizes across the four forests revealed no statistically significant differences (perpendicular distance: H (3, N= 73) = 5.1175; p = 0.1634; cluster size: H (3, N= 73) = 6.9546; p = 0.07336; Fig. 13a and c). Perpendicular distance was not statistically different between seasons (Mann-Whitney U = 804.5; p = 0.09685; Fig. 13b), and also group size (U = 219; p > 0.2, Fig. 13d). The correlation between perpendicular distances and cluster size was not significantly different (p>0.2, Fig. 13e).




(b)
Distance by Season
U = 804.5; p = 0.09685
Distance (m)
10
20
30
40
50
Dry
Wet


(c)
Cluster size by Stratum
H (3, N= 73) = 6.9546; p = 0.07336
Cluster size
2
4
6
8
10
12
14
DDF
GMF
HDF
JKMWS



Cluster size vs. Distance

Spearman r = 0.1256; p = 0.2896; N = 73

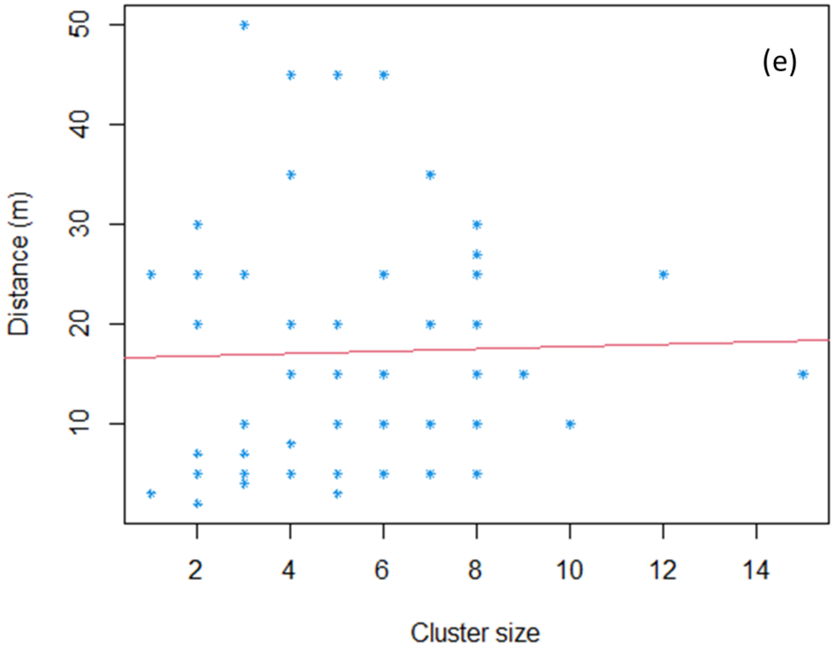


Figure 13. Comparison of perpendicular distances (a and b) and cluster sizes (c and d) among the four forests, and the two seasons and the correlation between cluster size and

perpendicular distance (e). Dindin Forest (DDF), Jallo Kuni-Muktar Wildlife Sanctuary (JKMWS), Hades Forest (HDF), and Gara Muleta Forest (GMF).

4.1.2. Cluster size and composition

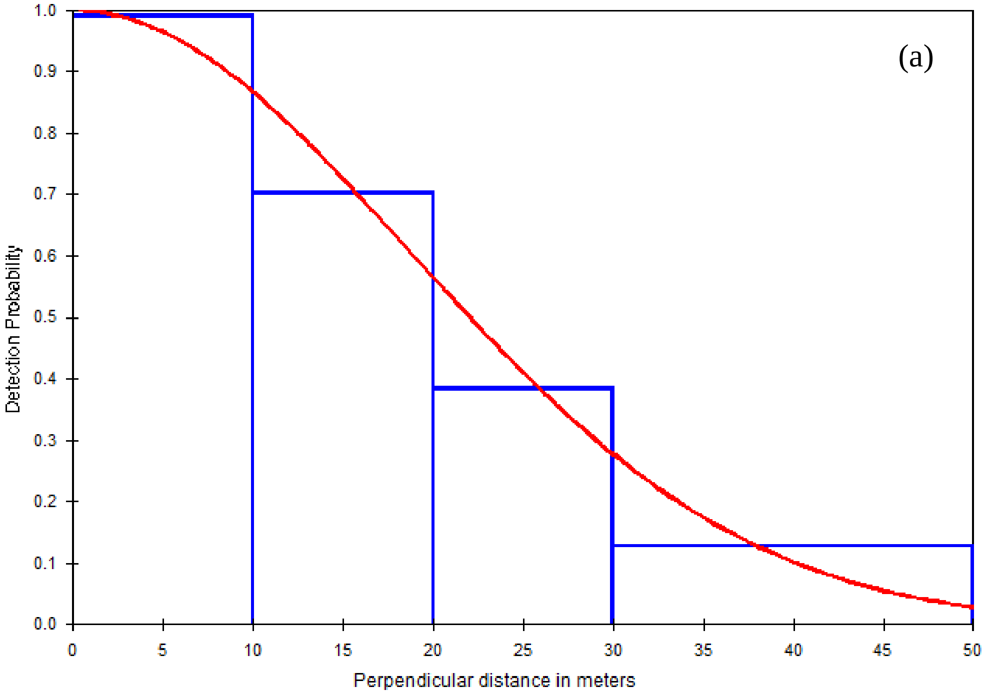
A group of *C. g. gallarum* consists of up to 15 individuals, including 1–3 adult males and several adult females and young. Djaffa Mountains guereza individuals per cluster varied from 1 to 15 (N = 73), with an overall mean cluster size of 5.3 ± 2.5 (mean ± standard deviation (SD)). The mean cluster size observed during dry season was 5.28 ± 2.5 (mean ± SD), while during wet season of 5.32 ± 2.54 (mean ± SD). Of the total 73 groups encountered, 54 (74%) were one-male groups and 19 (26%) contained more than one adult males.

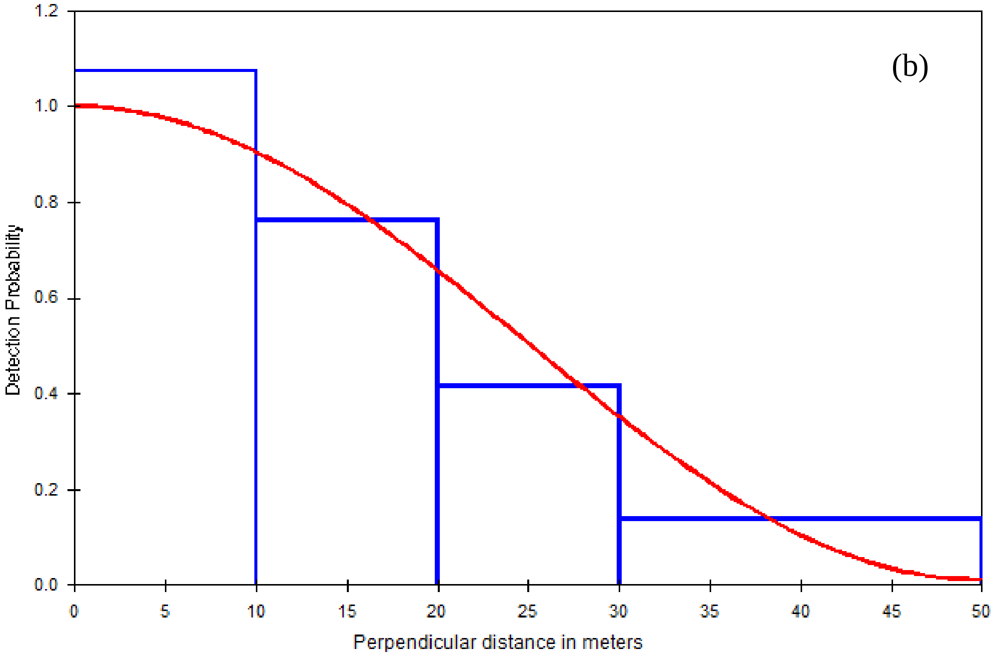
Within 73 sighted groups, 387 individuals of *C. g. gallarum* were recorded, of which 32.8% (127) were adult females, 24% (93) adult males, 38.5% (149) juveniles and 4.6% (18) infants (Appendix 7). The sex ratio of adult females to males was 1:0.73 and adult females to infants was 1:0.14.

Group sizes and proportion of one-male groups did not differ significantly among four different forest sites (Appendix 8). The study found 41 clusters at DDF (5.5 ± 2.8, range 1–15), of which, 30 were one-male clusters and 11 were multi-male clusters. The study counted 10 clusters at GMF, with an average of 6.4 ± 1.6, six being one-male and the remaining two-male clusters. The study recorded 15 clusters in HDF, of which 12 were one-male and the remaining three being two-male clusters, with a mean of 4.47 ± 1.9. At JKF, seven clusters were identified and recorded with a mean of 4.3 ± 1.8 of which one consisted of two-male clusters.

4.1.3. Modelling detection function

The result of model selection suggested the best detection model was a half-normal key function and no adjustment (Table 4). Chi-square goodness-of-fit tests show that grouped distance data provides an adequate fit ($\chi^2 = 0.1682$, DF = 2, P = 0.9193; Appendix 6). Figure 14 depicts the fitted detection function averaged over the observed perpendicular distance for different key functions (labelled a-d). Histograms of detected distances show higher detections close to the line transect, fitting the assumption of distance sampling analyses.





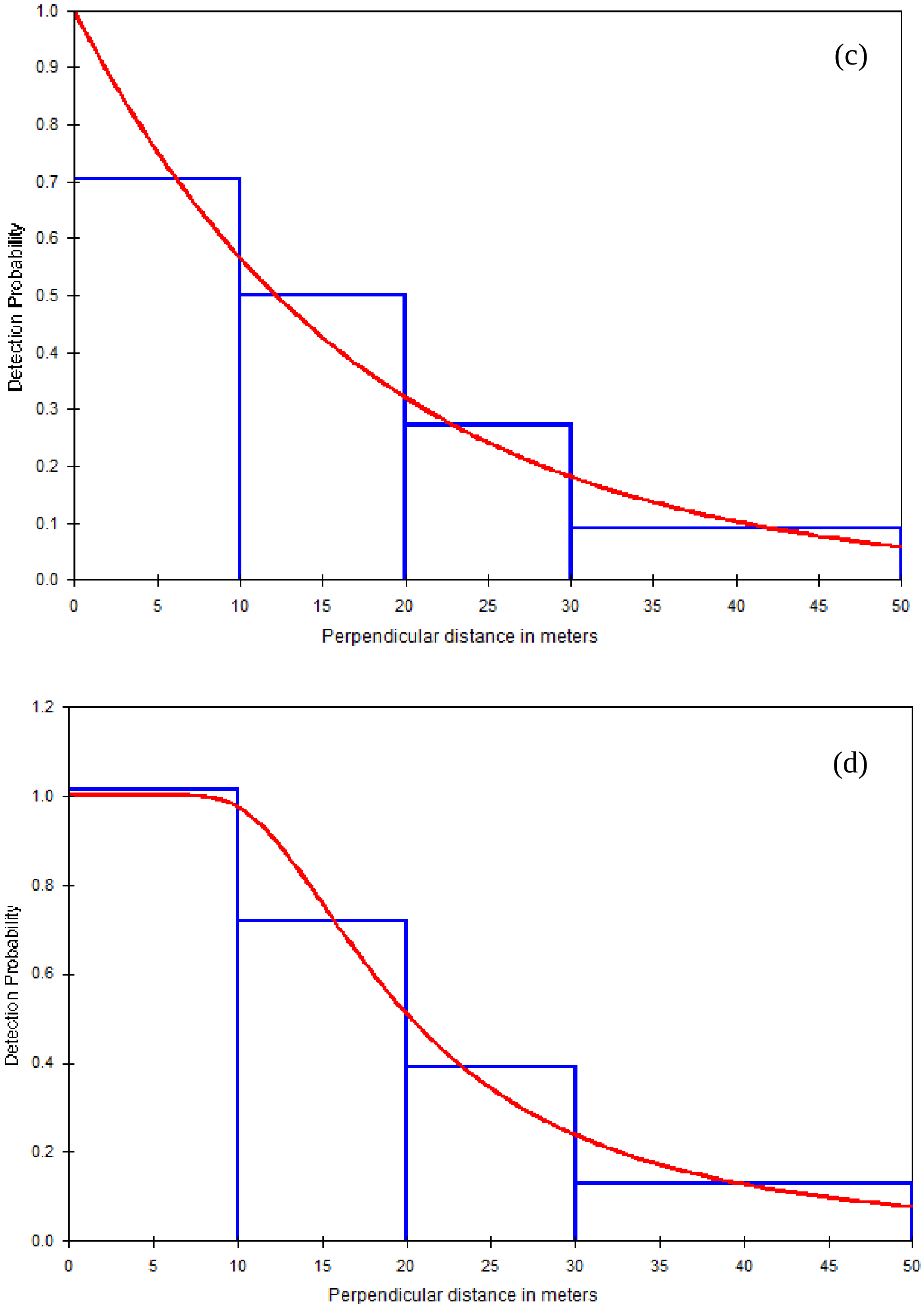


Figure 14. The detection function models of *C. g. gallarum* fitted using different key functions for all data combined and encountered during the field surveys across the forest fragments in the Ahmar Mountains, Eastern Ethiopia (a) half normal, (b) uniform, (c) negative exponential, (d) hazard rate.

Table 4. Results from fitting different detection models for Djaffa Mountains guerezas across the four forest sites during the survey periods.

Model (series)	np	ΔAIC*	AIC	Pa	ESW (m, 95%CI)	D (95% CI)	D (CV)
CDS: HN	1	0.00	186.75	0.47(0.39–0.56)	23.31 (19.28–28.19)	109.62 (75.99–158.13)	0.183
CDS: UN (CS)	1	0.70	187.45	0.51 (0.45–0.57)	25.28 (22.49–28.42)	101.06 (72.05–141.76)	0.167
CDS: NE	1	0.88	187.64	0.33 (0.25–0.44)	16.60 (12.41–22.20)	153.96 (100.85–235.05)	0.214
CDS: HR	2	2.04	188.79	0.48 (0.36–0.63)	23.86 (18.05–31.54)	107.11 (70.69–162.28)	0.210

4.1.4. Abundance and density estimate

We estimated the group density as 20.6 clusters/km^2 (95% CI: 14.5–29.3; %CV = 17. 5; DF = 35.1) and the population density of Djaffa Mountains guerezas as 109.6 individuals/km^2 (95% CI: 76.0–158.1; %CV = 18.3 %; DF = 42.3) (Table 5). The estimated total population size for the complete study area of 183 km^2 was 20,061 individuals (95% CI: 13,907–28,938; %CV = 18.3).

Table 5. Parameter estimates and inference for *C. g. gallarum* across the forest fragments during the survey periods using the best model selected.

Parameter	Point Estimate	SE	% CV	DF	95 % CI	
A (1)	18.74	1.91	-	-	-	-
f (0)	0.04	0.004	9.55	72.00	0.04	0.05
p	0.47	0.05	9.55	72.00	0.39	0.56
ESW	23.31	2.23	9.55	72.00	19.28	28.19
n/L	0.96	-	14.60	18.00	0.71	1.31
DS	20.63	3.60	17.45	35.07	14.51	29.31
E(S)	5.32	0.30	5.55	72.00	4.76	5.94
D	109.62	20.07	18.31	42.32	75.99	158.13
N	20,061	3673.3	18.31	42.32	13,907	28,938

4.2. Habitat suitability and distribution using MaxEnt

4.2.1. Model efficacy and the significance of the variables

The correlation coefficients of the ecological predictors were tested for final MaxEnt model (Appendix 4). The variable inflation factor for all predictor variables incorporated into the model showed less than 10 (R^2 = 0.6364, F = 9.946, DF = 9, P = 1.483e-07) (Table 3). The omission rate for the test data and the predicted area are based on the value of the cumulative threshold and are presented in Figure 15. The MaxEnt model for Djaffa Mountains guereza provided a high value AUC equal to 0.973±0.014, averaged over 10 replicate runs (Fig. 16).

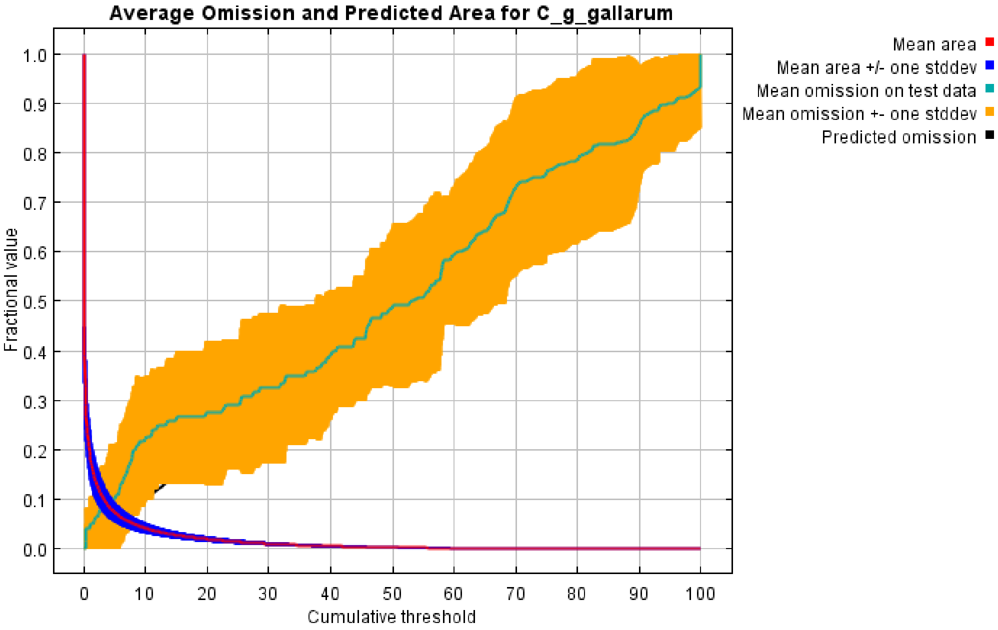


Figure 15. The omission rate for the test data and the predicted area based on the value of the cumulative threshold for current predictor variables used for modelling.

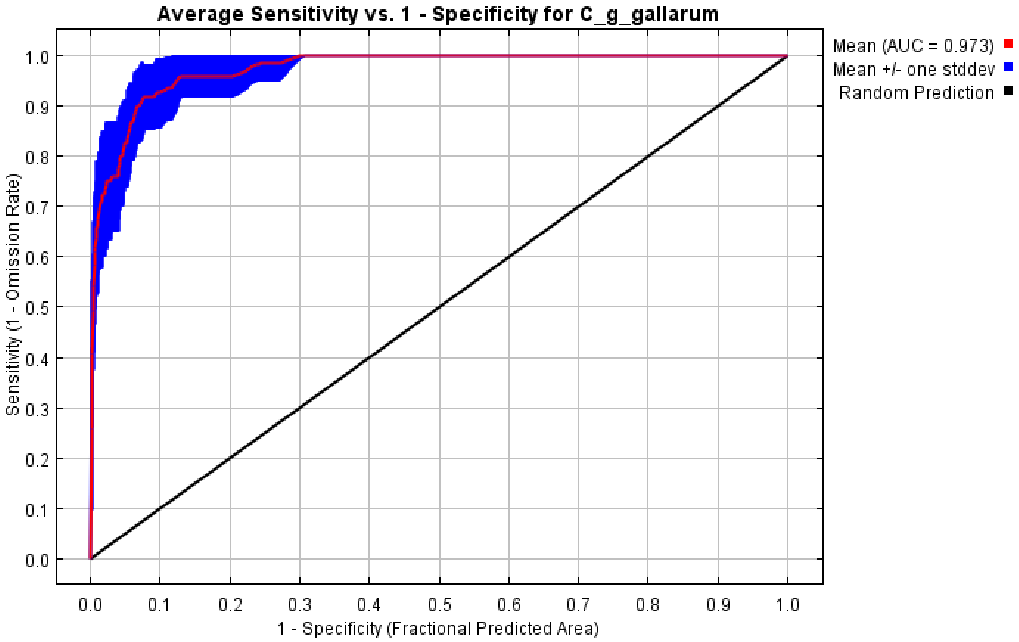


Figure 16. Djaffa Mountains guerezas, *C. g. gallarum*, habitat suitability prediction averaged over 10 replicate runs produced AUC value using test data.

An estimate of ecological predictors contribution to the MaxEnt model was given (Table 6). Precipitation in the wettest quarter (65.9%), land cover (17.4%), temperature seasonality (6.1%) and mean diurnal range (5.3%) were the four predictors with variable importance greater than 5%.

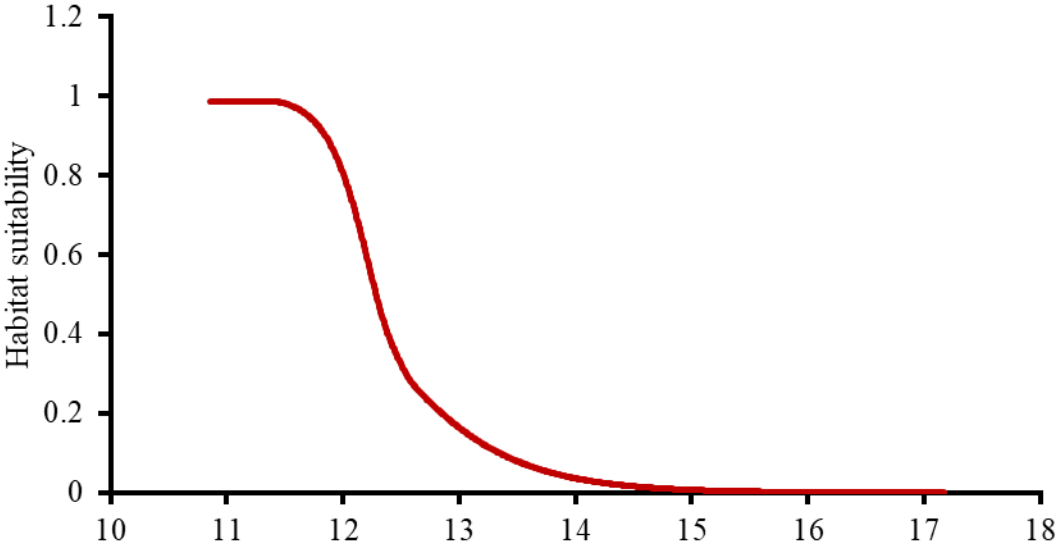
Table 6. Influence of predictor variables to model habitat suitability and distribution of *C. g. gallarum*.

Variable	Percent contribution*	Permutation importance
Bio16	65.90	80.30
Lulc	17.40	0.40
Bio4	6.10	5.30
Bio2	5.30	1.10
DistRvr	1.40	0.90
DistPopD	1.30	9.00
Bio15	1.20	0.00
Asp	1.00	1.10

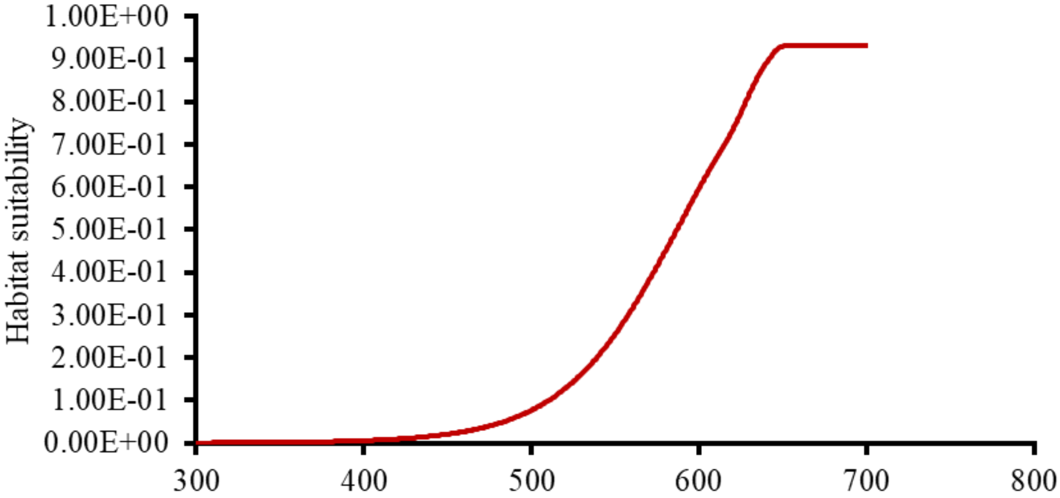
*Only variables with greater than 1 percent contributions were presented.

Response curves display a different model, namely, a Maxent model created using only the corresponding variable (Fig. 17). These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. Habitat suitability of *C. g. gallarum* decreases when the mean diurnal range increases (Fig. 17a). On the other hand, suitability was increasing with precipitation of the wettest quarter (Fig. 17b) and precipitation seasonally (Fig. 17c). Temperature seasonality influence on the habitat suitability of *C. g. gallarum* fluctuated (Fig. 17d). The habitat suitability map (in a clockwise direction, the aspect is indicated as North-East-South-West; Fig. 17e) revealed that aspect has a positive relationship with the *C. g. gallarum* occurrence. From the landscape composition perspective, broadleaved evergreen forest (0.83) was the best predictor, followed by the broadleaved deciduous forest (0.41) (Fig. 17f). A single limiting variable changes shortly and the distribution is truncated for continuous variables (labelled as Fig. 17 a-e).

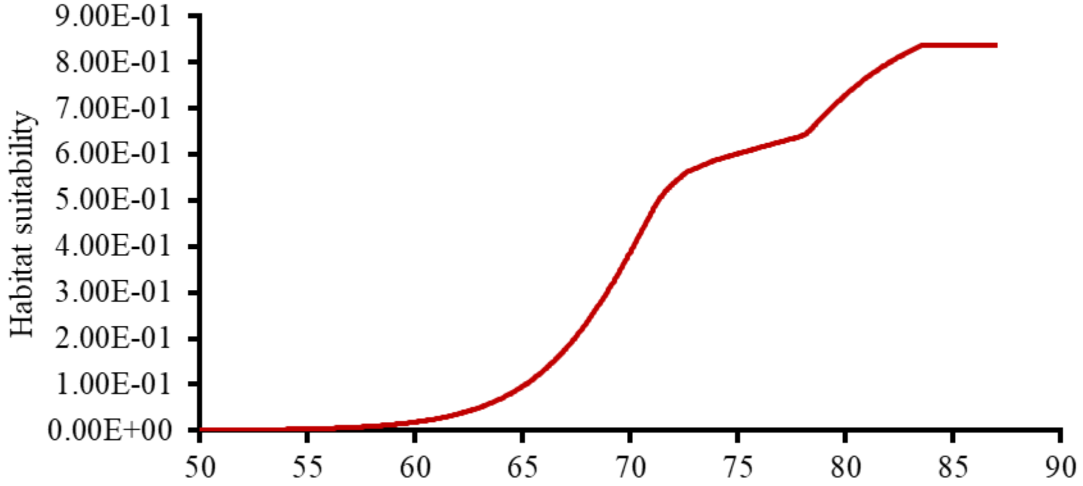
MaxEnt model evaluated by jackknife AUC for *C. g. gallarum* habitat suitability prediction also validated the importance of the precipitation of the wettest quarter (Fig. 18). In this study, altitude and slope were highly corelated with other variables and removed from model fitted. Note that all of these plots of habitat suitability distribution in gradients did not represent normal curves, suggesting at least one tail was missing when the distribution of the species extends beyond the measured gradients.



