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Drivers and facilitators of the illegal killing of elephants across 64 African sites

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Relevant information will appear here if provided.

Ethics

Does your article include research that required ethical approval or permits?:
This article does not present research with ethical considerations

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Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
Raw data, R statistical code, and instructions for reproducing this analysis are available online within the Harvard Dataverse repository: https://doi.org/10.7910/DVN/GNI6DS

Conflict of interest

I/We declare we have no competing interests

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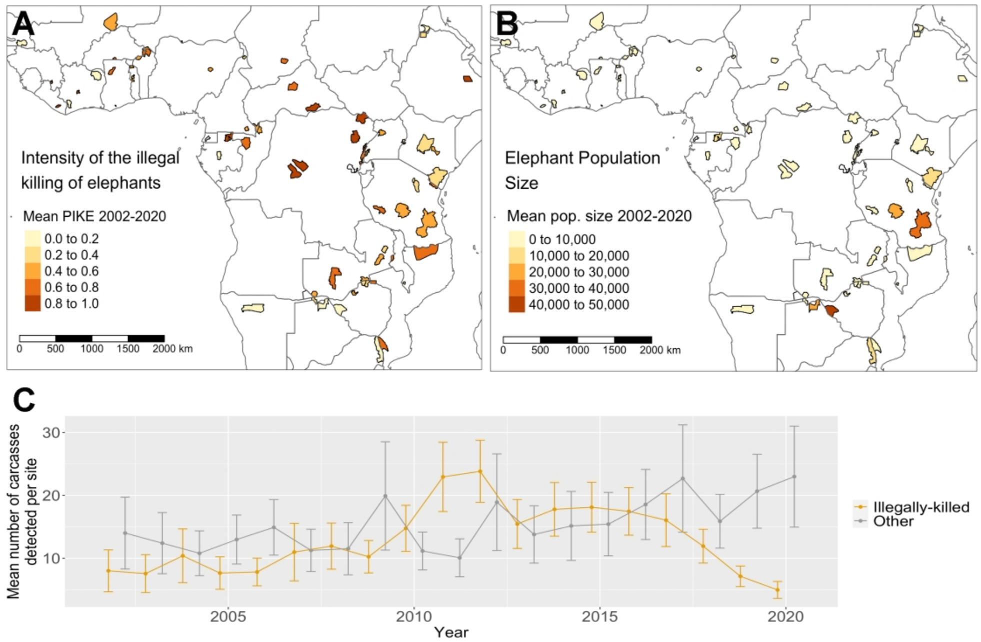

Figure 1. The 64 African sites contributing to the programme for Monitoring the Illegal Killing of Elephants (MIKE). (A) The intensity of the illegal killing of elephants at each site (measured as the Proportion of Illegally Killed Elephants; PIKE, see Methods). (B) Mean elephant population sizes from the African Elephant Database (4). (C) The mean number of carcasses detected per site (mostly by wildlife rangers) between 2002 and 2020.

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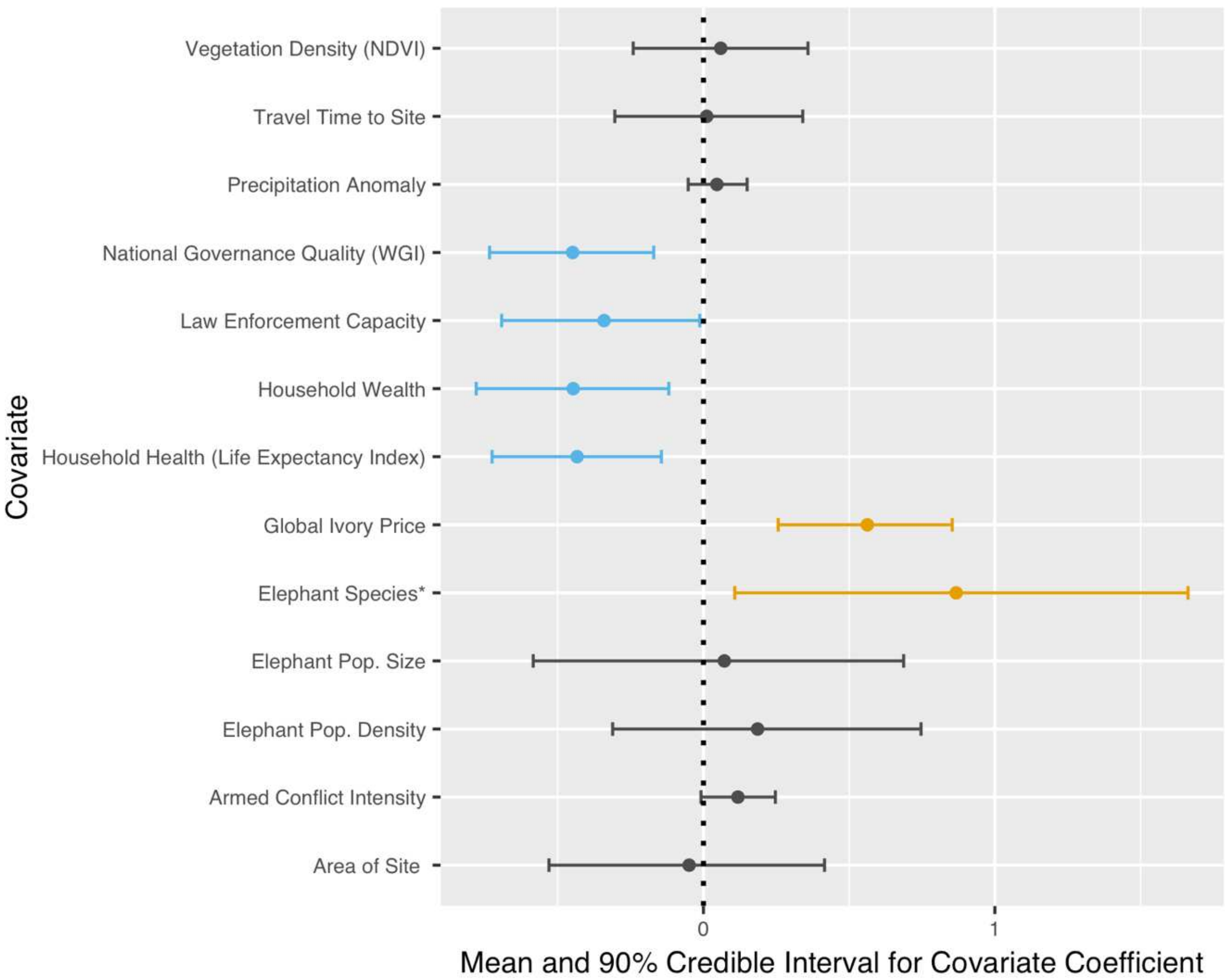
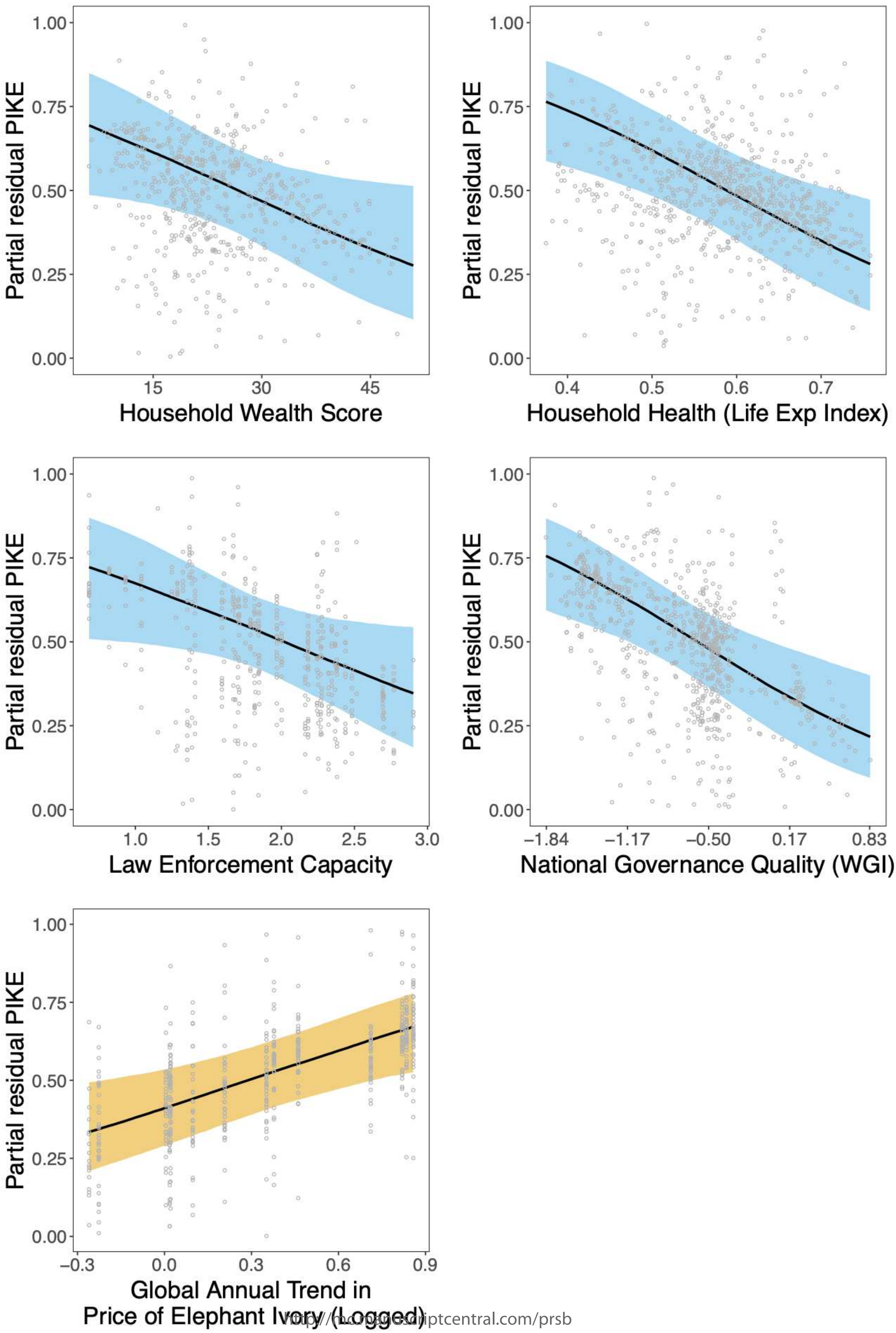
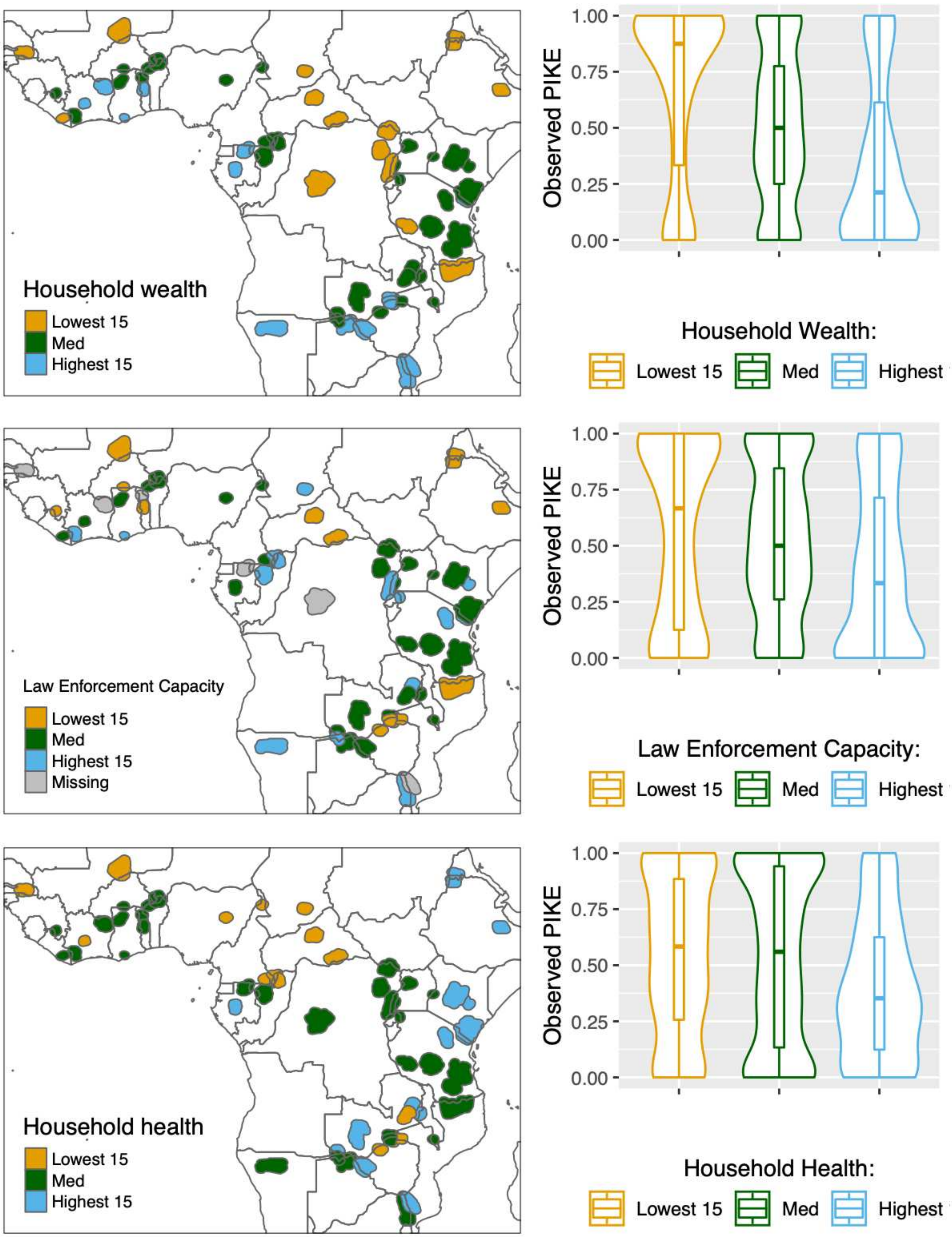

