A Journal of Conservation Biogeography

Diversity and Distributions

BIODIVERSITY RESEARCH

Recent decline in suitable environmental conditions for African great apes

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ABSTRACT

Aim To predict the distribution of suitable environmental conditions (SEC) for eight African great ape taxa for a first time period, the 1990s and then project it to a second time period, the 2000s; to assess the relative importance of factors influencing SEC distribution and to estimate rates of SEC loss, isolation and fragmentation over the last two decades.

Location Twenty-two African great ape range countries.

Methods We extracted 15,051 presence localities collected between 1995 and 2010 from 68 different areas surveyed across the African ape range. We combined a maximum entropy algorithm and logistic regression to relate ape presence information to environmental and human impact variables from the 1990s with a resolution of 5×5 km across the entire ape range. We then made SEC projections for the 2000s using updated human impact variables.

Results Total SEC area was approximately 2,015,480 and 1,807,653 km^2 in the 1990s and 2000s, respectively. Loss of predicted SEC appeared highest for Cross River gorillas (−59%), followed by eastern gorillas (−52%), western gorillas (−32%), bonobos (−29%), central chimpanzees (−17%) and western chimpanzees (−11%). SEC for Nigeria-Cameroon chimpanzees and eastern chimpanzees was not greatly reduced. Except for Cross River and eastern gorillas, the number of SEC patches did not change significantly, suggesting that SEC loss was caused mainly by patch size reduction.

Main conclusions The first continent-wide perspective of African ape SEC distribution shows dramatic declines in recent years. The model has clear limitations for use at small geographic scales, given the quality of available data and the coarse resolution of predictions. However, at the large scale it has potential for informing international policymaking, mitigation of resource extraction and infrastructure development, as well as for spatial prioritization of conservation effort and evaluating conservation effectiveness.

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INTRODUCTION

In recent years, thousands of species have declined dramatically, and many populations are close to extinction owing to anthropogenic impacts (Koh *et al.*, 2004). The effects of this conservation crisis have been particularly severe in tropical regions, which support *c.* 50% of described species (Wright, 2005), including our closest living relatives, the great apes. Bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*), gorillas (*Gorilla beringei*, *Gorilla gorilla*) and orangutans (*Pongo abelii*, *Pongo pygmaeus*) are particularly important for biodiversity conservation. They fulfil the multiple roles of charismatic

flagship species, umbrella species and environmental indicator species (Wrangham *et al.*, 2008). Focusing on ape populations and their habitats raises public awareness and funding for bio-diversity conservation, overlaps with conservation priorities identified for many other tropical plant and animal species, and helps maintain tropical ecosystem services.

During the past 30 years, there have been alarming declines in great ape populations (Oates, 1996). Ape populations in Gabon were halved between 1983 and 2000 owing to outbreaks of Ebola and poaching for bushmeat (Walsh *et al.*, 2003); an estimated 5000 gorillas died in the Republic of the Congo following an Ebola outbreak (Bermejo *et al.*, 2006); 90% of chimpanzees in Côte d'Ivoire died between 1990 and 2007 (Campbell *et al.*, 2008); in Senegal a formerly contiguous chim-panzee population was fragmented into three blocks with large unoccupied areas in between (Galat-Luong *et al.*, 2000), and in south-western Nigeria, chimpanzee population size and distri-bution sharply declined over a decade (Greengrass, 2009). Even in areas with large intact ape populations, such as northern Democratic Republic of Congo, evidence of the sale of large numbers of chimpanzee orphans and carcasses testify to a rapid recent increase in illegal hunting (Hicks *et al.*, 2010).

Much of the remaining African ape range, previously relatively intact, is now rapidly being converted to human-dominated mosaics (Laporte *et al.*, 2007). In many ape range states this has created isolated remnants of prime ape habitat, often inside protected areas, within a landscape dominated by agriculture and agro-forestry (e.g. Plumptre *et al.*, 2010).

Whether or not great apes will survive within these human-modified landscapes depends on whether protected areas are large enough and, more importantly, adequately protected (Tranquilli *et al.*, 2011). Encouragingly, if poaching pressure is low, some ape taxa may survive in heterogeneous land-use mosa-ics that include extensive agricultural activity. For example, chim-panzees occur at low density throughout Sierra Leone, where only a small proportion of the original forest cover remains in a landscape dominated by traditional small-scale slash-and-burn agricultural fields (Brncic *et al.*, 2010). Other studies report simi-lar situations in Guinea (Hockings *et al.*, 2009), Guinea-Bissau (Torres *et al.*, 2010) and Uganda (McLennan, 2008).

At the other end of this spectrum lie the large and contig-uous forest blocks of Central Africa. However, human popu-lation densities, hunting, logging and mining activities are now rapidly increasing, destroying ape habitat in their wake (Laporte *et al.*, 2007; Hicks *et al.*, 2010).

Recent site-specific or landscape-scale surveys have provided information on the effects of these threats on density and abundance (Morgan *et al.*, 2006; Kuehl *et al.*, 2009; Stokes *et al.*, 2010; Campbell *et al.*, 2008), and on spatial and tempo-ral trends in ape populations (e.g. Hall *et al.*, 1998; Blom *et al.*, 2001; Reinartz *et al.*, 2008). Surprisingly, only very few studies exist which have attempted to combine the wealth of available GIS and remote sensing information and data on ape popula-tions in a predictive modelling context. Pintea *et al.* (2003) used data on chimpanzee presence in Tanzania and related it to multiscale remote sensing imagery; Bergl *et al.* (2010) used

a set of Landsat imagery and other predictors to develop a hab-itat suitability model for Cross River Gorillas (*Gorilla gorilla diehli*) to assess dispersal corridors and available non-occupied habitat; similarly Torres *et al.* (2010) suggested a habitat suit-ability model for an area in south-western Guinea-Bissau and three distinct time periods to asses rates of change in available chimpanzee habitat.

However, effective conservation also requires range-wide information on spatial and temporal trends in ape distribu-tion, to inform global policy-making (Norconk *et al.*, 2010) and donor decisions, and to foresee and confront emerging threats, such as habitat destruction, large-scale infrastructure developments and resource exploitation projects, as well as increasing poaching pressure and climate change impacts (Kormos *et al.*, 2003; Tutin *et al.*, 2005; Oates *et al.*, 2007; Plumptre *et al.*, 2010; Morgan *et al.*, 2011). Eventually this information will allow us to evaluate the effectiveness of ape conservation worldwide. The only attempt to provide a range-wide predictive model of African ape biogeography has been derived from behavioural observations at the several long-term field sites (Lehmann *et al.*, 2008). This model uses information on body mass and climate conditions to first predict time allocation for key activities and subsequently for group size that is predicted across the entire range.

In an effort to further bridge the gap between local scale information and global ape population trends, we conducted a first continent-wide analysis of data compiled in the IUCN/SSC A.P.E.S. (Ape Populations, Environments and Surveys) database (http://apes.eva.mpg.de). A.P.E.S. serves to centralize and standardize all existing ape survey informa-tion, providing a universal platform from which these data may be accessed by the scientific and conservation commu-nity following a strict data access and release policy.