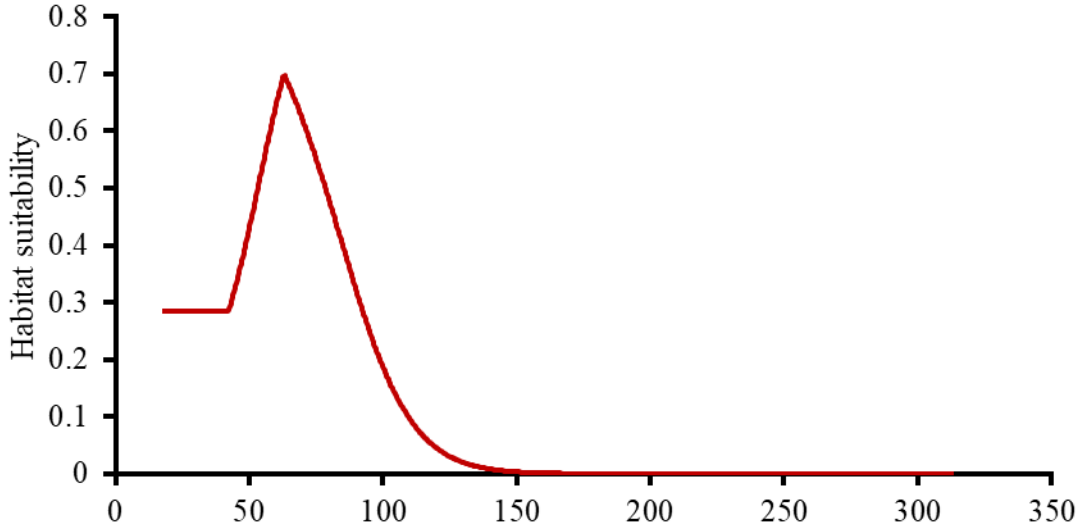
(a) Mean Diurnal Range (Mean of monthly (max temp - min temp)) (°C)



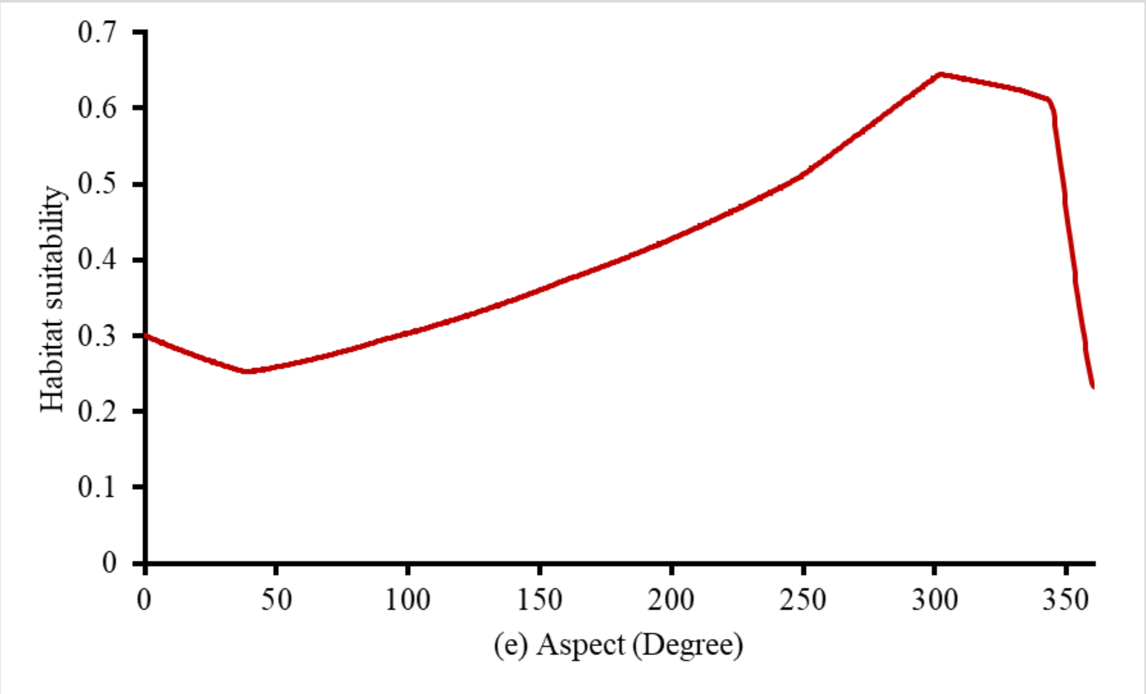
(b) Precipitation of Wettest Quarter (mm)



(c) Precipitation Seasonality
(Coefficient of Variation) (mm)



(d) Temperature Seasonality (standard deviation ×100) (°C)



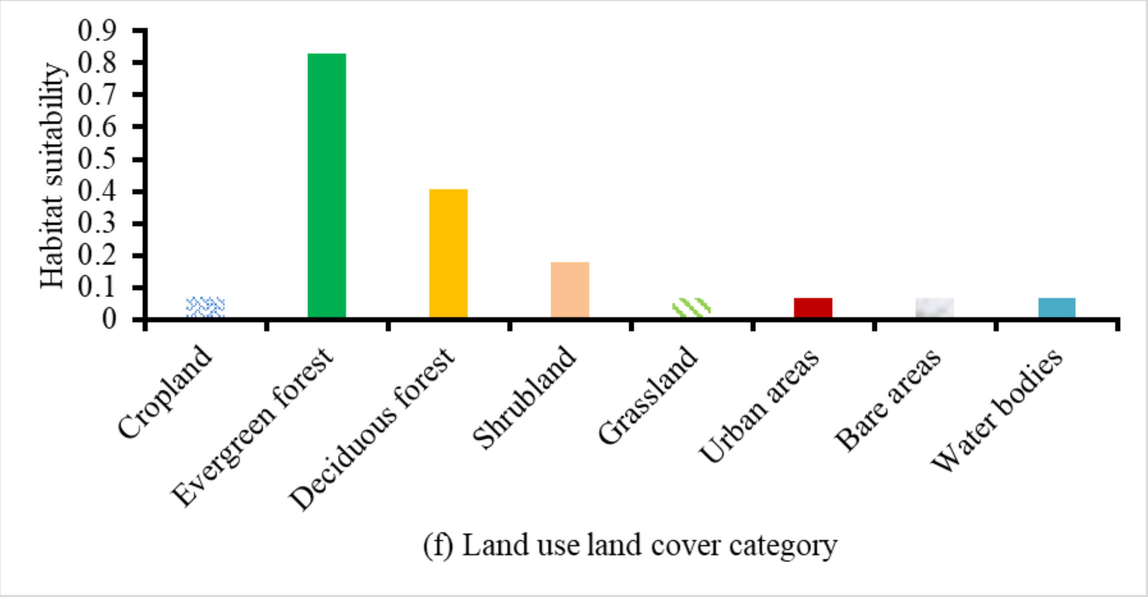


Figure 17. Response curves of the most important variables showing the mean response of habitat suitability of *C. g. gallarum* to predictor variables.

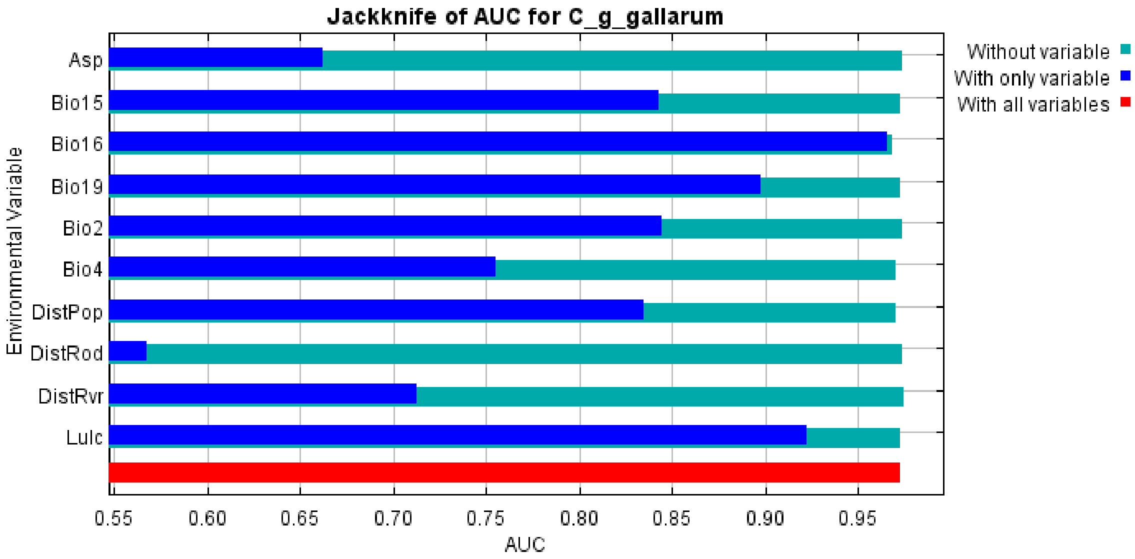
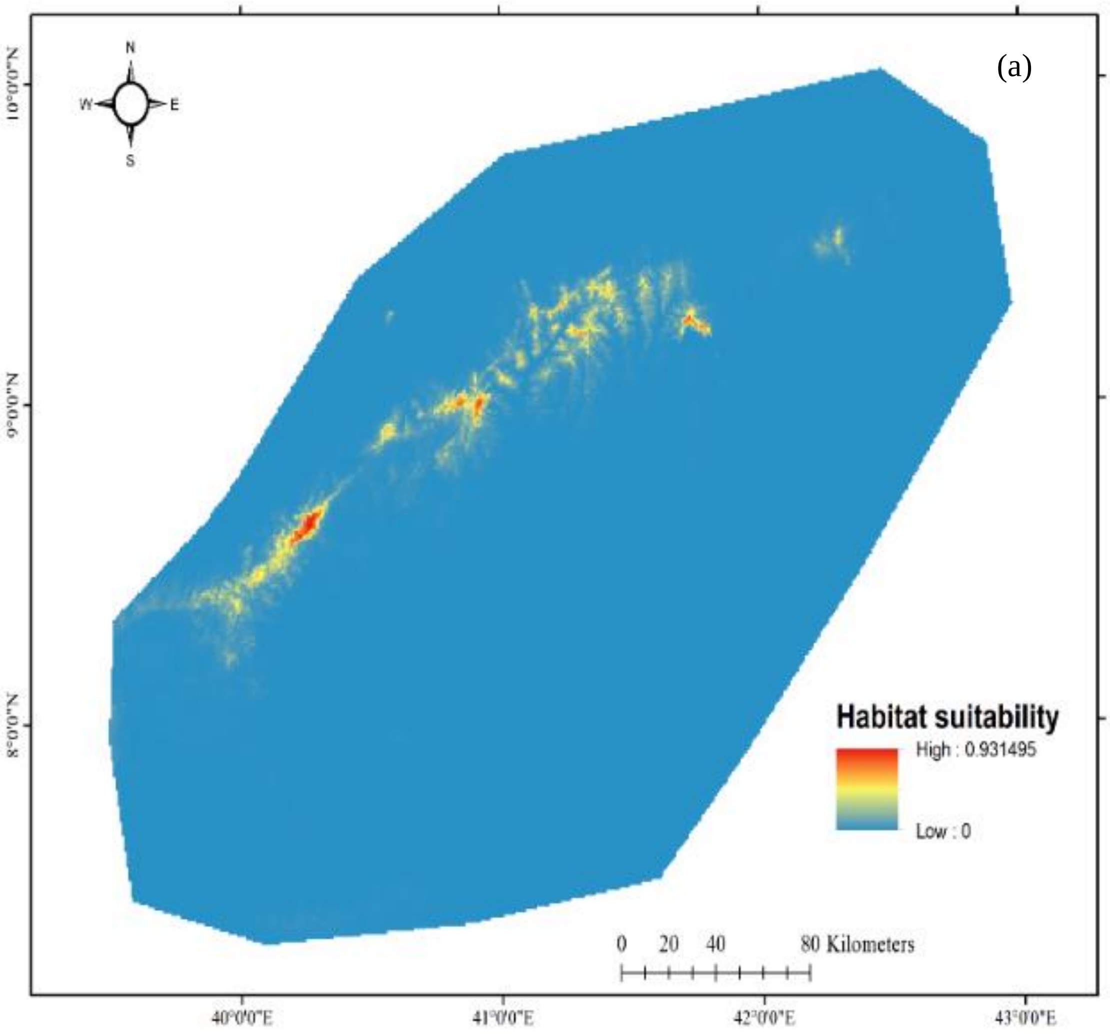


Figure 18. *Colobus g. gallarum* habitat suitability modelling evaluated by jackknife analysis.

4.2.2. Current predicted habitat suitability

The suitability and spatial distribution of *C. g. gallarum* habitat was predicted. The model discriminates suitable habitat with an excellent power (AUC = 0.973±0.014) (Fig. 16). About 1,336.1 km^2 (1.8%) of suitable habitat exists for *C. g. gallarum* from a total of 75,307.49 km^2 geographic extent considered (Fig. 19a). This suitable area was further classified as highly suitable with an area of 183.26 km^2 (13.33%), whereas 86.67% of the remaining area was moderately suitable. The highly suitable habitats for the *C. g. gallarum* were highly fragmented and dispersed in different localities of the eastern Ethiopian highland, particularly where the National Forest Priority Protected area existed, including in Eastern Arsi, West Hararghe, and East Hararghe Zones (Fig. 19b).


(a)
N
S
W
E
10°0'0"N
9°0'0"N
8°0'0"N
40°0'0"E
41°0'0"E
42°0'0"E
43°0'0"E
Habitat suitability
High : 0.931495
Low : 0
0 20 40 80 Kilometers

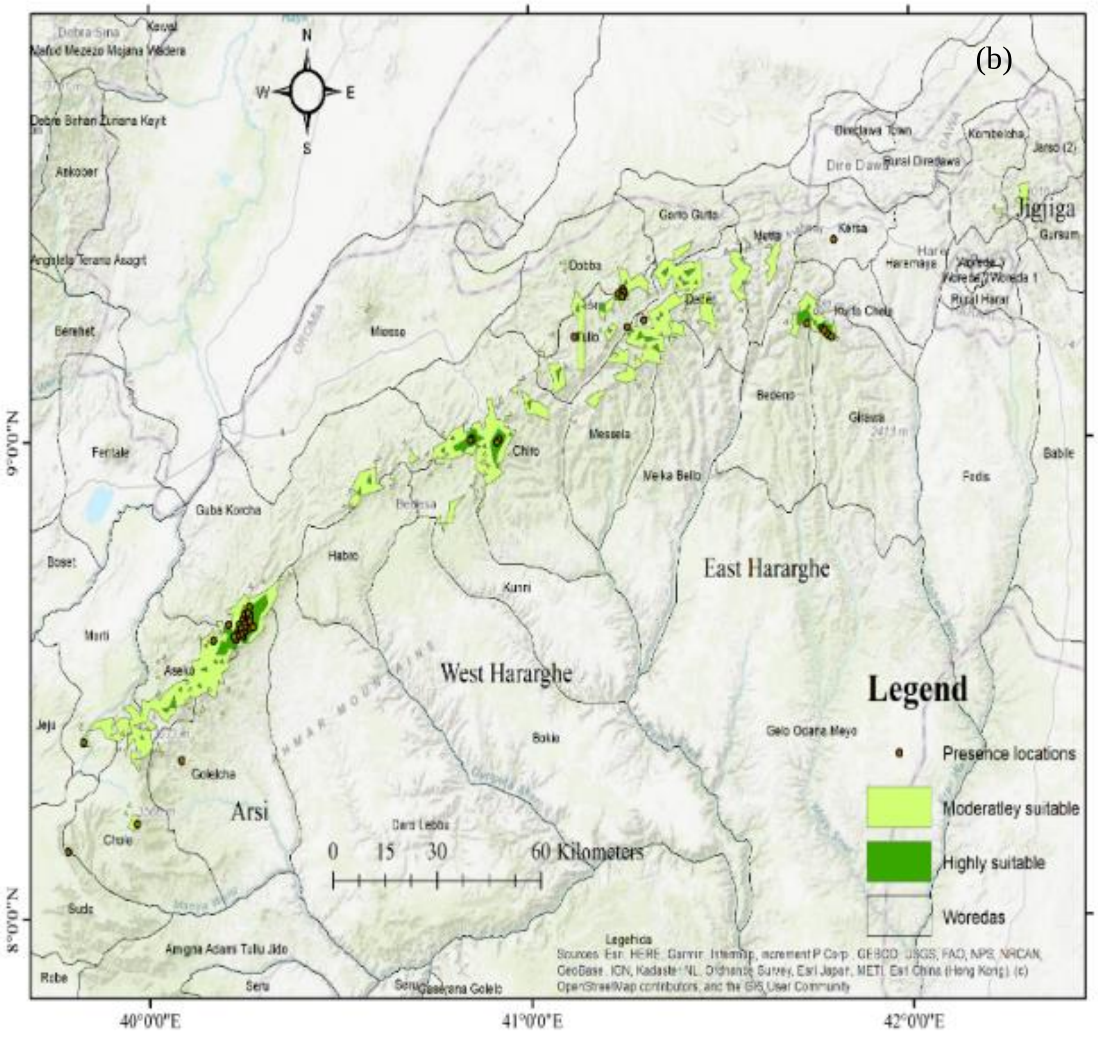


Figure 19. The current predicted habitat suitability of *C. g. gallarum* using the MaxEnt algorithm: a) Continuous MaxEnt model output showing areas with red colour as highly suitable and blue colour unsuitable and b) map indicating the reclassified suitable areas overlaid with the occurrence localities and topographic Base-map.

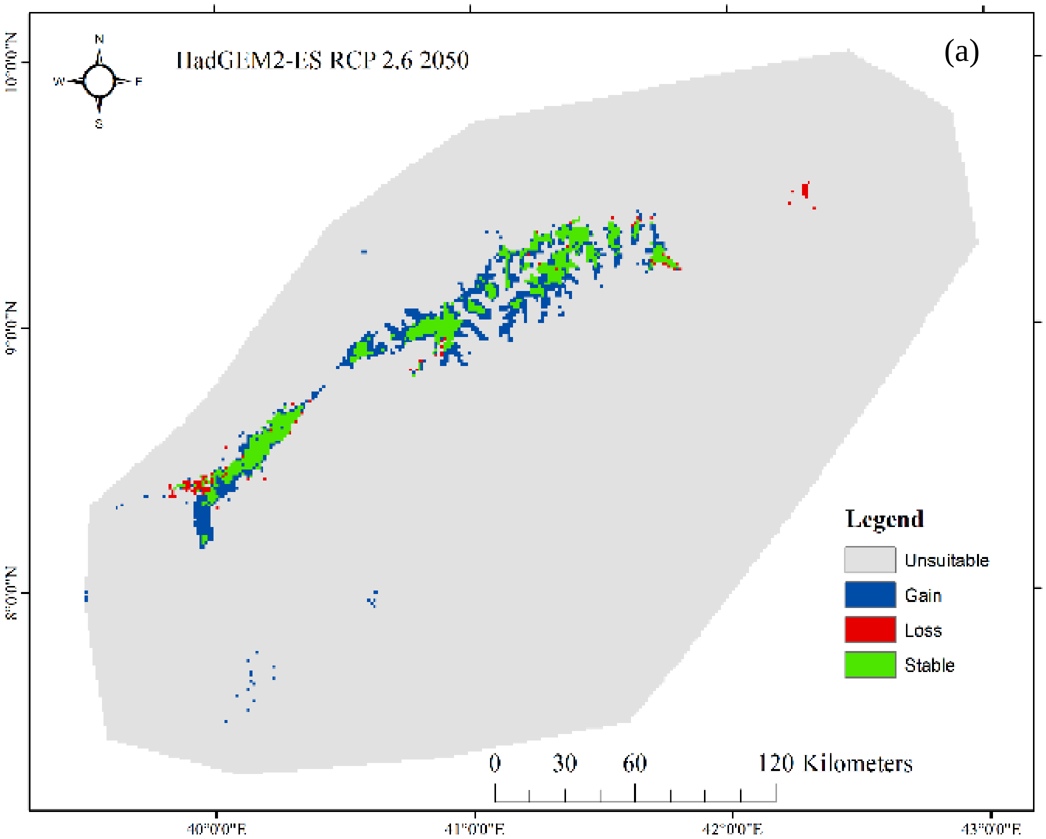
4.2.3. Future model evaluations and variable importance

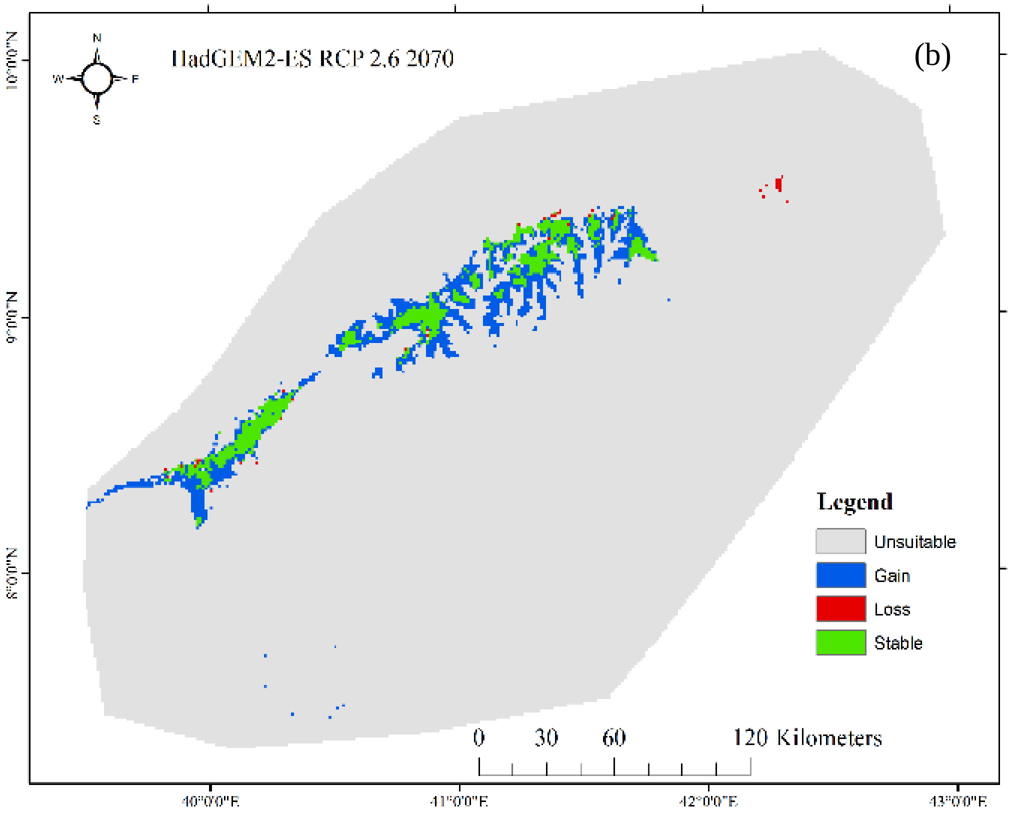
We predicted the suitable habitat distribution of *C. g. gallarum* under two RCP scenarios and GCM systems (Fig. 20). The range of AUC values for several climate change scenarios was 0.96 to 0.98, which indicates an "excellent" predictive power (Appendix 9). The jackknife test revealed the best predictor of suitable habitat was the precipitation of the wettest quarter (Bio16), with the percent contributions ranging between 62.90 and

91.40 under all future climate scenarios, whereas other predictor variables had variability in percent contributions and jackknife tests under different scenarios (Appendix 10).

4.2.4. Future habitat distribution model

Using two GCMs, suitable habitat and its distribution were predicted for *C. g. gallarum* under the worst (RCP 8.5) and most conventional (RCP 2.6) emission scenarios (Appendix 11). The model's output demonstrated the overall increase in *C. g. gallarum*'s suitable habitat under all future climatic scenarios (Fig. 20a-f, Table 7). According to RCP 2.6, the largest increase in *C. g. gallarum*'s suitable habitat was projected for the year 2070, at 182.58% for the BCC-CMS1-1 and 155.32% for the HadGEM2-ES model systems (Appendix 11). It was expected that in all route scenarios, the amount of habitat loss would be almost equal, except there is a very low amount of predicted habitat loss under of year 2050s the BCC-CMS1-1 and of year 2070s for the HadGEM2-ES (Table 7).

