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Range-wide indicators of African great ape density distribution

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Abstract

Species distributions are influenced by processes occurring at multiple spatial scales. It is therefore insufficient to model species distribution at a single geographic scale, as this does not provide the necessary understanding of determining factors. Instead, multiple approaches are needed, each differing in spatial extent, grain, and research objective. Here, we present the first attempt to model continent-wide great ape density distribution. We used site-level estimates of African great ape abundance to (1) identify socioeconomic and environmental factors that drive densities at the continental scale, and (2) predict range-wide great ape density. We collated great ape abundance estimates from 156 sites and defined 134 pseudo-absence sites to represent additional absence locations. The latter were based on locations of unsuitable environmental conditions for great apes, and on existing literature. We compiled seven socioeconomic and environmental covariate layers and fitted a generalized linear model to investigate their influence on great ape abundance. We used an Akaike-weighted average of full and subset models to predict the range-wide density distribution of African great apes for the year 2015. Great ape densities were lowest where there were high Human Footprint and Gross Domestic Product values; the highest predicted densities were in Central Africa, and the lowest in West Africa. Only 10.7% of the total predicted population was found in the International Union for Conservation of Nature Category I and II protected areas. For 16 out of 20 countries, our estimated abundances were largely in line with those from previous studies. For four countries, Central African Republic, Democratic Republic of the Congo, Liberia, and South Sudan, the estimated populations were excessively high. We propose further improvements to the model to overcome survey and predictor

data limitations, which would enable a temporally dynamic approach for monitoring great apes across their range based on key indicators.

KEYWORDS
Bonobo, chimpanzee, gorilla, IUCN SSC A.P.E.S. database, range-wide assessment

1 | INTRODUCTION

To manage and protect species effectively, knowledge of the density distribution of wildlife populations is fundamental. Species distribution modelers frequently use survey data to predict abundances in both sampled and unsampled locations (Pearce & Boyce, 2006). To this end, raw survey data (e.g., line transect data) have been used to derive predictions of density distribution or changes thereof at local (e.g., Dias et al., 2019), landscape (e.g., Stokes et al., 2010), national (e.g., Tweh et al., 2015), and taxon-wide scales (e.g., Heinicke et al., 2019a; Jantz et al., 2016; Strindberg et al., 2018). Alternatively, abundance estimates can be used to model species distributions (e.g., Regehr et al., 2016), where total abundance per survey site is derived from the raw survey data, with two important implications. First, the resulting abundance dataset may facilitate large-scale species distribution models (SDMs), as the approach can accommodate abundance estimates derived from a wide variety of survey methods (e.g., camera trapping, transect surveys, genetic analyses). Second, site level-abundance data have a coarser resolution than the raw survey data (which also reflect fine scale habitat-use), and thus smooth the resolution of predicted density distributions over large geographic scales. Site-level abundance data may therefore be suitable for large-scale SDMs, for which, accordingly, the aim is to obtain a global perspective of density distribution, as well as identifying key determinants of species distribution across wide geographic scales that can be used as highly informative indicators of species status.

Such large-scale assessments may also help identify blocks of potentially contiguous populations (e.g., Maisels et al., 2013), and the proportion of a taxon likely to be in any area, such as land-use management units. These studies are also of great use for assessments (e.g., Red List) regularly carried out by the International Union for Conservation of Nature (IUCN). At the other end of the spectrum, local-scale information on threats, abundance drivers, and social contexts can more easily translate into management strategies. Thus, rather than a dichotomy, there are different explanatory levels and a scale-dependent trade-off (Wennekes et al., 2012), which highlights the importance of a multiscale approach to understanding species abundance drivers along a range of spatial scales (Graf et al., 2005; Figure 1).

Recent assessments have revealed drastic great ape population declines (e.g., Kühl et al., 2017; Plumptre et al., 2016; Strindberg et al., 2018), and all species and subspecies of African great apes— bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes, P. t. ellioti, P. t. schweinfurthii, P. t. verus, P. t. troglodytes*), western gorillas (*Gorilla gorilla, G. g. diehli, G. g. gorilla*), and eastern gorillas (*Gorilla beringei, G. b. beringei, G. b. graueri*)—are listed as endangered or critically endangered (IUCN, 2021). Most African great apes require large forested areas and share life-history traits that make them particularly susceptible to population declines, such as late age at first reproduction and long inter-birth intervals, which result in overall low-reproductive rates (Kühl et al., 2017). African great apes also face three major threats: poaching, habitat destruction, and infectious disease. These major threats are driven by several underlying factors, often interconnected and present across a range of spatial scales (Arcus Foundation, 2014). For instance, the global demand for a natural resource may lead to infrastructure development across a region to facilitate its extraction, causing great ape habitat loss. Furthermore, as infrastructure development facilitates access to previously remote forest, hunting and the risk of zoonoses may be exacerbated at a local level.

