From popularity to preservation: large carnivore potential for ecosystem conservation

Stijn VERSCHUEREN* *Cheetah Conservation Fund, PO Box 1755, Otjiwarongo, Namibia and Evolutionary Ecology Group, Department of Biology, University of Antwerp, Universiteitsplein 1, Wilrijk 2610, Belgium. Email: stijn@cheetah.org*

Hans BAUER *Evolutionary Ecology Group, Department of Biology, University of Antwerp, Universiteitsplein 1, Wilrijk 2610, Belgium and Wildlife Conservation Research Unit (WildCRU), Department of Zoology, The Recanati-Kaplan Centre, Oxford University, Tubney House, Abingdon Road, Tubney OX13 5QL, UK. Email: hans.bauer@biology.ox.ac.uk*

Bogdan CRISTESCU *Cheetah Conservation Fund, PO Box 1755, Otjiwarongo, Namibia and Namibia University of Science and Technology, 13 Jackson Kaujeua, Windhoek, Namibia. Email: bogdan@cheetah.org*

Herwig LEIRS *Evolutionary Ecology Group, Department of Biology, University of Antwerp, Universiteitsplein 1, Wilrijk 2610, Belgium. Email: herwig.leirs@uantwerpen.be*

Carolina TORRES-URIBE *Cheetah Conservation Fund, PO Box 1755, Otjiwarongo, Namibia. Email: carolina@cheetah.org*

Laurie MARKER *Cheetah Conservation Fund, PO Box 1755, Otjiwarongo, Namibia. Email: director@cheetah.org*

ABSTRACT

1. Conservation efforts are challenged by lack of funding and ambiguity in strategic prioritisation. Flagship species generate public attention but may not adequately represent and protect biodiversity. Integrating species-centric approaches with area-based strategies may refine conservation outcomes and could improve achievements towards biodiversity targets.

2. We present this case for a globally appealing flagship species, the cheetah (*Acinonyx jubatus*).

3. We identified research trends and gaps, and estimated the biodiversity value associated with cheetah occurrence throughout its free-ranging distribution.

4. Although the existing body of literature encompasses insights from diverse interdisciplinary approaches, current knowledge is mostly derived from a limited number of localised study areas, whereas most populations are understudied. Cheetahs inhabit more than half of Africa's ecoregions and their contemporary occurrence coincides with areas valuable for biodiversity conservation, in particular, closer to the equator where ecoregions are poorly protected and human footprint is high.

5. Cheetah conservation efforts could yield substantial biodiversity benefits, particularly outside protected areas, thereby complementing current area protection networks. Growing pressures on remaining habitat will require adaptive conservation strategies; hence, it becomes imperative to embrace a more inclusive and comprehensive approach to the protection of cheetahs, a flagship species for drylands and landscapes shared with humans.

INTRODUCTION

The natural world is imperilled and suffers severely from inadequate funding and lack of political and public interest (Butchart et al. 2010, Waldron et al. 2013, Díaz et al. 2019). To allocate limited conservation resources, global biodiversity conservation priorities have been identified and include among others biodiversity hotspots, areas of endemism, taxon-specific approaches and securing ecosystem services (Myers et al. 2000, Brooks et al. 2006, Grenyer et al. 2006, Nicholson et al. 2009). Similarly, research prioritisation efforts have been comprehensive (Greggor et al. 2016, Sutherland et al. 2023), but the vast and expanding number of conservation challenges can be daunting (Cristescu & Boyce 2013) and pessimism can be prevalent and counterproductive in conservation (Swaisgood & Sheppard 2010). Ecoregions were created to map terrestrial life and act as conservation units comprising geographically distinct assemblages of natural communities and species (Olson et al. 2001). An aspirational goal of protecting half the terrestrial realm emerged as 'Nature Needs Half', yet only 12% of ecoregions exceed 'Half Protected' (Locke 2013, Dinerstein et al. 2017). Attracting sufficient conservation attention for area protection remains challenging and therefore hinders area-based conservation strategies (Maxwell et al. 2020).

Charismatic species on the other hand broadly appeal to the public and are central as flagship species in conservation marketing campaigns (Verissimo et al. 2011, Macdonald et al. 2015). While these species, particularly large mammals, receive substantial research attention and inform species-based conservation initiatives (Bonnet et al. 2002, Clark & May 2002), the flagship approach has faced criticism for misallocating funds and its failure to adequately represent broader biodiversity (Andelman & Fagan 2000, Williams et al. 2000, Joseph et al. 2011). In addition, even the most charismatic species fail to generate sufficient funding for effective ecosystem conservation (Lindsey et al. 2018), underscoring the need for innovative and smart approaches to inform decision making (Bottrill et al. 2008).

Integrating species-centric approaches with area-based strategies may refine conservation priorities (McGowan et al. 2020). For the most charismatic species with the highest fundraising potential, it would therefore be worthwhile to evaluate their biodiversity representativeness. In addition, identifying thematic and geographic research gaps may inform and redirect species-based conservation actions. We present this case for the cheetah (*Acinonyx jubatus*), a globally appealing flagship species of high conservation priority (Belbachir et al. 2015, Dickman et al. 2015, Albert et al. 2018). The International Union for the Conservation of Nature (IUCN) lists the cheetah as Vulnerable under the Red List of Threatened Species (Durant et al. 2022). Five subspecies are recognised, with two subspecies listed as Critically Endangered (*Acinonyx jubatus venaticus* in Asia and *Acinonyx jubatus hecki* in northwest Africa), one as Endangered (*Acinonyx jubatus soemmeringii* in northeast Africa), and two as Vulnerable (*Acinonyx jubatus jubatus* in southern Africa and *Acinonyx jubatus raineyi* in east Africa) (Schmidt-Küntzel et al. 2018, Durant et al. 2023).

Cheetahs have been subject of extensive research efforts, yet it is key to evaluate whether these research patterns comply with the principles and broader desired outcomes of biodiversity conservation (Czech et al. 1998, Bonnet et al. 2002, Clark & May 2002, Marker et al. 2018a). Cheetahs predominantly occur outside protected areas (Durant et al. 2017) and require wildlife-friendly land-use practices (i.e. land sharing approach) (Green et al. 2005, Powell et al. 2018). Across these unprotected lands, the cheetah's wide-ranging behaviour makes it a potential candidate as umbrella species (Roberge & Angelstam 2004). However, species with broad habitat tolerances may persist in degraded landscapes, and the umbrella concept has been challenged for wide-ranging species (Linnell et al. 2000, Rozylowicz et al. 2011). The potential of large carnivores to act as biodiversity indicators is therefore also debated, and case-by-case evaluations should bring clarity (Dalerum et al. 2008, Natsukawa & Sergio 2022).

