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Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis

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ABSTRACT

The densities and survival of many wild animals are presently at risk. Crucial for improving conservation actions is an understanding on a large scale of the relative importance of human and ecological factors in determining the distribution and densities of species. However, even for such charismatic species as the African elephant (*Loxodonta africana*), spatially explicit, large-scale analyses are lacking, although various local-scale studies are available. Here we show through continent-scale analysis that ecological factors, such as food availability, are correlated with the presence of elephants, but human factors are better predictors of elephant population densities where elephants are present. These densities strongly correlate with conservation policy, literacy rate, corruption and economic welfare, and associate less with the availability of food or water for these animals. Our results suggest that conservation strategies should be organized in a socioeconomic context. The successful conservation of large animal species could depend more on good human education, greater literacy, good governance, and less corruption, than merely setting aside areas for conservation.

1. Introduction

Many empirical studies that relate the distribution and density of species to ecological factors determining habitat suitability have been carried out to understand the reasons why species become endangered (Rodrigues et al., 2004). Obviously, human factors, such as land use and resource management, strongly interfere with these ecological factors, leading to problems like habitat fragmentation and overexploitation of food and water resources (Adams et al., 2004; Kareiva et al., 2008). Hence, conservation policies need analyses that include both ecological and human factors, in the knowledge that human factors are becoming dominant in determining the quality of the Earth's ecosystems (Vitousek et al., 1997). Crucial for improving conservation actions is an understanding on a large scale of the relative importance of human and ecological factors in determining the occurrence and densities of species. Many studies that investigate the distribution of species and their population density have a regional focus (Hoare and Du Toit, 1999; Khaemba and Stein, 2000), whereas spatially explicit, continent-wide analyses are often lacking.

Here we use the African elephant (*Loxodonta africana*, Fig. 1) to analyze the relation between both ecological and human factors and the spatial distribution and density of a large-bodied and charismatic species. We distinguish the occurrence (presence/absence) of the elephant as well as the densities at which it occurs. Besides the present-day distribution, we also analyze the historic distribution of elephants. We analyze a continent-wide data set of elephants and determine the relation with 19 ecological variables, including forage availability, rainfall, and water, and 15 human variables, including human density, welfare, literacy rate, and habitat fragmentation. Our choice of the African elephant arose from its indisputable importance to nature conservation.

2. Methods

The African Elephant Database supplied the data for the distribution and densities of elephants over the whole African continent (Blanc et al., 2007). The historic distribution was based on Dorst and Dandelot (1972) and Carruthers et al. (2009). The presence and absence of elephants (ELEPRES) and the mean elephant density

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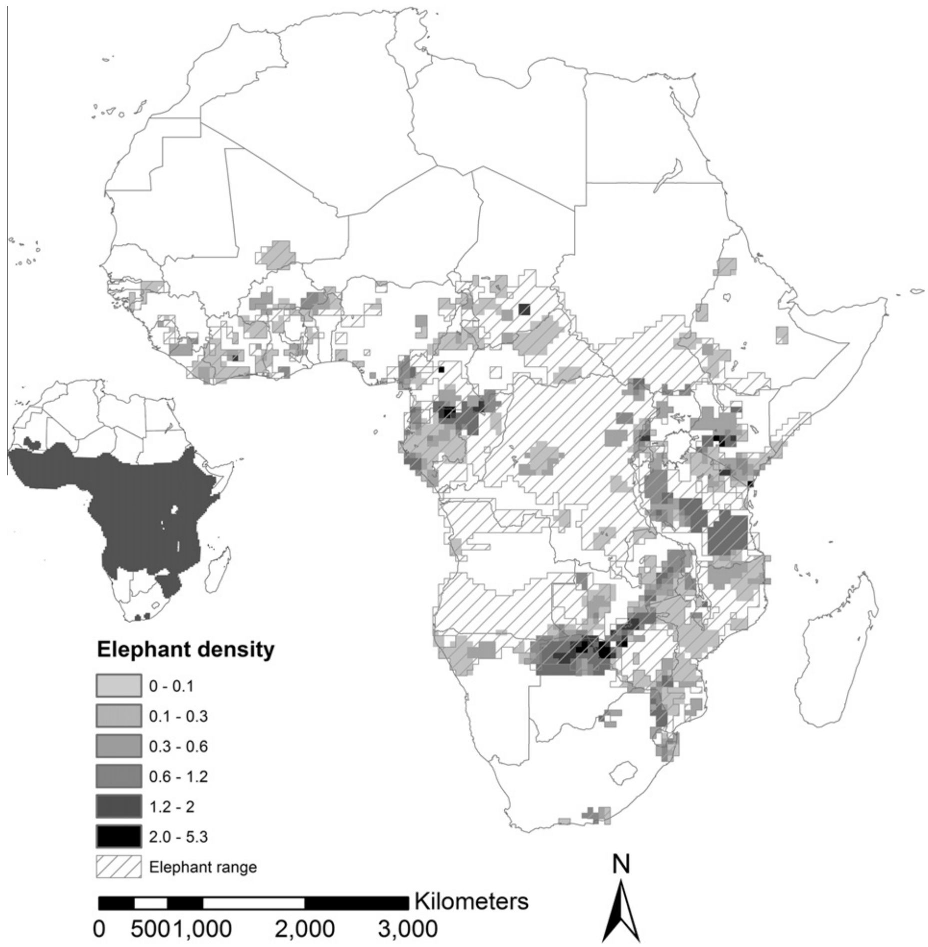

Fig. 1. Distribution of African elephants (*Loxodonta africana*). Current distribution of African elephants is illustrated by hatched areas if elephant presence was confirmed. Differences in known density estimates (n/km^2) are illustrated by gradients of shading (source: Blanc et al., 2007). Hatched areas without shading represent areas where elephant presence was confirmed but where elephant densities were unknown. Inset: historic distribution of elephants. *Source*: Dorst and Dandelot, 1972; Carruthers et al., 2009

