


RESEARCH ARTICLE

Where have all the lions gone? Establishing realistic baselines to assess decline and recovery of African lions

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Abstract

Aim: Predict empirically the current and recent historical (c1970) landscape connectivity and population size of the African lion as a baseline against which to assess conservation of the species.

Location: Continental Africa.

Methods: We compiled historical records of lion distribution to generate a recent historical range for the species. Historical population size was predicted using a generalized additive model. Resistant kernel and factorial least-cost path analyses were used to predict recent historical landscape connectivity and compare this with contemporary connectivity at continental, regional and country scales.

Results: We estimate a baseline population of ~92,054 (83,017–101,094 95% CI) lions in c1970, suggesting Africa's lion population has declined by ~75%, over the last five decades. Although greatly reduced from historical extents (c1500AD), recent historical lion habitat was substantially connected. However, in comparison, contemporary population connectivity has declined dramatically, with many populations now isolated, as well as large declines within remaining population core areas. This decline was most marked in the West and Central region, with a 90% decline in connected habitat compared with its c1970 extent. The Eastern and Southern regions have experienced lower, though significant, declines in connected habitat (44% and 55%, respectively). Contemporary populations are connected by three non-core habitat linkages and 15 potential corridors (spanning unconnected habitat) that may allow dispersal and gene flow. Declining connectivity mirrors recent studies showing loss of genetic diversity and increasing genetic isolation of lion populations.

Main conclusions: We provide an empirically derived baseline for African lion population size, habitat extent and connectivity in c1970 and at present against which to evaluate contemporary conservation of the species, avoiding a shifting baseline syndrome where conservation success/failure is measured only against recent population size or range. We recommend priorities for conservation of existing connections to avoid further fragmentation.

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KEYWORDS

African lion, habitat fragmentation, landscape connectivity, *Panthera leo*, population decline

1 | INTRODUCTION

Globally, large carnivores have experienced rapid population declines and geographic range reductions, largely due to loss and fragmentation of habitat, conflicts with livestock owners and over-exploitation (Ceballos & Ehrlich, 2002; Ripple et al., 2014). As human populations grow, conversion of wild habitat to agricultural land is expected to increase habitat fragmentation and species extinction risk across most terrestrial vertebrate taxa (Tilman et al., 2017). Mammalian species whose habitats are more fragmented face higher extinction risk (Crooks et al., 2017) and such risks may be particularly acute for large-bodied, wide-ranging species (Cardillo et al., 2005; Crooks, 2002; Woodroffe & Ginsberg, 1998). Populations living in fragmented, poorly connected habitats are at increased risk of genetic isolation and loss of heterozygosity, inbreeding depression and susceptibility to disease and stochastic events, further exacerbating the probability of local extinction (Benson et al., 2016; Delaney et al., 2010; Trinkel et al., 2008, 2011).

The African lion (*Panthera leo*) is an informative model species to understand the process of species range collapse as it is a widely distributed and charismatic umbrella species for African savanna ecosystems (Lindsey et al., 2018; Macdonald et al., 2015) and a strong indicator of the range collapse and fragmentation experienced by many large-bodied African mammals. Having once occurred throughout Africa, except for Equatorial forests and hyper-arid regions of the Sahara desert (Nowell & Jackson, 1996), the lion is known to have experienced a geographic range retraction of ~85% since 1500 AD (Morrison et al., 2007).

Contemporary African lion populations are accepted as being in the region of 23,000 individuals (Bauer et al., 2016). This disconcerting trend has resulted in a reassessment of the IUCN Red List status of the West African lion subpopulation as Critically Endangered (Henschel et al., 2015) and focussed the concern of conservationists on the, currently secure, but likely declining populations in Eastern and Southern Africa. In addition to population declines, recent comparisons between contemporary and historical genetic diversity have shown declines in diversity that are likely to be due to fragmentation and loss of habitat connectivity (Curry et al., 2020; Dures et al., 2019). Together these findings suggest that declining populations and collapsing geographic range, with accompanying loss of genetic diversity, could impact the viability of the African lion if ambitious conservation measures are not implemented.

Defining historical baselines against which to measure and understand the process of landscape fragmentation facilitates the alignment of conservation policy to mitigate further habitat loss. Recorded historical distributions of many species are often limited to generalized biogeographical maps based on sparse historical records and broad-scale expectations of habitat use (Boshoff et al., 2016;

Rookmaaker & Antoine, 2012), which often greatly overestimate biodiversity and conservation effectiveness (Macdonald et al., 2020).

In order to generate baseline estimates of recent historical, 20th century, landscape connectivity and population size for the African lion, against which to assess the conservation status of extant lion populations, we used published historical sources describing species range, along with species distribution models to reconstruct geographic range and population size for the period approximating 1970. We compared contemporary population size, and, using landscape connectivity models, lion's habitat connectivity with these recent historical baselines to assess the loss of range and continent-wide habitat connectivity.

2 | METHODS

2.1 | Mapping recent historical lion range

We reconstructed a detailed species range map for the period approximating 1970 (hereafter termed "recent historical" range), based on historical, published sources describing regional or localized geographic lion range. We chose this decade because (a) there are credible, suitably detailed, published sources of information for this period, (b) changes over the 50-year period between 1970 and the present are likely to be informative as human population and development have accelerated over this time period, with sub-Saharan human population doubling between 1975 and 2001 (United Nations, 2019), and (c) detailed continent-wide spatial datasets required to generate species distribution models and analyse patterns of landscape connectivity were available for this period. Data limitations inherent in using contemporary historical sources are discussed in Appendix S1, Supplementary materials.

Recent historical lion distribution was compiled (see Figure S1, Table S2) and digitized using ArcMap 10.6 (ESRI, Redlands, CA). We did not consider small, fenced protected areas of <1000 km² as part of free-ranging lion habitat as these are intensively managed and lions rarely disperse naturally into or out of these populations. We term range and population estimates for this period as the c1970 baseline.

2.2 | Modelling extant and historical African lion population densities

Mammalian herbivore biomass is known to be ultimately determined by rainfall and soil nutrient levels in African savanna systems (Bell, 1982; Coe et al., 1976). In turn, predator biomass correlates closely with herbivore biomass in African savannas (East, 1984;

Grange & Duncan, 2006; Loveridge & Canney, 2009) and in global ecosystems more generally (Hatton et al., 2015). Further proximate determinants of mammalian biodiversity are likely to include anthropogenic pressures on ecosystems and species, which in turn, are likely to be determined by protected status (Craigie et al., 2010; Lindsey et al., 2017) and human population (Harcourt et al., 2001).

