Emerging remote sensing technologies and population genetic analyses for chimpanzee conservation in Tanzania

Noémie Bonnin

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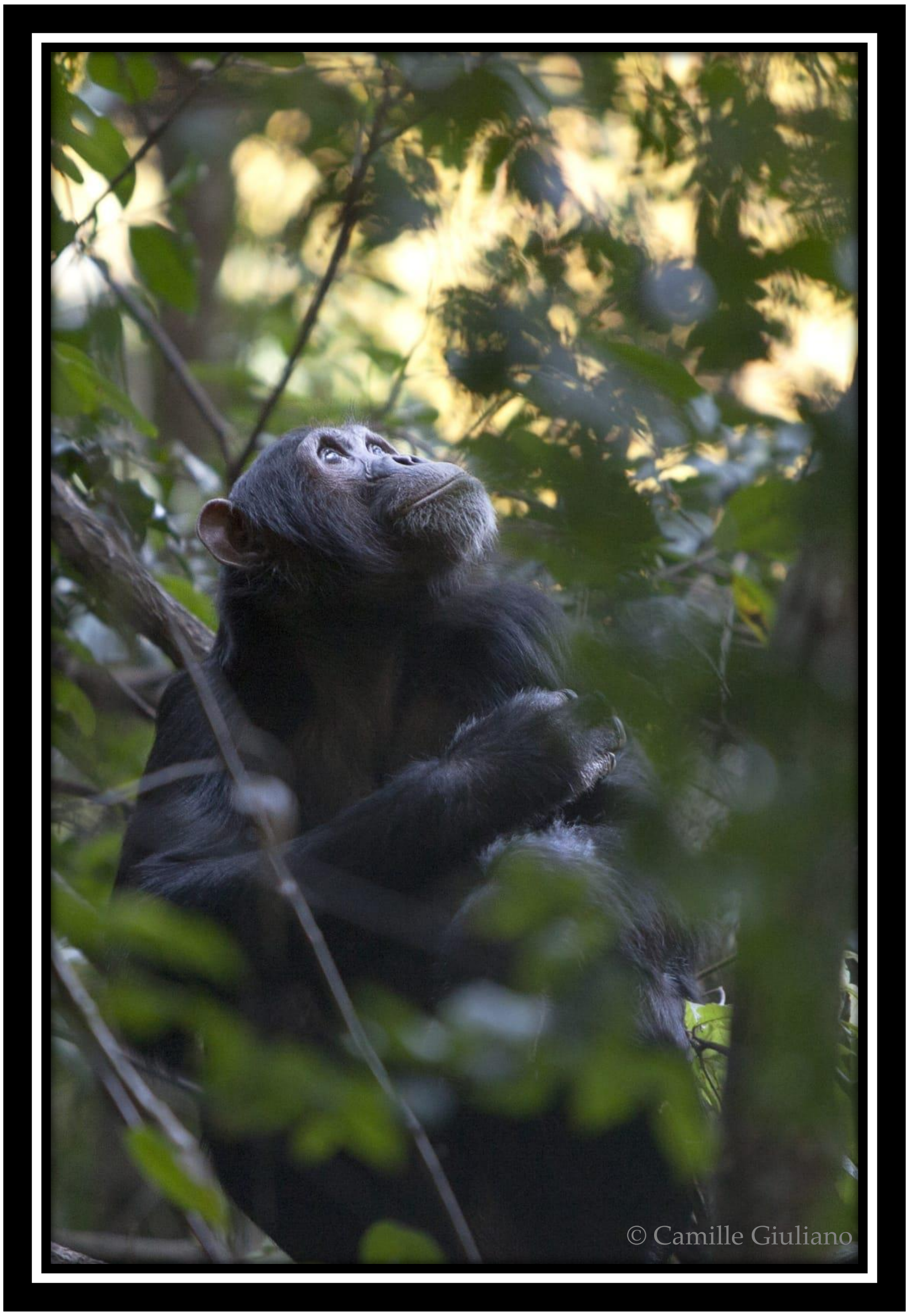

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Contents

Abstract

Chimpanzees are declining at a rate of up to 6.5% per year in some parts of Africa due to human impacts. Effective conservation relies on accurate and reliable information on population density, distribution and connectivity. Yet, traditional line transect surveys are costly to conduct over large areas and particularly at sufficiently regular intervals to determine trends in abundance. Moreover, they often fail to identify critical areas for animal movement. Given the vast landscape across which chimpanzees are found, we need new methods that are time and cost efficient while providing precise and accurate data across broad spatial scales. This thesis explores the potential of multiple remote sensing technologies along with molecular methods to provide critical information on population distribution, density and connectivity across broad spatial and temporal scales. My research first investigated the potential of drones for chimpanzee population surveys in Tanzania. More specifically, I evaluated drone performance in detecting chimpanzee nests by comparing ground and aerial surveys in the Issa valley, western Tanzania. I found ground and aerial nest numbers to be correlated, with an average of 10% of nests observed from the ground detectable from the air. Although I highlight challenges in using drones for chimpanzee surveys, the study provides guidance for future investigations and emphasises the importance of contrasting background and high-resolution images. Next, using satellite imagery from 1973 and 2018 and a landcover projection for 2027, I model landscape connectivity change for chimpanzees within the Greater Mahale Ecosystem (GME), an area containing nearly all of Tanzanian's chimpanzees. The model reveals a series of corridors allowing chimpanzee movement throughout the ecosystem, as well as a reduction of connectivity over time likely to continue through 2027. By identifying critical areas for chimpanzee movement, the model provides valuable guidance on where to focus conservation efforts. Finally, using two molecular markers (mitochondrial control region sequences and 10 microsatellite loci), I describe population structure and genetic diversity of Tanzania's chimpanzees. My analyses confirm historical gene flow between Gombe National Park (GNP) and the GME but also suggest complete interruption of chimpanzee movements between the two areas in recent years. Both genetic markers suggest high genetic diversity with no evidence of inbreeding and a greater mitochondrial DNA diversity within GNP. This surprising result might be explained by potential gene flow with extra-park chimpanzees and evidence of Gombe females preference for genetically dissimilar mates. Results of this study resolve previous contrasting findings on connectivity between GNP and the GME and support the establishment of two conservation units. Together, these chapters demonstrate the diversity of non-invasive technologies that can be applied, not only to help chimpanzee conservation, but also any large-bodied species facing accelerated rates of anthropogenic disturbance.

Declaration

I declare that that no portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

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Author contributions

Chapter 1

N. Bonnin	Writing - Original Draft, Writing - review & editing
S.A. Wich	Writing - review & editing
A.K. Piel	Writing - review & editing

Chapter 2

N. Bonnin	Data collection (Drone and ground surveys, September 2016, in the Issa Valley, Western Tanzania), Formal analysis, Writing - Original Draft, Writing - review & editing
A.C. Van Andel	Conceptualisation, Data collection (Drone and ground surveys, May 2015, in the Issa Valley, Western Tanzania), Writing - review & editing
J.T. Kerby	Conceptualisation, Data collection (Drone and ground surveys, May 2015, in the Issa Valley, Western Tanzania), Writing - review & editing
A.K. Piel	Conceptualisation, Data collection (Ground survey, May 2015, in the Issa Valley, Western Tanzania), Writing - review & editing, Supervision, Project administration, Funding acquisition
L. Pintea	Funding acquisition, Writing - review & editing
S.A. Wich	Conceptualisation, Data collection (Drone surveys, May 2015, in the Issa Valley, Western Tanzania), Writing - review & editing, Supervision, Funding acquisition

Chapter 3

N. Bonnin	Conceptualisation, Data collection (Ground survey, April – June 2017, across the GME), Formal analysis, Writing - Original Draft, Writing - review & editing
F.A. Stewart	Data collection (Ground survey, 2008 - 2014, across the GME), Writing - review & editing, Project administration
S.A. Wich	Conceptualization, Writing - review & editing, Supervision
L. Pintea	Methodology (created the landcovers), Formal analysis, Writing - review & editing
S.M. Jantz	Methodology (created the canopy cover layer for 2000), Formal analysis, Writing – original draft, Writing - review & editing
R. Dickson	Methodology (created the deforestation prediction layer), Writing - review & editing
J. Bellis	Methodology (provided habitat suitability modelling R codes), Writing - original draft, Writing - review & editing
A. Chitayat	Data collection (Ground survey, 2017 – 2020, across the GME)
R. Ingram	Data collection (Ground survey, June – August 2018, across the GME)
R.J. Moore	Data collection (Ground survey, May – July 2018, across the GME)
A.K. Piel	Data collection (Ground survey, 2008 - 2014, across the GME), Data Curation, Writing - review & editing, Project administration, Funding acquisition

Chapter 4

N. Bonnin	Conceptualisation, Data collection (Ground survey, April – June 2017, across the GME), Laboratory work (DNA extraction and amplification from GME samples, July – December 2018, in Beatrice Hahn Laboratory at the University of Pennsylvania, Philadelphia, USA), Formal analysis, Writing - Original Draft, Writing - review & editing
A.K. Piel	Data collection (Ground survey, 2008 - 2014, across the GME), Writing - review & editing, Supervision
R.P. Brown	Conceptualisation, Writing - review & editing, Supervision
J. Giles	Laboratory work (DNA extraction and amplification from GNP samples, 2017-2019, in Beatrice Hahn Laboratory at the University of Pennsylvania, Philadelphia, USA)
A.N. Avitto	Laboratory work (DNA extraction and amplification from GNP samples, 2017-2019, in Beatrice Hahn Laboratory at the University of Pennsylvania, Philadelphia, USA)
M. Gundlapally	Laboratory work (DNA extraction and amplification from GME samples, December 2017 – February 2018, in Beatrice Hahn Laboratory at the University of Pennsylvania, Philadelphia, USA)
A.J. Connell	Software (Chiimp software development), Data Curation (organized and integrated all genetic data from GNP samples)
Y. Li	Data curation (organized and integrated all genetic data from GNP samples)
B. Hahn	Resources (provision of laboratory supplies), Project administration (laboratory director)
P.M. Sharp	Writing - review & editing
D.C. Mjungu	Project administrator (Director of Gombe Stream Research Centre, overseed the collection, storage, and shipment of GNP samples)
J. Raphael	Project administrator (ran the Gombe Ecosystem Health Project, overseeing the collection, storage, and shipment of GNP samples)
I. Lipende	Project administrator (ran the Gombe Ecosystem Health Project, overseeing the collection, storage, and shipment of GNP samples)
D. Mwacha	Project administrator (ran the Gombe Ecosystem Health Project overseeing the collection, storage, and shipment of GNP samples)
M.L. Wilson	Project administrator (former Director of Field Research at Gombe), Writing - review & editing
E.V. Lonsdorf	Project administrator (overseed the collection, storage, and shipment of GNP samples)
E.E. Wroblewski	Writing - review & editing
A.E. Pusey	Data curation (organized and integrated all data collected in GNP)
A. Chitayat	Data collection (Ground survey, 2017 – 2020, across the GME)
S.A. Wich	Writing - review & editing, Supervision
F.A. Stewart	Conceptualisation, Data collection (Ground survey, 2008 - 2014, across the GME), Writing - review & editing, Supervision

Chapter 5

N. Bonnin	Writing - Original Draft, Writing - review & editing
S.A. Wich	Writing - review & editing
A.K. Piel	Writing - review & editing

List of abbreviations and notations

AGL	Above Ground Level
AMOVA	Analysis of Molecular Variance
APM	ArduPilot Mega
Ar	Allelic Richness
AUC	Area Under the Curve
CARTA	Center for Academic Research and Training in Anthropogeny
COSTECH	Commission for Science and Technology
DNA	Deoxyribonucleic Acid
F_{ST}	Fixation index
F'_{ST}	Standardized FST
F_{IS}	Inbreeding coefficient
GBM	Generalised Boosted Models
GCP	Ground Control Point
GEDI	Global Ecosystem Dynamics Investigation
GLAD	Global Land Analysis and Discovery
GLM	Generalized Linear Models
GME	Greater Mahale Ecosystem
GMERC	Greater Mahale Ecosyststem Research and Conservation
GNP	Gombe National Park
GPS	Global Positioning System
GSA	Ground Sampling Area
GSD	Ground Sampling Distance
h	Haplotype diversity
H_e	Expected heterozygosity
H_o	Observed heterozygosity
HWE	Hardy-Weinberg equilibrium
IUCN	International Union for Conservation of Nature
JGI	Jane Goodall Institute
LD	Linkage disequilibrium
LiDAR	Light Detection and Ranging
LJMU	Liverpool John Moores University
LPDAAC	Land Process Distributed Active Archive Center
MAXENT	Maximum Entropy distribution modeling
MMNP	Mahale Mountains National Park
MODIS	Moderate-Resolution Imaging Spectroradiometer
MPD	Mean Pairwise sequence Difference
mtDNA	Mitochondrial DNA

MUE	Masito-Ugalla Ecosystem
Na	Microsatellite number of alleles
NASA	National Aeronautics and Space Administration
NIR	Near Infra-Red
PCA	Principal Component Analysis
PCR	Polymerase Chain Reaction
REDD	Reducing Emissions from Deforestation and forest Degradation
RF	Random Forests
RGB	Red, Green, Blue - standard visual spectrum
SD	Standard deviation
SIV	Simian Immunodeficiency Virus
SNP	Single Nucleotide Repeat
SRTM	Shuttle Radar Topographic Mission
SWIR	shortwave infrared
TAWIRI	Tanzanian Wildlife Research Institute
TIR	Thermal Infrared
TSS	True Skill Statistic
UAV	Unmanned Aircraft Vehicles
USAID	United States Agency for International Development
VCF	Vegetation Continuous Fields
VIF	Variance Inflation Factor
π	Nucleotide diversity
φST	FST analogous for molecular sequence data

Chapter 1:
General introduction

Significance

Primates are important to tropical biodiversity, providing critical ecosystem functions and services (Estrada et al., 2017; Redmond and Goodall, 2008). As our closest living biological relatives, primates also offer insights into human evolution, biology, and behaviour. However, most primate populations are declining in numbers and ~60% of primate species are now under threat of extinction (Estrada et al., 2017). Habitat loss, degradation and fragmentation are the main causes of their decline along with hunting, anthropogenic diseases and climate change (Wich and Marshall, 2016). Global social and economic systems are changing rapidly, increasing global demand for natural resources. As a result, deforestation is occurring at an unprecedented rate (Hansen et al., 2013). This extensive forest loss represents a major threat to primates, which face subsequent challenges to adapt and respond to novel rates, types and scales of disturbance (Haddad et al., 2015). There is an urgent need to preserve the remaining populations and mediate species loss. To establish where and how many individuals remain and understand the potential ***connectivity*** between populations is a crucial first step to develop management plans. With this information, conservation planners can establish baseline estimates for prioritizing areas and assess effectiveness of their efforts over time (Nichols and Williams, 2006; Plumptre and Cox, 2006). Traditional ground surveys are a critical initial method to monitor ecosystems, however, they are costly in time and money across large spatial and temporal scales (Plumptre, 2000).

Integrating various emerging and established remote sensing technologies such as satellites and drones greatly increases the spatial and temporal scales over which an ecosystem can be surveyed and threats to be identified and potentially mitigated (Marvin et al., 2016). Besides remote sensing data, molecular tools are another fast-evolving technology able to provide a wide range of information across large spatial and temporal scale (Frankham et al., 2011). The DNA extracted from non-invasive samples (e.g. dung) provides scientists with detailed information about population demography, genetic variability and gene flow, without the need of capturing, disturbing or even seeing the individuals (Goossens and Bruford, 2009).

By integrating multiple remote sensing technologies and population genetic analyses, this thesis not only provides critical information on where to focus conservation effort to protect and preserve a viable large population of chimpanzees, but also demonstrate the potential of integrating technologies and methodologies for biodiversity conservation at broader scale.

Chimpanzee conservation in Tanzania

Chimpanzees, our closest living biological relatives, are classified as either Endangered (Nigeria-Cameroon chimpanzees *P. t. ellioti*, central chimpanzees *P. t. troglodytes,* and eastern chimpanzees *P. t. schweinfurthii)* or Critically Endangered (Western Chimpanzees *P. t. verus*) by the International Union for Conservation of Nature due to their declining populations across Africa (Humle et al., 2016). Tanzania represents the eastern and southern limit of their distribution (Figure 1.1) and hosts two of the longest studies of their behaviour: Gombe National Park (GNP), where Dr. Jane Goodall pioneered research on the species in 1960 (Goodall, 1968) and Mahale Mountains National Park (MMNP), where Dr. Toshisada Nishida established a permanent field station in 1965 (Nishida, 2011). Both study sites led to ground-breaking discoveries on chimpanzee behaviour and influenced the creation of the two national parks protecting wild chimpanzees in Tanzania. However, several surveys have now revealed that most (~75%) of Tanzanian chimpanzees are found outside national parks with the majority (~1 500) inhabiting the Greater Mahale Ecosystem (GME) (Kano et al. 1999; Yoshikawa et al. 2008; Plumptre et al. 2010; Nakamura et al. 2013; Piel and Stewart 2014, Figure 1.1b). This mosaic ecosystem, dominated by miombo-woodland interspersed with riparian forest, offers important diversity of resources for chimpanzees and is one of the driest places where they occur (Moore, 1992). As a result, they exhibit unique patterns not otherwise seen in forest-dwelling populations. For example, they are found at extremely low density (Kano et al., 1999; Moore and Vigilant, 2014; Piel and Stewart, 2014; Yoshikawa et al., 2008) and have large home ranges (Moore and Vigilant 2014; Piel and Stewart, unpublished data). Given the environmental similarity between this savanna landscape and reconstructions of hominin habitats, western Tanzania offer an insight into human evolution (Moore, 1992). Moreover, a recent study has shown that chimpanzees exhibit greater behavioural diversity in environments with more pronounced seasonality (such as savannah woodland habitats) (Kalan et al., 2020). With chimpanzee behavioural diversity currently threatened by increasing human pressure (Kühl et al., 2019) and the GME falling at the extreme end of the species habitat continuum (van Leeuwen et al., 2020), the importance of protecting GME chimpanzees cannot be overstated.

It is in the context of informing models of human evolution that Kyoto University African Primate Expedition (KUAPE) organised the first chimpanzee survey across Tanzania in 1961. About halfway between Gombe and Mahale, Kabogo station was established in the aim of studying chimpanzees living in an habitat similar to that in which early hominids evolved (Azuma and Toyoshima, 1961). Kabogo station was moved in 1963 to three additional camps (Kasakati, Filabanga and Kasoje), with the latest remaining as MMNP's long-term research site (Nishida, 2011). Kano led the first extensive survey across western Tanzania from 1965 to 1967 and noted the presence of chimpanzees all along the shore of Lake Tanganyika, with the Ugalla river representing the eastern limit and Wansisi mountains the southern limit of their distribution (Kano, 1972, 1971) (Figure 1.1c).

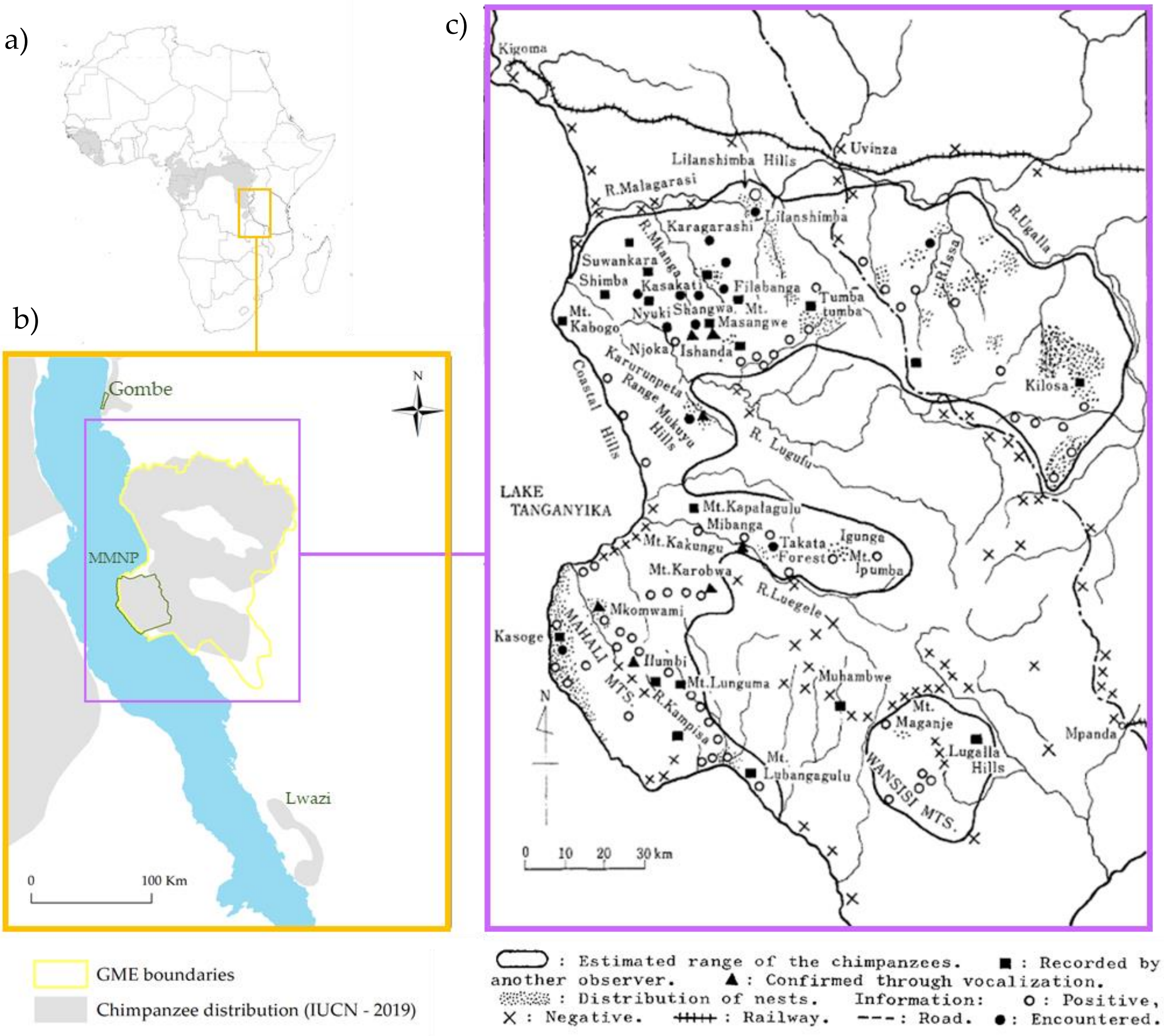

Figure 1.1 : Chimpanzee distribution a) across Africa; b) in Western Tanzania; c) map from Kano (1971) showing early chimpanzee survey sites in Tanzania .

In 1997, more that 25 years after Kano's first survey, another population of chimpanzees was reported further south, in the Lwazi river river basin (Ogawa, 1997). Later suveys confirmed the presence of large chimpanzee populations outside protected areas but also stressed the major human demographic changes and their threat to chimpanzee survival in Tanzania (Massawe 1992; Moyer et al. 2006; Yoshikawa et al. 2008; Ogawa et al. 2013; Piel and Stewart 2014; Piel et al. 2015). A major political event, the Ujamaa village resettlement scheme of the mid 1970s, had a significant impact on forest and woodland cover. This reform program shifted over five million small farmers and hunter-gathers from their scattered homesteads into nucleated settlements and collective farms. Although reducing human population in some remote habitats, population concentration has lead to heavy pressure on surrounding miombo woodland, increasing deforestation and habitat degradation (Massawe, E, 1992; McCall, 1985; Pintea et al., 2011). Tanzania has also received a large number of refugees from neighboring countries. Nearly 1.3 million people from Rwanda, Burundi, and the Democratic Republic of the Congo (DRC) sought refuge in western Tanzania between 1993 and 1998 (Whitaker, 2002). It is likely that the establishment of the refugee settlements and sudden increase in human population density has increased the pressure on chimpanzees through poaching (most newcomers not sharing the Tanzanian traditional taboo against eating primates) and increased conversion of land for agriculture (Jambiya et al., 2007; Ogawa et al., 2013, 2006a, 2006b; Whitaker, 1999).

Although historical events have played a role in the decline of Tanzanian chimpanzee populations, suitable habitat continues to decline and still represents the primary threat to the species persistance in the country (Davenport et al., 2010; Moyer et al., 2006; Piel et al., 2015a; Piel and Stewart, 2014; Plumptre et al., 2010). To protect the remaining chimpanzees, the Tanzanian governement, together with conservation organizations, and local stakeholders have developped a national conservation action plan for the species (Lasch et al., 2011; TAWIRI, 2018). The document identifies threats to chimpanzees in the country along with strategies necessary to counter these threats. Human activities such as agriculture, infrastructure and settlement development, logging and charcoal production, livestock keeping and mining, have been recognized as the leading threats to chimpanzees and their habitat. As part of the overall conservation strategy, the plan emphasised the needs of conducting regular and systematic chimpanzee surveys. This baseline information is necessary to implement the additional steps toward conservation progress: development of district land use framework plans, expansion / establishment of protected areas, reduction of human-chimpanzee conflict through and reduction of chimpanzee habitat loss. Given the sheer scale of chimpanzee distribution across western Tanzania (>20,000 km^2), we need new methods that are time and cost efficient while providing precise and accurate data across broad spatial scales.

Emerging remote sensing technologies for wildlife monitoring

Collecting baseline information on population distribution, abundance and trend is a vital first step for effective conservation. Not only are these data important for identifying priority areas under local threat and developing conservation management strategies (e.g. Nichols and Williams 2006; Plumptre and Cox 2006), but they also enable direct assessment of the effectiveness of conservation measures (e.g. Tranquilli et al. 2012; Akçakaya et al. 2018). There are several established methods for monitoring wild primate populations. Line transect surveys are widely used to estimate population density for a variety of mammal species, including great apes (e.g. Buckland et al., 2001; Piel et al., 2015a; Silveira et al., 2003; Stokes et al., 2010; Wich and Marshall, 2016). In these surveys, animal densities are estimated from counting direct or indirect signs of the animal presence. Given the elusive nature of great apes, scientists have traditionally relied on nests count (e.g. Kouakou et al., 2009; Spehar et al., 2010). To convert nest density to animal density, the nest decay rate and nest production rate are required. However, these factors require extensive studies as they vary considerably in time and space (Spehar et al., 2010) and thus are site-specific. Across large spatial and temporal scales, traditional line transect surveys are costly in time and for these reasons, geographically wide surveys are not repeated frequently (Kühl et al., 2009). Along with ground deployed technology such as passive acoustic monitoring (PAM) and camera trapping (CT) (Crunchant et al., 2020), emerging remote sensing technologies can help increase the spatial and temporal scales over which wildlife populations can be surveyed and monitored, especially when used in combination (Marvin et al., 2016).

Manned planes and helicopters

Manned planes and helicopters pioneered wildlife monitoring from ***remote sensing platforms***[1] and have been widely used by conservationists to obtain data on animal distribution and density (Wang et al., 2019). For instance, light aircraft have been used to assess the abundance of African wildlife since the mid-1950s (Jachmann, 2002) and five decades of aerial surveys provided important insights into changes in marine megafauna populations on the western pacific ocean (Martin et al., 2016). Helicopters have also been used to estimate orangutan density through aerial nest count (Ancrenaz et al., 2005). Detection of animals (or their signs) is either performed in real time by trained observers (e.g. Stoner et al., 2007) or using on-board cameras to collect aerial imagery (e.g. Descamps et al., 2011). While such surveys can greatly increase the spatial and temporal scales of wildlife surveys, they are expensive to implement and are of high risk for the operators (i.e. crashes) (Sasse, 2003).

Unmanned Aircraft Vehicles (UAV)

Unmanned Aircraft Vehicles (hereafter referred to as Drones) are rapidly gaining popularity as a powerful tool for wildlife monitoring (Chabot and Bird, 2015). These remotely operated aircrafts with pre-programmed flight capabilities offer the ability to collect rapid high-resolution data across moderate to broad spatial scales. Originally used for military applications, the use of drones has now widely spread across wildlife conservation applications including landcover mapping, anti-poaching efforts and wildlife monitoring (Wich, 2015). Several drone systems are available, and their different designs offer operational advantages. ***Fixed-wing drone*** models offer relatively long flight endurance (up to 1h30) allowing the coverage of larger areas but are limited by needing landing sites (e.g. large open areas). ***Multirotor drones*** have shorter flight time capacities

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[1] Throughout the thesis, bold italics indicate terms that are described in the Glossary

but can fly at lower altitudes and can be controlled in a more precise manner (Anderson and Gaston, 2013). Because some commercially produced systems remain cost prohibitive for conservationists, Koh and Wich (2012) were one of the firsts to develop a low-cost alternative to commercially available drones. Assembled from off the shelf components, these systems also offer much greater flexibility in terms of the sensors they can carry. Numerous types of sensors are available, and their numbers are expanding rapidly (Toth and Jóźków, 2016). In conservation research, drones are commonly equipped with RGB (Red, Green, Blue) cameras but recently, Multispectral, Hyperspectral, Thermal and ***Light Detection and Ranging (LiDAR)*** cameras have also been deployed and successfully used to detect animals and map vegetation (Wich and Koh, 2018). A common challenge in drone-based wildlife survey is the amount of data they produce (e.g. thousands of images) and the associated time to analyse them (Chabot and Bird, 2015). With the development of computer vision algorithms, scientists have recently been able to detect animals automatically, saving hours of tedious images examination (e.g. Gonzalez et al., 2016; Seymour et al., 2017).

Satellites

Satellite remote sensing platforms offer freely available images across most regions of the planet. Dating back to 1972, when the first non-military satellite program (Lansdat-1) was launched by the National Aeronautics and Space Administration (NASA), satellites offer the longest continuous global record of the Earth's surface (NASA, 2020). Such data have allowed consistent monitoring of worldwide forests (Hansen et al., 2013) and represent an unprecedented tool for conservation decision support (Rose et al., 2015). Continuously updated variables derived from satellite remote sensing can also be used to refine habitat suitability models for near real-time monitoring (Jantz et al., 2016). More than just monitoring wildlife habitat, satellite imagery can be used to detect animals or their signs. Löffler and Margules (1980) first demonstrated the feasibility of using Landsat-1 data to detect hairy-nosed wombat (*Lasiorhinus latifrons*) colonies. With the improvement of spatial resolution, it is now possible to detect a wide variety of animals ranging from birds (e.g. Fretwell et al., 2012) to mammals (e.g. Yang et al., 2014). However satellite images are hampered by atmospheric interference from clouds (Yang et al., 2014) and very high-resolution images (less than a meter resolution) necessary to detect small species also remain expensive (ranging from US $14.50-17.50 per km^2 depending on exact bands required (LLC 2020)).

Although any one of these methods has limitations (e.g. limited drone flying time, cloud cover hampering satellite images), together they can work as a powerful ensemble to address key questions for species conservation.

Population genetics for wildlife conservation

Besides remote sensing data, molecular information extracted from non-invasive samples (such as dung, hair, urine or extracts from discarded food items) represent another powerful tool to remotely monitor wildlife distribution and abundance, without the need of seeing the animals (Arandjelovic and Vigilant, 2018; Schwartz et al., 2007; Vigilant and Guschanski, 2009). Compared to the methods described above, only genetic markers provide an evolutionary context (Schwartz et al., 2007). The observed genetic signature reported by genetic diversity has enabled researchers to estimate the sizes of ancestral populations and date drastic population decline (e.g Okello et al., 2008). These data help to determine the role that historical events have played and are important for understanding long-term population viability. Indeed, population persistence is highly dependent on genetic mixing from migrating individuals (Young and Clarke, 2000). This not only avoids ***inbreeding*** and fixation of ***deleterious alleles***, but also increases the ***adaptive potential*** of a population (Crooks and Sanjayan, 2006).

The importance of applying genetic principles for nature conservation was first described by Otto Frankel and Michael Soulé (1981). These authors highlighted the long-term impact of ***inbreeding depression*** on population persistence (i.e. the reduced reproduction and survival of offspring from related parents) and urged the need to preserve genetic diversity. However, the contribution of genetic factors to species extinction was controversial and was generally considered minor (DeSalle, 2005; DeSalle and Amato, 2004). It was not until more recently that conservation genetics was recognised as an integral part of the field of conservation biology (Frankham et al., 2002). The use of genetic theory and techniques to reduce the risk of extinction in threatened species is now widely applied among conservationists and its applications keep expanding (DeSalle and Amato, 2004).

Advances in molecular marker technologies have played an important role in the development of conservation genetics. The first major advance was in the 1960s with the development of allozyme electrophoresis (i.e. separating proteins in an electrical potential gradient and subsequently visualising them using a locus-specific histochemical stain). As the first method allowing the direct measure of genetic diversity in natural populations, the technique quickly became widespread (e.g. Avise, 1974; Lewontin and Hubby, 1966). However, it required capturing or killing individuals to extract their blood; additionally, proteins evolve relatively slowly, hence were not suitable to study small populations of endangered species (Bertorelle et al., 2009). A latter breakthrough revolutionized population genetics: the PCR, or Polymerase Chain Reaction. With DNA fragments amplified millions of times, only a minute amount of DNA is needed to conduct genetic analyses (Mullis et al., 1986). This technique not only enabled genetic monitoring from non-invasive samples (usually containing low amount of DNA) (Frankham et al., 2004) but also facilitated the development of a wide range of genetic markers (e.g. ***Random amplified polymorphic DNA (RAPD)***; ***Amplified fragment length polymorphism (AFLP)***; ***mitochondrial DNA (mtDNA)***; ***minisatellite*** and ***microsatellite*** repeats, ***single nucleotide polymorphic markers (SNP's)***; see Avise (2012) for an extensive review).

