Understanding the consequences of refaunation in coexistence landscapes: integrating social and ecological dimensions

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Article impact statement: Simultaneous refaunation with cattle and elephants poses both ecological and governance challenges, emphasizing the need for balanced conservation policies

Abstract

Human-wildlife conflict poses a significant challenge to 21st-century conservation, with a limited understanding of these interactions within the broader social and ecological context of coexistence. Specifically, the impact of large-scale refaunation efforts on social-ecological dynamics in landscapes shared by humans and wildlife remains poorly understood. This study aims to enhance this understanding by jointly analyzing the consequences of refaunation involving wildlife and cattle in a mixed-use landscape in sub-Saharan Africa. Applying an interdisciplinary approach encompassing ecology, soil science, agricultural economics, and environmental anthropology, we reconstruct the coupling processes in social-ecological systems triggered by refaunation over the last five decades in Namibia's portion of the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA). To assess ecological impacts of refaunation with cattle or elephants, space-for-time substitutions are used.

The findings demonstrate that post-1960s increases in cattle numbers, and the surge in wildlife numbers since the 1990s have shaped the coexistence landscape. Elephant refaunation positively impacted herbaceous vegetation and soil conditions at intermediate elephant densities but negatively affected vegetation at higher densities. Wildlife refaunation, achieved through conservation and tourism, reduced income inequality. However, this effect was outweighed by the concentration of wealth among affluent cattle owners. Increasing rural inequality contributed challenges of local resource governance.

Our study highlights that refaunation has profound ecological and socio-economic repercussions, challenging existing forms of resource governance in KAZA-TFCA and similar coexistence landscapes in Africa, and emphasizing the need for further research on the simultaneous increase of wildlife and cattle and its socio-ecological consequences.

1. Introduction

Human-wildlife coexistence is among the most pressing challenges of 21st century conservation efforts (Nyhus 2016, Salerno et al. 2020). While negative aspects of this coexistence known as human-wildlife conflict (HWC) have been extensively documented in studies worldwide (e.g. Distefano 2005, Seoraj-Pillai and Pillay 2016, Fletcher and Toncheva 2021), our understanding of how human-wildlife interactions are embedded in broader social and ecological contexts remains limited (Dickman 2010, König et al. 2020, Bollig 2022). Specifically, we still lack understanding how large-scale refaunation impacts social-ecological dynamics in coexistence landscapes where humans, livestock and wildlife cohabit (Fiasco and Massarella 2022). This is also the case in transfrontier conservation areas (TFCAs) worldwide, which are created to better protect wildlife species through coordinated conservation management across national borders (Mason et al. 2020). In sub-Saharan Africa, wildlife corridors are often established in TFCAs to allow cross-border mobility of large herbivores such as elephants (Naidoo et al. 2022, Roque et al. 2022). In these areas, community conservation zones, wildlife corridors, and national parks typically create a mosaic of conservation areas interspersed with agricultural land (Hanks 2003, Meyer and Börner 2022). The subsequent increase in interactions of humans, their livestock and wildlife can bring about, or aggravate HWCs (König et al. 2020, Bollig 2022, Matata et al. 2022). These conflicts are commonly associated with negative, material and non-material damage to human well-being (Nyhus 2016, Methorst et al. 2020), posing a challenge to coexistence between human and wildlife..

In contrast to the common focus on HWC, the concept of a coexistence landscape stresses mutual adaptation over conflict (Fiasco and Massarella 2022). The concept underlines the turn from a strict protected area policy – where wildlife conservation can only happen in areas without human land-use – to a community-based conservation strategy. In this context, coexistence is seen as a state in which humans and wildlife dynamically co-adapt to living in shared landscapes (König et al. 2020). Under these conditions, human interactions with wildlife are governed by institutions that ensure long-term wildlife population persistence, social legitimacy, and tolerable levels of risk (König et al. 2020, Carter and Linnell 2023). Coexistence policies therefore assume that wildlife and humans can cohabit and co-adapt in a coexistence landscape (Fiasco and Massarella 2022). While the concept is certainly meaningful in widening the framework beyond a gaze on conflict, the embeddedness of coexisting species in a wider landscape is a further step necessary for making the concept operational for conservation. Moreover, the coexistence concept does not consider the impact of wildlife and livestock dynamics on the surrounding vegetation and soils, or the effects exerted on the political environment but focusses entirely on the immediate consequences of human-wildlife interaction for human livelihoods (Fiasco and Massarella 2022). Refaunation and the coexistence of wildlife, livestock, and humans might therefore pose a challenge to natural resource management.

In sub-Saharan Africa, refaunation with elephants can have profound effects on both soil and vegetation, as their selective foraging can alter the density and composition of woody vegetation (Guldemond et al. 2017, Kindermann et al. 2022a), and influence soil nutrient dynamics (Sandhage-Hofmann et al. 2022). Under increasing elephant densities, soil carbon sequestration can almost compensate for losses in woody biomass (Sandhage-Hofmann et al. 2021). Conversely, refaunation with cattle can also impact African savanna ecosystems, but in different ways: cattle grazing patterns are more targeted towards herbaceous vegetation and are less selective (Linstädter et al. 2016, Ferner et al. 2018). Surprisingly little is known on the differential impact of these divergent refaunation trajectories on the structure of woody and herbaceous vegetation, and subsequently on soil conditions.

Namibia’s Zambezi Region belongs to the Kavango-Zambezi Transfrontier Conservation Area (KAZA TFCA). In this area, three national parks, eighteen community-based conservancies and numerous wildlife corridors contribute to the realization of the nationally formulated conservation policies and the internationally endorsed and financed goals of this TFCA. Although wildlife formally belongs to the Namibian state, restricted rights to it are appropriated by the local society through community conservation efforts that emphasize local ownership. Regional and transnational conservation initiatives are effective at conserving and even increasing iconic wildlife species, in particular elephants (Naidoo et al. 2016, Meyer et al. 2021). Although these increases in wildlife populations inevitably come at the cost of increasing HWC, they also have the potential to generate income for rural households through tourism and conservation initiatives (Munthali et al. 2018, Meyer et al. 2021). While Barua et al. (2013) focus on psychological and social dimensions of human-wildlife conflict, in this contribution we deal with its social-ecological and economic consequences.

Given increasing numbers of wildlife, expanding livestock husbandry, and the increasing spatial extent of agricultural farms, it is unclear if the vision of a "coexistence landscape" can become reality in Namibia’s portion of the KAZA TFCA. Hoare and Du Toit (1999) established that elephants usually leave areas of intense human use, and give 19 persons per square kilometre as the upper threshold for human-elephant co-existence. However, several areas in northeastern Namibia nowadays have human population densities exceeding this threshold (Namibia Statistics Agency 2017), and elephants are nevertheless still present in these areas, impacting ecosystems and human livelihoods (Stoldt et al. 2020).

Like in many rural areas of sub-Saharan Africa, livestock ownership in Namibia’s portion of the KAZA TFCA is an expression of wealth, and income-earning community members invest ambitiously in cattle (Bollig and Vehrs 2020). Balancing income from both livestock and wildlife conservation is challenging (Meyer and Börner 2022). In this context, it remains unknown how both trajectories of refaunation are connected to income inequality and how a dynamic social-ecological system, in which major parameters have changed over the past decades, is to be governed.

Indeed, the establishment of coexistence landscapes, as envisioned for the Namibian portion of the KAZA TFCA, present considerable challenges to governance. Usually, the state is the owner of land, and some of the land is managed as national park or state forest, where a specialised administration operates according to the guidelines of a line ministry. Most land, however, is communal: while the state is the formal owner, the land is administered jointly by traditional authorities and their institutions and respective line ministries (Mosimane et al. 2023). Non-governmental organizations (NGOs) and Community-based organizations (CBOs) work together with traditional authorities to govern communal lands and their natural resources (Hulke et al. 2021). The governance of these lands has two challenges. First, both NGOs and CBOs are dependent on donor funding. The donors have their own visions and programs concerning conservation and sustainable resource governance. Second, NGO and CBOs rely on good and trustful relations with local communities. Hence, it is not only humans and wildlife that need to coexist, but also different forms of governance, differently legitimised stakeholders, and different social institutions.

In our interdisciplinary study, we investigate the socio-economic and ecological impacts of a simultaneous refaunation with elephants and cattle in the Namibian portion of the KAZA TFCA. This region hosts the largest elephant population in the world (Stoldt et al. 2020), with extensive over-spills of elephants from the national parks to adjacent community conservation areas. Specifically, we ask the following research questions addressing the challenges of coexistence in a landscape simultaneously refaunated by wildlife and cattle:

(1) What historical and contemporary patterns of de- and refaunation dynamics are discernible in Namibia's Zambezi Region?