Despite differing data collection methods, confirmed ape presence is standard information available across all archived data sets. Species presence localities can be used to model suit-able environmental conditions (SEC) (Pearce & Boyce, 2006). Applying such models simultaneously to different taxa, vary-ing environments and spatial scales is a great challenge and limitations are likely to arise from the quality and resolution of available predictor variables. In this study we aim to (1) estimate the distribution of SEC for African great apes for two time periods, the 1990s and 2000s, to (2) assess the relative importance of factors influencing SEC distribution, and (3) quantify temporal rates of SEC loss, fragmentation and isola-tion. We define SEC as the probability of ape occurrence given certain environmental conditions.

METHODS

To model SEC for African apes we combined a maximum entropy algorithm (MAXENT; Phillips *et al.*, 2006) with logistic regression. We chose this approach for two reasons. First, we had confirmed ape presence localities but only few confirmed absence locations. Although presence-only modelling app-roaches are widely used (Pearce & Boyce, 2006), we also wanted

to make use of the advantages of Generalized Linear Models (GLMs) (i.e. with regard to the inclusion of interactions and nonlinear terms) and multimodel inference, which is well developed for logistic regression (Burnham & Anderson, 2002). We therefore used MAXENT to generate pseudo-absences and then used logistic regression to build SEC models. Owing to lack of comparable ape presence data sets for the 1990s and 2000s, we modelled SEC for the 1990s and then projected SEC probability into the 2000s using updated predictor variables. We repeated the MAXENT analysis 50 times using different random selections of presence points for each taxon separately as test data. We generated 20 sets of pseudo-absences from each of the derived presence probability maps (i.e. a total of 1000 data sets), which we then combined with the presence localities and analysed using logistic regression. The results reported here are the averages revealed by these 1000 analyses per taxon. Details of the analysis are described below and in Appendix S1 in Supporting Information which also includes a flowchart (S1-1) depicting the analytical process. The text passages are directly linked to the respective steps in S1-1.

Presence localities

We extracted 15,051 great ape presence localities from the A.P.E.S. database (defined as GPS positions of sightings, nest sites, vocalizations, dung, carcasses, trails, tracks, feeding- and tool-use-sites) (step 1, Fig. S1-1 in Appendix S1). After referencing presence locality data to a 5 × 5 km grid, we eliminated all duplicates from the data set to reduce sample bias. The extracted and used presence points per (sub-) species were *Pan troglodytes verus*: 3033/325 extracted/used presence localities; *Pan troglodytes troglodytes*: 1317/272; *Pan troglodytes schweinfurthii*: 5866/537, *Pan troglodytes ellioti*: 477/143; *P. paniscus*: 896/121; *Gorilla gorilla gorilla*: 2293/387; *G. g. diehli*: 759/69; and *Gorilla beringei graueri*: 410/92 (Fig. S1-2 and Table S2–1 in Appendices S1 and S2). For areas with overlapping chimpanzee and gorilla range we did not use ape signs that could not be assigned to one or the other species. These presence localities were originally confirmed during ape and biodiversity surveys in 68 different areas. Survey areas ranged in size from a few km^2 to tens of thousands of km^2. We excluded localities for mountain gorillas as good estimates of this subspecies' population size and geographic range are available covering several decades (Guschanski *et al.*, 2009; Gray *et al.*, 2010). All ape presence locations used in this study were collected between 1995 and 2010 and are GPS-based. We dealt with obvious GPS errors by excluding all those points, which fell outside of the survey area defined for a particular survey data set. Additionally, because of the scale of the study, potential small-scale spatial error from GPS inaccuracies may not be significant.

Predictor variables

African apes are primarily forest dwelling species and many populations occur within the tropical forest belt, which is characterized by a humid climate, high rainfall and low temperature variability. However, at their range limits towards the Sahel zone in the north and east and in West Africa, chimpanzees range in drier woodland and savannah-dominated areas (Caldecott & Miles, 2005). Almost all ape populations are impacted to some degree by human activities in the form of habitat destruction and poaching (Kormos *et al.*, 2003; Plumptre *et al.*, 2003; Walsh *et al.*, 2003; Caldecott & Miles, 2005; Reinartz *et al.*, 2006; Campbell *et al.*, 2008; Greengrass, 2009; Kuehl *et al.*, 2009; Hicks *et al.*, 2010). Therefore, we chose 13 predictor variables of three categories (climate, vegetation and human impact) to model SEC (Table 1; step 1, Fig. S1-1 in Appendix S1). This choice was also influenced by the limited availability of high quality range-wide GIS data sets.

MAXENT analysis

We ran one MAXENT analysis per taxon using presence localities and seven environmental predictor variables, which were partially principal components analysis (PCA) scores (see Table 2, Table S1 in Appendix S1) derived for the 1990s (step 3 and 4, Fig. S1-1 in Appendix S1). We bootstrapped the models 50 times per taxon, and for each run we randomly selected 75% of the occurrence locality grid cells as training data with the remaining 25% reserved for testing the resulting model. We used recommended default values for the convergence threshold (10^5), maximum number of iterations (500) and regularization value (10^4), and let the program automatically select 'features' (environmental variables) following default rules according to the number of presence records (Phillips *et al.*, 2006). Overall model performance was evaluated by means of the 'Area under the Curve' (AUC) determined by the Receiver Operating Characteristic Curves (ROC) analysis (Phillips *et al.*, 2006).

For each taxon we used its broadly classified geographical range (provided by IUCN) to which we added a 100-km buffer where no obvious geographic barriers existed (for *G. g. diehli* we added a 10-km buffer because of their relatively small geographical range), to ensure that potential suitable habitat outside the defined distributional limit would be included in our analysis.

Absence localities

We generated pseudo-absences from the presence probability maps revealed by MAXENT (Engler *et al.*, 2004) (step 5, Fig. S1-1 in Appendix S1). We derived pseudo-absences by randomly drawing cells from the range of the respective taxon whereby the probability of each particular cell to be drawn equalled one minus the cell's ape occurrence probability (as derived from MAXENT). For presence cells and cells directly neighbouring them, the probability to be drawn was set to zero. The number of pseudo-absences generated (N_a) was determined as $N_a = (N_p \times H_{unsuitable})/H_{suitable}$, where $H_{suitable}$ and $H_{unsuitable}$ were the number of pixels with MAXENT

Table 1 Variables used, their sources, the year(s) for which data were available and the time period (past: 1990s; current: 2000s) for which each layer was included into the SEC model