These molecular markers represent a powerful tool to gather precise information for wildlife conservation such as population abundance (e.g. Solberg et al. 2006; Gray et al. 2013; Moore and Vigilant 2014; Arandjelovic and Vigilant 2018), demographic history (e.g. Okello et al. 2008; Pilot et al. 2014; Stoffel et al.

2018), population structure and gene flow (e.g. Wang et al. 2017; McCarthy et al. 2018; Hendricks et al. 2020), detecting hybridization (e.g. Gottelli et al. 1994; Rhymer and Simberloff 1996; Oliveira et al. 2008) and defining management unit (e.g. Moritz 1994; Liu et al. 2007; Hurt et al. 2017).

Thesis outline

In this dissertation, I apply two remote sensing technologies (drones and satellite imagery) as well as population genetic analyses to investigate chimpanzee distribution and connectivity across western Tanzania.

My research first investigated the potential of drones for chimpanzee population survey in Tanzania. More specifically, I evaluated the performance of two drone prototypes in detecting chimpanzee nest in the Issa Valley, Western Tanzania. I also assessed the factors influencing nest detectability from drone data (**Chapter 2**).

Next, using satellite imagery, I examined landscape connectivity change for chimpanzees within the GME (C**hapter 3**). I first developed habitat suitability models to create an index of habitat selection by chimpanzees. The resulting maps were used to model habitat connectivity independently of any a priori habitat patches or populations using circuit theory. To assess connectivity change over time and predict the impact of future forest loss on chimpanzees, I used satellite images from 1973 and a landcover projection for 2027.

In **Chapter 4**, I analysed 234 faecal samples from 16 different sampling locations within the GME along with genotypes from 136 individuals from Gombe National Park to explore chimpanzee population structure and genetic diversity across western Tanzania.

Chapter 5 synthesises the results of the previous research chapters, discusses the conservation implications of these findings, and highlight future research perspectives.

Each research chapter is presented as a manuscript in preparation for submission or already published in peer-reviewed journal.

Chapter 2:

Assessment of Chimpanzee Nest Detectability in Drone-Acquired Images

Noémie Bonnin [1,*], Alexander C. Van Andel [2], Jeffrey T. Kerby [3], Alex K. Piel [1], Lilian Pintea [4] and Serge A. Wich [1,5]

1. School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, UK; A.K.Piel@ljmu.ac.uk (A.K.P.); S.A.Wich@ljmu.ac.uk (S.A.W.)
2. IUCN National Committee of The Netherlands, Amsterdam, 1018 DD, The Netherlands; sander.vanandel@iucn.nl
3. Neukom Institute for Computational Science, Dartmouth College, Hanover, NH 03755, USA; jeffrey.t.kerby@dartmouth.edu
4. Conservation Science Department, the Jane Goodall Institute, 1595 Spring Hill Road, Suite 550, Vienna, VA 22182, USA; lpintea@janegoodall.org
5. Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Science Park 904, 1098 XH Amsterdam, The Netherlands

* Correspondence: N.Bonnin@2016.ljmu.ac.uk; Tel.: +44-7903-251803

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This chapter was published in April 2018 and reformatted to fit the thesis requirements.

Abstract

As with other species of great apes, chimpanzee numbers have declined over the past decades. Proper conservation of the remaining chimpanzees requires accurate and frequent data on their distribution and density. In Tanzania, 75% of the chimpanzees live at low densities on land outside national parks and little is known about their distribution, density, behavior or ecology. Given the sheer scale of chimpanzee distribution across western Tanzania (>20,000 km^2), we need new methods that are time and cost efficient while providing precise and accurate data across broad spatial scales. Scientists have recently demonstrated the usefulness of drones for detecting wildlife, including apes. Whilst direct observation of chimpanzees is unlikely given their elusiveness, we investigated the potential of drones to detect chimpanzee nests in the Issa valley, western Tanzania. Between 2015 and 2016, we tested and compared the capabilities of two fixed-wing drones. We surveyed twenty-two plots (50 × 500 m) in gallery forests and miombo woodlands to compare nest observations from the ground with those from the air. We performed mixed-effects logistic regression models to evaluate the impact of image resolution, seasonality, vegetation type, nest height and color on nest detectability. An average of 10% of the nests spotted from the ground were detected from the air. From the factors tested, only image resolution significantly influenced nest detectability in drone-acquired images. We discuss the potential, but also the limitations, of this technology for determining chimpanzee distribution and density and to provide guidance for future investigations on the use of drones for ape population surveys. Combining traditional and novel technological methods of surveying allows more accurate collection of data on animal distribution and habitat connectivity that has important implications for ape conservation in an increasingly anthropogenically-disturbed landscape.

Keywords: UAV; great apes; conservation; survey; Tanzania; image resolution

2.1. Introduction

As with other great ape species, chimpanzee numbers have declined over the past decades and the species is currently threatened by extinction (Humle et al., 2016). Several studies have documented the impact of habitat loss (Campbell et al., 2008; Junker et al., 2012; Wich et al., 2014), poaching (Bowen-jones and Pendry, 1999; McLennan et al., 2012; Piel et al., 2015b) and infectious disease (Rudicell et al., 2010; Walsh et al., 2003) on wild populations. In Tanzania, 75% of wild chimpanzees are found within a 20,000 km^2 area of national parks (Kano, 1972; Moore and Vigilant, 2014; Ogawa et al., 2011; Piel and Stewart, 2014; Plumptre et al., 2010; Zamma and Inoue, 2004). Monitoring these chimpanzees is therefore crucial for their conservation in Tanzania. For conservation management, it is important to establish where and how many individuals remain and to understand the potential connectivity between populations. These data represent key information that is used towards creating baseline estimates for assessing the effectiveness of conservation efforts over time (Nichols and Williams, 2006; Plumptre and Cox, 2006).

There are several established methods for studying and monitoring wild animal populations. Line transect surveys are widely used to estimate population density for a variety of mammal species, including great apes (Piel et al., 2015a; Silveira et al., 2003; Stokes et al., 2010; Wich et al., 2016). Data from direct observations of animals or indirect evidence such as dung (Moore and Vigilant, 2014), nests (Kouakou et al., 2009; Spehar et al., 2010) and calls (Kidney et al., 2016) can be converted into density and subsequently population estimates across larger landscapes (Buckland et al., 2001). Indirect evidence is especially important in great ape surveys given the elusive nature of the species and their extensive range and distribution(Kühl et al., 2009).

Traditional land-based transects are time-consuming and expensive, and for these reasons geographically wide surveys are not repeated frequently (Kühl et al., 2009). Aerial surveys with light aircraft can be effective across broad areas for counting large mammals (Jachmann, 2002; Kirkman et al., 2013), but have limitations. While such surveys may provide an unbiased population size estimate for large mammals found in open areas (e.g., elephants, buffalos, zebras), they are unlikely to provide accurate estimates for smaller species (e.g., black-backed jackal, bushbuck, vervet monkey) (Greene et al., 2017) or those that live in habitats with greater canopy cover. Furthermore, aircraft surveys are logistically difficult to implement due to their very high cost and the risk they pose to operators (i.e., aircraft crashes) (Sasse, 2003). Due to their increasing availability, high resolution satellite images have also been used to detect animals or their signs (Yang et al., 2014). Although promising, this method is also unlikely to provide accurate estimates for small species and is hampered by cost and atmospheric interference from clouds, especially problematic in the tropical regions where great apes are distributed (Hansen et al., 2008). Camera-traps and acoustic sensors are other promising remote technologies that enable broad spatiotemporal and precise information on animals that are elusive and otherwise difficult to study (Blumstein et al., 2011; Rowcliffe and Carbone, 2008). Nevertheless, these methods have high initial costs and still require intensive manual labor for deployment, memory card collection and substantial expertise in subsequent data analyses.

Recently, scientists have started to deploy drones—remotely operated aircraft with autonomous flight capabilities—for wildlife monitoring (Chabot and Bird, 2015; Koh and Wich, 2012a; Wich, 2015). This application allows for rapid and frequent monitoring across moderate to broad spatial extents while providing high-resolution spatial data. Several studies have now reported successful animal detection using drone-derived aerial imagery, ranging from birds (Chabot et al., 2014; Chabot and Bird, 2015) to large terrestrial (Mulero-Pázmány et al., 2014; Vermeulen et al., 2013) and marine (Hodgson et al., 2017, 2013; Koski et al., 2015, 2009) mammals. Recent studies on using drones to detect indirect signs of animals have also reported promising results in detecting orangutan (Wich et al., 2015) as well as chimpanzee (van Andel et al., 2015) nests.

Given the extent of the area in need of monitoring, exploring drone applications for chimpanzee population surveys in Tanzania may reduce cost and time investments. Visibility bias (i.e., failure to detect all animals within a sampled area) is a primary source of error in aerial surveys (Greene et al., 2017; Jachmann, 2002; Pollock and Kendall, 1987). Prior to the widespread deployment of drones for a census, it is important to first evaluate bias in the method (i.e., calculate a correction factor) by comparing the resulting detections with traditional ground survey results. Numerous factors can impact the detectability of a direct or indirect sign of wildlife (Buckland et al., 2001). Thus, it is critical to determine what affects chimpanzee nest detectability in drone-acquired images. In the current study, we assessed several factors known to affect target detectability in aerial images: image resolution (Dulava et al., 2015; Mulero-Pázmány et al., 2014); canopy cover and vegetation type (Greene et al., 2017; Mulero-Pázmány et al., 2014; Patterson et al., 2016; van Andel et al., 2015); and target size and color (Greene et al., 2017; Koski et al., 2009).

In summary, our objectives were to (1) evaluate drone performance for chimpanzee nest surveys by comparing ground and aerial surveys; and (2) assess the factors that influence detectability from drone data. Based on the results of the aforementioned studies, we hypothesized that using a higher resolution camera as well as flying at a lower altitude would increase the nest detection probability. We also expected a higher detection probability during the leaf-off season and in the more open miombo woodland vegetation than the closed riverine forest. Finally, we predicted that nests higher in the canopy and with a color that contrasts with their surroundings will be easier to detect.

2.2. Materials and Methods

2.2.1. *Study Site*

The study was conducted in May 2015 and September 2016 (beginning and end of dry seasons, respectively) in the Issa Valley, western Tanzania (Figures 2.1 and 2.2). The area is characterized by a landscape mosaic, dominated by miombo woodland (named for the dominant tree genera of *Brachystegia* and *Julbernardia*) interspersed with grasslands, swamps and gallery forest restricted to steep ravines. Open vegetation (e.g., miombo woodland, grassland and swamps) represents more than 90% of the 85 km^2 study area (Piel et al., unpublished data; Figure 2.1). The region is one of the driest, most open and seasonally extreme habitats in which chimpanzees live (Moore, 1992), with annual temperatures ranging from 11 °C to 35 °C and a dry season (<100 mm of rainfall) lasting from May to October.

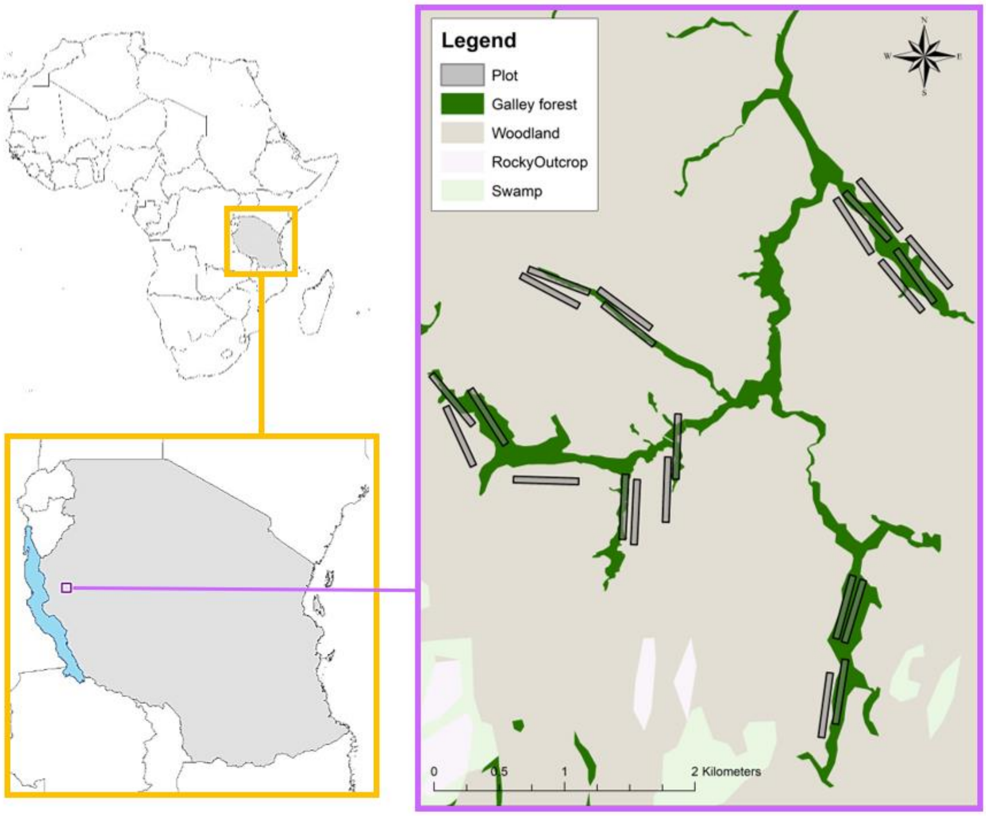

Figure 2.1: Location and map of the Issa Valley showing the distribution of all plots. Vegetation class layer produced by Caspian Johnson (unpublished).

Figure 2.2: Partial orthomosaics of the study site representative of the vegetation at the beginning (May 2015) and at the end (September 2016) of the dry season.

2.2.2. *Ground Surveys*

To collect chimpanzee nest data from the ground for comparison with drone observations, we created 22 plots, each 50x500 m, stratified equally across gallery forest and miombo woodland (Figure 2.2). Within each plot, two experienced observers walked slowly and recorded the GPS location of all observed chimpanzee nests. Only one inspection per plot was performed. During the 2015 survey, data were collected using the open data kit (https://opendatakit.org/) on NEXUS 7 tablets with an average accuracy of 15 m. In 2016, we used the ***global navigation satellite system (GNSS)*** Mobile Mapper 20 (MM20, http://www.spectraprecision.com), allowing us to collect data with a <1 m accuracy. For each nest, we collected additional data, including nest height from ground (estimated to the nearest meter), vegetation type (open or closed) and the nest color (green or brown).

2.2.3 *Aerial Surveys*

For the aerial surveys, we used two drone models paired with two different cameras (Figure 2.3).

Pairing A: The ConservationDrones.org X5 (Skywalker X5 frame; hobbyking.com [similar to HBS FX61]) equipped with a GPS-enabled Canon S100 camera (resolution: 4000 × 3000 pixels; sensor size: 7.6 × 5.7 mm) operating a Canon Hack Development Kit firmware modification (allowing pictures to be automatically taken every three seconds).

Pairing B: The more stable HBS Skywalker 100 km Long Range Fix Wings drone (Skywalker 2013 body 1880 mm; hobbyking.com) fitted with a Sony RX100M2 (resolution: 5472 × 3648 pixels; sensor size: 13.2 × 8.8 mm). Both were equipped with an autopilot system based on the 'ArduPilot Mega' (APM), which includes a computer processor, GPS, data logger, pressure and temperature sensor, airspeed sensor, triple-axis gyro, and accelerometer. Cameras were triggered automatically based on a predefined flight plan to produce at least 60% front- and side-overlap among images. Missions were planned using the open-source software APM Mission Planner (http://planner.ardupilot.com/) on a standard Windows-based laptop. Once we completed the missions, we geotagged the images from the Sony camera using the same software. ***Geotagging*** was not necessary for the Canon images as the camera was GPS-equipped.

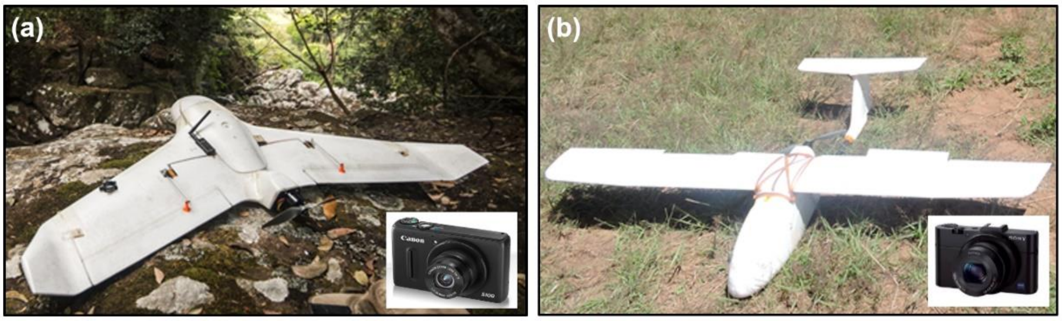

Figure 1.3: Types of drone/camera pairing deployed: **(a)** Pairing A; **(b)** Pairing B.

The drones performed two types of missions: straight line transects and grid missions (Figure 2.4).

Line transects: Straight line missions covering the areas within the ground plots at an average altitude of 90 m above ground level (AGL). We investigated aerial images obtained during these missions for the presence of chimpanzee nests.

Grid missions: Grid pattern missions flown at an average altitude of 120 m above ground level with extensive overlap (>60%) between flight legs to allow for the creation of ***orthomosaics***. We produced orthomosaics using the geotagged images in Pix4D mapper (https://pix4d.com, version 4.0.25). Although ***ground***

control points (GCPs)[2] were set up in each area for both years, the GCPs from 2015 could not be localized in the aerial images. The resulting accuracy of the orthomosaics was that of the Canon S100 camera GPS (average accuracy of 5 m). Improved GCPs were set up in 2016 allowing a ***georeferencing*** accuracy within a meter. We used the orthomosaics for the subsequent spatial relocation of aerial observations made while interpreting the photos from the nest counting missions.

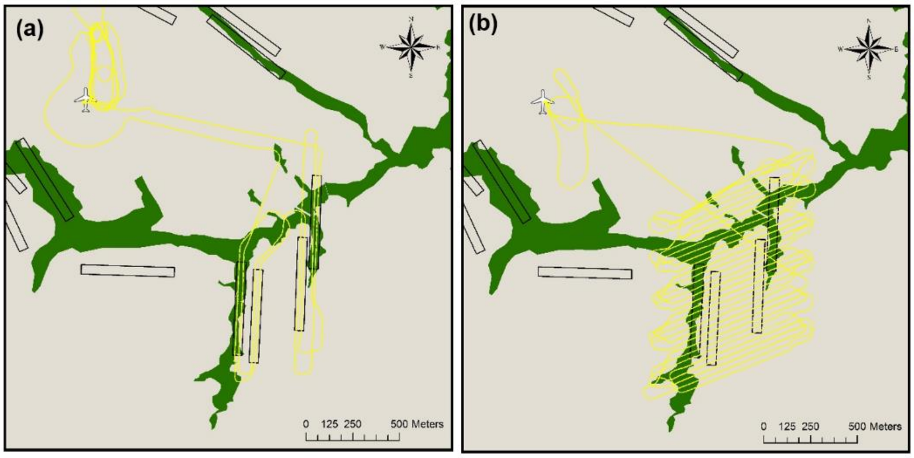

Figure 2.4 : Types of mission flown: **(a)** Line transect; **(b)** Grid mission.

2.2.4. Nest Detection

One observer (NB) examined the 1227 images resulting from the transect missions falling within the plots. Images were imported into the WiMUAS software (Linchant et al., 2015) and investigated for the presence of nests. The aerial observation location was subsequently exported to a georeferenced shapefile. Because the resulting file was accurate to within 50 m, each aerial observation was relocated using the orthomosaics. Due to the 15 m inaccuracy of the 2015 ground data, a buffer of 15 m was created around each nest and if an aerial observation was recorded within this 15 m radius that was considered an aerial nest detection.

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[2] 2015 GCPs were created from red fabric attached at the top of trees and 2016 GCPs consisted of white vinyl crosses pinned onto the ground.

2.2.5. Analyses

All statistical analyses were conducted in the R studio (version 1.0.136).

Performance of the Aerial Detection

We calculated recall and false alarm rates to estimate the performance of nest detection using drone imagery (Macmillan and Creelman, 2005). ***Recall rate*** is the percentage of successful detection (i.e., the proportion of nests observed from the ground detected during the aerial survey in relation to the total number of nests observed from the ground). The ***false alarm rate*** is the proportion of false detections (the number of aerial observations not aligning with nests found from the ground by the total number aerial observations). Because the data were not normally distributed, we used non-parametric statistics. A Wilcoxon-signed rank test was applied to compare the number of nests per plot found on the ground and on the aerial drone survey. We further ran a Spearman rank correlation to test for associations between the number of nests per plot across the two survey methods.

Factors Influencing Detectability

We used three generalized linear models (GLM) with a binomial error structure and logit-link function to evaluate which factors (drone/camera pairing, season, vegetation type, nest age, nest height and flight altitude above ground level (AGL)) influenced the recall rate and the false alarm rate. The models were fitted using the GLM function from the lme4 package (Bates et al., 2015). We fitted all terms of interest and tested significance via likelihood ratio tests to determine which factors resulted in a significant reduction in explanatory power when removed (Crawley, 2012).

Factors influencing the recall rate: For the first model, the recall rate was fitted following the method from Lopez-Bao (López-Bao et al., 2008). The number of nest detection successes vs. number of failures by plot (modelled as 1 = success and 0 = failure) was fitted as the dependent variable. Drone/camera pairing (Pairing A or Pairing B), season (May 2015 or September 2016) and vegetation type (open or closed) were each fitted as two-level fixed effects. As it was not possible to test the influence of all variables in this model (e.g., nest color and nest height required a perfect individual nest match between the ground and aerial survey), we fitted a second model. This second model included only the data from the 2016 survey, for which aerial observations could be more accurately matched to individual nests found on the ground. We fitted the nest detection event (not detected = 0, detected = 1) as the dependent variable. Vegetation type (open vs. closed) and nest color (green or brown) were each fitted as the two-level fixed effect and flight altitude AGL[3] and nest height were fitted as covariates. We determined flight altitude AGL by subtracting the elevation (extracted from a Shuttle Radar Topographic Mission (SRTM) layer—30 m resolution; http://earthexplorer.usgs.gov) from the flight altitude above mean sea level (extracted from the geotagged images) at each recorded nest location.

Factors influencing the false alarm rate: In the last model, the false detection event (true detection = 0, false detection = 1) was fitted as dependent variable. Drone/camera pairing (Pairing A or Pairing B), season (May 2015 or September 2016) and vegetation type (open or closed) were each fitted as two-level fixed effects and flight altitude AGL was fitted as a covariate.

2.3. Results

2.3.1. Performance of the Aerial Detection

Considering both survey seasons (May 2015 and September 2016) and the results from both drone/camera pairings (pairing A and pairing B), we documented 667 chimpanzee nests from the ground (Supplementary Figure S2.1) and 112 from aerial observations (Figure 2.5; Supplementary Figure S2.2). Of these aerial observations, 64 fell within the 15 m radius of a nest that had been spotted

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[3] Because flight altitude would have required to be averaged within survey plots to be used in the first model, we decided to only include it in the second model (with a flight altitude value above each individual nest).

from the ground and were considered to be nests, representing a 9.6% recall rate and 42.8% false alarm rate. Although the image analysis resulted in significantly fewer nest records per plot compared to what the ground teams documented (Wilcoxon- signed rank test: $v = 981$; $p < 0.001$; $n = 47$), the number of nests detected from aerial survey imagery showed a significantly positive correlation with those recorded on the ground per plot (Spearman's $\varrho = 0.53$; $p < 0.001$, $n = 47$).

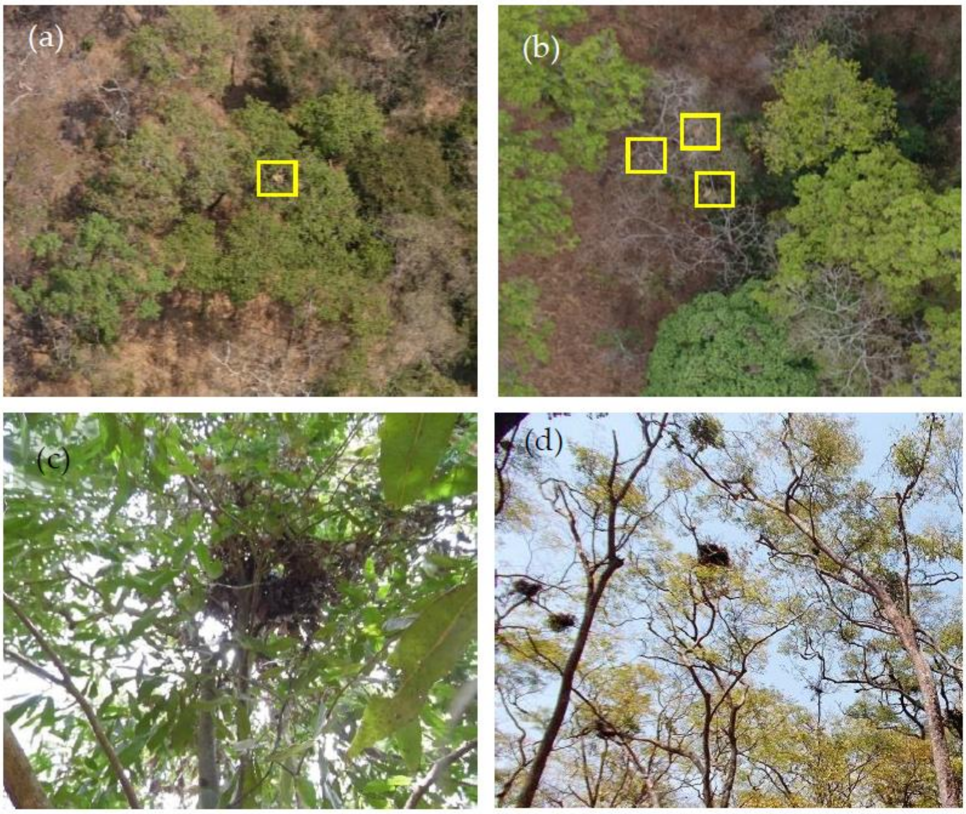

Figure 2.5: Examples of images of chimpanzee nests: captured during drone surveys (a,b) and observed from the ground (c,d).

2.3.2. Factors Influencing Detectability

Factors Influencing the Recall Rate

Our first model included drone/camera pairing and season and vegetation type. From these variables, only drone/camera pairing significantly influenced the recall rate (likelihood ratio test: $X^2 = -10.96$, $p < 0.001$), with the highest probability of nest detection with Pairing B (12.81% probability) (Figure 2.6). There was no significant difference in the recall rate between open and closed vegetation types (likelihood ratio test: $X^2 = 93.1$, df = 41, $p = 0.747$) or between the beginning and end of the dry season (likelihood ratio test: $X^2 = 93$, df = 43, $p = 0.551$) (Table 2.1).

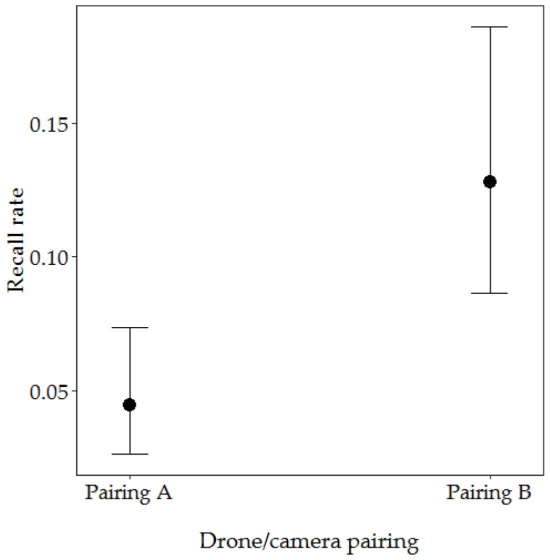

Figure 2.6: Effect of drone/camera pairing on the recall rate. Error bars represent 95% confidence intervals for the predicted probabilities.

Table 2.1: Outcomes of GLM to investigate the effect of drone/camera pairing, season and vegetation on the recall rate.

Predictors	LRT		Parameter Estimate			
	X^2	*p* Value	Estimate	Std. E.	*z* Value	Pr (>$\lvert z \rvert$)
(Intercept)			−2.96	0.59	−5.01	5.66×10^{-7}
Drone/camera pairing (Pairing A)	10.96	0.004 **				
Pairing B			1.43	0.57	−2.49	0.013 *
Vegetation (closed)	0.89	0.828				
Open			0.3	0.84	0.37	0.722
Season (May 2015)	0.40	0.818				
Sep-16			−0.35	0.78	−0.45	0.651
Drone/camera pairing: Vegetation	0.55	0.457				
Pairing A: Open vegetation			0.57	0.76	0.74	0.458
Vegetation: Season	7.29	0.993				
Open vegetation: September 2016			0.01	1	0.01	0.993

The *p* value for each term is based on the chi-squared test (likelihood ratio test (LRT)) for change in the deviance when comparing models with or without that term. Parameter estimates are reported for all terms in the full model. *=p<0.05; **=p<0.01.

Our second model (for 2016 data only) included flight altitude, nest height and vegetation type. We decided to remove nest color from our second model as of the 337 nests recorded by the ground survey team in 2016, only one was green. The recall rate differed significantly across flight altitude AGL (likelihood ratio test: $X^2 = 4.35$, $p < 0.05$), with nests more likely to be detected when flying at a lower altitude (19.58% probability) (Figure 2.7). We found a trend towards higher detectability in closed rather than open vegetation (likelihood ratio test: $X^2 = 2.79$, $p < 0.1$) (Table 2.2). There was no significant difference in nest detection depending on nest height within the tree (likelihood ratio test: $X^2 = 0.07$, $p = 0.789$).

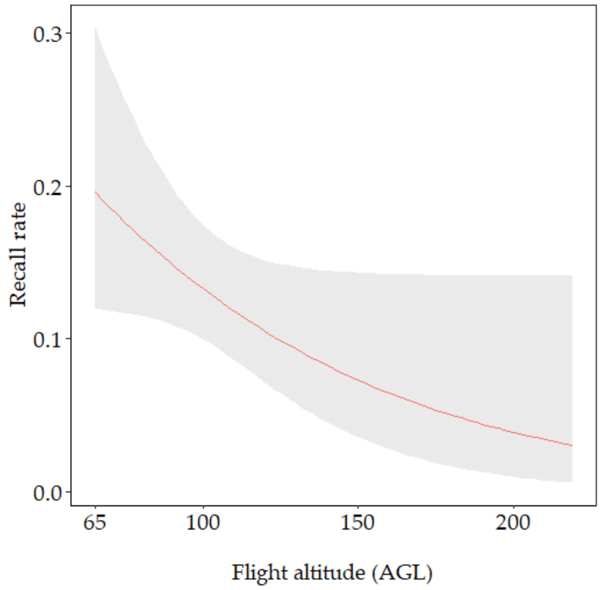

Figure 2.7: Effect of the flight altitude (AGL) on the recall rate. Grey ribbon represents 95% confidence intervals for predicted probabilities

Table 2.2: Outcomes of GLM to investigate the effect of altitude, vegetation type and nest height on the recall rate.

Predictors	LRT		Parameter Estimate			
	X^2	*p* Value	Estimate	Std. E.	*z* Value	Pr (>|*z*|)
(Intercept)			−1.53	0.28	−5.45	4.98×10^{-8}
Flight altitude AGL	4.35	0.037 *	−0.47	0.25	−1.90	0.057
Vegetation (closed)	2.79	0.094				
Open			−0.68	0.40	−1.70	0.089
Nest height	0.07	0.789	0.04	0.17	0.27	0.789

The *p* value for each term is based on the chi-squared test (likelihood ratio test (LRT)) for change in deviance when comparing models with or without that term. Parameter estimates are reported for all terms in the full model. *=p<0.05.

Factors Influencing the False Alarm Rate

For this model, we investigated the influence of drone/camera pairing, season, vegetation type and flight altitude AGL on the false alarm rate. Drone/camera pairing, vegetation type and flight altitude AGL significantly influenced the false alarm rate (Table 3.3). Aerial observations from Pairing A were more likely to be false positives (83% probability). The overall false alarm rate was higher in closed vegetation than in open vegetation but significantly differed between seasons (likelihood ratio test: $X^2 = 4.01$, $p < 0.05$). Aerial observations made at the beginning of the dry season (May 2015) were more likely to be false positives when recorded in open vegetation (0.94% probability opposed to 0.19% probability for closed vegetation). The false alarm rate significantly increased at lower altitude (likelihood ratio test: $X^2 = 9.55$, $p < 0.05$) (Figure 2.8).

