

Illegal killing for ivory drives global decline in African elephants

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Illegal wildlife trade has reached alarming levels globally, extirpating populations of commercially valuable species. As a driver of biodiversity loss, quantifying illegal harvest is essential for conservation and sociopolitical affairs but notoriously difficult. Here we combine field-based carcass monitoring with fine-scale demographic data from an intensively studied wild African elephant population in Samburu, Kenya, to partition mortality into natural and illegal causes. We then expand our analytical framework to model illegal killing rates and population trends of elephants at regional and continental scales using carcass data collected by a Convention on International Trade in Endangered Species program. At the intensively monitored site, illegal killing increased markedly after 2008 and was correlated strongly with the local black market ivory price and increased seizures of ivory destined for China. More broadly, results from application to continental data indicated illegal killing levels were unsustainable for the species between 2010 and 2012, peaking to ~8% in 2011 which extrapolates to ~40,000 elephants illegally killed and a probable species reduction of ~3% that year. Preliminary data from 2013 indicate overharvesting continued. In contrast to the rest of Africa, our analysis corroborates that Central African forest elephants experienced decline throughout the last decade. These results provide the most comprehensive assessment of illegal ivory harvest to date and confirm that current ivory consumption is not sustainable. Further, our approach provides a powerful basis to determine cryptic mortality and gain understanding of the demography of at-risk species.

poaching | overharvest | population estimation | extinction | endangered species consumption

Overharvest of wildlife for human consumption is currently the second leading driver of global biodiversity decline and local extinction of species (1–3). Overharvesting diminishes species occurrence and density and affects food webs and ecological processes extensively (4, 5). The repercussions of this harvest when driven by illegal commercial trade are not only ecological in nature, but raise human health (6) and socioeconomic concerns (2, 7) with broad implications for national and international policy and security (8). Recently, overharvest driven by illegal commercial trade has received renewed focus due to the extirpation of populations of commercially valuable species including rhinoceros, tigers, and elephants (9–12), but information on overharvest rates and resulting population trends for these species and others are lacking. Information on the levels and drivers of illegal harvest is broadly needed to facilitate conservation and management actions.

Despite the importance of assessing the magnitude of illegal trade and its impacts on local populations of commercially and ecologically valuable species (13, 14), it is cryptic and therefore notoriously difficult to quantify (15). Few approaches provide robust delineation of mortality drivers, such as natural mortality versus illegal offtake rates, although this information is critical for diagnosing population trends and risks and formulating regulatory frameworks (16, 17). In 2002, an elephant monitoring

system [Monitoring the Illegal Killing of Elephants (MIKE)] was instituted by the Convention on International Trade in Endangered Species (CITES) in 45 sites across Africa to ascertain the impact of legal ivory trade on the species (18). The cause of death and date of all elephant carcasses found during regular patrolling (by foot, vehicle, or air) were recorded. This monitoring system provides powerful data regarding the site-specific relative causes of mortality [i.e., the proportion of illegally killed elephants (PIKE)] (18) that has served to indicate regional levels of illegal harvest (19).

Here we develop an approach using carcass surveys to assess trends in relative causes of elephant deaths (PIKE) and population performance, an approach broadly applicable to other species with similar data. Initially, we used carcass survey data to partition the causes (illegal killing or natural) of known mortality among individually monitored elephants inhabiting the Samburu National Reserves complex (20). Although offering robust metrics for a local, intensively studied population, it was critical to expand our approach to estimate illegal killing levels at the country, regional, and species scales to assess the species' status. Therefore, we modified our approach to infer trends on the broader carcass data collected through the CITES MIKE program (19). At this continental scale, we applied and compared results from two parallel approaches representing alternative monitoring structures and related assumptions: (i) intense monitoring of a few sites versus (ii) coarse monitoring across many sites.

Significance

Illegal harvest for commercial trade has recently surged to become a major threat to some of the world's most endangered and charismatic species. Unfortunately, the cryptic nature of illegal killing makes estimation of rates and impacts difficult. Applying a model based on field census of carcasses, to our knowledge we provide the first detailed assessment of African elephant illegal killing rates at population, regional, and continental scales. Illegal harvest for commercial trade in ivory has recently surged, coinciding with increases in illegal ivory seizures and black market ivory prices. As a result, the species declined over the past 4 y, during which tens of thousands of elephants have been killed annually across the continent. Solutions to this crisis require global action.