Here, we investigate some of the drivers of great ape abundance at the continent-wide scale and predict great ape range-wide density distribution. We faced the problem that we could not include direct

	Level of detail			Spatial coverage	
	Local	**Landscape**	**Country**	**Region**	**Continent**
Study example	Assess impacts of a site-specific threat (Haurez et al., 2014)	Measure the effectiveness of conservation interventions (Stokes et al., 2010)	Assess nationwide status (Tweh et al., 2015)	Map density distribution and identify main abundance drivers across taxa (Strindberg et al., 2018; this study)	
Km	5	50	500	5000	

FIGURE 1 Trade-off between local accuracy and spatial extent of the assessment. Along the continuum of scales, the level of detail and specificity decreases with increasing spatial extent. Thus, the scale should be appropriately selected according to the study aim

measures of hunting and infectious diseases, as this information is not available at the range-wide scale and temporal resolution required for our study. Instead, we used the Human Footprint composite measure (Venter et al., 2016a), which is an accepted proxy for human impact, including the partial impact of hunting (Di Marco et al., 2018; Sanderson et al., 2002; Venter et al., 2016b; Wall et al., 2021). We also included the variable "food taboos" as a proxy for hunting and consumption of great apes (Heinicke et al., 2019b). For the impact of infectious diseases, we could not identify equally useful proxy variables. Information on the impact of infectious disease is only available for some regions and diseases, such as Ebola virus disease. However, we needed range-wide information for our models and thus highlight the resulting limitations in the discussion. With the extensive availability of remotely-sensed data and great ape survey data compiled in the IUCN SSC Ape Populations, Environments and Surveys (A.P.E.S.) database, we developed a modeling approach that uses site-level abundance. In brief, we used site-level abundance data to (1) evaluate the importance of different socio-economic and environmental factors for African great ape abundance, which could be used for monitoring great apes across their range, including future and scenario-based population trajectories, and (2) model their range-wide density distribution.

2 | METHODS

2.1 | Overview

For this study, we used a spatial layer of great ape sites represented by polygon areas with associated abundance estimates, and a set of eight predictor variables. We used these data to model the influence of the predictor variables on great ape densities, and then to predict the range-wide density distribution of great apes.

Our analysis consisted of two main steps (Figure S1 depicts the workflow). In Step I we used a generalized linear model (GLM) to estimate the effects of socioeconomic and environmental variables on great ape densities using data collected between 2000 and 2015. To counter a lack of confirmed absence sites of great apes, we created pseudo-absences before fitting the GLM. In Step II we used an Akaike's information criterion (AIC) weighted average of the model set (from Step I) to predict the range-wide density distribution of great apes for the year 2015. This study adhered to the American Society of Primatologists principles for the ethical treatment of primates.

2.2 | Model response

We compiled great ape abundance estimates for 156 sites (Table S5.1). We define a site as a survey area of known spatial extent that is represented as a polygon in our data. A variety of great ape survey methods exist (e.g., nest count line transect distance sampling, nest count reconnaissance surveys, camera trap distance sampling, dung-based genetic capture–recapture), of which nest count line transect distance sampling is the standard method (Kühl et al., 2008). The majority of

abundance estimates were provided in studies and biomonitoring reports; details on the survey methods and the sources are included in Table S5.1. All data are available on request from the IUCN SSC A.P.E.S. database (http://apesportal.eva.mpg.de/database/policy; also see Supporting Informations 3 and 4, comprising our final datasets). The surveys were conducted in 18 African countries between the years 2000 and 2015. Most surveys were conducted in areas where great apes were known to occur (only 24 surveys reported absence). To counter this low sampling intensity in areas of low and zero abundance that would likely produce biased estimates (Pearce & Boyce, 2006), we created pseudo-absence survey sites with abundance estimates of zero. The selection of pseudo-absence sites was based on suitable environmental conditions for African great apes (Junker et al., 2012), as well as available literature on areas known not to hold great apes (Brncic et al., 2010; Caldecott & Miles, 2005). To this end, we considered the average suitable environmental conditions value per each $490 \, km^2$ cell in a grid layer extending over the entire great ape range and a 100 km buffer around it. We selected cells with the lowest suitable environmental conditions (the average suitable environmental condition was 0.012), indicating very low habitat suitability for great apes (Junker et al., 2012), as well as cells coinciding with documented absence locations (Brncic et al., 2010; Caldecott & Miles, 2005). The resulting 134 pseudo-absence polygons ranged between 490 and $1960 \, km^2$ in size and were spread across 21 countries (Burkina Faso, Mali, and South Sudan contained only pseudo-absence sites).