Based on the rationale that current ecological, environmental and anthropogenic drivers of lion population density can be used to predict both current and historical lion numbers across the species range, we used a generalized additive model (GAM) to determine variables that predict lion population density across the species range (Wood, 2011). GAMs are an extension of generalized linear models that provide the flexibility of a non-linear relationship between the response and predictors in a model (Guisan et al., 2002). We used the IUCN red list map of current African lion distribution as the basis for describing contemporary lion distribution (Bauer et al., 2016; IUCN-SSC, 2018), modified with updated range information collated by the authors (Figure S1, Table S2, see Appendix S1 for discussion of potential data limitations). We generated a realistic point density distribution of lions across all subpopulations within the extant range using the total number of lions estimated to persist in each wild population ($N = 21,288$ points spaced at 1500m, Table S1, Figure 1b). Where more detailed information on population density was available, we subdivided large regional populations to

realistically reflect variation in population density across large landscapes. At each point, the variables expected to influence lion densities were extracted from GIS layers, including human population density, soil nutrient status, cumulative average rainfall, percentage tree cover and land use (Table S3). Covariates were resampled at 1 km resolution. To avoid autocorrelation and model overfitting, we used a random subset of 50% of the lion population points as training data. After testing for collinearity among the dependent variables (using a Pearson correlation coefficient of 0.7 as a threshold, [Zuur et al., 2009]) we modelled the lion densities using a gamma log-link GAM (R package "mgcv" Wood, 2011). To account for spatial autocorrelation, additional geographical components, Latitude, Longitude and their interaction, were added, and this model was found to perform better based on deltaAIC and Akaike weights (R package "MuMIn," Barton, 2020). Finally, the model was validated by the Pearson correlation coefficient between the raw densities of the remaining data (50%) and densities for these points predicted by the model.

To estimate lion population densities across lion range c1970, we projected the density model described above across the c1970 lion range (Figure 1). For this, we extracted the same covariates used in the model for the historical range and replaced both land use (World Database on Protected Areas, WDPA) and human density GIS data layers for the appropriate to the period c1970 (Table S3). The

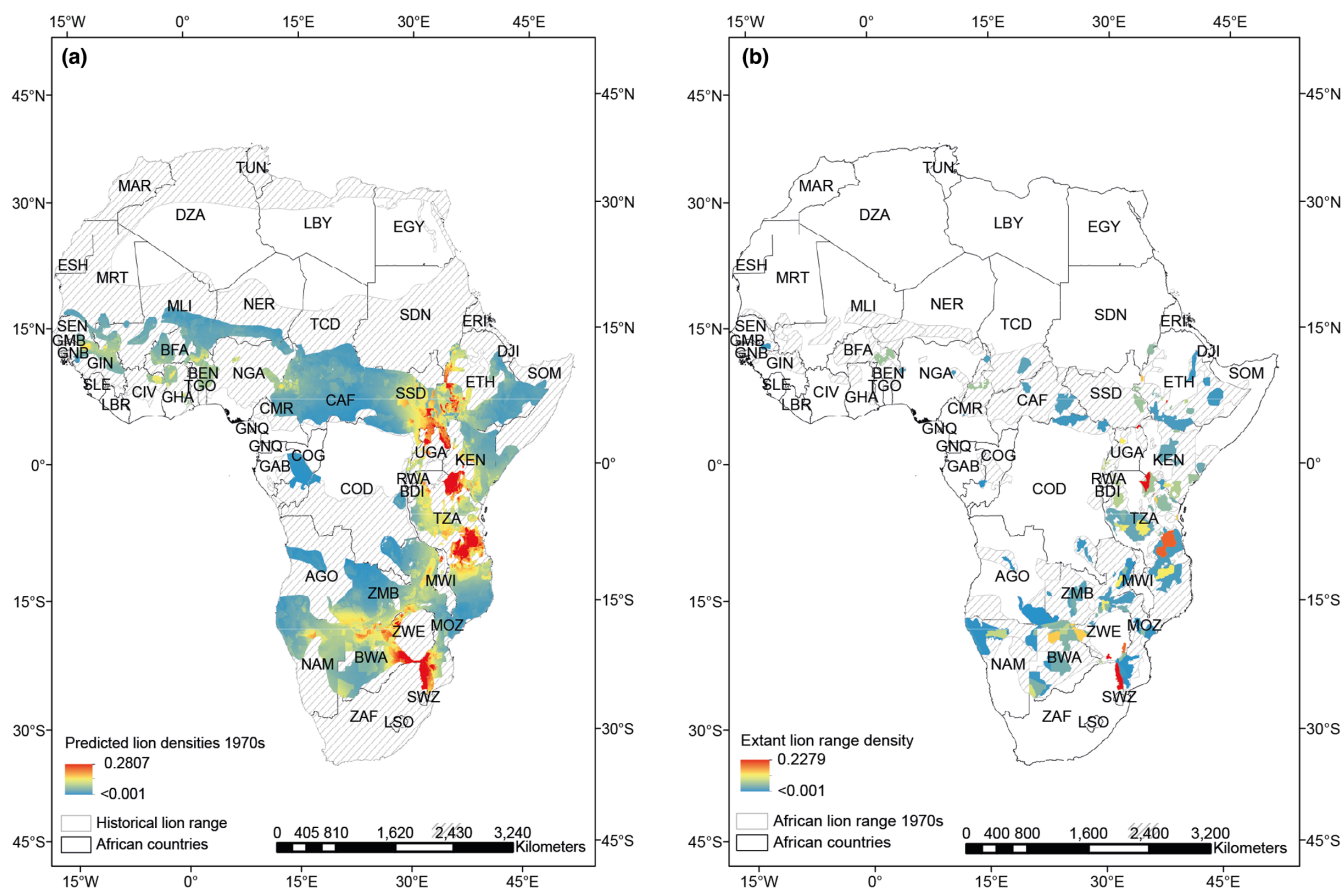


FIGURE 1 African lion density (N/km^2) across (a) recent historical (c1970) lion distribution with population density derived from a generalized additive model; and (b) extant range showing lion population densities (Source: IUCN-SSC, 2018).

predicted recent historical population densities at a 1 km resolution were then used to generate the lion source points for modelling historical landscape connectivity (see below), using Zonal statistics tool in ArcGIS to calculate the summed N/km² per population polygon. This final number of lions per polygon was used to generate random points in each polygon for connectivity analyses.

2.3 | Predictions of African lion habitat connectivity past and present

In lions, male natal dispersal is disproportionately important in determining population connectivity (Dolrenry et al., 2014; Elliot et al., 2014). To measure the impacts of habitat loss and fragmentation on the connectivity of African lion range, we generated a surface of landscape resistance to lion movement based on movement data collected from male dispersers in the Kavango–Zambezi Transfrontier Conservation Area (KAZA), empirically optimized using a multiscale, path-selection function (Cushman & Lewis, 2010) that included a total of ten different environmental and anthropogenic covariates (Elliot et al., 2014; See Table S4a,b). This was used to predict landscape resistance, with dispersing males selecting movement paths preferentially in protected areas and avoiding agricultural lands, areas in close proximity to towns, areas with high human population density and large roads (Cushman et al., 2015, 2018; Elliot et al., 2014). Using these empirical relationships, we calculated a resistance surface for recent historical and current time periods using GIS data layers appropriate to each period (see Elliot et al., 2014 for methods, Table S4a,b). The 500m resolution resistance surface provides resistance values for all locations in the study extent, in the form of the cost of crossing each pixel relative to the least-cost condition.