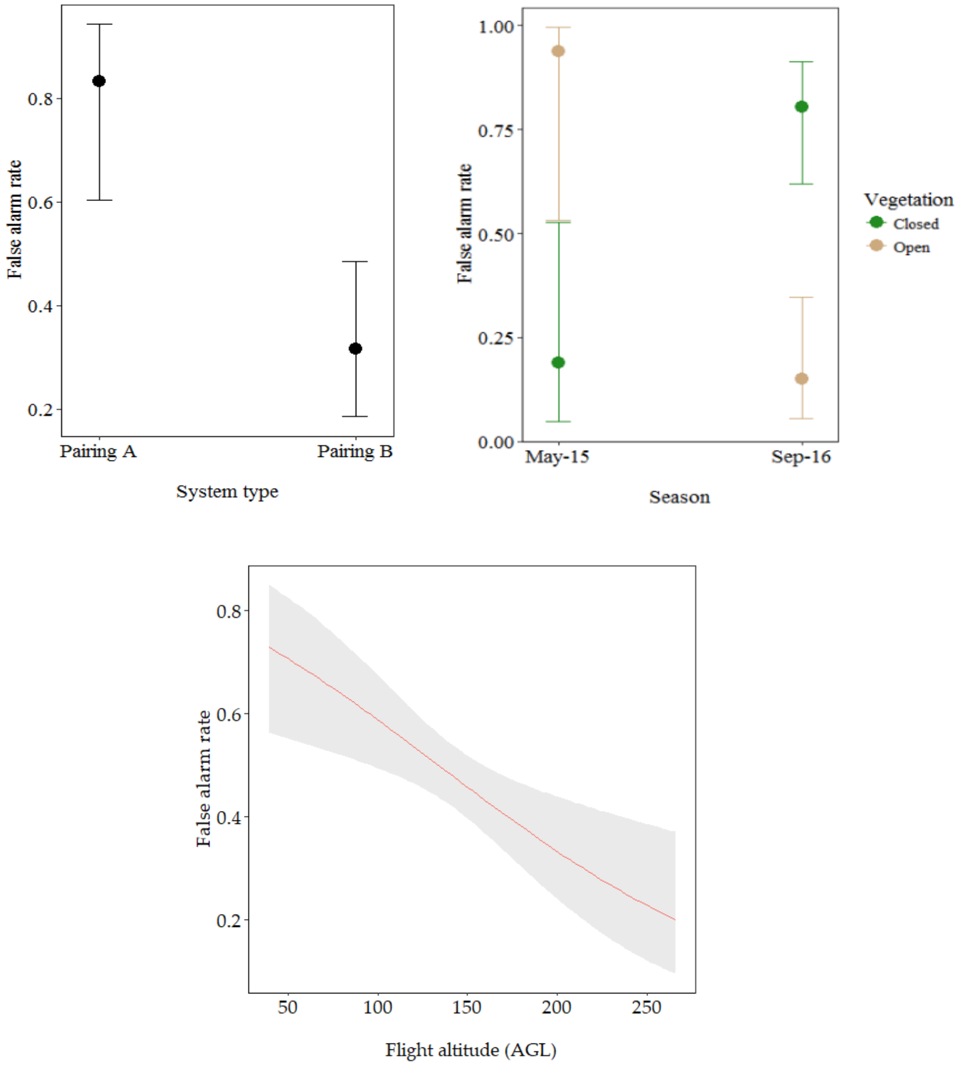

Figure 2.8: Effect of **(a)** drone/camera pairing; **(b)** vegetation type within season for pairing A and **(c)** flight altitude above ground level (AGL) on the false alarm rate for both pairing. Error bars and grey ribbon represent 95% confidence intervals for predicted probabilities.

Table 2.3. Outcomes of GLM investigating the effect of the drone/camera pairing, season, vegetation type and flight altitude AGL on the false alarm rate.

Predictors	LRT		Parameter Estimate			
	X^2	*p* Value	Estimate	Std. E.	*z* Value	Pr $(>\lvert z \rvert)$
(Intercept)			−3.03	1.19	−2.54	0.011 *
Drone/camera pairing (Pairing A)	14.14	1.17×10^{-4} ***				
Pairing B			3.69	1.08	3.40	6.73×10^{-4} ***
Vegetation (closed)	23.23	1.44×10^{-6} ***				
Open			5.72	1.99	2.87	0.004 **
Season (May 2015)	0.04	0.834				
Sep-16			2.86	1.16	2.47	0.013 *
Flight altitude AGL	9.55	0.002 **	2.01	0.90	2.24	0.025 *
Drone/camera pairing: Vegetation	0.05	0.824				
Pairing A: Open vegetation			−3.72	1.56	−2.38	0.017 *
Season: Vegetation	4.01	0.045 *				
Sept 2016: Open vegetation			−7.27	1.83	−3.98	6.83×10^{-5} ***
Vegetation: Flight altitude AGL	0.37	0.542				
Open vegetation: Flight altitude AGL			−5.98	1.63	−3.67	2.40×10^{-4} ***

The *p* value for each term is based on the chi-squared test (likelihood ratio test (LRT)) for change in deviance when comparing models with or without that term. Parameter estimates are reported for all terms in the full model. *=p<0.05; **=p<0.01; ***=p<0.001.

2.4. Discussion

We investigated the feasibility of using drones to detect chimpanzee nests in the Issa Valley, western Tanzania, and evaluated the influence of image resolution, seasonality, vegetation type, nest height and color on nest detectability. An average of 10% of the nests observed from the ground were detected from the air, with improved nest detection in imagery with higher spatial resolution. Our overall detection rate was lower than that previously reported for chimpanzee nests in Gabon (39.9%) (van Andel et al., 2015) and orangutan nests in Indonesia (17.4%) (Wich et al., 2015). This discrepancy is likely due to methodological differences and our systematic approach. In their study, van Andel et al. (2015) used two approaches that biased the probability of detection. In the first, they collected nest data first via ground surveys and then used the location of the recorded nests to confirm their presence in drone images. In the second, nests were first detected on drone images and then confirmed on the ground using the location of the aerial observations. These methods effectively demonstrated that it was indeed possible to detect chimpanzee nests from drones, although these specific approaches resulted in an increased probability of detecting a nest in the drone images for the first approach and on the ground for the second approach.

Wich et al. (Wich et al., 2015) used a buffer of 25 m around nests recorded on the ground to select which nest detected from the air would be included in the analyses, comparing the relative density of nests from the aerial and ground-based surveys. The smaller 15 m buffer used in our study could be associated with our smaller detection rate, i.e., we were more conservative regarding what constituted a match. Moreover, aerial nest surveys may be more efficient for orangutan nests as they tend to build nests higher in the tree canopy and visual contrasts of nest materials and canopy color are seemingly more apparent in these habitats (Ancrenaz et al., 2005; van Casteren et al., 2012).

Of the factors hypothesized to influence the probability of chimpanzee nest detection in drone-derived aerial imagery, only image resolution was identified as having a significant influence on the recall rate, with a higher probability of nest detection associated with the higher-resolution camera at a lower flight altitude AGL. This finding is consistent with that of Mulero-Pázmány et al. (2014), who also found that the targets (i.e., rhinoceros, people acting as poachers) were better detected with a lower-flying drone. Our results are also consistent with those of Dulava et al. (2015), who reported a significant negative relation between ***ground sampling distance (GSD)*** and correct waterbird identification with a minimum of 5 mm GSD. In our study, we favored flight altitude AGL above GSD as a measure of resolution because of identical camera parameters, however, the two are conceptually interchangeable. We obtained the highest probability of nest detection at the lowest possible flight altitude (AGL: 65 m), corresponding to 1.4 cm GSD. Flying at lower altitude would have threatened drone safety. These findings reflect the inherent trade-offs between monitoring at a high spatial resolution (grain) versus across broad spatial extents, such as ground sampling distance (GSD) and ***ground sampling area (GSA)***. This highlights the importance of the a priori identification of the minimum GSD required to detect ground targets from the air during the survey design period, particularly if planning for extensive area surveys where the balance between GSD and GSA should be optimized.

Contrary to expectations, we did not find a significant influence of nest height on aerial nest detection. Nests constructed higher in trees are expected to be more visible from the air, however, the visibility also depends on the height of the tree (i.e., a nest at 15 m will be more visible in a tree of 15 m height than in a tree of 20 m). The inclusion of tree height into models will be important in subsequent analyses.

Another surprising result of our study was the lack of influence of canopy cover and vegetation type, with no significant differences between the probability of nest detection in the leaf-off season and the "greener season" as well as between the more open miombo woodland vegetation and the closed, riverine forest. Even more surprising, the probability of nest detection tended to be higher in closed rather than in open vegetation. This finding contradicts numerous other studies that demonstrated a significant improvement of target detection from drone imagery in more open habitats (e.g., (Greene et al., 2017; Mulero-Pázmány et al., 2014; Patterson et al., 2016; Pearse et al., 2008; van Andel et al., 2015)). A possible explanation for this might be the difficulty of detecting brown nests against a similarly colored background, in this case the less continuous and more earth-toned colors of the Miombo woodland and the grassland mosaic. Light body color has been demonstrated to negatively influence animal detection during aerial surveys in a conservation area of northern Tanzania (e.g., dark Ostrich (*Struthio camelus*) better detected than light Grant's gazelle (*Nanger granti*)) (Greene et al., 2017).The results from Chabot and Bird (2012) further support the importance of contrast in target detection. In their investigation into the use drones to survey flocks of geese they reported a poor detection of low-contrast Canada Geese (*Branta canadensis*) but good aerial survey performance for the high-contrast Snow Geese (*Chen caerulescens*) resulting in more efficient aerial count compared to ground count (60% higher). We were unable to test the role of contrast in our study due to an insufficient sample of recent (green) nests.

Findings from the analysis of the factors influencing false alarm rates support this hypothesis. Different vegetation types significantly affected the false alarm rate depending on the season. The false alarm rate was higher in miombo woodland at the beginning of the dry season. The canopy cover in miombo woodland is much higher during this period than at the end of the dry season. At the beginning of the dry season, the miombo woodland reflects a mosaic of green leaves and a brown understory, leading to potential misinterpretation of aerial data. At the end of the dry season, however, reflection is mostly from the brown understory, making nest detection more difficult but more accurate. As only Paring A was flown in both seasons, we acknowledge that technological factors may play a role in these seasonal effects, however we strongly believe future studies will benefit from considering and further exploring the effects of seasonal canopy differences on nest detection.

The limitations on the use of drones to survey chimpanzees are threefold. Firstly, only a small proportion of chimpanzee nests are detectable from the air. Most chimpanzee nests are built in the middle of the tree crown (Stewart, 2011) making them undetectable from above the tree canopy (van Andel et al., 2015). Chimpanzees also exhibit ground night nesting (Hicks, 2010), which would also be difficult to detect from aerial surveys. Secondly, the high proportion of false alarm rate highlighted in this study is problematic. The false alarm rate is an important parameter that must be taken into consideration when assessing new wildlife survey methods, as it may lead to an overestimation of the population density (Greene et al., 2017). However, the false alarm rate has not been described in previous studies investigating the use of drones to detect great ape nests. In this study, we reported a 42.8% false alarm rate. These aerial observations, for which the location did not align with any of the nests spotted from the ground, can be explained in two ways: (1) These could be nests visible from the air, but not the ground, as would be the case of nests high in the canopy that might be obscured from ground teams by the mid-canopy. Van Schaik et al. (2005) noted that nests can go undetected during ground surveys, resulting in an underestimation of ape densities; (2) alternatively, false positives could represent dead leaves or canopy gaps revealing the brown understory that was mistaken for nests. This uncertainty represents an important problem in the deployment of drones to assess chimpanzee presence/density, especially in a new area where little information is available. We argue here that whilst aerial imagery offers an improvement in spatial coverage and data collection time and frequency, this approach still requires complementary validation from ground surveys. Finally, the time associated with analyzing thousands of images to identify nests represents an additional key limitation to using drones in this context.

The limitations we discussed above are significant but not prohibitive, and the findings from our study provide guidance for future investigation on the use of drones for ape population surveys. Firstly, it is important to generate high spatial resolution images and lower GSD, providing greater details and significantly increasing the probability of nest detection. For our survey, we decided to use fixed-wing drone models allowing longer flights that can cover larger areas. Because of the mountainous terrain, flying at lower altitude was not possible. Most chimpanzees do not live across mountainous terrain, therefore this problem would not affect large parts of their range. Multirotor drones have smaller flight time capacities but can fly at lower altitudes (Duffy and Anderson, 2016). This technology is improving rapidly (e.g., drone design optimization allowing longer flight time (Du et al., 2016; Magnussen et al., 2014)), which could make multirotors a viable option in the future. Meanwhile, camera resolution is improving, which will allow future studies to obtain higher resolution images from fixed wing surveys. Reliable detection also requires a high contrast background. During both our survey seasons, the brown understory made nest identification difficult. We therefore recommend conducting future surveys during seasons with green vegetation on the ground to contrast otherwise brown nests. We acknowledge that this context might reduce the probability of detecting fresh green nests, however, given their low abundance, their non-detectability is less likely to impact chimpanzee density estimations. Multispectral sensors may help address this problem. Widely used for landcover classification and vegetation monitoring (Arnold et al., 2013; Berni et al., 2009; De Biasio et al., 2010; Gini et al., 2014; Sugiura et al., 2005; Woll et al., 2011) this technology uses green, red, red-edge and near infrared wavebands to capture detail not available to standard RGB cameras. Green vegetation materials are characterized by high reflectance in the near infrared (NIR) domain (outside of the spectral range of human vision); a multispectral camera can provide useful contrast to discriminate between live and dead vegetation. Furthermore, it would be interesting to assess the potential of oblique aerial images. This perspective may offer better glimpses through foliage and more intuitively interpretable representations of the targets. Another step would be to assess the potential of 3D mapping of the canopy surface for nest detection. 3D models can now be created using point clouds from drone imagery (Greenwood, 2015) providing better perspectives for visual interpretation of the data. Another complementary approach would be to use light detection and ranging (LiDAR) technology. Recently developed at sizes suitable for drone payloads (Wallace et al., 2012), this remote sensing technique offers new insights beyond simple top of canopy structure that may help nest detectability algorithms. For example, these technologies could be used to better establish the habitat characteristics of trees holding nests. These data could be used in computer vision algorithms (Abd-Elrahman et al., 2005; Gonzalez et al., 2016; Hodgson et al., 2018; Selby et al., 2011) to refine automatic nest detection, possibly reducing the false alarm rate. A recent study on using a drone to detect eagle nests reported 75% nest detection using a semi-automated method (Andrew and Shephard, 2017). Similar to the difficulties encountered with chimpanzee nest detection, eagle nests are found in highly heterogeneous environments with many features that resemble nests, at small scale (~1–2 m), and with variable nest size, shape and context. This result is promising for broader nest detection applications, including those of great apes.

Given the shy and elusive nature of great apes, direct surveys are rarely feasible. Researchers thus must rely on indirect signs to estimate population density. However, to convert nest counts into ape density, the nest decay rate and nest production rate are required. These factors are highly dependent on ape species and environmental characteristics, and therefore require extensive study (Kühl et al., 2009). Recent studies have now shown the potential of thermal cameras mounted on drones for animal detection (Gonzalez et al., 2016; Gooday et al., 2018; Mulero-Pázmány et al., 2014). However, this approach would require extensive spatial coverage and further research is required to assess whether apes could be detected using a thermal camera mounted on a drone.

2.5. Conclusions

The design and execution of great ape surveys are crucial to allocating conservation efforts to where they are most needed, but face many logistical challenges, particularly when they must be implemented across broad areas. Drone surveys could be a revolutionary method, allowing rapid and frequent monitoring in remote and poorly-understood areas, with data accessible immediately and containing a rich variety of information about habitat and other conservation revelation conditions. The limitations we discussed above are meaningful but not prohibitive, and the rapid pace of technological improvement suggests many promising solutions in a near future. Assessing the potential of drones to detect chimpanzee nests has major implications, not only for chimpanzee monitoring across Tanzania, but also for all great apes monitoring. This technology could be applied to survey extensive areas filling problematic gaps in our current understanding of ape distribution and abundance (Hicks et al., 2014), providing key information for conservationists.

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Supplementary Materials

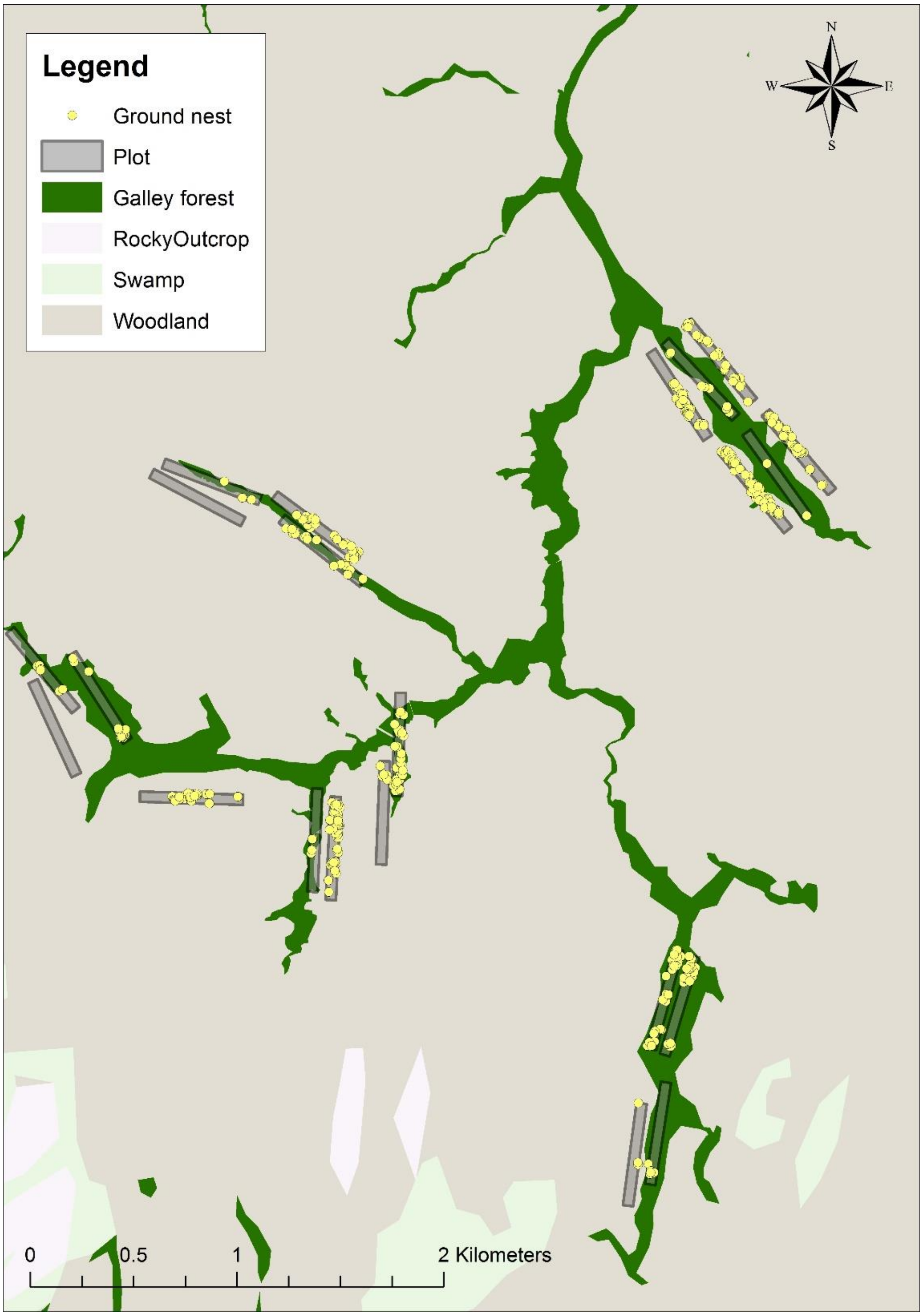

Figure S2.1: Locations of nests observed from the ground

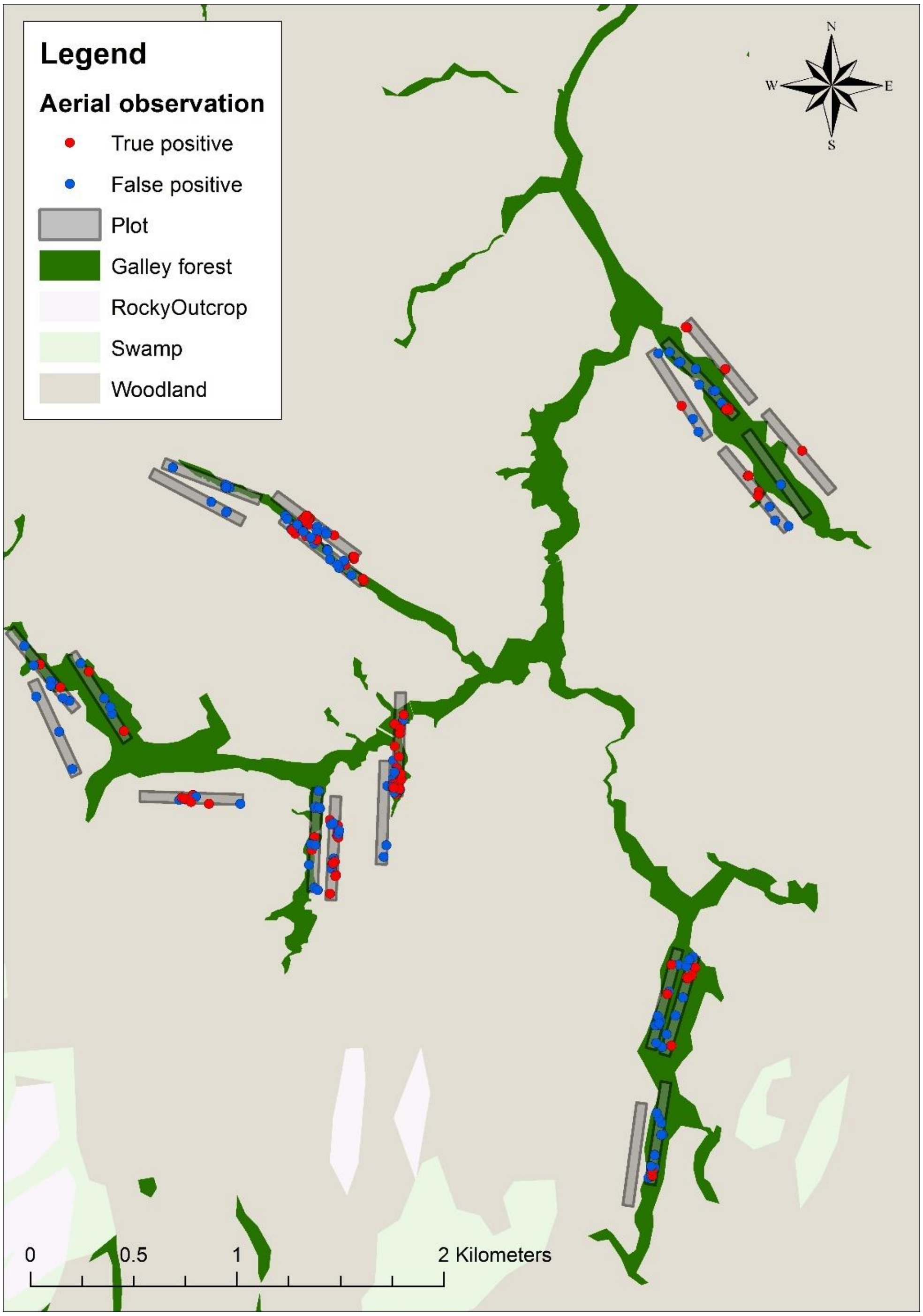

Figure S2.2: Aerial observations (true positives and false positives) recorded from drone surveys.

Chapter 3:

Modelling landscape connectivity change for chimpanzee conservation in Tanzania

Noémie Bonnin[1,*], Fiona A. Stewart[1,2,3], Serge A. Wich[1,4], Lilian Pintea[5], Samuel M. Jantz[6], Rebecca Dickson[7,8], Joe Bellis[1], Adrienne Chitayat[2,4], Rebecca Ingram[2], Richard J. Moore[2], Alex K. Piel[2,3]

1. School of Biological and Environmental Sciences, Liverpool John Moores University, UK
2. Greater Mahale Ecosystem Research and Conservation Project, Dar es Salaam, Tanzania
3. Department of Anthropology, University College London, UK
4. Institute of Biodiversity and Ecological Dynamics, University of Amsterdam, The Netherlands
5. Conservation Science Department, the Jane Goodall Institute, Vienna, VA 22182, USA
6. Department of Geographical Sciences, University of Maryland, College Park , MD 20742, USA
7. TerraCarbon, Illinois, USA
8. Wake Forest University, Winston-Salem, NC, USA

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Abstract

Chimpanzees, like all great ape species, have experienced a dramatic decline in global numbers during the past decades. The degradation, fragmentation and loss of suitable habitat impede chimpanzee movements, reducing the potential for dispersal and thus population viability. In Tanzania, 90% of the 2 000-3 000 remaining chimpanzees are found within the Greater Mahale Ecosystem (GME), the majority of which live at low densities outside of national park boundaries. Recent genetic analyses have identified potential boundaries between the northern and southern populations of the GME. Using landscape connectivity modelling, we aimed to clarify population connectivity across this vast ecosystem (>20 000 km^2) and assess change over time. We developed habitat suitability models to create an index of habitat selection by chimpanzees and mapped connectivity using circuit theory. Our results suggest that, in recent history (1973), the entire ecosystem was linked by a series of corridors showing a high likelihood of chimpanzee movement. Our analysis also reveals a reduction of connectivity by 2017 impacting the two corridors linking the northern and southern GME. When projected to 2027, areas contributing to connectivity are predicted to continue to decline, threatening all available corridors between the northern and southern GME. By modelling connectivity across time, we were able to identify key areas to focus conservation efforts to maintain population viability within the largest chimpanzee population in Tanzania.

Keywords: Landscape connectivity; Primate conservation; Great Apes; Circuit theory; Habitat suitability

3.1. Introduction

Deforestation is occurring at an unprecedented rate (Hansen et al., 2013). This extensive forest loss represents a major threat to wildlife, which face subsequent challenges to adapt and respond to novel rates, types and scales of disturbance (Haddad et al., 2015). Fifteen percent of the world's terrestrial surfaces are now under some form of protection (IUCN and UNEP-WCMC, 2018). However, the establishment of isolated reserves will not alone suffice for the conservation of biodiversity. Effective conservation must consider ***connectivity*** between these areas (Rudnick et al., 2012). Landscape connectivity is defined as the extent to which a landscape facilitates or impedes the movements of organisms (Taylor et al., 1993). If dispersal routes are blocked or degraded, genetic exchange between remaining populations will be reduced or lost, increasing the level of ***inbreeding*** and ***genetic drift*** in small populations (Young and Clarke, 2000). Such effects eventually compromise ***adaptive potential*** and reduce ***fitness***, accelerating extinction of small populations (e.g. Gilpin and Soulé, 1986). Maintaining connectivity confers ecosystems with greater resilience to disturbance and ultimately facilitates species persistence (Crooks and Sanjayan, 2006).

Landscape connectivity models can help highlight important areas on which to focus conservation efforts. These models use estimates of landscape ***resistance*** (the degree to which landscape features impede animal movement) to predict the likelihood of connectivity between habitat patches (Taylor et al., 2006). Several studies have now shown the potential of landscape connectivity modelling to identify priority areas and support conservation planning of a wide range of species, from herptiles (e.g. Mui et al., 2017) and birds (e.g. Rayfield et al., 2016), to small (e.g. Fabrizio et al., 2019) and large mammals (e.g. Roever et al., 2013), including great ape species (Freeman et al., 2019; Vanthomme et al., 2019).

As with all the other species of great apes, chimpanzees are classified either as Endangered (Nigeria-Cameroon chimpanzees *P. t. ellioti*, central chimpanzees *P. t. troglodytes*, and eastern chimpanzees *P. t. schweinfurthii)* or Critically Endangered (Western Chimpanzees *P. t. verus*) by the International Union for Conservation of

Nature (www.iucnredlist.org). Tanzania represents the eastern and southern limit of chimpanzee distribution and hosts two of the longest studies of their behaviour (Gombe National Park: Pusey et al., 2007; and Mahale Mountains National Park: Nakamura et al., 2015; Figure 3.1). However, several surveys have now revealed that 75% of Tanzanian chimpanzees live outside of these two National Parks, with the majority (~1 500) inhabiting the Greater Mahale Ecosystem (GME) (Kano et al., 1999; Nakamura et al., 2013; Piel and Stewart, 2014; Plumptre et al., 2010; Yoshikawa et al., 2008). This mosaic ecosystem dominated by miombo-woodland (i.e. deciduous trees and shrubs with grass understory and discontinuous canopy) interspersed with riparian forest offers an important diversity of resources for chimpanzees but is under several pressures. Habitat loss through settlement expansion and conversion to agriculture represents the primary threat to chimpanzees within the ecosystem, followed by annual burning, logging, and poaching (Moyer et al., 2006; Piel and Stewart, 2014). Monitoring the impact of habitat loss on remaining chimpanzee populations is logistically challenging given that chimpanzees in this area are found at extremely low densities (Piel et al., 2015a). Remote sensing technologies can help to overcome these challenges by providing precise and accurate data across broad spatial and temporal scales (Marvin et al., 2016).

The GME has previously been regarded as one ecosystem that supports one continuous chimpanzee population (Inoue et al., 2011), however, other studies have highlighted potential barriers which may limit chimpanzee movement between northern and southern populations (Bonnin et al., 2015; Moyer et al., 2006; Piel et al., 2013; Rudicell et al., 2011). Given the long generation time of chimpanzees, the genetic consequences of recent habitat destruction have the potential to manifest decades into the future and have long-lasting effects on the genetic diversity of the remaining populations (Landguth et al., 2010).

In this study, we aimed to clarify chimpanzee habitat connectivity by developing a landscape connectivity map that is independent of any a priori habitat patches or populations. By using remote sensing data from 1973 and a land-cover projection for 2027, we also evaluated the impact of forest loss on habitat connectivity. We hypothesised the GME to be connected by multiple areas of high connectivity values in 1973. We also expected a reduction in connectivity associated with forest loss, now isolating the northern and southern populations. Identified areas of high likelihood of chimpanzee movement can be used by conservationists to support detailed conservation planning needs of local human communities and chimpanzees.

3.2. Methods

3.2.1. Study area

The GME is a ≈ 18 000 km2 region in western Tanzania, bordered to the north by the Malagarasi river, to the south by Katavi National Park, to the east by the Ugalla river and to the west by Lake Tanganyika (Figure 3.1). The area is dominated by miombo-woodland (*Brachystegia* spp. and *Julbernardia* spp., Fabaceae) with small patches of riparian forest, swamp, bamboo and grassland. The topography consists of broad valleys separated by steep mountains and flat plateaus ranging from 900 to 2 500 m above sea level. The GME represents the southern and eastern extreme of chimpanzee distribution and is one of the driest habitats in which they are found (Moore, 1992). The area includes the Mahale Mountains National Park (MMNP), which protects a high level of biodiversity, although it has been estimated that 75% of the chimpanzee population lives outside of MMNP (Moyer et al., 2006). To account for potential chimpanzee movement along the edges of the GME, we drew a 20km buffer around the GME boundary.

