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Socio-political and ecological fragility of threatened, free-ranging African lion populations

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Lions are one of the world's most iconic species but are threatened with extinction. Developing effective range-wide conservation plans are crucial but hampered by the relative lack of knowledge on specific threats facing each population and the socio-political context for conservation. Here, we present a range-wide examination of the relative fragility of lion populations, examining socio-political factors alongside ecological ones. We found Ethiopia's Maze National Park had the most ecologically fragile geographic population while Kavango-Zambezi was the least. At a country level, lion populations had highest ecological fragility in Cameroon and Malawi. When we examined socio-political fragility, Somalia was the most fragile lion range country, followed by South Sudan. When socio-political and ecological fragility were combined, lion populations in Maze National Park and Bush-Bush (Somalia) and more broadly, Somalian and Malawian lion populations were the most fragile. These insights should help inform more nuanced and appropriately targeted lion conservation plans.

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The African lion (Panthera leo) is one of the world's most iconic and charismatic species[1] and much of the global public imbues them with a high existence value and is passionate about their conservation[2]. Even in those places where lions pose a very real threat to peoples' livelihoods and sometimes their lives, they often have high cultural value amongst local communities, particularly traditional pastoralists[3]. As apex predators, lions also have substantial ecological value, and the removal of top carnivores from ecosystems can have significant and long-lasting negative ecological impacts[4]. In addition to their cultural and ecological significance, lions have high economic value, and are one of the top attractions for both photographic tourists and trophy hunters to the countries where they remain[5].

Despite their ecological, economic and existence value, lions have undergone striking declines in both geographic range and population size over recent decades. The latest range-wide estimates from 2023 estimate a remaining population between 20,000 and 25,000 African lions[6]. Alarmingly, lions are considered to have been extirpated from at least 92% of their historic range-wide distribution[6,7]. Lions are currently listed as Vulnerable based on an estimated 36% decline in the species range in the last 21 years[6]. As lions depend upon their habitat, it is therefore suspected that a similar population reduction has occurred[6]. This listing suggests a high risk of extinction in the wild[6,7]. However, there is a marked dichotomy in population trends between countries and regions - in four southern African countries (Botswana, Namibia, South Africa and Zimbabwe) lion populations increased by 12% between 1993 and 2014, but in the remainder of African range, sample lion populations declined by 60%[7]. Lions in West and Central Africa, meanwhile, have undergone particularly severe declines (estimated to be 66%[7]) and West African lions meet the criteria of being Critically Endangered, with fewer than 250 mature lions remaining[8].

The specific threats causing these declines vary substantially across lion range countries and regions. For example, in Eastern and Southern Africa, the most severe threats to lions include poaching of prey for bushmeat, indiscriminate killing (usually due to conflict with livestock-keepers), and small population size[9–11]. Meanwhile, in West and Central Africa the three primary threats are prey depletion, small population size and livestock encroachment[8,12]. Protected areas are vital strongholds for lions[13], but are not always effective in conserving them. For example, bushmeat poaching with snares most likely led to local extinctions of lions in Nsumbu National Park in Zambia (Dröge. pers. comm. 2022) while populations in Limpopo National Park in Mozambique have been driven to near extinction by increasing poaching for lion parts[14]. A substantial portion of lion range also falls outside of protected areas, exposing lions to higher risks of conflict, habitat loss, prey loss and other threats[7,15,16].

Although in some cases the direct cause of death of an individual lion may be easy to identify e.g., poisoning, the underlying drivers of that poisoning can be more difficult to understand. Human-lion conflict is described as a multi-dimensional and 'wicked problem,' with no easy solution and requiring multi-disciplinary and interdisciplinary research to understand[17,18]. However, human-lion conflict is not the only threat in which understanding the underlying drivers of a specific threat is important[16]. Conservation threats in general are driven and affected by a multitude of wider-scale socio-political factors[16,19–21]. Key factors include poverty, governance (particularly corruption), wildlife policies, human pressures, and the extent of armed conflict[8,12,20,21], yet they are rarely explicitly considered in conservation planning. The IUCN called for this broader perspective to be considered in lion conservation over 15 years ago[12,22], yet it is often still ignored in conservation assessments[20]. We argue the time has come to finally include and compare the socio-political contexts in which remaining lion populations survive. Assessing socio-political alongside ecological pressures is essential to understand threats and to develop effective conservation strategies and priorities.

Here, using recent, available data for extant free-ranging African lion populations, we examine their ecological and socio-political fragility at both a national and geographic population scale. Fragility is defined as a species or ecosystem that are vulnerable to damage/harm or even extinction[23]. This approach provides a novel tool for understanding the fragility of lion populations and range countries and will inform decision-makers regarding choices around lion conservation, such as funding strategies and priorities for action. For instance, different lion populations could be compared to better understand ecological factors that may affect population persistence as well as the socio-political factors that may enable successful conservation action. This model also has applicability for many other taxa, as remaining wildlife populations are subject to increasing anthropogenic threats from both an ecological and socio-political perspective.

Our analyses indicated 62 free-ranging geographic lion populations remain across 25 range countries. When transboundary populations were split according to national boundaries, we identified 84 national lion populations. Maze National Park in Ethiopia was identified as the most ecologically fragile population at both a geographic and national level. This can largely be attributed to intense edge effects from high densities of both cattle and people. When assessing at the national level, Cameroonian and Malawian lion populations were most ecologically fragile due to their small populations and isolation from other lion populations. Somalia was the most fragile lion range country from a socio-political perspective. Maze National Park and Bush-Bush (Somalia) were found to be the most fragile overall when ecological and socio-political fragility scores were combined.

Results

Our analyses indicated 62 free-ranging geographic lion populations across 25 range countries (Table 1, Supplementary Table 1, Supplementary Table 2, and Supplementary Fig. 1). This resulted in 84 national lion populations when transboundary populations were split according to national boundaries (Table 3, Supplementary Table 3, Supplementary Table 4, and Supplementary Fig. 2).

Ecological characteristics and fragility of geographic lion populations

Of the 62 geographic populations, 41.9% ($n = 26$) were estimated to have 50 or fewer lions (Supplementary Fig. 3). Another ten (16.1%) of Africa's geographic populations had between 51 and 100 lions and only seven populations (11.3%) were estimated to have 1,000 or more lions (Supplementary Fig. 3). The median category for population size was 51–100 lions, while the mode was 0–50.

The 62 geographic populations ranged in size from 156 km^2 (Manyara Ranch) to 249,754 km^2 (Kavango-Zambezi in Angola, Botswana, Namibia, Zambia, and Zimbabwe) with a mean of 30,575 km^2 and a median of 7,442 km^2 (Supplementary Table 2). Seven populations (10.7%) spanned over 100,000 km^2 (Etosha-Kunene, Katavi-Ruaha, Kavango-Zambezi, Luangwa-Mana-Tchuma Tchato, Maasai Steppe and Selous-Niassa). Based on WDPA data (UNEP-WCMC 2018), twelve of the populations (19.4%) were completely encompassed by existing protected areas with IUCN categories I-IV, while an additional 17 populations (27.4%) had at least 50% of their area covered by existing protected areas (Supplementary Table 1). However, nine populations (14.5%) did not appear to be covered by existing protected areas with categories I-IV to any extent. Collectively, these nine

Table 1 Socio-political, ecological and overall fragility scores of 62 geographic lion populations listed from most to least fragile.

	Population	Rescaled ecological fragility score	Rescaled socio-political fragility	Overall fragility		Population	Rescaled ecological fragility score	Rescaled socio-political fragility	Overall fragility		Population	Rescaled ecological fragility score	Rescaled socio-political fragility	Overall fragility
1	Bush-bush	0.53	1.00	1.53	22	Kasungu	0.46	0.54	1.00	43	Niokolo-Koba	0.45	0.35	0.80
2	Maze	1.00	0.49	1.49	23	Afar-Awash	0.48	0.49	0.97	44	Meru Conservation Area	0.50	0.23	0.73
3	Boma National Park	0.35	0.88	1.23	24	Welmel-Genale	0.45	0.49	0.94	45	Laikipia-Samburu-Marsabit	0.48	0.23	0.71
4	Garamba Complex	0.51	0.72	1.23	25	Bale	0.45	0.49	0.94	46	Lavushi Manda	0.44	0.27	0.71
5	Toro-Semiliki	0.70	0.49	1.19	26	Dinder, Alatash, Bejemis & surroundings	0.45	0.49	0.93	47	Southern Maasai Steppe	0.47	0.23	0.70
6	Nechisar	0.70	0.49	1.19	27	Murchison Falls	0.44	0.49	0.93	48	Greater Mapungubwe	0.37	0.32	0.70
7	Lake Manyara	0.94	0.23	1.17	28	Ogaden	0.44	0.49	0.93	49	Liuwa Plain	0.42	0.27	0.70
8	Bili-Uere Complex	0.44	0.72	1.16	29	Magoe	0.51	0.40	0.91	50	Bubye Valley	0.36	0.33	0.69
9	Yankari	0.52	0.64	1.16	30	Benoue Complex	0.45	0.45	0.90	51	Udzungwa Mountains	0.45	0.23	0.68
10	Integral Nature Reserve and the Luando	0.44	0.70	1.14	31	Akagera	0.38	0.52	0.90	52	Greater Kafue Ecosystem	0.37	0.27	0.64
11	Liwonde and Mangochi	0.60	0.54	1.13	32	Gambella	0.40	0.49	0.89	53	Moyowosi-Kigosi	0.40	0.23	0.63
12	Chebera Churchura, Kaffa,	0.64	0.49	1.13	33	W-Arly-Pendjari	0.43	0.45	0.88	54	Luangwa-Mana-Tchuma Tchato	0.19	0.41	0.60
13	Greater Virunga	0.58	0.54	1.12	34	South Omo Ecosystem	0.37	0.49	0.86	55	Greater Limpopo	0.16	0.40	0.56
14	Zakouma NP and Surrounds	0.42	0.69	1.11	35	Gorongosa-Marromeu	0.46	0.40	0.86	56	Kavango-Zambezi	0.00	0.46	0.46
15	Chinko and surroundings	0.40	0.68	1.08	36	Swaga Swaga	0.61	0.23	0.84	57	Katavi-Ruaha	0.20	0.23	0.43
16	Kainji Lake	0.44	0.64	1.08	37	Kidepo Valley	0.34	0.49	0.84	58	Maasai Steppe	0.07	0.34	0.41
17	Bamingui-Bangoran	0.40	0.68	1.08	38	Borana and South Omo Ecosystem	0.32	0.49	0.81	59	Kgalagadi	0.22	0.19	0.41
18	Waza	0.62	0.43	1.06	39	Manyara Ranch	0.57	0.23	0.80	60	Selous Niassa	0.00	0.38	0.38
19	Babille/ Eastern Hararghe	0.54	0.49	1.03	40	Burigi-Chato	0.57	0.23	0.80	61	Etosha-Kunene	0.34	0.03	0.38
20	Maokomo	0.53	0.49	1.02	41	Chizarira-Chirisa	0.47	0.33	0.80	62	Hluhluwe-Umfolozi	0.38	0.00	0.38
21	Vwaza Marsh	0.47	0.54	1.00	42	Saadani	0.57	0.23	0.80					

populations represented 64,116 km^2 (4.0%) of lion range and less than 1,000 lions ($n = 790$).