(ELEDENS; numbers/km^2) for each grid cell south of the Sahara were calculated at a resolution of 0.5° latitude–0.5° longitude (Fig. 1). This was the smallest cell size at which the data could be analyzed without spatial interpolation. Moreover, elephants have large home ranges (Shannon et al., 2010), their distribution is influenced by decisions taken over tens of kilometers (De Knegt et al., 2011), and the elephant survey data are subject to spatial uncertainty (Blanc et al., 2007), so that an analysis at a finer resolution is not justified. The analysis was based on 2932 and 3778 grid cells for elephant presence and absence, respectively, and 1370 grid cells with estimated elephant densities. The latter estimated elephant densities were obtained from a variety of methods, such aerial counts, road transects and dung counts, and for more information regarding methods, estimates and reliability we refer to Blanc et al. (2007). We took elephant range and density estimates at face value, although their reliability is undoubtedly influenced by survey method (Blanc et al., 2007). These estimates were regressed on several predictor variables at a similar resolution, obtained from different sources (Table A1). The sizes of the grid cells were not equal, because of the geographic coordinate system used, but 95.4% of all cells were within ±4% of the mean cell size (3025 km^2 ± 132 km). Where the original data were available at finer resolutions in a 0.5° × 0.5° grid cell, we calculated mean values weighted for the proportion of the grid cell. The probability of recording elephants depends to some extent on the proportion of a grid cell that is covered by land. To correct for these differences in land area, we used the variable LAND (land area in%) as a covariate. Several variables were only available per country; these variables were converted to grid cell values.

2.1. Vegetation and soil characteristics

Elephants are bulkfeeders and therefore have lower densities in areas with low plant biomass (Parker and Graham, 1989; Olff et al., 2002). We used Net Primary Production (NPP) and the Normalized Difference Vegetation Index (NDVI) as proxies for the amount of forage for elephants (Young et al., 2009). NDVI measures the reflection of green vegetation, and we calculated mean NDVI over the period 1981–1994. NDVI has been successfully correlated to elephant densities and distribution in other studies at smaller scales (Young et al., 2009; Murwira and Skidmore, 2010). It has the potential problem that it saturates at higher reflectance levels and can thus less accurately measure high levels of forage availability. NPP is highly correlated with NDVI but is more linearly related to plant biomass (Lu, 2006), and could therefore be a better predictor variable for forage biomass. In areas with high amounts of plant biomass, like rainforests, a relatively large part of the vegetation is inaccessible for elephants, which could result in lower elephant densities (Olff et al., 2002). Therefore, we anticipated a unimodal relationship between elephant density and both NDVI and NPP and added their squared terms as predictor variables (NDVI2 and NPP2).

Soil characteristics partly determine forage quality for elephants (Parker and Graham, 1989; Khaemba and Stein, 2000). However, other studies have indicated that elephant distribution was relatively unaffected by soil fertility (Fritz et al., 2002; Olff et al., 2002). We used soil type (SOILTYPE), total extractable bases (TEB) and cation exchange capacity (CEC) as soil nutrient status indicators. We also expected a positive correlation between elephant densities and soil water holding capacity (SOILH2O), because a higher capacity can increase plant available moisture and thereby elephant density (Olff et al., 2002).

Plant biomass is not the only important factor determining elephant distribution and density. Various studies have documented different elephant densities in different vegetation types, explained by differences in forage biomass, forage quality, shade, water availability, or plant species composition (Harris et al., 2008). Therefore, we expected differences in elephant densities over the main different vegetation types (VEGTYPE, following White, 1983), and an increase in elephant density with increasing tree cover (TREE).

Similarity in soil or vegetation does not automatically imply that wildlife density or species composition should be similar because large changes occur over time under the influence of species expansion and physical or natural barriers. We therefore also tested for differences in elephant density over the African zoogeographic provinces (ZOOGEO; following Werger, 1978).

2.2. Temperature, rainfall, surface water and evapotranspiration

Elephants might have difficulties controlling their body temperature when ambient temperatures are too high (Phillips and Heath, 1995), and water availability is therefore a key factor in determining elephant population changes (Fritz et al., 2002; Chamaillé-Jammes et al., 2008). We therefore related temperature (TEMP), rainfall (RAIN), and the amount of surface water (SURFH2O) to elephant distribution and density, expecting a positive effect of these terms. As there might be a unimodal effect of temperature and rainfall on elephant presence/absence and elephant density (Phillips and Heath, 1995; Olff et al., 2002), we also added their squared terms RAIN2 and TEMP2. Moreover, rainfall can also serve as a proxy for resource abundance because it is highly correlated with plant biomass (Coe et al., 1976). We also used the number of wet days per year (NWD) and the number of vegetation growing days per year (GROWTH) as proxies for water and forage availability. We expected a positive correlation between the number of wet days per year and elephant density, as elephant mortality decreases in longer wet seasons (Dudley et al., 2001).

Elephant densities are generally low when rainfall is low but are even lower when the variability in resource abundance is high (Parker and Graham, 1989). We thus anticipated negative correlations between the coefficient of variation of rainfall and of temperature (as a measure of inter-annual variability: CVRAIN, CVTEMP) and elephant densities. As the original temperature and rainfall data were available at finer resolutions in a $0.5° \times 0.5°$ grid cell, we calculated mean annual values, and coefficients of variation were calculated from the variation between these annual means. The rainfall data consisted of monthly averages in millimeters per day for the period 1979–1999. From these, we calculated the mean annual rainfall and its coefficient of variation. The temperature data provided the mean temperature for each month, from which we calculated the annual mean temperature and its coefficient of variation.

Parker and Graham (1989) suggested that elephant densities positively correlate with evapotranspiration because of their association with plant biomass production. We used both actual and potential evapotranspiration (AET and PET) in our analysis.