Landscape connectivity models calculate the relative probability of animal movement (dispersal) across a modelled landscape using cost (resistance to movement) surfaces, empirically optimized using movement data, and realistic species movement and distribution parameters in order to predict population connectivity and habitat fragmentation (Diniz et al., 2020). Predictions of both recent historical and current landscape connectivity for African lions were calculated using cumulative resistant kernels (KDE, Compton et al., 2007) and factorial least-cost paths (LCP, Cushman et al., 2014). The KDE method calculates movement paths between geographical source points (see below) and every pixel in the resistance surface. The LCP method predicts movements between pairs of source points. Source points reflect the distribution and density of the underlying population with the cost of moving between points or points and pixels in the resistance surface based on the value of the resistance surface (Figure S2). Source points for contemporary populations were established from the known distribution and population size of extant lions. Within each subpopulation polygon, points (each representing a source or destination location for a dispersing lion) were randomly distributed with a minimum spacing of 1.5 km a radius that is plausibly representative of the core of the smallest lion home

range (van Orsdol et al., 1985), with the density of points within each subpopulation polygon equivalent to population size. Source points for recent historical populations were generated from the modelled recent historical distribution and population density. As with the current lion population, we converted densities to source points by randomly generating a distribution of individuals matching the density within each range unit of the c1970 range. For computational efficiency, we used half the number of source points from both current and recent historical populations (11,318 and 46,029 source points, respectively).

We used UNICOR (Landguth et al., 2012) to calculate the KDE and LCP density maps. The KDE model calculates the expected movement of dispersing lions per pixel of the resistance surface, given the dispersal ability of the species, the density and distribution of the source population and the resistance of the landscape (Compton et al., 2007; Cushman & Lewis, 2010) and can be interpreted as the probability of a dispersing lion traversing each pixel. The LCP analysis calculates the least-cost paths among all combinations of source points and sums them to create a path density map reflecting the relative strength of linkages across the network (Cushman et al., 2009). The LCP approach complements the KDE by defining corridors between core habitat patches in the landscape and potential constraints to dispersal movement patterns (Cushman, McRae, et al., 2013).

We calibrated the cost units dispersal threshold for the resistant kernel analysis for both current and recent historical resistance surfaces against the dispersal ability of lions within a National Park (~80km²) established by Elliot et al. (2014), using the following conversions derived from linear regressions: Current Continental Resistance = $2.018 + (0.171 * \text{Elliot et al., 2014})$, where Elliot et al., 2014 refers to the resistance layer values of that study, and Recent Historical Resistance = $4.316 + (0.665 * \text{Current Continental Resistance})$. Based on these calibrations, we specified a dispersal threshold of 170,000 cost units for the resistant kernel analysis of current and 115,000 for recent historical lion landscape connectivity. The LCP network was calculated with a dispersal threshold 3.25 times higher than the threshold defined for the cumulative resistance kernels, (Cushman et al., 2018; Kaszta, Cushman, Htun, et al., 2020), to simulate the long-range dispersal of individuals recorded as dispersing between protected areas (mean 261 ± 77 km, range 150–347, $n = 8$). The resultant LCP density layers (current and recent historical) were smoothed using a focal mean of 5 km radius (ArcGIS, ESRI) to more realistically highlight linkage width for highly mobile species such as African lions and termed “corridors” hereafter (e.g., Cushman, Landguth, et al., 2013).

To account for uncertainty in both the population estimates and dispersal ability, we undertook a sensitivity analysis by running cumulative resistance kernel and least-cost path models at two different dispersal thresholds (3.25 and 6.5 times dispersal thresholds—see above) and using three different population estimates (actual plus $\pm 10\%$ of the current lion estimates). We then calculated Pearson's correlation and averaged absolute difference between the kernels and the least-cost paths layers.

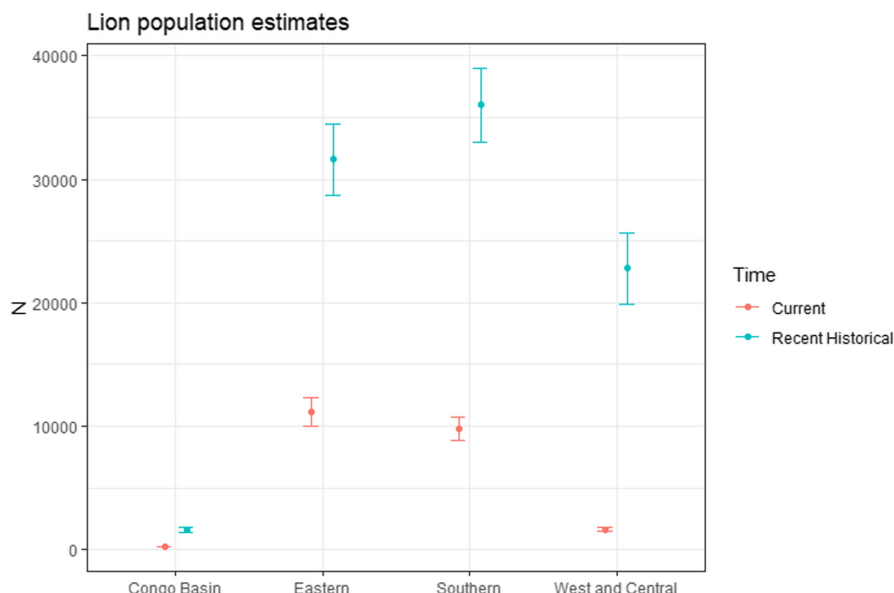


FIGURE 2 Estimated recent historical regional subpopulation sizes compared with extant populations for the same regions. Regionally, the West and Central African subpopulation has declined by 87%, the Eastern African subpopulation by 65% and the southern African subpopulation by 73%. The Congo Basin population has been almost entirely extirpated, declining by 93%. Error bars represent $\pm 10\%$ of the current estimated populations and $\pm 2SE$ (95% CI) for the projected population estimates for ~1970.

2.4 | Metrics to define landscape connectivity

KDE GIS layers were classified as: “0” (background where no connectivity is present); “1” (non-core connected areas where the kernel density probability of dispersal was less than the 1st quartile of the kernel values) and “2” (core connected areas as all the remaining connected habitat) after Cushman and Landguth (Cushman & Landguth, 2012). For the recent historical range, background values were defined as the maximum-historical African Lion range, equating to the extent of lion range in Africa c1500AD (IUCN-SSC, 2006; Morrison et al., 2007). For the current lion range, background values were defined against both the historical and the recent historical range in order to assess total habitat loss and fragmentation occurring over the last 50 years. To characterize and compare temporal and spatial (at continental, regional and country levels) changes in connectivity in core and non-core habitats, for both recent historical and current lion ranges, we calculated six measures of landscape fragmentation in Fragstats (McGarigal et al., 2012, Table S5).

