

1 1. Introduction

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

17 Landscape connectivity models can help highlight important areas on which to focus
18 conservation efforts. These models use estimates of landscape resistance (the degree to
19 which landscape features facilitate or impede animal movement) to predict the likelihood
20 of connectivity between habitat patches (Taylor et al., 2006). Several studies have now
21 shown the potential of landscape connectivity modelling to identify priority areas and
22 support conservation planning of a wide range of species, from herptiles (e.g. Mui et al.,
23 2017) and birds (e.g. Rayfield et al., 2016), to small (e.g. Fabrizio et al., 2019) and large
24 mammals (e.g. Roeber et al., 2013), including great ape species (Freeman et al., 2019;
25 Vanthomme et al., 2019).

26 As with all the other species of great apes, chimpanzees are classified either as Endangered
27 (Nigeria-Cameroon chimpanzees *P. t. ellioti*, central chimpanzees *P. t. troglodytes*, and
28 eastern chimpanzees *P. t. schweinfurthii*) or Critically Endangered (Western Chimpanzees
29 *P. t. verus*) by the International Union for Conservation of Nature (www.iucnredlist.org).
30 Tanzania represents the eastern and southern limit of chimpanzee distribution and hosts
31 two of the longest studies of their behaviour ([Gombe National Park](#): Pusey et al., 2007; and
32 [Mahale Mountains National Park](#): Nakamura et al., 2015; Fig. 1). However, several surveys
33 have now revealed that 75% of Tanzanian chimpanzees live outside of these two National
34 Parks, with the majority (~1 500) inhabiting the Greater Mahale Ecosystem (GME) (Kano et
35 al., 1999; Nakamura et al., 2013; Piel and Stewart, 2014; Plumptre et al., 2010; Yoshikawa et
36 al., 2008). This mosaic ecosystem dominated by miombo-woodland (*i.e.* [deciduous trees
37 and shrubs with grass understory and discontinuous canopy](#)) interspersed with riparian
38 forest offers an important diversity of resources for chimpanzees but is under several
39 pressures. Habitat loss through settlement expansion and conversion to agriculture
40 represents the primary threat to chimpanzees within the ecosystem, followed by annual

41 burning, logging, and poaching (Moyer et al., 2006; Piel and Stewart, 2014). Monitoring the
42 impact of habitat loss on remaining chimpanzee populations is logistically challenging
43 given that chimpanzees in this area are found at extremely low densities (Piel et al., 2015a).
44 Remote sensing technologies can help to overcome these challenges by providing precise
45 and accurate data across broad spatial and temporal scales (Marvin et al., 2016).

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

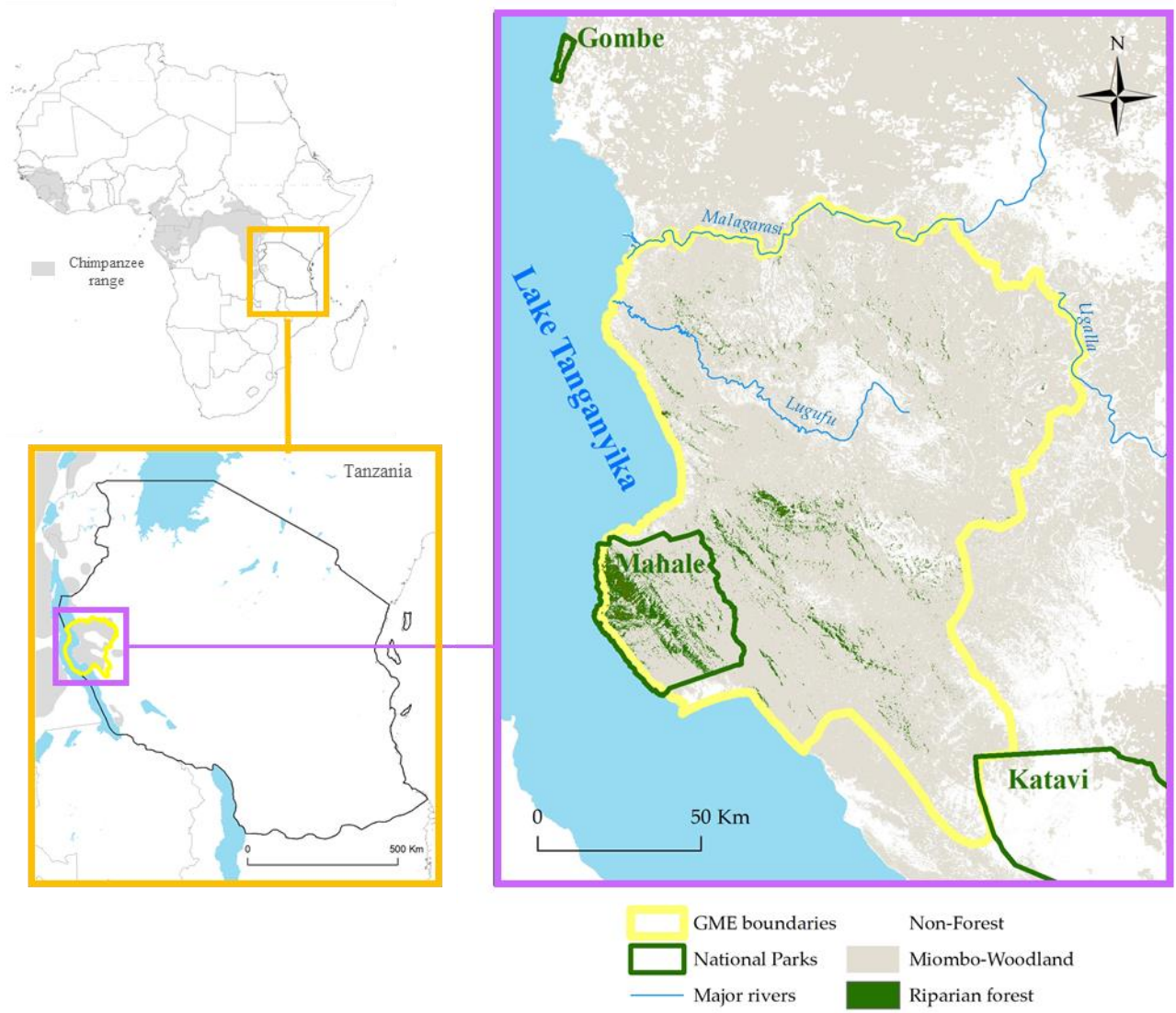
53 In this study, we aimed to (1) develop a habitat suitability model to create an index of
54 habitat selection by chimpanzees within the GME; (2) map functional habitat connectivity
55 independently of any a priori habitat patches or populations using circuit theory and our
56 resulting habitat selection model; finally (3) evaluate the impact of forest loss on habitat
57 connectivity by using remote sensing data from 1973 and a land-cover projection for 2027.
58 We hypothesised the GME to be connected by multiple area of high connectivity values in
59 1973. We also expected a reduction in connectivity associated with forest loss, now
60 isolating the northern and southern populations. Our results provide key information on
61 where to focus conservation efforts, not only to protect current chimpanzee habitat, but
62 also areas critical for connectivity that might be classified as only moderately suitable for
63 chimpanzee habitat. Identified areas of high likelihood of chimpanzee movement can be
64 used by conservationists to support detailed conservation planning needs of local human
65 communities and chimpanzees.