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Results

We partitioned known mortality in the intensively monitored Samburu elephant population (20) between natural and illegal sources using our analytical framework based on carcass survey data. The population was subjected to unsustainable rates of illegal killing between 2009 and 2012, escalating from a mean of 0.6% (SD = 0.4%) between 1998 and 2008 to a high of 8% in 2011 (Fig. 1). Annual illegal killing of elephants in the Samburu population during 2009 to 2012 exceeded those of all previous years of monitoring (1998–2008) with an estimated aggregate of 20.8% of the known elephants illegally killed during that 4-y period. Preliminary numbers from 2013 indicated the annual rate of illegal offtake remained concerning at around 3.7%, although below the peak levels experienced in 2011. Illegal killing rates were strongly correlated with black market ivory prices in the Samburu ecosystem (Pearson's $r = 0.85$, $P = 0.015$; Fig. 1A) and mirrored increases in raw ivory seizures in or from Kenya (21) and modeled continental seizure rates (22), both of which demonstrate increased trafficking to China (Fig. 1B). As a result of this illegal killing, the population currently suffers from few prime-aged males, strongly skewed sex ratios, and social disruption in the form of some collapsed families and increased numbers of orphans (immature elephants without a parent) (23).

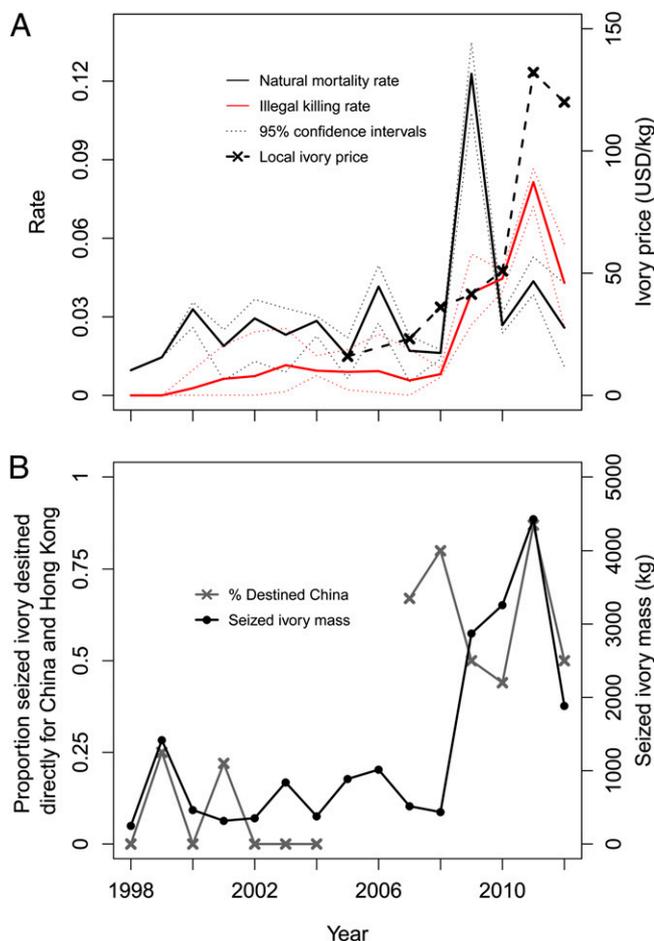


Fig. 1. (A) Estimated natural (gray line) and illegal killing (red line) rates (with 95% confidence interval) contrasted with local prices of ivory (black line) to the poachers in the Laikipia/Samburu ecosystem. (B) Mass of annual ivory seizures in Kenya (no data in 2005–2006) and the proportion of seizures destined for China (including Hong Kong). Data is represented by a black or gray “x.”

