Global Ecology and Conservation 38 (2022) e02221

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Africa's drylands in a changing world: Challenges for wildlife conservation under climate and land-use changes in the Greater Etosha Landscape

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Abbreviations: GEL, Greater Etosha Landscape; EEI, Etosha Ecological Institute; MEFT, Ministry of Environment, Forestry and Tourism; HWC, human-wildlife conflict.

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https://doi.org/10.1016/j.gecco.2022.e02221
Received 11 February 2022; Received in revised form 29 June 2022; Accepted 7 July 2022
Available online 12 July 2022

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A R T I C L E I N F O

Keywords:
Dryland research
Ecosystem services
Etosha National Park
Etosha Ecological Institute
Global change
Human dimensions
Human-wildlife conflict
Landscape ecology
Namibia
Savanna ecology

A B S T R A C T

Proclaimed in 1907, Etosha National Park in northern Namibia is an iconic dryland system with a rich history of wildlife conservation and research. A recent research symposium on wildlife conservation in the Greater Etosha Landscape (GEL) highlighted increased concern of how intensification of global change will affect wildlife conservation based on participant responses to a questionnaire. The GEL includes Etosha and surrounding areas, the latter divided by a veterinary fence into large, private farms to the south and communal areas of residential and farming land to the north. Here, we leverage our knowledge of this ecosystem to provide insight into the broader challenges facing wildlife conservation in this vulnerable dryland environment. We first look backward, summarizing the history of wildlife conservation and research trends in the GEL based on a literature review, providing a broad-scale understanding of the socioecological processes that drive dryland system dynamics. We then look forward, focusing on eight key areas of challenge and opportunity for this ecosystem: climate change, water availability and quality, vegetation and fire management, adaptability of wildlife populations, disease risk, human-wildlife conflict, wildlife crime, and human dimensions of wildlife conservation. Using this model system, we summarize key lessons and identify critical threats highlighting future research needs to support wildlife management. Research in the GEL has followed a trajectory seen elsewhere reflecting an increase in complexity and integration across biological scales over time. Yet, despite these trends, a gap exists between the scope of recent research efforts and the needs of wildlife conservation to adapt to climate and land-use changes. Given the complex nature of climate change, in addition to locally existing system stressors, a framework of forward-thinking adaptive management to address these challenges, supported by integrative and multidisciplinary research could be beneficial. One critical area for growth is to better integrate research and wildlife management across land-use types. Such efforts have the potential to support wildlife conservation efforts and human development goals, while building resilience against the impacts of climate change. While our conclusions reflect the specifics of the GEL ecosystem, they have direct relevance for other African dryland systems impacted by global change.

1. Introduction

Approximately 47 % of global land area is characterized as dryland that, despite low productivity, is home to ∼40 % of the world's human population (Koutroulis, 2019; Mirzabaev et al., 2019). These dryland systems support nearly 30 % of all endangered and endemic plant and animal species (Millennium Ecosystem Assessment, 2005). The competing pressures of changing climate, multiple land-uses, and human population growth, together with increasingly unpredictable ecosystem dynamics, make drylands a "hot spot" of animal and human population vulnerability. Under even modest predictions of climate change, global dryland area and human population growth within these regions is expected to increase (Koutroulis, 2019). Thus, drylands encapsulate the challenges of changing environments expected globally, but with potential for more extreme impacts given the already low productivity of these areas and their demonstrated susceptibility to land-use changes (Walther, 2016).

Dryland ecosystems are characterized by high evaporation, low rainfall, frequent droughts, heatwaves, and low-fertility soils vulnerable to erosion. Although drylands support high plant functional diversity (Maestre et al., 2021), these ecosystems are subject to desertification and woody plant encroachment (García Criado et al., 2020; Martens et al., 2021), leading to biodiversity loss (Soto-Shoender et al., 2018; Stanton et al., 2018), shifting species interactions, and changing biomes (McCluney et al., 2012). Drylands are resource limited ecosystems, where strong seasonal and inter-annual variation in rainfall drive resource availability, influencing the dynamics of consumers (Illius and O'Connor, 2000). In addition to the challenges caused by variability in conditions, climate-driven shifts toward increasing aridity in these landscapes intensifies agricultural land use and increases the need for freshwater, adding unrelenting pressure on these ecosystems (Bestelmeyer et al., 2015; Lian et al., 2021; Stringer et al., 2021), and the ecosystem services they provide (Lu et al., 2018; Maestre et al., 2021).

African dryland ecosystems are relatively more intact functionally and taxonomically than many other dryland ecosystems that have depleted megaherbivore (i.e., body sizes >1000 kg, Malhi et al., 2016; Ripple et al., 2015) and carnivore guilds (e.g., Dalerum et al., 2009; Ripple et al., 2014). Losses of these larger species can result in ecological changes including trophic downgrading (Estes et al., 2011), reduced long-distance seed dispersal (e.g., Bunney et al., 2017; Pires et al., 2018), changes in nutrient recycling (Abraham et al., 2021; Poulsen et al., 2018) and altered fire regimes (Hempson et al., 2015) and interspecific interactions. The loss of interspecific interactions reduces ecological complexity and resilience (Johnson et al., 2016; le Roux et al., 2018), and the importance of biodiversity for ecosystem functioning is a key question in conservation biology (Dalerum et al., 2012; Sutherland et al., 2009). Such "depleted" ecosystems may require different management approaches but rely on information from more intact ecosystems to inform recovery efforts (Bowman, 2012), making megafaunal ecosystems a useful model for management and conservation (Corlett, 2013). Consequently, African dryland ecosystems are not only vitally important for understanding the effects of a changing environment in a particular area, but also for providing insight into the management challenges that other dryland environments are facing globally.

Seventy-five percent of Africa's total area is characterized as drylands (Prăvălie, 2016) where significant temperature changes have already occurred due to global climate change, and more warming is anticipated this century (Engelbrecht et al., 2015). Temperatures in Africa's drylands are projected to increase twice as fast as the global mean temperature, with increasing risk of heatwave days, high fire-danger days, and decreased annual rainfall (Engelbrecht et al., 2015). Etosha National Park (hereafter Etosha) in northern Namibia (Fig. 1), has been a focal research area in the drylands of Africa, and is at the epicenter of predicted increases in temperature and aridity. Etosha has a rich ecological research record providing a unique foundation for long-term research in this fast-changing region of Africa. Given the breadth and depth of research on this ecosystem, we focus on the Greater Etosha Landscape (GEL), here defined as Etosha surrounded by a 40-km buffer. Our compilation of knowledge provides unique insights and lessons with application to the general issues currently facing human and animal vulnerability within global drylands.

This perspective was motivated by discussions that arose during a research symposium in Etosha in June 2019 and participant responses to a questionnaire regarding future challenges to wildlife conservation in this region. Here, we extract key lessons from over a century's worth of wildlife management and research on dryland ecology, identify emerging challenges in the face of climate and land-use change, note gaps in our knowledge, and identify future research needs based on the history of wildlife conservation and a literature review of research conducted in this region. We further evaluate how the knowledge base from this relatively intact ecosystem can be applied to mitigate the pressures impacting wildlife conservation in the GEL and other dryland systems under an increasingly unpredictable future.

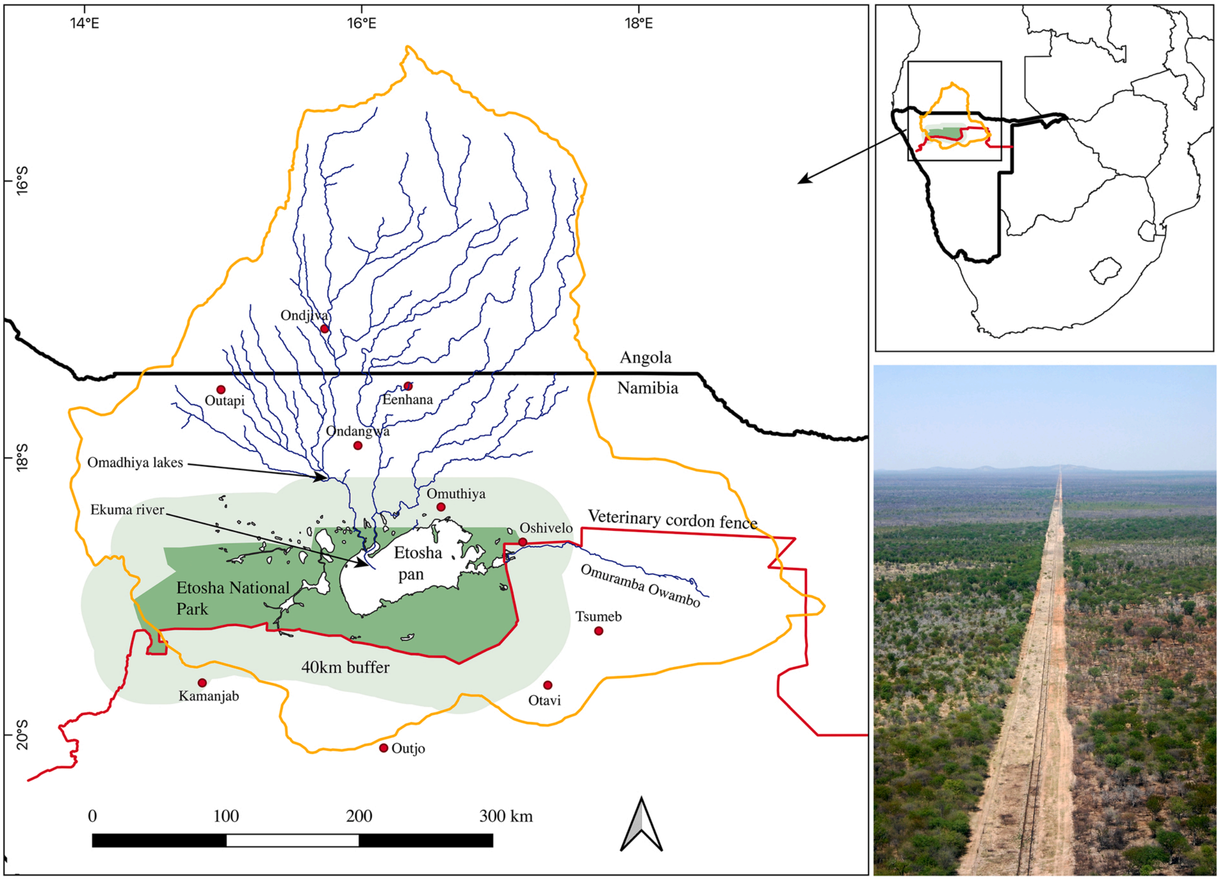

Fig. 1. The Cuvelai Basin in southern Africa and the location of the Greater Etosha Landscape (GEL). The Cuvelai Basin (yellow boundary) spans the border between Angola and Namibia. The Greater Etosha Landscape as defined here consists of the Etosha National Park (dark green) and a 40-kilometer surrounding buffer area (pale green). The GEL has a series of saline pans (white) of which the Etosha Pan is the largest. The river channels of the Cuvelai Basin (blue lines) are often dry. The veterinary cordon fence (red line) stretches across northern Namibia (an aerial view of the veterinary cordon fence's double fence lines along Etosha is shown in the inset photo). Main towns or cities (red dots) in the region are also shown. Photo by J. Werner Kilian.