Vegetation Density (NDVI)
Travel Time to Site
Precipitation Anomaly
National Governance Quality (WGI)
Law Enforcement Capacity
Household Wealth
Household Health (Life Expectancy Index)
Global Ivory Price
Elephant Species*
Elephant Pop. Size
Elephant Pop. Density
Armed Conflict Intensity
Area of Site
Covariate
0
1
Mean and 90% Credible Interval for Covariate Coefficient


Partial residual PIKE
Household Wealth Score
Partial residual PIKE
Household Health (Life Exp Index)
Partial residual PIKE
Law Enforcement Capacity
Partial residual PIKE
National Governance Quality (WGI)
Partial residual PIKE
Global Annual Trend in
Price of Elephant Ivory (Logged)


Household wealth
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Observed PIKE
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Lowest 15
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Highest
Law Enforcement Capacity
Lowest 15
Med
Highest 15
Missing
Law Enforcement Capacity:
Lowest 15
Med
Highest
Household health
Lowest 15
Med
Highest 15
Household Health:
Lowest 15
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Highest

Drivers and facilitators of the illegal killing of elephants across 64 African sites

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Abstract

Ivory poaching continues to threaten African elephants. We (1) used criminology theory and literature evidence to generate hypotheses about factors that may drive, facilitate, or motivate poaching, (2) identified datasets representing these factors, and (3) tested those factors with strong hypotheses and sufficient data quality for empirical associations with poaching. We advance on previous analyses of correlates of elephant poaching by using additional poaching data and leveraging new datasets for previously untested explanatory variables. Using data on 10,286 illegally-killed elephants detected at 64 sites in 30 African countries (2002-2020), we found strong evidence to support the hypotheses that the illegal killing of elephants is associated with poor national governance, low law enforcement capacity, low household wealth and health, and global elephant ivory prices. Forest elephant populations suffered higher rates of illegal killing than savannah elephants. We found only weak evidence that armed conflicts may increase the illegal killing of elephants, and no evidence for effects of site accessibility, vegetation density, elephant population density, precipitation, or site area. Results suggest that addressing wider systemic challenges of human development, corruption, and consumer demand would help reduce poaching, corroborating broader work highlighting these more ultimate drivers of the global illegal wildlife trade.

Introduction

The illegal wildlife trade is one of the highest value illicit trade sectors globally, threatening both human well-being and biodiversity (Sas-Rolfes et al. 2019; Esmail et al. 2020). African elephant populations have experienced significant declines (~30%) since 2006 (Chase et al. 2016; Thouless et al. 2016), correlating with high rates of illegal killing (Wittemyer et al. 2014; Schlossberg et al. 2020a) and large seizures of trafficked ivory (Underwood et al. 2013; Wasser et al. 2015). This threat to a charismatic species results in lost tourism revenues for African states (Naidoo et al. 2016), dilutes the important ecosystem function of elephants (Robson et al. 2017) and results in both hunters and rangers losing their lives (Büscher & Ramutsindela 2016; Belecky et al. 2019). Conservation responses have involved a diversity of local and international interventions, from law enforcement and community engagement at the local level, to demand reduction and global ivory trade bans.

Our aim in this research was to help inform strategies to tackle elephant poaching by empirically identifying local to global factors that may drive or facilitate poaching across Africa. The Convention on the International Trade in Endangered Species of Fauna and Flora (CITES) established the Monitoring of the Illegal Killing of Elephants (MIKE) programme in 2002 to monitor rates of illegal elephant killing at over 90 sites in Africa and Asia (CITES Secretariat 2019; Fig. 1). MIKE monitors poaching levels and trends by analysing data associated with elephant carcasses detected at MIKE sites. According to MIKE protocols, illegal killing includes poaching to harvest ivory as well as mortality related to human-elephant conflict (though only ~3% of all carcass records are associated with conflict; CITES Secretariat 2022). Trends in illegal killing from multiple sites are aggregated to the sub-regional and continental levels to help inform international decisions on the ivory trade and elephant conservation at various inter-governmental wildlife trade forums (CITES Secretariat 2019). The intensity of illegal killing for each site and year is measured as the Proportion of Illegally Killed Elephants (PIKE; see Methods). By using PIKE as an index of relative poaching rates and by considering patterns across all populations, we seek to identify general drivers/facilitators of illegal killing across the continent. Our analysis does not, therefore, necessarily identify factors that may be important at a few sites where absolute numbers of illegally killed elephants may be high.

When seeking to identify factors associated with elephant poaching, it is essential to understand what drives the decisions of key actors in the system. It is important to explore factors that may help explain the full range of drivers and facilitators of illegal killing. Oyanedel et al. (*2020*) review two main approaches to studying crime and non-compliance with rules; the actor-based approach considers the motivations of individual people to comply or not, while opportunity-based approaches consider how the immediate environment/context may create opportunities for non-compliance. For example, poverty may act on the motivations of individuals to be complicit in illegal killing, while corrupt park officials or low law enforcement capacity may create the context that facilitates this killing. Poaching of high-value species like elephants and rhinoceros is driven primarily by criminal networks or syndicates as opposed to opportunistic subsistence hunters (Warchol 2004; Underwood et al. 2013; Douglas & Alie 2014; Titeca 2019). Why do these networks choose to operate in the countries and sites that they do, at the times and in the ways that they do? A second set of decision-makers are individuals who choose to join hunting operations on the ground, to be complicit with, or turn a blind eye to, illegal killing in their local areas. The connection between higher-level syndicates and local poachers is often fluid, with syndicates relying on middlemen to acquire ivory from a wide array of poachers (Wasser et al., 2022). We are interested in understanding what factors influence the decisions of both groups.

To address our research aim, we took a hypothesis-driven approach that involved four stages:

(1) First, we reviewed evidence from the literature to generate hypotheses about socio-economic, political, and environmental factors (or covariates) that may plausibly drive, facilitate, motivate, or hinder the illegal killing of elephants at different scales (from site-level to national to global).
(2) Second, for each covariate identified we reviewed available datasets and assessed how well they represented the factor of interest (for example, we assessed four alternative measures of wealth/poverty).
(3) Third, we ranked each covariate by both the plausibility of the hypotheses associated with it (strength of logic and evidence in the literature) and the quality of available datasets.
(4) Fourth, covariates with adequately high plausibility and data quality were tested for associations with annual data on the illegal killing of elephants from 64 African MIKE sites in 30 countries over 19 years (2002-2020; Fig. 1). This established the degree of support for each hypothesis in (1). We fitted a Bayesian hierarchical Generalised Linear Mixed Model to the poaching/covariate data, with site, year, site-year, and country random effects to fit the data structure. Model selection was performed using LASSO-regularisation (26). Regularisation and multiple random effects tend to reduce the effect sizes and precision of poorly supported covariates (Tibshirani 1996; Zuur et al. 2009a), helping ensure that only those covariates with strong empirical associations with the illegal killing of elephants were identified as important (see Methods).

We build on similar previous analyses of correlates of elephant poaching (Burn et al. 2011; Hauenstein et al. 2019) by taking advantage of several years of additional poaching data, data from several additional sites, as well as improved covariate datasets not previously tested (Table 1). This includes geo-referenced data on armed conflicts in the vicinity of monitored elephant populations (Sundberg & Melander 2013), internationally comparable wealth and development data recently constructed from long-term surveys of households adjacent to monitored sites (Smits & Steendijk 2015; Smits & Permanyer 2019), improved measures of site-level law enforcement capacity (updated MIKE assessments; see Supplementary Material S2), data on site accessibility (Weiss et al. 2018), and a newly collated global dataset on 3012 raw elephant ivory price samples (Do et al. 2021) as a proxy for ivory demand (Table 1). Furthermore, our extensive review of evidence to generate and interrogate specific hypotheses and associated data sources further advances previous work and helps us better scrutinise possible mechanisms underlying complex relationships, such as those between illegal killing and poverty or armed conflict.

Methods

MIKE sites and data on the illegal killing of elephants

Here we use 19 years (2002-2020) of annual elephant carcass data (collected mostly by wildlife rangers) from 64 protected sites in 30 African countries (Fig. 1). Levels of illegal killing are estimated for each site, each year, as the Proportion of Illegally Killed Elephants (PIKE): the number of illegally killed elephant carcasses detected as a proportion of all carcasses detected (including natural mortalities, management related deaths, and mortalities of unknown cause). Some sites were established more recently, and each site has a variable number of years of PIKE data (Fig. 1), so our final data set consisted of 780 site-year observations of PIKE. The PIKE index is subject to several biases (such as sensitivity to natural mortality variation and higher detectability of poached versus natural mortalities in different habitats), but also has several advantages such as being relatively robust to variation in patrol effort and elephant density (see https://citesmike.org/analysis for a full discussion). The index has also been profitably used in various published analyses (Burn et al. 2011; Hauenstein et al. 2019; Schlossberg et al. 2020a). Our rainfall anomaly covariate also partly controls for changes in drought-related natural mortality (Table 1).

Statistical model

To match the data structure, we used a Bayesian hierarchical Generalized Linear Mixed Model (GLMM) with a binomial error structure to determine which covariates had a strong empirical association with PIKE across sites, countries, and years. We used a PIKE-covariate model previously developed by Hauenstein et al. (2019) with the significant addition of a site-year random effect alongside the site, country, and year random effects. This error structure was chosen to represent the data structure, account for pseudo replication at the different levels, and ensure a more conservative interpretation of main effects. The site-year effect deals with pseudo-replication of multiple carcass observations within a site-year while also reducing the possibility of false positives for the main site-year effects like wealth and armed conflict (by reducing effect precision; Zuur et al. 2009b). The site-year effect also substantially improved model fit (Bayesian p-value test for goodness of fit; see below). Model selection was performed using LASSO regularization which penalizes overly complex models by shrinking covariate effects towards zero (Tibshirani 1996; Tredennick et al. 2021). Our model was conservative in that the multiple random effects and LASSO regularization ensured that a very strong empirical association between a particular covariate and PIKE is required for sufficient evidence of an effect.

We model PIKE for each site-year observation by treating the number of illegally killed carcasses detected ($N.illegal_{sy}$) at each site (s) and year (y) as a binomial random variable:

$$N.illegal_{sy} \sim Binomial\ (PIKE_{sy}, N.total_{sy})$$

where $N.total_{sy}$ is the total number of carcasses detected at each site and year. We then model PIKE as a function of the 11 covariates and normally distributed random intercepts ($\mathcal{N}$) for site, site-year, year, and country:

$$logit(PIKE_{sy}) = \beta_0 + \sum_{k=1}^{6} \beta_k X_{sy} + \beta_7 Gov_{country \ni s,\ y} + \mathcal{N}(\mu_{site}, \sigma_{site}) + \mathcal{N}(\mu_{year}, \sigma_{year}) + \mathcal{N}(0, \sigma_{site-year}) + \mathcal{N}(0, \sigma_{country})$$

Where $Gov_{country \ni s,\ y}$ represents the governance quality of the country that contains site *s*, in the year *y*. X_{sy} represents the six site-by-year covariates (Table 1). We model the hierarchical level means for the site random intercept (μ_{site}) as a function of the site covariates that had only one measurement across all years (area of site, law enforcement capacity, and travel time to the nearest city):

$$\mu_{site} = \beta_9 Area_{site} + \beta_{10} LawEnf_{site} + \beta_{11} TravelTime_{site}$$

Finally, we model the hierarchical level mean for the year random intercept as a function of the global trend in the price of elephant ivory:

$$\mu_{year} = \beta_{12} IvoryPrice_{year}$$

We fitted the model using Markov chain Monte Carlo (MCMC) sampling, implemented using the software JAGS (Plummer 2003), integrated with the R package R2jags (Su & Yajima 2015). We found that 100 000 MCMC iterations with a 50 000 burn in was sufficient to ensure convergence, which was confirmed by visual examination of chain-iteration trace plots as well as Gelman Rubin potential scale reduction factor ($\hat{R}$) values of less than 1.1. We used gamma (1,1) priors for the standard deviations of the site, year, site-year, and country random intercepts, and Laplace priors on the covariate coefficients to achieve LASSO regularization (see Hauenstein et al. 2019 for details). All covariates were Z-transformed to ensure the same scale.

To test model fit, we used the model equation to simulate response (PIKE) data and then compared discrepancy measures (observed versus predicted) for both the empirical and simulated data using Bayesian p-values (Kéry & Royle 2020). Most covariates had complete data, however the trend in ivory price was missing data for the years 2016-2020, rainfall anomaly data were missing for the year 2020, governance data were not available for 2020, and law enforcement capacity and community participation data were missing for 6 of the 64 sites. We imputed missing data for these covariates using draws from a standard normal distribution, noting that covariates were standardized to this scale (van Buuren & Groothuis-Oudshoorn 2011). Finally, the 'shrinkage' effect helped ensure that estimated covariate effects were influenced more by sites with more reliable estimates of PIKE (by virtue of larger carcass sample sizes) (Burn et al. 2011).

To test model predictive performance, we split the raw data into training and testing sets, using a 75% to 25% random split. We then compared observed PIKE values to median PIKE estimates for the testing set, based on 5000 MCMC samples of the model fitted to the training data only, and calculated R^2 values for the correlation. Then, to account for spatial dependencies in the data (Roberts et al. 2016), we tested predictive performance by excluding 15 randomly selected MIKE sites (~25% of all observations) for the training set and then followed the same procedures as above for testing. Finally, to estimate the proportion of spatial, temporal, and spatio-temporal variation in PIKE accounted for by the covariates (fixed effects), we compared the size of the variance components of the random effects in the full model to a model with only the random effects (a proportional change in variance analysis following equation 31 in Nakagawa & Schielzeth 2013).