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HadGEM2-ES RCP 2.6 2070
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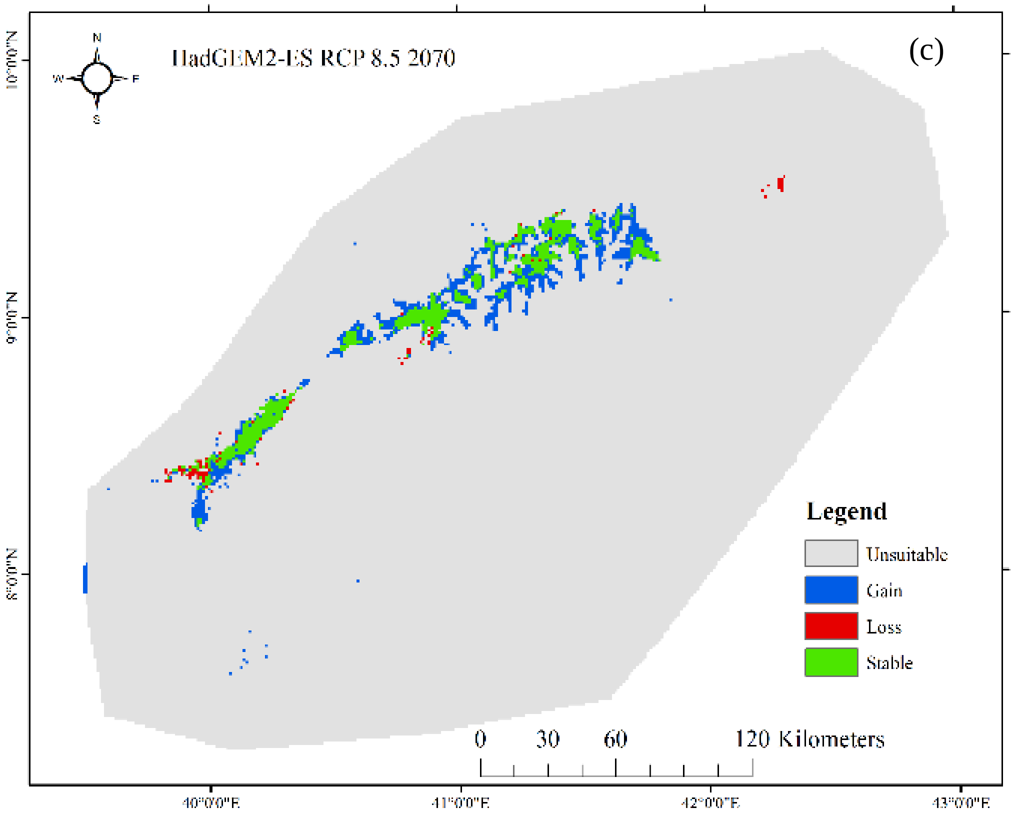
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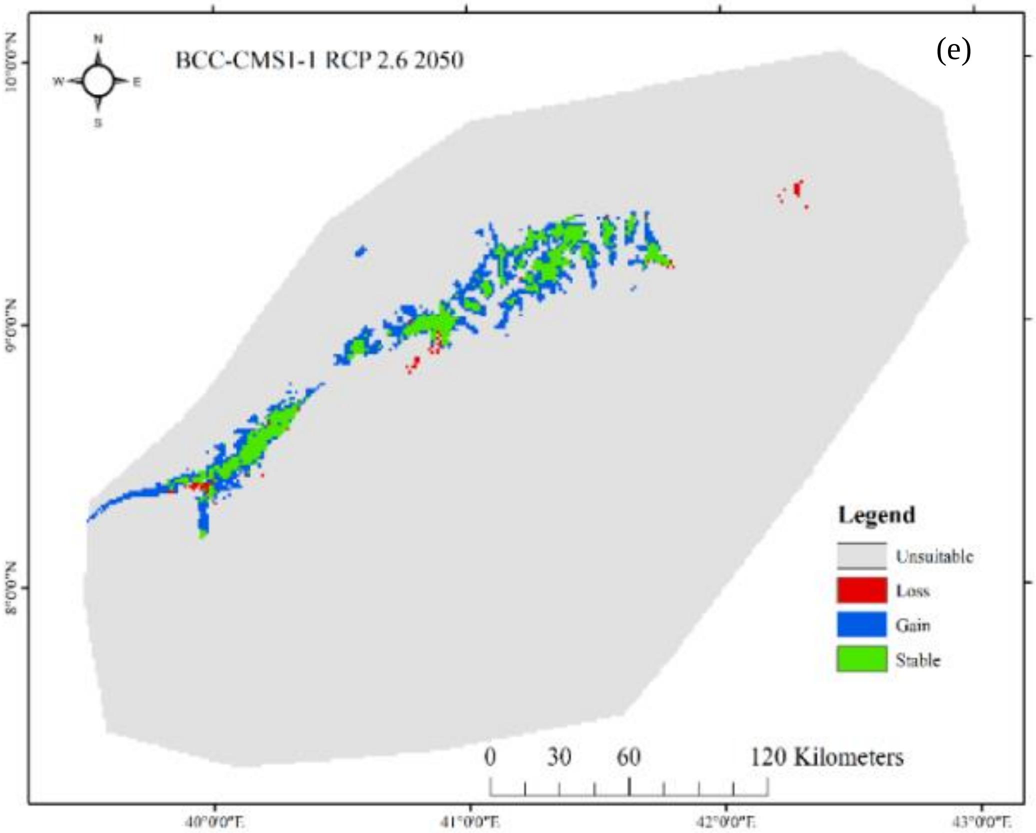
42°0'0"E
43°0'0"E


BCC-CMS1-1 RCP 2.6 2050
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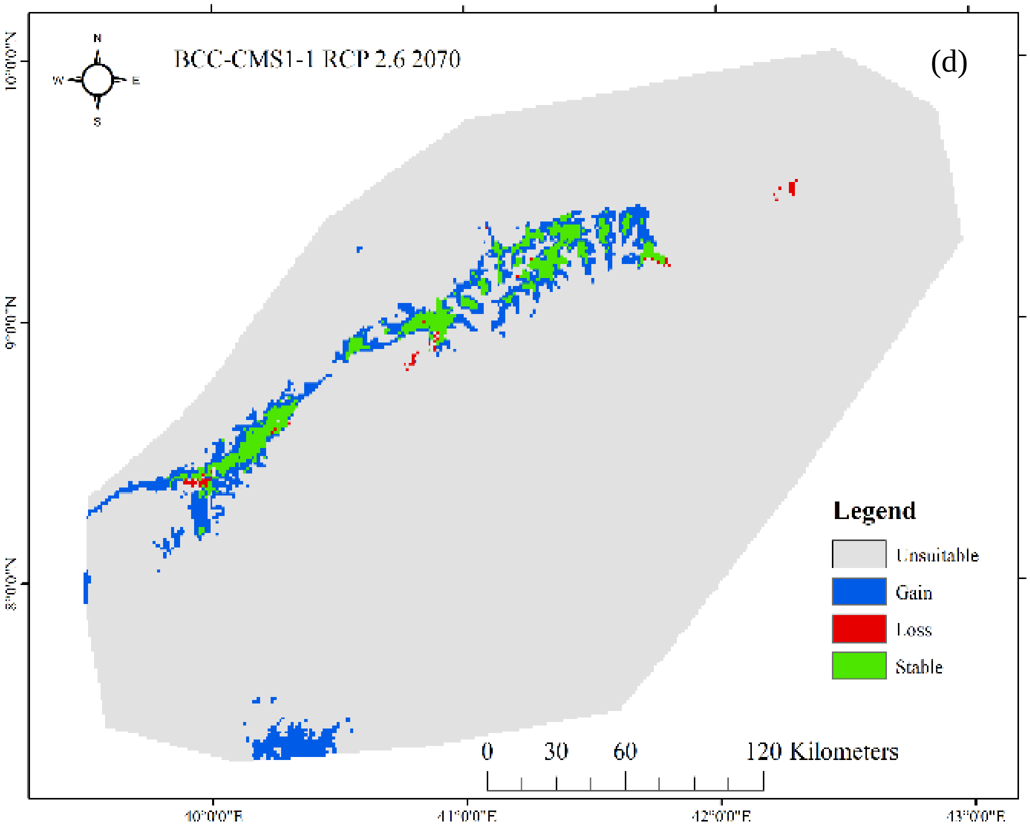
BCC-CMS1-1 RCP 2.6 2070
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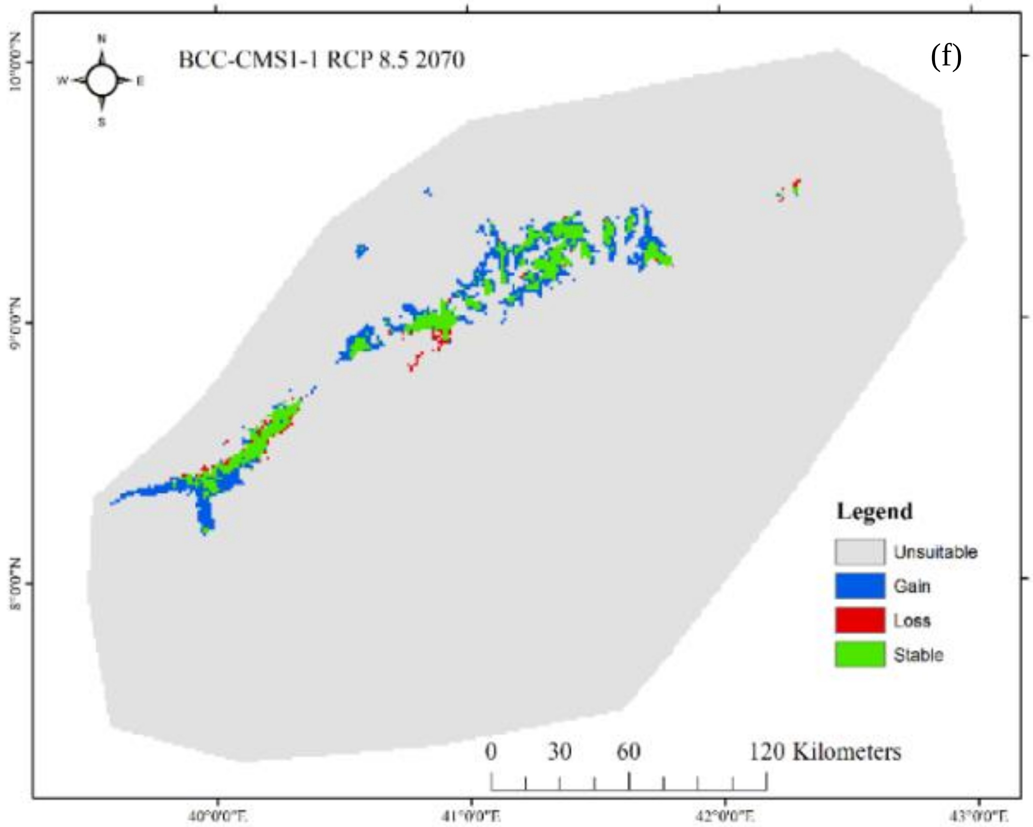


Figure 20. Habitat suitability of *C. g. gallarum* predicted by MaxEnt, including the RCP 2.6 and RCP 8.5 scenarios, for the 2050s and 2070s, using two climate models.

Table 7. Average rang size changes of *C. g. gallarum* predicted under all scenarios using two global climate models.

GCM		BCC-CMS1-1		HadGEM2-ES	
Suitability models scenarios	Current	RCP 2050	RCP 2070	RCP 2050	RCP 2070
Suitable habitat (km^2)	1336.05	3096.36	3049.58	2578.98	2954.96
Stable habitat (km^2)	1336.05	1249.23	1207.05	1178.72	1221.12
Stable habitat (%)	100.00	93.50	90.30	88.20	91.40
Gain (km^2)		1847.13	1842.53	1400.25	1733.84
Gain (%)		138.20	137.90	104.80	129.80
Loss (km^2)		86.82	128.99	157.32	114.93
Loss (%)		6.50	9.70	11.80	8.60
Net gain/net loss (km^2)		1760.31	1713.53	1242.93	1618.91

4.3. Ecological niche determinants and Anthropocene refugia

4.3.1. Model optimal and accuracy

The general distribution of the AUC values among the algorithms and subspecies varied (Table 8). Except for RF model predicted suitable habitats for *C. g. gallarum*, all the models had an excellent predictive performance (AUC > 0.90) (Table 8). The COR values computed using the five state-of-art models different between and within the subspecies. The variables that have contributed the most to predict the suitable habitat of *C. g. gallarum* include Max Temperature of Warmest Month, Precipitation Seasonality and Temperature Annual Range, whereas Annual Precipitation, Min Temperature of Coldest Month, and Precipitation of Wettest Quarter were the environmental factors that best predict the habitat suitability for *C. g. guereza* in increasing order.

Table 8. Metrics used for all algorithms to evaluate the performance of the models run (AUC, COR), indicating their maximum sensitivity and specificity (maxSS) as well as predicted habitat suitability (HS).

Algorithm	Subspecies							
	C. g. gallarum				*C. g. guereza*			
	AUC	COR	maxSS	HS predicted (km^2)	AUC	COR	maxSS	HS predicted (km^2)
GAM	0.98	0.29	0.15	132,523.70	0.93	0.15	0.33	193,503.64
GLM	0.98	0.21	0.44	58,773.62	0.93	0.15	0.32	216,285.15
MaxEnt	0.99	0.47	0.01	39,983.00	0.95	0.30	0.53	91,373.01
MaxEnt tuned	0.99	0.49	0.002	74,006.62	0.96	0.32	0.51	81,618.21
RF	0.79	0.55	0.001	19,544.95	0.93	0.41	0.02	105,684.97
Mean	0.95	0.40	0.12	64,966.38	0.94	0.27	0.34	137,693.00
SD	0.09	0.14	0.19	42,928.26	0.01	0.11	0.20	62,461.97

4.3.2. Ensemble potential predicted suitable habitats

The potential suitable habitats predicted were different between algorithms and subspecies (Table 8). The potential predicted suitable niche for *C. g. guereza* was 168,731 km^2 and suitable habitats for *C. g. gallarum* was 69,542 km^2 (Fig. 21; Table 9).

As expected, the suitable habitat of *C. g. gallarum* was mainly concentrated in its current range, whereas the predicted suitable habitat of *C. g. guereza* extended to geographic range of *C. g. gallarum*.

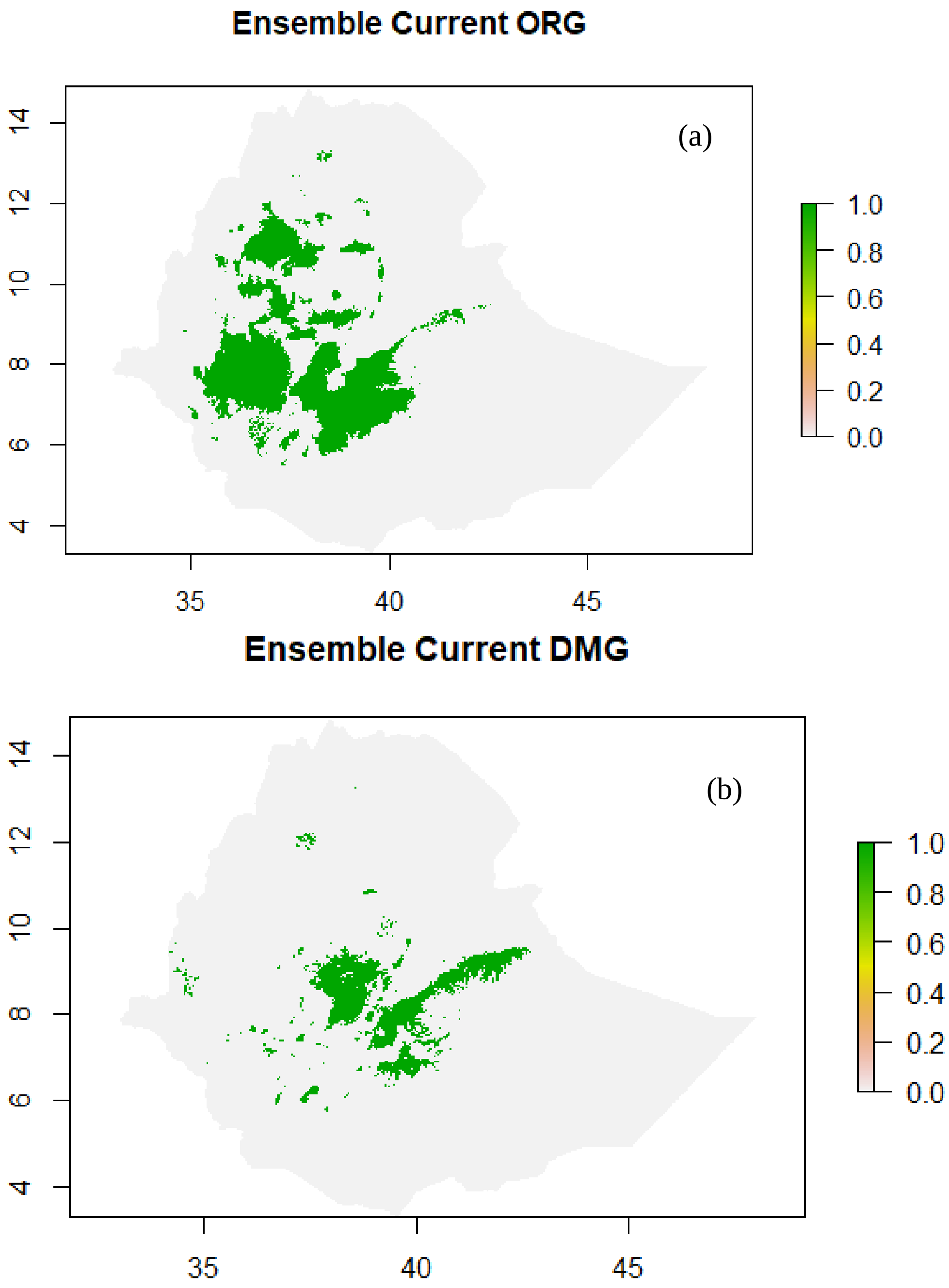


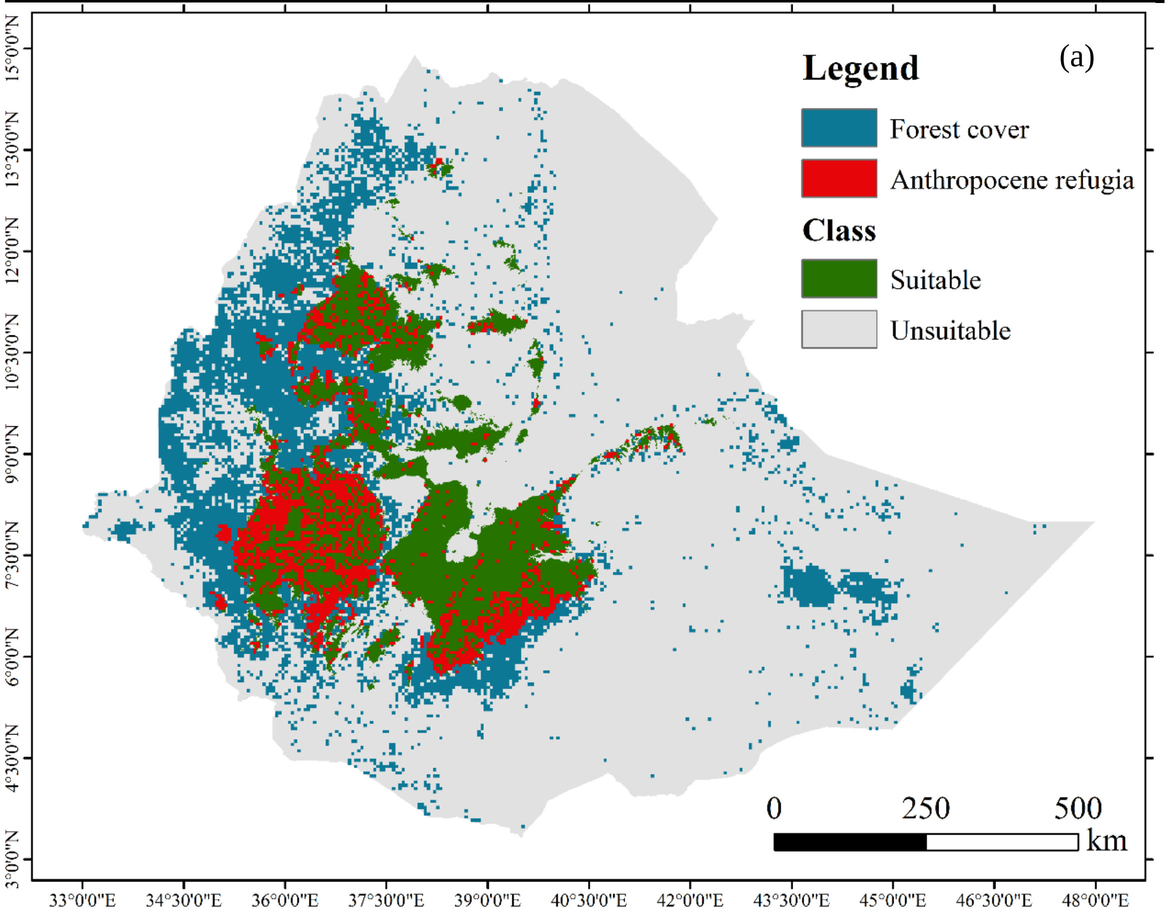
Figure 21. Current weighted mean ensemble habitat suitability maps produced for closely related sister taxa of Ethiopian guereza.

4.3.3. Anthropocene refugia

The Anthropocene refugia of the taxa obtained from the recent forest cover map of Ethiopia (Fig. 22a and b) showed that the suitable habitat for the *C. g. guereza* was 47,101.34 km^2 of the predicted fundamental niche, whereas that for the *C. g. gallarum* was 8,429.93 km^2 limited to the forest cover.

Table 9. Areas of suitable habitats of Ethiopian guereza (in km^2).

Taxa	Potential niche	Anthropocene refugia (AR)	AR within PA	AR outside PA	Potential niche within PAs
C. g. guereza	168,731	47,101.34 (27.92%)	18,729.29 (39.76%)	28,372.05 (60.24%)	42,500.88 (25.19%)
C. g. gallarum	69,542	8,429.93 (12.12%)	4,527.27 (53.70%)	3,902.66 (46.29%)	19,297.29 (27.75%)



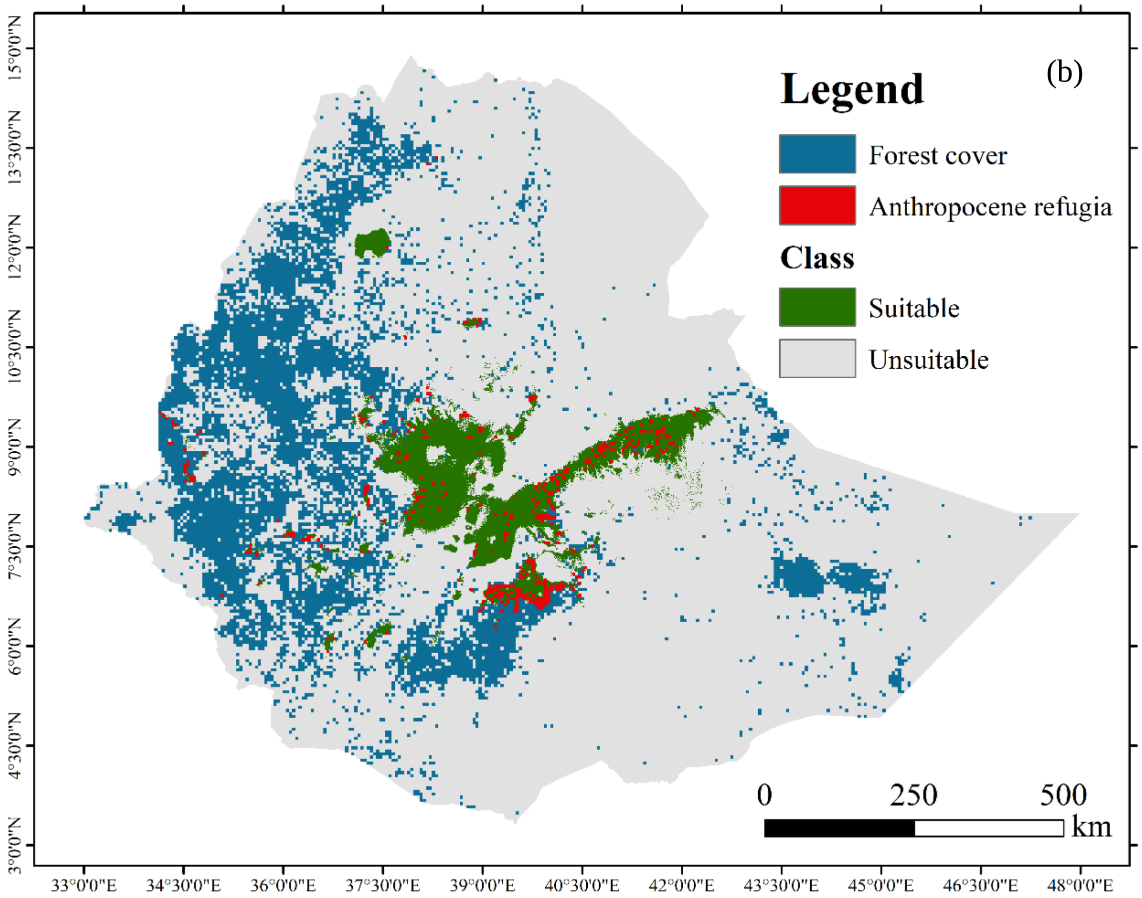


Figure 22. The predicted suitable habitats of Ethiopia's guereza confined within forest cover (Anthropocene refugia) predicted by ecological niche modelling: a) *C. g. guereza*, b) *C. g. gallarum*.

4.3.4. Protected Anthropocene refugia

A large proportion of the Anthropocene refugia (53.70%) coincided with the present PAs network for *C. g. gallarum*. However, *C. g. guereza* overlapped comparatively medium proportion of Anthropocene refugia (39.76%) with the current PAs system. The potential suitable habitats examined within PAs revealed that 42,500.88 km^2 and 19,297.29 km^2 of the suitable area were found within the Ethiopia's protected area network for *C. g. guereza* and *C. g. gallarum*, respectively.

4.3.5. Conservation and Anthropogenic threats

Anthropogenic disturbance had a significant impact on habitat suitability for the *C. g. gallarum* ($F_{1, 98}$ = 7.255, 95% CI = 0.0073–0.057, adjusted R^2 = 0.05943, p = 0.00832). In contrast, as expected, the habitat suitability of *C. g. guereza* was not significantly affected by the risk of anthropogenic threats ($F_{1, 98}$ = 0.7919, 95% CI = -0.0053–0.015, adjusted R^2 = -0.002106, p = 0.3757).

4.3.6. Niche overlap and climate syndromes

It was discovered that two subspecies' ecological niche were divergent than anticipated, meaning that their initial overlap values were in the lowest 5% of the null distribution. The ecological niche overlap estimates between subspecies show overlap indices of 0.244 and 0.378 for Schoener's *D* and Hellinger's *I*, respectively (Fig. 23). Of the 238,273 km^2 of potential predicted suitable habitats for both taxa, the niche overlap area was 41,055 km^2, while the suitable area account only for *C. g. guereza* was 127,675 km^2 and for *C. g. gallarum* was only 28,487 km^2.

