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ORIGINAL PAPER

Large mammal diversity and their conservation in the human-dominated land-use mosaic of Sierra Leone

Terry Brncic[1,2] · **Bala Amarasekaran**[2] · **Anita McKenna**[2] ·
Roger Mundry[3] · **Hjalmar S. Kühl**[3,4]

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Abstract Like elsewhere in West Africa, the landscapes of Sierra Leone are strongly human-dominated with consequences for large mammal distribution and diversity. Sierra Leone is currently going through a phase of post-war recovery, with accelerating development of the mining, forestry, agricultural and infrastructure sectors. As environmental issues are increasingly considered, comprehensive biodiversity information is required. Here we evaluate spatial patterns of large mammal diversity throughout Sierra Leone to make inferences about species persistence. We used systematic line transect sampling for assessing large mammal distribution. GLMs and canonical correspondence analyses were used to evaluate the relative importance of human impact for every species while controlling for environmental gradients and to make countrywide spatial model predictions. We further developed an algorithm to identify core distributional ranges for the most common species. A total of 562 km of transects were surveyed and 35 large mammal species encountered. Species diversity was impoverished in the country's south and center and strongly increased towards the north and east. Human impact did not determine the distribution of four species (*brushed-tailed porcupine*, *bushbuck*, *giant rat*, *warthog*), but was very influential on *chimpanzee* and *yellow-backed duiker* occurrence with U-shaped and negative responses, respectively. The remaining species showed mixed responses to

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✉ Hjalmar S. Kühl
kuehl@eva.mpg.de

[1] World Resources Institute, Kinshasa, Democratic Republic of Congo

[2] Tacugama Chimpanzee Sanctuary, Freetown, Sierra Leone

[3] Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany

[4] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,
Deutscher Platz 5e, 04103 Leipzig, Germany

human impact and environmental gradients. Predicting species persistence in West African human-dominated landscapes is complex. Pooling of species for land-use planning is therefore not recommended. Our study provides key information for land-use planning to separate areas with post-depletion species assemblages from more diverse regions with high conservation value.

Keywords Core distributional range areas · Distribution · Hunting · Line transect · Post-depletion · Spatial model

Introduction

In the face of global change and ensuing modifications of biodiversity patterns, research on species distribution is a prime focus in ecology and conservation (e.g. Austin 2002; Dormann 2007; McMahon et al. 2011). Large scale land conversion, resource exploitation, industrial agricultural and climate change are posing considerable pressure on species (e.g. Parmesan and Yohe 2003; Foley et al. 2005; Wich et al. 2014). The question of how this impact will modify community assemblages, species interactions and eventually ecosystems and their services requires first and foremost a solid understanding of the mechanisms determining species distribution and biodiversity patterns (e.g. Gaston 2000; Balvanera et al. 2006). Furthermore, this information is fundamental to find solutions for adaptively planning appropriate conservation measures, including the prioritization of key areas across scales (Wilson et al. 2006), for evaluating existing protected area networks (Bruner et al. 2001; Geldmann et al. 2013) and to assess the effectiveness of conservation interventions (Tranquilli et al. 2012).

The distribution of species and biodiversity is determined by a large number of abiotic and biotic factors, of which usually only a few are well established for any given species (Araujo and Guisan 2006; Elith and Leathwick 2009). Much research effort has been devoted to identifying such factors for individual species and patterns of biodiversity, including climate and other geophysical conditions, geographical features, the productivity, quality and heterogeneity of habitats, predation, disease, demographic effects, human impact and species interactions (Atauri and de Lucio 2001; Tews et al. 2004; Araujo and Guisan 2006; Austin 2007; Elith and Leathwick 2009). For instance in human-dominated landscapes the productivity and structural heterogeneity is heavily modified compared to less human impacted environments. Consequently certain species are no longer able to persist, if they cannot meet their energy requirements (Yamaura et al. 2011) or if reproductive and survival rates decrease for other reasons (Rodewald et al. 2011). In contrast other species may thrive as human-dominated landscapes offer improved living conditions (Chown et al. 2003). Consequently, depending on the taxa of interest these effects then lead to both positive or negative relationships between biodiversity and human impact (Luck 2007).

There is overwhelming evidence that the recent human impact has a dramatic negative effect on the Earth's biodiversity with species' extinction rates exceeding those observed in geological times (Barnosky et al. 2011). However, this relationship does not always hold when looking at particular species, taxa, regions and scales. Certain species groups may even benefit from increased human impact as indicated by positive relationships between the densities of these species and human impact. However, underlying mechanisms are not always clear and more research is needed (Chown et al. 2003; Luck 2007).

Generally, large body sized species with extended home ranges, or those with limited dispersal ability, will be affected more negatively by habitat fragmentation compared to highly mobile species which are able to persist as meta-populations in fragmented landscapes (Purvis et al. 2000). Similarly, species with high reproductive rates are more likely to persist under high hunting pressure than species with extended inter-birth intervals and lower number of offspring (Fa and Brown 2009). These differences can lead to the phenomenon of post-depletion community assemblages (Cowlishaw et al. 2005). Such assemblages consist of a considerably reduced species richness compared to less human-impacted areas and contain only those that can persist under high human impact. Remaining species can then sometimes increase in density due to the effect of competitor and/or predator release (Ritchie and Johnson 2009; Azevedo et al. 2012).

Like many other regions, the landscapes of West Africa have become strongly human-dominated over the last few decades with far-reaching consequences for populations of large mammals (Craigie et al. 2010; Junker et al. 2012). Information on biodiversity and species distribution, however, is very limited and makes strategic conservation planning and evaluation of conservation effectiveness extremely difficult (e.g. Kormos et al. 2003).

The small West African country Sierra Leone is a good example for this lack of information on biodiversity and large mammal distribution. It is currently going through a phase of post-war recovery, with accelerating development of the mining, forestry, industrial agriculture and infrastructure sectors all requiring detailed information on species distribution and biodiversity (Brncic et al. 2010). The very limited information on wildlife distribution in Sierra Leone mostly stems from the period before the war (the 1970s–1980s or even earlier) (Robinson 1971; Lowes 1970) and is largely out-dated. At that time it was suggested that species diversity and abundance was higher in the Northern provinces compared to the southern part of the country (Lowes 1970). The past studies on wildlife distribution in Sierra Leone are dominated by a great concern of wildlife exploitation through excessive hunting and trade to national, regional and international markets and resulting species extinctions. As it was unlikely that this massive exploitation of wildlife has stopped since conservationists became increasingly worried about the situation.

In the east, bounty payments were made for over 240,000 monkey carcasses during pest control programmes between 1947 and 1962 (Teleki and Baldwin 1981). A lucrative international trade continued, with over ten 30-ton lorries carrying smoked bushmeat to Liberia each month during the dry season until 1985 (Davies and Palmer 1989). Wildlife overexploitation had already led to species decline and extinction a long time ago. Lions were considered extinct by 1905 (Fairtlough 1905), although there have been sightings more recently (Robinson 1971); the Derby eland (*Taurotragus derbianu*) is considered to have gone extinct around the same time. Already in the early 1970s the list of rare and uncommon species comprised the pygmy hippopotamus (*Choeropsis liberiensis*), Jentink's duiker (*Cephalophus jentinki*), zebra duiker (*Cephalophus zebra*), *the* bongo (*Boocercus eurycerus*), leopard (*Panthera pardus*), and chimpanzee (*Pan troglodytes verus*). Species that were more common at that time included elephant (*Loxodonta africana cyclotis*), buffalo (*Syncerus caffer nanus*), several duiker species, hogs and small bodied primates. The killing of large and medium sized predators in the more densely populated areas apparently resulted in a massive increase in the density of the giant cane rat (*Thryonomys swinderianus*) through the effect of predation pressure release (Lowes 1970).