To facilitate regional analyses, we defined the Regions of Africa as Southern (savanna regions South of the Angolan woodland-forest transition and West of the southern Rift Valley, Figure S2), Eastern (savannas to the east of the Albertine Rift and including Ethiopia and Somalia), West and Central (forest and savanna mosaic North of the Equatorial forest and West of the Nile Valley, corresponding broadly with the West/ Central African lion genetic clade, Bertola et al., 2021) and Congo Basin (forest-savanna mosaics South of the Equatorial Forest and West of the Rift Valley). These regions broadly coincide with phylogeographic and genetic patterns found in African mammalian taxa, including lions (Bertola et al., 2016, 2021; de Manuel et al., 2020), and align with regional indices of conservation performance described by Craigie et al. (2010). Regional extents follow political boundaries to facilitate per country analysis (see below).

Multitemporal principal component analysis (PCA, Cushman & McGarigal, 2019) of country-level Fragstats metrics was implemented

(R package “vegan,” Oksanen et al., 2020) to identify the similarity in landscape connectivity and lion habitat fragmentation between countries as well as the trajectory of the core connectivity areas through time from the recent historical to the current period. This analysis generated a ranking of countries based on habitat loss and landscape subdivision of lion range over the past 50 years.

Finally, we ranked connections between patches of core habitat across the continental lion range. We distinguish between two different categories of habitat connection. Firstly, LCPs linking two or more core areas, falling within non-core connected habitat (defined as above), termed habitat linkages, and LCPs between core habitats that did not fall within connected non-core areas, termed corridors. We ranked non-core connected habitat linkages according to the combined weighted area of core habitat they linked (total area of core areas combined divided by the ratio of larger/smaller patch (Kasza, Cushman, & Macdonald, 2020)). Dispersal corridors formed by LCP links were ranked (Table S6) according to the number of paths (as the proportion of maximum links); the combined size of core areas they connected (divided by the ratio of larger/smaller patch) and intensity (LCP value), following Cushman et al. (2018). See Figure S6 for a synthesis of the methodological approach.

3 | RESULTS

3.1 | Population density estimation

The global GAM model was found to be the most parsimonious, with all variables being significant determinants of lion population density (Tables S7, S8, Figures S3 and S4). This model was further validated by the correlation between the predicted lion densities and the hold-out dataset (Pearson's coefficient 0.8693; $t = 181.26$, d.f. = 10,618, p -value $< 2.2e-16$). Overall, the model explained 69.6% of the deviation in lion density across extant range. This model, substituting variables corresponding to c1970, was used

to generate a population density map across the recent historical range (Figure 1a), giving an estimated population of 92,054 (83,017–101,094 95% CI) lions for this period. These numbers suggest that, compared with current estimates, lion populations have declined by approximately 70,000 (~75%) in 50 years, or by roughly 1400 lions per year over five decades.

Regionally, the West and Central African subpopulation has declined by 87% (from 1600 to ~200, Figure 2), the Eastern African subpopulation by 65% (~31,000 to ~11,000) and the southern African subpopulation by 73% (~36,000 to ~9800). The Congo Basin population, estimated at ~1600 lions in c1970, has been almost entirely extirpated, declining by 93% to 211 lions currently.

3.2 | Sensitivity analysis

The sensitivity analyses (Table S21) suggest that simulations using $\pm 10\%$ of population size (number of source points) had little effect on calculated kernel density or least-cost paths, with layers being highly correlated with low absolute average difference (KDE: $r \geq 0.88$, AAD ≤ 0.12 ; LCP: $r \geq 0.82$, AAD ≤ 2.6). Outputs were more sensitive to doubling the maximum dispersal distance (unit cost), although correlations between calculated kernel density or least-cost paths were still high (KDE: $r \geq 0.88$; LCP ≥ 0.81) and absolute average difference relatively low for kernel density (KDE: AAD ≤ 0.74), although due to the biologically unrealistic dispersal distance ($>500\text{ km}$) had a larger effect on absolute average difference between least-cost paths (LCP: AAD ≤ 24).

3.3 | Recent historical connectivity compared with historical range

Landscape connectivity for lions for c1970 shows that relatively recently much of extant African lion habitat was well connected (Figure 3a), although some fragmentation was apparent in populations in the far West of the West and Central region, those in Congo Basin and in the Northwest of the Southern region. Overall, the recent historical lion range is estimated to have contracted 59% from its historical maximum (Figure 4, Table S9) with only 31% of the total historical area representing a core habitat for lions. The largest decrease in landscape extent occurred in the Congo Basin region (82%) followed by the West–Central region (63%), with the smallest, but nonetheless substantial, contractions occurring in the Southern (42%) and Eastern (40%) regions.

Regionally, the Eastern and Southern recent historical areas contained relatively more core and non-core habitat patches (Number Patches, NP) and these were less fragmented than those in Congo Basin, as indicated by higher Largest Patch Index (LPI, Table S9). The Largest Patch Index of core habitat in c1970 occupied 41% of the Southern region, 47% in the Eastern and only 14% of the West and Central, and 4% of the Congo Basin. The ability of a lion to traverse extant non-core patches (Gyrates-AM, Table S9), approximating habitat

extent, was similar between Southern, Eastern and West regions, but 4 to 7 times lower in the Congo Basin. The same regional pattern is found in relation to the isolation of core areas, with Southern, Eastern and Western regions showing a higher level of proximity (Prox-AM, Table S9). Core areas in the Congo Basin were more isolated. However, core habitat extent was largest in the Southern area, with average patches 1.4 times larger than the Eastern, ~3 times greater than the West and Central and 55 times greater than in core patches in Congo Basin. There were fewer, smaller core habitat patches in the West and Central and Congo Basin than Eastern and Southern regions. LCP analysis suggests that, historically, core habitats were linked by ten corridors: six in the Congo Basin and two in each of the Eastern and Southern Regions (Figure 3c).

3.4 | Current lion population connectivity

Current, continent-wide lion populations occupied 13% of the maximum-historical range of the species, with only 9.9% of historical range currently constituting core connected habitat (Figure 3b). Range loss was most severe in the Congo Basin area with ~97% loss, with only small remnant populations remaining, and West and Central region, with 96% loss relative to the maximum-historical range, and extant core connected habitat constituting less than 2.3% of historical range. The Southern and Eastern areas have lost ~75% of range relative to the maximum-historical range, with current core connected habitat making up 19% and 23% relative to this baseline. At a continental scale, lion range has declined by 66% against the recent historical baseline. Regionally, the West and Central habitat has shrunk by 90% and Southern and Eastern regions by 55 and 44%, respectively.

In terms of connectivity of the current landscape, the West and Central and Congo Basin habitats were highly fragmented, with fewer, smaller and more widely isolated patches of both core and non-core habitat compared with the recent historical range, indicating a catastrophic collapse in range and habitat connectivity over the last 50 years (See Fragstats landscape indices, Table S10). The Southern and Eastern habitats were also more fragmented compared with recent historical extents with, respectively, the connected largest patch index (LPI) declining from 44 to 20% and 50 to 12% of the maximum-historical extent over 50 years. Extent of core connected habitat (Gyrates-AM) declined by a factor of ~2.3 in the Southern, ~3.7 in East ~7.2 in West and Central and ~2.1 in Congo Basin, suggesting core habitat fragmentation was least severe in the Congo Basin and Southern regions and most severe in the West and Central region compared with the recent historical period. Metrics characterizing landscape fragmentation suggest that the Southern region is composed of fewer (NP), larger (Gyrates-AM) but more isolated (Prox-AM) patches of connected habitat and the Eastern area of relatively more, smaller and more proximate patches. See Tables S17–S20 for detailed country-level metrics.