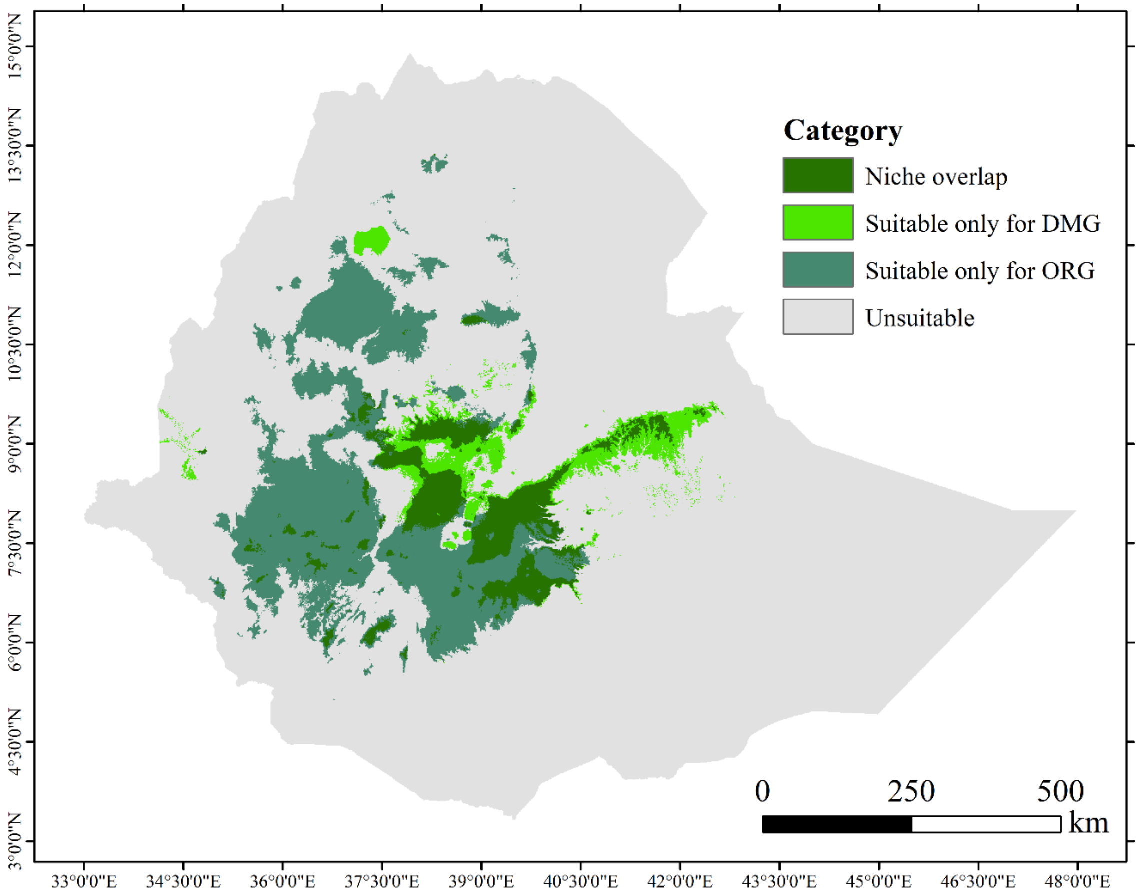


Figure 23. Computed niche overlap (divergence) to illuminate niche requirements between the two taxa.

Evidence for climate response syndromes was discovered when looking at the subspecies' appearances in multivariate climate space (Fig. 24). There was no significant grouping of taxa in the climate-response space. For each subspecies, the top two PCA described 65.2 % variance. The top two components, PC1 and PC2, explained 42.8% and 22.4% of variation in 163 occurrence points, respectively, with PC1 positively correlated with all variables except biol14, while PC2 positively correlated with Biol12, Biol15 and Biol16.

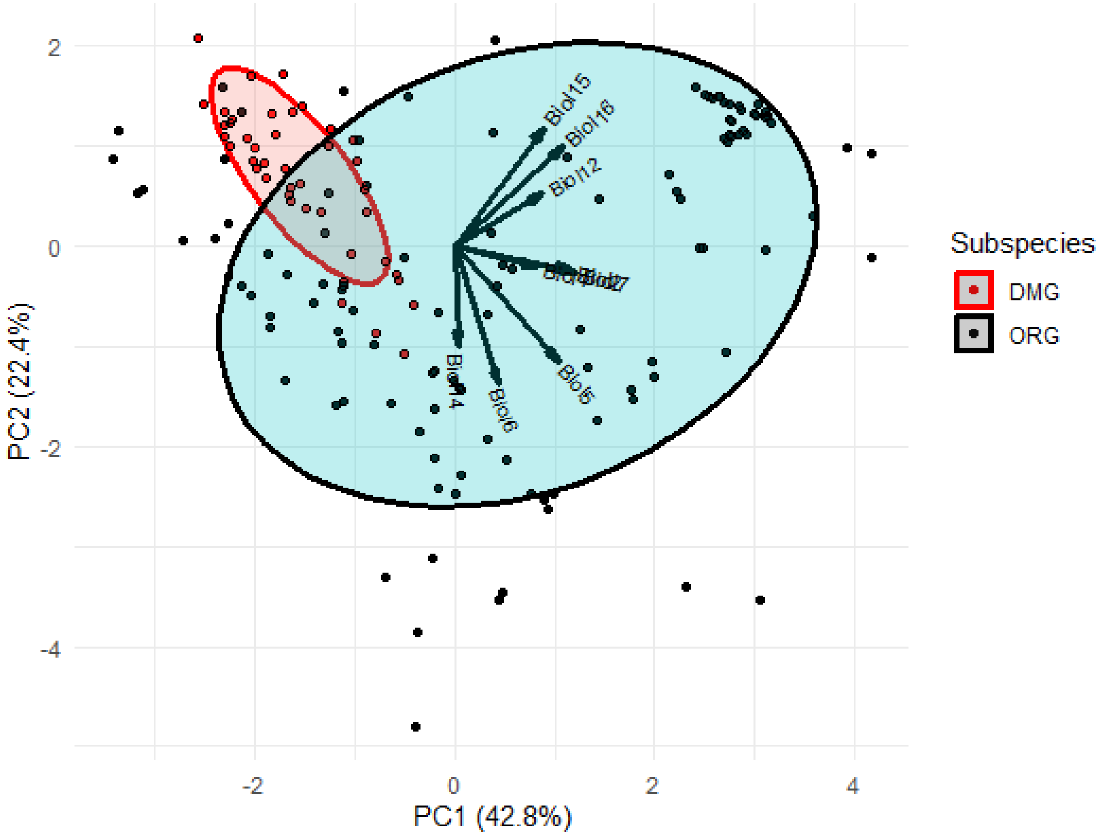


Figure 24. Principal component analysis ordination of the environmental variable space requirements of the two subspecies throughout their ranges. Each point represents estimated regression coefficients for a subspecies. Vectors indicate the direction and magnitude of correlations of climatic indications determining occurrence. Ellipses were the 95% confidence interval surrounding the centroid for each taxon's occurrence. DMG stands for Djaffa Mountains guereza whereas ORG is for Omo River guereza.

4.3.7. Abundance-suitability prediction patterns

The observed abundance of *C. g. gallarum* and habitat suitability index had positive association ($\rho = 1$, $p < 2.2e-16$), with strong predictive power (deviance explained = 50% of the variation in local abundance, on average), predicting abundance across the subspecies' geographical range (Fig. 25).

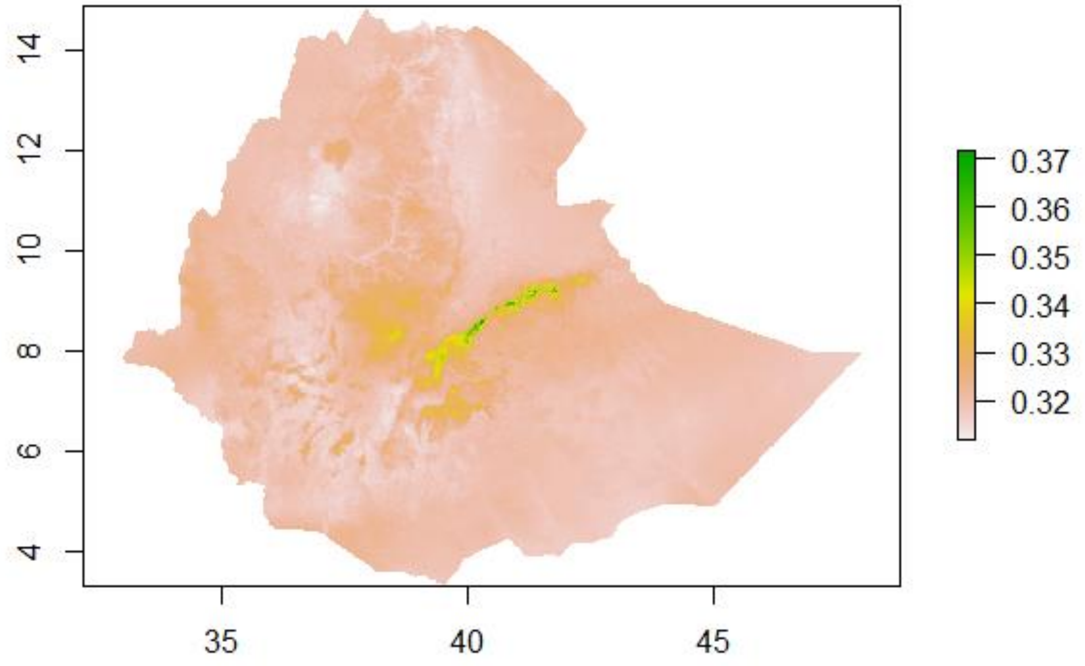


Figure 25. Distribution of predicted spatial variation in abundance for *C. g. gallarum* as a function of habitat suitability by implementing the ecological niche theory. Green shades represent higher predicted abundance.

The OLS regression revealed a weak abundance-suitability relationship for endemic little-known *C. g. gallarum* in the Ahmar Mountains, with slope quantiles ranging from β_1 (0.10) = -0.12133 to β_1(0.95) = 0.51282 (Table 10; Fig. 26).

Table 10. Five selected regression quantiles (rq) used to estimate the intercept (β0) and slope (β1), together with a 90% confidence interval (CI) for β1, in models y. The local abundance of *C. g. gallarum* (yabundance = β0 + β1xsuitability index) is determined by climatic conditions.

τ	β_0	β_1	90 % CI for β_1	p
10th	0.25346	-0.12133	-0.15033−1.797693	0.19585
25th	0.26667	0.00000	-0.22357–0.13579	1.00000
LAD	0.25346	-0.12133	-0.150–1.7e+303	0.19585
75TH	0.37672	0.10585	-0.25263–0.33066	0.53699
95th	0.30738	0.51282	-6.5205–0.530	0.57078

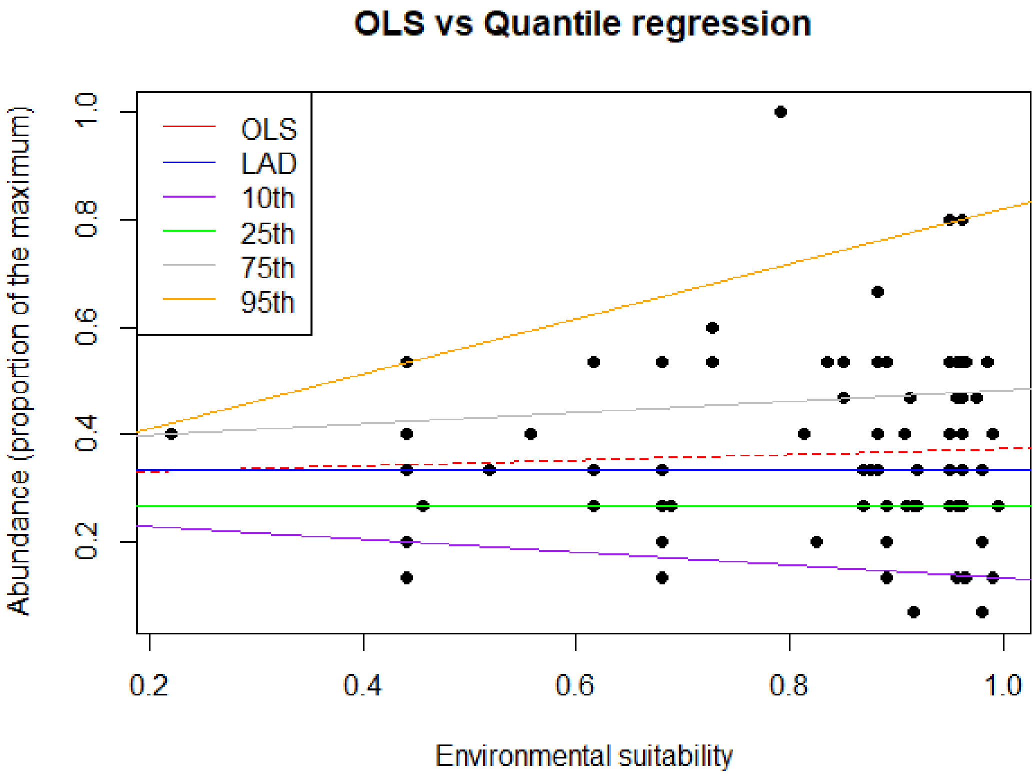


Figure 26. Scatterplot of *C. g. gallarum* local abundance vs predicted suitable habitat. Depicted by the regression lines: 10th, 25th, LAD (median (50th), 75th and 95th percentiles of quantile regressions.

4.4. Species-habitat association

4.4.1. Vegetation community

A 25,600 m^2 area was sampled from 64 plots in five forest patches, revealing 51 tree species from 16 families (Appendix 12). Of these, 88.46% (46) were woody plants while 11.54% (6) were climbers. During vegetation sampling, the species number varied from two to twelve per plot. The estimator estimated between 58 and 73 species within the surveyed area. The study revealed that *A. abyssinica*, *J. procera*, *P. falcatus*, *M. lancolata* and *C. lusitanica* highly abundant in more than 20 plots, indicating that *C. g. gallarum* relies more on these species to meet its daily basic needs (Appendix 13).

4.4.2. Community types and indicator species

Four communities were identified using agglomerate and objective dataset clustering in the forest patches of Ahmar Mountains (Fig. 27). The objective method indicates that the optimal number of clusters showed a sharp bend at the fourth cluster. The communities were named after tree and/or climber species with highest indicator values (Tables 11 and 12).

Community 1 (***Allophylus abyssinicus- Embelia schimperi-Croton macrostachyus***) was found mainly in the Dindin Forest, but a few plots from the Jalo-Kuni Forest and Hades Forest also harbours these species. This community hand 21 plot and four indicator species that had significant value ($p<0.05$).

Community 2 (***Buddlejia polystachya-Malva venticillata-Prunus africana***) was composed of 15 plots and 21 species. In this community type, six species were significant in their indicator values ($p<0.01$).

Community 3 (***Podocarpus falcatus-Juniperus procera-Cuperssus lusitanica***) comprised 18 plots and 22 species. Of the eight indicator species associated with this community, four were significant ($p<0.05$).

Community 4 (***Maesa lanceolata-Maytenus* spp.- *Dombeya torrida*)** contained 10 plots with 22 species. This community is associated with 11 indicator species, of which six were significant in their value ($p<0.05$).

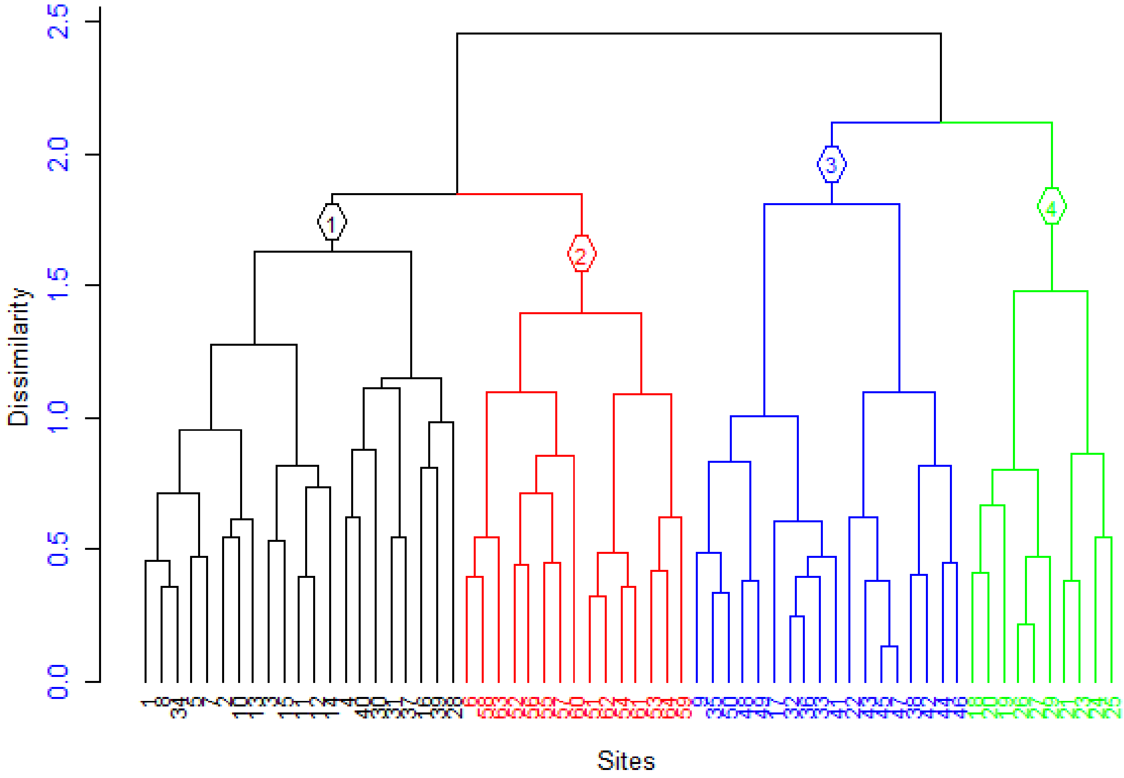


Figure 27. Hierarchical cluster analysis of vegetation data collected in Ahmar Mountains.

Table 11. Indicator of the abundance values of plant species in Ahmar Mountains.

Indicator species	Indicator value (%)			
	C1	C2	C3	C4
Allophylus abyssinicus	**30.7**	46.0	0.7	0.2
Embelia schimperi	**22.7**	0.0	1.1	1.2
Croton macrostachyus	**22.4**	0.4	0.9	1.9
Maytenus arbutifolia	21.8	3.2	0.0	0.0
Olea capensis	20.2	0.7	1.0	0.0
Ekebergia capensis	18.8	8.8	1.2	0.0

Juniperus procera	14.9	0.3	**29.5**	0.3
Suregada procera	14.3	0.0	0.0	0.0
Cissus rotundifolia	14.3	0.0	0.0	0.0
Myrsine melanophloeos	14.3	0.0	0.0	0.0
Podocarpus falcatus	10.4	0.1	**57.9**	3.4
Grewia ferruginea	9.5	0.0	0.0	0.0
Celtis africana	9.5	0.0	0.0	0.0
Schefflera abyssinica	8.0	0.0	2.4	0.0
Bersama abyssinica	7.9	1.0	0.0	8.8
Rhus natalensis	7.2	0.0	11.0	0.0
Ficus sur	6.9	0.0	1.6	0.0
Psydrax schimperiana	4.8	0.0	0.0	0.0
Olea hochstetteri	4.8	0.0	0.0	0.0
Asparagus africanus	4.8	0.0	0.0	0.0
Schefflera volkensii	4.8	0.0	0.0	0.0
Maesa lanceolata	4.8	0.0	0.0	0.0
Rhamnus staddo	4.8	0.0	0.0	0.0
Dovyalis caffra	4.8	0.0	0.0	0.0
Erythrina bruce	4.8	0.0	0.0	0.0
Maesa lanceolata	4.8	3.5	0.2	**59.1**
Hagenia abyssinica	4.6	0.0	0.0	5.1
Rosa abyssinica	4.0	0.0	3.6	3.9
Teclea nobilis	3.6	12.0	0.3	1.1
Euphorbia dalettiensis	3.2	2.1	0.0	0.0
Carissa spinarum	3.0	0.0	2.0	0.0
Cussonia holstii	1.2	46.7	0.0	0.0
Hagenia abyssinica	1.2	12.2	0.0	8.2
Rytigna neglecta	1.0	41.7	0.0	0.0
Dombeya torrida	0.9	14.7	0.0	**23.2**
Cuperssus lusitanica	0.8	0.2	**24.1**	21.7
Malva venticillata	0.2	**51.9**	0.2	0.5
Maytenus **spp.**	0.1	0.0	1.6	**33.1**
Prunus africana	0.0	**51.1**	0.2	0.0
Maytenus arbutifolia	0.0	6.7	0.0	0.0

Buddlejia polystachya	0.0	**53.3**	0.0	0.0
Bercium gradiflorim	0.0	6.7	0.0	0.0
Olea europaea	0.0	0.0	23.5	1.5
Rhus glutinosa	0.0	0.0	11.1	0.0
Jasminum abyssinicum	0.0	0.0	5.6	0.0
Oncoba spinosa	0.0	0.0	5.6	0.0
Canthium oligocarpum	0.0	0.0	0.0	10.0
Embelia schimperi	0.0	0.0	0.0	10.0
Vernonia urticifolia	0.0	0.0	0.0	20.0
Rhamnus prinoides	0.0	0.0	0.0	20.0
Calpurnia aurea	0.0	0.0	0.0	10.0
Lepidotrichilia volkensii	0.0	0.0	0.0	20.0

C1, *Allophylus abyssinicus - Embelia schimperi - Croton macrostachyus*; C2, *Buddlejia polystachya - Malva venticillata - Prunus africana;* C3, *Podocarpus falcatus - Juniperus procera - Cuperssus lusitanica;* C4, *Maesa lanceolata - Maytenus* spp. - *Dombeya torrida* community.

Table 12. Name of indicator tree species used to nominate the community clusters in the remnants of forests from Ahmar Mountains.

Name of indicator species	Community type (C)	Indicator value	*P*-value
Maytenus arbutifolia	1	0.218	0.033*
Olea capensis	1	0.202	0.031*
Embelia schimperi	1	0.227	0.036*
Allophylus abyssinicus	2	0.46	0.002**
Croton macrostachyus	1	0.224	0.046*
Prunus africana	2	0.511	0.001***
Rytigna neglecta	2	0.417	0.001***
Cussonia holstii	2	0.467	0.002**
Malva venticillata	2	0.519	0.001***
Buddlejia polystachya	2	0.533	0.001***
Podocarpus falcatus	3	0.579	0.001***
Juniperus procera	3	0.295	0.047*
Dombeya torrida	4	0.232	0.054*

Olea europaea	3	0.235	0.016*
Maesa lanceolata	4	0.591	0.001***
Maytenus **spp**.	4	0.331	0.003*
Vernonia urticifolia	4	0.2	0.021*
Rhamnus prinoides	4	0.2	0.017*
Lepidotrichilia volkensii	4	0.2	0.016*

C1, *Allophylus abyssinicus - Embelia schimperi - Croton macrostachyus*; C2, *Buddlejia polystachya - Malva venticillata - Prunus africana;* C3, *Podocarpus falcatus - Juniperus procera - Cuperssus lusitanica;* C4, *Maesa lanceolata - Maytenus* spp. *- Dombeya torrida* community.

Table 13 displays diversity indices among the four community types, with community 1 having higher values across all indices.

Table 13. Indices of species diversity among communities.

Community type	Richness	Species diversity (H)	Shannon Evenness (J)
1	38	3.17	0.87
2	21	2.50	0.82
3	22	2.19	0.71
4	22	2.41	0.78

4.4.3. Dissimilarity between plant communities

The study found minor differences between plant communities (S <0.4), with the lowest observed value between C2 and C3, C2 and C4, and C3 and C4, and the greatest dissimilarity between C1 and C2 (Table 14).

Table 14. Index of Sorensen similarity among communities.

	C1	C2	C3
C2	0.37	1	
C3	0.22	0.20	1

C4	0.20	0.20	0.21

4.4.4. Habitat association

The mean abundance of *C. g. gallarum* did not show a significant difference among communities (F3, 32 = 1.704, P = 0.186; Fig. 28).

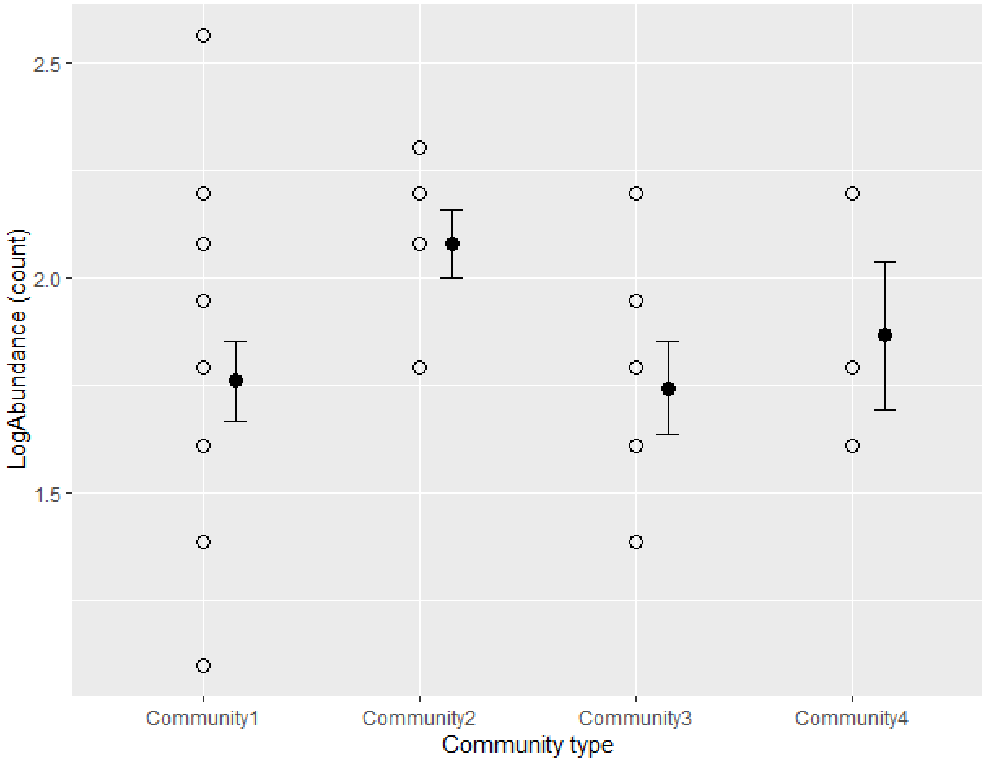


Figure 28. Plot of log-abundance of *C. g. gallarum* vs. vegetation clustered.