Lion populations appeared to be severely depleted compared to their predicted carrying capacity. The populations examined here could potentially hold over four times as many lions (approximately 100,000) based on ecological characteristics[24,25] (Supplementary Fig. 4). On average, lions were estimated to be at around 33.3% (range 1.9% − 328.2%) of predicted carrying capacity (Supplementary Table 2). Almost a third of populations ($n = 20$, 32.3%) maintained lions at less than 10% the predicted carrying capacity, while only three populations (5%) had lions at between 50 and 100% of carrying capacity (i.e., Akagera, Greater Limpopo, Lake Manyara). In addition, five populations (8.1%) had lion populations exceeding carrying capacity, ranging from 121.3% to 328.1% of the predicted level (i.e., Bubye Valley Conservancy, Greater Mapungubwe, Hluhluwe-Umfolozi, Kidepo Valley and Manyara Ranch).

In terms of connectedness, the most well-connected populations were in East Africa, such as the Southern Maasai Steppe, Katavi-Ruaha and Selous-Niassa. On the other hand, some populations were critically isolated (i.e., the bottom 5%) with almost no connectedness, such as Niokolo-Koba, Hluhluwe-Umfolozi and Luando Integral Nature Reserve (Supplementary Table 1). Both human and cattle densities tended to be higher in the Horn of Africa, particularly in Ethiopia, while human and cattle densities were generally lower across lion populations in Southern Africa (Supplementary Table 1).

Ethiopia's Maze National Park lion population was the most ecologically fragile, mainly due to high cattle and human densities within lion range (Fig. 1, Fig. 2, and Fig. 3). Other ecologically fragile geographic populations were Lake Manyara, Nechisar and Toro-Semiliki (Table 1, Fig. 2, and Fig. 3). Meanwhile, the lion populations in Selous-Niassa (Tanzania and Mozambique) and Kavango-Zambezi (Angola, Botswana, Namibia, Zambia and Zimbabwe) were the least ecologically fragile (Fig. 1, and Fig. 2), mainly due to their large sizes and relatively large lion populations, although their fragility scores were increased by relatively low protected area coverage (Fig. 1).

Ecological characteristics and fragility of national lion populations and lion range countries

The 62 geographic populations were split into 84 national populations and subpopulations (if a geographic population was split across 2 or more countries, we called each country-level population a national population or a 'subpopulation') (Table 2, Supplementary Fig. 2, Supplementary Table 3, and Supplementary Table 4). The Selous-Mikumi and Okavango-Chobe subpopulations emerged as the least ecologically fragile, with Lake Manyara and Maze the most fragile (Fig. 2., Table 2, Supplementary Table 3, and Supplementary Table 4).

Fragility score of lion populations and subpopulations were then averaged (if a country had >1 population) and national scores compared (Table 2). Based on the data available here, six (24%) of the 25 lion range countries had a total of fewer than 50 lions and eight countries (32%) had 1,000 or more (Supplementary Fig. 3). Over half of Africa's remaining lion range countries ($n = 14$, 56%) each supported less than 1% of the overall lion population examined in this study (Table 3). Current available data (which is often very poor) suggested that Tanzania had by far the largest number of lions, with over 8,000 (34% of the study total), and just two countries (Tanzania and Botswana) accounted for almost half (48%) of the total number of lions examined.

Lion range per country varied from just over 1,000 km^2 in Rwanda to over 383,503 km^2 in Tanzania (Table 3). Range countries formally protected on average 62.9% of their area occupied by resident lions, although this varied considerably, from 0% in Somalia to 100% or just shy of this in Senegal, South Sudan, Sudan, Uganda and Rwanda (Table 3). More than a quarter ($n = 7$; 28%) of range countries' lion populations were at <10% of potential ecological carrying capacity, with South African populations existing at the highest percentage of carrying capacity and Angola the lowest (Table 3, Supplementary Fig. 4). Edge effects on lion populations were particularly high in Democratic Republic of Congo, Malawi and Uganda, while they were lowest in Botswana, Central African Republic and Namibia (Table 3). Senegal's only lion population was the most isolated, with no other populations within 350 km, while Tanzania and Zimbabwe's lion populations were the most well-connected (Table 3). Human population density within lion population areas was highest in Tanzania, followed by Ethiopia, while it was very low in both Botswana and Central African Republic (Table 3). Cattle density within lion population areas was particularly high in Somalia, followed by Ethiopia, while this was lowest in Angola, the Central African Republic and Niger (Table 3).

When considering national lion populations, Cameroon, Malawi and Ethiopia had the most ecologically fragile lion populations (Fig. 4 and Table 3), with populations in the first two countries suffering from large edge effects and small population sizes relative to potential carrying capacity (Fig. 1 and Table 3). National lion populations in South Sudan, Botswana and Angola were the least fragile (Fig. 1, Fig. 2, and Table 3). In Botswana, high lion population numbers and the population size relative to expected carrying capacity contributed to less fragile scores (Fig. 1). South Sudan had only a single population, within Boma National Park, which was less fragile primarily because it had low human and cattle densities within and surrounding the lion area and it was well-connected to other populations in Ethiopia (Fig. 1). Angola's two populations both had low human and cattle densities within and surrounding the lion areas.

Socio-political characteristics and fragility

The 25 range countries assessed here varied markedly in terms of characteristics across the four socio-political categories (Supplementary Table 5). Note that these scores were calculated at the national level such that all lion population(s) within the country all had the same socio-political score. On our indices, Somalia was the most socio-politically fragile lion range country (Fig. 4, and Table 3, and Supplementary Table 5). It scored above average in fragility for three of the four categories and was particularly vulnerable in terms of the governance and conservation policy categories (Fig. 5, and Supplementary Table 5). The next most fragile country was South Sudan, where poor scores in both governance and conservation policy categories contributed most to its high fragility (Fig. 2, Fig. 5, and Supplementary Table 5). Botswana, South Africa and Namibia were ranked as the least socio-political fragile lion range countries, with relatively good governance and economic scores compared to the other countries examined (Fig. 2, and Supplementary Table 5).

Socio-political fragility of geographic lion populations was very similar to the results at the national level. Geographic populations largely within Botswana (Kgalagadi and Greater Mapungubwe) were the least fragile. On the other hand, Bush-Bush is entirely within Somalia, the most fragile range country, and therefore is also the most fragile geographic population. Similarly, Boma is the second most fragile population as it is entirely within the second most fragile country, South Sudan.

Overall fragility of lion populations

Combining the ecological and socio-political scores of each range country provided an overall fragility score. This revealed Somalia as

