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Predictors of elephant poaching in a wildlife crime hotspot: The Ruvuma landscape of southern Tanzania and northern Mozambique

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ABSTRACT

Understanding the spatial distribution of elephant carcasses in relation to ecological characteristics and human activities is critical to developing targeted management strategies for reducing poaching. We employ a spatial modelling approach to quantify the relative contribution of multiple climatic, ecological, human and protected area management predictors of the number of elephant carcasses in a recognized poaching hotspot: the Ruvuma landscape of northern Mozambique and southern Tanzania. This includes the Niassa Reserve in the south and the Selous Game Reserve in the north. In Mozambique, the number of elephant carcasses is positively associated with State-managed protected areas such as Niassa Reserve, but particularly with environmental variables including low rainfall and high temperatures. In Tanzania, elephant carcasses are positively associated with community-managed sites. A strong focus on effective management of protected areas in the Ruvuma landscape is crucial to reducing the killing of elephants.

1. Introduction

Poaching of elephants is currently the main driver of elephant population declines in Africa (Bouche et al., 2011; Chase et al., 2016; Maisels et al., 2013). During the period 2008–2012, one hundred thousand elephants are estimated to have been killed across the African continent (Wittemyer et al., 2014). Reduced elephant populations have long term implications for vegetation composition, affect ecosystem function and service provision (Campos-Arceiz & Blake 2011; Ribeiro, Shugart, & Washington-Allen 2008), and human livelihoods through reduced tourism income potential (Lindsey, Roulet, & Romañach, 2007; Naidoo, Fisher, Manica, & Balmford, 2016; Wilfred & MacColl, 2010). Moreover, the trafficking of ivory is known to have implications for national and international security (Douglas & Alie, 2014).

Availability of data about the spatial distribution of elephants and elephant carcasses is frequently limited. Efforts to identify predictors of elephant poaching have anticipated a diverse set of factors. On a continental scale, sites with extensive forest cover, where patrolling and enforcement are relatively more challenging than in open savannah, experience higher levels of elephant poaching (Burn, Underwood, & Blanc 2011). At the country level, human factors such as poor governance and low economic development (Burn et al., 2011), low literacy rates (de Boer et al., 2013) and economic downturns (Wittemyer 2011) increase killing of elephants. Conversely, improved economic opportunities of local people (Kyando, 2014), building broad-based law enforcement capacity (Nyirenda et al., 2015), roads and rivers facilitating patrolling (Maingi, Mukeka, Kyale, & Muasya, 2012), increasing operational management budgets (Jachmann 2008), decreasing number of hunter camps (Dunham, 2008) and some types of tenure systems (Ihwagi et al., 2015; Kahindi et al., 2010), are associated with decreased poaching within protected sites. Recently, livelihood strategies of communities adjacent to areas of high levels of illegal killing of elephants (Knapp, 2007; Nuno, Bunnefeld, Naiman, & Milner-Gulland, 2013), and the relationship between enforcement and compliance (Keane, Jones, Edward-Jones, & Milner-Gulland, 2008; Solomon, Gavin, & Gore, 2015), have received a renewed focus in an attempt to identify the ultimate causes of individual participation in wildlife crime. Despite the above, information on the relative contribution of different ecological and human drivers of poaching to the number of killed elephants is limited.

Understanding what factors determine the spatial distribution of elephant carcasses is crucial to developing effective anti-poaching actions and protect areas. The success of anti-poaching actions are likely to depend on context-specific circumstances, thus more information

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about what determines the spatial distribution of elephants carcasses in known poaching hotspots is therefore urgently needed. The Ruvuma landscape in Tanzania and Mozambique is a major wildlife crime hotspot in Africa (CITES 2016; Wasser et al., 2008; Wasser et al., 2015). The elephant population in the Tanzanian Selous-Mikumi ecosystem has declined from about 50,000 elephants in 2006 to about 13,000 in 2013 (Kyando 2014). In the Mozambique part, the Niassa Reserve lost almost half of its population, declining from about 20,000 elephants in 2009 to about 12,000 in 2011, where 1000 elephants was poached just in 2011 (Booth & Dunham, 2016). The main reason for these population declines is illegal killing of elephants for their ivory (Wasser et al., 2015).

We aim to describe the distribution of live and dead elephants in different protected areas in the Ruvuma landscape and to identify the ecological and human related predictors associated with the number of elephant carcasses. We employ an explicit spatial modelling approach to quantify the relative contribution of multiple potential predictors described in the literature as a priori explaining the observed total number of elephant carcasses. We hypothesized that carcass numbers would be associated with (1) water availability and climate, (2) vegetation (detectability), (3) accessibility (roads and topography), (4) proximity of human settlements and land uses, (5) protected areas management and tenure system. The results provided aim to explore the comparative relevance of all these types of explanatory variables, with the purpose of contributing to facilitate the development of effective and optimally targeted management strategies to reduce poaching in a critical poaching hotspot such as the Ruvuma landscape, and elsewhere.