ID	Category	Variable name	Reference	Year	Time period
1	Climatic*	Mean temperature (bio1)	Hijmans *et al.* (2005)	1950–2000	Both
2		Mean precipitation (bio12)			Both
3		Range in temperature (bio4)			Both
4		Range in precipitation (bio15)			Both
5		Minimum temperature (bio6)			Both
6		Minimum precipitation (bio14)			Both
7	Human impact	Human population density†	Center for International Earth Science Information Network (CIESIN), Columbia University and Centro Internacional de Agricultura Tropical (CIAT) (2005)	1990	Past
				2010	Current
8		Human Influence Index	Fotheringham (1981)	1990	Past
				2010	Current
9		Poverty index	Elvidge *et al.* (1997)	1993	Past
				2003	Current
10		Distance to nearest road	Digital Chart of the World (DCW)	1992	Both
11		Distance to nearest river	Food and Agriculture Organization of the United Nations (FAO)	Undated	Both
12	Vegetation	Percentage forest cover‡	DeFries *et al.* (2000)	1992/93	Both
			Hansen *et al.* (2006)	2000	Both
13		Forest in neighbourhood	DeFries *et al.* (2000)	1992/93	Both
			Hansen *et al.* (2006)	2000	Both

*WorldClim Bioclimatic Variables.
†Gridded Population of the World, version 3 (GPWv3), 2.
‡1992/1993: GLCF AVHRR Continuous Fields Tree Cover Project; 2000: MODIS Vegetation Continuous Fields.

Table 2 Predictor variables used for the SEC model

Variable name	After PCA analysis	Variable no.	Anticipated effect
Human population density	Human impact (Factor 1)	1	Negative linear, potentially interacting with var. 4 and 5
Human influence index	Human impact (Factor 1)	1	Negative linear, potentially interacting with var. 4 and 5
Poverty	Human impact (Factor 1)	1	Negative linear, potentially interacting with var. 4 and 5
Precipitation driest	Climatic (Factor 2)	2	Negative quadratic – apes occur within an optimal climatic range
Seasonality precipitation	Climatic (Factor 2)	2	Negative quadratic – apes occur within an optimal climatic range
Seasonality temperature	Climatic (Factor 2)	2	Negative quadratic – apes occur within an optimal climatic range
Mean annual precipitation	Climatic (Factor 2)	2	Negative quadratic – apes occur within an optimal climatic range
Minimum temperature	Climatic (Factor 2)	2	Negative quadratic – apes occur within an optimal climatic range
Mean annual temperature	Climatic (Factor 3)	3	Negative quadratic
Distance to roads	Distance to roads	4	Positive linear (but see var. 1)
Distance to rivers	Distance to rivers	5	Negative or positive linear (but see var. 1)
Percentage forest cover	Percentage forest cover	6	Positive linear
Forest in neighbourhood	Forest in neighbourhood	7	Positive linear

The variables indicated in the first column were partly highly correlated and thus combined using a principal component analysis (PCA). Numbers in the third column label the derived principal components or original variables which entered our models as predictors.

output values ≥ 0.5 and < 0.5, respectively, and N_p was the number of presence cells for a taxon. Per cell, only one pseudo-absence could be placed. For the small range of *G. g. diehli* we selected as many pseudo-absences as there were cells with presence localities.

As the number of pseudo-absences was usually small compared with the number of available cells, we expected large variability in the particular locations at which pseudo-absences would be placed. To avoid an undue influence of

any particular selection of cells with pseudo-absences, we generated 20 sets of pseudo-absences for each of the 50 occurrence probability maps per taxon, creating 1000 data sets per taxon (step 6, Fig. S1-1 in Appendix S1).

SEC model

Based on the presence localities and the derived pseudo-absences we ran GLMs (McCullagh & Nelder, 1989) with

binomial error distribution and *logit* link function (i.e. logistic regressions) to estimate (1) the relative probabilities of apes occurring at a specific location within their potential geographical range under past and current environmental conditions and (2) the relative importance of the predictor variables in explaining ape presence or absence (step 7 and 8, Fig. S1-1 in Appendix S1). Models were built using the predictors as derived for the 1990s and then projected to the 2000s using updated layers of human impact variables (step 9 and 10, Fig. S1-1). See Appendix S1 for details of the analyses, model specification and formal inference.

Temporal change in SEC

To determine changes in SEC between the 1990s and 2000s, we first converted the continuous prediction maps into binary suitability maps. We defined a given pixel as suitable for apes when the model average of predicted ape occurrence probability was above a certain threshold. For each taxon we used nine different thresholds which were the quantiles (10, 20, etc., up to 90%) of the average ape occurrence probabilities derived for those pixels on the 1990s map, in which each respective taxon was actually present (Pearce & Boyce, 2006). The same thresholds were then also used to determine SEC on the map with average ape occurrence probabilities projected for the 2000s (step 11 and 12, Fig. S1-1 in Appendix S1). The derived maps (total of 9 thresholds × 2 periods × 8 taxa = 144 maps) were then characterized as follows (step 13 and 14, Fig. S1-1 in Appendix S1).

To estimate total ape range for the 1990s and 2000s and rate of change between the two decades, we first counted the number of pixels predicted as SEC for each map. Next, we determined patches of SEC. We defined a patch as a group of all SEC pixels directly neighbouring one another. We then determined for each patch its size (number of pixels) and its degree of isolation (closest distance from its border to the nearest border of any other patch). Finally, we counted the number of patches. To estimate mean rates of change in SEC, SEC patch size and degree of isolation for each taxon, we averaged values across all nine thresholds. We calculated total extent of SEC for the 1990s and 2000s by converting SEC predictions into a binary map using a threshold, which we derived by maximizing the product of the true positive rate and the proportion of the area predicted as nonsuitable for the 1990s data set. We then applied the same threshold to the 2000s SEC predictions. All statistical analyses were done in R (R Development Core Team, 2010).

RESULTS

Current SEC distribution

SEC showed a high degree of spatial heterogeneity both within and among taxa (Fig. 1). This resulted, for instance, in a highly variable SEC patch size distribution for the different taxa (Appendix S2). Although, the total number of SEC patches was dominated in general by very small patches, mean patch size and range differed considerably between taxa (Fig. S2-1 to S2-8). The largest SEC patches occurred in Central Africa within the ranges of *G. g. gorilla*, *P. t. troglodytes*, *P. t. schweinfurthii* and *P. paniscus*. Countries with SEC values predicted highest by our model were Democratic Republic of Congo (DRC), Gabon, Liberia and Republic of the Congo.

Where environmental predictor variables contributed substantially to predicted SEC distribution (i.e. mean Akaike weight was larger than expected), our hypotheses about their effects on ape SEC were mostly confirmed (Tables 2 & 3). However, variable contributions to predictions of SEC differed considerably between taxa. Human impact had a clear negative effect on all taxa except *P. t. schweinfurthii*. Looking at all variables combined in the 'human impact' factor and the 'human impact' factor itself, clearly demonstrates the differences in human pressure on the different taxa with Central Africa having lower human impact values than in East and West Africa (Fig. 2). Model predictions of most taxa were influenced heavily by distance to rivers and distance to roads; for most taxa these two predictors interacted in their impact or distance to rivers interacted with human impact, making the direct interpretation of the results difficult. Climate variables heavily weighted models of all eight taxa. In this case, however, the coefficients did not always behave as expected [e.g. factor 2 squared (climate variables) had a positive impact on *P. paniscus* and *P. t. schweinfurthii*, implying these taxa would be least common at intermediate values of this factor].