Due to correlations between the wealth and development covariates (Supplementary Material Fig. S1), we constructed several supplementary models for these covariates (see Results). Also, the literature suggests that the effects of armed conflict (disruptions to law enforcement, socio-economic change, corruption, and lawlessness) may not be immediate (Douglas & Alie 2014; Gaynor et al. 2016) . Therefore, we present models with conflict intensity measured for each site as the total battle deaths in the current year, over two years (the current year and previous year), three years (the current and previous two years), and five years (the current and previous four years).

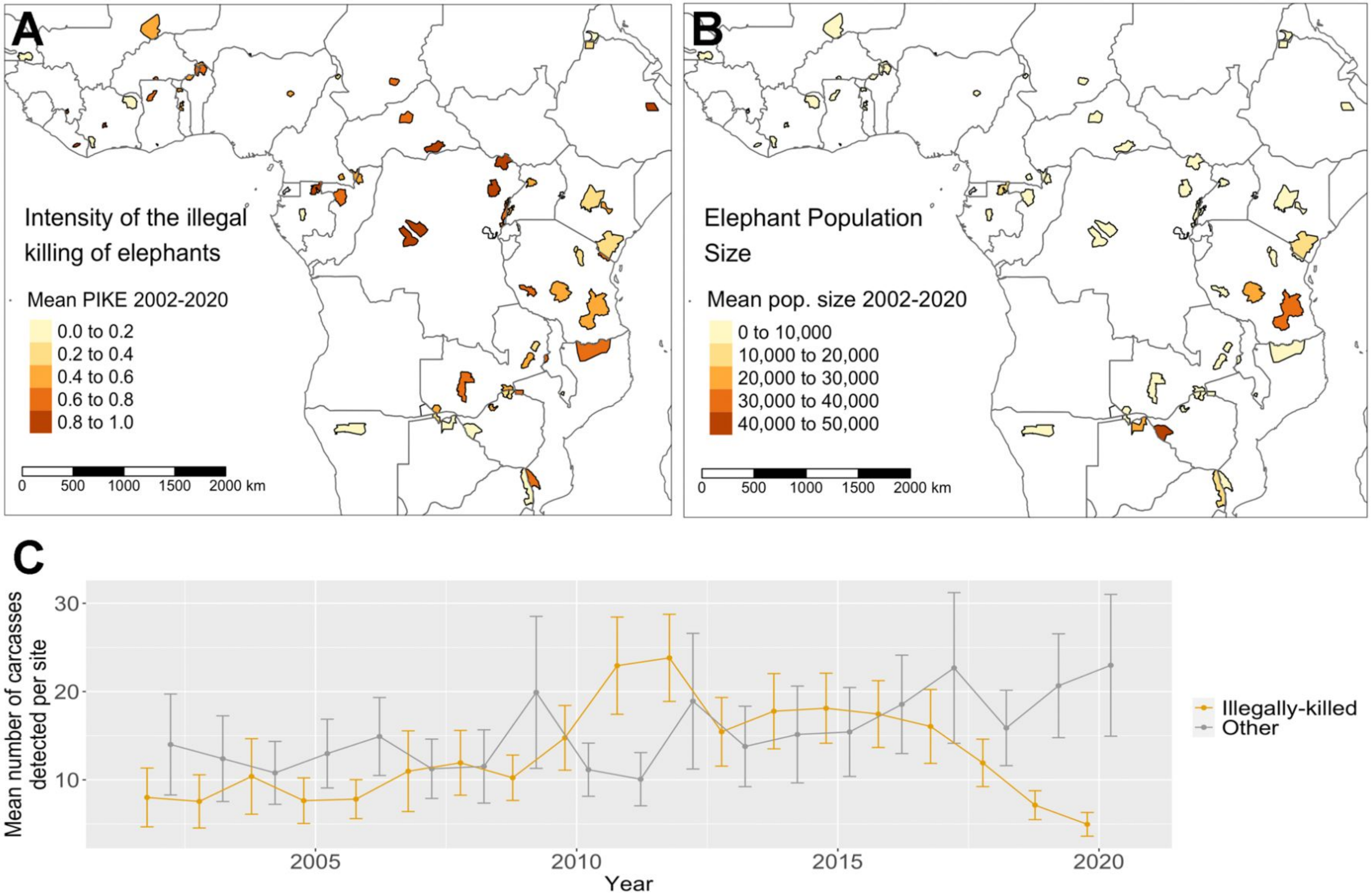

Figure 1. The 64 African sites contributing to the programme for Monitoring the Illegal Killing of Elephants (MIKE). (A) The intensity of the illegal killing of elephants at each site (measured as the Proportion of Illegally Killed Elephants; PIKE, see Methods). (B) Mean elephant population sizes from the African Elephant Database (4). (C) The mean number of carcasses detected per site (mostly by wildlife rangers) between 2002 and 2020.

Table 1: The 12 factors/covariates (out of 20 reviewed) identified as having sufficient plausibility and data quality for testing for empirical associations with the illegal killing of elephants (PIKE; Proportion of Illegally Killed Elephants). Evidence for the hypothesis underlying each covariate, the candidate data sources reviewed for each covariate (e.g., four measures of wealth/poverty were considered), details on how data were extracted to sites/years/countries, and information on the eight excluded covariates are included in Supplementary Materials section S2 and S3. All correlations between covariates were r<0.6, except wealth and development which were modelled separately (see Methods and Supplementary Material Fig. S1)

Factor (plus proxy data and link)	**Hypothesis for how factor might influence poaching (PIKE)**	**Scale**
Drivers: factors hypothesised to drive illegal killing		
Ivory demand (Annual trend in global elephant ivory price)	Ivory demand may incentivise illegal killing. If demand increases (e.g., due to increased disposable income) and supply cannot meet demand, ivory price may increase and further incentivise illegal killing*.	Global-by-year
Facilitators: factors hypothesised to facilitate illegal killing and ivory trafficking		
Governance quality (World Governance Indicators)	Poor governance may facilitate illegal killing at the site level and the trafficking of ivory within and out of source countries as officials (park managers and border staff) accept bribes or turn a blind eye.	Country-by-year
Accessibility (Travel time from site to the nearest city)	Sites that are easier for syndicates and hunters to access, and from which ivory can be easily and quickly transported, may experience higher levels of illegal killing.	Site
Accessibility (Size/area of site)	Smaller sites have a higher edge/area ratio making it easier for hunters to access and leave quickly, while larger sites may be difficult to police	Site
Armed conflict (Total battle deaths per site-year derived from the *Uppsala* Conflict Geo Dataset)	Armed conflicts lead to institutional and socioeconomic changes that may facilitate illegal killing, or ivory may be used to fund the operations of warring militias.	Site-by-year
Elephant populations (Size and density)	Sites with larger or more dense elephant populations may be more attractive targets to hunters and syndicates due to higher encounter rates.	Site-by-year
Motivators: factors hypothesised to increase or decrease the motivation to poach elephants		
Household wealth (Sub-national Household Wealth)	The socio-economic conditions of poverty may compel individuals to engage with illegal killing to earn income to meet basic needs, in the absence of viable alternatives.	Site-by-year
Human development (Sub-national Human Development Index - income/health/education)	Less developed communities (not necessarily in poverty) may be more likely to participate in or facilitate illegal killing to earn extra income or through turning a blind eye.	Site-by-year
Law enforcement capacity (MIKE LE Capacity Assessments)	Enhanced law enforcement allows for more committed and effective rangers, more effective apprehension and deterrence, and may thus result in lower illegal killing.	Site
Others: Confounding factors which are unrelated to illegal killing but that may influence the PIKE index		
Precipitation/drought (Rainfall anomaly from CHIRPS data)	PIKE is sensitive to natural mortality rates, so factors explaining natural mortality variation (e.g., rainfall/drought) may explain variation in PIKE both among sites and over time within a site.	Site-by-year
Carcass detectability (Vegetation density from MODIS NDVI)	Densely vegetated sites may have higher PIKE due to low detectability of natural mortalities which do not have the same detection cues as illegally killed carcasses (forest may also help conceal hunters).	Site-by-year
Elephant species (forest or savannah) (delineation from IUCN Red List assessments)	For various difficult to measure reasons, previous evidence suggests forest elephants may suffer higher poaching rates than savannah elephants, which may explain variation in the PIKE index across the continent.	Site (Population)
*We identified price as the best demand proxy, though price is dynamically determined by both supply and demand (See Supplementary Material S2 for a full discussion).		

Results

We identified 20 plausible covariates of the illegal killing of elephants, of which a final set of 12 covariates (those with adequately high plausibility and data quality) were tested in the statistical model to establish support for the hypotheses underlying their influence on the illegal killing of elephants (see Table 1). More detail on how each covariate considered in our analysis may relate to the decision-making of criminal syndicates is included in Supplementary Material S2.

We found evidence for negative associations between the illegal killing of elephants and each of national governance quality, site-level law enforcement capacity, and the wealth and health of households in the vicinity of MIKE sites (Bayesian GLMM 90% credible intervals for covariate coefficients do not include zero: Fig. 2). The credible interval for armed conflict intensity suggests that sites with more intense conflict (higher total battle deaths by site and year) tend to have higher rates of illegal killing, but the evidence is not strong (Fig. 2, 90% credible interval includes zero). We find no evidence for effects on the illegal killing of elephants of the precipitation anomaly, vegetation density, elephant population size and density, travel time from the site to the nearest city, or site area (km^2). We also found evidence for a positive association between the global annual trend in the price of elephant ivory (based on 3012 raw ivory price samples; see Supplementary Material S2) and the temporal trend in the illegal killing of elephants as represented by PIKE (Fig. 2). Finally, we found evidence that forest elephant populations tended to suffer higher rates of illegal killing than savannah elephant populations (Fig. 2).

We also found a strong negative association between human development and the illegal killing of elephants (Supplementary Material Fig. S2), a strong negative association between the illegal killing of elephants and the health and income dimensions of subnational human development, and a positive association between illegal killing and the education dimension (see Supplementary Material Fig. S3). Focussing in on the best-supported site-level covariates, there are relatively consistent geographical patterns in the location of the top and bottom 15 sites for household wealth and health, but variation in law enforcement capacity is spread across the continent (Fig. 4).

We explored the effect of armed conflict intensity further, to test whether the time-period over which it is measured affects associations. Conflict aggregated over the current and previous year had a strong positive association with the illegal killing of elephants (90% credible interval excludes zero: Supplementary Material Fig. S4). However, we found a weaker association with conflict in the current year alone, and no evidence for an effect of conflict intensity when measured over three- and five-year periods (Fig. S4).

Model predictive capacity was adequate to high, with R^2 of 0.36 for prediction of PIKE at 15 excluded sites (90% CI 0.07-0.51) and R^2 of 0.73 (90% CI 0.62-0.81) for a random test-train split (see Methods). Bayesian p-values >0.40 (see Methods) confirmed model fit for the main and supplementary models, as did a plot of observed versus predicted PIKE values (Supplementary Material Fig. S5). The variance components of the site, year, site-year, and country random effects in a random-effects-only model did not reduce significantly when the covariates were added in the full model (Supplementary Material Fig. S6). This indicates that the covariates left a large amount of unexplained variation in the illegal killing of elephants, though covariates were better at explaining spatial versus temporal variation (larger declines in the variance components for the spatial random effects; Fig. S6). The lambda parameter for the LASSO-regularisation in the main model was large (1.92, 90% credible interval: 1.26-2.64) indicating relatively high shrinkage of covariate effects towards zero (suggesting strong evidence for observed covariate effects).

