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Distinguishing ecological constraints from human activity in species range fragmentation: the case of Cross River gorillas

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Abstract

The geographic range of many species has been reduced and fragmented by human impact, and ever more species live in human-dominated landscapes where they are confined to small and often suboptimal refuge areas. A detailed understanding of the causation of species' persistence and disappearance is crucial to inform management of which interventions are likely to be most effective. Yet this information is often not available to decision makers and may, in the worst case, lead to erroneous management decisions. To clarify whether Cross River gorilla *Gorilla gorilla diehli* (CRG) occurrence is restricted due to ecological constraints or human disturbance, we collected extensive field data on food availability, habitat structure, human activity and wildlife abundance, which we related to CRG occurrence. We also related spatial variation in hunting pressure to human density, household forest use and topography. Our results clearly show that CRG are currently confined to refuge areas because of ongoing detrimental human activities and not because of lack of food resources. Current hunting pressure is driven by human population pressure, accessibility and socioeconomic conditions influencing household dependence on forest. A substantial amount of ecologically suitable but currently unoccupied habitat could potentially carry a much larger CRG population. Conservation management should therefore focus on reducing hunting and disturbance of CRG. In contrast, ecological restoration would not improve CRG living conditions. Our field and analytical approach is widely applicable to the rapidly increasing number of species inhabiting heavily human-influenced landscapes for identifying appropriate management interventions for their protection.

Introduction

Due to human impact, the geographic range of many species has been reduced and fragmented, and an increasing number of species live in human-dominated landscapes (Channell & Lomolino, 2000). This situation is common among all taxa including mammals (e.g. Asian elephant *Elephas maximus*: Rood, Ganie & Nijman, 2010; jaguar *Panthera onca*: Haag *et al*., 2010; brown bear *Ursus arctos*: Naves *et al*., 2003; Güthlin *et al*., 2011), birds (e.g. hen harrier *Circus cyaneus*: Anderson *et al*., 2009), amphibians (e.g. Moor frog *Rana arvalis*: Vos & Chardon, 1998), butterflies (e.g. *Melitaea cinxia*, *Polyommatus bellargus*: Thomas *et al*., 2001), reptiles (e.g. agamid lizard *Amphibolurus nobbi*: Driscoll & Hardy, 2005) and fen plants (e.g. *Carex lasiocarpa, Menyanthes trifoliata:* Soomers *et al*., 2012).

Efficient conservation management requires a detailed understanding of the relative influence of limiting ecological conditions versus detrimental human activities. However, it is often difficult to infer which factors determine the current distribution of a threatened species and their potential for recovery because of the potentially overriding influence of human activities relative to ecological factors (e.g. *Circus cyaneus* and *Aquila chrysaetos:* Whitfield *et al*., 2007; Anderson *et al*., 2009). Under conditions of intense hunting, even high quality habitat may function as a population sink, reducing its conservation value (e.g. culpeo fox *Pseudalopex culpaeus:* Novaro, Funes & Walker, 2005; brown bear *Ursus arctos*: Naves *et al*., 2003; Iberian lynx *Lynx pardinus:* Gaona, Ferreras & Delibes, 1998). In such situations, reducing hunting should be a priority for conservation management to reestablish suitable conditions for possible future population expansion. In contrast, if no potentially suitable habitat is available outside current areas of occurrence of a species, conservation management needs to focus on existing occupied areas; possibly connecting them through corridors by ecological restoration to enable dispersal.

Here, we use the Cross River gorilla (CRG), endemic to the southern Nigeria – Cameroon border region to further investigate this issue. The CRG population is small and highly fragmented (<300 individuals estimated to survive as of 2007), concentrated in about 14 small hilly areas (~600 km^2 in total) interspersed among large areas of unoccupied but potentially suitable habitat across a landscape of ~12 000 km^2 (Oates *et al*., 2007; Bergl *et al*., 2012; Fig. 1). Genetic evidence and historical records suggest that CRG were historically more abundant and probably more widespread across the Cross River landscape (Mansfield, 1908; Bergl *et al*., 2008; Thalmann *et al*., 2011), but their precise historical distribution and whether the gorillas have distinct preferences for certain habitat types is not known (Oates *et al*., 2003). Using detailed field data, we modeled CRG occurrence across their entire range in Nigeria to assess the relative importance of potentially limiting resource availability versus detrimental human activity. Additionally, we modeled spatial variation in hunting pressure using local household forest use and other socioeconomic data as well as topographic data.