Table 15 reveals structural complexity and floristic composition differences among community types, with complex microhabitats like community types 1 and 2 having greater total plant importance value, Shannon diversity and evenness, but no difference in other habitat characteristics (stem density/ha, BA/m^2/ha, and standard deviation of tree height).

There were significant differences between community types in terms importance value (F = 3.80, p < 0.05), average mean height of trees (F = 4.95, p < 0.01), richness (F = 10.52, p < 0.001), species diversity index (F = 12.74, p < 0.001) and evenness (F = 4.80, p < 0.01).

A *post-hoc* test showed that community type 3 had a considerably lower importance value than community types 1 and 2 ($p<0.05$). Two communities (community types 1 and 2) had considerably greater mean tree heights than did the fourth community ($p<0.01$); however, there were no deviations in heights among the communities. The first community had much greater species richness than the other communities ($p < 0.001$) while the third community hand lower diversity ($p<0.05$).

Table 15. Results of analysis of variances computed among four community types based on local habitat metrics recorded during the study period.

Variables (unit)	Community type				ANOVA	
	C1	C2	C3	C4	*F*	*P*
Density	15.8^{a}	16.5^{a}	15.4^{a}	14.1^{a}	0.41	0.743
BA (m^2/ha)	0.1^{a}	0.1^{a}	0.1^{a}	0.3^{a}	0.67	0.575
IVI	226.6^{a}	205.3^{a}	132.2^{b}	186.8^{a}	3.76	**0.01536**
MeanHeight (m)	30.8^{a}	32.3^{a}	25.2^{a,c}	20.7^{b,c}	4.95	**0.00388**
SDHeight	11.8^{a}	15.1^{a}	11.5^{a}	16.9^{a}	2.61	0.0596
Richness	38^{a}	21^{b}	22^{b}	22^{b}	10.52	**<0.001**
ShannIndex (H)	3.17^{a}	2.50^{a}	2.19^{b,c}	2.41^{a,c}	12.74	**<0.001**
ShannEvenness (J)	0.87^{a}	0.82^{a}	0.71^{b,c}	0.78^{a,c}	4.76	**0.00484**

C1, *Allophylus abyssinicus - Embelia schimperi - Croton macrostachyus*; C2, *Buddlejia polystachya - Malva venticillata - Prunus africana;* C3, *Podocarpus falcatus - Juniperus procera - Cuperssus lusitanica;* C4, *Maesa lanceolata - Maytenus* spp. - *Dombeya torrida* community. Superscript letters represent significant difference.

Correlation tests also revealed strong relationships between many habitat metrics and abundance of *C. g. gallarum*, notably the importance value and species richness, as well as the Shannon index (Table 16).

Colobus g. gallarum was detected in 36 plots but was not detected in the other 28 plots (Appendix 14). Independent sample *t*-tests revealed that the presence plots had substantially greater mean tree heights, species richness, and diversity indices than did the absence plots ($p < 0.05$; Table 17). Thus, the chance of *C. g. gallarum* occurrence was significantly related to tree height and Shannon index. Nonetheless, there were notable differences in these attributes between the occupied and unoccupied plots ($p<0.05$).

Table 16. Multi-collinearity analyses between the local abundance of *C. g. gallarum* and metrics of local habitat computed at each plot during the survey period.

	A	BA	D	IVI	mH	sdH	R	H	VIF
Abundance	-								1.42
BA (m^2/ha)	-0.03	-							1.07
Density/ha	0.18	-0.04	-						1.81
IVI	0.23	0.08	0.44	-					5.64
Mean tree Height (mH)	0.28	0.00	0.03	0.50	-				1.78
SD of tree Height (sdH)	-0.11	-0.02	0.22	0.38	0.29	-			1.31
Richness (R)	0.38	0.00	0.56	0.84	0.28	0.25	-		5.71
ShannIndex (H)	0.36	-0.02	0.49	0.84	0.30	0.27	0.97	-	61.55
ShannEvenness (J)	0.16	-0.13	-0.13	0.33	0.24	0.02	0.35	0.53	1.45

Table 17. Results of an independent sample t-test showing group mean differences of the local habitat attributes measured for the plots occupied by *C. g. gallarum* and not occupied during the study period.

Variables	Group		*Student t-test*	
	Presence	Absence	*t*	*P*
N	36	28	-	-
BA(m^2/ha)	0.11	0.12	-0.128	0.8989
Density/ha	2.8	2.69	1.2441	0.2181
IVI	5.22	5	1.7633	0.08278
MeanHeight (mH)	3.39	3.21	2.189	**0.03237**
SDHeight (sdH)	2.52	2.66	-1.3663	0.1768
Richness	1.87	1.65	2.9085	**0.005035**
ShannIndex (H)	0.93	0.81	2.8056	**0.006702**

ShannEvenness (J)	0.66	0.67	2.1673	**0.03672**

The study found that mean tree height, standard deviation of tree heights and richness significantly influences the presence of *C. g. gallarum* in a plot ($p<0.05$; Table 18). The probability of finding *C. g. gallarum* increases with tree height and species richness, but decreases with importance value and standard deviation of the height of trees. As a result, factors with positive connections define (at least in part) the habitat of *C. g. gallarum* and hence constitute habitat features. As expected, the taxon prefers taller trees for occupancy (Table 18; Appendix 14).

Table 18. Results of regression models analyzing the predictor variables that best predicts *C. g. gallarum* occupancy.

Variable	β	βstd.	*Z*	*P*
Intercept	0.3681	0.3071	1.198	0.23072
Richness	2.0213	0.7114	2.841	**0.00449**
SDHeight	-0.8280	0.3607	-2.296	**0.02168**
Mean height	1.0028	0.3850	2.605	**0.00919**
IVI	-1.2642	0.7010	-1.803	0.07133
Density	0.5844	0.3566	1.638	0.10132

The Poisson distribution model showed that *C. g. gallarum* abundance was negatively related to tree importance values ($\beta = -0.61050$) and the standard deviation of tree height ($\beta = -0.15014$), while positively related to mean tree height ($\beta = 0.46857$) and richness ($\beta = 0.76747$) (Table 19).

Table 19. Poisson distribution model showing the predictor variables significantly related to the abundance of *C. g. gallarum* within occupied sites.

	β	Std. Error	*Z*	*P*
Intercept	0.99881	0.08060	12.392	**< 2e-16** ***
BA	-0.01127	0.11192	-0.101	0.91982

Density	0.03688	0.11029	0.334	0.73810
IVI	-0.61050	0.18765	-3.253	**0.00114** **
Meanheight	0.46857	0.10177	4.604	**4.14e-06** ***
SDHeight	-0.15014	0.07945	-1.890	0.05880.
Richness	0.76747	0.15862	4.838	**1.31e-06** ***
ShanEvenness	-0.04118	0.10246	-0.402	0.68775

5. DISCUSSION

To effectively direct conservation and management activities, it is essential to understand the abundance, distribution, niche utilisation, and habitat suitability of colobus monkeys in the human-dominated landscape. In this regard, *C. g. gallarum* estimated population density in the Ahmar Mountains is about 109.6 individuals/km^2 (~20,061 individuals). This population density is relatively high compared to most populations of other *C. guereza* subspecies (Fashing, 2011; Fashing and Oates, 2013). Similarly, the current findings of population density estimate fits into the range of African black-and-white colobus population densities found at other sites (4.9 to 150 ind/km^2, with one outlier of 315 ind/km^2, Appendix 15), although one has to be careful when directly compare population densities from different sites, with different ecologies, and most important, when different census methods were applied (Spaan *et al*., 2019; Kiffner *et al*., 2022b). Since there is lack of baseline data, it was not possible to show the population dynamics of *C. g. gallarum* has increased, stable or declined due to dynamics that happened in the fragmented forests of the Ahmar Mountains. However, this subspecies is suspected to have undergone a population reduction of 30% over the last three generations (~60 years) with declining habitat quality and area (Yahya *et al*., 2020).

Densities of Djaffa Mountains guereza in Ahmar Mountains are higher than those for *C. g. guereza* in one of the natural state forests located in central Ethiopia, Wof-Washa (Dereje Yazezew *et al*., 2022) and in the northern Ethiopia, Borena-Sayint NP (Hussein Ibrahim *et al*., 2017). Densities of *C. guereza* vary between localities due to habitat quality, forest cover, and food trees (Dunbar and Dunbar, 1974). In Rwanda, *C. angolensis* has large groups due to high mature leaf consumption (Fimbel *et al*., 2001). A study in Kenya found that the diversity of dietary trees correlates with the densities of *C. guereza* and *Cercopithecus mitis*, suggesting food availability may positively influence densities (Mbora and Meikle, 2004; Mammides *et al*., 2009), signifying that the availability of diets might positively affect densities. Indeed, ecological constraints, social factors, and group size in folivorous primates are associated with habitat quality (Von Hippel, 1996; Chapman and Pavelka, 2005), thus requiring further investigation for this study taxon.

The mean cluster size of *C. g. gallarum* (with an overall mean: 5.3 individuals) did not differ among the four study sites. If one assumes that the cluster size corresponds to the size of their social groups, this figure is at the lower end reported average group sizes for other *C. guereza* subspecies (5.4 to 19; Fashing, 2011; Dereje Yazezew *et al*., 2022). Other *Colobus* taxa with greater group size include *C. satanas*: 17 in Gabon (Fleury and Gautier-Hion, 1999); *C. polykomos*: 16.2 in Taï, Côte d'Ivoire (Korstjens, 2001); *C. a. cottoni*:13.9 in the Ituri Forest (Bocian, 1997); and *C. vellerosus*: 15.1 in Boabeng-Fiema Monkey Sanctuary (BFMS) as well as in neighboring forest remains: 10.3 (Wong and Sicotte, 2006). Similarly, Dunbar and Dunbar (1974) found that the size of *C. g. guereza* (6.7) is certainly associated to quantity of large trees of Bole Valley, central Ethiopia. Indeed, Guerezas often exhibit high ecological flexibility, little variation in social structure and organization within their habitats, and smaller in riparian or disturbed forests and larger in continuous forests (Von Hippel, 1996). However, it remains an open question, whether the relatively low group size of *C. g. gallarum* is taxon-specific or is caused by ecological factors.

The encounter rate (0.96 clusters/km) shown in this study is comparable to other related studies elsewhere (1.2 clusters/km, Kakamega Forest, Kenya, Fashing and Cords, 2000; 1.65 clusters/km, central Ethiopia, Dereje Yazezew *et al*., 2022). The low sex ratio of adult females to infants in *C. g. gallarum* suggests low reproductive success. This might be attributable to high mortality of infants and the presences of predators such as Eagle and Leopard at this study area. Similarly, equivalent trend was found with very large monkey's populations (*Alouatta palliata*) in forest fragments (Cristobal-Azkarate *et al*., 2005). This is linked with their dispersal patterns of maturing adults (Ostro *et al*., 2001) and may also be associated with high juvenile mortality in forest fragments (Umapathy *et al*., 2011). Forest fragmentation may cause stress due to increased food scarcity or competition, potentially reducing reproduction and increasing mortality rates.

Colobus g. gallarum groups consist of up to 15 individuals, with one-male group was not significantly different across forest sites. Different *C. g. guereza* groups were discovered in Ethiopia based on population density and structure; these groups included small-one male, large one-male, and multi-male groupings (Dunbar and Dunbar, 1974), which may represent different phase in *Colobus* group life cycles (Dunbar and Dunbar, 1976).

Generally, guerezas are ecologically relatively flexible and they can survive even in small forest fragments (e.g., just a few trees surrounding a church in Ethiopia) (Dunbar and Dunbar, 1974; Fashing *et al*., 2019b). They can also even subsist in parks or can be found in tiny forest remnants in towns and are, in general, tolerant of the presence of humans (Yalden *et al*., 1977). Given the density of *C. g. gallarum* within the four study forests, the conservation concern seems not to be a low population density per fragments but might be more due to the small range and low number of suitable forests within the range of *C. g. gallarum*. Habitat suitability models revealed that only 1,336 km^2 (1.8%) of the 75,307 km^2 study area consist of highly suitable habitat for *C. g. gallarum* under current climate condition. Given that the subspecies occurs mainly at higher altitudes, changing climates can negatively affect the habitat of *C. g. gallarum*, in particular if the vegetation belts are “pushed” uphill, similar to what is expected for other high-altitude species in Ethiopia (Ahmed Seid *et al*., 2023).

This dissertation produced maps of ecological niche models using closely related parapatric taxa of Ethiopia’s guereza as model subspecies to evaluate the range of suitable habitats of the taxa and deliver a better reference point for the progress of conservation plans. The study predicted the habitat suitability of *C. g. gallarum* to evaluate the effects of climate change and provide valuable insights intended for conservation initiatives. The findings show that the suitable areas are fragmented and restricted to the National Forest Priority Protected Area for *C. g. gallarum*. The highly suitable habitats for this subspecies under current conditions have less area in contrast to a widely distributed sister taxon, *C. g. guereza* (Zinner *et al*., 2019). Our findings exhibit an excellent prediction suitability for the taxa. These discriminated areas of high habitat suitability lay the foundation for conservation initiatives (Thorn *et al*., 2009). As a result, conservationists will benefit from this predicted habitat suitability model to launch the campaign for conservation of wildlife. Further information about areas inhabited by a species within its distribution range and connectivity among patches are also needed (Boitani *et al*., 2008). To sustainably conserve and manage threatened species, more precise habitat distribution maps are required, which may be generated using machine learning techniques (Di Pasquale *et al*., 2020; Rather *et al*., 2020).

The findings of this study highlight the need for further study on species distribution and connectivity among patches. Habitats of *C. g. gallarum* were found in fragments and distributed across the Ahmar Mountain range, including Arba Gugu Mountain Forest, Angada and Asako forests and Urgan-Bula gorges in the Arsi Zone. Similar to the current study, fragmented suitable habitats are predicted for the endangered Javan gibbon (*Hylobates moloch*) (Widyastuti *et al*., 2020) and red-shanked douc (*Pygathrix nemaeus*) (Coudrat *et al.*, 2021). Beside fragmentation in suitable habitats, habitats predicted for some species also show up outside a protected area due to degradation and habitat conversion (Atmoko *et al*., 2020). This might associate with adaptability to Anthropogenically modified landscape. The OFWE initiated plantations in study area where *C. g. gallarum* occurs, aiming for sustainable development and community participation. However, challenges such as deforestation, wood logging, grazing, and human settlement expansion persist in protected areas, potentially impacting the survival of the subspecies and wildlife.

Habitat suitability models relate factors to species likelihood and the species-environment relationship (Hirzel and Le Lay, 2008). The present study reveals that environmental predictors for species distribution models have different optimal conditions but are niche truncated because the potential equilibrium environmental factors of a taxon are unknown for all points in the geographic range, calling for further exploration of the taxon's niche equilibrium. Grinnell (1917) enumerated causes that may have disrupted the distribution of species a century ago. It is evident that climatic conditions, coupled with species habitats and occurrences, are required to arrange conservation or restoration sites as well as to advise landscape plans (Préau *et al*., 2020). Climate patterns, including monthly to seasonal temperature and precipitation, influence the behaviour, physiology, distribution, abundance and interactions of biological species (Walther *et al*., 2002; Hirzel and Le Lay, 2008). Climate indirectly impacts animals by shaping vegetation and soils, affecting food abundance and cover in deciduous plants, and influencing their behavioral ecology (Van Schaik and Brockman, 2005). Anthropogenic climate changes significantly impact the predicted distribution, habitat connectivity and genetic diversity as seen in the endangered primate, *Rhinopithecus bieti* (Zhao *et al*., 2019).

Of the three genera of African colobines, *Colobus* lives in the greatest ranges of altitude, rainfall and temperature (Butynski and De Jong, 2022a). The study reveals that the predicted habitat suitability model for *C. g. gallarum* is influenced by climatic factors like wettest quarter precipitation, seasonal temperature and mean diurnal temperature range. However, precipitation-related variables like seasonality and the coldest quarter contribute to *C. g. gallarum* habitat as seen in the distribution models. A study in Brazil found that annual precipitation is the primary factor affecting the habitat suitability of primates (Moraes *et al*., 2020). Africa's colobines live under a wide range of temperature regimes (Butynski and De Jong, 2022a). Temperature annual range and coldest quarter average temperature greatly influenced on parapatric howlers' distribution (Holzmann *et al*., 2015). Variation in contribution of bioclimatic variables to species distribution in different localities may be influenced by agro-ecological variability.

The predicted habitat suitability of *C. g. gallarum* was significantly influenced by various aspects, as per the developed habitat suitability models based on subspecies relationships. The suitability is increasing clockwise from north to southwestern side mountain range's suitability may be due to convergent variability of its vegetation and moisture regime (Demele Teketay, 1996). Other derivatives of topography, such as elevation, are not significantly impacting the current mapping of *C. g. gallarum* habitat suitability models. In contrast, Hansen *et al*. (2020) study discovered that the habitat suitability of East Javan langur (*Trachypithecus auratus*) declined with altitude rise. This might attribute its forest primate status and its use of savannah habitats, similar to the strict arboreality of the current study subspecies. A review conducted showed that the altitudinal range for the genus *Colobus* ranges from 0 to 3400 m asl (Butynski and De Jong, 2022a). However, *C. guereza* reaches higher altitudes than others, with *C. g. gallarum* occupying up to 3400 m asl in some parts of its geographic range. Except at the subspecies level, *C. guereza* is a high-altitude species. For instance, *C. s. satanas*, on Bioko Island, has the highest altitudinal gradient of any *Colobus* subspecies (0–3010 m asl; Butynski and Koster, 1994). Overall, topography indirectly impacts species through its association with other environmental variables while directly affecting wildlife movement (Hirzel and Le Lay, 2008).

Anthropogenic disturbances have also affected the suitable habitats and distribution of wildlife (Guisan and Zimmermann, 2000; Ehrlén and Morris, 2015; Rezende *et al*., 2020). The MaxEnt model revealed the highest suitability for *C. g. gallarum* in the evergreen forest, followed by deciduous forest, which highlights the uses of dense forest with a fastened canopy. Similarly, the habitat suitability of *Hylobates moloch* and *Alouatta ululata* in less-protected Dieng Mountains, Central Java, Indonesia, and north-eastern Brazil is influenced by natural forest (Widyastuti *et al*., 2020) and good tree cover (Filho and Palmeirim, 2020). Gray *et al*. (2010) found that gibbon occupancy is higher in evergreen forests than semi-evergreen forests, suggesting that evergreen forests influence arboreal monkey abundance and distribution. Thus, land-cover data significantly impacts ecological niches. As primary forest's cover decreases, plantation forests are occupying more land, but their suitability as wildlife habitats remains unclear (Fashing *et al*., 2012). Although the plantation forests have the ability to aid in the preservation of certain monkeys, benefits of plantation and reforestation initiated by the OFWE to conserve wildlife require further research. Furthermore, it is vital to comprehend the impact of landscape structure on species in order to enhance management approaches (Galán-Acedo *et al*., 2018).

Anthropocentric activities are increasingly disrupting the biotic and abiotic habitats of species (Newbold *et al*., 2015), also disturb species distribution by limiting accessibility to suitable patches (Mangiacotti *et al*., 2013) and shaping its geographical range (Sala *et al*., 2000). The distance from the human population settlements had less of an influence on *C. g. gallarum* predicted habitat suitability. A pronounced negative influence of rural human population growth on several mammal species is indicated in the highlands of southwestern Ethiopia (Rodrigues *et al*., 2021). There was correlation found between the *C. g. gallarum* habitat suitability model and a varied distance to roads. Similarly, Hansen *et al*. (2020) found a negative correlation between this variable and lutung occurrences. However, the habitat suitability model of the proboscis monkey (*Nasalis larvatus*) is mostly influenced by the distance to riverine habitat, the distance from a pond, and the distance from the shoreline (Atmoko *et al*., 2020). As developing countries give priority to economic growth, the effects of development threaten natural habitats and species distribution, thus requiring further investigation on the impact of the development threat index on biodiversity in general.

For the future scenarios of changing climates, the projected habitat suitability models of the years 2050 and 2070 made a significant contribution for providing a stable (i.e., climate refugia) suitable habitat for the conservation of *C. g. gallarum* for long-term survival. Analysis of jackknife assessment revealed that the wettest quarter precipitation mainly influenced habitat suitability modelling of *C. g. gallarum* under all future climate scenarios. A considerable overall gain in suitable habitat is observed for this taxon under all climate emission scenarios. In contrast, the black-tailed marmosets extent of suitable habitats are declined in percent from 21 to 27 under the most optimistic (SSP2-4.5) scenario and in the worst-case scenario (SSP5-8.5) during the projected fifty-years in Brazil (Gusmão *et al*., 2021), respectively. Despite the overall gain, the currently suitable habitat for *C. g. gallarum* declined by 8.6 % under the conservative scenario (RCP 2.6) of the projected 50-year period and by 11.3% during the highest greenhouse gas emissions (RCP 8.5) of the projected 70-year period developed by the BCC-CMS1-1. On the other hand, the loss of current suitable habitat increased from 5.3 % to 11.9 % under different RCP developed by HadGEM2-ES. These suitable habitat area dynamics might be associated with changing climates, which signifies an extraordinary risk via affecting distributional pattern of global biodiversity (Sales *et al*., 2020). Such changes reduce connectivity and might resulted in local species extinction (Préau *et al*., 2020). The climate refugia maintained under each climate change scenario would be better to safeguard the survival of the subspecies as a safe heaven under the changing climate conditions. Therefore, novel strategies may be required to avoid biodiversity loss resulted due to effects of changes in climate across study region, even beyond the country or at the global level.

Besides utilizing only climate related factors to assess the extent of predicted suitable habitats, incorporating other ecological predictors such as land cover, anthropogenic disturbances and vegetation index could improve the resultant models under future climate conditions. This dissertation is not the sole, but other studies have also used only the climatic variables for future predictions (Hosni *et al*., 2020; Smeraldo *et al*., 2021). Even while the biological responses to the present shift in climate are now readily apparent (Walther *et al*., 2002; Sales *et al*., 2020), the projected trends of global warming effects on biodiversity need further investigation by incorporating Anthropocene effects. However, lack of future data on these variables might limit their use for studies that consider the influences of climate change on future distribution models (Hosni *et al*., 2020).

Different species are likely to react differently to predicted changes, and therefore, conservation suggestions based on habitat suitability models need to be examined with care. Habitat suitability and distribution models, alongside other ecological niches and range predictions for primates, are an essential step towards defining conservation management plans for threatened taxa (Singh *et al*., 2018). The present models indicate that the climatic conditions and landscape composition played roles in predicting the suitable habitats for *C. g. gallarum*, even though they were fragmented. Indeed, habitat fragmentation is the largest threat to primate species, accounting for 76% of primates declining due to habitat loss from agriculture and 2-13% declining due to the impacts of infrastructure construction and mining (Estrada *et al*., 2017). Habitat protection is a common conservation intervention (Junker *et al*., 2017), involving legally protected areas and community conservation areas to preserve important primate habitats during selective logging and agricultural activities (Chapman *et al*., 2000). Focus should be given to habitat restoration, corridor creation, and forest patch protection to protect wildlife (Junker *et al*., 2017) and reduce greenhouse gas emissions based on predicted wildlife habitat distribution (Moraes *et al*., 2020). These should be carried out considering the climate refugia sites (remained steady in habitat suitability) that are predicted for future climates to sustain the survival of the species.

The study modelled Anthropocene refugia for closely related and parapatric guereza taxa, identifying suitable habitats within forest cover and examining protected suitable areas within the country's PA network systems. This type of modelling approach is essential to identify species-environment relationships, map distribution and assess conservation threats (Hending *et al*., 2023). The findings of ecological niche models for both taxa showed that all of the algorithms utilized for predicting the extent of suitable habitat had the highest performance; however, the performances of the algorithms varied among the subspecies. Such performance is also evidenced in a study conducted on high-altitude species in Ethiopia, particularly *T. gelada* (Ahmed Seid *et al*., 2023).

The potential suitable habitat predicted for *C. g. guereza* was almost triple that of *C. g. gallarum*. However, small portions of these predicted suitable habitats are considered Anthropocene refugia (i.e., suitable habitats unaffected by human impacts or suitable habitats in forest land cover) for both taxa. These sites would be very crucial for *in-situ* conservation. For species conservation in the suitable habitat predicted outside of the forest land cover, *ex-situ* conservation might be an alternative option to initiate conservation actions. Lively conservation techniques like aided colonisation may be necessary when terrain circumstances prohibit species from accessing *ex-situ* refugia, such as high altitudes or other isolated environments (Hoegh-Guldberg *et al*., 2008). Almost half of Anthropocene refugia is preserved within Ethiopia’s protected area network for *C. g. gallarum*, while the majority of the Anthropocene refugia are found outside of the PAs network for *C. g. guereza*. The current PA system of high coverage for Anthropocene refugia suggests efficient sites for target subspecies, while low coverage suggests inadequacy in climate change, highlighting the need for adaptation (Brambilla *et al*., 2022). Overall, more effort is needed to protect the areas outside the protected area network and to conserve the endemic Ethiopia’s guereza from extinction.

Closely related taxa of Ethiopia's guereza exhibit divergent niches under the current climate conditions. Our research revealed that the variations in distribution between these closely related species are shaped by a complex array of bioclimatic factors, such as temperature and precipitation. Annual precipitation (Biol12), precipitation seasonality (Biol 15), and precipitation of wettest quarter (Biol 16) were found to be significantly correlated with PC1 and PC2, indicating their significant role in determining the distribution difference between these taxa. This might support the ecological parapatric speciation scenario between the two taxa, where there might be no hybridization in the contact zone (Bull, 1991). Similarly, niche divergence is discovered across the pairs of *Papio* species via ecological niche modelling (Fuchs *et al*., 2018). According to Agostini *et al*. (2010), this kind of niche differentiation permits closely related species to cohabit peacefully. Four macaque species are predicted to have suitable habitats that show niche segregation and gradual geographical distribution based on environmental gradients, as per the Coudrat and Nekaris (2013) study. These exhibited niche divergences between different species that might be because parapatric species seem to adapt to different ecological conditions (Bull, 1991). This will have a big impact on how these species are managed and studied in the future.