2. Methods

2.1. Study area

The Ruvuma landscape is located in northern Mozambique and southern Tanzania (Fig. 1). It contains three State-managed protected areas: Selous Game Reserve (SGR) (48,000 km^2), Niassa Reserve (NR) (42,000 km^2; of which 19,000 km^2 are private hunting block concessions) and Quirimbas National Park (QNP) (7500 km^2). In Mozambique, there is a community-managed site north-west of NR (Chipanje Chetu, 6000 km^2). In Tanzania there are a number of community-managed Village Land Forest Reserves (VLFR) (2500 km^2), Wildlife Management Areas (WMAs) (22,000 km^2), and State-managed Forest Reserves (FR) (1000 km^2) on the southern side of the SGR. The landscape has two main wildlife corridors. The first is the Selous Niassa Wildlife Protection Corridor (SNWPC) (9000 km^2). It is situated between NR and SGR and consists largely of WMAs. The second corridor is between QNP and NR, the Quirimbas Niassa Corridor (QNC) (7200 km^2) and is formed of privately-managed areas mainly used for logging and trophy hunting ("fazendas").

The temperature range from mean monthly temperature of 31 °C in the hot season to 27 °C during the cold season, and from driest (800 mm/year) in the East, to colder (30–20 °C) and wetter (1500 mm/year) areas at higher altitudes (1,400m) in the West. The rain season falls during the hot season, beginning in late October and ending in late March. The landscape has three main rivers (Rufiji, Ruvuma and Lugenda) and there is a broad network of small seasonal rivers that dry out during the dry season. Most of the landscape is covered by miombo woodland, with scattered bushland, savannah and grassland.

The Ruvuma landscape is traversed by two development corridors from East to West, one in each country (Mtwara corridor in Tanzania and Pemba-Lichinga corridor in Mozambique) with mostly continuous paved roads. There are a number of gravel roads that link both development corridors from North to South and a bridge over the Ruvuma River, which connect the countries by road. Human population density increases from West to East. Communities are mainly subsistence farmers who, to varying degrees complement agriculture with livestock production of mainly poultry and goats. Communities collect firewood for household cooking, bamboo and poles for construction, and non-timber products from surrounding forests. They hunt small and medium size mammals for own subsistence purposes (meat) and bigger animals (including elephants) for income generation through the bushmeat and ivory trade.

2.2. Data

Our analysis uses number of elephant carcasses and number of live elephants in each 20 × 20 km grid cell in the landscape; n = 142 in Mozambique and n = 101 in Tanzania (Fig. 1). This grid size is 6% of the largest home range estimated for elephant bulls in the landscape (Mpanduji & Ngomello, 2007), and provides balance to manage the spatial uncertainty in the predictor variables (Hunsaker, Goodchil, Friedl, & Case, 2001). Predictors variables were selected on the basis of our a priori expectation of their relevance to the killing of elephants as previously identified in the literature (see Table 1). We extracted information for all predictors based on spatial layers from the Ruvuma Interactive Map (World Wildlife Fund, 2011), except for the climatic variables, where we used the WorldClim database (http://www.worldclim.org/; last acceded 15th of October 2017); and elevation, where we used EarthData from NASA (http://reverb.echo.nasa.gov; last acceded 15th of October 2017). Data covered 2010 except logging (2012), elevation (2012). Climatic predictors are not temporally aligned with elephants and elephant carcasses data but they are interpolated values reflecting average conditions from 1950 to 2000. Due to data differences between countries, we developed separate models and analyses for each country.

Elephant data are the number of elephant carcasses and live elephants in each grid cell observed from aerial censuses during the dry season (September/October). Data for Mozambique were extracted from published maps from 2009 and 2011 (Craig, 2009, 2011) using ArcGIS 10 software (ESRI, 2011); while data for Tanzania are unpublished data for 2011 and 2014 (unpublished data; World Wildlife Fund and Poverty and Ecosystem Services Impact of Tanzania's Wildlife Management Areas, PIMA, http://www.ucl.ac.uk/pima; last acceded 15th of October 2017). Sampling intensity reported was 10% in Mozambique and 24–40% in Tanzania.

The data have a number of constraints. First, we do not have data for all grid cells in which aerial censuses have actually been conducted. In order to deal with this constraint, we consider grid cells where live elephants have been observed as surveyed grid cells where no elephant carcasses have been found (n = 57 Mozambique and n = 12 Tanzania). Second, there are grid cells where elephant data have been surveyed in both survey years (77 of 142 grid cells in Mozambique and 16 of 101 grid cells in Tanzania). These data cannot be treated as independent since carcasses (mainly elephant bones registred as old carcasess) may remain in the field for several years and we do not have information about the age of the carcasses. To resolve this issue, we used the average number of live elephants and carcasses recorded in these grid cells. A third limitation is lack of information on the proportion of carcasses that represent illegally killed elephants. However, available data from the CITES-MIKE programme on the proportion of illegally killed elephants (PIKE) indicates that the ratio was 0.89 in Niassa in 2011 and 0.74 in Selous-Mikumi in 2013 (CITES, 2014). This suggests that most of the elephant carcasses observed represent illegally killed individuals.