We provide an overview of cheetah research trends and themes to synthesise past research efforts and to identify gaps and avenues for future conservation research (1). Additionally, we overlay the cheetah's range with species richness and ecoregion layers to estimate its biodiversity value and to identify conservation priority areas, ultimately aiming to facilitate more efficient and directed conservation actions (2).

METHODS

Research trends

We performed a literature search in Scopus (https://www.scopus.com/) on 17 August 2022, with the search term 'TITLE-ABS-KEY (cheetah OR acinonyx)'. We retained only empirical research articles and reviews, and discarded duplicate items, errata, editorials, book chapters, conference proceedings, data papers, letters, commentaries and responses. We classified each article under a specific research theme, described in Appendix S1. If more than one research theme was suited, we assigned two or at most three research themes to one article. We explored interdisciplinarity of cheetah research based on network analysis of research themes classified together. The

classification was performed by two researchers independently to account for extraction errors, and we discussed disagreements until consensus was reached. To identify the relative importance of each research theme, we calculated the total number of articles, the mean number of citations of articles and the mean number of annual citations of articles (i.e. the average of the number of citations per article divided by the number of years since published). The latter was done to account for the positive relationship between time since publication and citation rate. Additionally, we derived the h-index per research theme (i.e. the number of publications for which a research theme has been cited by other publications at least that same number of times). We present the cumulative increase of research outputs over time for articles published since 1990, when more than 10 articles per year were published that met our search criteria. When applicable, we recorded the country where the research was performed to identify geographical bias in research efforts focusing on cheetahs. We acknowledge that research articles that considered regional distributions, or distributions of carnivore communities more broadly may have been omitted for this analysis. Our literature search followed the guidelines of PRISMA in ecology and evolutionary biology (O'Dea et al. 2021).

Biodiversity value

Cheetahs occur across various landscapes, but typically more so in semi-arid to arid environments (Durant et al. 2022). These ecosystems harbour unique species compositions, yet species richness is lower compared to more tropical systems (Kareiva & Marvier 2003). To address this, we explored ecoregion coverage by the cheetah's range and compared species richness values of the cheetah-covered portion of each ecoregion to the entire ecoregion. We used the most recent distribution map of the cheetah as determined by the International Union for the Conservation of Nature (IUCN, Fig. 1a) (Durant et al. 2022) and derived terrestrial ecoregion layers (Dinerstein et al. 2017) (Fig. 1d). We overlaid both data sources with four species richness rasters assessed by IUCN: all amphibians, birds and mammals (ABM, Fig. 1c); amphibians, birds and mammals that are listed as threatened ('Vulnerable', 'Endangered', 'Critically endangered'; tABM); all mammals (M); and mammals that are listed as threatened (tM) (IUCN 2021). The species richness rasters date from 2021 and reflect the number of species in 30 km × 30 km pixels, which roughly corresponds with mean cheetah home range size across published studies (Marker et al. 2018b). We extracted pixel-based means for the extant cheetah range and for the different ecoregions. Subsequently, we calculated for each ecoregion and for each IUCN species richness raster the difference in mean species richness between the extant cheetah range of the ecoregion and the entire ecoregion. For example, the average number of species present per 30 km × 30 km pixel in the West Sudanian savanna ecoregion was 437 (ABM), 81 (M), 14 (tABM) and 1 (tM). The average number of species present per 30 km × 30 km pixel in the cheetah-covered portion of the West Sudanian savanna ecoregion was 478 (ABM), 94 (M), 22 (tABM) and 7 (tM). Subsequently, this resulted in species richness difference values of 41 (ABM), 13 (M), 8 (tABM) and 5 (tM).

We derived four sets of species richness difference values consisting of 54 data points each, corresponding with the number of overlapping ecoregions of the extant cheetah range. Values above zero indicated that mean species richness for the cheetah-covered portion of the ecoregion was higher compared to the respective ecoregion, and values below zero indicated that mean species richness was lower compared to the respective ecoregion. The differences in species richness were interpreted as a proxy for the biodiversity value of cheetah occurrence, where large positive values may indicate ecologically valuable areas for cheetah conservation efforts.

We explored variation in species richness differences with a Principal Component Analysis (PCA) of ecoregions (observations) based on the four sets of difference values (active variables). We added supplementary variables that were related to geographical, environmental and anthropogenic attributes of ecoregions to better understand the dimensions of the variation (Table 1).

All statistical analyses were done in R version 4.2.2 (R Core Team 2022) using the packages igraph (Csardi & Nepusz 2006) and factoextra (Kassambara & Mundt 2020).