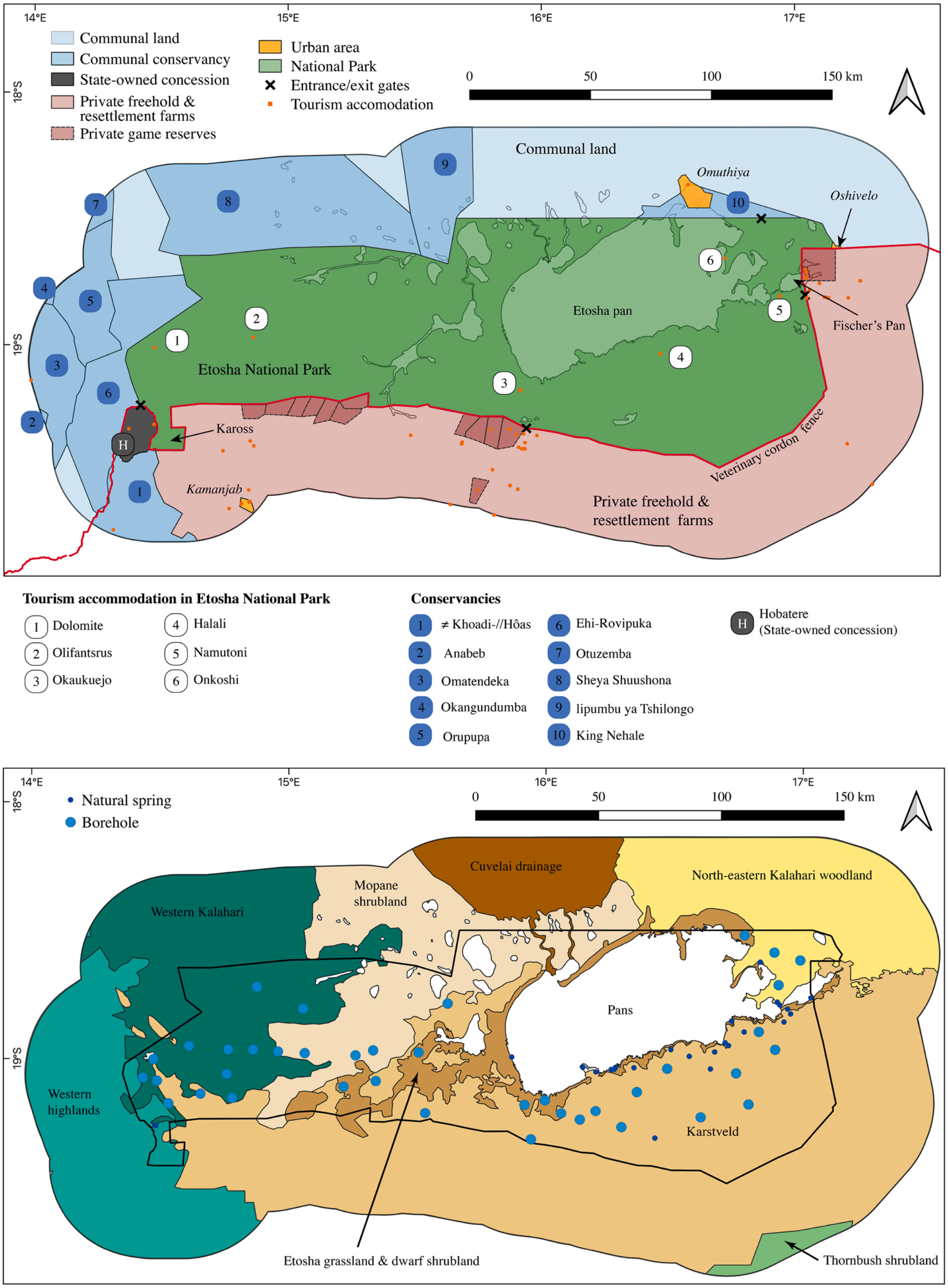

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Fig. 2. Land tenure and vegetation communities in the Greater Etosha Landscape (GEL). Land tenure in the GEL (top panel) includes Etosha National Park (shown in green). The buffer is divided into communal land (blue shades, occurring north of the veterinary cordon fence, shown with a red line) and private freehold and resettlement farms (pink shades occurring south of the veterinary cordon fence), with urban areas marked as yellow polygons. Conservancies in the buffer are marked with numbered blue circles. Tourist accommodation in the GEL is marked with orange dots; tourist camps within Etosha are further labeled with numbered white circles. The lower panel shows vegetation communities in different colors with text labels, saline pans are shown as white polygons, and within Etosha, perennial water sources, including natural springs (blue dots), and locations of boreholes (aqua dots) that may or may not supplement the flow of natural springs. Vegetation communities are derived from Mendelsohn et al. (2013), water sources and types from the Etosha Ecological Institute.

2. The Greater Etosha Landscape

2.1. Social context and changing land use

Before the 20th century, the GEL and surrounding areas were largely inhabited by hunting and gathering Hai||om and !Xun San people. To the west and northwest of the GEL were pastoralist Damara and Herero (including Himba) people. The San are one of the most marginalized people in Namibia, and the Hai||om are the largest and most widely distributed tribe of the San (Dieckmann, 2003). Areas occupied by San were greatly reduced by their exclusion from Etosha and private farms established to its south and east, and by the spread of agro-pastoralist Aawambo from the north (Mendelsohn et al., 2013; Namibia Atlas Team, 2022). Etosha, proclaimed as Game Reserve Number 2 in 1907, initially covered approximately 80,000 km^2 extending to the Skeleton Coast. Its boundaries were reconfigured several times, with major alterations occurring in 1958 (to 55,000 km^2) and 1970 (to its current size of 22,941 km^2). The boundary is entirely fenced, with fences erected between 1961 and 1973 (Berry, 1997).

The veterinary cordon fence, colloquially referred to as the Red Line, crosses northern Namibia and follows the southern and eastern borders of Etosha (Fig. 1). The Red Line was initially a patrolled boundary area that restricted movement and settlement to prevent the spread of diseases (Schneider, 2012; Miescher, 2012a). It was formalized as a double veterinary cordon fence after an outbreak of foot and mouth disease in 1961 (FMD, Schneider, 2012), despite FMD not being endemic in northern Namibia (Amuthenu, 2015). Placement of this fence as an internal border is a legacy of Namibia's colonial past, and has repercussions today for economics, equity, and wildlife conservation (Miescher, 2012b). The veterinary cordon fence is highlighted as one of the biggest challenges for expanding protected areas or for integrating management efforts around Etosha (Mannetti et al., 2019).

Residents of lands neighboring protected areas are those mostly likely to benefit from the economic value and ecological services of the protected area, or to suffer negative consequences such as human-wildlife conflict (HWC) (Anthony, 2007; Wittemyer et al., 2008). A 40-km buffer around Etosha comprises an area of 36,160 km^2, which, together with Etosha, forms the GEL. The veterinary cordon fence divides the buffer into two regions with different land tenure (Fig. 2). Communal areas are found north of the veterinary cordon fence where a few community conservancies have been established, although most have not yet realized tourism and conservation objectives (Ministry of Environment, Forestry and Tourism (MEFT) and Namibian Association of Community-Based Natural Resource Management Support Organisations, 2021). These communal lands also support residential, farming and livestock keeping with limited commercial agriculture production (Mendelsohn et al., 2013). In contrast, lands south of the veterinary cordon fence are populated with large farms used for commercial production of meat (from wildlife and livestock), trophy hunting, charcoal, tourism, and residential resettlement purposes (Mendelsohn et al., 2013).

The social and economic circumstances around Etosha have changed substantially in recent decades. The number and distribution of people and livestock living in communal areas has increased over the last century. The income of these residents is largely from off-farm sources, such as grants, remittances and the trade of goods and labor (Mendelsohn et al., 2013). In communal areas, cattle numbers have doubled since the 1980s, whereas in private farm areas, they have decreased by half (Veterinary Census Data, available at http://the-eis.com/). Similar trends were reported for both sheep and goats in these areas (Veterinary Census Data). The dual land tenure system of communal and freehold land is an artifact of Namibia's colonial past, and was largely formed along racial lines (Lenggenhager et al., 2021; Nghitevelekwa, 2022). Prior to Namibian independence in 1990, the majority of private farms were owned by white people, while by 2020, approximately 42 % of private farms were owned by previously disadvantaged people or allocated for their use as resettlement farms (Namibia Agricultural Union data).

The different land uses in areas surrounding Etosha have led to different costs and benefits to those living in proximity to the park, providing an important context to wildlife conservation, especially given changing environmental conditions. Those in communal areas may benefit little from Etosha and may have crop and livestock losses caused by wildlife leaving the park (Mfune et al., 2005). Livestock farmers south of Etosha share the same concerns, where livestock losses historically seem more severe than elsewhere (Lendelvo et al., 2015; Stander, 2004). However, many on private farms also benefit from Etosha, where in the last two decades there has been a switch in the uses of many private farms from livestock production to tourism, trophy hunting, game production, and game viewing, in particular for those located near the entrances to Etosha (Fig. 2). Thus, the differing social and economic circumstances in the northern/western and southern/eastern buffer areas affect perceptions of the Park, and the opportunities, costs and benefits of being its neighbor (Mannetti et al., 2019).

2.2. Biophysical environment

The GEL lies at the southern end of the endorheic Cuvelai Drainage Basin, a mostly flat and shallow basin spanning 175,870 km^2 across southern Angola and northern Namibia (Fig. 1; Mendelsohn et al., 2013). At the base of the Cuvelai is the Etosha saline deflation pan, once a large paleolake (Hipondoka et al., 2006; Miller, 1997). The Etosha Pan currently covers 4812 km^2 with many smaller saline pans to its west and north. A network of channels periodically carry water across the Angola-Namibia border into the Omadhiya Lakes and, sporadically, along the Ekuma River into the Etosha Pan. The Pan also receives water from local rainfall and, less frequently, from the Owambo Omuramba to the east (Friederich and Lempp, 2014). The Pan is a wetland of national and international importance for breeding birds (Kolberg, 2015, Kolberg undated; Simmons, 1996; Simmons et al., 1998) and grasslands along its edges support the Namibian population of Blue Cranes (*Grus paradisea*) (Simmons, 2015).

The structure and fertility of the soil has strong effects on vegetation, wildlife density, and land use, and surface water is scarce and seasonally ephemeral, further affecting animal density. Much of the soil in the northern half of the GEL is sandy arenosols, holding few nutrients and water, while in the southern half of the GEL soils are a mix of leptosols, regosols, cambisols or rock outcrops (Mendelsohn et al., 2013). However, the potential of these soils to support more wild or domestic mammals is often limited by shallow depths and aridity (Mendelsohn et al., 2013). Woodlands predominate in the southern half and northeastern areas of the GEL and grasslands and shrublands surround the Pan and occupy the saline soils to its west (le Roux et al., 1988; Fig. 2). The northwestern areas consist largely of shrubby growth forms of *Colophospermum mopane* (le Roux et al., 1988; Mendelsohn et al., 2013). The most productive soils and forage in Etosha are found southwest of the Pan, supporting a high density of grazing herbivores in the wet season (le Roux, 1979). Historically, the only permanent sources of fresh water were artesian and contact springs, most of them around and to the south of the Etosha Pan. Today, fresh water is supplied by springs and artificial water sources (Fig. 2).

Heterogeneous rainfall creates patchy pulses of vegetation growth (du Plessis, 2001), and many mammals and birds in the GEL have evolved to move and exploit the products of these pulses. Grazing herbivores once migrated annually around the Pan, but the erection of game-proof fences around Etosha prevented access to the relatively more productive grazing areas north of Etosha. Fencing greatly reduced the population sizes of Etosha's large herbivores (Gasaway et al., 1996) and changed grassland ecology and species utilization patterns around the Pan (le Roux, 1979; Ntinda et al., 2012). Animals move freely within Etosha, but movements outside the protected area are affected by human presence, and outside the southern and eastern borders, by many fences.