2.3. Statistical analysis

We used Generalized Linear Models (GLMs) to quantify first the independent explanatory capacity of each predictor described in Table 1 in the number of elephant carcasses (see Dobson, 1999). We used a Poisson error distribution for the response variable which was related to the predictor variables via a logarithmic link function (see

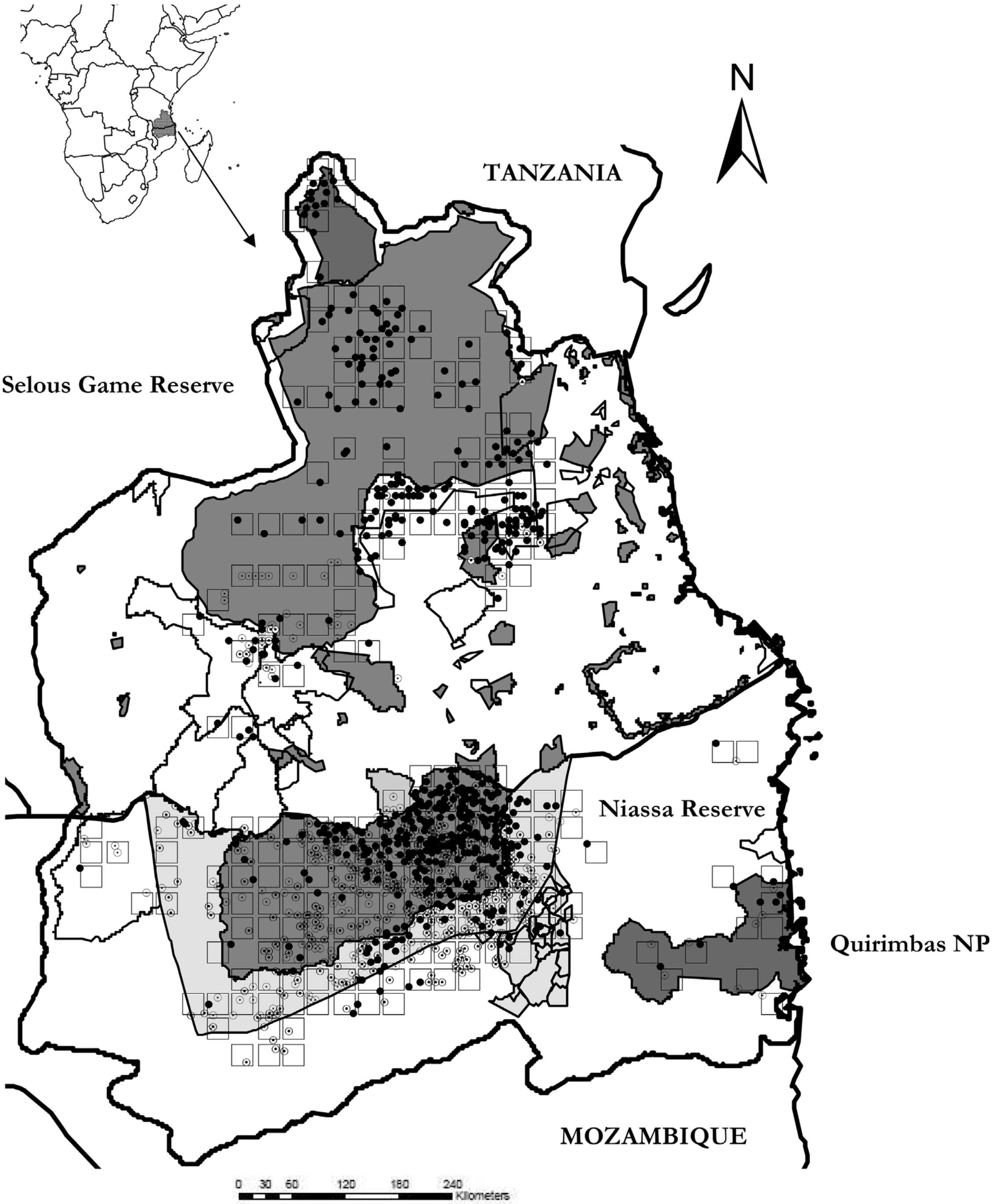

Fig. 1. The Ruvuma landscape, which spans southern Tanzania and northern Mozambique. Community-managed protected areas are coloured in white, privately-managed protected areas in light grey, and State-managed protected areas in dark grey. Black spots show points where elephant carcasses have been observed during the sample surveys, while white spoted spots show points where live elephants have been observed. 20 × 20 UTM grid cells showed in black outline indicate the grid cells included in the analysis.

