

Modelling landscape connectivity change for chimpanzee conservation in Tanzania

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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 2000–3000 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 km²) 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.

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).

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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 facilitate or 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., 2015b; Fig. 1). However,

several surveys have now revealed that 75% of Tanzanian chimpanzees live outside of these two National Parks, with the majority (~1500) 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

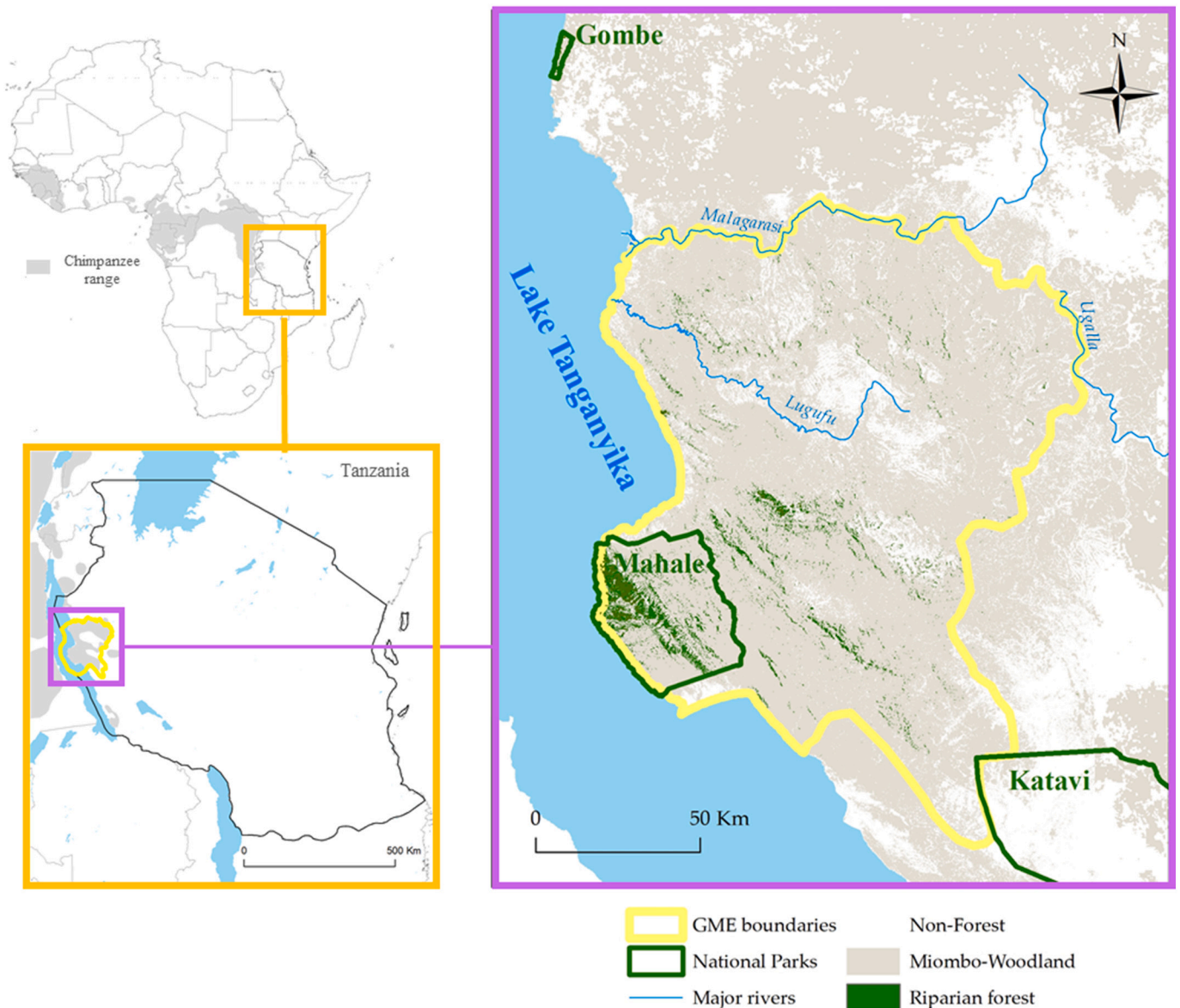


Fig. 1. Location and map of the GME.

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 (1) develop a habitat suitability model to create an index of habitat selection by chimpanzees within the GME; (2) map functional habitat connectivity independently of any a priori habitat patches or populations using circuit theory and our resulting habitat selection model; finally (3) evaluate the impact of forest loss on habitat connectivity by using remote sensing data from 1973 and a land-cover projection for 2027. We hypothesised the GME to be connected by multiple area of high connectivity values in 1973. We also expected a reduction in connectivity associated with forest loss, now isolating the northern and southern populations. Our results provide key information on where to focus conservation efforts, not only to protect current chimpanzee habitat, but also areas critical for connectivity that might be classified as only moderately suitable for chimpanzee habitat. 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.

