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# 1 **Predicting range shifts of African apes under global change** 2 **scenarios**

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4

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73 **ABSTRACT**

74 **Aim:** Modelling African great ape distribution has until now focused on current or past  
75 conditions, whilst future scenarios remain scarcely explored. Using an ensemble forecasting  
76 approach, we predicted changes in taxon-specific distribution under future scenarios of  
77 climate, land-use and human population changes.

78 **Location:** Sub-Saharan Africa

79 **Methods:** We compiled occurrence data on African ape populations from the IUCN A.P.E.S.  
80 database and extracted relevant human-, climate- and habitat-related predictors representing  
81 current and future (2050) conditions to predict taxon-specific distribution under a best- and a  
82 worst-case scenario, using ensemble forecasting. Given the large effect on model predictions,  
83 we further tested algorithm sensitivity by considering *default* and *non-default* modelling  
84 options. The latter included interactions between predictors and polynomial terms in  
85 correlative algorithms.

86 **Results:** The future distributions of gorilla and bonobo populations are likely to be directly  
87 determined by climate-related variables. In contrast, future chimpanzee distribution is  
88 influenced mostly by anthropogenic variables. Both our modelling approaches produced  
89 similar model accuracy, although a slight difference in the magnitude of range change was  
90 found for *Gorilla beringei beringei*, *G. gorilla diehli*, and *Pan troglodytes schweinfurthii*. On  
91 average, a decline of 50% of the geographic range (*non-default*; or 55% *default*) is expected  
92 under the best scenario if no dispersal occurs (57% *non-default* or 58% *default* in worst  
93 scenario). However, new areas of suitable habitat are predicted to become available for most  
94 taxa if dispersal occurs (81% or 103% best, 93% or 91% worst, *non-default* and *default*,  
95 respectively), except for *G. b. beringei*.

96 **Main Conclusions:** Despite the uncertainty in predicting the precise proportion of suitable  
97 habitat by 2050, both modelling approaches predict large range losses for all African apes.  
98 Thus, conservation planners urgently need to integrate land-use planning and simultaneously  
99 support conservation and climate change mitigation measures at all decision-making levels  
100 both in range countries and abroad.

101

102 **KEYWORDS:**

103 Bonobo, chimpanzee, climate change, configuration option settings, gorilla, great ape, habitat  
104 loss, human population scenarios, IUCN SSC A.P.E.S. database, species distribution  
105 modelling

106

## 107 INTRODUCTION

108 Currently, a major conservation challenge is to assess the potential future effects of climate  
109 and land-use changes on species distributions, typically through the use of species  
110 distribution models (SDMs), and usually under a range of future environmental scenarios.  
111 SDMs are widely used to predict and map species' ecological niches through time and space  
112 (Elith & Leathwick, 2009; Guillera-Arroita et al., 2015; Hao, Elith, Guillera-Arroita, &  
113 Lahoz-Monfort, 2019). Importantly, SDMs can inform spatial prioritization decisions for  
114 conservation and management actions, such as identification of strategic locations for new  
115 conservation or survey sites, and predicting future distributions (Araújo & New, 2007; Elith  
116 & Leathwick, 2009; Guillera-Arroita et al., 2015).

117 Changes in climate and land use are among the main global threats to biodiversity, therefore,  
118 how the synergistic interactions between these drivers impact species is an important area of  
119 research (Oliver & Morecroft, 2014). Newbold et al. (2018) assessed the single and combined  
120 effects of future climate and land-use change on local vertebrate biodiversity. They found that  
121 climate change is likely to be the principal driver of species distribution change in coming  
122 decades, equalling or surpassing the potential effects of land-use change by 2070. Because  
123 human population growth is already an extinction threat to many species (McKee, Chambers,  
124 & Guseman, 2013), it is important to determine how human distribution will impact future  
125 species presence (Jones & O'Neill, 2016).

126 Many primates are facing imminent extinction, due to extensive habitat loss and  
127 fragmentation, land-use change, global commodity growth and trade, and hunting (Estrada et  
128 al., 2018). Climate change is a delocalised, multi-faceted driver to add to the list. It exposes  
129 many species, especially forest-dwelling primates, to climatically unsuitable conditions  
130 (Carvalho et al., 2019). Primates have relatively limited dispersal abilities for their body size,  
131 slow reproduction, low population densities, dietary requirements and poor thermoregulation,  
132 and a predicted reduction of up to 86% of the Neotropical primate ranges with >3°C warming  
133 is likely to constrain their dispersal, resulting in elevated risks of extinction (Carvalho et al.,  
134 2019).

135 All African great apes (hereafter African apes) are classified either as Endangered (mountain  
136 gorillas *G. b. beringei*, bonobos *Pan paniscus*, Nigeria-Cameroon chimpanzees *P. t. ellioti*,  
137 eastern chimpanzees *P. t. schweinfurthii* and central chimpanzees *P. t. troglodytes*) or  
138 Critically Endangered (Grauer's gorillas *G. b. graueri*, Cross River gorillas *G. g. diehli*,  
139 western lowland gorillas *G. g. gorilla* and western chimpanzees *P. t. verus*) on the IUCN Red  
140 List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org)) and are regarded as flagship species for  
141 conservation. African apes have faced dramatic changes in suitable environmental conditions  
142 over the past 20 years (Junker et al., 2012) as well as large population losses (Kuehl et al.,  
143 2017; Plumptre et al., 2016; Strindberg et al., 2018) caused by human activities and/or  
144 infectious epidemics (Walsh et al., 2003). Many African apes live in areas that are suitable  
145 for agricultural expansion and 58.7% of oil-palm concessions currently overlap with African  
146 ape ranges (Wich et al., 2014). Moreover, massive development corridors (Heinicke et al.,  
147 2019) and mining activities (Howard, 2019) in their geographic ranges are projected to  
148 expand considerably, and to disrupt ape habitat connectivity and accelerate habitat loss.

149 Most African apes occur outside protected areas (Freeman, Roehrdanz, & Peterson, 2018;  
150 Heinicke et al., 2019; Strindberg et al., 2018). Importantly, protected areas will not be exempt

151 from climate change (Araújo, Alagador, Cabeza, Nogués-Bravo, & Thuiller, 2011), and shifts  
152 in species ranges as predicted by future scenarios would certainly determine the degree of  
153 species representation within protected areas. Improving the effectiveness of conservation  
154 efforts in protected areas as well as habitat connectivity would allow apes to disperse to new  
155 climatically suitable areas, and favour ape population survival in the long term.