Crawley, 1993). For each predictor, we tested the significance of linear and quadratic functions to consider possible curvilinear relationships. The model goodness-of fit was measured by the deviance statistic and the statistical significance of the obtained parameters by the Wald statistic. All models were checked for overdispersion. We included the number of living elephants as a covariable in the models in order to understand their relationship to the number of carcasses. Models were also estimated without the number of live elephants as a covariable to examine the consistency of results. If the number of carcasses is not influenced by the number of live elephants, we would expect results from the two modelling procedures to coincide.

Then, statistically significant predictors explaining more than 5% of total deviance (Melletti, Penteriani, Mirabile, & Boitani, 2007; Supple et al., 2017), were included in a subsequent model submitted to a best subset procedure in which all possible regression models were compared using the Akaike Information Criterion (AIC). Analysis was carried out using the Statistica 8.0 package (StatSoft Inc., 2007). Residuals of all models were checked for autocorrelation in order to determine if a structured spatial pattern exists (Diniz-Filho, Bini, & Hawkins, 2003). This was achieved by calculating Moran's *I* values for ten classes separated by a lag distance of 40 km, and evaluating their statistical significance through a Monte Carlo procedure (n = 199).

Table 1
Predictors of killing of elephants used in the statistical analysis, identified as potentially relevant in the literature; their units, range and mean values in Mozambique and Tanzania. Predictors identified with NA (not aplicable) were not included in the statistical analysis for the country.

Predictor	Units	Mozambique		Tanzania		Relevance reported previously in the literature
		Range	Mean	Range	Mean	
Water availability and climate						
Rivers	Number of kilometres of rivers in each grid cell. We allocated a weight of 1 to permanent rivers and 0.2 to seasonal rivers	0–99	25	0–98	25	Water is a limiting variable for elephants; droughts can affect population trends by increasing calf mortality and reducing conception rates (Foley, Pettorelli, & Foley, 2008; Shrader, Pimm, & van Aarde, 2010). Water availability is also a potential determinant of poaching activity as previous studies indicate that most illegal killing of elephants takes place during the dry season when elephants tend to concentrate near water reservoirs of big rivers (Maingi et al., 2012). Water availability depends largely on rainfall and temperature and we hyphotesize water availability related factors, such as rivers and climate variables, could be determining the distribution of the number of elephant carcasses.
Annual Mean Temperature	°C * 10	228–265	251	226–263	243	
Mean Diurnal Range	Mean of monthly (max temp − min temp)	91–116	105	68–106	86	
Isothermality	Mean Diurnal Range/Temperature Annual Range (* 100)	57–79	63	53–68	62	
Temperature Seasonality	standard deviation *100	1047–2099	1790	1181–1952	1530	
Max Temperature of Warmest Month	°C * 10	306–347	332	290–323	305	
Min Temperature of Coldest Month	°C * 10	138–192	165	142–195	168	
Temperature Annual Range	Max Temperature of Warmest Month – Min Temperature of Coldest Month	130–183	167	118–160	138	
Annual Precipitation	Millimetre	923–1327	1150	859–1499	1134	
Precipitation of Wettest Month	Millimetre	201–310	266	178–348	236	
Precipitation of Driest Month	Millimetre	1–8	2	1–11	4	
Precipitation Seasonality (Coefficient of Variation)	Millimetre	92–112	110	77–108	92	
Detectability (vegetation)						
Natural forest	Number of hectares covered by natural forest in each grid cell	0–40,000	2893	0–13,050	533	We hypothesize vegetation type influences the number and distribution of elephant carcasses found in aerial censuses. Vegetation type influences the distribution of poaching activities, because dense vegetation reduces visibility and hence decreases the likelihood of aerial detection of poachers by patrol guards (Burn et al., 2011). Vegetation type also influences elephant habitat use and enforcement effort as dense vegetation with low accessibility makes non-aerial patrolling and anti-poaching efforts more difficult (Ndey, 2005).
Closed woodland	Number of hectares covered by closed woodland in each grid cell	0–40,000	18,396	0–23,249	2507	
Open woodland	Number of hectares covered by open woodland in each grid cell	0–40,000	12702	0–40,000	24,801	
Bushland	Number of hectares covered by bushland in each grid cell	0–36,701	1515	0–24,535	1327	
Grassland	Number of hectares covered by grassland in each grid cell	0–35,358	2298	0–33,366	8088	
Accessibility (elevation, roads)						
Elevation	Mean number of meters of elevation over sea level in each grid cell	84–864	441	109–875	458	We hypothesize accesibility influence the number and distribution of elephant carcasses. Elevation has been recognized as a relevant predictor of the spatial distribution of elephant poaching in other studies in Africa (de Boer et al., 2013). Recent research in Tanzania suggests that mountains have likely served as refuges for elephants enabling them to escape poaching (Jones & Nowak, 2015). Roads have been documented as a strong predictor of elephant population decline (de Boer et al., 2013; Kyale, Ngene, & Maingi, 2011). Expansion and improvement of road networks is making elephant habitat more accessible to poachers.
Roads	Number of kilometres of roads in each grid cell. We allocated a weight of 1 to paved roads, 0.8 to gravel roads and 0.4 to dirt roads	0–34	5	0–26	4	
Human pressure (human density and land use)						
Number of villages	Number of villages in each grid cell, independently of their population number	0–35	3	0–12	1	High human population density can be considered a relevant predictor of general elephant decline in Africa due to land use change, habitat loss and human-elephant conflicts (Kahindi et al., 2010; Selier, Slotow, & Di Minin, 2016). The potential for human-elephant conflicts, generating incentives and support for elephant poaching is assumed to be greater where human population density is highest and where agricultural production is more intense. Logging was also included as a predictor for Mozambique, where this activity is widespread and it has been associated with elephant poaching (A. Ali, pers. comm., 2013). Detailed spatial data on areas actually supporting trophy hunting were not available; we excluded this issue from the analysis.
Population density	Population density in each grid cell calculated at the district level in inhabitants per km^2	1–124	7	3–31	10	
Agriculture	Number of hectares under agriculture in each grid cell	0–32,487	1491	0–26,510	1495	
Production of maize	Tons per hectare of maize produced in each grid cell	0–3.84	1	0.10–8.72	1.40	
Production of rice	Tons per hectare of rice produced in each grid cell	0–1.82	1	0.25–18.11	1.40	
Logging	Number of hectares under logging concessions in each grid cell	0–39,811	1792	NA	NA	