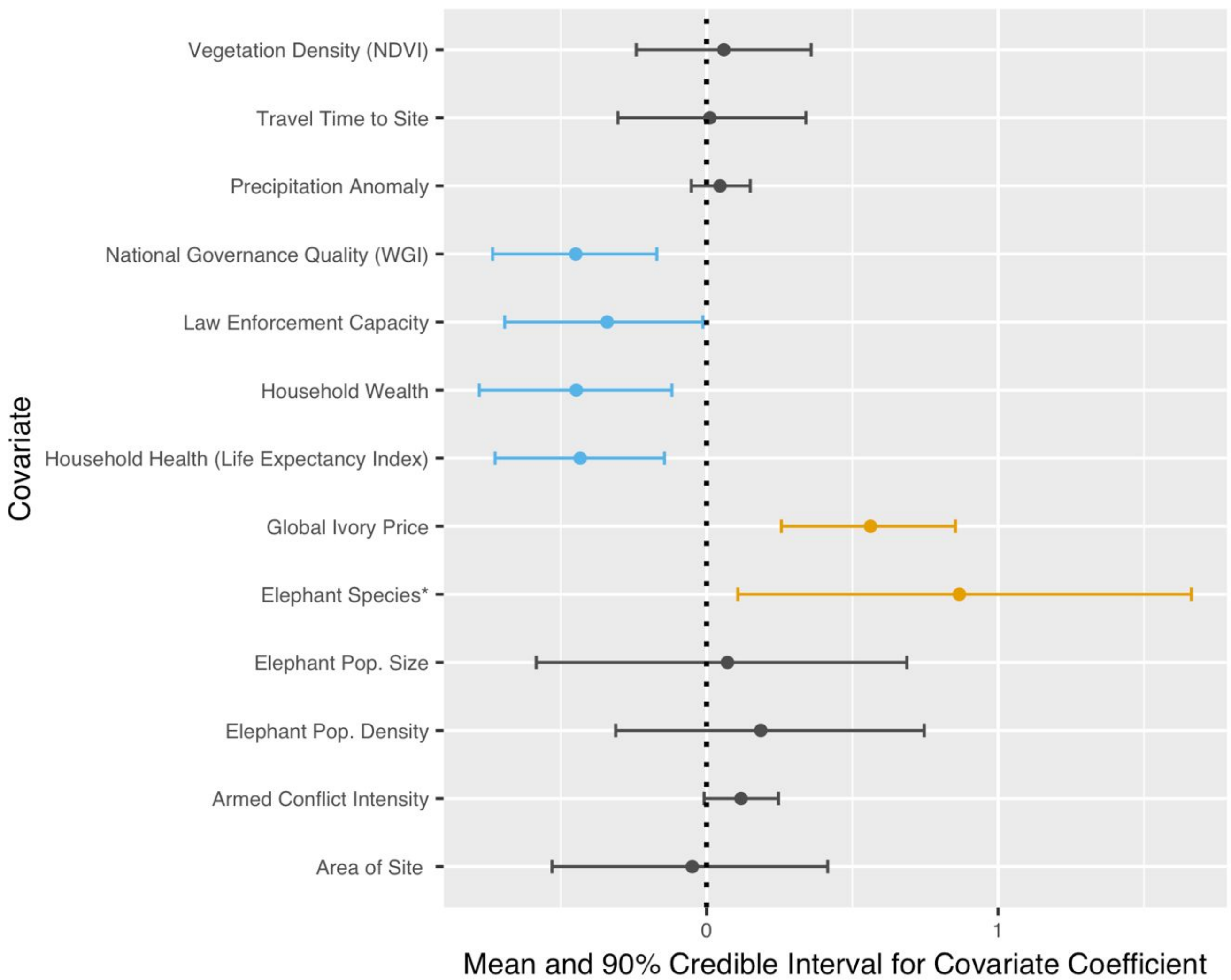

Figure 2. The effect of tested covariates on the illegal killing of elephants (PIKE), based on the LASSO-regulated Bayesian Generalised Linear Mixed Model. Blue lines (coefficient values <0) represent covariates with strong evidence for a negative effect (illegal killing tends to decrease as the covariate increases), while orange represents a strong positive effect. Points and bars represent mean and 90% credible intervals for covariate coefficients (5000 MCMC posterior samples). Covariates were standardized so coefficient effect sizes are directly comparable. Elephant species was coded as 0 for sites with savannah elephant (*Loxodonta africana*) populations and 1 for those with forest elephant populations, so values greater than 0 represent higher estimated illegal killing for forest elephants.

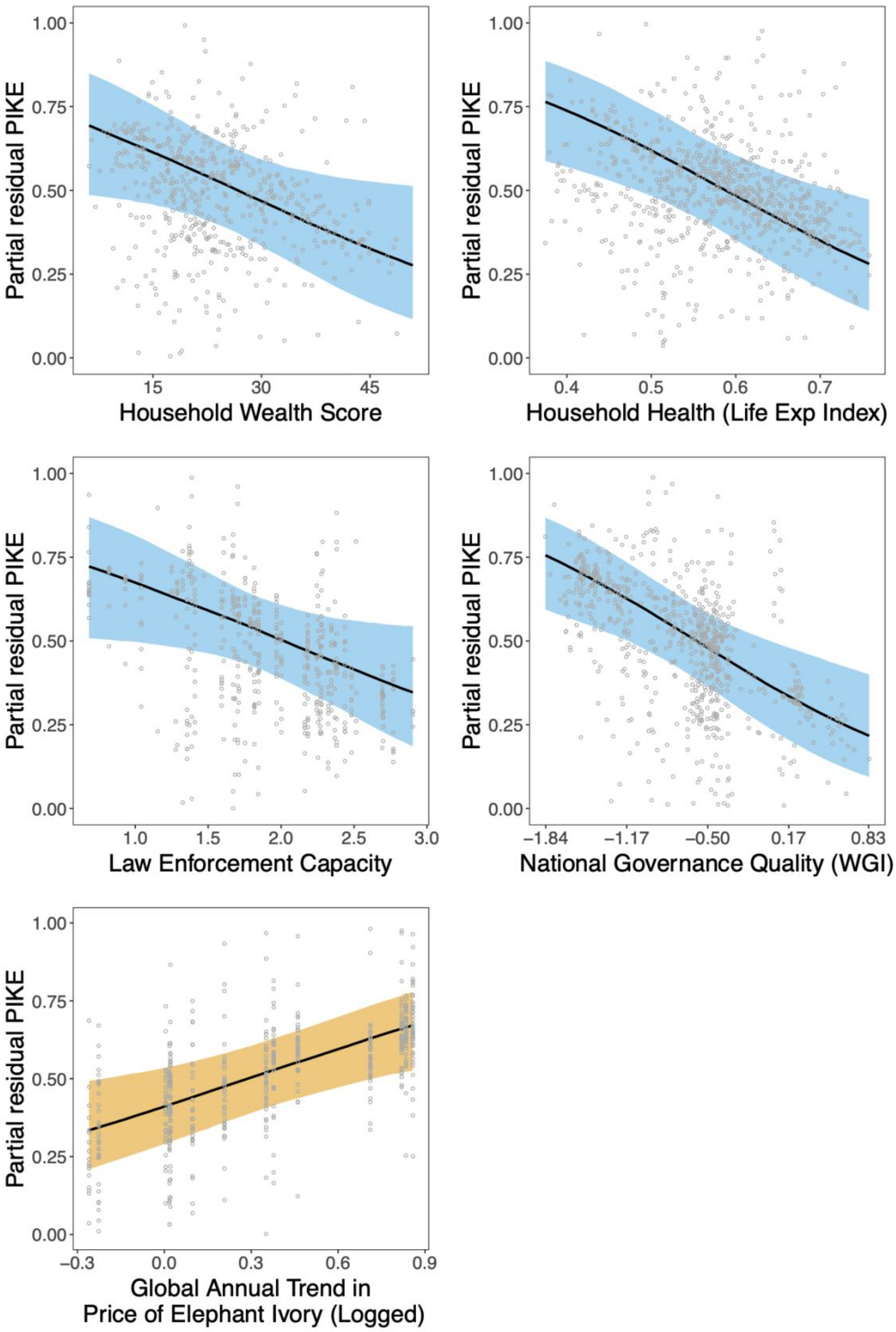

Figure 3. The estimated effect of well-supported covariates (90% credible interval for their effect excludes zero) on the proportion of illegally killed elephants (PIKE), as represented by conditional effects (partial residuals account for other covariates and random effects) from the LASSO-regularised Bayesian Generalised Linear Mixed Model. Bands represent 90% credible intervals from 5000 MCMC samples, and grey circles represent response-scale partial residuals. Orange = positive association, blue = negative associations. The units for ivory price represent median residuals from a regression of log-transformed price data against several control variables (see Do et al. 2021).

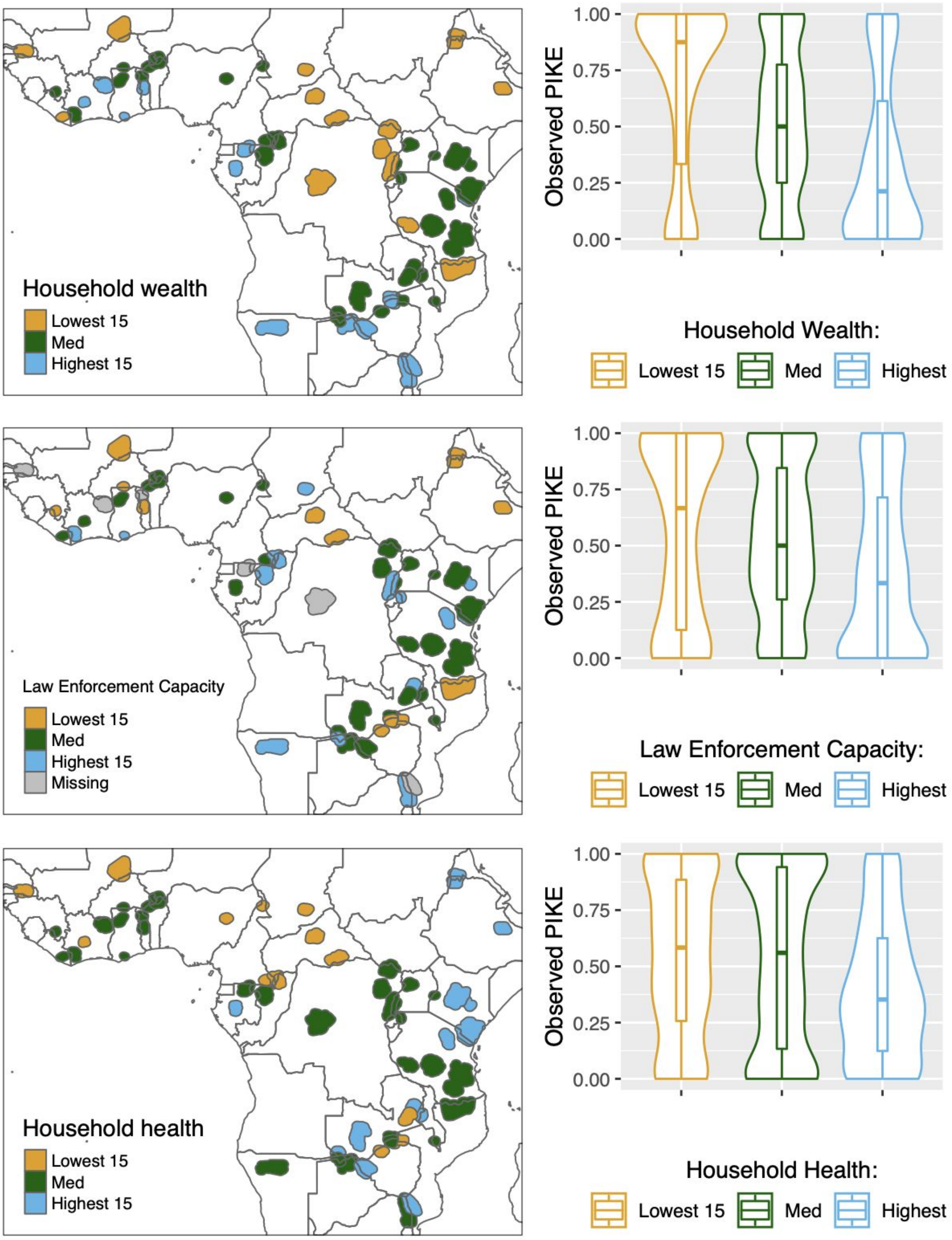

Figure 4. **Right panels:** Observed PIKE (Proportion of Illegally Killed Elephants) for different categories of MIKE sites ordered by the well-supported site-level covariates (Household Wealth, Household Health, and Law Enforcement Capacity), with categories representing the 15 MIKE sites with the highest and lowest mean values for each covariate. "Med" represents the 34 sites with intermediate values for each covariate (there were 64 sites with data in our sample). Observed PIKE is summarized using violin plots (showing data distribution kernels) and box plots (horizontal lines are median and upper/lower quartiles). **Left panels**: Maps of the location of the MIKE sites in each of the categories for each covariate.

Discussion

The unsustainable and illegal killing of elephants for ivory is ongoing across Africa (Wittemyer et al. 2014; Schlossberg et al. 2020a). We found evidence to support the hypotheses that strong national governance, higher levels of local human development (health and wealth), and stronger site-level law enforcement capacity help mitigate elephant poaching. We also found evidence consistent with the hypothesis that demand-driven increases in ivory price may lead to greater incentives for illegal killing of elephants across Africa. Addressing these systemic drivers of poaching will require wider policies and interventions beyond the traditional remit of biodiversity conservation, such demand reduction in consumer countries, reforms to government institutions to promote greater accountability and transparency, and programmes to promote adequate access to educational, health, and economic opportunities where they are lacking. While such interventions are of course an enormous task and already at the forefront of the global Sustainable Development Goals, our results suggest they will have co-benefits for biodiversity conservation.

Hauenstein et al. (2019) found similar associations between Africa-wide elephant killing and poverty, corruption, and ivory price. However, we used a more direct and finer-scale measure of poverty (household wealth, rather than infant mortality rate), a more direct measure of ivory prices (global elephant ivory price compared to mammoth ivory prices), and data for 11 additional sites and three additional years. We also used a more comprehensive measure of law enforcement capacity than Hauenstein et al. (see Supplementary Material S2) and found stronger evidence for a mitigating effect on illegal killing. In another similar analysis, Schlossberg et al. (2020b) did not find correlations between elephant mortality and human national human development or governance, although they acknowledge lower statistical power (they focussed on savannah elephants in 17 countries while we focus on both savannah and forest elephants across 30 countries). We considered using Schlossberg et al's (2020b) measure of poverty (the Night Lights Poverty Index), but most MIKE sites are in rural areas so there is little contrast in light intensity among sites. Our household wealth dataset is based on a local, direct, and internationally comparable metric of material well-being (Smits & Steendijk 2015) and had greater contrast among sites.

The health dimension of subnational human development that we used is based on the under-5 mortality rate (Smits & Permanyer 2019), so the observed positive association with PIKE accords with Hauenstein et al. (2019) who found that PIKE was positively associated with infant mortality rate. However, our household wealth and health (infant mortality) covariates were not strongly correlated, and both had an effect, suggesting that wealth levels affect poaching over and above the health effects observed here and by Hauenstein et al. (2019). Thus, our results provide more conclusive evidence that illegal elephant killing is related to local poverty.