We implemented two approaches representing alternative monitoring frameworks to model illegal killing and population trends at broader scales. The first approach (hereafter referred to as the empirical approach) analyzed carcass data from the 12 MIKE site populations with carcass samples allowing robust inference (averaging ≥ 20 carcasses annually; see *SI Materials and Methods* for details of sensitivity analyses used to define this threshold). The second approach (hereafter referred to as the model approach) used a quasibinomial predictive model (18, 19) based on site, region, and global predictors to estimate site-specific PIKE and the variance around these estimates for 306 elephant populations across the continent (see *SI Materials and Methods* for model details; the populations of West Africa, representing $\sim 2\%$ of the species, were excluded). Site-specific annual PIKE (empirical and modeled) were fed into a demographic model, assuming an average annual population increase of 4.2% in the absence of illegal killing, to estimate trends (*Materials and Methods*) which were compiled into regional and continental estimates (note: 5 East, 4 Southern, and 3 Central African sites comprised the 12 used in the empirical model). In aggregate, results demonstrated an overharvest-driven decline in African elephants likely began in 2010 (Table 1). Illegal killing rates were estimated to average $\sim 6.8\%$ between 2010 and 2012, equating to an average of $\sim 33,630$ elephants killed per y based on current estimates of the species total (24) (Table 1). The three regions of Africa (Central, East, and Southern) demonstrated different trends that were captured by both approaches. Illegal killing was most pervasive in the populations of Central Africa (Figs. 2 and 3), where results supported probable annual declines each year since at least 2007 (Fig. 2A), with the empirical approach estimating a 63.7% decline between 2002 and 2012 on par with the 62% estimated from dung surveys over a similar period (12). Our results suggest savanna populations in East (Fig. 2B) and Southern Africa (Fig. 2C) were relatively stable or growing between 2002 and 2009, after which they started declining. Results for Southern Africa varied between approaches, with empirical results suggesting decline during all 3 y, and modeled results suggesting stability in 2010 and decline in 2011–2012 (Table 1). At the site level, 42% of the 12 populations analyzed empirically and 60% of the 306 populations modeled were projected to have declined over the 10-y period (Fig. 2D). The majority of declines occurred in the last few years, with 75% and 77% of sites respectively estimated to have declined after 2009 (Fig. 3), although site-specific results differed between the two methods. Preliminary data from 2013 suggests regional and continental offtake levels were slightly lower to those reported for 2012, but still unsustainable.

As a verification exercise, we directly compared our PIKE model to intersurvey mean estimates of population change in 19 sites (39 survey periods) for which repeated, population surveys (aerial counts, spoor surveys, or individual-based monitoring) were conducted during the MIKE program period (Fig. 4). Survey and PIKE-based modeling estimates of annual population trends were correlated (empirical results: Pearson's $r = 0.675$, $P < 0.001$; model results: Pearson's $r = 0.372$, $P = 0.024$), with the empirical-based result averaging 0.33% slower growth (*SI Materials and Methods*). Simulated confidence intervals of our model relating PIKE to mean population change largely contained calculated trends (Fig. 4).

Discussion

Our analysis demonstrates the heavy toll illegal ivory trade is taking on African elephants, and suggests current offtake exceeds the intrinsic growth capacity of the species. It is important to recognize that the number of elephants being illegally killed annually is based on current species estimates, which are uncertain (24). Should fewer elephants be on the continent than estimated, the numbers illegally killed would be less than that

Table 1. Regional and total estimates of population change, illegal killing rates, and number of elephants poached for 2010–2012

Region	Empirical method, 12 sites			Model-based method, 306 sites		
	2010	2011	2012	2010	2011	2012
Africa						
Population growth rate	0.978	0.976	0.977	1.001	0.971	0.979
Poaching rate	0.063	0.083	0.065	0.045	0.077	0.077
No. poached	29,124	41,044	31,616	21,477	39,692	38,828
Central Africa						
Population growth rate	0.979	0.795	0.790	0.969	0.926	0.932
Poaching rate	0.142	0.248	0.235	0.100	0.160	0.177
No. poached	11,228	21,148	16,148	7,871	13,649	13,607
East Africa						
Population growth rate	0.988	0.988	0.983	0.994	0.960	0.979
Poaching rate	0.054	0.054	0.059	0.042	0.074	0.059
No. poached	7,187	7,763	8,695	5,645	10,631	8,515
Southern Africa						
Population growth rate	0.978	0.974	0.980	1.019	0.996	0.996
Poaching rate	0.064	0.068	0.062	0.023	0.046	0.048
No. poached	15,800	18,176	16,583	5,740	12,285	13,303

The variations around these estimates are presented in *SI Materials and Methods*.

reported (although undoubtedly still in the tens of thousands per y). As such, we emphasize estimates of the illegal killing rate and resulting trend in elephant numbers, rather than the numbers themselves (Fig. 3).