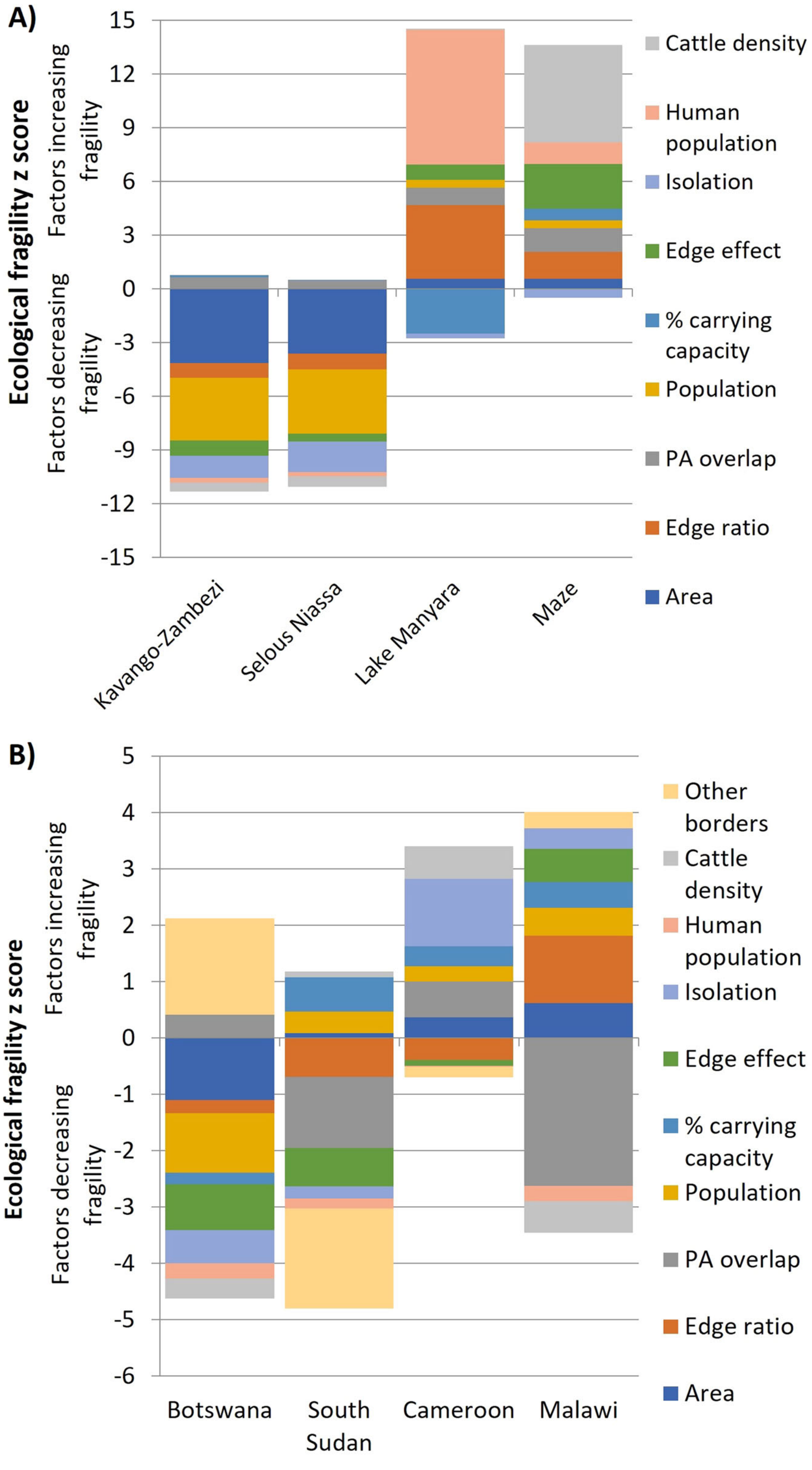

Fig. 1 Factors contributing towards ecological fragility scores. Factors which rank positively on the y axis increase ecological fragility for those populations, while those which rank negatively reduce ecological fragility. Total z-score is the sum of both positive and negative values. **A** Selous-Niassa, Kavango-Zambezi were the least ecologically fragile geographic populations while Lake Manyara and Maze the most. **B** Botswana and South Sudan were the least ecologically countries and Cameroon and Malawi the most fragile.

the most fragile lion range country overall, while Botswana was the least fragile (Fig. 4, and Table 3). Almost half of range countries ($n = 12$; 48%) scored as highly fragile (above mean) in both metrics: together, those countries represented 39.0% (735,984 km^2) of lion range.

There was an evident geographic pattern in terms of the location of the most fragile national populations or subpopulations. Those populations with above-average overall fragility were mostly in the northern parts of the lion's remaining range (e.g., Bush-Bush, Afar, Awash and Waza), while the least fragile populations

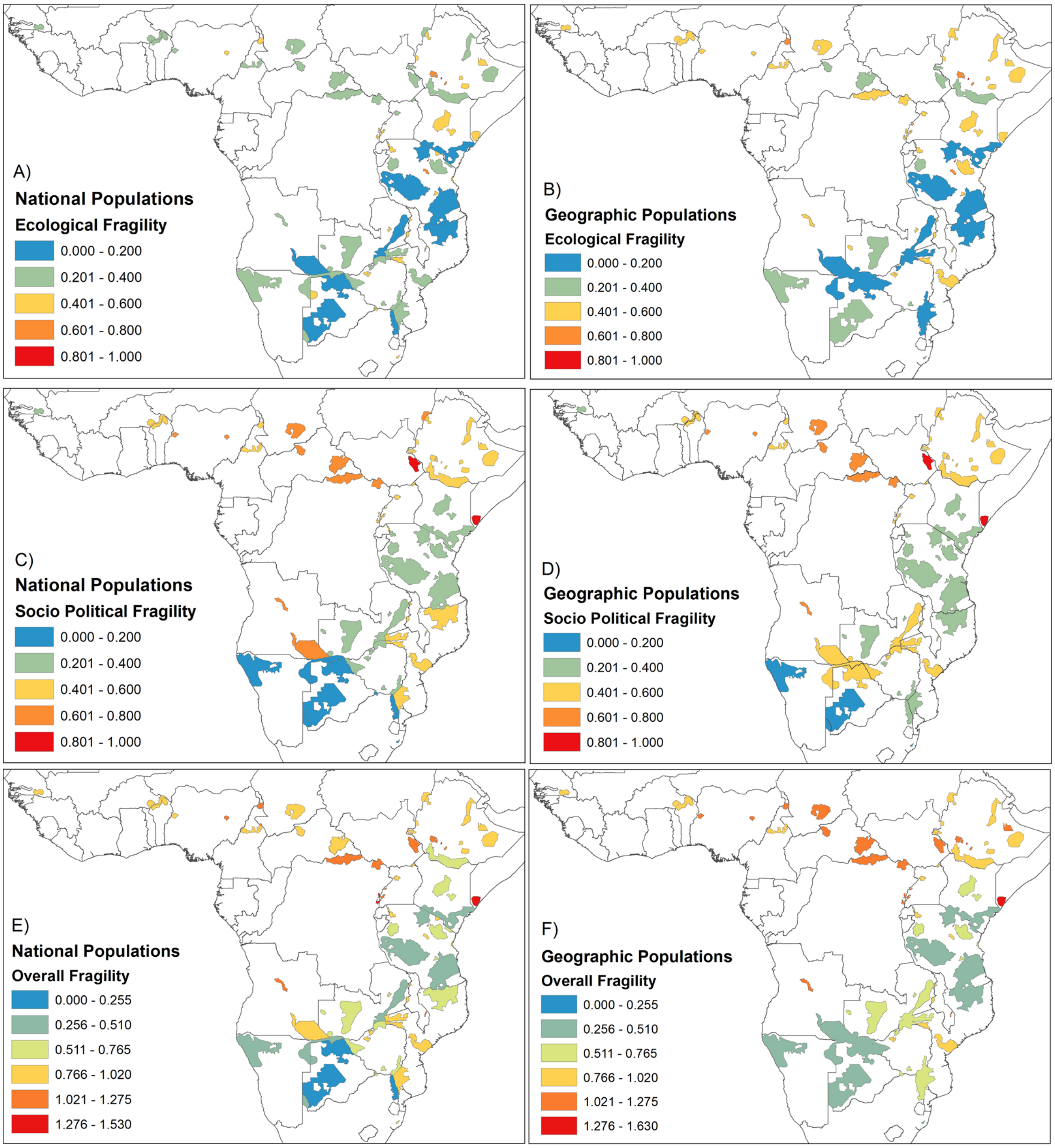

Fig. 2 The ecological, socio-political and overall fragility scores of 84 national populations (separated by national boundaries) and 62 geographic populations of free-ranging African Lions. Ecological fragility of (**A**) national populations and (**B**) geographic populations. Socio-political fragility of (**C**) national populations and (**D**) geographic populations. The overall fragility score for populations is calculated by summing their ecological and socio-political fragility scores. Overall fragility of (**E**) national populations and (**F**) geographic populations.

mostly occurred in eastern and southern Africa (e.g., Kruger and Okavango-Chobe; Fig. 6).

When examined at a geographic population level, Maze National Park in Ethiopia and Bush-Bush in Somalia emerged as the overall two most fragile populations (Fig. 3 and Table 1). On the other hand, the large lion populations in Kavango-Zambezi and Selous-Niassa were the two least fragile overall (Fig. 3 and Table 1).

Eight geographic populations (Boma National Park, Bush-Bush, Garamba Complex, Lake Manyara, Maze, Nechisar and Toro-Semiliki) had an overall fragility score more than one standard deviation above the mean (Table 1), and three of them were in a single country, Ethiopia. Together, these accounted for 1.3% of Africa's wild lions and 2.4% of their range (Table 1).

Ten geographic populations (Hluhluwe-Umfolozi, Katavi-Ruaha, Etosha-Kunene, Greater Mapungubwe, Luangwa-Mana-Tchuma-Tchato, Greater Limpopo, Maasai Steppe, Kgalagadi, Selous-Niassa and Kavango-Zambezi) each had combined fragility scores at least one standard deviation below the mean (Table 1). Collectively, these relatively less fragile populations represented nearly three quarters (75.8%) of remaining wild lions, and over half (63%) of their range (Table 1).

Discussion

These results highlight the need for urgent lion conservation action – there are 62 remaining free-ranging wild lion populations known to be extant in Africa, less than half of which have over 100 lions. Eight range countries only have a single wild lion population left, and almost half of all range countries have lion populations estimated at fewer than 250 individuals. Given that lions have innate biological characteristics linked to high extinction risk (e.g., high trophic level, low population density,

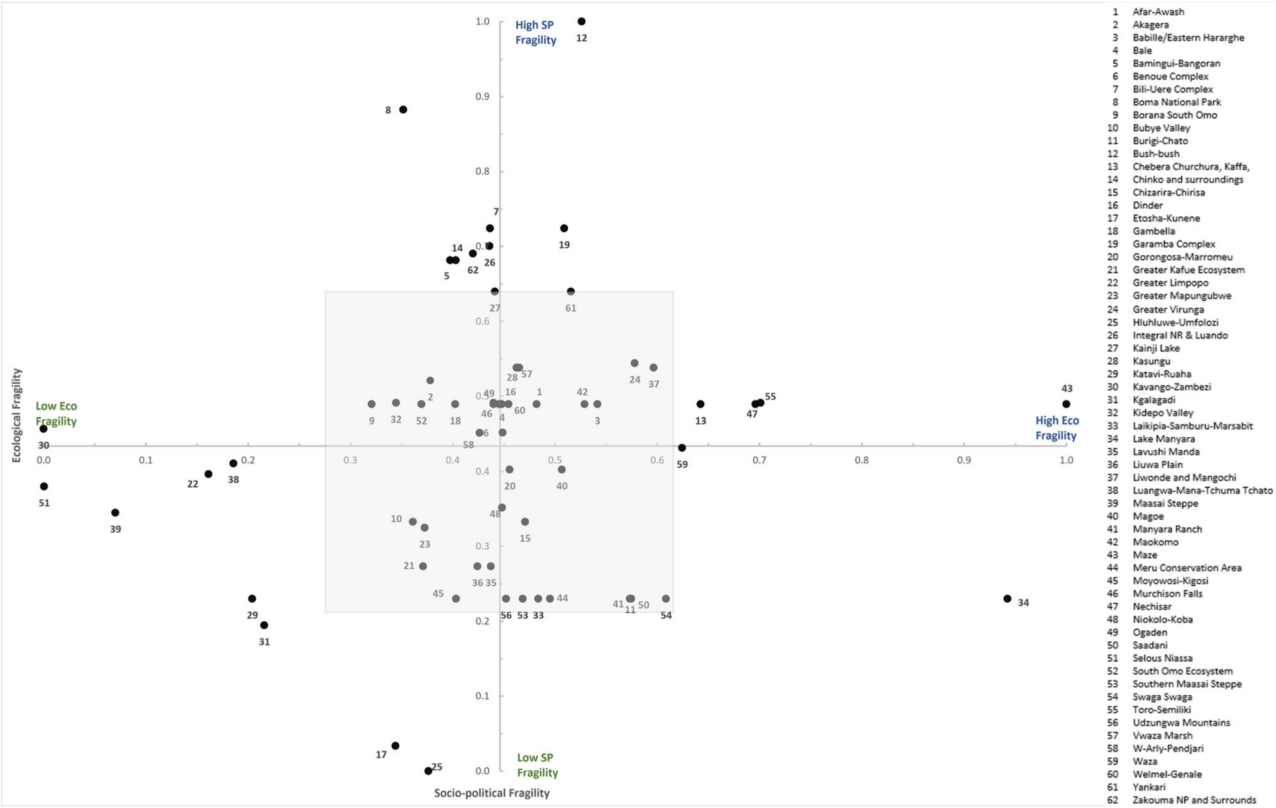

Fig. 3 Ranking of the 62 geographic lion populations in overall fragility. Populations higher on the y-axis or further to the right on the x-axis are more fragile. The axis lines are drawn at the mean value not at the mid-point of the index. The shaded grid depicts those populations which fall within one standard deviation of the mean on both axes.

