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A diminished large carnivore guild with contrasting species-habitat associations persists outside national parks in Namibia's central-eastern landscape

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ABSTRACT

Understanding species distributions is key for effective biodiversity conservation. We conducted a large-scale camera trapping survey in five systematic grids across central-eastern Namibia to identify drivers of large carnivore occupancy and to predict occurrence across a broader mixed-use landscape spanning 161,629 km^2. Through targeted searches for intensive-use areas and pooling detections across camera trap stations, we reliably detected the most elusive carnivores. We identified a diminished large carnivore guild with the two top predators (lion (*Panthera leo*) and spotted hyena (*Crocuta crocuta*)) functionally absent, although present historically. While brown hyenas (*Parahyaena brunnea*) were omnipresent, we found local variations in guild composition. African wild dogs (*Lycaon pictus*) were more common near their resident population eastwards and in areas of greater vegetation productivity. The distribution of cheetahs (*Acinonyx jubatus*) was determined by the proportional cover of grass, consequently woody encroachment of grasslands may pose a threat. Leopard (*Panthera pardus*) occurrence was low in areas with a high human footprint, and high in areas with rugged terrain and greater vegetation productivity. The diminished large carnivore guild with contrasting species-habitat associations may enable persistence of subordinate carnivores, such as the cheetah and African wild dog, across this mixed-use landscape. However, we underscore the importance of multi-species conservation approaches to maintain ecological interactions. The large proportion (80 %) of suitable habitat identified, i.e. where probability of occupancy exceeded 0.5, is an encouraging outcome for the region's potential to hold value for carnivore persistence and potentially recolonization. Considering the limited space for protected area expansion, holistic conservation approaches are warranted to ensure viable large carnivore guilds and functional ecosystems.

1. Introduction

Biodiversity conservation across large landscapes is key for maintaining ecosystem functionality and services (Mace et al., 2012). Although critical for conservation when management and resources are adequate (Cristescu et al., 2018), protected areas often fall short in effectively covering large extents (Lindsey et al., 2017), emphasizing the need for sustainable land-use practices beyond their borders (Kremen and Merenlender, 2018). Diversifying local livelihoods and effectively operationalizing multifunctional landscapes can provide environmental, social, and economic benefits, thereby leading to improved landscape structure and ecosystem resilience (Wright et al., 2016). Namibia, located in southern Africa and with a very low human population density (Atlas of Namibia Team, 2022), developed an extensive conservation network of national parks and conservancies. The country serves as a prime example of successful community-based conservation efforts

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and provides a stronghold for various threatened species with a substantial portion of the country's wildlife numbers residing outside of national parks (Barnes et al., 2004; Lindsey et al., 2013).

Despite Namibia's conservation successes, costs of living with wildlife remain high (Stoldt et al., 2020). This predicament often results in depleted prey populations and persecution of predators, which is particularly pronounced in the country's central-eastern communal conservancies (Verschueren et al., 2020). Here, community-benefits from wildlife conservation are typically low, despite the region's critical position in relation to the southern African conservation network, especially the Kavango-Zambezi Transfrontier Conservation Area (KAZA-TFCA). Understanding wildlife distributions across large spatial scales may be key for identifying conservation priorities, especially when considering the limited resources available and threats associated with future land-use and climatic changes (Bottrill et al., 2008).

Carnivores play vital roles in trophic dynamics and are therefore important conservation research priorities (Cristescu and Boyce, 2013), with their distributions and densities influenced by resource availability, intraguild interactions and anthropogenic activities (Ripple et al., 2014). An intact carnivore guild serves as an indicator of a healthy ecosystem (Dalerum et al., 2008), however the availability of large and continuous tracts of suitable and safe habitat is diminishing due to human expansion and isolation of remaining habitat patches (Newmark, 2008). Under natural conditions, species-specific habitat preferences at different scales enable multiple-species coexistence within a diverse and functional guild (Davis et al., 2018). However, human pressures increasingly narrow niche breadths for many species, which intensifies competitive relations and complicates carnivore conservation efforts (Manlick and Pauli, 2020). Across human-impacted lands, co-occurring species may become increasingly vulnerable to critical habitat thresholds (Swift and Hannon, 2010), possibly leading to local extinctions and diminished carnivore guilds (i.e. where current carnivore richness is lower than historic large carnivore richness due to range contractions) (Wolf and Ripple, 2017).

Large carnivores (i.e. species from the Order Carnivora with body mass > 15 kg, Ripple et al., 2014) are particularly prone to human disturbance since they are wide-ranging and have high energetic requirements. Preventive or retaliatory killings following livestock depredation are among the major threats to their survival, alongside depleted prey populations and habitat loss (Ripple et al., 2014). The southern African large carnivore guild consists of six species (African wild dog (*Lycaon pictus*), brown hyena (*Parahyaena brunnea*), cheetah (*Acinonyx jubatus*), leopard (*Panthera pardus*), lion (*Panthera leo*), spotted hyena (*Crocuta crocuta*)) and has received substantial research attention (Strampelli et al., 2022a). The lion, among the most charismatic and well-studied species, is largely confined to protected areas due to its limited ability to persist in human-dominated landscapes and its reliance on stable prey populations (Bauer et al., 2015). Spotted hyenas are considerably more tolerant to humans, but as a large-bodied and group-living species encounter similar challenges to lions in some areas (Wilkinson et al., 2023). African wild dogs are highly mobile and can persist on smaller prey items, increasing their chances of survival across unprotected lands (Woodroffe et al., 2007). Leopards live solitarily, have broad habitat tolerances and are likely some of the most adaptable large carnivores, provided they are not subjected to intense direct persecution (Jacobson et al., 2016). Cheetahs often live at higher densities outside protected areas because of competitive release from dominant predators (Durant, 1998). However on unprotected lands, cheetahs face challenges with human persecution and woody encroachment of open grassland habitats (Atkinson et al., 2022; Marker et al., 2003). Brown hyenas are perceived to be less conflict-prone and play a critical role as scavenger within southern African systems (Wilkinson et al., 2023).

