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Title: 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 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

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 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., 2015; Fig. 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 (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 ≈ 18 000 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 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). 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 20km buffer around the GME boundary.

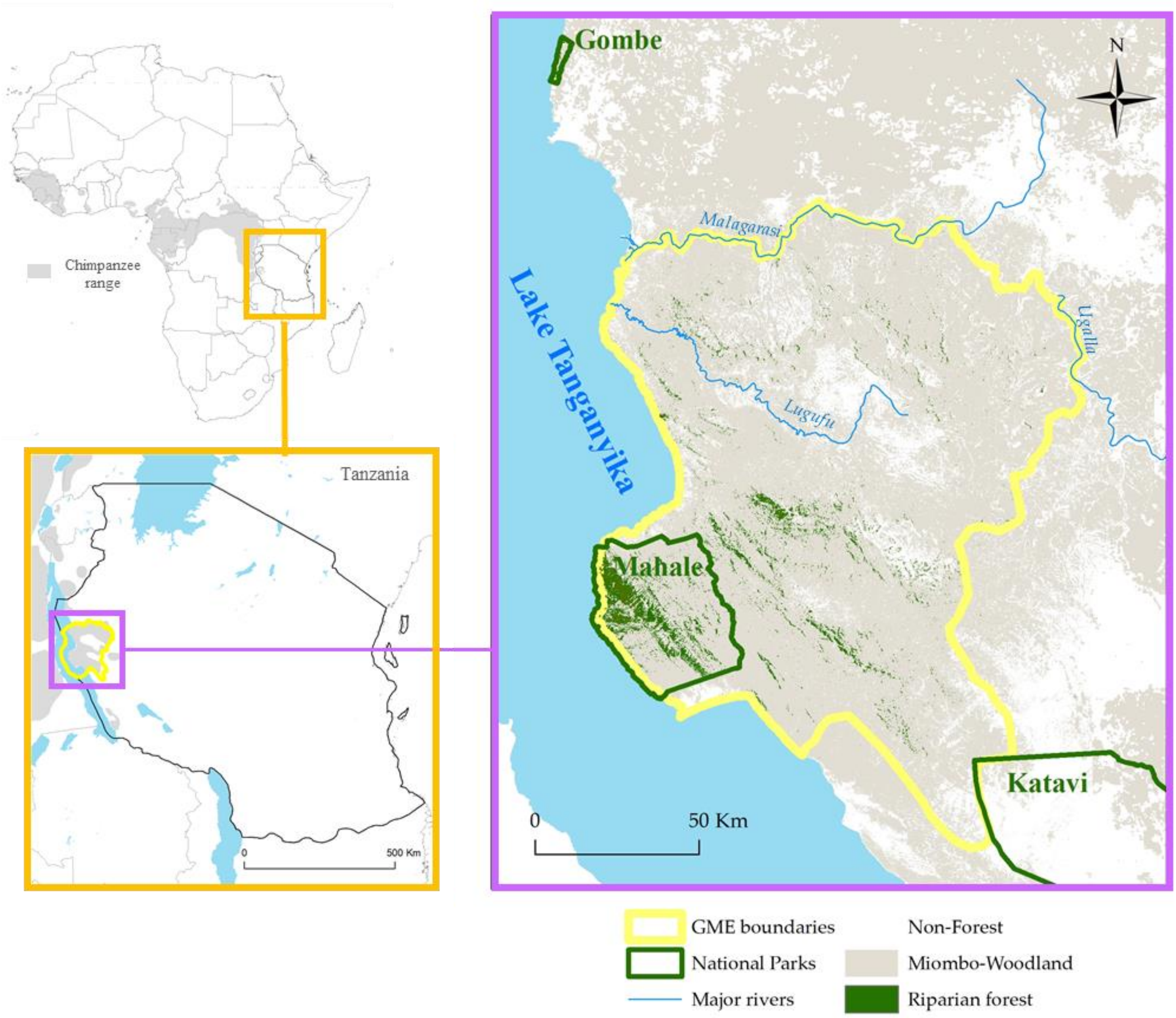

Figure 1: Location and map of the GME

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 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 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 & 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.

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 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 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, J. 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 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 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).