Recent decline in SEC

Comparisons of SEC area between the 1990s and 2000s revealed much stronger declines for *P. paniscus* and the three gorilla taxa than for *P. troglodytes*. SEC declined by 59% for *G. g. diehli*, 52% for *G. b. graueri*, followed by 32% for *G. g. gorilla* and 29% for *P. paniscus*. For *P. troglodytes* SEC decrease was highest in West Central Africa (Figs 3a & 4).

In West Africa, SEC levels decreased in areas previously predicted as very suitable for apes such as in Liberia (Fig. 1a) and similar decreases occurred in the Central African range countries, that is, Cameroon, DRC, Gabon and Republic of the Congo. Our model predicted much less SEC loss for other countries (Fig. 4).

Comparing the number of SEC patches between the two time periods revealed that the total number of SEC patches declined significantly for *G. b. graueri* only (Fig. 3b). Furthermore, because patch size distribution was dominated by very small SEC fragments neither mean SEC patch size nor distance between SEC patches changed significantly over time (Appendix S2).

DISCUSSION

This is the first range-wide study that attempts to quantify African ape SEC distribution and its changes over time.
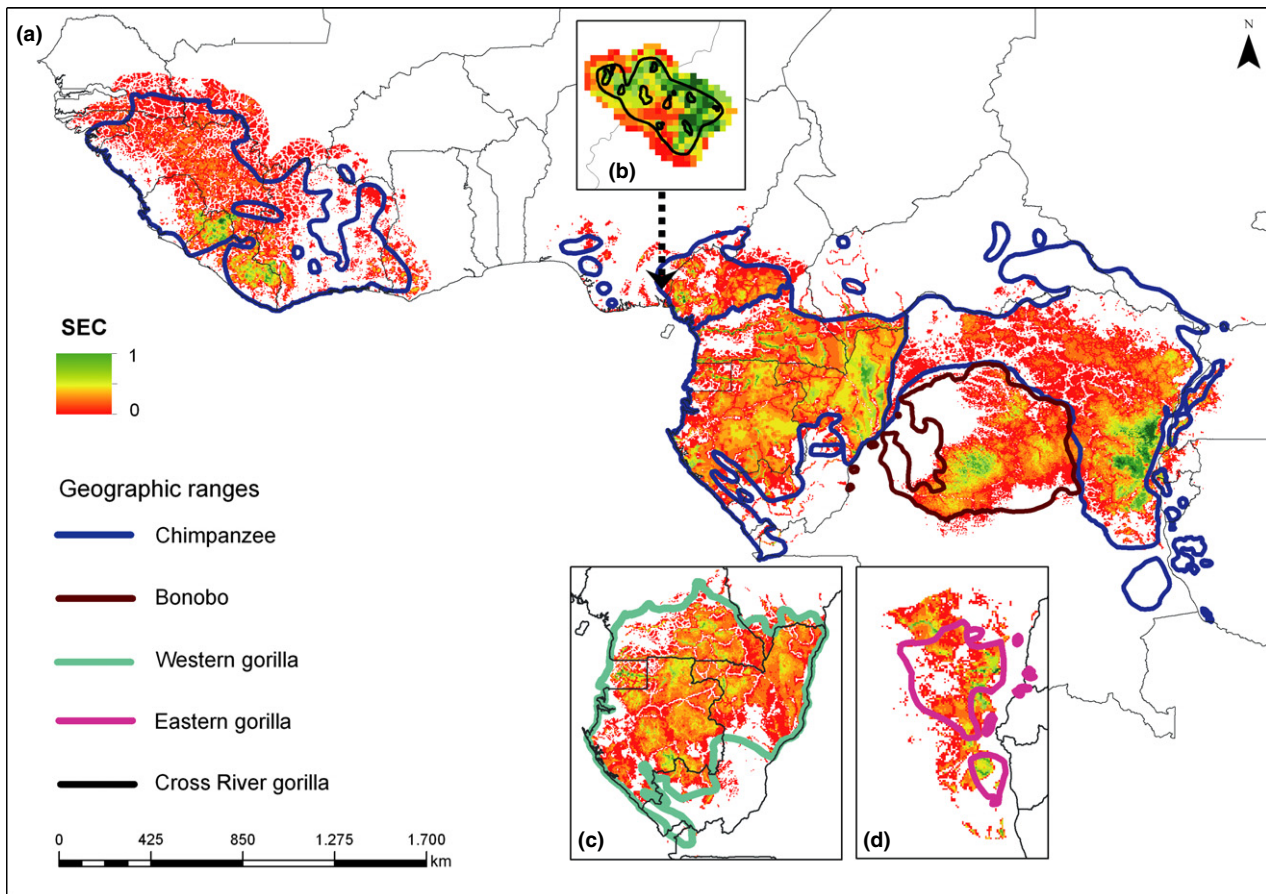
Figure 1 Predicted distribution of SEC for the 2000s: (a) chimpanzee and bonobo, (b) Cross River gorilla (c) western lowland gorilla and (d) eastern lowland gorilla. Colours indicate the gradient in SEC ranging from red to yellow to green, indicating low, intermediate and high values, respectively. White indicates unsuitable environmental conditions for great apes.

Between the 1990s and 2000s about 208,000 km² of SEC appeared to have been lost. In general, SEC for the three gorilla subspecies and bonobos was affected more than SEC for chimpanzees. SEC decline rates were as high as 59% and 52% for *G. g. diehli* and *G. b. graueri*, respectively, but showed almost no change for *P. t. schweinfurthii*. The regions that experienced the greatest loss of SEC were central and eastern DRC, western Equatorial Africa and the upper Guinean forest in Liberia. Importantly, the lack of decline in other areas may reflect the fact that much SEC had already been lost before the 1990s (i.e. East and West Africa). Within the Central African forest block for example, the areas highlighted as having had the highest SEC loss are currently the remaining strongholds of the great apes, however, even in these areas, the vast, once-remote forest tracts have been interlaced with logging and mining roads, and subsequent human immigration (Laporte *et al.*, 2007).

To interpret our estimated SEC loss and its effect on ape populations, both the delay effects in population response and the potential counterbalancing of human pressure by conservation measures need to be considered. Increased human pressure does not necessarily lead to instantaneous extinction of wildlife populations. Rather there is a time-lag

effect, during which populations still exist under increased human pressure and show decline only years later (Findlay & Bourdages, 1999). Great apes are particularly susceptible to such effects as they are long lived and have a low reproductive rate. Increased offspring mortality but relatively high adult survival may therefore mask critical changes before population decline becomes clearly evident. Our data set was presence-based and not density-based, so immediate decline will be less easy to pick up at the scale used. In some areas, effective conservation and/or an improved environmental awareness and attitude towards apes may counterbalance even relatively high human pressure and impact (Hockings & Humle, 2009; Tranquilli *et al.*, 2011). Consequently, observed SEC decline rates cannot be equalized in a linear way with ape population decline, but could mean reduced long-term survival of ape populations.