While prey availability is central in determining carnivore distributions, each species has uniquely adapted to fulfill its ecological requirements, displaying varying degrees of human tolerance and behavioral plasticity (Carter and Linnell, 2016). Current knowledge on large carnivore distributions and their habitat preferences is predominantly derived from research conducted within national parks and in geographically confined areas (Strampelli et al., 2022a). This bias may be attributed to the complex socio-political context of the continent (Bauer et al., 2020), easiness of carrying out research in parks compared to unprotected lands, as well as the challenges related with detecting elusive species (Kelly et al., 2012). Across southern and eastern Africa, carnivore research from rangelands is becoming more common, with most large carnivore species negatively affected by agricultural practices (Kiffner et al., 2015; Schuette et al., 2013). The development of mixed-use landscapes, however, can be conducive to carnivore conservation efforts outside of protected areas (Drouilly et al., 2018; Van der Weyde et al., 2018). Yet, many studies are focused on rather small spatial scales, and some of the widest-ranging species (e.g. African wild dog and cheetah) often remain undetected or at rates too low to be used in a reliable modelling framework (Strampelli et al., 2021). Two recent nationwide efforts integrated carnivore occurrence data from multiple data sources to empirically predict large carnivore distributions across Kenya and Botswana (Broekhuis et al., 2022; Van der Weyde et al., 2022). This responds to the growing need to better understand patterns of large carnivore distributions in understudied and unprotected parts of their range, and across a scale that matches the species' ranging requirements.

The continuous development of both technological and analytical tools enables researchers to survey larger landscapes more efficiently, and to derive meaningful (i.e. with measures of variance) estimates of carnivore occurrence and their habitat associations on a large scale. In this study, we identified distribution patterns of large carnivores across a large landscape of central-eastern Namibia covering two ecoregions and two biomes. In addition, we identified conservation priority areas based on the predicted probabilities of large carnivore occurrence and quantified the degree of their co-occurrence within these regions. We hypothesized that the distribution patterns and species richness of the large carnivore guild were affected by human pressures. An intact and diverse guild would suggest limited human disturbance and/or availability of abundant resources, while a diminished guild with species-specific habitat associations would be indicative of adaptive responses to cope with these human pressures. Conversely, overall low probabilities of carnivore occurrence within this landscape would suggest functional absence and inability to survive the human impact.

2. Material and methods

2.1. Study area

We conducted the study in the central and northern Kalahari of Namibia, covering the ‘Kalahari xeric savanna’ and ‘Kalahari acacia woodland’ ecoregions (Fig. 1). We focused on the area North of the Trans-Kalahari Corridor highway, covering an extent of 161,629 km^2. This region has a semi-arid climate with annual rainfall of 300–400 mm, typically falling from November until April (Atlas of Namibia Team, 2022). The soil is acidic, nutrient poor, and dominated by sand (Wang et al., 2007). Vegetation is characterized by thorny bushes and grasslands, but woody encroachment is widespread as a result of overgrazing, droughts, megaherbivore removal and altered fire regimes (Strohbach and Kutuahuripa, 2014). Free-ranging wildlife persist throughout the landscape but conflict with people because of grazing competition with livestock, bushmeat hunting and livestock depredation is threatening sustainable coexistence across this human-dominated landscape (Verschueren et al., 2020).

The study area is a mixed-use landscape, with multiple land designations and land use practices. The western and southern parts are designated as freehold farmland (i.e. privately-owned), where land use practices include livestock farming and wildlife-based activities (i.e. game meat production, trophy hunting, ecotourism, wildlife conservation), and where wildlife populations are relatively abundant but