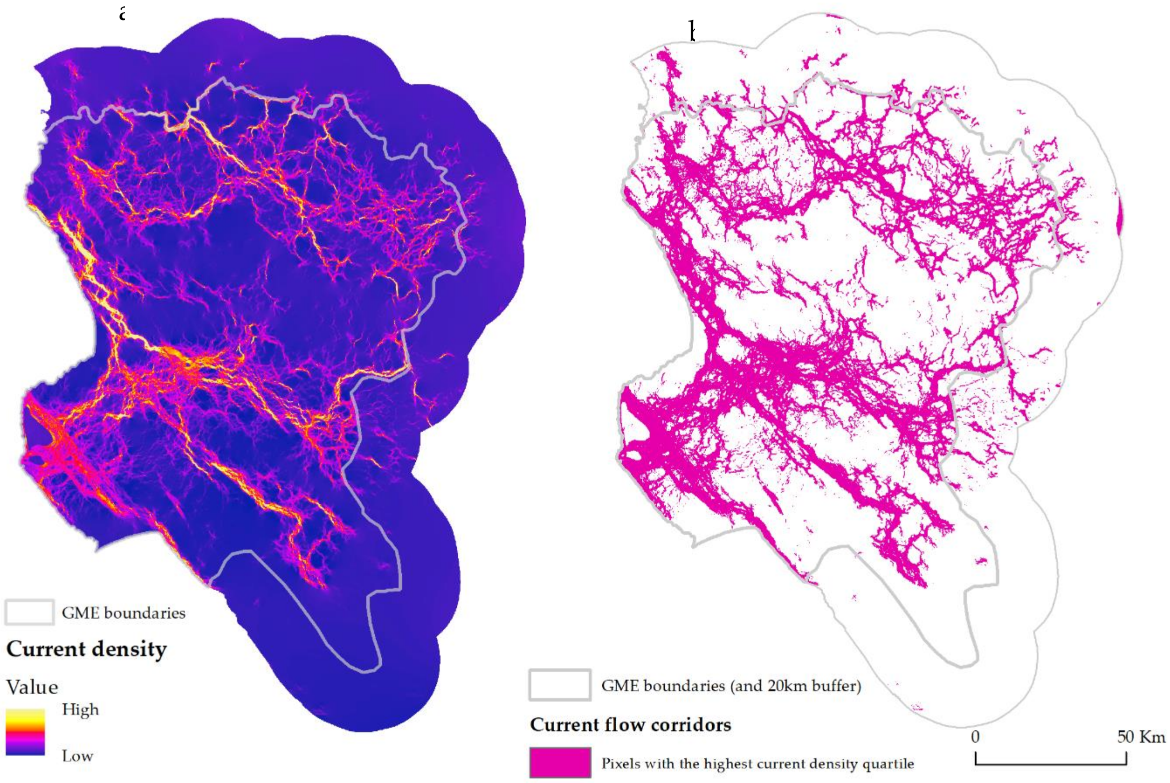

Figure 2: Habitat connectivity maps derived from Circuitscape for 1973 a) Current density map, b) current flow corridors

Although the pattern of landscape connectivity remained broadly similar over time (Appendix S2, Fig. S2.5), 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 (Fig. 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 (Fig. 3b). Increase in current flow is also observed for both time periods corresponding to displacement of probability of movement.

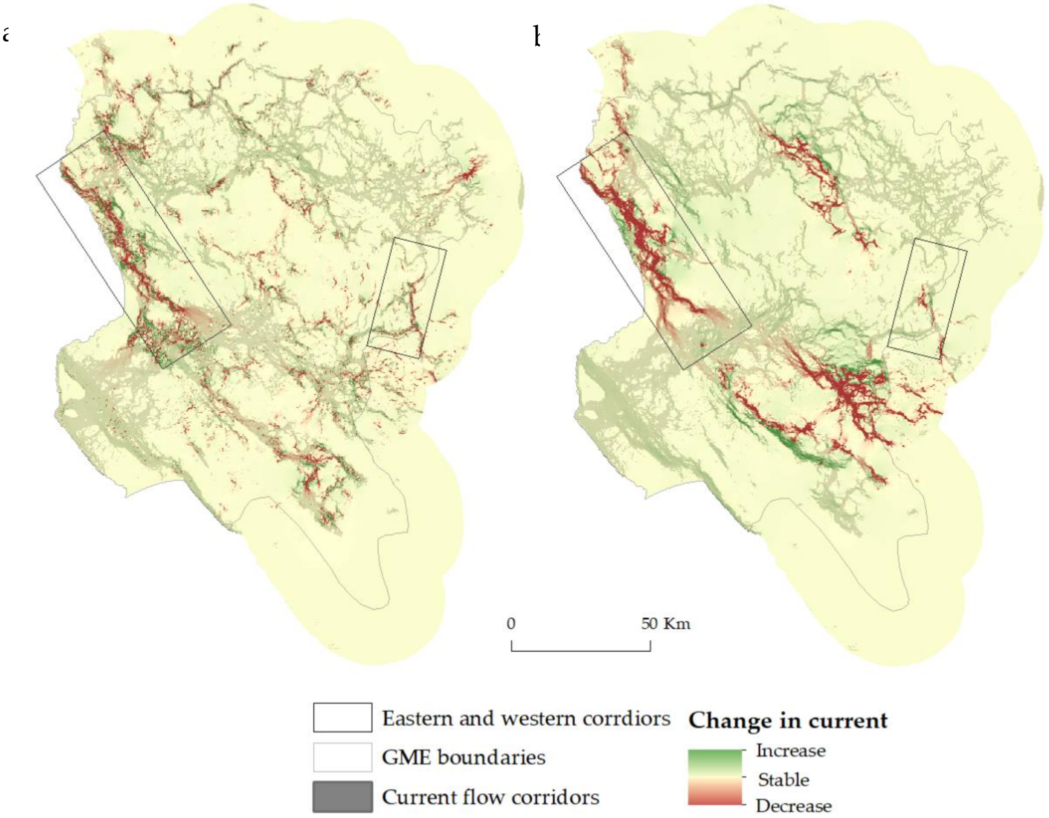

Figure 3: Current density change between a) 1973 and 2019, b) 2019 and 2027

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 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 1 677 km^2 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 2 426 km^2 of forest to be lost by 2027, threatening a large area in the south-east of the GME (Fig. 3b; Fig. 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.