66 **2. Methods**

67 *2.1. Study area*

68 The GME is a $\approx 18\,000\text{ km}^2$ region in western Tanzania, bordered to the north by the
69 Malagarasi river, to the south by Katavi National Park, to the east by the Ugalla river and
70 to the west by Lake Tanganyika (Fig. 1). The area is dominated by miombo-woodland
71 (*Brachystegia* and *Julbernardia*, Fabaceae) with small patches of riparian forest, swamp,
72 bamboo and grassland. The topography consists of broad valleys separated by steep
73 mountains and flat plateaus ranging from 900 to 2 500 m above sea level. The GME
74 represents the southern and eastern extreme of chimpanzee distribution and is one of the
75 driest habitats in which they are found (Moore, 1992). The area includes the Mahale
76 Mountains National Park (MMNP), which protects a high level of biodiversity, although it
77 has been estimated that 75% of the chimpanzee population lives outside of MMNP (Moyer
78 et al., 2006). Since 2005, the Greater Mahale Ecosystem Research and Conservation Project
79 (GMERC) in collaboration with The Nature Conservancy (TNC), Frankfurt Zoological
80 Society (FZS), the Jane Goodall Institute (JGI), Tanzania Wildlife Research Institute
81 (TAWIRI), Tanzania National Parks (TANAPA) and District government partners have led

82 surveys to monitor chimpanzee populations. To account for potential chimpanzee
83 movement along the edges of the GME, we drew a 20km buffer around the GME
84 boundary.



98 woodland as vegetation types with tree canopy cover between 30% and 70%. We used the
99 global forest change product from GLAD (Global Land Analysis & Discovery) between
100 2000 to 2019 to estimate riparian forest and miombo-woodland areas in 2019. The 16-day
101 Landsat composites used to generate canopy cover for the 2000's is only available from
102 1997 onward. In order to map historical vegetation type, we acquired a 60-meter resolution
103 Landsat MSS scene for August 17, 1973 downloaded from <http://earthexplorer.usgs.gov>.
104 We georeferenced the image to the 2000 canopy cover layer using ArcGIS Desktop (Esri).
105 Both 2000 and 2019 vegetation layers were resampled from 30-meter to 60-meter
106 resolution to match 1973 coarser spatial resolution and support comparison between 1973,
107 2000 and 2019 vegetation types. To further improve comparison between the datasets, 2000
108 forest and woodland areas were masked out from the 1973 image, assuming that if areas
109 were forested in 2000 they were also forested in 1973. The remaining 1973 image was
110 classified in riparian forest, miombo-woodland and other non-forest/non-woodland
111 classes using unsupervised Iso Cluster algorithm in ArcGIS Desktop. To validate our 1973
112 vegetation layer, we used "Create Accuracy Assessment Points" function in ArcGIS
113 Desktop and generated 100 randomly distributed points within each class using the
114 Equalized Stratified Random sampling strategy (see Appendix S1 for more details).