Here we present a recent study on the distribution of wildlife and large mammal diversity patterns on a nationwide scale throughout Sierra Leone. We address the following key question: To what extent have the strongly human-dominated landscapes shaped large mammal diversity patterns in the country? We evaluate the hypotheses that (a) the human impact has shifted large mammal diversity to characteristic post depletion assemblages with reduced species richness and only those species with high reproductive rates remaining, (b) certain species benefit from increased human pressure and show a positive relationship with it, (c) the species that are not able to persist under high human pressure are now mainly confined to the north of the country, where human population density is lower than in the south and (d) the north-east of the country is most suitable for the extension of the protected area network planned by the Sierra Leonean government. Finally we discuss the implications of this study for other regions of West Africa.

Methods

Study area

Sierra Leone is a small West African country (71,740 km^2) bounded by Guinea, Liberia, and the Atlantic Ocean (Fig. 1). Elevation ranges from below sea-level to the north-eastern plateau (300–600 m). The climate is moist tropical, with annual precipitation ranging from >3000 mm in the southwest to around 2000 mm in the north. Rainfall is seasonal, with the main wet season from June to September; seasons are more pronounced in the west than east. Average temperature is around 27 °C.

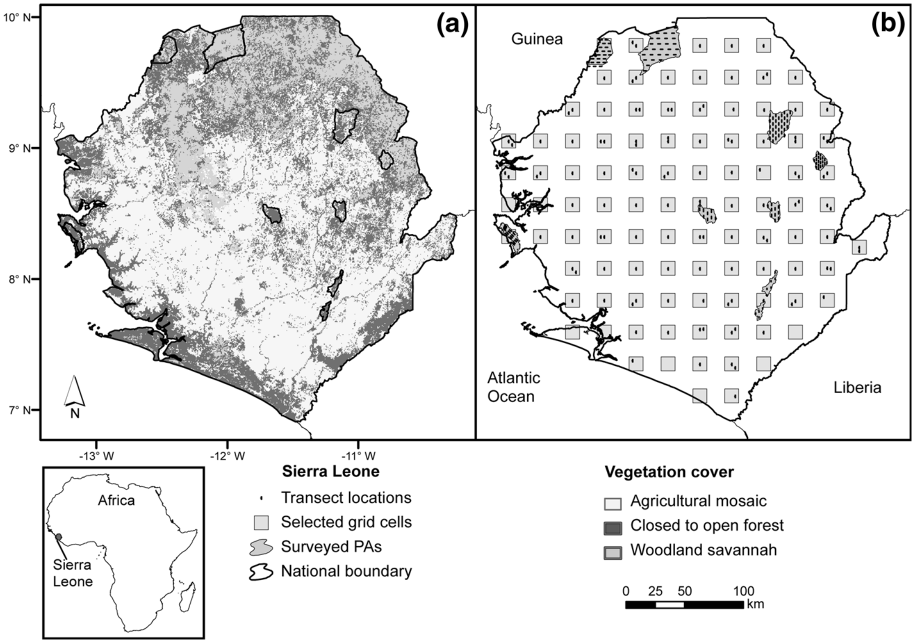

Fig. 1 Map of Sierra Leone showing **a** all transects and the placement of surveyed 9 × 9 km grid cells (*grey squares*) and surveyed protected areas in *dark grey*; and **b** vegetation cover of Sierra Leone adapted from ESA GlobCover Project (MEDIAS-France)

Sierra Leone lies at the western end of the Upper Guinean Forest and major vegetation types include moist equatorial lowland forest, forest-savannah mosaic in the north, and mangrove swamps along the coast. Over 60 % of Sierra Leone has the climatic and edaphic conditions for the establishment of closed-canopy moist evergreen and semi-deciduous forest. Now most of the former forest area is dominated by a patchwork of agriculture, bush fallow, and secondary forest (Davies and Palmer 1989; Norris et al. 2010) (Fig. 1a).

Field methods

Survey design

The study took place from February 2009 to April 2010. To systematically survey the entire country, a grid of 9 × 9 km cells with random starting point was laid across the country. Each of these blocks was further divided into 3 × 3 km cells. We selected every 3rd block and surveyed the centre 3 × 3 km cell with a 3-km long transect on a north–south bearing. Thus transects were about 27 km apart. Additionally, for about half of the blocks, we collected data on a second transect in that block to increase sample size (Fig. 1b).

For protected areas, line transects of 2 km length (1.5 km for Tingi Hills) were placed systematically across survey areas using the survey design module in DISTANCE 6.0 (Thomas et al. 2010). The number of transects in each reserve varied from 8 to 31. The Gola Forest Reserves were not surveyed as part of this study. At the time of survey the Gola Forest Programme ran its own chimpanzee survey in parallel, but did not record other mammals.

For Sierra Leone outside of protected areas, 89 blocks were sampled with 124 transects with a total length of 299 km. Within the eight protected areas that were surveyed, 142 transects were walked for a total distance of 262.6 km. Therefore a total of 266 transects and 561.6 km of survey effort were included in our analysis (Fig. 1; Appendix S2).

All signs of medium and large mammals were recorded along transects by teams of 3–4 experienced observers and locations were marked with a Garmin 60CSx GPS. Signs included direct sightings, vocalizations, footprints, dung, nests (chimpanzees), dens (burrowing animals), carcasses, and feeding remains. Signs of human activity, including signs of power-saw logging, hunting (hunters, snares, hunting camps, shotgun shells), human trails or roads, and farms, were also recorded. Furthermore, vegetation type was recorded along each transect. Forest types were assigned based on forest structure rather than species composition (e.g., closed forest, secondary forest, woodland savannah, farms).

Analytical methods

The analytical approaches used include (A) generalized linear mixed modelling (GLMM) to (i) assess the importance of variables influencing species distribution (*analytical model*), generalized linear modelling (GLM) to (ii) make countrywide predictions of each species' distribution (*distribution model*); (B) canonical correspondence analysis (CCA) to visualize relationships between species abundance and particular variables and (C) the development of an algorithm to identify core distributional range areas (CDRA) of species.