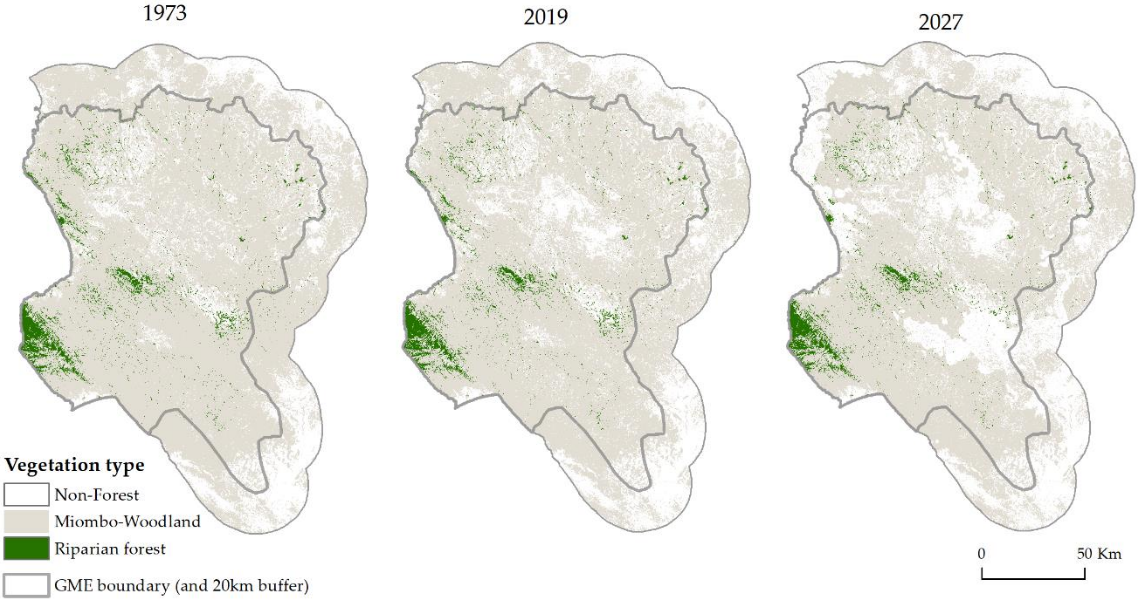

Figure 4: Vegetation change from 1973 to 2027

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 (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 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).

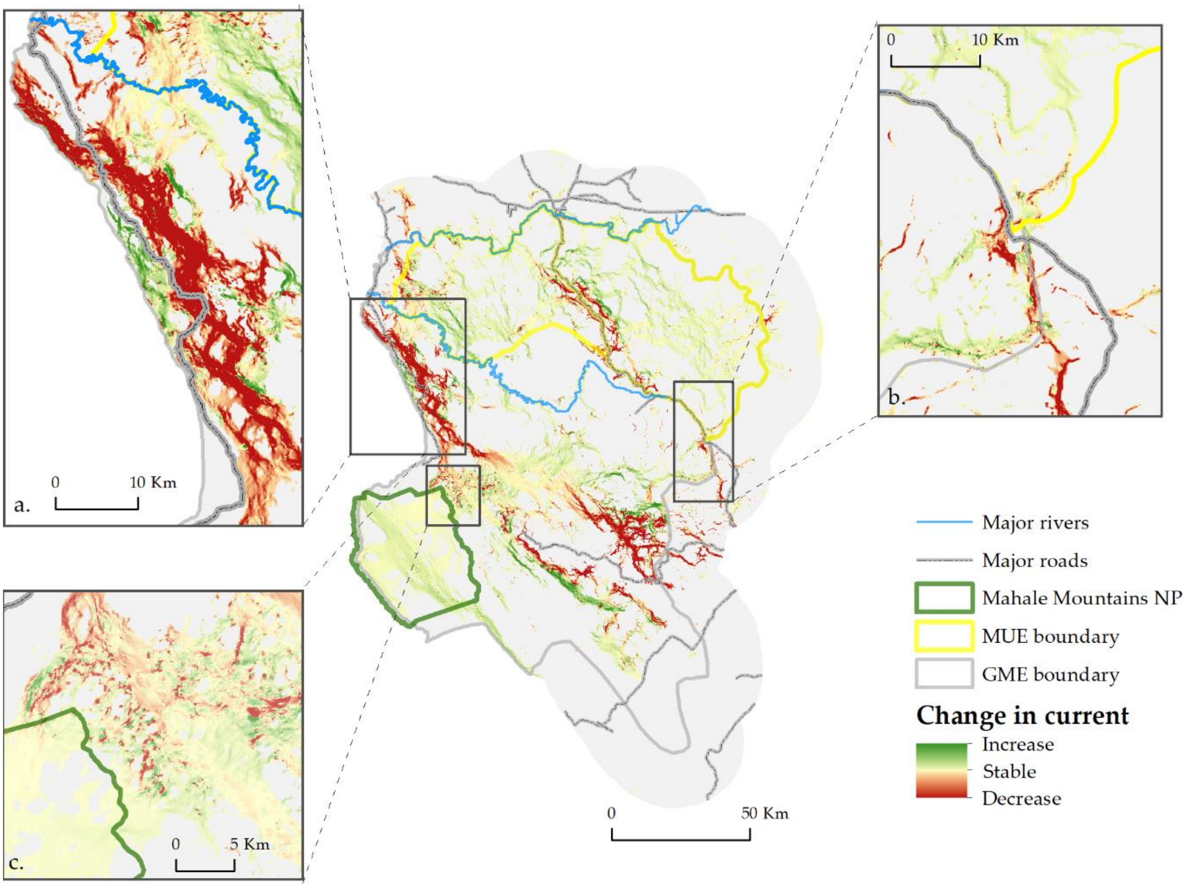

Figure 5: Priority areas to maintain connectivity for chimpanzee conservation within the GME. Background represents current density change between 1973 and 2027 within current flow corridors delineated for 1973. Box a. western corridor running through the Lugufu river; Box b. eastern corridor crossing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

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. (2013) 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 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.