115 The resulting land-cover map comprised three types representing non-forest, miombo-
116 woodland and riparian forest, the latter two being the main chimpanzee habitats in the
117 GME. Distance from riparian forest was calculated such that each grid value reflected the
118 linear distance from riparian forest (riparian forest pixels getting a zero value). We used
119 these landscape features because chimpanzees are highly dependent upon trees, many of
120 which host important food sources (Nishida et al., 1983; Piel et al., 2017) and for their role
121 as shelter e.g. nesting sites (Stewart et al., 2011). We extracted elevation and distance from
122 steep slopes (> 20 degrees) from a Shuttle Radar Topographic Mission (SRTM) layer (30 m
123 resolution; <http://earthexplorer.usgs.gov>) (Pintea & Plumptre 2006; Jantz et al. 2016). We
124 included topographic measures because altitude has an influence on chimpanzee
125 distribution (Fitzgerald et al., 2018; Plumptre et al., 2010). Elevation may act as a proxy for
126 suitable climatic conditions, affecting nesting site preference and food resource
127 distribution (Jantz et al., 2016). Moreover, in western Tanzania, studies have shown that
128 nesting sites are associated with steep slopes (Hernandez-Aguilar, 2009; Pintea and
129 Plumptre, 2006; Stewart, 2011). We fitted all four variables at 60 m resolution and
130 accounted for chimpanzee responses to vegetation type at a larger scale by creating a new
131 layer reflecting the proportion of riparian forest within a 30.8 km² neighbourhood, using
132 focal statistics in ArcGIS Desktop. We used 30.8 km², as this represents the average home
133 range size based on three habituated chimpanzee communities in the GME (55km² at Issa,
134 Piel and Stewart, unpublished data; 27.4 km² for M-group (MMNP), Nakamura et al., 2015
135 and 10km² for K-group (MMNP), Nishida, 2011). We did not include settlements or roads
136 as a predictor variable because of the difficulty of accessing reliable data for 1973. We
137 checked for collinearity by estimating the variance inflation factor (VIF; values>3
138 considered highly correlated predictors (Zuur et al. 2010)). We did not find
139 multicollinearity among our five predictor variables (VIF <1.3) and thus used all predictors
140 for further analyses.

141 *2.3.Land-cover change projections*

142 For future time periods, we used a model of predicted deforestation by 2027 developed for
143 the Ntakata REDD project (Shoch et al., 2019) which used Multi-Layer Perceptron neural
144 network to predict the likelihood of deforestation based on historical deforestation
145 occurring between 2007 and 2017. Predicted deforestation was used to create land-cover
146 map representing 2027 by reclassifying forest pixels mapped in 2017 to non-forest in 2027
147 where deforestation was projected.

148 *2.4. Habitat suitability modelling*

149 We decided to base our resistance values on a habitat suitability model, which is a
150 preferred alternative to expert opinion when empirical data on animal movement or
151 genetic distance are insufficient or not available (Beier et al., 2008; Stevenson-Holt et al.,
152 2014). To build our model, we used evidence of chimpanzee presence from surveys led by
153 GMERC between 2008 and 2020. By a combination of transects and reconnaissance walks
154 we have documented over 11 947 observations of chimpanzee presence (direct
155 observations, vocalizations, feces, feeding remains, nests, prints, and tools). For our
156 analysis, we removed vocalizations as chimpanzee calls can be heard up to 3km (Piel,
157 2014) and our modelling resolution is 60 m. In order to reduce spatial bias caused by
158 unequal sampling effort, we followed Kramer-Schadt et al.'s (2013) recommendations and
159 used spatial filtering and balancing of occurrence data, to reduce spatial autocorrelation.
160 For spatial filtering, we used Spatial Rarefy Tool in the SDM ToolBox v2.2 under ArcGIS
161 10.7 (Brown, 2014) to allow only one record per 60 x 60m. We chose this value to allow
162 sampling bias reduction and to keep a high spatial resolution on how landscape features
163 impact chimpanzee distribution. After spatial filtering, records were still heavily biased
164 towards the Issa valley, the GMERC long-term field site (Piel et al., 2015b). We thus further
165 reduced the number of records in Issa by randomly selecting 90 records to produce a
166 sample with the same density as the average density of the total covered area (Kramer-
167 Schadt et al., 2013). This resulted in N= 2 554 occurrence points used to train the final
168 model (Appendix S2, Fig. S2.1).

169 We used an ensemble of species distribution model algorithms because this approach
170 reduces the uncertainty associated with relying on a single method when projecting to a
171 different time period (Araújo and New, 2007; Buisson et al., 2010). We applied three
172 algorithms that have been shown to perform well when modelling species distributions:
173 Random Forests (RF), Generalised Boosted Models (GBM) and MAXENT (Elith, J. et al.,
174 2006; Elith and Graham, 2009). We used the default settings in the biomod2 package
175 (Version 3.3-7)] in the open-source software R (v. 3.6.1; <http://www.R-project.org/>) for
176 each algorithm (Thuiller et al., 2016)

177 We sampled 10 000 pseudo-absence records at random from the background extent,
178 excluding cells with previously removed true-presence points due to spatial filtering and
179 balancing of occurrences. We randomly divided the original dataset, using 70% to
180 construct the models and 30% to validate their accuracy. We replicated five runs to obtain
181 a robust estimate and tested accuracy using the Area Under the Curve (AUC). Only

182 models with AUC values equal to or greater than 0.9 were included in our final ensemble,
183 with the contribution of each model proportional to its goodness-of-fit statistics. The True
184 Skill Statistic (TSS) was also calculated for our final ensemble as an additional measure of
185 accuracy (Allouche et al., 2006).