Methods

Study area and data collection

CRG occur in the mountainous southern border region of Nigeria and Cameroon (Fig. 1). The area surveyed in this study (8°50′–9°21′ E, 6°4′–6°28′ N) covers four protected areas in Nigeria with a combined area of about 1000 km^2. Human population in this region is one of the highest in Africa resulting in high pressure on the habitat (Oates *et al*., 2004; Junker *et al*., 2012). Gorilla presence has been recorded over a wide altitudinal range, from below 200 to about 2000 m. However, the majority of gorilla signs in this region have been found between 400 and 1600 m and in areas of high relief and rugged terrain. The current occupied range covers *c*. 600 km^2 (Fig. 1) although analysis of satellite imagery showed that *c*. 8000 km^2 of the *c*. 12 000 km^2 landscape was forest in 2003 (Bergl *et al*., 2012). Threats to CRG include hunting, agricultural conversion, logging, seasonal bush fires and expanding human settlements and roads (Oates *et al*., 2007).

Data on the presence of gorillas in the landscape were obtained from surveys conducted between 1987 (when gorillas were 'rediscovered' in Nigeria) and 2008 (Harcourt, Stewart & Inahoro, 1989; Oates *et al*., 2003, 2004;

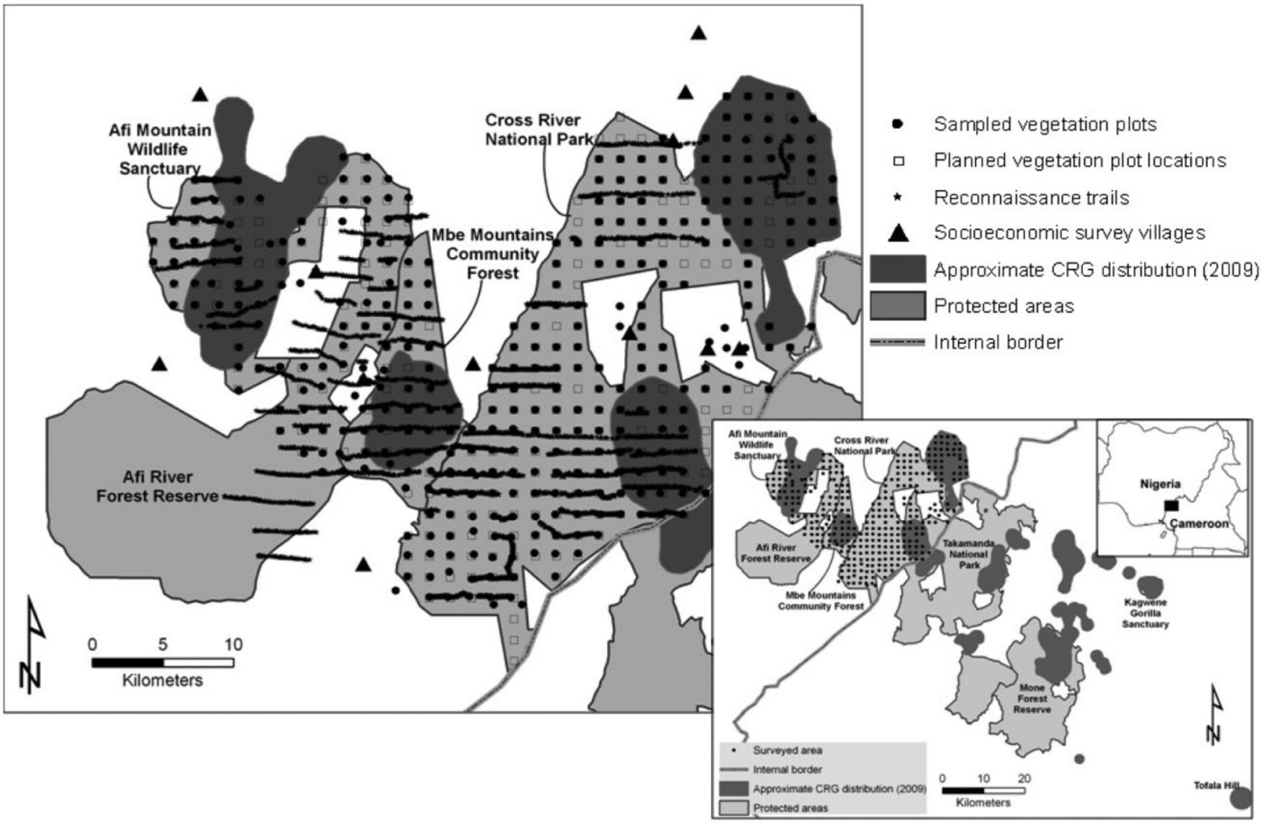

Figure 1 Range of the Cross River gorilla *Gorilla gorilla diehli* in the Nigeria – Cameroon border region and current distribution as of 2009 (right), the surveyed area (left) showing locations of sampled vegetation plots (black dots), all plots in original survey design (black squares) and reconnaissance trails (black lines).

Sunderland-Groves, Maisels & Ekinde, 2003; Bergl *et al.*, 2012). The surveys employed both 'travel' and 'guided' reconnaissance (recce) walk methods (White & Edwards, 2000; Kühl *et al.*, 2008). Signs of gorilla presence recorded include nests, dung, feeding remains, vocalizations and direct encounters. Inclusion of data from earlier surveys did not alter the current distribution of CRG, as more recent surveys showed continued presence of gorillas in all earlier known occupied areas (Bergl *et al.*, 2012). There are, therefore, no potential issues of incompatibility of gorilla presence data with vegetation, human activity and large mammal abundance data collected later. The occupied range was estimated by applying a 1.5 km buffer to the presence locations, and then manually edited to exclude areas where gorillas were known to be absent (e.g. villages) and to include contiguous forested hill areas (Bergl *et al.*, 2012). We applied a buffer around presence locations to account for gorillas occasionally using adjacent areas of suitable habitat. We chose a distance of 1.5 km for the buffer because it is roughly the mean daily travel distance of CRG (McFarland, 2007), so it represented a reasonable and conservative additional area that could have been used by the gorillas.