The present findings indicate that there is a positive correlation between abundance of *C. g. gallarum* and environmental suitability, however, with high prediction. Supporting the findings of this study, some studies have obtained a significant positive relationship between local abundance and environmental suitability (VanDerWal *et al.*, 2009; Weber *et al*., 2017). Other studies have found negative associations between abundance and environmental suitability (Pearce and Ferrier, 2001; Nielsen *et al*., 2005), contradicting the current findings. Therefore, care must be taken when generalizing the theory that local abundance, which is a direct outcome of ecological niches occupied by species, reflects how those species adapt to local circumstances (Brown, 1984). At high resolution, niche theory may be able to accurately forecast the spatial variance in species distribution (Fuente *et al.*, 2021). Previous studies suggested a wedge or triangular shape for the abundance-suitability relationship, with higher suitability indicating high or low abundance, and lowest suitability indicating predominantly low abundance (VanDerWal *et al*., 2009; Jiménez-Valverde, 2011; Braz *et al*., 2020; Jiménez-Valverde *et al*., 2021). This could be due to the difficulties of obtaining biotic components like species interaction that might possibly impact species spreading, spatial variation in abundance and are not included in SDMs (Fuente *et al*., 2021). In fact, due to a shortage of logistics and time constraints, there is a lack of abundance data that restricts our ability to comprehend biological pattern of the populations. Thus, robust abundance estimates using occurrence-based ecological niche models might be useful for conservation and ecological applications (Wilson *et al*., 2011a, b; Malone *et al*., 2018). Moreover, enhancing species conservation and management choices may be greatly aided by such a modelling method (Fuente *et al*., 2021). Therefore, modelling association between population demography and local-scale ecological conditions most likely add to reduce species extinction, because in areas with high-quality of habitats, species flourish more and succeed in survival (Araújo *et al*., 2002; Morrison *et al*., 2012; Weber *et al*., 2017).

Colobus g. gallarum occurs in dry Afroalpine evergreen forests and woodlands in the Ahmar Mountains. Preliminary data suggest that *C. g. gallarum* eats mainly leaves during the dry season, with upsurge fruits feeding during the wet season. They consume on a diversity of plants. While the dietary variability of black and white colobus is highest (Fashing, 2011), *C. satanas* consumed on average of 86 species (ranging 65–109; McKey *et al*., 1981; Gautier-Hion *et al*., 1997; Fleury and Gautier-Hion, 1999), *C. guereza* consumed on average of 46 species (ranging 27–73; Oates 1977a, 1994; Bocian, 1997; Fashing, 2001b; Matsuda *et al*., 2020; Dereje Tesfaye *et al*., 2021), *C. angolensis* consumed on average of 59 species (ranging 37–73; Bocian, 1997; Fimbel *et al*., 2001; Vedder and Fashing, 2002; Dunham, 2017; Miller *et al*., 2020), *C. polykomos* ate more than 46 species (Dasilva, 1989), and *C. vellerosus* consumed 56 species (Saj and Sicotte, 2007). These black and white colobus monkeys' dietary shift patterns revealed that there is nutritional variance both within and between species and sites (Fashing, 2022).

Colobus g. gallarum is found in forest remnants, where the intensity of human-modified landscapes increases. It was frequently observed on multifunctional trees like *A. abyssinicus, C. macrostachyus, P. africana, P. falcatus, J. procera, C. lusitanica*, and *M. lanceolata*. Black and white colobus monkeys utilize trees for various purposes, including diets (Fashing, 2011, 2022; Dereje Tesfaye *et al*., 2021; Miller *et al*., 2020), sleeping (Von Hippel, 1998; Teichroeb *et al*., 2012), sources of minerals (i.e., these are critical to growth, reproduction and survival) and medicine (Rode *et al*., 2003; Fashing, 2004; Fashing *et al*., 2007; Wasserman *et al*., 2012), basking (Dasilva, 1993; Decker, 1994), and shelters (Gautier-Hion *et al*., 1981; Dunbar, 1987). Humans also use trees for different purposes, including food, fodder for livestock, extractive goods, and other benefits like soil conservation as well as nitrogen fixation (Mesele Worku and Abay Bantihun, 2017; Latamo Lameso, 2021). The human-dominated world has exploited multipurpose trees for human needs, affecting biodiversity, including arboreal primates that rely on indigenous trees. The study taxon is experiencing increased pressures on wildlife due to timber production, requiring halting and maintaining measures.

Indeed, floral structural complexity influences habitat selection and preferences, requiring future ecological analyses. There is a trade-off between studies regarding whether habitat characteristics predict the status, distribution, occupancy, and abundance of primates. Some studies reported that no characteristics of forest patches predicted the presence of particular primate species in Kibale National Park, Uganda (Onderdonk and Chapman, 2000; Stickler and Southworth, 2008). In contrary, studies conducted on African colobines showed that the characteristics of the forest patches can influence their demography, occupancy, abundance, and distribution (Mbora and Meikle, 2004; Anderson *et al*., 2007b). Forest structure significantly influences density and habitat preference for sympatric gibbons, with canopy connectivity and height being key factors (Hankinson *et al*., 2021). The complexity of the canopy creates diverse microhabitats and ecological niches, allowing species to coexist. These differences in prediction between studies caution to make generalities about primates' responses to the fragmentation of forests.

Colobus g. gallarum, a subspecies relying on trees for their livelihood, prefers vegetation complexity and tree height. Tree height is positively correlated with abundance, possibly due to predator avoidance or leaf availability. The structural complexity of forests, influenced by species richness, also positively influences taxon abundance. However, general trends are not applicable across taxa, as populations, subspecies, and species respond differently to habitat changes (Cowlishaw and Dunbar, 2000), suggesting that detailed studies of individual species are need to make generalizations across taxa (Anderson *et al*., 2007b).

Long-term survival of many species, including *C. g. gallarum*, hinge on their ability to adjust to fluctuations of their environment, including microclimate, vertical stratification, and diet source (Purvis *et al*., 2000; Tabarelli *et al*., 2012; Neam and Lacher, 2018). Tall trees offer stable sleeping spots and can shield their species from predators that could attack from the air or the ground (Von Hippel, 1998). Studies show a positive correlation amongst the abundance of *Colobus* and characteristics of the forests like food trees basal area (Mbora and Meikle, 2004), leaf protein-to-fiber ratio (Wasserman and Chapman, 2003), tree cover and canopy height (Medley, 1993). Differences in tree height and importance values negatively related to abundance might be due to canopy structure that affects its dispersion or movement and human logging and deforestation vulnerability, respectively. Gouveia *et al*. (2014) found canopy height as one of the most predictors of primates than precipitation or productivity. This suggests that forests structural attributes are main drivers, potentially impacting diversity, abundance and distribution.

The impacts of anthropogenic disturbance (i.e. human footprint pressure) significantly affected the habitat suitability of *C. g. gallarum* but not that of *C. g. guereza* (Campera *et al*., 2020; Di Marco *et al*., 2018). This might be because *C. g. guereza* is more tolerant to disturbance than *C. g. gallarum*. Because the target study taxon, *C. g. gallarum*, is more restricted, it might be found in the Anthropocene refugia in the only remnant forests of the Ahmar Mountains. The main threats to *C. g. gallarum* personally observed during the study periods are conversion of forest into farmland and settlements, overgrazing, extracting trees for lumber, firewood, charcoal, and production of beehives. Climate change is an additional threat, particularly if vegetation belts are ’pushed’ uphill, as expected for other high-altitude species in Ethiopia (Ahmed Seid *et al*., 2023). All threats are linked to a large and increasing human population. The human population of Ethiopia has a ‘Rate of Natural Increase’ of 2.5%, compared to a global average of 0.9% (PRB, 2023). Hunting for the colobus pelt trade led to population decline in the past (Mittermeier, 1973, Dunbar and Dunbar, 1975, Oates, 1977c). The current level of this illegal trade and its impacts are much lower, although this needs to be investigated. Species-climate models predict that the habitat for *C. g. gallarum* will become even more fragmented and decline over the coming 50 to 70 years, and that anthropogenic pressures will have considerable negative impacts on the habitat of this subspecies.

Colobus guereza is registered on Appendix II of the CITES and in Class B of the ACCNNR. *Colobus g. gallarum* occurs in some protected areas, including Gara Muleta National Forest Priority Area (29 km^2), Dindin-Arba Gugu National Forest Priority Area (691.90 km^2), Jalo-Ades National Forest Priority Area (227.19 km^2) and Urgan-Bula Controlled Hunting Area (78.16 km^2) (UNEP-WCMC and IUCN, 2023). It is also informally protected in some small monastery forests scattered across the eastern Hararghe Zone, particularly around Hara Wacha. To the best, *C. g. gallarum* is not given emphasis at all continuing conservation act. Because of its limited geographic distribution (Zinner *et al*., 2019) and relatively small population size, *C. g. gallarum* is facing a higher risk of extinction than *C. g. guereza*. Also, the remnant forests where *C. g. gallarum* occurs are isolated, making genetic exchange among populations difficult, if not impossible. This can lead to an increase in inbreeding and genetic diversity loss. A population genetic study to assess the genetic status of *C. g. gallarum* would help to clarify this issue. The geographic distribution of *C. g. gallarum* needs to be better understood. Several forests with suitable habitats for *C. g. gallarum* have not been surveyed, such as Angada Forest, Aseko Forest, Hara Wacha Forest and the Arba-Gugu Mountains (340.45 km^2).

6. CONCLUSION AND RECOMMENDATIONS

6.1. Conclusion

This dissertation aims to assess the abundance and distribution patterns of the endemic *C. g. gallarum* in the remanent forests of the Ahmar Mountains, eastern Ethiopia. In addition, examining habitat ecology and factors affecting its distribution patterns and abundance are the goals of this study. Precipitation, temperature and evergreen forests are important variables that determine habitat suitability of *C. g. gallarum*. The predicted areas suitable for the taxon are more fragmented and restricted to its geographic range.

Though the size and density of a population are essential parameters in primate ecology and conservation, this dissertation has estimated a population density. This density is relatively high compared to other *C. guereza* taxa, but relatively small population size in terms of restricted geographic range. However, the detection distances and cluster sizes did not differ among the four forests and seasons. The study reveals that the ecological niches of two closely related and parapatric Ethiopian guereza taxa exhibit divergent characteristics under current climate conditions. There are differences in prediction values among algorithms and subspecies; however, all models predicted had excellent performance (i.e., except RF for *C. g. gallarum*) and their models ran consistently. *C. g. gallarum*'s suitable habitat is primarily found in its current range, indicating minimally suitable habitats. Anthropogenic disturbance exhibited significant effects on the suitable habitats for *C. g. gallarum*; in contrast, as expected, the habitat suitability of *C. g. guereza* is not significantly affected by the risks of anthropogenic threats.

A deeper understanding of forest habitat ecology, including structural complexity and floristic composition has been made possible by this dissertation for managing and conserving the endemic *Colobus g. gallarum*. *C. g. gallarum* clusters are located in four different types of communities. The mean tree heights, diversity indices and species richness significantly greater with the plots where *C. g. gallarum* is found.

This dissertation research is incomplete in terms of general biology, life history, and behavioural ecology analyses for *C. g. gallarum* across the Eastern Ethiopian highland. In spite of its limitations, the study certainly adds to the understanding of the *subspecies-climate* and *subspecies-habitat* associations in terms of distribution and abundance, which are very crucial to subspecies-specific conservation and management plans. This study has found that, generally, because of their assumed limited geographic distribution and, therefore, a relatively small population size within the overall distributional assortment, *C. g. gallarum* is utmost expected to be in danger of extinction risks. Thus, this taxon is reassessed and designated as Vulnerable (VU). The remnant forests where *C. g. gallarum* is found are isolated, which might make genetic exchange among the local populations of *C. g. gallarum* difficult. This can lead to an increase in inbreeding and a loss of genetic diversity.

6.2. Recommendations

Given the distribution pattern and population size estimate of *C. g. gallarum,* as well as its habitat suitability and ecological niche overlap with sister taxa under different ecological conditions in the time series of climate change, the present finding suggests that:

- Conservation action should be implemented to protect the forests and conserve the populations of *C. g. gallarum* through restocking of the fragmented forests.

- Future studies should investigate the long-term population assessment of the *C. g. gallarum* to understand its conservation status, population size and change, as well as its biology, life history, and behaviour.
- Furthermore, its population size in Ahmar Mountains remains unfamiliar, requiring new plan to assess population genetic differentiation and gene flow.
- Assumed that the suitable habitats and populations of *C. g. gallarum* are now vastly scrappy, urgent monitoring of populations and re-joining habitats are crucial for taxon conservation, with anthropogenic factors to consider for future modeling.
- Remedial actions should be taken by concerned bodies, such as habitat protection or restocking of the forest, reassessment of the threats, and reducing the challenges that contribute to habitat loss.
- A population genetic study to assess the genetic status of *C. g. gallarum* and a comprehensive survey to collect samples for genetic analysis (non-invasive sampling, e.g. faecal material) could be a next step.
- Determining the geographic distribution of *C. g. gallarum* is needed, because several forests that constitute suitable habitat for *C. g. gallarum* are unexplored, e.g., in the Arba-Gugu Mountains. It is also important to collect data along the common distribution border between *C. g. gallarum* and other guereza taxa to check for possible sympatry and hybridization.
- Studies are looked-for towards examining the influence of forest fragmentation on taxon occupancy and abundance, considering spatial, food, structural, and human disturbance factors.
- Conservation management programmes should focus on reconnecting forest fragments to re-establish dispersal routes among currently isolated local populations of C. g. gallarum. However, this should be accompanied by a public awareness campaign and discussion with the stakeholders involved.

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APPENDICES

Appendix 1. The occurrence localities of *C. g. gallarum* in its geographic range.

Species	Site	Long	Lat	References a)
C. g. gallarum	Bala Adi, Dindin	40.23858523	8.617606474	1
C. g. gallarum	Defo, Dindin	40.23858518	8.617588388	1
C. g. gallarum	Defo Giduu, Dindin	40.24945389543201	8.606855075544688	1
C. g. gallarum	Defo Giduu, Dindin	40.2436906	8.611079	1
C. g. gallarum	Defo Giduu, Dindin	40.245702	8.6069485	1
C. g. gallarum	Defo Giduu, Dindin	40.2474077	8.5770815	1
C. g. gallarum	Bal'a Heexoo (plantation)	40.2434311	8.6016389	1
C. g. gallarum	Bal'a Heexoo (plantation)	40.236797998346326	8.604490475232305	1
C. g. gallarum	Bal'a Heexoo, Dindin	40.24192981393097	8.5955211369613	1
C. g. gallarum	Bal'a Heexoo, Dindin	40.24193887049534	8.595512064514319	1
C. g. gallarum	Molticha, Dindin	40.24583175496563	8.61342316070789	1
C. g. gallarum	Molticha, Dindin	40.25579722188107	8.615443531624933	1
C. g. gallarum	Balada, Dindin	40.26238376596687	8.626038620898807	1
C. g. gallarum	Lemen, Dindin	40.264053968189934	8.636432747673236	1
C. g. gallarum	Dildila Rabbi, Dindin	40.257951781462474	8.640467987683094	1
C. g. gallarum	Derar, Dindin	40.24743002040305	8.638051678388809	1
C. g. gallarum	Najabas, Sorroro Torgam	40.84715074710257	9.004272971924532	1
C. g. gallarum	Kuni-Muktar Nyala Sanctuary	40.91925446102449	9.002918710655653	1
C. g. gallarum	Kuni-Muktar Nyala Sanctuary	40.9128622237146	8.99605425757812	1
C. g. gallarum	Hades	41.234854391614725	9.307785283363927	1
C. g. gallarum	Hades	41.24596463259242	9.316347034775411	1
C. g. gallarum	Hades	41.23851541577758	9.308277497041944	1
C. g. gallarum	Hades	41.23842523244958	9.308404600343756	1
C. g. gallarum	Hades	41.235896855409564	9.307164136888929	1
C. g. gallarum	Hades	41.23907909306767	9.30677359061122	1
C. g. gallarum	Hades	41.24605099184285	9.308501240810187	1
C. g. gallarum	Hades	41.245661511792356	9.307355829599214	1
C. g. gallarum	Hades	41.24475141923093	9.303050284888684	1
C. g. gallarum	Hades	41.24565330121285	9.304644388091633	1
C. g. gallarum	Hades	41.2477373936425	9.308978677796494	1
C. g. gallarum	Hades	41.24899123309786	9.30584351953096	1
C. g. gallarum	Arada Raasaa, Bedeno forest	41.25659243178694	9.236625678530636	1

C. g. gallarum	Arada Raasaa, Bedeno forest	41.7281769741179	9.240860948143329	1
C. g. gallarum	Girawa, Gara Muleta	41.76867841670173	9.22989861208806	1
C. g. gallarum	Girawa, Gara Muleta	41.78175241102974	9.219118481574657	1
C. g. gallarum	Girawa, Gara Muleta	41.79408474583481	9.212418510275157	1
C. g. gallarum	Midhagdu, Dindin	40.261445494103604	8.655404833180281	1
C. g. gallarum	Midhagdu, Dindin	40.26232217756455	8.653964080844217	1
C. g. gallarum	Derar, Dindin	40.25810302079563	8.64223090865166	1
C. g. gallarum	Derar, Dindin	40.2457970310524	8.63887087855484	1
C. g. gallarum	Tulu Adam Aniya, Dindin	40.243787534168575	8.627392518864262	1
C. g. gallarum	Tulu Adam Aniya, Dindin	40.24473409219606	8.625083429079506	1
C. g. gallarum	Tulu Adam Aniya, Dindin	40.24595152112411	8.622248952843199	1
C. g. gallarum	Tulu Adam Aniya, Dindin	40.24729884448552	8.620236985367287	1
C. g. gallarum	Tulu Adam Aniya, Dindin	40.24882904253515	8.618577105551479	1
C. g. gallarum	Molticha, Dindin	40.252750936902714	8.617506280839125	1
C. g. gallarum	Molticha, Dindin	40.256466393598565	8.614464680180527	1
C. g. gallarum	Molticha, Dindin	40.256333334330215	8.612692650927132	1
C. g. gallarum	Defo, Dindin	40.257373676774655	8.608547471282908	1
C. g. gallarum	Defo, Dindin	40.2544152502314	8.606920315129901	1
C. g. gallarum	Defo, Dindin	40.252862723293205	8.60729614669667	1
C. g. gallarum	Defo, Dindin	40.25138232330361	8.610267137161811	1
C. g. gallarum	Defo, Dindin	40.24942864441332	8.610237318210372	1
C. g. gallarum	Defo, Dindin	40.24846407035591	8.609806377376321	1
C. g. gallarum	Defo, Dindin	40.271181133660086	8.61286086819563	1
C. g. gallarum	Toma Heexoo, Dindin	40.23484714133572	8.616533317398138	1
C. g. gallarum	Toma Heexoo, Dindin	40.23886507213693	8.608661804147602	1
C. g. gallarum	Toma Heexoo, Dindin	40.24205302069861	8.605450215167961	1
C. g. gallarum	Toma Heexoo, Dindin	40.24784997123944	8.599860832039099	1
C. g. gallarum	Toma Heexoo, Dindin	40.248207820132464	8.598150503484922	1
C. g. gallarum	Toma Heexoo, Dindin	40.24632019899415	8.59329136302104	1
C. g. gallarum	Toma Heexoo, Dindin	40.24324991679492	8.593536408677137	1
C. g. gallarum	Toma Heexoo, Dindin	40.23978266113254	8.597445223685465	1
C. g. gallarum	Sidisaa, Dindin	40.22896032783049	8.597226707316857	1
C. g. gallarum	Sidisaa, Dindin	40.23063380093552	8.592093823577493	1
C. g. gallarum	Sidisaa, Dindin	40.22913135661318	8.588264266979875	1
C. g. gallarum	Sidisaa, Dindin	40.22707875204164	8.58569346869238	1
C. g. gallarum	Sidisaa, Dindin	40.22483232014285	8.585004277769933	1
C. g. gallarum	Seka, Dindin	40.22376662683251	8.587015275230954	1

C. g. gallarum	Seka, Dindin	40.22386973063203	8.588000667973006	1
C. g. gallarum	Seka, Dindin	40.22150331954704	8.59241226655124	1
C. g. gallarum	Seka, Dindin	40.206460323100735	8.616514985421592	1
C. g. gallarum	Hades forest	41.247063351835685	9.303171299669623	1
C. g. gallarum	Hades forest	41.24660999833511	9.300571123573597	1
C. g. gallarum	Hades forest	41.24375395055771	9.300733712785012	1
C. g. gallarum	Hades forest	41.244268545994224	9.301525847800901	1
C. g. gallarum	Hades forest	41.2458775168653	9.306983898080519	1
C. g. gallarum	Hades forest	41.245749215038856	9.311115213547588	1
C. g. gallarum	Hades forest	41.24160685403599	9.312198781529984	1
C. g. gallarum	Hades forest	41.241747711259876	9.311456752123574	1
C. g. gallarum	Hades forest	41.238942207936276	9.306711181900122	1
C. g. gallarum	Hades forest	41.2405684184763	9.30916843157626	1
C. g. gallarum	Hades forest	41.23734305560993	9.30707371780488	1
C. g. gallarum	Najabas, Sorroro Torgam	40.8445206	9.0009367	1
C. g. gallarum	Najabas, Sorroro Torgam	40.8474885	9.0040894	1
C. g. gallarum	Kuni Muktar	40.918315860421416	8.995637171339395	1
C. g. gallarum	Kuni Muktar	40.91241567839757	8.995866730157907	1
C. g. gallarum	Arada Raasaa, Bedeno forest	41.726432643702296	9.241091049940282	1
C. g. gallarum	Arada Raasaa, Bedeno forest	41.768637807601664	9.22819132991581	1
C. g. gallarum	Girawa forest, Gara Muleta	41.76818231328146	9.23041742426684	1
C. g. gallarum	Girawa forest, Gara Muleta	41.78316412682471	9.219405708074104	1
C. g. gallarum	Girawa forest, Gara Muleta	41.79411557569155	9.212870006669005	1
C. g. gallarum	Worgan bula	39.78533620356748	8.14115700924516	1
C. g. gallarum	Angada (Husa)	39.8266961652094	8.371140648308128	1
C. g. gallarum	Angada (Husa)	39.826296484019174	8.371105306336025	1
C. g. gallarum	Dindin (Toma Heto)	40.244347194846455	8.609584599136557	1
C. g. gallarum	Dindin (Defo)	40.24420982526923	8.606474173335544	1
C. g. gallarum	Dindin (Defo Oli)	40.252627658766855	8.604891420963641	1
C. g. gallarum	Dindin (Defo Gadi)	40.246930669866224	8.607704283448738	1
C. g. gallarum	Sorroro Torgam	40.84818321193268	9.005235131981868	1
C. g. gallarum	Hades forest	41.245244888967406	9.309084771628289	1
C. g. gallarum	Hades forest	41.24616291407129	9.310353388291857	1
C. g. gallarum	Hades forest	41.24576429534274	9.310627049869897	1
C. g. gallarum	Gara Muleta	41.783660333181565	9.218904954373258	1
C. g. gallarum	Gara Muleta	41.77528051175257	9.226423463789326	1
C. g. gallarum	Mt Arba Gugu, Arsi	39.966671	8.2	2

C. g. gallarum	Abul Casim ("Abu el Kassim")	37.883335	6.7	2
C. g. gallarum	Sagatta, 20 mi S, Webi Shebele	41.216667	8.383333	2
C. g. gallarum	Sagatta, 12 mi S, Webi Shebele	41.25	8.27423	2
C. g. gallarum	Djaffa Mts	40.16666667	7.666666667	3
C. g. gallarum	Arsi Mts near headwaters of Webi Shebeli	39.33333333	7.5	3
C. g. gallarum	near Burka	41.3	9.25	3
C. g. gallarum	Mt Kulubi	41.8	9.416666667	3
C. g. gallarum	Harar	42.41666667	9.2	3
C. g. gallarum	above Hirna valley	41.11666667	9.216666667	3
C. g. gallarum	Dindin Mts	40.16666667	8.583333333	3
C. g. gallarum	Gugu Mts, N of Gololcha	40.08333333	8.333333333	3
C. g. gallarum	Hades forest	41.2449	9.3087	4
C. g. gallarum	Hades forest	41.2453	9.3098	4
C. g. gallarum	Hades forest	41.2453	9.3106	4
C. g. gallarum	Kuni Muktar	40.8402	9.0208	4
C. g. gallarum	Kuni Muktar	40.8567	9.0258	4
C. g. gallarum	Kuni Muktar	40.8424	9.0291	4
C. g. gallarum	Kuni Muktar	40.855	9.0292	4
C. g. gallarum	Kuni Muktar	40.8476	9.0106	4
C. g. gallarum	Kuni Muktar	40.8303	9.0172	4

a) The occurrence localities of Djaffa Mountains guereza in the study area were mentioned in addition to the personal collection from the following literatures.

1: This study (Field collection)

2: GBIF (GBIF.org (Date 16 February 2021) GBIF Occurrence Download (DOI10.15468/dl.4ug5xa)

3: Yalden, D. W., Largen, M. J. and Kock, D. (1997). Catalogue of the Mammals of Ethiopia. *Mon. Zool. Ital. J. Zool.* **9**: 1–52.

4: Zinner, D., Tesfaye, D., Stenseth, N. C., Bekele, A. and Mekonnen, A. (2019). Is Colobus guereza gallarum a valid endemic Ethiopian taxon ? *Primate Biol.* **6**: 7–16.

Appendix 2. Ethiopian guereza occurrence used for species distribution modelling and niches overlap analysis.