(*continued on next page*)

Table 1 (*continued*)

Predictor	Units	Mozambique		Tanzania		Relevance reported previously in the literature
		Range	Mean	Range	Mean	
Protected areas management and tenure system						
Selous Game Reserve	Number of hectares in each grid cell covered by Selous Game Reserve	NA	NA	0–40,000	21,437	The protected area network has been shown to be correlated with both densities (Stokes et al., 2010) and illegal killing of elephants (Kahindi et al., 2010).
Forest Reserve	Number of hectares in each grid cell covered by Forest Reserve	NA	NA	0–40,000	2093	
Village Land Forest Reserve	Number of hectares in each grid cell covered by Village Land Forest Reserve	NA	NA	0–17,727	421	
Wildlife Management Area	Number of hectares in each grid cell covered by Wildlife Management Area	NA	NA	0–40,000	7105	
Niassa Reserve	Number of hectares in each grid cell covered by Niassa Reserve	0–40,000	15750	NA	NA	
Community-managed protected areas	Number of hectares in each grid cell covered by Community-managed protected areas	0–40,000	1391	NA	NA	
Quirimbas National Park	Number of hectares in each grid cell covered by Quirimbas National Park	0–40,000	1960	NA	NA	
Privately-managed protected areas	Number of hectares in each grid cell covered by Privately-managed protected areas	0–40,000	11681	NA	NA	
Elephants						
Elephants	Number of live elephants observed during the aerial censuses	0–9	2.58	0–4	0.40	
Elephant Carcasses						
Elephant carcasses	Number of elephant carcasses observed during the aerial censuses	0–15	1.72	0–7	1.79	

Table 2
Number of live (NE) and dead elephants (carcasses; NEC) observed during the aerial censuses (2009 and 2011 for Mozambique; 2011 and 2014 for Tanzania) within different protected area management and tenure systems. We estimated the number of elephant carcasses per square kilometre by dividing the number of elephant carcasses observed during the aerial censuses per the approximate number of square kilometres covered by each protected area management category; and the carcass ratio, as number of elephant carcasses/(number of elephants + number of elephant carcasses).

	NEC	NE	Area (Km^2)	NEC/km^2 *1000	Carcass ratio
Mozambique					
State-managed PAs (NR)	308	416	20,000	15.4	0.42
Privately-managed PAs (Niassa hunting blocks + QNC)	182	324	19,500	9.3	0.36
Community-managed PAs (Chipanje Chetu)	1	10	2000	0.5	0.09
Tanzania					
State-managed PAs (SGR)	116	33	16,000	7.3	0.77
Forest Reserves	39	5	2000	19	0.88
Village Forest Reserves	8	1	500	16	0.89
Wildlife Management Areas	119	31	7000	17	0.79

3. Results

3.1. Distribution of elephants and elephant carcasses

The distribution of elephant carcases and live elephants in relation to protected area management and tenure systems are described in Table 2. The number of carcasses and live elephants was highest in State-managed reserves in Mozambique (Niassa Reserve) but in Forest Reserves and community-managed protected sites in Tanzania (VFRs and WMAs). Very few elephant carcasses were reported from community managed sites in Mozambique. In general, the number of elephant carcasses was higher in Tanzania than in Mozambique whereas the number of live elephant was lower.