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

$$188 \quad r = 100^{1-SDM}$$

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

193 *2.5. Circuit-based connectivity modelling*

194 We developed landscape connectivity maps using electricity circuit theory implemented
195 through Circuitscape 4.0.5 (Mcrae et al., 2008) using the pairwise mode which considers
196 conductance across all pairs of nodes in the study area. We decided to focus on circuit
197 theory rather than other commonly used modelling approaches (e.g. least-cost analysis)
198 because of its success to quantify animal movement and gene flow (Dickson et al., 2018)
199 and because of its ability to create a [quantitative proxy of probabilities](#) of connectivity
200 across an entire surface without the need to define focal patches. We followed the method
201 of Koen et al., (2014) to develop landscape connectivity maps that were independent of a
202 priori source or destination locations by randomly placing regularly distanced nodes
203 around a 40 km buffer perimeter (20% of the max length of the GME). To identify the
204 optimum number of nodes required to generate an unbiased landscape-scale permeability
205 map, we created 10 current density maps using 10–100 nodes at intervals of 10. We
206 selected 10 000 cells randomly in each current density map and used Pearson correlation to
207 compare estimates extracted from each current density map (i.e. 10 to 90 nodes) with
208 estimates from the full current density map (developed using 100 nodes). We considered
209 that our modelling was sufficient when the curve comparing correlation coefficients to the
210 number of node pairs reached an asymptote.

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

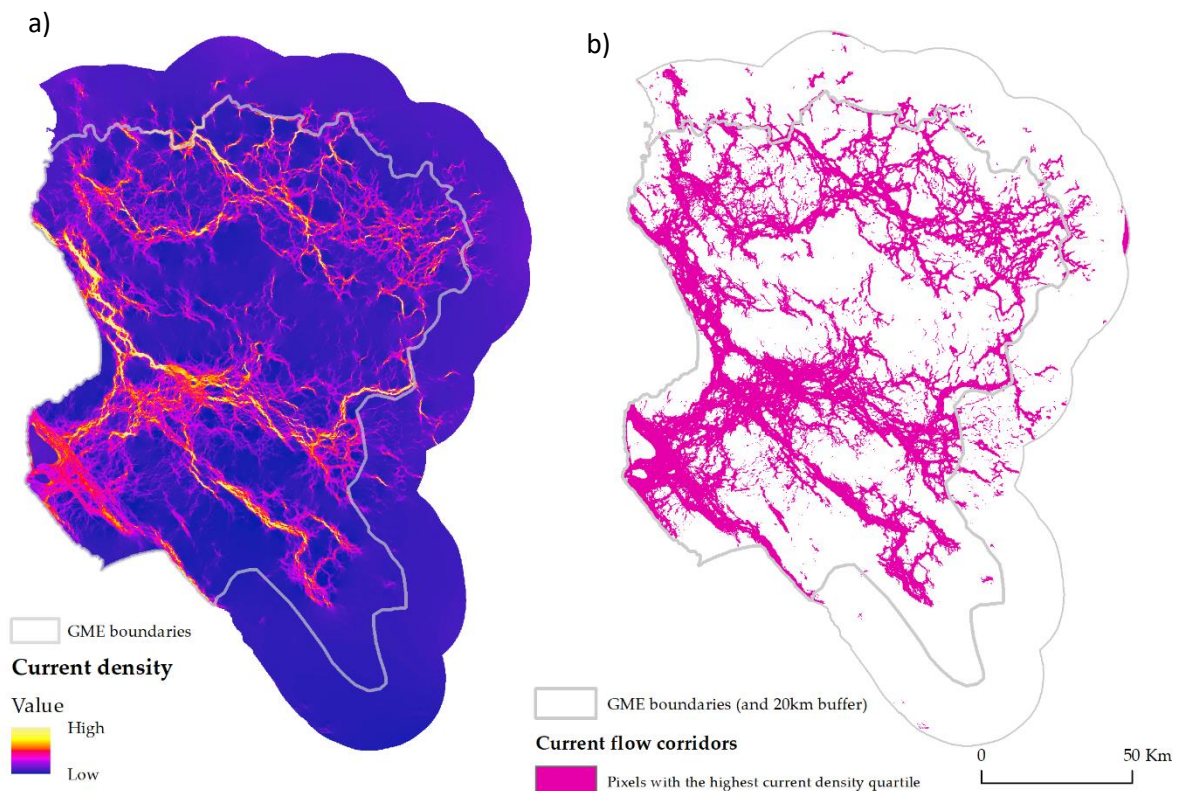
217 **3. Results**

218 The fit of the final chimpanzee habitat suitability model was 0.817 for TSS and 0.971 for
219 AUC, thus indicating a high level of predictive power. [Predictive accuracy of individual](#)
220 [models ranged from 0.744 \(+/-0.010\) to 0.776 \(+/-0.009\) for TSS and from 0.937 \(+/-0.004\) to](#)
221 [0.950 \(+/-0.003\) for AUC, depending on the algorithm. On average, RF models performed](#)

222 best compared to GBM and MAXENT models (Table. S1). The contribution of each
223 variable to the model was as follows: distance from steep slope (46.4%), distance from
224 riparian forest (31.6%), proportion of riparian forest (11.2%), elevation (6.1%) and
225 vegetation type (4.7%). The response curves produced by the model indicate that the
226 relative probability of chimpanzee occurrence decreases with distance from steep slopes as
227 well as with distance from riparian forest whereas it increases with proportion of riparian
228 forest. Regarding elevation, chimpanzees were most likely found between 1000 and 1850
229 m. Further, probability of presence was highest in riparian forest and lowest in non-
230 forested areas; miombo-woodland showed intermediate probabilities (Appendix S2, Fig.
231 S2.2).