Our observed wealth effect provides support for the hypothesis that local socio-economic deprivation may increase the likelihood of elephants being illegally killed. One interpretation might be that in areas of economic deprivation, local residents participate in illegal killing to meet their basic needs or earn extra income, in the absence of viable alternatives. Another interpretation might be that criminal ivory syndicates seeking to recruit local hunters target these areas because they are able to operate more effectively there (for a range of possible reasons). Previous work points to exceedingly high levels of illegal killing in central Africa and the northern Mozambique southern Tanzania landscape (Maisels et al. 2013; Wasser et al. 2015), which may explain our results, in that MIKE sites in these regions had amongst the lowest household wealth scores (Fig. 4). Wealth scores near all MIKE sites were low by international standards (<45 on a 0-100 scale; Smits & Steendijk 2015), yet we still found that PIKE was higher for areas in more extreme poverty. This contrasts with previous ethnographic work suggesting that individuals involved in illegal killing of high-value species like rhinoceros and elephant are often not in poverty (Hübschle 2017; Paudel et al. 2020). The positive association between illegal killing and the education dimension of the subnational Human Development Index accords with some anecdotal evidence from the Serengeti and Katavi ecosystems in Tanzania where poachers were found to be generally well-educated (which may facilitate selection by syndicates). However, causal hypotheses need deep understanding through more focussed site-level research before they are accepted as the reason behind observed associations (Duffy et al. 2016).

Market demand for wildlife products is one of the most well-evidenced factors driving the global illegal wildlife trade (Wilkie et al. 2005; Sas-Rolfes et al. 2019). The positive ivory price effect we observed supports the hypothesis that demand-driven increases in ivory price may lead to greater incentives for illegal killing, and accords with previous work (Wittemyer et al. 2014; Hauenstein et al. 2019). While price is not a direct measure of demand, and there may be multiple mechanisms behind a positive price-PIKE relationship, we considered price to be the most robust available proxy for ivory demand (see Supplementary Material S2 for a full discussion). However, the relationship between ivory price and illegal killing may be reciprocal (price affects motivations to supply ivory and supply affects price) and stockpiling and speculative trading in ivory are known to occur. Notably, a comprehensive recent analysis by Do et al. (2021) of associations between a proxy ("instrumental variable") for ivory price and PIKE found an inelastic relationship, whereby PIKE increased less-than-proportionately as price increased (Do et al. 2021). They used gold price as their instrumental variable to control for possible endogeneity (whereby ivory price is correlated with other unmeasured drivers of illegal killing). However, low elasticity between price and PIKE does not necessarily imply no relationship, but rather that the effect is small in the observed data range. Given the close correlation Do et al. (2021) found between ivory and gold prices, it is possible that our positive ivory price effect may be due to geopolitical shifts in the global economy (as also reflected in gold prices) rather than factors specific to the ivory market.

Our results provide support for the hypothesis that enhanced law enforcement capacity reduces the illegal killing of elephants (which may operate through apprehension or deterrence of offenders). Criminal syndicates are more likely to target areas where the risk of apprehension is lower (Oyanedel et al. 2020). Similar evidence was found in studies in Tanzania, Zambia, and Malawi (Jachmann & Billiouw 1997; Hilborn et al. 2006; Moore et al. 2018). Although we selected our law enforcement covariate as the most robust of several considered (Supplementary Material S2), it does not account for changes in law enforcement capacity over time and the tendency to under- or overestimate law enforcement capacity may vary by site according to personnel (although experienced personnel provided the assessments). Finally, it is also possible that sites with higher law enforcement and patrolling capacity detect a higher proportion of available natural mortalities, which would lead to lower PIKE scores.

The link between corruption and organised is well established in the literature (Buscaglia and van Dijk 2003). There is growing evidence that poor governance may negatively affect various aspects of biodiversity protection (Smith et al. 2003; Wright et al. 2007; Sundström 2016). We observed governance quality to be strongly and negatively associated with the illegal killing of elephants, as in previous analyses of similar data (Burn et al. 2011; Hauenstein et al. 2019). Our result also accords with Bennett (2015) who describes how bribery and corruption opportunities exist all along ivory supply and value chains, where officials may turn a blind eye to, or actively engage in, site-level illegal killing, and ivory trafficking within and between countries. van Uhm & Moreto (2018) found that wildlife poachers in Uganda, Russia, China and Morocco and traders may interact with government enforcement agents in a diversity of corrupt ways that can facilitate harvest, transport, processing, and export of wildlife products.

The strong elephant species effect suggests that forest elephants on average suffer higher rates of illegal killing compared to savanna elephants (Maisels et al. 2013, Wittemyer et al. 2014). The species effect is interesting in that it is over and above any effect due to differences between savannah and forest elephant populations in vegetation density, precipitation, population density, or any other effects already captured in other covariates. This may, however, represent a geographic region effect as the vast majority of forest elephant populations are in West and Central Africa while savannah populations mostly occupy East and Southern Africa. One possible explanation might be that natural mortalities tend to be harder to detect in forested environments, artificially inflating PIKE estimates. However, we would expect the vegetation density covariate to capture this effect. Maisels et al. (2013) highlight expanding infrastructure and encroachment into core elephant habitat as a key driver of forest elephant poaching. While the difference might be explained by demand for harder Forest elephant ivory for certain items such as name seals and musical instrument components in key consumer countries like Japan, this specific demand has largely declined since its peak in the 1970s and 1980s (Nishihara, 2012).

It is important to note that our analysis does not necessarily identify factors that have led to the largest absolute number illegally-killed elephants. It is possible that the factors driving large numbers of elephant killings at a handful of sites (such as observed for Selous and Rungwa/Ruaha in Tanzania around 2010-2013) may be different from the drivers/facilitators of illegal killing that are general across sites (as identified in our analysis). However, the goal of this paper is to find common patterns across the continent, rather than try and explain drivers of poaching at a few key 'hotspot' sites. Furthermore, genetic seizure analyses suggest poaching hotspots have shifted over the last 20 years, the period of our analysis (Wasser et al. 2015, Wasser & Gobush 2019). Our analysis across the whole continent and relatively long time period means we can learn something useful about tackling future hotspots.

Our results must be considered in the light of the limitations of the underlying datasets. MIKE data do not cover all Africa elephant populations and the PIKE index may be sensitive to natural mortality rates and differential detectability of illegally killed carcasses and natural mortalities (see Methods). Also, measuring factors like wealth and law enforcement accurately and in a comparable way over many sites and countries is difficult, and so covariate data may be biased and incomplete. Furthermore, many plausible drivers of the illegal killing of elephants cannot be adequately captured in a covariate. Global one-off events, or significant local events, may influence illegal killing but remain unmeasured. Finally, our analyses of proportional change in variance and model predictive performance suggests that much variation in PIKE remains unexplained by our covariates. This is perhaps not surprising given that illegal killing is influenced by a complexity of human decision-making within equally complex social and political institutions and networks affecting both offenders and law enforcement, which themselves interact with ecological factors and change over time. It is likely that there are many site, year, and country-level idiosyncrasies that cannot easily be captured in a covariate.

Notwithstanding these caveats, our approach of seeking a hypothesis-driven *a priori* understanding of the dynamics of illegal elephant killing and management, identifying the best available covariates to represent these dynamics, and using a tailored statistical modelling approach, helped us shed light on drivers and facilitators of illegal elephant killing across Africa. Overall, our results suggest that addressing system-level challenges at a variety of scales (poor governance, low human development, and ivory market dynamics) is essential to tackling illegal elephant killing, alongside the traditional focus on law enforcement. This corroborates broader work that has highlighted the importance of these more ultimate drivers of the global illegal wildlife trade (Duffy et al. 2016; Sas-Rolfes et al. 2019; Liew et al. 2021).

Supporting Information

[illegible]

Additional information is available in Supplementary Materials:.

Raw data, R statistical code, and instructions for reproducing this analysis are available online within the *Harvard Dataverse* repository: https://doi.org/10.7910/DVN/GNI6DS

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Drivers and facilitators of the illegal killing of elephants across 64 African sites

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Abstract

Ivory poaching continues to threaten African elephants. We (1) used criminology theory and literature evidence to generate hypotheses about factors that may drive, facilitate, or motivate poaching, (2) identified datasets representing these factors, and (3) tested those factors with strong hypotheses and sufficient data quality for empirical associations with poaching. We advance on previous analyses of correlates of elephant poaching by using additional poaching data and leveraging new datasets for previously untested explanatory variables. Using data on 10,286 illegally-killed elephants detected at 64 sites in 30 African countries (2002-2020), we found strong ~~strong~~ evidence to support the hypotheses that the illegal killing of elephants is associated with poor national governance, low law enforcement capacity, low household wealth and health, and global elephant ivory prices. Forest elephant populations ~~tended to~~ suffered higher rates of illegal killing than savannah elephants. We found only weak evidence that armed conflicts may increase the illegal killing of elephants, and no evidence for effects of site accessibility, vegetation density, elephant population density, precipitation, or site area~~/size~~. Results suggest that addressing wider systemic challenges of human development, corruption, and consumer demand would help reduce poaching, corroborating broader work highlighting these more ultimate drivers of the global illegal wildlife trade.

Introduction

The illegal wildlife trade is one of the highest value illicit trade sectors globally, threatening both human well-being and biodiversity (Sas-Rolfes et al. 2019; Esmail et al. 2020). African elephant populations have experienced significant declines (~30%) since 2006 (Chase et al. 2016; Thouless et al. 2016), correlating with high rates of illegal killing (Wittemyer et al. 2014; Schlossberg et al. 2020a) and large seizures of trafficked ivory (Underwood et al. 2013; Wasser et al. 2015). This threat to a charismatic species results in lost tourism revenues for African states (Naidoo et al. 2016), dilutes the important ecosystem function of elephants (Robson et al. 2017) and results in both hunters and rangers losing their lives (Büscher & Ramutsindela 2016; Belecky et al. 2019). Conservation responses have involved a diversity of local and international interventions, from law enforcement and community engagement at the local level, to demand reduction and global ivory trade bans.

Our aim in this research was to help inform strategies to tackle elephant poaching by empirically identifying local to global factors that may drive or facilitate poaching across Africa. The Convention on the International Trade in Endangered Species of Fauna and Flora (CITES) established the Monitoring of the Illegal Killing of Elephants (MIKE) programme in 2002 to monitor rates of illegal elephant killing at over 90 sites in Africa and Asia (CITES Secretariat 2019; Fig. 1). MIKE monitors poaching levels and trends by analysing data associated with elephant carcasses detected at MIKE sites. According to MIKE protocols, illegal killing includes poaching to harvest ivory as well as mortality related to human-elephant conflict (though only ~3% of all carcass records are associated with conflict; CITES Secretariat 2022). Trends in illegal killing from multiple sites are aggregated to the sub-regional and continental levels to help inform international decisions on the ivory trade and elephant conservation at various inter-governmental wildlife trade forums (CITES Secretariat 2019). The intensity of illegal killing for each site and year is measured as the Proportion of Illegally Killed Elephants (PIKE; see Methods). By using PIKE as an index of relative poaching rates and by considering patterns across all populations, we seek to identify general drivers/facilitators of illegal killing across the continent. Our analysis does not, therefore, necessarily identify factors that may be important at a few sites where absolute numbers of illegally killed elephants may be high.

When seeking to identify factors associated with elephant poaching, it is essential to understand what drives the decisions of key actors in the system. It is important to explore factors that may help explain the full range of drivers and facilitators of illegal killing. Oyanedel et al. (*2020*) review two main approaches to studying crime and non-compliance with rules; the actor-based approach considers the motivations of individual people to comply or not, while opportunity-based approaches consider how the immediate environment/context may create opportunities for non-compliance. For example, poverty may act on the motivations of individuals to be complicit in illegal killing, while corrupt park officials or low law enforcement capacity may create the context that facilitates this killing. Poaching of high-value species like elephants and rhinoceros is driven primarily by criminal networks or syndicates as opposed to opportunistic subsistence hunters (Warchol 2004; Underwood et al. 2013; Douglas & Alie 2014; Titeca 2019). Why do these networks choose to operate in the countries and sites that they do, at the times and in the ways that they do? A second set of decision-makers are individuals who choose to join hunting operations on the ground, to be complicit with, or turn a blind eye to, illegal killing in their local areas. The connection between higher-level syndicates and local poachers is often fluid, with syndicates relying on middlemen to acquire ivory from a wide array of poachers (Wasser et al., 2022). We are interested in understanding what factors influence the decisions of both groups.

To address our research aim, we took a hypothesis-driven approach that involved four stages:

(1) First, we reviewed evidence from the literature to generate hypotheses about socio-economic, political, and environmental factors (or covariates) that may plausibly drive, facilitate, motivate, or hinder the illegal killing of elephants at different scales (from site-level to national to global).
(2) Second, for each covariate identified we reviewed available datasets and assessed how well they represented the factor of interest (for example, we assessed four alternative measures of wealth/poverty).
(3) Third, we ranked each covariate by both the plausibility of the hypotheses associated with it (strength of logic and evidence in the literature) and the quality of available datasets.
(4) Fourth, covariates with adequately high plausibility and data quality were tested for associations with annual data on the illegal killing of elephants from 64 African MIKE sites in 30 countries over 19 years (2002-2020; Fig. 1). This established the degree of support for each hypothesis in (1). We fitted a Bayesian hierarchical Generalised Linear Mixed Model to the poaching/covariate data, with site, year, site-year, and country random effects to fit the data structure. Model selection was performed using LASSO-regularisation (26). Regularisation and multiple random effects tend to reduce the effect sizes and precision of poorly supported covariates (Tibshirani 1996; Zuur et al. 2009a), helping ensure that only those covariates with strong empirical associations with the illegal killing of elephants were identified as important (see Methods).