(2) What are the specific consequences of refaunation with megaherbivores and livestock for vegetation structure and soil quality?

(3) What socio-economic implications arise from the simultaneous refaunation of wildlife and livestock, particularly in terms of wealth distribution and governance structures?

2. Materials & Methods

2.1. Study area

Our study was conducted in the western parts of Zambezi Region in Namibia, an important portion of the KAZA TFCA (Stoldt et al. 2020), the world' largest TFCA (Naidoo et al. 2022). The climate is semi-arid with average temperatures of 10°C in winter and 36°C in summer; mean annual precipitation is highly variable with values between 550 and 600 mm (Mendelsohn et al. 1997, Mendelsohn et al. 2003). The Zambezi Region is part of the Kalahari Basin and covered by thick deposits of Kalahari sand, on which sandy, infertile soils, Arenosols, have developed. Arenosols cover > 50% of the Zambezi Region (Mendelsohn et al. 2003). The study area falls in the Miombo ecoregion, an area of open savannas, savanna woodlands and dry open forests in south-central Africa (Frost 1996). It is classified as 'Kalahari woodland' (Mendelsohn et al. 1997, Mendelsohn et al. 2003) where the tree layer is dominated by species such as *Terminalia sericea*, *Burkea africana*, or *Baikiaea plurijuga* depending on the underlying soils or altered to other forms of shrubland depending on land-use (Sandhage-Hofmann et al. 2021, Kindermann et al. 2022b).

The study area, with its three national parks, i.e. Mudumu (737 km^2), Bwabwata (3.137 km^2), and Nkasa Rupara (337 km^2; Figure 1), hosts large populations of elephant and other mammal herbivore species such as giraffe, buffalo, impala, and wildebeest (Stoldt et al. 2020). The area serves as a corridor for large elephant herds that cross from Botswana via Mudumu National Park and the State Forest north of the park to Zambia's Sioma Ngwezi Park (Naidoo et al. 2022). These corridors connect the three park areas and community conservation zones with protected areas in neighbouring countries. In the year 2016, over 70% of the Zambezi Region's ca. 90,000 residents lived in rural areas and 39% lived below the poverty line, compared to 27% in the whole country (Republic of Namibia 2016, Namibia Statistics Agency 2017). Unemployment is high, affecting 37% of the working population, and the percentage is even higher amongst young people with half of the population aged between 15 and 34 being without formal employment (Namibia Statistics Agency 2019). Conflicts over land have increased during the past two decades. These conflicts occur between ethnically defined groups of actors, and entail disputes over territorial boundaries, the power of traditional authorities to govern specific places and resources, and the right to settle on certain land (Mosimane et al. 2023).

Conflicts are also frequent within village communities, with wealthier people taking up increasingly more land for the development of farms and estates. A third layer of conflict is added by confrontations between communities that have been relocated by past governments to give space to conservation projects or to get people out of Tsetse infested wetlands (Vehrs and Zickel 2023). Some of these communities nowadays launch demonstrations for the restitution of their ancestral lands. HWC has gained prominence in the past two decades, as increasing numbers of elephants and other herbivores cause major damage to farms during the rainy season (Salerno et al. 2021, Fabiano et al. 2023).

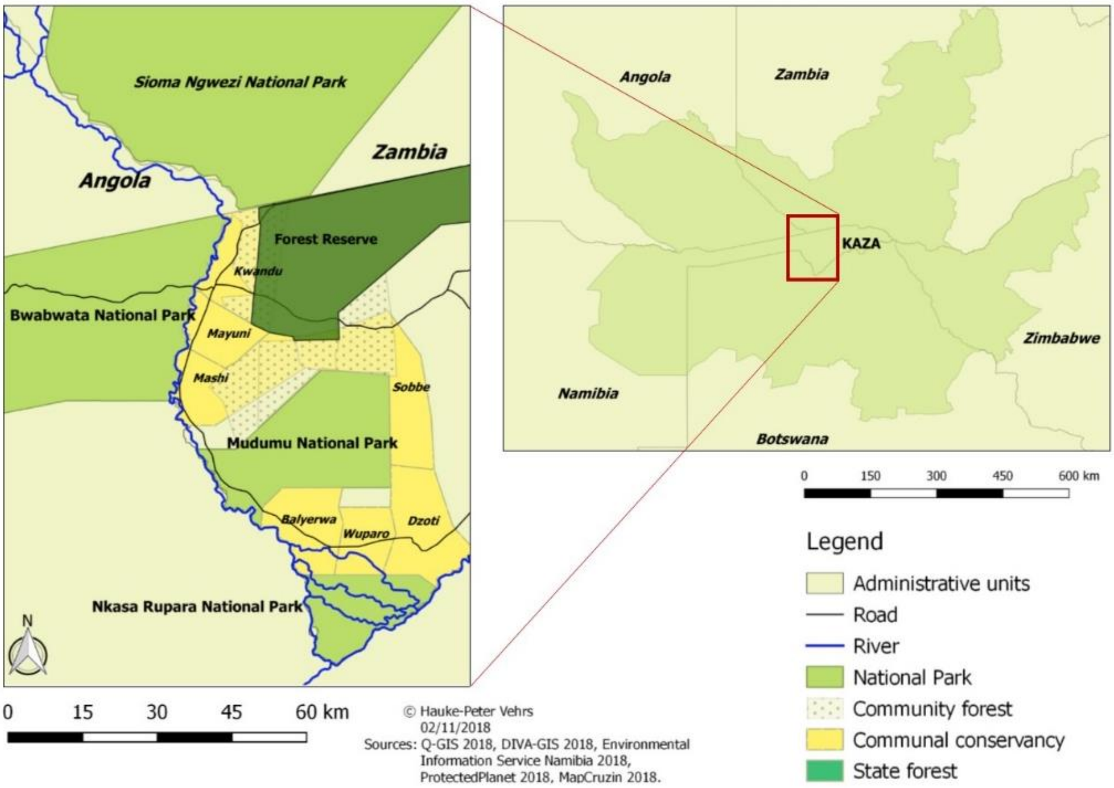

Figure 1 Study area in Namibia's Zambezi Region, depicting the adjacency of three national parks (functioning as a migratory corridor for elephant herds) to communal conservancies, where areas with low elephant densities and communal rangelands are located.

2.2. Methods for the reconstruction of historical de- and refaunation dynamics

To understand the historical dynamics of social-ecological relations, we analysed different historical sources, spanning the period from the 19th century to the present day. The Windhoek-based National Archives offer archival material to inform work on past population movements, political conflict and governmental projects of rural development. We consulted the files of the former East Caprivi Administration and found the files of the agricultural department to be of specific importance to our study. Additionally, about 30 interviews concerning settlement and land-use history took place in villages of Mudumu South (conservancies Balyerwa, Wuparo and Dzoti; Figure 1) and Mudumu North (conservancies Mashi, Sobbe, Mayuni and Kwando; Figure 1) between March 2018 and September 2022. These interviews were usually conducted with a person pointed out by the local traditional authority as being knowledgeable about history. The Department of Veterinary Services supplied historical and contemporary data on cattle numbers.

2.3. Analysis of refaunation effects on vegetation and soil

To analyse the ecological consequences of a refaunation with elephants and livestock, we used two space-for-time substitutions (sensu Pickett 1989) and sampled in five herbivore density classes (Figure 2). For a refaunation with elephants, we stratified our sampling into three elephant density classes, with low (L), medium (M) and high (H) densities. This study design captures sites representing past (L), current (M), and future (H) stages of the refaunation process with elephants in the study area (see Sandhage-Hofmann et al. 2021). To assess refaunation with cattle, we sampled on communal rangelands (R) representing the current state of medium cattle densities; and on an intensively used cattle farm (F) to capture a future refaunation stage with high cattle densities (Figure 2). Both refaunation pathways had the low elephant density (L) sites as referende, representing a past defaunated state.