We identified three LCP habitat linkages connecting two or more core areas within non-core habitat (Figure 3d, Table S11).

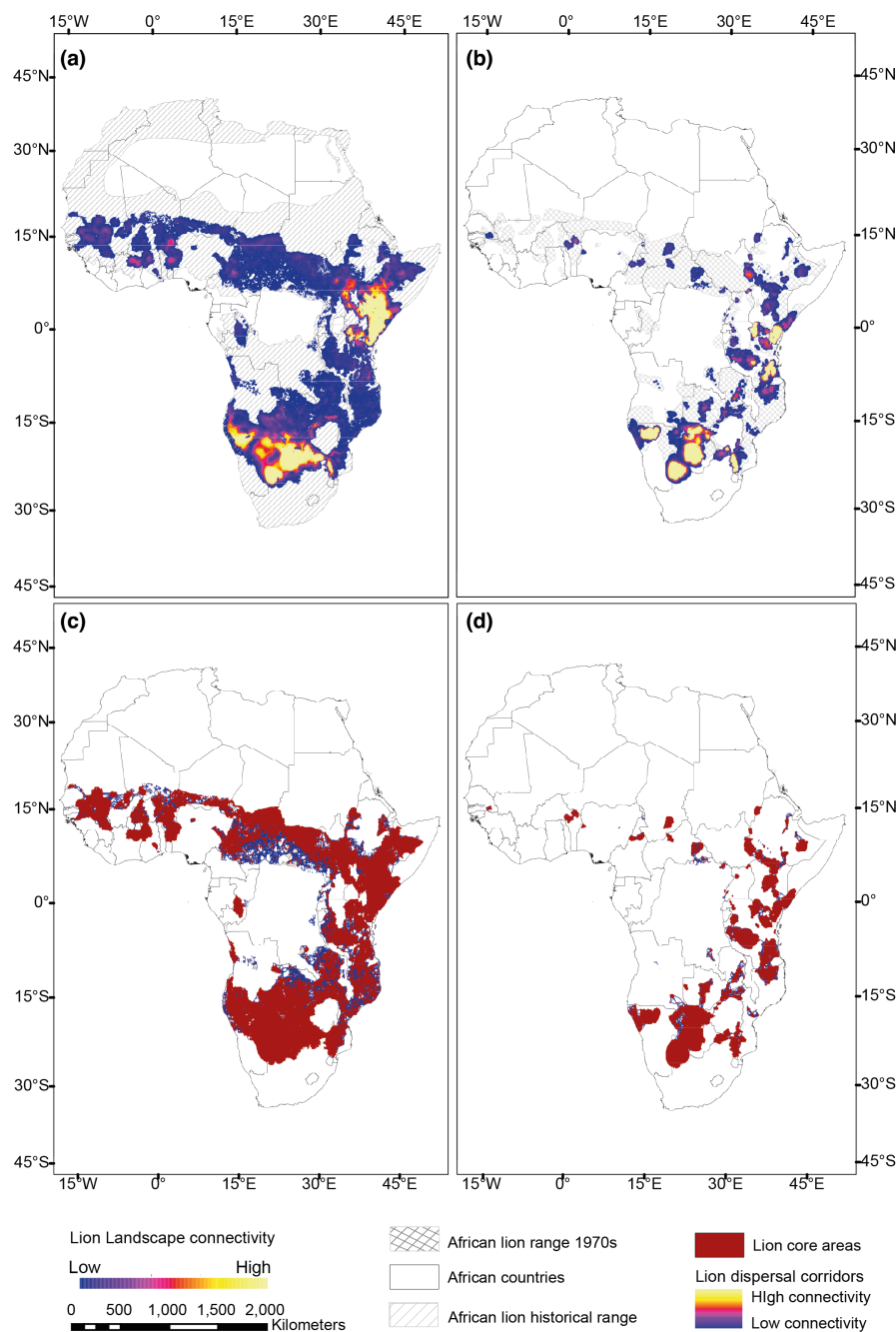


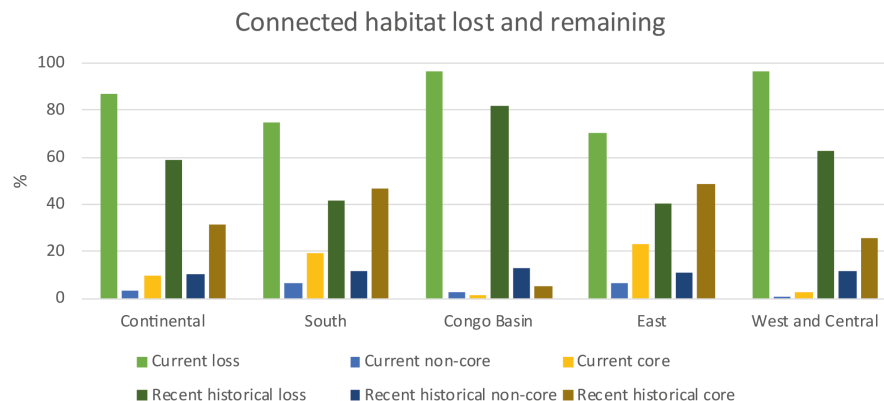
FIGURE 3 Maps showing landscape connectivity for c1970 and current time periods. Top panel: Landscape connectivity resistant kernels in (a) c1970 and (b) the current period. Bottom panel: least-cost paths in (c) c1970 and (d) the current period. The shaded area represents historical range extent (right-hand maps) and recent historical extent (left-hand maps).

These habitat linkages provide important connections between protected area complexes across the southern African savanna landscape (Figure 5c). In addition, we identified fifteen LCP corridors connecting core areas of adjacent patches of connected habitat falling outside connected habitat (Table S12). The highest ranked was in the East African region connecting the central Kenyan populations with the Maasai Steppe (Figure 5b). The model also reveals a corridor (ranked #4) connecting the Selous–Niassa with the Ruaha–Rungwa landscapes in Tanzania (Figure 5b). The top three corridors in the Southern region had relatively weak LCP values but connected large and highly connected core areas (namely linkages between the Greater Limpopo Transfrontier Conservation Area and the Mapungubwe TFCA (ranked #2), the

Zambezi Valley and Luangwa ecosystem (rank #3), the Kafue ecosystem with the Okavango–Hwange ecosystem (ranked #5) and the Zambezi Valley to the Okavango–Hwange ecosystem (ranked #6 and #14), Figure 5c). Of concern, we found only one corridor linking core areas, outside of non-core habitats, in the West and Central region linking Bili Uere–Garamba–Chinko (ranked # 10) and a second one connecting the Upemba and Kundelungu populations in DRC (ranked # 15) in the Congo Basin region (Figure 5a).