Table 1 Species recorded on transects, their IUCN status and number of signs recorded

Species	Scientific name	IUCN status	No. of transects		No. of signs	
			Lasting	Ephemeral	Lasting	Ephemeral
Maxwell's duiker	*Philantomba maxwellii*	LC	**131**	9	561	11
Western chimpanzee	*Pan troglodytes verus*	EN	**123**	16	1655	38
Cane rat	*Thryonomys swinderianus*	LC	**118**	3	1197	11
Bushbuck	*Tragelaphus scriptus*	LC	**103**	7	213	8
Red river hog	*Potamochoerus porcus*	LC	**95**	2	238	9
Black duiker	*Cephalophus niger*	LC	**72**	2	229	2
Bay duiker	*Cephalophus dorsalis*	LC	**65**	3	187	3
West African buffalo	*Syncerus caffer ssp.*	LC	**57**	1	186	1
Brush-tailed porcupine	*Atherurus africanus*	LC	**39**	1	76	1
Yellow-backed duiker	*Cephalophus silvicultor*	LC	**35**	1	54	1
Warthog	*Phacochoerus africanus*	LC	**30**		62	
Sooty mangabey	*Cercocebus atys*	VU	2	**21**	2	28
Civet[a]	*Civettictis/Nandinia*	LC	**20**		37	
Giant rat	*Cricetomys emini*	LC	**18**		27	
Campbell's monkey	*Cercopithecus campbelli*	LC	2	**17**	2	46
Waterbuck	*Kobus ellipsiprymnus*	LC	**17**		28	
Lesser spot-nosed guenon	*Cercopithecus petaurista buettikoferi*	LC		**15**		67
Crested porcupine	*Hystrix cristata*	LC	14	1	31	1
Aardvark	*Orycteropus afer*	LC	14		18	
Red-flanked duiker	*Cephalophus rufilatus*	LC	13	3	24	3
Western pied colobus	*Colobus polykomos*	VU		10		19
Olive/Guinea baboon[a]	*Papio anubis/papio*	LC/NT	8	2	14	17
Rock hyrax	*Procavia capensis*	LC	7	3	33	7
Elephant	*Loxodonta africana*	VU	6		48	
Western red colobus	*Procolobus badius*	EN		6		10
Western bongo	*Tragelaphus eurycerus eurycerus*	NT	3		3	
Royal antelope	*Neotragus pygmaeus*	LC	3		5	
Diana monkey	*Cercopithecus diana*	EN		3		11
Genet[a]	*Genetta maculate/thierryi*	LC	2		3	
Giant ground pangolin	*Smutsia gigantea*	NT	2		2	
Green (Vervet) monkey	*Chlorocebus sabaeus/ Cercopithecus aethiops*	LC		2		2

Table 1 continued

Species	Scientific name	IUCN status	No. of transects		No. of signs	
			Lasting	Ephemeral	Lasting	Ephemeral
Giant forest hog	*Hylochoerus meinertzhageni ivoriensis*	LC	1		1	
Pygmy hippopotamus	*Choeropsis liberiensis*	EN	1		1	
Tree pangolin	*Phataginus tricuspis*	NT	1		1	

Species included in the analysis are indicated in bold, and bold numbers indicate the type of sign used for each species

EN endangered, *VU* vulnerable, *NT* near threatened, *LC* least concern (IUCN, 2010)

[a] Not always able to distinguish species by their signs, so more than one species may be grouped

Species transect data

To determine species transect sign counts, we first distinguished two sign classes (lasting: carcass, dung, feeding remains, footprint, hole, sleeping site, trail, trap, footprint, nest; and ephemeral: call, sighting) and summed all observations separately per species, transect, and sign class. These two classes were considered separately because encounter rates are likely to differ between ephemeral and lasting signs. In fact, when correlating numbers of ephemeral and lasting signs by transect and species, we found only weak correlations (Spearman's correlation, conducted separately per species: largest $\rho = 0.2$, average $\rho = 0.04$, all N = 426 transects). In the following analyses we used for each species the most common sign class that was present on more transects and took this as a measure of its relative abundance. The selected sign classes were the ones which are usually also selected in other studies (e.g. Murai et al. 2013). Species found on fewer than 15 transects were excluded from the analysis to avoid model instability due to limited variation in the transect data (Table 1).

Predictor variables

We selected 19 predictor variables from two broad classes: eight environmental predictors (i.e., vegetation cover, topography, and climate) and eleven human impact predictors (i.e., hunting, logging, access, land use). Predictor variables were obtained either directly from transect sampling or from global datasets (Table 2). The most abundant human signs found on transects were grouped into three variables: hunting, logging, and access. The percentages of three main types of vegetation cover (agriculture, forest, woodland savannah) were derived from transect based vegetation coverage.

Distance to the nearest protected area only included those forest reserves and national parks which recently had some form of active protection (presence of guards, anti-poaching activities, environmental education). The GlobCover land cover classes defined with the UN Land Cover Classification System (European Space Agency (2008) were ground-truthed with available data points in Sierra Leone. These showed that the three most abundant land cover classes (closed to open forest, woodland savannah, agricultural mosaic) corresponded roughly to the three most common vegetation types found on the transects. Therefore the percentages of only these three types within a 2.5-km radius around each transect centre point were used.

Table 2 Environmental and human impact variables used as predictors in the analysis

Variable	Description	Source	Reference
Environmental			
GC-Forest	Percent of pixels classified in GlobCover as closed to open forest in 2.5 km radius around center point of transect	ESA/ESA GlobCover Project, led by MEDIAS-France (2006) and European Space Agency (2008) resolution 300 m	Campbell et al. (2011), Wich et al. (2012) and Junker et al. (2012)
Tr-Forest	Percent forest cover per transect (Forest, secondary forest, swamp forest, dry forest etc.)	This study	Barnes et al. (1991)
GC-WLS	Percent of pixels classified in GlobCover as woodland savanna (open deciduous forest) in 2.5 km radius around center point of transect	ESA/ESA GlobCover Project, led by MEDIAS-France (2006); resolution 300 m	Junker et al. (2012)
Tr-WLS	Percent woodland savanna per transect	This study	Serckx et al. (2014)
Elevation	GTOPO30—Elevation (meters above mean sea level) at center of transect	Data available from the U.S. Geological Survey and EROS Data Center (2008); resolution 1 km	Wich et al. (2012)
CTI	Compound Topographic (steady-state wetness) Index—related to soil moisture	Data available from the U.S. Geological Survey and EROS Data Center (2008), resolution 1 km	Elith et al. (2006)
MeanPrec	Mean annual precipitation (BIO12)	Hijmans et al. (2005); resolution ~1 km	Junker et al. (2012)
SeasPrec	Precipitation seasonality (BIO15)	Hijmans et al. (2005); resolution ~1 km	Junker et al. (2012)
Human impact			
DistVill	Distance to nearest village	Sierra Leone Information Services/UNDP (2007–2010) from http://www.statistics.sl	Junker et al. (2012)
DistMajRd	Distance to major roads	Sierra Leone Information Services/UNDP (2006) from http://www.statistics.sl	Junker et al. (2012)
DistMinRd	Distance to minor roads	Sierra Leone Information Services/UNDP (2006) from http://www.statistics.sl	Junker et al. (2012)
HPDens04	Human population density by chiefdom (2004)	Gridded Population of the World (CIESIN and CIAT 2005), Statistics Sierra Leone (2004) and Sierra Leone Information Services/UNDP (2004) from http://www.statistics.sl	Junker et al. (2012)
HPChange	Change in human population density (1985–2004)	Statistics Sierra Leone (2004) and Sierra Leone Information Services/UNDP (2004) from http://www.statistics.sl	Junker et al. (2012)
Logging	Number of logging signs per transect (tree stumps, power-saws, stacked timber)	This study	Remis et al. (2012)