Since the pseudo-absence sites did not have a survey year, we assigned them randomly chosen years from 2005 to 2015. We chose the year 2005 instead of 2000 (which was the earliest year for the real survey sites) to increase the likelihood that great apes were absent in the pseudo-absence sites, assuming that there is a time lag between the decrease in habitat suitability and the impact it had on great apes (Junker et al., 2012). We repeated this random assignment 100 times and conducted all the subsequent analyses for each of the 100 replicate datasets (see Supporting Information and Section 3 for results across the 100 datasets). For brevity and clarity, here we only report the results derived from the dataset that led to the most reasonable great ape abundance estimates based on a comparison with recent nationwide estimates (see Section 2.4).

2.3 | Predictor variables

We modeled great ape density as a function of different environmental and socioeconomic variables (Table 1). Predictor variables were selected based on two main criteria: (i) previously confirmed or assumed relevance for explaining great ape density distribution, and (ii) availability across the African great ape range. As some of the selected variables were strongly correlated (Table S1.1), namely climate and topographic variables, we chose minimum precipitation to represent limiting climatic conditions on great ape density. Also, as we were interested in the effect of elevation as a topographic variable, that is, assuming a refuge effect, we chose this variable over correlated climate variables. This limited the final number of predictors to eight, including the year in which a survey was conducted.

TABLE 1 Socioeconomic and environmental predictor variables considered in this study, their predicted effect on great ape density, and spatial and temporal resolution at which data were available

Variable name	Description	Spatial resolution	Temporal availability	Anticipated effect	Variable data source
Intact Forest Landscape	Forested areas larger than 500 km² and with a minimum width of 10 km, minimally influenced by human economic activity	The layer consists of polygon shapes	2000, 2013, 2016	Positive	Potapov et al. (2008)
Human Footprint[a]	Index based on human population density, night-time lights, pastureland, crop land, infrastructure, and access (e.g., roads)	30 arc-seconds (~1 km)	2009	Negative	Venter et al. (2016a)
GDP[b]	Gross Domestic Product (constant 2010, USD)	Nationwide	Yearly from 2000 to 2015	Negative, or positive/negative quadratic	World Bank (2017)
Corruption[a]	Index based on perception of corruption	Nationwide	Yearly from 2000 to 2015	Negative	Transparency International's Corruption Perceptions Index (2018)
Food taboos[a]	Proportion of Muslims	Subnational entities	Yearly from 1995 to 2009	Positive	Johnson and Grim (2021)
Minimum precipitation[a]	Precipitation of the driest month (mm)	30 arc-seconds (~1 km)	Average between 1970 and 2000	Positive	Fick and Hijmans (2017)
Elevation[c]	Elevation (m)	7.5 arc-seconds (~0.25 km)	2010	Positive	USGS (2010)
Survey year	Year of each great ape survey	Survey site	Yearly from 2000 to 2015	Negative	Our data

[a]Log-transformed to achieve a roughly symmetrical distribution and avoid influential cases.
[b]Log-transformed (see footnote a) and then squared to allow for a nonlinear relationship with the response.
[c]Square-root-transformed to achieve a roughly symmetrical distribution.

More specifically, we were interested in assessing the influence of socioeconomic factors on great ape density, as we expected them to have a substantial influence on their range-wide distribution. Thus, we included Human Footprint, Gross Domestic Product (GDP), corruption, food taboos, and Intact Forest Landscapes as test predictors. We included the Human Footprint index in our model, representing human impact and transformation of the landscape (Venter et al., 2016b). The Human Footprint includes proximity to roads, which has been linked to hunting activity and decreased wildlife densities for several taxa (Laurance et al., 2006; Wall et al., 2021), including great apes (Andrasi et al., in review; Stokes et al., 2010; Strindberg et al., 2018). We anticipated a negative correlation between Human Footprint and great ape density, as high Human Footprint values indicate increased habitat disturbance, and hunting pressure (Strindberg et al., 2018). We included Intact Forest Landscape as a predictor, as it describes forested areas minimally influenced by humans. To a certain extent, we expected higher great ape densities in areas with a higher proportion of Intact Forest Landscape, although we are aware that some well-managed logging concessions in Central Africa fall outside Intact Forest Landscape areas and hold large great ape populations (Brncic et al., 2018; Stokes et al., 2010). We further included corruption (as evaluated by Transparency International's Corruption Perceptions Index, 2018), because we assumed corruption to be a proxy variable for unmanaged extraction of natural resources (Smith & Walpole, 2005; Tacconi & Williams, 2020). Food taboos against eating great apes exist in certain regions, such as among Muslims in West Africa (Bachmann et al., 2019; Heinicke et al., 2019b). The adherence to taboos against consuming great apes has been shown to influence great ape densities in West Africa (Heinicke et al., 2019) and in Western Equatorial Africa (Strindberg et al., 2018). Thus, we included the proportion of Muslims in a population as a predictor variable, expecting increased great ape density in areas with a higher prevalence of food taboos. To explore the relationship between the size of each country's economy and great ape abundance, we included GDP, the annual monetary value of all finished products and services. We expected a negative relationship, in the scenario that a large GDP (resulting from increased economic activities, such as trade) led to adverse impacts on great apes and their habitat. To account for potential nonlinear effects, we included GDP squared.