We build on similar previous analyses of correlates of elephant poaching (Burn et al. 2011; Hauenstein et al. 2019) by taking advantage of several years of additional poaching data, data from several additional sites, as well as improved covariate datasets not previously tested (Table 1). This includes geo-referenced data on armed conflicts in the vicinity of monitored elephant populations (Sundberg & Melander 2013), internationally comparable wealth and development data recently constructed from long-term surveys of households adjacent to monitored sites (Smits & Steendijk 2015; Smits & Permanyer 2019), improved measures of site-level law enforcement capacity (updated MIKE assessments; see Supplementary Material S2), data on site accessibility (Weiss et al. 2018), and a newly collated global dataset on 3012 raw elephant ivory price samples (Do et al. 2021) as a proxy for ivory demand (Table 1). Furthermore, our extensive review of evidence to generate and interrogate specific hypotheses and associated data sources further advances previous work and helps us better scrutinise possible mechanisms underlying complex relationships, such as those between illegal killing and poverty or armed conflict.

Methods

MIKE sites and data on the illegal killing of elephants

Here we use 19 years (2002-2020) of annual elephant carcass data (collected mostly by wildlife rangers) from 64 protected sites in 30 African countries (Fig. 1). Levels of illegal killing are estimated for each site, each year, as the Proportion of Illegally Killed Elephants (PIKE): the number of illegally killed elephant carcasses detected as a proportion of all carcasses detected (including natural mortalities, management related deaths, and mortalities of unknown cause). Some sites were established more recently, and each site has a variable number of years of PIKE data (Fig. 1), so our final data set consisted of 780 site-year observations of PIKE. The PIKE index is subject to several biases (such as sensitivity to natural mortality variation and higher detectability of poached versus natural mortalities in different habitats), but also has several advantages such as being relatively robust to variation in patrol effort and elephant density (see https://citesmike.org/analysis for a full discussion). The index has also been profitably used in various published analyses (Burn et al. 2011; Hauenstein et al. 2019; Schlossberg et al. 2020a). Our rainfall anomaly covariate also partly controls for changes in drought-related natural mortality (Table 1).

Statistical model

To match the data structure, we used a Bayesian hierarchical Generalized Linear Mixed Model (GLMM) with a binomial error structure to determine which covariates had a strong empirical association with PIKE across sites, countries, and years. We used a PIKE-covariate model previously developed by Hauenstein et al. (2019) with the significant addition of a site-year random effect alongside the site, country, and year random effects. This error structure was chosen to represent the data structure, account for pseudo replication at the different levels, and ensure a more conservative interpretation of main effects. The site-year effect deals with pseudo-replication of multiple carcass observations within a site-year while also reducing the possibility of false positives for the main site-year effects like wealth and armed conflict (by reducing effect precision; Zuur et al. 2009b). The site-year effect also substantially improved model fit (Bayesian p-value test for goodness of fit; see below). Model selection was performed using LASSO regularization which penalizes overly complex models by shrinking covariate effects towards zero (Tibshirani 1996; Tredennick et al. 2021). Our model was conservative in that the multiple random effects and LASSO regularization ensured that a very strong empirical association between a particular covariate and PIKE is required for sufficient evidence of an effect.

We model PIKE for each site-year observation by treating the number of illegally killed carcasses detected ($N.illegal_{sy}$) at each site (s) and year (y) as a binomial random variable:

$$N.illegal_{sy} \sim Binomial\ (PIKE_{sy}, N.total_{sy})$$

where $N.total_{sy}$ is the total number of carcasses detected at each site and year. We then model PIKE as a function of the 11 covariates and normally distributed random intercepts ($\mathcal{N}$) for site, site-year, year, and country:

$$logit(PIKE_{sy}) = \beta_0 + \sum_{k=1}^{6} \beta_k X_{sy} + \beta_7 Gov_{country \ni s,\ y} + \mathcal{N}(\mu_{site}, \sigma_{site}) + \mathcal{N}(\mu_{year}, \sigma_{year}) + \mathcal{N}(0, \sigma_{site-year}) + \mathcal{N}(0, \sigma_{country})$$

Where $Gov_{country \ni s,\ y}$ represents the governance quality of the country that contains site s, in the year y. X_{sy} represents the six site-by-year covariates (Table 1). We model the hierarchical level means for the site random intercept (μ_{site}) as a function of the site covariates that had only one measurement across all years (area of site, law enforcement capacity, and travel time to the nearest city):

$$\mu_{site} = \beta_9 Area_{site} + \beta_{10} LawEnf_{site} + \beta_{11} TravelTime_{site}$$

Finally, we model the hierarchical level mean for the year random intercept as a function of the global trend in the price of elephant ivory:

$$\mu_{year} = \beta_{12} IvoryPrice_{year}$$

We fitted the model using Markov chain Monte Carlo (MCMC) sampling, implemented using the software JAGS (Plummer 2003), integrated with the R package R2jags (Su & Yajima 2015). We found that 100 000 MCMC iterations with a 50 000 burn in was sufficient to ensure convergence, which was confirmed by visual examination of chain-iteration trace plots as well as Gelman Rubin potential scale reduction factor ($\hat{R}$) values of less than 1.1. We used gamma (1,1) priors for the standard deviations of the site, year, site-year, and country random intercepts, and Laplace priors on the covariate coefficients to achieve LASSO regularization (see Hauenstein et al. 2019 for details). All covariates were Z-transformed to ensure the same scale.

To test model fit, we used the model equation to simulate response (PIKE) data and then compared discrepancy measures (observed versus predicted) for both the empirical and simulated data using Bayesian p-values (Kéry & Royle 2020). Most covariates had complete data, however the trend in ivory price was missing data for the years 2016-2020, rainfall anomaly data were missing for the year 2020, governance data were not available for 2020, and law enforcement capacity and community participation data were missing for 6 of the 64 sites. We imputed missing data for these covariates using draws from a standard normal distribution, noting that covariates were standardized to this scale (van Buuren & Groothuis-Oudshoorn 2011). Finally, the 'shrinkage' effect helped ensure that estimated covariate effects were influenced more by sites with more reliable estimates of PIKE (by virtue of larger carcass sample sizes) (Burn et al. 2011).

To test model predictive performance, we split the raw data into training and testing sets, using a 75% to 25% random split. We then compared observed PIKE values to median PIKE estimates for the testing set, based on 5000 MCMC samples of the model fitted to the training data only, and calculated R^2 values for the correlation. Then, to account for spatial dependencies in the data (Roberts et al. 2016), we tested predictive performance by excluding 15 randomly selected MIKE sites (~25% of all observations) for the training set and then followed the same procedures as above for testing. Finally, to estimate the proportion of spatial, temporal, and spatio-temporal variation in PIKE accounted for by the covariates (fixed effects), we compared the size of the variance components of the random effects in the full model to a model with only the random effects (a proportional change in variance analysis following equation 31 in Nakagawa & Schielzeth 2013).

Due to correlations between the wealth and development covariates (Supplementary Material Fig. S1), we constructed several supplementary models for these covariates (see Results). Also, the literature suggests that the effects of armed conflict (disruptions to law enforcement, socio-economic change, corruption, and lawlessness) may not be immediate (Douglas & Alie 2014; Gaynor et al. 2016) . Therefore, we present models with conflict intensity measured for each site as the total battle deaths in the current year, over two years (the current year and previous year), three years (the current and previous two years), and five years (the current and previous four years).

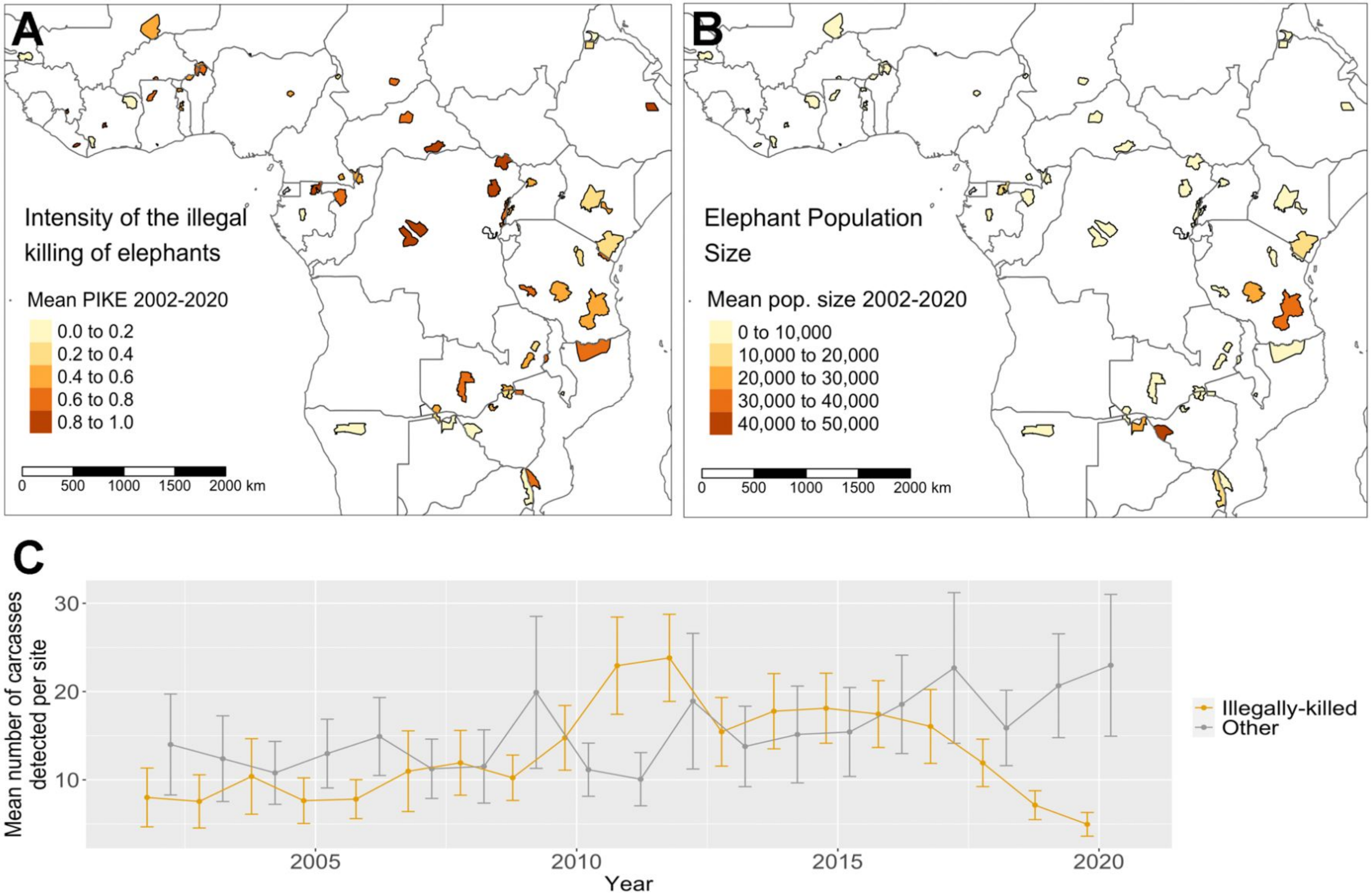

Figure 1. The 64 African sites contributing to the programme for Monitoring the Illegal Killing of Elephants (MIKE). (A) The intensity of the illegal killing of elephants at each site (measured as the Proportion of Illegally Killed Elephants; PIKE, see Methods). (B) Mean elephant population sizes from the African Elephant Database (4). (C) The mean number of carcasses detected per site (mostly by wildlife rangers) between 2002 and 2020.

Table 1: The 12 factors/covariates (out of 20 reviewed) identified as having sufficient plausibility and data quality for testing for empirical associations with the illegal killing of elephants (PIKE; Proportion of Illegally Killed Elephants). Evidence for the hypothesis underlying each covariate, the candidate data sources reviewed for each covariate (e.g., four measures of wealth/poverty were considered), details on how data were extracted to sites/years/countries, and information on the eight excluded covariates are included in Supplementary Materials section S2 and S3. All correlations between covariates were r<0.6, except wealth and development which were modelled separately (see Methods and Supplementary Material Fig. S1)

Factor (plus proxy data and link)	Hypothesis for how factor might influence poaching (PIKE)	Scale
Drivers: factors hypothesised to drive illegal killing		
Ivory demand (Annual trend in global elephant ivory price)	Ivory demand may incentivise illegal killing. If demand increases (e.g., due to increased disposable income) and supply cannot meet demand, ivory price may increase and further incentivise illegal killing*.	Global-by-year
Facilitators: factors hypothesised to facilitate illegal killing and ivory trafficking		
Governance quality (World Governance Indicators)	Poor governance may facilitate illegal killing at the site level and the trafficking of ivory within and out of source countries as officials (park managers and border staff) accept bribes or turn a blind eye.	Country-by-year
Accessibility (Travel time from site to the nearest city)	Sites that are easier for syndicates and hunters to access, and from which ivory can be easily and quickly transported, may experience higher levels of illegal killing.	Site
Accessibility (Size/area of site)	Smaller sites have a higher edge/area ratio making it easier for hunters to access and leave quickly, while larger sites may be difficult to police	Site
Armed conflict (Total battle deaths per site-year derived from the *Uppsala* Conflict Geo Dataset)	Armed conflicts lead to institutional and socioeconomic changes that may facilitate illegal killing, or ivory may be used to fund the operations of warring militias.	Site-by-year
Elephant populations (Size and density)	Sites with larger or more dense elephant populations may be more attractive targets to hunters and syndicates due to higher encounter rates.	Site-by-year
Motivators: factors hypothesised to increase or decrease the motivation to poach elephants		
Household wealth (Sub-national Household Wealth)	The socio-economic conditions of poverty may compel individuals to engage with illegal killing to earn income to meet basic needs, in the absence of viable alternatives.	Site-by-year
Human development (Sub-national Human Development Index - income/health/education)	Less developed communities (not necessarily in poverty) may be more likely to participate in or facilitate illegal killing to earn extra income or through turning a blind eye.	Site-by-year
Law enforcement capacity (MIKE LE Capacity Assessments)	Enhanced law enforcement allows for more committed and effective rangers, more effective apprehension and deterrence, and may thus result in lower illegal killing.	Site
Others: Confounding factors which are unrelated to illegal killing but that may influence the PIKE index		
Precipitation/drought (Rainfall anomaly from CHIRPS data)	PIKE is sensitive to natural mortality rates, so factors explaining natural mortality variation (e.g., rainfall/drought) may explain variation in PIKE both among sites and over time within a site.	Site-by-year
Carcass detectability (Vegetation density from MODIS NDVI)	Densely vegetated sites may have higher PIKE due to low detectability of natural mortalities which do not have the same detection cues as illegally killed carcasses (forest may also help conceal hunters).	Site-by-year
Elephant species (forest or savannah) (delineation from IUCN Red List assessments)	For various difficult to measure reasons, previous evidence suggests forest elephants may suffer higher poaching rates than savannah elephants, which may explain variation in the PIKE index across the continent.	Site (Population)
*We identified price as the best demand proxy, though price is dynamically determined by both supply and demand (See Supplementary Material S2 for a full discussion).		