2.3. Elevation

Areas located at higher elevation differ in soil type, vegetation, plant biomass, rainfall, and temperature, affecting the distribution of elephants (Ngene et al., 2009). We therefore calculated the average elevation for all grid cells from a digital elevation model (ALTI). Because >99% of the grid cells were <2000 m above sea level, we expected a positive effect of elevation on elephant presence and density, because rainfall is higher and temperatures are lower at higher altitudes.

2.4. Human density

Human density (HUMDENS) was expected to be negatively related to elephant density and distribution (Parker and Graham, 1989). Hoare (1999) and Hoare and Du Toit (1999) suggested that elephant densities were negatively related to human densities below a specific threshold. The area under cultivation and the number of livestock also reflect human presence. To test for these effects, we included land-cover classes following Mayaux et al. (2004) in our analysis and tested for the negative effects of agricultural areas (COVER) compared to natural vegetation (combined class of forests, woodlands, grasslands, and others), and for the effect of livestock densities (CATTLE, SHEEP and GOAT, together with the total metabolic weight of the Tropical Livestock Units, TLU; Wint and Robinson, 2007).

2.5. Human welfare and development

The per capita Gross Domestic Product (GDP/cap) varies widely in sub-Saharan Africa from <700 US$ in Burundi or Malawi to >10,000 US$ in South Africa or Botswana (UNDP, 2007). These differences are expected to influence the efficacy of conservation policies (Wittemyer et al., 2008; Burn et al., 2011). Elephant densities may react positively to the amount of resources invested in conservation (Leader-Williams and Albon, 1988). Differences between countries in human welfare, such as reflected in differences in GDP/cap or life expectancy (LEI), are known positively to influence attitudes towards conservation (Teel et al., 2007; Burn et al., 2011) and we therefore also included LEI as a predictor variable in the analysis.

2.6. Conservation policy and education

Scout density and bonuses paid for arrest of poachers had a significant negative effect on the number of illegally killed elephants (Jachmann and Billiouw, 1997). The conservation status of an area and protection efforts are positively correlated with wildlife population trends (Bruner et al., 2001; Caro and Scholte, 2007). To quantify conservation effort, we calculated the proportion of land per grid cell that was under protection (PROTECT). However, protection not only depends on the existence of reserves but also on the policy of a country or region, the level of corruption, and the capacity of a country successfully to implement such a policy (Smith et al., 2003). We therefore included an index of the level of corruption (Corruption Perception Index, CPI; Burn et al., 2011), and the Failed State Index (FSI, Shikida et al., 2011) for each country as predictor variables. State failure is characterized by the loss of physical control of its territory, the erosion of legitimate authority to make collective decisions, the inability to provide reasonable public services, and the inability to interact with other states as a full member of the international community (Fund for Peace, 2008).

A population's educational background is positively correlated with attitudes towards conservation (Vanclay, 2001; Kideghesho et al., 2007) and has therefore been regarded as a key to improving the conservation status of areas or animals. We therefore included the literacy rate of African countries (LIT) in the analysis.

2.7. Habitat fragmentation

Elephants have large home ranges and need extensive areas (Shannon et al., 2010). Habitat fragmentation leads to the reduction of the total habitat area, and the isolation and breaking up of habitat into smaller patches. Habitat fragmentation is therefore expected to negatively correlate with elephant distribution (Leimgruber et al., 2003), similar to its effects on many other species. We used the elephant presence per grid cell as an indicator of the range occupied by elephants (RANGE). We tested whether the size of the range per grid cell can explain elephant densities. We calculated the fractal dimension *D* of the elephant distribution (Olff and Ritchie, 2002), which represents the connectivity and isolation of the areas where elephants occur (FRACTAL). The proportion of the habitat area for large mammals is mainly determined by human land use. Therefore, we considered RANGE as a human variable in the elephant density analysis.

2.8. Statistical analyses

Cases (grid cells) with missing values were deleted from the entire database (<5% of the total number of cases) to allow comparison of the accuracy of the different models. All statistical tests were two-tailed.

2.8.1. Presence/absence analysis

We analyzed the current and historic presence/absence of elephants (ELEPRES; sample size: 6710 grid cells for each analysis) using binary logistic regression by regressing all predictor variables one by one. We used the Akaike Information Criterion (AIC) to compare the fit of the different models, with ΔAIC > 10 indicating that the model is unlikely to perform better than the model with the lowest AIC (Burnham and Anderson, 2002). To test whether the different models predicted the current and the historic elephant distribution equally well, we used a sign test for differences in the percentages of correctly predicted cells for the current and historic presence/absence of elephants.

We carried out a hierarchical partitioning to quantify and compare the importance of the individual predictor variables in multiple regression models using the six best human predictor variables and the six best ecological variables, together with their squared terms when a unimodal relation was expected. Hierarchical partitioning quantifies the contribution of each predictor to the total explained variance, calculated over all possible candidate models (Quinn and Keough, 2002). The current presence/absence data of elephants was used as a dependent variable. The variables that were selected for this hierarchical partitioning were the six variables with the lowest AIC values in the one by one analyses.

2.8.2. Density analysis

For the analysis of elephant density (ELEDENS; sample size: 1370 grid cells) we used only the grid cells where elephants were present, because the mechanisms responsible for presence/absence and density might be different (Quinn and Keough, 2002).

Table 1
Results of the binary logistic regression in which all predictor (human and ecological: Hum and Ecol) variables were tested one by one against the present-day distribution of elephants (n = 6710), with the sign of the expected relationship (H0), the sign of the relationship found (β), the AIC and ΔAIC, and the Wald statistics, degrees of freedom (df), and associated significance (p, ns is not significant); variables are ordered according to increasing AIC.