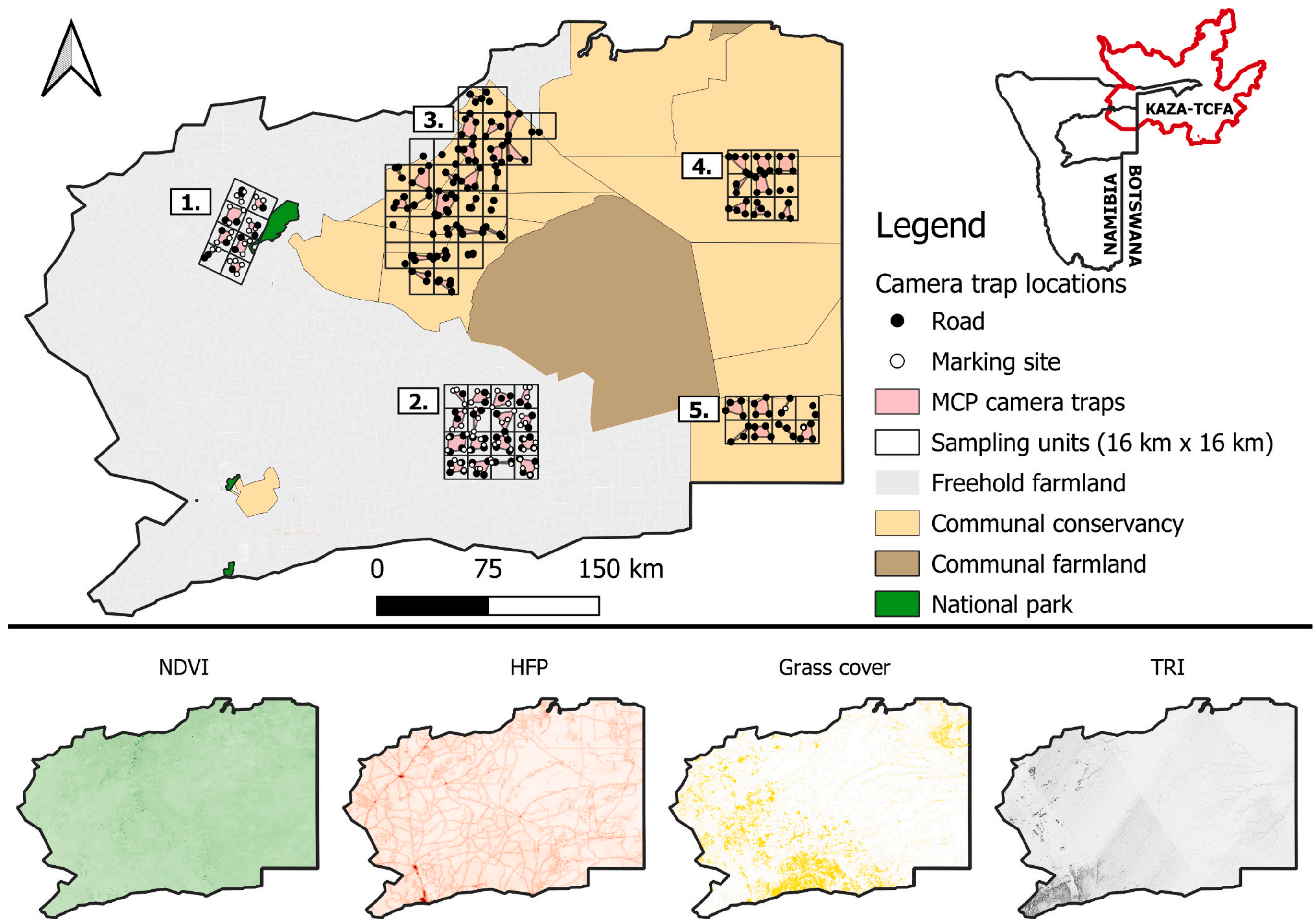

Fig. 1. Study area map with camera trapping surveys and site covariates hypothesized to predict large carnivore occurrence in eastern Namibia. MCP = Minimum Convex Polygon, NDVI = Normalized Difference Vegetation Index, HFP = Human Footprint Index, TRI = Terrain Ruggedness Index.

predator persecution prevalent (Verschueren et al., 2021b). The eastern and northern parts are designated as communal land with the majority gazetted as communal conservancies, where community-based natural resource management aims to facilitate human-wildlife coexistence. Despite this status, the low tourism potential stemming from depleted wildlife populations and remoteness hinders sectoral development, and conflict with carnivore species remains high (Verschueren et al., 2020).

The study area is located partially within but primarily adjacent to the southwestern region of the KAZA-TCFA, the largest terrestrial transboundary conservation initiative in the world. In addition, the study area covers three small national parks, 11 communal conservancies and 2872 freehold farms. Hence the study landscape may be of substantial biodiversity value to the southern African conservation network.

2.2. Data collection

Between 2018 and 2023, we conducted camera trapping surveys across five different grids over 17,580 camera trap nights (Fig. 1, Supplementary material Table S1). Grids were selected based on accessibility and established contact with the local communities. We placed camera traps in 16 km × 16 km grid cells (i.e. sampling units), approximately corresponding to large carnivore home ranges (Strampelli et al., 2022b). We sampled a total area of 18,688 km^2 (12 % of the study area), using 293 camera trap stations deployed over 73 sampling units (Strampelli et al., 2022b). We placed multiple camera trap stations per sampling unit, ranging from one to nine, and we pooled observations across camera traps within the same sampling unit to increase detection probability (Evans et al., 2019; Hofmeester et al., 2021; Iannarilli et al., 2021). We aimed for camera traps to be proportionally spread across the sampling unit, targeting coverage of each of the four quadrants within each sampling unit, although this was not always possible due to limited accessibility.

We placed camera traps alongside roads where a game trail intersected, and where available, at marking sites (i.e. trees) identified by a prior spoor survey effort supported by a scat detection dog to increase chances of detecting cheetahs (Hofmann et al., 2021). We placed double-sided cameras per station to increase detection, except during ‘Survey 3’ due to logistical constraints. We used Bushnell Trophy Cam (Survey 3) and Browning Strike Force Pro XD (all other surveys) infrared camera traps. We placed camera traps approximately 60 cm above the ground attached to trees, metal poles or fence posts. Camera traps placed at roads were programmed to take a burst of five images per trigger, and triggers were separated by 5 min. Camera traps placed at marking sites were programmed to take a burst of three images per trigger, and triggers were separated by 1 min. Camera traps were active for a minimum of 60 days and serviced for functionality every 30–60 days.

The total study duration extended over five years but was mainly focused on the dry seasons as long-term carnivore distributions appear to be influenced by availability of dry season resources (Verschueren et al., 2021b). However, due to logistical constraints, ‘Survey 1’ was done in the wet season, and ‘Survey 3’ was partially done in the wet season and partially in the dry season. Prior research on cheetah and leopard in the area covered by ‘Survey 1’ found equivalent probabilities of occupancy and detection in both wet and dry season (Fabiano et al., 2020; Verschueren et al., 2021b), hence we did not consider this as limiting factor and accounted for seasonality in the detection sub-model (see later). While the population closure assumption was not violated for the individual surveys, we adjusted the interpretation of the occupancy parameter from true occupancy to proportion of sites used, rather than the probability of continuous site occupation (MacKenzie et al., 2006).

Camera trap images were classified to species-level using TrapTagger, an open-source web application that uses artificial intelligence in combination with a manual annotation interface to process camera trap data (WildEye, 2023). Independent camera trap observations were separated by a 30 min threshold (O'Brien et al., 2003).