Results

We identified 20 plausible covariates of the illegal killing of elephants, of which a final set of 12 covariates (those with adequately high plausibility and data quality) were tested in the statistical model to establish support for the hypotheses underlying their influence on the illegal killing of elephants (see Table 1). More detail on how each covariate considered in our analysis may relate to the decision-making of criminal syndicates is included in Supplementary Material S2.

We found evidence for negative associations between the illegal killing of elephants and each of national governance quality, site-level law enforcement capacity, and the wealth and health of households in the vicinity of MIKE sites (Bayesian GLMM 90% credible intervals for covariate coefficients do not include zero: Fig. 2). The credible interval for armed conflict intensity suggests that sites with more intense conflict (higher total battle deaths by site and year) tend to have higher rates of illegal killing, but the evidence is not strong (Fig. 2, 90% credible interval includes zero). We find no evidence for effects on the illegal killing of elephants of the precipitation anomaly, vegetation density, elephant population size and density, travel time from the site to the nearest city, or site area (km^2). We also found evidence for a positive association between the global annual trend in the price of elephant ivory (based on 3012 raw ivory price samples; see Supplementary Material S2) and the temporal trend in the illegal killing of elephants as represented by PIKE (Fig. 2). Finally, we found evidence that forest elephant populations tended to suffer higher rates of illegal killing than savannah elephant populations (Fig. 2).

We also found a strong negative association between human development and the illegal killing of elephants (Supplementary Material Fig. S2), a strong negative association between the illegal killing of elephants and the health and income dimensions of subnational human development, and a positive association between illegal killing and the education dimension (see Supplementary Material Fig. S3). Focussing in on the best-supported site-level covariates, there are relatively consistent geographical patterns in the location of the top and bottom 15 sites for household wealth and health, but variation in law enforcement capacity is spread across the continent (Fig. 4).

We explored the effect of armed conflict intensity further, to test whether the time-period over which it is measured affects associations. Conflict aggregated over the current and previous year had a strong positive association with the illegal killing of elephants (90% credible interval excludes zero: Supplementary Material Fig. S4). However, we found a weaker association with conflict in the current year alone, and no evidence for an effect of conflict intensity when measured over three- and five-year periods (Fig. S4).

Model predictive capacity was adequate to high, with R^2 of 0.36 for prediction of PIKE at 15 excluded sites (90% CI 0.07-0.51) and R^2 of 0.73 (90% CI 0.62-0.81) for a random test-train split (see Methods). Bayesian p-values >0.40 (see Methods) confirmed model fit for the main and supplementary models, as did a plot of observed versus predicted PIKE values (Supplementary Material Fig. S5). The variance components of the site, year, site-year, and country random effects in a random-effects-only model did not reduce significantly when the covariates were added in the full model (Supplementary Material Fig. S6). This indicates that the covariates left a large amount of unexplained variation in the illegal killing of elephants, though covariates were better at explaining spatial versus temporal variation (larger declines in the variance components for the spatial random effects; Fig. S6). The lambda parameter for the LASSO-regularisation in the main model was large (1.92, 90% credible interval: 1.26-2.64) indicating relatively high shrinkage of covariate effects towards zero (suggesting strong evidence for observed covariate effects).

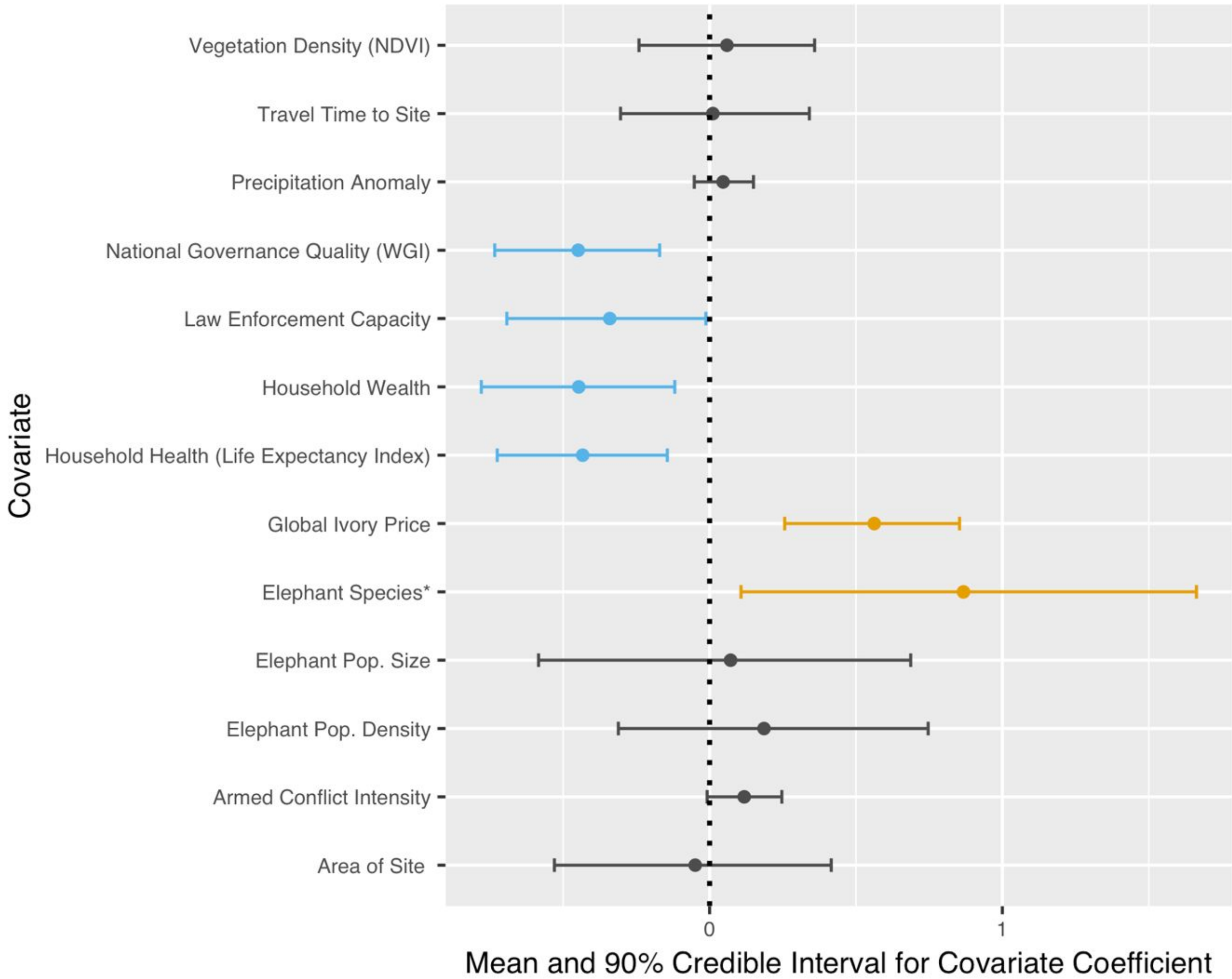

Figure 2. The effect of tested covariates on the illegal killing of elephants (PIKE), based on the LASSO-regulated Bayesian Generalised Linear Mixed Model. Blue lines (coefficient values <0) represent covariates with strong evidence for a negative effect (illegal killing tends to decrease as the covariate increases), while orange represents a strong positive effect. Points and bars represent mean and 90% credible intervals for covariate coefficients (5000 MCMC posterior samples). Covariates were standardized so coefficient effect sizes are directly comparable. Elephant species was coded as 0 for sites with savannah elephant (*Loxodonta africana*) populations and 1 for those with forest elephant populations, so values greater than 0 represent higher estimated illegal killing for forest elephants.

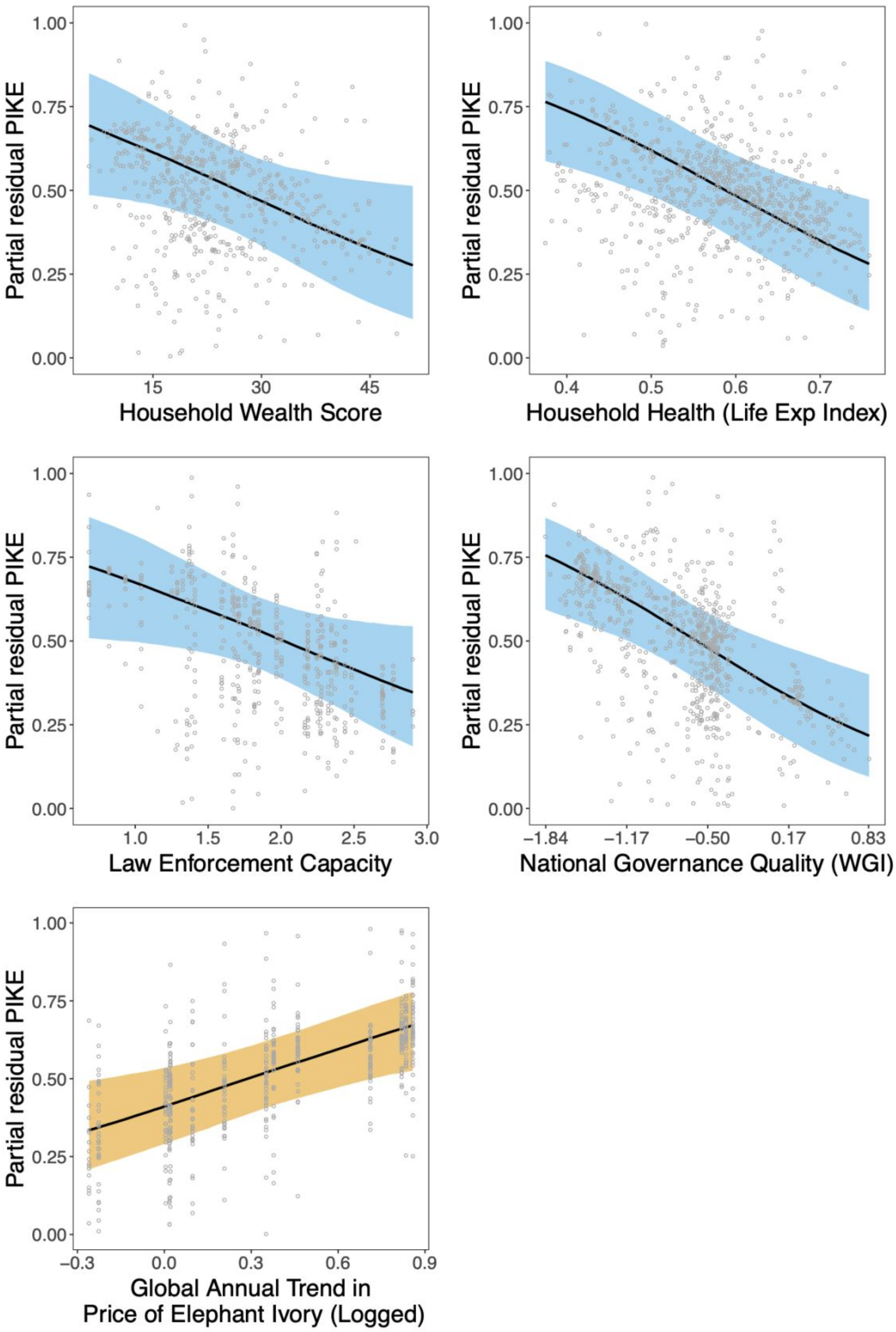

Figure 3. The estimated effect of well-supported covariates (90% credible interval for their effect excludes zero) on the proportion of illegally killed elephants (PIKE), as represented by conditional effects (partial residuals account for other covariates and random effects) from the LASSO-regularised Bayesian Generalised Linear Mixed Model. Bands represent 90% credible intervals from 5000 MCMC samples, and grey circles represent response-scale partial residuals. Orange = positive association, blue = negative associations. The units for ivory price represent median residuals from a regression of log-transformed price data against several control variables (see Do et al. 2021).

