From unusual suspect to serial killer: Cyanotoxins boosted by climate change may jeopardize megafauna

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The recent mass mortality event of more than 330 African elephants in Botswana has been attributed to biotoxins produced by cyanobacteria; however, scientific evidence for this is lacking. Here, by synthesizing multiple sources of data, we show that, during the past decades, the widespread hypertrophic waters in Southern Africa have entailed an extremely high risk and frequent exposure of cyanotoxins to the wildlife within this area, which functions as a hotspot of mammal species richness. The hot and dry climatic extremes have most likely acted as the primary trigger of the recent and perhaps also of prehistoric mass mortality events. As such climate extremes are projected to become more frequent in Southern Africa in the near future, there is a risk that similar tragedies may take place, rendering African megafauna species, especially those that are already endangered, in risk of extinction. Moreover, cyanotoxin poisoning amplified by climate change may have unexpected cascading effects on human societies. Seen within this perspective, the tragic mass death of the world's largest terrestrial mammal species serves as an alarming early warning signal of future environmental catastrophes in Southern Africa. We suggest that systematic, quantitative cyanotoxin risk assessments are made and precautionary actions to mitigate the risks are taken without hesitation to ensure the health and sustainability of the megafauna and human societies within the region.

KEYWORDS: **cyanobacteria toxin; climate change; eutrophication; mammal conservation; environmental health**

The sudden deaths of at least 330 African savanna elephants (*Loxodonta africana*) in Botswana during May and June 2020 sparked much attention and concern worldwide (as seen in mainstream media, such as *New York Times*, *Washington Post*, *Chicago Tribune*, and *BBC News*. Viral and bacterial agents were initially suggested to be the most plausible cause of the tragic events, while the possibility of malicious poisoning, poaching, starvation, and anthrax was ruled out.[1] Aerial images and lab tests indicate that biotoxins or diseases are the culprit (see Text S1 for analyses of possible causes). Particularly, ingestion of cyanobacterial neurotoxins through drinking water rich in cyanobacteria is the suggested cause (see Text S2 for more information on cyanobacteria, cyanotoxins, and eutrophication).

However, questions remain as to the causal role of cyanotoxin poisoning in the elephant mass mortality event. Ideally, adequate measurements of water quality, cyanobacteria species, and cyanotoxin concentrations, combined with histopathological analyses, could have identified whether cyanotoxin poisoning was indeed the trigger of the mysterious mass deaths. However, the global coronavirus pandemic (COVID-19) and the remoteness of the mass mortality location render such measurements difficult. Also, most waters had gone dry, and many carcasses had already strongly decayed when the event started to attract attention. Here, we collected data on cyanotoxins and examined relevant historical records on the African continent and conducted a retrospective toxicity analysis to unravel how these pachyderms might have been killed. Then, using long-term meteorological records, we also examined the possibility of climate change as a trigger of this tragic event. Finally, we forecast the future risk of exposure of megafauna to cyanotoxins by identifying spatial congruence of hotspots of megafauna diversity, high cyanotoxins, hot and dry climates, and other factors favoring cyanobacteria growth.