Variable	Explanation	Type	H0	β	AIC	ΔAIC	Wald	df	p
COUNTRY	Country	Hum			6709	0	1537.27	37	0.001
ZOOGEO	Zoogeographic province	Ecol			6925	216	1011.52	16	0.001
VEGTYPE	Vegetation type	Ecol			7030	321	1081.67	17	0.001
NPP	Net primary productivity	Ecol	+	+	7041	332	1535.68	1	0.001
NDVI	Normalized difference vegetation index	Ecol	+	+	7143	434	1417.27	1	0.001
AET	Actual evapotranspiration	Ecol	+	+	7251	542	1344.88	1	0.001
TREE	Tree cover	Ecol	+	+	7261	552	1214.53	1	0.001
NWD	Number of wet days	Ecol	+	+	7450	741	1190.18	1	0.001
CVRAIN	Rainfall coefficient of variation	Ecol	–	–	7516	807	924.734	1	0.001
GROWTH	Annual number of growing days	Ecol	+	+	7553	844	1271.45	1	0.001
RAIN	Mean annual rainfall	Ecol	+	+	7689	980	1182.69	1	0.001
CVTEMP	Temperature coefficient of variation	Ecol	–	–	7704	995	1020.65	1	0.001
SOILTYPE	Soil type	Ecol			7828	1119	1074.54	19	0.001
FRACTAL	Index of fragmentation	Hum	+	+	8481	1772	569.169	1	0.001
LEI	Life expectancy index	Hum	+	–	8487	1778	636.468	1	0.001
SHEEP	Sheep density	Hum	–	–	8757	2048	291.070	1	0.001
SOILH2O	Soil water holding capacity	Ecol	+	+	8822	2113	319.098	1	0.001
LIT	Adult literacy rate	Hum	+	+	8933	2224	252.921	1	0.001
PET	Potential evapotranspiration	Ecol	+	+	8958	2249	213.306	1	0.001
PROTECT	Conservation status	Hum	+	+	8982	2273	191.024	1	0.001
GDP/cap	Gross domestic product per capita	Hum	+	+	9033	2324	148.173	1	0.001
TEB	Total extractable bases	Ecol	+	–	9044	2335	139.211	1	0.001
CPI	Corruption perception index	Hum	+	–	9053	2344	136.689	1	0.001
TLU	Tropical livestock unit	Hum	–	+	9072	2363	103.631	1	0.001
GOAT	Goat density	Hum	–	–	9082	2373	95.329	1	0.001
CATTLE	Cattle density	Hum	–	–	9083	2374	97.119	1	0.001
FSI	Failed state index	Hum	–	+	9155	2428	43.461	1	0.001
HUMDENS	Human density	Hum	–	–	9137	2446	51.764	1	0.001
COVER	Presence of agricultural production	Hum	–	–	9165	2456	33.254	1	0.001
TEMP	Temperature	Ecol	+	–	9174	2465	24.852	1	0.001
CEC	Cation exchange capacity	Ecol	+	–	9192	2483	7.274	1	0.01
ALTI	Altitude	Ecol	+	+	9192	2483	6.951	1	0.01
SURFH2O	Surface water	Ecol	+	+	9194	2485	5.345	1	0.05
LAND	Land surface area	Ecol	+	–	9199	2490	0.164	1	ns

Note: The model with RANGE as independent variable could not be calculated because of singularity, as presence/absence of elephants is highly correlated with RANGE.

For this latter zero-truncated density analysis, we used a univariate general linear model (GLM) on logarithmically transformed elephant density, which followed a normal distribution. All predictor variables were regressed one by one on the dependent variable, and the Akaike Information Criterion (AIC) was used to compare the fit of the different models.

We also tested for a unimodal relationship of TEMP, NDVI, RAIN and NPP on elephant densities by including the respective main and squared terms using linear regression.

The relationship between elephant densities and human densities (Hoare, 1999; Hoare and Du Toit, 1999; Du Toit et al., 2004) was tested with linear regression. To test for the effect of protection status on elephant density, we calculated per grid cell the elephant density as supplied in the African Elephant Database, and the proportion of the area of the cell that was under protection, which was obtained from the database of the WDPA (2005), so that the analysis was not confounded by the coarse scale of our analysis using $0.5^\circ \times 0.5^\circ$ grid cells. To compare the different elephant densities in protected versus unprotected areas, we selected only the polygons with a known elephant density and calculated the total area of the protected areas within these polygons, and the total number of elephants in these polygons.

To quantify the contribution of the best predictor variables to the total explained variance, we carried out a hierarchical partitioning using the six best human predictor variables and the six best ecological variables together with their squared terms, and elephant density as the dependent variable. Variable selection and statistical analysis were as for the presence/absence analysis.

The analysis of elephant density allowed us further to distinguish the importance of human and ecological factors acknowledging the correlation between the independent variables. We corrected for this multicollinearity by performing two factor analyses, one for the human and one for the ecological variables, using only the available continuous variables (Quinn and Keough, 2002; Field, 2009). A factor analysis extracts the information from various, often collinear variables into a smaller subset of variables (factors) that are independent from each other. In the factor analysis we only saved the calculated human and ecological factors with eigenvalues > 1 (Field, 2009) for further use. We applied a varimax orthogonal rotation to ensure independence between factors, calculated the determinants of the matrix to check for multicollinearity, and reported the KMO statistics to provide a choice between models according to their sampling accuracy (Field, 2009). These new factor-variables were subsequently used as predictors in