Species and regions

There were clear regional differences in loss of SEC and among taxa. One striking pattern that emerged from our analysis was a difference in rates of SEC decline for gorillas and bonobos compared with chimpanzees. Likely explanations include (1)
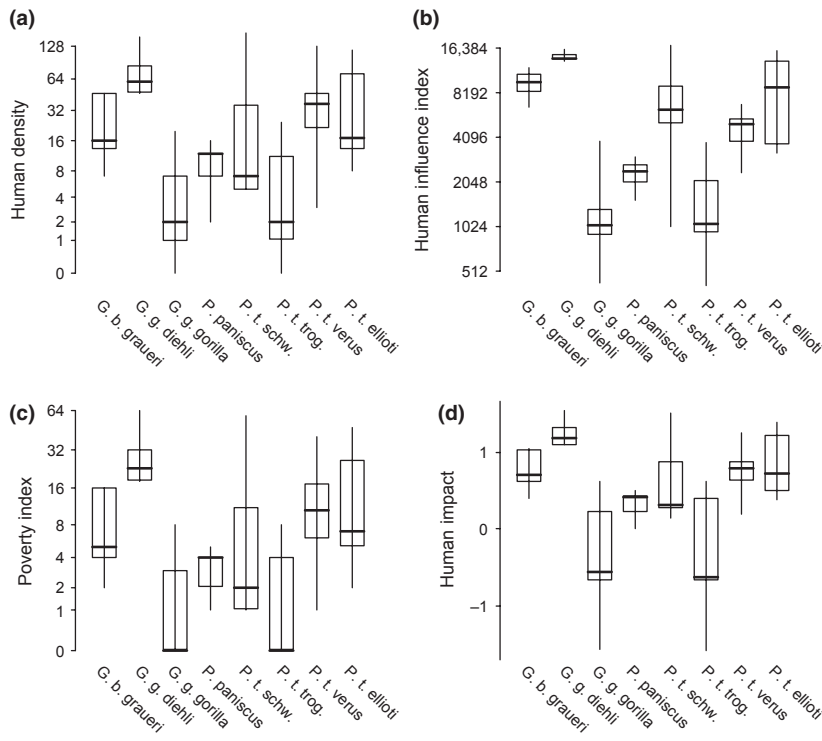
Figure 2 Values extracted for (a) human density, (b) human influence index, (c) poverty index and (d) human impact (PCA1) for all presence localities of the different taxa of great apes. Shown are medians, quartiles and percentiles (2.5% and 97.5%).

differences in species-specific ecological requirements, such as dietary preferences and niche specialization (Tutin *et al.*, 1991), and (2) differences in vulnerability to poaching related to behaviour and social structure (Caro *et al.*, 2009). Chimpanzees show considerably more behavioural flexibility than gorillas, enabling them to survive in human-modified landscapes (McLennan, 2008; Hockings *et al.*, 2009; Brncic *et al.*, 2010). In contrast, the killing of a dominant male gorilla disrupts the whole group and reduces likelihood of infants survival if their mothers are obliged to join another male (owing to infanticide by a new dominant male) (Robbins, 1995). Additionally, variation in poaching pressure across Africa can partially explain the observed patterns, with little direct hunting of chimpanzees in East Africa and high poaching pressure in Central and parts of West Africa. It is likely that SEC for bonobos declines at similar rates to that of gorillas owing to the particularly heavy impacts of human land-use and poaching in DRC, where the human population is growing by 2.6% per year and an enormous commercial bushmeat trade is emptying huge forest blocks at an accelerating rate (e.g. Hart *et al.*, 2008; Liengola *et al.*, 2010).

It is not surprising that rates of SEC loss are so marked in Central Africa, as this region experienced the greatest socio-economic changes during the 1990s and 2000s with, for example, previously remote forests being carved up by logging roads (Laporte *et al.*, 2007; Blake *et al.*, 2008; Stokes *et al.*, 2010). By contrast, East and West Africa had already experienced relatively high human impacts. For a more detailed discussion of model results, please see Appendix S1.

Model evaluation

Unfortunately, we could not quantitatively evaluate our SEC model predictions with independent data across the ape range. The only exception is Liberia for which an independent survey data set was available, suggesting SEC to be a good predictor of chimpanzee density (Appendix S1). We made further qualitative comparisons using other published and unpublished sources that suggest a relatively good agreement with our SEC model predictions, although for some regions ambiguity remains (Appendix S1). In West Africa, the low SEC predictions for Côte d'Ivoire are supported by a recent nationwide survey Campbell *et al.* (2008). Discrepancies between our SEC change projection and the results of Campbell *et al.* (2008) are owing to the lack of a suitable forest cover layer for the recent period in our study, thereby underestimating SEC destruction in recent years.

An on-going large-scale field survey in Western Guinea confirms a widespread chimpanzee population as suggested by the SEC model (S. Regnaut, pers. comm.). Similarly, Brncic *et al.* (2010) found an elevated chimpanzee density in the northern part of Sierra Leone. A study on a range-wide bonobo distribution model suggests the same for regions to which bonobo populations are now confined (J. Hickey, University of Georgia, Athens, *et al.*, in prep.). For eastern chimpanzees a comparison with a distribution model by Plumptre *et al.* (2010) reveals obvious discrepancies. Solving these discrepancies will require an in-depth investigation of both models and more likely an independent data set. On-going fieldwork in the region, in particular northern DRC will provide this opportunity in the near future.

Table 3 Results of the taxon-specific logistic regression, indicated are the coefficients derived (average of 198–324 models; 468 in case of the intercept, weighted by Akaike weights), as well as summed Akaike weights, and these weights divided by their respective expected value (for details see Appendix S1). Variables in bold had Akaike weights considerably in excess of the expected value