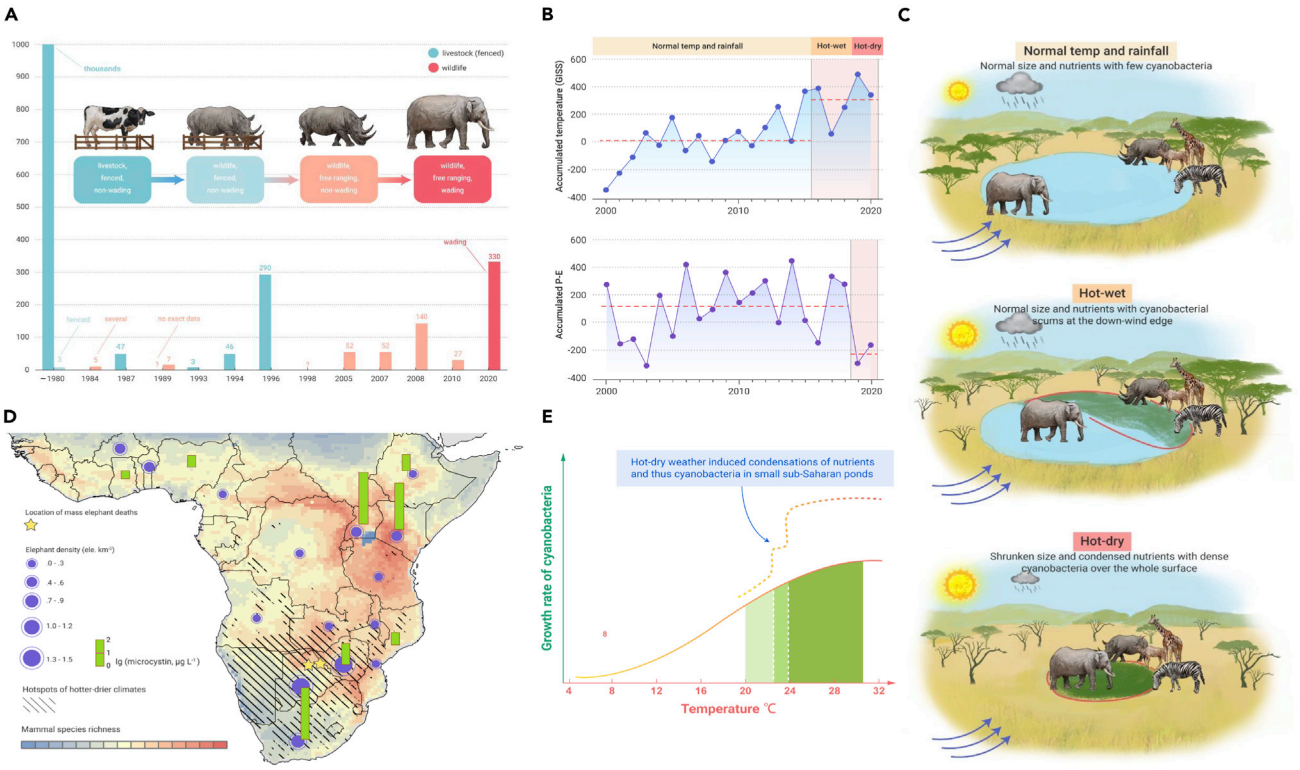

Figure 1. Lethal poisoning of cyanotoxin on megafauna in relation to changing environments Reported livestock and wildlife deaths in Africa with cyanotoxin poisoning as the suspected cause (A). Anomalies of effective accumulated temperature (°C days) and net precipitation (precipitation minus evaporation, mm) during 2000–2020 in the Seronga Village, Okavango Delta of Botswana, against the baseline climatology of 1986–2005 (B). Schematic representation of changes in vegetation, water area, and cyanobacteria concentrations and their poisoning risks to elephants under combined changing conditions of temperature and rainfall (C). Southern Africa identified as a hotspot of cyanotoxin risk at present and in the future (D). Response of cyanobacteria growth to climate warming (E).

High levels of cyanotoxins as a killer

One may doubt whether cyanobacteria in natural ecosystems are sufficiently toxic to kill hundreds of the world's largest terrestrial animals all at once. Indeed, cyanotoxin-induced mass mortalities have mostly been recorded for small-bodied animals such as fish, birds, and turtles.[2] Our literature review reveals that cyanotoxins have frequently been the suspected cause of the (mass) deaths of medium and large-sized terrestrial mammals in Africa, including livestock (cattle and sheep) as well as non-wading wild mammals (white rhinoceros, blue wildebeests, giraffes, zebras, and impalas) (Figure 1A) (see Table S1 for a compilation of historic events). Interestingly, due to vigilance against predators many of these species drink at the downwind edge of waters where dense cyanobacteria scum tends to accumulate, thus exposing them to high levels of cyanotoxins (Figure 1C). In contrast, elephants, being a wading species, tend to drink in the middle of the waters and are therefore expectedly less exposed to cyanotoxins if cyanobacterial scums are limited to the downwind edge. Hence, the behavior of the animals is expected to affect their susceptibility to toxic cyanobacteria.

Although *in situ* data on cyanotoxin concentrations in the elephant die-off locations are so far unavailable, our collected data on the water quality of relatively large waterbodies in Africa show that concentrations of cyanotoxin (using as a proxy microcystins, MCs for short, the most common and most toxic species) ranged between 0.36 and 124,460 $\mu g\ L^{-1}$. Most values were much higher (an 8,836 times average) than the provisional guideline value of 1.0 $\mu g\ L^{-1}$ recommended by the World Health Organization for mammals and humans (see Table S2 for details).[3] The situation is particularly serious in the southern part of Africa, where averaged MCs are over 13,400 times the guideline. Importantly, MCs in two waterbodies (103 and 124 $mg\ L^{-1}$) of southeastern Africa almost reached the acute lethal dose of 125 $mg\ L^{-1}$ (see Table S2 for the derivation of acute lethal dose).[3] Similar results are found for the daily intake of toxins. In small ponds and puddles serving as important sources of drinking water for wild mammals, cyanotoxin concentrations are expected to be even higher due to accelerated water evaporation at high summer temperatures.[4] Such high concentrations of cyanobacteria/cyanotoxins in this region are not surprising, as hypertrophic (e.g., nitrogen-rich sewage and feces from wildlife resulting in ammonium levels as high as 273 mg L^{-1} in the Hartbeespoort Dam, which is 10 times the level of raw domestic sewage), hydrologically stagnant, and climatically hot conditions together create an ideal environment for cyanobacterial blooming in almost every aspect.

Our analysis indicates that cyanotoxins were indeed the most likely cause of this event, which would be the first confirmed case of cyanotoxin-induced elephant mass mortality. In a broader context, our retrospective analysis also demonstrates a likely increasing risk during the last decades, with mammal victims extending from fenced livestock to fenced wildlife, over free and non-wading wildlife, and finally to free and wading wildlife (Figure 1A). Despite a caveat of "survivorship bias," our findings nevertheless have profound implications, suggesting that cyanotoxins have rapidly become a life-threatening stressor for an increasingly wide range of African megafauna, including the largest species (i.e., the African savanna elephant). The consequences of cyanotoxin poisoning for the already endangered elephant could be catastrophic since the number of carcasses from the Botswana mass die-off was close to that of poaching (385 ± 54) (the primary cause of elephant deaths) in Botswana for a whole year.[5]

Hot and dry weather as a trigger

Cyanobacterial blooms, driven by eutrophication and global warming, have rapidly increased in frequency, intensity, and duration across the globe.[6,7] While hot weather is the primary trigger of dense cyanobacterial blooms, the high inputs of wildlife and livestock feces and sewage will lead to cyanobacterial growth spurts in Southern Africa. Our analysis of climate records reveals that hot and dry conditions occurred for multiple years in a row in the areas where most of the elephant carcasses in Botswana were found (Figure 1B).

This finding seems unlikely to be a coincidence because similar climatic conditions were also associated with mass mortalities of elephants in Zimbabwe and non-wading mammals in South Africa (Figure S1). Hot and dry weather could have boosted the production of cyanotoxins (Figure 1C). Also, the dry weather amplified the risk of poisoning—the shrinking water areas led to elevated cyanotoxin concentrations and an increasing demand for drinking water by the mammals. Our remote sensing analyses on the event area showed that, during March–July 2020, FAI (Floating Algae Index, an approximate indicator of cyanobacteria abundance) increased continuously along with shrinking water bodies (Figure S2). This demonstrates the increasing risk of cyanotoxin exposure associated with a drying trend of surface water cover.