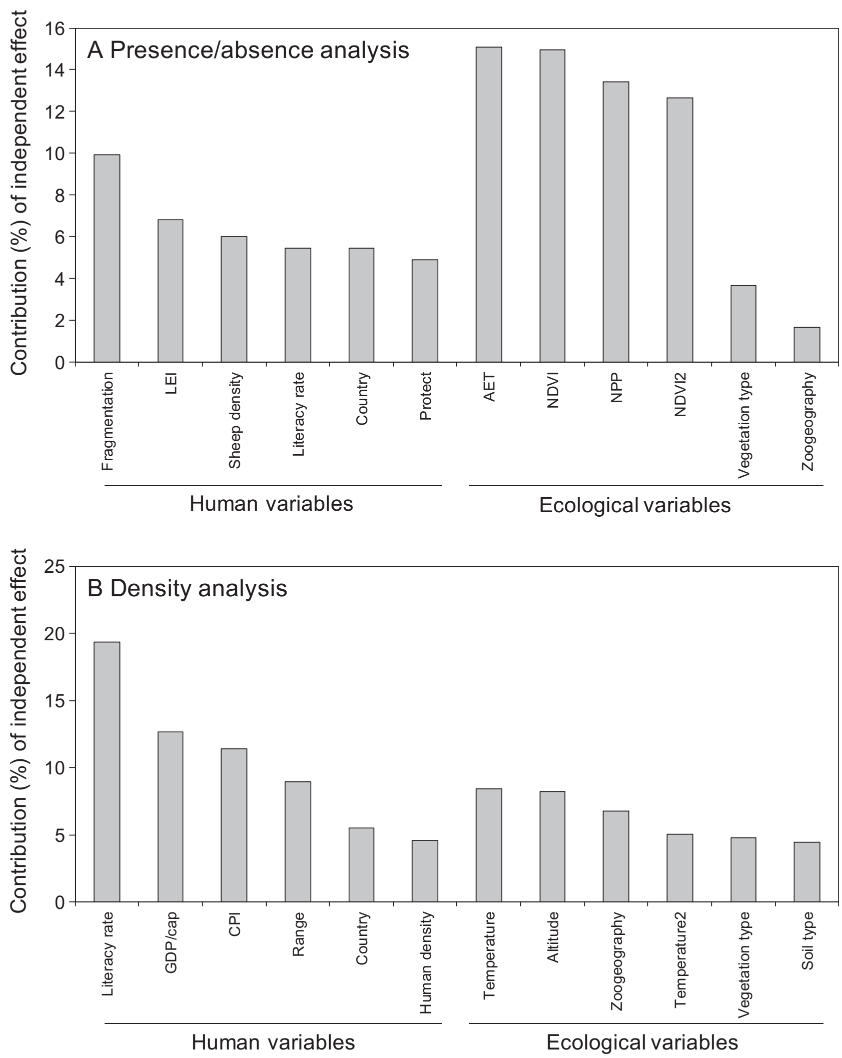

Fig. 2. The contribution of independent effects by the 12 best human and ecological variables as calculated from a hierarchical partitioning. The independent contribution for (A) the present-day presence/absence analysis and (B) density analysis of African elephant, south of the Sahara. The selected human variables are fragmentation, life expectancy index (LEI), sheep density, literacy rate, country, proportion of land under conservation protection (PROTECT), per capita gross domestic product (GDP/cap), corruption perception index (CPI), elephant range, and human density. Ecological variables are actual evapotranspiration (AET), temperature plus its quadratic effect, temperature2), normalized difference vegetation index (NDVI plus its quadratic effect, NDVI2), net primary productivity (NPP), altitude, zoogeographic provinces, vegetation type, and soil type.

Table 2
Results of the binary logistic regression in which all ecological predictor variables and the variable COUNTRY were tested one by one against the historic distribution of elephants (n = 6710), with the sign of the expected relationship (H0), the sign of the relationship found (β), the AIC, ΔAIC, and the Wald statistics, degrees of freedom (df) and associated significance levels (p, ns is not significant).

Variable	H0	β	AIC	ΔAIC	Wald	df	p
ZOOGEO			3428	0	989.140	16	0.001
RAIN	+	+	3503	75	1409.226	1	0.001
CVTEMP	–	–	3600	172	1599.146	1	0.001
NWD	+	+	3759	331	2057.011	1	0.001
AET	+	+	3868	440	1640.485	1	0.001
COUNTRY			3897	469	719.644	37	0.001
NPP	+	+	3945	517	1417.343	1	0.001
VEGTYPE			4091	663	1815.223	17	0.001
CVRAIN	–	–	4138	710	1475.829	1	0.001
GROWTH	+	+	4315	887	1622.663	1	0.001
NDVI	+	+	4358	930	1823.827	1	0.001
TREE	+	+	4607	1179	1109.802	1	0.001
SOILTYPE			5610	2182	936.526	19	0.001
SOILH2O	+	+	7351	3923	650.208	1	0.001
PET	+	+	7452	4024	574.786	1	0.001
TEB	+	–	7678	4250	398.364	1	0.001
CEC	+	–	8132	4704	20.139	1	0.001
ALTI	+	+	8141	4713	11.608	1	0.001
TEMP	+	+	8143	4715	9.438	1	0.01
SURFH2O	+	+	8146	4718	5.172	1	0.05
LAND	+	–	8146	4718	3.696	1	ns

two multiple regression models, one for human variables and one for ecological variables, to explain differences in elephant density. Only significant factors were maintained in the regression model. Both forward and backward selection of significant variables (factors) yielded similar final models.

To correct our analyses for effects of spatial autocorrelation, we applied a simultaneous autoregression technique based on maximum likelihood estimation (Dormann, 2007) in the multiple regression models for density (Rangel et al., 2006). We calculated Moran's I of the residuals from these multiple regression models to test for the presence of spatial autocorrelation (De Knegt et al., 2010).

3. Results

3.1. Presence/absence analysis

The majority of the variables were significantly correlated with the presence/absence of elephants in the binary logistic regression (Table 1); about two-thirds of the regression coefficients of the significant human and ecological variables followed our predictions. The AIC values indicated that COUNTRY was by far the best one-variable model (AIC = 6709), and Akaike evidence ratios of the best 12 models were, ranked in order of AIC, >3 in all cases, indicating that models with a lower AIC were better than subsequent models with a higher AIC.