Species	Variable name	Estimates	Wgt	Wgt/exp	Species	Variable name	Estimates	Wgt	Wgt/exp
Gorilla gorilla diehli	Intercept	−0.865			*Pan troglodytes schweinfurthii*	Intercept	−4.994		
	Distance to rivers	**2.297**	**0.999**	**1.444**		Distance to rivers	−0.056	0.675	0.975
	Distance to roads	0.395	0.532	0.865		Distance to roads	**0.471**	**1.000**	**1.625**
	Forest in neighbourhood	0.831	0.477	0.955		Forest in neighbourhood	**0.759**	**0.998**	**1.996**
	% Forest cover	**1.363**	**0.798**	**1.597**		% forest cover	**0.722**	**0.999**	**1.998**
	Factor 1 (human impact)	**−0.942**	**0.795**	**1.293**		Factor 1 (human impact)	−0.043	0.429	0.697
	Factor 2 (climatic)	**3.873**	**0.723**	**1.084**		Factor 2 (climatic)	**1.544**	**1.000**	**1.500**
	Factor 3 (climatic)	**−4.126**	**0.845**	**1.268**		Factor 3 (climatic)	**−1.912**	**1.000**	**1.500**
	Dist. rivers : dist. roads	0.676	0.177	0.768		Dist. rivers : dist. roads	−0.736	0.293	1.270
	Factor 1 : dist. rivers	0.783	0.247	1.072		Factor 1 : dist. to rivers	0.066	0.174	0.754
	Factor 2^2	0.353	0.299	0.897		Factor 2^2	**−0.069**	**1.000**	**3.000**
	Factor 3^2	1.464	0.360	1.079		Factor 3^2	0.527	0.382	1.146
Gorilla beringei graueri	Intercept	−6.504			*Pan troglodytes troglodytes*	Intercept	−5.068		
	Distance to rivers	**−0.387**	**0.981**	**1.417**		Distance to rivers	**−0.273**	**1.000**	**1.444**
	Distance to roads	−0.320	0.687	1.116		Distance to roads	**0.463**	**0.999**	**1.623**
	Forest in neighbourhood	**2.676**	**0.999**	**1.998**		Forest in neighbourhood	**0.811**	**0.994**	**1.988**
	% Forest cover	0.077	0.284	0.568		% Forest cover	0.057	0.293	0.586
	Factor 1 (human impact)	**−1.106**	**0.972**	**1.580**		Factor 1 (human impact)	**−0.253**	**1.000**	**1.625**
	Factor 2 (climatic)	**−2.225**	**0.946**	**1.419**		Factor 2 (climatic)	**0.353**	**0.903**	**1.355**
	Factor 3 (climatic)	−0.545	0.553	0.830		Factor 3 (climatic)	−0.221	0.695	1.043
	Dist. rivers : dist. roads	−0.784	0.307	1.330		Dist. rivers : dist. roads	**0.650**	**0.303**	**1.313**
	Factor 1 : dist. rivers	**0.158**	**0.295**	**1.278**		Factor 1 : dist. to rivers	**0.613**	**1.000**	**4.333**
	Factor 2^2	**0.620**	**0.765**	**2.295**		Factor 2^2	0.784	0.329	0.987
	Factor 3^2	0.732	0.320	0.960		Factor 3^2	0.891	0.199	0.597
Gorilla gorilla gorilla	Intercept	−4.397			*Pan troglodytes verus*	Intercept	−5.608		
	Distance to rivers	**−0.333**	**1.000**	**1.444**		Distance to rivers	**−0.151**	**0.947**	**1.368**
	Distance to roads	**0.713**	**1.000**	**1.625**		Distance to roads	**0.411**	**1.000**	**1.625**
	Forest in neighbourhood	**0.448**	**0.691**	**1.382**		Forest in neighbourhood	**0.429**	**1.000**	**2.000**
	% Forest cover	**0.416**	**0.738**	**1.476**		% Forest cover	**0.354**	**0.958**	**1.916**
	Factor 1 (human impact)	**−0.399**	**1.000**	**1.625**		Factor 1 (human impact)	**−0.146**	**0.731**	**1.188**
	Factor 2 (climatic)	**0.290**	**0.992**	**1.488**		Factor 2 (climatic)	**−0.436**	**0.999**	**1.499**
	Factor 3 (climatic)	**−0.652**	**1.000**	**1.500**		Factor 3 (climatic)	−0.129	0.572	0.858
	Dist. rivers : dist. roads	**−0.236**	**0.315**	**1.365**		Dist. rivers : dist. roads	**0.735**	**0.767**	**3.324**
	Factor 1 : dist. to rivers	**−0.048**	**0.977**	**4.234**		Factor 1 : dist. to rivers	**0.665**	**0.345**	**1.495**
	Factor 2^2	**0.658**	**0.968**	**2.904**		Factor 2^2	0.699	0.335	1.005
	Factor 3^2	**1.125**	**0.957**	**2.871**		Factor 3^2	0.704	0.195	0.585
Pan paniscus	Intercept	−5.956			*Pan troglodytes ellioti*	Intercept	−6.310		
	Distance to rivers	−0.110	0.485	0.701		Distance to rivers	**0.662**	**0.992**	**1.433**
	Distance to roads	**0.564**	**0.779**	**1.266**		Distance to roads	**0.372**	**0.987**	**1.604**
	Forest in neighbourhood	−0.128	0.310	0.620		Forest in neighbourhood	**0.305**	**0.926**	**1.852**
	% Forest cover	0.248	0.349	0.698		% Forest cover	0.122	0.332	0.664
	Factor 1 (human impact)	**−0.574**	**0.928**	**1.508**		Factor 1 (human impact)	**−0.122**	**0.964**	**1.567**
	Factor 2 (climatic)	**−0.350**	**0.940**	**1.410**		Factor 2 (climatic)	**1.618**	**0.990**	**1.485**
	Factor 3 (climatic)	**−0.947**	**0.931**	**1.397**		Factor 3 (climatic)	**−2.424**	**1.000**	**1.500**
	Dist. rivers : dist. roads	−1.632	0.123	0.533		Dist. rivers : dist. roads	**−0.634**	**0.704**	**3.051**
	Factor 1 : dist. to rivers	−0.767	0.136	0.589		Factor 1 : dist. to rivers	**0.412**	**0.945**	**4.095**
	Factor 2^2	**−1.136**	**0.908**	**2.724**		Factor 2^2	0.641	0.316	0.948
	Factor 3^2	0.265	0.284	0.852		Factor 3^2	**0.575**	**0.946**	**2.838**

Limitations of SEC model

Although our results seem reasonable, it is important to keep in mind that our predictions represent only a rough approxi-mation of the true distribution of SEC for African great apes. Development of our model was limited by the quality and resolution of available data: the non-random distribution of

(a)