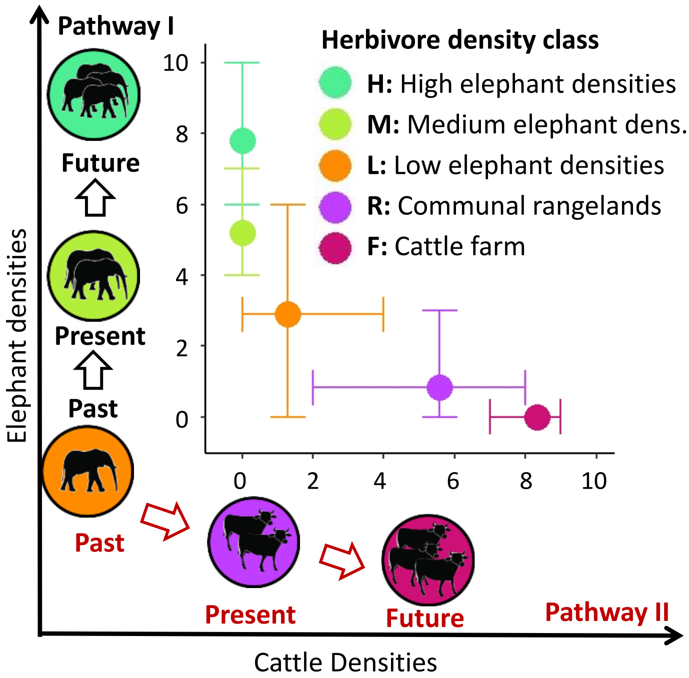

Figure 2 Study design capturing ecological effects of refaunation through two separate space-for-time substitutions. The figure depicts the past, present, and anticipated future effects of refaunation, focusing on elephants (Pathway I) and cattle (Pathway II), categorized into five herbivore density classes. The inserted graph presents recorded densities (mean values and standard deviations) of cattle and elephants on the plots, ranging from zero (absent) to ten (highly abundant).

The M and H sites were located in Mudumu National Park, while L and R sites were located within the conservancies Wuparo and Mashi (Figure 1), either in their designated wildlife conservation areas (L) or on rangelands close to villages (R). F sites were located on the farmland of the Sachinga Livestock Development Centre, a government-owned farm intended for livestock improvement programs. Here, the open woodlands are being replaced by close shrublands dominated by low *Baphia massaiensis, Bauhinia petersiana*, and thornbush species of the genera *Vachellia* and *Senegalia* (Lisao 2015). Sites in the national park were selected with the help of experienced park rangers, while sites in the conservancies were selected with the assistance of local guides.
Data were recorded on 1,000 m^2 plots, with six (R, F) or ten plots (L, M, H) per site. As R and L sampling was repeated in two conservancies, these herbivore density classes were sampled with n =12 and n = 20 plots, respectively (58 in total). Sampling took place from September to November 2018 and from April to June 2019. For an expert assessment of elephant and cattle densities, physical indicators of their activities (tracks, dung deposits, and recent signs of browsing or grazing) were combined (see Linstädter et al. 2014, Sandhage-Hofmann et al. 2021). Data were recorded on an ordinal scale ranging from zero (herbivore not present) to ten (herbivore highly abundant).

To assess the effects of refaunation on vegetation structure, we recorded the canopy cover of trees and shrubs (‘woody cover’), losses of woody biomass attributable to elephant damages, and the cover of herbaceous plants (‘grass cover’; visually estimated as percentage cover). For woody cover and biomass, we recorded tree and shrub individuals on our plots with their species identity and size parameters. This was done with a flexible sampling strategy to keep the sampling effort within reasonable limits (Kindermann et al. 2022b). Two allometric equations (Chave et al. 2014, Conti et al. 2019) were applied to estimate woody plants’ individual aboveground biomass (AGB) from measures of plant height, stem diameter, canopy diameters and specific wood density. Individual biomass losses attributable to elephant browsing were calculated based on a damage assessment (see Kindermann et al. 2022b), and added up per plot. For woody cover, crown areas of all trees and shrubs were added up per plot.

Soil samples were taken on all plots to a depth of 50 cm with an electrical soil auger of 6 cm diameter (Geotool). A smaller part of the plots was sampled using a hand auger of 5 cm diameter (Ecotech). Auger cores were subdivided into depth classes (0-10 cm, 10-20 cm, 20-30 cm, 30-50 cm). Dry bulk density was determined by weighing the air-dried samples and dividing them by the respective auger volume (Walter et al. 2016). The sieve-pipette method was used for particle-size analyses according to the (IUSS Working Group WRB 2015). To estimate total carbon (C) contents as a measure for soil fertility, samples were analysed by dry combustion with a CHNS analyser. No inorganic C was detected, meaning that total C was equal to organic C (referred to as SOC). $\delta^{13}C$ were analysed using an isotope ratio mass spectrometer (Delta V Advantage IRMS, Thermo Electron Corporation, Germany); isotope values were calculated following the equation in Appendix S1. To obtain information on the origin of SOC, we calculated the relative proportion of SOC derived from the woody biomass (FC_3; Appendix S2), based on $\delta^{13}C$ of -27.1 ‰ for woody components and $\delta^{13}C$ of -14.3 ‰ for grass (Boutton et al. 1998).

2.4. Analysis of economic effects of refaunation and coexistence

We assessed the economic dynamics of refaunation in three steps. First, we used an original household (HH) dataset from a representative cross-sectional survey to quantify income from various sources, including livestock and wildlife through community-based conservation and tourism employment for rural households (Meyer et al. 2021). This survey was conducted between April and September 2019 and covered 633 HHs throughout the whole rural part of Namibia's Zambezi Region (see Figure 1). The questionnaire used a 12-month recall period and followed a two-stage stratified random sampling process. Second, we calculated the Gini coefficient, which displays the income inequality of a given population, using the definition of Lerman and Yitzhaki (1985). Third, we constructed a decomposition of the Gini coefficient (Appendix S3), which helped us to understand the contribution of each income source to total income inequality (López-Feldman 2006).

We further conducted village-based surveys in the North and South of Mudumu National Park to ascertain livestock ownership. In selected villages, we chose five local informants who were known to be knowledgeable about herd ownership. We noted each village household on a card and asked these five informants to rank all households according to their cattle ownership. Rankings were unanimous in pointing out the divide between households that owned cattle and those that did not. Wealthy herd owners were easily identified as their cattle herd was clearly visible in the area. For each household we also asked whether the household received income from formal employment or a pension from a former employment and inquired where the herd was located at that time.

2.5. Analysis of governance of refaunation

To gain insight into governance structures in the Zambezi Region, we conducted about 40 qualitative interviews between September 2018 and April 2023 with local farmers, traditional authorities, NGO staff members, staff of the respective ministerial departments, and tourist entrepreneurs (Kalvelage et al. 2020). Interviews were mostly conducted with single interviewees and only occasionally in a focus group discussion format. During interviews, we frequently worked with translators, with some interviews conducted in the English language. We also participated in a number of formal and informal gatherings to observe the ways natural resource governance unfolded at the local level.

3. Results

3.1 Historical dynamics of de- and refaunation

Wildlife numbers in general and elephant numbers in particular declined drastically in the late 19th and early 20th centuries (Stoldt et al. 2020). Reid (1901), a British traveller passing through the area in 1899, reported that elephants had been nearly exterminated due to intensive hunting at the end of the 19th century. While elephant numbers gradually picked up due to colonial proscription of hunting, another drastic decline in wildlife numbers occurred in the 1970s and 1980s (Lenggenhager 2018). By the end of the colonial period (1989), wildlife was almost extinct.

Comprehensive conservation measures instituted in the 1980s and 1990s led to a resurgence of wildlife. In the mid 1990s, Mendelsohn et al. (1997) reported that elephant numbers in the region were on the increase, and estimated the population at about 5,000 to 6,000 individuals. The period 2006-2013 saw increases in numbers of elephant, impala, sable antelope and zebra (Namibian Ministry for Lands and Resettlement 2015). The Integrated Land Use Plan of 2015 (ibid.) estimated the number of elephants at 8,401 (for 2013). The Elephant Status Report for Africa 2016 (Thouless et al. 2016) gave 13,116 elephants for the entire Zambezi Region. A recent report (MET and NACSO 2020) stated that while the two National Parks, Mudumu and Nkasa Rupara, held 4,598 (resulting in an elephant density of 4.6 elephants/km²) and 2,151 elephants (6.7 elephants/km²), respectively, the number of elephants for Mudumu North's conservancies was only 467 and for Mudumu South's conservancies 446 (meaning 7,662 elephants for the entire Mudumu Landscape).

Cattle numbers also fluctuated tremendously throughout the last century (Appendix S4). Early German sources estimated the seasonal presence of about 30,000 cattle of the Lozi elite in the region around 1900. Once these herders retreated to southern Zambia in 1909 to avoid taxation or confiscation by the German administration, the region was devoid of significant cattle numbers for several decades (Bollig and Vehrs 2021). While there was some increase in cattle numbers in the 1930s and 1940s, an upsurge in Trypanosomiasis in the 1950s depleted cattle herds again, and by the early 1960s hardly any cattle were kept in the Mudumu landscape. Intensive spraying with insecticides and programmes directly targeted at the establishment of large cattle herds since the 1960s both contributed to a rapid increase of cattle populations throughout the last three decades of the 20th century. Now, in the early 2020s, about 180,000 cattle are kept in the Zambezi Region (source: Veterinary Office Windhoek); of these about 7,500 are herded in Mudumu South (Bollig and Vehrs 2021) and 6,100 in Mudumu North (personal com. M. Bollig with Veterinary Officer, Katima Mulilo). In summary, substantial increases in cattle have only occurred since the 1980s, reaching a peak in the early 2000s, and then settling at around 140,000.