Climate change as a risk amplifier

A critical question arising from the elephant mass die-off event in Botswana is how the ongoing climate change will influence the risks posed by cyanotoxins in the future. Our analysis identifies several "hotspots of cyanotoxin risks" in southeastern Africa where high megafauna diversity (including major elephant populations), high risks of exposure to cyanotoxins (MCs), and most historical cyanotoxin-related mortalities occur (Figure 1D). The first reported MC-attributed damage to human health under natural conditions also took place in this region (Zimbabwe).[8] Climate models project that, in the near future, this region will experience the highest warming rates across Africa, with a mean annual temperature increase of above 4°C and less precipitation than under the current conditions by 2070 predicted in a high-emission scenario SSP585 (Figure 1D; see also Figures S3 and S4). Of major concern is the circumstance that the poisoning risks will plausibly increase with the future warmer and drier climate. These hotter and drier climates will create more favorable conditions for cyanobacteria growth when both nutrient and cyanobacterial concentrations condense (Figure 1E).

With climate change, lake surface water temperatures are predicted to increase at a similar or even higher rate than the air temperatures.[9] Besides stimulating the release of toxins, warming will also promote dominance of a few highly toxic variants. At local scale, hot dry weather can drive more animals to gather more frequently around the remaining surface waters, which may accelerate eutrophication via feces and consequently further amplify the exposure risk (Figure 1C). In a worst-case scenario, the synergistic effects of warming and eutrophication promoting cyanobacteria growth and toxin release may create an existential risk for the vulnerable wildlife populations already subject to starvation and thirst induced by more frequent climate extremes.[10]

This study indicates an increased risk of mass die-off events with global warming, yet more research is needed to quantitatively predict the future (cyanotoxin-induced) mortality of African savanna elephants as well as other megafauna species that are prone to extinction with climate change. Interestingly, fossil records include evidence of prehistoric mass deaths of elephants and other megafauna in Pleistocene and Eocene lakes, which have been attributed to recurrent toxic cyanobacterial blooms, likely driven by climate change.[7] Further development of quantitative models on the link between cyanotoxins and animal death could provide robust explanations of these prehistoric mass mortality events as well as allow forecasts of future risks to wildlife populations.

In addition, cyanotoxin poisoning tragedies such as this tragic event may have unexpected cascading effects on humans and society. Thus, increasing exposure to cyanotoxins in polluted water will inevitably be harmful to the health and livelihoods of humans who rely on livestock and wildlife or use the polluted water for drinking or irrigation purposes. The substantial role of cyanotoxins in the Botswana die-off event emphasizes that more comprehensive and systematic (re-)assessments of the risks of cyanotoxins for both wildlife and humans are needed in the face of climate change to permit implementation of effective precautionary actions ameliorating the cyanotoxin threat to the vulnerable African socio-ecological systems.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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Supplemental Information

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Methods for climatic data processing and analyses

To investigate the climatic conditions associated with cyanobacterial blooms, temperature and precipitation records are examined. To account for potential observational uncertainty, multiple observational datasets are used. Global monthly temperature datasets used include: (1) GISS (NASA Goddard Institute for Space Studies; 2°X2°) and (2) BEST (Berkeley Earth Surface Temperature); 1°X1°.[1,2] Global monthly precipitation observation is from the GPCP (Global Precipitation Climatology Project); 2.5°X2.5°.[3] Monthly precipitation and evaporation data from the ERA5 reanalysis (0.25°X0.25°) are also used.[4]

Accumulated temperature for cyanobacteria is defined as follows[5,6]:

$$K = N(T - C)$$

where K is the accumulated temperature, C is the temperature threshold above which cyanobacteria recruit (C=9°C), N is the length of the cyanobacterial growing period (i.e. when $T>C$), and T is the mean temperature over the growing period. In this study, annual accumulated temperature is computed from preceding June to May (in °C days).

Likewise, the annual accumulated net precipitation is calculated from preceding June to May (in mm), which represents the availability of surface water. Here net precipitation (i.e. precipitation minus evaporation) is used so that the enhanced evaporation accompanying hot conditions is taken into account.

The temperature and precpitation records from different datasets consistently reveal the anomalous hot and dry conditions during 2019-2020 in Botswana and Zimbabwe (figure not shown). Thus, only the results from the GISS and ERA5 datasets are provided in the manuscript for brevity.

Methods for remote sensing analyses

NDWI (Normalized Difference Water Index) was calculated according to REF[7]:

NDWI = (GREEN-NIR)/(GREEN+NIR)

where GREEN and NIR represent green band and near infrared band of MSI and OLI. And pixels with NDWI greater than 0 are defined as constant water body.

FAI (Floating Algae Index) was calculated according to REF[8]:

FAI = RED - NIR'

NIR' = RED + [(SWIR-RED)]*[(λ(NIR)-λ(RED)/(λ(SWIR)-λ(RED))]

where RED, SWIR and NIR represent red band, near infrared band and shortwave infrared band of MSI and OLI. λ(RED), λ(NIR) and λ(SWIR) represent the center wavelength of red band, near infrared band and shortwave infrared band of MSI and OLI.

Methods for Figure 1 D

Response curve of growth rate of cyanobacteria to temperature was modified from REF[9]; Data on elephant density were collected from REF,[10] and data on mammal species richness were compiled based on their distribution range maps from the African Mammal Databank.

Text S1 Potential leading causes underlying the mysterious mass mortality.

Ruled-out causes

1 Poaching for ivory – carcasses intact.
2 Sabotage by farmers (nine commonly used pesticides) – lab test.
3 Starvation or dehydration – found in an area with an abundance of woodlands, 70% near waterholes and ponds.
4 Anthrax poisoning – differing from its selective effects on old and young individuals, carcasses of all ages found.

Possible causes

1 Cyanotoxins
– Lab test (posted by Botswana Department of Wildlife and National Parks) (*1*).
– Carcasses found in/near waterholes or ponds with heavy scum of cyanobacteria.
– Massive hemorrhage.
– Walk in circles and appear dizzy before suddenly dropping dead (sometimes face-first), typical neurological symptoms of (*2*,*3*).