232 Thirty node pairs were sufficient to generate unbiased connectivity maps (Appendix S2,
233 Fig. S2.3). The current density map derived from Circuitscape reflects relative probability
234 of movement, with areas of high current density representing higher probability of
235 movement. The GME appears to be connected by several current flow corridors facilitating
236 chimpanzee movement in 1973 (Fig. 2; Appendix S2, Fig. S2.4).

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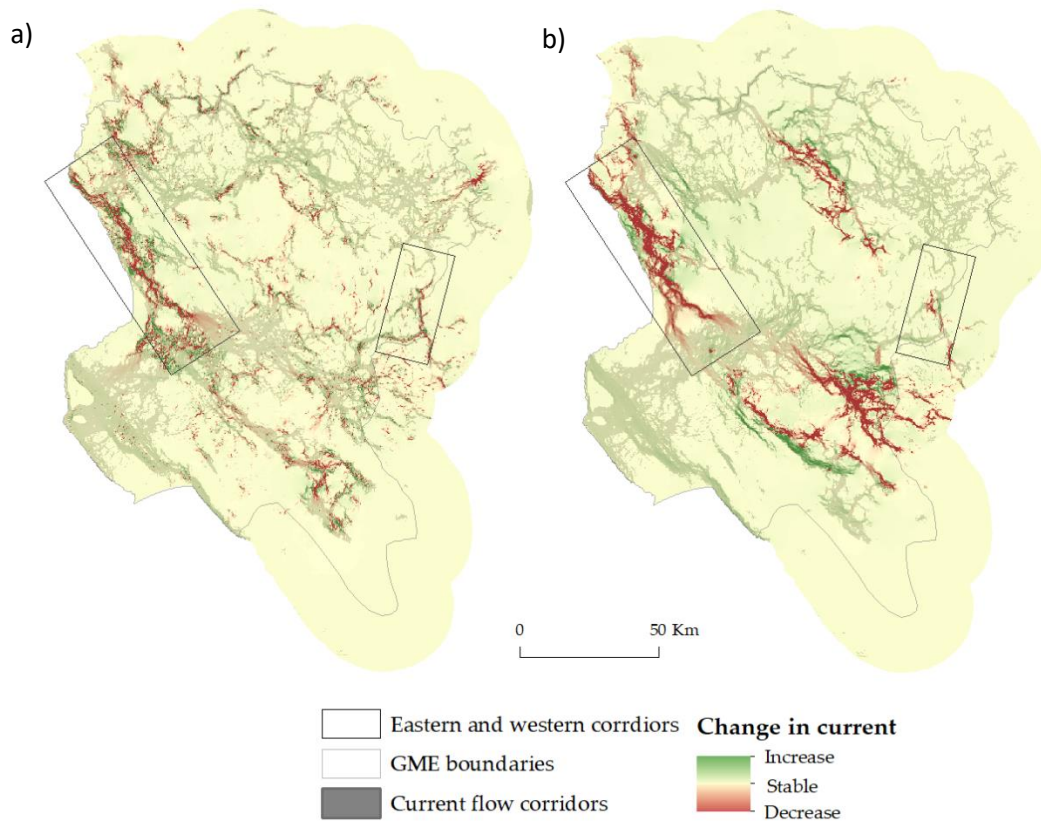


238

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

241 Although the pattern of landscape connectivity remained broadly similar over time
242 (Appendix S2, Fig. S2.5), a reduction in current density is observed for 1 966.7 km²
243 between 1973 and 2019. This reduction is impacting both current flow corridors linking the
244 northern and southern GME (Fig. 3a). When projecting to 2027, we predict 2 152.3 km²

245 further decline, severely impacting the western current flow corridor linking the northern
246 and southern GME and affecting a large area in the south-east of the GME (Fig. 3b).
247 Increase in current flow is also observed for both time periods corresponding to
248 displacement of probability of movement.