3.2. Predictors

Twelve predictors were statistically significant in predicting the number of elephant carcasses in Mozambique. The number of elephant carcasses was positively associated with the kilometres of rivers, higher temperatures, open woodlands, and the Niassa Reserve (Fig. 2). Among these, open woodlands had a curvilinear relationship with the number of elephant carcasses, with higher numbers of elephant carcasses in areas intermediately covered by open woodlands. Predictors denoting water availability and climate were particularly relevant, accounting for up to 33% of total deviance. Elephant carcass numbers were lower with higher rainfall and elevation, and where natural forest dominates. Only one of the human and protected area management predictors was important in explaining elephant carcass numbers: Niassa Reserve, which has a positive association with number of elephant carcasses. When all significant predictors explaining more than 5% of total deviance were jointly submitted to a best subset procedure, the selected model was composed of only six variables (annual mean temperature, isothermality, temperature seasonality, annual precipitation, Niassa and the quadratic function of open woodlands) accounting for 51% of total deviance.

When the regression models did not include the number of live elephants as a covariable, the same twelve predictors remain statistically significant explaining a similar proportion of total deviance, except in the case of isothermality and temperature seasonality that became not significant. Niassa, open woodlands and annual mean temperature were included in the best model (53% of explained deviance). For both models, the residuals did not show statistically significant spatial autocorrelation, except for the first lag of 40 km