Application of carcass monitoring to estimate population change provides a powerful framework but relies on a number of assumptions regardless of whether the analyses relied on the empirical or model approach (18), most substantively that mortality events and the detection probability of carcasses were

independent of the cause of death. Although a pilot study on four MIKE sites found these assumptions were met and PIKE accurately represented mortality patterns in well-monitored sites (25), assessments across all MIKE sites were not possible. As such, unidentifiable bias in the underlying data could skew results (see *SI Text* for discussion). Our implementation of the PIKE-based estimates of illegal killing rates was likely conservative on account of (i) relying on the best sampled populations and, therefore, those experiencing relatively intensive patrolling

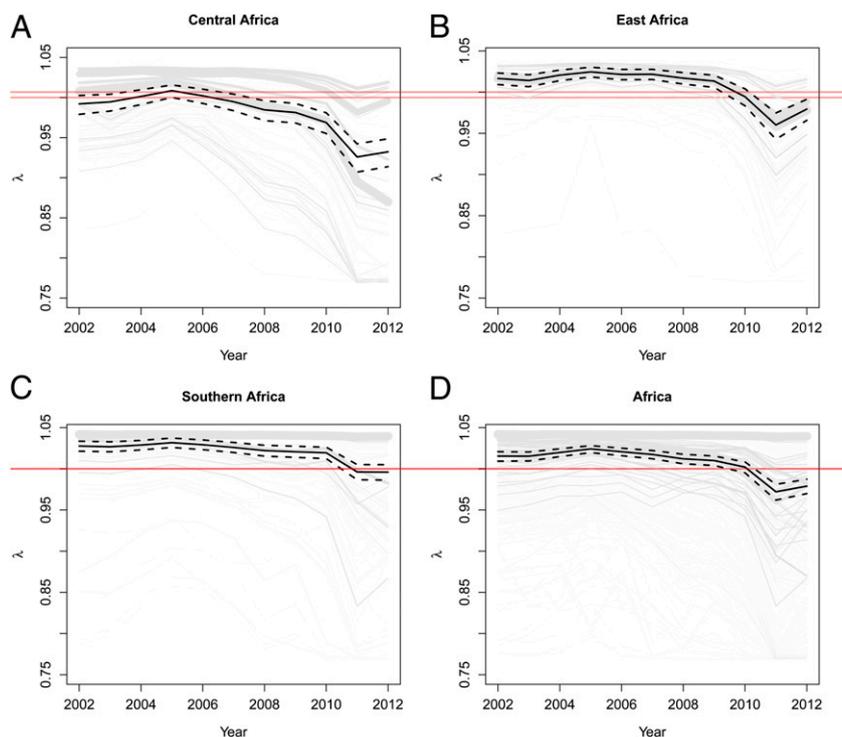


Fig. 2. Modeled trends in annual population changes between 2002 and 2012 for 306 elephant populations across Africa presented by region: (A) Central, (B) East, and (C) Southern Africa regions and (D) all combined. Gray lines represent the site-specific annual population changes, where the thickness represents relative population size. Black lines represent the aggregate trends. Dashed lines represent the 95% confidence interval of aggregate trends.

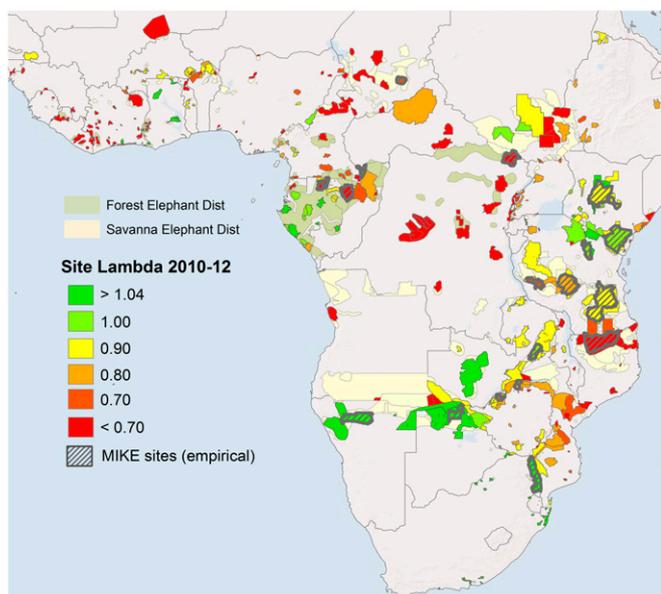


Fig. 3. Average annual population changes (λ) between 2010 and 2012 portrayed for 19 empirically calculated MIKE sites that averaged >10 carcasses per year (outlined and striped) and 287 populations calculated using a predictive model.