At the country level, lions have been extirpated from six countries in sub-Saharan Africa prior to 1970. Of 35 countries with extant lion habitat in 1970, ten (all in West and Central Africa) lost all habitat in the subsequent 50 years. Twenty-five countries currently retain core connected lion habitat (Table S13).

FIGURE 4 Percentage connected habitat lost and remaining in c1970 (recent historical) and at the current time against a baseline of maximum extent of historical lion range.



The results of the PCA analysis of Fragstats metrics reveal that almost all countries showed a clear signal of loss of core habitat area between c1970 and the present (Figure 6, Tables S14–S16) even though from different initial conditions and to different degrees. For example, South Sudan, Zambia Ethiopia and Mozambique exhibited large decreases in core habitat (axis 1, Figure 6). On the contrary, the degree of subdivision showed a mixed signal (axis 2, Figure 6), with some countries showing increases in subdivision, for example, Zimbabwe, Rwanda, Kenya and Benin and others showing decreased subdivision, for example, Mozambique and Malawi. Increases in subdivision likely result from patches being fragmented and broken up, whereas decreases in subdivision almost certainly result from loss of entire areas of core habitat, resulting in fewer patches and less total subdivision. See Tables S17–S20 for detailed differences in both area extent and subdivision per country.

4 | DISCUSSION

African lions were once one of the most widely distributed African savanna mammal species, with their geographic range extending from the Mediterranean to the southern tip of the African continent (Guggisberg, 1961). Range collapse driven by habitat loss and persecution by humans has resulted in the extinction of the northern and southernmost populations, and severe fragmentation and population decline across the remainder of the species range. These threats are predicted to accelerate and become more severe in the next 50–100 years (Tilman et al., 2017). Here, we quantify this decline over the last half-century, a period of unprecedented social and environmental change on the African continent, to generate a baseline against which to measure future conservation interventions.

Contemporary views of species conservation suffer from shifting baseline syndrome (Pauly, 1995; Plummeridge & Roberts, 2017), in that modern attempts to halt biodiversity decline often focus on existing geographical ranges and ignore or underestimate historical declines or trends. Failure to appreciate the magnitude and drivers of past loss may lead to an underestimation of contemporary extinction risk. Equally, pessimistic views of past population decline can hamper the realistic assessment of species conservation status and downplay conservation successes and population recovery

(Roman et al., 2015). Using population and landscape connectivity models, we estimate population size, range extent and connectivity for the African lion, providing a baseline for c1970.

4.1 | Population size

Accurate estimates of historical African lion population size are absent. A baseline figure, frequently caveated with regard to the uncertainty, of 200,000 is often cited relating to either the 1970s (e.g., Hazzah et al., 2009; Main, 2020) or the early 20th century (IUCN-SSC, 2006; Panthera, 2021). This estimate does not appear to be based on any empirical data or analysis and is likely to be derived from an article by Myers (1975) that speculates populations could be “as low as 200,000 or less,” having been “halved since the 1950s.” Our findings, based on a projection of lion range and population density c1970, suggest that the continental population was in the region of between 83,000 and 101,000 lions at this time. The estimate of 200,000 derived from Myers (1975), when used as a population baseline for the 1970s, is therefore likely a substantial overestimate, though may be plausible as a baseline for an earlier period. Our estimate implies that, while undoubtedly severe, population collapse since the 1970s may not have been as catastrophic as previously thought. Nevertheless, even against this more realistic baseline, continental lion populations have declined by over 75% (72%–77%) in the last 50 years. Regionally, they have declined by 93% in West and Central, 65% in Eastern, 73% in Southern Africa and 95% in Congo Basin. Despite differing in the analytical approach and temporal scales of analysis, this finding is consistent with declines of 42% over two decades from the mid-1990s estimated by Bauer et al. (2015). Our historical population model suggests there may have been ~1600 lions in sub-Equatorial West Africa in Gabon and S.W. Congo Basin, within a sizeable area of connected savanna habitat. This estimate is difficult to verify as there is sparse historical data on population size available for the region; nevertheless, lions were described as “widespread” in the Congolese Savanna in the 1940s (Malbrant & Maclatchy 1949, in Chardonnet, 2002) and there are sporadic contemporary records of lions in the Batéké Plateau region of Gabon and Northern Congo (Hedwig et al., 2018; Henschel et al., 2014), suggesting a remnant