(b)
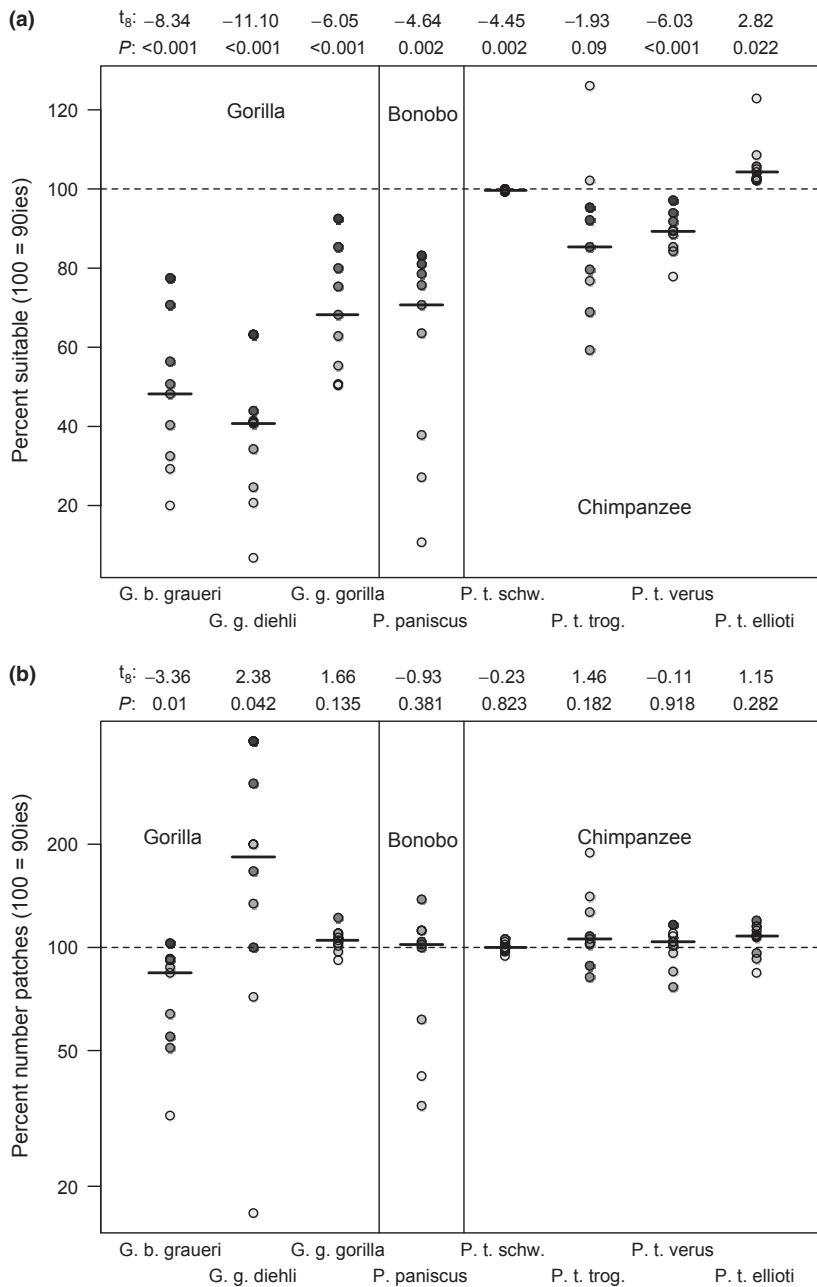
Figure 3 (a) Percentage change in area of SEC between the 1990s and 2000s for all African ape taxa and (b) percentage change in number of SEC patches for all African ape taxa. The points depict the different thresholds (quantiles 10, 20, etc., until 90%) used to define conditions as suitable, whereby darker points denote a lower threshold and hence a larger amount of area considered suitable. The short line represents the median. On top of the plots the results of one-sample tests (H_0: average change = 0) are shown. However, these should be treated cautiously as the degrees of freedom are arbitrary (i.e. depend solely on the number of thresholds used).

presence points and the lack of confirmed absence localities, the lack of consistent predictor variables at resolutions above 5 km, and the lack of comparable and detailed vegetation maps and other predictors for the two time periods at global scales. These issues and their effects on model predictions need to be investigated in more detail.

A large proportion of the presence points we used were collected in protected areas. This non-random distribution of presence localities may have biased our model, probably towards lower environmental suitability outside protected areas. In addition, the use of pseudo- instead of true absences certainly introduced more noise to the model predictions (Wisz & Guisan, 2009).

The use of predictor variables with a relatively coarse resolution of 5 × 5 km prohibits the use of model predictions at a local scale. This limitation is particularly relevant for taxa with particularly small ranges, such as *G. g. diehli*. The inevitable averaging of environmental conditions masks any small-scale variation of habitat and human impact that might be of particular importance for variation in ape occurrence.

Furthermore, because of the lack of comparable time-specific global GIS data sets, the variable 'human impact' was the sole predictor of change in SEC in our model. Although the variables combined in the 'human impact' factor can be interpreted as proxy for the impact of
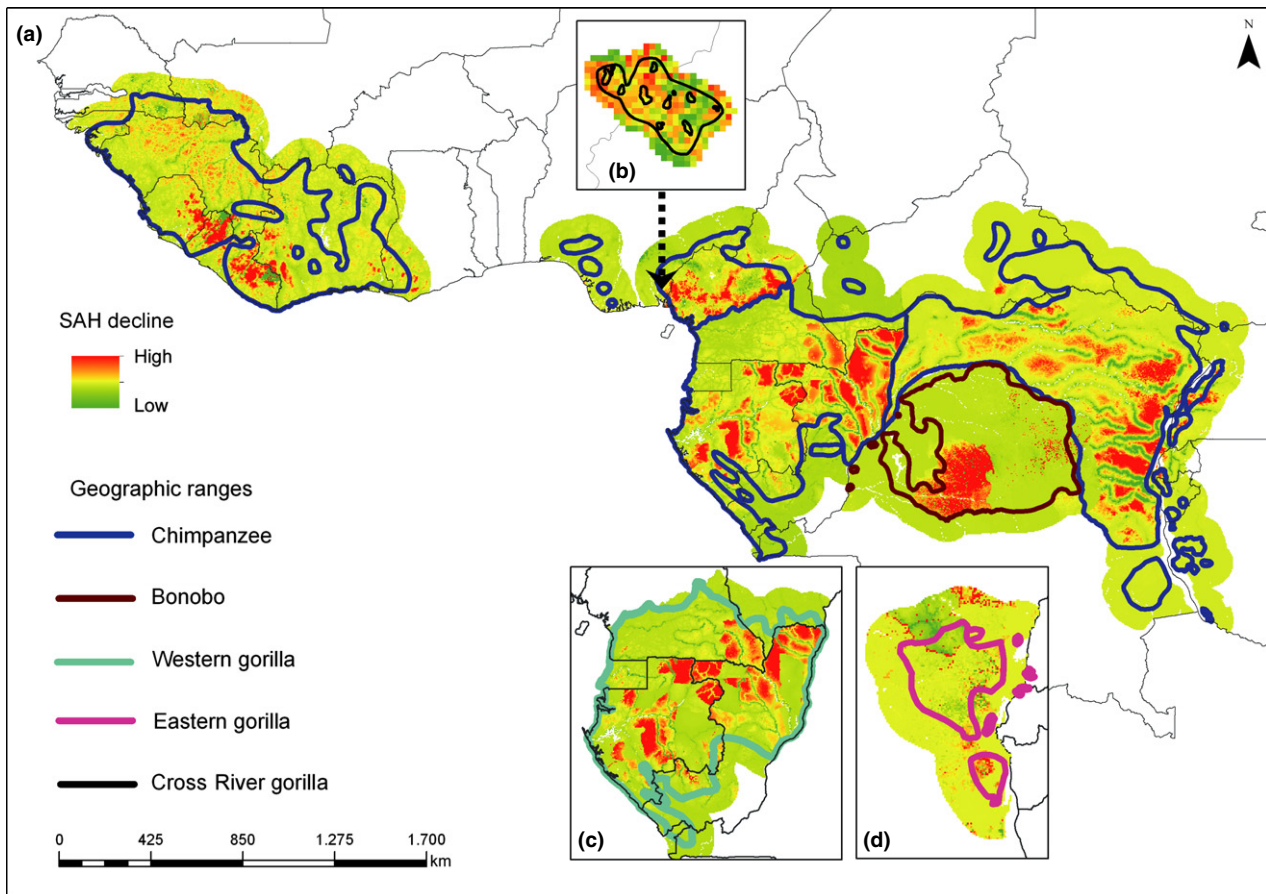
Figure 4 Estimated decrease in SEC between the 1990s and 2000s for (a) chimpanzee and bonobo, (b) Cross River gorilla, (c) western lowland gorilla and (d) eastern lowland gorilla. Colours indicate the gradient in SEC decrease ranging from green to yellow to red, indicating low, intermediate and high decrease in SEC. Note that areas previously characterized by high values of SEC may experience high rates of SEC decline.