156 A few studies have examined the future effects of climate change on African apes (Lehmann,  
157 Korstjens, & Dunbar, 2010; Thorne et al., 2013). Lehmann et al. (2010) investigated how  
158 climate change is likely to influence survival and reported that chimpanzees may lose 10% of  
159 their range, and gorillas 75% by year 2100. Given the small range of mountain gorillas and  
160 their highly restricted occurrence in mountain refuges as a result of human encroachment and  
161 the geographic barrier of the Rift Valley, one would expect them to be particularly  
162 susceptible to global warming and extinction (Thorne et al., 2013). However, in general, how  
163 future synergetic interactions among climate, land-use and human population changes will  
164 affect African apes and their habitat has been largely unexplored.

165 Here we combine data on projected climate, land-use and human population changes to  
166 model African ape distribution for the year 2050. We use the most comprehensive database  
167 on ape populations available, the IUCN SSC Ape Populations, Environments and Surveys  
168 database (A.P.E.S.) to predict the distribution of great apes on the African continent under  
169 best- and worst-case scenarios. We subsequently consider an ensemble forecasting approach  
170 to reduce the uncertainty among different models and future scenarios (Araújo & New, 2007;  
171 Thuiller, 2004) and estimate the proportional change in range size in 2050 relative to current  
172 estimated range sizes for African apes.

173

## 174 **METHODS**

### 175 **African ape data**

176 We compiled information on African ape occurrence held in the IUCN SSC A.P.E.S.  
177 database, a repository that includes a remarkable amount of information on population status,  
178 threats and conservation for several hundred sites (Heinicke et al., 2019; Kuehl, Williamson,  
179 Sanz, Morgan, & Boesch, 2007). We extracted all occurrence data, which are georeferenced  
180 point data of direct sightings and great ape sign (mostly night nests) collected over 20 years  
181 (1998-2017, see Appendix S1 in Supporting Information, Table S1.1). We obtained a total of  
182 62,469 presence records across all African ape taxa (occurrence data for each species in  
183 Table S1.1).

184 Although these data may be spatially biased as sampling effort is unevenly spread over the  
185 ape range, presence-only data are commonly the most available and hence most frequently  
186 used in SDMs (Phillips et al., 2009). The (sub)species (hereafter taxon) occurrence data we  
187 used were collected during systematic site-based wildlife and human impact surveys, which  
188 were generally based on some prior knowledge of occurrence, often in or close to protected  
189 areas, FSC-certified and other logging concessions, and from habituated populations, factors  
190 that can distort an SDM (Phillips et al., 2009). Different approaches have been applied to  
191 account for biased datasets: random background, bias background, geographic  
192 thinning/filtering, and environmental filtering (Aiello-Lammens, Boria, Radosavljevic,  
193 Vilela, & Anderson, 2015; Fourcade, Engler, Rödder, & Secondi, 2014; Phillips et al., 2009;

194 Varela, Anderson, García-Valdés, & Fernández-González, 2014). Thus, we considered all  
195 approaches, and for the bias background distances to roads, protected areas and villages were  
196 included. We favoured the approach with the best performance by visually inspecting the  
197 greatest overlap between taxon occurrence and each sampling bias (Fig. S1.1). Given that the  
198 geographic thinning approach performed best for all taxa, we integrated it into the SDMs for  
199 sampling bias correction (Fig. S1.1, Table S1.1).

200 Model algorithms require presence and absence data, so we generated a set of 10,000 pseudo-  
201 absence occurrences (Guillera-Arroita et al., 2015; Phillips et al., 2009) in the range of each  
202 taxon, except for *G. b. beringei*. Only 1,000 background occurrences were created for  
203 mountain gorillas due to their small range.

204 We delineated taxon-specific study regions to avoid unrealistic geographical predictions  
205 (Anderson & Gonzalez, 2011). For this, we created buffers bounding IUCN range polygons  
206 (IUCN, 2018) and included all occurrence data for each taxon (Table S1.1) (Jantz, Pinteá,  
207 Nackoney, & Hansen, 2016; Junker et al., 2012; Thorne et al., 2013). Whenever the buffer  
208 overpassed a known geographic barrier to ape dispersal (e.g. major rivers), we disregarded  
209 that area.

210

## 211 **Predictor variables**

212 We selected predictor variables based on their importance for African ape ecology, whilst  
213 guaranteeing data availability for current and future conditions (2050) under best- and worst-  
214 case scenarios and minimizing correlation between variables. We compiled altitude and  
215 climatic variables ( $N=19$ ) for the present and future conditions from Worldclim (periods of  
216 1950-2000 and 2050, respectively; Table S1.1, (Hijmans, Cameron, Parra, Jones, & Jarvis,  
217 2005)). For future predictions, we chose a best-case scenario (i.e. high mitigation scenario,  
218 CCSM4 RCP 4.5) and a worst-case scenario (i.e. low mitigation scenario, HadGEM-ES RCP  
219 8.5) (for more details see (Carvalho et al., 2019)). Land-use/cover data for current conditions  
220 and 2050 projections were compiled from the Land-use Harmonization Project (period of  
221 1500-2100, Table S1.1, (Chini, Hurtt, & Froking, 2014; Hurtt et al., 2011)). This dataset  
222 represents a set of land-use change and emission scenarios for studies of human impact on the  
223 past and future global carbon-climate system. Again, we considered a best-case scenario  
224 (MiniCam RCP 4.5) and a worst-case scenario (MESSAGE RCP 8.5) (Carvalho et al., 2019).  
225 We focused on the land-use states that best represent biomes where great apes can be found:  
226 primary (i.e. natural vegetation (either forest or non-forest) undisturbed by humans),  
227 secondary (i.e. natural vegetation previously disturbed by agriculture or wood harvesting),  
228 and cropland.

229 We based human population scenarios on a new set of future societal development scenarios,  
230 namely Shared Socioeconomic Pathways (SSP) (Table S1.1) (Jones & O'Neill, 2016). These  
231 future scenarios are based on both qualitative narratives of future development and  
232 quantitative projections of key elements such as human population growth at the national  
233 level, educational composition, urbanization and economic growth. These data are available  
234 from 2010 to 2100 for urban and rural population. We used two future scenarios, SSP1 and  
235 SSP3, given that they represent best- and worst-case scenarios, respectively.

236 We also considered distances to roads, villages and rivers as they are known to influence the  
237 distribution of African apes (Table S1.1) (Carvalho, Marques, & Vicente, 2013). We  
238 extracted data on protected areas in each taxon distribution from the most comprehensive  
239 global database on terrestrial and marine protected areas, the World Database on Protected  
240 Areas (Table S1.1).