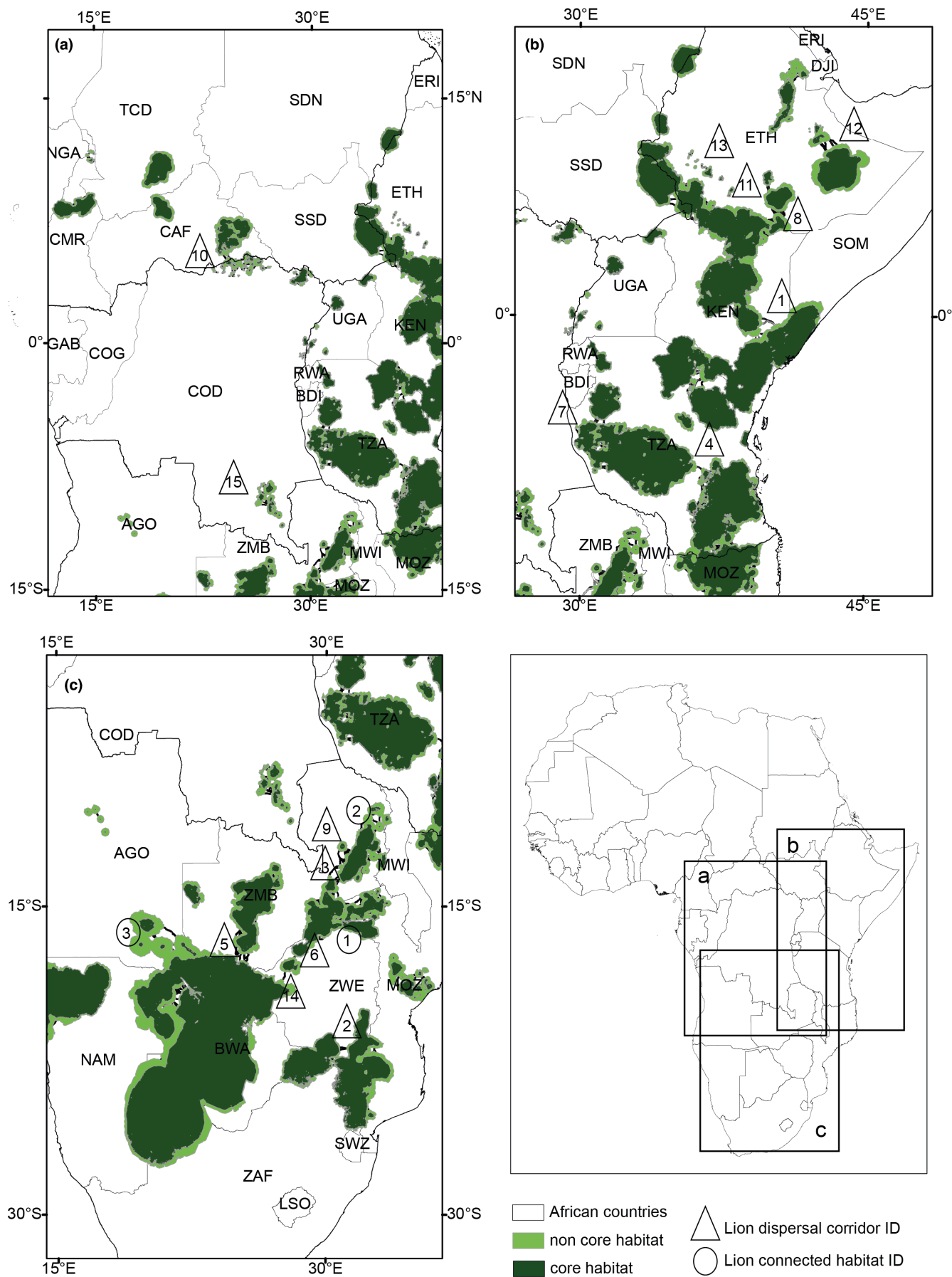


FIGURE 5 Showing the top three prioritized non-core habitat linkages (numbers in circles) and top 15 prioritized least-cost paths traversing non-core habitat (numbers in triangles) in four regions (a–d) of Africa (see map E). Numbered circles: 1- Zambezi Valley–Tchuma Tchato, 2- Luangwa–Luangwa Vwaza and 3- Kavango–Luenge Luiana. Numbered triangles (see Table S12 for details): 1- Central Kenyan populations–South Maasai Steppe, 2- Limpopo–Bubye, 3- Luangwa–Zambezi Valley, 4- Katavi–Ruaha–Selous, 5- Kavango–Kafue, 6- Zambezi Valley–Chirisa, 7- Moyowosi–Katavi–Ruaha, 8- Welmel–South Omo, 9- Lavushi–Luangwa, 10- BiliUere–Garamba–Chinko, 11- Bale–Welmel, 12- Hararghe–Ogaden, 13- Kafa–Chebera, 14- Kavango–Chirisa, 15- Upemba–Kundelungu. Country codes conform to the ISO-Alpha 3 naming convention.

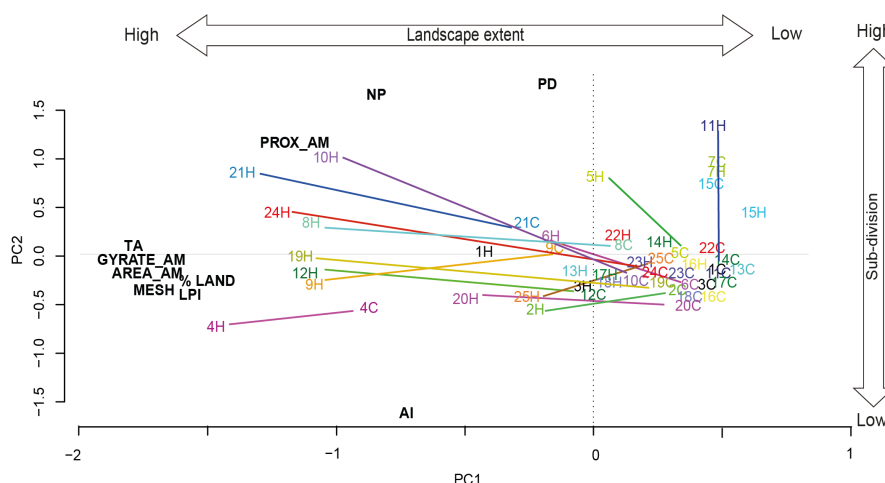


FIGURE 6 Core connectivity trajectory through time. Multitemporal PCA on landscape metrics in relation to a lion population core area. The axes illustrate the changes in the core areas per country. C denotes the current state of that country core area, whereas H refers to the historical core area. Multitemporal PCA analysis shows that 81.3% of the variance is explained by the first two axes (Tables S14–S16, Figure 6). Axis 1 is a gradient in the extent of lion core areas; landscapes characterized by large, extensive, connected patches of habitat lie on the left side of the axis, while landscapes with little or no habitat lie to the right. Axis 2 shows a gradient in subdivision of core connected habitat; lion cores characterized by a larger number of separate patches of habitat lie on the top of the Y axis, while landscapes with comparatively fewer patches lie on the opposite end. Countries are numbered as follows:

| | | | | | |
|---|----------------------------------|----|------------|----|--------------|
| 1 | Angola | 10 | Mozambique | 19 | South Sudan |
| 2 | Benin | 11 | Malawi | 20 | Chad |
| 3 | B. Faso | 12 | Namibia | 21 | Tanzania |
| 4 | Botswana | 13 | Niger | 22 | Uganda |
| 5 | CAF | 14 | Nigeria | 23 | South Africa |
| 6 | Cameroon | 15 | Rwanda | 24 | Zambia |
| 7 | Democratic Republic of the Congo | 16 | Sudan | 25 | Zimbabwe |
| 8 | Ethiopia | 17 | Senegal | | |
| 9 | Kenya | 18 | Somalia | | |

of a possibly once widespread regional population may persist. It is suggested that lions from this region are more closely related to southern African populations, than those from West and Central Africa (Barnett et al., 2018), indicating possible historical connectivity with more southerly populations.

4.2 | Population connectivity

Analysis of recent historical and current lion landscapes identifies three distinct classes of habitat connectivity. First, core connected

habitats are areas that are highly likely to be traversed by dispersing lions and protect breeding populations. Core habitats for lions are almost invariably centred on one or more large protected areas. Second, non-core connected habitats are less permeable to lions, but nevertheless represent critical habitat linkages that could support lions and facilitate movement and gene flow. Non-core habitat usually surrounds areas of core habitat or is formed by smaller protected areas. Finally, we identified corridors that traverse unconnected habitat and provide links that dispersing lions might infrequently use to move between patches of suitable habitat and represent critical linkages for gene flow.

The c1970s lion landscapes, while having contracted by ~60% from the maximum-historical extent, nevertheless consisted of expansive core habitats surrounded by a relatively continuous matrix of non-core habitat. Apart from isolated patches in the far West and Congo Basin regions, lion range was largely contiguous and connectivity models suggest there was potential for a high degree of dispersal movement across the landscape. By contrast, contemporary lion range is significantly more fragmented than 50 years ago, with overall range declining by ~87% from the maximum-historical extent and ~66% from recent historical range, demonstrating that habitat loss has accelerated significantly. This far exceeds the ~18% loss of African savanna habitat since 1960 estimated by Riggio et al. (2013), though is consistent with ~71% loss of potential lion range described by these authors. Of the 34 sub-Saharan countries containing connected lion habitat in 1970, only 26 retain connected habitat currently, and of these, only 25 retain core lion habitat. At a national level, the extent of core lion habitat has almost universally declined and become increasingly fragmented.