2.3. Data analysis

For species with a naïve occupancy between 0.1 and 0.9 (i.e. African wild dog, cheetah and leopard), we modelled carnivore occupancy within a Bayesian framework using the R package *spOccupancy* (Doser et al., 2022). We compiled single-species encounter histories based on pooled detection-non-detection data from camera traps deployed within the same sampling unit (Evans et al., 2019). We considered four sampling occasions of 15 days each. For cheetah and leopard, we used data from all camera trapping grids. Historic predator eradication efforts restricted the largest and group living carnivore species predominantly to the communal lands (Heydinger, 2020), hence for African wild dogs, we only used data from the camera trapping grids in the communal lands.

To explain variation in detection probability (p), we considered the number of camera trap stations per sampling unit (n), area covered by the minimum convex polygon of camera trap stations per sampling unit (MCP), presence of surveyed marking site(s) per sampling unit (M), number of camera traps per camera trap station (T) and season of the survey (S). We hypothesized that the number of camera trap stations and MCP area accounted for variability in detection across sampling units, the inclusion of marking site(s) and number of camera traps per station accounted for variability in detection across camera trap stations, and the seasonal covariate accounted for variability in detection across surveys (Supplementary material Table S2).

To explain variation in occupancy (ψ), we considered the proportion of grass cover (G), Human Footprint Index (HFP), Terrain Ruggedness Index (TRI), Normalized Difference Vegetation Index (NDVI), longitude (LON) and probability of leopard occurrence (LE). The rationale for covariate selection in the single-species models was based on a priori hypotheses of species-specific habitat preferences (Supplementary material Table S2). Site covariates were estimated at the scale of the sampling unit and were derived from publicly available sources. G was a measure of availability of open habitat and was derived from a global land cover map for 2021 at 10 m resolution based on Sentinel-1 and Sentinel-2 data (Zanaga et al., 2022). HFP represented a composite measure of intensity of built environments, human population density, nighttime lights, crop and pasture lands, roads and railways, and navigable waterways (Mu et al., 2022). TRI indicated the jaggedness or flatness of the terrain and was based on the elevation differences between adjacent cells (Atlas of Namibia Team, 2022). NDVI quantified vegetation greenness and may be correlated with prey availability (Pettorelli et al., 2005). NDVI values were derived for the same period when the camera trap survey was conducted, thereby accounting for seasonal differences in vegetation productivity. LON represented the west-east gradient and may be indicative of source-sink dynamics for African wild dogs moving between their resident range eastwards and the broader study area (Woodroffe and Sillero-Zubiri, 2020). LE, as determined from the leopard model output, was hypothesized to affect cheetah occurrence due to their role as dominant competitor and recent indications of leopard range expansion into cheetah habitat (Richmond-Coggan, 2019). We did not include this covariate in the model for African wild dogs as competitive interactions between leopards and African wild dogs can be bidirectional (Strampelli et al., 2023).

Covariates were checked for correlation using Spearman correlation tests. We ensured no strong collinearity existed between covariates ($|r| > 0.7$) and we scaled all covariates before analysis to have a mean of 0 and standard deviation of 1.

We modelled the probability of large carnivore occurrence in a two-step model selection framework based on the Widely Applicable Information Criterion (WAIC, MacKenzie et al., 2006). Firstly, the most parsimonious combination for detection probability was assessed keeping occupancy constant. Then, the top detection model was used and kept constant while applying WAIC to select the most parsimonious covariate combination for occupancy. Model fit was assessed using a Goodness of Fit (GoF) assessment, whereby replicated values for all detection-non-detection data points were generated and validated for alignment with the observed data. Reported Bayesian *p*-values close to 0.5 indicated adequate model fit, while values <0.1 or >0.9 suggested the model did not fit the data well (Hobbs and Hooten, 2015). Predictive performance of model outputs was evaluated using a *k*-fold cross-validation metric of model deviance (KCV), where smaller values indicated better performance (Broms et al., 2016). Covariate associations were considered strong when the 95 % confidence intervals of the parameter estimates did not include zero, while associations were considered weak when covariates were included in the top model, but the 95 % confidence intervals of the parameter estimates included zero.

We extrapolated carnivore probability of occurrence across the broader landscape based on the parameter estimates from the top model for each species and associated covariate values. For NDVI, we used the values for the dry season from August 2023. For cheetah and leopard, we predicted occurrence across the entire study area, while for African wild dog, we predicted occurrence across the communal lands only. We identified focal conservation areas based on the predicted probabilities of carnivore occurrence. We determined three suitability levels at a resolution of 16 km × 16 km cell size (priority, suitable and potential) based on the occupancy estimates of grid cells exceeding respectively 0.75, 0.50 and 0.25. We then identified multi-species conservation areas by stacking the single-species occurrence rasters to derive species overlap at each level of suitability.

3. Results

Our camera trapping effort resulted in independent detections of African wild dog ($n = 58$), brown hyena ($n = 1329$), cheetah ($n = 112$), leopard ($n = 183$), and spotted hyena ($n = 6$; Supplementary material Table S1). Lions were not detected in any of the surveys. Spotted hyenas had a naïve occupancy of <0.1, while brown hyenas had a naïve occupancy of over 0.9 and were not further examined.

The top-ranked detection models for the three carnivore species with a naïve occupancy between 0.1 and 0.9 (i.e. African wild dog, cheetah, leopard) included all considered detection covariates (Tables 1, 2). The number of camera trap stations per sampling unit showed a strong positive association with the detection probability of African wild dog, while double-sided camera traps positively associated with the detection probability of leopard. Seasonality also affected the probability of carnivore detection, with the wet season resulting in a lower detection probability of cheetah, and a higher detection probability of leopard. Additional variation in the detection models explained by covariates where the 95 % confidence intervals of the parameter estimates included zero followed our predictions, except that detection probability tended to decrease when MCP covered a larger extent.