241 Firstly, we extracted all variables for the extent of the range of each taxon, resampled onto a  
242 5km x 5km equal-area grid and projected them into the WGS 1984 geographic coordinate  
243 system. Secondly, we used Spearman rank correlations to select a subset of least correlated  
244 variables to minimize multicollinearity (Brun et al., 2019). For this, we used a graphical  
245 representation of the correlation values between variables to identify five least correlated  
246 variables for each species to avoid overfitting in model predictions (Fig. S1.2) (Thorne et al.,  
247 2013). We performed data analyses using the software R version 3.6.1 (R Development Core  
248 Team, 2019) and ArcMap version 10.4.1 (ESRI, 2011).

249

## 250 **SDM performance and ensemble forecasting**

251 We predicted future African ape distributions using an ensemble forecasting approach (i.e.  
252 combining predictions from individual models into an ensemble as implemented in the  
253 ‘biomod2’ package in R (version 3.3-7)) (Thuiller, Georges, & Engler, 2016). We selected  
254 two correlative algorithms, generalised linear model (GLM) and generalised additive model  
255 (GAM), and three machine-learning techniques, Maxent, random forest (RF) and artificial  
256 neural networks (ANN) to build predictive SDMs for each species. These algorithms have  
257 been shown to perform well in previous SDMs (Elith et al., 2006; Thuiller, Lafourcade,  
258 Engler, & Araújo, 2009). As the choice of configuration settings of individual modelling  
259 algorithms has potentially considerable impacts on predicted distributions (Hallgren, Santana,  
260 Low-Choy, Zhao, & Mackey, 2019), we contrasted results under two modelling approaches  
261 by 1) using the default tuning options of algorithms (i.e. *default*), and 2) changing the  
262 configuration settings of algorithms (i.e. *non-default*). The latter included changes in the  
263 correlative algorithms, particularly defining interactions between predictors as well as  
264 polynomial terms, to better represent assumptions about the ecological niche of each taxon  
265 (see R code in Appendix S2).

266 For the present time period only, we assessed the predictive performance of each model  
267 through cross validation using a bootstrap approach, i.e. partitioning of the presence data,  
268 using 80% of presences, randomly selected, for model calibration and 20% for evaluation,  
269 and repeating this procedure 5 times (Thuiller et al., 2009). We evaluated the performance of  
270 each model by the ‘true skill statistic’ metric (TSS) (Allouche, Tsoar, & Kadmon, 2006). TSS  
271 is an accuracy measure that accounts both for omission errors (i.e. the percentage of true  
272 presences predicted as absences are minimised) and commission errors (i.e. the percentage of  
273 true absences predicted as presences are minimised), is unaffected by prevalence, and ranges  
274 from -1 to 1, with a prediction accuracy considered similar to ‘random’ when  $\leq 0$ , ‘poor’ in  
275 the range 0.2-0.5, ‘useful’ in the range 0.6-0.8, and ‘good’ to ‘excellent’ when  $> 0.8$  (Allouche  
276 et al., 2006).

277 Ensemble forecasting has been widely employed to reduce the uncertainties associated with  
278 using a single algorithm, and is a useful method to account for uncertainties of extrapolation  
279 of species-environment relationships outside the environments sampled by the species data



280 (Araújo & New, 2007; Hao et al., 2019; Thuiller, Guéguen, Renaud, Karger, & Zimmermann,  
281 2019; Thuiller et al., 2009). We chose to apply the weighted mean ensemble method, which  
282 scales predictions of different models by weights based on some measure of predictive  
283 performance (Araújo & New, 2007; Thuiller et al., 2009). We included only individual  
284 models that reached very ‘good’ predictive accuracies (TSS>0.8) in ensemble models to map  
285 the current and future habitat suitability predicted for each taxon (Thuiller et al., 2019). For  
286 each modelling approach, we repeated the modelling five times (cross-validation) and given  
287 the five modelling algorithms and the three repetitions for variable importance (see below),  
288 we obtained an ensemble of 75 predicted distributions for each species for each time period  
289 (present and 2050) and future scenarios (best- and worst-case scenarios).

290

### 291 **Relative importance of predictors**

292 For each taxon and modelling approach, we calculated the importance of each predictor by  
293 correlating the fitted values of the full models with those from the model in which the values  
294 of the predictor were randomly permuted. We repeated this procedure three times (default  
295 settings of ‘biomod2’ were used) and used the average Pearson’s correlation to measure  
296 variable importance. A high correlation between the values from the full and permuted  
297 models indicates that the variable has a low importance, contributing poorly to the model. We  
298 then ranked each variable value based on the correlation coefficients and reversed its relative  
299 importance and scaled from 0 to 1, the more influential variables for the model representing  
300 those with a higher relative importance (Thuiller et al., 2009).

301

### 302 **Species range change**

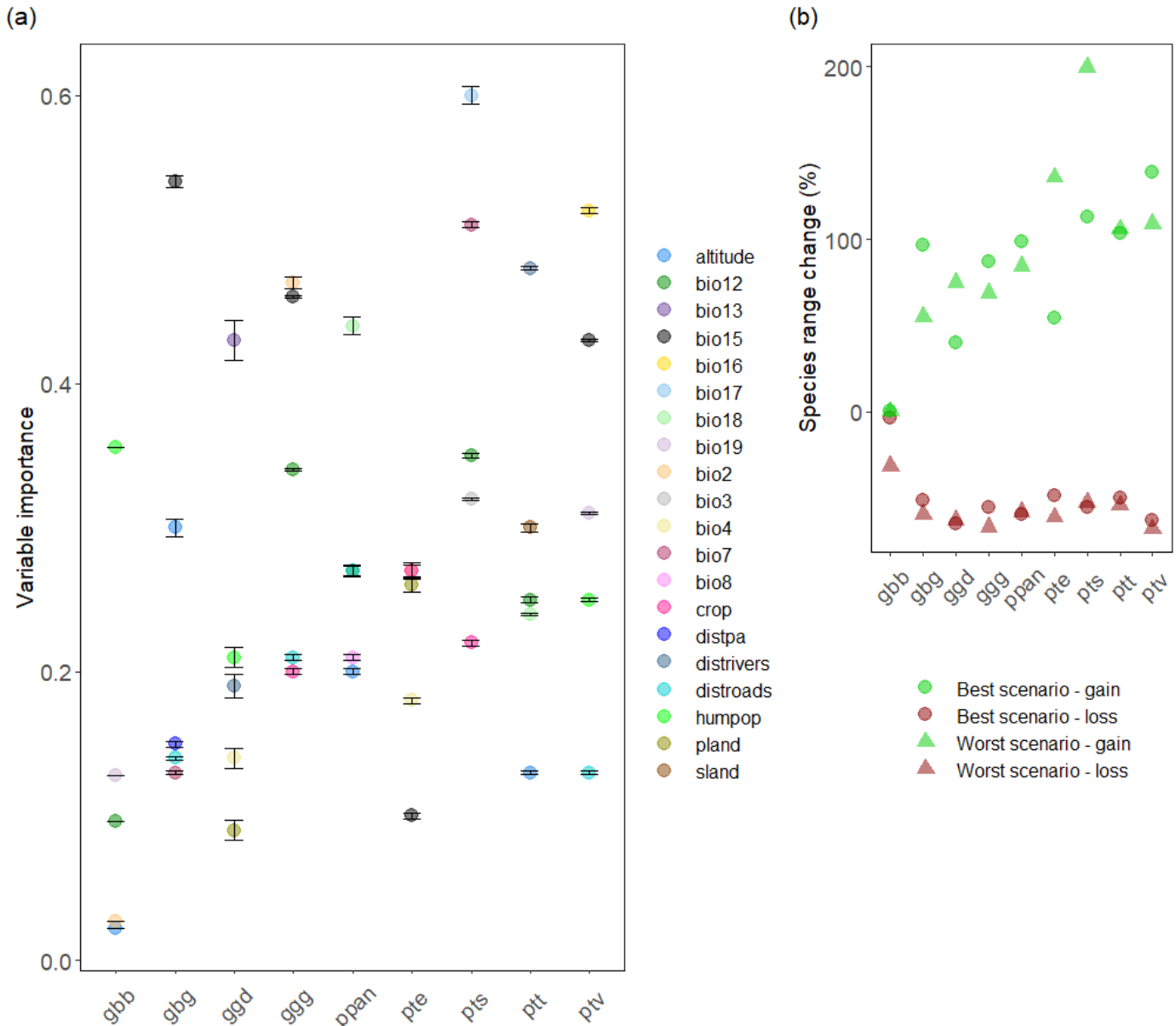
303 We estimated the proportional change in range size, in 2050 compared to the present, for  
304 each taxon by subtracting the future prediction ensemble output from the SDMs for the best-  
305 and worst-case scenarios from that under current conditions. We considered continuous  
306 predictive outputs from ensemble models as they provide richer information over outputs  
307 classified into binary maps, particularly when the purpose of our study is to inform spatial  
308 prioritization decisions for conservation and management actions (Guillera-Aroita et al.,  
309 2015).