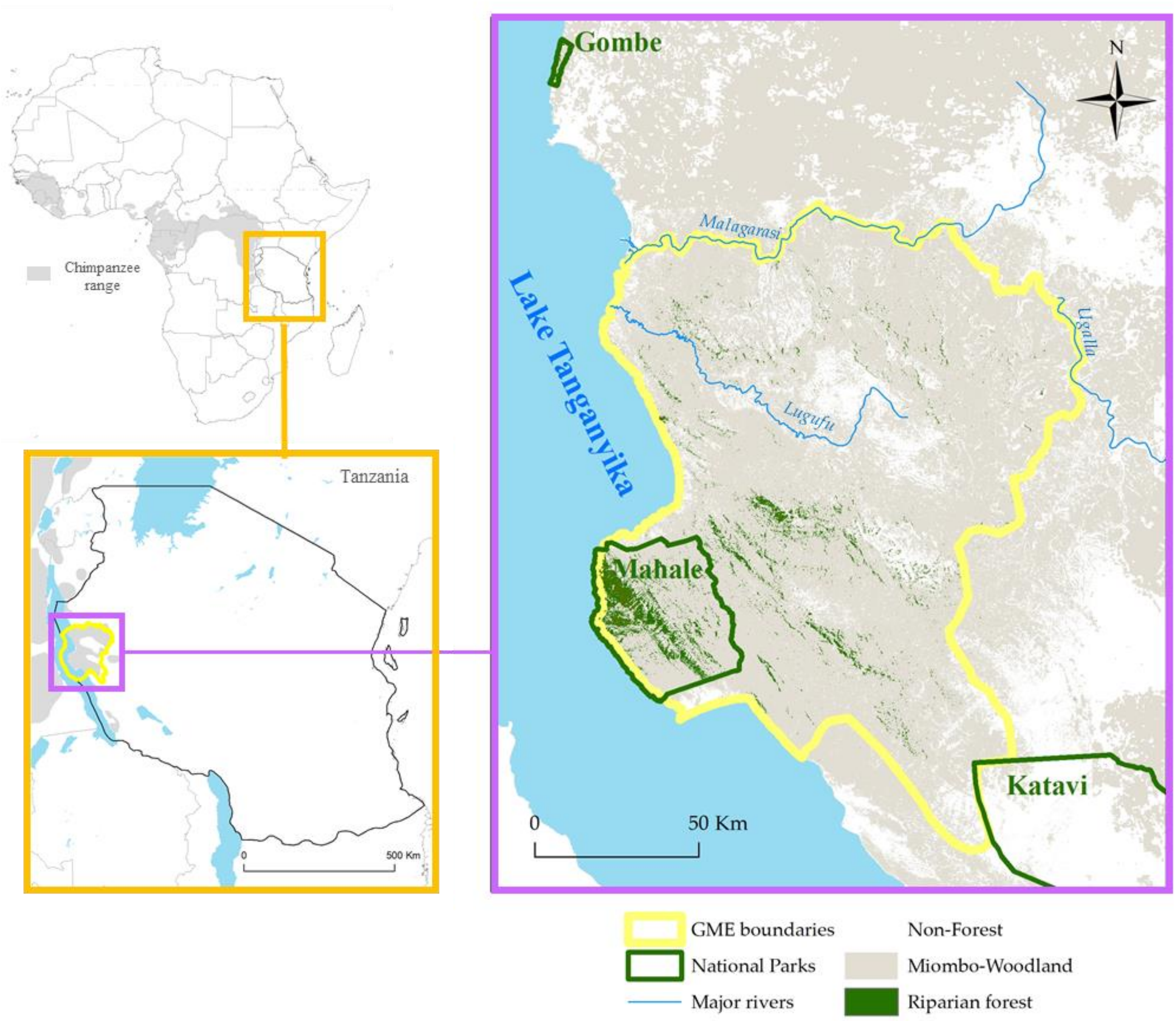


Figure 3.1: Location and map of the GME

3.2.2. Environmental variables

We selected five biophysical variables to integrate into our species distribution model: Vegetation type, proportion of riparian forest, distance from riparian forest, elevation and distance from steep slopes.

We created our vegetation layers based on a previously developed canopy cover product for the year 2000 (Appendix S3.1). We defined riparian forest as areas with tree canopy cover > 70% and miombo-woodland as vegetation types with tree canopy cover between 30% and 70%. To create a land-cover map for 2019, we used the global forest change product from GLAD (Global Land Analysis & Discovery) between 2000 to 2019 and reclassified deforested pixels to non-forest from our 2000 landcover product. In order to map historical vegetation type, we acquired a 60-meter resolution Landsat Multispectral Scanner (MSS) scene for August 17, 1973 downloaded from http://earthexplorer.usgs.gov. We georeferenced the image to the 2000 canopy cover layer using ArcGIS Desktop (Esri). Both 2000 and 2019 vegetation layers were resampled from 30-meter to 60-meter resolution to match 1973 coarser spatial resolution and support comparison between 1973, 2000 and 2019 vegetation types. To further improve comparison between the datasets, 2000 forest and woodland areas were masked out from the 1973 image, assuming that if areas were forested in 2000 they were also forested in 1973. We confirmed that 2000 forest areas were still forests in 1973 by visually inspecting the 1973 Landsat image. The remaining 1973 image was classified in riparian forest, miombo-woodland and other non-forest/non-woodland classes using unsupervised Iso Cluster algorithm in ArcGIS Desktop. To validate our 1973 vegetation layer, we used "Create Accuracy Assessment Points" function in ArcGIS Desktop and generated 100 randomly distributed points within each class using the Equalized Stratified Random sampling strategy (see Appendix S3.1 for more details).

The resulting land-cover map comprised three types representing non-forest, miombo-woodland and riparian forest, the latter two being the main chimpanzee habitats in the GME. Distance from riparian forest was calculated such that each grid value reflected the linear distance from riparian forest (riparian forest pixels getting a zero value). We used these landscape features because chimpanzees are highly dependent upon trees, many of which host important food sources (Nishida et al., 1983; Piel et al., 2017) and for their role as shelter e.g. nesting sites (Stewart et al., 2011). We extracted elevation and distance from steep slopes (> 20 degrees) from a Shuttle Radar Topographic Mission (SRTM) layer (30 m resolution; http://earthexplorer.usgs.gov) (Pintea & Plumptre 2006; Jantz et al. 2016). We included topographic measures because altitude has an influence on chimpanzee distribution (Fitzgerald et al., 2018; Plumptre et al., 2010). Elevation may act as a proxy for suitable climatic conditions, affecting nesting site preference and food resource distribution (Jantz et al., 2016). Moreover, in western

Tanzania, studies have shown that nesting sites are associated with steep slopes (Hernandez-Aguilar, 2009; Pintea and Plumptre, 2006; Stewart, 2011). We fitted all four variables at 60 m resolution and accounted for chimpanzee responses to vegetation type at a larger scale by creating a new layer reflecting the proportion of riparian forest within a 30.8 km^2 neighbourhood, using focal statistics in ArcGIS Desktop. We used 30.8 km^2, as this represents the average home range size based on three habituated chimpanzee communities in the GME (55km^2 at Issa, Piel and Stewart, unpublished data; 27.4 km2 for M-group (MMNP), Nakamura et al., 2015 and 10km^2 for K-group (MMNP), Nishida, 2011). We did not include settlements or roads as a predictor variable because of the difficulty of accessing reliable data for 1973. We checked for collinearity by estimating the variance inflation factor (VIF; values>3 considered highly correlated predictors (Zuur et al., 2010)). We did not find multicollinearity among our five predictor variables (VIF <1.3) and thus used all predictors for further analyses.

3.2.3.Land-cover change projections

For future time periods, we used a model of predicted deforestation by 2027 developed for the Ntakata REDD project (Shoch et al., 2019) which used Multi-Layer Perceptron neural network to predict the likelihood of deforestation based on historical deforestation occurring between 2007 and 2019. Predicted deforestation was used to create land-cover map representing 2027 by reclassifying forest pixels mapped in 2019 to non-forest in 2027 where deforestation was projected.

3.2.4. Habitat suitability modelling

We decided to base our ***resistance values*** on a habitat suitability model, which is a preferred alternative to expert opinion when empirical data on animal movement or genetic distance are insufficient or not available (Beier et al., 2008; Stevenson-Holt et al., 2014). To build our model, we used evidence of chimpanzee presence from surveys led by Greater Mahale Ecosystem Research and Conservation (GMERC) between 2008 and 2020. By a combination of transects and reconnaissance walks we have documented over 11 947 observations of chimpanzee presence (direct observations, vocalizations, feces, feeding remains, nests, prints, and tools). For our analysis, we removed vocalizations as chimpanzee calls can be heard up to 3km (Piel, 2014) and our modelling resolution is 60 m. In order to reduce spatial bias caused by unequal sampling effort, we followed Kramer-Schadt et al.'s (2013) recommendations and used spatial filtering and balancing of occurrence data, to reduce spatial autocorrelation. For spatial filtering, we used Spatial Rarefy Tool in the SDM ToolBox v2.2 under ArcGIS 10.7 (Brown, 2014) to allow only one record per 60 x 60m. We chose this value to allow sampling bias reduction and to keep a high spatial resolution on how landscape features impact chimpanzee distribution. After spatial filtering, records were still heavily biased towards the Issa valley, the GMERC long-term field site (Piel et al., 2015b). We thus further reduced the number of records in Issa by randomly selecting 90 records to produce a sample with the same density as the average density of the total covered area (Kramer-Schadt et al., 2013). This resulted in N= 2 554 occurrence points used to train the final model (Appendix S3.2, Figure S3.2.1).

We used an ensemble of species distribution model algorithms because this approach reduces the uncertainty associated with relying on a single method when projecting to a different time period (Araújo and New, 2007; Buisson et al., 2010). We applied three algorithms that have been shown to perform well when modelling species distributions: Random Forests (RF), Generalised Boosted Models (GBM) and MAXENT (Elith and Graham, 2009; Elith et al., 2006). We used the default settings in the biomod2 package (Version 3.3-7)] in the open-source software R (v. 3.6.1; http://www.R-project.org/) for each algorithm (Thuiller et al., 2016)

We sampled 10 000 pseudo-absence records at random from the background extent, excluding cells with previously removed true-presence points due to spatial filtering and balancing of occurrences. We randomly divided the original dataset, using 70% to construct the models and 30% to validate their accuracy. We replicated five runs to obtain a robust estimate and tested accuracy using the Area Under the Curve (AUC). Only models with AUC values equal to or greater than 0.9 were included in our final ensemble, with the contribution of each model proportional to its goodness-of-fit statistics. The True Skill Statistic (TSS) was also calculated for our final ensemble as an additional measure of accuracy (Allouche et al., 2006).

We derived resistance values using a negative exponential function of the suitability model output (Keeley et al., 2017, 2016; Mateo-Sánchez et al., 2015; Trainor et al., 2013).

$$r = 100^{1-SDM}$$

where r is the resistance value of a given cell and SDM is the suitability value associated to the cell. This transformation takes into consideration that during long-distance movements animals might be able to move through areas that would be classified as moderately suitable in the home range.

3.2.5. Circuit-based connectivity modelling

We developed landscape connectivity maps using electricity ***circuit theory*** implemented through Circuitscape 4.0.5 (Mcrae et al., 2008) using the pairwise mode which considers conductance across all pairs of nodes in the study area. We decided to focus on circuit theory rather than other commonly used modelling approaches (e.g. ***least-cost path analysis***) because of its success to quantify animal movement and gene flow (Dickson et al., 2018) and because of its ability to create a quantitative proxy of probabilities of connectivity across an entire surface without the need to define focal patches. We followed the method of Koen et al., (2014) to develop landscape connectivity maps that were independent of a priori source or destination locations by randomly placing regularly distanced nodes around a 40 km buffer perimeter (20% of the max length of the GME). To identify the optimum number of nodes required to generate an unbiased landscape-scale ***permeability map***, we created 10 current density maps using 10–100 nodes at intervals of 10. We selected 10 000 cells randomly in each current density map and used Pearson correlation to compare estimates extracted from each current density map (i.e. 10

to 90 nodes) with estimates from the full current density map (developed using 100 nodes). We considered that our modelling was sufficient when the curve comparing correlation coefficients to the number of node pairs reached an asymptote.

To help delineate the area of highest likelihood of chimpanzee movement, we selected all pixels with the highest current density quartile (Vanthomme et al., 2019), which for the purposes of this study, we term “current flow corridors”. To test the sensitivity of the identified corridors to the choice of our quartile threshold, we also used geometrical interval classification and selected all pixels in the upper class (Ersoy et al., 2019) (resulting maps are presented in supplementary material).

3.3. Results

The fit of the final chimpanzee habitat suitability model was 0.817 for TSS and 0.971 for AUC, thus indicating a high level of predictive power. Predictive accuracy of individual models ranged from 0.744 (+/-0.010) to 0.776 (+/-0.009) for TSS and from 0.937 (+/-0.004) to 0.950 (+/-0.003) for AUC, depending on the algorithm. On average, RF models performed best compared to GBM and MAXENT models (Table. S2.1). The contribution of each variable to the model was as follows: distance from steep slope (46.4%), distance from riparian forest (31.6%), proportion of riparian forest (11.2%), elevation (6.1%) and vegetation type (4.7%). The response curves produced by the model indicate that the relative probability of chimpanzee occurrence decreases with distance from steep slopes as well as with distance form riparian forest whereas it increases with proportion of riparian forest. Regarding elevation, chimpanzees were most likely found between 1000 and 1850 m. Further, probability of presence was highest in riparian forest and lowest in non-forested areas; miombo-woodland showed intermediate probabilities (Appendix S3.2, Figure S3.2.2).

Thirty node pairs were sufficient to generate unbiased connectivity maps (Appendix S3.2, Figure S3.2.3). The current density map derived from Circuitscape reflects relative probability of movement, with areas of high current density representing higher probability of movement. The GME appears to have been connected by several current flow corridors facilitating chimpanzee movement in 1973 (Figure 3.2; Appendix S2, Figure S3.2.4).

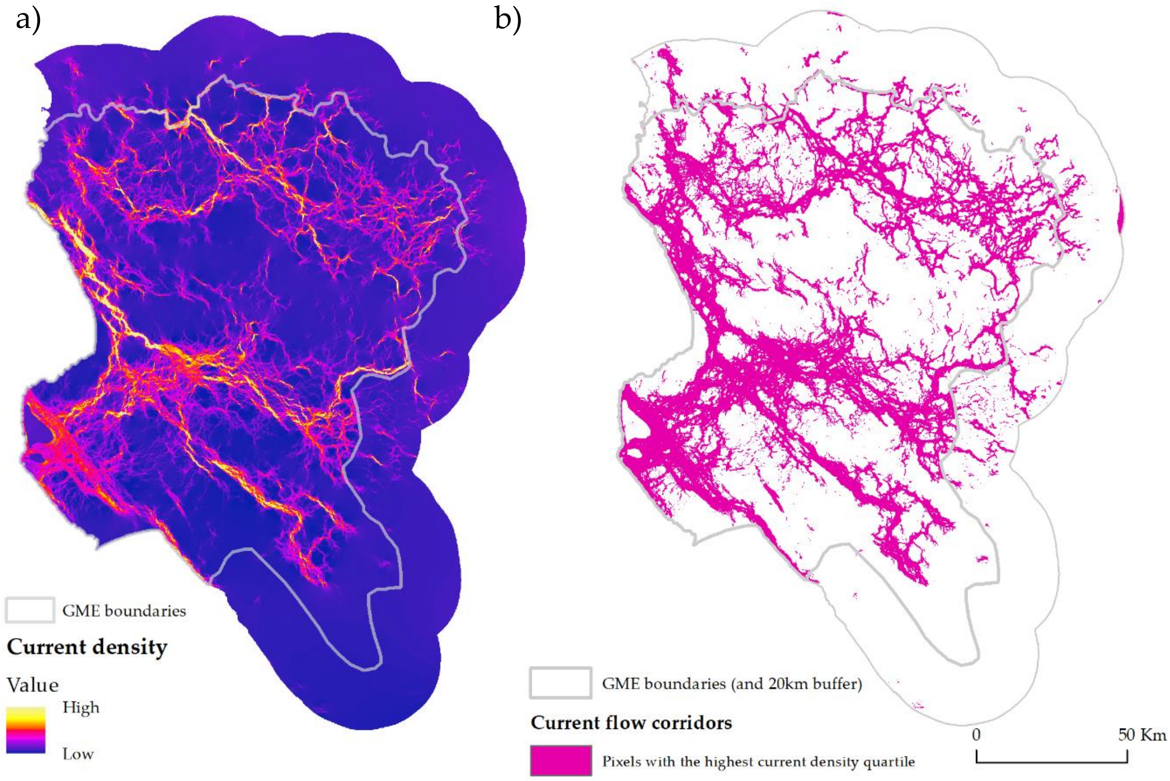


Figure 3.2: Habitat connectivity maps derived from Circuitscape for 1973 a) Current density map, b) current flow corridors

Although the pattern of landscape connectivity remained broadly similar over time (Appendix S3.2, Figue S3.2.5), a reduction in current density is observed for 1 966.7 km^2 between 1973 and 2019. This reduction is impacting both current flow corridors linking the northern and southern GME (Figure 3.3a). When projecting to 2027, we predict 2 152.3 km^2 further decline, severely impacting the western current flow corridor linking the northern and southern GME and affecting a large area in the south-east of the GME (Figure 3.3b). Increase in current flow is also observed for both time periods corresponding to displacement of probability of movement.

3.4. Discussion

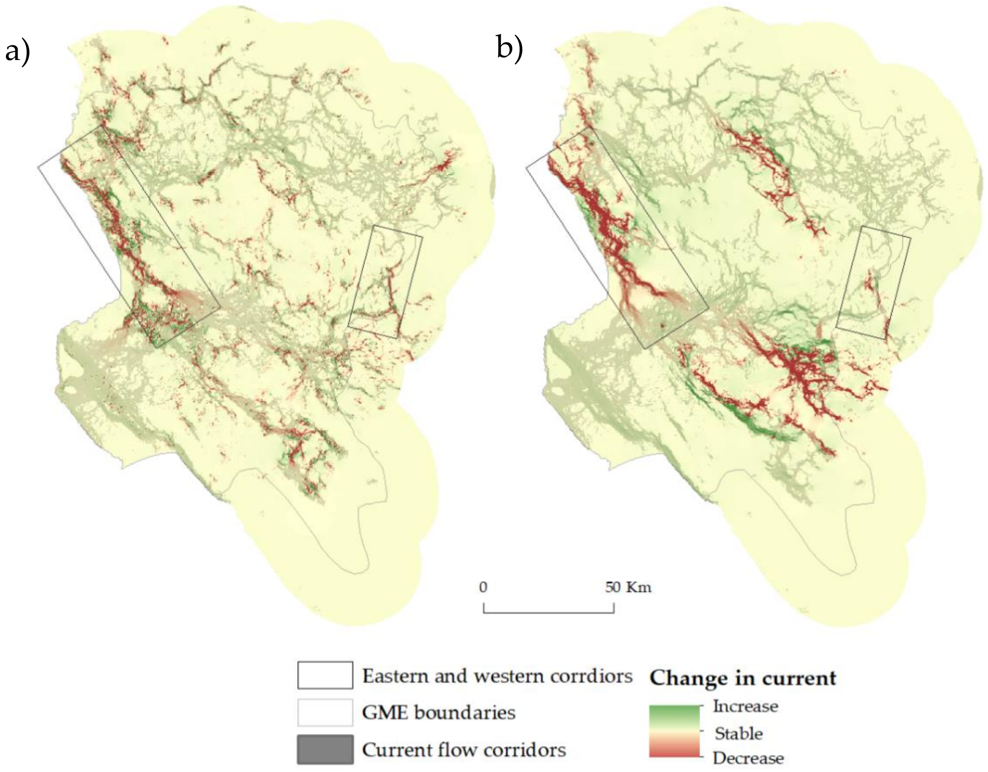


Figure 3.3: Current density change between a) 1973 and 2019, b) 2019 and 2027

Landscape connectivity is of central importance to maintain population viability, especially in increasingly anthropogenically disturbed landscapes. We used circuit theory to assess chimpanzee habitat connectivity within the GME, an area containing nearly the entire free-ranging population of Tanzania’s chimpanzees (Plumptre et al., 2010). Our results suggest that the ecosystem was linked by a series of corridors showing a relatively high probability of chimpanzee movement in 1973. This result is consistent with previous population genetic analyses suggesting recent gene flow throughout the GME (Inoue et al., 2011). Our analysis also reveals a reduction of connectivity impacting the two current flow corridors linking the northern and southern GME. Mishamo, a refugee settlement established in 1981 to host 35 000 Burundian refugees was hypothesised to separate the ecosystem or at least hinder chimpanzee movement between the northern and the southern population of the GME (Moyer et al., 2006; Piel and Stewart, 2015; Rudicell et al., 2011). However, our 1973 model shows that the central part of the ecosystem was already unsuitable for chimpanzees prior to the establishment of this settlement (Appendix S3.2, Figure S3.2.6). This result is supported by Kano's (1971) early work on chimpanzee distribution in Tanzania, when he reported no chimpanzees in the Lugufu basin (location of Mishamo establishment) following his extensive 1965-1967 surveys. The Lugufu Basin/Mishamo region is mainly flat and was dominated by Miombo-woodland and grassland (Bomans et al., 1981), whereas surveys indicate that chimpanzees select hilly areas with riparian forests (Hernandez-Aguilar, 2006; Kano, 1972; Moyer et al., 2006; Ogawa et al., 2013; Piel and Stewart, 2014, this study). While the Mishamo refugee settlement expansion occurred outside of chimpanzee habitat, the impact of increased human population density cannot be overlooked. It is likely that the establishment of the refugee settlement and the arrival of tens of thousands of people to the region has increased pressure on forests through consumption of firewood, charcoal production, conversion of land for agriculture and poaching (Jambiya et al., 2007; Ogawa et al., 2013, 2006a, 2006b; Whitaker, 1999).

A survey led 40 years after Kano's first expedition reported a reduction in chimpanzee density in each revisited area within the GME, but no extinction of local populations (Yoshikawa et al., 2008). Following surveys from Piel et al. (2015a) reported similar pattern and found an overall decline in mean chimpanzee nest density between 2007 and 2014 in the northern GME (previously identified as the Masito-Ugalla Ecosystem, MUE) and an association between habitat loss and a decline in chimpanzee density. Our analysis of Landsat images reveals a total forest (i.e. riparian forest and miombo-woodland) decline of 1 677 km^2 between 1973 and 2017 (Figure 3.4). Surprisingly, vegetation type contributed relatively little to our model (4.7%) and deforestation of miombo-woodland did not have a large impact on our landscape connectivity change. Instead, destruction of entire blocks of riparian forests were responsible for the observed reduction of connectivity between 1973 and 2017 and have disproportionately affected current flow corridors. Although travelling through more open miombo-woodland without nearby riparian forests may represent a higher risk of predation, miombo-woodland could still have been used by chimpanzees to a certain extent to reach sparsely distributed resources. The significant deforestation of miombo-woodland in the centre of the GME and settling of thousands of humans in the area is now likely to prevent any chimpanzee movements. This is particularly alarming given that the Shoch et al. (2019) model predicts another 2 426 km^2 of forest to be lost by 2027, threatening a large area in the south-east of the GME (Figure 3.3b; Figure 3.4). The consequences of habitat loss in this area will have a devastating impact on chimpanzees, not only reducing suitable habitat, but also an area of high movement probability. This area falls within the Ntakata REDD project boundaries, a project initiated in May 2017 with the goals of engaging and supporting local communities in the protection of their village land forest reserves (Shoch et al., 2019). By providing support for community patrols and monitoring by village game scouts, we are hopeful that this approach results in increased conservation of this large, critical area for chimpanzees.

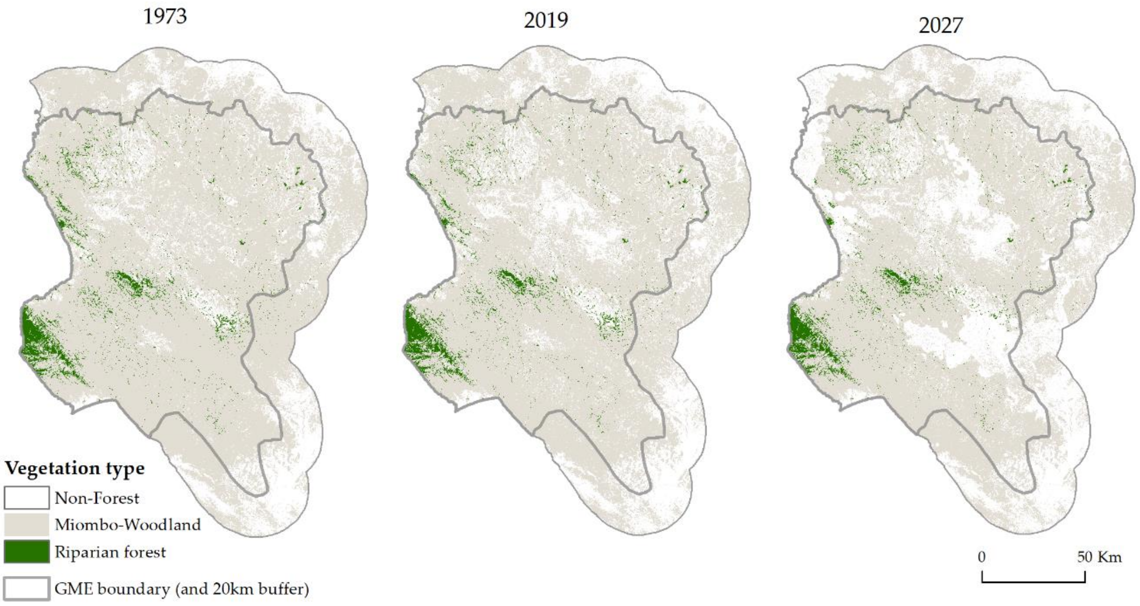


Figure 3.4: Vegetation change from 1973 to 2027

Along with forest loss, the Mpanda-Uvinza road may have potentially played a role in the current density reduction within the eastern corridor. Splitting the ecosystem, the road crosses the only migration route available for movement of individuals from eastern MUE to the south (Figure 3.5 Box b). Even though chimpanzees have been reported crossing and even using roads (Cibot et al., 2015; Hockings et al., 2006), roads can impede animal movement through mortality during crossing (McLennan and Asiimwe, 2016). Probably impacting chimpanzees more than the road itself, the associated deforestation enabled by easier access to forest resources is affecting habitat at a larger scale (Laurance et al., 2009; Palminteri et al., 2019; this study). Although this road was already established in 1973 (Kano, 1971), increases in traffic and other associated anthropogenic pressures may have negatively impacted animal movement. Chimpanzee presence has been reported on both sides of the road in the north of the ecosystem (Piel and Stewart, 2014), however, chimpanzee movement across the road still needs to be confirmed. Investigations into what extent this road and its associated land use change limit chimpanzee movement and thus gene flow will have important implications for conservation, especially because the (currently, dirt) road is now in the process of being paved (NB pers. obs). The Ilagala-Mahale road running to the west of the ecosystem may also have deleterious impacts on chimpanzee habitat and movement. Its construction in 2006 was correlated with a dramatic increase in forest loss and construction plans foresee an extension of the road to the south of MMNP (Palminteri et al., 2019). Our model highlights critical areas for chimpanzees and could be used for the development of detailed land use planning along the road. By establishing new village forest reserves and wildlife crossing structures across developing roads in these critical areas for chimpanzee movements we could help maintain movement and balance needs of local communities and chimpanzees (Gloyne and Clevenger, 2001; Lasch et al., 2011; Plumptre et al., 2010; TAWIRI, 2018).

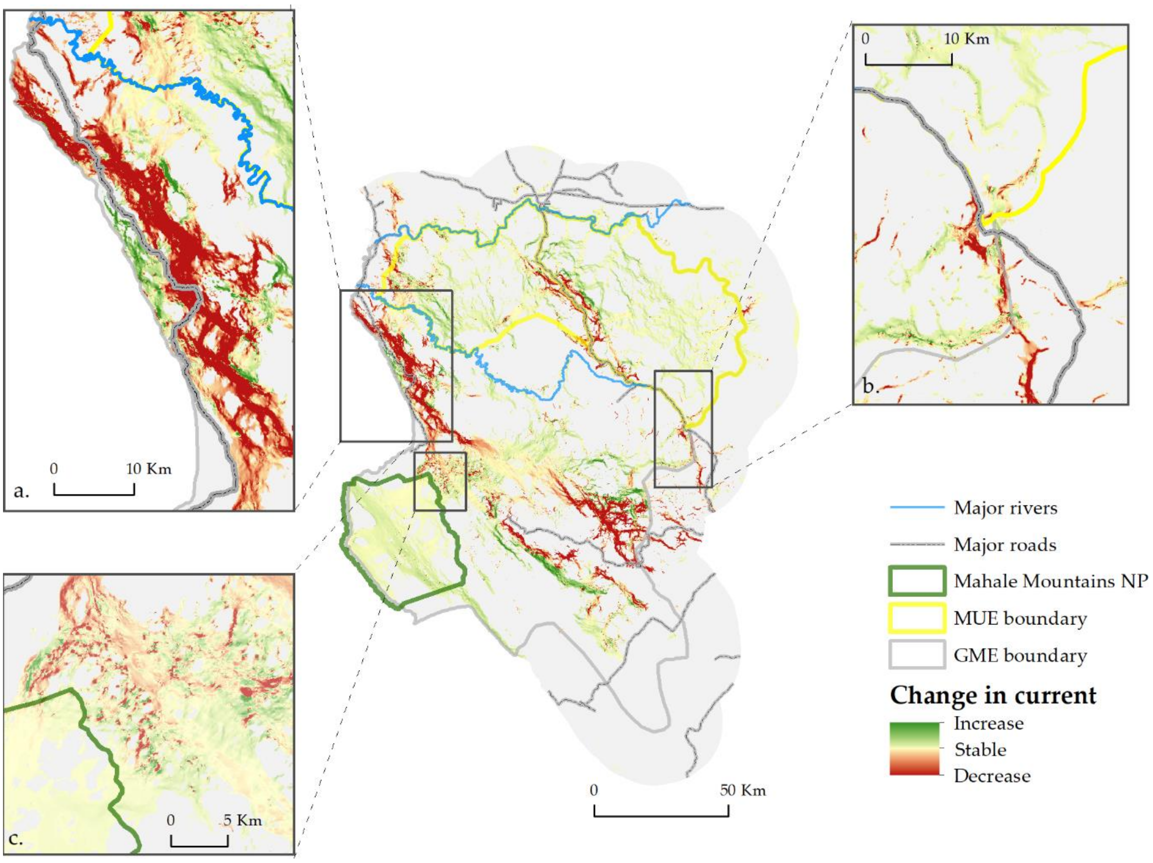


Figure 3.5: Priority areas to maintain connectivity for chimpanzee conservation within the GME. Background represents current density change between 1973 and 2027 within current flow corridors delineated for 1973. Box a. western corridor running through the Lugufu river; Box b. eastern corridor crossing Uvinza-Mpanda road; Box c. corridor allowing movement in/out MMNP

Large rivers may also act as barriers to animal movement (e.g. Eriksson et al. 2004). The GME is bordered by a large river, the Malagarasi, to the north, and segmented by the Lugufu river running through the north west of the ecosystem (Figure 3.5 Box a). Inoue et al. (2011) proposed the Malagarasi river to be a major biogeographical boundary preventing chimpanzee movement into the GME from the north, however circumstantial evidence suggests that chimpanzees can move across the 100m wide river using natural, shallow fords, which together with further genetic evidence, suggests that the river does not form a complete barrier to gene flow (Piel et al., 2013). The Lugufu river is only 15 m wide (at its widest), and so may similarly allow some movement across it, especially in the dry season; however, more investigation is needed. Given the extreme seasonality of the ecosystem, with a six months dry season (<100 mm of rainfall/month), temporal variation of connectivity also remains to be examined. Variation of river flow and depth could result in temporal barriers to chimpanzee movement (Eriksson et al., 2004), but also affect the availability of water resources from smaller streams. Other resources such as plants also show important seasonal variation and are known to influence chimpanzee ranging patterns (Doran, 1997; Hasegawa, 1990; Wrangham, 1977). Adding phenological data (e.g. resource availability) to our model would allow a better understanding of chimpanzee movement within this extremely seasonal ecosystem.

Here we chose to derive resistance values from habitat suitability modelling, which is recommended over expert opinions although often underperforms compared to direct movement data or genetic methods when sufficient genetic data are available (Beier et al., 2008; Stevenson-Holt et al., 2014). Less biased and more data-driven than expert opinions, habitat suitability modelling allows the creation of a more precise **resistance surface** at a fine-scale. However, our occurrence data are skewed towards sleeping sites, with nest locations comprising 81% of our presence points. This may explain the major contribution of steep slopes to our model as chimpanzee nests are often associated with steep slopes within the ecosystem (Hernandez-Aguilar, 2009; Stewart, 2011), whereas feeding and travel behaviour is likely not. Similarly, the importance of distance from riparian forest may represent sleeping site preferences although chimpanzees use miombo-woodland extensively for feeding and travelling (Hernandez-Aguilar, 2009; Nishida, 1989). Further work integrating genetic data (e.g. landscape genetic analysis) will help us better understand how landscape features impact chimpanzee movement across the GME.

Our models have confirmed historical connectivity throughout the GME and have highlighted priority areas for chimpanzee conservation in Tanzania. First, our results revealed potential corridors linking the northern and southern population of the GME (Figure 3.5 Box a. and b). Additional ground surveys and genetic analysis could confirm whether chimpanzee movement is possible along this potential corridor and if there is genetic exchange. Our model also identified corridors to the north-east of MMNP (Figure 3.5 Box c). Previous surveys have confirmed chimpanzee presence in this area in 2011-2012 (Piel and Stewart, 2014). However, as for the eastern and western corridors linking the northern and southern population of the GME, increasing anthropogenic pressure and associated deforestation is threatening this corridor. We recommend focusing conservation efforts on maintaining riparian forest, which is not only necessary for chimpanzee survival, but also essential for the provision of natural resources on which local human livelihoods depend. Our model supports evidence of large areas within the GME that are suitable for chimpanzee habitat and movement. Preference of GME chimpanzees for steep terrain may have allowed their continued persistence, as such areas are difficult for humans to access and are less favourable for conversion to other land-uses (Heinicke et al., 2019; Kinnaird et al., 2003). By maintaining and possibly enhancing connectivity identified in this study and giving priority to those areas currently under threat, we are optimistic that Tanzania can continue to host a large viable population of chimpanzees.