Cattle ownership was found to be noticeably uneven. A recent report by the Ministry of Lands and Resettlement (MLR 2015: 74) estimates that in the Zambezi Region 42% of all households had no cattle at all, while 43% had between 1-30 head of cattle and only 15% possessed more than 30 head of cattle. Bollig and Vehrs (2020) reported similar figures from a survey of 109 households in the Mudumu landscape where only about 50% of the households owned cattle and most cattle herds were rather small, having fewer than 10 animals.

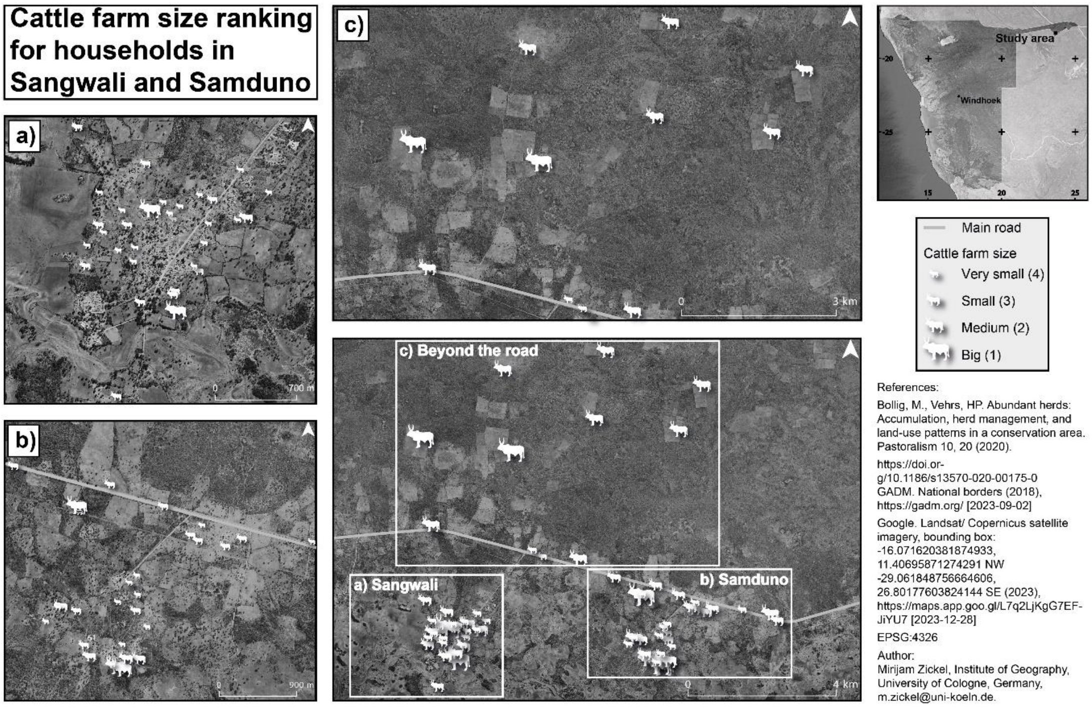

Figure 3 Cattle herds and cattle ownership in a location within Wuparo Conservancy (Mudumu South). The map shows that only large herds stay north of the Kongola-Katima Mulilo tarred road in a zone adjoining Mudumu National Park. These herds stay permanently in this landscape as all herd owners have drilled their own boreholes and do not rely on water from the Kwando/Linyanti river. Small and medium herds concentrate around Samuduno village.

The few wealthy cattle owners had their cattle herded in camps away from the villages where grazing pressure was lower, and the grazing quality was judged to be better (Bollig and Vehrs 2020). Notably, wealthy herd-owners could drill private boreholes there. These larger herds of cattle, typically having 100-150 animals, were herded by employed shepherds while the owners resided in the village. No farmers with small herds of cattle had their livestock herded north of the road during the dry season of 2019 (Figure 3). Cattle herded north of the road relied almost entirely on boreholes that these wealthy cattle owners often had drilled with their own funding, whereas those living in the village relied on the Kwando River for watering. In contrast to these large herds, smaller cattle herds were herded in the vicinity of the village (Figure 3).

3.2 Refaunation effects on vegetation structure and soils

The two refaunation pathways affected vegetation structure differently. Refaunation with elephants resulted in woody biomass losses due to elephant damages increasing from 2.5 t ha^{-1} ± 1.9 on L plots to 7.2 t ha^{-1} ± 4.2 on H plots (Figure 4a), which corresponds to recordable woody biomass losses of up to 50%. Accordingly, significant decreases of woody cover on M and H plots were observable compared to L plots (Figure 4b). Under a refaunation with cattle, woody cover increased dramatically on F plots as compared to L plots (from 78% ± 21 to 156% ± 43), and could reach > 200% due to a considerable overlap of tree and shrub crowns in different height layers. Aboveground woody biomass itself displayed similar trends as woody cover (Appendix S5). In contrast, grass cover showed roughly opposite trends to woody cover across herbivore density classes (Figure 4c), and was basically absent on F plots (1.0% ± 2.0) where woody cover was extremely high. Although vegetation structure at the endpoints of the two refaunation pathways always differed significantly from the structure at the pathways' starting point of defaunated reference sites (L plots), the relationship with increasing herbivore densities was never linear but instead hinds at ecological tipping points.

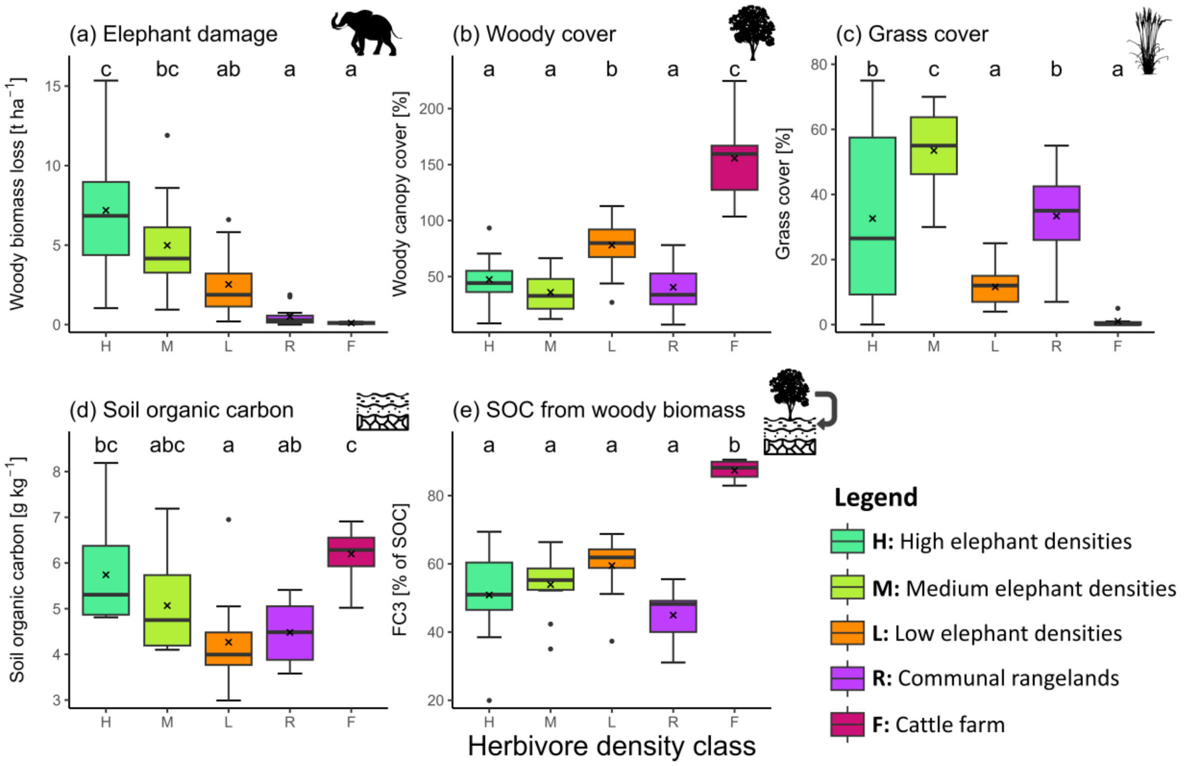

Figure 4 Vegetation and soil characteristics as impacted by a refaunation with elephants and cattle, with a) recorded losses of woody aboveground biomass due to elephant damages; b) woody cover of trees and shrubs; c) percentage cover of grasses and other herbaceous plants; d) soil organic carbon (SOC) concentrations in the topsoil (0-10 cm), and (e) relative proportion of SOC in topsoils derived from woody biomass (FC_3). Differences in lowercase superscripts indicate significant differences between herbivore density classes.