Table 2 continued

Variable	Description	Source	Reference
Hunting	Number of hunting signs per transect (guns, gun shells, gunshots heard, snares, snare fences)	This study	Campbell et al. (2011)
Access	Number of roads or footpaths per transect	This study	Serckx et al. (2014)
DistPA	Distance to nearest non-hunting forest reserve or national park (Outamba-Kilimi NP, Loma FR, Tingi Hills FR, Gola FR, Tiwai Island, or Western Area FR)	Maps modified from Sierra Leone Information Services/UNDP (2004) from http://www.statistics.sl	Murai et al. (2013)
Tr-Ag	Percent agricultural land per transect	This study	Serckx et al. (2014)
GC-Ag	Percent of agricultural mosaic pixels in 2.5 km radius around center point of transect	ESA/ESA GlobCover Project, led by MEDIAS-France (2006); resolution 300 m	Junker et al. (2012)

All datasets were used in the latitude/longitude coordinate reference system with datum WGS 1984. For raster data the pixel resolution is given; transect level predictor data collected during this study are labelled with ‘This study’, the remaining datasets are vector data

Table 3 Results of Factor Analysis with human impact variables including the loadings of each variable on the two factors, the factor’s Eigenvalues and the explained variance

Variable	Description	Transformation	HFactor1	HFactor2
Tr-Ag	% agricultural land per transect	Square root(x)	**0.86**	−0.08
DistPA	Distance to nearest protected areas	Square root(x)	**0.73**	0.14
GC-Ag	% satellite derived agricultural mosaic	Square root(x)	**0.73**	0.20
DistMinRd	Distance to minor roads	Square root(x)	**−0.71**	−0.27
DistVill	Distance to nearest villages	Square root(x)	**−0.70**	−0.06
Access	Number of roads or footpaths per transect	Log(x + 1)	**0.65**	0.20
Hunting	Number of hunting signs per transect		**0.35**	0.01
HPDens04	Human population density by chiefdom	Log(x)	0.20	**0.89**
Logging	Number of logging signs per transect		−0.18	**0.56**
DistMajRd	Distance to major roads	Square root(x)	−0.49	**−0.51**
HPChange	Change in human population density	Square root(x)	0.21	**0.47**
Eigenvalue			3.70	1.77
% variance explained			33.70	16.10

The strongest loadings per variable are indicated in bold. The first factor can be interpreted as indicating the degree to which the habitat is influenced by humans; the second largely represents human population density

Compound Topographic Index (CTI) was used as a proxy for steady-state wetness. CTI is highly correlated to several soil attributes such as horizon depth, silt percentage, organic matter content, and phosphorus, and is an indicator of soil moisture (Moore et al. 1993).

Since the human impact and environmental covariates were in part highly interrelated, we used two Factor Analyses (FA) to reduce their number and avoid collinearity (Field 2005). We checked all covariates for their distribution, and when a distribution was asymmetric, we transformed the variable to achieve a more symmetrical distribution prior to running the FA, (Tables 3, 4). The FA yielded only two factors for the human variables (HFactor 1 and 2) with Eigenvalues above 1, additional factors with Eigenvalues less than 1 were excluded. This criterion is commonly used for selecting the number of factors to be included into further analysis (McGregor 1992). HFactor 1 and 2 explained only 50 % of the total variance (Table 3). The FA for the environmental variables yielded three factors (EFactor 1–3), together explaining 69 % of their total variance (Table 4) (Appendix S1).

High values of human factor 1 are associated with high levels of agriculture, large distances from protected areas, short distances to minor roads and settlements and generally easily accessible areas. High values of human factor 2 correspond to high human population density, logging, short distances to major roads and human population increase. High levels of the environmental factors are associated with woodland savannah (EFactor1); high elevation, reduced soil moisture (CTI), large forest cover (EFactor2), or high levels of precipitation and seasonality (EFactor3). Thus we had for the 'analytical model' five factors as predictors for large mammal distribution in Sierra Leone.

Analytical model

To account for non-linear effects, we included in addition to the five factors the first human factor and all three environmental factors as squared terms into the GLMM. Furthermore, we included species ID and the interactions between species ID and the squared and all unsquared terms as fixed effects into the model. The second human factor, which was largely related to human population density, we did not include as a squared term because we assumed that the species investigated would more or less show a linear or sigmoidal

Table 4 Results of Factor Analysis with environmental variables including the loadings of each variable on the three factors, the factor's Eigenvalues and the explained variance

Variable	Description	Transformation	EFactor1	EFactor2	EFactor3
Tr-WLS	% woodland savanna on transect		**0.89**	−0.17	0.13
GC-WLS	% satellite derived woodland savanna		**0.83**	−0.04	−0.01
Elevation	Altitude in meter	Square root(x)	−0.03	**0.82**	−0.49
CTI	Compound Topographic Index	Square root(x)	0.06	**−0.72**	0.08
Tr-Forest	% forest cover per transect		−0.44	**0.63**	0.03
GC-Forest	% satellite derived forest	Square root(x)	−0.02	**0.48**	0.18
SeasPrec	Precipitation seasonality	Square root(x)	0.16	−0.02	**0.90**
MeanPrec	Mean annual precipitation		−0.64	0.03	**0.69**
Eigenvalue			2.12	1.84	1.57
% variance explained			26.40	23.00	19.60

The strongest loadings per variable are indicated in bold. The first factor can be interpreted as representing habitat characterized by a mixture of open and wooden patches, the second represents elevated, dry and forested habitat, and the last correlates positively with precipitation. See Table 2 for variable explanations relationship with it. In addition to these factors we included a term into the model which accounted for spatial autocorrelation ('autocorrelation term') and the logarithm of transect length as an offset variable ('offset') to account for varying transect length. Finally, we included transect ID as a random effect into the model. Hence the final full analytical model was

$$\begin{aligned} &\text{transect sign count} \sim \text{speciesID} \times \left(\text{HFactor1} + \text{HFactor1}^2 + \text{HFactor2} + \text{EFactor1}\right. \\ &\quad \left. + \text{EFactor1}^2 + \text{EFactor2} + \text{EFactor2}^2 + \text{EFactor3} + \text{EFactor3}^2\right) \\ &\quad + \text{autocorrelation term} + \text{offset} + (1|\text{transect ID}), \end{aligned}$$

where (1ltransect ID) represents the random intercepts effect of transect ID.

We used a GLMM (Baayen 2008) with negative binomial error distribution and log link function (McCullagh and Nelder 2008). Prior to model fitting, we z-transformed all environmental and human impact gradients (Cohen and Cohen 1983; Aiken and West 1991; for details on data processing and preparation, and the derivation of the autocorrelation term see in Appendix S1). Significance tests for sets of variables (i.e., interactions between species and human impact and environmental factors combined; interaction between species and human impact factors; interaction between species and environmental factors) we based on comparing the full model with a reduced model without the variable of interest using a likelihood ratio test (Cohen and Cohen 1983; Dobson 2002). To estimate to what extent the result of the negative binomial GLMM was unduly influenced by particularly influential transect sign counts, we removed transects one at a time, ran the full model on the reduced data set and compared the estimates derived with those obtained from the full model. This did not reveal any influential transects.