RESULTS

Research trends

We identified 1860 articles that met our search terms and filtered this number down to 1424 items to only include research articles and reviews. We discarded an additional 492 items which were articles irrelevant for our purposes and mostly pertaining to the development of new applications, processes and technologies that were named after or with reference to cheetahs because of certain properties, most often their speed. Although these articles were not included, they may reflect the perception of cheetah in modern-day society. We retained 932 empirical research articles on cheetahs of which 655 articles were assigned to one research theme, 255 articles were assigned to two research themes and 22 articles were assigned to three research themes. The number of articles showed a substantial increase over the past three decades and gradually expanded across the different research themes (Fig. 2, Table 2). Most research articles were
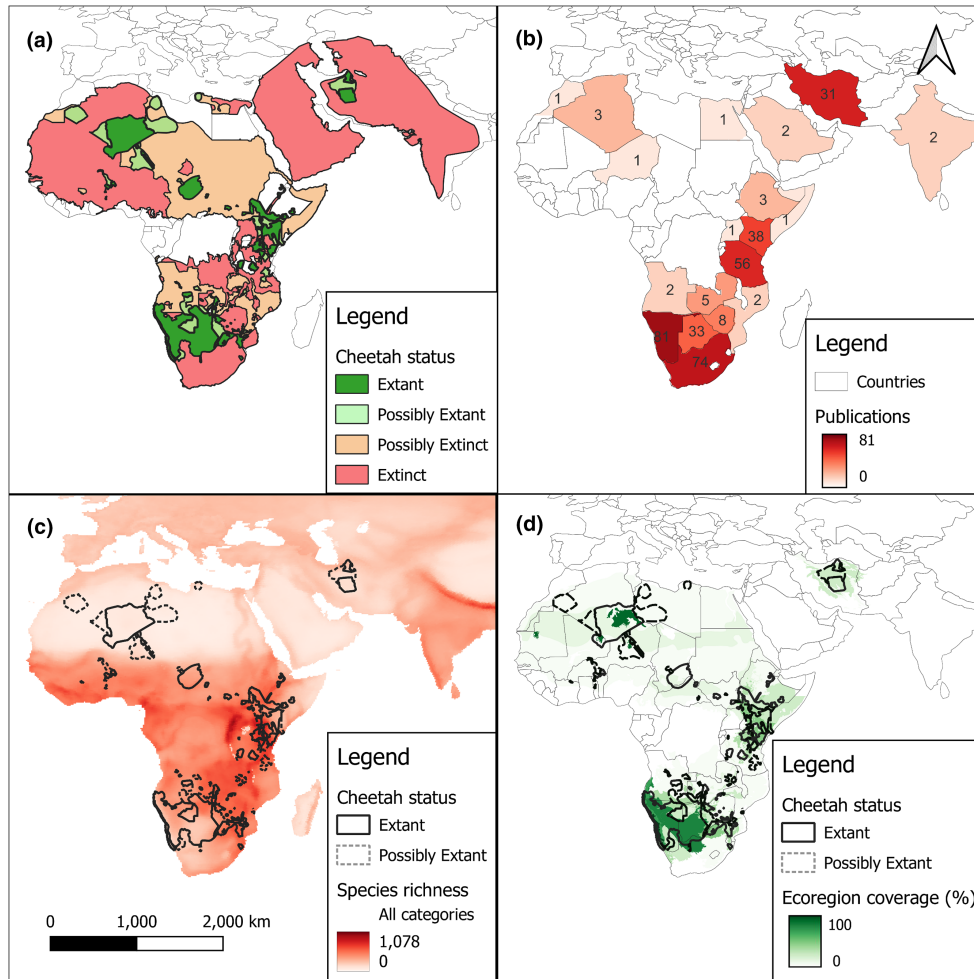
Fig. 1. (a) IUCN cheetah range (Durant et al. 2022); (b) Published literature on cheetah per country; (c) Species richness raster for all amphibians, birds and mammals assessed by IUCN overlaid with extant cheetah range; (d) Ecoregion coverage by the extant cheetah range (Dinerstein et al. 2017).

classified under the theme 'Disease' (*n*=309), with studies focusing on the formation, course, transmission and treatment of various kinds of disease in captive and free-ranging individuals and populations. Studies pertaining to themes 'Behaviour', 'Conservation', 'MorphoPhysio' and 'Population' were well-represented, and of particular relevance to the umbrella concept were the studies on inter-specific interactions, population ecology, distribution and conservation management. Dietary studies and reviews were less represented, but the high number of citations reflects their relevance within the field.

Cheetah research was interdisciplinary with 30% of research articles classifying under two or three research themes. 'Conservation' and 'MorphoPhysio' were the most connected and most central research themes, with both themes having a node degree of 8 (i.e. number of connecting themes) and a betweenness centrality of 1.35 (i.e. measure of centrality based on shortest paths) (Fig. 2). 'Conservation' was most often connected with 'Behaviour' (36 research articles) and

'Population' (30 research articles), while 'MorphoPhysio' was most often connected with 'Disease' (30 research articles).

The majority of in situ research performed on cheetahs was focused on Namibia, South Africa, Tanzania, Kenya and Botswana, as well as on the Iranian cheetah population (Fig. 1b). Other cheetah range countries were notably underrepresented, in particular, in northwest and central Africa and in the Horn of Africa. One hundred forty-nine publications (16%) included the term 'captive' in their title and reflected ex situ research.

Biodiversity value

The cheetah's current range covers 54 ecoregions where it is extant and 49 ecoregions where it is possibly extant, totalling a combined coverage of 57 ecoregions out of 119 ecoregions present in Africa, and a remaining 4 ecoregions out of 193 ecoregions in mainland Asia excluding

Table 1. Active and supplementary variables used in the principal component analysis to understand variation in species richness differences

Variable	Description	Source
Δ Species richness (ABM)	Differences in species richness between the cheetah-covered portion of each ecoregion and the entire ecoregion for all amphibians, birds and mammals	IUCN (2021), Durant et al. (2022)
Δ Species richness (M)	Differences in species richness between the cheetah-covered portion of each ecoregion and the entire ecoregion for all mammals	IUCN (2021), Durant et al. (2022)
Δ Species richness (tABM)	Differences in species richness between the cheetah-covered portion of each ecoregion and the entire ecoregion for amphibians, birds and mammals that are listed as threatened	IUCN (2021), Durant et al. (2022)
Δ Species richness (tM)	Differences in species richness between the cheetah-covered portion of each ecoregion and the entire ecoregion for mammals that are listed as threatened	IUCN (2021), Durant et al. (2022)
Latitude (x)	Latitude of ecoregion centroid	Dinerstein et al. (2017)
Longitude (y)	Longitude of ecoregion centroid	Dinerstein et al. (2017)
Area (A)	Area of ecoregion	Dinerstein et al. (2017)
Natural habitat remaining (H)	Remaining natural habitat of ecoregion	Dinerstein et al. (2017)
Average annual precipitation (R)	Long-term average of annual precipitation in the ecoregion (pixel-based mean)	Fick and Hijmans (2017)
Average annual temperature (T)	Long-term average of annual temperature in the ecoregion (pixel-based mean)	Fick and Hijmans (2017)
Species richness (S)	Number of amphibians, birds and mammals in the ecoregion assessed by IUCN (pixel-based mean)	IUCN (2021)
Cheetah coverage (Ch)	Proportion of ecoregion covered by the extant cheetah range	Dinerstein et al. (2017), IUCN (2021)
Human footprint (HFP)	Human pressure imposed on the ecoregion based on built environments, population density, nighttime lights, crop and pasture lands, roads and railways, and navigable waterways (pixel-based mean)	Mu et al. (2022)
Protected area coverage (PA)	Proportion of ecoregion covered by protected areas designated under IUCN categories I to VI	Dinerstein et al. (2017)
Protection status (*Categorical*)	Ecoregion classification based on the extent of both remaining natural habitat and protected area coverage: Half Protected (HP), Nature Could Reach Half (NCRH), Nature Could Recover (NCR), Nature Imperilled (NI)	Dinerstein et al. (2017)
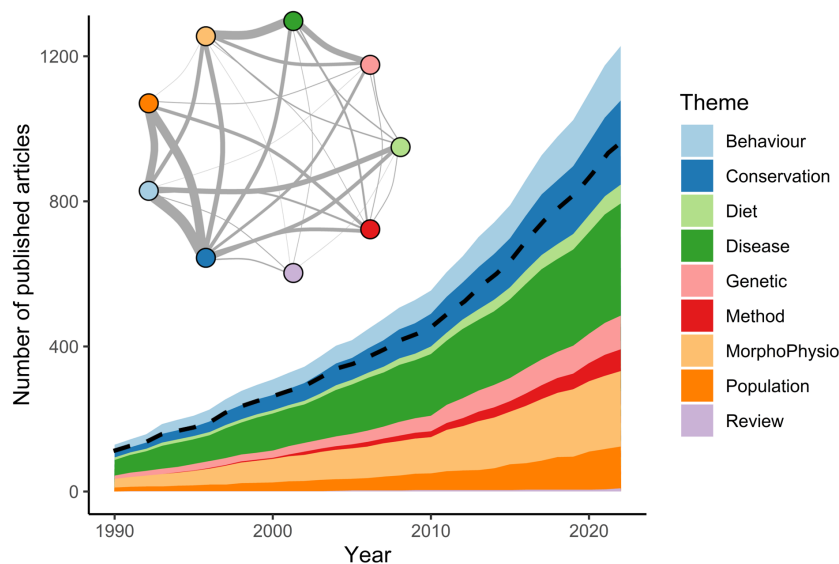
Fig. 2. Cumulative increase of published articles on cheetah *Acinonyx jubatus* (dashed line) and categorised per research theme (colours) since 1990. The network represents connections between research themes classified together.