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Supplementary Materials

Appendix S1

Generation of the 2000 continuous tree cover dataset

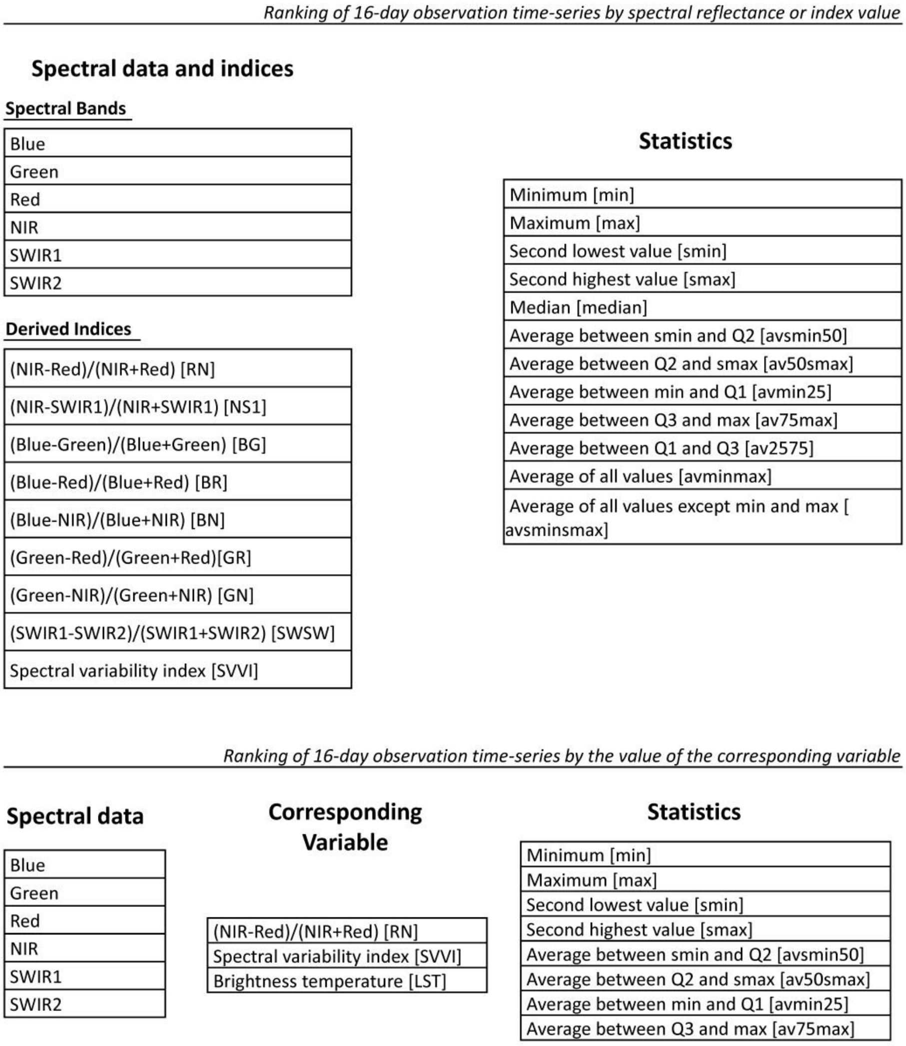
In this section we detail how we created and evaluated our tree cover product. We used a similar methodology compared to Sexton et al. (2013) but with key differences in the reflectance data and modelling algorithm. Instead of using Landsat reflectance data directly our approach uses a set annual multi-temporal 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 land cover 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 S1.1. 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 [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 S1.1: 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 S1.2). For example, the global product over predicts tree cover over sloped terrain.

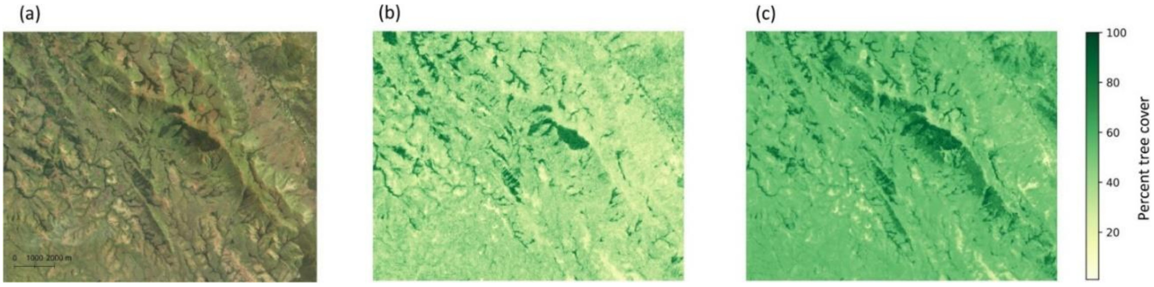


Figure S1.2: A zoomed region of the study area showing high resolution Google Earth imagery (a), our percent tree cover product (b), and percent tree cover from Hansen et al. (2013).

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 S1.3).