Acknowledgments

We thank the Tanzanian Wildlife Research Institute (TAWIRI) and Commission for Science and Technology (COSTECH) for permission to carry out research in Tanzania and village and District governments for their facilitation to conduct this work. We are also extremely grateful to GMERC field assistants in Tanzania. The UCSD/Salk Center for Academic Research and Training in Anthropogeny (CARTA) for long-term support of GMERC. We also thank L. Nelli for helpful discussions on suitability modelling and Nathaniel Robinson for his help on landcover classification. The Arcus Foundation, The Nature Conservancy, Frankfurt Zoological Society, the United States Agency for International Development (USAID) and the Jane Goodall Institute were all instrumental in supporting, facilitating, and funding this work.

Supplementary Materials

Appendix S3.1

Generation of the 2000 continuous tree cover dataset

In this section we detail how we created and evaluated our tree cover product. We used a similar methodology compared to Sexton et al. (2013) but with key differences in the reflectance data and modelling algorithm. Instead of using Landsat reflectance data directly our approach uses a set annual multi-temporal metrics and in place of piece-wise linear regression, we use gradient boosted regression trees as implemented in the XGBoost software (Chen and Guestrin, 2016). We evaluated our product using a hold-out sample from our dataset and independent reference data gathered from the Global Ecosystem Dynamics Investigation (GEDI) LiDAR sensor attached to the International Space Station.

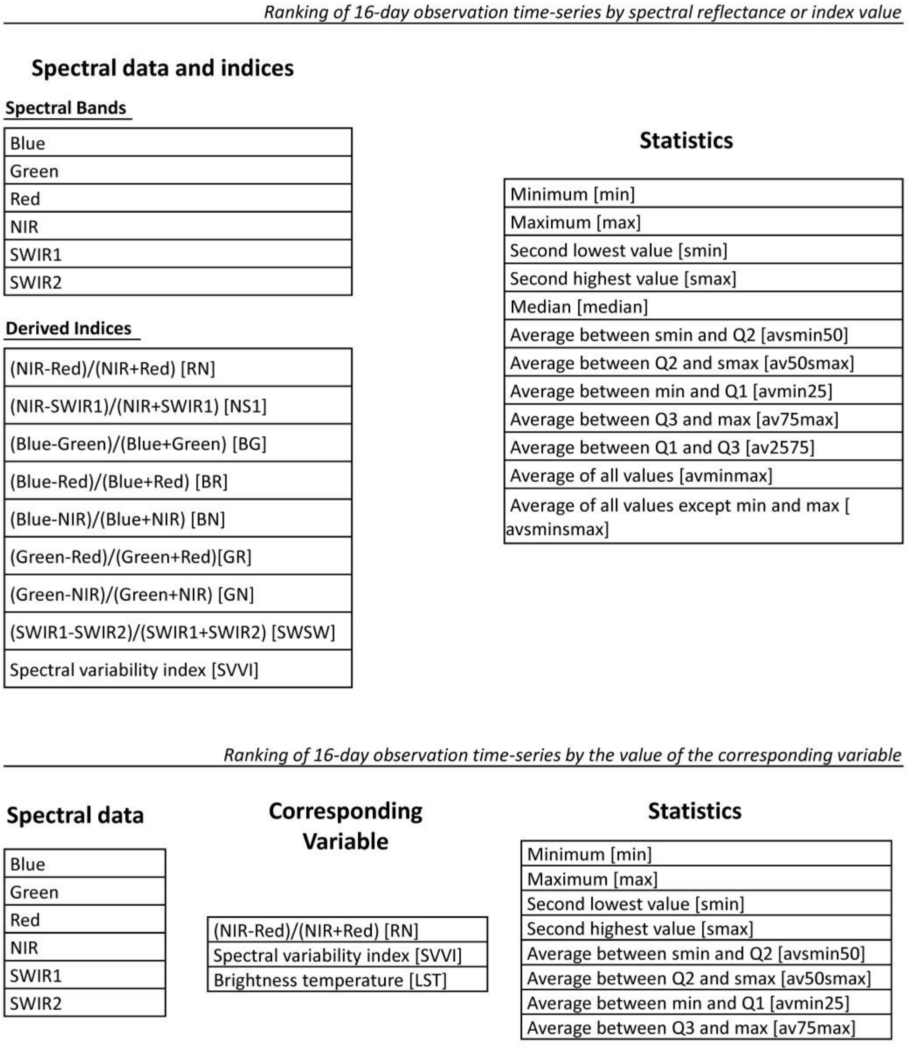
Training Data

Tree cover training data were derived from the MODerate-resolution Imaging Spectroradiometer (MODIS) Vegetation Continuous Fields (VCF) Tree Cover dataset (MOD44B), currently in Version 6, which has a spatial resolution of 250 meters and is produced on an annual basis from 2000 to 2019 (Dimiceli et al., 2015). MODIS VCF data have been used for several studies such as quantifying forest loss in and around tropical protected areas (Defries et al., 2005), climate modelling (Lawrence and Chase, 2007), quantifying global gross forest cover loss (Hansen et al., 2010) and mapping carbon emissions from tropical deforestation (Harris et al., 2012). We acquired MODIS VCF data for the period 2000-2019 for the study area from the NASA Land Processes Distributed Active Archive Center (LPDAAC) using the Application for Extracting and Exploring Analysis Ready Samples (AppEEARS Team, 2020).

Multi-temporal Landsat Metrics

We used Landsat Analysis Ready Data produced by the Global Land Analysis and Discovery team at the University of Maryland (GLAD ARD) to create a set of annual metrics for the study area from 2000 to 2019. The GLAD

ARD are 16-day composites of tiled Landsat (TM, ETM+ and OLI sensors) normalized surface reflectance from 1997 to the present updated annually, and designed for landcover monitoring at global to local scales (Potapov et al., 2020). In addition to a layer describing per pixel quality, each 1° by 1° tile contains normalized surface reflectance for the blue, green, red, near-infrared (NIR), shortwave infrared band 1 (SWIR1), shortwave infrared band 2 (SWIR2) and surface brightness temperature (LST). For a number of reasons, such as uneven cloud cover and differing acquisition strategies among the constellation of Landsat satellites, it is infeasible to use the 16-day composites directly. The metrics approach increases spatial and temporal consistency by building an annual time-series of the highest quality observations, and subsequently computing a set of metrics that represent salient phenological features across a landscape. We generated a set of 354 annual phenological metrics from the GLAD ARD tiles as detailed in Potapov et al. 2020 and displayed in figure S3.1.1. The tiled Landsat data and software to create the annual phenological metrics are freely available and can be downloaded at https://glad.umd.edu/ard/home. We supplemented our dataset with elevation data from Shuttle Radar Topography Mission (SRTM) (http://srtm.csi.cgiar.org/).



Ranking of 16-day observation time-series by spectral reflectance or index value

Spectral data and indices

Spectral Bands

Blue
Green
Red
NIR
SWIR1
SWIR2

Derived Indices

(NIR-Red)/(NIR+Red) [RN]
(NIR-SWIR1)/(NIR+SWIR1) [NS1]
(Blue-Green)/(Blue+Green) [BG]
(Blue-Red)/(Blue+Red) [BR]
(Blue-NIR)/(Blue+NIR) [BN]
(Green-Red)/(Green+Red)[GR]
(Green-NIR)/(Green+NIR) [GN]
(SWIR1-SWIR2)/(SWIR1+SWIR2) [SWSW]
Spectral variability index [SVVI]

Statistics

Minimum [min]
Maximum [max]
Second lowest value [smin]
Second highest value [smax]
Median [median]
Average between smin and Q2 [avsmin50]
Average between Q2 and smax [av50smax]
Average between min and Q1 [avmin25]
Average between Q3 and max [av75max]
Average between Q1 and Q3 [av2575]
Average of all values [avminmax]
Average of all values except min and max [avsminsmax]

Ranking of 16-day observation time-series by the value of the corresponding variable

Spectral data

Blue
Green
Red
NIR
SWIR1
SWIR2

Corresponding Variable

(NIR-Red)/(NIR+Red) [RN]
Spectral variability index [SVVI]
Brightness temperature [LST]

Statistics

Minimum [min]
Maximum [max]
Second lowest value [smin]
Second highest value [smax]
Average between smin and Q2 [avsmin50]
Average between Q2 and smax [av50smax]
Average between min and Q1 [avmin25]
Average between Q3 and max [av75max]

Figure S3.1.1: Adapted from figure 10 in Potapov et al. 2020. Phenological metrics with names in brackets.

The first set of metrics represents statistics calculated from 16-day observation time-series ranked by the spectral reflectance or index value. The ranking is performed independently for each spectral band or index. The second set of metrics represents statistics calculated from 16-day observation time-series ranked by the value of a corresponding variable (NDVI, SVVI, and brightness temperature). Q1, Q2, and Q3 represent the 1st, 2nd, and 3rd quartiles, respectively.

Reference Data

We obtained independent reference data from Global Ecosystem Dynamics Investigation (GEDI) Lidar attached to the International Space Station (ISS). GEDI is a full waveform Lidar specifically designed for measuring vegetation canopy structure and data from this mission is being used to create a suite of vegetation and aboveground biomass products (Dubayah et al., 2020). The footprint-level (25 meter diameter) vegetation canopy height and cover metrics for the first 9 months of GEDI observations (April - December 2019) have been processed and are publicly available. We retrieved Level 2B canopy structure metrics, including percent canopy cover, from the NASA Land Process Distributed Active Archive Center (LPDAAC).

Methods

For each year in the 2000 to 2019 period, we aggregated and co-located all metrics to match the 250 meter resolution MODIS VCF product and extracted all 250 meter pixels over land. Samples from all years were pooled together to create a single dataset. We then randomly divided the data into three subsets for training, early stopping and evaluation. We used the XGBoost software to model MODIS VCF percent tree cover as a function of the multi-temporal metrics as well as elevation, slope and aspect derived from the SRTM data. For model evaluation, we computed the root mean square error (*RMSE*), mean absolute error (MAE), mean bias error (*MBE)*, and Pearson's correlation coefficient (ϱ) (Willmott, 1982) using GEDI percent canopy cover as a reference.

$$RMSE = \sqrt{\frac{\sum_{i=1}^{n}(tc_i - r_i)^2}{n}}$$

$$MAE = \frac{\sum_{i=1}^{n}|tc_i - r_i|}{n}$$

$$MBE = \frac{\sum_{i=1}^{n}(tc_i - r_i)}{n}$$

$$\rho = \frac{cov(tc, r)}{\sigma_{tc} * \sigma_r}$$

where i = pixel index

tc_i = modelled percent tree cover

r_i = reference percent canopy cover from GEDI Lidar

n = sample size

cov = covariance function

σ = standard deviation

Results

Qualitatively, our product better captures tree cover in the region compared with the widely used Hansen et al. (2013) global product (Figure S3.1.2). For example, the global product over predicts tree cover over sloped terrain.

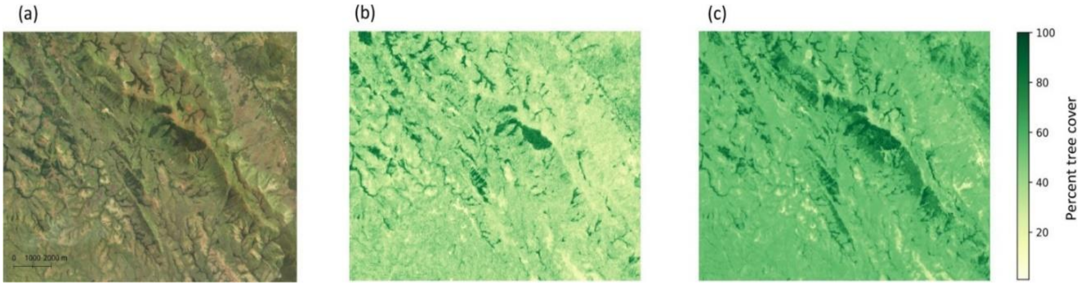


Figure S3.1.2: A zoomed region of the study area showing high resolution Google Earth imagery (a), our percent tree cover product (b), and percent tree cover from Hansen et al. (2013).

We were able model the MODIS VCF data well with *RMSE* of 5.61%, *MAE* of 4.23%, no bias error and ϱ of 0.88 on the hold-out sample. Our modelled tree cover and MODIS VCF tree cover are tightly distributed along the one-to-one line (Figure S3.1.3).

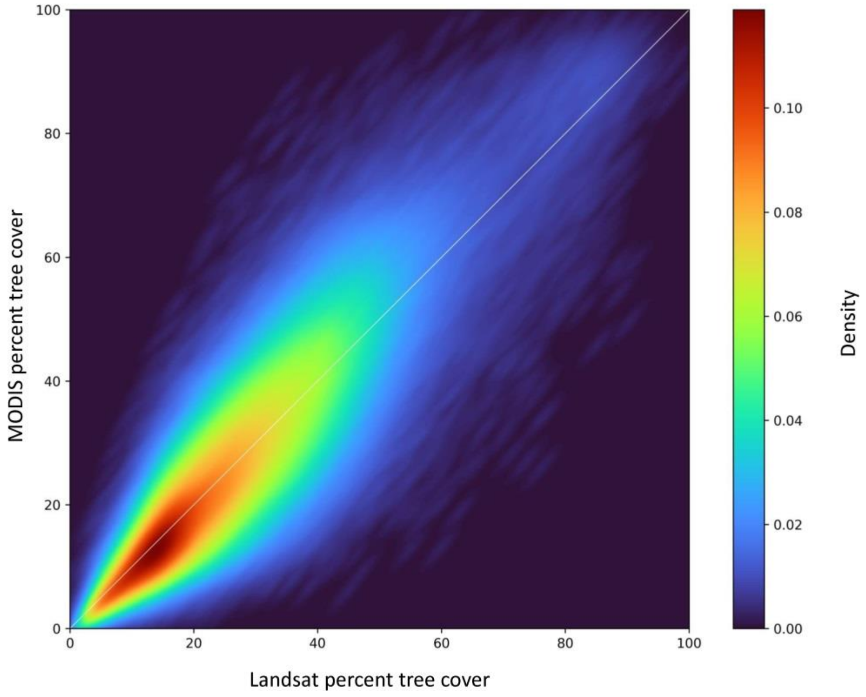


Figure S3.1.3: 2 dimensional density plot with Landsat predicted tree cover on the x-axis and MODIS VCF tree cover on the y-axis. The one-to-one line is shown in white.

Our product better matched the Lidar derived canopy cover compared to the MODIS VCF with smaller error and higher correlation (Table S3.1.1).

Table S3.1.1: Error metrics for tree cover predicted from Landsat data as well as the MODIS VCF product. Reference data are canopy cover as measured from the GEDI Lidar sensor.

	RMSE (%)	*MAE* (%)	*MBE* (%)	ρ
Landsat	13.3	10.3	-1	0.6
MODIS	15.4	11.9	-2.2	0.4

Both our product and the MODIS VCF tended to over predict low canopy cover values and under predict high canopy cover values (Figure S3.1.4). The MODIS VCF product is known to saturate at approximately 85% canopy cover (Hansen et al., 2002; Sexton et al., 2013) and this artifact is present in our product as well. Neither product predicts tree cover above 85% and the non-linear trend is evident in our product (Figure S3.1.4b).

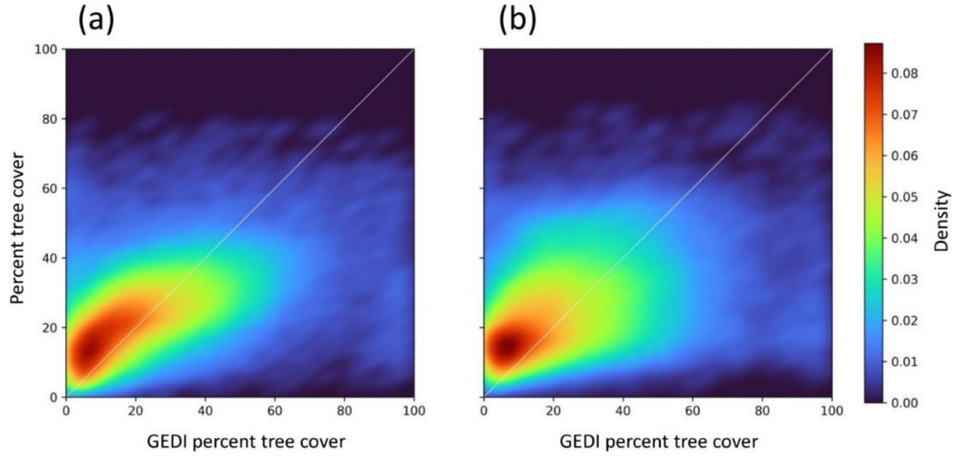


Figure S3.1.4: 2 dimensional density plots with canopy cover from GEDI Lidar on the x axes, percent tree cover from Landsat on the y-axis (a), and MODIS VCF tree cover on the y-axis (b). The one-to-one lines are shown in white.

Classification and evaluation of the 1973 image

Classification

The bare lands from 2000 image were masked from 1973 image and the resulting masked 1973 images was than classified using unsupervised Iso Cluster algorithm in ArcGIS Desktop, using 20 number of classes with minimum class size of 20 ad sampling interval of 10. This produced a raster with 17 classes that was than reclassified in forest and non-forest classes.

Evaluation

To validate 1973 vegetation we used "Create Accuracy Assessment Points" function in ArcGIS Desktop and generated 100 randomly distributed points within each class: Other, Woodland, Forest using Equalized Stratified Random sampling strategy.

We generated a distance layer from tree cover loss points from Hansen 2000-2019 and removed any points that were less than two pixels (120 meters) from deforestation pixels to focus on areas least impacted by people because our high resolution satellite imagery were acquired within 2010 to 2019 time interval. Total left points for ground-truthing were Other=77, Woodland=76 and Forest=80. The total overall Kappa accuracy was 0.83. The User Accuracy for the Forest was 0.95 and for Woodland was 0.91.

We used human interpretation of high-resolution satellite imagery to ground-truth the points by overlaying in ArcGIS Desktop using Maxar/DigitalGlobe ImmageConnect extension random points with Maxar 50 cm to 1-meter multitemporal satellite imagery collected between 2010-2019 along with Esri Imagery basemaps and Landsat MSS scene from 1973

Appendix S3.2

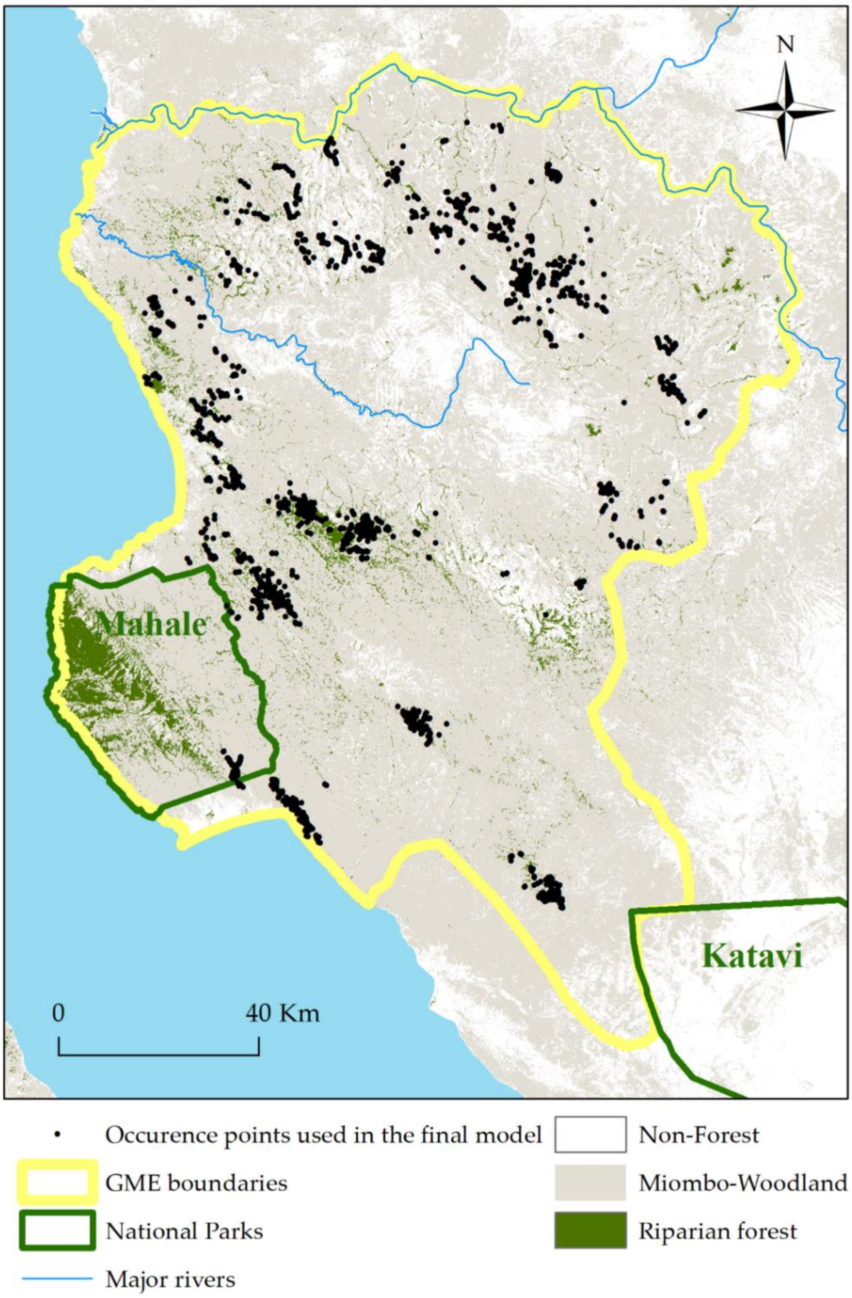


Figure S3.2.1: Locations of the occurrence points used in the final habitat suitability model

Table S3.2.1: Predictive accuracy and standard deviation (SD) of the 5 replicates for the 3 algorithms.

	Individual runs				**Ensemble**	
	TSS	**SD**	**AUC**	**SD**	**TSS**	**AUC**
RF	0.776	0.009	0.950	0.003	0.914	0.991
GBM	0.762	0.010	0.945	0.003	0.777	0.949
MAXENT	0.744	0.010	0.937	0.004	0.758	0.943

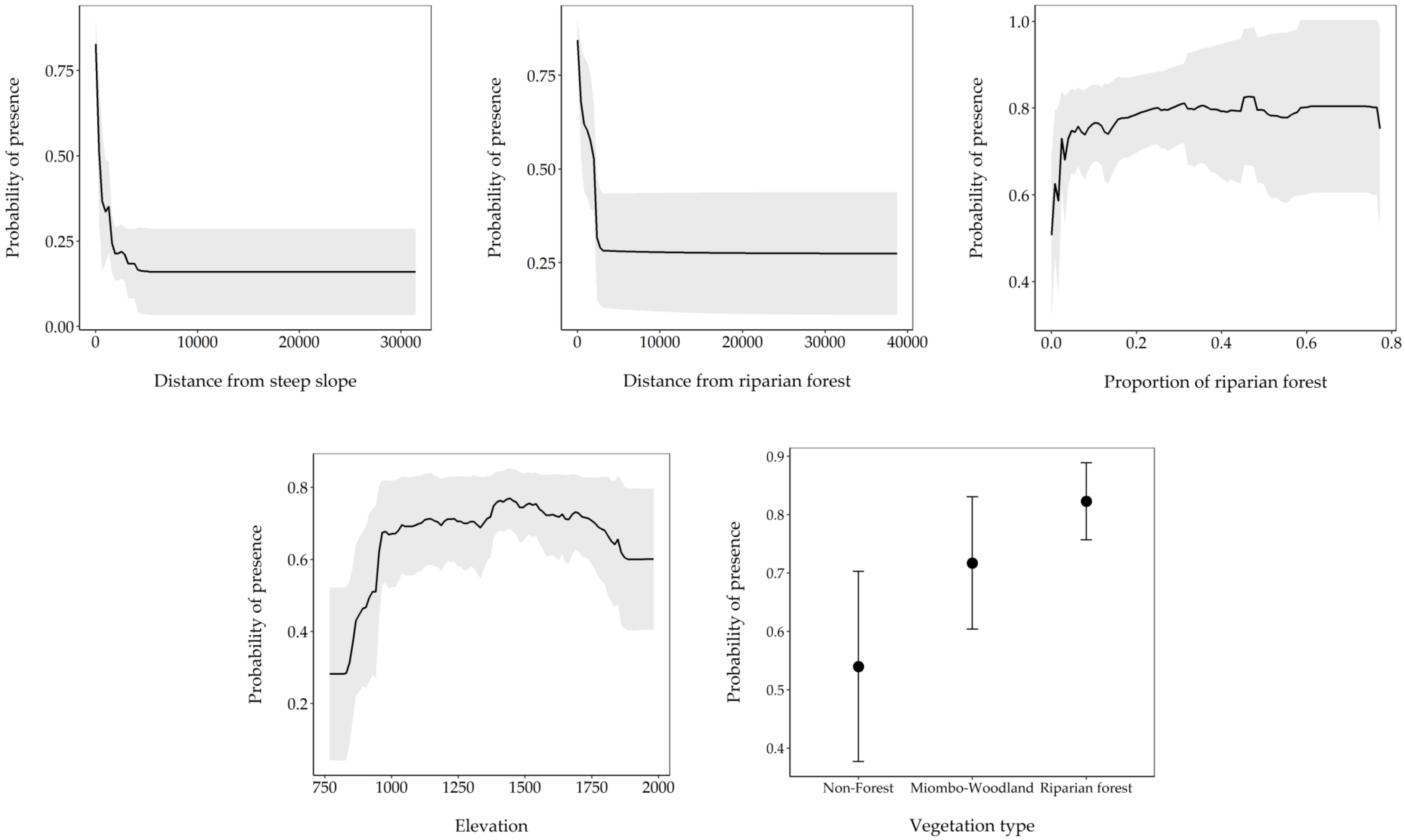


Figure S3.2.2: Response curves derived by the ensemble prediction. The plots show the mean response (dark line and dark points) and the standard deviation (error bars and grey ribbon) of the 5 replicates of the 3 algorithms. The curves display how the predicted probability of presence vary in function of each environmental variable. These response curves do not account for interactions between variables.

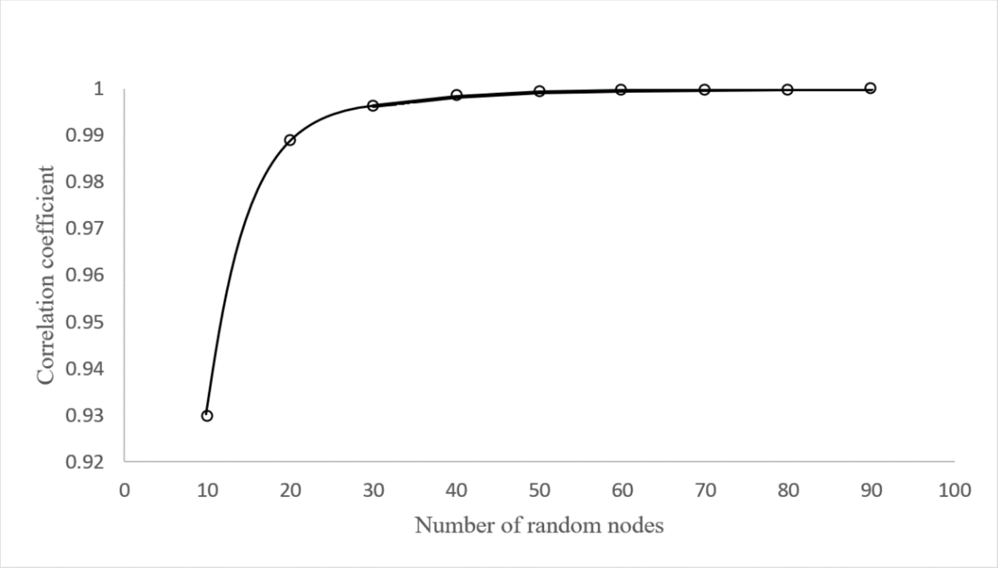


Figure S3.2.3: Pearson correlation coefficients of extracted values (n = 100 000) from a full permeability map developed using 100 random nodes compared to extracted values from permeability maps developed using fewer random nodes (i.e. 10–100).

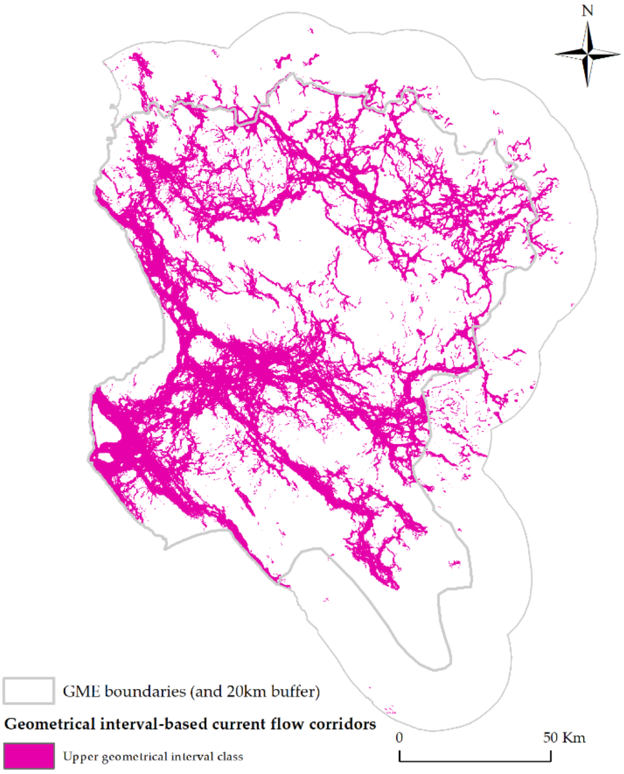


Figure S3.2.4: Current flow corridors for 1973 derived from upper geometrical interval

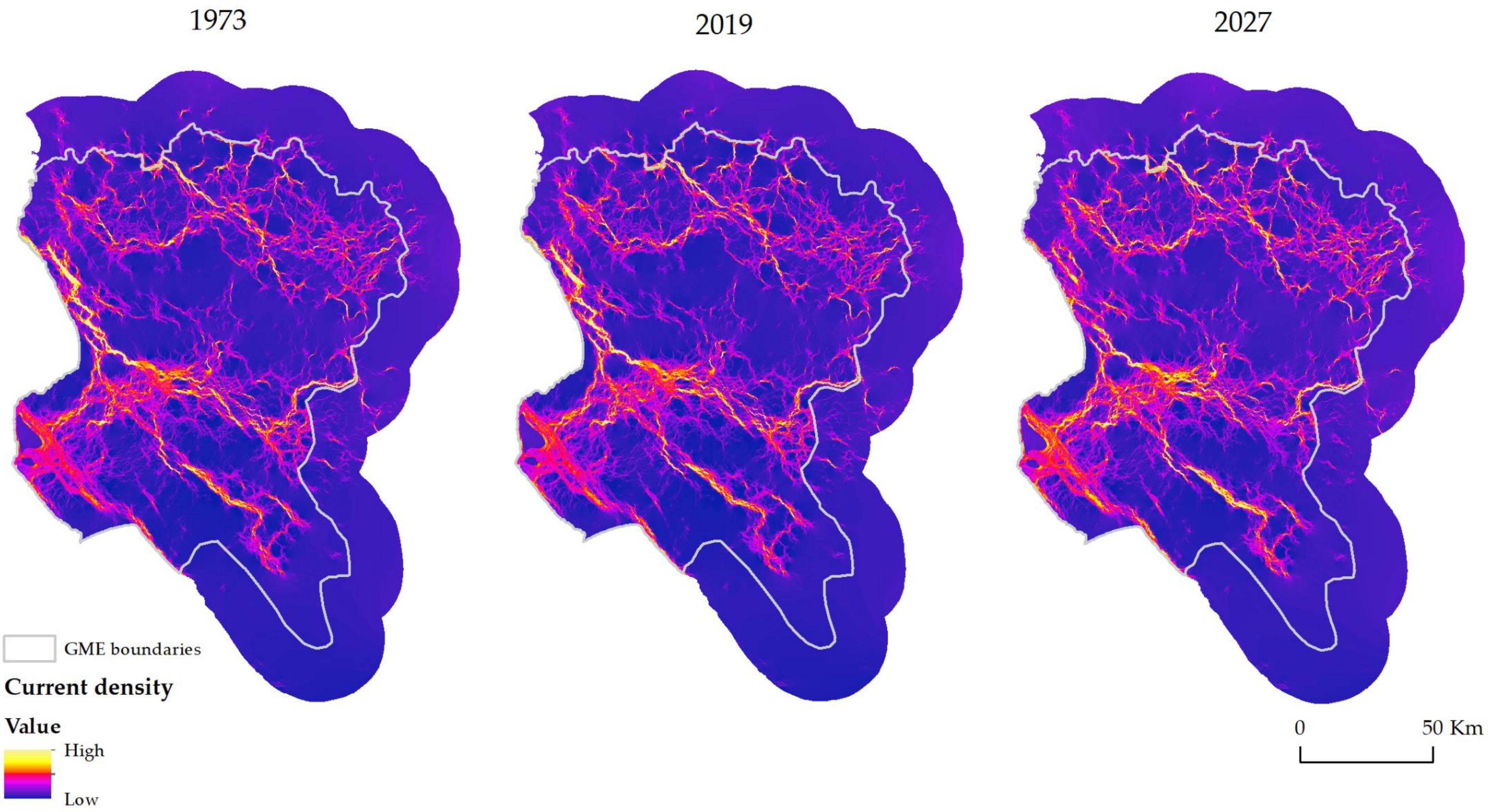


Figure S3.2.5: Current density map for 1973, 2017 and 2027 within the GME and a 20km buffer