Subspecies	longitude	latitude
C. g. guereza	39.6784	7.9853
C. g. guereza	36.0702	7.3172
C. g. guereza	38.5	6.3121
C. g. guereza	36.118	7.5256
C. g. guereza	38.6362	7.0209
C. g. guereza	35.6091	8.2895
C. g. guereza	36.1302	7.5094
C. g. guereza	36.2224	7.3202
C. g. guereza	38.5455	8.9668
C. g. guereza	36.7628	11.018
C. g. guereza	39.8366	6.6827
C. g. guereza	37.5724	9.7213
C. g. guereza	38.222	6.4499
C. g. guereza	39.7139	6.7476
C. g. guereza	36.8861	7.6679
C. g. guereza	36.087	7.3193
C. g. guereza	37.34	6.15
C. g. guereza	39.7175	7.22
C. g. guereza	37.2656	11.3716
C. g. guereza	39.6839	11.0251
C. g. guereza	37.981	8.5348
C. g. guereza	39.5463	7.0443
C. g. guereza	36.3618	8.4592
C. g. guereza	35.6992	8.4879
C. g. guereza	38.618896	7.084168
C. g. guereza	36.476923	10.952175
C. g. guereza	40.009714	8.845228
C. g. guereza	38.637552	7.080321
C. g. guereza	38.6277	7.101144
C. g. guereza	37.033328	10.842028
C. g. guereza	38.534329	8.961754
C. g. guereza	37.982304	8.514145
C. g. guereza	37.5552	6.035703
C. g. guereza	35.61945	8.323156
C. g. guereza	36.822036	7.688687
C. g. guereza	36.833586	7.677721
C. g. guereza	36.251106	7.280605
C. g. guereza	37.1333	11.0333
C. g. guereza	39.75	6.6667
C. g. guereza	38	6.6667
C. g. guereza	36.8833	10.2667
C. g. guereza	39.75	7.6667
C. g. guereza	34.85	8.1833
C. g. guereza	38.760378	9.185278
C. g. guereza	38.993568	8.777529
C. g. guereza	36.363372	5.505272
C. g. guereza	38.716667	6.666667
C. g. guereza	36.966667	10.966666
C. g. guereza	39.166668	6.916667
C. g. guereza	38.200001	10.416667
C. g. guereza	38.633335	6.666667
C. g. guereza	38.450001	6.6
C. g. guereza	39.183334	6.983333
C. g. guereza	38.583332	9.033334
C. g. guereza	39.723769	6.713382
C. g. guereza	39.702358	6.924126
C. g. guereza	38.809918	7.540078
C. g. guereza	39.79002	7.09673
C. g. guereza	38.469866	7.057013
C. g. guereza	38.207757	6.199775
C. g. guereza	39.729409	6.683811
C. g. guereza	39.737098	6.728019
C. g. guereza	39.728478	6.694372
C. g. guereza	38.483258	7.08728
C. g. guereza	38.529926	6.737175
C. g. guereza	38.443457	6.749635
C. g. guereza	38.82843	7.570799
C. g. guereza	39.822006	6.610726
C. g. guereza	37.616665	11.883333
C. g. guereza	38.166668	10.666667

C. g. guereza	38.200001	10.45
C. g. guereza	37.2451757	10.6709564
C. g. guereza	39.5682317	6.4145312
C. g. guereza	38.55	9.416666667
C. g. guereza	36.1045749	7.5256305
C. g. guereza	38.5586874	8.9779319
C. g. guereza	37.8197374	5.8395449
C. g. guereza	39.8447941	6.5523802
C. g. guereza	37.7063705	6.2144545
C. g. guereza	38.0551051	6.5610582
C. g. guereza	39.7581339	9.7501853
C. g. guereza	38.8850761	7.461899
C. g. guereza	37.4987333	6.7379675
C. g. guereza	39.1799875	7.9164483
C. g. guereza	38.7	7.12
C. g. guereza	39.1178137	7.9319391
C. g. guereza	39.2275324	6.9325476
C. g. guereza	36.2087929	7.2641251
C. g. guereza	37.6608657	8.2467703
C. g. guereza	36.54444	9.1270221
C. g. guereza	35.0724594	7.8304438
C. g. guereza	37.0383085	7.0406375
C. g. guereza	36.59370592	10.86275711
C. g. guereza	36.58118069	10.78651666
C. g. guereza	36.59263806	10.88987667
C. g. guereza	36.60335779	11.74954506
C. g. guereza	36.55020307	10.78244155
C. g. guereza	36.6425777	10.75658107
C. g. guereza	36.70925565	10.92273493
C. g. guereza	36.70849066	10.85897098
C. g. guereza	36.68238118	10.92491824
C. g. guereza	36.90134741	11.17028124
C. g. guereza	36.82330315	11.18922762
C. g. guereza	36.92841047	11.14240547
C. g. guereza	36.765292	11.06521142
C. g. guereza	36.66858068	10.99282607
C. g. guereza	36.69408065	11.03638994

C. g. guereza	36.7014137	10.94000953
C. g. guereza	37.02019878	10.81939353
C. g. guereza	36.7326298	11.00191422
C. g. guereza	36.99684974	10.78729921
C. g. guereza	36.66013902	10.9683704
C. g. guereza	36.7252742	10.97701552
C. g. guereza	36.84724701	10.82175143
C. g. guereza	36.96367301	10.91160056
C. g. guereza	36.99863218	10.84798018
C. g. gallarum	40.23858523	8.617606474
C. g. gallarum	40.23858518	8.617588388
C. g. gallarum	40.25579722	8.615443532
C. g. gallarum	40.26238377	8.626038621
C. g. gallarum	40.26405397	8.636432748
C. g. gallarum	40.24743002	8.638051678
C. g. gallarum	41.23485439	9.307785283
C. g. gallarum	41.24596463	9.316347035
C. g. gallarum	41.24899123	9.30584352
C. g. gallarum	41.25659243	9.236625679
C. g. gallarum	41.72817697	9.240860948
C. g. gallarum	41.76867842	9.229898612
C. g. gallarum	41.78175241	9.219118482
C. g. gallarum	41.79408475	9.21241851
C. g. gallarum	39.7853362	8.141157009
C. g. gallarum	39.82629648	8.371105306
C. g. gallarum	40.91925446	9.002918711
C. g. gallarum	40.91286222	8.996054258
C. g. gallarum	40.84818321	9.005235132
C. g. gallarum	41.24524489	9.309084772
C. g. gallarum	41.77528051	9.226423464
C. g. gallarum	40.26144549	8.655404833
C. g. gallarum	40.25810302	8.642230909
C. g. gallarum	40.24378753	8.627392519
C. g. gallarum	40.24882904	8.618577106
C. g. gallarum	40.25737368	8.608547471
C. g. gallarum	40.24942864	8.610237318
C. g. gallarum	40.27118113	8.612860868

C. g. gallarum	40.23484714	8.616533317
C. g. gallarum	40.23886507	8.608661804
C. g. gallarum	40.24784997	8.599860832
C. g. gallarum	40.2463202	8.593291363
C. g. gallarum	40.24324992	8.593536409
C. g. gallarum	40.23978266	8.597445224
C. g. gallarum	40.22896033	8.597226707
C. g. gallarum	40.2306338	8.592093824
C. g. gallarum	40.22483232	8.585004278
C. g. gallarum	40.22150332	8.592412267
C. g. gallarum	40.20646032	8.616514985
C. g. gallarum	41.24375395	9.300733713
C. g. gallarum	40.8445206	9.0009367
C. g. gallarum	41.3	9.25
C. g. gallarum	41.8	9.416666667
C. g. gallarum	41.11666667	9.216666667
C. g. gallarum	40.08333333	8.333333333
C. g. gallarum	40.16666667	8.583333333
C. g. gallarum	39.966671	8.2

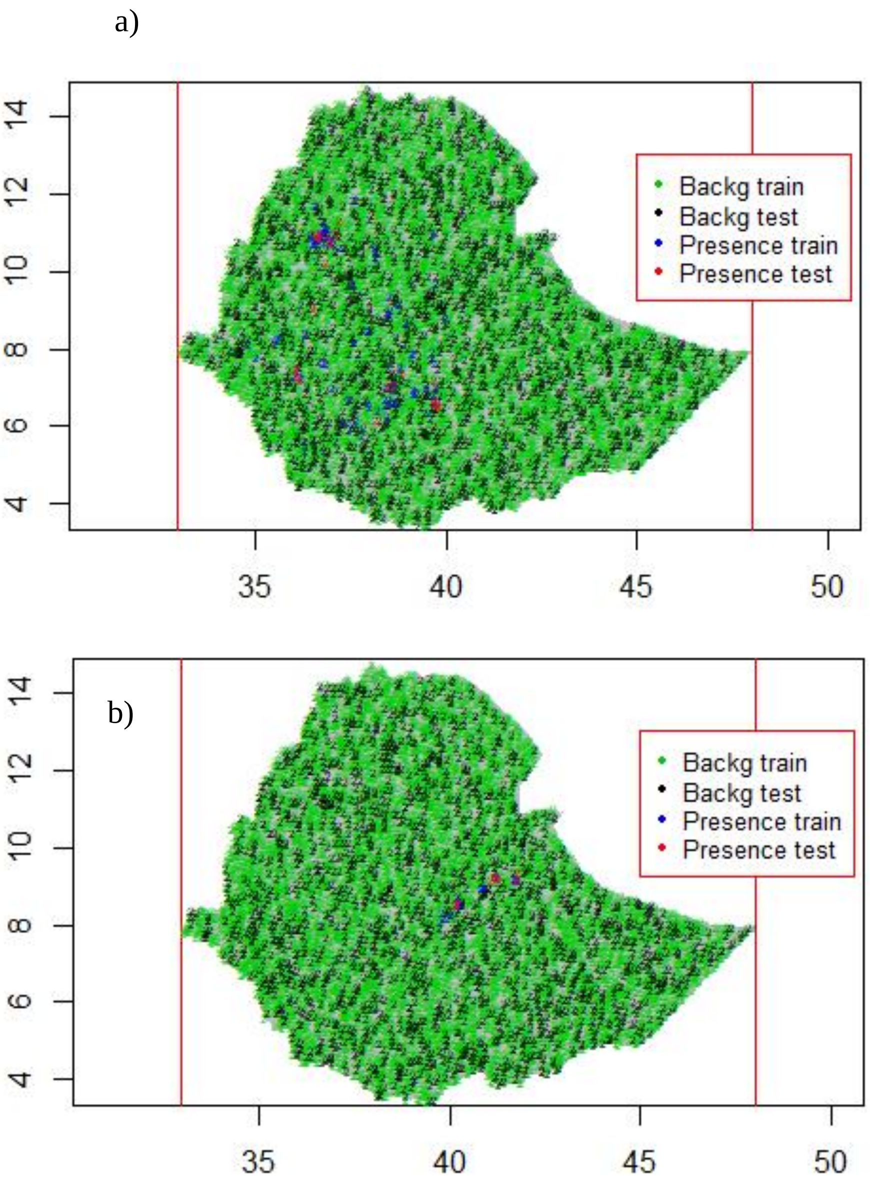
Appendix 3. Environmental predictors considered during the habitat suitability and distribution models of Djaffa Mountains guereza.

Category	Variables	Code	Units	Data sources
Bioclimatic	Annual Mean Temperature	BIO1	Degree Celsius	http://www.worldclim.org
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	BIO2	Degree Celsius	
	Isothermality (BIO2/BIO7) (×100)	BIO3	Degree Celsius	
	Temperature Seasonality (standard deviation ×100)	BIO4	Degree Celsius	
	Max Temperature of Warmest Month	BIO5	Degree Celsius	
	Min Temperature of Coldest Month	BIO6	Degree Celsius	
	Temperature Annual Range (BIO5-BIO6)	BIO7	Degree Celsius	
	Mean Temperature of Wettest Quarter	BIO8	Degree Celsius	
	Mean Temperature of Driest Quarter	BIO9	Degree Celsius	
	Mean Temperature of Warmest Quarter	BIO10	Degree Celsius	
	Mean Temperature of Coldest Quarter	BIO11	Degree Celsius	
	Annual Precipitation	BIO12	Millimeters	
	Precipitation of Wettest Month	BIO13	Millimeters	
	Precipitation of Driest Month	BIO14	Millimeters	
	Precipitation Seasonality (Coefficient of Variation)	BIO15	Millimeters	
	Precipitation of Wettest Quarter	BIO16	Millimeters	
	Precipitation of Driest Quarter	BIO17	Millimeters	
	Precipitation of Warmest Quarter	BIO18	Millimeters	
	Precipitation of Coldest Quarter	BIO19	Millimeters	
Disturbance	Distance to roads	DistRod	Meters	GEOFABRIK
	Distance to settlements	DistPopD	Meters	GEOFABRIK
Topographic attribute	Elevation	Alt	Meters	https://earthexplorer.usgs.gov
	Slope	Slop	Degrees	
	Aspect	Asp	Degrees	
	Distance to rivers	DistRvr	Meters	GEOFABRIK
Landscape attribute	Land cover class	LCC	Unitless	https://cds.climate.copernicus.eu/
Resource	Vegetation type	VegT	Unitless	

Appendix 4. Multicollinearity test by using correlation analysis among environmental variables.

	Bio1	Bio2	Bio3	Bio4	Bio5	Bio6	Bio7	Bio8	Bio9	Bio10	Bio11	Bio12	Bio13	Bio14	Bio15	Bio16	Bio17	Bio18	Bio19	LULC	VegT	Asp	Alt	Slop	DistRod	DistRvr
Bio2	0.3	-																								
Bio3	-0.5	-0.7	-																							
Bio4	0.7	0.5	-0.8	-																						
Bio5	1.0	0.6	-0.7	0.8	-																					
Bio6	1.0	0.1	-0.4	0.6	0.9	-																				
Bio7	0.4	1.0	-0.8	0.7	0.7	0.2	-																			
Bio8	1.0	0.2	-0.5	0.6	0.9	1.0	0.3	-																		
Bio9	1.0	0.3	-0.5	0.6	1.0	1.0	0.4	1.0	-																	
Bio10	1.0	0.4	-0.6	0.7	1.0	1.0	0.5	1.0	1.0	-																
Bio11	1.0	0.3	-0.5	0.6	1.0	1.0	0.4	1.0	1.0	1.0	-															
Bio12	-0.7	-0.7	0.7	-0.7	-0.9	-0.6	-0.8	-0.6	-0.7	-0.8	-0.7	-														
Bio13	-0.9	-0.4	0.4	-0.5	-0.9	-0.8	-0.5	-0.8	-0.9	-0.8	-0.9	0.8	-													
Bio14	-0.8	-0.2	0.5	-0.7	-0.8	-0.8	-0.3	-0.8	-0.8	-0.8	-0.8	0.5	0.6	-												
Bio15	-0.4	0.2	-0.3	0.3	-0.2	-0.5	0.2	-0.4	-0.4	-0.3	-0.4	0.0	0.6	0.2	-											
Bio16	-0.7	-0.7	0.6	-0.6	-0.8	-0.6	-0.7	-0.6	-0.7	-0.7	-0.7	1.0	0.9	0.5	0.3	-										
Bio17	-0.8	-0.7	0.8	-0.8	-0.9	-0.7	-0.8	-0.7	-0.8	-0.8	-0.8	0.9	0.7	0.7	-0.1	0.8	-									
Bio18	-0.7	-0.6	0.7	-0.8	-0.8	-0.6	-0.7	-0.6	-0.6	-0.7	-0.7	0.9	0.6	0.5	-0.2	0.7	0.9	-								
Bio19	-0.6	-0.4	0.5	-0.7	-0.7	-0.6	-0.4	-0.6	-0.6	-0.7	-0.6	0.6	0.4	0.7	-0.3	0.5	0.8	0.6	-							
LULC	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	-0.1	0.0	-0.1	0.0	0.1	-0.1	0.2	0.1	0.0	-0.1	0.0	-						
VegT	-0.3	-0.1	0.2	-0.4	-0.3	-0.3	-0.2	-0.3	-0.3	-0.3	-0.3	0.3	0.1	0.5	-0.3	0.2	0.4	0.2	0.7	0.1	-					
Asp	-0.1	0.0	0.0	0.1	0.0	-0.1	0.0	0.0	-0.1	0.0	-0.1	0.1	0.2	0.0	0.2	0.2	0.0	-0.1	0.0	-0.1	-0.1	-				
Alt	-0.9	-0.5	0.7	-0.7	-0.9	-0.8	-0.6	-0.9	-0.9	-0.9	-0.9	0.8	0.8	0.8	0.2	0.8	0.9	0.7	0.7	0.1	0.4	0.0	-			
Slop	-0.4	-0.2	0.2	-0.2	-0.4	-0.4	-0.2	-0.4	-0.4	-0.4	-0.4	0.4	0.4	0.3	0.2	0.4	0.4	0.3	0.2	0.1	0.0	-0.2	0.4	-		
DistRod	0.0	-0.6	0.4	-0.4	-0.2	0.2	-0.6	0.1	0.0	0.0	0.0	0.4	0.0	0.1	-0.5	0.3	0.4	0.4	0.3	-0.1	0.3	0.1	0.2	0.0	-	
DistRvr	-0.5	0.2	0.1	-0.2	-0.4	-0.6	0.1	-0.6	-0.5	-0.5	-0.5	0.1	0.3	0.2	0.2	0.1	0.2	0.4	0.0	0.1	-0.1	-0.1	0.2	0.2	-0.3	-
DistPopD	-0.3	-0.1	0.2	-0.3	-0.3	-0.3	-0.2	-0.3	-0.3	-0.3	-0.3	0.3	0.3	0.3	0.1	0.3	0.3	0.4	0.1	-0.2	0.0	0.1	0.3	0.1	0.1	0.1

Appendix 5. The Ethiopian guereza presence and background training and testing data sets utilized for ecological niche modellings.



Appendix 6. The chi-square test of goodness of fit for models fitted to the right-truncation value of 50 metres for the perpendicular distance of the Djaffa Mountains guereza survey data.

Sr/no	cut points	observed value	expected value	chi-square
1	0.0 – 10.0	31	29.89	0.041
2	10.0 – 20.0	22	22.64	0.018
3	20.0 – 30.0	12	12.98	0.074
4	30.0 – 50.0	8	7.49	0.035

Total Chi-square value = 0.1682 Degrees of Freedom = 2.00

Probability of a greater chi-square value, P = 0.91932

Appendix 7. Djaffa Mountains guereza population surveys dataset used for abundance estimation in Distance.

Stratum	Line/Stra	Area	Transect	Length	walk	Season	mode	date (GC)	time (24hr)	Distance	Cluster size
DDF	1	83	1	2.95	1	Dry	vis	12/30/2020	11:05	25	8
DDF	1	83	1	2.95	1	Dry	vis	12/30/2020	13:00	10	6
DDF	1	83	1	2.95	1	Dry	vis	12/30/2020	13:30	20	5
DDF	1	83	1	2.95	1	Wet	vis	7/17/2020	14:30	4	3
DDF	1	83	1	2.95	1	Wet	vis	7/17/2020	14:45	25	1
DDF	1	83	1	2.95	1	Wet	vis	7/17/2020	15:00	5	5
DDF	1	83	1	2.95	1	Wet	vis	7/17/2020	15:10	10	5
DDF	1	83	1	2.95	1	Wet	vis	7/17/2020	15:40	5	7
DDF	1	83	1	2.95	1	Wet	vis	7/17/2020	16:10	15	8
DDF	2	83	2	6	1	Dry	vis	12/30/2020	15:00	20	5
DDF	2	83	2	6	1	Dry	vis	12/30/2020	15:20	15	15
DDF	2	83	2	6	1	Dry	vis	12/30/2020	16:00	25	6
DDF	2	83	2	6	1	Dry	vis	12/30/2020	16:30	35	4
DDF	2	83	2	6	1	Wet	vis	7/18/2020	11:05	10	10
DDF	2	83	2	6	1	Wet	vis	7/18/2020	11:49	20	7
DDF	2	83	2	6	1	Wet	vis	7/18/2020	12:20	45	5
DDF	2	83	2	6	1	Wet	vis	7/18/2020	13:05	5	6
DDF	3	83	3	5.3	1	Dry	vis	12/31/2020	9:30	15	4
DDF	3	83	3	5.3	1	Dry	vis	12/31/2020	11:00	25	2
DDF	3	83	3	5.3	1	Dry	vis	12/31/2020	11:25	5	2
DDF	3	83	3	5.3	1	Dry	vis	12/31/2020	15:10	27	8
DDF	3	83	3	5.3	1	Dry	vis	12/31/2020	15:45	20	4
DDF	3	83	3	5.3	1	Dry	vis	12/31/2020	16:00	25	8
DDF	3	83	3	5.3	1	Wet	vis	7/18/2021	14:00	10	5
DDF	3	83	3	5.3	1	Wet	vis	7/18/2021	14:30	15	6
DDF	3	83	3	5.3	1	Wet	vis	7/18/2021	15:10	10	7
DDF	4	83	4	3.2	1	Dry	vis	1/1/2021	10:00	10	8
DDF	4	83	4	3.2	1	Dry	vis	1/1/2021	11:50	5	2
DDF	4	83	4	3.2	1	Wet	vis	8/16/2021	13:25	5	8
DDF	4	83	4	3.2	1	Wet	vis	8/16/2021	16:10	7	3
DDF	6	83	5	5.42	1	Dry	vis	1/1/2021	15:00	45	4
DDF	6	83	5	5.42	1	Dry	vis	1/1/2021	16:00	25	6
DDF	6	83	5	5.42	1	Wet	vis	7/16/2021	14:40	8	4

DDF	7	83	6	2.85	1	Wet	vis	7/16/2021	12:20	10	7
DDF	8	83	7	2	1	Wet	vis	7/16/2021	12:07	45	4
DDF	8	83	7	2	1	Wet	vis	7/16/2021	13:00	3	1
DDF	9	83	8	5	1	Wet	vis	7/19/2021	11:45	20	4
DDF	9	83	8	5	1	Wet	vis	7/19/2021	13:20	2	2
DDF	10	83	9	6.55	1	Wet	vis	7/19/2021	14:10	20	4
DDF	10	83	9	6.55	1	Wet	vis	7/19/2021	14:20	15	5
DDF	10	83	9	6.55	1	Wet	vis	7/19/2021	14:45	25	12
GMF	1	28.8	10	5	1	Dry	vis	1/12/2021	14:05	45	6
GMF	1	28.8	10	5	1	Dry	vis	1/12/2021	15:05	5	5
GMF	1	28.8	10	5	1	Wet	vis	9/5/2021	13:10	15	4
GMF	1	28.8	10	5	1	Wet	vis	9/5/2021	14:40	25	8
GMF	2	28.8	11	2.97	1	Dry	vis	1/13/2021	11:20	35	7
GMF	2	28.8	11	2.97	1	Wet	vis	9/6/2021	14:55	20	8
GMF	3	28.8	12	2.7	1	Dry	vis	1/12/2021	14:00	30	8
GMF	3	28.8	12	2.7	1	Wet	vis	9/6/2021	15:45	15	9
GMF	4	28.8	13	1.8	1	Dry	vis	1/13/2021	16:00	20	5
GMF	4	28.8	13	1.8	1	Wet	vis	9/6/2021	11:50	15	5
HDF	1	6.1	14	2	1	Dry	vis	1/9/2021	13:30	5	6
HDF	1	6.1	14	2	1	Dry	vis	1/9/2021	14:45	10	5
HDF	1	6.1	14	2	1	Dry	vis	1/9/2021	15:00	50	3
HDF	1	6.1	14	2	1	Wet	vis	7/22/2021	16:56	7	2
HDF	2	6.1	15	3.4	1	Dry	vis	1/9/2021	15:30	10	3
HDF	2	6.1	15	3.4	1	Wet	vis	7/22/2021	16:25	5	3
HDF	2	6.1	15	3.4	1	Wet	vis	7/22/2021	16:42	10	8
HDF	2	6.1	15	3.4	1	Wet	vis	7/22/2021	17:04	15	6
HDF	3	6.1	16	4.08	1	Dry	vis	1/10/2021	13:30	5	5
HDF	3	6.1	16	4.08	1	Dry	vis	1/10/2021	14:00	25	3
HDF	3	6.1	16	4.08	1	Wet	vis	7/22/2021	15:00	5	4
HDF	3	6.1	16	4.08	1	Wet	vis	7/22/2021	17:23	20	2
HDF	4	6.1	17	2.5	1	Dry	vis	1/10/2021	15:30	10	5
HDF	4	6.1	17	2.5	1	Wet	vis	7/22/2021	12:38	5	4
HDF	4	6.1	17	2.5	1	Wet	vis	7/22/2021	13:02	15	8
JKMWS	2	65.1	18	7	1	Dry	vis	1/5/2021	11:50	20	4
JKMWS	2	65.1	18	7	1	Wet	vis	7/23/2021	13:30	30	2
JKMWS	2	65.1	18	7	1	Wet	vis	7/23/2021	14:00	50	3
JKMWS	3	65.1	19	5.2	1	Dry	vis	1/6/2021	10:00	5	3

JKMWS	3	65.1	19	5.2	1	Dry	vis	1/6/2021	12:20	3	5
JKMWS	3	65.1	19	5.2	1	Wet	vis	8/28/2021	10:00	15	8
JKMWS	3	65.1	19	5.2	1	Wet	vis	8/28/2021	9:15	20	5

Appendix 8. Cluster size and composition of Djaffa Mountains guerezas in the remanent forest of the Ahmar Mountains, eastern Ethiopia during the study periods.