3. Looking backward: Wildlife conservation and research in the GEL

3.1. Wildlife conservation – The first 115 years

In the 1800s, unrestricted hunting and predator control profoundly reduced biodiversity of the GEL (Berry et al., 2007). The last herds of elephants (*Loxodonta africana*) were reportedly hunted out by 1881, and when the park was proclaimed, there were no elephants, rhinoceros (*Diceros bicornis, Ceratotherium simum*), or lions (*Panthera leo*) in the region (Berry et al., 2007). The return of lions to Etosha was first reported in 1912 and the return of elephants in 1946 (Berry et al., 2007). From the late 1880s through the first decades after Etosha's proclamation, management in the GEL focused on law enforcement, with military outposts at Okaukuejo and Namutoni (Fig. 2). While a Game Warden was appointed in 1907, this post was abolished in 1928, and little was recorded about wildlife in Etosha from the first census in the 1920s until the 1950s (Berry et al., 2007). A mandate for wildlife management developed in the 1950s with the establishment of a section for game management, and expanded in 1974, with the opening of the Etosha Ecological Institute (EEI) in Okaukuejo (de la Bat, 1982).

The first wildlife census in the 1920s reported high numbers of wild dogs (*Lycaon pictus*; $n = 2000$; now locally extirpated), and 10 times current estimates of the blue wildebeest (*Connochaetes taurinus*) population (Nelson, 1926). The decline in wild dogs could have been facilitated by reported "vermin" eradication efforts for wild dogs and black-backed jackals (*Lupulella mesomelas*) through poisoning, trapping, and hunting (Nelson, 1926). High numbers of plains zebra (*Equus quagga*), springbok (*Antidorcas marsupialis*), and black-backed jackal were reported in this first census, species that are similarly abundant in the region today.

From the 1950s there was a stark change in the management of Etosha, with the establishment of a nature conservation section for wildlife monitoring, the eviction of the Hai||om, and the rise of mass tourism. Namutoni and Okaukuejo military posts were transformed into tourist camps. Beyond predator control, some of the earliest active management of the system were culls of plains zebra and blue wildebeest in central Etosha in 1952, in response to overgrazing concerns (Berry, 1997). In the late 1960s and 1970s, wildlife management initiatives included flamingo rescues (Berry, 1972), establishment of a breeding facility for rare animal species (i.e., Kaross in southwestern Etosha; Fig. 2), and species (re)introductions (Berry, 1997). Successful (re)introductions included black rhinoceros and black-faced impala (*Aepyceros melampus petersi*) populations that have since flourished (Joubert, 1996; Green and Rothstein, 1998). Namibia supports the world's largest population of the southwestern black rhinoceros (*Diceros bicornis bicornis*, Knight, 2019), of which the vast majority occurs in Etosha (Kilian et al., 2021). Additionally, half of the total population of black-faced impala (Matson et al., 2006) are found in Etosha. Other introductions were not successful, including wild dog, roan (*Hippotragus equinus*), and sable (*Hippotragus niger*).

A combination of fencing, disease outbreaks, and severe drought led to a period of wildlife population control in the 1980s. Elephant culls in 1983 and 1985 reduced their population size by an estimated 8–14 % (Lindeque, 1988). The social disruption of culling caused elephants to move out of the culling area and outside park boundaries, creating HWC, and as a result further elephant culls were abandoned (Lindeque, 1988). Populations of mountain zebra (*Equus zebra hartmannae*) and plains zebra were also reduced in the 1980s through sales or culling (Berry, 1997). The mountain zebra population never recovered from these removals (of 2235 individuals), with a population estimate of only 875 (350–1400 95 % CI) individuals in 2015 (Kilian, 2015).

Active management interventions today focus on infrastructure (fence line, roads, and borehole maintenance), mitigating HWC, and reducing rhinoceros poaching (MEFT, 2021). Etosha's wildlife, in particular plains zebra, giraffe, black-faced impala and black rhinoceros, are regarded as potential source populations, with animals captured and translocated to support conservation efforts elsewhere (MEFT, 2021). As an example, the Rhino Custodianship Program, initiated in 1993, has successfully created a meta-population of black rhinoceros on private and communal lands across Namibia (Jewell et al., 2020).

The current mission statement of the MEFT is "To promote biodiversity conservation in the Namibian environment through sustainable utilization of natural resources and tourism development for the maximum social and economic benefit of its citizens" (MEFT, 2020b). From this mission statement, strategic objectives for the management of Etosha include: (i) to protect and maintain biodiversity, (ii) to secure and increase landscape connectivity, (iii) to provide and sustain human benefits in the form of high quality diverse tourism, environmental education, park-neighbor relations, and staff loyalty and commitment, and (iv) to maximize economic development, based on the principles of sustainable utilization, coexistence and collaborative management (Ministry of Environment, Forestry and Tourism, 2021).

3.2. Research conducted in the GEL

We conducted a literature review to investigate research trends over time in the GEL. We focused the literature search on peer-reviewed material from three online databases (Web of Science, Scopus, and SABINET), using "Etosha" as a search term. We identified 448 references meeting our inclusion criteria (see Appendix and Figure A1 for details). From these, we recorded the focal organisms and topics of study, levels of biological organization investigated, number of citations to date, and how these topics changed over time (classification scheme in Table A1; type of research in Figure A2; list of sources and their classifications is in Table S1).

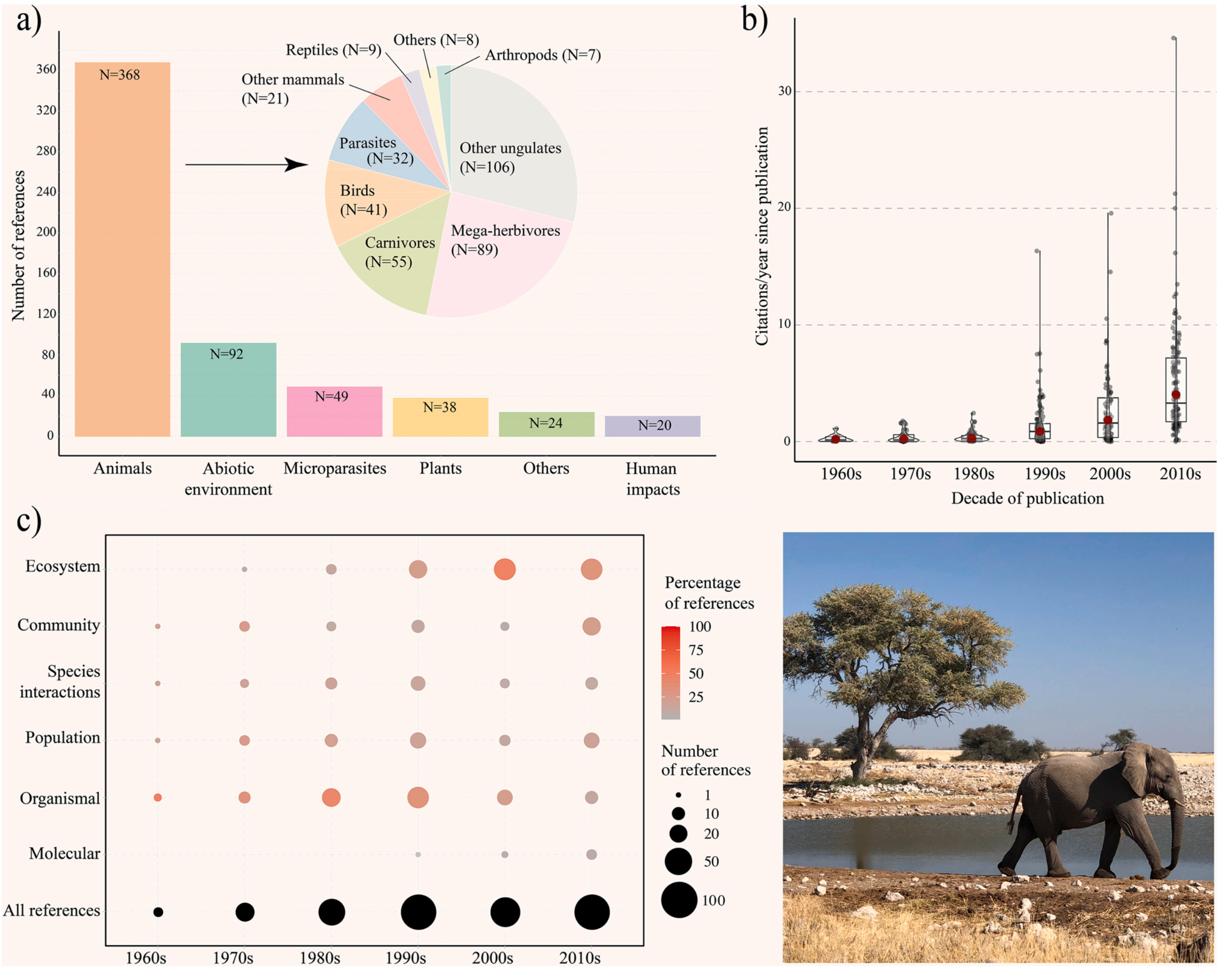

Fig. 3. Research in the Greater Etosha Landscape showing (a) the distribution of focal research areas investigated, (b) the number of citations per year for publications and (c) biological levels of organization studied through time for n = 448 peer reviewed references. Some references (n = 143) had more than one focal area, hence the numbers in the bar and pie charts in (a) do not sum to 100 %. The violin plot (b) shows the density distribution of citations around the mean (red dot) with the box plot showing the median and first and last quartiles. The bubble plot (c) gives the number of references in each decade for each level of biological organization (based on size of the circle) while color intensity represents the percentage of total references from a decade conducting research at that particular level of biological organization. The total number of references per decade is shown in black circles at the bottom of the chart. Data supporting this figure are available in Table S1. Photo: Wendy Turner.

Most research in the GEL has concentrated on large, common, charismatic species, and/or those at conservation risk (trends noted in other ecosystems: Clark and May, 2002; Tensen, 2018). Most references focused on animals (Animalia, $n = 368$, 82.1 %) or the abiotic environment ($n = 92$, 20.5 %, Fig. 3). Among references with an animal focus, most investigated ungulates ($n = 195$, 53 %) with 89 of those (24.2 % in total) on mega-herbivores (Fig. 3). The second most commonly researched taxa were carnivores ($n = 55$, 14.9 %), with 48 of these references focusing on large species (>45 kg), six on medium-sized species (10–45 kg) and only one on small carnivore species (2–10 kg).

The knowledge gathered on ecosystem engineers (e.g., elephants or other large herbivores) or ecosystem drivers (e.g., large carnivores) has great potential to inform models of future system changes and their consequences. However, our review also highlights numerous gaps in research in the GEL; for example, relatively little has been published on plants, small mammals, birds, reptiles and amphibians, invertebrates, human impacts or other ecosystem drivers and engineers. A detailed understanding of plant community composition and functioning, especially focused on resilience to global changes, is necessary to support informed management and conservation decisions for wildlife populations. Similarly, some of the largest and growing concerns for park management at present (e.g., wildlife crime, HWC) have yielded very few peer-reviewed publications in the last decade. While confidentiality and security might be in part why there are few publications in the public domain to date, humans and their activities are one component of the system which can be readily influenced. If we do not understand how humans interact with and affect the ecosystem, it will be difficult to direct and implement any changes to support wildlife conservation into the future.