To estimate which of the two groups of gradients (human impact or environmental) had the larger impact on a given species' abundance we also ran separate models per species. For each species we ran three models, a full model with all gradients and two reduced models comprising only the environmental or only the human impact gradients, respectively (and the respective squared terms). We compared the model's AIC-values and considered those models as the 'best' which had the smallest AIC with a difference of at least two compared to other models (Burnham and Anderson 2002). In all these models we included the autocorrelation term as derived from the full model and the offset variable.

Canonical correspondence analysis

To visualize the relation between species abundance and environmental and human impact variables we ran a single CCA including all species. We used the original environmental and human impact variables rather than the scores revealed from the Factor Analysis. Prior to running the CCA we transformed all covariates to achieve distributions as symmetric as possible (Appendix S1). Species abundances were expressed as number of signs per kilometer transect to account for various transect lengths. It has to be noted that these abundance values were very skewed, since most species were not encountered on the far majority of transects and, hence, the results of the CCA have to be treated cautiously.

Countrywide prediction of species distribution and key areas

For addressing the hypotheses that the north of Sierra Leone is still the most diverse and thus suitable region (Lowes 1970) for future creation of new protected areas, we located the CDRA of species in two steps. First, we fitted distribution models (GLMs) for every species and then used these models to make countrywide predictions ("Distribution model using GIS and remote sensing data" section). Second, we identified for every species an area equivalent to approximately 20 % of the size of Sierra Leone ($\sim$15,000 km^2) that maximized abundance and structural connectivity and minimized number of fragments and perimeter to surface ratio ("Species core distributional ranges" section).

Distribution model using GIS and remote sensing data

We repeated the model fitting approach as described above (see 'Predictor variables' and 'Analytical model' sections), but with the exception that we used a GLM and did not use covariates collected on transects (Table 2). We did this to make predictions of species distribution for locations between transects, for which only remotely sensed and GIS predictors were available. We then ran a Factor Analysis to aggregate the remaining 13 variables, which resulted in two human impact factors explaining about 50 % of the variance and two environmental factors explaining about 55 % of the variance (Appendices S1, S2). Furthermore, we divided Sierra Leone into a grid with cell size of 0.05° ($\sim$5 km) and assigned the original variables and corresponding values from the FA to each cell. Finally, we used multi-model inference to make predictions of species distribution for each cell based on fitted models (further details in Appendix S1).

Species core distributional ranges

To identify the most important area of a species' distribution in terms of relative abundance, we used the following procedure to define 'core distributional range areas' (CDRA). Many countries aim for protected area coverage of about 20 % (e.g. Tweh et al. 2014). For each species we selected those 20 % grid cells (N) for which the species specific distribution models had predicted the largest relative abundance. We then derived three metrics on the shape of the area representing the selected 20 % of the country and species abundance to use them as measures in the subsequent CDRA search. When developing the CDRA search algorithm, the principal idea was to define an area for each species that is minimally fragmented, i.e. has a minimum edge and reduces at the same time any loss in abundance.

The three metrics included (a) the total edge length of the selected areas divided by the total number (N) of pixels, which characterized the 'current edge-to-area ratio'; (b) the 'ideal edge-to-area ratio' assuming only a single area as CDRA and having the shape of a circle (i.e. minimum circumference for a given area, the 'ideal edge-to-area ratio' is calculated as 2/sqrt[N/π]); (c) the total abundance (sum of pixel values of distribution model) of the species in the initially selected pixels ('ideal abundance') and the pixels that are selected at each step of the CDRA search ('current abundance').

The combined measure of the shape and the total abundance was then defined as Q_{tot} = (ideal edge-to-area ratio/current edge-to-area ratio) × (current abundance/ideal abundance). Q_{tot} is reduced when there are many separated areas with low structural connectivity and/or when the areas have a very rugged, irregular, shape. It is also reduced when the total relative abundance in these areas decreases as compared to what could be selected if the initially selected N cells were chosen. Searching those N cells that maximize Q_{tot} means to search for a compromise between having only a few and regularly shaped areas with high structural connectivity and maximum abundance. We then implemented the algorithm to maximize Q_{tot} (Appendix S1). All analyses were conducted in R Development Core Team (2012).

Results

Analytical model and species specific responses

Overall, species abundance was clearly influenced by the environmental and human impact gradients (likelihood ratio test comparing full and null model comprising only the autocorrelation and the offset term: LR statistic = 1434.84, df = 169, $P < 0.0001$). Species clearly responded differently to human impact (interactions between species and human impact gradients: LR statistic = 151.48, df = 48, $P < 0.0001$) and also to environmental gradients (interactions between species and environmental gradients: LR statistic = 312.48, df = 96, $P < 0.0001$).

Four species (chimpanzees, spot-nosed monkeys, civets, and yellow-backed duikers) responded more strongly to human impact variables (smallest AIC revealed for the model with only human impact gradients), and four other species responded mainly to environmental gradients (brush-tailed porcupine, bushbuck, giant rat, and warthog; although for the Warthog the full model was only slightly worse than the environmental variables only model; Table 5). The other eight species' abundances were best explained by a mixture of environmental and human impact gradients.

The responses of individual species to the covariates followed a complex pattern (Fig. 2). With regard to human influence (largely represented by human impact factor 1) three species (chimpanzee, black duiker, Maxwell's duiker) showed increased relative abundance at both low and high values of human factor 1 whereas cane rats were more

Table 5 Results of likelihood ratio tests comparing full and null models, separately per species (columns LR stat., df and P), AIC-values of full model (AIC full), as well as models comprising only environmental variables including their squares (AIC env.) or only human impact variables and one human impact variable squared (AIC hum.)

Observations	LR stat.	df	P	AIC full	AIC env.	AIC hum.
Chimpanzee	52.01	9	<0.001	1057.3	1077.0	**1055.0**
Sooty mangabey*	29.98	9	<0.001	**174.9**	177.6	186.9
Lesser spot-nose guenon*	7.85	9	0.550	158.2	156.8	**149.4**
Bay duiker	50.69	9	<0.001	**463.5**	469.6	481.4
Black duiker	37.01	9	<0.001	**542.7**	554.6	565.0
Brush-tailed porcupine	27.49	9	0.001	306.1	**301.5**	313.9
Buffalo	63.34	9	<0.001	**405.6**	409.8	422.1
Bushbuck	35.82	9	<0.001	592.3	**589.9**	603.9
Cane rat	72.04	9	<0.001	**829.2**	850.4	853.2
Civet	9.03	9	0.434	175.4	174.4	**168.7**
Giant rat	17.20	9	0.046	123.3	**119.9**	123.1
Maxwell's duiker	50.27	9	<0.001	**871.8**	877.5	893.6
Red river hog	36.54	9	<0.001	**591.0**	594.6	597.2
Warthog	85.85	9	<0.001	**196.6**	**195.9**	221.2
Waterbuck	40.40	9	<0.001	**89.0**	91.9	106.2
Yellow-backed duiker	38.21	9	<0.001	259.8	267.8	**253.7**

The best model(s) per species are marked in bold. For all species long-lasting signs were used except for those marked with an asterisk common in areas with high values of human disturbance. Buffalos preferred areas with low levels of human influence.