2 Encephalomyocarditis virus (hemorrhagic septicemia, a rodent-borne virus infection)

– Neurological symptoms.
– Massive hemorrhage.

Related media reports:

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URL link for photos showing dead elephants in the Okavango Delta. https://www.reuters.com/article/us-botswana-elephants-idUSKCN24N2JK

Text S2 Concepts of cyanobacteria, cyanotoxin, and eutrophication.

Cyanobacteria

Cyanobacteria, also known as blue-green algae, are oxygen-producing bacteria and the Earth's oldest (~ 3.5 bya) organisms, with a major shaping effect on the origin of our modern-day biosphere through oxidization of the Earth's atmosphere.[11] Cyanobacteria occur throughout the world, especially in calm water rich in nutrients. Cyanobacteria can form dense blooms under nutrient-rich conditions, resulting in increased turbidity, smothering of submersed macrophytes, and oxygen depletion followed by massive deaths of fish and sensitive macroinvertebrates. Cyanobacteria can interfere with the recreational function of waters and their use for drinking water purposes by their generation of obnoxious taste and odor compounds. Cyanobacteria can also produce a variety of toxins, called cyanotoxins, which are detrimental and even lethal to birds, mammals and humans.[12] Cyanobacteria are particularly abundant in nutrient-rich and hot environments such as southeastern Africa.[13,14]

Cyanotoxins

Cyanotoxins can be classified into various types according to their modes of action and target cells and organs: hepatotoxins (the most frequently encountered), neurotoxins, dermatotoxins, and cytotoxins.[12,15] The symptoms of cyanotoxin poisoning include skin irritation, stomach aches, vomiting, nausea, diarrhea, fever, sore throat, and headache. The largest group of cyanotoxins is the cyclic heptapeptide hepatotoxins called microcystins (MCs), in which MC-LR is the best known and most toxic structural variant.[16] Microcystins predominantly cause liver injury.[17,18] An acute, lethal dose exposure can result in almost total breakdown of the tissue architecture and blood accumulation in the liver, where blood loss from the circulation causes death to the animal. Besides hepatotoxicity and tumor promotion, MCs may also induce neurotoxicity, reproductive toxicity, genotoxicity, and potential carcinogenicity.[19–22] Despite their aquatic origin, most cyanotoxins tend to be more hazardous to terrestrial mammals than to aquatic biota.[23] Furthermore, the proportion of toxic species or strain and release of toxins tend to increase with global warming.[24,25]

Eutrophication

Eutrophication is an enrichment process in aquatic ecosystems created by excessive loading of nutrients (e.g. nitrogen and phosphorus), which promotes massive growth of phytoplankton, including cyanobacteria. A shift from a macrophyte-dominated state to a phytoplankton-dominated state will happen when nutrient loading surpasses a critical level.[26,27] Human activities are a common cause of eutrophication, with both point-source and non-point-source discharges accelerating the rate at which nutrients enter ecosystems. In parts of Africa, wild mammals such as hippos contribute significantly to the nutrient loading of freshwater ecosystems by moving nutrients from terrestrial to aquatic ecosystems, and by foraging on land, whereas much non-feeding time is spent in water.[28] Therefore, savanna waters can become highly eutrophic also without the influence of human activities.

Text S3 Derivation of the tolerable daily intake and half lethal dose of microcystin for African savanna elephant

Provisional guideline of cyanotoxins by World Health Organization (WHO)

In order to set safe levels of cyanotoxins, extensive experimental studies on their toxicity have been carried out. Microcystin-LR (MC-LR), the most frequently occurring and most toxic form, is also the most studied. As direct assessment of the risk of cyanotoxin exposure to humans is not feasible, animal studies have been conducted to address the issue. Among these, a 13-week study of mice exposed to pure MC-LR (by gavage) was considered suitable for deriving a guideline value for MC-LR.[29] Based on liver histopathology and serum enzyme level changes, a NOAEL (No Observed Adverse Effect Level) of 40 μg kg^{-1} bw day^{-1} was determined. By applying a total uncertainty factor of 1,000, a provisional TDI (Tolerable Daily Intake) of 0.04 μg kg^{-1} bw day^{-1} was established as the guideline of safe level.[23] A level of 1.0 μg L^{-1} was then adopted as the provisional guideline based on an average adult body weight of 60 kg and an average water intake for adults of 2 liters per day. For acute exposures, a half lethal dose (LD50) of 5 mg kg^{-1} bw, administered by gavage, is commonly accepted based on tests on one mouse strain.[29]

TDI and LD50 for African savanna elephants

We derived TDI and LD50 for African savanna elephant (*Loxodonta africana*) as follows, based on an average elephant (5000 kg in body weight, 200 L water ingestion per day)[30]:

$TDI_{L.africana}$

$= TDI_{WHO2011} * bw_{L.africana}/\text{Water ingestion}$

$= 0.04\ \mu g\ kg^{-1}\ bw\ day^{-1} * 5000\ kg/200\ L$

$=1.0\ \mu g\ L^{-1}\ d^{-1}$

$LD50_{L.africana}$

$= LD50_{WHO2011} * bw_{L.africana}/\text{Water ingestion}$

$=5\ mg\ kg^{-1} * 5000\ kg/200\ L$

=125 mg L

Table S1. Historic events of cyanotoxin-caused animal mortality

Year	Country	Location	Cyanobacteria species	Toxin	Impacts reported		Reference number
					Death	Illness	
1913-1943	South Africa	Free State and Southeast Transvaal	*Microcystis aeruginosa*	microcystin	thousands of livestock (horses, sheep, cattle and rabbits)		31
1942	South Africa	Vaal Dam	*Microcystis* sp.	microcystin	thousands of cattle and sheep		32,33
1973-1974	South Africa	Hartbeespoort Dam	*M. aeruginosa*	microcystin	cattle		34
1979	South Africa	Klipvoor Dam	*M. aeruginosa*	microcystin	3 white rhinoceroses		35
1980	South Africa	Vaal Dam	*M. aeruginosa*	microcystin	cattle		31
1984	South Africa	William Pretorius Game Reserve	*M. aeruginosa*	microcystin	several black wildebeests		35
1987	South Africa	Eastern Transvaal	*M. aeruginosa*	microcystin	47 cattle		36
1989	South Africa	Reservoir Bloemhof Dam	*M. aeruginosa*	microcystin	7 giraffes		37
1989	South Africa	Reservoir Klipdrif Dam	*M. aeruginosa*	microcystin	livestock	livestock	38
1993	South Africa	Malmesbury	*Nodularia spumigena*	nodularin	3 cattle	10 cattle	39
1994	South Africa	Lake Zeekoevlei	*N. spumigena, M. aeruginosa*	nodularin, microcystin	dog (bull terrier bitch)		39,40
1994	South Africa	Malmesbury	*N. spumigena*	nodularin	34 cattle		39
1994	South Africa	Paarl	*M. aeruginosa*	microcystin	11 sheep	30 sheep	39
1996	South Africa	Kareedouw	*Oscillatoria* sp.	microcystin	290 dairy cows	70 stock	41
1998	South Africa	Erfenis Dam	*Anabaena* spp.	cyanotoxin	livestock		31,42

2000	South Africa	Orange River system downstream of the confluence with the Harts River	*Cylindrospermopsis raciborski Anabaena* sp., *Oscillatoria* sp.	not available	fish		41,43
2001	Kenya	Lake Bogoria	*Phormidium terebriformis, O. willei, Spirulina subsalsa, Synechococcus bigranulatus*	microcystin, anatoxin	mass lesser flamingos		44
2005	South Africa	Nhlanganzwane Dam	*M. aeruginosa*	microcystin	7 white rhinoceroses, 2 lions, 2 cheetahs, 9 zebras, 23 wildebeest, 1 hippopotamus, 1 giraffe, 5 buffalos, 1 warthog, 1 Kudu		45
2007	South Africa	Nhlanganzwane Dam[a]	*M. aeruginosa*	microcystin	15 white rhinoceroses, 10 zebras, 10 blue wildebeests	wild animals	43,45,46
2007	South Africa	Sunset Dam	*M. aeruginosa*	microcystin	1 white rhinoceros, 6 impalas		46
2008	South Africa	Lake Loskop Dam	*M. aeruginosa, M. flos-aquae*	microcystin	fish		47
2008	South Africa	Shilolweni Dam	*Microcystis* sp.	microcystin	70 wild animals (zebras, wildebeest, impalas, white rhinoceroses)		45
2008	Botswana	Tuli block	*Oscillatoria* sp.	microcystin	70 bushbucks and impalas		43
2010	South Africa	Shilolweni Dam	*Microcystis* sp.	microcystin	17 zebras, 7 wildebeests, 3 white rhinoceroses		45

Table S2. List of published concentrations of microcystins (MCs) /manuscripts on African waters, with calculation of daily intake by African savanna elephant per body weight based on an average individual.

Code	Zone	Country	Waters	MCs, µg/L	Daily intake by African elephant per body weight (MCs*200L/5000 kg), µg kg^{-1}bw	Reference number
1	Northern	Algeria	Ain Zada Dam	69.3	2.8	48
2	Northern	Algeria	Cheffia Dam	28.9	1.2	49
3	Northern	Algeria	Lake Oubcim	46.2	1.8	14
4	Northern	Egypt	Nile River	7.1	0.3	50
5	Northern	Morocco	Lake Lalla Takerkoust	19.9	0.8	14
6	Western	Ghana	Kpong Dam	0.03	0.001	51
7	Western	Ghana	Weija Dam	3.21	0.1	51
8	Western	Nigeria	Zaria aquaculture ponds	6.34	0.3	14
9	Eastern	Ethiopia	Lake Chamo	28.9	1.2	14
10	Eastern	Ethiopia	Lake Chamo	6.1	0.2	52
11	Eastern	Ethiopia	Lake Koka	3.9	0.2	14
12	Eastern	Ethiopia	Lake Koka	51	2.0	52
13	Eastern	Ethiopia	Lake Langano	1.3	0.1	52
14	Eastern	Ethiopia	Lake Ziway	1.3	0.1	52
15	Eastern	Kenya	Lake Simbi	29163	1167	53
16	Eastern	Kenya	Lake Sonachi	64.8	2.6	53
17	Eastern	Kenya	Lake Victoria, Nyanza Gulf	0.4	0.02	54
18	Eastern	Kenya	Nakuru oxidation ponds	1.72	0.1	14
19	Eastern	Kenya	Nyanza Gulf	82.5	3.3	14
20	Eastern	Kenya, Tanzania, Uganda	Lake Victoria	1	0.04	55
21	Eastern	Uganda	Lake Saka	31783	1271	14