The impact of publications from the GEL, evaluated based on their number of citations per year, has significantly increased from 1960 to 2019 ($n = 410$ publications, $F_{(5,56.12)} = 27.47$, $p < 0.0001$, Fig. 3) which is above the background rate of increase (Peterson et al., 2019). This positive trend suggests that research outputs from this ecosystem are increasingly contributing to an understanding of wildlife and conservation beyond Namibia, particularly the increase in very highly cited papers as well as the average citation rate. Bringing international attention to an arid ecosystem such as the GEL can stimulate interest in similar areas around the globe and influence the direction of future research beyond this particular area. This growing awareness may lead to a better understanding of the GEL and other ecosystems, fostering international collaborations and allowing for comparisons among arid ecosystems.

Between 1960 and 2019, the scope of research, based on biological levels of organization, also changed ($n = 327$ references, $\chi^2 = 63.98$, df $= 25$, $p < 0.0001$, Fig. 3) with a positive correlation between the decade of publication and the proportion of references addressing questions at the molecular ($\rho = 0.84$, $t = 3.14$, $p = 0.03$) and ecosystem levels ($\rho = 0.95$, $t = 6.43$, $p = 0.003$). While this temporal shift might be partly due to technological advances, we believe it also reflects a deeper understanding of the system, and an increased awareness about the connections among ecosystem components. Genetic studies are now common and increasingly easier and cheaper to conduct. These will be key components in deciphering the effects of global changes on population connectivity (e.g., in lions, elephants, rhinoceros), hybridization (e.g., between plains zebras and Hartmann's mountain zebras), or genetic adaptation. Similarly, the increase in ecosystem level studies may be driven by the development of remote sensing methods and availability of increasingly detailed environmental datasets, allowing for the study of processes such as rainfall and fire at both larger and finer spatiotemporal scales, which can be integrated with insights about wildlife populations.

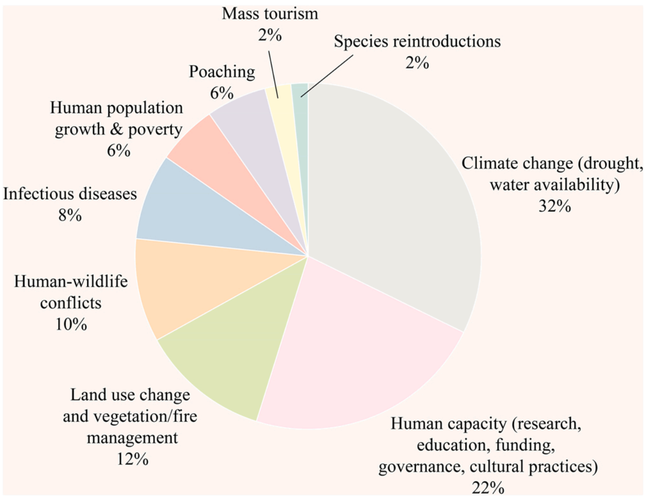

Fig. 4. Results of a survey of conference attendees asked to list their opinion of the biggest threat(s) or challenge(s) to wildlife conservation in the Greater Etosha Landscape. Of the 124 responses from 77 attendees (some listed multiple concerns), the dominant concern was climate change, either directly (16 %) or indirectly (16 %) through its effects on drought and water availability. Changing human capacity was the next biggest concern, regarding local research capacity and research and monitoring funding, education, cultural practices and governance affecting wildlife conservation. Conference attendees were primarily scientists or wildlife managers from Namibia (45 %), with additional scientists attending from the USA (23 %), South Africa (17 %), Germany (5 %) and other countries (10 %), i.e., UK, Australia, Botswana, New Zealand and Norway (based on institutional affiliations).

4. Looking forward: Challenges and opportunities for wildlife conservation in the GEL

We leverage the knowledge generated in the GEL to highlight key lessons for current challenges to wildlife conservation and to identify opportunities and gaps to guide future drylands research. This effort arose out of a participant survey conducted during a research symposium about Etosha in June 2019, which identified climate and socio-ecological changes in the ecosystem as the biggest threats to wildlife conservation in Etosha (Fig. 4). In the following subsections, we evaluate eight key challenges and opportunities for future research within the GEL identified through this process: climate change, water availability and quality, fire and vegetation management, individual variability and adaptation in wildlife, disease risk, human-wildlife conflict, commercial wildlife crime, and human dimensions of wildlife conservation. To give more context, we present publishing trends on these eight topics and where within the GEL research has occurred based on papers identified in our literature review (Fig. 5). Research efforts for several of these topics have increased over time, although key gaps include the study of climate change, human-wildlife conflict, and wildlife crime. While a substantial amount of research in the GEL has been conducted on variation among individuals by age or sex in their biology, ecology, and behavior (Fig. 5a), very few studies have linked individual variation to adaptive capacity, which is an important connection for understanding the impacts of changing environments on populations (de Meester et al., 2018). While most of the research effort has been focused on the National Park, there is a proportionally small but increasing effort to address questions in its buffer area. For each of these topic areas, we summarize what is known about the topic in the GEL and describe challenges and opportunities for future research and conservation efforts in the sections below.

4.1. Climate change

Surface temperatures in the region of the GEL have increased rapidly over the last half-century, by more than 3.2 °C/century (Engelbrecht et al., 2015). Between 1975 and 2004, annual mean maximum and minimum air temperatures in central Etosha increased by 1.1 °C and 1.3 °C respectively (Fig. 6a). The number of cold days per year with air temperature below 5 °C halved over the same period (Fig. 6b). Rainfall in Etosha is variable, with oscillating periods of above or below average rainfall, with each period lasting 2–20 years (Engert, 1997). Thus, detecting changes to rainfall in the system is sensitive to the time period examined. Etosha experienced periods of above average rainfall in the 1940s to mid-1950s, the mid 1960s through most of the 1970s, and the 2000s to 2012, with droughts occurring in the mid-1950s to the mid-1960s, the 1980s and 1990s, and from 2013 to 2020 (Engert, 1997; Etosha Ecological Institute data). As a result of the high variability in rainfall, there was no evidence for a change in annual rainfall over time (Fig. 6c), nor a change in the length of the wet season (Fig. 6d). Central Etosha received an average annual rainfall of 358 ± 124 mm, with most rain falling between January and March. In addition to temporal variation, Etosha has a spatial gradient of increasing rainfall from west to east (Fig. 7). Annual rainfall is lower and more variable in the western GEL than in the east, and these differences are exacerbated by the effects of evaporation. Evaporative water losses in the east represent 4–5 times the annual rainfall, whereas these represents as much as 10 times the annual rainfall in the west (Mendelsohn et al., 2013).

If temperatures in the region continue to rise as predicted at twice the global average, Etosha may experience a temperature increase between 4 and 6 °C by the end of the century (Engelbrecht et al., 2015). These increasing temperatures may be associated with an increase in the frequency and intensity of extreme events, such as heatwaves, heavy precipitation, and droughts (Intergovernmental

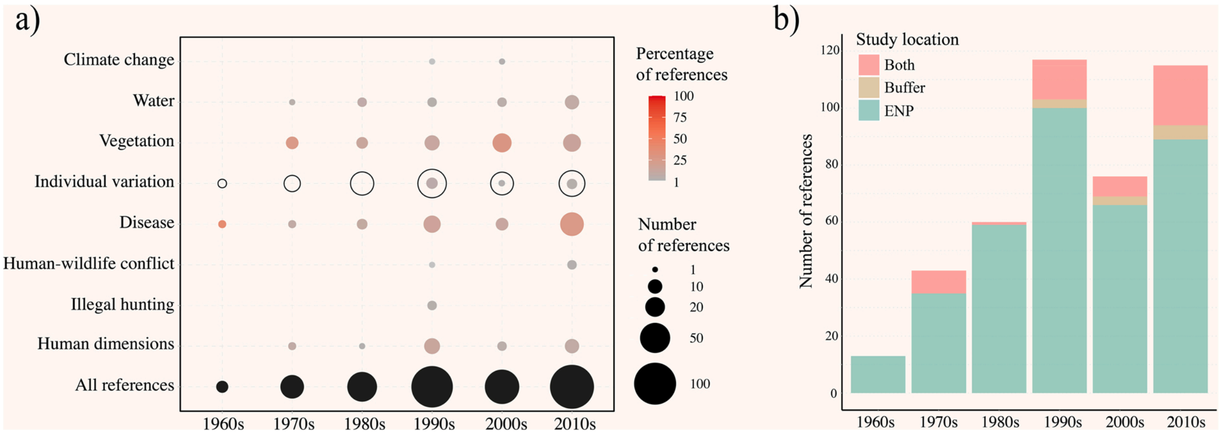

Fig. 5. Research in the Greater Etosha Landscape, showing (a) the eight key topics considered in this paper and the number of papers published over time in those topic areas, and (b) the study areas investigated, grouped into Etosha, the buffer around Etosha, or both. In (a), we show two types of individual variation: a strict definition of studies that examined individual variation linked to adaptation (colored circles) and a more liberal definition of studies documenting any sort of variation among individuals (black open circles). The size of bubbles denotes the number of studies in that topic area/decade, while the color represents the percentage of all references from a decade that address a given topic. The total number of references per decade is shown in black circles at the bottom of the chart. These results come from the 448 peer reviewed references from our literature search, with data supporting this figure available in Table S1. From this reference list we recorded studies that addressed research on these eight topics.

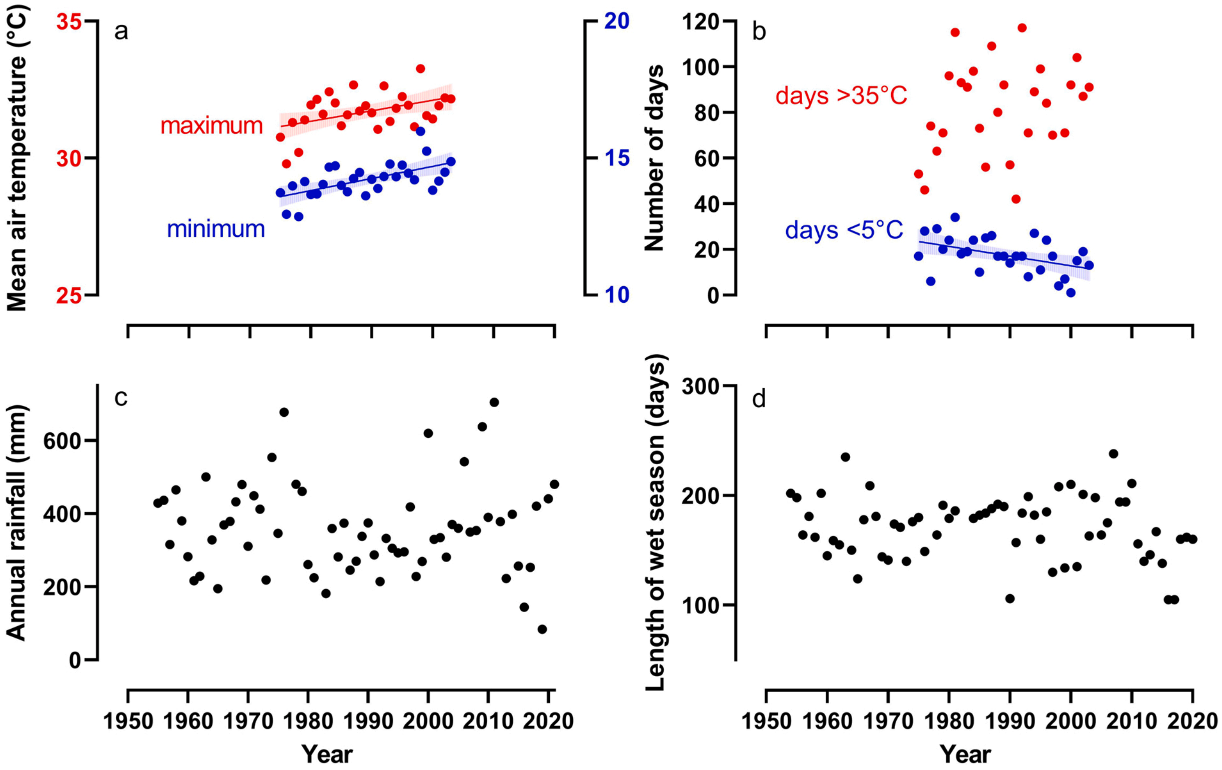

Fig. 6. Temperature and rainfall data recorded at Okaukuejo in central Etosha National Park. Rainfall data encompass the years from 1954 to 2021, whereas daily maximum and minimum temperatures encompass the years from 1975 to 2004. (a) the mean minimum and maximum air temperatures; (b) the number of days in a year with temperatures above 35 °C or below 5 °C; (c) the total annual rainfall (July to June); (d) the length of the wet season from the first to the last rainfall event of > 1 mm. Plots with lines show statistically significant changes in temperature trends over time. Data are from the Etosha Ecological Institute.