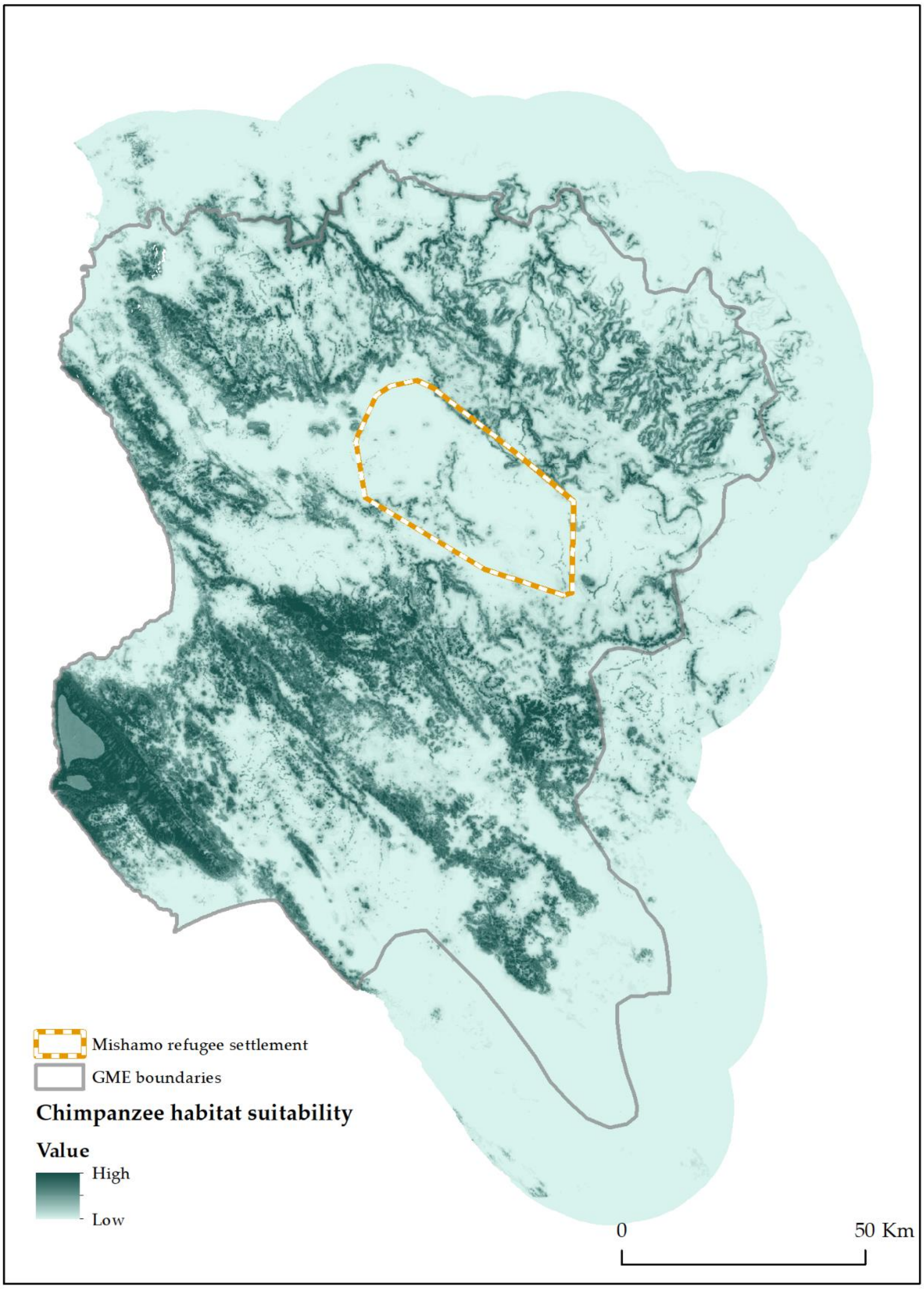


Figure S3.2.6: Area of Mishamo refugee settlement establishment overlaid with chimpanzee habitat suitability for 1973 within the GME and a 20km buffer

Chapter 4:

Genetic diversity and population structure of Tanzanian chimpanzees

Noémie Bonnin[1], Alex K. Piel[2], Richard P. Brown[1], Jasmin Giles[3], Alexa N. Avitto[3], Madhurima Gundlapally[3], Andrew J. Connell[3]; Yingying Li[3], Beatrice Hahn[3], Paul M. Sharp[4,5], Deus C. Mjungu[6], Jane Raphael[7], Iddi Lipende[8], Dismas Mwacha[6], Michael L. Wilson[9,10,11], Elizabeth V. Lonsdorf[12], Emily E. Wroblewski[13], Anne E. Pusey[14], Adrienne Chitayat[15], Serge A. Wich[1,15], Fiona A. Stewart[1,2]

[1] School of Biological and Environmental Sciences, Liverpool John Moores University, UK
[2] Department of Anthropology, University College London, London, UK
[3] Departments of Medicine and Microbiology, University of Pennsylvania, Philadelphia, Pennsylvania, United States of America
[4] Institute of Evolutionary Biology, University of Edinburgh, Edinburgh EH9 3FL, United Kingdom
[5] Centre for Immunity, Infection and Evolution, University of Edinburgh, Edinburgh EH9 3FL, United Kingdom
[6] Gombe Stream Research Centre, The Jane Goodall Institute–Tanzania, P.O. Box 1182, Kigoma, Tanzania
[7] Gombe National Park, Kigoma, Tanzania
[8] Tanzania Wildlife Research Institute (TAWIRI), Arusha, Tanzania
[9] Department of Anthropology, University of Minnesota, Minneapolis, MN 55455, USA
[10] Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA
[11] Institute on the Environment, University of Minnesota, St. Paul, MN 55108, USA
[10] Biological Foundations of Behavior Program, Franklin and Marshall College, Lancaster, PA, USA
[11] Department of Structural Biology, Stanford University School of Medicine, Stanford, CA, USA
[12] Department of Psychology, Franklin and Marshall College, Lancaster, PA 17604, USA
[13] Department of Anthropology, Washington University in St. Louis, USA
[14] Department of Evolutionary Anthropology, Duke University, Durham, NC, USA
[15] Institute of Biodiversity and Ecological Dynamics, University of Amsterdam, The Netherlands

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Abstract

Rapid habitat loss across chimpanzees' range threatens their viability and can result in small, isolated populations likely to suffer from inbreeding. Tanzania is home to two of the longest studies of chimpanzees, both in national parks and in their 6th and 7th decade. Most Tanzanian chimpanzees, however, live outside of national parks. Initial studies on gene flow and genetic diversity of Tanzanian chimpanzees have provided contrasting findings regarding population connectivity. Here we use both mitochondrial control region sequences and genotypes from 10 microsatellite loci to describe population structure and genetic diversity of chimpanzees across Tanzania. Although mitochondrial sequence analysis supports historical gene flow across their distribution, nuclear loci revealed two distinct genetic clusters corresponding to Gombe National Park (GNP) and the Greater Mahale Ecosystem (GME). The absence of admixed individuals suggests complete interruption of gene flow between the two ecosystems in recent years. However, a high level of gene flow appeared to be maintained within each ecosystem with no clear structure identified by Bayesian cluster analyses. Despite increasing anthropogenic pressures, Tanzanian chimpanzees have maintained high genetic diversity with no evidence of inbreeding at any sites and a greater mitochondrial DNA diversity within GNP. Restoring or strengthening connectivity between GNP and northern populations (i.e. Burundi) and maintaining connectivity within the GME through the protection of key areas for chimpanzee movements would help to safeguard genetic diversity and is of high significance for the species long term survival.

Keywords: Conservation genetics, great apes, gene flow, gene diversity, microsatellites, mitochondrial DNA

1. Introduction

Species are disappearing at an unprecedented rate with destruction of natural habitats and hunting representing the primary drivers (Lewis and Maslin, 2015; Pimm et al., 2014). The creation of protected areas is essential to reducing extinctions but by itself will not secure the conservation of biodiversity. A critical aspect of biodiversity conservation requires identifying, maintaining, and possibly enhancing connectivity between protected habitat patches (Rudnick et al., 2012). Genetic exchanges are vital to population persistence, not only preventing the deleterious effects of inbreeding and genetic drift (Frankham, 2015, 2005), but also providing opportunities to mitigate the negative impacts of new climatic and environmental pressures (Bijlsma and Loeschcke, 2005; Jump et al., 2009). Hence, quantifying genetic diversity and assessing of the amount of gene flow among populations represent key information for conservation planning (Frankham et al., 2011).

Chimpanzees are part of the ~30 000 species facing extinction (IUCN, 2020). Habitat loss (e.g. Junker et al., 2012; Kühl et al., 2017), poaching (e.g. McLennan et al., 2012; Strindberg et al., 2018) and infectious disease (Keele et al., 2009; Walsh et al., 2003) have all been documented to threaten chimpanzees' long-term survival. Tanzania is home to ~2 700 chimpanzees (Moyer et al., 2006), most of which are found at low density and outside of national parks (Piel and Stewart, 2014). Forest conversion to agricultural land, unsustainable timber extraction, and human settlement expansion are threatening the future of Tanzania's chimpanzees (Lasch et al., 2011; TAWIRI, 2018). Historically, two national parks were created to protect part of their distribution: Gombe National Park (GNP) was established in 1968 and now protects ~100 chimpanzees (Foerster et al. 2016, this study), while Mahale Mountains National Park (MMNP), which was created in 1985, is home to ~235 chimpanzees (Chitayat et al., 2021). The latter is part of the Greater Mahale Ecosystem (GME), an area of 18 000 km^2 estimated to host ~90% of Tanzania's chimpanzee population (Kano et al., 1999; Nakamura et al., 2013; Piel and Stewart, 2014; Plumptre et al., 2010; Yoshikawa et al., 2008). This mosaic ecosystem is mostly comprised of miombo woodland interspersed with riverine forest and is one of the driest places where chimpanzees occur (Moore, 1992). Across the GME, chimpanzees live at extremely low densities (range: 0.01 – 1.5) and have correspondingly large home ranges (Kano, 1972; Moore and Vigilant, 2014; Ogawa et al., 2007). These extraordinary patterns are logistically challenging to those trying to monitor the free-ranging populations of Tanzania's chimpanzees. To help protect the remaining chimpanzees, it is crucial to understand how genetic diversity is spatially distributed and maintain connectivity between populations.

Initial studies on gene flow and genetic diversity of Tanzanian chimpanzees have provided contrasting findings regarding connectivity between populations. Analysis of mitochondrial sequences of 138 fecal samples collected across western Tanzania revealed no shared haplotypes between GNP and other areas, although haplotypes were shared between GME chimpanzees and individuals from Lwazi, the southern part of their distribution, located 200 km further south (Inoue et al., 2011). Inoue et al. (2011) concluded that the Malagarasi River, a pre-rift time tributary of the Congo river (Kullander and Roberts, 2011) running between the GME and GNP (Figure 4.1), represented a barrier to chimpanzee movement, limiting gene flow. They also reported a low genetic differentiation index across the GME, suggesting the ecosystem was a single population and proposed historical chimpanzee dispersal from the southern population (i.e. Lwazi). However, later analyses revealed mitochondrial DNA haplotypes are shared between chimpanzees in GNP and the GME (Piel et al. 2013). Piel et al. (2013) also reported circumstantial evidence that chimpanzees cross the Malagarasi river using natural, shallow fords. Chimpanzees in GNP and northern GME are also infected with closely related strains of simian immunodeficiency virus (SIVcpz) (Rudicell et al., 2011), which suggests that the river does not form a complete barrier to chimpanzee movement. Further analysis found no SIVcpz positive infections in over 400 samples collected across the southern GME, which suggest potential barriers within the GME (Piel et al. 2013). Whether a large refugee settlement – Mishamo - established in the 1980s in the middle of the ecosystem hinders chimpanzee gene flow across the GME is unknown (Moyer et al., 2006; Rudicell et al., 2011). The Lugufu river, which runs through the middle of the ecosystem, may also limit chimpanzee movement between the northern and southern GME populations (Piel and Stewart, 2014). Given the increasing pressure on chimpanzee habitat from settlement expansion and conversion to agriculture (Moyer et al., 2006; Piel and Stewart, 2014), clarifying connectivity and maintaining genetic diversity is vital to the species' long term survival.

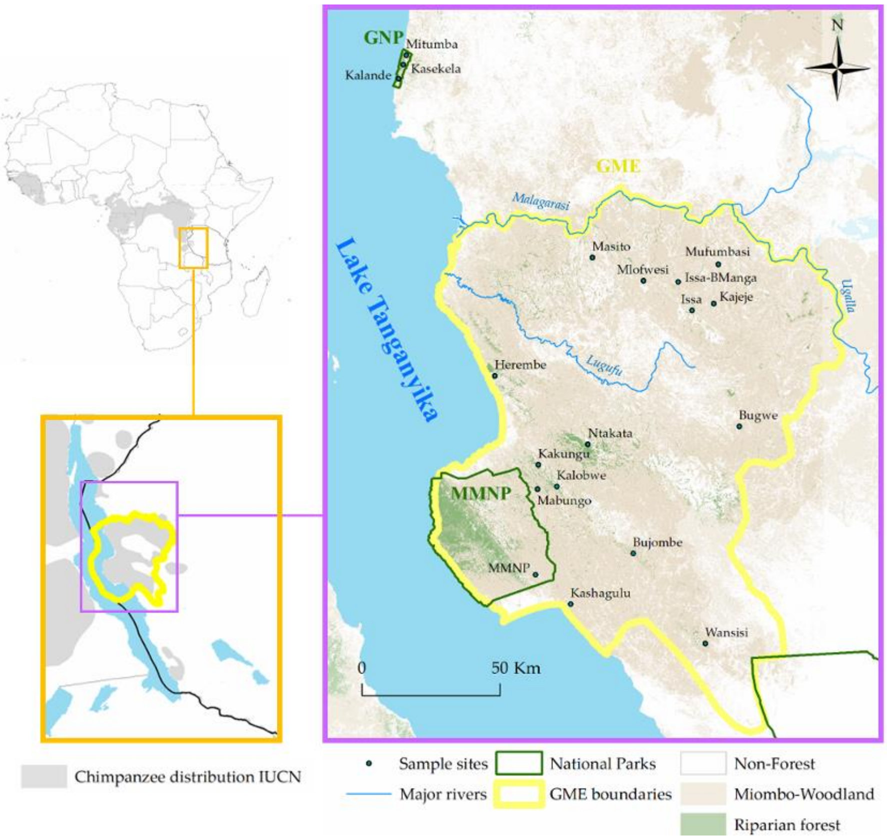
In this study, we aimed to clarify the population genetic structure and examined the genetic diversity of chimpanzees across Tanzania by using both mitochondrial control region sequences and genotypes from 10 microsatellite loci. Specifically, our objectives were to: (1) detect historical or current connectivity between GNP and the GME: from previous studies, we hypothesized that historical gene flow occurred between the two ecosystems but that the two populations are now genetically isolated from one another, (2) investigate potential genetic structure within the GME: here we predict some structuring within GME due to potential barriers to movement and (3) assess genetic diversity within those ecosystems, i.e., is there any evidence of inbreeding that could impact on the long-term viability of this population?

2. Materials and Methods

2.1. Samples

We analysed 234 faecal samples from 16 different sampling locations within the GME (Figure 4.1). We collected fresh samples opportunistically on transects and reconnaissance walks during a series of surveys led by the Greater Mahale Ecosystem Research and Conservation Project (GMERC) from 2011 to 2019. For each sample, approximately 15g of chimpanzee feces was collected into a tube containing 15-20ml of RNAlater (Ambion) and frozen on site at approximately -20°C from the day of collection. We mailed samples monthly to the Hahn laboratory at the Department of Microbiology, University of Pennsylvania, USA, where they were then stored at −80°C until analysis.

We also included genotypes from 135 individuals from GNP. Samples collected from 2002 were genotyped for previous analyses (Barbian et al., 2018; Keele et al., 2009) and updated with samples collected up to 2019. For the purposes of this study, the three GNP chimpanzee communities (i.e. Mitumba, Kasekela and Kalande) were used as representative "sample sites"; GNP and GME are hereafter referred to as ecosystems.



	Sample	Ind.
GNP	-	135
Mitumba	-	34
Kasekela	-	82
Kalande	-	19
GME	234	156
Masito	15	10
Mlofwesi	8	4
Issa – BManga	14	11
Mufumbasi	12	7
Issa	19	13
Kajeje	17	12
Herembe	14	9
Ntakata	25	18
Kakungu	10	6
Mabungo	21	16
Kalobwe	15	11
Bugwe	14	9
MMNP	11	8
Bujombe	10	3
Kashagulu	14	9
Wansisi	15	10

Figure 4.1: Distribution and location of faecal samples. Ind.: corresponding number of individual chimpanzees used for analyses

2.2. Molecular techniques

2.2.1. DNA extraction

We extracted faecal DNA using the QIAamp Stool DNA Mini kit (Qiagen, Valencia) as described in Keele et al. (2006). Briefly, 1.5 ml of fecal RNAlater mixture was resuspended in stool lysis buffer, clarified by centrifugation, reacted with an InhibitEx tablet (Qiagen, Valencia, CA), treated with proteinase K, and passed through a DNA binding column. Bound DNA was finally eluted in 200 µl elution buffer.

2.2.2. mtDNA sequencing

We amplified a 498bp fragment of the mitochondrial hypervariable D-loop control region 1 (HV1) by Polymerase Chain Reaction (PCR) using the primers L15997 (5′-CACCATTAGCACCCAAAGCT-3′) and H16498 (5′-CCTGAAGT AGGAACCAGATG-3′). PCR conditions were the same as for mtDNA amplification (Morin et al., 1994) except that an annealing temperature of 55°C was used and 55 amplification cycles were performed.

We assembled and aligned the resulting sequences with Mega 7.0.26 (Kumar et al., 2016), along with georeferenced sequences from previous studies (Keele et al., 2006; Liu et al., 2008; Rudicell et al., 2011).

2.2.3. Microsatellite genotyping

We amplified 10 polymorphic autosomal microsatellite loci (Table S4.1) following the MiSeq-based approach developed by Barbian et al. (2018). Loci were amplified in one-step multiplex reaction using cycling conditions described in Barbian et al. (2018). For each sample, three replicate PCR reactions were combined in equal volume and diluted in nuclease-free sterile water (1:10) prior to MiSeq sequencing. Details about sequencing and data analysis pipeline using CHIIMP can be found in Barbian et al. (2018). Homozygous alleles were confirmed by sequencing at least two independent PCR amplicons. All samples with less than 8 loci confirmed were excluded from further analyses. In contrast with previously established methods, this approach can detect alleles of similar size that differ in their sequence. To be able to differentiate each allele and to fit the required integer input format of most population genetic software, we used sequential index numbers as identifiers. We chose microsatellites as opposed to single nucleotide repeats (SNPs) for our study because data were already available for GNP. Furthermore, microsatellites have been shown to perform comparably to SNPs in estimates of population genetic structure (Lemopoulos et al., 2019).

2.3. Dataset preparation

Given non-invasive sampling of unhabituated chimpanzees across the GME, some individuals may have been sampled more than once. We conducted an identity analysis in Cervus 3.0.7 (Kalinowski et al., 2007) to distinguish individuals. Genotypes that mismatched at one or two loci were re-examined for possible genotyping errors or ***allelic dropout***. We calculated the probability of identity pID and pIDsib (Waits et al., 2001) for each putative match in Cervus and used it to ensure that our loci could reliably discriminate individuals (e.g. pID < 0.0001) before merging the data into consensus genotypes. From the 234 samples collected across the GME, we identified 156 individuals.

The presence of related individuals can increase the signal of genetic differentiation. We thus calculated pairwise estimates of relatedness for all individuals (GNP and GME) using Coancestry 1.0.1.9 (Wang, 2011). We used 1000 bootstrap permutations to estimate relatedness at 95% confidence intervals. We excluded 62 individuals (61 from GNP and 1 from the GME) with a relatedness index above 0.75 (Mitchell et al., 2015) based on the triadic likelihood estimator (Wang, 2007). We used data for the remaining 229 unrelated individuals for subsequent analyses on population genetic structure and kept all individuals (291) for genetic diversity analyses.

We tested for the presence of possible ***null alleles***, large ***allelic dropout*** or scoring error due to ***stuttering*** using the program Micro-checker 2.2.3 (Van Oosterhout et al., 2004). None of the loci showed evidence of genotyping error across GNP and the GME. We also tested for ***linkage disequilibrium*** (LD) and deviation from ***Hardy-Weinberg equilibrium*** (HWE) between all pairs of loci in Genepop 4.7.5 (Rousset, 2008). We observed no deviation from HWE and no evidence of LD after ***sequential Bonferroni correction*** when GNP and the GME were analysed separately. We therefore included all loci for further analyses.

2.4. Population genetic analysis

2.3.1. Mitochondrial control region

We constructed a Median-joining haplotype network (Bandelt et al., 1999) using PopART 1.7 (Leigh and Bryant, 2015). We estimated measures of molecular diversity (***haplotype diversity*** (h), ***mean pairwise sequence difference*** (MPD) and ***nucleotide diversity*** (π)) using ARLEQUIN 3.5.2.2 (Excoffier and Lischer, 2010).

We also performed analysis of molecular variance (AMOVA) (Excoffier et al., 1992) in ARLEQUIN to estimate the variance between and within GNP and GME samples, with individuals grouped by sample site within these two areas. The obtained degree of genetic differentiation for haplotypic data (φ-statistics, analogous to Wright's ***F-statistics*** (Wright, 1943)) is calculated using information on the allelic content of haplotypes, as well as their frequencies (Excoffier et al., 1992). We subsequently investigated population structure using BAPS 6.0 (Cheng et al., 2013; Corander et al., 2003). We performed genetic mixture analyses with an upper bound of K = 19 and without prior information on geographic location. Results from mixture clustering were used to determine the optimal number of clusters, which were used to perform an admixture analysis.

2.3.2. Microsatellites

We computed general statistics of microsatellite diversity for each sample site and among GNP and the GME. Microsatellite number of alleles (Na), ***rarefied allelic richness*** **(Ar)**, ***expected and observed heterozygosity*** (H_e and H_o, respectively) and ***inbreeding coefficients*** **(F_{IS})** were obtained using the R package diveRsity 1.9.90 (Keenan et al., 2013).

We next examined hierarchical partitioning of genetic variation within and between populations and between ecosystems using analysis of molecular variance (AMOVA) as implemented in the software ARLEQUIN (Excoffier and Lischer 2010). Estimates of pairwise F_{ST} values were obtained using diveRsity 1.9.90 with significance of deviations from zero assessed using 1 000 bootstrap steps to generate 95% confidence intervals (Keenan et al., 2013). As recommended (Meirmans and Hedrick, 2011), we also calculated **standardized F_{ST} (F'_{ST})** as it is most suited for microsatellite loci due to their high polymorphism. Mantel tests were performed in GenAlex (Peakall and Smouse, 2012) to examine correlation between genotypic and geographic (Euclidean) distances.

To detect population structure, we ran admixture models in STRUCTURE v2.3.4 (Pritchard et al., 2000) without a priori assignment of samples to populations. Because STRUCTURE tends to underestimate the number of contributing populations when using unbalanced sample sizes, we used Wang (2017) recommendations and set the population-specific ancestry prior, decreased the initial α to 1/K and used the uncorrelated allele frequency model. We conducted 10 independent runs for each assumed number of clusters (K) from 1 to 19 (e.g. number of sample sites). We used a burn-in of 10,000 and 100,000 Markov Chain Monte Carlo (MCMC) iterations. The independent runs of each cluster were merged and visualized using the R package Pophelper 2.3 (Francis, 2017). Optimal K values were determined in Pophelper using the log probability of the data [ln Pr (X|K)] (Pritchard et al., 2000) and the ad hoc statistic ΔK based on the rate of change in the log probability (Evanno et al., 2005). To investigate substructure, main clusters were subsequently analysed using the same method. As all individuals were available for GNP communities, Wang (2017) recommendations were not applied for cluster only comprising GNP. We also performed a principal component analysis (PCA) using the R package Adegenet 2.1.1. (Jombart, 2008) to visualize the genetic variability across Tanzania and within both ecosystems.

3. Results

3.1. Mitochondrial control region

We identified 20 different mtDNA HV1 haplotypes with 38 variable sites from 293 individuals sampled across GNP and the GME (two samples failed to amplify). Of these, four haplotypes were shared between the GME and GNP, nine were specific to GNP and seven were specific to the GME.

Although the majority of haplotypes (16 out of 20) were specific to either GNP or the GME, no geographical partitioning appeared in the Median-joining haplotype network with GNP and the GME clustering together either by haplotype sharing or sequence similarity (Figure 4.2). A small number of mutational steps (1-4) were observed between each haplotype except for UG59 which diverged by 7 mutations (Figure 4.2). We observed two predominant haplotypes (GM7 and MH32) shared by two third of the individuals sampled within GME while a balanced distribution was found within GNP (Figure 4.2; Table S4.2).

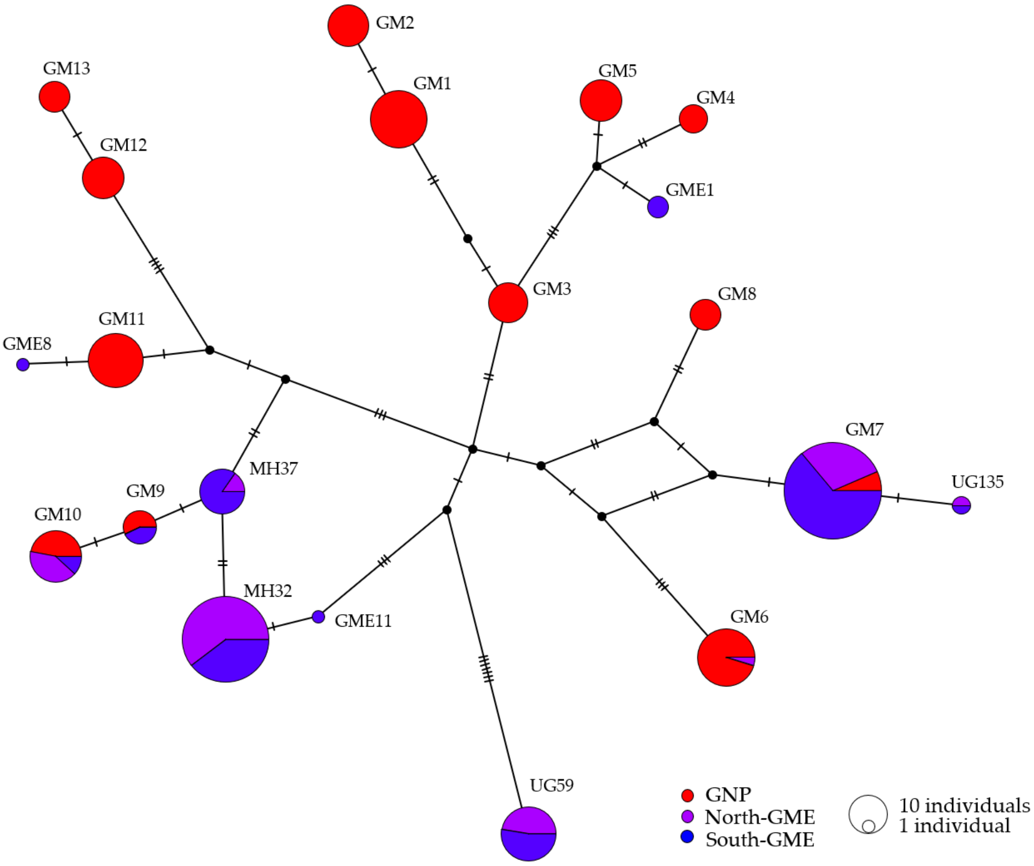


Figure 4.2: Median-joining haplotype network of chimpanzee mitochondrial HV1 sequences. Haplotypes colours represent the geographic repartition. Hash marks on the haplotype edges indicate individual mutational steps.

Haplotype diversity was significantly higher in GNP than in the GME (P_H <0.01, two-tailed Mann-Whitney U test). There was no significant difference between GNP and the GME for Nucleotide diversity ($P_{SD} = 0.261$, two-tailed Mann-Whitney U test) and Mean pairwise difference ($P_{MPD} = 0.211$, two-tailed Mann-Whitney U test). Among all sample sites, haplotype diversity was highest in Kalande (H = 0.985), whilst nucleotide diversity was highest in Kalobwe (SD = 0.019). Issa-BManga had the lowest haplotype and nucleotide diversity (H = 0.200, SD = 0.001) (Table S4.3).

Results from the AMOVA revealed that most of the mtDNA genetic variation (76.12%) was found within sample sites (Table S4.4). Genetic variation between GNP and the GME accounted for 16.19% of the total variation. The remaining 7.69% was found among sample sites within ecosystems (i.e. GNP and GME). The fixation index between ecosystems was low ($\varphi_{CT} = 0.162$) but significantly different from zero (p<0.0001). The global φ_{ST} value for the 19 sample sites across Tanzania was 0.239 and was significantly different from zero (p<0.0001).

A similar pattern was observed within GNP and the GME with most of the variation detected within sample sites (Table S4.4). No mtDNA structuring was detected within GNP ($\varphi_{ST} = 0.000$; p-value = 0. 0.459), whereas significant structuring was found between sample sites within the GME ($\varphi_{ST} = 0.137$; p-value = <0.0001). Only 1.36% of the genetic variance was attributed to differences between the north and south of the GME and the fixation index did not significantly differ from zero ($\varphi_{CT} = 0.014$; p-value = 0.2268).

Mixture analyses using BAPS indicated that the data were optimally described by K = 10 clusters (highest Log likelihood -901.5562). Although some clusters were mainly found in GNP or in the GME, clusters did not sort by geographic location (Figure 4.3). This absence of a clear geographical pattern also held true when K=2 clusters was used (in accordance with the two main areas) (Figure 4.3).

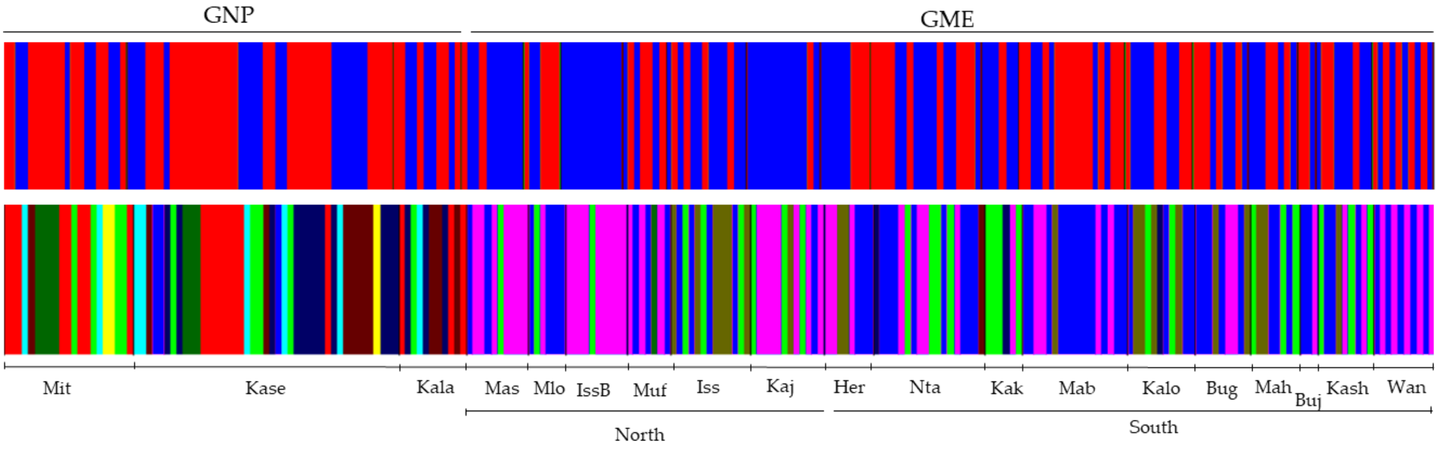


Figure 4.3: Results of individual clustering analyses for mitochondrial data using BAPS for both K=2 and K=10 analyses. Vertical bars represent individuals with different colours corresponding to different inferred cluster. Mit: Mitumba; Kase: Kasekela; Kala: Kalande; Mas: Masito; ; Mlo: Mlofwesi; Her: Herembe; IssB : Issa-Bmanga; Muf: Mufumbasi; ; Iss: Issa; Kaj: Kajeje; Nta: Ntakata;

Kak: Kakungu; ; Mab: Mabungo; Kalo: Kalobwe; Bug: Bugwe; Mah: MMNP; Buj: Bujombe; Kash: Kashagulu; Wan: Wansisi

3.1. Microsatellites

Overall genetic diversity estimates did not differ significantly between GNP and the GME (P_{Na} = 0.835, P_{Ar}=0.943, P_{Ho} = 1.000 ,P_{He} = 0.933, 2-sample t-test). We observed no evidence of inbreeding at any sites (as indicated by the lower 95% confidence interval of F_{IS} never above 0) (Table S4.5).