Soils on our plots were found to be Arenosols, with high sand contents ranging from 94-96% across all herbivore density classes except for rangelands with only around 90% (Appendix S6). Due to the sandy texture of the soils, carbon concentrations and stocks were generally low. In the topsoils, we found carbon concentrations (Fig. 4d) and stocks (Appendix S7a) to be consistently higher with increasing elephant and cattle densities. This effect was most pronounced for the cattle farm, but SOC was also significantly higher on H and M plots. Defaunated sites (L plots) showed the lowest carbon concentrations (2.6 g kg^{-1} ± 1.3). The effect of refaunation on carbon was highest in the topsoils and declined with depth (Appendix S7b). This resulted in highest carbon stocks (25.5 t ha^{-1} ± 6) being stored in H plots between 0-50 cm soil depth, compared to 21 t carbon ha^{-1} ± 4 in F plots.

FC3 values, an indicator of the contribution of different plants on SOC based on $\delta\ ^{13}C$, showed that for topsoils, most parts of the origin of SOC in the cattle farm (87% ± 0.1) originated from woody plants (Fig. 4e). This was still evident in 50 cm soil depth (Appendix S8). On H plots, the input of woody plants and grasses was balanced in toposils, whereas in R plots, input of grasses dominated; they contributed 55% ± 0.2 to SOC. This conforms to the different grazing and browsing patterns of cattle and elephants, respectively.

3.3 Wealth and inequality

We found the Gini coefficient for total income to be 0.71 (Table 1), which indicates a very high degree of inequality in a rural setting. A 1% increase in livestock income, under otherwise similar conditions, was associated with an increase in income inequality (Gini coefficient) by 0.30%, indicating a substantial increase in inequality.

Table 1 Gini decomposition results by income source, where column 1 indicates the changes in income inequality by the respective income source, column 2 the share on total income of the respective income source and column 3 the Gini coefficient by each respective source.

Income source	Percent change in income inequality	Share of income source on total income	Source Gini
Livestock	0.30	0.33	8.97
Tourism employment	-0.87	0.014	0.85
Conservancy	-0.002	0.01	0.97
Total income			0.71

Note: Using descogini in Stata by López-Feldman (2006), other income sources are included in the calculation and details can be found in appendix S3. Marginal effects are indicated as percent change.

On the other hand, a 1% increase in income from employment in tourism was associated with a decrease in income inequality by 0.87%. Income from conservancies, as a form of wildlife economics, had a negative but small effect on income inequality. The share of each income source on total income indicates that livestock income took up the largest share of 0.33. However, livestock-related income was extremely unequally distributed (Source Gini: 8.97). Despite the large potential for decreasing income inequality through wildlife economies, especially from tourism employment, the share of these sources of income were found to be small (tourism employment income: 1.37%, conservancy income: 0.50%). This suggests a limited overall relevance of income from wildlife through tourism and conservancies. To summarise, livestock income was associated with wealth but also wealth inequality, while income from wildlife was associated with an income equalizing effect through tourism and conservancies. These empirical findings match well with our field observations which suggest that local income inequality has been rapidly increasing in recent years. Well-built houses springing up at the road-sides, and expensive four-wheel drive cars are highly visible signs of increasing wealth. The proximity of comparatively luxurious housing adjacent to simple traditional huts can be seen as a conspicuous indication of increasing inequality.

3.4 Governance

The communities under study were found to have a complex political set-up. Communal lands and the state governed national parks were clearly set apart. The communal lands fell under three separate chieftaincies, notably the Mayei Chieftaincy with its headquarter at Sangwali, the Mafwe Chieftaincy with its headquarter at Chinchimani (outside the research region) and the Mayuni Chieftaincy with its headquarter at Choi. The chiefs were supported by a council (the khuta). This structure of traditional governance is replicated at the village level, where headmen and their councils are responsible for day-to-day decisions pertaining to land and civil law issues. Since 1998 community-based conservation entities, conservancies, have been established throughout the region. The conservancies have their own elected leadership and have endorsed land management plans that provide space for wildlife corridors and conservation areas where little human use is encouraged. The conservancies are supported by NGOs which have their own staff. The NGOs in turn depend almost entirely on foreign donor funding. The Directorate of Veterinary Services in the Ministry of Agriculture, Water and Land Reform and the Directorate of Forestry, in the Ministry of Environment, Forestry and Tourism is also active in the area. Each conservancy submits and continuously develops a land zonation plan that differentiates core conservation zones, buffer-zones, settlement zones, zones used for tourism and zones used for livestock husbandry and/or agriculture. The zones are regarded as commons and governance of these common pool resources is effected via an elected committee.

The governance of rural landscapes has been made more complex with the Communal Land Reform Act 5 of 2002 which opens a route to formally endorse customary land titles for individual owners and thereby paves the way for privatisation. The Act was only fully rolled out in a programme in the Zambezi Region since the early 2010s and the titling of customary farmlands is still ongoing. All large cattle owners in the village survey had private customary land titles of this kind. The Mudumu landscape has experienced a run on such land titles, leading to a considerable erosion of the commons (Figure 5).

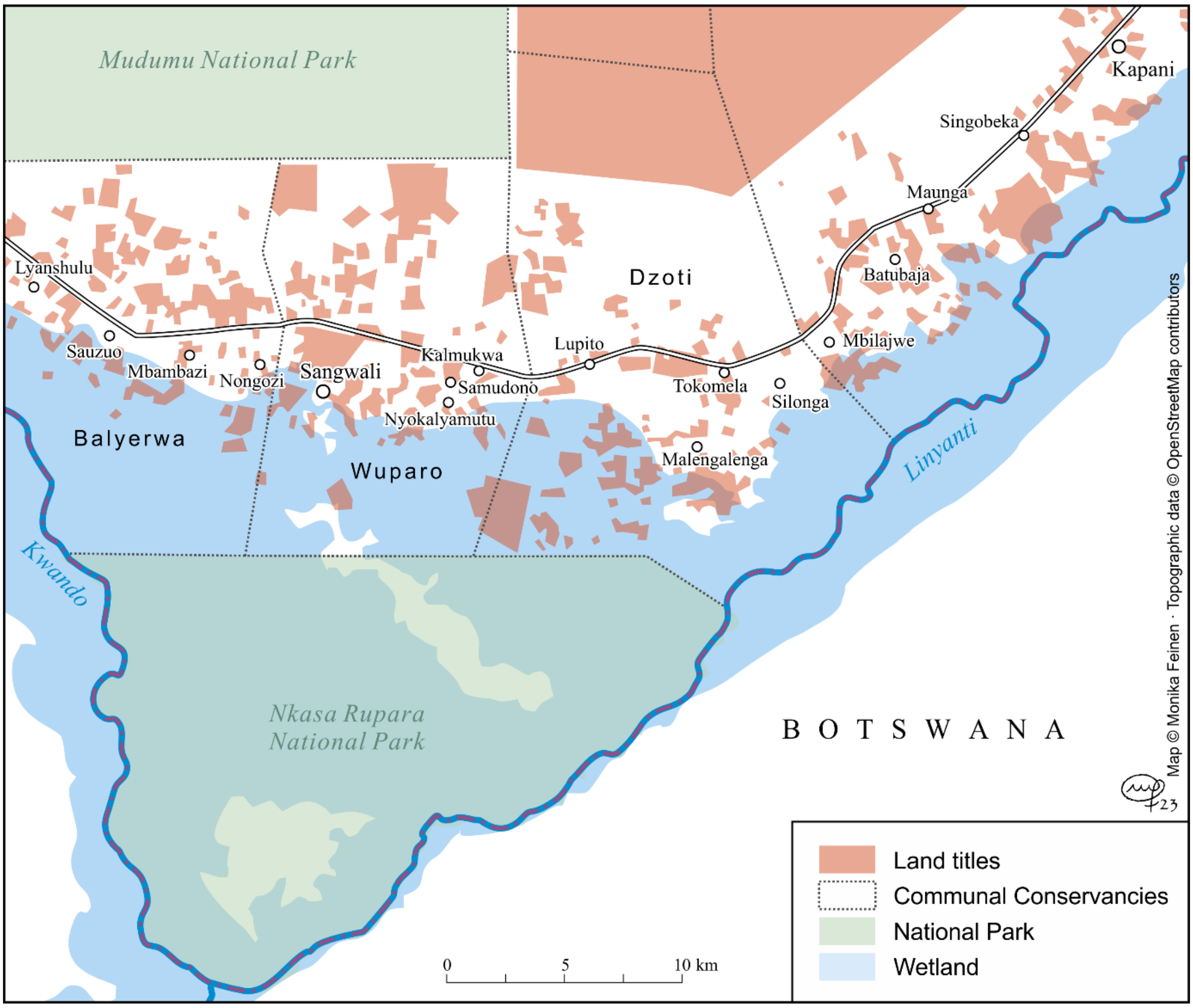

Figure 5 Customary land titling in Mudumu South; Source: WWF, based on Taylor (2022).