Before our analysis, we extracted the values of all predictor variables for (i) each survey site, and (ii) across the African great ape geographic range using a 5 arc-min resolution grid (average cell size: 85.4 km^2; hereafter "prediction grid"). Whenever predictor variables were available for multiple years, we extracted the ones temporally closest to the survey years of the sites. For the prediction grid we extracted them for 2015, or the year closest to 2015 (see Figure S1.1 for the time lags between the survey years and closest year for which predictor data were available). Further details on the predictor variable extraction are included in the Supporting Information and Section 1.

2.4 | Statistical analysis

2.4.1 | Model implementation

We fitted a GLM with negative binomial error distribution and log link function (Hilbe, 2011; McCullagh & Nelder, 1989). The response in the model was the estimated great ape abundance per site, with a sample size of 285 sites. We included GDP, corruption, food taboos, Human Footprint, and Intact Forest Landscape as test predictors, representing human pressure on great ape abundance and habitat. To control for environmental factors influencing ape abundance, we included minimum precipitation and elevation. The survey year was also included as a control predictor. Finally, we checked for spatial autocorrelation by fitting the model and extracting the residuals. Then, for each data point, we averaged the residuals of all other data points, and weighted their contribution by their distance to the data point. The weights followed a normal distribution with a mean of zero (i.e., maximum weight at a distance of zero) and a standard deviation chosen such that the log-likelihood of the model with the derived autocorrelation term included was maximized (Fürtbauer et al., 2011). The model revealed that the autocorrelation term was positive and significant ($p < 0.001$), therefore it was included in the full model. To control for variation in the size of survey sites, we included their area (in square kilometers and log-transformed) as an offset term (McCullagh & Nelder, 1989), noting that by means of the offset term we effectively modeled great ape density. Thus, the full model was:

Great ape abundance ∼ Intact Forest Landscape + human influence + corruption + GDP + GDP^2 + food taboos + minimum precipitation + elevation + survey year + autocorrelation + offset term.

Before model fitting, we inspected the distribution of all predictors, log-transformed (base e) several of them (Table 1) to achieve more symmetrical distributions and avoid influential cases. We then z-transformed all predictors to a mean of zero and a standard deviation of one to obtain comparable model coefficient estimates. To test the influence of the test predictors on great ape abundance, and to avoid "cryptic multiple testing" we compared the full model with a null model (Forstmeier & Schielzeth, 2011) that did not include those predictor variables. We used a likelihood ratio test (Dobson, 2002) for the full-null model comparison, and tests of the individual predictors were based on Wald's z-approximation (Quinn & Keough, 2010). Over-dispersion was not an issue (dispersion parameter: 0.627). Collinearity, assessed from a standard linear model lacking the squared term, was also no issue (largest variance inflation factor: 1.726; Field, 2005), and model stability was acceptable (for details see Table S2.1). We obtained confidence intervals (CIs) for model coefficients by means of a nonparametric bootstrap in combination with the percentile method (Manly, 2007). All models were fitted in R (R Core Team, 2019) using a self-written function based on the R function "optim."

In addition to inference based on null hypothesis significance testing, we applied multimodel inference (MMI; Burnham & Anderson, 2010). To this end, we constructed all possible subsets of the set of terms in the full model (total of 384 models). All models

included the offset and the autocorrelation term as derived for the full model. For each model, we then determined AIC (corrected for small sample size), as well as AIC weight. We further evaluated the number of models in the 95% best model confidence set and determined whether the null model was in the 95% best model confidence set (Mundry, 2011). Since not all models converged, the actual number of models evaluated was 321.

2.4.2 | Predicting range-wide great ape density distribution

For the second part of our analysis, we obtained a range-wide prediction of great ape density distribution using a multimodel-based approach. We obtained model predictions for all 321 models in linear predictor space, then averaged these (Cade, 2015) by weighting the contribution of each model by its Akaike weight, and finally exponentiated the result to obtain the predicted great ape density.