slow life history[26]), and are particularly susceptible to anthropogenic risk factors such as habitat conversion, illegal or unsustainable hunting, prey depletion and conflict[15,27–29], these figures are concerning and warrant greater emphasis on urgent and effective conservation effort. Anthropogenic pressures are likely to grow, especially as more than half the global human population growth between now and 2050 is predicted to occur in Africa (United Nations DESA/ Population Division). Alongside growing global demand for goods and services, we expect rapidly increasing human pressures on land[30] and biological resources to have severe impacts on the persistence of lions, especially in many of these small remaining populations.

There is a long history of papers estimating lion population size and range across Africa, starting in 1975[31] and continuing through to present day[6,13,15,32]. This focus on numbers and range is essential, and when conducted in a robust, repeatable way, provides invaluable insights into lion trends and threats. It is relatively straightforward to collect data on ecological aspects of a population, such as its size, extent of formal protection, or the distance to the next closest population. Indeed, these are critically important elements in conservation biology and should be considered in conservation planning for lions[7,16,33–37]. However, despite the long focus on understanding lion population dynamics, there has been limited data on specific threats facing each population[16] (but see Everatt et al.[14]). Furthermore, the explicit consideration or evaluation of socio-political factors has been almost completely neglected in wider lion range-wide analyses, despite the critical significance of such factors for conservation.

To better understand and counteract threats, and to develop lion conservation plans that have the highest likelihood of success, socio-political factors must be considered alongside ecological ones[16,21]. For example, poor governance is often a major limiting factor to effective conservation[38], and countries which face major challenges such as conflict, poverty, political instability, low human development or rapidly growing human populations are unlikely to be able to prioritise conservation or conduct it effectively[16,20,39–41]. Therefore, two populations with similar levels of ecological threat could face very different socio-political challenges, and therefore require quite different conservation approaches, engagement of different stakeholders and varying levels of investment. Understanding these differences is necessary to developing effective and meaningful conservation action and a central goal of this research.

For example, populations or range countries with similar scores could have different drivers of fragility. The Etosha-Kunene and Kidepo Valley populations emerged with the same ecological fragility scores of 0.34, suggesting they are both relatively fragile on that index (Fig. 7). However, the drivers of those scores differed between the two populations: in Kidepo Valley, ecological fragility was driven mainly by a lack of connectedness, relatively small area and high edge-to-area ratio (Fig. 7). Meanwhile, the primary drivers of fragility for the Etosha-Kunene population were a lack of connectedness with other populations and limited protected area coverage (Fig. 7). In another example, Cameroon and DRC had very high, and similar, overall fragility scores of 1.47 and 1.48. Yet, the driver of Cameroon's high overall fragility was very high ecological fragility, despite relatively less socio-political fragility. DRC, on the other hand, was relatively fragile ecologically but highly fragile due to socio-political factors such as poor governance and policy indicators. Thus, conservation work may be more needed, and potentially more effective, in the relatively more stable socio-political climate of Cameroon than DRC.

Table 2 Socio-political, ecological and overall fragility scores of 84 national lion populations listed from most to least fragile.

	Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score		Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score		Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score
1	Maze	1.00	0.53	1.53	29	Welmel-Genale	0.41	0.53	0.94	57	Mana Pools, Hurungwe, Sapi, Chewore, Dande and Doma	0.36	0.38	0.74
2	Bush-bush	0.41	1.00	1.41	30	Bale	0.40	0.53	0.93	58	Udzungwa Mountains	0.44	0.29	0.73
3	Virunga	0.54	0.74	1.28	31	Afar-Awash	0.39	0.53	0.92	59	Laikipia-Samburu-Marsabit	0.43	0.29	0.72
4	Lake Manyara	0.99	0.29	1.28	32	Luengue-Luiana and Mavinga	0.19	0.72	0.91	60	Liuwa Plain	0.38	0.33	0.71
5	Nechisar	0.65	0.53	1.18	33	Murchison Falls	0.37	0.53	0.90	61	Bubye Valley	0.31	0.38	0.69
6	Chebera Churchura, Kaffa	0.62	0.53	1.15	34	Swaga Swaga	0.60	0.29	0.89	62	Gonarezhou-Save Valley	0.30	0.38	0.68
7	Toro-Semiliki	0.61	0.53	1.14	35	Manyara Ranch	0.59	0.29	0.88	63	Moyowosi-Kigosi	0.39	0.29	0.68
8	Garamba Complex	0.39	0.74	1.13	36	Ogaden	0.34	0.53	0.87	64	Southern Maasai Steppe	0.38	0.29	0.67
9	Liwonde and Mangochi	0.55	0.57	1.12	37	Magoe	0.42	0.45	0.87	65	Niassa-Quirimbas	0.18	0.45	0.63
10	Boma National Park	0.21	0.89	1.10	38	Saadani	0.58	0.29	0.87	66	Mkomazi	0.33	0.29	0.62
11	Sena Oura	0.39	0.71	1.10	39	Burigi-Chato	0.56	0.29	0.85	67	Sioma Ngwezi	0.27	0.33	0.60
12	Queen Elizabeth	0.55	0.53	1.08	40	Benoue Complex	0.38	0.47	0.85	68	Hwange	0.20	0.38	0.58
13	Yankari	0.41	0.67	1.08	41	South Omo Ecosystem	0.31	0.53	0.84	69	Shashe-Limpopo	0.51	0.07	0.58
14	Waza	0.58	0.47	1.05	42	WAP, Burkina Faso	0.33	0.50	0.83	70	Greater Kafue Ecosystem	0.22	0.33	0.55
15	Bili-Uere Complex	0.30	0.74	1.04	43	WAP, Benin	0.37	0.46	0.83	71	Hluhluwe-Umfolozi	0.45	0.07	0.52
16	Integral Nature Reserve and the Luando	0.32	0.72	1.04	44	WAP, Niger	0.35	0.48	0.83	72	Xaxa	0.49	0.00	0.49
17	Vwaza Marsh	0.44	0.57	1.01	45	Gorongosa-Marromeu	0.38	0.45	0.83	73	Luangwa Valley	0.15	0.33	0.48
18	Babille/ Eastern Hararghe	0.48	0.53	1.01	46	Gambella	0.29	0.53	0.82	74	Serengeti-Ngorongoro-Loliondo	0.14	0.29	0.43
19	Kasungu	0.43	0.57	1.00	47	Kidepo Valley	0.29	0.53	0.82	75	Mara-Amboseli-Chyulu-Tsavo-BoniDodori	0.14	0.29	0.43
20	Kainji Lake	0.33	0.67	1.00	48	Niokolo-Koba	0.39	0.40	0.79	76	Khaudum-Caprivi	0.31	0.10	0.41
21	Zakouma NP and Surrounds	0.29	0.71	1.00	49	Greater Limpopo (including Karingani, Banhine)	0.34	0.45	0.79	77	Kalahari Gemsbok	0.32	0.07	0.39
22	Bamingui-Bangoran	0.28	0.70	0.98	50	Chizarira-Chirisa	0.40	0.38	0.78	78	Etosha-Kunene	0.29	0.10	0.39

Table 2 (continued)

	Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score		Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score		Population	Rescaled ecological fragility score	Rescaled socio-political score	Overall fragility score
23	Chinko and surroundings	0.28	0.70	0.98	51	Tchuma Tchato	0.33	0.45	0.78	79	Katavi-Ruaha	0.08	0.29	0.37
24	Maokomo	0.44	0.53	0.97	52	Longido	0.48	0.29	0.77	80	Northern Tuli	0.35	0.00	0.35
25	Akagera	0.41	0.56	0.97	53	Matusadona and Omay	0.39	0.38	0.77	81	Selous-Mikumi	0.00	0.29	0.29
26	Tuli Circle	0.58	0.38	0.96	54	Borana and South Omo Ecosystem	0.23	0.53	0.76	82	Kruger National Park and Adjoining Private Nature Reserves	0.10	0.07	0.17
27	Alatash, Bejemis & surroundings	0.42	0.53	0.95	55	Meru Conservation Area	0.47	0.29	0.76	83	Central Kalahari-Khutse-Gemsbok	0.13	0.00	0.13
28	Dinder	0.31	0.63	0.94	56	Lavushi Manda	0.41	0.33	0.74	84	Okavango-Chobe	0.04	0.00	0.04

A few geographic populations and countries scored highly on one index of fragility but relatively low on the other. This suggests a need to carefully consider conservation action in these areas due to potentially divergent threats. For example, Lake Manyara was highly fragile ecologically (due in that case largely to its high edge-to-area ratio) but had a relatively low socio-political fragility score. This could suggest a more stable political climate to invest in where focus could be spent on improving local ecological conditions (although in this particular case, Lake Manyara is relatively close to predicted carrying capacity). Similarly, the Maze population has a close-to-average socio-political score but very high ecological fragility score, so here, ecological restoration could result in greater improvement in lion numbers. Other populations, such as Boma and Bush-Bush, score very highly on socio-political fragility but are about average for ecological fragility. This suggests that improving socio-political conditions, rather than ecological ones, should be the primary focus for stemming lion decline or restoring populations.