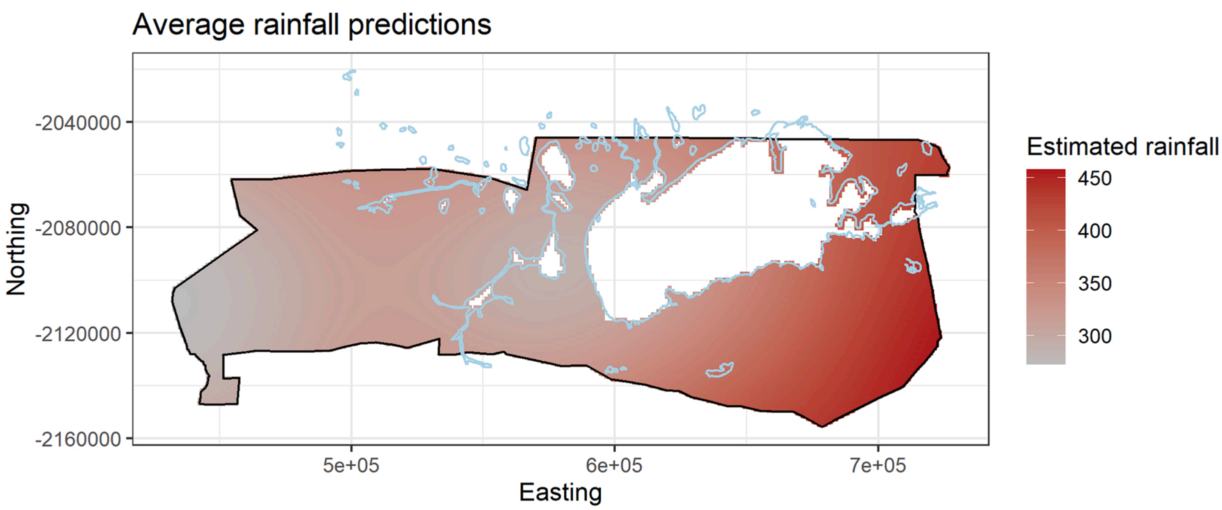

Fig. 7. Spatial patterns of rainfall across Etosha National Park showing a gradient of increasing rainfall from west to east. This map was generated from 168 annual rainfall gauges dispersed across Etosha, with data from 1983 to 2020, extending the analysis of this dataset previously presented in (Engert, 1997). Data are from the Etosha Ecological Institute.

Panel on Climate Change, 2021), further exacerbating the high temperatures and alternating floods and droughts that already characterize the Cuvelai-Etosha Basin region. Most climate change models predict a 10–20 % decrease in annual precipitation for the region, with increased evapotranspiration further drying the soils (Maúre et al., 2018). This increased aridity is likely to extend the end of the dry season from September to November, reducing the length of the growing season and increasing the risk of fire (Engelbrecht et al., 2015; Maúre et al., 2018). Because of the complexity in modeling water-limited ecosystems (Lian et al., 2021), there is some uncertainty surrounding the impact of climate change on net primary production and vegetation biomes. While there is a low probability of a complete biome change for the region (Martens et al., 2021), there may be a substantial shift in plant species composition in Etosha by the end of the century (Thuiller et al., 2006). These climatic changes may compound existing threats to biodiversity and ecosystem services (Archer et al., 2021). As an example, environmental changes may in particular affect species existing at the edges of their ranges, such as the serval (*Leptailurus serval*) (Edwards et al., 2018). Servals are medium-sized carnivores considered specialists for well-watered savanna grasslands and wetlands (Thiel, 2015), habitats which are only marginally present within the GEL.

4.2. Water availability and quality

Increasingly hotter and drier climatic conditions will continue to increase the pressure on already water-limited ecosystems, where higher levels of evaporation will further decrease water availability and quality (Engelbrecht et al., 2015; Prăvălie, 2016; Tietjen et al., 2010). Hotter environments will increase the water requirements of wildlife, as they will have to increasingly rely on evaporative cooling to dissipate excess heat (Hetem et al., 2016). Their body water balance will be further stressed because declining water availability and quality, and the consequent depletion of forage resources near potable water (Tietjen et al., 2010), may force wildlife to move further to meet their resource requirements. Increased salinization of water sources is common in drylands and correlates with decreases in biodiversity and productivity in an ecosystem (Williams, 1999). These changes in water can affect wildlife, agriculture, and humans living in increasingly drier landscapes.

Limited water availability can alter animal physiology, behavior, and species interactions (McCluney et al., 2012). For example, movement patterns are heavily influenced by water availability and the distribution of waterholes (Loarie et al., 2009; Tsalyuk et al., 2019). Individuals of many prey species congregate around waterholes (Valeix et al., 2008), which attracts predators (Trinkel et al., 2004; Valeix et al., 2009) and aggregates parasites (Titcomb et al., 2021). In the vicinity of waterholes, competition can be high and may alter interactions (Crosmary et al., 2012; Sirot et al., 2016; Valeix et al., 2010). These include aggressive interactions for access to water, for example among elephants (O'Connell-Rodwell et al., 2011), other ungulates (Ferry et al., 2020), or between predators (Périquet et al., 2021). These competitive interactions may be exacerbated as water availability decreases, with the potential for competitive exclusion.

Variable water quality is an important factor in the Etosha region as well as other dryland systems. Groundwater quality in the GEL varies, being derived from five different aquifers, ranging in water quality from fresh (south of the Pan) to hyper saline (north of the Pan), with most of Etosha's natural springs fed by the relatively fresh Etosha limestone aquifer in the south and east of the Pan (Auer, 1997; Mendelsohn et al., 2013). High levels of dissolved minerals including sodium, chloride, and sulfate are found in Etosha's waters (Auer, 1997), and have been highlighted as a concern in other dryland ecosystems (Selebatso et al., 2018). The high levels of dissolved minerals in water within the GEL create health risks to human and livestock consumers, with wildlife being assumed to be more tolerant. However, safe water quality standards have not been established for wildlife and it is unclear how a decline in water quality will influence the various species that occur in the region (Auer, 1997). Further work could include determining how the quality of water available today compares to previous time periods, and the impact on wildlife drinking preferences and health.

Previous and current water mitigation efforts in Etosha include managing the fresh water supply through the creation or closure of artificial watering points. The first artificial water point in Etosha was the borehole at Andoni, dug in 1923; thereafter water provisioning increased only after 1948 (Etosha Ecological Institute data). The biggest expansion of artificial water points was in the 1960s to (i) provide supplemental water during a drought, (ii) reduce the detrimental effects on vegetation of wildlife concentrating around relatively few natural springs, (iii) provide additional game viewing locations for tourism, and (iv) reduce HWC in the buffer zone surrounding Etosha (Ebedes, 1976). Before that, wildlife, particularly elephants, depended on farmlands south of the park for seasonal water (Ebedes, 1976). During construction of the veterinary cordon fence, water provisioning across western Etosha aimed to keep elephants inside the park (de la Bat, 1982; Ebedes, 1976).

The combination of fencing and water provisioning led to overutilization of grasslands northeast and southwest of the Etosha pan, as these previously seasonally used grasslands became home to resident herds of grazing wildlife. In 1964, the first cases of anthrax (*Bacillus anthracis*) were detected in Etosha, affecting herbivores on these grasslands (Ebedes, 1976). In combination with high rainfall periods in the late 1960s, Etosha experienced its largest anthrax outbreaks in the years 1967–1974 with over 1500 anthrax mortalities recorded (Ebedes, 1976). Overgrazing of these grasslands coupled with the outbreaks of anthrax led to a re-evaluation of the water provisioning policy (le Roux, 1979). As a result, gravel pits, providing ephemeral water, were decontaminated or removed to prevent them holding water, and boreholes on the grasslands were closed in the late 1970–1980s (Ebedes, 1976). This change in water management returned these grasslands to seasonal use, and reduced anthrax incidence (Lindeque and Turnbull, 1994). These changes in water provisioning in Etosha mirror fluctuations in water provisioning in other ecosystems, such as Kruger National Park, South Africa, where reducing the density of artificial water sources increased vegetation heterogeneity and reduced drought associated herbivore mortalities (Smit et al., 2020; Smit and Bond, 2020). Today, there is again pressure to add more boreholes, to provide more watering opportunities for wildlife, and more game viewing locations for tourism, and five boreholes have been opened in Etosha since 2016. However, any changes to water management may result in unintended negative outcomes of increased water provisioning, such as changing species interactions and diversity (Harrington et al., 1999) or reduced ecosystem resilience (Parker and Witkowski, 1999). For wildlife in the GEL, the distribution and quality of available surface water is a key concern, as predicted changes in precipitation and evaporation will continue to raise the amount of dissolved solids in surface water, increasing the spatial distribution of brackish water (Auer, 1997; Williams, 1999).

4.3. Fire and vegetation management

Fire is a major determinant of savanna vegetation structure and floristic composition (Scholes and Walker, 1993) and plays a critical role in shaping African savannas (Bond, 2019; Joubert et al., 2012, 2008). Under global climate change, increasing aridity in drylands has important implications for fire risks to society and ecosystem functioning (Hantson et al., 2017; Wei et al., 2021). Fires in dryland savannas occur less frequently compared to in wetter savannas, but the spatial extent of fires rises sharply in areas with mean annual precipitation below 550 mm (Hantson et al., 2017). Yet, fire is a natural part of the ecosystem and it can serve an important role in opening up the grass canopy and stimulating grass recruitment in the system (Zimmermann et al., 2008). While fire has been used successfully as a management tool in the past (Joubert et al., 2012; Lohmann et al., 2014; Mulqueeny et al., 2010; van Wilgen et al., 2008), the effects of climate change on vegetation and fire dynamics may be important to consider in developing future fire management plans.