Most of the variation in microsatellite allele frequencies was found within sample sites, both across GNP and the GME and within each ecosystem (Table S4.6). Allele frequency variation between GNP and the GME accounted for 9.04% of the total variation. Only 0.80% of the total variation found within the GME was attributed to north-south separation of the ecosystem. Fixation indices were significant for all partitions.

Indices of genetic differentiation between sample sites ranged from 0 to 0.180 for F_{ST} and from 0 to 0.620 for F'_{ST} (Figure S4.1). The lower 95% confidence interval indicated significant population differentiation between GNP communities and all GME samples sites for both F_{ST} and F'_{ST}. GNP communities were all significantly different from one another based on the latter index, although Mitumba and Kalande did not show significant differentiation for F_{ST}. Within the GME, 43 and 54 out of 120 sample site comparisons showed significant differentiation for F_{ST} and F'_{ST}, respectively (Figure S4.1).

We found a pattern of isolation by distance (IBD) across all sample sites with significant correlation between F_{ST} and geographic distances (Mantel test: R = 0.626, P <0.001). However, this pattern was not detected within GNP (Mantel test: R = 0.039, P = 0.560) or within the GME (Mantel test, R = 0.141, P = 0.150) (Figure S4.2).

The STRUCTURE analysis that specified K=2 correctly assigned individuals to either GNP or GME clusters with high probability (mean estimate membership coefficient q= 0.99) (Figure 4.4). The highest proportion of admixture was 29% for one individual sampled in Wansisi. The PCA corroborated STRUCTURE results and clearly separated GNP and the GME along the first axis. The first component explained 6.3% of the total variation while the second axis represented 2.4% of the variation.

We repeated STRUCTURE analyses within each cluster and found no clear evidence of substructure (Figure S4.3). Within GNP, K = 3 was favoured by Evanno's method but the highest Log likelihood was found for K = 1. Nonetheless, neither STRUCTURE nor the PCA revealed any clear structuring (Figure S4.3 - GNP). In the GME, both Evanno's method and the Log likelihood favoured K = 2 but no clear geographic pattern emerged from either STRUCTURE or PCA analyses (Figure S4.3 – GME).

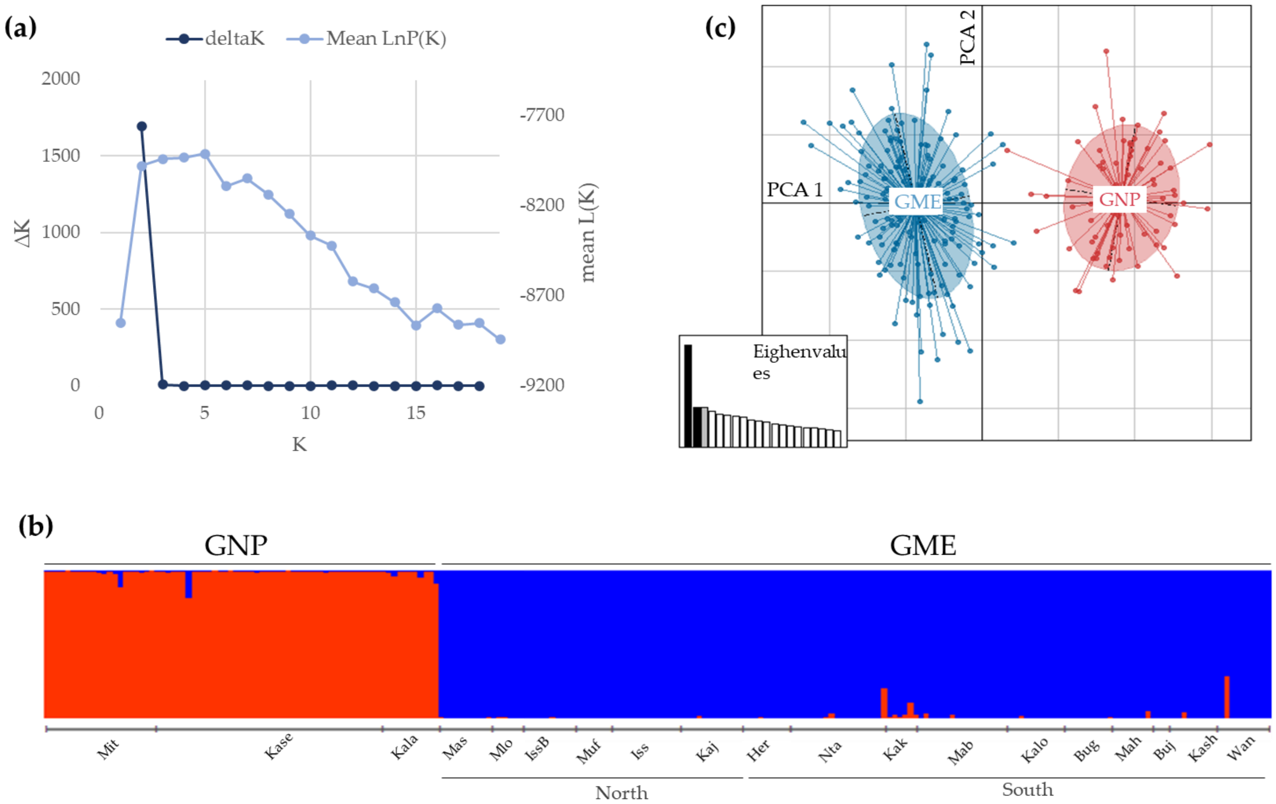


Figure 4.4: Results of individual clustering analyses. **(a)** Plot of mean L(K) and ΔK over 10 runs for each K value. **(b)** Bar plot created from STRUCTURE runs at K=2. Each vertical bar represents an individual with colours indicating the proportion of each individual assigned to each inferred cluster. **(c)** PCA plot of the 10 microsatellite loci for the entire dataset. Eigenvalues corresponding to the represented components are filled in black. Points represent genotypes; Populations are labelled inside their 95% inertia ellipses

4. Discussion

Despite extensive research into two focal communities – GNP and MMNP – we know relatively little about the conservation status of most of Tanzania's chimpanzees. Here, we built on previous genetic studies to investigate the potential connectivity and genetic diversity of Tanzanian chimpanzees. By incorporating new non-invasive samples across a large spatial scale and analysing two molecular markers, we were able to resolve previous contrasting findings. We confirmed historical chimpanzee movement across GNP and the GME, which today represent two populations completely isolated from one another. We found no clear geographic pattern of genetic differentiation within the GME, suggesting a high level of gene flow throughout the ecosystem. Finally, we found no evidence of inbreeding at any sites and a greater mtDNA genetic diversity within GNP compared with the GME.

Connectivity between GNP and the GME

No clear geographic pattern emerged from mtDNA haplotypes while clear clusters corresponding to GNP and the GME were revealed using microsatellite genotypes. This contrasting pattern could be explained by the different modes of inheritance and mutation rates of our genetic markers. In chimpanzees, as with most animals, mtDNA is inherited maternally, meaning that it is passed down from mothers to their offspring, while microsatellite genotypes are inherited from both parents. With female chimpanzees typically dispersing from their natal community and male typically being philopatric (e.g. Boesch and Boesch-Achermann, 2000; Michio Nakamura et al., 2015), we expect mtDNA to spread over longer distances and to see a greater genetic structure in microsatellite genotypes. Microsatellite markers also have higher evolutionary rates and are more likely to reveal contemporary genetic patterns while mtDNA are useful to reveal recent historical events (Frankham et al., 2004). The lack of geographic structuring in mtDNA haplotypes was therefore expected within GNP and supports the hypothesis of historical gene flow between GNP and the GME. Microsatellite distinct clusters, on the other hand, indicate a recent interruption of gene flow. The small amount of mtDNA haplotype-sharing between GNP and the GME could be explained by incomplete **lineage sorting**.

Evidence of widespread historic gene flow among eastern chimpanzee populations is well established with shared mtDNA haplotypes across the entire range of the subspecies (Goldberg and Ruvolo, 1997a; Morin et al., 1994). Our pattern of genetic variation across Tanzania is similar to the one reported across the eastern chimpanzee range (Goldberg and Ruvolo, 1997b) with most of the variation found within sample sites. However, our measure of genetic differentiation (global φ_{ST} value of 0.239) is twice as high as the one reported (0.129) by Goldberg and Ruvolo (1997b), which is rather surprising given the smaller scale of our analysis. Greater genetic differentiation observed in our study could be the result of a reduction in gene flow due to increasing anthropogenic pressure on chimpanzee habitats in the 20 years since Goldberg and Ruvolo’s (1997b) study. Nonetheless, given that GNP was the southern sample locality in Goldberg and Ruvolo's (1997b) study, genetic differentiation reported here between the GME and GNP could be greater than genetic differentiation between GNP and more northern populations despite being separated by longer geographic distances. Supporting this hypothesis, a more recent study comparing nine wild chimpanzee populations found higher φ_{ST} between GNP and M-group (from MMNP) than between GNP and three communities sampled in Uganda (Langergraber et al., 2011). Such differentiation could be due to the matrix of human settlements separating GNP and the GME (Pintea, 2007) and long standing geographic barriers (e.g. rivers) reducing the amount of gene flow between the two habitats.

The GNP and GME are indeed separated by more than 50km of flat terrain with sparse gallery forest and a relatively dense human population. Given that chimpanzees in Tanzania are known to select hilly areas with riparian forests (Hernandez-Aguilar, 2006; Kano, 1972; Moyer et al., 2006; Ogawa et al., 2013; Piel and Stewart, 2014), these unsuitable chimpanzee habitats could limit chimpanzee movement. In addition, the Malagarasi river separates GNP and the GME. Circumstantial evidence suggests that chimpanzees can move across the river using a natural, shallow ford (Piel et al., 2013) and there is evidence of historical gene flow across Tanzania (Piel et al.,2013; this study). However, the 100m wide river surely limits gene flow and could be responsible for the higher genetic distance observed between GNP and other Tanzanian populations then GNP and northern populations (i.e. Ugandan sites). Further investigation that includes all eastern chimpanzee haplotypes would allow us to better understand the genetic position of GNP and GME chimpanzees within the species' range.

Genetic structure within the GME

Previous studies proposed that the GME comprised one panmictic population (Inoue et al., 2011; Yoshikawa et al., 2008). However, other studies have highlighted potential barriers limiting chimpanzee movement between northern and southern populations in the GME (Moyer et al., 2006; Piel et al., 2013; Rudicell et al., 2011). Our AMOVA analysis revealed significant differentiation within the GME, however a division north-south of the ecosystem explained less than 2% of the total mtDNA variation and less than 1% of the microsatellite variation (Table S4.4 and S4.6). Pairwise F_{ST} values also indicated significant differentiation between one third of all sample sites, although this should be interpreted with caution given the large sampling error when estimated from small sample sizes (Puechmaille, 2016). A large refugee settlement established in the 80s located in the middle of the GME was hypothesized to separate the ecosystem or at least hinder chimpanzee movement (Moyer et al., 2006; Rudicell et al., 2011). Although the genetic consequences of this relatively recent event are unlikely to be already visible (50 years representing ~2 chimpanzee generations), unsuitable chimpanzee habitats in the area prior to the establishment of this settlement could have hindered chimpanzee movement north-south of the ecosystem (Bonnin et al., 2020). Habitat connectivity modelling revealed narrow corridors allowing gene flow throughout the ecosystem (Bonnin et al., 2020). This could explain the absence of both genetic structuring and genetic isolation by distance within the GME. It is possible that different landscape features have shaped the genetic structure of GME chimpanzees. Future landscape genetic analyses will help to better understand how landscape features are impacting chimpanzee movement. Across the GME, chimpanzees live at extremely low densities and have large home ranges (Moore and Vigilant 2014; Piel and Stewart, unpublished data). These extraordinary patterns may also result in a shift in social structure and consequently, affect population genetic structure. Further analyses using sex-specific markers or conducting separated analyses for each sex would help us to examine the role of sex-specific dispersal patterns.

Genetic diversity

Our data provide no evidence of inbreeding at any sites and even suggest a greater mtDNA genetic diversity within GNP than across the GME. This is surprising given that GNP is much smaller than the GME and is thought to be isolated from other nearby populations (Pintea et al., 2011; Pusey et al., 2007). Morin et al. (1994) reported surprisingly high within-community mtDNA genetic diversity and attributed it to females mediating gene flow. Inoue et al. (2011) also found greater genetic diversity in GNP than in five other sampled Tanzanian habitats. Evidence of Gombe females' preference for genetically dissimilar mates might have played a role in avoiding inbreeding and optimizing genetic diversity (Walker et al., 2016). It is also possible that GNP chimpanzees are not completely isolated and exchange genes with northern populations. With GNP chimpanzees sharing mtDNA haplotypes reported up to Uganda (Goldberg and Ruvolo, 1997a; Inoue et al., 2011; Morin et al., 1994). GNP may still be part of a large population including Burundi, Rwanda, Uganda and DRC. Females periodically arrive in GNP from unknown origin (Walker et al., 2016). Although the park is primarily surrounded by anthropogenic landscapes, chimpanzees have been reported crossing highly fragmented landscapes in other parts of their range (McCarthy et al., 2015). On the other hand, the unusual geographic location of GME chimpanzees - which marks the southeastern limit of *Pan* distribution may also be responsible for the lower mtDNA diversity observed (Lester et al. in press). With Lake Tanganyika separating them from western populations and the Malagarasi river and unsuitable habitats limiting gene flow from the north, new alleles coming from neighbouring populations are less likely to reach the GME chimpanzees. It is also possible that due to the opportunistic nature of sampling within the GME, some genetic variability was missed. Contrary to GNP, for which we had access to genotype data for nearly all individuals, we estimate that we sampled less than 10% of chimpanzees present in the GME. Larger sampling would confirm the pattern observed. Combining our data with published haplotypes reported by Inoue and colleagues (2011) would have increased our sample size and would have allowed the inclusion of Lwazi, the southern part of chimpanzee distribution in Tanzania. However, Inoue and colleague's sequences were 167bp shorter and missing mutation sites revealed in our haplotypes, thus, we decided not to include them in our analysis.

5. Conclusion

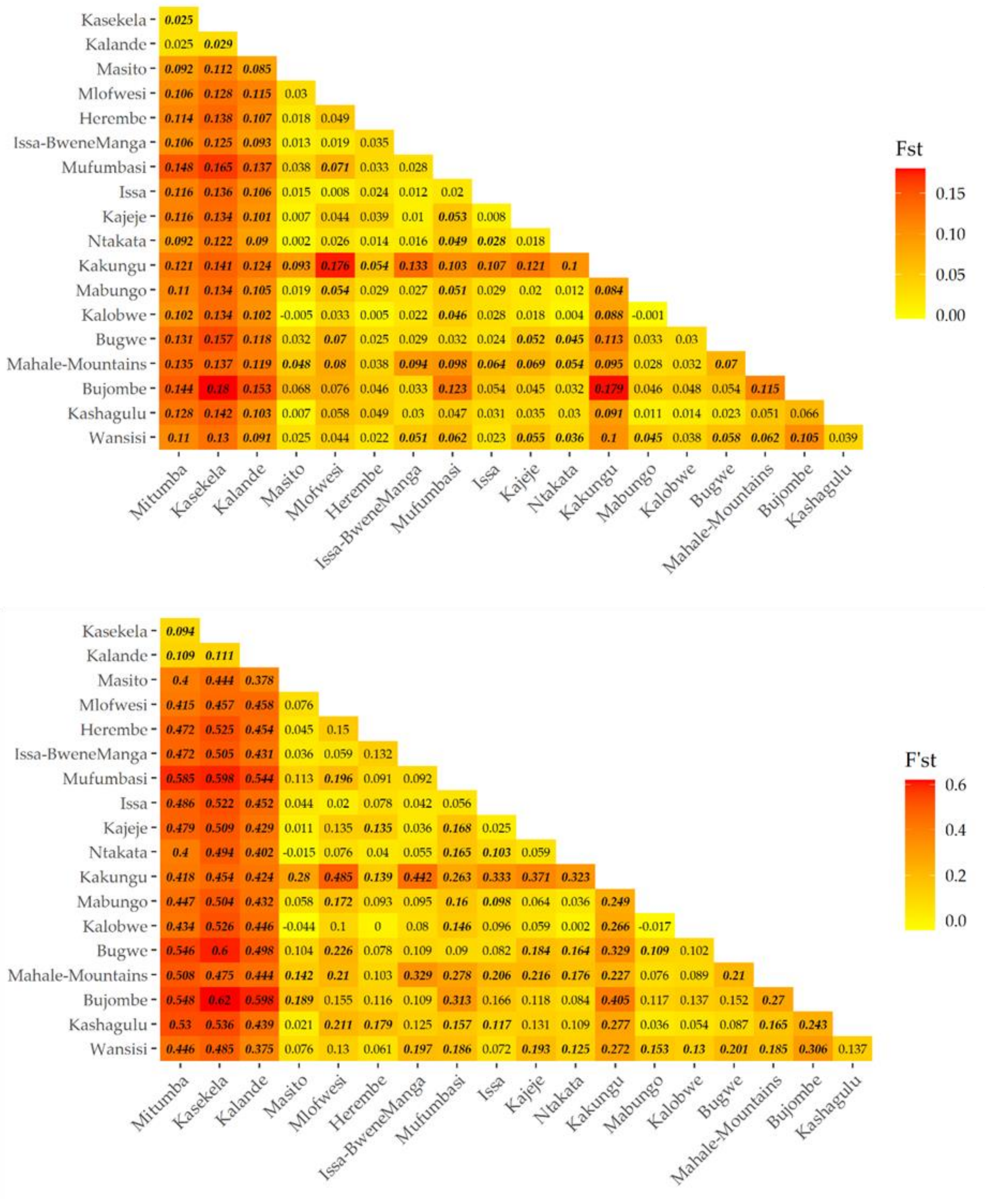
Our results provide additional evidence for historical gene flow between GNP and the GME, which now represent two distinct genetic clusters completely isolated from one another. The current population structure supports the designation of GNP and GME as two managements units, in that they represent the logical unit for population monitoring and demographic study (Moritz, 1994). In addition to a complete loss of gene flow between the two areas, chimpanzees in the GME seems to be adapted to a very different type of habitat, ranging across larger home ranges in a more open and dry landscape. However, the evidence of historical gene flow through mtDNA haplotype sharing suggests that habitat restoration could allow the two populations to exchange migrants again.

Despite loss of connectivity between the two ecosystems and increasing anthropogenic pressure on chimpanzee habitat (Piel et al., 2015a; Piel and Stewart, 2014; TAWIRI, 2018; Yoshikawa et al., 2008), we found high levels of gene flow and genetic diversity within both the GNP and the GME. Given the long generation time of chimpanzees, the genetic consequences of recent landscape changes may not be detectable yet. If the GNP is also isolated from populations to the north, the population of ~100 chimpanzees remains vulnerable to inbreeding depression. Restoring or strengthening connectivity between GNP and northern populations could help to safeguard their genetic diversity and long-term viability. With the GME hosting over 90% of Tanzania's chimpanzee population, protecting remaining suitable habitats and maintaining connectivity across this vast ecosystem is of key importance to maintain a large viable population of chimpanzee. By focusing conservation effort on key corridors highlighted by habitat connectivity models (Bonnin et al., in press), we can best maintain gene flow and balance needs of communities and chimpanzees.

Acknowledgments

We are grateful to TAWIRI, COSTECH, and the Uvinza, Mpanda and Kigoma Districts for permission to conduct research in western Tanzania. The Nature Conservancy, Frankfurt Zoological Society, and the Jane Goodall Institute provided substantial financial, logistical, and administrative support. We are also extremely grateful to JGI and GMERC field assistants in Tanzania. The UCSD/Salk Center for Academic Research and Training in Anthropogeny (CARTA) for long-term support of GMERC. Many thanks to Dr Begoña Martínez-Cruz and Adeline Morez for helpful discussions on population genetic analyses.

Supplementary Materials



	Mitumba	Kasekela	Kalande	Masito	Mlofwesi	Herembe	Issa-BweneManga	Mufumbasi	Issa	Kajeje	Ntakata	Kakungu	Mabungo	Kalobwe	Bugwe	Mahale-Mountains	Bujombe	Kashagulu
Kasekela	***0.025***																	
Kalande	0.025	***0.029***																
Masito	***0.092***	***0.112***	***0.085***															
Mlofwesi	***0.106***	***0.128***	***0.115***	0.03														
Herembe	***0.114***	***0.138***	***0.107***	0.018	0.049													
Issa-BweneManga	***0.106***	***0.125***	***0.093***	0.013	0.019	0.035												
Mufumbasi	***0.148***	***0.165***	***0.137***	0.038	***0.071***	0.033	0.028											
Issa	***0.116***	***0.136***	***0.106***	0.015	0.008	0.024	0.012	0.02										
Kajeje	***0.116***	***0.134***	***0.101***	0.007	0.044	0.039	0.01	***0.053***	0.008									
Ntakata	***0.092***	***0.122***	***0.09***	0.002	0.026	0.014	0.016	***0.049***	***0.028***	0.018								
Kakungu	***0.121***	***0.141***	***0.124***	***0.093***	***0.176***	***0.054***	***0.133***	***0.103***	***0.107***	***0.121***	***0.1***							
Mabungo	***0.11***	***0.134***	***0.105***	0.019	***0.054***	0.029	0.027	***0.051***	0.029	0.02	0.012	***0.084***						
Kalobwe	***0.102***	***0.134***	***0.102***	-0.005	0.033	0.005	0.022	***0.046***	0.028	0.018	0.004	***0.088***	-0.001					
Bugwe	***0.131***	***0.157***	***0.118***	0.032	***0.07***	0.025	0.029	0.032	0.024	***0.052***	***0.045***	***0.113***	0.033	0.03				
Mahale-Mountains	***0.135***	***0.137***	***0.119***	***0.048***	***0.08***	0.038	***0.094***	***0.098***	***0.064***	***0.069***	***0.054***	***0.095***	0.028	0.032	***0.07***			
Bujombe	***0.144***	***0.18***	***0.153***	0.068	0.076	0.046	0.033	***0.123***	0.054	0.045	0.032	***0.179***	0.046	0.048	0.054	***0.115***		
Kashagulu	***0.128***	***0.142***	***0.103***	0.007	0.058	0.049	0.03	0.047	0.031	0.035	0.03	***0.091***	0.011	0.014	0.023	0.051	0.066	
Wansisi	***0.11***	***0.13***	***0.091***	0.025	0.044	0.022	***0.051***	***0.062***	0.023	***0.055***	***0.036***	***0.1***	***0.045***	0.038	***0.058***	***0.062***	***0.105***	0.039

	Mitumba	Kasekela	Kalande	Masito	Mlofwesi	Herembe	Issa-BweneManga	Mufumbasi	Issa	Kajeje	Ntakata	Kakungu	Mabungo	Kalobwe	Bugwe	Mahale-Mountains	Bujombe	Kashagulu
Kasekela	***0.094***																	
Kalande	***0.109***	***0.111***																
Masito	***0.4***	***0.444***	***0.378***															
Mlofwesi	***0.415***	***0.457***	***0.458***	0.076														
Herembe	***0.472***	***0.525***	***0.454***	0.045	0.15													
Issa-BweneManga	***0.472***	***0.505***	***0.431***	0.036	0.059	0.132												
Mufumbasi	***0.585***	***0.598***	***0.544***	0.113	***0.196***	0.091	0.092											
Issa	***0.486***	***0.522***	***0.452***	0.044	0.02	0.078	0.042	0.056										
Kajeje	***0.479***	***0.509***	***0.429***	0.011	0.135	***0.135***	0.036	***0.168***	0.025									
Ntakata	***0.4***	***0.494***	***0.402***	-0.015	0.076	0.04	0.055	***0.165***	***0.103***	0.059								
Kakungu	***0.418***	***0.454***	***0.424***	***0.28***	***0.485***	***0.139***	***0.442***	***0.263***	***0.333***	***0.371***	***0.323***							
Mabungo	***0.447***	***0.504***	***0.432***	0.058	***0.172***	0.093	0.095	***0.16***	***0.098***	0.064	0.036	***0.249***						
Kalobwe	***0.434***	***0.526***	***0.446***	-0.044	0.1	0	0.08	***0.146***	0.096	0.059	0.002	***0.266***	-0.017					
Bugwe	***0.546***	***0.6***	***0.498***	0.104	***0.226***	0.078	0.109	0.09	0.082	***0.184***	***0.164***	***0.329***	***0.109***	0.102				
Mahale-Mountains	***0.508***	***0.475***	***0.444***	***0.142***	***0.21***	0.103	***0.329***	***0.278***	***0.206***	***0.216***	***0.176***	***0.227***	0.076	0.089	***0.21***			
Bujombe	***0.548***	***0.62***	***0.598***	***0.189***	0.155	0.116	0.109	***0.313***	0.166	0.118	0.084	***0.405***	0.117	0.137	0.152	***0.27***		
Kashagulu	***0.53***	***0.536***	***0.439***	0.021	***0.211***	***0.179***	0.125	***0.157***	***0.117***	0.131	0.109	***0.277***	0.036	0.054	0.087	***0.165***	***0.243***	
Wansisi	***0.446***	***0.485***	***0.375***	0.076	0.13	0.061	***0.197***	***0.186***	0.072	***0.193***	***0.125***	***0.272***	***0.153***	***0.13***	***0.201***	***0.185***	***0.306***	0.137

Figure S4.1: Genetic differentiation index between sample sites. a) F_{ST} (Weir & Cockerham, 1984) b) F'_{ST} (Hedrick, 2005). Italic and bold indicate significant population differentiation (lower 95% confidence interval > 0)

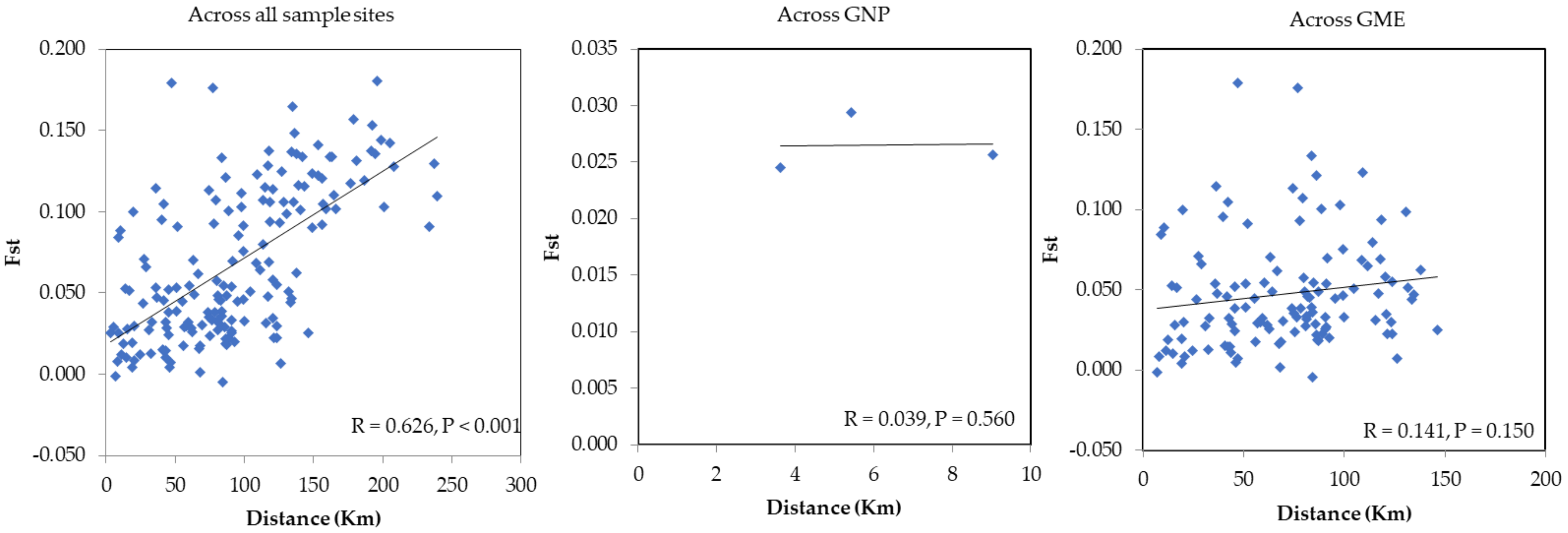


Figure S4.2: Isolation by distance analysis.

Genetic distances plotted against geographic distance for the full dataset and within each ecosystem. Each point represents pairwise comparison between sample. The trend line indicates the least-squares regression estimate. Mantel test results for correlation between genetic and geographic distance are displayed at the bottom of each plot

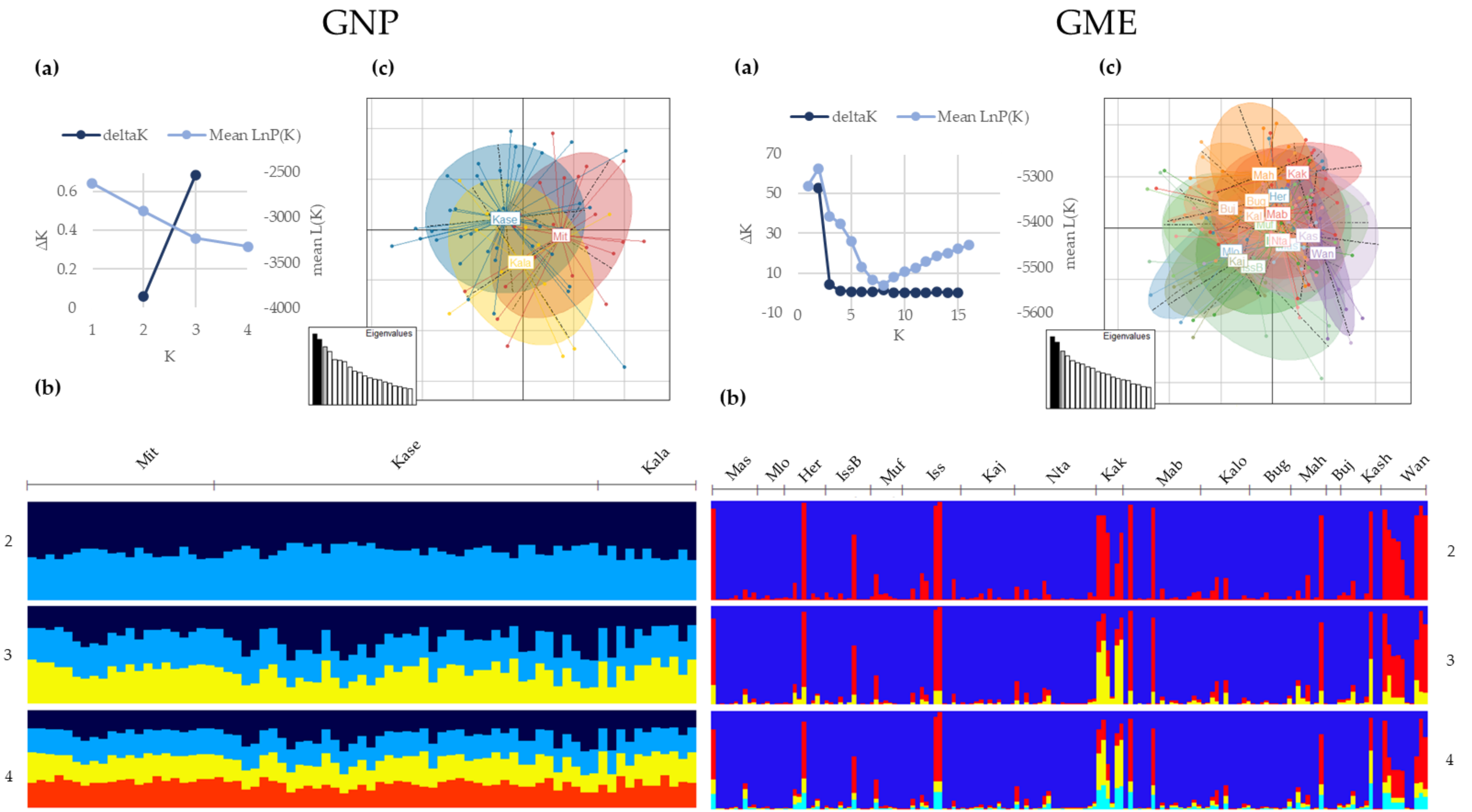


Figure S4.3: Results of individual clustering analyses for GNP and the GME. **(a)** Plot of mean L(K) and ΔK over 10 runs for each K value. **(b)** Bar plot created from structure. Each vertical bar represents an individual with colours indicating the proportion of each individual assigned to each of the inferred cluster. **(c)** PCA plot of the 10 microsatellite loci for the entire dataset. Eigenvalues corresponding to the represented components are filled in black. Points represent genotypes; breeds are labelled inside their 95% inertia ellipses.