2. Methods

2.1. Study area

The GME is a $\approx 18,000 \text{ km}^2$ 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 (Fig. 1). The area is dominated by miombo-woodland (*Brachystegia* and *Julbernardia*, 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 2500 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). Since 2005, the Greater Mahale Ecosystem Research and Conservation Project (GMERC) in collaboration with The Nature Conservancy (TNC), Frankfurt Zoological Society (FZS), the Jane Goodall Institute (JGI), Tanzania Wildlife Research Institute (TAWIRI), Tanzania National Parks (TANAPA) and District government partners have led surveys to monitor chimpanzee populations. To account for potential chimpanzee movement along the edges of the GME, we drew a 20 km buffer around the GME boundary.

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 found that riparian forests are not well resolved by existing canopy cover products and since these forests are an essential component of chimpanzee habitat, we developed our own canopy cover product using Landsat spectral metrics derived from 16-day Landsat 7 ETM+ and Landsat 8 OLI image composites as outlined in Potapov et al. (2020). For a detailed explanation and evaluation of our product, we refer the reader to the Supplementary Material (Appendix S1). Our product represents canopy cover for the year 2000. 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

and 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 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. 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 S1 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 and Plumtre, 2006; Jantz et al., 2016). We included topographic measures because altitude has an influence on chimpanzee distribution (Fitzgerald et al., 2018; Plumtre 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 Plumtre, 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 (55 km^2 at Issa, Piel and Stewart, unpublished data; 27.4 km^2 for M-group (MMNP), Nakamura et al., 2015b and 10 km^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.

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.

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 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 3 km (Piel and Stewart, 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 60×60 m. 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 $N = 2554$ occurrence points used to train the final model (Appendix S2, Fig. S2.1).

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 et al., 2006; Elith and Graham, 2009). 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.

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 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. 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 S1). 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 from 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 S2, Fig. S2.2).

Thirty node pairs were sufficient to generate unbiased connectivity maps (Appendix S2, Fig. S2.3). 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 be connected by several current flow corridors facilitating chimpanzee movement in 1973 (Fig. 2; Appendix S2, Fig. S2.4).

Although the pattern of landscape connectivity remained broadly similar over time (Appendix S2, Fig. S2.5), a reduction in current density is observed for 1966.7 km² between 1973 and 2019. This reduction is impacting both current flow corridors linking the northern and southern GME (Fig. 3a). When projecting to 2027, we predict 2152.3 km² 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 (Fig. 3b). Increase in current flow is also observed for both time periods corresponding to displacement of probability of movement.