249
250 **Figure 3:** Current density change between a) 1973 and 2019, b) 2019 and 2027
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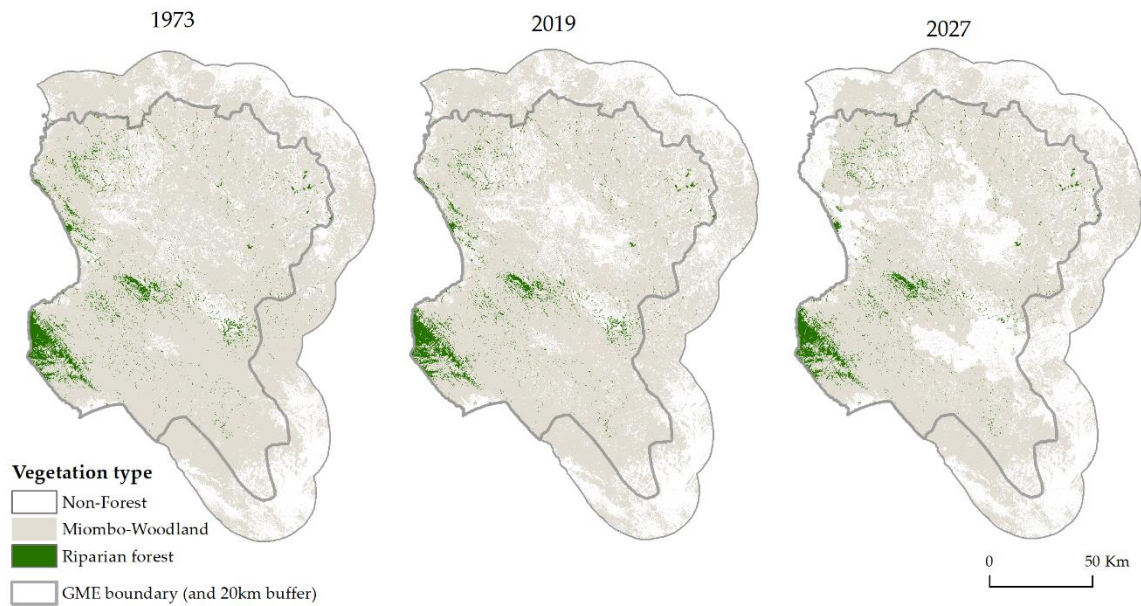
252 4. Discussion

253 Landscape connectivity is of central importance to maintain population viability,
254 especially in increasingly anthropogenically disturbed landscapes. We used circuit theory
255 to assess chimpanzee habitat connectivity within the GME, an area containing nearly the
256 entire free-ranging population of Tanzania's chimpanzees (Plumptre et al., 2010). Our
257 results suggest that the ecosystem was linked by a series of corridors showing a relatively
258 high probability of chimpanzee movement in 1973. This result is consistent with previous
259 population genetic analyses suggesting recent gene flow throughout the GME (Inoue et al.,
260 2011). Our analysis also reveals a reduction of connectivity impacting the two current flow
261 corridors linking the northern and southern GME. Mishamo, a refugee settlement
262 established in 1981 to host 35 000 Burundian refugees was hypothesised to separate the
263 ecosystem or at least hinder chimpanzee movement between the northern and the
264 southern population of the GME (Moyer et al., 2006; Piel and Stewart, 2015; Rudicell et al.,
265 2011). However, our 1973 model shows that the central part of the ecosystem was already
266 unsuitable for chimpanzees prior to the establishment of this settlement (Appendix S2, Fig.
267 S2.6). This result is supported by Kano's (1971) early work on chimpanzee distribution in

268 Tanzania, when he reported no chimpanzees in the Lugufu basin (location of Mishamo
269 establishment) following his extensive 1965-1967 surveys. The Lugufu Basin/Mishamo
270 region is mainly flat and was dominated by Miombo-woodland and grassland (Bomans et
271 al., 1981), whereas surveys indicate that chimpanzees select hilly areas with riparian
272 forests (Hernandez-aguilar, 2006; Kano, 1972; Moyer et al., 2006; Ogawa et al., 2013; Piel
273 and Stewart, 2014, [this study](#)). While the Mishamo refugee settlement expansion occurred
274 outside of chimpanzee habitat, the impact of increased human population density cannot
275 be overlooked. It is likely that the establishment of the refugee settlement and the arrival
276 of tens of thousands of people to the region has increased pressure on forests through
277 consumption of firewood, charcoal production, conversion of land for agriculture and
278 poaching (Jambiya et al., 2007; Ogawa et al., 2013, 2006a, 2006b; Whitaker, 1999).

279 A survey led 40 years after Kano's first expedition reported a reduction in chimpanzee
280 density in each revisited area within the GME, but no extinction of local populations
281 (Yoshikawa et al., 2008). Following surveys from Piel et al. (2015a) reported similar pattern
282 and found an overall decline in mean chimpanzee nest density between 2007 and 2014 in
283 the northern GME (previously identified as the Masito-Ugalla Ecosystem, MUE) and an
284 association between habitat loss and a decline in chimpanzee density. Our analysis of
285 Landsat images reveals a total forest (i.e. riparian forest and miombo-woodland) decline of
286 1 677 km² between 1973 and 2017 (Fig. 4). [Surprisingly, vegetation type contributes](#)
287 [relatively little to our model \(4.7%\) and deforestation of miombo-woodland did not have a](#)
288 [large impact on our landscape connectivity change. Instead, destruction of entire blocks of](#)
289 [riparian forests were responsible for the observed reduction of connectivity between 1973](#)
290 [and 2017 and have disproportionately affected current flow corridors. Although travelling](#)
291 [through more open miombo-woodland without nearby riparian forests may represent a](#)
292 [higher risk of predation, miombo-woodland could still have been used by chimpanzees to](#)
293 [a certain extent to reach sparsely distributed resources. The significant deforestation of](#)
294 [miombo-woodland in the centre of the GME and settling of thousands of humans in the](#)
295 [area is now likely to prevent any chimpanzee movements. This is particularly alarming](#)
296 [given that the Shoch et al. \(2019\) model predicts another 2 426 km² of forest to be lost by](#)
297 [2027, threatening a large area in the south-east of the GME \(Fig. 3b; Fig. 4\). The](#)
298 [consequences of habitat loss in this area will have a devastating impact on chimpanzees,](#)
299 [not only reducing suitable habitat, but also an area of high movement probability. This](#)
300 [area falls within the Ntakata REDD project boundaries, a project initiated in May 2017](#)
301 [with the goals of engaging and supporting local communities in the protection of their](#)
302 [village land forest reserves \(Shoch et al., 2019\). By providing support for community](#)
303 [patrols and monitoring by village game scouts, we are hopeful that this approach results](#)
304 [in increased conservation of this large, critical area of for chimpanzees.](#)