4. Discussion

4.1. Refaunation effects on vegetation and soil

We found refaunation dynamics to gravely impact local ecosystems. In areas where elephants were dominant, their browsing activities resulted in a reduction of woody cover to values often well below 40% of plot area falling under any tree or shrub cover, corresponding to woody biomass losses close to 50% (Kindermann et al. 2022b). These values are in the same range as losses reported for adjacent protected areas in the KAZA-TFCA, such as in Zimbabwe's Zambezi National Park. In this national park, up to 40% of woody biomass was lost in areas close to waterpoints (Wilson et al. 2021). Generally, elephants are known to open up landscapes i.e. removing trees, which benefits the herbaceous vegetation (Voysey et al. 2021, Coetsee et al. 2023). Our results from the space-for-time substitution approach highlight these impacts on vegetation. In comparison to the reference state (L) that stands exemplary for the defaunated past with low wildlife densities (1880s-1910s & 1970s-1980s) today's higher elephant impact in the 'medium' herbivore density class significantly reduces tree cover but increases grass cover. Further increases in elephants to 'high' levels of herbivore density leaves woody cover unchanged, but significantly reduces grass cover as the herbaceous vegetation layer suffers from trampling. The currently localized impact elephants mainly have in the national parks provide an outlook of future conditions for the larger KAZA TFCA area if elephant numbers are to increase further. Furthermore, rising elephant numbers may lead to losses not only of woody cover and biomass, but also alter the taxonomic and functional diversity of woody vegetation (Rutina and Moe 2014, Ferry et al. 2021). These structural and functional changes will most likely extend to the protected areas of conservancies outside the national parks. The pathway of refaunation with cattle revealed an interesting difference between extensive cattle rangelands in the conservancies and intensive cattle farming in the Sachinga livestock farm. The extensive use had positive influences of reducing woody cover while promoting grass cover in comparison to the low disturbance reference site i.e. they are combatting potential bush encroachment thereby demonstrating that livestock can to some degree replace natural wild herbivore communities (Buisson et al. 2021). Intensive cattle farming and total exclusion of elephants on the other hand led to closed canopy of the tree layer while the grass layer seems to have been completely depleted, indicating that the rangeland degraded through unbalanced refaunation (Tobler et al. 2003, Buisson et al. 2021).

Interestingly, high elephant densities were correlated with higher levels of soil carbon storage and soil nutrients compared to other herbivore density classes. This indicates that elephants replenish nutrients in the savanna soils (Sandhage-Hofmann et al. 2021). Such a process may lay the basis for a dense and productive grass layer on comparatively poor soils, corresponding to the significantly higher grass cover values which were particularly observed in plots with medium elephant densities. From a soil-science perspective, elephants are important intermediaries that return the nutrients stored in woody vegetation to the soils and hence indirectly support primary production. This is in line with findings that megaherbivores including elephants up to certain population densities contribute significantly to the nutrient cycle in the savanna and are therefore essential, perhaps even irreplaceable, components of a resilient savanna landscape (Svenning et al. 2016, Buisson et al. 2021).

In contrast, refaunation with cattle changed the ecosystem differently, but only at high cattle densities. Cattle populations at moderate levels had only minor effects on soil fertility and nutrient cycling, and even had positive effects on grass cover. For the latter, our findings are in line with studies from other African savanna rangelands, where the effects of moderate cattle densities were also found to be negligible or even positive – with only high cattle densities having adverse effects on grass cover (Linstädter et al. 2014, Guuroh et al. 2018) and on soil fertility (Sandhage-Hofmann et al. 2020). Elevated cattle densities, however, may even alter the savanna ecosystem toward a woody plant encroached system (O'Connor et al. 2014). In our study, this was the case on the cattle farm, where megaherbivores had been excluded. Such ecological shifts pose a threat to the underlying principles of robust livestock management. This potential scenario becomes more critical with the increasing privatization of communal land and potentially unregulated future growth in cattle density, which is already nowadays observed in the Zambezi Region.

Due to low to moderate herbivore densities in the study region, the coexistence of elephants and cattle did not lead to a pronounced ecosystem degradation. However, as observed in neighbouring Botswana (Buchholtz et al. 2019, Redmore et al. 2023), further increases of elephants and cattle populations will result in substantial changes in ecosystem functions and subsequently to losses of critical ecosystem services such as carbon storage, forage provision, and soil fertility. While the concrete payouts of human-elephant interaction are complex to account for – Buchholtz et al. (2019) for example show that villagers in the Okavango Panhandle profit from high elephant densities as a major percentage of the firewood gathered by villagers results from trees and branches broken down by elephants – the overall ecosystem changes are certainly challenging bringing about biodiversity loss and degradation.

4.2 Wealth Distribution

In aligning the empirical evidence with our field observations, we observe that the increase in cattle ownership is not the cause of income inequalities, but a consequence. None of the cattle owners has earned his (indeed, it is mostly men) wealth through livestock husbandry. The big cattle herds are owned by professionals such as former headmasters, school inspectors and high-ranking government officials. While they are still working, they invest part of their income in the accumulation of livestock. Upon receiving their pension packages at retirement, they take this as the starting capital for a cattle ranch, drilling of boreholes, establishment or construction of paddock and recruitment of herders. They normally apply for a customary land title to ascertain that the ranch they develop is their personal property.

The logic of the cattle owners is simple. The herd will reproduce quicker than any bank savings and, once established, contribute to the further increase of wealth. Surplus income and particularly pension packages are invariably invested into the expansion of herds, the infrastructure of a ranch, and combined with that (and often in direct proximity), the acquisition of large fields intended for commercial maize production. The increasing regional herd is, therefore, directly linked to the growing wealth inequality in the local population – a trend that is, of course, not peculiar to Namibia (for a similar trend in Botswana, see Bolt and Hillbom (2016).

About 15% of the community possess large cattle herds, while another 30-40% manage smaller cattle herds. The remaining ~ 50% of the population, do not own livestock. This population does not profit in any significant way from their neighbours' ownership of cattle. Habitually, they will have to rent oxen for ploughing in the early rainy season.

Although the increase of wildlife populations can have positive effects on single rural households, our empirical results suggest that these are small for the rural population as a whole. That is because the share of income from tourism and conservancies are relatively small. The wealthy are not usually prominently engaged in community-based conservation activities. However, two factors seem to determine who profits directly from community-based conservation that is invariably connected to the increase of wildlife: first, those who live close to a touristic establishment that is linked contractually to the conservancy (see also Meyer et al. 2022) and second, those who possess a certain degree of education. These people are the primary beneficiaries of community-based conservation as they become conservancy employees or are able to secure jobs for themselves in lodges and touristic enterprises. Hence, the increase in wildlife does not benefit the rural poor in any statistically detectable way on a regional level, but it does benefit the rural unemployed who live close enough to a touristic establishment.

4.3 Governance

The governance of natural resources in the coexistence landscape is fragmented and it is difficult to come up with consensual decisions on how to govern resources best and in a sustainable manner. Livestock mobility and livestock demographics depend on individual decisions and are progressively becoming linked to privately owned lands held under customary land titles. Increase in individually owned livestock herds beyond a subsistence minimum is invariably tied to capital generated through off-farm incomes. The Ministry of Agriculture, Water and Forests creates an enabling environment (e.g. drilling boreholes, facilitating customary land titles) without, for example, stipulating any thresholds or carrying capacities.

There are currently some concerted attempts being made by wealthy livestock holders and local administrators to improve the marketing system through upgrading abattoir facilities and advocating a commodity-based trade in canned meat. These initiatives will inevitably be of most benefit to those who hold substantial herds of cattle.