To measure food availability and its spatial variation, we surveyed 358 vegetation plots (spaced by 1.5 km and distributed over the study area) to record tree, liana and terrestrial herb species (trees: 20 × 20 m, lianas: 5 × 5 m and herbs: 1 × 5 m) from July 2010 to August 2011. We surveyed vegetation at a 1.5 km resolution because it is fine scaled enough given the scale at which vegetation structure and composition vary but at the same time still feasible with regard to the sampling effort required. Food availability assessment was based on existing knowledge of CRG food species, a potential limitation of our study (Supporting Information Appendix S1). We collected data on human activity and large mammal abundance using the standard field method of 'guided' reconnaissance walk (White & Edwards, 2000; Kühl *et al.*, 2008) between February 2008 and May 2011 covering a total distance of 298 km (Fig. 1).

We collected household forest use data through questionnaire interviews conducted in 12 villages (240 households in total) within the study area (Fig. 1) between 2010 and 2011. Households were selected using a stratified random sampling method such that the main occupations in the study area (hunting, farming, forest products collection and non-forest-based occupation) were proportionately represented in the sample. This was done in order to have a sample that was not biased toward certain occupations. To achieve this, a household list was created for each village with main occupation of household heads indicated. From the household list, the proportion of households engaged in different primary occupations was determined. We defined a household as 'a group of persons living together under the same roof or several roofs within the same dwelling, making common provision for food and other living arrangements' (Kideghesho, Røskaft & Kaltenborn, 2007). Respondents were heads of the households. To ensure that respondents provided reliable information, given the sensitive nature of the issues investigated; the purpose of the study was explained and made clear before the start of the interview.

Topographical data were obtained from the Shuttle Radar Topography Mission Digital Elevation Model (90 m resolution) (USGS, 2004) and human population data (population size per village, for 59 villages in and around the surveyed area) from the Nigeria National Population Commission census database, respectively. Because of issues of reliability of more recent census figures and difficulties in obtaining them, we used data for the year 1996 which we projected to 2010 using the formula:

$$p_t = p_o(1+r)^t$$

Where p_o = basal population of the area (i.e. population for the year 1996)
p_t = projected population t years later (i.e. 2010)
t = time interval in calendar years between p_o and p_t (i.e. 1996 to 2010)
r = growth rate of population per year, assumed to remain constant over the time interval, t.