4. Discussion

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

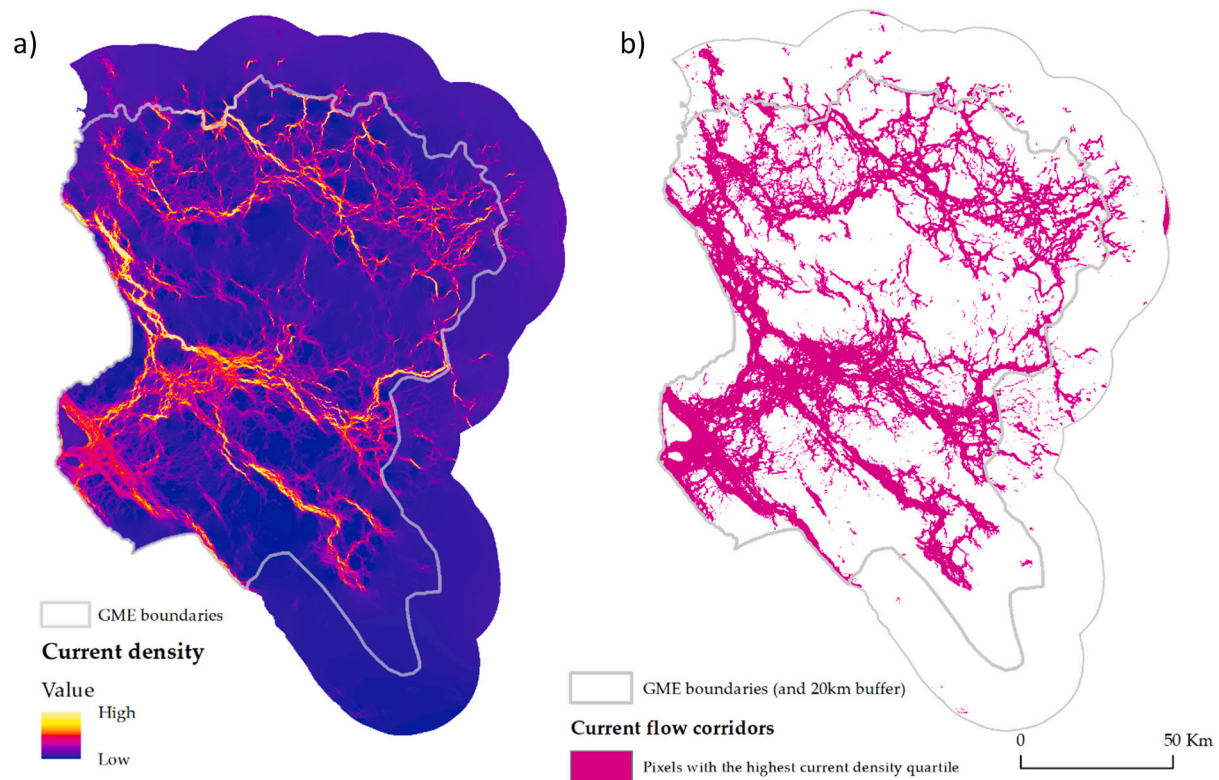


Fig. 2. Habitat connectivity maps derived from Circuitscape for 1973 a) current density map, b) current flow corridors.

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 S2, Fig. S2.6). 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 1677 km² between 1973 and 2017 (Fig. 4). Surprisingly, vegetation type

contributes 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 2426 km² of forest to be lost by 2027, threatening a large area in the south-east of the GME (Figs. 3b; 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 of for chimpanzees.

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 (Fig. 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 Asimwe, 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