Group	Season	Adult Male	Adult Female	Juvenile	Infant
DDF1	Dry	2	3	3	0
DDF2	Dry	1	2	3	0
DDF3	Dry	1	2	2	0
DDF4	Wet	1	1	1	0
DDF5	Wet	1	0	0	0
DDF6	Wet	2	1	2	0
DDF7	Wet	1	2	2	0
DDF8	Wet	2	2	3	0
DDF9	Wet	2	4	2	0
DDF10	Dry	1	2	2	0
DDF11	Dry	3	4	8	0
DDF12	Dry	1	2	3	0
DDF13	Dry	1	1	2	0
DDF14	Wet	2	3	5	0
DDF15	Wet	1	3	2	1
DDF16	Wet	1	2	1	1
DDF17	Wet	1	2	3	0
DDF18	Dry	1	1	2	0
DDF19	Dry	1	1	0	0
DDF20	Dry	1	1	0	0
DDF21	Dry	1	3	4	0
DDF22	Dry	1	1	2	0
DDF23	Dry	2	3	3	0
DDF24	Wet	1	2	1	1
DDF25	Wet	1	2	3	0
DDF26	Wet	2	3	2	0
DDF27	Dry	2	2	4	0
DDF28	Dry	1	1	0	0
DDF29	Wet	1	3	2	2
DDF30	Wet	1	1	1	0
DDF31	Dry	1	1	2	0
DDF32	Dry	2	2	2	0
DDF33	Wet	1	1	2	0
DDF34	Wet	1	2	4	0
DDF35	Wet	1	1	2	0
DDF36	Wet	1	0	0	0
DDF37	Wet	1	1	2	0
DDF38	Wet	1	1	0	0
DDF39	Wet	1	1	1	1
DDF40	Wet	1	1	2	1

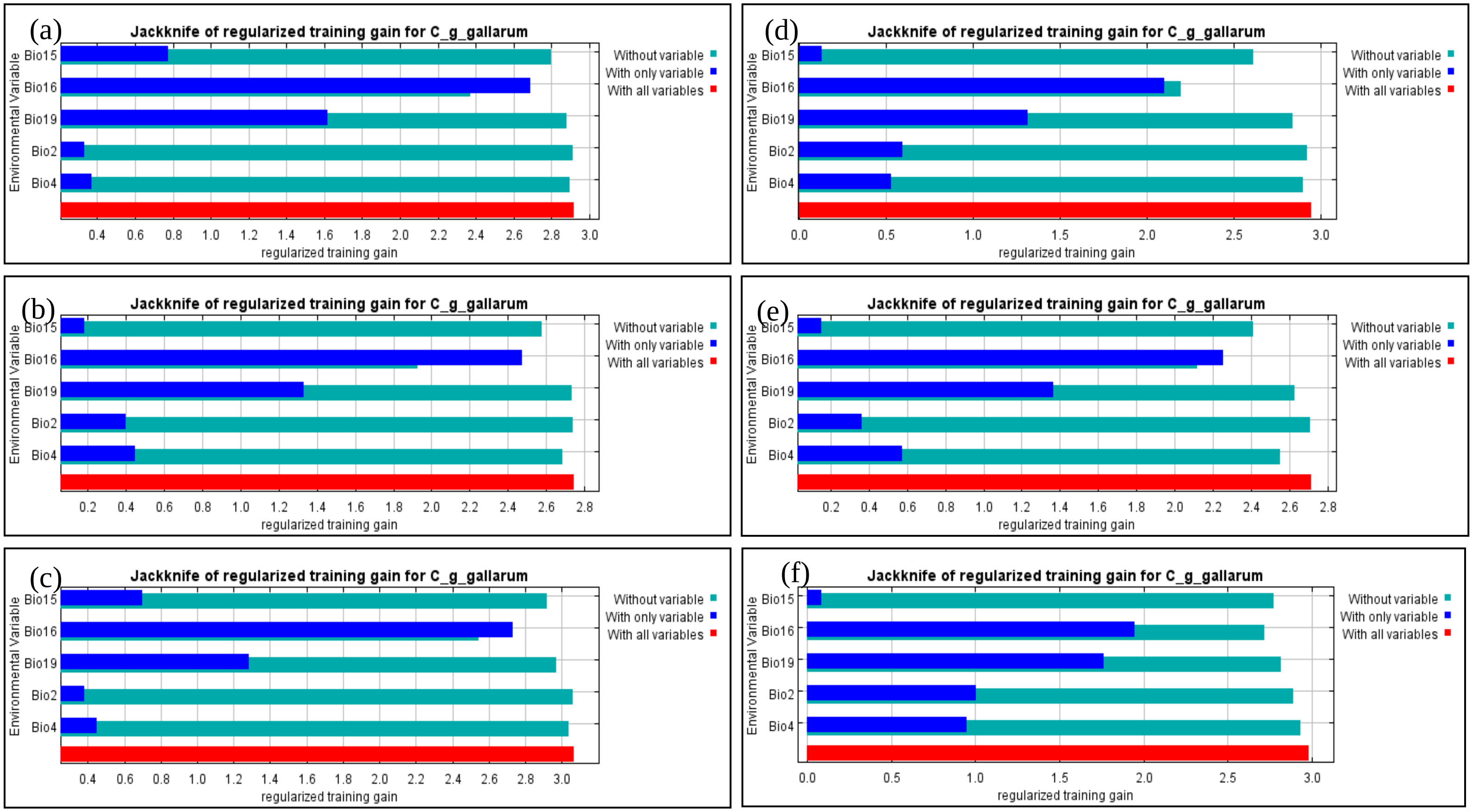
DDF41	Wet	2	3	5	2
GMF1	Dry	1	2	3	0
GMF2	Dry	1	1	3	0
GMF3	Wet	1	1	2	0
GMF4	Wet	2	3	3	0
GMF5	Dry	2	2	3	0
GMF6	Wet	2	2	4	0
GMF7	Dry	1	2	4	0
GMF8	Wet	2	3	3	1
GMF9	Dry	1	2	2	0
GMF10	Wet	1	1	3	0
HDF1	Dry	1	2	3	0
HDF2	Dry	1	2	2	0
HDF3	Dry	2	1	0	0
HDF4	Wet	2	0	0	0
HDF5	Dry	1	1	1	0
HDF6	Wet	1	2	0	0
HDF7	Wet	1	2	3	2
HDF8	Wet	1	2	3	0
HDF9	Dry	1	2	2	0
HDF10	Dry	1	1	1	0
HDF11	Wet	1	1	2	0
HDF12	Wet	1	1	0	0
HDF13	Dry	2	3	0	0
HDF14	Wet	1	1	1	1
HDF15	Wet	1	3	2	2
JKMWS1	Dry	1	1	2	0
JKMWS2	Wet	1	1	0	0
JKMWS3	Wet	1	1	1	0
JKMWS4	Dry	1	1	1	0
JKMWS5	Dry	1	2	2	0
JKMWS6	Wet	2	3	1	2
JKMWS7	Wet	1	1	2	1

Appendix 9. The climate-only predictor variables contribute to the predicted habitat suitability modeling of Djaffa Mountains guereza using low and high RCP scenarios during the periods of the 2050s and 2070s under two Global Circulation Models (GCM).

Time	RCPs	Variable	Bio16	Bio2	Bio4	Bio15	Bio19	AUC* ± (SD)
50BCC-CMS1-1	2.6	% contribution	90.00	0.10	1.20	8.20	0.60	0.98
		Permutation importance	90.90	0.20	3.80	2.60	2.40	(0.01)
	8.5	% contribution	91.40	0.10	2.40	5.10	1.10	0.98
		Permutation importance	73.20	0.10	17.80	7.50	1.40	(0.01)
70BCC-CMS1-1	2.6	% contribution	90.80	0.90	1.20	5.80	1.20	0.96
		Permutation importance	80.40	3.40	2.00	10.90	3.40	(0.01)
	8.5	% contribution	87.30	0.10	1.90	6.10	4.60	0.97
		Permutation importance	77.20	0.10	1.30	17.90	3.40	(0.02)
50HadGEM2-ES	2.6	% contribution	75.30	5.00	1.50	14.80	3.40	0.98
		Permutation importance	61.50	1.50	17.70	17.70	1.60	(0.01)
	8.5	% contribution	73.10	5.00	4.20	12.30	5.40	0.98
		Permutation importance	50.30	2.00	22.70	20.90	4.10	(0.01)
70HadGEM2-ES	2.6	% contribution	86.10	0.10	4.10	7.70	2.00	0.98
		Permutation importance	56.00	0.30	37.20	3.70	2.80	(0.01)
	8.5	% contribution	62.90	14.70	2.10	12.30	8.00	0.98
		Permutation importance	55.00	6.30	15.40	15.30	8.00	(0.01)

* AUC, the area under the curve, SD, standard deviation.

Appendix 10. The MaxEnt models for *C. g. gallarum* show the relative prediction performance under two scenarios with climate-only ecological predictors, as illustrated by the jackknife test using regularized training gain. (a) BCC-CMS1-1 low_RCP_2050s, (b) BCC-CMS1-1 high_RCP_2050s, (c) BCC-CMS1-1 high_RCP_2070s, (d) HadGEM2-ES low_RCP_2050s, (e) HadGEM2-ES low_RCP_2070s, and (f) HadGEM2-ES high_RCP_2070s.



Appendix 11. The Global Circulation Model predicts changes in Djaffa Mountains guereza habitat distributions in the Eastern Ethiopian Highlands under low and high Representative Concentration Pathway scenarios for the mid-decade 2050s and late decade 2070s.

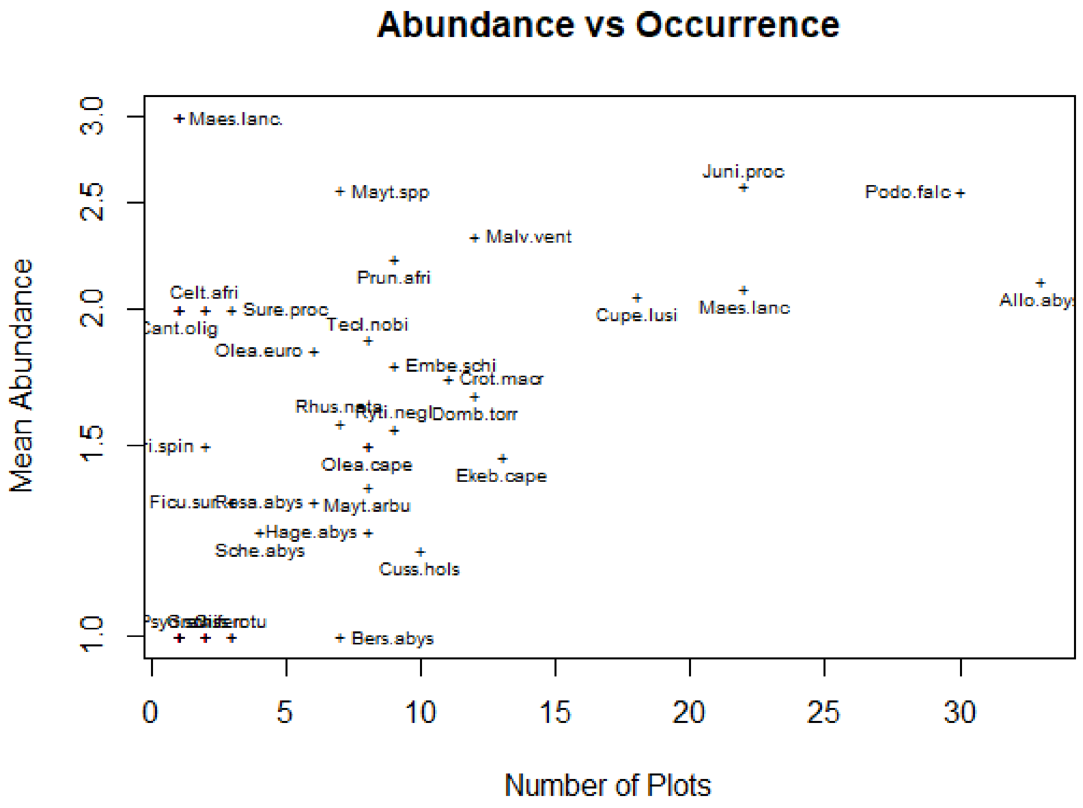
GCM	Suitability models scenarios	Habitat predicted to be suitable (ha)	Steady habitat (ha)	Steady habitat (%)	Gain (ha)	Gain (%)	Loss (ha)	Loss (%)	Net gain/net loss (ha)
	Current	133604.52	133604.52	100.00					
BCC-CMS1-1	RCP 2.6 (2050)	281,214.75	122,139.90	91.42	159,074.85	119.06	11,464.62	8.58	147,610.23
	RCP 8.5 (2050)	338,056.36	127,705.80	95.58	210,350.56	157.44	5,898.72	4.42	204,451.84
	RCP 2.6 (2070)	366,802.53	122,863.63	91.96	243,938.90	182.58	10,740.89	8.04	233,198.01
	RCP 8.5 (2070)	243,113.34	118,546.92	88.73	124,566.42	93.24	15,057.59	11.27	109,508.83
HadGEM2-ES	RCP 2.6 (2050)	251,887.97	117,959.77	88.29	133,928.20	100.24	15,644.75	11.71	118,283.45
	RCP 8.5 (2050)	263,907.16	117,785.07	88.16	146,122.09	109.37	15,819.45	11.84	130,302.64
	RCP 2.6 (2070)	333,985.70	126,473.12	94.66	207,512.58	155.32	7,131.39	5.34	200,381.19
	RCP 8.5 (2070)	257,005.69	117,749.86	88.13	139,255.83	104.23	15,854.66	11.87	123,401.17

Appendix 12. Lists of plant species in Ahmar Mountains, Eastern Ethiopia. [a] local name = Afaan Oromo.

No.	Scientific name	Family	Local names[a]	Habit
1	Allophylus abyssinicus (Hochst.) Radlk	Sapindaceae	Hirqamu, Yaayaa	Tree
2	Asparagus racemosus Wild.	Asparagaceae	Seriitii	Climber
3	Bercium gradiflorim (Lam.) PichSerm	Lamiaceae	Huruuba	Tree
4	Bersama abyssinica Fres.	Melianthaceae	Qilisa, lolchiisaa	Tree
5	Buddlejia polystachya Fresen.	Buddlejiaceae	Qawissa/Anfar	Tree
6	Calpurnia aurea (Aiton) Benth.	Fabaceae	Ceekataa	Tree
7	Canthium oligocarpum Hiern.	Rubiaceae	Wanta fullas	Tree
8	Carissa spinarum L./Carissa edulis	Apocynaceae	Agamsa	Shrub
9	Celtis africana Burm	Ulmaceae	Mataqoma	Tree
10	Cissus rotundifolia (Forssk.) Vahl	Vitaceae	Balcha	Climber
11	Croton macrostachyus Del.	Euphorbiaceae	Makkanniisa	Tree
12	Cuperssus lusitanica Mill.	Cupressaceace	Gattiraa Ferji	Tree
13	Cussonia holstii Harms ex Engl.	Araliaceae	Harfattuu	Tree
14	Dombeya torrida (J.F. Gmel) Bamps	Sterculiaceae	Daannisa	Tree
15	Dovyalis caffra (Hook. & Harv.) Hook. f.	Flacourtiaceae	Koshimi	Tree
16	Ekebergia capensis Sparrm.	Meliaceae	Somboo	Tree
17	Embelia schimperi Vatke	Embenaceae	Hanquu	Climber
18	Erythrina bruce	Fabaceae	Walensuu	Tree
19	Euphorbia dalettiensis	Euphorbiaceae	Adamii	Shrub
20	Ficus sur Forssk.	Moraceae	Harbuu	Tree
21	Grewia ferruginea (Hochst.ex A. Rich)	Tiliaceae	Laanqisaa	Climber
22	Hagenia abyssinica (Bruce) J.F. Gmel.	Rosaceae	Heexoo	Tree
23	Jasminum abyssinicum	Oleaceae	Biluu	Tree
24	Juniperus procera Eiille	Cupressaceace	Gatira Habasha	Tree
25	Lepidotrichilia volkensii (Gürke) Leroy	Meliaceae	Halaba	Tree
26	Maesa lanceolata Forssk	Myrsinaceae	Abayyi	Tree
27	Malva venticillata L	Malvaceae	Liitii	Climber
28	Maytenus arbutifolia (A.Rich.) Wilczek	Celastraceae	Kombolcha	Tree
29	Maytenus sp.	Celastraceae	Qaxammee	Tree
30	Myrsine melanophloeos (L.)	Sapotaceae	Tullaa	Tree
31	Olea capensis L. subsp. Macrocarp (C.H.Wright) Verde)	Oleaceae	Gagamaa	Tree
32	Olea europaea L. subsp. Cuspidata	Oleaceae	Ejersa	Tree

	(Wall.exG.Don). CF			
33	Olea hochstetteri Baker	Oleaceae	Ejersa Korma	Tree
34	Oncoba spinosa Forssk	Flacouriaceae	Garabagush	Tree
35	Podocarpus falcatus (Thunb.) Mirb.	Podocarpaceae	Birbirsa	Tree
36	Prunus africana (Hook.f.) Kalkman	Rosaceae	Sukkee, Mechaloo, Tikur Enchet	Tree
37	Psydrax schimperiana (A. Rich.) Bridson	Rubiaceae	Gaallee	Tree
38	Dracaena steudneri Engl	Dracaenaceae		
39	Rhamnus prinoides LHerit	Rhamnaceae	Garaba Gosh	Tree
40	Rhus glutinosa A. Rich	Anacardiaceae	Waka	Tree
41	Rhus natalensis Krauss	Anacardiaceae	Xaxesa	Shrub
42	Rhus glutinosa			
43	Rosa abyssinica Lindley	Rosaceae	Goraa	Climber
44	Rubus apetalus			
45	Rytigna neglecta (Hiern) Robyns	Polygonaceae	Mixoo	Tree
46	Schefflera abyssinica (Hochst.ex.A. Rich.)	Araliaceae	Gatamee	Tree
47	Suregada procera (Prain) Croizat	Euphorbiaceae	Xillo	Tree
48	Teclea nobilis Del.	Rutaceae	Hadhessa	Tree
49	Vernonia urticifolia A. Rich	Asteraceae	Ibicha Adii	Tree
50	Schefflera volkensii	Araliaceae	Anshaa	Tree
51	Rhamnus staddo	Rhamnaceae	Geesho	Tree

Appendix 13. Plot that demonstrated the connection between the mean species abundance and the number of plots where plant species occur in.



Appendix 14. Dataset of 64 sampling plots and eleven predictor variables used to conducted the habitat associations of a Djaffa Mountains guereza. “Community type (CT)” shows the plant communities clustered based on dissimilarity of the plot in plant species in one of the four community. The data included information on DMG abundance (A), tree density (D), basal area (BA), importance value (IV), mean tree height (mH), richness (R), Shannon diversity index (H), and Shannon evenness (SE).

Plot	P/A	A	CT	BA	D	IV	mH	SdH	R	H	SE	Forest
1	1	5	1	0.51	22.06	544.50	40.73	17.61	8	1.96	0.94	Dindin
2	1	7	1	0.11	27.94	384.83	28.65	14.62	12	2.34	0.94	Dindin
3	1	5	1	0.10	20.59	276.67	35.39	12.33	10	2.18	0.95	Dindin
4	1	5	1	0.22	14.71	314.00	43.50	11.80	7	1.89	0.97	Dindin
5	1	7	1	0.13	17.65	383.50	29.42	13.09	11	2.37	0.99	Dindin
6	1	8	2	0.09	14.71	209.00	31.90	17.85	7	1.83	0.94	Dindin
7	1	7	1	0.18	13.24	247.50	38.50	19.73	6	1.74	0.97	Dindin
8	1	4	1	0.15	17.65	298.17	43.36	15.96	8	1.95	0.94	Dindin
9	1	4	3	0.24	26.47	247.39	47.94	10.55	5	1.46	0.91	Dindin
10	1	2	1	0.22	14.71	270.50	40.90	11.95	6	1.73	0.97	Dindin
11	1	5	1	0.08	14.71	113.08	30.45	6.88	4	1.26	0.91	Dindin
12	1	12	1	0.06	13.24	101.92	29.00	8.37	4	1.26	0.91	Dindin
13	1	8	1	0.15	22.06	228.33	36.47	11.69	6	1.70	0.95	Dindin
14	1	2	1	0.15	14.71	227.00	28.85	8.09	6	1.70	0.95	Dindin
15	0	0	1	0.06	16.18	175.25	25.64	15.57	7	1.83	0.94	Dindin
16	1	4	1	0.05	13.24	153.50	23.33	2.50	7	1.89	0.97	Dindin
17	1	6	3	0.43	11.76	313.00	43.56	14.08	5	1.49	0.93	Dindin
18	0	0	4	2.71	10.29	81.00	14.00	9.83	3	0.87	0.79	Jallo-Kuni
19	0	0	4	0.13	10.29	441.00	21.14	17.21	6	1.75	0.98	Jallo-Kuni
20	0	0	4	0.01	27.94	304.83	18.74	12.28	7	1.63	0.84	Jallo-Kuni
21	1	4	4	0.02	11.76	104.33	14.88	13.27	4	1.32	0.95	Jallo-Kuni
22	0	0	3	0.01	13.24	124.83	30.11	21.89	3	1.08	0.99	Jallo-Kuni
23	0	0	4	0.01	14.71	159.17	14.10	9.53	5	1.50	0.93	Jallo-Kuni
24	0	0	4	0.01	7.35	197.00	25.00	23.40	5	1.56	0.97	Jallo-Kuni
25	1	5	4	0.01	17.65	211.17	33.67	33.84	5	1.37	0.85	Jallo-Kuni
26	0	0	4	0.01	14.71	192.67	29.30	23.34	4	1.21	0.88	Jallo-Kuni
27	1	8	4	0.01	13.24	107.20	17.45	20.13	5	1.43	0.89	Jallo-Kuni
28	1	3	1	0.01	16.18	128.50	18.64	12.41	6	1.67	0.93	Jallo-Kuni
29	0	0	4	0.01	13.24	69.70	18.33	5.96	3	1.04	0.95	Jallo-Kuni
30	0	0	1	0.01	16.18	142.50	24.42	17.79	4	1.17	0.84	Jallo-Kuni
31	0	0	1	0.00	2.94	79.50	32.67	4.04	2	0.64	0.92	Hades
32	0	0	3	0.01	7.35	52.25	38.60	12.32	2	0.56	0.81	Hades
33	1	3	3	0.17	4.41	45.25	16.75	2.75	2	0.64	0.92	Hades
34	1	6	1	0.06	13.24	114.33	23.00	13.07	5	1.52	0.95	Hades
35	1	5	3	0.05	16.18	104.00	28.36	13.21	4	1.07	0.77	Hades
36	1	8	3	0.05	8.82	149.33	35.50	8.92	3	0.95	0.86	Hades

37	1	3	1	0.06	10.29	204.00	31.43	9.00	5	1.55	0.96	Hades
38	1	3	3	0.15	14.71	188.10	28.00	6.75	4	1.21	0.88	Hades
39	0	0	1	0.18	17.65	181.92	14.67	7.69	6	1.67	0.93	Hades
40	1	4	1	0.15	11.76	189.83	26.88	14.62	5	1.48	0.92	Hades
41	0	0	3	0.09	7.35	78.00	15.75	17.73	3	1.04	0.95	Hades
42	0	0	3	0.15	13.24	152.83	20.44	14.26	4	1.37	0.99	Hades
43	0	0	3	0.07	16.18	127.83	24.27	13.70	4	1.17	0.84	Hades
44	1	5	3	0.15	25.00	113.35	15.29	10.49	5	1.49	0.93	Hades
45	1	3	3	0.10	22.06	67.30	17.87	11.11	2	0.56	0.81	Hades
46	0	0	3	0.04	14.71	55.19	14.80	7.81	2	0.64	0.92	Hades
47	0	0	3	0.08	17.65	123.22	12.25	10.85	4	0.94	0.68	Hades
48	0	0	3	0.06	20.59	140.05	23.79	9.99	4	1.29	0.93	Hades
49	1	8	3	0.07	17.65	135.75	17.08	8.60	5	1.42	0.88	Hades
50	0	0	3	0.16	20.59	162.78	22.71	11.21	4	1.08	0.78	Hades
51	0	0	2	0.11	23.53	199.33	28.53	14.55	6	1.66	0.93	Gara Muleta
52	0	0	2	0.13	13.24	144.42	18.40	14.18	4	1.26	0.91	Gara Muleta
53	0	0	2	0.10	22.06	188.70	25.67	11.58	6	1.71	0.95	Gara Muleta
54	0	0	2	0.22	14.71	271.00	28.24	11.31	6	1.68	0.94	Gara Muleta
55	0	0	2	0.13	19.12	214.86	41.56	21.03	6	1.47	0.82	Gara Muleta
56	0	0	2	0.16	14.71	194.50	33.69	26.20	5	1.56	0.97	Gara Muleta
57	1	5	2	0.12	13.24	138.75	33.91	11.18	4	1.32	0.95	Gara Muleta
58	1	8	2	0.17	17.65	280.00	34.25	8.92	7	1.77	0.91	Gara Muleta
59	1	7	2	0.18	16.18	289.50	32.81	13.80	7	1.85	0.95	Gara Muleta
60	0	0	2	0.27	7.35	200.00	52.50	24.86	4	1.33	0.96	Gara Muleta
61	1	8	2	0.11	16.18	162.50	31.67	12.31	5	1.50	0.93	Gara Muleta
62	1	9	2	0.10	20.59	216.50	33.33	15.31	7	1.73	0.89	Gara Muleta
63	0	0	2	0.13	17.65	145.25	38.38	13.57	4	1.28	0.92	Gara Muleta
64	1	5	2	0.08	16.18	225.50	19.27	10.57	8	1.97	0.95	Gara Muleta

Appendix 15. Population parameters of African black-and-white colobus

Taxon	Site	Area km^2	Cluster density/km^2	Individual density/km^2	Reference
C. g. gallarum	Ahmar Mts, ETH	183	20.6	109.6	this study
C. g. guereza	Wof-Washa Forest, ETH	25.6	14.3	94.4	Dereje Yazezew *et al.*, 2022
	Borena-Sayint NP, ETH	19	14.8	114.2	Hussein Ibrahim *et al.*, 2017
	Bole Valley, ETH	0.1	-	315	Dunbar, 1987
C. g. occidentalis	Kakamega, KEN			150	Fashing, 2001a
	Kibale NP, UGA	766	0.8-9.1	26	Chapman and Lambert, 2000
	Kibale NP, UGA			100	Oates 1977a, b
	Entebbe, UGA			63	Grimes, 2000
	Budongo Forest, UGA			49	Suzuki, 1979
	Budongo Forest, UGA	428	39.3	-	Plumptre and Reynolds, 1994
	Budongo Forest, UGA	793	15.0	56	Hobaiter *et al.*, 2017
	lturi, COD			17	Bocian, 1997
	Dja Reserve, CMR	526	-	4.9	Poulsen *et al.*, 2001
C. angolensis	Ituri Forest, COD	-	1.2	7.7	Thomas, 1991
C. a. palliatus	Shimba Hills Nat. Reserve, GHA	-	2.9	15.3	Anderson *et al.*, 2007a
	Okapi Faunal Reserve, COD	-	1.2	16.7	Bocian, 1997
C. satanas anthracinus	Lope Reserve, GAB	5360	0.75	11	Brugière, 1998
	Forêt des Abeilles, Makandé, GAB	-	-	7	Brugière *et al.*, 2002
	Taï National Park, CIV	-	2.8	47	Korstjens, 2001
C. vellerosus	Boabeng-Fiema, GHA	-	15	-	Wong and Sicotte, 2006

CMR = Cameroon; CIV = Ivory Coast; COD = Democratic Republic of Congo; ETH = Ethiopia; GAB = Gabon; GHA = Ghana; KEN = Kenya; TZA = Tanzania; UGA = Uganda

List of Publications and Papers Presented

Kufa, C. A., Bekele, A. and Atickem, A. (2022). Impacts of climate change on predicted habitat suitability and distribution of Djaffa Mountains Guereza (*Colobus guereza gallarum*, Neumann 1902) using MaxEnt algorithm in Eastern Ethiopian Highland. *Global Ecology and Conservation 35*, e02094.?????

Kufa, C. A., Bekele, A., Atickem, A. and Zinner, D. (2023). Djaffa Mountains guereza (*Colobus guereza gallarum*) abundance in forests of the Ahmar Mountains, Ethiopia. *Primate Biology 10*(2), 13-23.