Many formerly contiguous core areas have been fragmented into small, isolated and less permeable habitat patches. The West and Central and Congo Basin regions have been most heavily affected, losing 90% and 83% of range, respectively, relative to the 1970s extent. These regions also showed the highest levels of loss and fragmentation in comparison with maximum-historical range, suggesting that processes contributing to range decline were already taking place by the middle of the 20th century. Eastern and Southern regions have suffered lower loss of connectivity, overall losing ~50% of connected habitat, but maintaining several core areas of continuous habitat centred on large protected area complexes. This regional pattern of loss is mirrored in declines of mammalian species in protected areas across these regions (Bouché et al., 2010, 2011; Craigie et al., 2010) and is likely a reflection of higher levels of protected area management and budgets in eastern and southern Africa (Lindsey et al., 2017, 2018).

Species with highly fragmented ranges face a high risk of extinction (Crooks et al., 2017), with small isolated populations more vulnerable to environmental and demographic stochasticity. They are more likely to suffer from loss of genetic diversity and inbreeding depression as a result of reduced effective breeding population size and reduced gene flow, with strong correlations between loss of heterozygosity and declines in population fitness (Reed & Frankham, 2003). The effects of inbreeding and loss of genetic variability following population fragmentation or isolation have been demonstrated for several large felid populations (de Manuel et al., 2020; van de Kerk et al., 2019), manifesting as deleterious genetic abnormalities affecting breeding success, such as reduced testosterone, sperm abnormalities and cryptorchidism (Onorato et al., 2010; Packer et al., 1991; Wildt et al., 1987), as well as increased vulnerability to disease as a result of eroded genetic variability (Trinkel et al., 2011). Recent analysis of African lion genetic diversity has shown marked declines in allelic richness, heterozygosity and private alleles in modern compared with

historic lion populations (Antunes et al., 2008; Curry et al., 2020; Dures et al., 2019). Furthermore, modern continental lion populations are more highly structured genetically than in the past, when lion populations were likely regionally panmictic with high levels of male-mediated gene flow (Curry et al., 2020), suggesting that barriers to gene flow exist in the modern landscape that were absent historically. Genetic isolation appears to align closely with observed patterns of habitat fragmentation (Curry et al., 2019; Dubach et al., 2013; Morandin et al., 2014; Smitz et al., 2018; Tende et al., 2014) and conforms closely to the declines in habitat connectivity from recent historic to current times we predicted here (see Figure S5a–d).

4.3 | Conservation implications

In our models, increasing human population density, more widespread infrastructure and larger urban extents greatly increase landscape resistance in the current compared with the c1970s landscape, reducing the permeability of the landscape and the movements of lions. Human population growth in Africa has accelerated since the 1950s, with populations increasing by 59% and per capita resource use having increased by 73% by the 1970s (Bongaarts, 2009; Holdren & Ehrlich, 1974). The population of sub-Saharan Africa doubled between 1975 and 2001 and will double again by 2034 (United Nations, 2019), likely resulting in significant clearance of natural habitat for agricultural production and increasing resource extraction and consumption (Díaz et al., 2019; Tilman et al., 2017) and increasing settlement, urban areas and transportation infrastructure (Laurance et al., 2014). This rapid growth of the human enterprise has already resulted in severe environmental degradation across much of Africa and will continue to do so (Bradshaw & Di Minin, 2019) and is expected to accelerate existing trends of habitat fragmentation and isolation of protected areas (Newmark, 2008; Östberg et al., 2018).

Our analysis suggests that core connected habitat for lions has been continuously eroded since historical times, with ~26% of African countries losing all core habitat since 1970, with increased human impact in current models greatly reducing the ability of lions to move through the landscape, with areas with currently weak or absent connectivity coinciding closely with regions where high risk of human conflict with lions and elephants (*Loxodonta africana*) is predicted (Di Minin et al., 2021). Much of the remaining core habitat for lions is centred on large protected areas and the future of lions and Africa's large mammal diversity depends critically on the management of these protected areas, which are worryingly under-resourced and many are failing (Lindsey et al., 2018; Robson et al., 2021). As such, securing the protection of African conservation areas through greater investment in protected area management is crucial.

Nevertheless, even if core areas are secured, genetic diversity in populations of wide-ranging species, such as lions, is likely to continue to decline without adequate connectivity between

populations. To maintain what remains of lion genetic diversity will require, either, intensive and resource-expensive meta-population management with animals translocated between isolated core areas to maintain gene flow (Bertola et al., 2021), or protection of existing movement corridors that allow movement of both lions and other species between patches of natural habitat. The former approach is currently widely practised for the management of predator genetic diversity and population dynamics in small fenced populations in South Africa (Miller et al., 2015), but also might be appropriate in regions, such as West and Central Africa where populations are already irretrievably isolated. The latter approach, where existing dispersal corridors can be identified, prioritized and protected, is critical for maintaining existing levels of habitat connectivity for lions, gene flow and future genetic diversity. This may yet be a viable strategy in large connected landscapes in East and Southern Africa and importantly would also provide genetic and demographic exchange for a wide range of other non-target species. However, even in regions where landscape connectivity remains, these connections are likely to be highly vulnerable in the face of growing human populations and agricultural activity, particularly in the vicinity of protected areas where human population growth has been shown to be high (Wittemyer et al., 2008). Of the two types of connectivity linkage, LCP corridors across unconnected habitats are the most vulnerable to loss, as they generally traverse unprotected, human-occupied lands, where lions are less likely to be tolerated and more likely to face various sources of anthropogenic mortality (Loveridge et al., 2017). Encouragingly though, movement data collected from lions fitted with GPS telemetry in the KAZA region provide evidence that, at least in this region, these empirically modelled linkages are realistic and still used by dispersing lions (Elliot et al., 2014; Matshisela et al., 2021). This suggests that it is not too late for conservation managers to implement initiatives to secure these connectivity corridors, through integrated land use planning exercises (Estrada-Carmona et al., 2014; Kaszta, Cushman, Htun, et al., 2020), implementation of human-wildlife conflict mitigation strategies (Marchini et al., 2019; Sibanda et al., 2021) and enhancement of sustainable, wildlife-based livelihoods as part of landscape-scale conservation programmes (Schroth & McNeely, 2011). Future work should focus on scenario analyses that can optimize the trade-offs between development and conservation (Kaszta, Cushman, Htun, et al., 2020) across the lion range to allocate conservation resources to effective landscape-scale planning.

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CONFLICT OF INTEREST

The authors declare there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

All datasets and analytical software used is open source and freely available. Datasets used in analysis are available via the Dryad Digital Repository: <https://doi.org/10.5061/dryad.h44j0zpp6>.

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BIOSKETCH

The authors belong to the Wildlife Conservation Research Unit at Oxford University. Established in 1986 in the Department of Zoology, WildCRU is a pioneering, interdisciplinary research unit in a world-class academic centre. WildCRU aims to underpin solutions to conservation problems with primary scientific research of the highest calibre. Our approach is empirical, interdisciplinary and collaborative, seeking to understand and address conservation problems using empirical methods; provide education to explain them; involve communities to ensure participation and acceptance; and implementation of long-term solutions. Loveridge and Macdonald have undertaken research and conservation work on African lions in the Kavango–Zambezi Transfrontier Conservation area for over two decades.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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