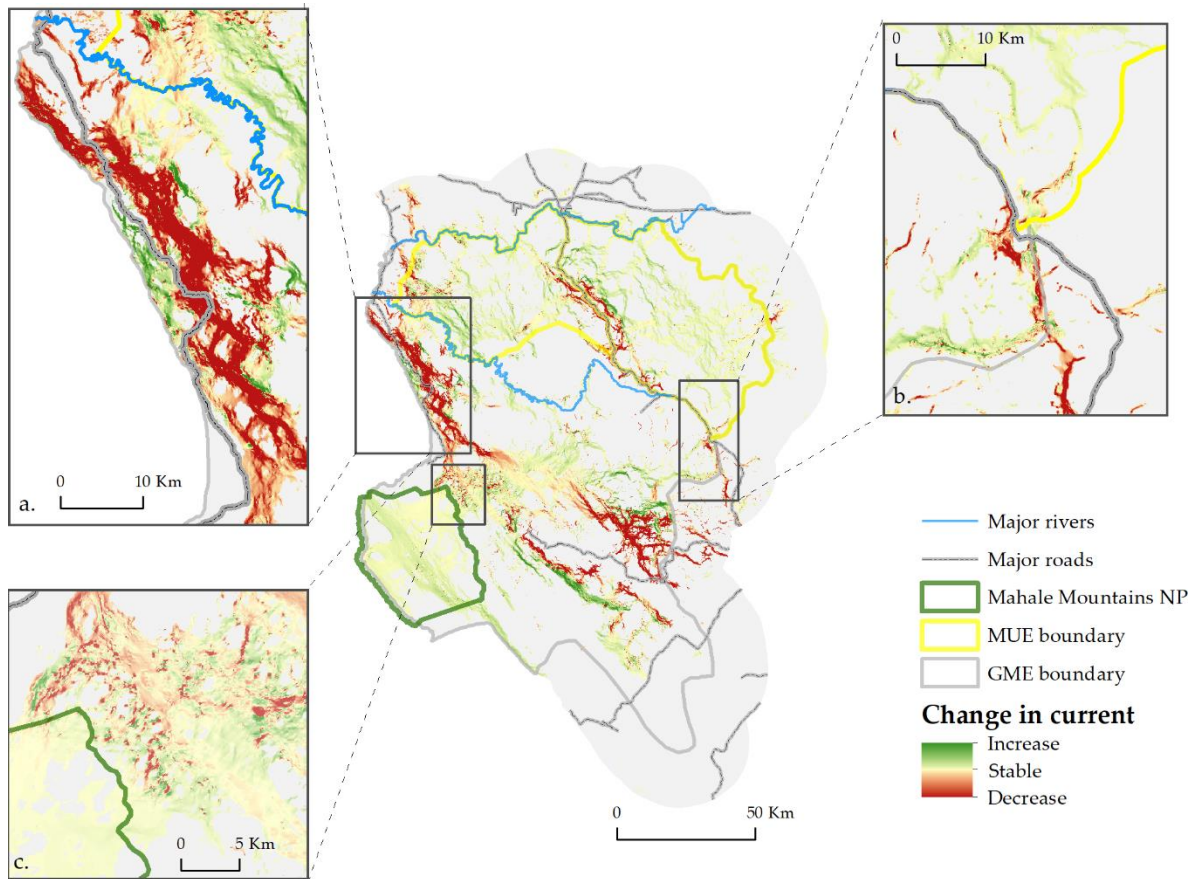
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306