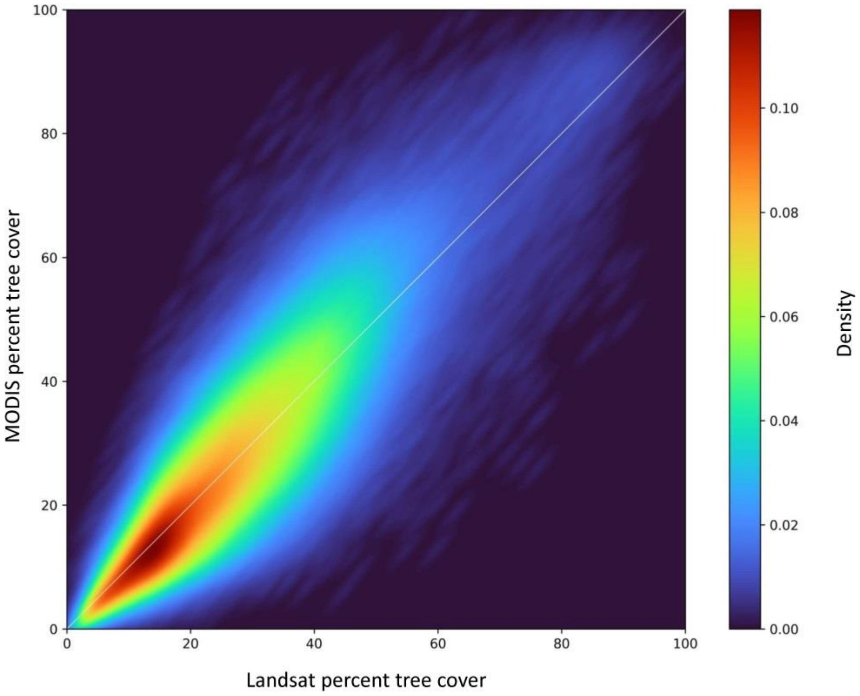


Figure S1.3: 2 dimensional density plot with Landsat predicted tree cover on the x-axis and MODIS VCF tree cover on the y-axis. The one-to-one line is shown in white.

Our product better matched the Lidar derived canopy cover compared to the MODIS VCF with smaller error and higher correlation (Table S1).

Table S1: 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 S1.4). 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 S1.4b).

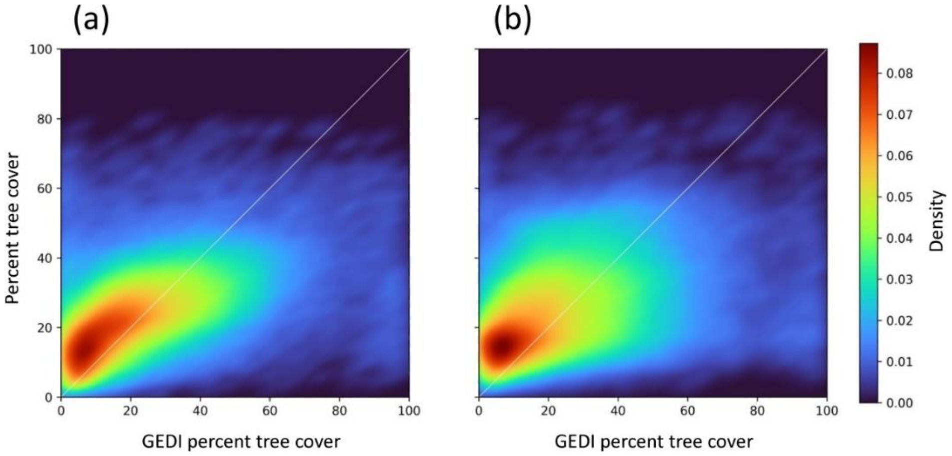


Figure S1.4: 2 dimensional density plots with canopy cover from GEDI Lidar on the x axes, percent tree cover from Landsat on the y-axis (a), and MODIS VCF tree cover on the y-axis (b). The one-to-one lines are shown in white.

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 withing 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

Literature cited in Appendix S1

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Appendix S2

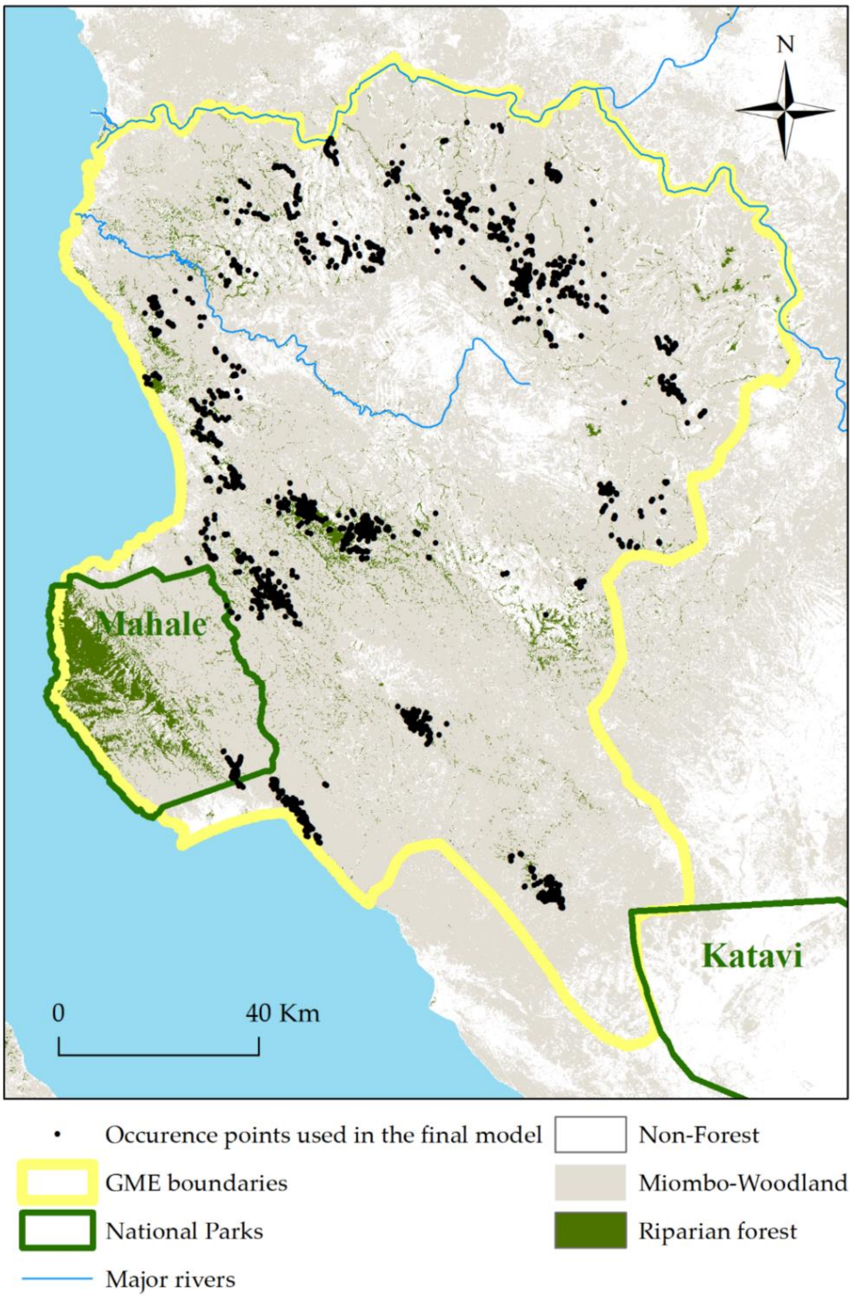

Figure S2.1: Locations of the occurrence points used in the final habitat suitability model