310 We subsequently identified areas of range loss (i.e. sites where the species is present at the  
311 moment but is likely to be absent in the future), gain (i.e., sites where the species is absent at  
312 the moment but is likely to be present in the future), and stability (i.e., sites where the species  
313 is potentially present at the moment and is likely to be present in the future). For this, we  
314 considered range change under two contrasting dispersal scenarios: 1) full dispersal, which  
315 assumes that the species can disperse to new suitable areas in the future; and 2) no dispersal,  
316 which assumes that the species will be unable to disperse and only the overlap between  
317 present and future distributions will be the expected suitable habitat for the species (Thomas  
318 et al., 2004).

319

## 320 **RESULTS**

321 In general, both modelling approaches (*default* and *non-default*) resulted in similar predictive  
 322 accuracy of individual and ensemble models and in the relative importance of the variable  
 323 predictors (Fig. 1, S1.3-4). Predictive accuracy of the individual models based on TSS was  
 324 ‘useful’ to ‘excellent’, depending on the algorithm (Fig. S1.3). On average, RF models  
 325 performed best relative to ANN and GLM models which performed worst at predicting  
 326 species distributions (Fig. S1.3a). Importantly, with TSS scores >0.9 ensemble models had  
 327 excellent predictive accuracy and clearly outperformed individual models (Fig. S1.3b).



329 Figure 1. Results for the modelling approach where algorithm settings were changed for each African ape  
 330 species (i.e. *non-default*). (a) Variable importance (mean and standard deviation (SD) of the correlation values)  
 331 for the ensemble models, and (b) Predicted percentage change in African ape ranges by 2050 under the best- and  
 332 the worst-case scenario, assuming no dispersal (loss) and dispersal (gain) scenarios. Variable predictor  
 333 abbreviations: bio12 – annual precipitation, bio13 – precipitation of wettest month, bio15 – Seasonal variation  
 334 of precipitation, bio16 – precipitation of wettest quarter, bio17 – precipitation of driest quarter, bio18 –  
 335 precipitation of warmest quarter, bio19 – precipitation of coldest quarter, bio2 – mean diurnal range, bio3 –  
 336 isothermality, bio4 – temperature seasonality, bio7 – temperature annual range, bio8 – mean temperature of

337 wettest quarter, crop – cropland, distpa – distance to protected areas, distrivers – distances to rivers, distroads –  
338 distances to roads, humpop – human population density, pland – primary land, sland – secondary land.

339

340 Our ensemble models indicated that the current distribution of *G. b. beringei*, *P. t. ellioti* and  
341 *P. t. troglodytes* is strongly determined by anthropogenic variables, in contrast to the greater  
342 influence of climate-related variables on the distribution of *G. b. graueri*, *G. g. diehli*, *G. g.*  
343 *gorilla*, *P. paniscus*, *P. t. schweinfurthii* and *P. t. verus* (Fig. 1, S1.4-6). Our models indicate  
344 that the future distributions of most gorillas and bonobos will be more heavily influenced by  
345 climate-related variables, contrasting with the greater influence of anthropogenic variables in  
346 shaping the chimpanzee distribution (Fig. S1.5-6).

347 On average, the same trend in species range change was estimated for both *default* and *non-*  
348 *default* modelling approaches (Fig. 2, 3, S1.7-8). However, the *non-default* approach  
349 predicted a slightly lower range loss (50% or 57% under the best and worst scenarios,  
350 respectively) and lower range gain (81% or 93% under the best and worst scenarios,  
351 respectively) than the *default* approach (loss: 55% or 58%, gain: 103% or 91%, under the best  
352 and worst scenarios, respectively) (Fig. 3, S1.8). Moreover, differences were found in the  
353 magnitude of change for some taxa, particularly for *G. b. beringei*, *G. g. diehli* and *P. t.*  
354 *schweinfurthii*. To simplify, only results from the *non-default* approach are presented below  
355 (details for the *default* approach are provided in Appendix S1).