22	Eastern	Uganda	Murchison Bay	3.1	0.1	[14]
23	Southern	Mozambique	Maputo and Gaza provinces	7.31	0.3	[13]
24	Southern	South Africa	Hartbeespoort Dam	580	23.2	[56]
25	Southern	South Africa	Hartbeespoort Dam	1965	78.6	[41]
26	Southern	South Africa	Hartbeespoort Dam	1861	74.4	[41]
27	Southern	South Africa	Hartbeespoort Dam	1698	67.9	[41]
28	Southern	South Africa	Hartbeespoort Dam	414	16.6	[41]
29	Southern	South Africa	Hartbeespoort Dam	1538	61.5	[41]
30	Southern	South Africa	Hartbeespoort Dam	1314	52.6	[41]
31	Southern	South Africa	Hartbeespoort Dam	474	19.0	[41]
32	Southern	South Africa	Hartbeespoort Dam	4.65	0.2	[57]
33	Southern	South Africa	Hartbeespoort Dam	12300	492	[58]
34	Southern	South Africa	Hartbeespoort Dam	44878	1795	[59]
35	Southern	South Africa	Klipvoor Dam	22330	893	[41]
36	Southern	South Africa	Klipvoor Dam	21100	844	[41]
37	Southern	South Africa	Loskop Dam	0.36	0.01	[14]
38	Southern	South Africa	Loskop Dam	0.09	0.004	[14]
39	Southern	South Africa	Loskop Dam	3.173	0.1	[60]
40	Southern	South Africa	Makhohlola Dam	0.2	0.01	[46]
41	Southern	South Africa	Makhohlolo Dam	3.38	0.1	[14]
42	Southern	South Africa	Mpanamana Dam	1	0.04	[46]
43	Southern	South Africa	Nhlanganzwane Dam	24951	998	[14]
44	Southern	South Africa	Nhlanganzwane Dam	103160	4126	[46]
45	Southern	South Africa	Nhlanganzwane Dam	23720	949	[47]
46	Southern	South Africa	Rietvlei Dam	198	7.9	[41]
47	Southern	South Africa	Rietvlei Dam	184	7.4	[41]
48	Southern	South Africa	Roodeplaat Dam	981	39.2	[41]
49	Southern	South Africa	Sunset Dam	124460	4978	[46]

50	Southern	South Africa	Sunset Dam	1110	44.4	[46]
51	Southern	Zimbabwe	Lake Chivero	19.86	0.8	[61]
Average	Northern Africa			34.28		
	Western Africa			3.19		
	Eastern Africa			4371		
	Southern Africa			13423		

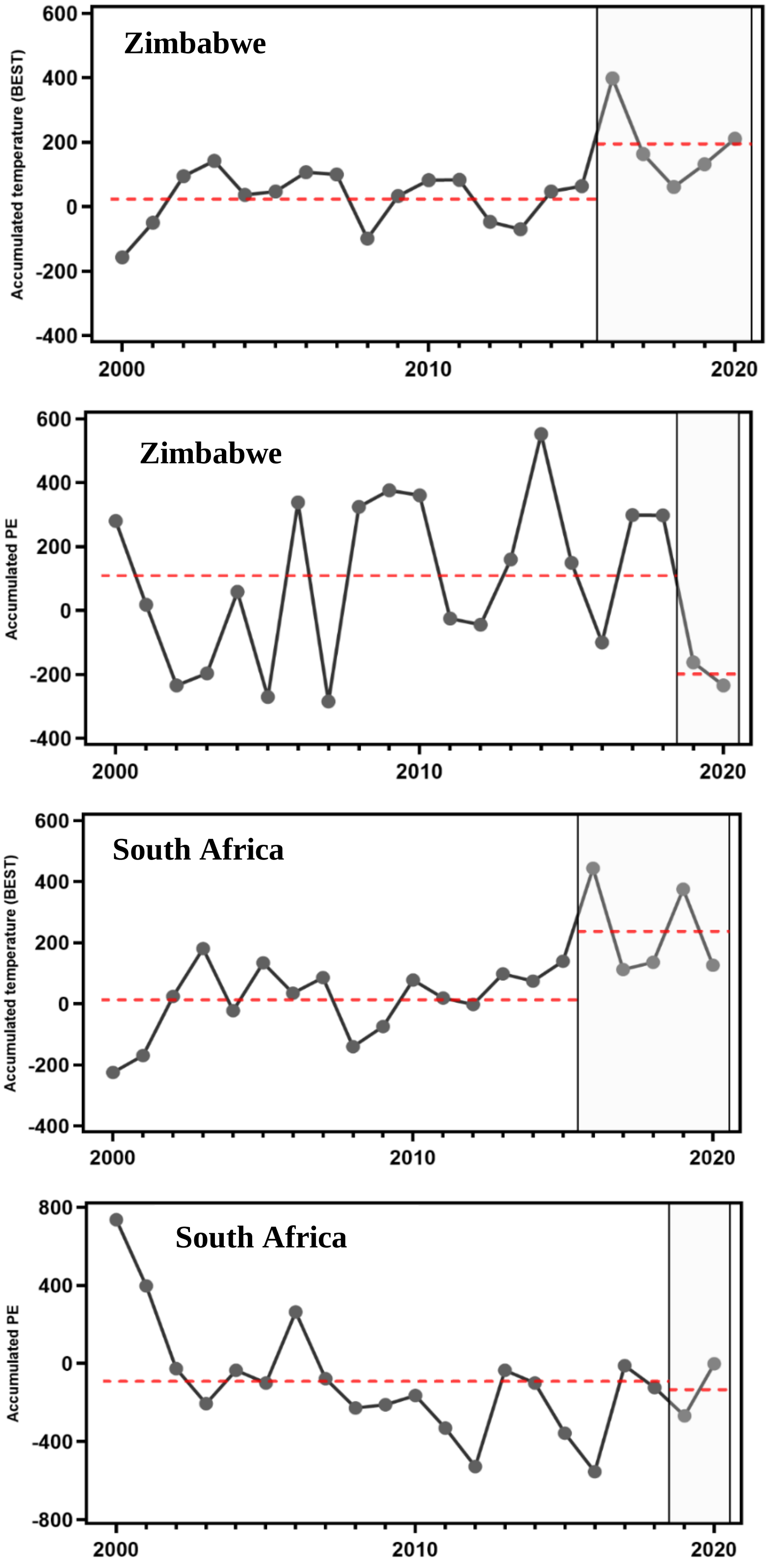


Fig. S1. Anomalies (against the 1986-2005 baseline climatology) of accumulated (from preceding June to May) temperature (℃ days) and net precipitation (precipitation minus evaporation, mm) during 2000-2020 in Zimbabwe and South Africa