Table S2.1: 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

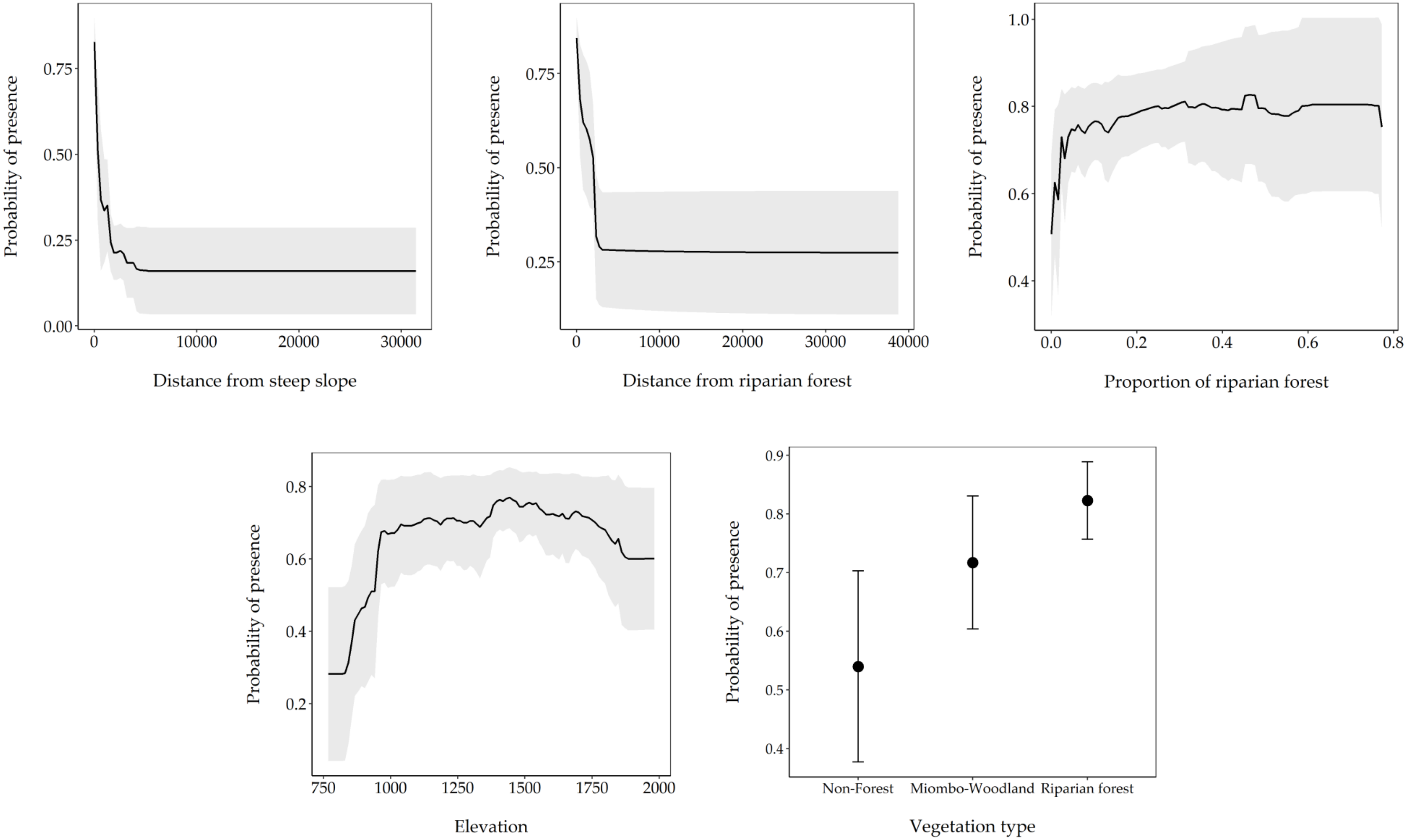

Figure S2.2: Response curves derived by the ensemble prediction. The plots show the mean response (dark line and dark points) and the standard deviation (error bars and grey ribbon) of the 5 replicates of the 3 algorithms. The curves display how the predicted probability of presence vary in function of each environmental variable. These response curves do not account for interactions between variables.