356

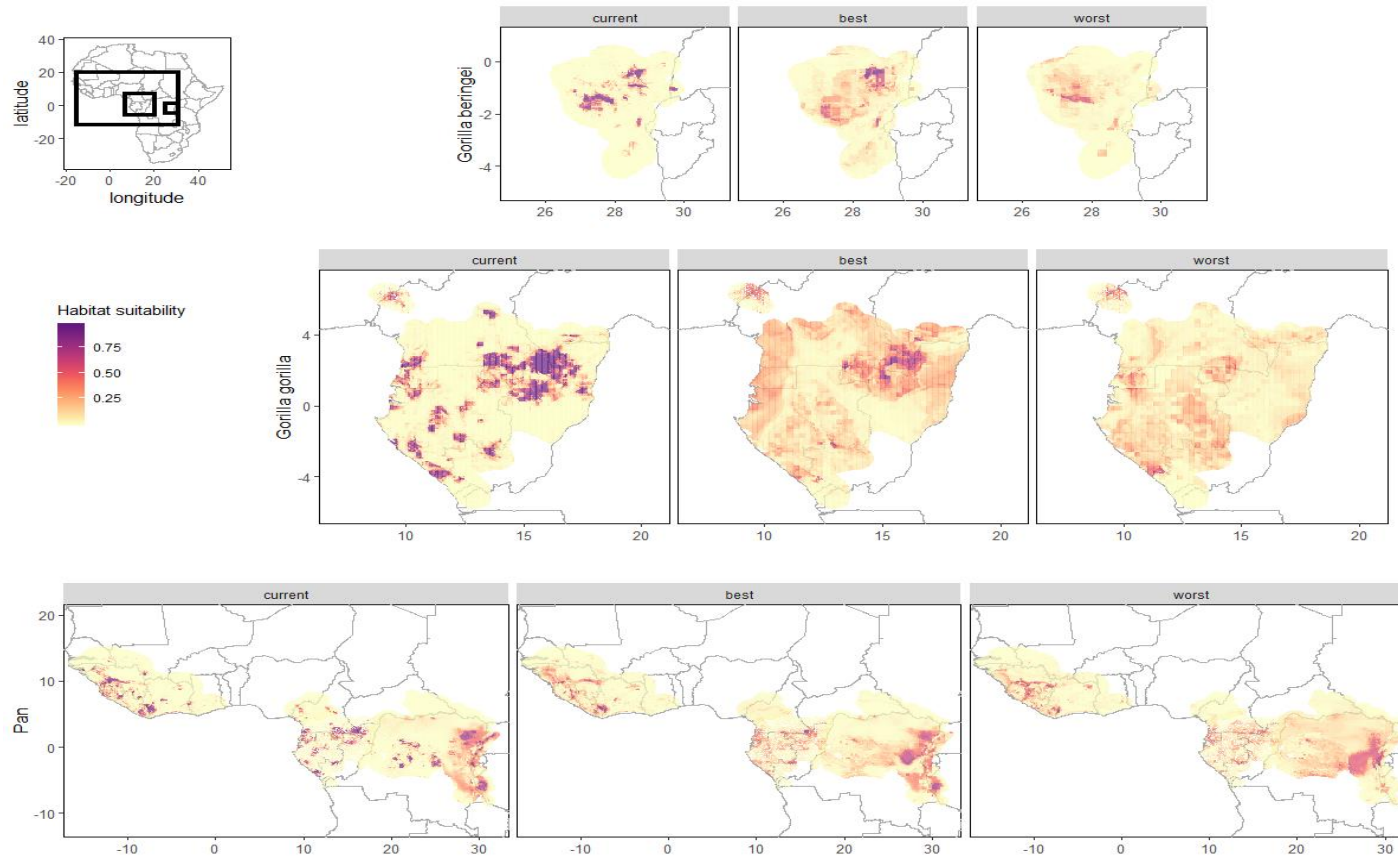
### 357 ***Gorilla beringei beringei*** (mountain gorilla)

358 Annual precipitation contributed most in the correlative models, whereas human population  
359 density was the strongest determinant of mountain gorilla distribution in machine-learning  
360 and ensemble models (Fig. S1.4). This taxon is confined to artificial ‘island’ areas in a sea of  
361 agriculture where annual precipitation (1,200-1,500 mm), diurnal temperature range (11-12  
362 °C), human population (3,000-10,000 people/km<sup>2</sup>), and elevation (1,500-2,200 m) are high,  
363 and precipitation in the coldest quarter is low (180-440 mm) (Fig. S1.5-6). Precipitation  
364 variables will increase and diurnal temperature range will decrease by 2050 under the best  
365 scenario (Fig. S1.5-6). However, the opposite is predicted under the worst scenario. Human  
366 population growth is predicted to occur under both future scenarios.

367 Range stability is predicted to occur under the best scenario, but one-third of current suitable  
368 habitat is predicted to be lost under the worst scenario (Fig. 3, S1.7). Moreover, both future  
369 scenarios agree that dispersal is unlikely given that no new suitable habitat will become  
370 available for mountain gorillas.

### 371 ***Gorilla beringei graueri*** (Grauer's gorilla)

372 Seasonal variation in precipitation (precipitation seasonality) was the most important variable  
373 in both individual and ensemble models in predicting the distribution of Grauer's gorillas  
374 (Fig. S1.4). This taxon is predicted to persist where seasonal variation of precipitation is low  
375 (25-40 mm), diurnal temperature range (12-13 °C) and altitude (500-1500 m) are high, close  
376 to roads (<6 km) and far from protected areas (<30 km) (Fig. S1.5-6). Both climatic variables