Data analysis

We derived five food availability factors using a Factor Analysis (FA; Supporting Information Appendix S1). Variables were defined based on basal area, density and species richness of different categories of CRG food plants (McFarland, 2007; Table 1). To process human activity and large mammal abundance data, we laid a 1.5 × 1.5 km grid over the study area. This was done to summarize the data collected on reconnaissance trails into discrete spatial units for subsequent integration with vegetation data collected within plots. We chose a 1.5 × 1.5 km resolution for the grid to match the spacing of vegetation plots (1.5 km). Per grid cell, we determined survey effort (as recce length), the number of observed signs of human activity and the abundance of large mammals other than gorillas (Supporting Information Appendix S1). To account for varying survey effort, we divided the summed scores of human activity and large mammal abundance per grid cell by the respective number of kilometers surveyed. To derive the intensity of human activities (divided into hunting and other human activities) and large mammal abundance per vegetation plot, we calculated the inverse distance-weighted mean of the respective signs of all grid cells (Supporting Information Appendix S1). We derived two variables describing household forest use: non-timber forest products (NTFP) collection man-days and primary occupation of household (i.e. primarily forest-based or otherwise, see Supporting Information Appendix S1).

Modeling gorilla presence and hunting pressure

Data were analyzed within a generalized linear model framework. The gorilla presence model was fitted with a

Table 1 Results of the Factor Analysis (FA) conducted on food availability variables

Variable	FA1	FA2	FA3	FA4	FA5
Density of important staple lianas	0.95	0.02	–0.02	–0.10	0.12
Density of important fruit lianas	0.95	0.02	–0.02	–0.09	0.12
Density of important fallback lianas	0.95	0.01	–0.01	–0.09	0.11
Density of lianas	0.85	0.20	0.03	0.07	0.13
Species richness of all lianas	0.79	0.22	0.05	0.04	0.16
Density of important herbs	0.02	0.89	0.11	0.30	0.07
Density of important fallback herbs	0.08	0.89	0.09	–0.22	0.11
Density of all herbs	0.13	0.88	0.11	0.30	0.09
Species richness of all herbs	0.22	0.84	0.10	0.21	0.12
Density of tree bark species	–0.03	0.08	0.81	0.12	0.26
Density of important staple trees	–0.07	0.04	0.79	0.06	–0.10
Density of important fruit trees	0.16	0.05	0.70	–0.02	0.46
Density of Aframomum spp. and Anchomanes deformes	–0.04	0.17	–0.03	0.87	–0.05
Density of important staple herbs	–0.10	0.21	0.20	0.87	0.02
Species richness of all trees	0.28	0.11	0.35	–0.05	0.80
Density of all trees	0.29	0.09	0.35	–0.07	0.79
Basal area of all trees	0.13	0.03	0.12	–0.01	0.79
Density of important fallback trees	0.00	0.15	–0.18	0.04	0.67
Eigenvalue	5.75	3.43	2.61	1.49	1.09
Proportion of variance explained	0.24	0.18	0.15	0.12	0.10

FA1 correlates with density and species richness of food lianas; FA2 largely correlates with density and species richness of herbaceous foods; FA3 correlates with density of important bark, fruit and staple food trees; FA4 correlates with density of the two most important herb species in the CRG diet; FA5 correlates with density, basal area and species richness of food trees.

binomial error structure and logit link function, whereas the hunting pressure model was fitted with negative binomial error structure and log link function. We modeled gorilla presence (yes/no) on individual vegetation plots ($n = 358$) as a function of the five food availability factors (FA1–FA5, Table 1), hunting pressure, other human activities, large mammal abundance and a term accounting for spatial autocorrelation (Supporting Information Appendix S1). We included large mammal abundance in the model because we reasoned that the distribution of other hunted large mammals may predict the distribution of gorillas. In addition, we considered that since gorillas are not targeted by hunters but are hunted opportunistically, the abundance and distribution of other large mammals may allow a clearer understanding of patterns of hunting pressure. The model was:

$$\begin{aligned}&\text{Gorilla presence(yes/no)} \sim \text{FA factor 1} + \text{FA factor 2}\\&\quad + \text{FA factor 3} + \text{FA factor 4} + \text{FA factor}\\&\quad 5 + \text{hunting pressure} + \text{other human activities}\\&\quad + \text{large mammal abundance} + \text{autocorrelation term.}\end{aligned}$$

Although linear barriers such as rivers and roads influence species occurrence (Schippers *et al.*, 1996), we did not include these variables directly in our model because for our study species, dispersal is not likely to be limited by such linear barriers themselves but rather by the associated human disturbance (which we incorporated directly in our model). There are no rivers in the study area large enough to constitute a total barrier to movement of gorillas. Also, for relatively long distance dispersers like gorillas movement between resource patches is not likely to be limited by a road per se (typically 20–30 m wide), but by associated human disturbance.