(exclusively for the empirical approach and relatively in the model approach in respect to greater influence of sites with larger carcass sample sizes on model outputs); (ii) the structure of our population growth model (assuming 4.2% annual growth in the absence of illegal killing and capping the maximum annual rate of decline at 28.8%); and (iii) the assumption that carcasses from unknown origins were naturally caused. Illegal killing was not compensatory in the Samburu system and, therefore, assumed to be additive in our model of population change (*SI Text*). Simulation results given our demographic parameterization indicated populations with PIKE of 0.54 were likely at equilibrium, with higher proportions associated with greater probabilities of decline (Fig. 4). This threshold PIKE value can serve as a rule of thumb indicating excessive pressure that requires intervention if the corresponding population is to avoid extirpation.

The two approaches implemented in our broad-scale analysis provided similar results when contrasted at the regional or continental scales, but relied on starkly different data (a limited empirical sample from well-monitored populations versus a coarse-scale model that provides predictions on all elephant populations across Africa). The differences in outputs from the two approaches were driven by the temporal trend in macro-scale covariates used in the model approach. Although the two approaches have different merits, it is not clear which approach is more accurate, but it is notable that both agree that the rate of illegal killing is unsustainable. As the MIKE system progresses, assessing underlying assumptions is critical but likely only possible at a few, well-sampled populations (25). Investment in the 12 sites used here in the empirical analysis to allow more refined modeling is suggested, as such a sensitive approach can serve to identify local drivers of illegal killing (26) and the efficacy of interventions. On the other hand, broad-scale modeling as conducted by the second approach provides estimates of the status of populations where ground monitoring is difficult (Figs. 2 and 3), and can identify broad-scale predictors of illegal killing that can facilitate targeted interventions. For example, the correlation of PIKE to the Chinese household consumption expenditure variable suggests reduction of demand for illegal ivory in China should be a priority (19). Although the reliability of any single site estimate

by the modeling approach is uncertain, efforts to refine the model to improve accuracy will undoubtedly enhance its utility.

Intriguingly, our analysis suggests the rate of killing slowed after the peak in 2011 both locally in Samburu and globally, although it still remained unsustainable. It is critical to identify the drivers of this change in the rate of illegal killing. Speculation regarding the influences of restriction in ivory auctions in China at the end of 2011 should be explored and expanded should this action be found to be substantive (27), although it is notable the black market ivory price in Samburu did not appear to change in 2012. Increased global attention on MIKE carcass data and the adoption of PIKE as a measure of conservation success may serve the function of drawing attention to the problem, but also may risk the integrity of future data, as without standards of verification it could easily be manipulated. It is important to ensure the neutrality of such monitoring data rather than tying incentives to this metric.

Carcass monitoring in combination with knowledge of underlying demographic processes provides the potential to disentangle drivers of population trends that can serve to target conservation and management actions (2) and enhance the theoretical understanding of population and evolutionary responses to different types of mortality (28). Our approach provides a detailed understanding of the scope of the illegal killing problem for a widely dispersed species, but is applicable to numerous systems (human, disease, or predation influenced) where mechanistic information on survival is desired (17). In respect to this study on African elephants, it is obvious that stemming the rate of illegal killing is paramount. Heavy in situ conservation efforts have been shown to stem illegal harvesting (29) and, therefore, need to be enhanced in the face of the current offtake rates (30). Enforcement of end-user markets is also critical, and curbing demand—particularly in the Far East (21)—appears necessary to reduce black market ivory prices and alleviate the unsustainable