Making detailed data available on both the ecological and socio-political characteristics of remaining populations should help inform both the actions of conservation practitioners on the ground, and the decisions of those (often outside the field) who allocate scarce resources to conservation, as there is frequently a disconnect between those groups[42]. This work helps inform decision making, or at least provides a framework that can be modified and specialised for future use, as decisions on prioritising where scarce conservation resources are allocated should be transparent[43]. The importance of this approach is demonstrated by considering two populations which may look superficially similar in the context normally examined by conservationists. Lions in Swaga Swaga in Tanzania and Yankari in Nigeria are both small populations (<50 individuals each), each covering around 3,000 km^2, and score similarly fragile in terms of their ecological context. However, they occur in very different socio-political contexts – in Yankari, relatively poor government effectiveness, high political instability, high corruption, conflict and high human population densities make it far more socio-politically fragile than the Swaga Swaga population and a very different proposition for investors, as it is likely to need greater resource allocation to effectively manage it. This does not mean that conservation efforts in Yankari are less important (indeed they could be viewed as more ecologically important given that West African lions are Critically Endangered) but that a similar financial investment at the two populations may not result in the same outcomes, and may need to be spent differently. If investors are clear about the level of risk and investment they are happy with, these data could be useful for informing a lion equivalent to the Rhino Impact Investment Project, the first pay-for-results financial instrument for species conservation where investments are scaled to risk and likely outcomes (http://www.rhinoimpact.com/).

This initial analysis is not intended to be a priority-setting exercise, as different conservation groups and funders will have different individual aims. Some stakeholders will prioritise the most imperilled lion populations, others may prefer those with genetic distinctiveness[44] or the last lions in a country or region[8,9], while others, equally justifiably, will prioritise safeguarding the few remaining large lion populations[45]. However, the results presented here will help inform any of those strategies, as they reveal the most notable threats to whichever target populations are chosen and potentially, how to implement effective conservation action.

The lion populations examined fell into one of four quadrants relative to one another, and the categorisation can broadly inform conservation planning. Countries and populations which are classed as above-average for both fragility indices are likely to be viewed by some as top conservation priorities, given the urgency

Table 3 Mean results per country and overall ecological and sociopolitical scores per country ($n = 25$), which when summed provide an overall fragility score (denote most fragile countries overall).**

Country	No. lion populations	Overall lion range area (km2)	% of overall lion range in country	Mean edge to area ratio	Mean % area overlap with WDPA	Approx % of overall wild lions in country	Mean % of carrying capacity	Mean intensity of edge effect	Mean exposure to other borders	Mean population connectedness (lack of isolation)	Mean human density in lion range	Mean cattle density in lion range	Mean ecological fragility score per country	Rescaled ecological fragility score	Rescaled socio-political score	Country-wide fragility score
Angola	2	95309	7.64	0.05	57.11	0.20	1.64	4.85	0.69	13.50	1.54	0.00	0.26	0.16	0.72	0.88
Benin	1	12347	10.70	0.08	68.96	0.63	16.15	39.71	0.51	12.00	11.82	0.05	0.37	0.60	0.46	1.06
Botswana	4	240521	41.62	0.07	46.43	14.52	47.52	1.88	0.09	22.75	0.83	0.03	0.25	0.13	0.00	0.13
Burkina Faso	1	10407	3.81	0.09	84.12	0.90	19.35	27.68	0.51	12.00	11.02	0.02	0.33	0.45	0.50	0.96
Cameroon	2	19854	4.26	0.06	38.06	1.14	16.43	41.66	0.50	4.50	24.79	0.16	0.48	1.00	0.47	1.47
Central African Republic	2	54949	8.86	0.04	65.77	0.89	12.95	1.86	0.72	4.50	0.41	0.00	0.28	0.25	0.70	0.95
Chad	2	38420	3.03	0.09	87.49	0.74	5.07	19.94	0.73	6.50	14.22	0.08	0.34	0.47	0.71	1.18
Democratic Republic of the Congo	3	61116	2.63	0.09	52.24	0.35	5.28	102.38	0.75	10.67	33.43	0.01	0.41	0.74	0.74	1.48
Ethiopia	13	180314	15.96	0.08	36.07	5.06	17.69	69.56	0.64	14.92	40.74	0.20	0.46	0.93	0.53	1.46
Kenya	3	116819	19.94	0.04	25.02	7.34	23.23	62.70	0.40	20.33	8.55	0.10	0.35	0.50	0.29	0.78
Malawi	3	4268	3.62	0.19	84.83	0.12	11.10	80.45	0.40	13.00	0.81	0.01	0.48	0.99	0.57	1.56**
Mozambique	5	197780	25.12	0.04	10.60	6.18	11.01	20.73	0.44	18.60	8.57	0.01	0.33	0.44	0.45	0.89
Namibia	2	170643	20.71	0.03	19.15	2.93	12.65	2.56	0.13	21.00	1.75	0.05	0.30	0.31	0.10	0.42
Niger	1	2688	0.23	0.13	98.66	0.20	28.29	29.71	0.51	12.00	5.58	0.00	0.35	0.52	0.48	1.00
Nigeria	2	6773	0.75	0.08	97.13	0.08	5.65	53.09	0.70	4.50	23.04	0.02	0.37	0.58	0.67	1.25
Rwanda	1	1001	3.96	0.20	98.70	0.15	86.57	74.02	0.31	15.00	0.00	0.00	0.41	0.72	0.56	1.28
Senegal	1	8234	4.18	0.06	100.00	0.12	2.63	20.05	0.42	0.00	5.04	0.01	0.39	0.68	0.40	1.08
Somalia	1	12346	1.95	0.05	0.00	0.62	44.84	8.92	0.96	8.00	11.08	0.34	0.41	0.72	1.00	1.72**
South Africa	4	33035	2.71	0.12	68.70	9.83	93.85	16.45	0.15	11.75	8.33	0.01	0.34	0.49	0.07	0.56
South Sudan	1	19757	3.15	0.04	100.00	0.31	1.88	9.71	0.85	19.00	9.23	0.10	0.21	0.00	0.89	0.89
Sudan	1	8428	0.45	0.06	99.70	0.65	11.35	12.83	0.64	6.00	14.31	0.05	0.31	0.38	0.63	1.01
Tanzania	13	383503	40.77	0.13	32.03	33.51	39.44	69.27	0.33	25.85	88.35	0.15	0.43	0.81	0.29	1.10
Uganda	4	7808	3.23	0.18	99.31	1.41	49.08	164.54	0.72	11.00	12.56	0.07	0.46	0.91	0.53	1.44
Zambia	5	149720	19.93	0.07	72.07	4.63	7.81	9.06	0.35	21.80	3.92	0.01	0.29	0.28	0.33	0.61
Zimbabwe	7	59438	15.21	0.10	31.29	7.47	44.35	12.39	0.32	23.57	10.49	0.05	0.37	0.57	0.38	0.95

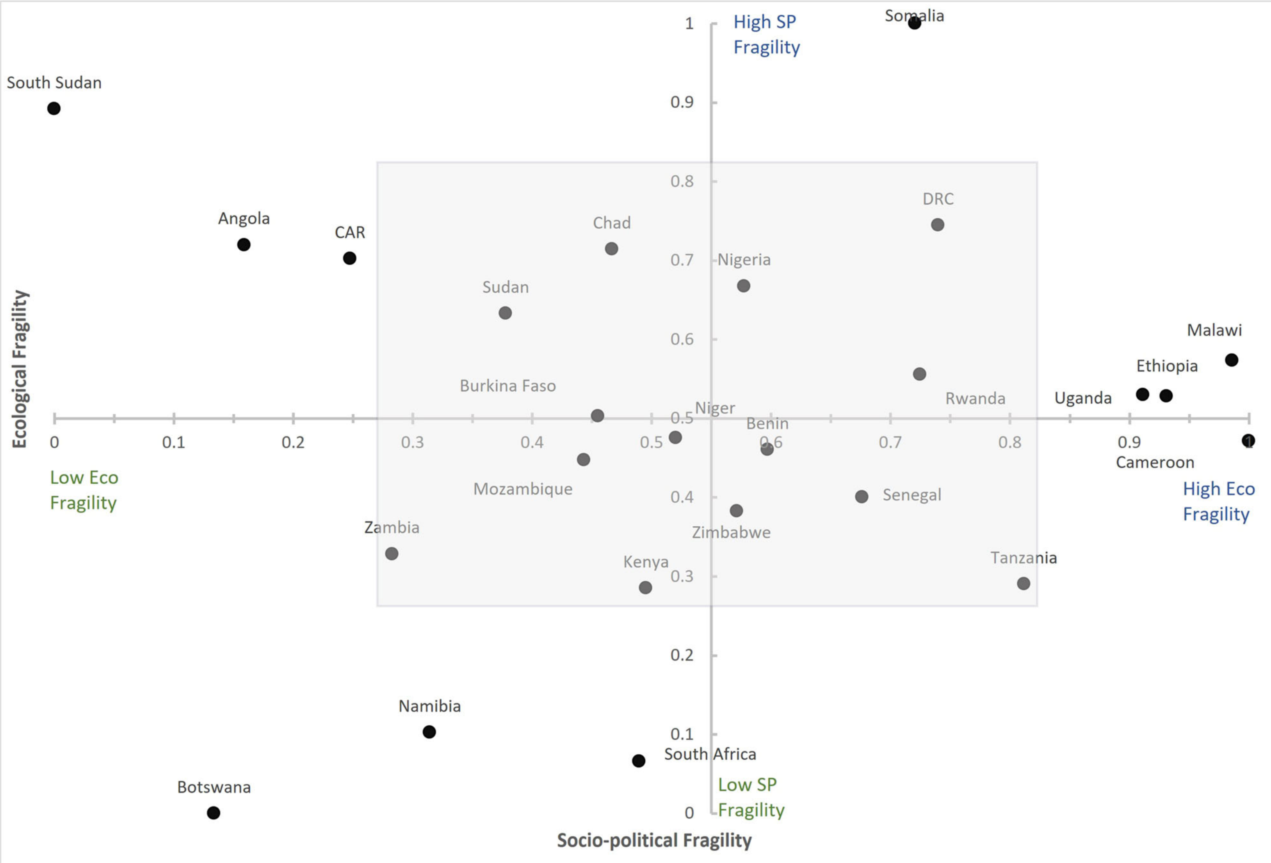

Fig. 4 Ranking of countries in overall fragility of their lion populations, relative to other lion range countries. Countries higher on the y-axis or further to the right on the x-axis are more fragile. The axis lines are drawn at the mean value not at the mid-point of the index. The shaded grid depicts those populations which fall within one standard deviation of the mean on both axes.

of threats facing them[8]. Others, however, may decide that resources should rather be focused on those populations which scored below average on both fragility indices, as those populations may have the best chance of long-term persistence. Conservationists are likely to be most well-equipped to deal with the threats facing populations which have relatively high ecological fragility but relatively low socio-political fragility. For those, interventions aimed at things like reducing the intensity of edge effects or improving connectivity between populations[46] could substantially improve the overall outlook in terms of fragility. Conversely, improving the status of populations which rank relatively high on socio-political fragility will require a broad suite of involvement from other stakeholders such as policymakers, and rely less on the expertise of conservationists, particularly if they are not particularly ecologically fragile.