In a second model, we investigated whether 'NTFP collection man-days' and 'primary occupation of households' (forest vs. non-forest related) ($n = 240$ households), as measures of households' dependence on the forest, as well as human population pressure, topography and protection status of sites (as a measure of conservation effort) influenced hunting pressure in individual grid cells ($n = 228$) in the study area (Supporting Information Appendix S1). We used the hunting pressure score as described above. To determine the specific value of a predictor in a given grid cell, we used the distance-weighted average of the variable for each grid cell sampled. As weight, we used the inverse of the cost-weighted distance (based on slope steepness) from the grid cell to each of the 12 surveyed villages (Supporting Information Appendix S1). We also included in the model protection status (yes or no) and an autocorrelation term. We assumed that the distance-weighted average of 'NTFP collection man-days' and 'primary occupation of households' would more strongly impact grid cells that are more accessible, therefore we included the interaction between 'human population pressure', on the one hand, and 'NTFP collection man-days' and 'primary occupation of households', on the other hand, into the model. The model was:

$$\begin{aligned}&\text{Hunting pressure} \sim \text{NTFP collection man} - \text{days}\\&\quad + \text{primary occupation of households} + \text{human}\\&\quad \text{population pressure} + \text{NTFP collection man}\\&\quad - \text{days*human population pressure} + \text{primary}\\&\quad \text{occupation of households*human population pressure}\\&\quad + \text{protection status} + \text{autocorrelation term.}\end{aligned}$$

For both models, we compared the full with a null model comprising only the autocorrelation term to assess overall significance (Forstmeier & Schielzeth, 2011) using a likelihood ratio test (Dobson, 2002). We also report Nagelkerke's pseudo R^2 as measures of effect size (Field, 2005). Data analysis was carried out in R (R Development Core Team, 2011). We considered $P \leq 0.05$ as significant and $0.05 < P \leq 0.1$ as a trend.

Results

Gorilla presence

Overall, gorilla presence was clearly influenced by the variables investigated (likelihood ratio test comparing full and null model: $\chi^2 = 34.93$, d.f. = 8, $P < 0.001$). Regarding food availability, the only significant variable was lianas (FA1), correlating negatively with gorilla presence (Table 2; Figs 2a and 3). Gorilla presence was not influenced by the abundance of other large mammals (Table 2; Fig. 3), but was strongly influenced by human activity (Table 2). Specifically, while non-hunting human activity (farming, logging, NTFP collection, etc.) influenced gorilla presence negatively (Fig. 2b), hunting pressure was positively correlated with gorilla presence (Fig. 2c). Using different weights for hunting signs and replacing large mammal abundance with species richness in the model did not change the results (Supporting Information Table S4 and S5).

Table 2 Results of the model of gorilla presence as a function of food availability, human activity and large mammal abundance

Predictor	Estimate	SE	z	P	R^2
Intercept	–2.172	0.337	(1)	(1)	(1)
FA 1	–0.751	0.280	–2.682	0.007	0.065
FA 2	–0.103	0.250	–0.412	0.680	0.002
FA 3	–0.201	0.266	–0.754	0.451	0.004
FA 4	–0.239	0.246	–0.970	0.332	0.009
FA 5	–0.189	0.257	–0.736	0.462	0.033
Hunting pressure	1.109	0.373	2.972	0.003	0.006
Wildlife abundance	0.272	0.239	1.137	0.255	0.005
Other human activities	–1.801	0.395	–4.561	< 0.001	0.162
Autocorrelation term	3.254	0.398	8.169	< 0.001	(1)

(1), not indicated because it has no meaningful interpretation; FA, factor analysis.
All predictors were z-transformed. R^2 is Nagelkerke's pseudo R^2.