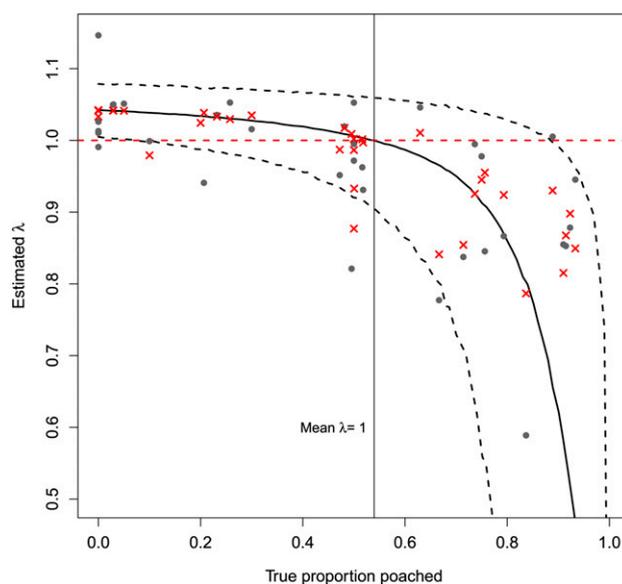


Fig. 4. Actual annual population change (those surveyed are represented by gray circles) and carcass-based, empirical-modeled population change (red "x"s) relative to PIKE (the proportion of illegally killed elephants) for the 19 MIKE sites with the largest annual average number of carcasses surveyed (*SI Materials and Methods*). The mean (thick black line) and 95% confidence interval (dashed line) of simulations exploring the predicted relationship between population change and PIKE are shown for reference. The red dashed line indicates population stability ($\lambda = 1$) and the thin black line depicts PIKE = 0.54, where the mean simulation indicates population stability.

pressure from illegal killing on wild populations (31). Ultimately, interventions are needed to tackle all levels of the supply chain (32) and the underlying factors contributing to increasing levels of illegal offtake (33).

Materials and Methods

Whereas total annual mortality rates (m_t) (and number of elephants that died) for the intensively studied Samburu population were known (20), all carcasses were not found, so the illegal killing (m_p) and natural mortality (m_n) rates were not known. Monte Carlo simulation was used to adjust annual m_t by the binomial sample proportion ($p_p = c_p/c_t$) and variance ($\text{var}_p = [p_p(1-p_p)]/c_t$) of carcasses illegally killed (c_p), where c_t is the annual total number of carcasses found, to estimate annual illegal killing rates as $m_p = m_t p_p$ (see details in *SI Materials and Methods*). Further, uncertainty introduced by carcasses for which the cause of demise was unknown was integrated into this estimate (see *SI Materials and Methods* for formal model structure).

Building on this approach to offer insight at broader scales, we combined PIKE data (empirical or model derived) with a compilation of published natural mortality rates to estimate illegal killing rates and population trends (20). Specifically, we calculated a distribution for illegal killing rates (m_p) per site as a function of the natural mortality rate (m_n): $m_p = [p_p/(1-p_p)]m_n$, where p_p (PIKE) was calculated empirically from carcass survey data at MIKE sites for the empirical approach or derived from model outputs for the model approach. The distribution of plausible annual natural mortality (m_n) was compiled from published metrics (*SI Materials and Methods*). Annual intrinsic population growth rates and associated variance were then modeled for each MIKE site as $\lambda = 1 - m_p - m_n + R$, using a Monte Carlo simulation framework where the distribution of natality (R) was compiled from

published metrics (*SI Materials and Methods*). Population size and number of illegally killed elephants were then estimated through forward or backward calculation using the most recent population estimate, and amalgamated to obtain regional and continental metrics (see *SI Materials and Methods* for formal model structure and description).

We used simulations to assess the performance of the above methods for estimating the poaching rate under different levels of poaching and carcass samples (detailed in *SI Materials and Methods*) and to estimate threshold levels where p_p indicates population decline (Fig. 4). Simulation results suggested sites with fewer than 20 carcasses surveyed per year provided relatively weak precision on estimates of p_p , undermining the efficacy of our approach to estimate illegal killing rates. This was used as the cutoff for site inclusion in the empirical approach. We also assessed the sensitivity of metrics derived empirically in relation to this cutoff, finding estimates of illegal killing rate and population decline increased when increasing the number of sites in the empirical approach by using 10 carcasses per year as the cutoff (*SI Materials and Methods*), results of which are portrayed in Fig. 3. Further assessment and discussion of assumptions are provided in *SI Materials and Methods*.

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