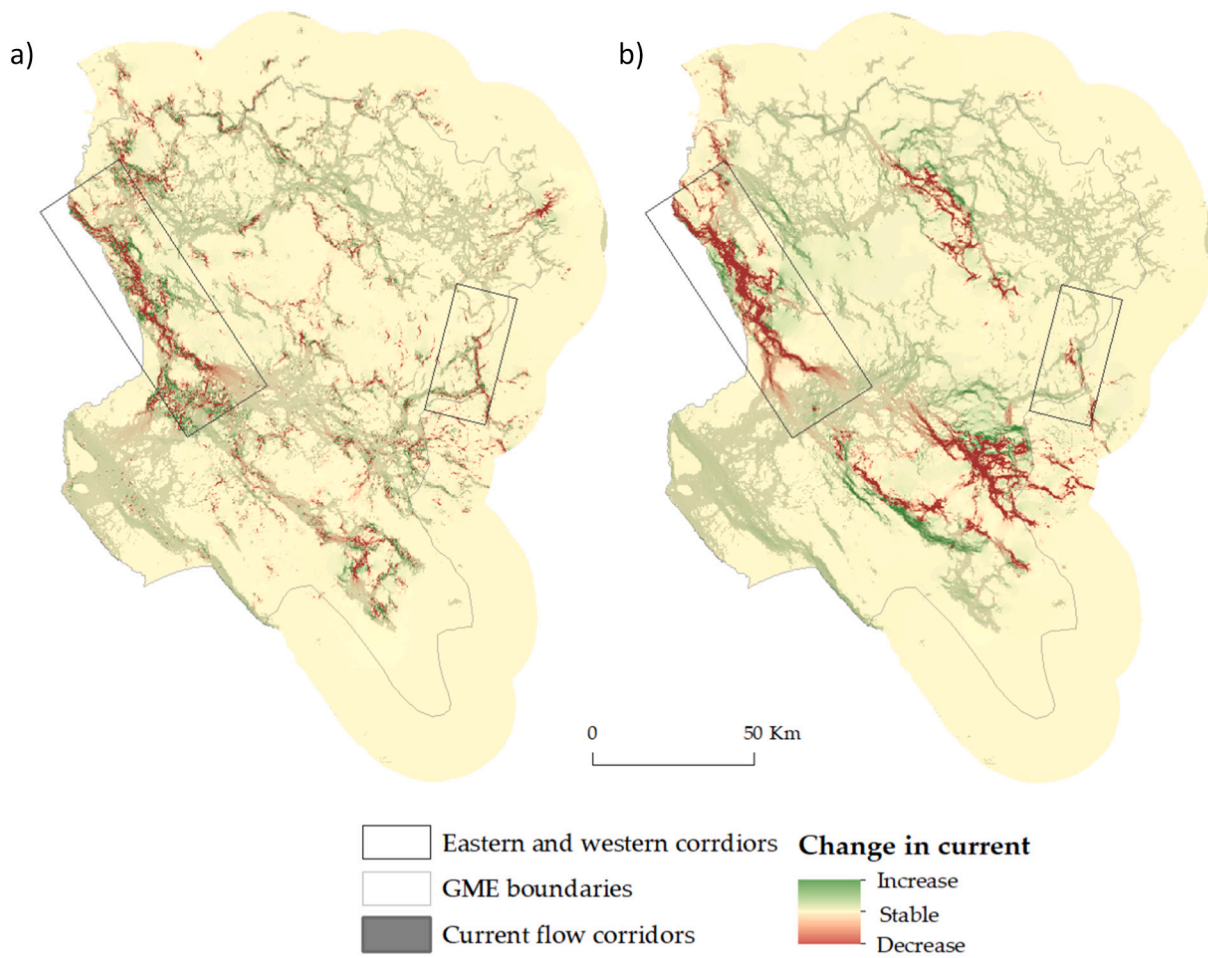


Fig. 3. Current density change between a) 1973 and 2019, b) 2019 and 2027.

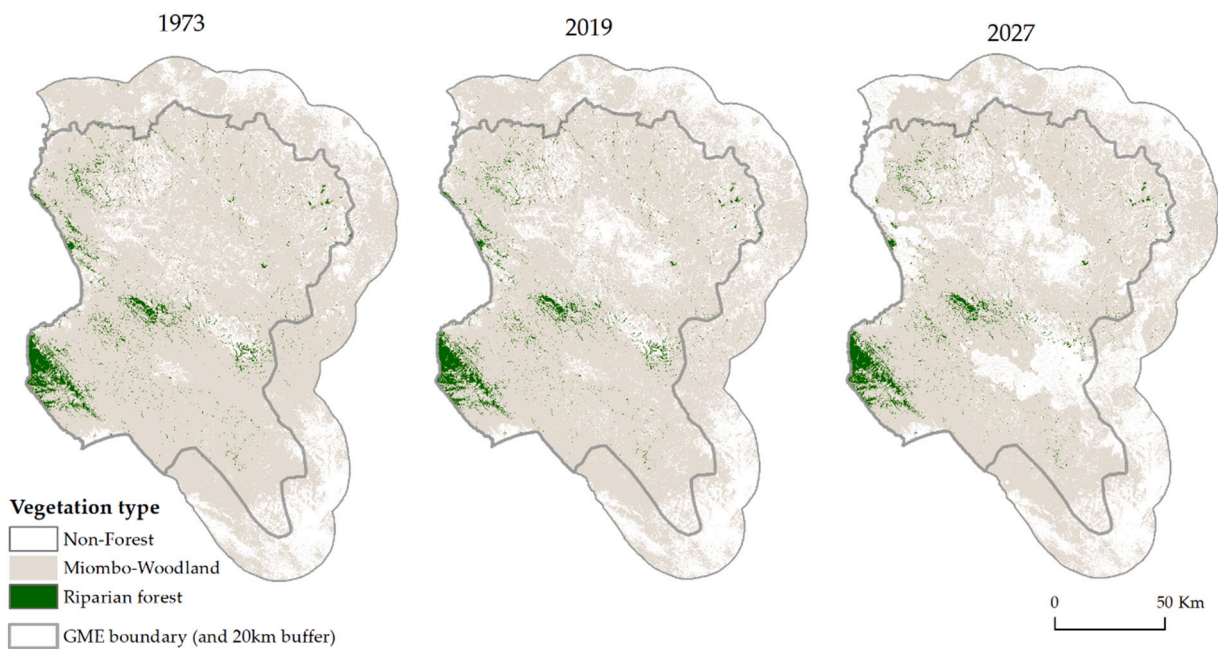


Fig. 4. Vegetation change from 1973 to 2027.