The top-ranked occupancy models for each of the three carnivore species included a different set of covariates (Tables 1, 2). The probability of occurrence of African wild dog was positively associated with NDVI and LON. The probability of occurrence of cheetahs was determined by G only, which showed a strong positive association. The probability of occurrence of leopards was positively associated with TRI, and negatively associated with HFP. Additional variation was explained

Table 1
Model selection and performance metrics of the intercept only model, the full detection model, the full occupancy model, and the top model for three large carnivore species with sufficient detections. AWD = African wild dog, CH = cheetah, LE = leopard, k = number of parameters, WAIC = Widely Applicable Information Criterion, KCV = k-fold cross-validation metric, GoF = Bayesian *p*-values for Goodness of Fit tests.

Species	Model		k	WAIC	KCV	GoF
AWD	ψ(.)p(.)	*Intercept only model*	2	130.64	147.77	0.36
	ψ(.)p(n,MCP,T,S)	*Full detection model*	6	113.57	128.71	0.49
	ψ(G,HFP,TRI, NDVI,LON)p(n, MCP,T,S)	*Full occupancy model*	11	105.04	111.25	0.64
	ψ(NDVI,LON)p(n, MCP,T,S)	*Top model*	8	101.60	109.55	0.64
CH	ψ(.)p(.)	*Intercept only model*	2	227.09	281.55	0.27
	ψ(.)p(n,MCP,M,T, S)	*Full detection model*	7	170.16	169.74	0.31
	ψ(G,HFP,TRI, NDVI,LE)p(n, MCP,M,T,S)	*Full occupancy model*	12	160.23	163.49	0.53
	ψ(G)p(n,MCP,M, T,S)	*Top model*	8	157.17	158.86	0.59
LE	ψ(.)p(.)	*Intercept only model*	2	210.63	290.83	0.25
	ψ(.)p(n,MCP,M,T, S)	*Full detection model*	7	176.21	202.69	0.16
	ψ(G,HFP,TRI, NDVI)p(n,MCP,M, T,S)	*Full occupancy model*	11	168.68	201.16	0.28
	ψ(HFP,TRI,NDVI) p(n,MCP,M,T,S)	*Top model*	10	166.80	194.98	0.28

by NDVI that showed a weak positive association with leopard probability of occurrence. The top model for each species showed an adequate model fit with good predictive power (Table 1).

Extrapolating our model outputs across the study area extent resulted in an estimated average probability of occurrence of 0.10 (± 0.07 SD) for African wild dog, 0.65 (± 0.10 SD) for cheetah and 0.46 (± 0.17 SD) for leopard (Fig. 2). Variations in site-specific occupancy estimates ranged from 0.01 to 0.92 for African wild dog, 0.29 to 0.99 for cheetah, and 0.01 to 0.97 for leopard.

When considering grid cells with predicted probabilities of carnivore occurrence higher than 0.75, we identified 55 % of the study area as conservation priority. However, no areas were identified where all three species overlapped; two species overlapped in only 6 % of the study area, and 49 % was prioritized for a single species (Fig. 3). Expanding the threshold to 0.50, we found that 80 % of the study area was suitable for conservation for at least one carnivore species. Here, the three species overlapped in just 1 % of the area, while two species overlapped in 26 %, and 53 % was suitable for a single species. Lowering the threshold to 0.25, the entire study area was deemed potentially suitable for conservation. Under this scenario, the three species overlapped in 8 % of the area, two species overlapped in 67 %, and the remaining 25 % was potentially suitable for a single species.

4. Discussion

The study area was characterized by a diminished large carnivore guild, where the contrasting patterns of carnivore distributions suggest that habitat heterogeneity is key for carnivore survival (Davies et al., 2021). This may be particularly true across rangelands, where human activities may restrict resource access and exacerbate competition (Manlick and Pauli, 2020). We identified species of global conservation priority, and the collective importance of species-specific niches within this landscape may offer great complementarity to the KAZA-TCFA.

Table 2
Parameter estimates with 95 % confidence intervals from the top model for detection (p), occupancy (ψ) and covariate associations (β) for three carnivore species: AWD = African wild dog, CH = cheetah, LE = leopard. Values in bold were parameter estimates where the 95 % confidence intervals did not include zero. The levels for the categorical detection covariates were: No vs. Yes (Marking site), Double vs. Single (Type), and Both vs. Dry vs. Wet (Season), with the reference level given first.

Model	Parameter	AWD	CH	LE
Detection (p)	p(log)	−0.81 (−2.81–1.06)	**−2.24 (−4.11 to −0.44)**	0.02 (−1.75–1.78)
	p	0.31 (0.06–0.74)	**0.1 (0.02–0.39)**	0.5 (0.15–0.86)
	β_{n}	**2.38 (0.88–3.85)**	0.39 (−0.29–1.06)	−0.16 (−1.16–0.79)
	β_{MCP}	−0.93 (−1.9–0.07)	−0.34 (−1.07–0.35)	−0.08 (−0.88–0.69)
	β_{M}	–	1.1 (−0.09–2.3)	−0.89 (−2.48–0.72)
	β_{T}	−1.6 (−3.66–0.48)	−1.28 (−3.37–0.87)	**−2.62 (−4.58 to −0.65)**
	β_{Sdry}	0.72 (−1.24–2.69)	1.56 (−0.26–3.47)	−0.07 (−1.76–1.7)
	β_{Swet}	–	**−2.47 (−4.81 to −0.28)**	**2.72 (0.79–4.73)**
Occupancy (ψ)	ψ(log)	−0.3 (−1.54–1.02)	**1.14 (0.05–2.47)**	0.34 (−0.77–1.64)
	ψ	0.43 (0.18–0.74)	**0.76 (0.51–0.92)**	0.58 (0.32–0.84)
	β_{G}	–	**3.19 (1.18–5.47)**	–
	β_{HFP}	–	–	**−1.31 (−2.51 to −0.26)**
	β_{TRI}	–	–	**1.43 (0.09–2.94)**
	β_{NDVI}	**1.91 (0.76–3.28)**	–	1.35 (−0.07–3.29)
	β_{LON}	**1.59 (0.34–3.06)**	–	–
	β_{LE}	–	–	–

Nevertheless, throughout much of the study area, only one to two large carnivore species were predominantly present (omitting the widely distributed scavenger, the brown hyena), which was largely driven by the restricted distribution of African wild dog to the extreme eastern section of the study area, and the functional absence of lion and spotted hyena.