Hunting pressure

Overall, the number of hunting signs per grid cell was not influenced by the predictors in the model as a whole ($\chi^2 = 10.00$, d.f. = 6, $P = 0.125$). We found no significant interaction between 'primary occupation of households' and 'human population pressure' ($P = 0.619$; Supporting Information Table S6) but a potential interaction between household 'NTFP collection man-days' and 'human population pressure' ($P = 0.046$; Table 3) suggesting that the impact of household forest use on hunting pressure varied with human population pressure. We also found a tendency for an increased number of hunting signs in grid cells within protected areas ($P = 0.068$; Table 3). However, these results should be considered with caution because they might arise from multiple testing (since the full and null model comparison did not reveal significance; Forstmeier & Schielzeth, 2011).

Discussion

The key finding of our study is that at a landscape-scale CRG are confined to their current distribution because of human disturbance and not because of a lack of food resources. A large amount of ecologically suitable habitat is available outside the current occupied area that presumably could support a much larger gorilla population. We found higher intensity of hunting in difficult to reach hilly areas generally occupied by CRG. This likely reflects a transient situation emerging in many regions throughout the world where hunting is advancing into previously inaccessible

Table 3 Results of the model of hunting pressure (weighted number of hunting signs) as a function of local household forest use, human population pressure (weighted by accessibility) and protection status

Predictor	Estimate	SE	Z	P	R^2
Intercept	–7.000	0.482	(1)	(1)	(1)
Household NTFP collection man-days	–0.213	0.268	(1)	(1)	(1)
Human population pressure	0.140	0.239	(1)	(1)	(1)
Primary occupation of household (forest/non-forest related)	0.084	0.197	0.424	0.671	0.002
Protection status (no = 0; yes = 1)	0.891	0.488	1.825	0.068	0.014
NTFP collection man-days*human population pressure	–0.355	0.178	–1.996	0.046	0.011
Autocorrelation term	0.298	0.155	1.925	0.054	(1)

(1), not indicated because it has no meaningful interpretation.
All predictors were z-transformed. R^2 is Nagelkerke's pseudo R^2. Household non-timber forest products (NTFP) collection man-days is number of days spend collecting forest products multiplied by number of household members collecting forest products.

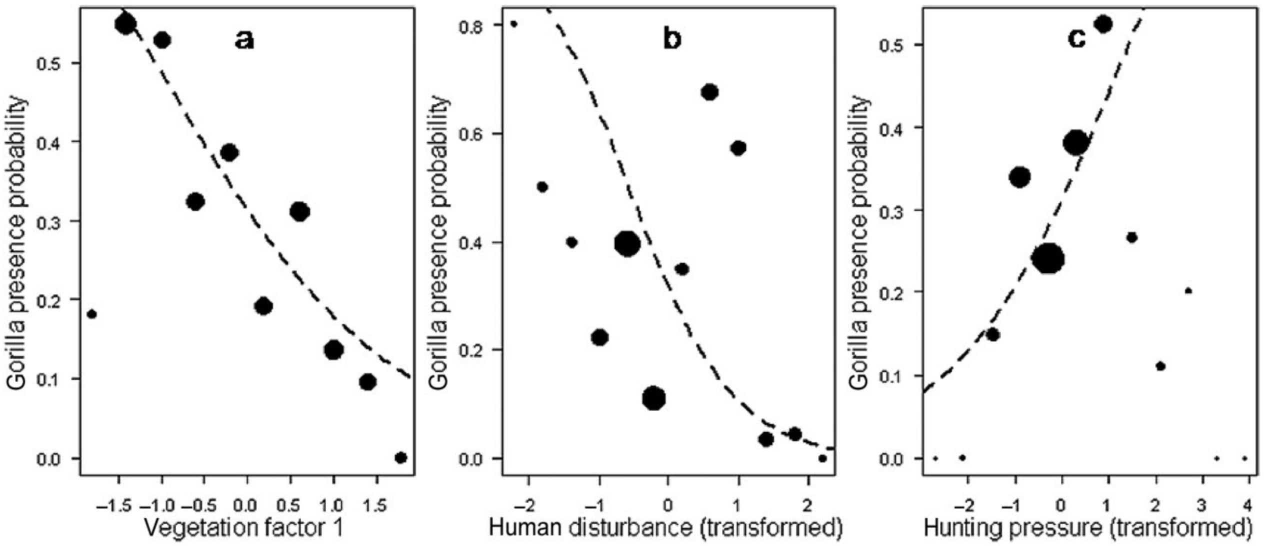

Figure 2 Gorilla presence probability as a function of vegetation factor 1 (Lianas) (a) human disturbance (b) and hunting pressure (c). Shown are presence probabilities per binned value of the respective predictor. The dashed line indicates the fitted response (determined using a generalized linear model with multiple predictors). The area of the dots is proportional to the sample size per bin.