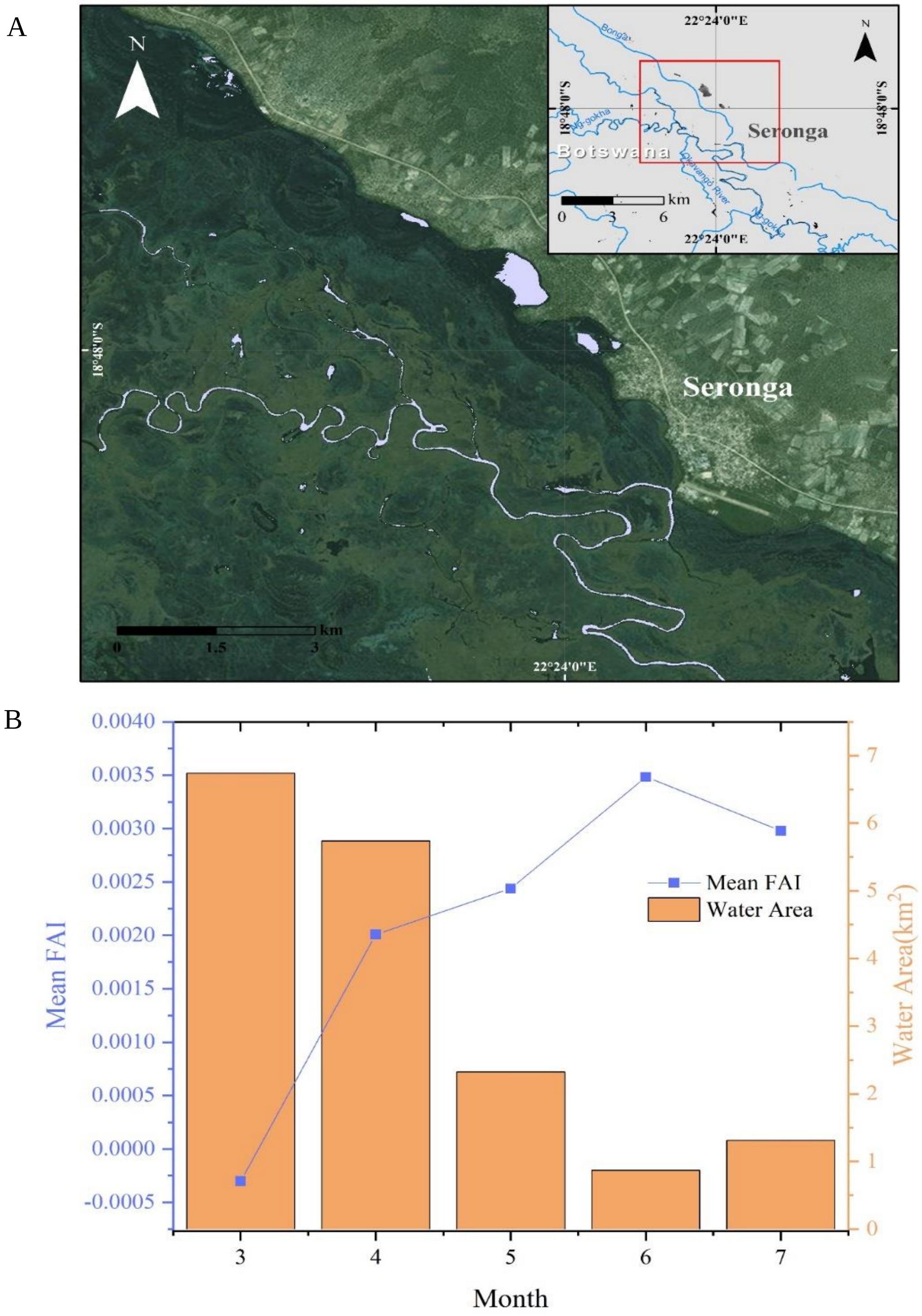
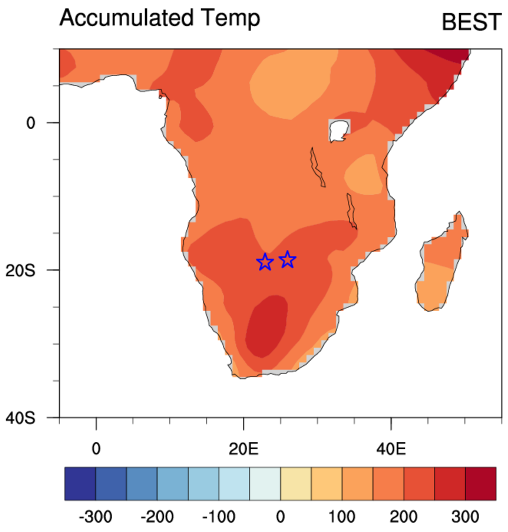
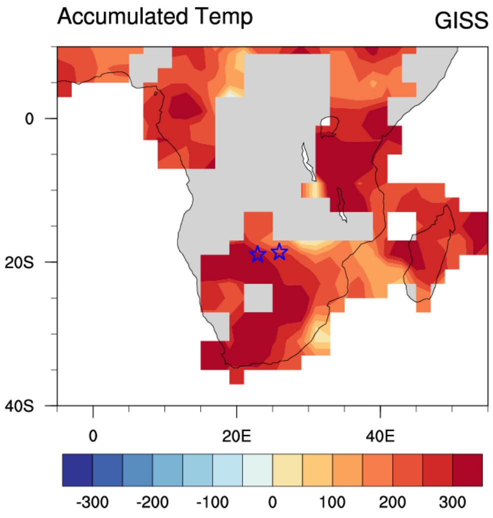