Areas identified as 'priority' and 'suitable' were found on freehold farmlands, and in the communal conservancies in the northeastern part of the study area, overlapping with KAZA-TCFA. Both privately-owned farmland and community-led conservation initiatives can make substantial contributions to biodiversity conservation, and the combined implementation across the region may facilitate long-term human-wildlife coexistence. Freehold farmlands specifically hold substantial value for carnivore conservation, largely due to the viable wild prey populations supported through wildlife-based land uses (Verschueren et al. 2021). Across southern and eastern Africa, rangelands support relatively diverse carnivore communities with estimates of occupancy and diversity comparable to national park systems (Broekhuis et al., 2022; Drouilly et al., 2018). On the other hand, there is a need to equally support community-based natural resource management practices across all communal areas, providing greater incentives to people living alongside wildlife (Kansky and Kidd, 2024). The communal lands in the central parts of the study area were of lower conservation value, but when effectively managed, could yield considerable socio-ecological benefits (MET/NACSO, 2018). Despite potentially acting as a barrier to carnivore connectivity, the amount of potential habitat present may facilitate future restoration efforts, which could be particularly important for African wild dog persistence within this landscape.

Although we covered five extensive grids with camera traps, we

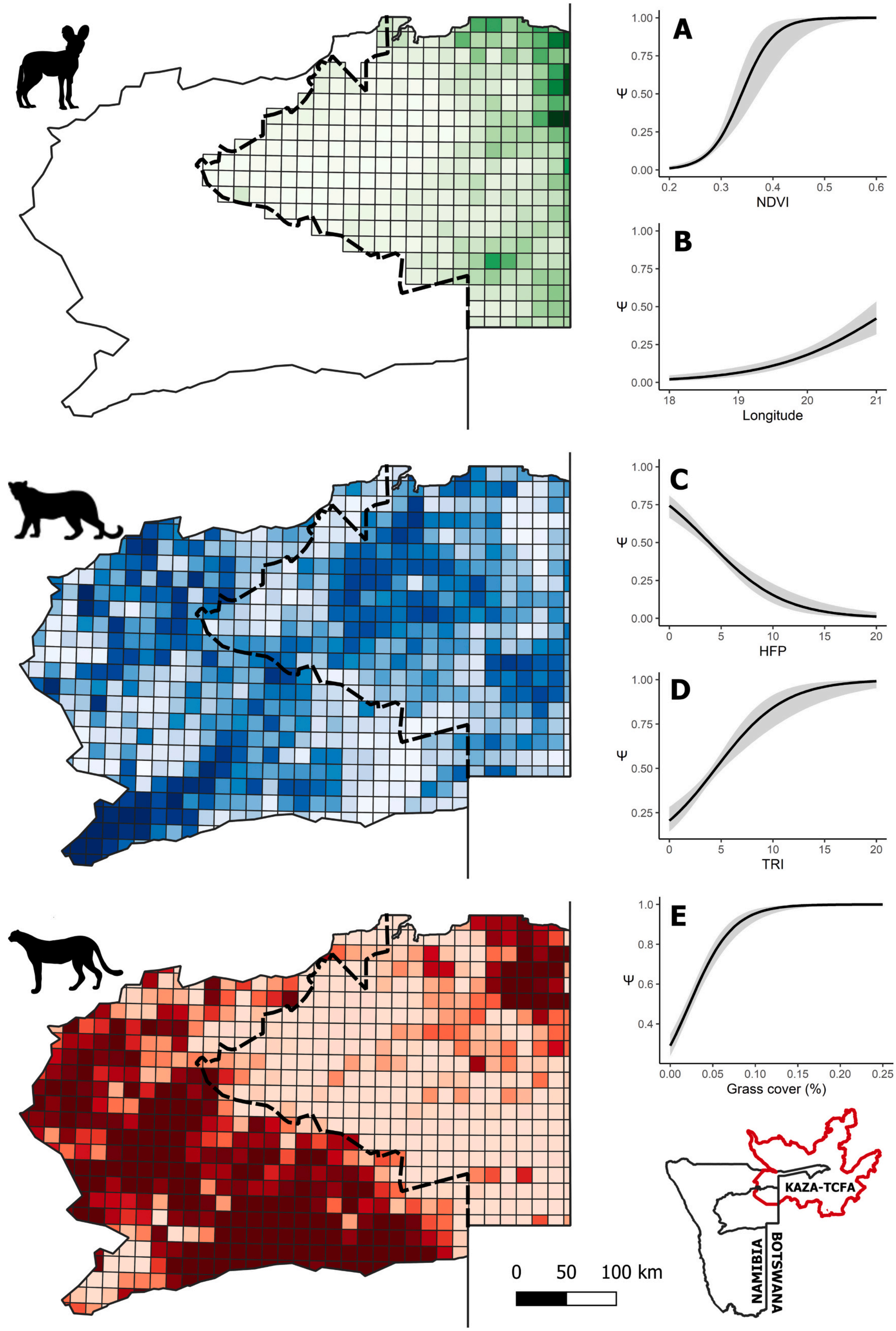

Fig. 2. Predicted probabilities of occupancy for the three carnivore species (i.e. African wild dog, leopard, cheetah) with adequate detections extrapolated across the study area extent. The extrapolation of African wild dog occurrence was restricted to the communal lands. Darker shades indicate greater probability of occupancy. The dashed line shows the divide between freehold (left) and communal (right) farmland. Species-specific responses to covariates explaining the probability of occupancy are presented right of the maps: African wild dog response to NDVI (A) and Longitude (B); Leopard response to Human Footprint (C) and Terrain Ruggedness Index (D); Cheetah response to proportional grass cover (E).