The ecological role of fire in structuring vegetation communities was recognized in Etosha in 1981, when a fire policy guided by seasonal rainfall, time since last burn, and grass fuel load was established (du Plessis, 1997; Owen-Smith, 2010; Stander et al., 1993). Prior to 1981, fires were not used as a tool in Etosha's wildlife management and were suppressed through the application of backburning (Siegfried, 1981). In 1997, a prescribed fire in western Etosha could not be contained, and as a result prescribed burning was again abandoned. From 1997–2011, all fires within Etosha were suppressed through active interventions with backburns. In 2011, numerous animals, including black and white rhinoceros, elephants, and lions were trapped and killed in backburns in eastern Etosha (written communication, Werner Kilian, August 2021). This prompted a revision of the fire policy to support a patch mosaic burning approach (Ministry of Environment and Tourism, 2016). This approach is based on a system in which the season, area burnt, and fire intensities are spatially and temporally varied across the landscape (Brockett, 2001). This policy included igniting prescribed fires in the cool-dry season (May-August), designed to break up and fragment the landscape and prevent more intense fires from spreading over large areas in the hot dry season (Loehle, 2004).

The implementation of patch mosaic burns in Etosha has proven to be challenging due to a lack of clear guidelines, varied fire suppression policies in the areas surrounding Etosha, and difficulties in changing negative perceptions of fire. To enable management plans that are feasible, fire policies based on scientifically proven best practices and aligned between the government and park neighbors could create more common ground for decision-making (Archibald, 2016). There are many challenges and research opportunities to contribute to an improved understanding, through monitoring and ultimately informing management, of rainfall-soil-vegetation-fire dynamics in the changing landscape of the GEL.

The potential for shifts in species composition of plant communities by the end of the century (Thuiller et al., 2006) could compound existing threats to biodiversity and ecosystem services (Archer et al., 2021). These risks to plant communities, and the wildlife populations they support, highlight an information gap in monitoring and research on plant diversity and distributions in the GEL. The only park-wide assessment of plant communities occurred in the 1980s (le Roux et al., 1988). Long-term vegetation monitoring in Etosha was initiated in 1984 through a ground-based, photographic library, with panchromatic photographs taken at 400 fixed points approximately every six years. This sampling technique was validated and recommended to support satellite remote sensing data, with early analyses for south-central Etosha showing either no change or a modest increase in woody vegetation structure over a 15-year period (Hipondoka and Versfeld, 2003).

Although Etosha is a large, relatively intact dryland ecosystem, historical records of animal movement patterns reveal that the current protected area is only a portion of the range previously used by wildlife in the GEL. Changes in land management such as fencing and water provisioning have restricted animal movements, causing increased year-round foraging pressure on vegetation that historically supported migratory herds of herbivores. These impacts, coupled with periods of drought, have led to degradation of the grasslands surrounding the Etosha Pan (le Roux, 1979), and in the areas surrounding water points (Franz et al., 2010). This degradation includes overgrazing, trampling and denudation of vegetation, an increase in annual plant species and invasive species, a reduction in rare plant species, and increased soil erosion (Beugler-Bell and Buch, 1997; le Roux et al., 1988). Elephants have a strong impact on woody vegetation and were responsible for a decline in woody plant survival noted within an 8 km radius of water points, which corresponds to an area covering 42 % of Etosha (Van Aarde et al., 2004). Studies on the interactions between vegetation dynamics, herbivores and fire in the GEL are therefore highly important for future research, as these vegetation changes may shift biomes and hence alter species interactions (McCluney et al., 2012), ultimately increasing extinction risk (Cahill et al., 2013).

4.4. Individual variability and adaptation in wildlife

Within an integrative framework, the vulnerability of a species to environmental change depends on its exposure and sensitivity to change, which in turn is influenced by its adaptive capacity and resilience to change (Williams et al., 2008; de Meester et al., 2018; Donelan et al., 2020). Drylands not only impose an increased risk of exposure to extreme and rapidly changing conditions, but the individual organisms inhabiting those drylands may already be living at the edge of their physiological limits (Hetem et al., 2014; Vale and Brito, 2015). The adaptive capacity and resilience of a species is often dependent on a combination of genetics (i.e., microevolution) and phenotypic flexibility (i.e., non-heritable variation), whereby a single genotype may result in an array of functional types depending on the environment (Wong and Candolin, 2015). Phenotypic flexibility includes reversible changes in physiological and behavioral responses that may provide a fitness advantage, enabling an individual to acclimatize to rapidly changing conditions (Rymer et al., 2016). In plants, responses of phenotypically flexible traits have been associated with variation in water availability

(Bradshaw, 1965) and intensity of herbivory (Mboumba and Ward, 2008; Wang et al., 2017). Animal studies have revealed flexible responses to predatory pressure (e.g., color change for camouflage; Stevens, 2016), ambient temperature (e.g., body size variation and early emergence from hibernation, Ozgul et al., 2010), and water availability (e.g., selective brain cooling, Strauss et al., 2017; or variation in body temperature, Hetem et al., 2016).

As the climate in many of southern Africa's arid and semi-arid ecosystems is expected to become hotter and drier, with increased frequency and intensity of drought (Engelbrecht et al., 2015), flexibility in behavioral (e.g., modifying activity patterns and seeking shade) and autonomic thermoregulation (e.g., evaporative cooling) will be critical for the persistence of species in the GEL as well as other dryland ecosystems. However, there are limits to such flexibility, as well as associated costs (Fuller et al., 2021). For example, changes in activity patterns may affect the temporal overlap and interactions among wildlife species, leading to altered predator-prey and competitive interactions (Haswell et al., 2020; Sévêque et al., 2021). In addition, time spent seeking shade may reduce the time available for foraging. Certain species may be more at risk than others, with those more dependent on surface water being particularly vulnerable to droughts (Boyers et al., 2021; Veldhuis et al., 2019). Additionally, fencing or surrounding non-protected areas could restrict movement and limit adaptive behavioral strategies. For example, blue wildebeest require daily access to water and faced a population decline when the erection of the Etosha fence prevented their seasonal migration to permanent water sources during drought (Berry, 1982).

While considerable research in Etosha has focused on individual variation, including differences in behavior, demography, and infection status, little work has addressed how individual variation leads to adaptation and resilience (Fig. 5). Such research is vital as physiological mechanisms underlie observed ecological responses, including movement (Wu and Seebacher, 2022), foraging behavior, and prey selection (Warne et al., 2019). As such, measuring variability in the physiology of individual animals in drylands could help clarify ecological dynamics (Warne et al., 2019). In Etosha, genetic studies have largely focused on examining genetic variation, substructure, and connectivity in wildlife species of conservation concern, such as the black rhinoceros (van Coeverden de Groot et al., 2011), giraffe (Winter et al., 2018), black-faced impala (Miller et al., 2020), and Blue Crane (Simmons, 2015). While valuable for identifying taxonomic or management units, these studies do not link individual variation to adaptation. Further, few studies have examined genetic or physiological adaptive responses to environmental factors in particular, with the exception of those documenting parasite-mediated evolution in plains zebra immune genes (Kamath et al., 2014; Kamath and Getz, 2012) or temperature effects on striping patterns in zebras (Larison et al., 2015). Nonetheless, genetic variation is an important index for predicting adaptability into the future. For example, the small and isolated Blue Crane population in Namibia may be prone to inbreeding effects if genetic heterogeneity is lost (Simmons, 2015). Small populations coupled with other threats, including increasing human density in the GEL and long-term changes in surface water availability, could push Blue Cranes, as well as other threatened populations in the region, to local extinction within a few generations (Morrison et al., 2019).

Population genetic differentiation and phenotypic flexibility have been cited as non-mutually exclusive, concomitant strategies for adaptation (Volis et al., 2015). Individuals may differ in the variability of their behavioral response, with some being more predictable than others (Hertel et al., 2021). In addition, phenotypic flexibility itself may be locally adaptive, having a genetic basis (Mboumba and Ward, 2008). Heritable epigenetic variation, or molecular changes in response to environmental variation that affect gene expression without altering the DNA sequence (e.g. histone modification, DNA methylation), is increasingly recognized as playing a large role in determining phenotypic responses and adaptation, in part due to higher rates of spontaneous mutation (Hu and Barrett, 2017; Schmitz et al., 2011). Maternal effects, such as hormones passed to offspring through gestation and lactation can influence development and provide an important source of flexibility to enable a rapid inter-generational response to dynamic environmental and social cues (e.g., Mateo, 2014). Future research could provide a better understanding of phenotypic flexibility, epigenetic variation, and maternal effects, and how these may contribute to adaptation of free-ranging wildlife in the GEL under changing climate and land use. While previous work on individual variation has focused mostly on behavior, and, to a degree, describing neutral genetic variation in key species, much remains unknown about the drivers and efficacy of genetic and phenotypic variation.

4.5. Disease risk

Global analyses of emerging infectious diseases typically predict pathogen emergence risk to be highest in tropical forests and areas of high mammal diversity (Allen et al., 2017) and areas with high livestock abundance (Johnson et al., 2020). Zoonotic and vector-borne diseases have had a large impact in African drylands, where the coexistence of humans, livestock, and wildlife creates a heightened risk of contact and potential for pathogen spillover (Hassell et al., 2020), with African drylands supporting an estimated 63% of the continent's cattle populations, 82 % of sheep populations, and 70 % of goat populations (Butterbach-Bahl et al., 2020). Climate and land-use changes are expected to exacerbate disease risk in drylands (Middleton and Sternberg, 2013; Prăvălie, 2016; Wilcox et al., 2019; but see Cohen et al., 2020), with climate and landscape features in dryland systems increasing pathogen transmission risk, complicating both disease forecasting and control.

The unpredictability of resource availability and quality in drylands can directly influence disease transmission risk. Resource heterogeneity can affect host health, host or vector density, and host movement patterns (e.g., Huang et al., 2021). Many important infectious diseases are also considered "climate-sensitive," varying in their incidence based on temperature and humidity, including a range of vector-borne and environmentally transmitted pathogens (Couper et al., 2021; Moreira et al., 2020). Seasonal extremes and landscape variation may thus alter the spatial distribution of hosts, vectors, and pathogen populations, influencing contact networks of hosts and parasites, pathogen persistence, and transmission potential. Among parasitic or pathogenic species, increasing temperatures are expected to benefit helminths more than other parasitic organisms, leading to the largest increases in infection prevalence (Cohen et al., 2020). Climate change and land-use change together increase the risk of virus sharing among species, with sub-Saharan Africa showing considerable future risk (Carlson et al., 2022).

In ecosystems with relatively low host population densities, pathogens that can persist in the environment may be favored over those requiring direct, host-to-host contact for transmission. A good example in the GEL is anthrax, a generalist disease of mammals able to form highly resistant spores that can persist for years in alkaline grassland soils through periods of low host density (Turner et al., 2016, 2014). Other important pathogens of concern for spillover among domestic animals, wildlife, or humans in the GEL include rabies virus, canine distemper virus, rift valley fever virus, and a range of parasites including nematodes, protists, and ticks.

Wildlife disease has undoubtedly shaped animal distributions in the Etosha ecosystem. For example, anthrax is an important source of mortality maintaining plains zebra, blue wildebeest, and springbok populations below their resource carrying capacity (Gasaway et al., 1996), and in elephants, is the most common cause of adult mortality (Lindeque, 1988). Anthrax also creates seasonal carcass subsidies that support an abundant scavenger guild (Borchering et al., 2017). In turn, these carcasses likely increase the incidence of other infectious diseases, such as rabies or canine distemper, through agonistic interactions at carcasses (Bellan et al., 2012; Borchering et al., 2017). Further, anthrax may explain why cheetahs (*Acinonyx jubatus*) are not more abundant on the Etosha grasslands, with research in the early 1990s recording anthrax as the cause of death in 7 of 8 collared individuals (Lindeque et al., 1998). Failures to reintroduce wild dogs into the Etosha system are attributed to rabies (Scheepers and Venzke, 1995), which may be more prevalent due to the effects of endemic anthrax on scavenger populations. Future research could disentangle how disease could prevent reintroduction success into a region where wild dogs once thrived (based on Nelson, 1926). Concerns about the risk of FMD and bovine tuberculosis in African buffalo populations is one of the reasons why this species has not been (re)introduced into Etosha, preventing it from being marketed as a "Big Five" attraction for tourism.