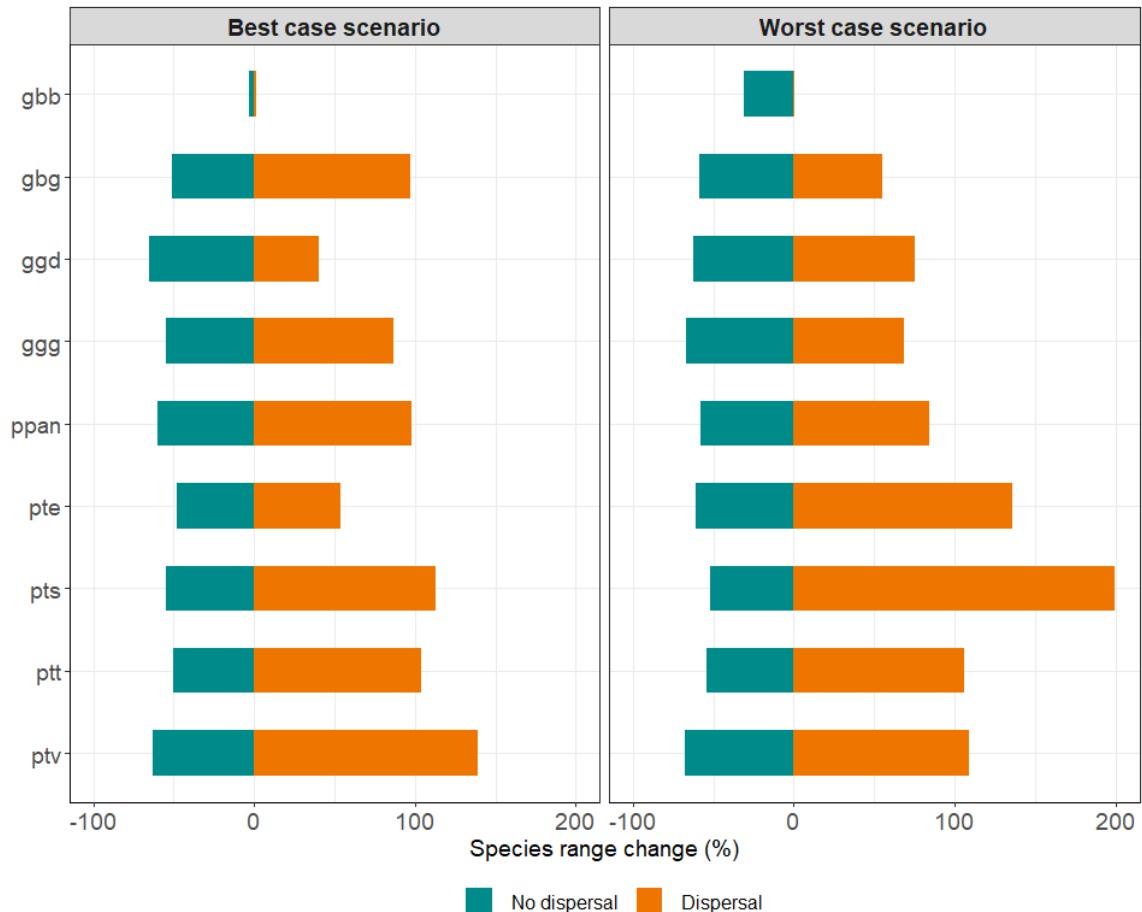
377

378 Figure 2. Ensemble forecasting of the current and future (best- and worst-case scenarios) habitat suitability for *Gorilla beringei* spp, *Gorilla gorilla* spp and  
 379 *Pan* spp based on weighted mean and the true skill statistics (TSS) for the *non-default* approach. Note that only results for the no dispersal scenario are  
 380 presented here.

381 are expected to decrease under the best scenario or increase under the worst scenario (Fig.  
 382 S1.5-6).

383 If no dispersal occurs, this taxon is predicted to lose half of its current habitat under both  
 384 scenarios (Fig. 3, S1.7). However, if dispersal occurs, a 97% range gain is predicted under the  
 385 best scenario, but only 55% under the worst scenario.

386



387 Figure 3. Predicted percentage change in African ape ranges by 2050 under the best- and the worst-  
 388 case scenario, assuming either no dispersal (loss) and dispersal (gain) for the *non-default* approach.  
 389

390

391 ***Gorilla gorilla diehli*** (Cross River gorilla)

392 Precipitation in the wettest month was the most important predictor of Cross River gorilla  
 393 distribution in both individual and ensemble models (Fig. S1.4). High precipitation during the  
 394 wettest month (340-400 mm) and seasonal variation in temperature (9-10 °C), very low  
 395 human population (<2,500 people/km<sup>2</sup>), a large distance to main rivers (>400 km) and  
 396 presence of large tracts of primary land (>95%) are suitable conditions for the distribution of  
 397 this species (Fig. S1.5-6). Precipitation in the wettest month is predicted to increase and  
 398 seasonal variation in temperature to decrease under the best scenario, whereas the opposite  
 399 pattern is predicted under the worst scenario (Fig. S1.5-6). According to both future

400 scenarios, human population is predicted to increase, and primary land is predicted to be  
401 completely lost.

402 If no dispersal occurs, more than two-thirds of the current range is predicted to disappear  
403 under both future scenarios (Fig. 3, S1.7). In contrast, if Cross River gorillas could disperse,  
404 range gains of 40% or 75% are predicted under the best and worst scenarios, respectively.

405 ***Gorilla gorilla gorilla*** (western lowland gorilla)

406 All climatic variables were important predictors of western lowland gorilla distribution,  
407 particularly seasonal variation of precipitation and diurnal temperature range (Fig. S1.4).  
408 Areas characterised by low seasonal variation in precipitation (50-70 °C), high annual  
409 precipitation (1,600-1,800 mm) and diurnal temperature range (9-11 °C), absence of cropland  
410 and close to roads (0-15 km) harbour suitable conditions for the persistence of this subspecies  
411 (Fig. S1.5-6). According to both future scenarios, precipitation variables will not change, but  
412 decrease in diurnal temperature is predicted to occur. Cropland is predicted to increase under  
413 the worst scenario.

414 Assuming no dispersal, loss of more than half the suitable area is predicted under both future  
415 scenarios (Fig. 3, S1.7). With dispersal, however, a large increase in suitable habitat under  
416 both future scenarios is predicted (87% best, 69% worst).

417 ***Pan paniscus*** (bonobo)

418 Precipitation in the warmest quarter is an important predictor of bonobo distribution in both  
419 individual and ensemble models (Fig. S1.4). Favourable environmental conditions shaping  
420 this species distribution are high precipitation (450-500 mm) and temperature (24-25 °C) of  
421 the warmest quarter and annual precipitation (1,750-1,950 mm), mid altitudes (350-450 m)  
422 and close proximity to roads (<6 km) (Fig. S1.5). All climatic variables are predicted to  
423 increase in the future (Fig. S1.5-6).

424 Under both future scenarios, more than half of the area of suitable habitat is predicted to be  
425 lost if no dispersal occurs (Fig. 3, S1.7). Suitable habitat is predicted to expand to new areas  
426 and, if bonobos disperse, range gains of 98% or 84% are predicted under the best and worst  
427 scenarios, respectively.

428 ***Pan troglodytes ellioti*** (Nigeria-Cameroon chimpanzee)

429 Cropland and primary land were the best predictors in GLM and Maxent models, in contrast  
430 to diurnal temperature range, which was the variable with the highest importance in GAM  
431 and RF models as well as in the ensemble models (Fig. S1.4). Areas with a low proportion of  
432 cropland (<7%), very high proportion of primary land (>90%), high diurnal temperature  
433 range (9-11 °C), pronounced seasonal variation of both precipitation (67-75 mm) and  
434 temperature (8-11 °C) offer suitable conditions for Nigeria-Cameroon chimpanzees (Fig.  
435 S1.5). An increase in cropland and a large reduction in primary land are predicted under the  
436 worst scenario. In contrast, no cropland expansion and a smaller decrease in primary land are  
437 expected under the best scenario. Under both future scenarios, seasonal variation of  
438 precipitation and temperature are predicted to increase and diurnal temperature range to  
439 decrease (Fig. S1.5-6).

440 If no dispersal occurs, almost half of the area of suitable habitat is predicted to be lost under  
441 both future scenarios (Fig. 3, S1.7). However, if dispersal occurs, substantial range gains are  
442 predicted to occur, particularly under the worst scenario (137% vs. 83% best scenario).