Mit: Mitumba; Kase: Kasekela; Kala: Kalande; Bug: Bugwe; Iss: Issa; IssB : Issa-Bmanga; Kaj: Kajeje; Mas: Masito; Mlo: Mlofwesi; Muf: Mufumbasi; Buj: Bujombe; Her: Herembe; Kak: Kakungu; Kalo: Kalobwe; Kash: Kashagulu; Mab: Mabungo; Mah: MMNP; Nta: Ntakata; Wan: Wansisi

Table S4.1: STR loci used for MiSeq genotyping

Locus	Code	Forward primer sequence[a]	Reverse primer sequence[a]	Size range (bp)[b]
D18S536	A	5′-ATTATCACTGGTGTTAGTCCTCTG-3′	5′-CACAGTTGTGTGAGCCAGTC-3′	131-179
D4S243	B	5′-TCAGTCTCTCTTTCTCCTTGCA-3′	5′-TAGGAGCCTGTGGTCCTGTT-3′	194-235
D10S676	C	5′-GAGAACAGACCCCCAAATCT-3′	5′-ATTTCAGTTTTACTATGTGCATGC-3′	155-200
D9S922	D	5′-TCAGAGGACCACTGCCTAAG-3′	5′-CTGATGGGATTTGTGCCTAT-3′	263-307
D2S1326	1	5′-AGACAGTCAAGAATAACTGCCC-3′	5′-CTGTGGCTCAAAAGCTGAAT-3′	232-270
D5s1457	FP1	5′-TAGGTTCTGGGCATGTCTGT-3′	5′-TGCTTGGCACACTTCAGG-3′	91-147
D1s550	FP2	5′-CCTGTTGCCACCTACAAAAG-3′	5′-TAAGTTAGTTCAAATTCATCAGTGC-3′	136-180
D4s2408	FP3	5′-AATAAACTTCAACTTCAATTCATCC-3′	5′-AGGTAAAGGCTCTTCTTGGC-3′	274-298
D11s2002	FP4	5′-CATGGCCCTTCTTTTCATAG-3′	5′-AGTGTGAGCCACCACACCAGC-3′	136-160
D17S974	NMS5	5′-AGACCCTGTCTCAGATAGATGG-3′	5′-TAAAATAGAAAGTGCCCCTCC-3′	188-216

[a] STR loci were amplified as previously described (Keele *et al.* 2009b; Rudicell *et al.* 2010), except for the addition of MiSeq adapters at the 5′ end of both forward (5′-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-3)′ and reverse (5′-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-3′) primers.

[b] All selected loci fell within the size range of the sequencing chemistry (Illumina v2 chemistry, 500 cycle kit) and were thus sequenced without fragmentation using only the forward reads (<400 bp).

Table S4.2: Nucleotide sequence differences and geographic distribution of Tanzanian' chimpanzees mtDNA control region haplotypes

	Nucleotides positions of variables sites																																						Sample sites																			
Haplotypes	**74**	**77**	**93**	**94**	**97**	**144**	**168**	**169**	**176**	**180**	**182**	**184**	**189**	**194**	**208**	**224**	**247**	**260**	**272**	**274**	**275**	**276**	**279**	**285**	**290**	**291**	**292**	**294**	**295**	**296**	**312**	**328**	**345**	**358**	**386**	**401**	**439**	**489**	Mitumba	Kasekela	Kalande	Masito	Mlofwesi	Issa-BManga	Mufumbasi	Issa	Kajeje	Herembe	Ntakata	Kakungu	Mabungo	Kalobwe	Bugwe	MMNP	Bujombe	Kashagulu	Wansisi	Total
GM1	T	A	A	C	C	C	C	T	A	T	C	A	C	C	C	C	A	T	C	C	G	A	T	A	A	T	C	T	C	T	T	C	C	C	A	C	G	C	7	14																		**21**
GM2	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	3																	**11**
GM3	.	.	.	T	C	.	.	C	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	4																	**10**
GM4	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	G	.	.	.	.	.	.	.	C	.	.	T	.	.	.	.	.		4	1																	**5**
GM5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	A	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.		11																		**11**
GM6	.	A	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	C	.	G	.	C	G	.	C	A	.	.	C	.	.	C	.	.	.	.	T	7	13					1													**21**
GM7	.	.	.	.	.	.	.	.	.	.	.	.	T	C	.	.	T	.	.	.	.	.	.	.	G	T	.	.	.	.	.	.	.	.	.	.	.	C		4		2	4		3	3	1	3	7		12	4	5	3	2	3	5	**61**
GM8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	A	.	.	.	.	.	.	A	.	.	.	C	.	.	.	.	.	.	.	.	.	.	3	2	1																	**6**
GM9	C	.	.	.	.	.	.	.	.	.	C	G	C	.	C	.	.	C	.	T	.	.	.	.	A	.	.	T	.	T	C	.	.	.	.	.	.	.	1	2	1									3								**7**
GM10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	4	1	3	1	1			2	3		1					1				**17**
GM11	T	.	.	.	.	T	.	.	.	.	.	A	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	C	.	.	.	C	.	.	.	.	.	.	3	13	3																	**19**
GM12	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	T	.	T	.	T	.	.	4	7																		**11**
GM13	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	3																	**6**
GME1	.	G	.	.	.	C	.	.	.	T	T	.	.	.	.	.	.	T	.	.	A	.	T	.	.	.	C	.	.	.	T	C	T	C	.	C	.	.											1	1		1						**3**
GME8	.	A	.	.	.	T	.	C	.	.	C	.	.	.	.	.	.	C	.	.	G	.	C	.	.	.	A	C	.	C	C	.	C	.	.	.	.	.											1									**1**
GME11	.	.	.	.	.	C	.	.	.	.	.	G	.	.	.	T	.	T	.	T	.	.	.	.	.	.	.	T	.	T	T	.	.	.	.	.	.	.											1									**1**
UG59[a]	.	.	.	.	.	.	T	.	G	.	T	A	.	.	T	C	.	.	.	.	.	.	.	.	.	.	.	.	T	.	.	.	.	T	G	.	A	.								6	1	2			1	4	2	2		1		**19**
UG135[a]	.	.	G	.	.	.	C	.	A	.	.	.	T	.	C	.	T	.	.	C	.	.	.	G	G	.	.	.	C	C	.	.	.	C	A	.	G	.								1			1									**2**
MH32[a]	.	.	A	.	.	.	.	.	.	.	C	G	C	.	.	T	A	.	.	T	.	.	.	A	A	.	.	.	.	T	C	.	.	.	.	.	.	.				7	1	9	3		7	3	3	1	4		2		1	2	5	**48**
MH37[a]	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.						1		1			3	1		2		2		3		**13**
Total																																							**35**	**82**	**19**	**10**	**6**	**10**	**7**	**13**	**12**	**8**	**18**	**6**	**17**	**11**	**9**	**8**	**3**	**9**	**10**	**293***

In red, haplotypes found in GNP; in bleu, haplotypes found in the GME; in black, haplotypes found both in GNP and the GME.

[a] Haplotype already documented in GenBank

* Two samples failed to amplify

Table S4.3: Genetic variability of mtDNA observed in the GNP and the GME and across sample sites

	N	Hp	H	SD	MPD
GNP	**136**	**13**	**0.906 +/- 0.008**	**0.016 +/- 0.008**	**8.158 +/- 3.808**
Mitumba	35	10	0.889 +/- 0.024	0.017 +/- 0.009	8.232 +/- 3.909
Kasekela	82	13	0.893 +/- 0.013	0.016 +/- 0.008	8.114 +/- 3.804
Kalande	19	8	0.895 +/- 0.035	0.015 +/- 0.008	7.649 +/- 3.732
GME	**157***	**11**	**0.754 +/- 0.021**	**0.015 +/- 0.008**	**7.137 +/- 3.365**
Masito	10	3	0.511 +/- 0.164	0.009 +/- 0.005	4.267 +/- 2.309
Mlofwesi	6	3	0.600 +/- 0.215	0.013 +/- 0.008	6.133 +/- 3.399
Issa-BManga	10	2	0.200 +/- 0.154	0.001 +/- 0.001	0.400 +/- 0.403
Mufumbasi	7	3	0.714 +/- 0.127	0.014 +/- 0.008	6.571 +/- 3.535
Issa	13	5	0.756 +/- 0.097	0.018 +/- 0.010	8.795 +/- 4.340
Kajeje	12	4	0.636 +/- 0.128	0.010 +/- 0.006	4.833 +/- 2.537
Herembe	8	3	0.750 +/- 0.097	0.017 +/- 0.010	8.357 +/- 4.333
Ntakata	18	8	0.824 +/- 0.072	0.014 +/- 0.008	6.732 +/- 3.329
Kakungu	6	4	0.800 +/- 0.172	0.010 +/- 0.007	4.800 +/- 2.728
Mabungo	17	3	0.471 +/- 0.118	0.010 +/- 0.006	5.000 +/- 2.557
Kalobwe	11	4	0.764 +/- 0.083	0.019 +/- 0.011	9.055 +/- 4.518
Bugwe	9	3	0.667 +/- 0.132	0.016 +/- 0.009	7.611 +/- 3.922
MMNP	8	4	0.821 +/- 0.101	0.018 +/- 0.011	8.857 +/- 4.574
Bujombe	3	2	0.667 +/- 0.314	0.014 +/- 0.011	6.667 +/ -4.328
Kashagulu	9	4	0.806 +/- 0.089	0.015 +/- 0.009	7.111 +/- 3.685
Wansisi	10	2	0.556 +/- 0.075	0.012 +/- 0.007	5.556 +/- 2.916

Sample size (N), number of haplotypes (Hp), haplotype (gene) diversity (H), nucleotide diversity (SD) and mean pairwise difference (MPD)

* Two samples failed to amplify

Table S4.4: Hierarchical analyses of molecular variation (AMOVA) for mtDNA HVRI

Partition	**Variance components**	**Percentage of variation**	**Fixation Indices**	**p-value**
	Across GNP and GME			
Among ecosystems (φCT)	0.762	16.45	0.164	<0.01
Among sample sites within ecosystems (φSC)	0.305	6.58	0.079	<0.0001
Within sample sites (φST)	3.565	76.97	0.230	<0.0001
	Within GNP			
Among sample sites	0.042	1.03		
Within sample sites (φST)	4.045	98.97	0.010	0.151
	Within GME			
Among regions[b] (φCT)	0.049	1.36	0.014	0.2268
Among sample sites within regions[b] (φSC)	0.448	12.36	0.125	<0.0001
Within sample sites (φST)	3.125	86.28	0.137	<0.0001

[a] Ecosystems referring to GNP and GME

[b] Regions defined as north and south of the GME

Table S4.5: Summary statistics of genetic diversity averaged across 10 microsatellite loci across GNP and the GME

	N	Na	Ar	Ho	He	FIS (LL,UL)
GNP	**136**	**9.6**	**9.320**	**0.800**	**0.780**	**-0.034 (-0.060,-0.007)**
Mitumba	35	7.7	3.520	0.790	0.770	-0.020 (-0.064,0.022)
Kasekela	82	8.7	3.490	0.810	0.750	-0.088 (-0.122,-0.054)
Kalande	19	7.4	3.650	0.780	0.780	-0.002 (-0.103,0.097)
GME	**159**	**9.9**	**9.23**	**0.81**	**0.78**	**-0.039 (-0.064,-0.013)**
Masito	10	6.1	3.59	0.900	0.750	-0.193 (-0.309,-0.107)
Mlofwesi	6	3.6	2.72	0.800	0.650	-0.221 (-0.486,-0.036)
Issa-BManga	11	5.5	3.29	0.790	0.740	-0.067 (-0.201,0.064)
Mufumbasi	7	4.4	3.01	0.810	0.670	-0.207 (-0.391,-0.051)
Issa	13	5.6	3.3	0.790	0.730	-0.077 (-0.179,-0.005)
Kajeje	12	5.2	3.04	0.770	0.720	-0.071 (-0.198,0.041)
Herembe	9	5.9	3.33	0.820	0.720	-0.143 (-0.259,-0.069)
Ntakata	18	6.8	3.57	0.880	0.770	-0.143 (-0.210,-0.081)
Kakungu	6	4.4	2.91	0.740	0.590	-0.256 (-0.467,-0.140)
Mabungo	17	6.6	3.31	0.800	0.730	-0.096 (-0.174,-0.026)
Kalobwe	11	5.7	3.38	0.840	0.740	-0.138 (-0.228,-0.078)
Bugwe	9	5.4	3.31	0.790	0.710	-0.110 (-0.249,-0.020)
Bujombe	3	2.7	2.28	0.750	0.530	-0.421 (-0.939,-0.050)
MMNP	8	4.7	3.04	0.800	0.660	-0.216 (-0.399,-0.085)
Kashagulu	9	5.2	3.01	0.680	0.700	0.017 (-0.192,0.230)
Wansisi	10	5.1	3.19	0.840	0.710	-0.171 (-0.274,-0.087)

Sample size (N), Mean number of alleles per locus (Na), rarefied allelic richness (Ar), observed and expected heterozygosity (Ho and He, respectively), inbreeding coefficient (FIS) and 95% confidence intervals lower (LL) and upper (UL) limits.

Table S4.6: Hierarchical analyses of molecular variation (AMOVA) for 10 microsatellite loci

Partition	**Variance components**	**Percentage of variation**	**Fixation Indices**	**p-value**
	Across GNP and GME			
Among ecosystems[a] (F_{CT})	0.264	9.04	0.09	<0.0001
Among sample sites within ecosystems[a] (F_{SC})	0.07	2.39	0.026	<0.0001
Within sample sites (F_{ST})	2.588	88.56	0.114	<0.0001
	Within GNP			
Among sample sites	0.07	2.21		
Within sample sites (F_{ST})	3.087	97.79	0.022	<0.001
	Within GME			
Among regions[b] (F_{CT})	0.02	0.8	0.008	<0.05
Among sample sites within regions[b] (F_{SC})	0.06	2.11	0.021	<0.0001
Within sample sites (F_{ST})	2.86	97.1	0.029	<0.0001

[a] Ecosystems referring to GNP and GME

[b] Regions defined as north and south of the GME

Chapter 5:
General conclusion

In this dissertation, I have demonstrated the potential of combining remote sensing and genetic approaches to monitor chimpanzees and their habitat across large spatial and temporal scales. This dissertation has highlighted some of the opportunities in using emerging remote sensing technologies for chimpanzee monitoring and has provided detailed information on where to focus conservation efforts to protect and preserve a large, viable population of chimpanzee.

Findings overview

Drones for chimpanzee monitoring

The results from chapter 2 demonstrate the feasibility of using drones to detect chimpanzee nests in the mosaic landscape of western Tanzania. This study adds to a growing body of literature on the potential of drone technology for wildlife monitoring (Wich and Koh, 2018). Although the technology has been used across a wide range of taxa, only few studies have investigated the potential of drones for primate monitoring (3 out of 68 studies reported in Which and Koh 2018). Nearly a decade ago, Koh and Wich (2012) first demonstrated the feasibility of using a drone to detect Sumatran orangutans (*Pongo abelii*). Their low-cost prototype drone fitted with a standard camera was able to capture a wild Sumatran orangutan on top of a palm tree. Three years later, chimpanzee (*Pan troglodytes*) nests were counted from drone-acquired images in Gabon (van Andel et al., 2015), followed by a similar study on orangutan nests in Indonesia (Wich et al., 2015). Both studies reported successful detection of great ape nests and highlighted the potential of drones for great ape surveys, especially in open habitat, where nest detection was higher. The study presented in chapter 2 follows-up on these findings. With most (~75%) Tanzanian chimpanzees found outside national parks in an area characterised as one of the most open habitats in which chimpanzee inhabit (Moore, 1992), drones appeared as a promising tool for chimpanzee surveys in the country. A significant correlation was observed between the number of nests detected from the air and those recorded on the ground but only a small proportion (9.6%) of the nests spotted from the ground were detected from the air. Surprisingly, detection tended to be lower in open vegetation than in closed forest. The discontinuous miombo-woodland colours composed by green leaves and visible brown understory had created a difficult background from which to accurately identify brown nests. Although the chapter highlighted potential challenges in using drones for chimpanzee surveys, the study provided guidance for future investigations and highlighted the importance of contrasting background and high resolution images.

Satellite imagery and molecular markers to assess chimpanzee connectivity and viability

In chapters 3 and 4, I used satellite imagery and molecular markers to investigate chimpanzee connectivity across western Tanzania. By using remote sensing data from 1973 and a land-cover projection for 2027, I was able to map historical habitat connectivity for chimpanzees and predict the impact of future forest loss. The results suggest historical connectivity throughout the Greater Mahale Ecosystem (GME), the ecosystem containing nearly the entire free-ranging population of Tanzania's chimpanzees (Plumptre et al., 2010). The analysis also revealed a reduction of connectivity since 1973, which is likely to continue through 2027 and beyond if no effective conservation actions are enacted. In fact, 2 426 km^2 of forest are predicted to be lost by 2027 (Shoch et al., 2019), adding to the 1 677 km^2 already lost since 1973 (as revealed by the Landsat analyses from chapter 2). The reduction of forest, especially the destruction of entire blocks of riparian forests, and arrival of thousands of humans in the ecosystem has had a significant impact on chimpanzee habitat and movement corridors.

In chapter 4, I investigated the potential consequences of such disruptions on the genetic diversity and population structure of Tanzanian chimpanzees. I analysed 234 faecal samples collected across the GME along with genotypes from 136 individuals from Gombe National Park (GNP) and found no evidence of inbreeding and a greater genetic diversity within GNP compared with the GME. This result was rather surprising given that GNP is significantly smaller than the GME and was thought to be isolated from any other chimpanzee populations for decades (Pintea et al., 2011; Pusey et al., 2007). Behavioural adaptations to avoid inbreeding such as selecting mates genetically distant (Walker et al., 2016) and possible connectivity between GNP chimpanzees and northern populations (e.g. Burundi) may explain this unexpected result. Using both mitochondrial control region sequences and genotypes from 10 microsatellite markers, I was also able to resolve previous contrasting findings on connectivity between GNP and the GME (Inoue et al., 2011; Piel et al., 2013). Mitochondrial DNA analyses confirmed historical chimpanzee movement across GNP and the GME while microsatellite markers revealed a complete interruption of gene flow in recent years. No clear geographic pattern emerged within the GME for both markers from Bayesian cluster analyses. However, AMOVA analysis and Pairwise F_{ST} values indicated significant differentiation between sample sites which could not be explained by a division North-South of the ecosystem, nor via isolation by distance. The narrow corridors connecting the ecosystem revealed in chapter 3 could be responsible for the observed genetic pattern.

Conservation implications

Fifteen years ago, Tanzania was estimated to be home to ~2 700 chimpanzees (Moyer et al., 2006), scattered across ~20 000 km^2 (Humle et al., 2016). With less than 10% of their range protected by national parks, the majority of Tanzanian chimpanzees are facing increasing pressure from habitat loss, degradation and fragmentation (Davenport et al., 2010; Moyer et al., 2006; Piel et al., 2015a; Piel and Stewart, 2014; Plumptre et al., 2010). Improving connectivity and enhancing protection of chimpanzees outside of national parks was identified as essential by the most recent national conservation action plan for the species (TAWIRI, 2018). The results from chapters 3 and 4 compiled key information to support decision-making and guide management of the remaining chimpanzees. Chapter 3 has highlighted areas on where to focus conservation efforts (Figure 3.5), not only to protect current chimpanzee habitat, but also critical corridors for connectivity that might be classified as only moderately suitable chimpanzee habitat. Our model output represents a useful base on which to build detailed land-use planning, benefiting the long-term chimpanzee conservation and the local community (e.g. Zeller et al. 2013). By identifying critical areas for chimpanzee movement, our output map could help to better allocate land for biodiversity conservation but also for food production and economic development. Our connectivity map can also provide guidance on mitigation projects such as providing the most suitable location for wildlife crossing structures over roads (e.g. tunnels, bridges, speed bumps, informative signs). Finally, by providing fine scale measure of habitat importance for chimpanzees, landscape connectivity models along with species distance models can be used to quantify biodiversity co-benefit of climate mitigation projects such as REDD+ projects (Dickson et al., in press).

Results from chapter 4 also provide guidance for effective conservation. Our genetic data provide evidence of complete interruption of gene flow between GNP and the GME supporting the establishment of two conservation units (e.g. isolated populations identified within species that are used to help guide management and conservation efforts (Fraser and Bernatchez, 2001)). In addition to being adapted to very different types of habitat (GNP chimpanzees live in forest while most GME individuals range across a more open and dry landscape), the two ecosystems now represent distinct genetic clusters completely isolated from one another. Our findings suggested a high level of gene flow and genetic diversity maintained within both GNP and the GME. The GNP population of ~100 chimpanzees distributed across 35km^2 remains vulnerable to inbreeding – especially because genetic consequences of recent landscape changes have the potential to manifest decades into the future (Landguth et al., 2010) - however, our results suggest possible connectivity with northern chimpanzee populations which could act as a genetic rescue. We have shared our results with GNP researchers and conservationists and are hopeful that GNP can continue hosting a viable population of chimpanzees by restoring or strengthening connectivity with northern populations. With the GME hosting over 90% of Tanzania's chimpanzee population, we propose protecting the remaining suitable habitat and maintaining connectivity by focusing conservation effort on the key corridors highlighted in chapter 3 as key strategies to maintain a large viable population of chimpanzees.

Research perspectives

The future of drones for primate monitoring

Since our results from chapter 2 were published, several other studies have been released describing similarly encouraging results for drones to become a valuable tool for primate monitoring. Contrary to earlier studies, which used standard visual spectrum (RGB) cameras, several of the recent studies used drones fitted with Thermal Infrared (TIR) cameras. Using infrared radiation, these cameras detect the body heat emitted from animals. This drone/ TIR camera pairing has now demonstrated successful detection for seven species of primate across Asia and South America : Howler monkey (*Alouatta palliata*), Black-handed spider monkeys (*Ateles geoffroyi*) (Kays et al., 2018), Geoffroy's spider monkeys (*A. geoffroyi*) (Spaan et al., 2019), Bornean orangutans (*Pongo pygmaeus*), proboscis monkeys (*Nasalis larvatus*) (Burke et al., 2019), Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) (Gang et al., 2020) and Hainan gibbon (*Nomascus hainanus*) (Zhang et al., 2020). These studies all indicate that a TIR camera fitted to a drone offers an exciting new tool to monitor primate populations. However, false positives (e.g. incorrect detection) and species identification remain a challenge. When the canopy structure is composed of numerous emergent trees, drone altitude is limited, necessarily higher than the tallest trees. As a consequence, pixel resolution is generally insufficient to detect clear shapes and identify animals at the species level (Kays et al., 2018; Spaan et al., 2019; Zhang et al., 2020). Several solutions to address the challenges have been proposed. Kays et al. (2018) suggested that future work should combine thermal imagery with infrared spotlights or colour flash so that additional bands in the electromagnetic spectrum could be used to facilitate species identification. Burke et al. (2019) suggested developing an autonomous on-board system halting the drone and reducing its flight altitude above automatically detected animals, allowing sufficient resolution to identify the species.

With detection mainly influenced by image resolution (Bonnin et al., 2018), the rapid pace at which drone and sensor technologies are improving along with the developments in the field of Computer Science, in particular machine learning (Lamba et al., 2019), suggests many promising opportunities in the near-future for monitoring distribution and potentially density of chimpanzees and other great apes.

Connectivity model improvement and genetic data integration

Modelling connectivity for wildlife conservation is a growing field with a wide range of methods now available to measure and map landscape resistance to movements (Bocedi et al., 2014; Correa Ayram et al., 2016). In chapter 3, I chose to derive resistance values using circuit theory (Mcrae et al., 2008), allowing me to develop a landscape-scale permeability map that was independent of an priori source or destination locations. Contrary to least-cost path, the other popular modelling approach for identifying and quantifying landscape connectivity, circuit theory considers all possible routes and does not assume that individuals have perfect knowledge of the landscape (McClure et al., 2016). Not only is this approach more likely to accurately represent chimpanzee long distance movement, but it can also be performed by randomly placing regularly distanced nodes around a buffer perimeter, removing the challenge of defining focal nodes within the study areas (Koen et al., 2014). With the majority of Tanzanian chimpanzees found outside national park boundaries and an unknown number of populations, this approach has reduced the bias associated with choosing random nodes within the GME. However, a recent study using both modelling approaches to identify corridors between two Gabonese national parks found that least-cost path performed better than circuit theory in predicting corridors for western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) (Vanthomme et al., 2019). Further work testing the sensitivity of using least-cost path analyses on the landscape connectivity output will help us to better understand how chimpanzees move across the landscape. Large continuous suitable habitat patches could be used to define nodes within the study area (D'Elia et al., 2019; Maiorano et al., 2019). By projecting our model to 1973 and 2027, we were able to assess connectivity change for chimpanzees across a large temporal scale, however, the approach restricted the number of predictor variables we could include in our model (e.g. difficulty of accessing reliable settlement and road data for 1973). Future investigations focusing on current predictions would benefit from including additional variables such as roads, rivers, settlements, and vegetation indices.

To fully exploit the potential of our connectivity model to informing sustainable management decisions, validating our model would be a crucial step forward. One way to achieve this would be to collect independent field data (Crooks and Sanjayan, 2006). Chimpanzee data collected through additional line transect surveys, camera traps, or passive acoustic monitoring could be used to evaluate the model by assessing the correlation between connectivity values and chimpanzee density (Laliberté and St-Laurent, 2020). Another approach would be to integrate genetic data to parameterise resistance surface. Landscape genetic methods assess multiple alternative resistance models to determine the optimal resistance values that best describe pairwise genetic differentiation (e.g. F_{ST}). This approach thoroughly investigates the relationship between landscape features and gene flow, allowing a detailed understanding of how landscape features affect animal movements (Balkenhol et al., 2016). Applied with our data, this method would help us to better understand the impact of roads, rivers and land-cover change for chimpanzee movement within Tanzania. Additionally, by extending our analysis to the entire Tanzanian chimpanzee range and including samples across the Tanzania - Burundi border, we could investigate chimpanzee movement at the trans-national scale. Not only would these additional data inform protection of the entire Tanzanian chimpanzee population, but also make a difference at the eastern chimpanzee subspecies level.

Glossary

Adaptive potential: Potential to adapt to environmental change.

Amplified fragment length polymorphism (AFLP): A dominant molecular marker that genotypes individuals at multiple loci. Amplified DNA is digested with restriction enzymes,
adapters are attached to the ends of amplified fragments, and a subset of fragments is then
re-amplified to generate a multi-band pattern

Allelic dropout: Failure of a microsatellite allele to amplify in some PCR reactions, especially when low-quality DNA is the template.

Allelic Richness (Ar): Allelic diversity (average number of allele per locus) standardized to a particular sample size

Circuit theory: Principles applied to electric circuits in which electric current flow from one node (connection point) to another through resistors (electrical components that conduct current). Applied to movement ecology, circuit theory treats the landscape as if it were a large electrical surface with low resistance values assigned to landscape features facilitating movement, and high resistances assigned to movement barriers. Current flow can then be calculated between pairs of nodes (representing habitat patches or populations) and can be related to the probability of animal movement across the landscape. In contrast with Least-cost path analysis, the other popular connectivity modelling approach, circuit theory simultaneously considers all possible pathways and does not assume that the animals have perfect knowledge of the landscape.

Connectivity: The degree of movement of organisms or processes. The more movement, the more connectivity, and conversely, the less movement, the less connectivity.

Deleterious alleles: Alleles reducing the viability and fitness (see **fitness**) of individuals when homozygous.

False alarm rate: Proportion of false detections. Calculated as the ratio between the number of false detections (in this thesis, aerial observations not aligning with nests found from the ground) to the total number of detections (here aerial observations).

Fitness: The relative ability of an individual to survive and reproduce compared with other.

Fixation index (F-statistics): Provides an estimate of the genetic differentiation between subpopulations. F_{ST} ranges from 0 (no differentiation between subpopulation) to 1 (fixation of different alleles in subpopulation).

Fixed-wing drone: Drone with a rigid structure which generates lift under the wing due to forward airspeed.

Genetic drift: Changes in the genetic composition of a population due to random sampling in finite populations

Georeferencing: The inclusion of geographic coordinates in a digital map or aerial photo of an area. A georeferenced digital map or image has been tied to a known Earth coordinate system, so users can determine where every point on the map or aerial photo is located on the Earth's surface.

Geotagging*:* process of adding a geographical location to a media.

Global Navigation Satellite System (GNSS): Constellation of satellites providing signals from space that transmit positioning and timing data to GNSS receivers.

Ground Control Points (GCP): Ground control points are large marked targets on the ground, spaced strategically throughout the area of interest, with known spatial coordinates. These points are used to accurately georeferenced and calibrate images.

Ground Sampling Area (GSA): The area on the ground covered by one aerial image.

Ground Sampling Distance (GSD): The length on the ground corresponding to the side of one pixel in an aerial image.

Haplotype diversity (h): A measure of genetic diversity, represents the probability that two randomly sampled alleles are different

Hardy-Weinberg equilibrium (HWE): The equilibrium genotype frequencies achieved in a random mating population with no perturbating forces from mutation, migration, selection or chance.

Inbreeding coefficient (F_{IS}): Measures the degree of inbreeding within individuals relative to the rest of their subpopulation. Positive Fis values indicate that individuals in a population are more related than you would expect under a model of random mating.

Inbreeding depression: A reduction in the fitness of offspring that result from matings between close relatives.

Inbreeding: Mating between closely related individuals

least-cost path analysis: Identify the path with the least accumulated resistance between two locations across a resistance surface (see **resistance surface**). In contrast with circuit theory which take into consideration all possible routes, least-cost path analysis assume that individuals have perfect knowledge of the landscape and select a single optimal route which is only one cell wide. Least-cost models can therefore better identify long-distance movement which are passed down through generation.

Light Detection and Ranging (LiDAR): Active remote sensing system that uses light in the form of a pulsed laser to measure ranges (variable distances) to the Earth. These light pulses—combined with other data recorded by the airborne system — generate precise, three-dimensional information about the shape of the Earth and its surface characteristics.

Lineage sorting: Fixation of different alleles (or haplotypes) in different lineages (populations or species reproductively isolated from one another).

Linkage disequilibrium (LD): Non-random association of alleles at two or more loci. These alleles tend to be inherited together significantly more than expected by random mating.

Mean pairwise sequence difference (MPD): The mean number of loci for which two haplotypes are different.

Microsatellite: A stretch of DNA that consists of a short tandem sequence of up to five base pairs that is repeated multiple times (typically showing variable number of repeats).

Minisatellite: Repetitive DNA sequences that are each 10-100 bases long and are dispersed throughout the genome.

Mitochondrial DNA (mtDNA): The circular DNA molecule of the mitochondrion. Haploid (contains only one set of chromosomes) and generally passed on only from mother to offspring.

Multirotor drones: Drones with rotary wings or rotor blades, which generate lift by rotating around a vertical mast.

Nucleotide diversity (π): A measure of genetic diversity at the nucleotide level. Quantifies the mean sequence divergence among several haplotypes by factoring in both the frequencies and the pairwise divergences of different sequences.

Null alleles: Alleles that fail to amplify during a PCR reaction. Microsatellite null alleles can lead to the erroneous identification of homozygotes.

Orthomosaics: A mosaic of orthorectified images. Orthorectifying imagery is the process of aligning the images that have been captured usually using photogrammetry techniques and processing them so that the geometric angles are aligned correctly creating a geometrically correct map with a uniform scale.

Permeability: The degree to which a landscape feature or a habitat location facilitate animal movement (inverse of **resistance**).

Random amplified polymorphic DNA (RAPD): Dominant molecular marker that generates multiple DNA fragments through the random PCR amplification of multiple regions of the genome using single arbitrary primers.

Recall rate: Proportion of successful detections. Calculated as the ratio between the number of true detections (in this thesis, nests observed from the ground detected during the aerial survey) to the total number of detectable events (nests observed by the ground survey).

Remote sensing platforms: Technologies acquiring information from a distance.

Resistance surface: A representation of the landscape in which each location is assigned a resistance value which affect movement through the landscape.

Resistance: The degree to which a landscape feature or a habitat location impede animal movement (inverse of **permeability**).

Sequential Bonferroni correction: Procedure whereby the significance level of a statistical test is adjusted in order to protect against Type I errors (also called false positives) when multiple comparisons are being made. Bonferroni correction consists in multiplying the significance level by the total number of tests performed. For the sequential version, considered more powerful, the statistical tests are first performed to obtain their "p-values." The tests are then ordered from the one with the smallest p-value to the one with the largest p-value. The test with the lowest probability is tested first with a Bonferroni correction involving all tests. The second test is tested with a Bonferroni correction involving one less test and so on for the remaining tests.

Single Nucleotide Repeat (SNP): A variation between two sequences of DNA that is caused by a single nucleotide substitution

Standardized F_{ST} (F'_{ST}): Corrected so that it scales 0–1 (F_{ST} divided by F_{ST} max)

Stuttering: Artefact seen when amplifying short tandem repeats and typically occurs at one repeat unit shorter in length than the parent allele caused by slippage of the DNA polymerase during DNA synthesis.

Unmanned Aircraft Vehicles (UAV) or drones: an aircraft that does not have a human pilot on board but is controlled by someone on the ground.

φ_{ST}: F_{ST} analogous for molecular sequence data - Use information on the allelic content of their haplotypes as well as their frequency.

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