Disease management is a common concern for protected areas, and is typically addressed by controlling animal movements across borders of the protected area (de Vos et al., 2016; Mysterud and Rolandsen, 2019; Taylor and Martin, 1987). Although fences are used to constrain animal movement and hence disease transmission, they often do not provide a hard boundary, given the significant economic and logistical challenges to maintaining such infrastructure (Somers and Hayward, 2012). Despite the erection of a double fence to prevent disease transmission between wildlife and livestock, Etosha is by no means a closed system, with herbivores and carnivores, both small and large, regularly crossing the veterinary cordon fence (Trinkel et al., 2016).

Although pathogens can be of concern for the conservation of vulnerable host species, they are also an integral part of natural ecosystems (Hudson et al., 2006). Ecological communities evolved in the presence of pathogens. Thus, any attempts to remove or reduce pathogens can have implications for maintaining the stability and biodiversity of the ecosystem itself (Buck, 2019; Hatcher et al., 2012). For example, in Etosha, the seasonal pulse of anthrax carcasses during the rainy season supports a vibrant vertebrate scavenger community. Any attempts to reduce anthrax could have indirect negative effects on the scavenger community with unknown cascading effects through trophic links in the system. Thus, control of pathogens may be best reserved for instances where host species conservation is threatened, or for pathogens with the potential for significant spillover to domestic animals and humans. Parasites can also be used as biological indicators of ecosystem health and can serve as a tool to support wildlife conservation efforts (Gagne et al., 2021), an approach which could be used to evaluate future conservation efforts in the GEL.

4.6. Human-wildlife conflict

Human-wildlife conflict is a serious threat to wildlife conservation today and is predicted to worsen as human populations increase and suitable habitat for wildlife decreases as a result of climate change and habitat conversion (Abrahms, 2021; Nyhus, 2016). Wildlife dispersing out of protected areas commonly leads to HWC and wildlife mortalities (e.g., Trinkel et al., 2016), thus, non-protected areas can become population sinks (Woodroffe and Ginsberg, 1998), especially for large carnivores and migratory megaherbivores with large range needs. In the GEL, the most common types of HWC are crop destruction, infrastructure damage by megaherbivores and depredation of livestock by carnivores (Lendelvo et al., 2015; Mfune et al., 2005). Elephants may raid crops and destroy windmills, waterholes, and fencing as they move through buffer areas (Lendelvo et al., 2015; MEFT, 2020a). The elephant population in the GEL increased through the 1970s–1980s, and has remained fairly stable since (Craig et al., 2021; Lindeque, 1991). Today, elephants have recolonized Etosha as well as the communal conservancies to the west and north and private farms in the southwest (Craig et al., 2021). Increasing elephant density over time has meant that farmstead infrastructure previously constructed without protection from elephants may no longer be adequate.

Human-carnivore conflicts during the 1900s were most prevalent on commercial livestock farms in southern boundary areas of the GEL (Stander, 2005, 2004; Trinkel, 2013). Recent changes in land use and livestock density in northern and western areas of the buffer zone have led to increased livestock depredations (Lendelvo et al., 2015). How changing land use from livestock to wildlife ranching in southern buffer areas has affected HWC is unknown. Wildlife depredation is harder to prevent than livestock depredation, since farmers cannot use typical livestock practices such as kraaling to protect free-ranging wildlife (Abade et al., 2014; Inskip and Zimmermann, 2009). In the last decade, a small number of large, private, mixed use (game/livestock) farms on the southern boundary were responsible for a disproportionately large percentage of lion and cheetah mortalities from human-carnivore conflicts in the GEL (Goelst, 2018). Communal and commercial farmers who live along the borders of Etosha often use indigenous knowledge to employ practices to mitigate livestock depredations and protect their crops, families and properties from predators and megaherbivores (Lendelvo et al., 2015). However, conflicts also occur within Etosha; local herders along the northern boundary allow their cattle to graze inside the park (Mfune et al., 2005), which may increase depredation risk. Retaliatory killings in response to HWC are common, including placing poison on depredated livestock, which is particularly detrimental for social carnivore species that scavenge (Inskip and Zimmermann, 2009). Poisoning carcasses to kill mammalian predators can adversely affect other species, for example, worldwide declines in vulture populations are attributed in part to poisoning (Murn and Botha, 2018; Ogada et al., 2016a,b).

As in many dryland ecosystems, the complexities of multiple, shifting land tenure and land-use systems contribute to changing landscape and land-use practices in rural areas today, exacerbating HWC (Lindsey et al., 2013; Schumann et al., 2012). People reliant on farming for their livelihood are less tolerant of damages and losses, and human-induced wildlife mortalities are markedly higher close to the boundaries of protected areas where human and livestock densities are high (Miller, 2015; Winterbach et al., 2013). Inhabitants of communal lands to the north of Etosha are less tolerant of wildlife as they have little financial capacity to compensate for HWC derived losses (Ministry of Environment and Tourism, 2018). The historical exclusion of indigenous people from Etosha has also likely contributed to decreased tolerance of wildlife (Hoole and Berkes, 2010). Human-wildlife conflicts are costly, with farmers suffering losses to their livelihood and the MEFT in partnership with neighboring conservancies assuming large costs for conflict mitigation and compensation for depredations.

In addition to fluctuating meat prices and societal and government demands for human-wildlife coexistence, farming in drylands will become increasingly challenging with climate change (Zeidler, 2008). For example, livestock depredations in Namibian communal conservancies increase during droughts (MEFT and Namibian Association of CBNRM Support Organisations, 2021). Climate change and associated increases in drought severity and frequency will likely decrease farmland productivity, reducing the economic capacity of communities to cope with HWC losses. However, this will also encourage a shift to alternative land uses including wildlife ranching or concessions. The concern remains that further habitat loss and increasing competition for resources could lead to an increase in HWC and greater intolerance of wildlife in the GEL. Since negative attitudes and actions towards wildlife often persist long after HWCs have occurred, pre-emptive mitigation strategies are preferable to retroactive management (Abade et al., 2014). Effective prevention strategies can be improved by contextualizing wildlife location data and HWC events across the GEL, particularly where HWCs are increasing, to identify priority locations for targeted conflict mitigation based on social and ecological factors (Miller, 2015). For example, migrant pastoralism, shifting agriculture, seasonal crop fields, and shifting cattle posts that use grazing areas communally are potential contributing factors to the occurrence of human-carnivore conflicts (Abade et al., 2014). Yet, these factors are not currently monitored during the registration or reallocation of communal farmlands in the GEL (Malan, 2003; Communal Land, 2002). Long-term wildlife monitoring studies with GPS technology offer an opportunity to bring credible evidence to inform mitigation strategies, by identifying important areas for wildlife under a range of environmental conditions (Breitenmoser et al., 2012; Melzheimer et al., 2020). Additionally, we emphasize the importance of long-term movement data to develop predictive models of depredation or other HWC risk under climate change (Boitani and Powell, 2012).

4.7. Commercial wildlife crime

Wildlife crime is the illegal trading, taking, exploiting, possessing, or killing of animals (Kurland et al., 2017; Wilson-Wilde, 2010). Here, we focus on commercial wildlife crime because of the different scales and unique challenges in mitigating this form of wildlife crime (Gonçalves, 2017). Within Namibia, elephants (Scott-Hayward et al., 2022), rhinoceros, pangolin (*Smutsia temminckii*), and, to a lesser extent, carnivores and reptiles, are targeted by crime syndicates for commercial gain. However, in Etosha, rhinoceros poaching, targeting both black and white rhinoceros, is the most commonly documented form of commercial wildlife crime, and thus the focus of this section.

Commercial poaching targeting Etosha's black rhinoceros population occurred in two waves. The first started in 1981 and peaked in 1989 (Martin, 1994); the second started in late 2014 and peaked with an estimated 80 rhinoceros killed in 2015. During both poaching surges, cooperation with the Namibian Police Force and Namibian Defence Force, development of specialized intelligence, and information gathering proved successful in the reduction of rhinoceros poaching. However, there is concern that intensified military interventions could be counterproductive and undermine other conservation priorities. Such "green militarization"–or the use of military and paramilitary techniques in pursuit of conservation–can have significant negative impacts on relationships with park neighbors, and on the people tasked with enforcing such techniques (Annecke and Masubelele, 2016; Duffy et al., 2019; Lunstrum, 2014). Incorporating multi-pronged approaches where policies are in place to engage, empower, and benefit neighboring residents living with rhinoceros or adjacent to key rhinoceros range areas, are crucial to effect efficient and sustainable long-term anti-poaching strategies (Annecke and Masubelele, 2016; Muntifering et al., 2017). As an example, anti-poaching efforts to protect the free-ranging black rhinoceros population in Kunene (distributed west of Etosha) are based on monitoring and community engagement (Muntifering, 2019), and there have been only a few rhinoceros poached.

Law enforcement efforts to curb rhinoceros poaching in the GEL are supported by biological monitoring efforts. These include using population estimates from aerial block counts and age-structure data to determine trends in the rhinoceros population (Ferreira et al., 2018; Kilian et al., 2021), and using GPS telemetry data to understand rhinoceros movement patterns (Seidel et al., 2019). Such indicators are vital in prioritizing biological management activities. In 2016, Etosha implemented SMART (Spatial Monitoring and Reporting Tool) to measure and improve mortality surveillance to inform law enforcement efforts with the aim of reducing poaching threats to targeted species. Another monitoring tool being developed in Etosha is an early warning system for poaching risk assessment that integrates mortality and environmental covariate data to predict rhinoceros mortality risk across the Etosha landscape. Given that detected carcasses are underestimates of actual mortalities (Huso, 2011), it remains a key challenge to evaluate the impact of poaching on black rhinoceros population dynamics (Ferreira et al., 2012). Furthermore, it may be important to apply and adapt methods to improve the early detection of rhino carcasses to aid rapid deployment of patrols and expedite site investigations.

Little is known about how environmental changes may influence rates of wildlife crime in the GEL. Socioeconomic factors are a main motivation for individuals to participate in rhinoceros poaching (Naro et al., 2020), hence management planning may benefit from considering climate and land-use changes and their potential to alter the incidence of wildlife crime. Future research could evaluate the socioeconomic impacts of climate change on human livelihoods and wellbeing in the GEL, and if these impact wildlife crime and, by extension, wildlife conservation. Anecdotally, we note that the two waves of rhinoceros poaching in Etosha occurred during droughts. Ultimately, conservation planning occurs at a very different time scale than responding to an immediate threat of illegal hunting. An important consideration in developing wildlife crime responses is to balance trade-offs between short- and long-term conservation goals, without negatively affecting the relationships between wildlife managers and neighboring communities that are necessary for adaptation to climate change (Ranjan, 2018).