Four species (cane rat, warthog, bushbuck, and buffalo) were particularly common in woodland savannah habitat (large values of environmental factor 1), two species (sooty mangabey and giant rat) avoided such habitat, and Maxwell's duiker preferred areas where

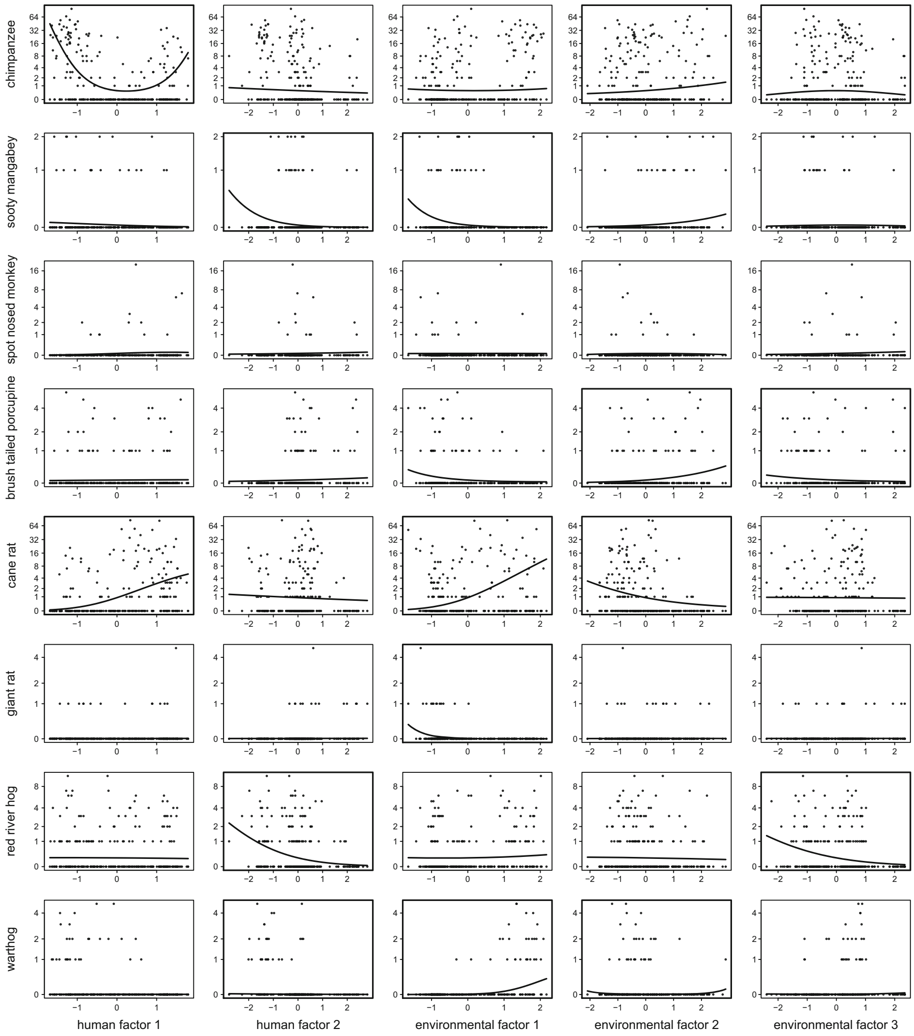

Fig. 2 Influence of human impact and environmental gradients on the abundance of species investigated. Each row represents one species and each column one gradient (from *left to right* human factors 1 and 2, environmental factors 1–3). *Lines* represent relations estimated from models run separately per species. Note that abundance values (y-axis) are shown on a log-scale. Variables having a significant impact ($P \leq 0.05$ for the squared term or the linear term in a model not comprising the squared term since it was not significant in the full model) are highlighted by *thick frames*. For waterbuck, no trend lines are indicated since some instability problems occurred, and Campbell's monkey is not shown because the model did not converge for this species

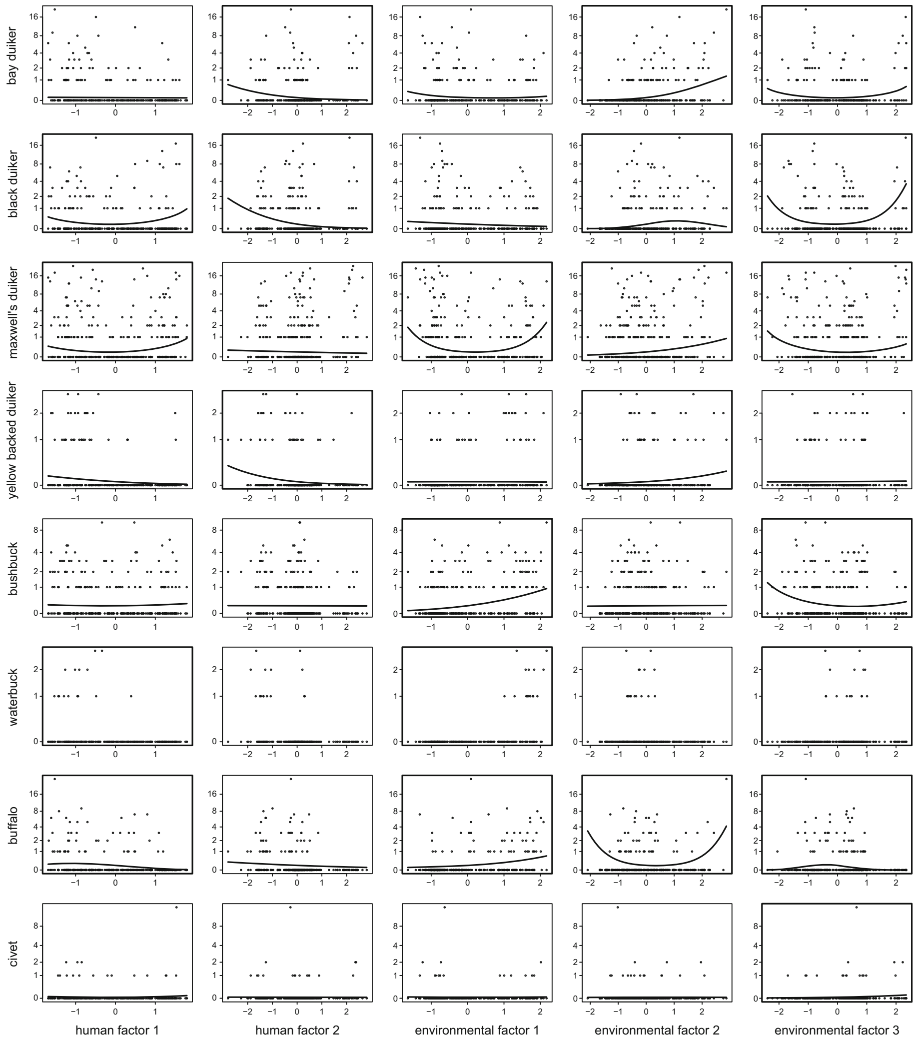

Fig. 2 continued

such habitat was rare as well as areas where it was common (Fig. 2). Drier, more elevated and forested areas (i.e., larger values of environmental factor 2) were preferred by five species (chimpanzee, brush-tailed porcupine, bay duiker, Maxwell's duiker, and yellow-backed duiker) and avoided by cane rats. Warthogs and buffalos preferred small and large values of this gradient and black duiker preferred intermediate values of it. As indicated by the impact of environmental factor 3, largely representing precipitation, two species (brush-tailed porcupine, red river hog, and, to some extent, Maxwell's duiker and bushbuck) were more common in drier habitats whereas civets seemed to have a weak preference for wetter areas.