Russia. Average ecoregion coverage by the cheetah's range was 23% (±28 SD) where it is extant and 11% (±16 SD) where it is possibly extant (Fig. 1d, Appendix S2).

Species richness was generally higher within the cheetah-covered portion of the ecoregion compared to the entire ecoregion. Based on different species groupings assessed

Table 2. Summary of research themes identified in published literature on cheetahs. Relative importance of each research theme is identified by the number of articles, the mean number of citations per article, the mean number of annual citations per article and the h-index for each research theme. Description of research themes is presented in Table S1

Theme	Number of articles	Mean number of citations (±SD)	Mean number of annual citations (±SD)	h-index
NA*	223	–	–	–
Application*	269	–	–	–
Behaviour	150	44 (±53)	2.86 (±3.72)	45
Conservation	232	27 (±33)	1.67 (±2.28)	41
Diet	52	38 (±53)	2.43 (±3.69)	21
Disease	309	24 (±45)	1.52 (±3.04)	40
Genetic	93	35 (±48)	2.31 (±3.38)	31
Method	60	23 (±28)	1.42 (±1.94)	20
MorphoPhysio	208	31 (±43)	2.00 (±2.95)	43
Population	115	28 (±39)	1.85 (±2.72)	32
Review	9	55 (±76)	2.18 (±4.35)	4
Taxonomy**	3	18 (±13)	0.86 (±0.98)	2

*Not included and irrelevant for further analyses.
**Before 1990.

by IUCN, 50% (ABM), 69% (M), 81% (tABM) and 83% (tM) of ecoregions had a higher species number in areas where cheetahs were extant (Figs 3 and 4). We identified two principal components (PC) that explained 93% of variation in the differences in species richness (PC1 = 61%, PC2 = 32%; Fig. 4). We found a positive correlation along the first principal component (i.e. *x*-axis) for all active variables (ABM, M, tABM, tM), and a negative correlation along the second principal component (i.e. *y*-axis) between the variables including threatened species (tABM, tM) and the variables including all species (ABM, M).

The correlations with ecoregion attributes showed that poorly protected ecoregions with little natural habitat remaining (i.e. 'Nature Imperilled') had a higher species number in areas where cheetahs were present than where they were not, while ecoregions with a better protection status and more natural habitat (i.e. 'Half Protected', 'Nature Could Reach Half Protected') had only small differences in species number regardless of cheetah presence. Similarly, ecoregions under high human pressure had a higher species number in areas where cheetahs were still
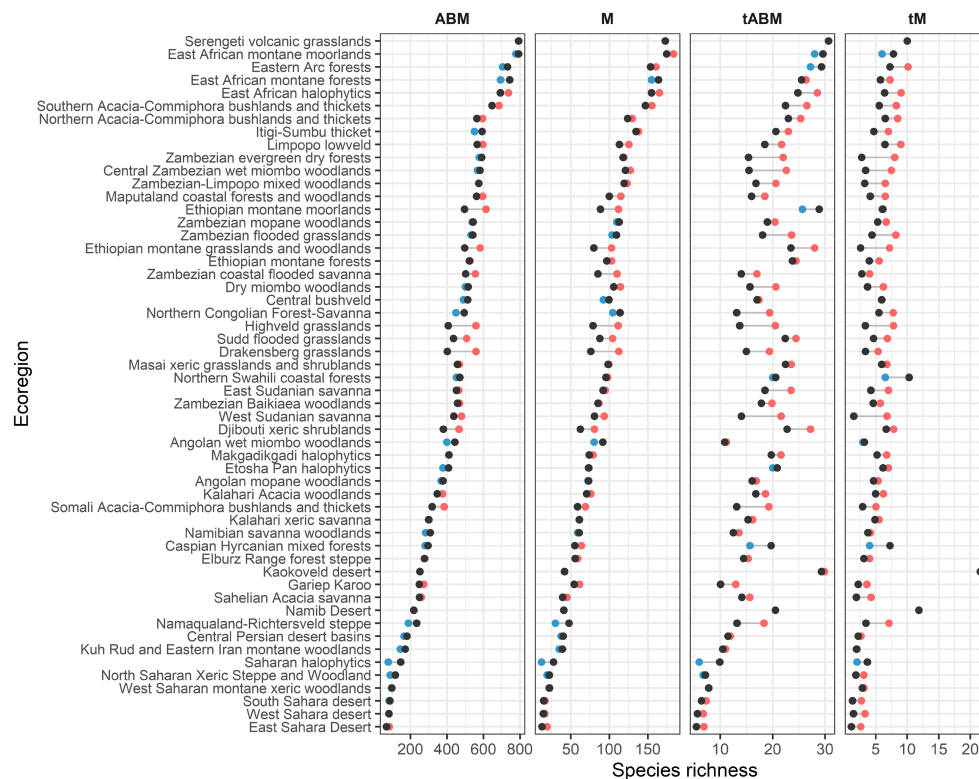