We compared average great ape abundance estimates summed per country from recent estimates (see Table S1) to the summed estimates per country obtained from our own predictions (derived from the multimodel-based predictions for our 100 datasets). We then identified the dataset (i.e., random assignment of years) that produced the smallest differences for each pairwise country comparison, based on their relative deviations, and used this dataset to bootstrap CIs for the range-wide prediction. We used a nonparametric bootstrap (N = 1000) to obtain these CIs (Manly, 2007). Using data from the World Database on Protected Areas (WDPA), we further evaluated the proportion of the total predicted great ape population found within protected areas with IUCN Categories I and II, as well as the predicted proportion of the population that is found within all protected areas documented in the WDPA (UNEP-WCMC & IUCN, 2019). Finally, we assessed the

influence of the number of our pseudo-absence sites on our predicted density distribution by implementing a sensitivity analysis (see Supporting Information and Section 4 for details and results).

3 | RESULTS

3.1 | Model results

Regarding the full-null model comparison, which tests the overall influence of the socioeconomic variables on great ape abundance, we found a significant difference (likelihood ratio test: $\chi^2 = 29.023$, $df = 6$, $p < 0.001$). The Human Footprint and GDP were important predictors of great ape density (Table 2). Great ape density was inversely related to Human Footprint values (Figure 2a). The relationship between great ape density and GDP was negative quadratic, with decreasing great ape densities above a GDP of $5 billion annually (Figure 2b). Great ape density tended to be negatively correlated with corruption (Figure S2.1). The autocorrelation term was highly significant (Table 2), indicating that the abundances of sites that were geographically closer to one another were more similar to each other than to more distant ones. Hence, this hints at predictors missed in the model that contribute to spatial variation in great ape densities or to demographic processes largely independent of external predictors. Regarding the MMI there were 152 (47%) models in the 95% best model confidence set, which did not include the null model.

3.2 | Range-wide prediction of great ape density distribution

Our prediction was based on the dataset that predicted nationwide estimates closest to those from other studies and reports (Figure 3).

TABLE 2 Estimated model coefficients for the full model

Term[a]	Estimate	SE	z	p	Lower CL	Upper CL
Intercept	−1.428	0.207	[b]	[b]	−1.610	0.589
Human footprint	**−0.671**	**0.180**	**−3.737**	**<0.001**	**−2.739**	**−0.744**
GDP	−0.347	0.185	[b]	[b]	−1.805	0.195
GDP²	**−0.204**	**0.103**	**−1.989**	**0.047**	**−0.819**	**0.253**
Intact Forest Landscape	0.271	0.216	1.258	0.208	−0.163	1.682
Corruption	**−0.357**	**0.213**	**−1.673**	**0.094**	**−1.958**	**0.510**
Food taboos	−0.069	0.213	−0.322	0.747	−0.900	1.084
Min. precipitation	0.182	0.205	0.888	0.375	−1.229	0.626
Elevation	0.277	0.174	1.593	0.111	−0.079	1.453
Survey year	−0.063	0.212	−0.300	0.764	−0.419	1.271
Autocorrelation	**1.888**	**0.459**	**4.114**	**<0.001**	**−0.073**	**3.264**

Note: Predictor variables with significant effects or trends are indicated in bold.

Abbreviations: CL, confidence limit; GDP, Gross Domestic Product.

[a]All predictors were z-transformed to a mean of zero and a standard deviation of 1.

[b]Not shown because of having a very limited interpretation.
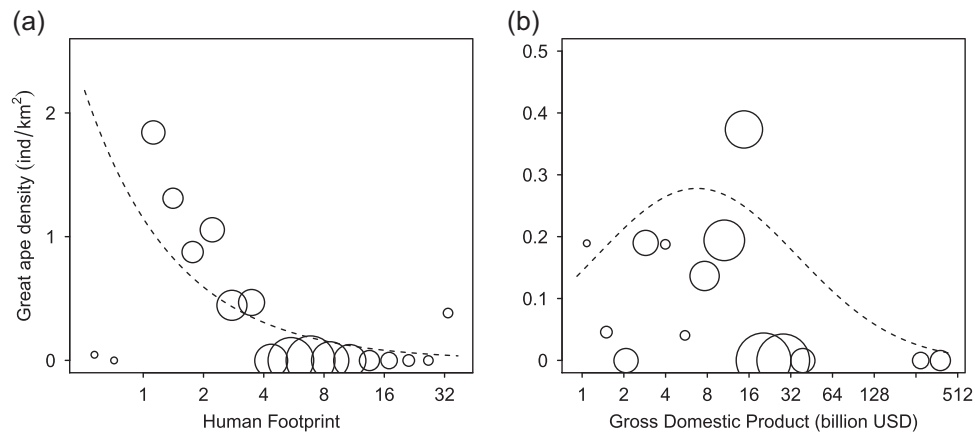
FIGURE 2 Great ape density as a function of (a) Human Footprint, and (b) GDP. The area of the dots depicts the number of survey sites per binned Human Footprint (N = 1–55) and GDP (N = 1–69). GDP, Gross Domestic Product