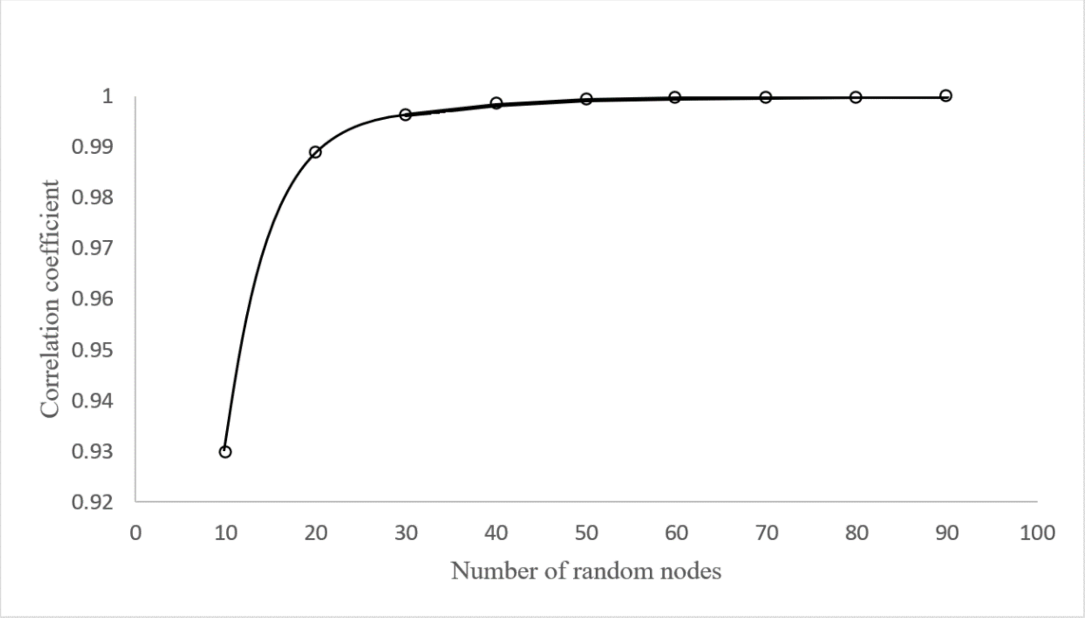

Figure S2.3: Pearson correlation coefficients of extracted values (n = 100 000) from a full permeability map developed using 100 random nodes compared to extracted values from permeability maps developed using fewer random nodes (i.e. 10–100).

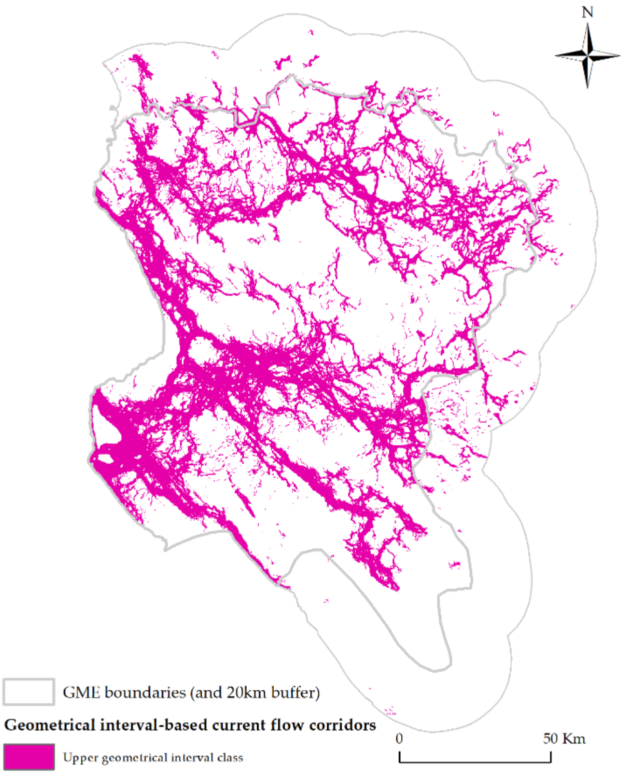

Figure S2.4: Current flow corridors for 1973 derived from upper geometrical interval