443 ***Pan troglodytes schweinfurthii*** (eastern chimpanzee)

444 Precipitation of driest quarter was an important predictor in most individual models, except  
445 for GLM and ANN models, where annual precipitation performed best (Fig. S1.4). However,  
446 all predictors ranked equally in importance in ensemble models. Eastern chimpanzees  
447 encounter suitable conditions where precipitation of the driest quarter is low (30-190 mm),  
448 annual precipitation (1,250-1,750 mm), isothermality (7-8 °C) and diurnal temperature range  
449 (13-17 °C) are high, and cropland is rare (<5%) (Fig. S1.5-6). Under the best scenario,  
450 climatic variables are unlikely to change, but a decrease in isothermality is predicted under  
451 the worst scenario. The latter also predicts expansion of cropland by 2050.

452 According to both future scenarios, suitable habitat is predicted to be confined to the core of  
453 the species' current distribution (Fig. 3, S1.7). In terms of range change, half of suitable  
454 habitat is predicted to be lost under both future scenarios if no dispersal occurs. In contrast, if  
455 dispersal occurs, range expansion of 113% or 199% into new areas is expected under the best  
456 and worst scenarios, respectively.

457 ***Pan troglodytes troglodytes*** (central chimpanzee)

458 Secondary land and distances to main rivers were the predictors of greatest importance in  
459 individual and ensemble models, except for GLM models, where only secondary land was a  
460 slightly better predictor (Fig. S1.4). Suitable environmental conditions for central  
461 chimpanzees are characterised by a high percentage of secondary land (12.5-75%), large  
462 distance to main rivers (>450 km), high annual precipitation (1,600-1,800 mm) and  
463 precipitation in the warmest quarter (400-500 mm), and mid-altitudes (300-600 m) (Fig.  
464 S1.5-6). According to both future scenarios, climatic variables are predicted to remain  
465 unchanged, but expansion of secondary land is expected by 2050.

466 A reduction of half the current area of suitable habitat is expected under both future scenarios  
467 if no dispersal occurs (Fig. 3, S1.7). Predictions of range gains for central chimpanzees  
468 suggest that 104% or 106% of suitable habitat will become available in new areas under the  
469 best and future scenarios, respectively.

470 ***Pan troglodytes verus*** (western chimpanzee)

471 Precipitation in the wettest quarter was the most important variable in individual and  
472 ensemble models (Fig. S1.4). Current suitable conditions for western chimpanzees are very  
473 high precipitation of the wettest quarter (600-900 mm), high seasonal variation of  
474 precipitation (60-110 mm) and precipitation of coldest quarter (100-600 mm), low human  
475 population (<5,000 people/km<sup>2</sup>) and low proximity to roads (<2 km) (Fig. S1.5-6). A greater  
476 increase in both seasonal variation in precipitation and precipitation of the coldest quarter is  
477 predicted under the worst scenario.

478 Western chimpanzees have the widest geographic distribution among African apes, however,  
479 loss of more than half their present range is predicted under both future scenarios if no  
480 dispersal occurs (Fig. 3, S1.7). On the other hand, high range gains are anticipated under both  
481 future scenarios if there is dispersal (best: 139%, worst: 109%).

## 482 DISCUSSION

483 This is the first study to combine climate, land-use and human population changes in an  
484 ensemble forecasting approach to predict African ape distribution by 2050. Customizing the  
485 model specifications relative to the default settings in the correlative algorithms revealed  
486 uncertainty in predicting the amount of suitable habitat available by 2050. However, both  
487 approaches agreed that all African ape taxa are likely to experience marked range losses  
488 (best: 55% *default* or 50% *non-default*; worst: 58% *default* or 57% *non-default*), and that  
489 these reductions may not be as severe if dispersal to new areas of suitable habitat occurs  
490 (best: 103% *default* or 81% *non-default*; worst: 91% *default* or 93% *non-default*).

491 A previous study quantified changes in suitable environmental conditions for African apes  
492 between 1990 and 2000, and found that the greatest proportional reductions occurred for  
493 gorillas (*G. g. diehli*, range loss of 59%; *G. b. graueri*, 52%; *G. g. gorilla*, 32%) and bonobos  
494 (*P. paniscus*, 29%) compared with chimpanzees (*P. t. troglodytes*, 17%; *P. t. verus*, 11%)  
495 (Junker et al., 2012). Lehmann and colleagues (2010) employed a mechanistic approach to  
496 investigate how climate change under a worst scenario would influence African ape survival  
497 and reported that chimpanzees might lose 10% of current range and gorillas 75%. Our study  
498 concurs with these results for most gorilla taxa, but more than half of suitable habitat area for  
499 chimpanzees is predicted to be lost under both future scenarios if no dispersal occurs.  
500 However, our full dispersal scenario predicts gains of suitable conditions in new areas under  
501 both future scenarios for all taxa, except mountain gorillas.

502 The variables that best predicted current distribution were taxon-specific: anthropogenic  
503 variables were key predictors in most models for mountain gorillas, Nigeria-Cameroon and  
504 central chimpanzees, and climate-related variables for Grauer's, Cross River and western  
505 lowland gorillas, bonobos, eastern and western chimpanzees. However, future scenarios  
506 suggest that the distribution of most gorillas and bonobos is predicted to be determined by  
507 changes in climatic variables, and that of chimpanzees by land-use changes. Moreover, the  
508 forecast variation in both climatic and human population variables can explain the predicted  
509 habitat stability for mountain gorillas. Interestingly, habitat gains predicted for Cross River  
510 gorillas, Nigeria-Cameroon and eastern chimpanzees under the worst scenario are likely to be  
511 explained by stability of climatic variables and changes in anthropogenic variables by 2050.

512 Despite the importance of climatic variables in determining African ape time budgets, and  
513 consequently their effects on distributions, gorillas and chimpanzees are more sensitive to  
514 variations in temperature than in precipitation and they persist better in habitats with lower  
515 monthly temperature variation (Lehmann et al., 2010). Moreover, gorillas are predicted to be  
516 affected more than chimpanzees given the more restricted behavioural flexibility of gorillas  
517 to cope with temperature variation (Lehmann et al., 2010). Our study suggests that diurnal  
518 and seasonal variability influence the distribution of most gorillas, yet only play a similar role  
519 for Nigeria-Cameroon and eastern chimpanzees. Additionally, annual precipitation, and  
520 particularly its distribution over the wet and dry seasons, affects the distribution of most  
521 gorillas and chimpanzees, as well as bonobos. These results are indirect evidence of the  
522 marked influence of temperature and precipitation on species ecological niche with regard to  
523 dehydration and thermoregulation (Wessling et al., 2018). The influence of climate change on  
524 great ape ecology has been poorly explored compared with anthropogenic disturbance;  
525 nonetheless, we can expect temperature extremes to exacerbate habitat loss for African apes



526 and consequently pose serious threats to species persistence, as they are anticipated to impact  
527 other non-primate species (Araújo et al., 2011; Newbold, 2018). By integrating future climate  
528 and land-use changes as well as human population scenarios, our predictions provide strong  
529 evidence for synergistic interactions among these global drivers constraining species  
530 distributions.