The results of any analysis depend upon which metrics were selected for inclusion, and the methods and scoring systems used[42]. Here, we assumed a linear relationship between our variables and lion fragility, whereas, in reality, relationships (such as between human poverty and wildlife fragility) are likely to be complex, non-linear and site-specific[47,48]. In addition, we were limited to national-level socio-political statistics, which are unlikely to fully reflect the specific conditions in the rural areas where lions persist. Variables needed to be available across all range countries for inclusion, which limited those which could be selected for analysis.

Furthermore, the data presented here (for all aspects) are a snapshot in time of the situation in each lion range and range country as it is best known at present (and that knowledge may have been gathered some years ago). Some of these variables, such as human-human conflict, could change suddenly and drastically with repercussions for estimates of fragility (see Masiaine et al.[49] regarding impacts from the incursion of pastoralists into Loisaba Conservancy in 2017 due to widespread, severe drought). Therefore, this study is intended as a first attempt at collating current knowledge for lion fragility and developing an analytical method, which will hopefully be refined, adjusted and enhanced by others as detailed range-wide knowledge of lion populations and their threats improves.

We are also aware that conservation is rarely aimed at one species – it is important to maintain a functioning ecosystem where species negatively affected by lions, such as smaller carnivores such as wild dogs (Lycaon pictus) or cheetahs (Acinonyx jubatus) (Swanson et al. 2014), can also thrive. Although this analysis was done for a single species, it can be replicated for other taxa and guilds. A final caveat is that we restricted our analyses to what we defined as 'free-ranging' lion populations, defined as all unfenced populations and partially or fully fenced populations of at least 500 km^2 or 1,000 km^2 respectively. Therefore, this excludes lions in several places, including smaller fenced areas in South Africa (~800 lions), in Nairobi National Park and those reintroduced into fenced areas such as Liwonde National Park in Malawi, making the overall lion population figures look unexpectedly small for those countries.

The results of interdisciplinary analyses such as these can be daunting for conservationists, as many of the most pressing threats, such as poor governance, low human development, and rapidly growing anthropogenic pressures, need to be tackled by other stakeholders, often at national scale and could take a long time to change. This is far from saying that conservation in socio-

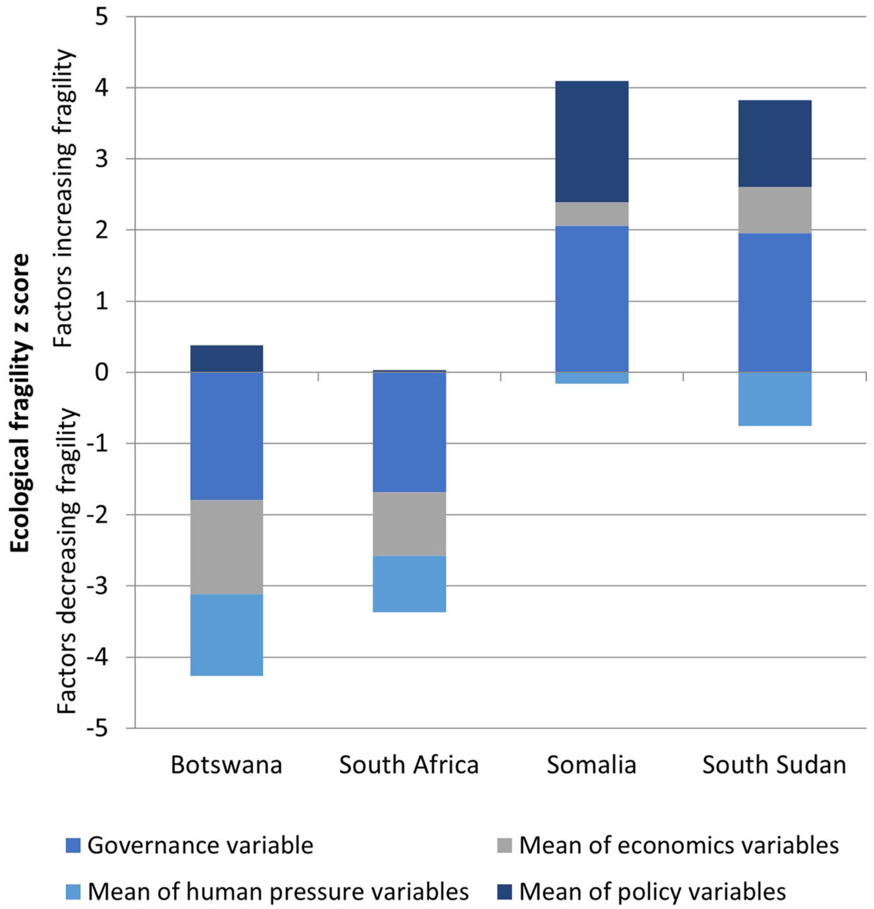

Fig. 5 Factors contributing towards four countries socio-political fragility scores. Botswana and South Africa were the least socio-politically fragile lion range countries, and South Sudan and Somalia were the most. Factors which rank positively on the y-axis increase socio-political fragility for those countries, while those which rank negatively decrease socio-political fragility. Total z-score is the sum of both positive and negative values.

politically challenging areas is not worthwhile, but rather that for realistic conservation planning, everyone should be aware of the magnitude and specific drivers of threats, so that appropriate actions, timescales and levels of funding can be put in place. Inadequate funding is one of the key constraints in conservation, and this is a particularly pressing issue given the scale of action needed for lions. More than US$1 billion would be needed annually to maintain lions within current protected areas, with a major shortfall at present[25]. Importantly, this estimate assumes equal costs for all populations, but some of the costs are likely to be substantially higher in those countries with poor socio-political conditions such as poor governance (particularly with high levels of corruption) and intense human pressures. Conversely, conservation dollars may go further in countries with lower purchasing power parity (PPP), so it is a complex scenario and one that requires further in-depth analysis. As a rough estimate based on Packer et al.'s [50] costs for fenced and unfenced areas, we estimate that the cost of effective lion conservation would likely exceed US$3 billion per year[50].

An important detail of the results presented here is that lion range countries presented as more or less fragile in a socio-political sense are done so relative to other lion range countries. These all scored poorly in the Global Multidimensional Poverty Index[51]. Almost all African lion range countries are in the top 50% (highest poverty), with nearly three quarters in the top 25%. The 10 countries with the most ecologically fragile lion populations are all in the top 50% of acutely poor countries[51]. The global community are expecting some of the poorest countries to carry an expensive burden, which is inequitable and likely unsustainable[52]. Indeed, historically, the lion ranged over wealthier countries within northern Africa, the Middle East and Central Asia, but has been extirpated from those areas. It seems incumbent upon the richest countries to shoulder far more of the cost of future lion conservation.

Conclusion

Ultimately, these results make clear that given the importance of factors such as governance and economics on the fragility of wildlife populations, effective lion conservation cannot be achieved by conservationists alone. It requires the engagement of many diverse stakeholders, including policymakers, development experts, economists, land-use planners, local communities, local traditional leadership, and all levels of government. Maintaining wild lion populations – whichever ones may be prioritised - will require sustained effort and significant levels of international investment and sustainable funding mechanisms, particularly as many of the key challenges identified here, such as human population and livestock density, are likely to rapidly increase in key lion areas over the coming years. Without such efforts, lion populations will increase in fragility (some possibly beyond recovery), and we will come substantially closer to losing ecologically meaningful populations of this most iconic African predator.