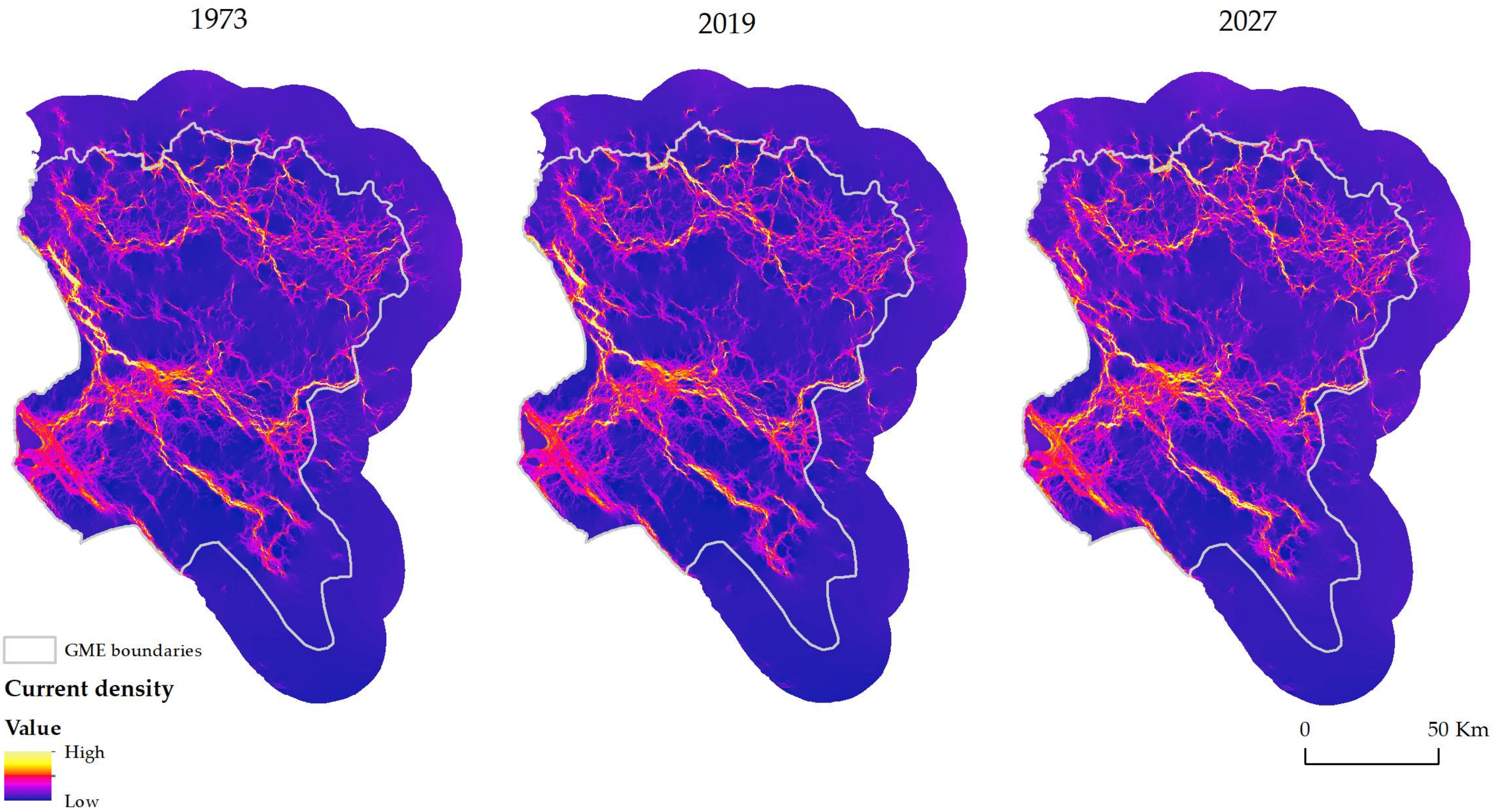

Figure S2.5: Current density map for 1973, 2017 and 2027.

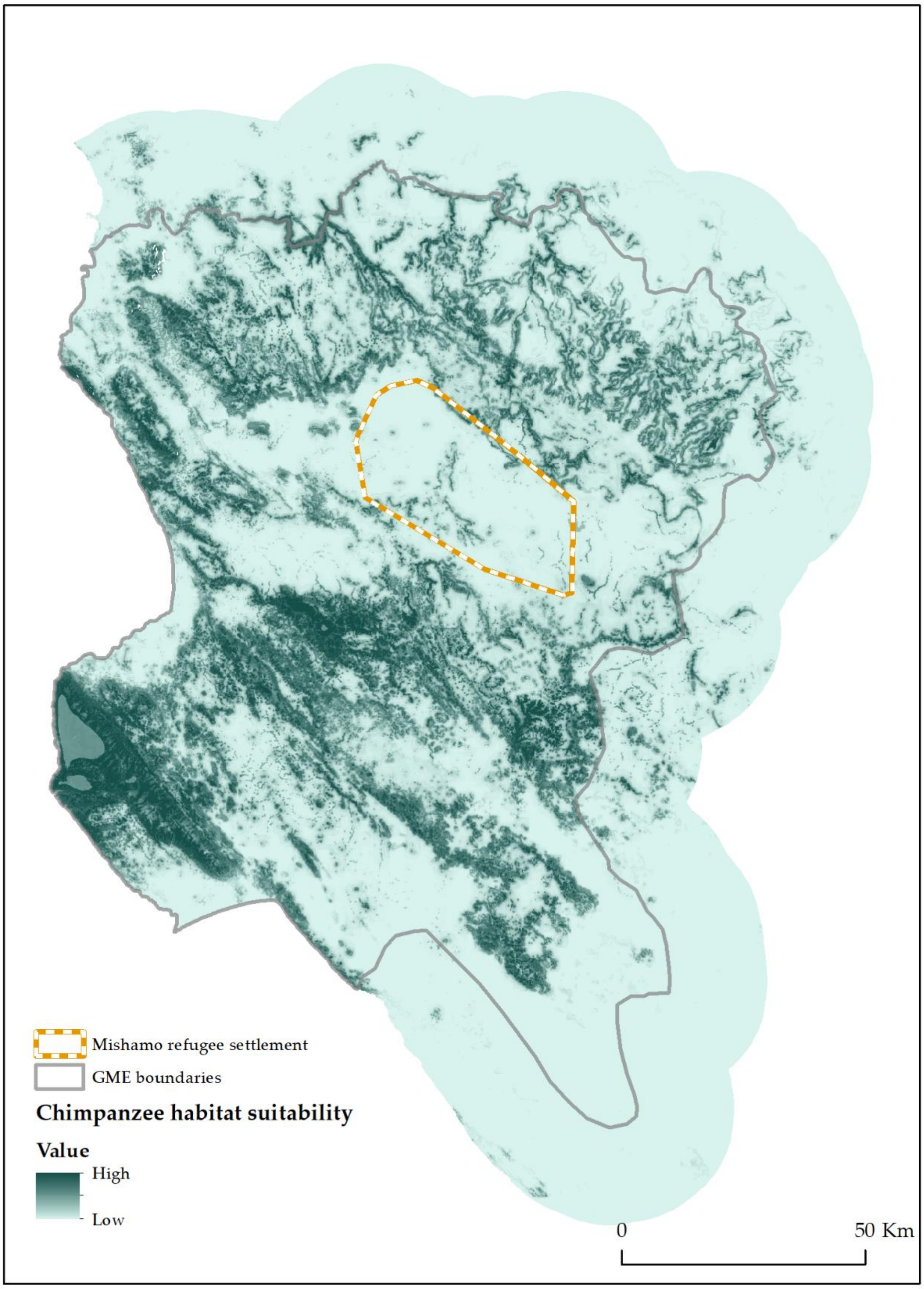

Figure S2.6: Area of Mishamo refugee settlement establishment overlaid with chimpanzee habitat suitability for 1973