Fig. 3. Species richness per ecoregion (black) and for the cheetah-covered portion of the ecoregion (coloured) for four species groupings assessed by IUCN: All amphibians, birds and mammals (ABM); all mammals (M); threatened amphibians, birds and mammals (tABM); threatened mammals (tM). Red dots are mean species richness values for the cheetah range higher compared to the respective ecoregion; blue dots are mean species richness values lower compared to the respective ecoregion.
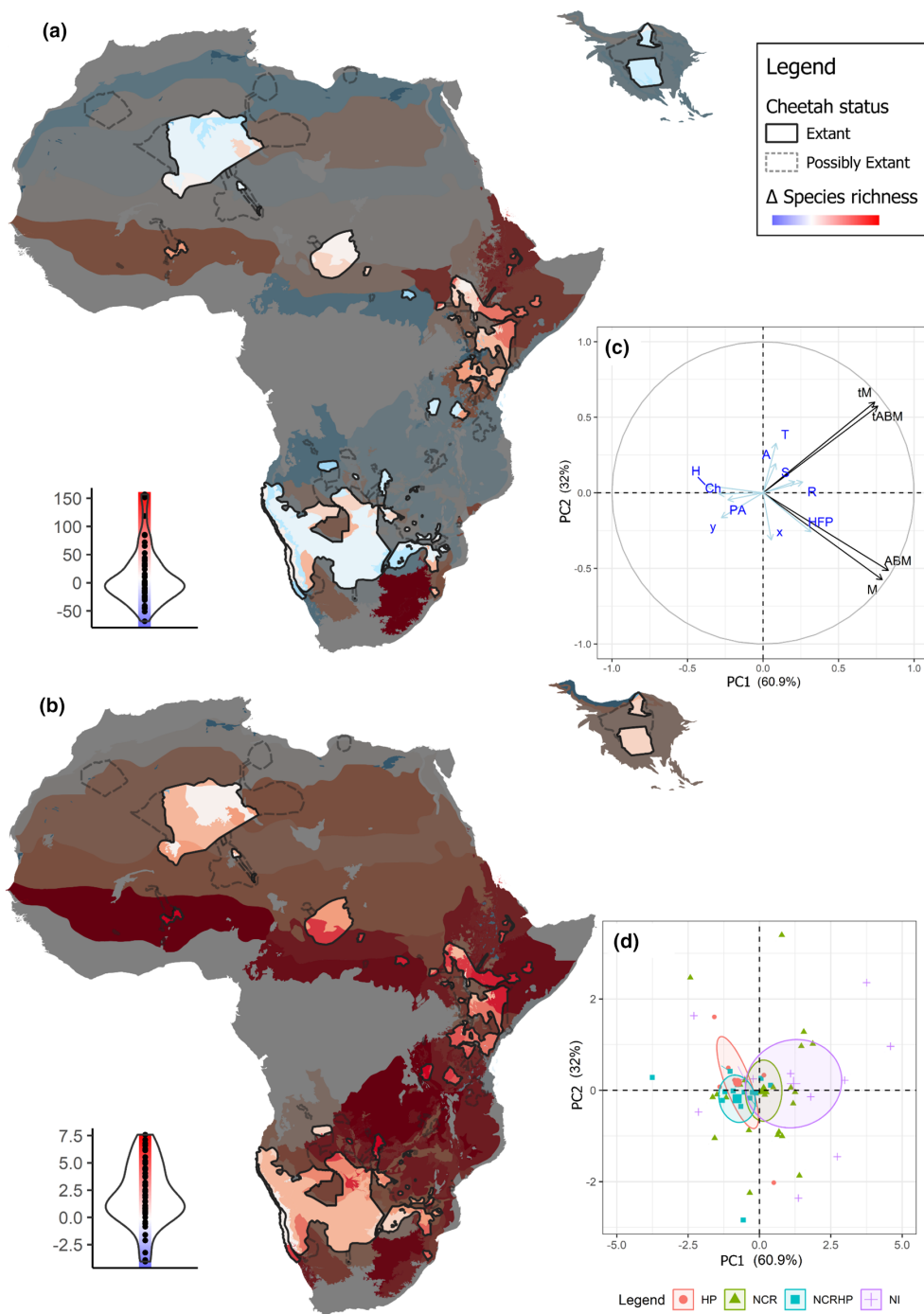
Fig. 4. Spatial visualisation of the differences in mean species richness values of the cheetah-covered portion of ecoregion compared to their respective ecoregions for (a) all amphibians, birds and mammals assessed by IUCN (ABM), and (b) amphibians, birds and mammals listed as threatened by IUCN (tABM). The extant cheetah range overlaps with highlighted areas. Red shading indicates areas where mean species richness values for the cheetah range are higher compared to the respective ecoregion; blue shading indicates areas where mean species richness values are lower compared to the respective ecoregion. Principal Component Analysis output is presented for (c) active (black) and supplementary (blue) variables, and (d) ecoregions categorised per protection status (Dinerstein et al. 2017). A, area; ABM, all amphibians, birds and mammals; Ch, Cheetah coverage; H, natural habitat remaining; HFP, human footprint; HP, Half Protected; M, all mammals; NCR, Nature Could Recover; NCRHP, Nature Could Reach Half Protected; NI, Nature Imperilled; PA, protected area coverage; R, average annual precipitation; S, species richness; T, average annual temperature; tABM, threatened amphibians, birds and mammals; tM, threatened mammals; x, latitude; y, longitude.

present, in particular, when considering threatened species groupings. When a large portion of the ecoregion was covered by cheetahs, the difference was naturally small. Geographically, the differences in species richness tended to be larger closer to the equator, reflecting remnant cheetah populations in western Africa (e.g. W-Arly-Pendjari complex in Benin, Burkina Faso and Niger), central Africa (e.g. Greater Zakouma Ecosystem in Chad), eastern Africa (e.g. transboundary population in Ethiopia, South Sudan, Uganda and Kenya) and the Horn of Africa (e.g. Somali Regional State in Ethiopia). Temperature, rainfall, species richness and area of the ecoregion showed weak positive associations with differences in species richness, mostly for threatened species groupings.