Methods

Lion population estimates and geographic range were initially taken from the IUCN's "Guidelines for the Conservation of Lions

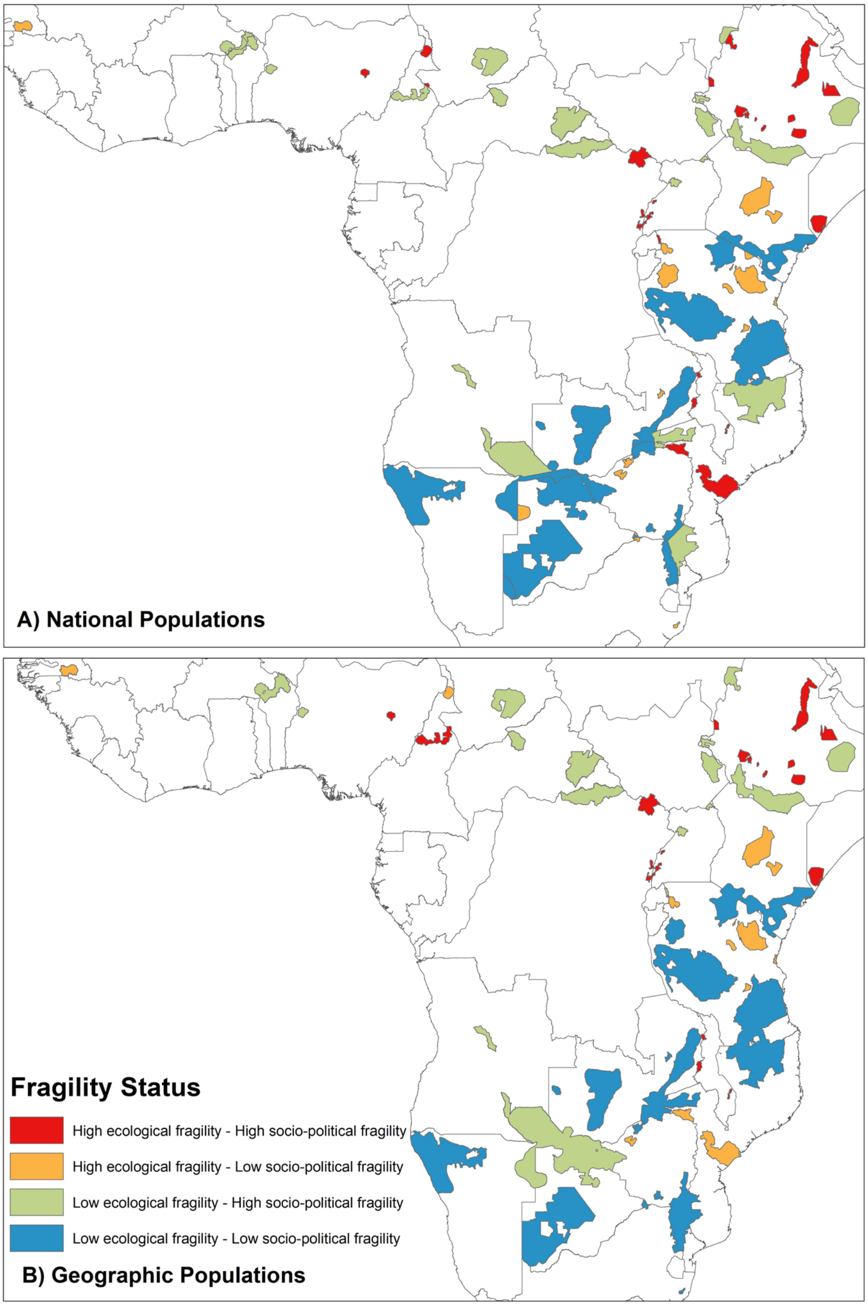

Fig. 6 The fragility status of all 84 national and 62 geographic lion populations. Populations are colour-coded according to whether they scored high (above-mean) or low (below-mean) on both the ecological and socio-political fragility scale. **A** The fragility status of 84 national lion populations. **B** The fragility status of 62 geographic lion populations.

in Africa" (GCLA[53]) as it was approved by African Lion Range States and numerous lion experts. Minor edits were then made based on the IUCN SSC Cat Specialist Group's African Lion Database (Supplementary Table 6 for full list of populations and references used for this study). In both cases, in the absence of updated survey data, we used expert opinion to provide population estimates and spatial extent of range. Experts were defined as conservation biologists that have extensive knowledge of lions in that region.

Analyses were restricted to free-ranging lion populations (termed a 'geographic population'), which we defined as consisting of all individuals connected via contiguous habitat. If a geographic population crossed national boundaries, it was split into a national subpopulation for analysis at the national level. We included all unfenced lion populations and those populations which were partially fenced but were at least 500 km^2 in extent, and populations which were fully fenced but at least 1,000 km^2 in extent. Although this was a necessarily arbitrary cut-off, these large, fenced areas were classed as free-ranging because they probably allow for ecologically functional lion populations, assuming even the lower end of 1.5 adult lions/100 km^2 cited for southern African semi-deserts[7,15]. Populations which were within 10% of that cut-off were considered for inclusion. Only one fell within that scope (South Africa's Hluhluwe-iMfolozi) so that was included in the final analysis. We only included areas where experts said there was confirmed lion presence in the last two lion generations (15 years; since 2006) as our aim was to assess fragility of known populations.

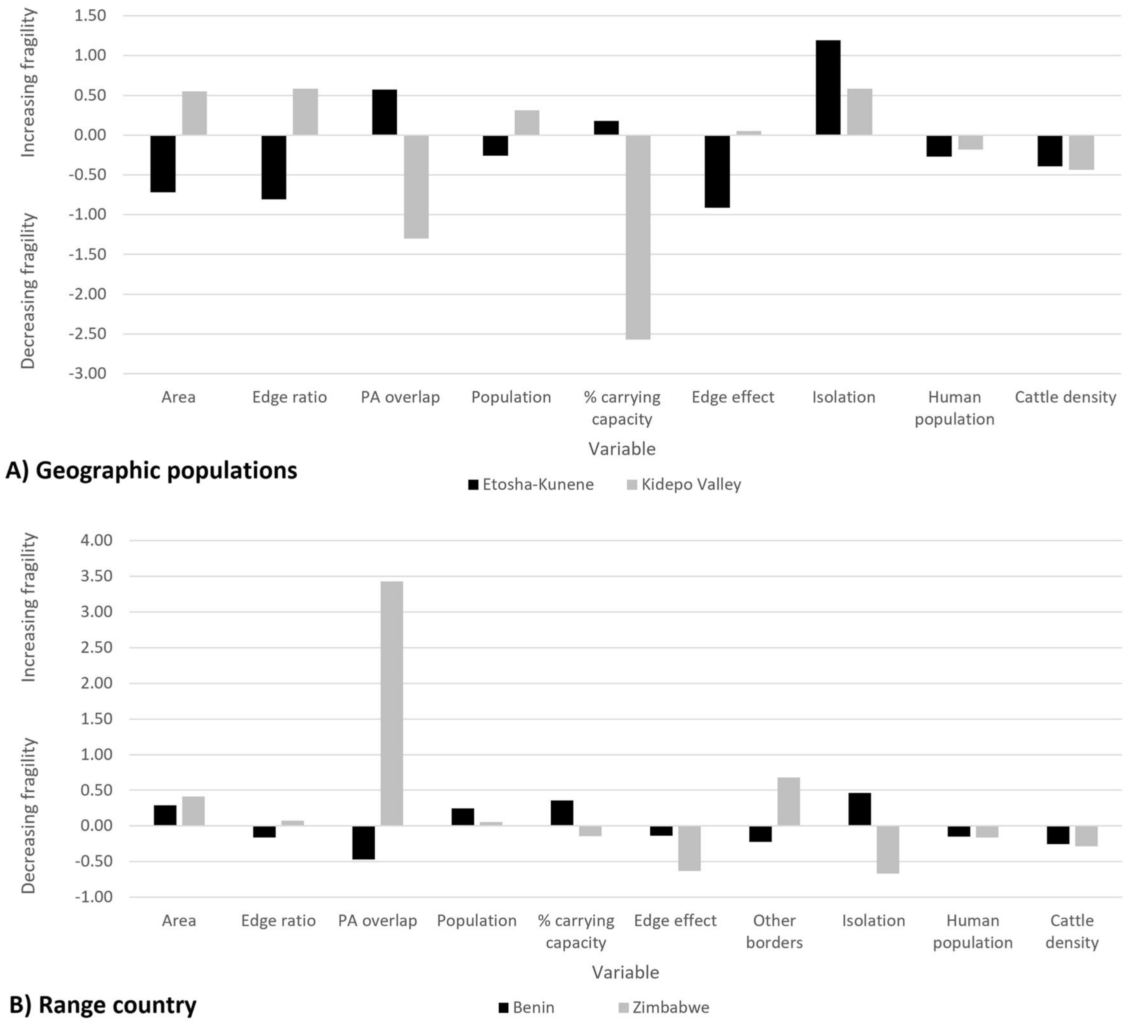

Fig. 7 Mean z-scores of the constituent variables contributing to the ecological fragility score. Positive z-scores increase ecological fragility while negative ones decrease ecological fragility. Total z-score is the sum of both positive and negative values. **A** Two geographic lion populations (Etosha-Kunene and Kidepo Valley) that both had an ecological fragility score of 0.34 but different drivers of fragility. **B** Two range countries (Benin and Zimbabwe) are shown that had similar ecological scores (0.372 and 0.366 respectively).

Country boundaries were obtained from the Global Administrative Areas database (GADM 2016) and all spatial analyses were conducted in ArcMap 10.4 (Release 10.4.1; ESRI, Redlands, CA). It is imperative to note that the resultant map does not depict a conclusive current range map for lions, and the estimates do not constitute the total number of wild lions in Africa, but this analysis represents the populations where sufficiently reliable data were available to examine fragility.

Lion populations were assessed at three spatial scales. The first scale was the 'geographic' population scale (i.e., the entire population regardless of whether it spans national boundaries), which accommodates the transboundary nature of many lion populations. We also assessed at a 'national' scale, where geographic populations were split at a national boundary (if a geographic population was split by a country boundary, the population within a single country we called a 'subpopulation'), as countries are the management units at which most policies and decisions are made. Lastly, we assessed fragility at the country level in which we averaged multiple national populations and subpopulations, if appropriate.

Calculation of ecological and socio-political fragility scores. We calculated two fragility scores for lion populations: an ecological and a socio-political score. Both scores comprised a sum of individual variables (see below), which were standardised to produce z-scores before summing. Higher scores represented greater fragility. Some z-scores were inverted from negative to positive in instances when a higher value was associated with lower fragility (e.g., a larger population is less fragile). Individual z-scores were summed to produce a composite measure of fragility[20]. Combining factors can provide a more informative picture than examining factors individually, and summing z-scores is an established method for producing composite measures[54,55]. Although it could be argued that some factors should be weighted more heavily in our calculations of fragility than others, this was beyond the scope of this study. Researchers interested in developing a weighted index could do so using a similar approach.

Calculating the ecological fragility score of lion populations. The ecological fragility of each lion population was calculated as the sum of standardised values of the ten variables described below (details in Supplementary Table 7). The 'exposure to bordering countries' variable was not relevant at the geographic scale and was only calculated at the 'national' and 'country' scales.

(i) Geographic area – populations covering a smaller area were assumed to be more ecologically fragile, as they would be more susceptible to edge effects even if the core population was protected[56].

(ii) Percentage of wild lions remaining - smaller lion population sizes were assumed to be more vulnerable to extinction and therefore more ecologically fragile.