The hierarchical partitioning, only including continuous variables, showed that several ecological variables (AET, NDVI, NDVI2, and NPP) were the most important in the different regression models (Fig. 2A), whereas human variables like FRACTAL and LEI were less important.

The majority of the ecological variables and COUNTRY were significantly correlated with the historic presence/absence of elephants in the binary logistic regression (Table 2). A strong increase in model fit emerged using the historic elephant

Table 3
Results of the univariate tests in which all (human and ecological: Hum and Ecol) predictor variables and the zero-truncated elephant density data were tested one by one in a GLM (n = 1370), with the sign of the expected relationship (H0), the sign of the relationship found (β), the R^2_{adj}, the degrees of freedom (df), and the F values with associated significance values (p, ns is not significant); variables are ordered according to increasing AIC, together with their ΔAIC.

Variable	Type	H0	β	R^2_{adj}	AIC	ΔAIC	df	F	p
COUNTRY	Hum			0.314	–2540	0	361,333	18.370	0.001
ZOOGEO	Ecol			0.158	–2280	260	161,353	17.100	0.001
LIT	Hum	+	+	0.132	–2252	288	11,368	208.300	0.001
HUMDENS	Hum	–	–	0.014	–2178	362	11,368	19.770	0.001
CPI	Hum	+	+	0.058	–2141	399	11,368	82.290	0.001
VEGTYPE	Ecol			0.066	–2140	400	141,355	7.932	0.001
GDP/cap	Hum	+	+	0.055	–2137	403	11,368	81.050	0.001
TEMP	Ecol	+	–	0.045	–2121	419	11,368	65.040	0.001
ALTI	Ecol	+	+	0.041	–2116	424	11,368	59.520	0.001
SOILTYPE	Ecol			0.043	–2102	438	181,351	4.388	0.001
RANGE	Hum	+	+	0.031	–2101	439	11,368	44.490	0.001
CVTEMP	Ecol	–	+	0.025	–2094	446	11,368	36.110	0.001
PROTECT	Hum	+	+	0.024	–2092	448	11,368	34.420	0.001
TEB	Ecol	+	–	0.009	–2072	468	11,368	13.620	0.001
FSI	Hum	–	–	0.008	–2070	470	11,368	12.520	0.001
SOILH2O	Ecol	+	–	0.004	–2064	476	11,368	5.902	0.05
GROWTH	Ecol	+	–	0.004	–2064	476	11,368	6.251	0.05
NWD	Ecol	+	–	0.003	–2063	477	11,368	5.316	0.05
RAIN	Ecol	+	–	0.002	–2061	479	11,368	3.091	ns
CVRAIN	Ecol	–	+	0.001	–2061	479	11,368	3.049	ns
LAND	Ecol	+	+	0.001	–2061	479	11,368	2.564	ns
SHEEP	Hum	–	–	0.000	–2060	480	11,368	1.587	ns
TLU	Hum	–	+	0.000	–2060	480	11,368	1.560	ns
AET	Ecol	+	–	0.001	–2060	480	11,368	1.996	ns
PET	Ecol	+	–	0.001	–2060	480	11,368	2.022	ns
CATTLE	Hum	–	+	0.001	–2059	481	11,368	1.689	ns
LEI	Hum	+	+	0.000	–2059	481	11,368	0.599	ns
NPP	Ecol	+	+	0.001	–2059	481	11,368	1.221	ns
CEC	Ecol	+	–	0.000	–2059	481	11,368	1.128	ns
COVER	Hum	–	+	0.000	–2058	482	11,368	0.149	ns
GOAT	Hum	–	–	0.000	–2058	482	11,368	0.761	ns
FRACTAL	Hum	+	+	0.000	–2058	482	11,368	0.320	ns
NDVI	Ecol	+	+	0.001	–2058	482	11,368	0.001	ns
SURFH2O	Ecol	+	+	0.000	–2058	482	11,368	0.338	ns
TREE	Ecol	+	+	0.001	–2058	482	11,368	0.003	ns

distribution and the ecological predictors compared to the models with the present-day elephant distribution, as the percentage of correctly predicted cells was higher for models with the historic elephant distribution (Sign test, $n = 20$, $p < 0.001$). The mean percentage of correctly predicted cells increased from 65% for the present-day elephant distribution to 80% for the historic elephant distribution. The historic distribution of elephant was correlated better with ecological variables (RAIN, CVTEMP, NWD, and AET) and the zoogeographic provinces than by COUNTRY.

3.2. Density analysis

Elephant density was significantly correlated with most of the predictor variables when tested one by one in a GLM (Table 3). Relationships for all significant human variables followed our predictions. Elephant density was positively correlated with increasing literacy rate (LIT), Corruption Perception Index (CPI), income (GDP/cap), the proportion of the grid cell where elephants occurred (RANGE) and the proportion of the grid cell under protection (PROTECT), and with decreasing human density (HUMDENS) and decreasing Failed State Index (FSI). The explained variances of these variables were relatively high for COUNTRY ($R^2_{adj} = 0.31$), and LIT ($R^2_{adj} = 0.13$). The ecological variables had poor fits, and yielded only one significant continuous variable (ALTI) that was in agreement with our hypotheses, but with $R^2_{adj} < 0.05$. Other continuous ecological variables were either not significant ($n = 10$), or had signs contrary to our predictions ($n = 6$). However, the three categorical ecological variables (ZOOGEO, VEGTYPE, and SOILTYPE) were all significant, but this could also be due to site effects, as the COUNTRY model outperformed the vegetation and soil type models as well as the model based on differences in the zoogeographic provinces (ZOOGEO). When ordering the variables according to their AIC values, four out of the best five were human variables.