Wildlife demographics are scrutinised and co-managed by local conservancies, NGOs and the respective line ministry, the Ministry of Environment and Tourism. Through hunting quotas, the ministry facilitates a modest take off. There are also compensation schemes in place that pay farmers a small compensation for harvests or livestock lost to wildlife. Neither the conservancies nor the government are particularly concerned with livestock husbandry and nor does the ministry have a special mandate for it.

The Integrated Zambezi Land Use plan of 2015 tried to combine these perspectives but did not succeed in formulating either a clear-cut policy or the founding of overarching institutions dedicated to natural resource governance. Cattle husbandry and wildlife economics lead to new and contradicting forms of fragmented governance: on the one hand traditional authorities and elected committees govern community-based conservation efforts in cooperation with elected committees and NGOs, while on the other hand, wealthy herd owners together with planners and politicians govern lands that are factually (and through customary land titles also formally) privatised and thereby contribute to a rapid erosion of the commons that the conservancies are meant to manage.

To minimise unintended consequences of refaunation, such institutions need to be facilitated at both regional and local levels. Locally the conservancies have the institutional capacity to manage resources at a broader scale. In some conservancies (i.e. Kwandu, Sobbe) an integration of formerly independent community forest committees into the conservancies has taken place. Rangelands, however, are not collectively managed at all. In order to prevent a detrimental ecological degradation of these lands, a similar move towards comprehensive and holistic resource management at the local level is sorely needed.

4.4. Synthetic discussion: Coexistence landscape

When König et al. (2020) defined coexistence, they mentioned, importantly, that such landscapes are shaped by co-adaptation and the governance of effective institutions that ensure social legitimacy and long-term persistence of populations. Within the KAZA TCFA, such co-adaptation has indeed be found, with humans adjusting to high wildlife numbers, and wildlife adjusting to the continuous presence of human activities (Buchholtz et al. 2019, Redmore et al. 2023). However, our own results show that effective institutions that can ensure the governance of a simultaneous refaunation with elephants and cattle are as yet missing. The overall assumption seems to be that vegetation and soils can effectively buffer ever-increasing herbivore densities. However, we found that this is neither the case for woody nor for herbaceous vegetation cover. Although soils may act as a buffer to a certain extent (Sandhage-Hofmann et al. 2022), an increase in cattle densities may, in the long term, change all ecosystems compartments including soils (Figure 6). In economic terms, the coexistence of wildlife and cattle currently does not lead to a balancing of the existing wealth inequality. On the contrary, the strong growth of cattle herds exacerbates inequality, an effect that can only be partially offset by income from wildlife-dependent economies. The emerging coexistence of cattle-based economies and wildlife-based economies also remains unmanaged because it is linked to different centres of power and different competencies. Unless institutions develop which are capable of sustainable resource management at large – and not of wildlife, of forests, of rangelands in a siloed manner – the ecological future of the Mudumu landscape looks bleak despite the enormous gains from increasing wildlife populations and significant wealth storage in cattle herds (see Figure 6 for a conceptual summary).

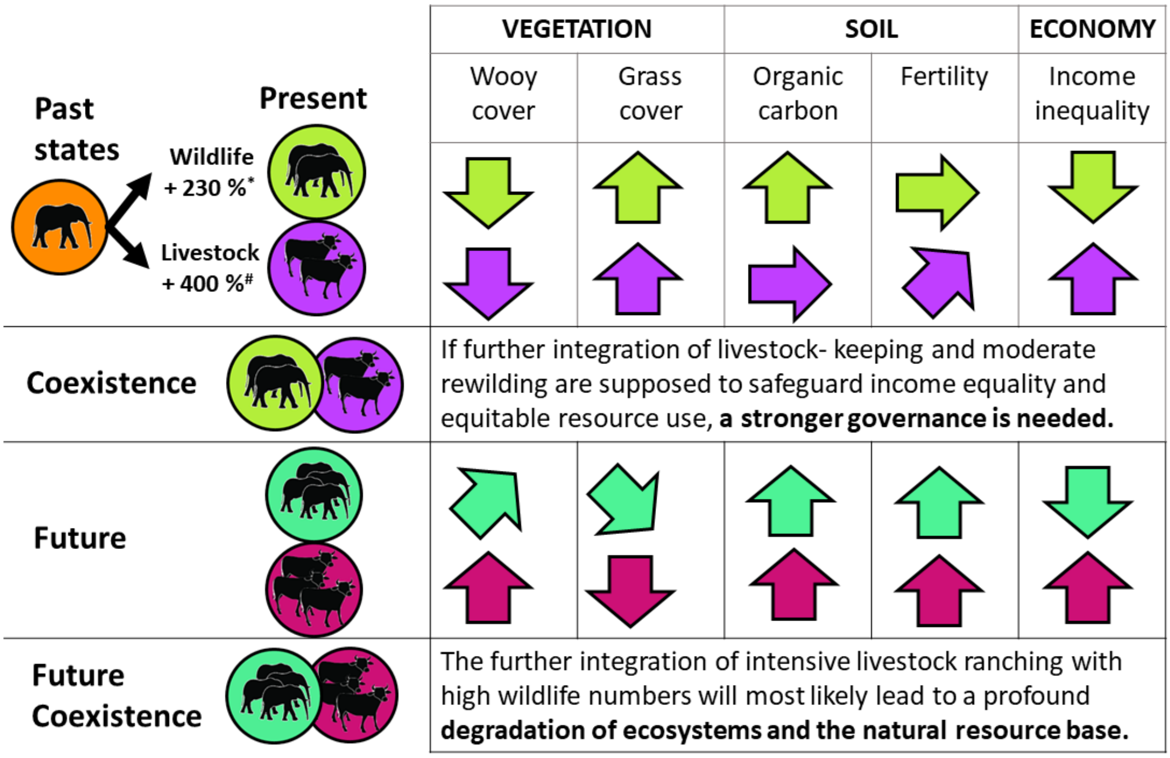

Figure 6 Conceptual graph summarizing ecological, economic and governance-related trends of resource use in a coexistence landscape: past, present and future trajectories. The coloured icons show the five herbivore density classes studied with a space-for-time substitution for their ecological impact on soil and vegetation (see Figure 2).

5. Conclusions and Outlook

Our study reveals that refaunation with elephants has partly non-linear effects on ecosystem characteristics, with unexpected positive impacts on grass cover, soil fertility, and soil quality at intermediate elephant densities. High elephant densities negatively affect grass cover, while effects on soil fertility remain positive. When elephant densities would increase even further, a desertified vegetation state with insufficient forage resources will eventually be reached, while a further increase of cattle densities would result in a bush-encroached state. In both cases, carbon input from plant biomass may no longer have positive effects on soil carbon storage and other soil-mediated ecosystem services. A simultaneous further increase in wildlife and cattle densities at the same location could not be conclusively assessed with our data. We speculate that, if both refaunation processes would coincide in high densities within a coexistence landscape, potentially interactive and unpredictable effects may occur, such as the passing of ecological tipping points. This development would pose severe challenges for management and governance.

Surprisingly, we found that wildlife refaunation, in the context of conservation and tourism, reduces income inequality at the household level. However, this positive effect is overshadowed on a community level by wealth concentration among a few affluent cattle owners, unrelated to refaunation with elephants and conservation efforts. The simultaneous refaunation with wildlife and cattle poses challenges to the governance of natural resources, with conservancy committees having a mandate for wildlife and competing with wealthy cattle herd owners. Attention should thus be given to the potential inequalities arising from the rapid increase and uneven distribution of cattle herds, impacting the ecological resource base of the social-ecological system. In light of our findings, future research and policy-making should address both the ecological and social limits of refaunation in coexistence landscapes, recognizing coexistence as a paradigm for conservation efforts in rural Africa.

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Supporting Information

Appendix S1: Calculation of isotope values

$$\delta = [(R(sample) – R(standard)) / R(standard)] * 100$$

where R(sample) is the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratio of the sample and R(standard*)* is the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ isotope ratio of the standard with respect to the V-PDB standard for carbon isotopes and the atmospheric dinitrogen standard for nitrogen isotopes (Coplen et al., 2006).