DISCUSSION

The cheetah is an iconic dryland species attracting international attention and support. The extensive body of scientific literature on cheetahs reflects this popularity, attracting the curiosity and interest of scientists worldwide. The various research themes emerging over the course of more than three decades underscore the diverse facets of cheetah biology, as well as the interdisciplinary nature of cheetah research and the concerted efforts to link scientific knowledge back to the conservation of this species.

Despite the research attention that the cheetah has received, much of our current knowledge stems from the study of a few populations, mostly inside protected areas (Cristescu et al. 2018), and from ex situ research. Populations that are large and found in protected areas located in countries that are relatively safe may decisively determine research outputs, a pattern similar to other African species (Strampelli et al. 2022, Gross & Heinsohn 2023, Visser et al. 2023). Most cheetahs are found in Africa and the conservation context of the continent is culturally, geographically and politically complex (Bauer et al. 2020). Global research and conservation priorities are influenced by socioeconomic dynamics (Czech et al. 1998), wherein the allocation of limited resources is determined by funding institutions and mechanisms with their own priorities and preferences, leading to an unbalanced pattern (Wilson et al. 2016, Watson et al. 2017). Consequently, research biases exist and impact range distribution maps and the accuracy and precision of population estimates, which ultimately affects conservation actions. We recommend a more coordinated, inclusive and comprehensive approach towards cheetah research and conservation. This will involve broadening the scope of efforts to encompass a wider range of populations and habitats, and will rely on collaborations across different regions and institutions.

Despite the limited geographical scope of published research to date, the cheetah is a wide-roaming, land sharing species inhabiting diverse habitats, ranging from dry forest and thick scrub to grasslands and hyper-arid deserts (Durant et al. 2022). Nearly half of Africa's ecoregions appear suitable for cheetahs, and their presence often coincides with areas rich in biodiversity. The cheetah's extant range overlaps with a substantial number of threatened species, which indicates that cheetahs inhabit important biodiversity areas and remaining pockets of relatively intact ecosystems, particularly for ecoregions that receive less protection (i.e. 'Nature Could Recover', 'Nature Imperilled'). With 77% of the current range occurring outside of protected areas (Durant et al. 2017, Marker et al. 2018c), cheetah conservation may yield substantial comparative gains for biodiversity, complementing the current protected areas network which hosts distinct flagship species, such as lion (Panthera leo). Lions are primarily considered a land sparing species as their distributions are more strongly influenced by area protection (Lindsey et al. 2017). Cheetahs could therefore play a critical role in biodiversity conservation beyond protected areas, but this requires complementary conservation approaches that include among others the coordination of large multiple-use landscapes (Durant et al. 2017, Powell et al. 2018) and the development of alternative human livelihoods (Wykstra et al. 2018). Unprotected land is under increasing pressure from human development, in particular, across the fragmented cheetah populations closer to the equator where conservation investments are lagging behind due to poor governance (Dickman et al. 2015).

The concepts of flagship and umbrella species have faced significant criticism (Andelman & Fagan 2000, Linnell et al. 2000, Joseph et al. 2011), and we recognise the identified biases in geographical and thematic research efforts towards cheetahs. We also acknowledge that any co-occurring species may exhibit similar biodiversity patterns across their range (Williams et al. 2000). Rather than seeking to independently validate these concepts for cheetah conservation, our intention was to evaluate and refocus research and conservation efforts for a globally valued and IUCN Vulnerable red-listed species.

Our investigation into the umbrella role of a flagship species, the cheetah, revealed that tangible biodiversity benefits could be achieved across the cheetah's range, with key areas identified of high biodiversity value, especially for threatened animal taxa. Leveraging the wealth of knowledge accumulated on cheetah over the past decades may increase the effectiveness of area-based conservation strategies to protect the biodiversity patterns across the cheetahs' range.

Species ranges are dynamic and current delineations often rely on expert opinion (Schipper et al. 2008). Consequently, species richness maps may overestimate species occurrence, in particular, for narrow-ranging species and ecological specialists (Jetz et al. 2008). Moreover, species distributions are often clipped to protected area

and ecoregion polygons, whereas species boundaries are not strictly delineated in reality (Bailey 2004). Similarly, ecoregion protection status may not necessarily be reflective of cheetah status and ecosystem integrity (e.g. the Critically Endangered Asiatic cheetah in Iran covers ecoregions listed as 'Nature Could Reach Half Protected' (Farhadinia et al. 2017)), while data deficiencies from understudied landscapes introduce additional uncertainties (e.g. recent confirmation of cheetah presence in Djibouti and Somaliland in areas with IUCN cheetah status 'Possibly Extinct' (Marker et al. 2023, Murgatroyd et al. 2023)). Given the broad scope of our study, using coarse-scale information may yield relevant continental-level findings (Hurlbert & White 2005), yet caution is warranted when conducting and interpreting macroecological analyses (Herkt et al. 2017). Additionally, up-to-date and empirically derived range maps are essential to effectively inform and guide conservation initiatives, especially for IUCN red-listed species like the cheetah.

Eventually, the long-term survival of free-ranging cheetahs and co-occurring wildlife will depend on the availability and connectivity of suitable habitat and on effective strategies for coexistence. With over 90% of the cheetah's historic range already lost (Durant et al. 2017), and Africa's human population projected to more than triple by 2100 (Gerland et al. 2014), conservation scientists and society face unprecedented challenges that will require adaptive and timely approaches that safeguard current populations but also consider potential range shifts (Durant et al. 2022) and reintroductions (Tordiffe et al. 2023). This requires collaborative efforts at national and international levels, with the recent adoption of the Global Biodiversity Framework offering hope to mobilise increased international support. Recognising the global interest in cheetahs, sharing costs involved with wildlife coexistence at global levels may be one solution to empower local communities to actively embrace and engage in conservation efforts, which will be vital to safeguard dryland systems.

CONFLICT OF INTEREST STATEMENT

We have no competing interests to declare.

ACKNOWLEDGEMENTS

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

REFERENCES

Albert C, Luque GM, Courchamp F (2018) The twenty most charismatic species. *PLoS One* 13: e0199149.

Andelman SJ, Fagan WF (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proceedings of the National Academy of Sciences of the United States of America* 97: 5954–5959.