The postulated relations of TEMP, NDVI, or NPP together with their squared terms yielded significant unimodal models for TEMP and NDVI (linear regression, $F_{2,1367} > 8.552$, $p < 0.001$), but with low R^2_{adj} (respectively 0.07 and 0.01). Highest elephant densities were predicted at intermediate TEMP (Fig. 3A) and NDVI values (Fig. 3B), as both models had positive linear terms and negative squared terms (model for TEMP: $b = -0.072$, $t = -5.281$, $p < 0.001$; TEMP2: $b = -0.002$, $t = -5.988$, $p < 0.001$; model for NDVI: $b = 0.247$, $t = 3.854$, $p < 0.001$; NDVI2: $b = -0.327$, $t = -4.136$, $p < 0.001$). The highest R^2_{adj} could be obtained by combining TEMP and NDVI in a multiple regression, resulting in significant positive main terms and negative squared terms for both temperature and NDVI ($F_{5,1364} = 30.474$, $R^2_{adj} = 0.10$).

We found that elephant density was negatively correlated with increasing human density (Fig. 4; $F_{1,1369} = 19.770$, $b = -0.024$, $p < 0.001$), yet the explained variance was small ($R^2_{adj} = 0.01$). Other studies have suggested the existence of a threshold at approximately 15–20 people per km^2 above which elephant density is relatively low (Hoare, 1999; Hoare and Du Toit, 1999; Du Toit et al., 2004), but such a threshold could not be confirmed at the continental scale. In fact, some grid cells in Kenya ($n = 10$) and Uganda ($n = 3$) had relatively high elephant densities (>0.2 $\log_{10}$ elephants/km^2) under a high human density (>2 $\log_{10}$ humans/km^2; Fig. 4).

Elephant densities were positively correlated with the proportion of grid cells under protection (PROTECT, Table 3). Grid cells that were 100% protected had a higher elephant density ($\log_{10}$ n/km^2) than partly protected grid cells, or cells without any protection status (GLM, $F_{2,1367} = 19.988$, $p < 0.001$, $R^2_{adj} = 0.03$). Around 14% of the area where elephants were found (RANGE) was under protection. When analyzing the maps of protected areas and elephant densities we calculated a mean density of 0.41 elephants/km^2 in protected areas, against 0.25 elephants/km^2 in areas with

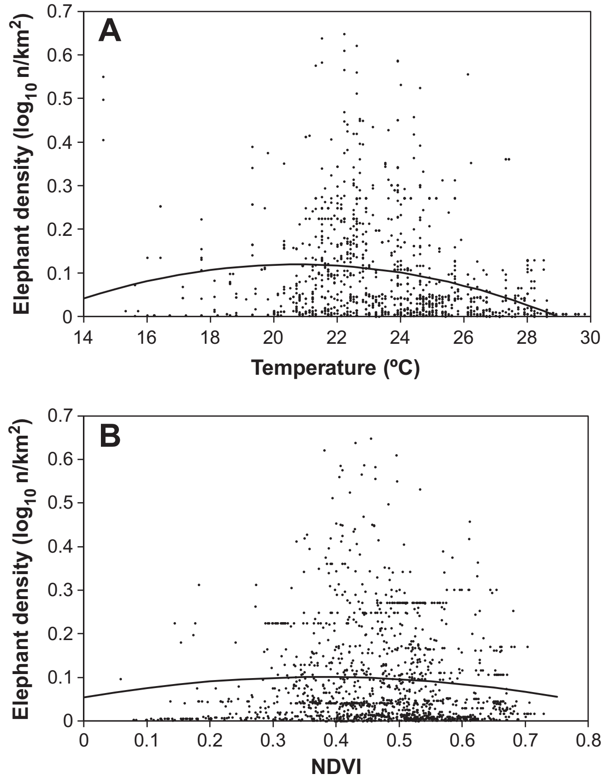

Fig. 3. Relationships between (A) temperature, and (B) Normalized Difference Vegetation Index (NDVI) with densities of African elephants, together with predicted values (line) derived from a regression equation that had significant positive single terms and negative squared terms for both temperature and NDVI.

no official protection status. There were in total more elephants in protected areas (3.47×10^5 elephants, 8.53×10^5 km^2) than in areas without protection status (6.20×10^5 elephants, 2.50×10^6 km^2).

The hierarchical partitioning showed that, unlike the presence/absence analysis, the human variables CPI, LIT, GDP/cap and RANGE contributed more to the explained variance of elephant density than the ecological variables (Fig. 2B).

The factor analysis resulted in four human and three ecological factors with eigenvalues > 1 (Table 4). Using these ecological and human factors as predictors in two separate regression models with elephant density as the dependent variable showed that

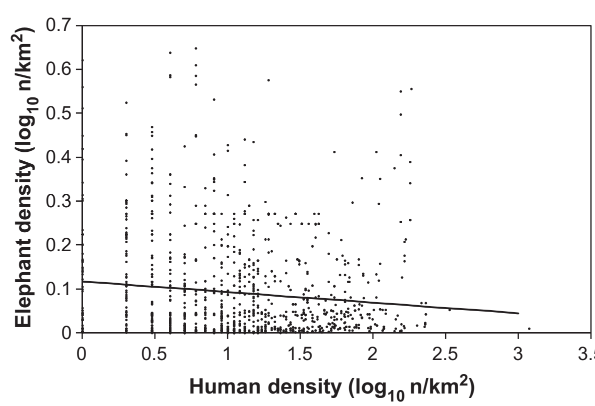

Fig. 4. Relationship between densities of people and African elephants. Our regression analysis indicated that elephant density decreased linearly with increasing human density.

Table 4
Results of the factor analysis on elephant densities, with the Determinant and KMO measure of sampling adequacy and the factor loadings (>0.400) for each variable for factors with eigenvalue > 1.