4.8. Human dimensions of wildlife conservation

Successful conservation of natural resources depends on various human dimensions, including human capacity in the management of resources, as well as the social, economic, and political aspects of tourism activities and park-neighbor relations. Etosha faces a series of challenges and opportunities related to human dimensions of wildlife conservation, an area on which there has been relatively little research. Successful biodiversity conservation is promoted if all stakeholders are fully capacitated (O'Connell et al., 2019; Siyaya et al., 2022). Etosha's current management plan highlights threats to achieving the Park's strategic goals (MEFT, 2021). Current threats related to human capacity include concerns such as insufficient funds to support managing the Park, staff shortages and unfilled vacancies, and a need for training and capacity building for management and scientific services (MEFT, 2021). Maintenance of Etosha's artificial water points, extensive road network, and 850 km boundary fence, as well as waste management from tourism/staff are critical and costly aspects of maintaining this resource. Research collaborations with tertiary institutions, facilitated by the EEI, have long promoted capacity building and funding for locally driven research, as well as access to technology.

Although tourism is one of the main contributors to Namibia's economy, the socio-economic, socio-cultural, political, and environmental impacts of tourism-based activities in and around Etosha are largely unexplored. Etosha is Namibia's most popular natural tourist destination, receiving more than 100,000 visitors each year (Ministry of Environment and Tourism, 2013), with national park entrance fees generating 65% of the Ministry's revenue nationally (MEFT, 2020b). As Etosha developed for tourism in the 1950s, the (then) South West Africa administration removed the Hai||om who inhabited Etosha, leaving them landless (Dieckmann, 2003). Similarly, some Herero-speaking communities living within western Etosha were forcibly relocated in the 1970s to what is now the Ehi-rovipuka Conservancy (Hoole and Berkes, 2010). After Namibia's independence in 1990, land reform and resettlement programs were enacted to redress historical injustices, for rural development, and to ultimately alleviate poverty (Werner, 2001). The government purchased farmland adjacent to Etosha for the resettlement program to grant the Hai||om the right to occupy resettlement farms as wildlife tourism concessions, with traversing rights within the southeastern part of Etosha (Dieckmann et al., 2014; Hitchcock, 2015). Through these efforts, the government aimed to support the Hai||om by providing greater social equity and by engaging in sustainable livelihood activities in and around Etosha.

In 2007, MEFT developed a policy to provide tourism concessions within protected areas to local communities living adjacent to parks as a strategy to enhance pro-conservation behavior through increasing income-generating opportunities (Thouless et al., 2014). The five communal conservancies bordering Etosha (Fig. 2) were thus awarded concessions in Etosha or in Hobatere. However, development of infrastructure and access to the park is currently limited to King Nehale Conservancy to northeast Etosha, and two conservancies in the west with concessions in Hobatere. The newest concession, in southeast Etosha, was awarded to the !Gobaub Association and Hai||om Traditional Authority in 2012, but has yet to be developed and is part of an ongoing legal dispute (Koot and Hitchcock, 2019; Odendaal and Hebinck, 2021).

Another opportunity for communal conservancies to profit from tourism is conservation fees (written communication from Claudine Cloete, September 2021). Before 2020, all park entry fees went to the central government. With the implementation of a conservation fee in 2020, tourists entering Namibia's National Parks directly contribute to wildlife conservation efforts through the Game Products Trust Fund. Park management and communal conservancies have access to this fund for conservation related projects. This funding offers potential for collaborative conservation efforts between Etosha and the surrounding conservancies.

There are many opportunities to integrate human dimensions into wildlife conservation programs in the GEL to help buffer this ecosystem against future changes. Increasing human population density in the buffer area, especially north of the park, puts pressure on water resources and may lead to land-use changes and a rise in HWC. This pressure is compounded by the fact that many Namibians have never visited the park, since the cost of in-park accommodation makes Etosha inaccessible for most people. When Etosha's neighbors are not aware of or provided access to benefits derived from proximity to the park, they may value this resource less. The Namutoni Environmental Education Centre hosts visits by school groups, but the impact of these visits on appreciation of this resource is unknown. Increasing tourism access and park neighbor involvement in Etosha through communal conservancy concessions opens doors to engagement with this resource, but this puts pressure on the park to upgrade and extend the road network and commission additional water points for tourism. As yet, little work has been done to integrate the rich cultural diversity of Namibia outside of the park with its rich biodiversity inside the park. In summary, there is an important gap in research on human dimensions, including perceptions, values, and behaviors relating to wildlife conservation in the GEL, and research in these areas could guide strategies for increasing park-neighbor communication and engagement in the park and in wildlife conservation.

5. New research directions: Looking to the future as informed by the past

Although scientists and managers working in and around Etosha have expressed concern about how changing climate, land use, human capacity, and other factors may affect the future of wildlife conservation in the GEL (Fig. 4), relatively little research has investigated these topics (Fig. 5). This gap between the needs of the wildlife conservation community and the scope of current research efforts is an important area for future work. Addressing the complex nature of climate change, which may exacerbate existing stressors in the system, could benefit from a forward-thinking adaptive management framework supported by integrative, multidisciplinary research. There is a promising trend toward tackling research questions with increased complexity in the GEL, with a rise in research conducted across Etosha's boundaries (Fig. 5) and in research addressing ecological community and ecosystem level questions (Fig. 3). These positive directions form a solid foundation to begin to address the complexity arising from increasing unpredictability in climate effects on wildlife conservation. The interface between GEL research and management already exemplifies the power of more integrated research programs, such as the interaction between water and disease management. However, key gaps remain as highlighted above, for example, in the lack of integrated research on herbivory and fire interactions, as well as the influence of water management on this interaction.

Research in Etosha has followed a shift from sporadic monitoring during the first 40 years, through command-and-control management practices from approximately the 1950s–1990s, to largely managing for heterogeneity at multiple scales in the ecosystem from the beginning of the 2000s onwards. The latter strategy matches the recommendations of du Toit et al. (2003) and may become increasingly important in the future. For example, anthrax research in Etosha shifted from initial efforts at disease control, to gaining an understanding of disease transmission dynamics, to a perspective that these dynamics are an important part of the ecosystem. These changes in research reflect changes in management philosophy. Given increased understanding of disease dynamics, anthrax has the potential to be used as a sentinel for ecosystem changes related to climate change, since anthrax is tied to rainfall dynamics as well as species interactions (Borchering et al., 2017; Huang et al., 2022). These changes in anthrax research reflect the general trend we identified in our literature review, moving from a focus on single species to more complex systems ecology, as the importance of heterogeneity across ecological levels is increasingly recognized. It is this heterogeneity coupled with an understanding of the system's ecology which may help managers determine approaches to buffer the effects of climate change.

Currently, more integration between park and private/communal lands in the buffer is occurring, driven by greater interest in diffusing economic benefits from the park to surrounding areas, and politically by greater interest in leveraging these relationships to reach human development goals. As a long-term vision, these growing connections between conservancies, private game reserves, and Etosha have the potential to lead to the removal of parts of the Etosha boundary fence. This would be akin to the Associated Private Nature Reserves connected to Kruger National Park (Kreuter et al., 2010). This trajectory could be one approach to easing pressures on managing wildlife movement or abiotic forces, such as fire acting across park borders, allowing for greater biophysical exchange across the GEL. Removing fences may be feasible only in areas with compatible land use in the buffer, or else such initiatives could lead to an increase in HWC and a decline in neighbor relations. However, the presence of the veterinary cordon fence on Etosha's boundary adds significant complexity to any initiatives aimed at altering or removing this landscape barrier. Collaborative, multidisciplinary approaches building on successful disciplinary foundations (i.e., in Fig. 3) are necessary for understanding dynamics in wildlife, disease, fire, and other ecological processes that spatially diffuse across the landscape, and how these interact with neighbors' attitudes and their livelihoods. These multidisciplinary approaches further have the potential to enhance beneficial socio-ecological interactions. In the GEL, these could include the development of a multi-faceted tourism industry leveraging different land uses in a single connected ecosystem (i.e., hunting, adventure tourism, cultural exchange) while reducing the challenges that come with an open system, such as illegal activities conducted across land management areas.

To continue to develop and respond to ecological fluxes in time and space, we have identified factors that have contributed to the success of research in Etosha, which could be used to inform development of research in other dryland areas. One of the keys to the success of Etosha's research and conservation programs has been the EEI, centered in the park. The EEI is in a single building, where the upper management, scientific, and veterinary staff of the park share office space, an arrangement that promotes frequent interactions, collaborations, and problem-solving along the interface of research and management concerns. This shared space facilitates communication between researchers and managers, and among researchers with different focal areas, and fosters integrative research, with increasing complexity and multidisciplinarity (akin to embedded researchers discussed in Roux et al., 2019). Further, the EEI takes a data-sharing, collaborative approach to research. This could be further advanced by having a data manager in MEFT to facilitate and coordinate the collation and storage of all data in a central database at the EEI. As the amount of long-term research conducted in Etosha increases, unpublished long-term datasets and internal reports provide a valuable resource on which researchers can build their current efforts. Bringing these long-term, largely unpublished studies together with published research in comprehensive reviews can be particularly valuable in planning future research priorities (e.g., Weise et al., 2021). Local efforts to digitize historic data could support ongoing efforts to make long term datasets more accessible through the Environmental Information Service of Namibia (http://the-eis.com/).

There are also several risks to research and wildlife conservation in Etosha. Tourism is a key contributor to the economy of conservation, which provides an uncertain foundation of support, demonstrated by the steep decline in tourism with the COVID-19 pandemic. A lack of stable financial revenue is likely to be a factor in many dryland ecosystems that are in areas reliant on tourism. The changing dynamics in dryland ecosystems may become less predictable, with greater oscillations between dry and wet years. Furthermore, our understanding of the biology of many species remains data limited. These data gaps present challenges to predicting population trajectories, particularly with the anticipated changing dynamics in a system managed for the retainment of flexibility, although promising research techniques can be applied (Horswill et al., 2021). Thus, the future looks likely to be less predictable both from socioeconomic and biological perspectives, increasing the difficulty of managing this and other ecosystems for heterogeneity. Responding to this uncertainty could be more effective with more collaboration to understand the different effects across biological scales, and coordination of research effort to inform management. In Etosha, this could include continued oversight within the EEI, and the maintenance of a critical mass of resident scientists and support staff to ensure the required collaboration and coordination are able to occur (e.g., Kenna and Berche, 2011).

The challenges for wildlife conservation in other drylands are likely to be similar to those described here for the GEL, or even more extreme, given that Etosha may have more ecosystem resilience due to its relatively large size and intact ecosystem. The key lines of inquiry we have identified in this review may be valuable, not only for formulating testable hypotheses in the GEL, but for developing these hypotheses in other dryland ecosystems facing similar challenges. Etosha is a global resource that demonstrates the benefits of collaborative approaches to research and management, particularly for understanding the challenges currently facing dryland ecosystems.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available in the supplementary materials.

Acknowledgments

We thank the attendees of the “Etosha 112 years and counting” symposium in June 2019, since this paper was inspired by the presentations and discussions that emerged from this meeting. We thank everyone who shared their knowledge of the history of the Etosha National Park, including Kallie Venzke, Willie Adank, Ingo Behrens, Louis Geldenhuys and Dries Malan. We thank Florian Weise for his help in classifying the German references. Thanks to librarians from the University of Wisconsin-Interlibrary Loan Department and from Columbia University in the City of New York Library of Science and Engineering and InterLibrary Loan staff who provided full texts for hard to find articles. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Data accessibility statement

Additional information about datasets and reports from the Etosha Ecological Institute can be obtained from Claudine Cloete (cloete.claudine@meft.gov.na). Additional information about the literature review can be obtained from Stéphanie Périquet (stephanie.periquet@gmail.com).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02221.

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