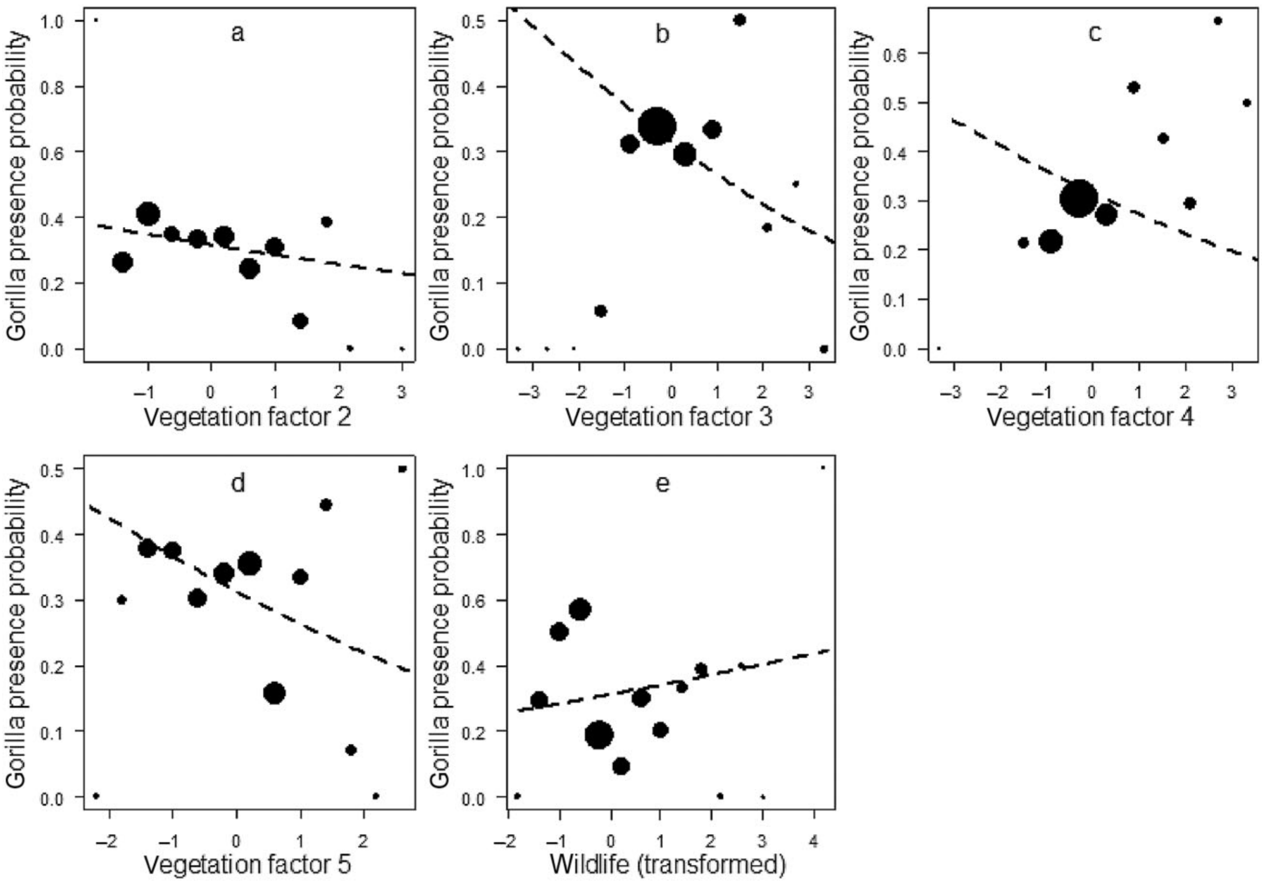

Figure 3 Gorilla presence probability as a function of food availability factors (plots 3a–d) and wildlife abundance (e). Shown are presence probabilities per binned value of the respective predictor. The dashed lines indicate the fitted response (determined using a generalized linear model with multiple predictors). The area of the dots is proportional to the sample size per bin.

wildlife refugia as human population and road access increase (Wilkie *et al.*, 2000; Kuehl *et al.*, 2009; Yackulic *et al.*, 2011). Our approach integrates detailed ecological and human activity data over a large spatial extent in a single model. It thus allows drawing firm conclusions about the determinants of CRG distribution and the suitability of currently unoccupied habitat which was impossible from previous spatially limited studies. Current high levels of hunting could be reduced through effective law enforcement informed by systematic monitoring data (N'goran *et al.*, 2012; Tranquilli *et al.*, 2012) thereby reestablishing suitable conditions for population expansion into currently unoccupied areas.