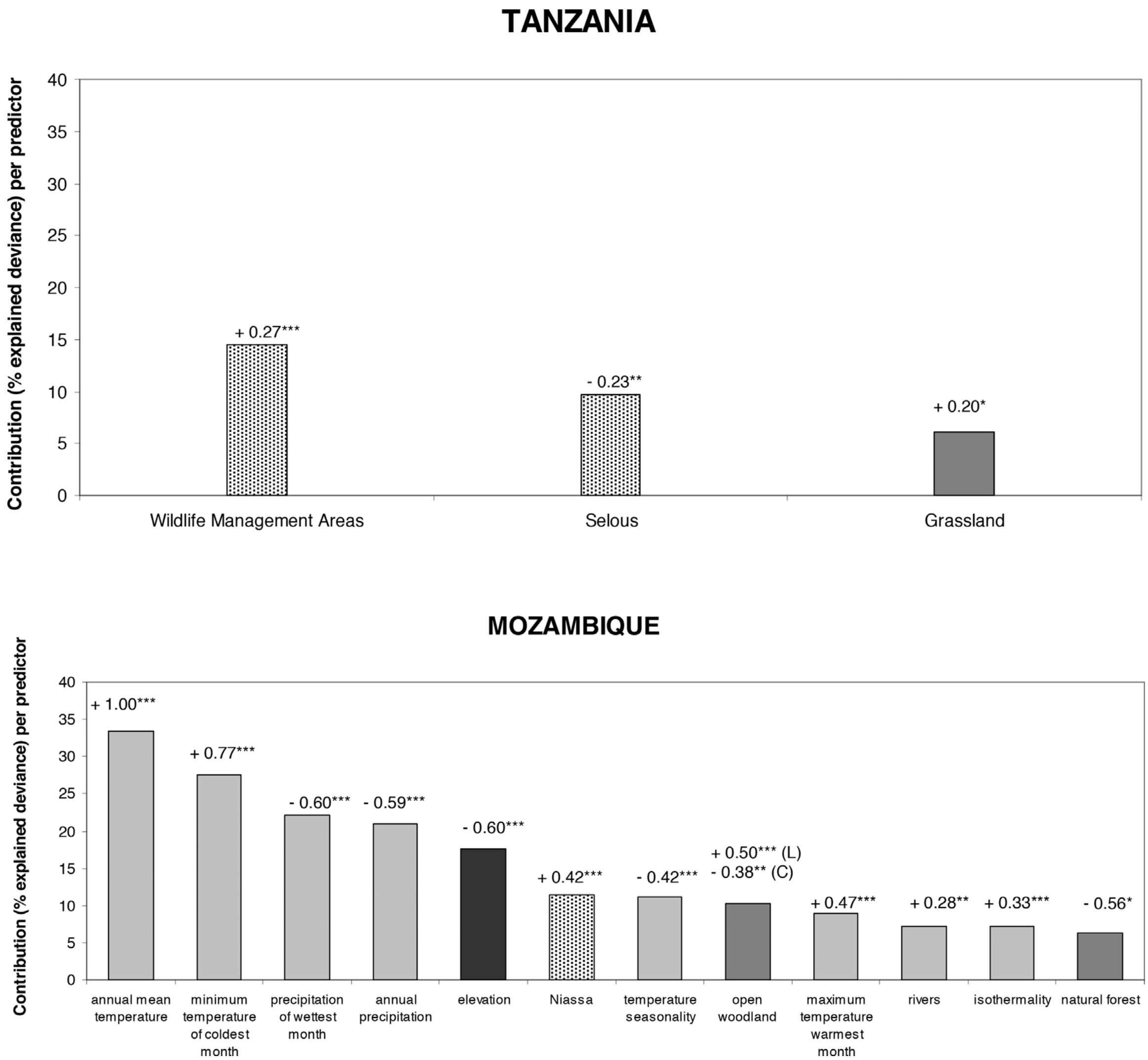

Fig. 2. Results of the Generalized Linear Models, produced by consecutively regressing each considered explanatory variable on the number of elephant carcasses, including the number of live elephants as a covariable. The regression coefficients of linear (L) and quadratic (C) terms of each variable are included, as well as their statistical significance measured as the Wald statistic (* $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$).% Dev is the percentage of total deviance explained by each variable. Only statistically significant variables accounting for more than 5% of total variability are showed; water availability and climatic variables are coloured in light grey, detectability in dark grey, accessibility in black and protected area management and tenure system are spotted.a.

(Moran's $I = 0.203$ and 0.167, $p = 0.005$).

In the case of Tanzania, three of the predictors were statistically significant and explained more than 5% of total variability in both models, i.e. including and excluding elephants as a covariable. These were grassland area, Selous and Wildlife Management Areas, with the latter having the highest predictive capacity (Fig. 2). Grassland biomes and community-managed protected areas were positively associated with the number of elephant carcasses. The model selected by AIC eliminated the Selous Game Reserve, with the two remaining variables explaining 19.45% of total deviance. Grassland and Wildlife Management Areas remain also significant when live elephants were not included as a covariable, accounting for 19.41% of the explained deviance. In this case the residuals of both models did not show statistically significant spatial autocorrelation values at any lag distance.

4. Discussion

4.1. Biophysical determinants

Our analysis suggests that the warmest sites with lowest rainfall are where the likelihood of finding elephant carcasses is highest. These sites are normally the lowest elevation areas in the eastern part of the landscape. Our results also indicate that fewer elephant carcasses are observed in areas at higher elevations, which are less accessible. In Northeast Mozambique, most of the lowland areas are drier and hotter areas with seasonal rivers that dry up during the dry season, forcing elephants to aggregate at the few remaining available sources of water, where they are more easily hunted (Sibanda et al., 2016). In addition, the drying of seasonal rivers allows increased accessibility to poachers and facilitates transporting tusks from remote regions. These areas are also mostly covered by open vegetation (Booth & Dunham, 2016; Kahindi et al., 2010), which predicts the number of elephant carcasses in Mozambique. These predictors are also good proxies of the detectability of poaching, and our results show fewer elephant carcasses in forested areas. Carcasses are more difficult observed in forested areas by aerial censuses and poachers presumably have as well greater freedom of action without been detected (Burn et al., 2011).

4.2. Management of protected areas and tenure systems

In Mozambique, Niassa Reserve (NR) has a strong positive correlation with the number of elephant carcasses. Evidence from other savannah and woodland habitats in Africa shows more elephant carcasses are observed in remote sites, with infrequent patrolling and weak management effectiveness (Kahindi et al., 2010). This would also explain results in NR, which was managed by a partnership between the State (51%) and private tourist investors (49%, Investimentos Niassa, S.A.R.L.) from 1998 until 2012. In this period only 100 dedicated rangers were available to cover the 4.2 million hectares of the reserve. From 2012, a special unit of rangers supported by security forces was created with the aim of stopping poaching (J. Perez, *personal communication* on 25th of February 2013).