agriculture, logging, artisanal mining, commercial and sub-sistence poaching on apes, other factors such as infectious diseases (Walsh *et al.*, 2003; Leendertz *et al.*, 2004; Bermejo *et al.*, 2006) and climate change are also important predictors of ape distribution. Cultural taboos and traditional proscriptions of eating apes in some ethnic groups and regions can impact ape SEC (Lahm, 2000; McLennan, 2008; Hockings *et al.*, 2009; Brncic *et al.*, 2010). Other factors may also have important roles in structuring human-ape interactions, including human warfare, land-use rights, indigenous hunting and farming traditions.

Because we lacked information on the attitudes of local people towards apes and because we modelled SEC on a global scale, we could not explicitly incorporate spatial differences in coexistence between humans and apes into our models. Here our results require particularly careful interpretation: our models usually detected only the generally negative correlation between human population density and ape presence. They are not representative of locations where apes and humans coexist in close proximity, such as parts of Guinea (Hockings *et al.*, 2009), Sierra Leone (Brncic *et al.*, 2010) and Uganda (McLennan, 2008). However, it remains

to be seen whether these are stable situations or transitional phenomena in the process of habitat conversion and development of human-dominated landscapes. Including such scenarios would need a more fine-scaled analysis and additional predictors (e.g. local attitudes towards apes and long-term human impacts, such as the modification of food-plant distribution and historical development of land-use by humans). Similarly, our model does not take into account the effects of conservation activities aimed at mitigating human impact (Tranquilli *et al.*, 2011). This is an obvious weakness, but could not be incorporated given the limitations of existing data.

Finally, we did not have two comparable vegetation maps to represent past and current habitat conditions, thereby underestimating the impact of continued habitat destruction on ape populations in Africa, although in the Central African forest blocks identified as the ape strongholds (Fig. 1) forest loss is still very low (Hansen *et al.*, 2008, 2011) Additionally, the model did not distinguish between swamp and *terra firma* forest, nor between closed-canopy-open-understory forests and open-canopy-closed-understory forests, which affected the SEC maps produced for both central chimpanzees and

western lowland gorillas. However, from our continental perspective this effect is less important than it would be from a regional perspective.

Given the number of limitations discussed above, we consider our model and estimates of change in SEC distribution over the past 20 years as only the first attempt to provide a continent-wide perspective of the situation ape populations face and much work needs to be done to improve this model (see Conclusion and outlook).

Fields of application

The results presented in this paper may provide another source of information to support researchers, wildlife managers, funding agencies, industry and politicians when making decisions in identifying priority conservation areas, research gaps, potential wildlife corridors and future survey sites, within the limitations of the model outlined above. However, given the complexity of decision-making in conservation, involving national and international politics, local communities and economical interests, we do not make specific recommendations about specific locations that deserve greater attention. This process will require studying our results in the context of the respective question, location, region or taxon of interest. We also strongly recommend to overlay the SEC models with a series of other GIS layers, including expert based ape priority areas, confirmed presence locations, survey areas, as well as various contextual layers related to human activities, landcover, topography, and conservation to help inform decisions (all available at http://apesportal.eva.mpg. de). This approach will help to identify obvious discrepancies between different sources of information (e.g. expert based priority areas and SEC model predictions) but at the same time provides a further source of information.

CONCLUSION AND OUTLOOK

Our results represent the best available estimate of continent-wide African SEC distribution and change over the past 20 years. This is also the first study to have amalgamated data from numerous sites across the African ape range in an attempt to bridge the gap between local efforts in the field and a global perspective of the distribution of ape populations. This is one of the major goals of the IUCN/SSC A.P.E.S. project, from which the presence localities used in this study were extracted.

We have demonstrated dramatic declines in SEC for great apes, which strongly suggest that conservation efforts must be radically stepped up. It is also highly likely that many other species within the apes' range have experienced similar declines in SEC.

Future studies are needed to further develop the model presented in this paper and we suggest the following. (1) Evaluation of model: in principle every new field data set (transect, recce, genetic or camera trap survey) can be compared against our SEC model prediction (see Appendix S1

for example method), elucidating over which spatial scale and in which regions model predictions are reasonable. (2) Improving current model: development of models that use real absences, which are likely to be more easily available in the near future; and comparison of different modelling techniques. (3) Development of regional and local models of ape population status taking more finely scaled spatial information into account and compare predictions against the SEC model of this study; (4) Explicit modelling of ape-human coexistence to evaluate whether ape persistence in human-dominated landscapes is likely to be long-term; (5) Evaluation of ape population changes under different conservation management scenarios.

Our work is only the beginning of modelling ape populations in relation to their environments, threats and conservation effort. This is a wide and open field with many interesting avenues to pursue.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Supplementary material on methods, results and discussion of this article.

Appendix S2 List of data sets (country and site name where data were collected, name of data provider and the year(s) during which the data were collected) from which ape presence localities were extracted and included in our model; results on patch size distribution and change.

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BIOSKETCHES

The authors are actively involved in biomonitoring and research of great ape populations across Africa to effectively inform management decisions and guide future conservation efforts. They also contributed their data sets to the IUCN/ SSC A.P.E.S. database (http://apes.eva.mpg.de) in an attempt to centralize all great ape survey data collected in the past and make these accessible to the scientific community. The main scientific interest of the first author focuses on large mammal temporal and spatial population dynamics and the factors influencing these. She also has a keen interest in conservation biology and the application of theoretical ecology to address ecological problems.

Author contributions: J.J. and H.K. conceived the ideas, compiled the data, conducted the analysis and led the writing; D.M. and C.S. assisted with the development, coordination and implementation of initial data contributions. C.B. conceived the ideas and provided comments on the manuscript; R.M. and L.d.T. conducted the analysis; S.T. compiled the data and all other authors developed the survey design of the study from which data were extracted, collected, compiled and processed the data and provided comments on the manuscript.

Editor: Michael Bode