This dataset revealed the lowest great ape densities in parts of West Africa and the highest in Central Africa (Figure 4). Densities ranged from 0 to 5.8 individuals per km². Nationwide abundance estimates for the Central African Republic (CAR), Democratic Republic of the Congo (DRC), Liberia, and South Sudan were unreasonably high and are therefore not shown (this was established by comparison with information from other sources and expert knowledge; see Table S2.4). Due to a lack of Human Footprint data for Angola's Cabinda province, we could not make a prediction for this area. With the exclusion of DRC, the largest predicted populations were found in the Republic of Congo (274,437 individuals; 2.5% confidence limit (CL) was 142,329; the 97.5% CL was not meaningful due to exceedingly high densities), Gabon (123,617 individuals; 97.5% CI: 41,232–380,911) and Cameroon (62,833 individuals; 97.5% CI: 25,432–123,586). All other estimated abundances per country are

included in Table S2.2. Of the total predicted abundance of great apes, although 23.2% were found in protected areas listed in the WDPA (UNEP-WCMC & IUCN, 2019), only 10.7% were found in IUCN Categories I and II protected areas.

4 | DISCUSSION

This study is the first to attempt a continent-wide prediction of African great ape density distribution and an evaluation of factors driving their abundance at this large spatial scale. It thus complements modeling efforts at the local, landscape, and regional scale (Figure 1). In analogy to large-scale remote sensing approaches of land-use changes that complement local-scale field studies, our large-scale modeling effort complements local- to regional-scale great ape monitoring, for example, for the establishment of a range-wide, indicator-based surveillance system. Great ape densities were inversely related to Human Footprint and GDP and tended to correlate negatively with the level of corruption. A high degree of spatial autocorrelation indicated that additional variables and demographic processes contributed to the density distribution of great apes not accounted for in the analysis. Model predictions of ape abundance were similar to previous estimates for 16 out of 20 countries but were likely too high for Liberia, CAR, South Sudan, and DRC.

4.1 | Key indicators of African great ape density

The severity and expansion of the Human Footprint is strongly related to the suitability of land for agriculture (Venter et al., 2016b). In West Africa, large-scale industrial agriculture (following, or in combination, with small-scale agriculture) has contributed greatly to chimpanzee population declines and to the reduction of their geographic range (Kühl et al., 2017). Deforestation rates have been comparatively lower in Central Africa, but hotspots can be found bordering the Congo Basin, as rapidly growing human populations
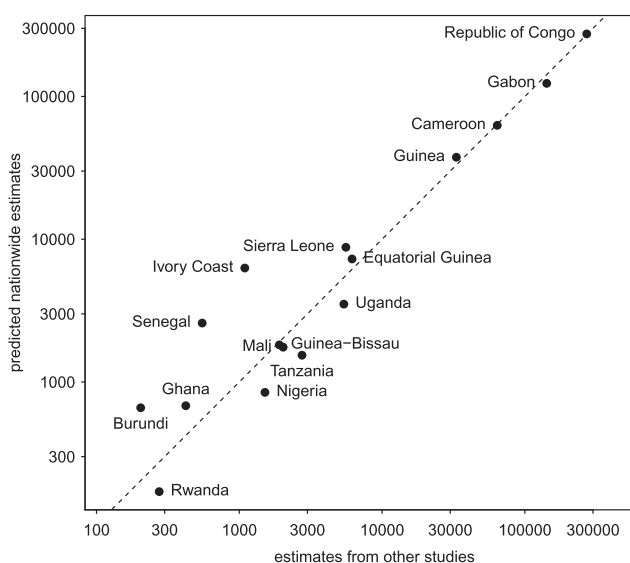