Although management effectiveness, mainly linked to patrolling and law enforcement capacity, has been broadly documented as a critical factor related to the illegal killing of elephants elsewhere (Martin 2010; Stokes et al., 2010; Watson, Dudley, Segan, & Hockings, 2014), evidence from other case studies also suggests that community engagement and collaboration with authorities managing adjacent protected areas are important in ensuring compliance and generating local support for conservation in protected areas and hence for conservation outcomes (Challender & MacMillan, 2014; Duffy, St. John, Büscher, & Brockington, 2015; Phelps, Shepherd, Reeve, Niissalo, & Webb, 2014). Community-managed protected sites (WMA) in Tanzania have a strong positive relation to the number of elephant carcasses. Implementation of these reserves has been considered top-down, reducing community support for conservation actions (Barua, Bhagwat, & Jadhav, 2013; Brooks, Waylen, & Mulder, 2012; Songorwa, 1999). Furthermore, increasing levels of human-wildlife conflicts and agricultural opportunity costs experienced by poor communities has been reported as factors explaining non-compliance with conservation regulations (Kangalawe & Noe, 2012; Kideghesho, 2016). For instance, in Tunduru, Mbarangandu (SNWPC) and Liwale (East border of SGR) WMA's, information from a household survey (n = 962) in 2014–2015 indicates significantly higher incidences of wildlife crop damage compared to propensity score matched control villages away from the WMA, with respectively 86, 65 and 84% of households experiencing loss of crops within the past 12 months in the three WMAs (unpublished results). In addition, the lack of tangible benefits from the WMA to communities provides extremely limited individual incentives for conservation (Kyando, Ikanda, & Røskaft, 2017). The main income generating option for the WMAs in Tanzania is leasing of concessions to private companies for trophy hunting. This has generated between $6000 and 11,000 per year in the three mentioned WMAs from 2012 (World Wildlife Fund, 2014), equivalent to around 0.10–0.75 USD per capita annually. Finally, experience from across Tanzania indicates frequent problems of elite capture, where some community members capture most of the benefits of the WMA and obtain higher well-being improvements (unpublished results). Similar incidences has been shown to perpetuate poaching by hunters that are dissatisfied with the individual level of benefits and act in defiance of the rules of the community based organization they perceive as corrupt and acting out of self-interest (Nielsen & Meilby, 2013).

4.3. Differences in predictability of killing of elephants between Mozambique and Tanzania

We find difference between the relative predictability of the number of elephant carcasses found in Mozambique ($\approx$50% of deviance explained by the best model) compared to Tanzania ($\approx$20%). The difference in autocorrelation of residuals indicates that this difference in the explanatory ability between datasets cannot be attributed to a common unaccounted spatially structured variable. Rather the predictors are responsible for them. The number of elephant carcasses in Mozambique is mainly determined by climatic and ecological variables, whereas non-environmental predictors appear to be most important in Tanzania. As the average number of elephant carcasses per area unit is similar in both countries (Tables 1 and 2), but there is a smaller number of live elephants recorded in Tanzania (average of 0.4 per grid cell, Table 1) compared to Mozambique (2.6 per grid cell, Table 1) (see also carcass ratios in Table 2), we suspect that poachers in Tanzania hunt elephants at any available site independently of their accessibility and biophysical caracteristics, while poachers in Mozambique may select the most favourable areas for killing elephants. This interpretation of our results suggests limitations in the effectiveness of the current strategy to safeguard elephant populations in both countries. It also suggest the importance of establishing urgent conservation management actions to deal with the high hunting pressure on the remaining elephants in southern Tanzania, enganging communities, managing human elephant conflicts and addressing elite capture in WMAs (Caro & Davenport, 2015). In Mozambique, increasing the number and capacity of staff and securing the budget, as well as improving patrolling efforts could contribute to limiting the actions of illegal hunters whitin the NR (White, 2014).

4.4. Sources of bias

There are various sources of bias underlying the analysis, which should be taken into account in the practical application of the results. First, we do not know which of the elephant carcasses have been illegally killed or died naturally and it is possible that the ecological determinants explain locations of higher natural elephant mortality. However, no droughts or diseases were reported in the landscape during the timeframe analysed (Booth & Dunham, 2016; Kyando, 2014), supporting that our results reflect predictors of illegal killing of elephants. Second, management effectiveness of protected areas is a critical factor explaining the intensity of illegal killing of elephants. Unfortunately, we did not have actual patrolling data or detailed data on diverse aspects of management effectiveness to include in the models. We encourage further analysis assessing the association between the illegal killing of elephants and patrolling effort in this landscape. Third, although management effectiveness of protected areas has been pointed out as an important factor determinig the level of elephant poaching in other studies (Ihwagi et al., 2015; Kahindi et al., 2010), our results could reflect the fact that most of our grid cells correspond to protected areas. Thus, additional analyses regarding elephant poaching on protected land versus non-protected land is needed to fully assess the efectivenes of the protected areas in conserving elephants. Elephant poaching is a complex issue and more detailed analysis of interactions and trade-offs between drivers, as well as further analysis comparing drivers at different spatial scales, could increase the deviance explained by the models and support additional informed decision-making about appropriate actions to tackle elephant poaching in the Ruvuma landscape.

5. Conclusions and conservation implications

This study disentangles drivers of killing of elephants in the Ruvuma landscape and can be used to devise targeted conservation and management strategies to reverse the current decline in elephant numbers. Specifically, places with low rainfall and high temperatures appear most suitable for killing elephants in Mozambique. There are still opportunities for further enhancement of the effectiveness of state-managed protected areas in Mozambique and community-managed sites in Tanzania to ensure the long-term protection and persistence of elephants in the Ruvuma landscape and potentially elsewhere.

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