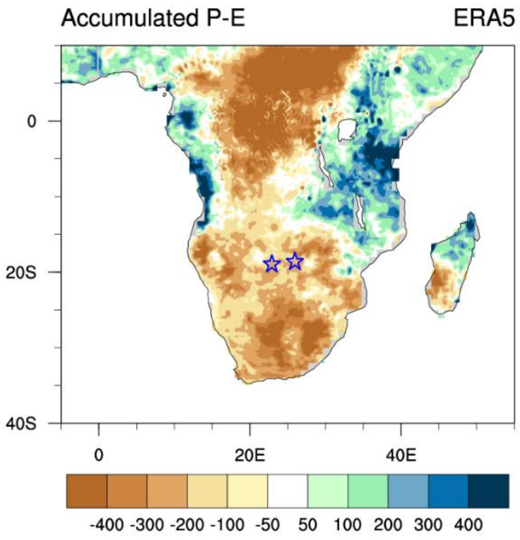
Fig. S2. The zone (framed) where most elephant mortality events took place (north-west of Seronga, Okavango Delta, Botswana) and for which the remote sensing analyses were performed (A) and changes in water area and floating algae index (FAI) in the framed area during the period of elephant death (March-July, 2020). The constant water extent area was extracted by NDWI with Sentinel-2/MSI images during the period of elephant death. Changes in water area and floating algae index (FAI) in the framed area were obtained Sentinel-2/MSI and Landsat-8/OLI with at the same time.



A. Annual accumulated effective temperature (from preceding June to May; ℃ days) during 2015-2020 relative to the 1986-2005 baseline climatology from the BEST data. Stars denote Botswana (18.84S, 22.90E) and Zimbabwe (18.51S, 25.95E).



B. Same as A but for temperature derived from the GISS data.



C. Same as A but for annual accumulated net precipitation (precipitation minus evaporation, mm) during 2019-2020 derived from the ERA5 data.

Fig. S3. Spatial distribution of extreme hot and dry climatic conditions associated with the deaths of African savanna elephants in 2020.

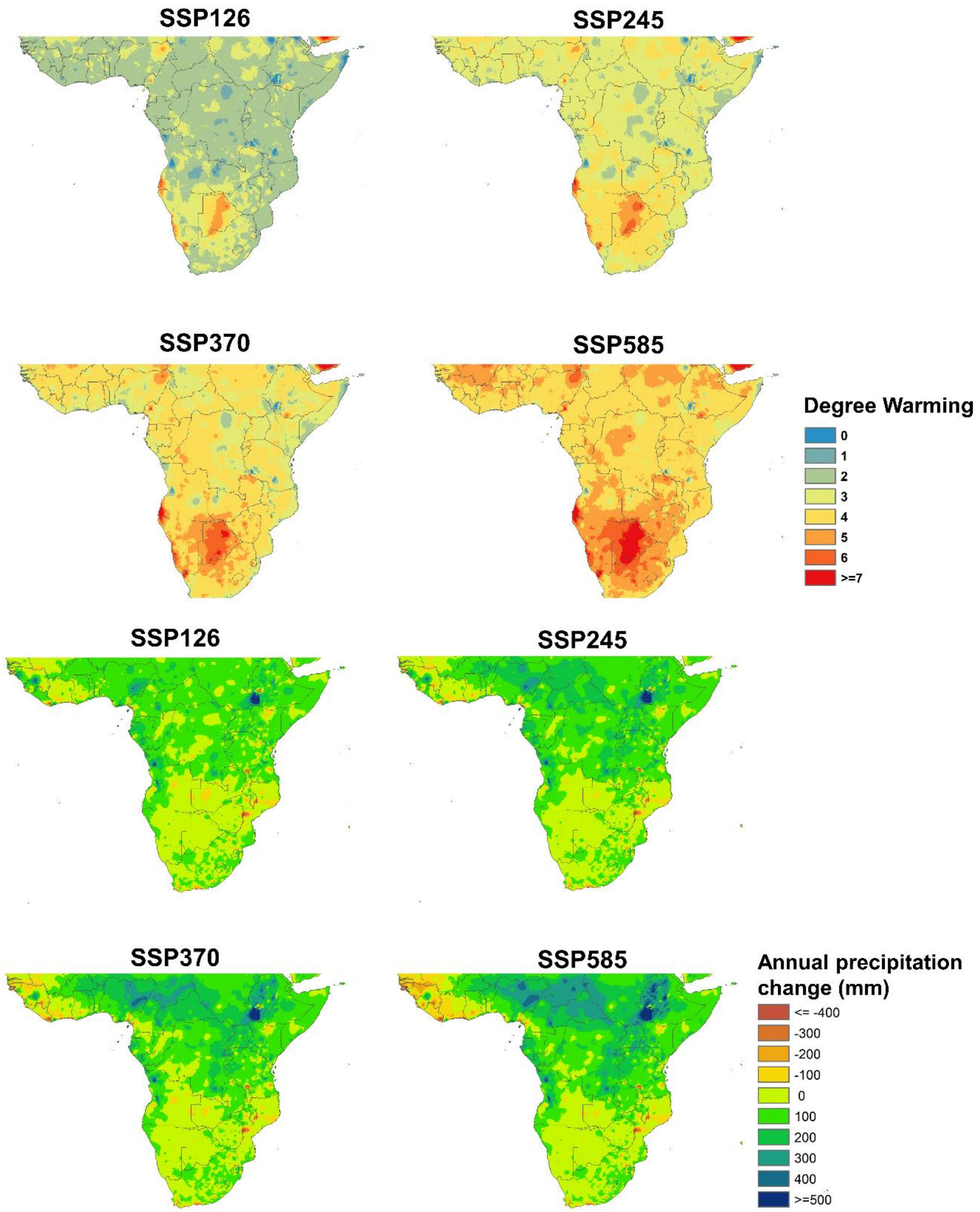


Fig. S4. Changes in mean annual temperature and precipitation around 2070, with southern Africa identified as a hotspot of climate warming and drying. The mean annual temperature and precipitation data projected for the time period of 2061-2080 are available from 9 CMIP6 global climate models (BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, GFDL-ESM4, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, MRI-ESM2-0) for 4 Shared Socio-economic Pathways (SSP126, 245, 370 and 585). WorldClim v2.1 data is used as the current baseline. The climate data with a spatial resolution of ~10 km is downloaded from the WorldClim website.

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