531 Strindberg and colleagues (2018) found that western lowland gorillas and central  
532 chimpanzees, two sympatric taxa with 97% range overlap, mostly occur outside protected  
533 areas, and argued for *'reinforcement of anti-poaching efforts both inside and outside*  
534 *protected areas (particularly where habitat quality is high and human impact is low), diligent*  
535 *disease control measures (including training, advocacy, and research into Ebola virus*  
536 *disease), and the preservation of high-quality habitat through integrated land-use planning*  
537 *and implementation of best practices by the extractive and agricultural industries'*. Our study  
538 suggests that both taxa will find environmentally suitable areas outside their current range, in  
539 line with our predictions for most African apes. Thus, outcomes from our SDMs should be  
540 integrated with a habitat connectivity analysis to optimize conservation land-use planning and  
541 identify priority areas for these species (Freeman et al., 2018; Jones et al., 2018). This is  
542 extremely important given that African protected areas are distant from each other (Santini,  
543 Saura, & Rondinini, 2016) and particularly because great apes have a low dispersal capacity  
544 due to their slow reproduction, low population densities, dietary requirements and poor  
545 thermoregulation. It will be important to ensure objective assessments of human pressures  
546 and habitat conditions in potential protected areas to avert species extinctions in the long term  
547 (Jones et al., 2018).

548 Taxon-specific frameworks of environmental and socio-economic trends (Estrada et al.,  
549 2018; Strindberg et al., 2018; Tranquilli et al., 2014) should be considered at all major  
550 decision-making levels in range countries and abroad to (1) improve the management and  
551 recovery of degraded habitat in protected areas and off-reserve management to increase  
552 resilience, (2) increase the size of protected areas, establish additional protected areas and  
553 ensure habitat connectivity, (3) incorporate climate change into land-use planning and  
554 propose mitigation measures on the conservation agenda for African apes and sympatric  
555 wildlife, and (4) implement more effective law enforcement in ape ranges, supplemented by  
556 environmental education, community development, tourism programmes and research (IUCN  
557 & ICCN, 2012; IUCN, 2014; Tranquilli et al., 2014, 2012). Public-private partnerships have  
558 proven highly effective across the forest and savanna zones, where an NGO or other  
559 organisation takes on management responsibility for a given site over one or more decades  
560 (Scholte et al., 2018).

561

## 562 **Limitations of distribution models**

563 Modelling species responses to global environmental changes carries many uncertainties  
564 (Araújo & New, 2007; Thuiller et al., 2019). Using two algorithm approaches, two future  
565 scenarios, two dispersal scenarios, an ensemble forecasting and including only a few but  
566 highly important predictors of the distribution of African apes, should have reduced  
567 uncertainties in our distribution models (Brun et al., 2019; Thorne et al., 2013). A recent  
568 study proposed that SDMs include historical records to produce better predictions of range  
569 shifts rather than relying on contemporary records alone (Faurby & Araújo, 2018). This is

570 important for large vertebrates given the direct effects of anthropogenic disturbances on their  
571 distribution, and many ranges being far from equilibrium under current environmental  
572 conditions (Faurby & Araújo, 2018). The species occurrences we used are from field sites  
573 and may represent realized niches as currently African apes may be absent from areas of  
574 potential distribution, but unfortunately, reliable information about historical ranges is not  
575 available. Thus, it is possible that our predictions of current African ape distribution have  
576 underestimated the diversity of niches suitable for these species, which consequently may  
577 have limited our model predictions under future conditions.

578 Mining concessions and granted mining claims are increasing dramatically across Africa,  
579 particularly threatening large ape populations in Guinea, Gabon and Liberia (Howard, 2019).  
580 It will be important to model the influence of this threat on future African ape distributions  
581 once appropriate spatial data sets become available.

582 Our results corroborate the other recent studies showing that African ape populations and  
583 their habitats are declining dramatically (Freeman et al., 2018; Hickey et al., 2013; Kuehl et  
584 al., 2017; Lehmann et al., 2010; Plumptre et al., 2016; Strindberg et al., 2018; Thorne et al.,  
585 2013), thus our findings should also be used to guide the prioritization of conservation efforts  
586 for these flagship species to avoid irreversible losses.

587

## 588 **Conclusions**

589 Given that the existing network of protected areas is inadequate for ensuring the long-term  
590 conservation of African apes (Strindberg et al., 2018), we support the argument that effective  
591 conservation strategies require taxon-specific conservation planning that focuses on existing  
592 and proposed protected areas, the creation and/or management of which can be informed by  
593 our habitat suitability models. Additionally, efforts to maintain connectivity between the  
594 habitats predicted to be suitable in the future will be crucial for the survival of African apes.  
595 For a species to shift to new climatically suitable areas, the availability of such habitat will  
596 need to be ensured through effective protection by antipoaching teams whether in a protected  
597 area or not, the enforcement of industrial extractive industry conservation regulations (for  
598 example, as currently practiced in logging concessions under FSC Standards), and by national  
599 land-use planning that ensures that the areas of current and future high conservation value are  
600 not transformed into agricultural plantations or fragmented by roads. As an example, this  
601 country-wide approach has been undertaken in Gabon, where planning for the development  
602 of agriculture, road and rail links, and mineral extraction has been informed by wildlife and  
603 vegetation data in order to locate these activities in areas that are already degraded, and to  
604 avoid closed-canopy old-growth and remote forests (Government of Gabon, 2012; Strindberg  
605 et al., 2018). This will be an effective way of promoting habitat connectivity to maintain  
606 African ape populations as well as sympatric wildlife.

607

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626

### 627 **Data Accessibility Statement**

628 The African ape data sets are available via the IUCN SSC A.P.E.S. database  
629 (<http://apesportal.eva.mpg.de>).  
630

### 631 **Biosketch**

632 Joana Carvalho is a postdoctoral researcher in the Faculty of Science, Liverpool John Moores  
633 University, UK, who has been working in the field of primate ecology and conservation. Her  
634 current research focuses on evaluating effects of future climate change and land-use/cover  
635 change on primates, through species distribution modelling, scenario analyses, and landscape  
636 connectivity analyses. Additionally, she has been working on density/distribution models for  
637 Tanzania chimpanzees.

638

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