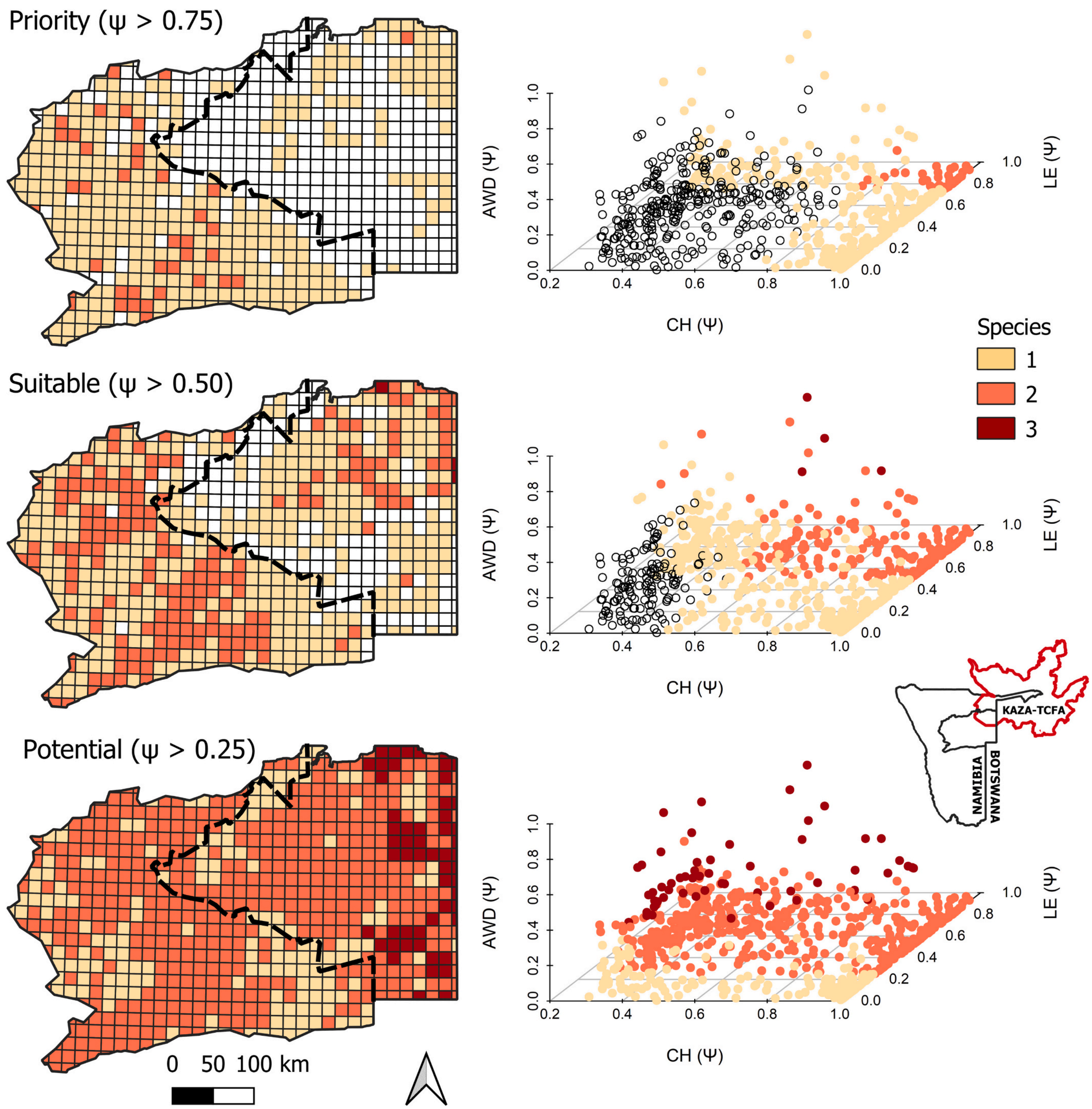

Fig. 3. Priority, suitable and potential conservation areas identified based on the occupancy estimates of grid cells exceeding respectively 0.75, 0.50 and 0.25. Left: Multi-species maps derived from stacking the single-species rasters. The dashed line shows the divide between freehold (left) and communal (right) farmland. Right: Three-dimensional scatterplots of predicted grid cell values corresponding with the occupancy estimates for the three carnivore species. Open black circles represent predicted grid cell values with occupancy estimates of all three carnivore species below the suitability threshold values.

acknowledge that the sampled region only represented a small portion of the entire study area and the large extrapolation of our results may warrant cautious interpretation. The delineation of this landscape was guided by ecoregion coverage and logistical constraints of covering this vast landscape. Within ecoregions, the vegetation across the landscape was largely homogeneous and characterized by thorny bushes and sparse grasslands (Strohbach and Kutuahuripa, 2014). In addition, the range of covariate values used for the predictions was largely similar to the range of covariate values that were sampled, with the exception of a few outliers. Subsequently, we considered our covariate selection and sampled sites to adequately represent the heterogeneity in habitat across this large landscape and the derived species distribution maps aligned well with our expectations and prior knowledge about the different species.

Our modelling approach did not include direct covariates relating to livestock and prey availability. Instead, we relied on HFP and NDVI as proxies for these factors. It is worth noting that NDVI may overestimate greenness of woodland environments, which may be less productive for large mammals compared to grassland environments, particularly if sampling occurred in the dry season (Pettorelli et al., 2005).

Additionally, HFP did not reflect human tolerance, which may differ with different land use types and among communities. However, due to the intricate nature of human tolerance, which may vary across various spatiotemporal scales, we did not include this complexity in our model. Acquiring direct metrics across the extent of the study area is challenging, hence satellite-derived metrics provided practical alternatives (Kerr and Ostrovsky, 2003), as supported by our statistically robust model outcomes.