We acknowledge that the accuracy of our food availability assessment could potentially be limited by the current state of knowledge of the diet of CRG which comes mainly from two relatively high elevation sites that are also at the periphery of the species' range (Oates *et al.*, 2003; McFarland, 2007) and may not be fully representative for the whole population. However, this is not likely to be a problem since food availability was not higher in the relatively higher elevation areas occupied by gorillas compared to unoccupied lower elevation areas. Furthermore, including additional food species present at lower elevations, but not found in occupied high elevation areas in the analysis is likely to result in even higher food availability in unoccupied areas. Moreover, selection of species that constitute 'important' food species may also influence accuracy when assessing the influence of food availability on a species' distribution (Forest *et al.*, 2008). To overcome this problem, we included all known food species in the analysis, grouped into a number of importance categories as well as according to plant form (McFarland, 2007).

Our results can be considered representative of the situation of many other threatened species inhabiting heavily human-influenced landscapes. Similar to many other regions, the CRG landscape represents a complex social-ecological system in which ecological processes and human activity are closely related and need to be considered together in order to understand conservation issues (Parrott & Meyer, 2012). Because complex landscapes have 'memory' (i.e. historical events influence future landscape states), current species distribution patterns and ecological processes often reflect past disturbance events such as intense hunting and land-use patterns. In the case of CRG, past hunting pressure and human disturbance have resulted in the disruption of the relationship between ecological conditions and CRG presence with the CRG being now confined to small suboptimal refuge areas.

Understanding the cross-scale nature of interactions between human activity and ecological processes in complex landscapes and the causes of emergent landscape patterns will inform decisions about which scales management actions might have the greatest impact. Although at the subpopulation level, the distribution of key food resources is an important determinant of CRG habitat use and ranging pattern (Sawyer & Brashares, 2013); at the landscape level, anthropogenic disturbance has led to a mismatch between CRG occurrence and ecological suitability. While in some cases conservation management may need to focus on occupied areas where species or populations are confined to small ranges due to total loss of habitat in surrounding areas (as in the case of mountain gorillas; Robbins *et al.*, 2011), our results highlight the importance of landscape-scale conservation planning and management to achieve biodiversity conservation as global change intensifies.

Our field and analytical approach can be easily transferred to other species and to other heavily human-influenced landscapes that represent complex social-ecological systems to identify appropriate management actions. Studies replicating our approach need to take into account species-specific habitat requirements, including food preferences. Furthermore, such studies should also consider appropriate spatial scales since the importance of ecological and human factors may vary at different spatial scales and thus affect results (e.g. subpopulation vs. landscape scale; Sawyer & Brashares, 2013). Field data collection designs should consider spatial heterogeneity of the study landscape in terms of vegetation and other ecological variables, as well as human influence to ensure representativeness of data.

Studying the dynamics of complex landscapes and emergent patterns in response to disturbances through analysis of historical data is a useful way to understand current distributional patterns of species and ecological processes that lead to them and inform management strategies. Furthermore, modeling alternative future scenarios and assessing the potential impacts of different management actions will help to buffer against inherent uncertainties and enhance the persistence of endangered species in complex landscapes (Peterson, Cumming & Carpenter, 2003).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Detailed description of field and analytical methods and results of additional models

Table S1 List of large mammal species (other than gorilla) recorded during the reconnaissance survey

Table S2 Ranks assigned to signs of hunting and other human activities recorded during the reconnaissance survey. Ranks were used to weight signs in the analysis

Table S3 Alternative ranks assigned to signs of hunting used in a model to test the effects of different weighting schemes

Table S4 Results of the model of gorilla presence as a function of food availability, human activity and large mammal abundance. Hunting pressure, other human activities and wildlife abundance were derived using weighted values. All predictors were z-transformed

Table S5 Results of the model of gorilla presence as a function of food availability, unweighted human activity and large mammal species richness. All predictors were z-transformed

Table S6 Results of the initial full model of hunting pressure as function of household forest use, primary occupation of household, human population and protection status