FIGURE 3 Estimated nationwide great ape abundances obtained in this study compared to recent estimates from other studies (see Table S3.4). The dashed line depicts perfect concordance
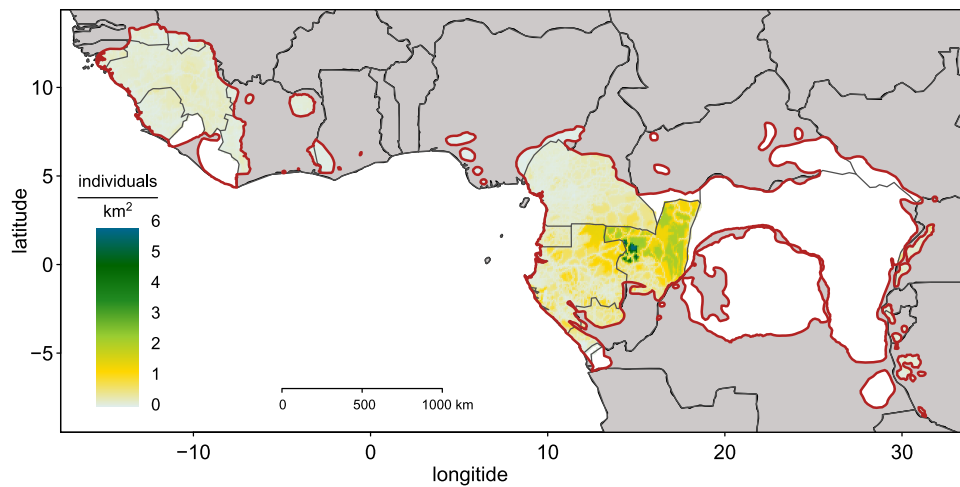
FIGURE 4 Predicted density distribution (number of individuals per km²) of African great apes for the year 2015. Throughout most of their geographic range (outlined in red), predicted densities ranged between zero and one

increase the demand for agricultural land (Tyukavina et al., 2018), including around mines and around agro-industry (Molinario et al., 2020). In addition, several planned development corridors (e.g., roads, railroads, and pipelines), some of which are underway, are likely to not only further degrade great ape habitats but also facilitate resource extraction, thereby enormously increasing the pressure on wildlife (Laurance et al., 2018). The international demand for crops such as coffee, cacao, rubber, and palm oil, as well as the extraction of minerals and timber, are contributing to rapid infrastructure development (Estrada et al., 2019; Laurance et al., 2018).

We approximated the influence of economic development on great ape populations and their habitat by including GDP in our model. Throughout our study period, the relationship between great ape density and GDP was negative quadratic. Notably, great ape densities were higher in the lower range of GDP values. The negative correlation between great ape density and higher GDP values is likely due to the indirect effects of economic development on great ape habitat, caused by infrastructure development, resource use, and land-use change. To undergo such development with minimal adverse impacts on great apes and their habitat, land-use planners and natural resource managers must take wildlife conservation into account (Heinicke et al., 2019a, Strindberg et al., 2018), as has been exemplified by the recent rerouting of the Cross River Highway (Mahmoud et al., 2017).

The level of corruption was identified as a trend in our analysis. Lower great ape abundance was associated with increased levels of corruption. This is in line with findings from other studies that have identified corruption as a global issue for wildlife conservation (Smith & Walpole, 2005; Tacconi & Williams, 2020). None of the other predictors were as important for explaining remaining variation in great ape abundance, although they were found to be relevant in other local- to regional-scale studies. This pattern may be explained on three levels. First, some predictors may indeed have only explanatory power in specific regions due to specific characteristics of social–ecological systems. This may be the case for food taboos, for

example, as observed in West Africa among the Muslim population (Heinicke et al., 2019b). Additionally, potential nonlinearity of predictor effects may cause the relationship with ape abundance to collapse, when the proportion of the population adhering to food taboos drops below a certain level. Second, the absence of additional important predictors, such as actual hunting intensity may have diluted the effect of some predictors, such as Intact Forest Landscapes. With widespread poaching of great apes, the predictive power of Intact Forest Landscapes on great ape abundance likely vanishes. Third, a large proportion of variation may already be captured by the composite Human Footprint index and GDP, which may be considered as key indicators of great ape density distribution at the large scale.

4.2 | Predicted great ape density distribution

Of the 20 countries for which we predicted density distribution, the nationwide estimates for 16 were in line with previous estimates (Figure 3). For four countries they notably diverged; these were Liberia, CAR, South Sudan, and DRC. The high estimate for Liberia was likely due to the combination of relatively low Human Footprint values (compared to other West African countries; see Figure S3.2), high forest cover, and high poaching rates in the country (Tweh et al., 2015) that was not captured by any of the predictor variables. Similarly, the high estimate for CAR may be explained by the remarkably low Human Footprint values in the country—in fact, the lowest across the entire great ape range (Figure S3.2). Since low Human Footprint values were strongly correlated with high great ape densities, this likely contributed to high densities in the CAR. In South Sudan, a lack of great ape surveys in the country likely played a role in the high predicted population estimate, as predictions were mainly informed by the relationship between great ape abundance and predictors in other regions. Likewise, only a fraction of DRC has been surveyed; for instance, the eastern chimpanzee population has

scarcely been surveyed in the western part of their geographic range, north of the Congo River (Plumptre et al., 2010). Furthermore, the lack of a direct hunting intensity variable in the model has likely contributed to high predicted densities in DRC. While model predictions for several of the remaining 16 countries are very similar to previous estimates, some show deviations, such as Senegal, Burundi, or Nigeria. Here, it is important to note that no survey-based nationwide estimates are available, and deviations in Figure 2 may simply reflect this. Similarly, for some countries (e.g., Cameroon) our predicted nationwide estimates were compared to the summed estimates of multiple surveys that were conducted within each country.