Challenges remain with the study of large carnivores, particularly the low rates of detection. We addressed this by pooling detections across multiple camera trap stations deployed within the same sampling unit, and by surveying the area beforehand in search for marking sites of cheetahs, and to a lesser degree of leopards (Verschueren et al., 2021a). These efforts generally resulted in sufficient detections for the various species to be used in an occupancy modelling framework, and we recommend these practices for future studies that are challenged with low detection rates.

Cheetahs were common, especially across freehold farmlands that sustain viable prey populations and maintain relatively open grassland habitats. Southern Africa is a global hotspot for cheetah presence (Weise et al., 2017), and the southwestern section of our study area appears of key importance. In contrast, the central part of the study area may be limiting connectivity and was characterized by widespread woody encroachment. While the modelled cheetah occurrence showed a relatively high degree of tolerance to woody environments, our findings illustrate that resident cheetah populations may become transient when grass cover falls below 10 %. This likely relates to reduced availability of preferred prey (Hayward et al., 2006) as well as reduced predation success (Atkinson et al., 2022), while some woody cover may help in concealing cubs and kills (Broomhall et al., 2003). Given that much of the cheetah's range is threatened by woody encroachment (Venter et al., 2018), our findings may inform habitat restoration initiatives aiming to restore heterogeneous savanna landscapes, ensuring minimally 10 % of open grassland habitat.

No other occupancy covariates were retained in the top model for cheetah. The species is a flagship for semi-arid and arid environments; hence, cheetahs may persist in low productivity ecosystems. In addition, its high mobility may facilitate survival across rangelands (Creel et al., 2019), although high rates of persecution remain (Marker et al., 2003). Cheetahs may cope with persecution by having a high reproductive output and profit from the absence of competing carnivores (Wachter et al., 2011). We hypothesized that leopards would negatively influence cheetah occurrence. However, the absence of this effect may be attributed to the cheetah's fine-scale avoidance strategies (Broekhuis et al., 2013).

Habitat associations identified for leopard followed our predictions of the species preferences, notably with the covariate HFP retained in the top model. While leopards have broad habitat tolerances with a preference for rugged terrain, limited human disturbance appears important for their survival. This aligns with earlier findings identifying the importance of adequate habitat protection and sufficient prey throughout the KAZA-TFCA (Searle et al., 2020). Our measure for HFP mainly reflected public roads and towns, hence our findings suggest the avoidance of these infrastructures by leopards. While recognizing regional variations where certain leopard populations rely on urban environments (Surve et al., 2022), differences observed in tolerance to humans could be attributed to the presence of human-induced fear through legal and illegal hunting practices in our study area.

African wild dogs were confined to the communal lands and were more common towards their resident population eastwards. During the wet season source-sink dynamics may sustain African wild dogs more widely across the study area. This time of year is characterized by an increase in vegetation productivity, where prey may become more widely available across the landscape. Our predictions were however based on the dry season NDVI values as dry season resource availability likely determines long-term predator distributions (Verschueren et al., 2021b). African wild dogs may also reproduce during the dry season, with confined home ranges surrounding their dens (Comley et al., 2023). This may lead to increased risk of livestock-carnivore conflict, when wild prey resources are limited (Woodroffe et al., 2005). African wild dogs may however hunt smaller prey items and alter pack dynamics to persist in rangelands (Woodroffe et al., 2007).

Brown hyenas were omnipresent across the landscape and appear to be less impacted by the threats faced by other large carnivores. Their opportunistic nature may allow them to exploit human-dominated landscapes more effectively, while their strictly nocturnal behavior renders them seldomly seen (Maude and Mills, 2005). Within their limited range, our study area functions as a stronghold for the species, where they fulfill a vital role as scavenger (Wilkinson et al., 2023).

Lions were not detected and spotted hyenas had few detections. Both species were restricted to the northeast of the study area, mainly residing within a well-managed conservancy that borders a national park at the periphery of the KAZA-TFCA. The local costs of coexistence with lions and spotted hyenas are substantially higher compared to the other large carnivores (Jacobsen et al., 2022), and conflict with humans possibly explains their confined distribution and functional absence from much of the region, despite their critical role as apex predators within African ecosystems.

5. Conclusion

National parks rarely match the scale required to support viable large carnivore guilds and there is limited space for future expansion of protected area networks. Facilitating human-carnivore coexistence across unprotected lands is therefore key for carnivore conservation, however their persistence appears limited by varying degrees of human impact and species-specific habitat preferences. As a result, much of our study area was characterized by a diminished large carnivore guild that varied across the region. This may enable persistence of subordinate carnivores such as the cheetah and African wild dog across human-dominated landscapes, although trophic cascading effects, such as mesopredator release, and human-induced imbalances, such as prey depletion, are possibly prevalent across this landscape and warrant investigation. Even though large national parks were absent, the large proportion of suitable habitat for carnivores is an encouraging outcome for the potential of this area to hold value for carnivore survival and potentially recolonization. The realized value for carnivores will decrease if intensity and types of land use experience unfavorable change in the future. We recommend more diversified land use types in central-eastern Namibia and an increased focus on wildlife-based economies (Lindsey et al., 2013), which can reinforce KAZA-TFCA as a conservation stronghold while accommodating sustainable livelihoods.

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CRediT authorship contribution statement

Stijn Verschueren: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Tim Hofmann:** Writing – review & editing, Investigation. **Willem D. Briers-Louw:** Writing – review & editing, Investigation. **Mikael Kakove:** Writing – review & editing, Investigation. **Herwig Leirs:** Writing – review & editing, Supervision. **Hans Bauer:** Writing – review & editing, Supervision. **Laurie Marker:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Bogdan Cristescu:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization.

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 will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110741.

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