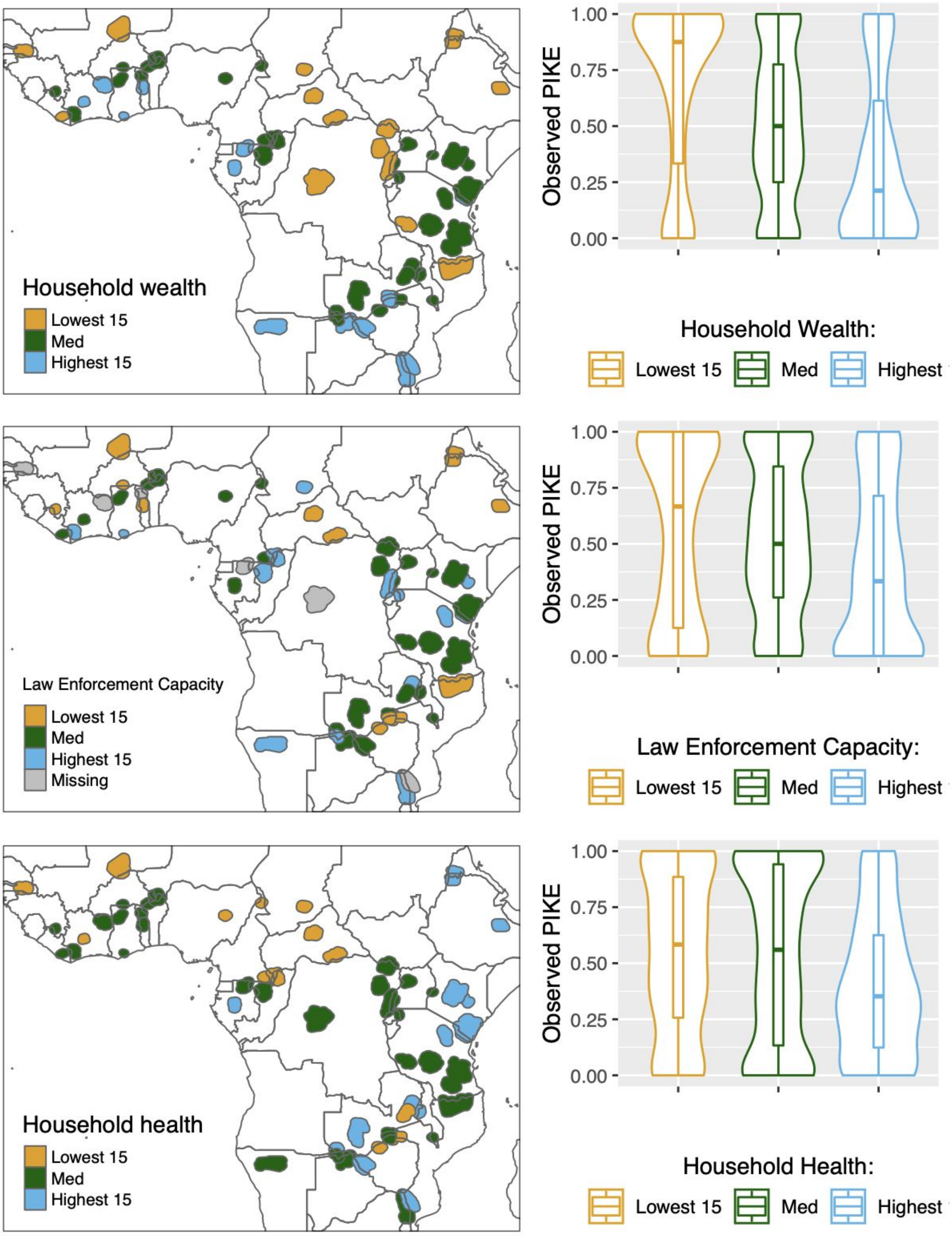

Figure 4. **Right panels:** Observed PIKE (Proportion of Illegally Killed Elephants) for different categories of MIKE sites ordered by the well-supported site-level covariates (Household Wealth, Household Health, and Law Enforcement Capacity), with categories representing the 15 MIKE sites with the highest and lowest mean values for each covariate. “Med” represents the 34 sites with intermediate values for each covariate (there were 64 sites with data in our sample). Observed PIKE is summarized using violin plots (showing data distribution kernels) and box plots (horizontal lines are median and upper/lower quartiles). **Left panels**: Maps of the location of the MIKE sites in each of the categories for each covariate.

Discussion

The unsustainable and illegal killing of elephants for ivory is ongoing across Africa (Wittemyer et al. 2014; Schlossberg et al. 2020a). We found evidence to support the hypotheses that strong national governance, higher levels of local human development (health and wealth), and stronger site-level law enforcement capacity help mitigate elephant poaching. We also found evidence consistent with the hypothesis that demand-driven increases in ivory price may lead to greater incentives for illegal killing of elephants across Africa. Addressing these systemic drivers of poaching will require wider policies and interventions beyond the traditional remit of biodiversity conservation, such demand reduction in consumer countries, reforms to government institutions to promote greater accountability and transparency, and programmes to promote adequate access to educational, health, and economic opportunities where they are lacking. While such interventions are of course an enormous task and already at the forefront of the global Sustainable Development Goals, our results suggest they will have co-benefits for biodiversity conservation.

Hauenstein et al. (2019) found similar associations between Africa-wide elephant killing and poverty, corruption, and ivory price. However, we used a more direct and finer-scale measure of poverty (household wealth, rather than infant mortality rate), a more direct measure of ivory prices (global elephant ivory price compared to mammoth ivory prices), and data for 11 additional sites and three additional years. We also used a more comprehensive measure of law enforcement capacity than Hauenstein et al. (see Supplementary Material S2) and found stronger evidence for a mitigating effect on illegal killing. In another similar analysis, Schlossberg et al. (2020b) did not find correlations between elephant mortality and human national human development or governance, although they acknowledge lower statistical power (they focussed on savannah elephants in 17 countries while we focus on both savannah and forest elephants across 30 countries). We considered using Schlossberg et al's (2020b) measure of poverty (the Night Lights Poverty Index), but most MIKE sites are in rural areas so there is little contrast in light intensity among sites. Our household wealth dataset is based on a local, direct, and internationally comparable metric of material well-being (Smits & Steendijk 2015) and had greater contrast among sites.

The health dimension of subnational human development that we used is based on the under-5 mortality rate (Smits & Permanyer 2019), so the observed positive association with PIKE accords with Hauenstein et al. (2019) who found that PIKE was positively associated with infant mortality rate. However, our household wealth and health (infant mortality) covariates were not strongly correlated, and both had an effect, suggesting that wealth levels affect poaching over and above the health effects observed here and by Hauenstein et al. (2019). Thus, our results provide more conclusive evidence that illegal elephant killing is related to local poverty.

Our observed wealth effect provides support for the hypothesis that local socio-economic deprivation may increase the likelihood of elephants being illegally killed. One interpretation might be that in areas of economic deprivation, local residents participate in illegal killing to meet their basic needs or earn extra income, in the absence of viable alternatives. Another interpretation might be that criminal ivory syndicates seeking to recruit local hunters target these areas because they are able to operate more effectively there (for a range of possible reasons). Previous work points to exceedingly high levels of illegal killing in central Africa and the northern Mozambique southern Tanzania landscape (Maisels et al. 2013; Wasser et al. 2015), which may explain our results, in that MIKE sites in these regions had amongst the lowest household wealth scores (Fig. 4). Wealth scores near all MIKE sites were low by international standards (<45 on a 0-100 scale; Smits & Steendijk 2015), yet we still found that PIKE was higher for areas in more extreme poverty. This contrasts with previous ethnographic work suggesting that individuals involved in illegal killing of high-value species like rhinoceros and elephant are often not in poverty (Hübschle 2017; Paudel et al. 2020). The positive association between illegal killing and the education dimension of the subnational Human Development Index accords with some anecdotal evidence from the Serengeti and Katavi ecosystems in Tanzania where poachers were found to be generally well-educated (which may facilitate selection by syndicates). However, causal hypotheses need deep understanding through more focussed site-level research before they are accepted as the reason behind observed associations (Duffy et al. 2016).

Market demand for wildlife products is one of the most well-evidenced factors driving the global illegal wildlife trade (Wilkie et al. 2005; Sas-Rolfes et al. 2019). The positive ivory price effect we observed supports the hypothesis that demand-driven increases in ivory price may lead to greater incentives for illegal killing, and accords with previous work (Wittemyer et al. 2014; Hauenstein et al. 2019). While price is not a direct measure of demand, and there may be multiple mechanisms behind a positive price-PIKE relationship, we considered price to be the most robust available proxy for ivory demand (see Supplementary Material S2 for a full discussion). However, the relationship between ivory price and illegal killing may be reciprocal (price affects motivations to supply ivory and supply affects price) and stockpiling and speculative trading in ivory are known to occur. Notably, a comprehensive recent analysis by Do et al. (2021) of associations between a proxy ("instrumental variable") for ivory price and PIKE found an inelastic relationship, whereby PIKE increased less-than-proportionately as price increased (Do et al. 2021). They used gold price as their instrumental variable to control for possible endogeneity (whereby ivory price is correlated with other unmeasured drivers of illegal killing). However, low elasticity between price and PIKE does not necessarily imply no relationship, but rather that the effect is small in the observed data range. Given the close correlation Do et al. (2021) found between ivory and gold prices, it is possible that our positive ivory price effect may be due to geopolitical shifts in the global economy (as also reflected in gold prices) rather than factors specific to the ivory market.

Our results provide support for the hypothesis that enhanced law enforcement capacity reduces the illegal killing of elephants (which may operate through apprehension or deterrence of offenders). Criminal syndicates are more likely to target areas where the risk of apprehension is lower (Oyanedel et al. 2020). Similar evidence was found in studies in Tanzania, Zambia, and Malawi (Jachmann & Billiouw 1997; Hilborn et al. 2006; Moore et al. 2018). Although we selected our law enforcement covariate as the most robust of several considered (Supplementary Material S2), it does not account for changes in law enforcement capacity over time and the tendency to under- or overestimate law enforcement capacity may vary by site according to personnel (although experienced personnel provided the assessments). Finally, it is also possible that sites with higher law enforcement and patrolling capacity detect a higher proportion of available natural mortalities, which would lead to lower PIKE scores.

The link between corruption and organised is well established in the literature (Buscaglia and van Dijk 2003). There is growing evidence that poor governance may negatively affect various aspects of biodiversity protection (Smith et al. 2003; Wright et al. 2007; Sundström 2016). We observed governance quality to be strongly and negatively associated with the illegal killing of elephants, as in previous analyses of similar data (Burn et al. 2011; Hauenstein et al. 2019). Our result also accords with Bennett (2015) who describes how bribery and corruption opportunities exist all along ivory supply and value chains, where officials may turn a blind eye to, or actively engage in, site-level illegal killing, and ivory trafficking within and between countries. van Uhm & Moreto (2018) found that wildlife poachers in Uganda, Russia, China and Morocco and traders may interact with government enforcement agents in a diversity of corrupt ways that can facilitate harvest, transport, processing, and export of wildlife products.

The strong elephant species effect suggests that forest elephants on average suffer higher rates of illegal killing compared to savanna elephants (Maisels et al. 2013, Wittemyer et al. 2014). The species effect is interesting in that it is over and above any effect due to differences between savannah and forest elephant populations in vegetation density, precipitation, population density, or any other effects already captured in other covariates. This may, however, represent a geographic region effect as the vast majority of forest elephant populations are in West and Central Africa while savannah populations mostly occupy East and Southern Africa. One possible explanation might be that natural mortalities tend to be harder to detect in forested environments, artificially inflating PIKE estimates. However, we would expect the vegetation density covariate to capture this effect. Maisels et al. (2013) highlight expanding infrastructure and encroachment into core elephant habitat as a key driver of forest elephant poaching. While the difference might be explained by demand for harder Forest elephant ivory for certain items such as name seals and musical instrument components in key consumer countries like Japan, this specific demand has largely declined since its peak in the 1970s and 1980s (Nishihara, 2012).

It is important to note that our analysis does not necessarily identify factors that have led to the largest absolute number illegally-killed elephants. It is possible that the factors driving large numbers of elephant killings at a handful of sites (such as observed for Selous and Rungwa/Ruaha in Tanzania around 2010-2013) may be different from the drivers/facilitators of illegal killing that are general across sites (as identified in our analysis). However, the goal of this paper is to find common patterns across the continent, rather than try and explain drivers of poaching at a few key 'hotspot' sites. Furthermore, genetic seizure analyses suggest poaching hotspots have shifted over the last 20 years, the period of our analysis (Wasser et al. 2015, Wasser & Gobush 2019). Our analysis across the whole continent and relatively long time period means we can learn something useful about tackling future hotspots.

Our results must be considered in the light of the limitations of the underlying datasets. MIKE data do not cover all Africa elephant populations and the PIKE index may be sensitive to natural mortality rates and differential detectability of illegally killed carcasses and natural mortalities (see Methods). Also, measuring factors like wealth and law enforcement accurately and in a comparable way over many sites and countries is difficult, and so covariate data may be biased and incomplete. Furthermore, many plausible drivers of the illegal killing of elephants cannot be adequately captured in a covariate. Global one-off events, or significant local events, may influence illegal killing but remain unmeasured. Finally, our analyses of proportional change in variance and model predictive performance suggests that much variation in PIKE remains unexplained by our covariates. This is perhaps not surprising given that illegal killing is influenced by a complexity of human decision-making within equally complex social and political institutions and networks affecting both offenders and law enforcement, which themselves interact with ecological factors and change over time. It is likely that there are many site, year, and country-level idiosyncrasies that cannot easily be captured in a covariate.

Notwithstanding these caveats, our approach of seeking a hypothesis-driven *a priori* understanding of the dynamics of illegal elephant killing and management, identifying the best available covariates to represent these dynamics, and using a tailored statistical modelling approach, helped us shed light on drivers and facilitators of illegal elephant killing across Africa. Overall, our results suggest that addressing system-level challenges at a variety of scales (poor governance, low human development, and ivory market dynamics) is essential to tackling illegal elephant killing, alongside the traditional focus on law enforcement. This corroborates broader work that has highlighted the importance of these more ultimate drivers of the global illegal wildlife trade (Duffy et al. 2016; Sas-Rolfes et al. 2019; Liew et al. 2021).

Supporting Information

[illegible]

Additional information is available in Supplementary Materials:

Raw data, R statistical code, and instructions for reproducing this analysis are available online within the *Harvard Dataverse* repository: https://doi.org/10.7910/DVN/GNI6DS

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