Alarmingly, only 10.7% of the predicted great ape population was found in IUCN Category I and II protected areas, and an additional 12.5% of the population was found in areas with a lower level of protection—the same kind of results noted by Strindberg et al. (2018) for Western Equatorial Africa's great apes. We commend existing efforts to increase protected area networks and their connectivity, and strongly support moves towards improved management of existing protected areas and of selectively logged timber concessions.

4.3 | Model evaluation and limitations

Our prediction covered the entire geographic range of African great apes, including areas that have not yet been surveyed. Although seemingly isolated, large forest blocks in Central Africa are accessible to hunters through networks of paths (Abernethy et al., 2013; Plumptre et al., 2021), and hunting pressure in some of these areas has been predicted to be very high (Ziegler et al., 2016). Using actual data on hunting intensity instead of a crude proxy (e.g., proximity to roads) would likely improve the over-estimated densities in some areas. Efforts to map faunal and ecologically functional intactness, as well as hunting impact, are quickly developing (Gallego-Zamorano et al., 2020; Plumptre et al., 2021). Although these are also proxy, composite variables (i.e., not direct hunting measures), they may be able to more extensively account for the impacts of hunting in future models.

We could also not account for the impact of disease in our model, which likely contributed to an overestimation of densities in some areas. Most notably, the Ebola virus disease has eliminated large numbers of great apes in the Republic of Congo and Gabon (Strindberg et al., 2018). Specifically, abundance in the areas of northeast Gabon and across the border in the Republic of Congo (Strindberg et al., 2018) was overestimated by our model. Thus, we believe that the absence of predictors estimating actual hunting pressure and spread of infectious diseases contributed to an overestimation of our predicted abundances, especially in areas that appear to otherwise have high habitat suitability. However, the inclusion of the autocorrelation term captured at least part of the unexplained variability in the density distribution of great apes, which could, for instance, be due to local or regional variation in hunting pressure not accounted for in the model.

Based on the comparison of our nationwide estimates to those from previous studies (Figure 3), our predictive model performed better in areas covered by a larger proportion of survey sites. Model accuracy would therefore improve not only with increased confirmed absences but also increased occurrence data in regions that have been sparsely surveyed, such as DRC and South Sudan. Other limitations relate to the unavailability of predictor variables, as well as to the quality and resolution of available variables. These limitations are magnified with the large scale of our study, which attempts to model the density distribution of different taxa in varying socioeconomic contexts. However, as the availability and quality of environmental, socioeconomic, and great ape survey data continue to improve, future range-wide assessments are likely to increase in accuracy.

4.4 | Conclusion and outlook

We consider our study a starting point for continent-wide assessments of African great ape status, acknowledging at the same time important limitations that led to overestimates in great ape abundance in four countries. For future studies building on our work, we suggest in particular the following five points: (1) since the absence of great apes is still uncertain in many areas, the number of confirmed absence or near absence locations need to increase; (2) for areas that are currently underrepresented, a larger number of sampled sites will improve accuracy of predictive models and will allow for cross-scale assessments (i.e., from local to continental scales); (3) the approach we have taken here can incorporate abundance estimates derived from different types of surveys and can be further expanded to include additional data types. The recent emergence of integrated population models provides a powerful tool to make use of all types of data (Santika et al., 2017; e.g., line transect nest counts, camera trap observations, passive acoustic monitoring, genetic surveys) and make the most of existing and new survey datasets in the A.P.E.S. database. (4) We have identified the Human Footprint and GDP as important predictors of range-wide great ape density. Thus, we recommend using these variables as important indicators to assess great ape status at this scale and constructing future population trajectories; (5) the sourcing and development of additional predictors that measure hunting and spread of infectious diseases, will be key to improve model performance. Additional variables related to the export of natural and mineral resources, agricultural products or international trade in general may be important predictors to be considered. Finally, we emphasize that merely 10.7% of the total great ape population was found in areas with higher levels of legal protection. This highlights the urgent need to develop conservation activities outside protected areas that integrate sustainable development, human well-being, and health with the continued persistence of African great apes.

DATA AVAILABILITY STATEMENT

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