Bailey RG (2004) Identifying ecoregion boundaries. *Environmental Management* 34: S14–S26.

Bauer H, Chardonnet B, Scholte P, Kamgang SA, Tiomoko DA, Tehou AC et al. (2020) Consider divergent regional perspectives to enhance wildlife conservation across Africa. *Nature Ecology & Evolution* 5: 1–4.

Belbachir F, Pettorelli N, Wacher T, Belbachir-bazi A (2015) Monitoring rarity: the critically endangered Saharan cheetah as a flagship species for a threatened ecosystem. *PLoS One* 10: e0115136.

Bonnet X, Shine R, Lourdais O (2002) Taxonomic chauvinism. *Trends in Ecology & Evolution* 17: 1–3.

Bottrill MC, Joseph LN, Carwardine J, Bode M, Cook C, Game ET et al. (2008) Is conservation triage just smart decision making? *Trends in Ecology & Evolution* 23: 649–654.

Brooks TM, Mittermeier RA, Da Fonseca GAB, Gerlach J, Hoffmann M, Lamoreux JF, Mittermeier CG, Pilgrim JD, Rodrigues ASL (2006) Global biodiversity conservation priorities. *Science* 313: 58–61.

Butchart SHM, Walpole M, Collen B, Van Strien A, Scharlemann JPW, Almond REA et al. (2010) Global biodiversity: indicators of recent declines. *Science* 328: 1164–1168.

Clark JA, May RM (2002) Taxonomic bias in conservation research. *Science* 297: 191–192.

Cristescu B, Boyce MS (2013) Focusing ecological research for conservation. *Ambio* 42: 805–815.

Cristescu B, Lindsey P, Maes O, Bissett C, Mills G, Marker L (2018) Protected areas for cheetah conservation. In: Marker L, Boast LK, Schmidt-Küntzel A (eds) *Cheetahs: Biology and Conservation*, 265–274. Academic Press, London, UK.

Csardi G, Nepusz T (2006) The igraph software package for complex network research. *InterJournal, Complex Systems* 1695: 1–9.

Czech B, Krausman PR, Borkhataria R (1998) Social construction, political power, and the allocation of benefits to endangered species. *Conservation Biology* 12: 1103–1112.

Dalerum F, Somers MJ, Kunkel KE, Cameron EZ (2008) The potential for large carnivores to act as biodiversity surrogates in southern Africa. *Biodiversity and Conservation* 17: 2939–2949.

Díaz S, Settele J, Brondízio E (2019) The global assessment report on biodiversity and ecosystem services: summary for policy makers.

Dickman AJ, Hinks AE, Macdonald EA, Burnham D, Macdonald DW (2015) Priorities for global felid conservation. *Conservation Biology* 29: 854–864.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E et al. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67: 534–545.

Durant SM, Mitchell N, Groom R, Pettorelli N, Ipavec A, Jacobson AP et al. (2017) The global decline of cheetah *Acinonyx jubatus* and what it means for conservation. *Proceedings of the National Academy of Sciences of the United States of America* 114: 528–533.

Durant SM, Groom R, Ipavec A, Mitchell N, Khalatbari L (2022) *Acinonyx jubatus*. The IUCN Red List of Threatened Species: e.T219A124366642.

Durant SM, Broekhuis F, Evangelista P, Tricorache P, Asfaw T, Gedow O, Marker L (2023) *Acinonyx jubatus* ssp. *soemmeringii*. The IUCN Red List of Threatened Species: e.T231957008A232671735.

Farhadinia MS, Hunter LTB, Jourabchian A, Hosseini-Zavarei HA, Akbari H, Ziaie H et al. (2017) The critically endangered Asiatic cheetah *Acinonyx jubatus venaticus* in Iran: a review of recent distribution, and conservation status. *Biodiversity and Conservation* 26: 1027–1046.

Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315.

Gerland P, Raftery AE, Ševčíková H, Li N, Gu D, Spoorenberg T et al. (2014) World population stabilization unlikely this century. *Science* 346: 234–237.

Green RE, Cornell SJ, Scharlemann JPW, Balmford A (2005) Farming and the fate of wild nature. *Science* 307: 550–555.

Greggor AL, Berger-Tal O, Blumstein DT, Angeloni L, Bessa-Gomes C, Blackwell BF et al. (2016) Research priorities from animal behaviour for maximising conservation progress. *Trends in Ecology & Evolution* 31: 953–964.

Grenyer R, Orme CDL, Jackson SF, Thomas GH, Davies RG, Davies TJ et al. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature* 444: 93–96.

Gross RB, Heinsohn R (2023) Elephants not in the room: systematic review shows major geographic publication bias in African elephant ecological research. *Diversity* 15: 451.

Herkt KMB, Skidmore AK, Fahr J (2017) Macroecological conclusions based on IUCN expert maps: a call for caution. *Global Ecology and Biogeography* 26: 930–941.

Hurlbert AH, White EP (2005) Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters* 8: 319–327.

IUCN (2021) *Species Richness and Range Rarity Data.*

Jetz W, Sekercioglu CH, Watson JEM (2008) Ecological correlates and conservation implications of overestimating species geographic ranges. *Conservation Biology* 22: 110–119.

Joseph LN, Maloney RF, Watson JEM, Possingham HP, Blignaut J (2011) Securing nonflagship species from extinction. *Conservation Letters* 4: 324–325.

Kareiva P, Marvier M (2003) Conserving biodiversity coldspots: recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. *American Scientist* 91: 344–351.

Kassambara A, Mundt F (2020) factoextra: extract and visualize the results of multivariate data analyses. R package version 1.0.7.

Lindsey PA, Petracca LS, Funston PJ, Bauer H, Dickman A, Everatt K et al. (2017) The performance of African protected areas for lions and their prey. *Biological Conservation* 209: 137–149.

Lindsey PA, Miller JRB, Petracca LS, Coad L, Dickman AJ, Fitzgerald KH et al. (2018) More than $1 billion needed annually to secure Africa's protected areas with lions. *Proceedings of the National Academy of Sciences of the United States of America* 115: E10788–E10796.

Linnell JDC, Swenson JE, Andersen R (2000) Conservation of biodiversity in Scandinavian boreal forests: large carnivores as flagships, umbrellas, indicators, or keystones? *Biodiversity and Conservation* 9: 857–868.

Locke H (2013) Nature Needs Half: a necessary and hopeful new agenda for protected areas. *Parks* 19: 13–22.

Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW (2015) Conservation inequality and the charismatic cat: Felis felicis. *Global Ecology and Conservation* 3: 851–866.

Marker L, Boast L, Schmidt-Kuntel A (2018a) *Cheetahs: Biology and Conservation.* Academic Press, San Diego, CA.

Marker L, Cristescu B, Dickman A, Nghikembua MT, Boast LK, Morrison T et al. (2018b) Ecology of free-ranging cheetahs. In: *Cheetahs: Biology and Conservation*, 10–119. Academic Press, San Diego, CA.

Marker L, Cristescu B, Morrison T, Flyman MV, Horgan J, Sogbohossou EA et al. (2018c) Cheetah rangewide status and distribution. In: Marker L, Boast LK, Schmidt-Küntzel A (eds) *Cheetahs: Biology and Conservation*, 33–54. Academic Press, San Diego, CA.

Marker L, Connolly E, Saed AH, Reasoner E, Aden KY, Cristescu B (2023) Cheetahs persist in the wild in the remote Awdal region of Somaliland. *Oryx* 57: 1–4.

Maxwell SL, Cazalis V, Dudley N, Hoffmann M, Rodrigues ASL, Stolton S et al. (2020) Area-based conservation in the twenty-first century. *Nature* 586: 217–227.

McGowan J, Beaumont LJ, Smith RJ, Chauvenet ALM, Harcourt R, Atkinson SC et al. (2020) Conservation prioritization can resolve the flagship species conundrum. *Nature Communications* 11: 1–7.

Mu H, Li X, Wen Y, Huang J, Du P, Su W, Miao S, Geng M (2022) A global record of annual terrestrial human footprint dataset from 2000 to 2018. *Scientific Data* 9: 176.

Murgatroyd M, Chynoweth MW, Blount DJ, Rayaleh HA, Buechley ER (2023) First recent photographic record of cheetah in Djibouti. *CATnews* 77: 21–23.

Myers N, Mittermeler RA, Mittermeler CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Natsukawa H, Sergio F (2022) Top predators as biodiversity indicators: a meta-analysis. *Ecology Letters* 25: 2062–2075.

Nicholson E, MacE GM, Armsworth PR, Atkinson G, Buckle S, Clements T et al. (2009) Priority research areas for ecosystem services in a changing world. *Journal of Applied Ecology* 46: 1139–1144.

O'Dea RE, Lagisz M, Jennions MD, Koricheva J, Noble DWA, Parker TH et al. (2021) Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews* 96: 1695–1722.

Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC et al. (2001) Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience* 51: 933–938.

Powell LA, Kharuxab R, Marker L, Nghikembua MT, Omusula S, Reid RS, Snyman A, Weaver C, Wykstra M (2018) Coordination of large landscapes for cheetah conservation. In: Marker L, Boast LK, Schmidt-Küntzel A (eds) *Cheetahs: Biology and Conservation*, 239–250. Academic Press, London, UK.

R Core Team (2022) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.Rproject.org/

Roberge JM, Angelstam P (2004) Usefulness of the umbrella species concept as a conservation tool. *Conservation Biology* 18: 76–85.

Rozylowicz L, Popescu VD, Pătroescu M, Chişamera G (2011) The potential of large carnivores as conservation surrogates in the Romanian Carpathians. *Biodiversity and Conservation* 20: 561–579.

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V et al. (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225–230.

Schmidt-Küntzel A, Dalton DL, Menotti-Raymond M, Fabiano E, Charruau P, Johnson WE, Sommer S, Marker L, Kotzé A, O'Brien SJ (2018) Conservation genetics of the cheetah: genetic history and implication for conservation. In: Marker L, Boast LK, Schmidt-Küntzel A (eds) *Cheetahs: Biology and Conservation*, 71–92. Academic Press, San Diego, CA.

Strampelli P, Campbell LAD, Henschel P, Nicholson SK, Macdonald DW, Dickman AJ (2022) Trends and biases in African large carnivore population assessments: identifying priorities and opportunities from a systematic review of two decades of research. *PeerJ* 10: e14354.

Sutherland WJ, Bennett C, Brotherton PNM, Butterworth HM, Clout MN, Côté IM et al. (2023) A global biological conservation horizon scan of issues for 2023. *Trends in Ecology & Evolution* 38: 96–107.

Swaisgood RR, Sheppard JK (2010) The culture of conservation biologists: show me the hope! *Bioscience* 60: 626–630.

Tordiffe ASW, Jhala YV, Boitani L, Cristescu B, Kock RA, Meyer LRC et al. (2023) The case for the reintroduction of cheetahs to India. *Nature Ecology & Evolution* 7: 480–481.

Verissimo D, MacMillan DC, Smith RJ (2011) Toward a systematic approach for identifying conservation flagships. *Conservation Letters* 4: 1–8.

Visser F, Drouilly M, Moodley Y, Michaux JR, Somers MJ (2023) Mismatch between conservation needs and actual representation of lions from West and Central Africa in in situ and ex situ conservation. *Conservation Letters* 16: e12949.

Waldron A, Mooers AO, Miller DC, Nibbelink N, Redding D, Kuhn TS, Roberts JT, Gittleman JL (2013) Targeting global conservation funding to limit immediate biodiversity declines. *Proceedings of the National Academy of Sciences of the United States of America* 110: 12144–12148.

Watson JEM, Chapman S, Althor G, Kearney S, Watson JEM (2017) Changing trends and persisting biases in three decades of conservation science. *Global Ecology and Conservation* 10: 32–42.

Williams PH, Burgess ND, Rahbek C (2000) Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. *Animal Conservation* 3: 249–260.

Wilson KA, Auerbach NA, Sam K, Magini AG, Moss ASL, Langhans SD, Budiharta S, Terzano D, Meijaard E (2016) Conservation research is not happening where it is most needed. *PLoS Biology* 14: e1002413.

Wykstra M, Combes G, Oguge N, Klein R, Boast LK, Mosimane AW, Marker L (2018) Improved and alternative livelihoods: links between poverty alleviation, biodiversity, and cheetah conservation. In: *Cheetahs:*

Biology and Conservation: Biodiversity of the World: Conservation from Genes to Landscapes, 223–237. Academic Press, San Diego, CA.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Descriptions and examples of research themes used for classifying research articles on cheetahs.

Appendix S2. Absolute and relative coverage of ecoregions by the cheetahs (possibly) extant range. Ecoregions are categorised by protection status.