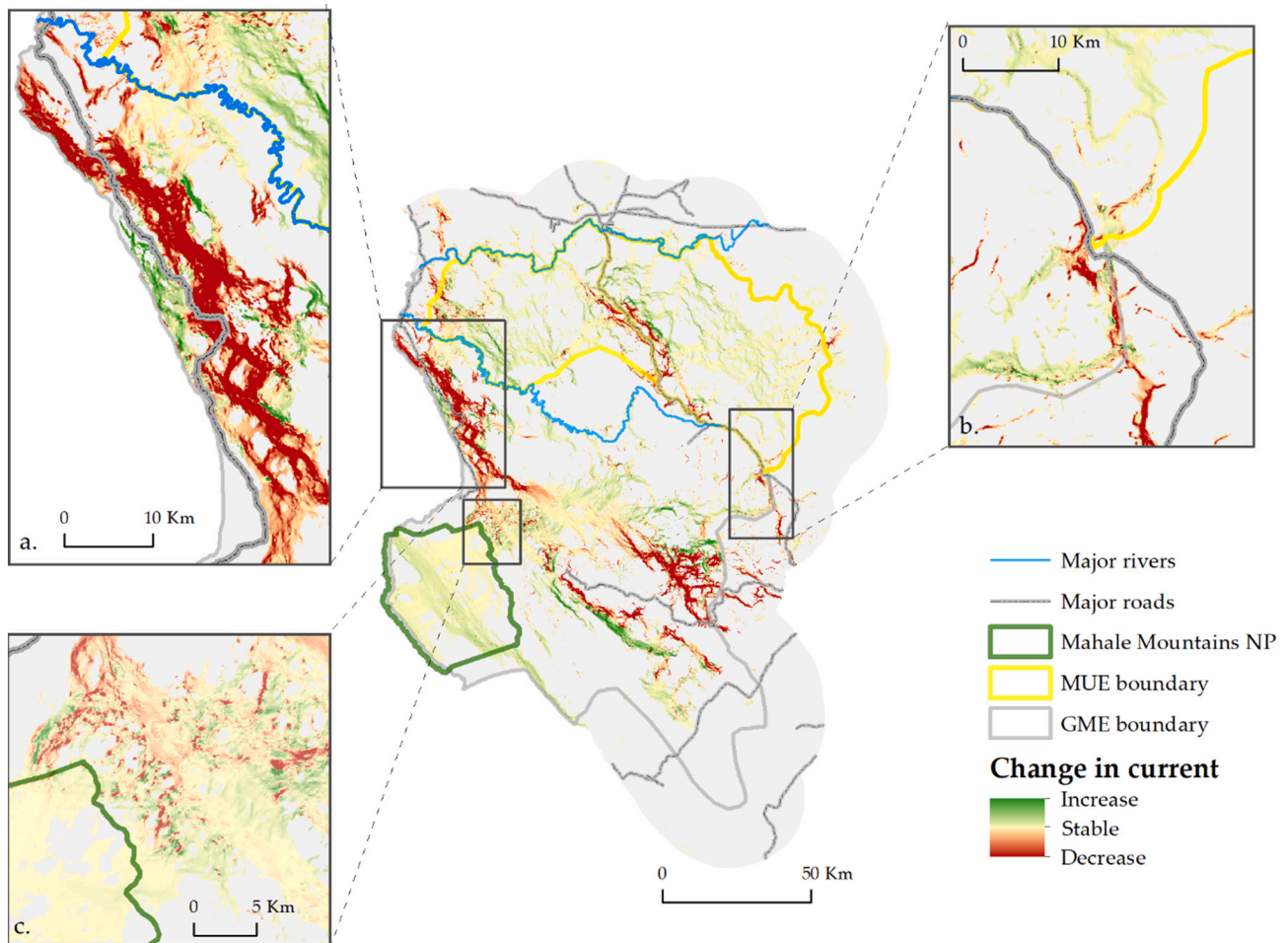


Fig. 5. Priority areas to maintain connectivity for chimpanzee conservation within the GME. Background represents current density change between 1973 and 2027 within current flow corridors delineated for 1973. Box a. western corridor running through the Lugufu river; Box b. eastern corridor crossing Uvinza-Mpanda road; Box c. corridor allowing movement in/out Mahale Mountains NP.

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 Cleverger, 2001; Lasch et al., 2011; Plumpré et al., 2010; TAWIRI, 2018).

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 (Fig. 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 100 m 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 month 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 opinion 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 opinion, habitat suitability modelling allow 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 (Fig. 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 (Fig. 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 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.

CRedit authorship contribution statement

Noémie Bonnin: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing.

Fiona A. Stewart: Investigation, Writing - original draft, Writing - review & editing, Supervision.

Serge A. Wich: Conceptualization, Writing - original draft, Writing - review & editing, Supervision.

Lilian Pintea: Methodology, Formal analysis, Writing - original draft, Writing - review & editing.

Samuel M. Jantz: Methodology, Formal analysis, Writing - original draft, Writing - review & editing.

Rebecca Dickson: Resources, Writing - original draft.

Joe Bellis: Methodology, Writing - original draft, Writing - review & editing.

Adrienne Chitayat: Investigation.

Rebecca Ingram: Investigation.

Richard J. Moore: Investigation.

Alex K. Piel: Investigation, Data Curation, Supervision, Writing - original draft, Writing - review & editing, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108816>.

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