Appendix S2: Calculation of the relative proportion of SOC derived from woody biomass (FC_3)

$$FC_3 = (\delta^{13}C_{soil} - \delta^{13}C_4) / (\delta^{13}C_3 - \delta^{13}C_4)$$

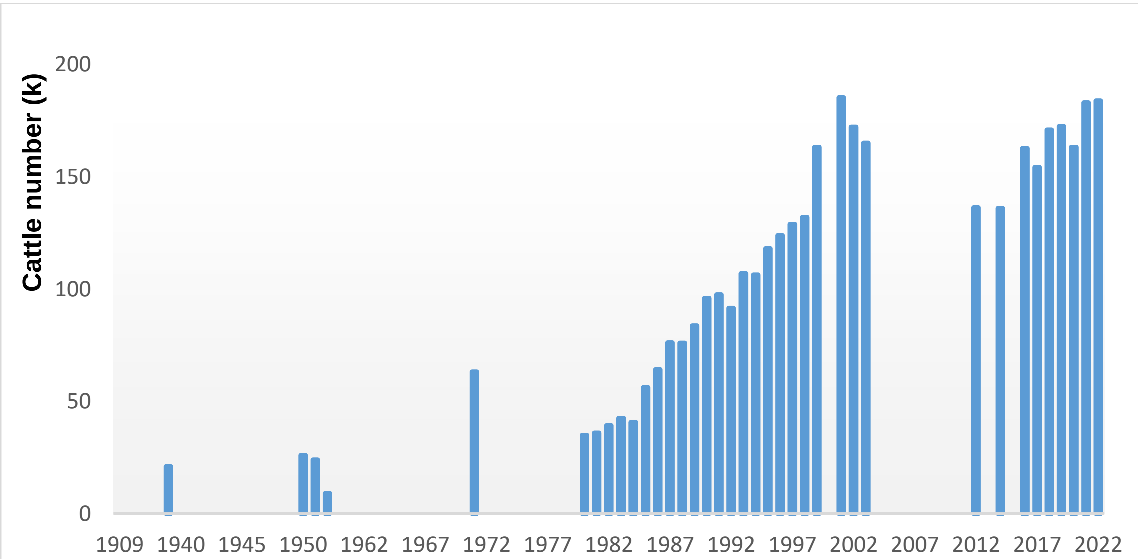
with $\delta^{13}C_{soil}$ being the measured $\delta^{13}C$ value of the soil sample, $\delta^{13}C_{grass}$ the average $\delta^{13}C$ value of remnant grass (-14.3‰,), and $\delta^{13}C_3$ the average $\delta^{13}C$ value of woody plant material from *Terminalia sericea* vegetation (-27.1‰)

Appendix S3: Gini decomposition using *descogini* (López-Feldman 2006)

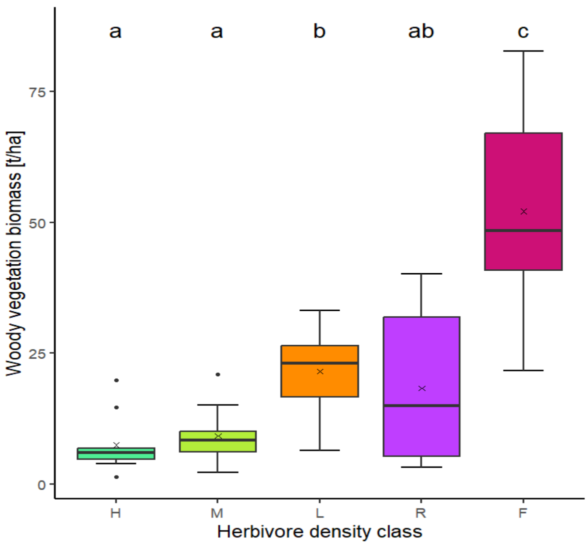
$$\frac{\Delta G}{\Delta e} = S_k(G_k R_k - G)$$

with G being the Gini coefficient, e the percentage change in source k, S_k the importance of each income source with respect to total income, G_k a measure for the (in-) equality of income distribution of source k, R_k the correlation between income source, k and the distribution of total income. We calculated income as net income, i.e. quantity times prices minus expenses.

Appendix S4: Development of cattle numbers in Namibia's Caprivi/Zambezi Region over the past decades. Source: Veterinary Offices Windhoek, for the years 1996 to 2003 Rep. of Namibia 2004. Housing and Population Census 2001 and 2011; and Kruger, C. E. 1984. *History of the Caprivi Strip 1890-1984.* (unpublished manuscript). NAN A0472.



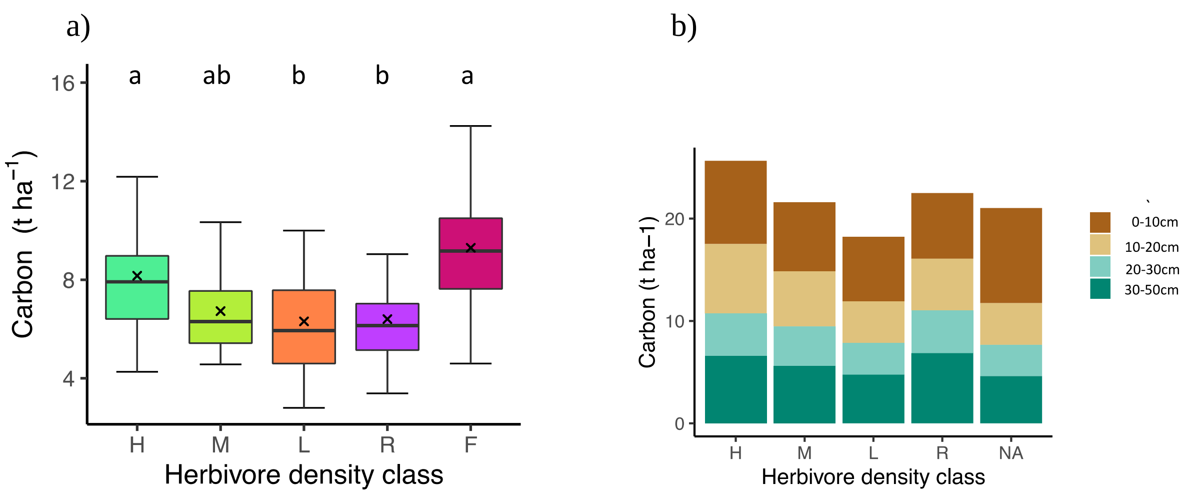
Appendix S5: Vegetation characteristics as impacted by a refaunation with elephants and cattle, aboveground woody biomass (t ha^{-1}). Differences in lowercase superscripts indicate significant differences between herbivore density classes, with H = high elephant densities, M= medium elephant densities, L = low elephant densities, R = communal rangelands, and F = cattle farm.


a
a
b
ab
c
75
50
25
0
Woody vegetation biomass [t/ha]
H
M
L
R
F
Herbivore density class

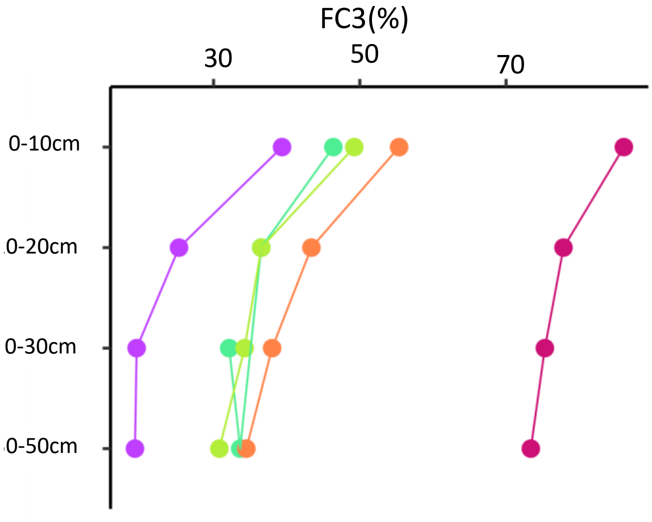
Appendix S6: Soil texture in plots within the five different herbivore density classes.

Texture class	High elephant plots	Medium elephant plots	Low elephant plots	Rangeland	Cattle Farm
Sand (%)	94.3±2.8	93.8±3.6	96.7±1.7	90.5±5	94.2±2.8
Silt (%)	3.3±0.5	4.0±3.2	1.8±1.4	4.2±2.3	1.9±0.6
Clay (%)	1.8±0.7	2.2±2.2	1.2±0.7	3.8±2.1	2.7±0.7

Appendix S7: Soil characteristics as impacted by a refaunation with elephants and cattle, with a) soil organic carbon stocks (t ha^{-1}) in topsoils (0-5cm), and b) soil organic carbon stocks (t ha^{-1}) in different soil depths. Differences in lowercase superscripts indicate significant differences between herbivore density classes, with H = high elephant densities, M= medium elephant densities, L = low elephant densities, R = communal rangelands, and F = cattle farm.



Appendix S8: Impact of refaunation with elephants and cattle on the relative proportion of soil organic carbon derived from woody biomass (FC_3) as a function of depth. For the colour codes of the herbivore classes, see Fig. S3a.



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