Canonical correspondence analysis and species specific responses

The CCA partly confirmed these conclusions from the GLMM analyses (Fig. 3). Warthog, waterbuck and cane rat abundance were largely correlated with CCA2 which in turn was particularly correlated with woodland savannah. Black duiker, bay duiker and Maxwell's duiker, as well as giant rat and brush-tailed porcupine abundances were particularly correlated with higher precipitation and more seasonality in precipitation. Cane rat and spot-nosed monkey occurred most commonly in areas dominated by agriculture and further away from protected areas. Buffalos and chimpanzees, finally, were indicated to be particularly common far away from roads and villages.

Distribution model and species core distributional ranges

For most species our analyses revealed a single CDRA. With a few exceptions (civet, cane and giant rat) selected CDRA were concentrated in the north and east of Sierra Leone (Fig. 4). For several species (particularly spot-nosed monkey, brush-tailed porcupine, Black and Maxwell's duiker; Fig. 4d, e, k, and l) selected CDRA extended also into the centre of the country. There is a distinct species diversity gradient in Sierra Leone with higher large mammal richness in the region extending from Outamba-Kilimi NP in the northwest to the Loma Mountains and to a lesser extent further southeast to the border to Guinea (Fig. 4r, s). The south and west of the country has much more reduced large mammal richness.

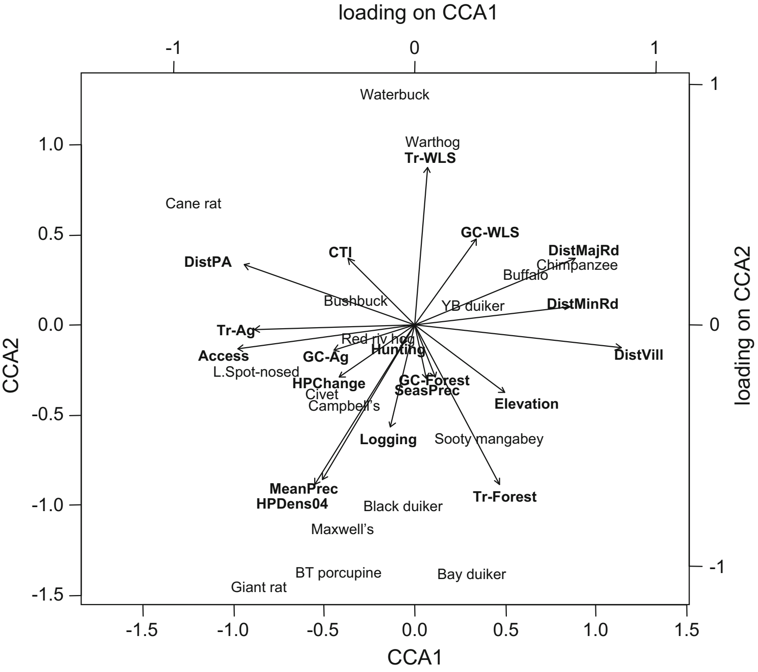

Fig. 3 Relation between environmental and human impact variables as revealed by a canonical correspondence analysis (CCA). Shown are loadings of the environmental and human impact variables (in *bold*) on the first two canonical axes and locations of the various species along these two axes. Some species names have been shortened for clarity. For abbreviations, please see Table 2

Discussion

Our study provides for the first time a systematic assessment of large mammal distribution and diversity throughout Sierra Leone; it shows how strongly human impact is nowadays determining species distribution, but also how variable different species respond to it. The most important findings that have emerged from our analyses are that (a) in large parts of Sierra Leone, i.e. the centre, south and west, mainly post-depletion species community assemblages are retained; (b) some species have benefitted from increasing human impact and species diversity decline, such as cane rats, brush-tailed porcupine, bushbuck, giant rat,

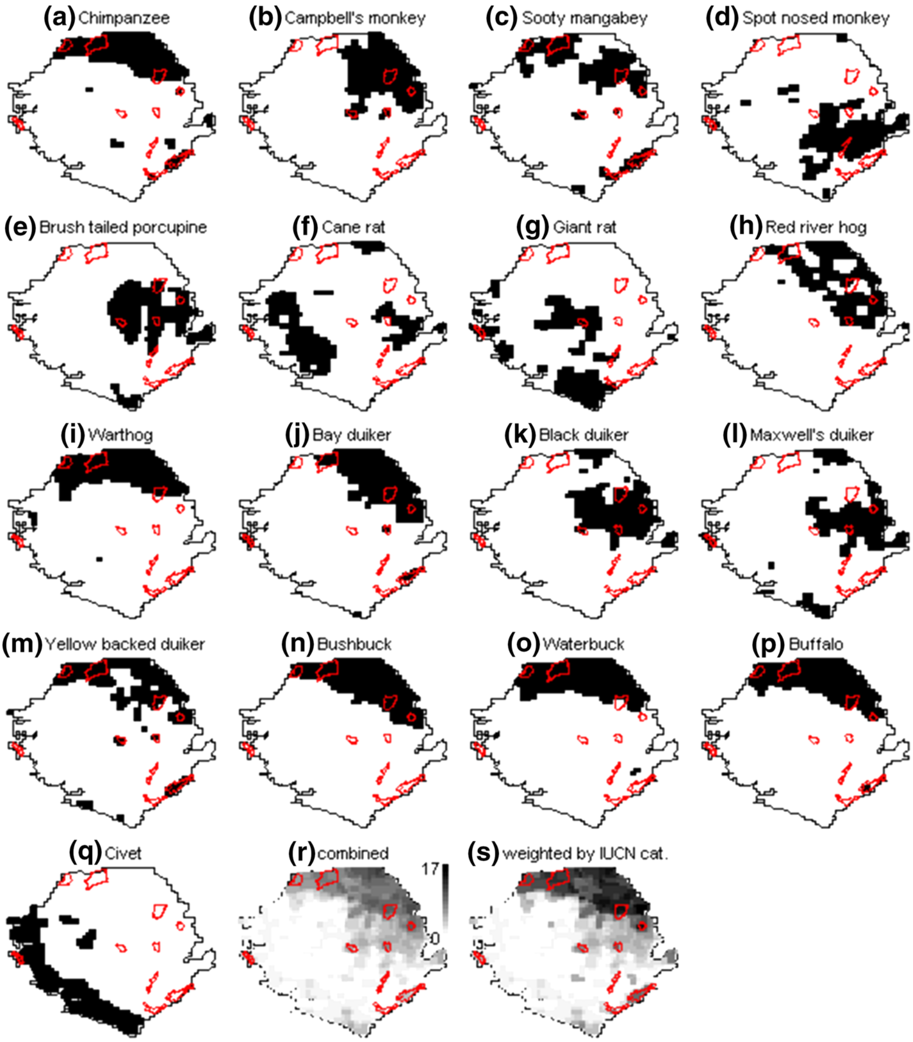

Fig. 4 Final selection of CDRA (*black*) per species (**a**–**q**), protected areas in *red*. **r** Per grid cell the number of species for which the respective cell was selected by the optimization to be inside an area and **s** the same but with the species contributions weighted by their IUCN category. (Color figure online)

which show no response to human impact or are even positively correlated with it; (c) the more sensitive species, such as sooty mangabey or yellow-backed duiker, are now mainly confined to the north of the country, where human population density is much lower than in the south and (d) that the region between Outamba-Kilimi NP and Loma Mountains is the area with the highest large mammal species diversity remaining in the country which is where efforts for extending the protected area network should focus on.