307 **Figure 4:** Vegetation change from 1973 to 2027

308 Along with forest loss, the Mpanda-Uvinza road may have potentially played a role [in the](#)
 309 [current density reduction within](#) the eastern corridor. Splitting the ecosystem, the road
 310 crosses the only migration route available for movement of individuals from eastern MUE
 311 to the south (Fig. 5 Box b). Even though chimpanzees have been reported crossing and
 312 even using roads (Cibot et al., 2015; Hockings et al., 2006), roads can impede animal
 313 movement through mortality during crossing (McLennan and Asiimwe, 2016). Probably
 314 impacting chimpanzees more than the road itself, the associated deforestation enabled by
 315 easier access to forest resources is affecting habitat at a larger scale (Laurance et al., 2009;
 316 Palminteri et al., 2019; this study). Although this road was already established in 1973
 317 (Kano, 1971), increases in traffic and other associated anthropogenic pressures may have
 318 negatively impacted animal movement. [Chimpanzee presence has been reported on both](#)
 319 [sides of the road in the north of the ecosystem \(Piel and Stewart, 2014\), however,](#)
 320 [chimpanzee movement across the road still needs to be confirmed.](#) Investigations into
 321 what extent this road and its associated land use change limit chimpanzee movement and
 322 thus gene flow will have important implications for conservation, especially because the
 323 (currently, dirt) road is now in the process of being paved (NB pers. obs). The Ilagala-
 324 Mahale road running to the west of the ecosystem may also have deleterious impacts on
 325 chimpanzee habitat and movement. Its construction in 2006 was correlated with a
 326 dramatic increase in forest loss and construction plans foresee an extension of the road to
 327 the south of MMNP (Palminteri et al., 2019). Our model highlights critical areas for
 328 chimpanzees and could be used for the development of detailed land use planning along
 329 the road. [By establishing new village forest reserves and wildlife crossing structures across](#)
 330 [developing roads in these critical areas for chimpanzee movements we could help](#)
 331 [maintain movement and balance needs of local communities and chimpanzees \(Gloyne](#)
 332 [and Clevenger, 2001; Lasch et al., 2011; Plumptre et al., 2010; TAWIRI, 2018\).](#)



333

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

339 Large rivers may also act as barriers to animal movement (e.g. Eriksson et al. 2004). The
 340 GME is bordered by a large river, the Malagarasi, to the north, and segmented by the
 341 Lugufu river running through the north west of the ecosystem (Fig. 5 Box a). Inoue et al.
 342 (2013) proposed the Malagarasi river to be a major biogeographical boundary preventing
 343 chimpanzee movement into the GME from the north, however circumstantial evidence
 344 suggests that chimpanzees can move across the 100m wide river using natural, shallow
 345 fords, which together with further genetic evidence, suggests that the river does not form a
 346 complete barrier to gene flow (Piel et al., 2013). The Lugufu river is only 15 m wide (at its
 347 widest), and so may similarly allow some movement across it, especially in the dry season;
 348 however, more investigation is needed. Given the extreme seasonality of the ecosystem,
 349 with a six month dry season (<100 mm of rainfall/month), temporal variation of
 350 connectivity also remains to be examined. Variation of river flow and depth could result in
 351 temporal barriers to chimpanzee movement (Eriksson et al., 2004), but also affect the
 352 availability of water resources from smaller streams. Other resources such as plants also
 353 show important seasonal variation and are known to influence chimpanzee ranging
 354 patterns (Doran, 1997; Hasegawa, 1990; Wrangham, 1977). Adding phenological data (e.g.

355 resource availability) to our model would allow a better understanding of chimpanzee
356 movement within this extremely seasonal ecosystem.

357 Here we chose to derive resistance values from habitat suitability modelling, [which is](#)
358 [recommended over expert opinion although often underperforms compared to direct](#)
359 [movement data or genetic methods when sufficient genetic data are available \(Beier et al.,](#)
360 [2008; Stevenson-Holt et al., 2014\)](#). Less biased and more data-driven than expert opinion,
361 habitat suitability modelling allow the creation of a more precise resistance surface at a
362 fine-scale. However, our occurrence data are skewed towards sleeping sites, with nest
363 locations comprising 81% of our presence points. This may explain the major contribution
364 of steep slopes to our model as chimpanzee nests are often associated with steep slopes
365 within the ecosystem (Hernandez-Aguilar, 2009; Stewart, 2011), whereas feeding and
366 travel behaviour is likely not. Similarly, the importance of distance from riparian forest
367 may represent sleeping site preferences although chimpanzees use miombo-woodland
368 extensively for feeding and travelling (Hernandez-Aguilar, 2009; Nishida, 1989). [Further](#)
369 [work integrating genetic data \(e.g. landscape genetic analysis\) will help us better](#)
370 [understand how landscape features impact chimpanzee movement across the GME.](#)

371 Our models have confirmed [historical](#) connectivity throughout the GME and have
372 highlighted priority areas for chimpanzee conservation in Tanzania. First, our results
373 revealed potential corridors linking the northern and southern population of the GME
374 (Fig. 5 Box a. and b). Additional ground surveys and genetic analysis could confirm
375 whether chimpanzee movement is possible along this potential corridor and if there is
376 genetic exchange. Our model also identified corridors to the north-east of MMNP (Fig. 5
377 Box c). Previous surveys have confirmed chimpanzee presence in this area in 2011-2012
378 (Piel and Stewart, 2014). However, as for the eastern and western corridors linking the
379 northern and southern population of the GME, increasing anthropogenic pressure and
380 associated deforestation is threatening this corridor. We recommend focusing conservation
381 efforts on maintaining riparian forest, which is not only necessary for chimpanzee
382 survival, but also essential for the provision of natural resources on which local livelihoods
383 depend. Our model supports evidence of large areas within the GME that are suitable for
384 chimpanzee habitat and movement. Preference of GME chimpanzees for steep terrain may
385 have allowed their continued persistence, as such areas are difficult for humans to access
386 and are less favourable for conversion to other land-uses (Heinicke et al., 2019; Kinnaird et
387 al., 2003). By maintaining and possibly enhancing connectivity identified in this study and
388 giving priority to those areas currently under threat, we are optimistic that Tanzania can
389 continue to host a large viable population of chimpanzees.

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