(iii) Edge-to-area ratio – populations with a higher edge-to-area ratio were assumed to be more ecologically fragile[27]. The edges of some populations bordered features like lakes, where edge effects would presumably be less than those bordering farming or pastoralist areas. The 'hardness' of the edge was not incorporated here, but within the 'intensity of edge effect' calculations.

(iv) Percentage of lion range covered by protected areas – populations with relatively little coverage by protected areas were assumed to be more ecologically fragile. Protected area boundaries were obtained from the World Database on Protected Areas (IUCN and UNEP-WCM, 2018). We minimally modified protected area categorization due to inconsistent designation across countries, and only used designated and terrestrial protected areas with IUCN categories I-IV[57].

(v) Population size as a percentage of predicted lion carrying capacity – populations at only a low percentage of predicted carrying capacity were assumed to be more ecologically fragile[26]. Fragility here was viewed as the likelihood of the population becoming extirpated, so higher population size relative to carrying capacity was viewed as being more secure, even in cases where populations exceeded the predicted carrying capacity (which would be likely to cause issues in the longer-term). Predicted lion carrying capacity was calculated for this analysis[24].

(vi) Population isolation – populations which were less connected to other lion populations were assumed to be more ecologically fragile, as there is less likely to be genetic mixing with, or recolonisation from, other populations. A connectedness score was calculated as the count of other extant lion populations within 350 km of the focal population, based on a maximum dispersal distance for a male lion of 343km[36], weighted by distance to the focal population. Neighbouring populations within 50 km were given a score of 5, populations between 50 and 99 km away were given a score of 4, populations 100 to 149 km away were given a score of 3, populations 150 to 249 km away were given a 2 and populations 250 to 349 km away were given a 1. These were summed to produce an overall population isolation figure.

(vii) Intensity of edge effect – populations with high human population density on the edges were assumed to be more ecologically fragile, as intense edge effects can have far-reaching impacts even within protected areas[27,56]. Non-overlapping 30 km buffers were drawn around each extant lion population and these were combined with a human population density map (WorldPop 2020 data)[58] to extract an estimate of human population density in the immediate surroundings of lion populations. Buffers were set at 30 km to reflect a reasonable daily movement of a lion, and thus the scale at which regular conflict with human presence is likely. This variable was weighted according to whether there was partial (25% reduction) or complete (50% reduction) fencing of the lion population, as fencing largely eliminates the impact of an edge effect[50].

(viii) Human population density within the lion population - higher human population density within the same area as the lion population was assumed to increase ecological fragility, due to associated threats such as resource extraction, habitat degradation, prey depletion and human-lion conflict. Human population estimates within the lion range were extracted from the WorldPop data for the year 2020[58]. In fully-fenced areas where no humans resided in the lion area, we reduced the WorldPop density to 0 humans/km^2. This applied to Akagera National Park (Rwanda), Liwonde National Park (Malawi), Hluhluwe-Umfolozi (South Africa) and Bubye Valley (Zimbabwe).

(ix) Cattle density within the lion population – greater cattle density within lion range was assumed to increase ecological fragility due to associated threats of human-carnivore conflict, particularly retaliatory or preventative lion killings over depredation[59,60]. As cattle density represents pastoralism the best and is one of the most important cases of human-wildlife conflict[59], we used cattle as a proxy for all livestock. Cattle data were obtained from the Université Libre de Bruxelles/ Food and Agriculture (FAO) Gridded Livestock of the World 2010 (GLW 3) dataset[61]. In fully-fenced areas where no humans resided in the lion area, we altered the cattle density to 0 cattle/km^2. This applied to Akagera National Park (Rwanda), Liwonde National Park (Malawi), Hluhluwe-Umfolozi (South Africa) and Bubye Valley (Zimbabwe).

(x) Immediate exposure to influence of bordering nations – a neighbouring country's policies and situation could affect lion populations that adjoin or cross borders[14]. The percentage of total area of a lion population influenced by the socio-political score of a neighbouring country (deemed as falling within a 30 km buffer of the border) was weighted by the difference in socio-political scores between the two countries. Hence, if a lion population existed largely in a less socio-politically fragile country (see below) but bordered a country with a higher fragility score, this would increase the fragility of the population.

Calculating the socio-political fragility score of lion populations. The fragility score was calculated by creating a composite measure from the z-scores of the following 12 national-level variables (Supplementary Table 7), as defined in source databases[20]. Although not an exhaustive list, these 12 variables were identified as key governance, economics, anthropogenic pressure and environmental policy indicators likely to influence the fragility of lion populations, and had comparable data for all 25 of the lion range countries. Each variable was standardised relative to all current lion range countries. The standardised variables contributing to each of the four metrics (governance, economics, anthropogenic pressure and environmental policy) were averaged within each category, and these four metrics summed and then re-scaled to produce an estimate of socio-political fragility[20]. Geographic population-level estimates of socio-political fragility were calculated as a percentage of a population's range in a given country multiplied by the socio-political score of that country, averaged across all the national population(s) (i.e., subpopulations of the single geographic population).

A. Governance

i. Government effectiveness – Less effective governments are likely to impede successful conservation efforts, so lower effectiveness was assumed to be linked to increased fragility. This was taken as a 10-year average (2011-2020) from the World Bank Worldwide Governance Indicators: http://info.worldbank.org/governance/wgi/.

ii. Political stability – Lower political stability is likely to divert attention and funding away from conservation efforts, limits the will of international agencies to work in the country and inhibits long-term planning. Lower political stability was therefore assumed to be linked to increased fragility. Data as above.

iii. Control of corruption – Corruption is likely to deter investment for conservation and lead to misappropriation of conservation funding, so higher levels of corruption was assumed to be linked to increased fragility. Data as above.

B. Economics

i. Gross Domestic Production (GDP) per capita based on Purchasing Power Parity (PPP) – lower GDP is likely to limit funding for conservation and means that other issues such as food security take priority, so lower GDP was assumed to be linked to increased fragility. GDP based on PPP was used to enable more accurate comparisons between countries. Data averaged across years 2011-2020 from World Bank World Development Indicators: https://databank.worldbank.org/source/world-development-indicators.

ii. Human Development Index (HDI) – With low HDI levels, a country is unlikely to have sufficient resources to invest in conservation, so lower HDI was assumed to be linked to increased fragility. Data as above.

iii. GINI Index – An estimate of the distribution of wealth that measures inequality in income between households, with greater inequality between the richest and poorest assumed to be linked to increased fragility. Data as above.

C. Anthropogenic pressure

i. Annual human population growth rate – higher human growth rates place increasing pressure on land and resources, so higher growth was assumed to be linked to increased fragility. National data averaged across years 2011-2020 from World Bank World Development Indicators: https://databank.worldbank.org/source/world-development-indicators.

i. Countrywide human population density – higher human density results in higher demand for land and resources, so higher density was assumed to be linked to increased fragility. Data as above.

ii. Global human modification – a measure of the level of human modification on terrestrial land accumulated across 13 stressors[62]. Values were averaged across a lion population. A higher level of modification was assumed to be linked to increased fragility.

A. Policy

i. Conservation Action Plan – Developing an Action Plan represents some level of governmental commitment to conservation, so the absence of a conservation action plan relevant to lions was assumed to be linked to increased fragility. Countries were scored 3 if they had a specific large carnivore action plan developed, 2 for an active National Biodiversity Strategies and Action Plans (NBSAP under the convention on Biological Diversity) that has nothing specific for lions, 1 for a developed but not apparently active NBSAP, or 0 for no carnivore action plan or NBSAP.

ii. Percentage of relevant wildlife treaties signed up to – Another measure of government-level commitment to conservation is the percentage of ten international wildlife treaties deemed relevant to lion conservation that lion range countries have signed up to (Ramsar Convention, World Heritage Convention, CITES, CMS, CBD, African Convention, Bern Convention, SADC Protocol, Lusaka Agreement and TFCA treaties)[63]. The fewer treaties a state signed up to, the higher the assumed fragility on this metric.

iii. Percentage of land designated as Protected Area – Setting aside protected areas is one example of a country's willingness to commit resources to conservation, so having a smaller percentage set aside at the national level was assumed to be linked to increased fragility. Countrywide data reported from Protected Planet in 2018 for all terrestrial and inland water coverage.

All variables were initially retained because each contributed additional value (e.g., small populations restricted to small, unprotected areas surrounded by high human population density merit more attention than those that are just small populations, even if the processes are related)[20]. However, if variables had high Pearson correlation coefficient (i.e., above 0.8), the correlated variables were removed. All governance variables were highly correlated, so only Government Effectiveness was retained after removing control of corruption and political stability (Supplementary Table 7).

To produce an indicator of overall fragility, both ecological and socio-political indices were re-scaled, so the minimum score became 0 (least fragile) and the maximum 1 (most fragile), and then the indices were summed together to produce one composite measure from 0 to 2.

Data availability

Information on the distribution and population sizes of lion are available from the IUCN SSC Cat Specialist Group's African Lion Database. Area specific population sizes are referenced accordingly in Supplementary Table 6. The study used openly available datasets of Gridded Population of the World Version 4, Gridded Livestock of the World database, and data on protected areas were available from the World Database on Protected Areas (http://www.protectedplanet.net). Data for the ecological and socio-political scores are openly available from sources such as FAO and links are provided in the 'Methods' section and in Supplementary Tables 1, 2. Our data tables with all variables, detailed results and calculations are available to download from https://doi.org/10.6084/m9.figshare.23685675.v1.

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Author contributions

A.D., A.H., D.B., E.M. and D.M. conceived the study and wrote the early drafts. All authors were involved in study design and contributed data for use in the study. S.N., A.D., A.H., H.B., J.R., and A.J. compiled the datasets. S.N., A.D., A.H. and J.R. carried out data preprocessing. A.L. ran the carrying capacity results required for the study analysis. S.N., A.D., and A.J. analysed the data. SN prepared figures, maps and tables. S.N., A.J. and A.D. led the writing of the final manuscript. All authors contributed to writing, reviewing, and editing the manuscript. S.N. and A.D. contributed equally. A.D. and A.J. jointly supervised the work.

Competing interests

The authors declare no competing interests.

Additional information

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