Human variables					Ecological variables			
Determinant	0.003					0.001		
KMO measure	0.657					0.894		
	Factor 1	Factor 2	Factor 3	Factor 4		Factor 1	Factor 2	Factor 3
Explained variance (%)	27.9	21.8	10.4	9.7		54.4	9.3	8.8
Correlated variables								
GDP/cap	−0.714	0.551			GROWTH	0.916		
HUMAN	0.697				NPP	0.903		
CPI	−0.683	0.648			RAIN	0.898		
GOAT	0.670	0.561			AET	0.876		
SHEEP	0.661	0.552			CVRAIN	−0.853		
TLU	0.604	0.514			TREE	0.832		
FSI	0.564	−0.593			NWD	0.797		
LEI		0.564			CVTEMP	−0.777		
FRACTAL			0.719		NDVI	0.688		
RANGE			0.531	0.466	ALTI		0.743	−0.553
LIT			−0.410	0.568	TEB		0.520	0.512
PROTECT				0.449	SOILH2O		0.482	0.489

human factors were stronger correlated with differences in elephant densities than ecological factors. Three human factors were significant in the regression model compared with two ecological factors (human factors: partial η^2 respectively 0.239, 0.237, and 0.210, total $R^2_{adj} = 0.15$, AIC = −2270; ecological factors: η^2 respectively 0.193, and 0.117, total $R^2_{adj} = 0.05$, AIC = −2126). The human variables that were highly correlated with the extracted factors were GDP/cap, HUMAN, CPI, and several livestock variables (GOAT, SHEEP, TLU), all with factor loadings > 0.600 (Table 4).

The results of the autocorrelation test showed that the values for Moran's I based on the residuals of these regression analyses were all between 0.24 and −0.101 for the human factors and between 0.312 and −0.114 for the ecological factors, suggesting that there is only weak spatial autocorrelation in the residuals.

4. Discussion

Ecological variables, especially mean annual rainfall, were strongly correlated with the historic distribution of elephants in terms of occurrence over the African continent (Table 2). The model fit of these variables was better for the historic distribution than for the present-day distribution of elephants (Table 1). Our results suggest, however, that these ecological variables continue to pose constraints on current elephant distribution (Fig. 2A), with the greatest explanatory power coming from variables that represent resource availability: actual evapotranspiration, net primary production, and vegetation biomass (NDVI). Country and habitat fragmentation were the human variables that best correlated with the presence and absence of elephants (Table 1).

The current distribution of elephants (presence/absence analysis) was strongly correlated with ecological variables, but these variables were weak predictors for present-day elephant densities (Fig. 2B). Rather, human variables were better correlated to elephant densities; these variables include literacy rate, corruption, and per capita gross domestic product. Elephant densities were positively correlated with increasing literacy rate and increasing per capita gross domestic product (Table 3), and decreased with increasing human density, even though the explained variance was small (Fig. 4; Smith et al., 2003). Other studies have also shown that education is an important variable in affecting the conservation behavior of people (Vanclay, 2001; Kideghesho et al., 2007). In our study ecological variables were poor predictors in explaining differences in elephant densities; elevation was the only significant continuous ecological variable influencing density that was in agreement with our hypotheses, and most ecological variables (n = 10) were not significantly correlated with elephant densities. Temperature and NDVI yielded unimodal relationships, but with a relatively low explanatory power. The negative squared term of NDVI indicated that the forage biomass might become out of reach at elevated NDVI values. Country-specific characteristics are apparently more important than ecological conditions in influencing elephant densities, as COUNTRY outperformed the models based on vegetation type, soil type and zoogeographic provinces. An important observation here is that the amount of variation that was explained by all human factors, composed out of all continuous human variables ($R^2_{adj} = 0.15$), is still less than what COUNTRY alone explained ($R^2_{adj} = 0.31$). Apparently, country-specific differences, which are not related to site effects such as differences in vegetation, soil types, or by human variables such as differences in literacy rate or human density, are important predictors in explaining differences in elephant density. In areas where elephants are present, we suggest that human variables might better explain the present-day density of elephants in Africa than ecological variables. At a local level the management of protected areas needs to take account not only of socio-political factors, but also of ecological factors.

This strong correlation of human factors with elephant densities can have different explanations, for example, the availability of food and water resources for wild animals might be higher in protected areas, and poaching might be lower in countries with a lower corruption index and a better education system (Jachmann and Billiouw, 1997; Caro and Scholte, 2007; Kideghesho et al., 2007; Burn et al., 2011). Bruner et al. (2001) identified a relationship between conservation effectiveness and the level of deterrents to illegal activities, such as the probability of apprehending or sanctioning violators. Outside protected areas, pressure on wild animals is often higher, as elevated human densities around conservation areas can explain local species extinction (Brashares et al., 2001). Thus, the efficacy of conservation policies is influenced by socioeconomic factors.

The pressure on natural ecosystems leads to a marked species decline especially of large terrestrial vertebrates (Schipper et al., 2008). Hence, governments have and need to establish policies for nature conservation, but the question remains about how effective such policies truly are. It has been suggested that effective protection is only achievable with the support of society at large as success in protecting wild animals may depend not only on protection status or law enforcement efforts, but also on the desire of people to respect the law, to put the law into effect, and to tolerate or even admire wildlife (Stern, 2001). Our results support the relevance of these trends for conservation: we found that higher elephant densities occur in countries with a higher per capita gross domestic product or a higher literacy rate. Hence, improving the conservation of African elephants might not rely solely on increasing the area under conservation or improving the ecological conditions of protected areas, such as by increasing resource availability (forage, water, or shade). Instead, our work suggests that the efficacy of conservation policies may especially improve with alleviation of poverty (Adams et al., 2004; Burn et al., 2011) or improved education (Sachs and Reid, 2006). Even at the coarse resolution of our analysis ($0.5^\circ \times 0.5^\circ$), we found many significant relationships between elephant distribution and various ecological and human factors. Such broad-scale findings have potentially high impact given the equally large-scale policies required to conserve African megafauna.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.10.015.

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