Species specific responses

Species varied considerably in their response to human and environmental variables. This finding cautions against pooling of species (Rist et al. 2009), as this may mask important differences in species specific responses to habitat disturbance and hunting (Cowlishaw et al. 2005; Laurance et al. 2006).

Species that occurred at high values of human disturbance may take advantage of new food resources in agricultural land or are released from interspecific competition for food resources with other, more heavily hunted species or predation pressure (Rist et al. 2009). Cane rat and lesser spot-nosed guenon were more abundant only at higher levels of disturbance. Cane rats are granivorous crop pests and have high rates of reproduction which compensates for high offtake levels. Lesser spot-nosed guenons are also frequent crop raiders, but their very small size (4 kg) and the need to hunt them primarily with guns makes them an inefficient species to hunt. They, along with Campbell's monkeys, can often be seen calling openly in trees around villages. A high degree of frugivory may contribute to their success in agricultural areas as compared to other monkey species (Fimbel 1994).

Three species had higher abundances at both high and low values of our measure of human influence (HF1): chimpanzee, black duiker, and Maxwell's duiker. These species occurred frequently outside of protected areas, adapting well to agricultural habitat. Although several studies suggest that chimpanzees should be vulnerable to disturbance, our results are consistent with other studies showing that chimpanzees can sometimes tolerate agriculture and/or low level of hunting (Isaac and Cowlishaw 2004; Rist et al. 2009), perhaps given an advantage by their behavioural flexibility, intelligence, omnivorous diet, and certain cultural taboos against eating chimpanzee meat. Two other popular bushmeat species (bushbuck and brush-tailed porcupine) did not respond significantly to human impact factors indicating that the benefits of human impacts may balance the losses to hunting (Rist et al. 2009).

The distinct distribution pattern of chimpanzees and other species in relation to human impact may be explained by transient effects. Increasing human impact in previously less impacted areas will cause a decline of chimpanzees and other species. However, from a certain level of human impact onwards, post-depletion communities will emerge, in which chimpanzees possibly coexist with only few other species. Due to competitor and predator reduction, persisting species may increase again in density. However, at this point this explanation is only hypothetical and requires further evaluation.

Only the West African buffalo had a significant negative response to increased human disturbance. Buffalos can cause damage to crops, so hunting, more than habitat loss, may be responsible for this pattern. The large body size makes them an easier target for hunters, so the restriction on guns in Sierra Leone may enable them to persist for the moment outside of protected areas. Although classified as Least Concern by IUCN, the western subspecies of African buffalo is estimated to have fewer than 27,000 remaining individuals

(IUCN 2010). We would therefore suggest that the Western African buffalo be prioritised for conservation within Sierra Leone.

Other species under pressure from increasing human population density are those that responded negatively to human factor 2. These species ranged from medium-sized ungulates and primates (bay and black duiker, sooty mangabey) to the larger yellow-backed duiker, warthog, and red river hog. These species have been shown to be some of the first to be lost due to hunting (Fa et al. 2005).

Rare species

The limited number of observations of rarer species prevented a statistical analysis of their response to predictor variables. However, our study still provides details on their distribution in Sierra Leone (Fig. S3) Diana monkeys, western pied colobus, and red colobus are all vulnerable to logging, agriculture, and hunting (Isaac and Cowlishaw 2004). These primates and the endangered pygmy hippopotamus prefer primary forest (Eltringham 1993; Fimbel 1994; Klop et al. 2008). Their persistence in Sierra Leone depends on the continued protection of remaining old-growth forest areas.

Elephant numbers have drastically declined in West Africa. They are in danger of becoming extinct in Sierra Leone. Outamba NP and Gola FR had the largest populations, but both of these have been severely hit by poaching in recent years. Overall, there are probably much fewer than 50 elephants left in Sierra Leone and immediate control of poaching is the only hope of preventing local extinction.

Conservation potential in Sierra Leone

Given the history of intensive bushmeat hunting in Sierra Leone, the occurrence of cane rat and Maxwell's duiker as two of the most common species suggests that the country is heading towards a depletion of larger species (Brugière and Magassouba 2009; Cowlishaw et al. 2005; Waite 2007).

Several factors may explain the persistence of some larger species and primates outside of protected areas. Sierra Leone's civil war from 1992 to 2002 caused many villages and farms to be abandoned. An arms embargo since the end of the war has reduced the use of firearms for hunting. Therefore larger species may not be targeted as much as in other countries where gun hunting is legal. Finally, commercial mechanized agriculture is rare in Sierra Leone, and subsistence agriculture allows for a mosaic of active cropland, bush fallow, and secondary forest which can provide suitable habitat for some of these species. Traditional taboos may also play a role. In theory, clans will not hunt their name-sake totem animals, and Muslims will not eat primates. However, it was revealed during village interviews that these practices are not always observed in the face of extreme poverty (Brncic pers.observ).

Protected areas in Sierra Leone also have a crucial role to play in protecting endangered or vulnerable species. Outamba NP had the highest mammal sign encounter rate of all protected areas, followed by Loma FR, Tingi Hills FR, Western Area Peninsula FR, and Kilimi NP. However, several forest reserves within Sierra Leone were impoverished in mammal abundance, even more so than outside of protected areas (Kambui Hills FR, Kangari Hills FR, and Nimini Hills FR). The threats posed to each protected area varied from hunting to forest clearance driven by illicit mining, charcoal production, or agriculture, requiring different management approaches to protect those species that continue to be found almost exclusively in protected areas (Appendices S2, S3). Currently, Sierra

Leone's protected area network is under revision and an extension has been proposed. Our study suggests that these efforts should concentrate on the north and east of the country.

There are a few limitations of our approach that need to be taken into account, when using the provided information for conservation planning. Because 18 of the 35 species where encountered only on few transects, we could not treat them the same way as the more common ones. However, when comparing the point locations of the rare species with the selected core distributional ranges of the more common ones (Figs. 4, S3) it becomes evident that their distribution is reflected in those of other species. Last, the approach we have taken in our study to link species distribution to human impact and environmental factors is only correlative. There may be also other reasons driving similar relationships between human impact, environmental factors and species distribution.

Conclusions

Our study is the first systematic nationwide multi-species assessment in Sierra Leone that aimed to understand the major drivers of mammal richness and abundance in highly fragmented biomes and that identified key range areas. Knowing species relative abundance and distribution at this scale can help focus conservation efforts and decide where a protected area or species focus may be more effective in preventing species extinctions. Conservation areas will continue to be crucial environments for long-term protection of vulnerable or endangered forest species and a spatially explicit focus on several key species could be more cost-effective.

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